grandidentata in the field at ambient and twice ambient CO2 in open bottom root boxes filled with organic matter poor native soil. Nitrogen was added to all root boxes at a rate equivalent to net N mineralization in local dry oak forests. Nitrogen added during August was enriched with N-25 to trace the flux of N within the plant-soil system. Above- and belowground growth, CO2 assimilation, and leaf N content were measured non- destructively over 142 d. After final destructive harvest, roots, stems, and leaves were analyzed for total N and N-15. There was no CO2 treatment effect on leaf area, root length, or net assimilation prior to the completion of N addition. Following the N addition, leaf N content increased in both CO2 treatments, but net assimilation showed a sustained increase only in elevated CO2 grown plants. Root relative extension rate was greater at elevated CO2, both before and after the N addition. Although final root biomass was greater at elevated CO2, there was no CO2 effect on plant N uptake or allocation. While low soil N availability severely inhibited CO2 responses, high CO2 grown plants were more responsive to N. This differential behavior must be considered in light of the temporal and spatial heterogeneity of soil resources, particularly N which often limits plant growth in temperate forests.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, NITROGEN, PHOTOSYNTHESIS, QUERCUS-ALBA, SEEDLING GROWTH, TREES

480
Cushman, J.C., and H.J. Bohnert. 1997. Molecular genetics of Crassulacean acid metabolism. *Plant Physiology 113(3):667-676.*

Most higher plants assimilate atmospheric CO2 through the C-3 pathway of photosynthesis using ributose-1,5-bisphosphate carboxylase/oxygenase (Rubisco). However, when CO2 availability is reduced by environmental stress conditions, the incomplete discrimination of CO2 over O-2 by Rubisco leads to increased photorespiration, a process that reduces the efficiency of C-3 photosynthesis. To overcome the wasteful process of photorespiration, approximately 10% of higher plant species have evolved two alternate strategies for photosynthetic CO2 assimilation, C-3 photosynthesis and Crassulacean acid metabolism. Both of these biochemical pathways employ a "CO2 pump" to elevate intracellular CO2 concentrations in the vicinity of Rubisco, suppressing photorespiration and therefore improving the competitiveness of these plants under conditions of high light intensity, high temperature, or low water availability. This CO2 pump consists of a primary carboxylating enzyme, phosphoenolpyruvate carboxylase. In C-4 plants, this CO2-concentrating mechanism is achieved by the coordination of two carboxylating reactions that are spatially separated into mesophyll and bundle-sheath cell types (for review, see R.T. Furbank, W.C. Taylor [1995] Plant Cell 7:797-802; M.S.B. Ku, Y. Kano-Murakami, M. Matsuoka [1996] Plant Physiol 111:949-957). In contrast, Crassulacean acid metabolism plants perform both carboxylation reactions within one cell type, but the two reactions are separated in time. Both pathways involve cell- specific changes in the expression of many genes that are not present in C-3 plants.

KEYWORDS: ABSCISIC- ACID, C-3 PHOTOSYNTHESIS, CAM, COMMON ICE PLANT, DIFFERENTIAL EXPRESSION, INDUCTION, MESEMBRYANTHEMUM-CRYSTALLINUM L, NADP-MALIC ENZYME, PHOSPHOENOLPYRUVATE CARBOXYLASE, SALT STRESS

481
Dacey, J.W.H., B.G. Drake, and M.J. Klug. 1994. Stimulation of methane emission by carbon-dioxide enrichment of marsh vegetation. *Nature 370(6484):47-49.*

THERE is substantial evidence that many plants respond to increased concentrations of atmospheric carbon dioxide by increasing their productivity(1-4) This observation has led to the suggestion that, by taking up CO2, the terrestrial biosphere might mitigate the potential greenhouse warming associated with anthropogenic CO2 emissions(5). Whiting and Chanton(6) have found, however, that for wetlands of varying productivity around the world, higher net primary production is associated with higher emissions of methane-another important greenhouse gas. Here we present measurements of methane emissions from a marsh that has been exposed to twice the present ambient concentration of atmospheric CO2. We find that over a one-week period, the CO2-enriched sites had significantly higher emissions of methane than the control sites. Our results suggest that future increases in atmospheric CO2 concentration may lead to significant increases in methane emissions from wetlands.

KEYWORDS: COMMUNITIES, ELEVATED CO2, ESTUARINE MARSH, FIELD, GROWTH, PLANTS, PRODUCTIVITY, RESPONSES, RICE PADDIES, WETLANDS

482
Dahlman, R.C. 1993. Co2 and plants - revisited. *Vegetatio 104:339-355.*

The decade-long USA research program on the direct effects of CO2 enrichment on vegetation has achieved important milestones and has produced a number of interesting and exciting findings. Research beginning in 1980 focused on field experiments to determine whether phenomena observed in the laboratory indeed occurred in natural environments. The answer is yes. Data obtained from numerous field studies show mixed response of crop and native species to CO2 enrichment however. Nearly all experiments demonstrate that plants exhibit positive gain when grown at elevated CO2; although the magnitude varies greatly. Most crop responses range from 30 to 50 % increase in yield. Results from long-term experiments with woody species and ecosystems are even more variable. Huge growth responses (100 to nearly 300 % increase relative to controls) are reported from several tree experiments and the salt-marsh ecosystem experiment. Other results from experiments with woody species and the tundra ecosystem suggest little no effect of CO2 on physiology, growth or productivity. Numerous studies of the physiology of the CO2 effect are continuing in attempts to understand controlling mechanisms and to explain the variable growth responses. Particular emphasis needs to be given to physiological measures of interactions involving the CO2 effect and other environmental influences, and to the wide-ranging observations of photosynthesis acclimation to CO2. Prospects for future research are identified.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CARBON-DIOXIDE, ELEVATED LEVELS, ENRICHMENT, GROWTH, INHIBITION, PHOTOSYNTHESIS, SEEDLINGS, SHORT- TERM, TEMPERATURE

483
Dale, H., and M.C. Press. 1998. Elevated atmospheric CO2 influences the interaction between the parasitic angiosperm Orobanche minor and its host Trifolium repens. *New Phytologist 140(1):65-73.*

The influence of the root holoparasitic angiosperm Orobanche minor Sm. on the biomass, photosynthesis, carbohydrate and nitrogen content of Trifolium repens L. was determined for plants grown at two CO2 concentrations (350 and 550 mu mol mol(-1)). Infected plants accumulated less biomass than their uninfected counterparts, although early in the association there was a transient stimulation of growth. Infection also influenced biomass allocation both between tissues (infected plants had lower root:shoot ratios) and within tissues: infected roots were considerably thicker before the point of parasite attachment and thinner below. Higher concentrations of starch were also found in roots above the point of attachment, particularly for plants grown in

elevated CO2. Elevated CO2 stimulated the growth of T. repens only during the early stages of development. There was a significant interaction between infection and CO2 on growth, with infected plants showing a greater response, such that elevated CO2 partly alleviated the effects of the parasite on host growth. Elevated CO2 did not affect total O. minor biomass per host, the number of individual parasites supported by each host, or their time of attachment to the host root system. Photosynthesis was stimulated by elevated CO2 but was unaffected by O. minor. There was no evidence of down-regulation of photosynthesis in T. repens grown at elevated CO2 in either infected or uninfected plants. The data are discussed with regard to the influence of elevated CO2 on other parasitic angiosperm-host associations and factors which control plant responses to elevated CO2.

KEYWORDS: CARBON DIOXIDE, GROWTH, METABOLISM, N2 FIXATION, NITROGEN, PHOTOSYNTHETIC ACCLIMATION, SORGHUM, STRIGA-HERMONTHICA, TEMPERATURE, WHITE CLOVER

484
Dalen, L.S., O. Johnsen, and G. Ogner. 1997. Frost hardiness development in young Picea abies seedlings under simulated autumn conditions in a phytotron - effects of elevated CO2, nitrogen and provenance. *Plant Physiology 114(3):576.*

485
Damesin, C., C. Galera, S. Rambal, and R. Joffre. 1996. Effects of elevated carbon dioxide on leaf gas exchange and growth of cork-oak (Quercus suber L) seedlings. *Annales Des Sciences Forestieres 53(2-3):461-467.*

Leaf gas exchange and growth were determined on cork-oak (Quercus suber L) seedlings which were grown from acorns for periods of up to 4 months in greenhouses at ambient (350 mu mol mol(-1)) and at elevated (700 mu mol mol(-1)) concentrations of carbon dioxide. In well-watered conditions, daily maximum photosynthesis (15 mu mol m(-2) s(-1)) and stomatal conductance (440 mmol m(-2) s(-1)) of plants grown and measured at 700 mu mol mol(-1) CO2 did not differ from those of plants grown and measured at 350 mu mol mol(-1). In conditions of moderate drought, net CO2 assimilation was at least twice as great in elevated CO2, but stomatal conductance was unchanged. Elevated CO2 affected total biomass production, the average increase being 76 and 97% at 3 and 4 months, respectively. Shoot biomass, root biomass, stem height and total leaf area were increased by elevated CO2. Root and stem ramification were also enhanced by elevated CO2, but no change in root/shoot ratio was observed.

KEYWORDS: AMBIENT, ATMOSPHERIC CO2, CO2 CONCENTRATION, PHOTOSYNTHESIS, PLANTS, PRODUCTIVITY, RESPONSES, STOMATAL CONDUCTANCE, TREES, WATER

486
Daniel, E. 1997. The temperature dependence of photoinhibition in leaves of Phaseolus vulgaris (L) - Influence of CO2 and O-2 concentrations. *Plant Science 124(1):1-8.*

The interactive effect of temperature and CO2 concentration on the susceptibility to photoinhibition was assessed using chlorophyll a fluorescence to estimate the reduction of the quantum yield of PSII photochemistry (F-w/F-m) after high-light exposure. Leaves exposed to high photon flux density always exhibit a decrease in F-w/F-m, resulting from both a decrease in the rate constant for photochemistry and an increase in the rate constant for non photochemical dissipation of excess excitation energy. At a-given CO2 concentration, there was almost no difference in the degree of photoinhibition between leaves exposed to high light in 10 or 210 mmol O-2/mol. But photoinhibition was more pronounced at 10 mmol O-2/mol and 0 mu mol CO2/mol than at 210 mmol O-2/mol and 50 pmol CO2/mol, i.e. when both photorespiration and CO2 refixation are suppressed. Despite this photoprotective role of photorespiration, photoinhibition was enhanced by decreasing CO2 concentration in bean leaves, especially at elevated (30-35 degrees C)temperatures. (C) 1997 Elsevier Science Ireland Ltd.

KEYWORDS: ASSIMILATION, CHLOROPHYLL FLUORESCENCE, CHLOROPLAST PROTEIN, DROUGHT, LIGHT, PHOTOCHEMICAL EFFICIENCY, PHOTORESPIRATION, PHOTOSYNTHETIC ELECTRON FLOW, PHOTOSYSTEM, WATER-STRESS

487
Darrah, P.R. 1996. Rhizodeposition under ambient and elevated CO2 levels. *Plant and Soil 187(2):265-275.*

As global CO2 levels rise, can soils store more carbon and so buffer atmospheric CO2 levels? Answering this question requires a knowledge of the rates of C inputs to soil and of CO2 outputs via decomposition. Below-ground inputs from roots are a major component of the C flow into soils but are still poorly understood. In this article, new techniques for measuring rhizodeposition are reviewed and discussed and the need for cross-comparisons between methods is identified. One component of rhizodeposition, root exudation, is examined in more detail and evidence is presented which suggests that current estimates of exudate flow into soils are incorrect. A mechanistic mathematical model is used to explore how exudate hows might change under elevated CO2.

KEYWORDS: AMINO-ACIDS, ARBUSCULAR MYCORRHIZAL FUNGUS, BRASSICA-NAPUS L, CARBON FLUXES, CITRIC-ACID, CUCUMIS-SATIVUS L, PSEUDOMONAS- FLUORESCENS, SOIL-ROOT INTERFACE, WHEAT RHIZOSPHERE, ZEA MAYS L

488
Darrigo, R.D., and G.C. Jacoby. 1993. Tree growth-climate relationships at the northern boreal forest tree line of north-america - evaluation of potential response to increasing carbon-dioxide. *Global Biogeochemical Cycles 7(3):525-535.*

Tree growth at the northern limit of the range of boreal forests is primarily limited by temperature-related factors. Thus the position of this range limit, and the growth rates of trees along the northern forest border, may undergo significant change if predictions of enhanced greenhouse warming at northern latitudes are realized. In this paper we evaluate tree ring width and maximum latewood density chronologies of white spruce for three temperature-sensitive tree line sites in northern North America: in the Brooks Range, Alaska, the Franklin Mountains, Northwest Territories, and Churchill, Manitoba. The ring width data, which more strongly integrate low-frequency temperature trends than the density series, show overall enhanced growth and inferred warming during the period of anthropogenic increase in greenhouse gases. The recent growth at these sites equals or exceeds that which has occurred during earlier centuries of more clearly natural climate variability. When the ring width and density variations are estimated using temperature and precipitation data in principal components regession analysis, no substantial residual trends are detected which might require CO2 or other nutrient fertilization as an additional explanation for recent growth changes.

KEYWORDS: ATMOSPHERIC CO2, CANADA, CHRONOLOGY, CIRCULATION, DENSITY, ENHANCEMENT, RING DATA, TEMPERATURE, TRENDS, WIDTH

489

Davey, P.A., A.J. Parsons, L. Atkinson, K. Wadge, and S.P. Long. 1999. Does photosynthetic acclimation to elevated CO2 increase photosynthetic nitrogen-use efficiency? A study of three native UK grassland species in open-top chambers. *Functional Ecology 13:21-28.*

1, The photosynthetic response to elevated CO2 and nutrient stress was investigated in Agrostis capillaris, Lolium perenne and Trifolium repens grown in an open-top chamber facility for 2 years under two nutrient regimes. Acclimation was evaluated by measuring the response of light-saturated photosynthesis to changes in the substomatal CO2 concentration. 2. Growth at elevated CO2 resulted in reductions in apparent Rubisco activity in vivo in all three species, which were associated with reductions of total leaf nitrogen content on a unit area basis for A. capillaris and L. perenne. Despite this acclimation, photosynthesis was significantly higher at elevated CO2 for T. repens and A. capillaris, the latter exhibiting the greatest increase of carbon uptake at the lowest nutrient supply. 3. The photosynthetic nitrogen-use efficiency (the rate of carbon assimilation per unit leaf nitrogen) increased at elevated CO2, Mot purely owing to higher values of photosynthesis at elevated CO2, but also as a result of lower leaf nitrogen contents. 4. Contrary to most previous studies, this investigation indicates that elevated CO2 can stimulate photosynthesis under a severely limited nutrient supply. Changes in photosynthetic nitrogen-use efficiency may be a critical determinant of competition within low nutrient ecosystems and low input agricultural systems.

KEYWORDS: C-3 PLANTS, CAPACITY, COTTON, GAS-EXCHANGE, GROWTH, LEAVES, NUTRIENT STATUS, NUTRITION, RISING ATMOSPHERIC CO2, SEEDLINGS

490

Davies, S.J., and L. Unam. 1999. Smoke-haze from the 1997 Indonesian forest fires: effects on pollution levels, local climate, atmospheric CO2 concentrations, and tree photosynthesis. *Forest Ecology and Management 124(2-3):137-144.*

Atmospheric composition, local climate and sapling gas exchange were monitored to assess the short-term effects of smoke-haze from the 1997 Indonesian forest fires. Atmospheric concentrations of particulate matter, SO2, CO, CH4 and CO2, and relative humidity were elevated, and photosynthetically active radiation and ambient temperature were reduced by the smoke- haze. Despite elevated CO2 levels, photosynthesis in three tree species was reduced by the smoke-haze, both indirectly through reduced PAR levels, and directly through elevated aerosol and atmospheric pollutant levels.

KEYWORDS: ASIA, BIOMASS, CARBON DIOXIDE, DEFORESTATION, ELEVATED CO2, EMISSIONS, GROWTH, LAND-USE CHANGE, LATIN-AMERICA, PLANTS

491

Day, F.P., E.P. Weber, C.R. Hinkle, and B.G. Drake. 1996. Effects of elevated atmospheric CO2 on fine root length and distribution in an oak-palmetto scrub ecosystem in central Florida. *Global Change Biology 2(2):143-148.*

Atmospheric CO2 concentration is rising and it has been suggested that a portion of the additional carbon is being sequestered in terrestrial vegetation and much of that in below-ground structures. The objective of the present study was to quantify the effects of elevated atmospheric CO2 on fine root length and distribution with depth with minirhizotrons in an open-top chamber experiment in an oak-palmetto scrub ecosystem at Kennedy Space Centre, Florida, USA. Observations were made five times over a period of one and a half years in three ambient chambers (350 p.p.m. CO2), three CO2 enriched chambers (700 p.p.m. CO2), and three unchambered plots. Greater root length densities were produced in the elevated CO2 chambers (14.2 mm cm(-2)) compared to the ambient chambers (8.7 mm cm(-2)). More roots may presumably lead to more efficient acquisition of resources. Fine root abundance varied significantly with soil depth, and there appeared to be enhanced proliferation of fine roots near the surface (0-12 cm) and at greater depth (49-61 cm) in the elevated CO2 chambers. The vertical root distribution pattern may be a response to availability of nutrients and water. More studies are needed to determine if increased root length under CO2 enriched conditions actually results in greater sequestering of carbon below ground.

KEYWORDS: CARBON, CLIMATE CHANGE, GROWTH, HETEROGENEITY, MICROSITES, RESPONSES

492

Dayan, E., H. Vankeulen, J.W. Jones, I. Zipori, D. Shmuel, and H. Challa. 1993. Development, calibration and validation of a greenhouse tomato growth-model .1. Description of the model. *Agricultural Systems 43(2):145-163.*

A dynamic crop growth model. TOMGRO, for an indeterminate tomato variety is presented. The model describes the phenological development and increase in dry weight of various organs (roots, stem nodes, leaves and fruits) from planting till maturity under variable environmental conditions. Phenological development is governed by genetic plant properties and environmental conditions (e.g. air temperature and CO2 level) and expressed in a plastochron index, i.e. the current stem node number. Total dry matter accumulation is based on a quantitative description of the carbon balance, including gross CO2 assimilation, maintenance respiration and growth respiration. Partitioning of dry matter increase over the various organs is governed by their relative sink strengh, defined on the basis of a genetically determined 'potential' growth rate, achieved under non-limiting carbohydrate supply. The model is both schematic and modular in set-up. This means it can be adapted easily and most of its subroutines can be replaced easily by others if better descriptions become available. It can also be combined with a more comprehensive model describing greenhouse climate and appears robust for use in procedures of economic optimization of climate conditions in greenhouses or for management purposes.

KEYWORDS: CARBON-DIOXIDE ENRICHMENT, FRUIT- GROWTH, IMPORT, LEAF, LYCOPERSICON-ESCULENTUM MILL, NITROGEN, PHOTOSYNTHESIS, PLANTS, RESPONSES, TRANSLOCATION

493

Daymond, A.J., T.R. Wheeler, P. Hadley, R.H. Ellis, and J.I.L. Morison. 1997. The growth, development and yield of onion (Allium cepa L) in response to temperature and CO2. *Journal of Horticultural Science 72(1):135-145.*

Stands of two cultivars (cv. Hysam and Site) of onion (Allium cepa L.) were grown in the held within polyethylene-covered tunnels along which a temperature adient was imposed. Pairs of tunnels were maintained at either 374 or 532 mu mol mol(-1) CO2. The rates of progress from transplanting to bulbing, and from bulbing to harvest maturity, were positive linear functions of mean temperature for each cultivar. At a given temperature, the time of bulbing was earlier, but the duration of bulb growth longer, at elevated compared with normal CO2. Canopy architecture was not affected by CO2, temperature or cultivar; an estimate of 0.25 for the canopy light extinction coefficient was common to all treatment combinations. Radiation use efficiency was greater at elevated compared with normal CO2 in the period up to bulbing, but was the same at both CO2 concentrations during subsequent bulb growth. Total crop dry weight at bulbing was increased by 32-44% due to

elevated CO2. Bulb yields at harvest maturity declined with progressively warmer temperatures and to a greater extent in cv. Site than cv. Hysam. Enrichment with CO2 increased bulb yields by 29-37% and by 35-51% in cvs Hysam and Site, respectively. From comparison of the temperature rise needed to offset entirely the yield increases of each cultivar due to elevated CO2, it is concluded that current estimates of climate change should be beneficial for bulb onion production, particularly for long- season cultivars.

KEYWORDS: AIR- TEMPERATURE, ATMOSPHERIC CO2, CARBON DIOXIDE, ENRICHMENT, FIELD, LEAF-AREA, NITROGEN, PHOTOSYNTHESIS, PLANT GROWTH, PRODUCTIVITY

494

De Angelis, P., and G.E. Scarascia-Mugnozza. 1998. Long-term CO2-enrichment in a Mediterranean natural forest: An application of large open top chambers. *Chemosphere 36(4-5):763-770.*

It is crucial to be able to anticipate the possible effects of environmental changes on the Mediterranean woodland communities given their essential role on protecting lands that are under a strong pressure by man and climate. Predictions of the effects of increasing CO2 concentration on plants have been inferred by short- and long-term studies, conducted at different scales and by different technologies. Open Top Chambers (OTCs) are experimental facilities that have been widely used to expose field grown plants to different pollutant gases, and more recently to elevated [CO2]. In this paper, we present the natural site and the experimental system (six large OTCs enclosing clumps of natural vegetation) that we have been utilizing for 3 years, to assess the impact of elevated [CO2] on a Mediterranean natural forest community. The results show that large OTCs can be usefully used to simulate CO2 doubling even under the harsh environmental conditions of the mediterranean region. (C) 1998 Elsevier Science Ltd.

KEYWORDS: BALANCE, CARBON DIOXIDE, CLIMATE, ECOSYSTEMS, ELEVATED CO2, EXCHANGE, RESPONSES

495

Debevec, E.M., and S.F. Maclean. 1993. Design of greenhouses for the manipulation of temperature in tundra plant-communities. *Arctic and Alpine Research 25(1):56-62.*

Passive greenhouses can be used to elevate the temperature of natural communities, but they also introduce other effects. We tested the effects of potential greenhouse materials-clear polyethylene plastic film, polyester fabric, and rigid fiberglass panels-on light transmission, photosynthesis of Salix planifolia, elevation of air and soil temperature, and thaw depth. Plastic had the greatest light transmittance and caused the least depression of photosynthesis (- 5%). Greenhouses covered with plastic elevated daily maximum and daily mean air temperatures by an average of 7.8 and 2.0- degrees-C and depressed daily minimum temperature by 1.1- degrees-C compared with the control. Plastic is impervious to gases and may alter CO2 concentration and humidity within greenhouses. Fiberglass had lower transmittance, especially of short wavelength radiation. Fabric had the lowest light transmission and reduced photosynthesis by 10%, but it has the advantage of permeability to CO2 and water vapor. Greenhouses covered with fabric, alone, produced only a small effect (daily mean temperature elevated 0.4-degrees-C above controls). A mixed greenhouse design (plastic and fabric) raised daily mean temperatures by 0.9-degrees-C and may minimize adverse effects on gas diffusion. Because of the effect of the materials on amount and spectral distribution of radiation and on photosynthesis, the appropriate treatment control for any greenhouse design is an open plot shaded with the same material. Soil temperature at 10 cm depth was elevated in all greenhouses, but no effect on depth of thaw was detected.

KEYWORDS: CARBON NUTRIENT BALANCE

496

Debruin, H.A.R., and C.M.J. Jacobs. 1993. Impact of co2 enrichment on the regional evapotranspiration of agroecosystems, a theoretical and numerical modeling study. *Vegetatio 104:307-318.*

This paper gives a brief overview of factors determining evapotranspiration of vegetated surfaces. It indicates which of these factors are sensitive to CO2 enrichment. A qualitative analysis is presented of the impact of large scale climate changes. Data in literature indicate that the surface resistance of vegetated areas may change within the range -25 % and +50 % if the atmospheric CO2-concentration doubles. The impact of such changes on regional scale transpiration is evaluated using a numerical model in which the interaction between the evapotranspiration and the Planetary Boundary Layer is accounted for. It is concluded that the impact of CO2 enrichment on the transpiration at the regional scale is relatively small for aerodynamically smooth surfaces (between +7 % and -11 %). For aerodynamically rough surfaces the effects are somewhat larger (between +15 % and -21 %).

KEYWORDS: ATMOSPHERIC BOUNDARY-LAYER, CANOPY RESISTANCE, CARBON DIOXIDE, CONDUCTANCE, EVAPORATION, FOREST, SCALE, SENSITIVITY, STOMATAL CONTROL, TRANSPIRATION

497

Deepak, S.S., and M. Agrawal. 1999. Growth and yield responses of wheat plants to elevated levels of CO2 and SO2, singly and in combination. *Environmental Pollution 104(3):411-419.*

Wheat plants (Triticum aestivum L. cv. Malviya 234) were exposed to 600 ppm of carbon dioxide (CO2) and 0.06 ppm sulphur dioxide (SO2), singly and in combination for 8 h daily (8 a.m. to 4 p.m.) from germination to maturity in open top chambers (OTCs) in field conditions to investigate their individual as well as interactive influence on plant growth and yield. Exposure of plants to 0.06 ppm SO2 significantly reduced plant height, leaf area, biomass and yield. Elevated CO2, on the other hand, stimulated the growth and yield of plants. Combination of CO2 and SO2 showed a similar response pattern as that of CO2 alone. Pattern of biomass allocation also varied in response to different treatments. RGR was significantly increased due to CO2 and CO2 + SO2 treatments, whereas the same reduced due to SO2 exposure. Root/shoot ratio decreased significantly due to CO2 and CO2 + SO2 treatment at 45 days age. CO2 modified the responses of plants to SO2. Combined exposure of SO2 and CO2 stimulated the growth as well as the yield maximally. This suggests that the CO2 enrichment has not only reduced the adverse effect of low level of SO2, but at the same time the extra carbon provided by CO2 enrichment took the advantage of air borne sulphur as nutrient and showed maximum increment in growth and yield. (C) 1999 Elsevier Science Ltd. All rights reserved.

KEYWORDS: AIR- POLLUTANTS, CARBON DIOXIDE, FUMIGATION, LEAVES, PHOTOSYNTHESIS, RESPIRATION, STOMATAL CONDUCTANCE, SULFUR-DIOXIDE, TEMPERATURE, WINTER-WHEAT

498

Dehaan, B.J., M. Jonas, O. Klepper, J. Krabec, M.S. Krol, and K. Olendrzynski. 1994. An atmosphere-ocean model for integrated assessment of global change. *Water, Air, and Soil Pollution 76(1-2):283-318.*

This paper describes the atmosphere-ocean system of the integrated model IMAGE 2.0. The system consists of four linked models, for

atmospheric composition, atmospheric climate, ocean climate and for ocean biosphere and chemistry. The first model is globally averaged, the latter are zonally averaged with additional resolution in the vertical. The models reflect a compromise between describing the physical, chemical and biological processes and moderate computational requirements. The system is validated with direct observations for current conditions (climate, chemistry) and is consistent with results from General Circulation Model experiments. The system is used in the integrated setting of the IMAGE 2.0 model to give transient climate projections. Global surface temperature is simulated to increase by 2.5 K over the next century for socio- economic scenarios with continuing economic and population growth. In a scenario study with reduced ocean circulation, the climate system and the global C cycle are found to be appreciably sensitive to such changes.

KEYWORDS: ANTHROPOGENIC CO2, BALANCE, BUDGET, CARBON DIOXIDE, CLIMATE, SEA

499
Delatorre, A., B. Delgado, and C. Lara. 1991. Nitrate-dependent O2 evolution in intact leaves. *Plant Physiology 96(3):898-901.*

Evolution Of O2 by illuminated intact detached leaves from barley (Hordeum vulgare L. cv Athos) and pea (Pisum sativum L. cv Lincoln) in a CO2-saturating atmosphere was enhanced when KNO3 (1-2.5 millimolar) had been previously supplied through the transpiration stream. The extra O2 evolution observed after feeding KNO3 increased with the light intensity, being maximal at near saturating photon flux densities and resulting in no changes in the initial slope of the O2 versus light-intensity curve. No stimulation Of O2 evolution was otherwise observed after feeding KCl or NH4Cl. The data indicate that nitrate assimilation uses photosynthetically generated reductant and stimulates the rate of noncyclic electron flow by acting as a second electron-accepting assimilatory process in addition to CO2 fixation.

KEYWORDS: ANACYSTIS-NIDULANS, ASSIMILATION, CHLOROPLASTS, OXYGEN, REDUCTION, TRANSLOCATOR

500
de la Vina, G., F. Pliego-Alfaro, S.P. Driscoll, V.J. Mitchell, M.A. Parry, and D.W. Lawlor. 1999. Effects of CO2 and sugars on photosynthesis and composition of avocado leaves grown in vitro. *Plant Physiology and Biochemistry 37(7-8):587-595.*

The effects of micropropagation conditions on avocado (Persea americana Mill.) have been measured in leaves and plants cultured in vitro. The consequences of the type and concentration of sugar in the medium and of carbon dioxide concentration in the atmosphere on the rates of photosynthesis and amounts of ribulose 1,5-biphosphate carboxylase-oxygenase (EC 4.1.1.39; Rubisco) and total soluble protein (TSP) were measured. At the highest sucrose supply (87.6 mM), Rubisco content was substantially decreased in leaves, and even more when elevated CO2 (1 000 mu mol mol(-1)) was supplied. Maximum photosynthetic rate (P-max) was significantly decreased when plants developed in high sucrose and elevated CO2. However, Rubisco concentration was significantly greater when glucose was supplied at the same molar concentration or when the concentration of sucrose was small (14.6 mM), and no differences were observed due to the CO2 concentration in the air in these treatments. The ratio of Rubisco to total soluble protein (Rubisco/TSP) was dramatically decreased in plants grown in the highest concentration of sucrose and with elevated CO2. Leaf area and ratio of leaf fresh weight/(stem + root) fresh weight, were greater in plants grown with CO2, enriched air. However, upon transplanting, survival was poorer in plants grown on low sucrose/high CO2 compared to those grown on high sucrose/high CO2. (C) Elsevier, Paris.

KEYWORDS: (CO2) C 14, ACCLIMATIZATION, EXPRESSION, FIXATION, INHIBITION, INVITRO, MECHANISM, PLANTS, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, SINK REGULATION

501
Delesalle, V.A., and S. Blum. 1994. Variation in germination and survival among families of sagittaria-latifolia in response to salinity and temperature. *International Journal of Plant Science 155(2):187-195.*

We studied seed germination and seedling growth in eight maternal families of Sagittaria latifolia (Alismataceae), a freshwater perennial, in response to salinity (four levels) and temperature effects (two levels) in the greenhouse. Salinity decreased germination, delayed emergence, and decreased survival and growth rates. The negative effects of salinity on germination were greater at the high-temperature regime, but the effects on growth were greater at the low-temperature regime. Some seeds were capable of germinating and surviving (with minimal growth) even in 0.8% NaCl solution. Families also differed in their response to salinity but not to temperature. In particular, high salinities had little effect on the germination of some families. Growth rate always decreased with increasing salinity, but again the magnitude of the effect differed among maternal families. Our data show that S. latifolia can germinate but cannot grow well under low-salinity conditions; thus, S. latifolia might be minimally affected by short-term salt intrusions. In order to understand how plant populations respond to disturbances, such as increased salinity or increased temperature, we need to consider the source, either environmental or genetic, of maternal effects.

KEYWORDS: ECOPHYSIOLOGY, ELEVATED CO2, EVOLUTIONARY CONSEQUENCES, GROWTH, HORDEUM-JUBATUM, INBREEDING DEPRESSION, INTRASPECIFIC VARIATION, PLANTS, SEED-GERMINATION, SIZE

502
Delgado, E., R.A.C. Mitchell, M.A.J. Parry, S.P. Driscoll, V.J. Mitchell, and D.W. Lawlor. 1994. Interacting effects of co2 concentration, temperature and nitrogen supply on the photosynthesis and composition of winter-wheat leaves. *Plant, Cell and Environment 17(11):1205-1213.*

Winter wheat (Triticum aestivum L., cv. Mercia) was grown at two different atmospheric CO, concentrations (350 and 700 mu mol mol(-1)) two temperatures [ambient temperature (i.e. tracking the open air) and ambient +4 degrees C] and two rates of nitrogen supply (equivalent to 489 kg ha(-1) and 87 kg ha(- 1)). Leaves grown at 700 mu mol mol(-1) CO2 had slightly greater photosynthetic capacity (10% mean increase over the experiment) than those grown at ambient CO2 concentration, but there were no differences in carboxylation efficiency or apparent quantum yield. The amounts of chlorophyll, soluble protein and ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) per unit leaf area did not change with long-term exposure to elevated CO2 concentration. Thus winter wheat, grown under simulated field conditions, for which total biomass was large compared to normal field production, did not experience loss of components of the photosynthetic system or loss of photosynthetic competence with elevated CO2 concentration. However, nitrogen supply and temperature had large effects on photosynthetic characteristics but did not interact with elevated CO2 concentration. Nitrogen deficiency resulted in decreases in the contents of protein, including Rubisco, and chlorophyll, and decreased photosynthetic capacity and carboxylation efficiency. An increase in temperature also reduced these components and shortened the effective life of the leaves, reducing the duration of high photosynthetic capacity.

KEYWORDS: ACCLIMATION, CARBON-DIOXIDE

CONCENTRATION, CARBOXYLASE-OXYGENASE, ELEVATED CO2, GROWTH, HIGH ATMOSPHERIC CO2, PLANTS, PROTEIN, RESPONSES, RUBISCO

503

Delmas, R.J. 1998. Ice-core records of global climate and environment changes. *Proceedings of the Indian Academy of Sciences-Earth and Planetary Sciences 107(4):307-319.*

Precipitation accumulating on the Greenland and Antarctic ice sheets records several key parameters (temperature, accumulation, composition of atmospheric gases and aerosols) of primary interest for documenting the past global environment over recent climatic cycles and the chemistry of the preindustrial, atmosphere. Several deep ice cores from Antarctica and Greenland have been studied over the last fifteen years. In both hemispheres, temperature records (based on stable isotope measurements in water) show the succession of glacial and interglacial periods. However, detailed features of the climatic stages are not identical in Antarctica and in Greenland. A tight link between global climate and greenhouse gas concentrations was discovered, CO2 and CH4 concentrations being lower in glacial conditions by about 80 and 0.3 ppmv, respectively, with respect to their pre-industrial levels of 280 and 0.65 ppmv. Coldest stages are also characterized by higher sea-salt and crustal aerosol concentrations. In Greenland, contrary to Antarctica, ice-age ice is alkaline. Gas-derived aerosol (in particular, sulfate) concentrations are generally higher for glacial periods, but not similar in both the hemispheres. Marine and continental biomass-related species are significant in Antarctica and Greenland ice, respectively. Finally, the growing impact of anthropogenic activities on the atmospheric composition is well recorded in both polar regions for long-lived compounds (in particular greenhouse gases), but mostly in Greenland for short-lived pollutants.

KEYWORDS: ANTARCTIC ICE, ATMOSPHERIC METHANE, CENTRAL GREENLAND ICE, CYCLE, DUST, GLACIAL PERIOD, HYDROGEN- PEROXIDE, NITRATE CONCENTRATIONS, SUMMIT, VOSTOK

504

Delucia, E.H., R.M. Callaway, and W.H. Schlesinger. 1994. Offsetting changes in biomass allocation and photosynthesis in ponderosa pine (pinus-ponderosa) in response to climate-change. *Tree Physiology 14(7-9):669-677.*

We examined the effect of climate on aboveground biomass allocation of ponderosa pine (Pinus ponderosa) by measuring trees in disjunct forest stands growing on the same substrate at high-elevation montane sites and low-elevation desert sites. Climatic differences between the sites were comparable to the difference between present and future climates of interior North America that is expected to result from a doubling of atmospheric CO2 concentration. Relative to the montane populations, the desert populations allocated a greater proportion of biomass to sapwood (functional xylem) at the expense of foliage. The leaf/sapwood area ratio and percent of aboveground biomass in sapwood for trees of the same height were 0.201 m2 cm-2 and 58% for montane trees and 0.104 m2 cm-2 and 71% for desert trees. In a phytotron experiment, increases in net photosynthesis and net assimilation rate for seedlings grown under future conditions of high CO2 and temperature were offset by a decrease in leaf area ratio. As was observed for large trees at different elevations, increased temperatures caused an increase in biomass allocation to stem in the phytotron seedlings. Thus, CO2- and temperature-driven shifts in biomass allocation negated the effect on growth of the CO2- driven increase in carbon assimilation rate. Our data from the controlled growth chamber and field experiments suggest that future climate conditions, including elevated atmospheric CO2, may not stimulate growth and productivity of ponderosa pine.

505

Delucia, E.H., R.M. Callaway, E.M. Thomas, and W.H. Schlesinger. 1997. Mechanisms of phosphorus acquisition for ponderosa pine seedlings under high CO2 and temperature. *Annals of Botany 79(2):111-120.*

To test the hypothesis that elevated atmospheric CO2 and elevated temperature, simulating current and predicted future growing season conditions, act antagonistically on phosphorus acquisition of ponderosa pine, seedlings were grown in controlled-environment chambers in a two temperature (25/10 degrees C and 30/15 degrees C)xtwo CO2 (350 and 700 mu l(-1)) experimental design. Mycorrhizal seedlings were watered daily with a nutrient solution with P added in organic form as inositol hexaphosphate (64ppm P). Thus seedlings were challenged to use active forms of P acquisition. Elevated CO2 increased the relative growth rate by approx. 5% which resulted in an approx. 33% increase in biomass after 4 months. There was no main effect of temperature on growth. Increased growth under elevated CO2 and temperature was supported by increases in specific absorption rate and the specific utilization rate of P. The contribution of mycorrhizae to P uptake may have been greater under simulated future conditions, as elevated CO2 increased the number of mycorrhizal roots. There was no main effect of temperature on root phosphatase activity, but elevated CO2 caused a decrease in activity. The inverse pattern of root phosphatase activity and mycorrhizal infection across treatments suggests a physiological coordination between these avenues of P acquisition. The concentration of oxalate in the soil increased under elevated CO2 and decreased under elevated temperature. This small molecular weight acid solubilizes inorganic P making it available for uptake. Increased mycorrhizal infection and exudation of oxalate increased P uptake in ponderosa pine seedlings under elevated CO2, and there was no net negative effect of increased temperature. The increased carbon status of pine under elevated CO2 may facilitate uptake of limiting P in native ecosystems. (C) 1997 Annals of Botany Company.

KEYWORDS: CALCIUM-OXALATE, CARBON DIOXIDE, COMPENSATORY RESPONSES, ELEVATED ATMOSPHERIC CO2, NUTRIENT, PHOSPHATASE-ACTIVITY, PLANTS, RHIZOSPHERE, SOILS, TAEDA L SEEDLINGS

506

DeLucia, E.H., J.G. Hamilton, S.L. Naidu, R.B. Thomas, J.A. Andrews, A. Finzi, M. Lavine, R. Matamala, J.E. Mohan, G.R. Hendrey, and W.H. Schlesinger. 1999. Net primary production of a forest ecosystem with experimental CO2 enrichment. *Science 284(5417):1177-1179.*

The concentration of atmospheric carbon dioxide was increased by 200 microliters per Liter in a forest plantation, where competition between organisms, resource Limitations, and environmental stresses may modulate biotic responses. After 2 years the growth rate of the dominant pine trees increased by about 26 percent relative to trees under ambient conditions. Carbon dioxide enrichment also increased Litterfall and fine-root increment. These changes increased the total net primary production by 25 percent. Such an increase in forest net primary production globally would fix about 50 percent of the anthropogenic carbon dioxide projected to be released into the atmosphere in the year 2050. The response of this young, rapidly growing forest to carbon dioxide may represent the upper Limit for forest carbon sequestration.

KEYWORDS: BIOMASS, CLIMATE, ELEVATED CO2, GROWTH TRENDS, LOBLOLLY-PINE, RESPONSES, RISING ATMOSPHERIC CO2, SODA-LIME, TREE GROWTH, UNITED-STATES

507
DeLucia, E.H., and W.H. Schlesinger. 1999. Effect on the biosphere of elevated atmospheric CO2 - Response. *Science 285(5435):1852.*

508
De Luis, I., J.J. Irigoyen, and M. Sanchez-Diaz. 1999. Elevated CO2 enhances plant growth in droughted N-2-fixing alfalfa without improving water status. *Physiologia Plantarum 107(1):84-89.*

The long-term interaction between elevated CO2 and soil mater deficit was analysed in N-2-fixing alfalfa plants in order to assess the possible drought tolerance effect of CO2. Elevated CO2 could delay the onset of drought stress by decreasing transpiration rates, but this effect was avoided by subjecting plants to the same soil water content. Nodulated alfalfa plants subjected to ambient (400 mu mol mol(-1)) or elevated (700 mu mol mol(-1)) CO2 were either men watered or partially watered by restricting water to obtain 30% of the water content at field capacity (approximately 0.55 g water cm(-3)). The negative effects of sop water deficit on plant growth were counterbalanced by elevated CO2. In droughted plants, elevated CO2 stimulated carbon fixation and, as a result, biomass production was even greater than in well-watered plants grown in ambient CO2. Below-ground production was preferentially stimulated by elevated CO2 in droughted plants, increasing nodule biomass production and the availability of photosynthates to the nodules. As a result, total nitrogen content in droughted plants was higher than in well-watered plants grown in ambient CO2. The beneficial effect of elevated CO2 was not correlated with a better plant water status. It is concluded that elevated CO2 enhances growth of droughted plants by stimulating carbon fixation, preferentially increasing the availability of photosynthates to below-ground production (roots and nodules) without improving water status. This means that elevated CO2 enhances the ability to produce more biomass in N-2-fixing alfalfa under given soil water stress, improving drought tolerance.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CARBON-DIOXIDE, ENRICHMENT, N2 FIXATION, PHOTOSYNTHESIS, PRODUCTIVITY, RESPONSES, SOIL, STARCH, TEMPERATURE

509
Demmers-Derks, H., R.A.C. Mitchell, V.J. Mitchell, and D.W. Lawlor. 1998. Response of sugar beet (Beta vulgaris L.) yield and biochemical composition to elevated CO2 and temperature at two nitrogen applications. *Plant, Cell and Environment 21(8):829-836.*

Effects on sugar beet (Beta vulgaris L.) of current and elevated CO2 and temperature alone and in combination and their interactions with abundant and deficient nitrogen supply (HN and LN, respectively) have been studied in three experiments in 1993, 1994 and 1995. Averaged over all experiments, elevated CO2 (600 mu mol mol(-1) in 1993 and 700 mu mol mol-l in 1994 and 1995) increased total dry mass at final harvest by 21% (95% confidence interval (CI) = 21, 22) and 11% (CI = 6, 15) and root dry mass by 26% (CI = 19, 32) and 12% (CI = 6, 18) for HN and LN plants, respectively. Warmer temperature decreased total dry mass by 11% (CI = - 15, - 7) and 9% (CI = - 15, - 5) and root dry mass by 7% (CI = - 12, - 2) and 7% (CI = - 10, 0) for HN and LN plants, respectively. There was no significant interaction between temperature and CO2 on total or root dry mass. Neither elevated CO2 nor temperature significantly affected sucrose concentration per unit root dry mass. Concentrations of glycinebetaine and of amino acids, measured as alpha-amino-N, decreased in elevated CO2 in both N applications; glycinebetaine by 13% (CI = - 21, - 5) and 16% (CI = - 24, - 8) and alpha-amino-N by 24% (CI = - 36, - 11) and 16% (CI = - 26, - 5) for HN and LN, respectively. Warmer temperature increased alpha-amino-N, by 76% (CI = 50, 107) for HN and 21% (CI = 7, 36) for LN plants, but not glycinebetaine.

KEYWORDS: CARBON DIOXIDE, CROPS, FIELD, GROWTH, PLANT, PRODUCTIVITY, SOURCE-SINK RELATIONS, WINTER-WHEAT

510
DeMothes, M.A.G. 1996. Effects of enhanced CO2 concentration on wheat photosynthesis and long- and short-term stomatal behaviour. *Photosynthetica 32(2):193-202.*

Wheat (Triticum aestivum L.) plants were cultivated in a growth chamber at normal (35 Pa = c(35)) and increased (70 Pa = c(70)) CO2 partial pressure. Environmental conditions other than CO2 concentration were similar for the c(35) and the c(70) plants. For the c(35) and the c(70) plants stomatal density was similar. When both variants were measured at growth conditions, the net photosynthetic rate (P-N) Of c(70) plants was 44 % higher and stomatal conductance to water vapour pressure (g(s)) was 22 % lower than those of the c(35) plants, while the relation between internal partial pressure of CO2 (pci) and external partial pressure (pea) was similar for both variants. Plants were also submitted to a sequence of increments in CO2 concentration (from 10 Pa up to saturating CO2 concentration) at saturating photosynthetically active radiation (PAR). Following 1.5 h at saturating CO2 concentration and PAR, CO2 concentration was decreased stepwise. Both variants showed hysteresis in the response of P-N, transpiration rate (E), g(s) and water use efficiency (WUE) to pci. While CO2 concentration was incremented, P-N and g(s) were linearly related indicating that mesophyll activity and g(s) were correlated. At saturating CO2 concentration and PAR, end product feedback inhibition on photosynthesis disrupted this correlation for both variants. Plants were also submitted to a sequence of increments in PAR (from 40 mu mol m(-2), s(-1) up to saturating PAR) at saturating CO2 concentration. Following 1.5 h at saturating CO2 concentration and PAR, PAR was decreased stepwise. While both variants showed hysteresis in the response of P-N, E and g(s), the c(35) plants showed also hysteresis in the response of pci/pca and WUE to PAR. Stomatal conductance and activity of mesophyll remained co-ordinated during the whole experiment for the c(70) plants, while for the c(35) plants the correlation between g(s) and mesophyll activity present during step-up PAR response was disrupted at saturating CO2 concentration and PAR.

KEYWORDS: FIELD, LEAF, WATER-USE EFFICIENCY

511
DeMothes, M.A.G., M. Baumgarten, and D. Knoppik. 1996. Hysteresis in the response of photosynthesis to CO2 and saccharide pools of wheat leaves grown at normal and enhanced CO2. *Photosynthetica 32(2):181-191.*

Wheat plants were cultivated in a growth chamber at 35 Pa (c(35) variant) and 70 Pa CO2 partial pressure (c(70) variant) during the whole vegetation period. The response of net photosynthetic rate (P-N) Of the nag leaf of both variants to successive increases in CO2 partial pressure (step-up curve) showed hysteresis when the direction of the sequence was reversed (step-down curve) after 1.5 h at saturating CO2 partial pressure and photosynthetically active radiation (PAR). Saccharose, glucose and fructose accumulated during the measurement of a step-up CO2 curve for the c(35) and c(70) plants as the export rate was not able to keep pace with the rate of saccharide synthesis. Remaining 1.5 h at saturating CO2 partial pressure and PAR, the saccharose pool increased further for both variants while glucose and fructose decreased reaching the values at growth conditions. The electron transport rate decreased after 1.5 h at saturating CO2 partial pressure and PAR for the two variants due to end product feedback. Glucose and fructose contents fell 50 % below the initial contents when partial pressure of CO2 was lowered stepwise. The c(35) plants showed a double fold increase in the content of saccharose at the end point of the hysteresis curve. Contents

of saccharose for the c(70) variant in contrast were similar to the initial values.

KEYWORDS: ACCLIMATION, ASSIMILATION, CARBON DIOXIDE, ELECTRON-TRANSPORT, ELEVATED CO2, ENRICHMENT, PHASEOLUS-VULGARIS L, RESPIRATION, TEMPERATURE

512

Demothes, M.A.G., and D. Knoppik. 1994. Effects of long-term enhanced co2 partial-pressure on gas- exchange parameters and saccharide pools of wheat leaves. *Photosynthetica 30(3):435-445.*

Wheat plants were cultivated in a growth chamber at normal (35 Pa, c35 plants) and enhanced (70 Pa, c70 plants) CO2 partial pressure. In C35 plants the net photosynthetic rate (P(N)) of flag leaves and the concentrations of saccharides such as sucrose, glucose, fructose and starch were increased. The c70 plants possessed higher chlorophyll (Chl) a and Chl b contents. The CO2 response of P(N) at saturating photosynthetically active radiation (PAR) was very similar for both variants. At the highest CO2 concentration saccharides accumulated in both variants as a consequence of decreased export rate. The response of P(N) to PAR at saturating CO2 concentrations was similar in the two variants. On the other hand, the response of water vapour pressure conductance (gH2O) to PAR in c35 plants followed a hyperbolic response to PAR, while in the c70 plants it was linearly related to PAR up to the mean PAR used for growth. In this variant gH2O seemed to change parallelly to changes in the mesophyll demand for CO2 caused by PAR.

KEYWORDS: ACCLIMATION, ASSIMILATION, ATMOSPHERIC CO2, CARBON DIOXIDE, ELEVATED CO2, PHOTOSYNTHESIS, RESPIRATION, RESPONSES, TEMPERATURE, YIELD

513

Denelzen, M.G.J., and J. Rotmans. 1993. Modeling climate related feedback processes. *Journal of Environmental Science and Health Part A- Environmental Science and Engineering & Toxic and Hazardous Substance Control 28(9):2095-2151.*

Feedback mechanisms play a crucial role in the climate system, amplifying or dampening the climate response to enhanced concentrations of greenhouse gases from anthropogenic perturbations. Many of these feedbacks are known, but most of them only potentially. This article evaluates the role of a number of these feedback processes within the climate system. In order to assess their impact, the feedbacks which at present can be quantified reasonably are built into the Integrated Model to Assess the Greenhouse Effect (IMAGE). Unlike previous studies, this study describes the scenario- and time-dependent role of biogeochemical feedbacks. A number of simulation experiments are performed with IMAGE to project climate changes. Besides estimates of their absolute importance, the relative importance of individual biogeochemical feedbacks is considered by calculating the gain for each feedback process. This study focuses on feedback processes in the carbon cycle and the methane (semi-) cycle. Modeled feedbacks are then used to balance the past and present carbon budget. This results in substantially lower projections for atmospheric carbon dioxide than the Intergovernmental Panel on Climate Change (IPCC) estimates. The difference is approximately 18% from the 1990 level for the IPCC "Business-as-Usual" scenario. Furthermore, the IPCC's "best guess" value of the CO2 concentration in the year 2100 falls outside the uncertainty range estimated with our balanced modeling approach. For the IPCC "Business-as- Usual" scenario, the calculated total gain of the feedbacks within the carbon cycle appears to be negative, a result of the dominant role of the fertilization feedback. This study also shows that if temperature feedbacks on methane emissions from wetlands, rice paddies, and hydrates do materialize, methane concentrations might be increased by 30% by 2100. The total effect of the methane feedbacks and the carbon dioxide feedbacks modeled can be expressed in the carbon dioxide- equivalent concentrations. Our simulated CO2-equivalent concentrations are lower than the IPCC estimates.

KEYWORDS: ATMOSPHERIC CO2, ECOSYSTEMS, GLOBAL CLIMATE, GREENHOUSE, ICE CORE, INCREASE, METHANE EMISSIONS, PAST 2 CENTURIES, SENSITIVITY, SIMULATION

514

Deng, R., and D.J. Donnelly. 1993. In-vitro hardening of red raspberry by co2 enrichment and reduced medium sucrose concentration. *Hortscience 28(10):1048-1051.*

Micropropagated 'Festival' red raspberry (Rubus idaeus L.) shoots were rooted in specially constructed plexiglass chambers in ambient (340 +/- 20 ppm) or enriched (1500 +/- 50 ppm) CO2 conditions on a medium containing 0, 10, 20, or 30 g sucrose/liter. Plantlet growth and leaf (CO2)-C-14 fixation rates were evaluated before and 4 weeks after ex vitro transplantation. In vitro CO2 enrichment promoted in vitro hardening; it increased root count and length, plantlet fresh weight, and photosynthetic capacity but did not affect other variables such as plantlet height, dry weight, or leaf count and area. No residual effects of in vitro CO2 enrichment were observed on 4-week-old transplants. Sucrose in the medium promoted plantlet growth but depressed photosynthesis and reduced in vitro hardening. Photoautotrophic plantlets were obtained on sucrose-free rooting medium under ambient and enriched CO2 conditions and they performed better ex vitro than mixotrophic plantlets grown with sucrose. Root hairs were more abundant and longer on root tips of photoautotrophic plantlets than on mixotrophic plantlets. The maximum CO2 uptake rate of plantlet leaves was 52% that of greenhouse control plant leaves. This did not change in the persistent leaves up to 4 weeks after ex vitro transplantation. The photosynthetic ability of persistent and new leaves of 4-week-old ex vitro transplants related neither to in vitro CO2 nor medium sucrose concentration. Consecutive new leaves of transplants took up more CO2 than persistent leaves. The third new leaf of transplants had photosynthetic rates up to 90% that of greenhouse control plant leaves. These results indicate that in vitro CO2 enrichment was beneficial to in vitro hardening and that sucrose may be reduced substantially or eliminated from red raspberry rooting medium when CO2 enrichment is used.

KEYWORDS: ACCLIMATIZATION, CULTURE, EXVITRO, FIXATION, GROWTH, LEAF ANATOMY, LEAVES, SOIL, STRAWBERRY PLANTLETS

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Deng, R., and D.J. Donnelly. 1993. In-vitro hardening of red raspberry through co2 enrichment and relative-humidity reduction on sugar-free medium. *Canadian Journal of Plant Science 73(4):1105-1113.*

Micropropagated shoots of red raspberry (Rubus idaeus L. 'Comet') were rooted on modified Murashige-Skoog medium lacking sucrose, in specially 'constructed plexiglass chambers, under ambient (340 +/- 20 ppm) or enriched (1500 +/- 50 PPM) CO2 and ambient (ca. 100 %) or reduced (90 +/- 5 %) relative humidity. Cultured plantlets were evaluated for their survival, rooting and relative vigor, leaf and root number, stem and root length, total leaf area, total fresh and dry weight, gas exchange rate, and stomatal features, prior to transplantation to soil and at intervals for 6 wk ex vitro. In vitro CO2 enrichment promoted plantlet growth, rooting and both the survival and early growth of transplants. CO2 enrichment increased stomatal aperture of plantlet leaves but did not apparently increase water stress at transplantation. Reduced in vitro RH did not affect plantlet growth but decreased stomatal apertures and stomatal index on leaves of cultured plantlets and promoted both the survival and early growth of transplants. In vitro CO2

and RH levels did not affect the photosynthetic rate of either plantlets or transplants. Only the stomata on leaves of plantlets from the ambient CO2 and reduced RH treatment were functional. Normal stomatal function was not observed in persistent leaves of transplants from the other treatments, even 2 wk after transplantation. In vitro CO2 enrichment acted synergistically with RH reduction in improving growth of plantlets both in vitro and ex vitro. Hardened red raspberry plantlets obtained through CO2 enrichment and RH reduction survived direct transfer to ambient greenhouse conditions without the necessity for specialized ex vitro acclimatization treatment.

KEYWORDS: ANATOMY, CULTURE, GROWTH, LEAVES, LIGHT, PLANTLETS INVITRO, SOIL, STRAWBERRY

516
Deng, X., and F.I. Woodward. 1998. The growth and yield responses of Fragaria ananassa to elevated CO2 and N supply. *Annals of Botany 81(1):67-71.*

Strawberry plants (Fragaria ananassa Duchesne var. Elsanta) were grown in pots at two concentrations of carbon dioxide (partial pressures of 39 and 56 Pa) and with three rates of nitrogen supply (0.04, 0.4 and 4 mM as nutrient solution) to study their individual and interactive effects on plant growth and fruit yield. Nitrogen deficiency reduced total dry biomass and relative growth rate (RGR), mainly through reductions in leaf area ratio (LAR) and plant N concentration (PNC), although both the net assimilation rare (NAR) and root weight ratio (RWR) increased. Elevated CO2 increased the N productivity (NP) but reduced the LAR. High CO2 increased the fruit yield by 42% at high N supply and by 17% at low N supply. The CO2 yield enhancement occurred through an increase in the flower and fruit number of individual plants. This resulted in an increase in the fruit weight ratio (FWR) of plants at high CO2. Nitrogen deficiency reduced the fruit yield by about 50% through decreases in fruit size, fruit set and the number of fruits. However, N deficiency increased the proportion of total plant dry biomass allocated to fruits. There were no significant interactions between CO2 and N supply on yield. (C) 1998 Annals of Botany Company.

KEYWORDS: ATMOSPHERIC CO2, AVAILABILITY, CARBON-DIOXIDE ENRICHMENT, DRY-MATTER, GRASSES, NITROGEN, NUTRITION, WHEAT

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denHertog, J., I. Stulen, F. Fonseca, and P. Delea. 1996. Modulation of carbon and nitrogen allocation in Urtica dioica and Plantago major by elevated CO2: Impact of accumulation of nonstructural carbohydrates and ontogenetic drift. *Physiologia Plantarum 98(1):77-88.*

Doubling the atmospheric CO2 concentration from 350 to 700 mu l l(-1) increased the relative growth rate (RGR) of hydroponically grown Urtica dioica L. and Plantago major ssp. pleiosperma Pilger only for the first 10-14 days. Previous experiments with P. major led to the conclusion that RGR did not respond in proportion to the rate of photosynthesis. The present paper is focussed on the analysis of the impact of changes in leaf morphology, dry matter partitioning, dry matter chemical composition and ontogenetic drift on this discrepancy. Soon after the start of the treatment, carbohydrate concentrations were higher at elevated CO2; a reaction that was largely due to starch accumulation. An increase in the percentage of leaf dry matter and decreases in the specific leaf area (SLA) and the shoot nitrogen concentration were correlated with an increase in the total nonstructural carbohydrate concentration (TNC). A combination of accumulation of soluble sugars and starch and ontogenetic drift explains the decrease in SLA at the elevated CO2 level. A similar ontogenetic effect of elevated CO2 was observed on the specific root length (SRL). Other variables such as shoot nitrogen concentration and percentage leaf dry matter were not affected by correction of data for TNC levels. The net diurnal fluctuation of the carbohydrate pool in P. major was equal for both CO2 concentrations, indicating that the growth response to elevated CO2 may be ruled by variables other than photosynthesis, as for instance sink strength. Elevated CO2 did not greatly influence the partitioning of nitrogen between soluble and insoluble, reduced N and nitrate, nor the allocation of dry matter between leaf, stem and root. The finding that the root to shoot ratio (R/S) was not affected by elevated CO2 implies that, in order to maintain a balanced activity between roots and shoot, no shift in partitioning of dry matter upon doubling of the atmospheric CO2 concentration is required. Our data on R/S are in good agreement with the response of R/S to high CO2 predicted by models based on such a theorem.

KEYWORDS: ASSIMILATION, ATMOSPHERIC CO2, DIOXIDE ENRICHMENT, LEAF-AREA, NITRATE, PHOTOSYNTHESIS, PRODUCTIVITY, RELATIVE GROWTH-RATE, ROOT, SHOOT RATIO

518
Denhertog, J., I. Stulen, and H. Lambers. 1993. Assimilation, respiration and allocation of carbon in plantago major as affected by atmospheric co2 levels - a case-study. *Vegetatio 104:369-378.*

The response of Plantago major ssp. pleiosperma plants, grown on nutrient solution in a climate chamber, to a doubling of the ambient atmospheric CO2 concentration was investigated. Total dry matter production was increased by 30 % after 3 weeks of exposure, due to a transient stimulation of the relative growth rate (RGR) during the first 10 days. Thereafter RGR returned to the level of control plants. Photosynthesis, expressed per unit leaf area, was stimulated during the first two weeks of the experiment, thereafter it dropped and nearly reached the level of the control plants. Root respiration was not affected by increased atmospheric CO2 levels, whereas shoot, dark respiration was stimulated throughout the experimental period. Dry matter allocation over leaves stems and roots was not affected by the CO2 level. SLA was reduced by 10%, which can partly be explained by an increased dry matter content of the leaves. Both in the early and later stages of the experiment, shoot respiration accounted for a larger part of the carbon budget in plants grown at elevated atmospheric CO2. Shifts in the total carbon budget were mainly due to the effects on shoot respiration. Leaf growth accounted for nearly 50 % of the C budget at all stages of the experiment and in both treatments.

KEYWORDS: DIOXIDE, ENRICHMENT, NITROGEN, PHOTOSYNTHESIS, RELATIVE GROWTH-RATE

519
den Hertog, J., I. Stulen, F. Posthumus, and H. Poorter. 1998. Interactive effects of growth-limiting N supply and elevated atmospheric CO2 concentration on growth and carbon balance of Plantago major. *Physiologia Plantarum 103(4):451-460.*

To assess the interactions between concentration of atmospheric CO2 and N supply, the response of Plantago major ssp. pleiosperma Pilger to a doubling of the ambient CO2 concentration of 350 mu l l(-1) was investigated in a range of exponential rates of N addition. The relative growth rate (RGR) as a function of the internal plant nitrogen concentration (Ni), was increased by elevated CO2 at optimal and intermediate N-i. The rate of photosynthesis, expressed per unit leaf area and plotted Versus N-i, was increased by 20-30% at elevated CO2 for N-i above 30 mg N g(-1) dry weight. However, the rate of photosynthesis, expressed on a leaf dry matter basis and plotted versus N-i, was not affected by the CO2 concentration. The allocation of dry matter between shoot and root was not affected by the CO2 concentration at any of the N addition rates. This is in good agreement with theoretical models, based on a balance between the rate of photosynthesis of the shoot and

the acquisition of N by the roots. The concentration of total nonstructural carbohydrates (TNC) was increased at elevated CO2 and at N limitation, resulting in a shift in the partitioning of photosynthates from structural to nonstructural and, in terms of carbon balance, unproductive dry matter. The increase in concentration of TNC led to a decrease in both specific leaf area (SLA) and Ni at all levels of nutrient supply, and was the cause of the increased rate of photosynthesis per unit leaf area. Correction of the relationship between RGR and Ni for the accumulation of TNC made the effect of elevated CO2 on the relationship between RGR and Ni disappear. We conclude that the shift in the relationship between RGR and Ni was due to the accumulation of TNC and not due to differences in physiological variables such as photosynthesis and shoot and root respiration, changes in leaf morphology or allocation of dry matter.

KEYWORDS: BETULA-PENDULA ROTH, DRY-MATTER, ENRICHMENT, LEAF-AREA, MINERAL NUTRITION, NITROGEN CONCENTRATION, NUTRIENT AVAILABILITY, PHOTON FLUX-DENSITY, PHOTOSYNTHETIC ACCLIMATION, SHOOT RATIO

520
Denmead, O.T., F.X. Dunin, S.C. Wong, and E.A.N. Greenwood. 1993. Measuring water-use efficiency of eucalypt trees with chambers and micrometeorological techniques. *Journal of Hydrology 150(2-4):649-664.*

Enclosure appears to be the only feasible way to examine the gas exchange of small groups of trees or to answer questions about the effects of increased atmospheric CO2 on the assimilation, evaporation and water use efficiency of forests. To be effective, enclosures must necessarily change the microclimate, but few studies have been made of the consequences. In this paper, the assimilation, evaporation and water use efficiency of a community of Eucalyptus trees inside a ventilated chamber are compared with the same attributes for the surrounding forest. Assimilation and evaporation for the chamber were measured by the depletion in CO2 and the enrichment in water vapour of air passing through the chamber. For the forest, assimilation and evaporation were determined by micrometeorological techniques based on the energy balance, and for CO2, additional chamber measurements of the soil efflux. Water use efficiencies were calculated as the ratio of mol CO2 assimilated to mol water evaporated. There are some important microclimatic differences between chamber and forest: net radiation is reduced by about 30% in the chamber, the vapour pressure deficit of the chamber air is lower, and the light climate there tends to be diffuse rather than direct. Despite these differences, evaporation rates for both chamber and forest were generally similar, perhaps due to compensating effects in the chamber from higher boundary layer conductances (because of greater ventilation rates) and higher stomatal conductances (because of increased humidity). However, assimilation rates and water use efficiencies were markedly different for the two communities in clear sky conditions, with higher values of both being recorded in the chamber for most of the daylight hours. Only on cloudy days, when the light climate was diffuse in both chamber and forest, were similar assimilation rates and water use efficiencies observed. This behaviour seems to be attributable in part to the light climate in the chamber being predominantly diffuse and that in the forest predominantly direct. Diffuse light enhances the photosynthesis of lower leaves in the canopy. This contention is supported by model calculations of canopy assimilation under diffuse and direct radiation which produced qualitatively the same light response functions as observed for chamber and forest. The study suggests that the use of chambers for exploring questions of forest productivity and water use efficiency must be circumspect. The act of enclosure, by itself, can change the daily water use efficiency of the tree community by as much as 50%.

KEYWORDS: FOREST, PHOTOSYNTHESIS, TRANSPIRATION, VENTILATED CHAMBER

521
Desjardins, Y., A. Gosselin, and M. Lamarre. 1990. Growth of transplants and invitro-cultured clones of asparagus in response to CO2 enrichment and supplemental lighting. *Journal of the American Society for Horticultural Science 115(3):364-368.*

522
Devakumar, A.S., M.S.S. Shayee, M. Udayakumar, and T.G. Prasad. 1998. Effect of elevated CO2 concentration on seedling growth rate and photosynthesis in Hevea brasiliensis. *Journal of Biosciences 23(1):33-36.*

To study the effect of elevated CO2 concentration on plant growth and photosynthesis, two clones of Hevea brasiliensis were grown in polybags and exposed to elevated concentration (700+/-25 ppm) for 60 days. There was higher biomass accumulation, leaf area and better growth when compared to ambient air grown plants. From A/Ci curves it is clear that photosynthetic rates increases with increase in CO2 concentrations. After 60 days of exposure to higher CO2 concentration, a decrease in the carbon assimilation rate was noticed.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, CARBON DIOXIDE, ENRICHMENT, FIELD, TEMPERATURE, YIELD

523
Devakumar, A.S., M. Udayakumar, and T.G. Prasad. 1996. A simple technique to expose tree seedlings to elevated CO2 for increased initial growth rates. *Current Science 71(6):469-472.*

Initial growth rates of most tree species that are used in afforestation programmes are very low. Therefore, polybag planted seedlings have to be maintained in the nurseries for a long period of time. Growing plants in an elevated CO2 atmosphere increases the growth rates as well as biomass production in many annual crop and tree species. Higher temperature and relative humidity in association with elevated CO2 concentration helps to boost the biomass and leaf area production. We demonstrate here an easy and cost-effective method for obtaining elevated CO2 concentrations for better growth of tree seedlings in the nursery.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, PLANTS, RESPIRATION, TEMPERATURE

524
de Wild, H.P.J., E.J. Woltering, and H.W. Peppelenbos. 1999. Carbon dioxide and 1-MCP inhibit ethylene production and respiration of pear fruit by different mechanisms. *Journal of Experimental Botany 50(335):837-844.*

Ethylene production in relation to O-2 partial pressure of whole pear fruit stored at 2 degrees C could be described by a Michaelis-Menten equation. This was indicated by the use of a gas exchange model. The maximum ethylene production rate was strongly inhibited while the K-mO2 value (1.25 kPa) was not affected by elevated CO2. Ethylene production was also inhibited by 1-MCP, an inhibitor of ethylene perception. The reduction in ethylene production by CO2 was similar for 1-MCP treated and untreated pears. Elevated CO2, therefore, must have had an influence on ethylene production other than through ethylene perception. A possible site of inhibition by CO2 is the conversion of ACC to ethylene. The O-2 uptake rate in relation to O-2 partial pressure of whole pear fruit could be described by a Michaelis-Menten equation. The O-2 uptake rate was inhibited by elevated CO2 at a level similar to the inhibition of ethylene production. Again the K-mO2 value (0.68 kPa)

was not affected by CO2. Using 1-MCP treatments it was shown that there was no direct effect of inhibited ethylene production on O-2 uptake rate.

KEYWORDS: 1-AMINOCYCLOPROPANE-1-CARBOXYLIC ACID, ACC OXIDASE, APPLES, ATMOSPHERES, AVOCADO FRUIT, BIOSYNTHESIS, ELEVATED CO2 CONCENTRATIONS, INTRACELLULAR PH, TISSUE, VEGETABLES

525

Deyton, D.E., C.E. Sams, and J.C. Cummins. 1992. Application of dormant oil to peach-trees modifies bud twig internal atmosphere. *Hortscience 27(12):1304-1305.*

Treatments of single applications of 0%, 3%, 6%, 9%, or 12% dormant oil were sprayed on peach (Prunus persica L. Batsch) trees on 6 Feb. 1990. A repeat application of 6% oil plus 6% oil applied 6 days later was also made. Internal CO2 concentrations of oil-treated buds and twigs were higher than the control the day after treatment and continued to be higher for 6 days. The second application of 10% oil prolonged the elevated CO2 concentration. Applications of 9% or 12% oil delayed flower bud development and bloom. The repeated application of 6% oil delayed bud development and bloom more than a single application of 6% oil. Damage to fruit buds increased as oil concentration increased, but repeated application of 6% oil resulted in less damage than a single application of 12% oil.

526

Dhakhwa, G.B., and C.L. Campbell. 1998. Potential effects of differential day-night warming in global climate change on crop production. *Climatic Change 40(3-4):647-667.*

Recent studies on the nature of global warming indicate the likelihood of an asymmetric change in temperature, where night- time minimum temperature increases more rapidly than the daytime maximum temperature. We used a physically based scenario of asymmetric warming combined with climate change scenarios from General Circulation Models (GCMs) outputs and the EPIC (Erosion Productivity Impact Calculator) plant process model to examine the effects of asymmetric temperature change on crop productivity. Our results indicated that the potential effects of global change on crop productivity may be less severe with asymmetric day-night warming than with equal day- night warming.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CO2 CONCENTRATIONS, EPIC MODEL, GROWTH, MAXIMUM, MINIMUM TEMPERATURE, SENSITIVITY, SOUR ORANGE TREES, VARIABILITY, YIELD

527

Dhakhwa, G.B., C.L. Campbell, S.K. LeDuc, and E.J. Cooter. 1997. Maize growth: assessing the effects of global warming and CO2 fertilization with crop models. *Agricultural and Forest Meteorology 87(4):253-272.*

Projected future climate change scenarios derived from two General Circulation Models (GCMs): Geophysical Fluid Dynamics Laboratory (GFDL) and United Kingdom Meteorological Office (UKMO), and two crop models: Crop Estimation through Resources and Environmental Synthesis (CERES), and Erosion/Productivity Impact Calculator (EPIC), were considered to assess the climate change impact on the yield and biomass of maize. Climate change scenarios included changes in temperature, precipitation and solar radiation from two GCMs interpolated to 1 degrees x1 degrees grid cells in the central Piedmont in North Carolina. Changes in mean monthly temperature and precipitation from the GCMs were used to adjust observed daily climate records from 1949-1988. There is convincing evidence that future temperature linked to global warming might be characterized by asymmetric change between daily daytime maxima and daily nighttime minima. Two hypotheses regarding how GCM temperature would alter observational record were examined. The first hypothesis assumed that daytime and nighttime warming occurs symmetrically, i.e., maximum and minimum temperatures are raised equally. The second hypothesis assumed that nighttime minima change is three times greater than daytime maxima change and the change in mean diurnal temperature range is approximately equal to the change in daily mean temperature. For the equal day-night warming scenario, when only the effects of climate change (i.e., changes in temperature, precipitation and solar radiation) were considered, simulations with CERES and EPIC indicated substantial losses in maize grain yield and total above ground biomass with both the GCM scenarios. For the asymmetric warming, the reduction in biomass and yield due to climate change was less than that obtained with symmetric warming. Simulated maize yield and biomass with CERES and EPIC increased when only effects due to CO2-fertilization were considered. The inclusion of CO2 fertilization effects with those due to climate change resulted in higher biomass and yield compared to values obtained with effects of climate change alone. When CERES was used with the GFDL scenario, and the effects of CO2 fertilization and the climate change were combined, no difference in simulated yield was found between the two hypotheses; only an 8% difference in aboveground biomass was found when the UKMO scenario was used. When EPIC was used, the differential day-night warming hypothesis resulted in 9-13% less reduction in biomass and yield than did the use of the equal day-night warming hypothesis. (C) 1997 Elsevier Science B.V.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CLIMATE CHANGE, ENRICHMENT, EPIC MODEL, PRODUCTIVITY, RESPONSES, TEMPERATURE, UNITED-STATES, WATER-USE, YIELD

528

Dhillion, S.S., J. Roy, and M. Abrams. 1996. Assessing the impact of elevated CO2 on soil microbial activity in a Mediterranean model ecosystem. *Plant and Soil 187(2):333-342.*

The fate, as well as the consequence for plant nutrition, of the additional carbon entering soil under elevated CO2 is largely determined by the activity of soil microorganisms. However, most elevated CO2 studies have documented changes (generally increases) in microbial biomass and total infection by symbiotic organisms, which is only a first step in the understanding of the modification of soil processes. Using a Mediterranean model ecosystem, we complemented these variables by analyzing changes in enzymatic activities, hyphal lengths, and bacterial substrate assimilation, to tentatively identify the specific components affected under elevated CO2 and those which suggest changes in soil organic matter pools. We also investigated changes in the functional structures of arbuscular mycorrhizas. Most of the microbial variables assessed showed significant and substantial increase under elevated CO? of the same order or less than those observed for root mass and length. The increase in dehydrogenase activity indicates that the larger biomass of microbes was accompanied by an increase in their activity. The increase in hyphal length (predominantly of saprophytic fungi), and xylanase, cellulase and phosphatase activities, suggests an overall stimulation of organic matter decomposition. The higher number of substrates utilized by microorganisms from the soil under elevated CO2 was significant for the amine/amide group. Total arbuscular and vesicular mycorrhizal infection of roots was higher under elevated CO2, but the proportion of functional structures was not modified. These insights into the CO2-induced changes in soil biological activity point towards potential areas of investigation complementary to a direct

analysis of the soil organic matter pools.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, BIOCIDAL TREATMENTS, BIOMASS, COMMUNITIES, ENRICHMENT, MYCORRHIZAL COLONIZATION, RESPIRATION, RESPONSES, RHIZOSPHERE, ROOTS

529
Diaz, S. 1995. Elevated CO2 responsiveness, interactions at the community level and plant functional types. *Journal of Biogeography 22(2-3):289-295.*

Plant responsiveness to elevated carbon dioxide (CO2) is a relevant dimension for the definition of functional types in the face of global change. Most traits reported to be associated with high CO2 responsiveness are derived from laboratory experiments on individually grown species. This paper suggests that physiological traits such as photosynthetic pathway and internal sink strength are necessary, but not enough for the prediction of plant responses in mixed stands. A number of examples from the literature are presented to illustrate how predictions based on single-species experiments may not match the behaviour of multi-species assemblages. Individual attributes associated to the interaction of the species with other members of the community should be also considered. Morphogenetic and architectural traits, as well as characteristics related to other trophic levels, such as the presence of root symbionts or the preferential allocation to growth or defences against herbivory, may be useful for a better prediction of plant responsiveness to high CO2 in the field.

KEYWORDS: ALLOCATION PATTERNS, ATMOSPHERIC CARBON-DIOXIDE, ECOSYSTEMS, ENRICHMENT, INSECT HERBIVORE, NITROGEN, PHOTOSYNTHESIS, RESPONSES, SEEDLING GROWTH, WATER-STRESS

530
Diaz, S. 1996. Effects of elevated [CO2] at the community level mediated by root symbionts. *Plant and Soil 187(2):309-320.*

This review examines the effects of elevated [CO2] on plant symbioses with mycorrhizal fungi and root nodule bacteria, with emphasis on community and ecosystem processes. The effects of elevated [CO2] on the relationships between single plant species and root symbionts are considered first. There is some evidence that plant infection by and/or biomass of root symbionts are stimulated by elevated [CO2], but growth enhancement of the host seemingly depends on its degree of dependence on symbiosis and on soil nutrient availability. Second, the effects of elevated [CO2] on the relationships between plant multispecies assemblages and soil, and likely impacts on above-ground and belowground diversity, are analysed. Experimental and modelling work have suggested the existence of complex feedbacks in the responses of plants and the rhizosphere to CO2 enrichment. By modifying C inputs from plants to soil, elevated [CO2] may affect the biomass, the infectivity, and the species/isolate composition of root symbionts. This has the potential to alter community structure and ecosystem functioning. Finally, the incorporation of type and degree of symbiotic dependence into the definition of plant functional types, and into experimental work within the context of global change research, are discussed. More experimental work on the effects of elevated [CO2] at the community/ecosystem level, explicitly considering the role of root symbioses, is urgently needed.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, BOUTELOUA-GRACILIS, ECTOMYCORRHIZAL FUNGI, EXTERNAL HYPHAE, NITROGEN NUTRITION, PLANT COMMUNITY, QUERCUS-ALBA, SEEDLING GROWTH, VESICULAR-ARBUSCULAR MYCORRHIZAS, WATER RELATIONS

531
Diaz, S., and M. Cabido. 1997. Plant functional types and ecosystem function in relation to global change. *Journal of Vegetation Science 8(4):463-474.*

Plant functional types (PFTs) bridge the gap between plant physiology and community and ecosystem processes, thus providing a powerful tool in climate change research. We aimed at identifying PFTs within the flora of central-western Argentina, and to explore their possible consequences for ecosystem function. We analyzed 24 vegetative and regenerative traits of the 100 most abundant species along a steep climatic gradient. Based on plant traits and standard multivariate techniques, we identified eight PFTs. Our results confirmed, over a wide range of climatic conditions, the occurrence of broad recurrent patterns of association among plant traits reported for other floras; namely trade-offs between high investment in photosynthesis and growth on the one hand, and preferential allocation to storage and defence on the other. Regenerative traits were only partially coupled with vegetative traits. Using easily-measured plant traits and individual species cover in 63 sites, we predicted main community- ecosystem processes along the regional gradient. We hypothesized likely impacts of global climatic change on PFTs and ecosystems ill situ, and analysed their probabilities of migrating in response to changing climatic conditions. Finally, we discuss the advantages and limitations of this kind of approach in predicting changes in plant distribution and in ecosystem processes over the next century.

KEYWORDS: ATTRIBUTES, CLASSIFICATION, CO2- ENRICHMENT, COMMUNITIES, ECOLOGY, GROWTH RATE, RESPONSES, SEED SIZE, STRATEGIES, VEGETATION

532
Diaz, S., M. Cabido, M. Zak, E.M. Carretero, and J. Aranibar. 1999. Plant functional traits, ecosystem structure and land-use history along a climatic gradient in central-western Argentina. *Journal of Vegetation Science 10(5):651-660.*

This paper deals with theoretical concepts, methodological steps, and case studies related to the use of plant functional traits in the assessment of vegetation responses to climate and land use. Trait-environment links are considered, and special emphasis is put on the links between vegetation structure and ecosystem function, and on the role of disturbance history in determining vegetation responses to land use at present. As a basis for discussion, published and new case studies from central-western Argentina are presented. Similar plant traits measured with different levels of precision are utilized in the description of ecosystem structure in different land-use situations along a steep regional climatic gradient. The general protocol followed in the case studies represents a data-driven, non-hierarchical, low-tech approach, that can be applied to a wide range of spatial scales, from plots to regions. Climatic factors (including extreme events and seasonality), disturbance frequency and intensity, and disturbance history are suggested as key factors to be considered in global comparisons of vegetation responses to land use and in predictive models of ecosystem dynamics.

KEYWORDS: ATMOSPHERIC CO2, BIODIVERSITY, COMMUNITIES, GLOBAL CHANGE, GRASSLAND, VEGETATION

533
Diaz, S., L.H. Fraser, J.P. Grime, and V. Falczuk. 1998. The impact of elevated CO2 on plant-herbivore interactions: experimental evidence of moderating effects at the community level. *Oecologia 117(1-2):177-186.*

Surprisingly little research has been published on the responses to elevated [CO2] at the community level, where herbivores can select their preferred food. We investigated the combined effects of atmospheric [CO2] and herbivory on synthesised plant communities growing on soils of different fertility. Factorial combinations of two [CO2] (350 or 700 mu l l(-1)), two fertility (fertilised or non-fertilised), and two herbivory (herbivores present or absent) treatments were applied to a standard mixture of seven fast- and eight slow- growing plants in outdoor microcosms. The herbivores used were the grain aphid (Sitobion avenae) and the garden snail (Helix aspersa). We measured plant biomass, foliar nitrogen and soluble tannin concentration, aphid fecundity, and snail growth, fecundity, and feeding preferences over one growing season. Elevated [CO2] did not have a significant impact on(1)the combined biomass of fast-growing or slow-growing plants, (2) herbivore feeding preferences, or (3) herbivore fitness. There was, however, a significant biomass increase of Carex flacca (which represented in all cases less than 5% of total live biomass), and some chemical changes in unpalatable plants under elevated [CO2]. The herbivory treatment significantly increased the biomass of slow-growing plants over fast-growing plants, whereas fertilisation significantly increased the abundance of fast-growing plants over slow- growing plants. Predictions on the effects of elevated [CO2] based on published single-species experiments were not supported by the results of this microcosm study.

KEYWORDS: ATMOSPHERIC CO2, CALCAREOUS GRASSLAND, CARBON DIOXIDE, CHEMICAL-COMPOSITION, DECOMPOSITION, EXPERIMENTAL MICROCOSMS, INSECT HERBIVORE, PERFORMANCE, RELATIVE GROWTH-RATE, RESPONSES

534

Diaz, S., J.P. Grime, J. Harris, and E. McPherson. 1993. Evidence of a feedback mechanism limiting plant-response to elevated carbon-dioxide. *Nature 364(6438):616-617.*

IN short-term experiments under productive laboratory conditions, native herbaceous plants differ widely in their potential to achieve higher yields at elevated concentrations of atmospheric carbon dioxide1-8. The most responsive species appear to be large fast-growing perennials of recently disturbed fertile soils7,8. These types of plants are currently increasing in abundance9 but it is not known whether this is an effect of rising carbon dioxide or is due to other factors. Doubts concerning the potential of natural vegetation for sustained response to rising carbon dioxide have arisen from experiments on infertile soils, where the stimulus to growth was curtailed by mineral nutrient limitations2,3,10. Here we present evidence that mineral nutrient constraints on the fertilizer effect of elevated carbon dioxide can also occur on fertile soil and in the earliest stages of secondary succession. Our data indicate that there may be a feedback mechanism in which elevated carbon dioxide causes an increase in substrate release into the rhizosphere by non-mycorrhizal plants, leading to mineral nutrient sequestration by the expanded microflora and a consequent nutritional limitation on plant growth.

KEYWORDS: CO2- ENRICHMENT, ECOSYSTEMS, GROWTH, NUTRITION, POPULATIONS, SOIL, TUNDRA

535

Dickson, R.E., M.D. Coleman, D.E. Riemenschneider, J.G. Isebrands, G.D. Hogan, and D.F. Karnosky. 1998. Growth of five hybrid poplar genotypes exposed to interacting elevated CO2 and O-3. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 28(11):1706-1716.*

A wide variety of hybrid poplar clones are being introduced for intensive culture biomass production, but the potential clonal or genotypic response to increasing tropospheric carbon dioxide (CO2), ozone (O-3), and their interactions are unknown. To study these effects, we exposed five different hybrid Populus clones to increased concentrations of CO2, O-3, and CO2 + O-3 in open-top chambers for one growing season and determined growth responses. Exposure to elevated CO2 increased height growth, dry mass, and basal area; exposure to O-3 decreased all three of these growth responses. Exposure impact differed among the different plant parts (leaf, stem, and roots) and among the crones. These differences were associated with different growth strategies or carbon allocation patterns inherent in the different clones. The fastest growing clones had the greatest response to O-3 treatment. The addition of CO2 to the O-3 exposure counteracted the negative impact of O-3 in all plant components except leaf mass (e.g., CO2 + O-3 plant mass equaled control plant mass) in all of the clones. But correspondingly, added O-3 negated increased growth from CO2. Genetic variation in response to atmospheric pollutants must be considered even in closely related genotypes found in Populus culture.

KEYWORDS: AIR-POLLUTION, ASPEN CLONES, ATMOSPHERIC CO2, BETULA-PUBESCENS EHRH, CARBON DIOXIDE, ESTABLISHMENT-YEAR, FOREST ECOSYSTEMS, PLANT GROWTH, POPULUS X EURAMERICANA, TROPOSPHERIC OZONE

536

Didham, R.K. 1998. Altered leaf-litter decomposition rates in tropical forest fragments. *Oecologia 116(3):397-406.*

The effects of forest fragmentation on leaf-litter decomposition rates were investigated for the first time in an experimentally fragmented tropical forest landscape in Central Amazonia. Leaf-litter decomposition rates were measured at seven distances (0-420 m) along forest edge-to-interior transects in two 100-ha fragments, two continuous forest edges, and at an identical series of distances along two deep continuous forest transects, as well as at the centers of two 1-ha and two 10-ha fragments. Decomposition rates increased significantly towards the edge of 100-ha forest fragments. Litter turnover times were 3-4 times faster within 50 m of the edge of 100-ha fragments than normally found in deep continuous forest. In contrast, there was no significant change in the rate of leaf-litter decomposition from the interior to the edge of continuous forest. It is difficult to account for these very different edge responses. Decomposition rates were not correlated with air temperature differentials, evaporative drying rates, litter depth, biomass or moisture content, or with total invertebrate densities, either within individual edge transects or across all sites. The difference in edge response may be due to chance, particularly the patchy removal of vast quantities of litter by litter-feeding termites, or may be a real, area-dependent phenomenon. Clearly, however, forest fragmentation increases the variability and unpredictability of litter decomposition rates near forest edges. In addition to edge effects, decomposition. rates were strongly affected by decreasing fragment area. While sites at the centers of 10-ha and 100-ha forest fragments and continuous forest had equivalent decomposition rates, rates were markedly lower at the centers of 1-ha fragments. Litter turnover times were 2-3 times slower in I-ha fragments than in continuous forest, and up to 13 times slower than at 100-ha edges. Litter structure and nutrient cycling dynamics are inevitably altered by forest fragmentation.

KEYWORDS: AMAZON, CLEAR-CUT, DECAY-RATES, DOUGLAS-FIR FOREST, ELEVATED CO2, GROWTH, LIGNIN CONTROL, NITROGEN, NUTRIENT DYNAMICS, RAIN FORESTS

537

Diemer, M.C., and C. Korner. 1996. Lifetime leaf carbon balances of herbaceous perennial plants from low and high altitudes in the central Alps. *Functional Ecology 10(1):33-43.*

1. A combination of demographic analysis of leaf growth, age- specific CO2 gas exchange and microclimate were employed to calculate lifetime sums of net photosynthesis and dark respiration, in order to obtain leaf carbon balances (Q(c)) of altitudinally disjunct Ranunculus and Geum species, as well as two altitudinal populations of Potentilla crantzii. If carbon costs for construction of leaf tissue are included, leaves fixed a lifetime carbon surplus ranging from 0.4 to 2.0 mmol CO2 cm(-2) independent of altitude, thereby exceeding initial investments by the plant three- to sixfold. 2. The lack of a consistent difference between the Q(c) of high and related low elevation taxa with similar leaf area ratios (LAR) challenges the view that carbon gain impairs growth and persistence of herbaceous perennials in harsh alpine climates to a greater extent than at low elevation. 3. Evidence from a sensitivity analysis of our carbon balance model as well as rank correlations indicate that the primary determinant of a leaf's carbon balance is its longevity. A comparison of leaf carbon balance data from the literature on wild plants of the temperate zone suggests that daily carbon gain on a leaf area basis is higher in herbaceous plants, compared to deciduous woody shrubs, which could explain the predominance of the herbaceous growth form at high altitudes.

KEYWORDS: COST, LONGEVITY, PHOTOSYNTHETIC CHARACTERISTICS, SEASONAL-CHANGES, SHRUB, SPANS

538
Diemer, M. 1992. Population-dynamics and spatial arrangement of ranunculus- glacialis L, an alpine perennial herb, in permanent plots. *Vegetatio 103(2):159-166.*

In 1986 sixteen permanent plots (625 cm2 each) were established in scree slopes dominated by Ranunculus glacialis at Mt. Glungezer, Austria (2600 m elevation) in order to document the population dynamics of herbaceous perennials near the upper altitudinal limits of plant existence. The abundance and sizes of individual R. glacialis shoots, their leaf numbers and reproductive status were evaluated over a 6-year period. On South-facing slopes the population sizes of adult and juvenile shoots remained constant over the years, while seedling numbers fluctuated significantly. Overall density of all developmental stages of R. glacialis was significantly lower on North-facing slopes and year-to-year fluctuations were greater, than on thermally-favorable Southern slopes. The spatial pattern of adult shoots and seedlings was clumped, while juvenile shoots had a random or clumped distribution. Fertilization had no effects on population dynamics. Proposed greenhouse effects, e.g. increases in CO2 and temperature, should result in population growth on North-facing slopes and may increase mortality on South-facing sites.

KEYWORDS: AREA, FINNISH LAPLAND, PLANTS

539
Diemer, M.W. 1994. Mid-season gas-exchange of an alpine grassland under elevated co2. *Oecologia 98(3-4):429-435.*

Ecosystem net CO2 uptake, evapotranspiration (ET) and night- time CO2 efflux were measured in an alpine grassland dominated by Carex curvula, treated with doubled ambient partial pressure of CO2 via open-top chambers. One quarter of the plots were treated with mineral nutrients to simulate the effect of lowland nitrogen deposition rates. Depending upon fertilizer supply, ecosystem net CO2 uptake per ground area in full sunlight (NCE(max)) was 41-81% higher in open-top chambers supplied with doubled ambient partial pressure (p(a)) of CO2 than in plots receiving ambient CO2. Short-term reversals of the CO2 level suggest that the extent of downward adjustment of canopy photosynthesis under elevated CO2 was 30-40%. ET tended to decline, while water use efficiency (WUE), expressed as the NCE(max):ET ratio, increased more than twofold under elevated CO2. Night-time ecosystem CO2 efflux did not respond to changes in CO2 p(a). NCE(max) and night-time CO2 efflux were more responsive to mineral fertilizer than the doubling of CO2. This suggests that in these alpine plant communities, atmospheric nutrient input may induce equal or greater effects on gas exchange than increased CO2.

KEYWORDS: ATMOSPHERIC CO2, BALANCE, CARBON DIOXIDE, COMMUNITIES, ECOSYSTEMS, RESPONSES, TUSSOCK TUNDRA

540
Diemer, M. 1996. The incidence of herbivory in high-elevation populations of Ranunculus glacialis: A re-evaluation of stress-tolerance in alpine environments. *Oikos 75(3):486-492.*

Growing conditions in the upper alpine zone are characterized by low temperature, low partial pressures of CO2 and, in the temperate zone, a short growing period. The plants which have evolved under these conditions presumably share a number of characteristics that were ascribed to stress-tolerance, namely slow growth, extended longevity, resource limitation and low palatability to herbivores. Hence chronic biomass removals by herbivores should be a threat to plant persistence in alpine environments. as predicted by Grime's C-S-R theory. I tested this hypothesis on populations of an alpine buttercup, Ranunculus glacialis. A survey along an altitudinal transect in the Central Alps of Austria indicated that between 15 and 26% of the R. glacialis plants in each population examined exhibited signs of herbivory damage. Merely a small population, isolated by glaciers, at the highest site (3310 m a.s.l.) showed no traces of herbivory. Ar two sites (2600 m and 3180 m a.s.l.) twenty plants each were tagged and examined for a two- year period. Herbivory damage was considerable: on an average nearly 25% of a plant's total leaf area was removed in 1987. primarily by snow mice (Microtus nivalis). Inflorescences of 65-85% of all flowering plants were removed as well. Ar the lower sire (2600 m, roughly 600 m above the treeline) up to 5 g dry matter and 140 mg nitrogen m(-2) were consumed in one season. Despite the magnitude of these losses both reproductive investment and the number of leaves initiated per plant did not change appreciably in the subsequent year. Since populations of R. glacialis are able to support populations of herbivores at the altitudinal limits of plant growth without obvious reductions in vigor,these plants and other food species (e.g. Oxyria digyna) cannot fit the stress-tolerator scheme proposed by Grime. The widespread occurrence of herbivory at high elevations and plant traits challenge the concept of stress- tolerance as it is commonly applied to alpine environments.

KEYWORDS: AVAILABILITY, DYNAMICS, GRADIENTS, HERB, LEAF, LIFE, PLANTS, SEED, ZONE

541
Diemer, M. 1997. Effects of elevated CO2 on gas exchange characteristics of alpine grassland. *Acta Oecologica-International Journal of Ecology 18(3):177-182.*

The ecosystem-level gas exchange characteristics of an alpine grassland treated with a combination of elevated CO2 and moderate additions of NPK fertilizer during the third season of experimental treatments are described. Mid-season maximum daytime net ecosystem CO2 flux (NEC)increased significantly under elevated CO2 (+45%), whereas nighttime NEC was unaffected by the CO2 treatment. Since daytime NEC under elevated CO2 underwent a seasonal decline, only moderate carbon surpluses accumulated under elevated CO2. The observed seasonal decline in daytime NEC may be due to reduced sink strength once maximum aboveground biomass is attained, and appears to be a reg ulatory mechanism of ecosystem carbon accumulation. Moderate additions of NPK fertilizer stimulated both day- (+39%) and nighttime NEC (+29%) due to increased plant biomass, independent of CO2 treatment. Yet there is no indication that enhanced mineral nutrient

status will increase ecosystem responsiveness to elevated CO2.

KEYWORDS: CARBON BALANCE

542
Diemer, M., and C. Korner. 1998. Transient enhancement of carbon uptake in an alpine grassland ecosystem under elevated CO2. *Arctic and Alpine Research 30(4):381-387.*

We investigated the carbon uptake and release of a Central European alpine grassland community subjected to doubled ambient CO2 during the third (1994) and fourth (1995) season of CO2 enrichment. Within this period net carbon uptake under elevated CO2 declined successively, providing evidence of carbon saturation in this high-elevation environment. Third year data were used to calculate a CO2 balance for the 13-wk growing season and indicated that the grassland still served as net carbon sink in 1994. Integrated over the growth period, plots exposed to doubled ambient CO2 fixed 22% more CO2 than control treatments receiving ambient CO2. Increased carbon uptake under elevated CO2 was entirely due to a stimulation of daytime net CO2 uptake, since nighttime CO2 release remained unaffected. However, enhancement of net canopy CO2 uptake showed a distinct seasonal response: following substantial net CO2 gains from snowmelt until attainment of peak biomass (ca. 6 wk), the relative effect of elevated CO2 declined over the remainder of the season. In contrast to controls, the C balance became negative under CO2 enrichment during the final weeks of the growth period. Estimates of wintertime respiratory CO2 losses of unfertilized plots (ca, 9 mo during which soils remain thawed under the snow) indicate a release of 73 to 89% of the amount of CO2 fixed during the snow-free period. Under elevated CO2 an estimated mean surplus of 41 g C m(-2) accreted during the third year of CO2 enrichment, which we hypothesize must been transferred belowground, since aboveground biomass remained unchanged. Moderate additions of mineral fertilizer (NPK) alone had a strong positive effect on seasonal net CO2 balance (57% increase) mediated by enhanced plant biomass. NPK- treated plots under elevated CO2 had a 38% higher seasonal CO2 balance, relative to NPK-plots at ambient CO2 concentration. Fourth-year (1995) data indicate no further stimulation of daytime net ecosystem CO2 flux under elevated CO2, both in unfertilized plots and plots treated with NPK. Hence, it is unlikely that alpine grasslands will serve as carbon sinks in a CO2-rich world in the long term.

KEYWORDS: ATMOSPHERIC CO2, CLIMATE, ENRICHMENT, ENVIRONMENTAL-CHANGE, GAS-EXCHANGE, GROWTH, HIGH-ALTITUDES, PLANTS, RESPONSES, TUSSOCK TUNDRA

543
Dietz, T., and E.A. Rosa. 1997. Effects of population and affluence on CO2 emissions. *Proceedings of the National Academy of Sciences of the United States of America 94(1):175-179.*

We developed a stochastic version of the Impact = Population Affluence Technology (IPAT) model to estimate the effects of population, affluence, and technology on national CO2 emissions. Our results suggest that, for population, there are diseconomies of scale for the largest nations that are not consistent with the assumption of direct proportionality (log- linear effects) common to most previous research. In contrast, the effects of affluence on CO2 emissions appear to reach a maximum at about $10,000 in per-capita gross domestic product and to decline at higher levels of affluence. These results confirm the general value of the IPAT model as a starting point for understanding the anthropogenic driving forces of global change and suggest that population and economic growth anticipated over the next decade will exacerbate greenhouse gas emissions.

KEYWORDS: ECONOMIC-GROWTH, ENVIRONMENTAL-QUALITY, ROBUST

544
Diiorio, A.A., R.D. Cheetham, and P.J. Weathers. 1992. Carbon-dioxide improves the growth of hairy roots cultured on solid medium and in nutrient mists. *Applied Microbiology and Biotechnology 37(4):463-467.*

The effect of varying CO2 concentrations on the growth of beet and safflower hairy roots was measured for tissues cultured in nutrient mists and on solid media in chambers fed mixtures of humidified air supplemented with different CO2 concentrations. Hairy root tissue grown on solid media in air enriched with CO2 showed increased growth, as measured by dry weight increases vs air-fed controls. Growth increased with CO2 enrichment as much as 2.5 times more than the air-fed control for safflower at 1.0 % CO2 and 1.4 times more than the air-fed control for beets at 1.5 % CO2 over a 12-day period. Beet hairy root tissue was also cultured aeroponically in nutrient mists. Beet hairy root cultured in nutrients mists enriched with 1.0 % CO2 showed a 15 % increase in biomass over a 7-day period vs tissue cultured in nutrient mists (with ambient air) or in shake flasks. The stimulation of root growth via CO2 enrichment reduced the time required for biomass accumulation.

KEYWORDS: ACID

545
Dijkstra, P., A.H.M.C. Schapendonk, K. Groenwold, M. Jansen, and S.C. Van de Geijn. 1999. Seasonal changes in the response of winter wheat to elevated atmospheric CO2 concentration grown in Open-Top Chambers and field tracking enclosures. *Global Change Biology 5(5):563-576.*

Winter wheat was grown at ambient and elevated (ambient plus 350 mu L L-1) CO2 concentrations in open top chambers and in field-tracking sun-lit climatized enclosures (elevated is 718 mu L L-1). There was no significant effect of CO2 concentration on sheath, leaf and root biomass and leaf area in the early spring (January to April). 24-h canopy CO2 exchange rate (CCER) was not significantly affected either. However, elevated CO2 concentration increased CCER at midday, decreased evapotranspiration rate and increased instantaneous water-use-efficiency during early spring. Leaf, sheath and root nitrogen concentration per unit dry weight decreased and nonstructural carbohydrate concentration increased under elevated CO2, and N-uptake per unit ground area decreased significantly (-22%) towards the end of this period. These results contrast with results from the final harvest, when grain yield and biomass were increased by 19% under elevated CO2. N concentration per dry weight was reduced by 5%, but N-uptake per unit ground area was significantly higher (+11%) for the elevated CO2 treatment. 24-h and midday-CCER increased significantly more in late spring (period of 21 April to 30 May) (respectively by + 40% and 53%) than in the early spring (respectively 5% and 19%) in response to elevated CO2. Midday evapotranspiration rate was reduced less by elevated CO2 in the late spring (-13%) than in early spring (-21%). The CO2 response of midday and 24-h CCER decreased again (+ 27% and + 23% resp.) towards the end of the growing season. We conclude that the low response to CO2 concentration during the early spring was associated with a growth-restriction, caused by low temperature and irradiance levels. The reduction of nitrogen concentration, the increase of nonstructural carbohydrate, and the lower evapotranspiration indicated that CO2 did have an effect towards the end of early spring; but not on biomass accumulation. Regression analysis showed that both irradiance and temperature affected the response to CO2.

KEYWORDS: ACCLIMATION, C-3, CARBON DIOXIDE,

CARBOXYLASE-OXYGENASE, ENRICHMENT, LOLIUM-PERENNE, TEMPERATURE, TRITICUM-AESTIVUM L, WATER-USE EFFICIENCY, YIELD

546
Ding, L., C.H. Zhang, K.Z. Bai, and T.Y. Kuang. 1997. Relation between seed size in different plant species and response of their seedlings to double CO2. *Chinese Science Bulletin 42(4):331-333.*

547
Dippery, J.K., D.T. Tissue, R.B. Thomas, and B.R. Strain. 1995. Effects of low and elevated co2 on C-3 and C-4 annuals .1. Growth and biomass allocation. *Oecologia 101(1):13-20.*

In order to study C-3 and C-4 plant growth in atmospheric CO2 levels ranging from past through predicted future levels, Abutilon theophrasti (C-3) and Amaran thus retroflexus (C-4) were grown from seed in growth chambers controlled at CO2 partial pressures of 15 Pa (below Pleistocene minimum) 27 Pa (pre-industrial), 35 Pa (current) and 70 Pa (predicted future). After 35 days of growth, CO2 had no effect on the relative growth rate, total biomass or partitioning of biomass in the C-4 species. However, the C-3 species had greater biomass accumulation with increasing CO2 partial pressure. C-3 plants grown in 15 Pa CO2 for 35 days had only 8% of the total biomass of plants grown in 35 Pa CO2. In 15 Pa CO2, C-3 plants had lower relative growth rates and lower specific leaf mass than plants grown in higher CO2 partial pressures, and aborted reproduction. C-3 plants grown in 70 Pa CO2 had greater root mass and root-to-shoot ratios than plants grown in lower CO2 partial pressures. These findings support other studies that show C-3 plant growth is more responsive to CO2 partial pressure than C-4 plant growth. Differences in growth responses to CO2 levels of the Pleistocene through the future suggest that competitive interactions of C-3 and C-4 annuals have changed through geologic time. This study also provided evidence that C-3 annuals may be operating near a minimum CO2 partial pressure for growth and reproduction at 15 Pa CO2.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, COMPETITION, ENRICHMENT, PERENNIALS, PHOTOSYNTHESIS, PLANTS, RESPONSES, SEEDLINGS, SUBAMBIENT

548
Dixon, M., D. Lethiec, and J.P. Garrec. 1995. The growth and gas-exchange response of soil-planted norway spruce [picea-abies (L) karst] and red oak (quercus-rubra L) exposed to elevated co2 and to naturally-occurring drought. *New Phytologist 129(2):265-273.*

Norway spruce and red oak trees were planted directly into the soil and exposed to 700 mu mol mol(-1) CO2 in open-top chambers. There were large inter-specific differences in response to naturally occurring drought during the second pear of exposure to elevated CO2. Both species had decreased assimilation rates. CO2-treated red oak had no loss of photosynthetic enhancement when undroughted, whereas CO2- treated Norway spruce showed a relative increase in assimilation rates only when droughted. The effect of CO2 on radial growth of both species was less marked in the second growing season, but this may have been a result of different biomass partitioning as Norway spruce shoot extension had a different pattern of growth in elevated CO2. Stomatal density and chlorophyll content were largely unaffected by the CO2 treatment. A precise method for measuring Norway spruce needle surface area was also developed.

KEYWORDS: ENHANCEMENT, ENRICHMENT, INCREASE, LIMITATIONS, PHOTOSYNTHESIS, SEEDLINGS, SITCHENSIS BONG CARR, STOMATAL DENSITY, WATER-STRESS

549
Dixon, R.K. 1995. Agroforestry systems - sources or sinks of greenhouse gases. *Agroforestry Systems 31(2):99-116.*

The prominent role of forestry and agroforestry systems in the flux and long-term storage of carbon (C) in the terrestrial biosphere has increased global interest in these land-use options to stabilize greenhouse gas (GHG) emissions. Preliminary assessments suggest that some agroforestry systems (e.g., agrosilvicultural) can be CO2 sinks and temporarily store C, while other systems (e.g., ruminant-based silvopastoral systems) are probably sources of GHG (e.g., CH4). Agroforestry;systems can be significant sources of GHG emissions, especially at low latitudes. Practices such as tillage, burning, manuring, chemical fertilization, and frequent disturbance can lead to emission of CO2, CH4, and N2O from soils and vegetation to the atmosphere. Establishment and management of agroforestry systems incompatible with prevailing edaphic and climatic conditions can accelerate soil GHG emissions. Non-sustainable agroforestry systems are quickly degraded, and woody and herbaceous crops can become significant GHG sources. Silvopastoral systems can result in soil compaction and erosion with significant loss of labile C and N compounds to the atmosphere. Ruminant-based silvopastoral systems and rice paddy agrisilvicultural systems are well documented sources of CH4 which significantly contribute to the global CH4 budget. Early assessments of national and global terrestrial CO2 sinks reveal two primary beneficial attributes of agroforestry systems: 1) direct near-term C storage (decades to centuries) in trees and soils, and, 2) potential to offset immediate GHG emissions associated with deforestation and subsequent shifting agriculture. Within the tropical latitudes, it is estimated that one ha of sustainable agroforestry can provide goods and services which potentially offset 5-20 ha of deforestation. At a global scale, agroforestry systems could potentially be established on 585-1275 x 10(6) ha of technically suitable land, and these systems could store 12-228 (median 95) Mg C ha(-1) under current climate and edaphic conditions.

550
Dixon, R.K., S. Brown, R.A. Houghton, A.M. Solomon, M.C. Trexler, and J. Wisniewski. 1994. Carbon pools and flux of global forest ecosystems. *Science 263(5144):185-190.*

Forest systems cover more than 4.1 x 10(9) hectares of the Earth's land area. Globally, forest vegetation and soils contain about 1146 petagrams of carbon, with approximately 37 percent of this carbon in low-latitude forests, 14 percent in mid-latitudes, and 49 percent at high latitudes. Over two- thirds of the carbon in forest ecosystems is contained in soils and associated peat deposits. In 1990, deforestation in the low latitudes emitted 1.6 +/- 0.4 petagrams of carbon per year, whereas forest area expansion and growth in mid- and high- latitude forest sequestered 0.7 +/- 0.2 petagrams of carbon per year, for a net flux to the atmosphere of 0.9 +/- 0.4 petagrams of carbon per year. Slowing deforestation, combined with an increase in forestation and other management measures to improve forest ecosystem productivity, could conserve or sequester significant quantities of carbon. Future forest carbon cycling trends attributable to losses and regrowth associated with global climate and land-use change are uncertain. Model projections and some results suggest that forests could be carbon sinks or sources in the future.

KEYWORDS: ATMOSPHERIC CARBON, BIOMASS, CLIMATE CHANGE, CO2 CONCENTRATION, ELEVATED CO2, INCREASING CO2, STORAGE, TRANSIENT-RESPONSE, TROPICAL FORESTS, UNITED-STATES

551
Dixon, R.K., J.B. Smith, S. Brown, O. Masera, L.J. Mata, and I.

Buksha. 1999. Simulations of forest system response and feedbacks to global change: experiences and results from the US Country Studies Program. *Ecological Modelling 122(3):289-305.*

Large shifts in the response and feedbacks of forest systems are implied by models and systems analysis driven by global change scenarios of general circulation models (GCMs). Prior climate change analyses and modeling efforts have been reported at a global scale in a few developed countries, but relatively few national assessments have been successfully completed in developing countries. Under the auspices of the U.S. Country Studies Program, analysts from 55 countries employed a common set of methods and models to characterize current carbon (C) pools in forests, future impacts of global change on forest distribution, and management options for conserving and sequestering carbon dioxide (CO2) in forest systems. The analysis revealed that the response and feedbacks of forest systems to global climate change will be profound in the 55 countries studied on five continents. Globally, forest vegetation and soils contain about 1146 Pg C, with approximately 37% of this C in low-latitude forests, 14% in mid-latitudes, and 49% at high latitudes. The impacts of future global change on forest distribution and productivity will be most significant at high latitudes, with more modest changes in distribution and productivity at low latitudes. Future opportunities to conserve and sequester CO2 in forest systems are potentially significant, but land-use practices and global change will influence the size of this C pool and CO2 sink. In the future, a greater proportion of forests at all latitudes could become a greenhouse gas (GHG) source if sustained management and conservation policies are not employed. The timing and magnitude of future changes in forest systems are dependent on global environmental factors (for example, global change, biogeochemical Sulphur and Nitrogen cycles), as well as on human factors such as demographics, economic growth, technology, and resource management policies.

KEYWORDS: AGROFOREST MANAGEMENT-PRACTICES, ATMOSPHERIC CARBON-DIOXIDE, BIOMASS, BUDGET, CO2-INDUCED CLIMATE CHANGE, EMISSIONS, MODEL, SENSITIVITY, STORAGE, TRANSIENT-RESPONSE

552

Dixon, R.K., J.K. Winjum, and P.E. Schroeder. 1993. Conservation and sequestration of carbon - the potential of forest and agroforest management-practices. *Global Environmental Change-Human and Policy Dimensions 3(2):159-173.*

Forests play a major role in Earth's carbon cycle through assimilation, storage, and emission of CO2. Establishment and management of boreal, temperate, and tropical forest and agroforest systems could potentially enhance sequestration of carbon in the terrestrial biosphere. A biological and economic analysis of forest establishment and management options from 94 nations revealed that forestation, agroforestry, and silviculture could be employed to conserve and sequester one Petagram (Pg) of carbon annually over a 50-year period. The marginal cost of implementing these options to sequester 55 Pg of carbon would be approximately $10/Mg.

553

Dixon, R.K., and J. Wisniewski. 1995. Global forest systems: An uncertain response to atmospheric pollutants and global climate change? *Water, Air, and Soil Pollution 85(1):101-110.*

Forest systems cover more than 4.1 x 10(9) ha of the Earth's land area. The future response and feedbacks of forest systems to atmospheric pollutants and projected climate change may be significant. Boreal, temperate and tropical forest systems play a prominent role in carbon (C), nitrogen (N) and sulfur (S) biogeochemical cycles at regional and global scales. The timing and magnitude of future changes in forest systems will depend on environmental factors such as a changing global climate, an accumulation of CO2 in the atmosphere, and increase global mineralization of nutrients such as N and S. The interactive effects of all these factors on the world's forest regions are complex and not intuitively obvious and are likely to differ among geographic regions. Although the potential effects of some atmospheric pollutants on forest systems have been observed or simulated, large uncertainty exists in our ability to project future forest distribution, composition and productivity under transient or nontransient global climate change scenarios. The potential to manage and adapt forests to future global environmental conditions varies widely among nations. Mitigation practices, such as liming or fertilization to ameliorate excess NOx or SOx or forest management to sequester CO2 are now being applied in selected nations worldwide.

KEYWORDS: CARBON, ECOSYSTEMS, ELEVATED CO2, NITROGEN DEPOSITION, SINK

554

Docherty, M., D.K. Hurst, J.K. Holopainen, J.B. Whittaker, P.J. Lea, and A.D. Watt. 1996. Carbon dioxide-induced changes in beech foliage cause female beech weevil larvae to feed in a compensatory manner. *Global Change Biology 2(4):335-341.*

The phenology of Fagus sylvatica was unaffected by exposure to an atmosphere of elevated CO2 (600 mu L L(-1)) after two years of fumigation. Non-significant changes in nitrogen and phenolic content of the leaves decreased the nutritional status of beech for female larvae in elevated CO2 such that they responded by eating in a compensatory manner; males were unaffected. Rates of development, mortality and adult biomass of Rhynchaenus fagi were no different from those in ambient CO2 concentrations (355 mu L L(-1)). It is possible that, with the changes in leaf chemistry affecting the females, fecundity will be altered, with important consequences for populations of beech weevil.

KEYWORDS: ATMOSPHERIC CO2, ELEVATED CO2, GROWTH, INSECT HERBIVORE INTERACTIONS, LEAF-MINER, PICEA-SITCHENSIS, RESPONSES, RHYNCHAENUS-FAGI, SITKA SPRUCE, WINTER MOTH

555

Docherty, M., F.A. Wade, D.K. Hurst, J.B. Whittaker, and P.J. Lea. 1997. Responses of tree sap-feeding herbivores to elevated CO2. *Global Change Biology 3(1):51-59.*

Five species of sap-feeding homoptera were studied on Fagus sylvatica and Acer pseudoplatanus and exposed to elevated concentrations of carbon dioxide (600 mu L L(-1)). The concentration of total soluble amino acids in foliage of F. sylvatica was unaffected by growing saplings in elevated atmospheric CO2 concentrations. Although experiments on individual aphids indicated poorer performance of Phyllaphis fagi (fewer, smaller nymphs produced), resultant populations did not differ from those in ambient (350 mu L L(-1)) conditions. The area of beech foliage stippled by the leafhopper Fagocyba cruenta was similar at ambient and elevated CO2 concentrations. The concentration of total amino acids and that of serine of A. pseudoplatanus foliage were significantly lower at elevated CO2 concentrations. However, the relative growth rates of two aphid species Drepanosiphum platanoidis and Periphyllus testudinaceus and one leafhopper Ossiannilssonola callosa were not significantly different in elevated CO2. No evidence was found that, under the conditions of these experiments, populations of aphids and leafhoppers will change as concentrations of CO2 increase.

KEYWORDS: AIR-POLLUTION, CARBON DIOXIDE, GROWTH,

INFESTATION, INSECT PERFORMANCE, PHLOEM SAP, PLANTS, POPULATIONS, REPRODUCTIVE ACTIVITY, SYCAMORE APHID

556
Doi, M., H. Oda, N. Ogasawara, and T. Asahira. 1992. Effects of co2 enrichment on the growth and development of invitro cultured plantlets. *Journal of the Japanese Society for Horticultural Science 60(4):963-970.*

Plantlets of Caladium bicolor (C3 plant), Saccharum officinarum (C4 plant), and Phalaenopsis hybrid (CAM plant) at the preparation stage for acclimatization (the final stage of in vitro culture) were cultured on the medium containing 2% sucrose. The culture vessels were kept under continuous, 16 hr, or 8 hr lighting conditions; half of the vessels were ventilated continuously with 0.8 +/- 0.4% CO2 enriched atmosphere; while the remainder was exposed to ambient atmosphere. The growth of plantlets was promoted with an increase in daylength under both ambient and CO2 enriched atmospheres. When the plantlets were supplied with adequate CO2, dry matter production increased under all daylength treatments except Caladium cultured under continuous lighting. This promotive effect of CO2 enrichment was especially noticeable in root growth. In Caladium and Phalaenopsis, the leaf chlorophyll content of plantlets cultured under CO2 enriched atmosphere was less than that of leaves from plantlets grown in ambient atmosphere. Although the chlorophyll was less concentrated in leaves of plantlets growing under the CO2 enriched treatment, the rate of CO2 uptake of these plantlets measured at the midpoint of the light period was higher than that of leaves exposed to ambient atmosphere. Increasing the O2 concentration in culture vessels to 37% also promoted the growth of Caladium and Dendrobium phalaenopsis (CAM plant) under CO2 enriched condition. Because of the development of photoautotrophy, the Caladium plantlets exposed to enriched CO2 atmosphere and cultured on sugar-free medium using ceramic wool plug system responded with vigorous growth when transplanted into pots.

557
DolcetSanjuan, R., E. Claveria, and A. Huerta. 1997. Androgenesis in Capsicum annuum L - Effects of carbohydrate and carbon dioxide enrichment. *Journal of the American Society for Horticultural Science 122(4):468-475.*

A new and simple protocol for androgenesis in bell pepper is described. The initial medium, a modification of Nitsch and Nitsch's H medium, consisted of a two-phase system of semi- solid and liquid medium and contained maltose as carbon source. The total number of embryos formed was greater with maltose at 40 g . L-1, but embryos developed better at 10 to 20 g . L-1. Depending on the genotype, the number of embryos and plants recovered ranged from 3 to 750 and 0.25 to 8, respectively, per 100 flowers. Further increases in the number of embryos (up to 3561 per 100 flowers) and plants (up to 23 per 100 flowers) could be attained by flushing cultures with air enriched with CO2 at 900 mu L . L-1. The ploidy level and the microspore origin of the recovered plants were determined by flow cytometry and zymograms for isocitrate dehydrogenase. Nearly 65% of the acclimated plants had undergone spontaneous doubling of the chromosome number, as confirmed by flow cytometry of leaf nuclei. Isocitrate dehydrogenase zymograms demonstrated that plants originated from microspores and that the two parental alleles were equally represented among the haploid and dihaploid plants.

KEYWORDS: ACTIVATED-CHARCOAL, ANTHER-CULTURE RESPONSE, GENETIC-MARKERS, HORDEUM VULGARE L, INDUCTION, INHERITANCE, MEDIA, PEPPER, PLANTS, SEGREGATION

558
Donnelly, A., M.B. Jones, J.I. Burke, and B. Schnieders. 1999. Does elevated CO2 protect grain yield of wheat from the effects of ozone stress? *Zeitschrift Fur Naturforschung C-A Journal of Biosciences 54(9-10):802-811.*

This study has investigated the effects of elevated CO2 and elevated O-3, both singly and in combination, on the yield of spring wheat (Triticum aestivum L., cv. Minaret). Plants were grown in open-top chambers and exposed to three CO2 concentrations (ambient, 510 and 680 ppmv) and two O-3 concentrations (ambient and ambient +50 or +90 ppbv) either from anthesis onwards or for the full growing season. To date, experiments that have investigated the interactive effects of these gases have shown a variety of responses, ranging from an amelioration of the damaging effects of high O-3 to a greater sensitivity to O-3, at elevated CO2. The effects on grain yield and yield components were determined. Our results confirm that elevated CO2 provides some protection to a wheat crop against the damaging effects of O-3 On grain yield. However, the level of protection varies from one growing season to the next and also appears to be related particularly to the timing of exposure to elevated O-3.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, DRY-MATTER, LEAF-AREA, OPEN-TOP CHAMBERS, PLANT GROWTH, SPRING WHEAT, TRITICUM-AESTIVUM L, TROPOSPHERIC OZONE, WATER-STRESS

559
Dorais, M., J. Charbonneau, and A. Gosselin. 1993. Gas-exchange in greenhouse tomatoes grown under supplemental light. *Canadian Journal of Plant Science 73(2):577-585.*

This study reports on in situ gas-exchange measurements in tomatoes grown under a sequential intercropping system with supplemental lighting provided by high-pressure sodium-vapour lamps. A supplemental photosynthetic photon flux (PPF) of 150 mumol m-2 s-1 significantly increased the amount of light energy penetrating the canopy of intercropped tomato seedlings. During the day, the supplemental 150 mumol m-2 s-1 light regime increased the photosynthetic rate of leaves 5 and 10 by 67%, while at night the increases were 93 and 12%, respectively. Regression analysis of the photosynthetic rate of leaves 5 and 10 as a function of PPF received accounts for 58 and 45% of the variation, respectively. Hierarchical analysis demonstrated a significant linear relationship between PPF received during the day and photosynthetic activity of leaves 5 and 10 accounting for 46 and 28%, respectively, of the variance in the model. Regression analysis of the photosynthetic activity as a function of PPF received at night accounts for 41 and 32 %, respectively, of the variation in the photosynthetic rate of leaves 5 and 10. Using a high level of supplemental lighting during the day or at night had no significant effect on stomatic conductance or on the transpiration rate of leaves.

KEYWORDS: CO2- ENRICHMENT, LEAF, PHOTOINHIBITION, PHOTOSYNTHESIS, PRODUCTIVITY, RESPONSES, TRANSPIRATION, TRANSPORT, YIELD

560
Downing, J.P., and D.A. Cataldo. 1992. Natural sinks of co2 - technical synthesis from the palmas-del- mar workshop. *Water, Air, and Soil Pollution 64(1-2):439-453.*

Natural CO2 sinks in terrestrial and marine environments are important components of the global carbon cycle, yet the sign and magnitudes of key fluxes among them are unknown. The results of the Palmas Del Mar Workshop - Natural Sinks of CO2 presented in this special issue and its companion hard-bound volume of Water, Air, & Soil Pollution, provide

a synthesis of current research on the carbon cycle, CO2 sinks and associated processes and fluxes, and critical research needs to assess the potential role of forest and land-use management in carbon sequestration. The papers in this volume present data, observations, and model simulations that demonstrate: 1) the existence of natural CO2 sinks that could mitigate a significant amount of CO2 emissions from fossil-fuel combustion; 2) probable, human-caused imbalances in C exchanges among vegetation, soils, and the atmosphere; 3) enhanced C storage in vegetation in response to excess atmospheric CO2; 4) strong interactions among carbon, nutrient and hydrological cycles; and 5) an excess of carbon production over consumption in several, large managed forests. Although it appears unlikely that the search for the "missing" C sink required to balance the C budget will end in the open ocean, new estimates of C storage in mangrove wood and peat, suggest that coastal ecosystems have the capacity to store significant amounts of carbon in vegetation and sediments. Convincing analyses are also presented indicating the technical and economical feasibility of managing existing lands to sequester additional carbon. Long-term field studies of CO2 fertilization effects and carbon cycling by plants and soils in geographically important systems, native forests, and coastal ecosystems will go a long way toward meeting the research needs identified at the workshop.

KEYWORDS: MODEL, OCEAN

561
Downton, W.J.S., and W.J.R. Grant. 1994. Photosynthetic and growth-responses of variegated ornamental species to elevated co2. *Australian Journal of Plant Physiology 21(3):273-279.*

Variegated and completely green cultivars of oleander (Nerium oleander L.) and willow myrtle (Agonis flexuosa (Willd.) Sweet) were grown in controlled environment cabinets for 3 and 5 months, respectively, under either ambient levels of CO2 or with supplementary CO2 to a partial pressure of 800 mu bar. Photosynthesis of entirely green leaves and the green portions of variegated leaves on both species was greatly stimulated by high CO2 and there was no evidence of downward adjustment (acclimation) of photosynthetic rates to high CO2 during the experiment. Dark respiration rates of these leaves were lowered by high CO2. The yellow portions of willow myrtle leaves showed a low level of photosynthetic activity which was stimulated by high CO2; however, dark respiration rates showed little response to elevated CO2. Green and yellow areas on variegated leaves of willow myrtle had much lower dark respiration rates than completely green leaves, but this difference was not evident for oleander. Yellow portions of oleander leaves showed little evidence of photosynthetic capacity. This was also confirmed by a low photochemical efficiency as determined by chlorophyll fluorescence. A major effect of variegation was to slow overall plant growth compared with completely green plants. The respective 3-fold and 6-7-fold differences in biomass between fully green and variegated cultivars of oleander and willow myrtle was closely related to estimated net carbon gain per day by the plant canopy. Variegation for both species averaged close to 50:50, green:yellow areas. Variegated plants developed about twice the leaf area ratio and specific leaf area compared with their completely green counterparts. The relative growth response to high CO2 was significantly greater for the variegated plants compared to the completely green plants.

KEYWORDS: ACCLIMATION, CARBON DIOXIDE, DARK RESPIRATION, LEAVES, PLANTS

562
Drake, B.G. 1992. A field-study of the effects of elevated CO2 on ecosystem processes in a Chesapeake Bay wetland. *Australian Journal of Botany 40(4-5):579-595.*

Open top chambers are being used in a long-term project to determine the effects of elevated CO2 on ecosystem processes on a Chesapeake Bay wetland. Three communities are studied: mono-specific stands of the C3 sedge, Scirpus olneyi, and the C4 grass, Spartina patens, and a mixed community of these two species and the C4 grass, Distichlis spicata. Treatment began in the spring of 1987 and will continue through the 1994 growing season. During the first 4 years of exposure, elevated CO2 had the following effects on mono-specific stands of the C3 sedge, Scirpus olneyi: increased quantum yield and photosynthetic capacity, reduced dark respiration, increased numbers of shoots, roots and rhizomes, reduced nitrogen concentration of all tissues, increased nitrogen fixation and increased ecosystem carbon accumulation. In a mixed community of the sedge and C4 grass species, Spartina patens and Distichlis spicata, biomass of the C3 component increased over 100% and this was accompanied by decreased biomass in the C4 component of the community. Elevated CO2 reduced water loss, increased water potential and delayed senescence in all three species. Many factors contributed to CO2 stimulated carbon accumulation in the plant community dominated by the C3 sedge, Scirpus olneyi, including: sustained high photosynthetic capacity, decreased respiration, delayed senescence, and allocation of the additional carbon to roots and rhizomes. The complex interaction of these diverse responses suggests that the rising atmospheric CO2 may have a significant impact on ecosystem processes.

KEYWORDS: ATMOSPHERIC CO2, CANOPY PHOTOSYNTHESIS, CARBON-DIOXIDE ENRICHMENT, ELECTRON-TRANSPORT CAPACITY, ESTUARINE MARSH, LONG-TERM EXPOSURE, PHOTOSYNTHETIC ACCLIMATION, RIBULOSE 1;5-BISPHOSPHATE, SOYBEAN CANOPIES, TRANSPIRATION RESPONSES

563
Drake, B.G. 1992. The impact of rising co2 on ecosystem production. *Water, Air, and Soil Pollution 64(1-2):25-44.*

A fundamental property of green plants is that the rate of photosynthesis is dependent in the ambient CO2 concentration. There is overwhelming experimental evidence that this effect increases plant production in most C3 Plants: hundreds of experiments with many species show that plant growth increases an average 30% to 40% for a doubling of the present normal ambient CO2 concentration (Kimball, 1986). External environmental factors, such as temperature and the availability of nutrients, modify this response. The greatest stimulation of photosynthesis and growth can be expected to occur at high temperatures and much smaller responses at low temperature. Factors which restrict growth, such as low nutrients, will reduce but usually do not eliminate the stimulation of production with increasing CO2 even when nitrogen is severly limiting. There are also reports of direct effects of ambient CO2 concentration on dark respiration which show that there is an immediate reduction in the rate of CO2 efflux or O2 consumption when the CO2 around plant tissues is increased. There have been very few long-term field studies of the effects of increased CO2 on whole plants and ecosystem processes but the data from these studies are consistent in showing an increase in plant production with an increase in CO2 concentration of the ambient air.

KEYWORDS: ABSCISIC- ACID, CARBON-DIOXIDE ENRICHMENT, ELEVATED ATMOSPHERIC CO2, GAS-EXCHANGE, LONG-TERM EXPOSURE, PHOTOSYNTHETIC INHIBITION, SOYBEAN LEAVES, STOMATAL CONDUCTANCE, TRANSPIRATION RESPONSES, TUSSOCK TUNDRA

564
Drake, B.G., J. Azcon-Bieto, J. Berry, J. Bunce, P. Dijkstra, J. Farrar, R.M. Gifford, M.A. Gonzalez-Meler, G. Koch, H. Lambers,

J. Siedow, and S. Wullschleger. 1999. Does elevated atmospheric CO2 concentration inhibit mitochondrial respiration in green plants? *Plant, Cell and Environment 22(6):649-657.*

There is abundant evidence that a reduction in mitochondrial respiration of plants occurs when atmospheric CO2 (C-a) is increased. Recent reviews suggest that doubling the present C-a will reduce the respiration rate [per unit dry weight (DW)] by 15 to 18%. The effect has two components: an immediate, reversible effect observed in leaves, stems, and roots of plants as well as soil microbes, and an irreversible effect which occurs as a consequence of growth in elevated C-a and appears to be specific to C-3 species. The direct effect has been correlated with inhibition of certain respiratory enzymes, namely cytochrome-c-oxidase and succinate dehydrogenase, and the indirect or acclimation effect may be related to changes in tissue composition. Although no satisfactory mechanisms to explain these effects have been demonstrated, plausible mechanisms have been proposed and await experimental testing. These are carbamylation of proteins and direct inhibition of enzymes of respiration. A reduction of foliar respiration of 15% by doubling present ambient C-a would represent 3 Gt of carbon per annum in the global carbon budget.

KEYWORDS: CARBON-DIOXIDE CONCENTRATION, CHEMICAL-COMPOSITION, CONSTRUCTION COSTS, DARK RESPIRATION, GAS-EXCHANGE, GROWTH, LEAF RESPIRATION, LOLIUM-PERENNE, MAINTENANCE RESPIRATION, WHEAT LEAVES

565

Drake, B.G., M.A. GonzalezMeler, and S.P. Long. 1997. More efficient plants: A consequence of rising atmospheric CO2? *Annual Review of Plant Physiology and Plant Molecular Biology 48:609-639.*

The primary effect of the response of plants to rising atmospheric CO2 (C-a) is to increase resource use efficiency. Elevated C-a reduces stomatal conductance and transpiration and improves water use efficiency, and at the same time it stimulates higher rates of photosynthesis and increases light- use efficiency. Acclimation of photosynthesis during long-term exposure to elevated C-a reduces key enzymes of the photosynthetic carbon reduction cycle, and this increases nutrient use efficiency. Improved soil-water balance, increased carbon uptake in the shade, greater carbon to nitrogen ratio, and reduced nutrient quality for insect and animal grazers are all possibilities that have been observed in field studies of the effects of elevated C-a. These effects have major consequences for agriculture and native ecosystems in a world of rising atmospheric C-a and climate change.

KEYWORDS: BETULA-PENDULA ROTH, CARBON-DIOXIDE ENRICHMENT, ELEVATED CO2, LEAF GAS- EXCHANGE, LIRIODENDRON-TULIPIFERA L, LONG-TERM EXPOSURE, PHASEOLUS-VULGARIS L, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, SOURCE-SINK RELATIONS, WATER-USE EFFICIENCY

566

Drake, B.G., and P.W. Leadley. 1991. Canopy photosynthesis of crops and native plant-communities exposed to long-term elevated CO2. *Plant, Cell and Environment 14(8):853-860.*

There have been seven studies of canopy photosynthesis of plants grown in elevated atmospheric CO2: three of seed crops, two of forage crops and two of native plant ecosystems. Growth in elevated CO2 increased canopy photosynthesis in all cases. The relative effect of CO2 was correlated with increasing temperature: the least stimulation occurred in tundra vegetation grown at an average temperature near 10-degrees-C and the greatest in rice grown at 43-degrees-C. In soybean, effects of CO2 were greater during leaf expansion and pod fill than at other stages of crop maturation. In the longest running experiment with elevated CO2 treatment to date, monospecific stands of a C3 sedge, Scirpus olneyi (Grey), and a C4 grass, Spartina patens (Ait.) Muhl., have been exposed to twice normal ambient CO2 concentrations for four growing seasons, in open top chambers on a Chesapeake Bay salt marsh. Net ecosystem CO2 exchange per unit green biomass (NCE(b)) increased by an average of 48% throughout the growing season of 1988, the second year of treatment. Elevated CO2 increased net ecosystem carbon assimilation by 88% in the Scirpus olneyi community and 40% in the Spartina patens community.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CO2-ENRICHMENT, ENRICHMENT, ESTUARINE MARSH, GROWTH, SALT-MARSH, SOYBEAN PHYSIOLOGY, TEMPERATURE, TRANSPIRATION RESPONSES, TUSSOCK TUNDRA

567

Drake, B.G., M.S. Muehe, G. Peresta, M.A. GonzalezMeler, and R. Matamala. 1996. Acclimation of photosynthesis, respiration and ecosystem carbon flux of a wetland on Chesapeake Bay, Maryland to elevated atmospheric CO2 concentration. *Plant and Soil 187(2):111-118.*

Acclimation of photosynthesis and respiration in shoots and ecosystem carbon dioxide fluxes to rising atmospheric carbon dioxide concentration (C-a) was studied in a brackish wetland. Open top chambers were used to create test atmospheres of normal ambient and elevated C-a(=normal ambient+34 Pa CO2) over mono-specific stands of the C-3 sedge Scirpus olneyi, the dominant C-3 species in the wetland ecosystem, throughout each growing season since April of 1987. Acclimation of photosynthesis and respiration were evaluated by measurements of gas exchange in excised shoots. The impact of elevated C-a on the accumulation of carbon in the ecosystem was determined by ecosystem gas exchange measurements made using the open top chamber as a cuvette. Elevated C-a increased carbohydrate and reduced Rubisco and soluble protein concentrations as well as photosynthetic capacity(A) and dark respiration (R-d; dry weight basis) in excised shoots and canopies (leaf area area basis) of Scirpus olneyi, Nevertheless, the rate of photosynthesis was stimulated 53% in shoots and 30% in canopies growing in elevated C-a compared to normal ambient concentration. Elevated C-a inhibited R-d measured in excised shoots (-19 to -40%) and in seasonally integrated ecosystem respiration (R-e; -36 to -57%). Growth of shoots in elevated C- a was stimulated 14-21%, but this effect was not statistically significant at peak standing biomass in midseason. Although the effect of elevated C-a on growth of shoots was relatively small, the combined effect of increased number of shoots and stimulation of photosynthesis produced a 30% stimulation in seasonally integrated gross primary production (GPP). The stimulation of photosynthesis and inhibition of respiration by elevated C-a increased net ecosystem production (NEP=GPP-R-e) 59% in 1993 and 50% in 1994. While this study consistently showed that elevated C-a produced a significant increase in NEP, we have not identified a correspondingly large pool of carbon below ground.

KEYWORDS: ENRICHMENT, ESTUARINE MARSH, EXPOSURE, FIELD, GAS-EXCHANGE, OPEN-TOP CHAMBERS, PERSPECTIVE, PLANT, SCIRPUS- OLNEYI, TUNDRA

568

Drake, S.R. 1994. Elevated carbon-dioxide storage of anjou pears using purge- controlled atmosphere. *Hortscience 29(4):299-301.*

'Anjou' pears (Pyrus communis L.) were placed in controlled-atmosphere (CA) storage immediately after harvest (<24 hours) or after a 10-day delay in refrigerated storage, and held there for 9 months at 1C. Oxygen in all atmospheres was 1.5% and CO2 was at either 1% or 3%.

Atmospheres in the flow-through system were computer-controlled at +/- 0.1%. After removal from CA storage, pears were evaluated immediately and after ripening at 21C for 8 days. Pears stored in 3% CO2 were firmer, greener, and displayed less scald, internal breakdown, and stem-end decay than pears stored in 1% CO2. In addition, no internal discoloration of 'Anjou' pears was evident when held with 3% CO2. 'Anjou' pears held in 3% CO2 retained the ability to ripen after long-term storage. A 10-day delay in atmosphere establishment had little or no influence on the long-term keeping quality or ripening ability of 'Anjou' pears.

KEYWORDS: DANJOU PEAR

569
Drake, S.R. 1999. Quality of 'Bosc' pears as influenced by elevated carbon dioxide storage. *Journal of Food Quality 22(4):417-425.*

'Bosc' pears (Pyrus communis L.) were placed in a purge-type controlled-atmosphere (CA) storage immediately after harvest (<24 h) and held for 180 days at IC. Oxygen in all atmospheres was 1.5% and CO2 was 1%, 3% or 5%. Pears were evaluated immediately after removal from CA storage and after ripening for an additional 7 days at 21 C. Pears stored in 3% CO2 were firmer, had a superior finish, with significantly reduced decay and internal breakdown than pears stored in 1% CO2. In 3% CO2, pears retained the ability to ripen after long-term storage. A 10 day delay in atmosphere establishment had little or no influence on the long-term keeping quality or ripening ability of 'Bosc 'pears. Firmness, soluble solids content and starch either alone or together were good indices of maturity for 'Bosc 'pears.

KEYWORDS: ATMOSPHERE, DANJOU PEAR

570
Drake, S.R., and D.C. Elfving. 1999. Response of three strains of 'Gala' apples to high carbon dioxide prior to controlled atmosphere storage. *Fruit Varieties Journal 53(1):16-21.*

The postharvest fruit quality of three strains ('Royal Gala: 'Imperial Gala' and 'Crimson Gala') of apples was evaluated over two or three storage seasons. To determine the influence of carbon dioxide treatment on storage quality, apples were stored in normal controlled atmosphere (1% O-2 & 1% CO2), or treated with 12% CO2 for 7 or 14 days prior to normal CA and evaluated after 90 or 150 days of storage. The use of 12% CO2 prior to storage helped to maintain firmness of 'Royal Gala' apples in 1 of 3 seasons. Firmness of 'Imperial Gala' and 'Crimson Gala' apples was not influenced by high CO2 treatment, regardless of storage season. Other quality factors (color, soluble solids, acidity and carbohydrates) were not influenced to the extent that high CO(2)would be a viable option for the quality enhancement of 'Gala' apples during storage, regardless of strain. Use of normal CA maintained 'Gala' apple quality for 150 days of storage. Harvest date had a major influence on 'Gala' apple quality. A delay of one week reduced firmness and acidity, but enhanced color and content of sucrose, glucose and fructose in 'Royal Gala: 'Imperial Gala' and 'Crimson Gala' apples.

KEYWORDS: CA

571
Drake, S.R., and A. Yazdaniha. 1999. Short-term controlled atmosphere storage for shelf-life extension of apricots. *Journal of Food Processing and Preservation 23(1):57-70.*

Shelf-life of 'Perfection' and 'Rival' apricots can be enhanced with the use of controlled atmosphere (CA) storage. Apricots were harvested at commercial maturity and immediately stored in CA at 1 or 2 % O-2 and 3, 6, 9, 12 or 15 % CO2 for 30, 45 and 60 days. No differences in fruit quality were evident between O-2 atmospheres of 1 and 2 %, except that fruit stored in 1 % O-2 displayed less rot development and higher acid content. Apricots stored in 9 % or less CO2 displayed reduced external and internal color, inadequate finish, increased internal breakdown and more rot development with unacceptable firmness retention for additional handling. Apricots stored in 12 or 15 % CO2 retained firmness and displayed enhanced finish with reduced rots and very little internal breakdown with storage duration of 60 days. Color was much slower to develop in apricots stored in 12 or 15 % CO2 for all storage periods.

KEYWORDS: NECTARINES, PHYSIOLOGICAL DISORDERS

572
Drennan, P.M., and P.S. Nobel. 1996. Temperature influences on root growth for Encelia farinosa (Asteraceae), Pleuraphis rigida (Poaceae), and Agave deserti (Agavaceae) under current and doubled CO2 concentrations. *American Journal of Botany 83(2):133-139.*

To help evaluate root distribution patterns, elongation rates of individual roots were measured as a function of soil temperature for Encelia farinosa (a C-3 species), Pleuraphis rigida (C-4), and Agave deserti (CAM), sympatric codominants in the northwestern Sonoran Desert. Measurements were made at current and doubled CO2 concentrations under winter and summer conditions of air temperature (day/night temperatures of 17 C/10 C and 33 C/22 C, respectively). The three species had different optimal temperatures for root elongation (T-opt) under winter conditions (25 C for E. farinosa, 35 C for P. rigida, and 30 C for A. deserti); T-opt increased by 2-3 C under summer conditions for all three species. The limiting temperatures for elongation also acclimated from winter to summer conditions. The rate of root elongation at T-opt was higher under summer than winter conditions for E. farinosa (3 vs. 6 mm d(-1)) and P. rigida (20 vs. 14 mm d(-1)), reflecting conditions for maximum photosynthesis; no difference occurred for A. deserti (9 vs. 10 mm d(-1)). Decreased elongation rates at extreme temperatures were associated with less cell division and reduced cell extension. The doubled CO2 concentration increased average daily root elongation rates for A. deserti under both winter (7%) and summer (12%) conditions, reflecting increased cell extension, but had no effect for the other two species. Simulations of root elongation as a function of soil temperatures showed that maximum elongation would occur at different depths (16-20 cm for E. farinosa, 4-8 cm for P. rigida, and 0-4 cm for A. deserti) and during different seasons (winter to spring for E. farinosa, spring to summer for P. rigida, and all year for A. deserti), contributing to their niche separation. Shading of the soil surface moderated daily variations in soil temperature, reducing seasonal root elongation for winter and spring and increasing elongation for summer. Shading also altered root distribution patterns, e.g., optimal rooting depth for A. deserti and especially P. rigida increased for a hot summer day.

KEYWORDS: C-4, CAM PLANT, CARBON DIOXIDE, COMPETITION, ELEVATED CO2, HILARIA-RIGIDA, RESPONSES, SUCCULENTS, WATER RELATIONS

573
Drennan, P.M., and P.S. Nobel. 1998. Root growth dependence on soil temperature for Opuntia ficus- indica: influences of air temperature and a doubled CO2 concentration. *Functional Ecology 12(6):959-964.*

1. Root elongation as a function of soil temperature was determined for the CAM succulent Opuntia ficus-indica, under three different day/night air temperatures (15 degrees C/5 degrees C, 25 degrees C/15 degrees C and 35 degrees C/25 degrees C) and an ambient (360 mu mol mol(-1)) vs a doubled CO2 concentration (720 mu mol mol(-1)) at 25 degrees

C/15 degrees C, the optimum temperature for net CO2 uptake. 2. Root elongation occurred at soil temperatures from 12 degrees C (at 15 degrees C/5 degrees C) to 43 degrees C (at 35 degrees C/25 degrees C) with optimum temperatures of 27-30 degrees C, similar to other CAM succulents and consistent with the distribution of this shallow-rooted species in warm regions. Although a doubled CO2 concentration did not alter the optimum or limiting soil temperatures, increases of up to 5 degrees C in these temperatures accompanied the 20 degrees C increase in day/night air temperatures. 3. Root elongation rates at optimum soil temperatures ranged from 5.4 mm day(-1) (15 degrees C/5 degrees C), through 6.6 mm day(-1) (25 degrees C/15 degrees C), to 10.4 mm day(-1) (35 degrees C/25 degrees C) with a 25% increase under a doubled CO2 concentration. Highest root elongation rates at 35 degrees C/25 degrees C may reflect changing root vs shoot sink strengths in a species with a highly plastic root system. 4. At limiting soil temperatures, the length of the cell division zone was reduced by an average of 20% and cell length at the mid-point of-the elongation zone by 10%. Increased root elongation rates under a doubled CO2 concentration reflected increased cell elongation. 5. The temperature response for the roots of O. ficus-indica and stimulation of elongation by a doubled CO2 concentration indicate that root growth for this highly productive species should be enhanced by predicted global climate change.

KEYWORDS: CAM PLANT, DESERT SUCCULENTS, ELEVATED CO2, ELONGATION, EXCHANGE, GLOBAL CLIMATE-CHANGE, NITROGEN, RESPONSES, WATER

574
Dube, S.L., and W. Vidaver. 1992. Photosynthetic competence of plantlets grown-invitro - an automated-system for measurement of photosynthesis invitro. *Physiologia Plantarum 84(3):409-416.*

An aseptic gas exchange and hydroponic system (AGEHS) has been developed in an attempt for characterization of physiological requirements for photoautotrophic growth in vitro and alleviation of the needs for ex vitro acclimatization. The AGEHS monitors and controls several parameters relevant to plant growth. Shootlets of Chrysanthemum, x morifolium Ramat. cv. Envy were treated with flow of air or CO2-enriched air under controlled relative humidity, elevated photosynthetic photon flux density (PPFD) and hydroponic irrigation. After 15 days of treatment, plantlets gained more than 3 times as much dry weight as those from a conventional culture tube treatment. This study shows that it is possible to favour photoautotrophic growth when elevated PPFD, enhanced air-exchange and hydroponic medium flow are provided concurrently. This enhancement is achievable through careful increments of light quanta, balanced with increments of humidified air flow and/or CO2 content in air which seem to be necessary to avoid potential photoinhibition and premature water exhaustion from gelled media.

KEYWORDS: ACCLIMATIZATION, CO2- ENRICHMENT, CULTURE, LEAVES, REGENERANTS, SOIL, SOYBEANS

575
Duchein, M.C., A. Bonicel, and T. Betsche. 1993. Photosynthetic net co2 uptake and leaf phosphate concentrations in co2 enriched clover (trifolium-subterraneum L) at 3 levels of phosphate nutrition. *Journal of Experimental Botany 44(258):17-22.*

Net CO2-uptake of sets of clover plants (Trifolium subterraneum L. was measured over three weeks in ambient air and in a highly CO2-enriched atmosphere (400 Pa CO2). Phosphate (P) in the nutrient solution was varied between 0-05 mol m-3 P (reduced P) and 2.0 mol m-3 P (high P). In ambient air, the daily increments of the daily rate of net CO2-uptake (DICU; a parameter related to relative growth) were higher at reduced P than at high P. Stimulation by high CO2 of net CO2-uptake in the first day was less at reduced P than at high P. In the following days, high CO2 markedly inhibited DICU at reduced P, and thus growth stimulation by high CO2 ceased after between 4 and 12 d. By contrast, at high P, DICU increased more than 2- fold upon CO2-enrichment, and thus growth stimulation by high CO2 was maintained. Intermediate results were obtained with half-strength Hoagland's solution (0-5 mol m-3 P). Leaf pools of inorganic ortho P, soluble esterified P, and total P declined markedly in high CO2 when P-nutrition had been reduced. Considerable decline also occurred in high CO2 when P- nutrition had been increased suggesting that P-uptake was not well tuned with net CO2-uptake (growth). It is proposed that high CO2 can perturb the P-metabolism of clover, the impairment being less at high levels of P-nutrition. With regard to high CO2 as a growth stimulus, these results demonstrate that increasing P-nutrition to a level supraoptimal in ambient air can considerably improve the growth of a C3-plant in high CO2.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CARBON-DIOXIDE, ELEVATED CO2, GROWTH, PHOSPHORUS, PLANTS, RESPONSES, SOURCE-SINK RELATIONS, SPINACH LEAVES, TEMPERATURE

576
Duff, G.A., C.A. Berryman, and D. Eamus. 1994. Growth, biomass allocation and foliar nutrient contents of 2 eucalyptus species of the wet dry tropics of australia grown under co2 enrichment. *Functional Ecology 8(4):502-508.*

1. Seeds of Eucalyptus tetrodonta and E. miniata were sown in duplicated air-conditioned tents which were ventilated with either ambient or CO2-enriched (700 mumol mol-1) air. Growth, foliar nutrient content, soluble protein and biomass allocation were investigated over the subsequent 32-week experimental period. 2. It was found that CO2 enrichment significantly increased the total biomass and tree height of E. tetrodonta, but had no effect on total biomass or tree height of E. miniata. 3. Allocation of biomass to main-stem wood and main- stem leaf mass increased and allocation to branch wood and branch leaves declined, under CO2 enrichment for E. tetrodonta. No change in allocation patterns for E miniata was observed in response to CO2 enrichment. 4. Foliar nitrogen, manganese and phosphorus contents were decreased under CO2 enrichment in E tetrodonta, but there was no effect of CO2 concentration in E. miniata. Soluble protein contents were not affected by CO2 enrichment in either species. These results are discussed in relation to the competitive relationship between these two species in northern Australia.

577
Dufrene, E., J.Y. Pontailler, and B. Saugier. 1993. A branch bag technique for simultaneous co2 enrichment and assimilation measurements on beech (fagus-sylvatica L). *Plant, Cell and Environment 16(9):1131-1138.*

A cheap CO2 enrichment system was designed to perform continuous gas exchange measurements of branches of mature European beech trees (Fagus sylvatica L.). Branches were grown at ambient (350 cm(3) m(-3)) and elevated CO2 (700 cm(3) m(-3)) during the whole 1992 leafy period. Leaks resulting from airtightness defaults in the system appeared to be low enough to measure accurately net CO2 assimilation and transpiration rates during the day. However, the CO2 exchange rates during the night (respiration) were too low to allow accurate measurements. Elevated CO2 had a great effect on the net assimilation rate of branches via its influence on both the C-3 photosynthetic pathway and the shade-tolerance of beech frees (85% increase). The A/C-a curves showed no acclimation effect to high CO2, both control and enriched branches increasing their net assimilation in the same way. The decrease of net assimilation rates in mature leaves was similar for

both control and enriched branches. The pattern of daily transpiration rates remained the same for both control and enriched branches, hence we can assume that there was no visible CO2 effect on stomata.

KEYWORDS: ATMOSPHERIC CO2, ELEVATED CARBON-DIOXIDE, GAS-EXCHANGE, GROWTH, PHOTOSYNTHETIC ACCLIMATION, PLANTS, RESPONSES, TREES

578

Dugal, A., S. Yelle, and A. Gosselin. 1990. Influence of CO2 enrichment and its method of distribution on the evolution of gas exchanges in greenhouse tomatoes. *Canadian Journal of Plant Science 70(1):345-356.*

579

Dugas, W.A., M.L. Heuer, D. Hunsaker, B.A. Kimball, K.F. Lewin, J. Nagy, and M. Johnson. 1994. Sap flow measurements of transpiration from cotton grown under ambient and enriched co2 concentrations. *Agricultural and Forest Meteorology 70(1-4):231-245.*

Increasing atmospheric CO2 concentration has many implications for agriculture and forestry, one of which is the effect it will have on transpiration (T). The objective of this work was to quantify T of cotton (Gossypium hirsutum L.) grown in the field under ambient (370 mumol mol-1) and enriched (550 mumol mol-1) CO2 concentrations. Measurements were made in 1990 and 1991 at the Maricopa Agricultural Center, Arizona. Constant- power sap flow gauges were used to measure T. In 1990, three plants and in 1991, 10 plants were simultaneously instrumented with gauges in each of the CO2 treatments. Leaf area of plants with gauges was measured. T measured by sap flow was compared with evapotranspiration (ET) calculated by water balance in 1990 and with T calculated by water balance in 1991. Soil evaporation was measured using microlysimeters in 1991, and was found to be essentially equal (approximately 0.8 mm day-1, or about 10% of T) in the two CO2 treatments. There were no consistent differences in leaf area of plants with gauges between the two CO2 treatments. Sap flow, for periods from 15 min to 2 weeks, was not significantly different between the two CO2 treatments in either year, except for a few days in 1990. In 1991, the coefficient of variation of daily sap flow across plants was the same (about 30%) for both CO2 treatments throughout the year. The water balance ET (1990) and T (1991) were similar to sap flow in both years, and also showed no effect of CO2 treatment. These results show that for this crop, grown under well-watered and high-fertility conditions, there was no effect of CO2 on T, on a per unit ground area or per plant basis. These results are relevant for assessing the effects of increasing atmospheric CO2 concentrations on transpiration by cotton.

KEYWORDS: CARBON DIOXIDE, CROP YIELD, ELEVATED CO2, EVAPORATION, HEAT-BALANCE, LEAF CONDUCTANCE, MASS-FLOW, PLANTS, STEM-FLOW, WATER-USE

580

Dugas, W.A., S.A. Prior, and H.H. Rogers. 1997. Transpiration from sorghum and soybean growing under ambient and elevated CO2 concentrations. *Agricultural and Forest Meteorology 83(1-2):37-48.*

The increasing concentration of carbon dioxide in the atmosphere ([CO2]) has several direct effects on plants and these effects may be different for C-3 and C-4 plants. Our objective was to measure hourly and daily whole-plant transpiration rates from the C-4 plant grain sorghum (Sorghum bicolor (L.) Moench) and the C-3 plant soybean (Glycine max (L.) Merr.) grown under ambient (359 mu molCO(2) mol(-1) dry atmospheric air) and elevated (705 mu molmol(-1)) [CO2] values. Transpiration measurements were made for 22 days in August 1994 at Auburn, Alabama, USA, using stem flow gauges on plants growing in open top chambers, n = 8 for each [CO2] and species. Leaf area averaged slightly more than 0.1m(2) per plant for sorghum and about 0.2 m(2) per plant for soybean, Averages (15 min and daily) of transpiration, per unit leaf area, were consistently greater from plants growing under the ambient [CO2,] for both sorghum and soybean. Average daily transpiration from plants growing under the elevated [CO2] was significantly smaller (P = 0.05) on all but 2 days for soybean and on 9 of the 22 days of measurements for sorghum. Average daily sorghum transpiration was 1128 gm(-2) day(-1) and 772 gm(-2) day(-1) from plants growing under an ambient and elevated [CO2], respectively. Corresponding soybean averages were 731 gm(-2) day(-1) and 416 gm(-2) day(-1). The transpiration reduction under elevated [CO2] was greater for the C-3 plant soybean than for the C-4, plant sorghum. These results support previous studies showing that transpiration, per unit leaf area, from sorghum and soybean will both be reduced if atmospheric [CO2] continues to increase, although the reduction may be greater for C-3, plants.

KEYWORDS: ATMOSPHERIC CO2, CARBON-DIOXIDE ENRICHMENT, COTTON, CROP TRANSPIRATION, HEAT-BALANCE, LEAF CONDUCTANCE, SAP FLOW, STEM-FLOW GAUGE, WATER-USE EFFICIENCY, YIELD

581

Dukes, J.S., and H.A. Mooney. 1999. Does global change increase the success of biological invaders? *Trends in Ecology and Evolution 14(4):135-139.*

Biological invasions are gaining attention as a major threat to biodiversity and an important element of global change. Recent research indicates that other components of global change, such as increases in nitrogen deposition and atmospheric CO2 concentration, favor groups of species that share certain physiological or life history traits. New evidence suggests that many invasive species share traits that will allow them to capitalize on the various elements of global change. Increases in the prevalence of some of these biological invaders would alter basic ecosystem properties in ways that feed back to affect many components of global change.

KEYWORDS: CARBON DIOXIDE, CLIMATE, COMMUNITY, CONSEQUENCES, DISTURBANCE, ELEVATED CO2, ENRICHMENT, MORPHOLOGY, NITROGEN, VEGETATION

582

Duquesnay, A., N. Breda, M. Stievenard, and J.L. Dupouey. 1998. Changes of tree-ring delta C-13 and water-use efficiency of beech (Fagus sylvatica L.) in north-eastern France during the past century. *Plant, Cell and Environment 21(6):565-572.*

We investigated variation in intrinsic water-use efficiency during the past century by analysing delta(13)C in tree rings of beech growing in north-eastern France. Two different silvicultural systems were studied: high forest and coppice- with-standards, We studied separately effects related to the age of the tree at the time the ring was formed and effects attributable to environmental changes. At young ages, delta(13)C shows an increase of more than 1 parts per thousand. However, age-related trends differ in high forest and coppice- with-standards. Changes in microenvironmental variables during stand maturation, and physiological changes related to structural development of the trees with ageing, could explain these results. During the past century, delta(13)C in tree rings shows a pattern of decline that is not paralleled by air delta(13)C changes. Isotopic discrimination has significantly decreased from 18.1 to 16.4 parts per thousand in high forest and varied insignificantly between 17.4 and 16.9 parts per thousand in coppice-

with-standards, As a consequence, intrinsic water-use efficiency has increased by 44% in high forest and 23% in coppice-with-standards during the past century. These results accord with the increased water-use efficiency observed in controlled experiments under a CO2-enriched atmosphere. However other environmental changes, such as nitrogen deposition, may be responsible for such trends.

KEYWORDS: ANTARCTIC ICE, ATMOSPHERIC CO2 CONCENTRATION, C 13/C 12, CARBON ISOTOPE DISCRIMINATION, CENTURIES, DIOXIDE, DOUGLAS-FIR, GAS-EXCHANGE, POLAR ICE CORES, STOMATAL DENSITY

583
During, H., and M. Harst. 1996. Stomatal behaviour, photosynthesis and photorespiration of in vitro-grown grapevines: Effects of light and CO2. *Vitis 35(4):163-167.*

To improve photosynthesis and growth of grapevines cultivated in vitro (Seyval blanc and SO 4) effects of light intensity, spectral irradiance and CO2 concentration on stomatal behaviour, CO2 fixation and photorespiration were studied. Stomata were shown to respond to changes of light intensity but, unlike photosynthesis, their reactions were delayed and stomatal closure was incomplete in the dark. In contrast, alterations of the CO2 concentration in the headspace (50-2200 ppm) did not cause stomatal reactions. Photosynthesis vs, light intensity relationships indicated lower light compensation points, higher quantum yield and higher rates of light- saturated photosynthesis with "Fluora" lamps (maximal spectral irradiance al 460 and 680 nm) compared to "projector" lamps (maximal spectral irradiance at 620 nm). Photosynthesis vs. intercellular CO2 concentration relationships indicated varietal differences, the carboxylation efficiency and rates of photosynthesis at CO2 saturation being distinctly higher in the more vigorous variety SO 4 compared to Seyval blanc. Under the usual light conditions of our in vitro culture (50-60 mu mol quanta . m(-2). s(-1), Fluora) the headspace CO2 concentration ranged from 145 to 155 ppm while at the end of a 10-hour dark period it increased to values >3000 ppm. Rates of photorespiration were high (>50 % of photosynthesis) due to the relative low CO2 concentrations and, presumably, due to elevated O-2 concentrations in the headspace. It is concluded that the often observed low rates of photosynthesis of in vitro plantlets are mainly due to low light intensity and CO2 concentration in the headspace, the latter depending on the low rates of gas diffusion between ambient air and headspace.

KEYWORDS: CULTURED INVITRO, LEAVES, PLANTLETS, VITIS

584
Dury, S.J., J.E.G. Good, C.M. Perrins, A. Buse, and T. Kaye. 1998. The effects of increasing CO2 and temperature on oak leaf palatability and the implications for herbivorous insects. *Global Change Biology 4(1):55-61.*

Rising levels of atmospheric CO2 are expected to perturb forest ecosystems, although the extent to which specific ecological interactions will be modified is unclear. This research evaluates the effects of elevated CO2 and temperature, alone and in combination, on the leaf nutritional quality of Pendunculate oak (Qeurcus robur L.), and the implications for herbiverous insect defoliators are discussed. A 3 degrees C temperature rise reduced leaf nutritional quality, by reducing foliar nitrogen concentration and increasing condensed tannin content. Doubling atmospheric CO2 temporarily increased total phenolics, but also reduced leaf toughness. The nutritional quality of the second leaf flush (lammas growth) was considerably reduced at elevated CO2. It is concluded that larval development of spring-feeding defoliators and hence adult fecundity may be adversely affected by increased temperatures.

KEYWORDS: CARBON-DIOXIDE ATMOSPHERES, ELEVATED ATMOSPHERIC CO2, LARVAL EMERGENCE, LEPIDOPTERA, MOTH, NUTRIENT BALANCE, PERFORMANCE, PHYTOCHEMISTRY, PLANTS, QUERCUS-ROBUR L

585
Eamus, D. 1991. The interaction of rising CO2 and temperatures with water-use efficiency. *Plant, Cell and Environment 14(8):843-852.*

Recent data concerning the impact of elevated atmospheric CO2 upon water use efficiency (WUE) and the related measure, instantaneous transpiration efficiency (ITE), are reviewed. It is concluded from both short and long-term studies that, at the scale of the individual leaf or plant, an increase in WUE or ITE is generally observed in response to increased atmospheric CO2 levels. However, the magnitude of this increase may decline with time. The opinion that elevated CO2 may substantially decrease transpiration at the regional scale is discussed. The mechanisms by which elevated CO2 may cause a change in these measures are discussed in terms of stomatal conductance, assimilation and respiration responses to elevated CO2. Finally, recent experimental data and model outputs concerning the impact of the interaction of increased temperature with elevated CO2 on WUE, ITE and yield are reviewed. It is concluded that substantially more data is required before reliable predictions about the regional scale response of WUE and catchment hydrology can be made.

KEYWORDS: ABSCISIC- ACID, ATMOSPHERIC CARBON-DIOXIDE, ELEVATED CO2, ENRICHMENT, GAS-EXCHANGE, LEAF, PLANT GROWTH, RESPONSES, STOMATAL GUARD-CELLS, STRESS

586
Eamus, D. 1996. Tree responses to CO2 enrichment: CO2 and temperature interactions, biomass allocation and stand-scale modeling. *Tree Physiology 16(1-2):43-47.*

In this review, I focus on modeling studies of tree responses to CO2 enrichment. First, I examine leaf-scale models of assimilation with respect to the interaction between low temperature and CO2 enrichment. Second, because changes in allocation within a tree may be significant in determining the growth response of trees to CO2 enrichment and low temperatures, I review models of the control of allocation in plants. Finally, models of stand-scale processes are discussed with respect to their ability to make reliable estimates of likely vegetation responses to predicted climate change. I conclude that our ability to make reliable predictions is hindered by our lack of understanding of several processes, namely: the interaction between increased atmospheric CO2 concentration and low temperatures; the control of allocation in plants; and the modeling of stand-scale processes.

KEYWORDS: AIR- TEMPERATURE, ATMOSPHERIC CO2, BALANCE, CARBON-DIOXIDE CONCENTRATION, ELEVATED CO2, GROWTH, PHOTOSYNTHESIS, ROOT, SEEDLINGS, TERM

587
Eamus, D., C.A. Berryman, and G.A. Duff. 1993. Assimilation, stomatal conductance, specific leaf-area and chlorophyll responses to elevated co2 of maranthes corymbosa, a tropical monsoon rain-forest species. *Australian Journal of Plant Physiology 20(6):741-755.*

Seeds of Maranthes corymbosa Blume, a monsoon rain forest species of northern Australia, were sown under ambient or elevated CO2 concentrations in tropical Australia. Seedlings were grown under conditions of photon flux density, temperature and atmospheric vapour pressure deficit which followed ambient variations as closely as possible. Specific leaf area, chlorophyll, stomatal density, stomatal conductance

and assimilation responses to photon flux density were measured after 30 weeks growth. Gas exchange characteristics were divided into morning and afternoon data sets and analysed separately. Stomatal density decreased and leaf area:dry weight ratio decreased in response to elevated CO2. In contrast there was no effect of elevated CO2 upon chlorophyll (total or ratio of a:b). Apparent quantum yield and rates of light saturated assimilation (A(max)) increased in response to elevated CO2. There was a significant decline in apparent quantum yield for both treatments between morning and afternoon. Stomatal conductance (g(s)) declined in response to elevated CO2. There was no significant difference in g(s) between morning and afternoon for ambient grown trees, but g(s) declined significantly between morning and afternoon for elevated CO2 grown trees. Instantaneous transpiration efficiency (ITE) was higher for elevated CO2 grown trees compared with control trees. There was a significant increase in ITE between morning and afternoon data for ambient grown trees; in contrast a significant decline in ITE was observed for elevated CO2 grown trees between morning anf afternoon data sets. The slope of the regression between assimilation rate and stomatal conductance increased for plants grown under elevated CO2. These data are discussed and compared with the responses of plants adapting to different photon flux densities.

KEYWORDS: ATMOSPHERIC CO2, CARBON-DIOXIDE ENRICHMENT, GROWTH, INCREASES, IRRADIANCE, LIGHT, ORANGE, PHOTOSYNTHESIS, SEEDLINGS, TREES

588

Eamus, D., C.A. Berryman, and G.A. Duff. 1995. The impact of co2 enrichment on water relations in maranthes- corymbosa and eucalyptus-tetrodonta. *Australian Journal of Botany 43(3):273-282.*

Seeds of Maranthes corymbosa Blume and Eucalyptus tetrodonta F.Muell were sown under ambient or CO2 enriched conditions (two replicate tents per treatment) in tropical Australia and allowed to grow, rooted in the ground, for 20 months. For both species, periodic measurements of leaf water potential, stomatal conductance and leaf temperature were made on four replicate leaves on each of four replicate trees within each tent. Measurements were made in November (M. corymbosa) and June (E. tetrodonta). At the same time, atmospheric wet and dry bulb temperatures were recorded and hence leaf-to-air vapour presure difference (LAVPD) calculated. Measurements of pre-dawn leaf water potential were also made on E. tetrodonta. Leaves were also taken to the laboratory, rehydrated to full turgor and pressure-volume analyses undertaken. For M. corymbosa, leaf water potential was lower throughout the day for control leaves compared to leaves growing in CO2 enriched air. Similarly, pre dawn leaf water potential was lower for control E. tetrodonta trees than for trees grown with CO2 enrichment. However, mid- morning and mid-afternoon values of leaf water potential for E. tetrodonta were slightly lower for plants growing in CO, enriched air compared to control plants. In both species, stomatal conductance was consistently lower for trees grown in CO2 enriched air than for controls. Whole plant hydraulic conductivity of both species was significantly lower for trees grown in CO2 enriched air than for control trees. For both species, maximum turgor and bulk volumetric elastic modulus increased and osmotic potential at zero turgor decreased for trees grown in CO2 enriched air.

KEYWORDS: ANATOMY, ATMOSPHERIC CO2, CARBON DIOXIDE, ELEVATED CO2, GROWTH, MORPHOLOGY, SEEDLINGS, STRESS

589

Eamus, D., G.A. Duff, and C.A. Berryman. 1995. Photosynthetic responses to temperature, light flux-density, co2 concentration and vapor-pressure deficit in eucalyptus tetrodonta crown under co2 enrichment. *Environmental Pollution 90(1):41-49.*

Seeds of Eucalyptus tetrodonta were sown under ambient or CO2 enriched (700 mu l litre(-1)) conditions in tropical Australia. Four sets of measurements were made, the first two after 12 months, on trees growing either in pots or planted in the ground. The third and fourth set were made after 18 and 30 months exposure to CO2 enrichment, on trees growing in the ground After 12 months exposure to CO2 enrichment, the rate of light-saturated assimilation (A(max)) of plants growing in the ground was determined. Responses of CO2 assimilation to variations in leaf temperature, leaf-to-air vapour,pressure deficit (LAVPD), Eight flux density and CO2 concentration were also measured in the laboratory using plants growing in large pots. There was no significant difference in A(max) between pot and ground located plants. Assimilation of E. tetrodonta was relatively insensitive to changes in LAVPD for both ambient and CO2 enriched plants but the temperature optimum of assimilation was increased in plants grown and measured under CO2 enrichment. Plants grown with CO2 enrichment had an increased rate of light-saturated assimilation and apparent quantum yield I-vas significantly inn eased by CO2 enrichment. rn contrast, carboxylation efficiency was decreased significantly by CO2 enrichment. After 18 months growth with CO2 enrichment, there was no sign of a decline in assimilation I ate compared to measurements undertaken after 12 months, At low LAVPD values, assimilation rate was not influenced by CO2 treatment but at moderate to high LAVPD, plants grown under CO2 enrichment exhibited a larger assimilation rate than control plants. Specific leaf area and chlorophyll contents decreased in response to CO2 enrichment, whilst foliar soluble protein contents and chlorophyll a/b ratios were unaffected by CO2 treatment. Changes in soluble protein and chlorophyll contents in response to CO2 enrichment did not account for changes in assimilation between treatments. After 30 months exposure to CO2 enrichment, the rate of light-saturated assimilation was approximately 50% larger than controls and this enhancement was larger than that observed after 18 months exposure to CO2 enrichment.

KEYWORDS: ACCLIMATION, CARBON DIOXIDE, CARBOXYLASE, ELEVATED CO2, GROWTH, L LEAVES, MARANTHES-CORYMBOSA, PHASEOLUS-VULGARIS L, SEEDLINGS, STOMATAL CONDUCTANCE

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Eamus, D., and M. Murray. 1991. Photosynthetic and stomatal conductance responses of norway spruce and beech to ozone, acid mist and frost - a conceptual-model. *Environmental Pollution 72(1):23-44.*

Two-year-old beech and Norway spruce seedlings were exposed to a combination of ozone and acid mist treatments in open-top chambers in Scotland during the months of July through to September 1988. Replicate pairs of chambers received charcoal- filtered air (control), ozone-enriched air (140 nl ozone litre- 1) or 140 nl ozone litre-1 plus a synthetic acid mist (pH 2.5) composed of ammonium nitrate and sulphuric acid. Field measurements of assimilation and stomatal conductance were made during August. In addition, measurements of assimilation and conductance were made during September in the laboratory. Light response curves of assimilation and conductance were determined using a GENSTAT non-rectangular hyperbolic model. During February 1988/9 the Norway spruce were subject to a four day warming period at 12-degrees-C and the light response of assimilation determined. The same plants were then subject to a 3-h night-time frost of -10-degrees-C. The following day the time-course of the recovery of assimilation was determined. It was found that ozone fumigation did not influence the light response of assimilation of beech trees in the field, although stomatal conductance was reduced in the ozone-fumigated trees. The rate of light-saturated assimilation of Norway spruce was increased by ozone fumigation when measured in the field. Measurements of assimilation of Norway spruce made during the winter showed that prior to rewarming there was no difference in the rate of light-saturated assimilation for control and ozone-fumigated trees. However, the ozone plus acid mist- treated trees exhibited a significantly

higher rate. The 4-day period of warming to 12-degrees-C increased the rate of light-saturated assimilation in all treatments but only the ozone plus acid mist-treated trees showed a significant increase. Following a 3-h frost to -10-degrees-C the control trees exhibited a reduction in the rate of light-saturated assimilation (A(max)) to 80% of the pre-frost value. In comparison, following the frost, the ozone-fumigated trees showed an A(max) of 74% of the pre-frost value. The ozone plus acid mist-treated trees showed an A(max) of 64% of the pre- frost trees. The time taken for A(max) to attain 50% of the pre-frost value increased from 30 min (control) to 85 min for ozone-fumigated trees to 190 min (ozone plus acid mist). These results are discussed in relation to the impact of mild, short- term frosts, which are known to occur with greater frequency than extreme, more catastrophic frost events. A simple conceptual framework is proposed to explain the variable results obtained in the literature with respect to the impact of ozone upon tree physiology.

KEYWORDS: ABIES L KARST, CO2 ASSIMILATION, FOREST DECLINE, GROWTH, HARDINESS, PINUS SYLVESTRIS, RAIN, SCOTS PINE, SEEDLINGS, TEMPERATURES

591

Easterling, W.E., P.R. Crosson, N.J. Rosenberg, M.S. McKenney, L.A. Katz, and K.M. Lemon. 1993. Agricultural impacts of and responses to climate-change in the missouri-iowa-nebraska-kansas (mink) region. *Climatic Change 24(1-2):23-61.*

The climate of the 1930s was used as an analog of the climate that might occur in Missouri, Iowa, Nebraska and Kansas (the MINK region) as a consequence of global warming. The analog climate was imposed on the agriculture of the region under technological and economic conditions prevailing in 1984/87 and again under a scenario of conditions that might prevail in 2030. The EPIC model of Williams et al. (1984), modified to allow consideration of the yield enhancing effects of CO2 enrichment, was used to evaluate the impacts of the analog climate on the productivity and water use of some 50 representative farm enterprises. Before farm level adjustments and adaptations to the changed climate, and absent CO2 enrichment (from 350 to 450 ppm), production of corn, sorghum and soybeans was depressed by the analog climate in about the same percent under both current and 2030 conditions. Production of dryland wheat was unaffected. Irrigated wheat production actually increased. Farm level adjustments using low-cost currently available technologies, combined with CO2 enrichment, eliminated about 80% of the negative impact of the analog climate on 1984/87 baseline crop production. The same farm level adjustments, plus new technologies developed in response to the analog climate, when combined with CO2 enrichment, converted the negative impact on 2030 crop production to a small increase. The analog climate would have little direct effect on animal production in MINK. The effect, if any, would be by way of the impact on production of feed-grains and soybeans. Since this impact would be small after on-farm adjustments and CO2 enrichment, animal production in MINK would be little affected by the analog climate.

KEYWORDS: CO2, CORN, EPIC MODEL, EROSION, PRODUCTIVITY

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Easterling, W.E., N.J. Rosenberg, K.M. Lemon, and M.S. McKenney. 1992. Simulations of crop responses to climate change - effects with present technology and currently available adjustments (the smart farmer scenario). *Agricultural and Forest Meteorology 59(1-2):75-102.*

If climate changes, farmers will have to adapt to a new set of climate constraints. In this paper we examine the efficacy of strategies for dealing with climate change that are currently available to farmers and that are inexpensive to use; we refer to this group of strategies as 'adjustments'. Adjustment schemes of various kinds were identified for us by agricultural experts in the Missouri-Iowa-Nebraska-Kansas (MINK) states. These can involve changes in land use, changes in variety and crop selection, changes in planting and harvesting practices, and changes in fertility and pest management. Using the erosion productivity impact calculator (EPIC) model on a small set of representative farms, we tested adjustments of these kinds. The simulations show that earlier planting, longer- season cultivars and the use of furrow diking for moisture conservation would offset some of the yield losses induced by climate change in warm-season crops. Longer-season varieties of wheat (a cool-season crop) and shorter-season varieties of the perennials wheatgrass and alfalfa were also effective. The adjustments to climate change diminished yield losses in all crops but irrigated wheat. Despite the positive effects of adjustments, however, yields of all dryland warm-season crops remained lower than control levels. The adjustments also increased demand for irrigation water. Carbon dioxide enrichment had the same incremental effect on crop yields with or without adjustments (see the fourth paper in this issue), except in the case of alfalfa and sorghum, where a CO2- adjustment interaction was found. We conclude that currently available techniques would partially offset the yield reductions caused by a 1930s-like climate, but that in most crops the yield reductions would still be substantial.

KEYWORDS: AGRICULTURE

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Edwards, N.T., and R.J. Norby. 1998. Below-ground respiratory responses of sugar maple and red maple saplings to atmospheric CO2 enrichment and elevated air temperature. *Plant and Soil 206(1):85-97.*

The research described in this paper represents a part of a much broader research project with the general objective of describing the effects of elevated [CO2] and temperature on tree growth, physiological processes, and ecosystem-level processes. The specific objective of this research was to examine the below-ground respiratory responses of sugar maple (Acer saccharum Marsh.) and red maple (Acer rubrum L.) seedlings to elevated atmospheric [CO2] and temperature. Red maple and sugar maple seedlings were planted in the ground in each of 12 open-top chambers and exposed from 1994 through 1997 to ambient air or air enriched with 30 Pa CO2, in combination with ambient or elevated (+4 degrees C) air temperatures. Carbon dioxide efflux was measured around the base of the seedlings and from root-exclusion zones at intervals during 1995 and 1996 and early 1997. The CO2 efflux rates averaged 0.4 mu mol CO2 m(-2) s(-1) in the root-exclusion zones and 0.75 mu mol CO2 m(-2) s-1 around the base of the seedlings. Mineral soil respiration in root-exclusion zones averaged 12% higher in the high temperature treatments than at ambient temperature, but was not affected by CO2 treatments. The fraction of total efflux attributable to root + rhizosphere respiration ranged from 14 to 61% in measurements made around red maple plants, and from 35 to 62% around sugar maple plants. Root respiration rates ranged from 0 to 0.94 mu mol CO2 s(-1) m(-2) of soil surface in red maple and from 0 to 1.02 in sugar maple. In both 1995 and 1996 root respiration rates of red maple were highest in high-CO2 treatments and lowest in high temperature treatments. Specific red maple root respiration rates of excised roots from near the soil surface in 1996 were also highest under CO2 enrichment and lowest in high temperature treatments. In sugar maple the highest rates of CO2 efflux were from around the base of plants exposed to both high temperature and high-CO2, even though specific respiration rates were lowest for this species under the high temperature and CO2 enrichment regime. In both species, patterns of response to treatments were similar in root respiration and root mass, indicating that the root respiration responses were due in part to differences in root mass. The results underscore the need for separating the processes occurring in the roots from those in the

forest floor and mineral soil in order to increase our understanding of the effects of global climate change on carbon sequestration and cycling in the below-ground systems of forests.

KEYWORDS: CARBON DIOXIDE, DECIDUOUS FOREST FLOOR, DROUGHT, EVOLUTION, GROWTH, NITROGEN, PONDEROSA PINE, ROOT RESPIRATION, SEEDLINGS, SOIL RESPIRATION

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Egli, P., and C. Korner. 1997. Growth responses to elevated CO2 and soil quality in beech- spruce model ecosystems. *Acta Oecologica-International Journal of Ecology 18(3):343-349.*

Growth responses of beech (Fagus sylvatica L.) and Norway spruce (Picea abies Karst.) to elevated atmospheric CO2 (366 and 550 mu l CO2 l(-1)) and increased wet deposition of nitrogen (2.5 and 25 kg N ha(-1) a(-1)) in combination with two soil types were studied in open-top chambers. Eight young beech and spruce trees, together with five understory species, were established in each of 32 model ecosystems. We present initial growth responses of trees during the first year of treatment which may set the trends for longer term responses to elevated CO2. Above-ground biomass production at the system level (biometric data) during the first year and root biomass (coring data) did not show significant responses to elevated CO2, irrespectively of other cc-treatments. Increased nitrogen deposition (treatment commencing by mid-season) also had no effect on above-ground biomass, whereas end of season root biomass was significantly increased in the high-nitrogen treated low fertility acidic soil (74 g m(-2) in the high-N versus 49 g m(-2)? in the low N-treatment), but not-in the more fertile calcareous soil. Stem diameter increment of beech was significantly increased (+9%) under elevated CO, in the calcareous soil, but not in the acidic soil. The opposite was found for spruce stems, which responded positively to elevated CO2 in the acidic soil (+ 11%; $P < 0.05$) but nor in the calcareous soil. These results suggest that soil type co- determines the CO2 response of young forest trees and that these interactions are species specific. These initial differences are likely to affect long-term responses of community structure and ecosystem functioning. Soil type appears to be a key factor in predictions of forest responses to continued atmospheric CO2 enrichment.

KEYWORDS: ATMOSPHERE, COMMUNITIES, PLANTS, TREES

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Egli, P., S. Maurer, M.S. Gunthardt-Goerg, and C. Korner. 1998. Effects of elevated CO2 and soil quality on leaf gas exchange and above-ground growth in beech-spruce model ecosystems. *New Phytologist 140(2):185-196.*

Responses of leaf gas exchange and above-ground growth of beech (Fagus sylvatica L.) and Norway spruce (Picea abies Karst.) to atmospheric CO2 enrichment (374 mu l l(-1) VS. 590 mu l l(-1)) and increased wet deposition of N (5 vs. 50 kg N ha(-1) a(-1)) in combination with two natural forest soil types ('acidic' and 'calcareous') were studied in large open-top chambers. Eight juvenile beech and spruce trees from different provenances, together with a ground cover composed of five understorey species, were established in each of 32 model ecosystems. Both beech and spruce showed sustained enhancement of photosynthesis in response to atmospheric CO2 enrichment during the first 2 yr of treatment. Nevertheless, switching measurement CO2 concentrations revealed partial downward adjustment of photosynthesis in trees grown in elevated CO2, beech generally showing more pronounced downward adjustment than spruce. The responsiveness of photosynthesis to CO2 enrichment did not vary significantly among trees from different provenances. Stomatal conductance was reduced under elevated CO2 in both tree species. In spruce, the radial growth of the main stem and the annual production of wood (shoot-wood dry mass of current-year lateral shoots), needle dry mass, and assimilation area per tree were stimulated both by CO2 enrichment and increased N deposition, but were not significantly affected by soil type by year 2. In contrast, in beech, the radial growth of the stem and the total leaf number, foliage dry mass, and assimilation area per tree were all not significantly affected by elevated CO2 and increased N deposition when responses of the two soil types were pooled, but were greater on calcareous than on acidic soil by year 2. However, CO2 interacted with soil type in beech: irrespective of the N deposition rate, saplings showed growth stimulation on the calcareous soil but responded negatively to CO2 enrichment on the acidic soil (where growth was slower). Our results suggest that complex interactions between CO2, species and soil quality need to be accounted for when attempting to predict forest development in a future CO2- rich world.

KEYWORDS: ATMOSPHERIC CO2, BRANCH BAG, CARBON DIOXIDE, ENRICHMENT, FAGUS-SYLVATICA, PHOTOSYNTHETIC ACCLIMATION, PINUS-TAEDA, RESPONSES, RISING CO2, TREES

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Ehler, N., and P. Karlsen. 1993. Optico - a model-based real-time expert-system for dynamic optimization of co2 enrichment of greenhouse vegetable crops. *Journal of Horticultural Science 68(4):485-494.*

To improve the economic yield of CO2 enrichment for greenhouse crops, an expert system (OPTICO) was constructed. The system continually adapts the setpoints of a standard climate computer to the climate, the greenhouse regulation equipment and the crop's physiological status and stage of development. Models describing air loss and photosynthesis were used for selecting an optimized CO2 setpoint by choosing the largest positive difference between expected income and cost. During the autumn of 1991 the sweet pepper (Capsicum annuum L.) cv. Trophy was used as experimental plant in two standard greenhouse compartments. One treatment used the optimized CO2 enrichment, the other a fixed CO2 level of 600 ppm. The optimized treatment resulted in greater yield using less CO2. The results stress the importance of adapting the CO2 level to the immediate irradiance and current leaf area and carbon partitioning behaviour of the crop.

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Ehleringer, J.R., and T.E. Cerling. 1995. Atmospheric co2 and the ratio of intercellular to ambient co2 concentrations in plants. *Tree Physiology 15(2):105-111.*

Much attention is focused today on predicting how plants will respond to anticipated changes in atmospheric composition and climate, and in particular to increases in CO2 concentration. Here we review the long-term global fluctuations in atmospheric CO2 concentration as a framework for understanding how current trends in atmospheric CO2 concentration fit into a selective, evolutionary context. We then focus on an integrated approach for understanding how gas exchange metabolism responds to current environmental conditions, how it previously responded to glacial-interglacial conditions, and how it may respond to future changes in atmospheric CO2 concentration.

KEYWORDS: CARBON ISOTOPE DISCRIMINATION, GAS-EXCHANGE, LAST 3 CENTURIES, LEAVES, PHOTOSYNTHESIS, SOIL CARBONATE, STOMATAL DENSITY, TRANSPIRATION EFFICIENCY, VOSTOK ICE-CORE, WATER-USE EFFICIENCY

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Ehleringer, J.R., T.E. Cerling, and B.R. Helliker. 1997. C-4 photosynthesis, atmospheric CO2 and climate. *Oecologia 112(3):285-299.*

The objectives of this synthesis are (1) to review the factors that influence the ecological, geographical, and palaeoecological distributions of plants possessing C-4 photosynthesis and (2) to propose a hypothesis/model to explain both the distribution of C-4 plants with respect to temperature and CO2 and why C-4 photosynthesis is relatively uncommon in dicotyledonous plants (hereafter dicots), especially in comparison with its widespread distribution in monocotyledonous species (hereafter monocots). Our goal is to stimulate discussion of the factors controlling distributions of C-4 plants today, historically, and under future elevated CO2 environments. Understanding the distributions of C-3/C-4 plants impacts not only primary productivity, but also the distribution, evolution, and migration of both invertebrates and vertebrates that graze on these plants. Sixteen separate studies all indicate that the current distributions of C-4 monocots are tightly correlated with temperature: elevated temperatures during the growing season favor C-4 monocots. In contrast, the seven studies on C-4 dicot distributions suggest that a different environmental parameter, such as aridity (combination of temperature and evaporative potential), more closely describes their distributions. Differences in the temperature dependence of the quantum yield for CO2 uptake (light-use efficiency) of C-3 and C-4 species relate well to observed plant distributions and light-use efficiency is the only mechanism that has been proposed to explain distributional differences in C-3/C-4 monocots. Modeling of C-3 and C-4 light- use efficiencies under different combinations of atmospheric CO2 and temperature predicts that C-4-dominated ecosystems should not have expanded until atmospheric CO2 concentrations reached the lower levels that are thought to have existed beginning near the end of the Miocene. At that time, palaeocarbonate and fossil data indicate a simultaneous, global expansion of C-4-dominated grasslands. The C-4 monocots generally have a higher quantum yield than C-4 dicots and it is proposed that leaf venation patterns play a role in increasing the light-use efficiency of most C-4 monocots. The reduced quantum yield of most C-4 dicots is consistent with their rarity, and it is suggested that C-4 dicots may not have been selected until CO2 concentrations reached their lowest levels during glacial maxima in the Quaternary. Given the intrinsic light-use efficiency advantage of C-4 monocots, C-4 dicots may have been limited in their distributions to the warmest ecosystems, saline ecosystems, and/or to highly disturbed ecosystems. All C-4 plants have a significant advantage over C- 3 plants under low atmospheric CO2 conditions and are predicted to have expanded significantly on a global scale during full- glacial periods, especially in tropical regions. Bog and lake sediment cores as well as pedogenic carbonates support the hypothesis that C-4 ecosystems were more extensive during the last glacial maximum and then decreased in abundance following deglaciation as atmospheric CO2 levels increased.

KEYWORDS: BUNDLE-SHEATH, C-4 PHOTOSYNTHESIS, CARBOXYLASE-OXYGENASE, ECOLOGICAL DISTRIBUTION, GEOGRAPHICAL-DISTRIBUTION, ICE CORE, LAST GLACIAL MAXIMUM, LEAF ANATOMY, ORGANIC-MATTER, QUANTUM YIELD

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Eichelmann, H., and A. Laisk. 1994. Co2 uptake and electron-transport rates in wild-type and a starchless mutant of nicotiana-sylvestris - the role and regulation of starch synthesis at saturating co2 concentrations. *Plant Physiology 106(2):679-687.*

CO2 uptake rate, chlorophyll fluorescence, and 830-nm absorbance were measured in wild-type (wt) Nicotiana sylvestris (Speg. et Comes) and starchless mutant NS 458 leaves at different light intensities and CO2 concentrations. Initial slopes of the relationships between CO2 uptake and light and CO2 were similar, but the maximum rate at CO2 and light saturation was only 30% in the mutant compared with the wt. O-2 enhancement of photosynthesis at CO2 and tight saturation was relatively much greater in the mutant than in the wt. In 21% O- 2, the electron transport rate (ETR) calculated from fluorescence peaked near the beginning of the CO2 saturation of photosynthesis. With the further increase of CO2 concentration ETR remained nearly constant or declined a little in the wt but drastically declined in the mutant. Absorbance measurements at 830 nm indicated photosystem I acceptor side reduction in both plants at saturating CO2 and light. Assimilatory charge (postillumination CO2 uptake) measurements indicated trapping of chloroplast inorganic phosphate, supposedly in hexose phosphates, in the mutant. It is concluded that starch synthesis gradually substitutes for photorespiration as electron acceptor with increasing CO2 concentration in the wt but not in the mutant. It is suggested that starch synthesis is co-controlled by the activity of the chloroplast fructose bisphosphatase.

KEYWORDS: CARBON METABOLISM, CHLOROPLAST, FLUORESCENCE, LEAVES, MATHEMATICAL-MODEL, PHOTOSYNTHESIS, PLASTID PHOSPHOGLUCOMUTASE, REDUCED-ACTIVITY, STEADY-STATE, SUCROSE SYNTHESIS

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Elhottova, D., J. Triska, H. Santruckova, J. Kveton, J. Santrucek, and M. Simkova. 1997. Rhizosphere microflora of winter wheat plants cultivated under elevated CO2. *Plant and Soil 197(2):251-259.*

We studied an effect of elevated atmospheric CO2 on rhizosphere microorganisms in a hydroponics system where young wheat plants provided the only source of C for microorganisms. Plants were cultivated in mineral solution in sterile silica sand and exposed to control (ambient) and elevated (double) CO2 concentrations for periods of 13, 20, 25 and 34 days. Microbial biomass C (C content in fraction of size 0.3-2.7 mu m) was not affected by the elevated CO2 concentration during the first 25 days of plant growth and was increased after 34 days of plant growth. A content of poly-beta-hydroxybutyrate (PHB) reserve compounds (measured as derivatized product of 3-hydroxy-butyric acid and N-tert-butyldimethylsilyl-N-methyltrifluoracetamide using GC-MS) was lowered significantly ($p<0.001$) in the elevated CO2 after 25 and 34 days. It was accompanied with a shift of bacterial distribution towards the nutritional groups utilising more complex organic material (number of CFUs on media with different sources of C and N). A coincidence of several events connected with plant and microbial carbon economy (decrease of an assimilation rate and relative growth rate of plants, small increase of microbial biomass, PHB decrease and suppression within the bacterial nutritional group requiring the most readily available source of C and energy) was observed in the system under elevated CO2 on the 25th day. A modification of the CC-MS method for the detection of low levels of PHB compounds in natural samples was developed. We excluded the lipids fractionation step and we used EI MS/MS detection of the main fragment ions of the derivatized compound. This guarantees that the ion profiles have high signal-to-noise ratio at correct retention time. The detection limit is then about 30 pg g(-1) of sand or soil. The rhizosphere microflora responded very sensitively to the short- term changes in C partitioning in plants caused by the elevated CO2.

KEYWORDS: ATMOSPHERIC CO2, AZOSPIRILLUM- BRASILENSE, CARBON, GROWTH, METABOLISM, POLY BETA HYDROXYBUTYRATE, RESPONSES

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Elkohen, A., and M. Mousseau. 1994. Interactive effects of elevated co2 and mineral-nutrition on growth and co2 exchange of sweet chestnut seedlings (castanea- sativa). *Tree Physiology 14(7-9):679-690.*

The effects of elevated atmospheric CO2 (700 mumol mol-1) and

fertilization were investigated on 2-year-old sweet chestnut (Castanea sativa Mill.) seedlings grown outdoors in pots in constantly ventilated open-sided chambers. Plants were divided into four groups: fertilized controls (+F/-CO2), unfertilized controls (-F/-CO2), fertilized + CO2-treated plants (+F/+CO2) and unfertilized + CO2-treated plants (-F/+CO2). Dry matter accumulation and allocation were measured after one growing season and CO2 exchange of whole shoots was measured throughout the growing season. Shoot growth and total leaf area of unfertilized plants were not affected by elevated CO2, whereas both parameters were enhanced by elevated CO2 in fertilized plants. Elevated CO2 increased total biomass by about 20% in both fertilized and unfertilized plants; however, biomass partitioning differed. In unfertilized plants, elevated CO2 caused an increase in root growth, whereas in fertilized plants, it stimulated aboveground growth. At the whole-shoot and leaf levels, photosynthetic activity of both fertilized and unfertilized plants increased in response to elevated CO2, but the seasonal pattern of this enhancement varied with nutrient treatment. In unfertilized plants, a downward acclimation of photosynthesis was observed early in the season (June), and was related to reductions in nitrogen and chlorophyll content and to starch accumulation. The decrease in the slope of the A/Ci curve suggested a decrease in Rubisco activity. In both fertilized and unfertilized plants, shoot respiration decreased during the night in response to elevated CO2 until mid-July. The decrease was not related to changes in sugar concentration.

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Elkohen, A., J.Y. Pontailler, and M. Mousseau. 1991. Effect of doubling of atmospheric CO2 concentration on dark respiration in aerial parts of young chestnut trees (Castanea sativa mill). *Comptes Rendus De L Academie Des Sciences Serie III-Sciences De La Vie-Life Sciences 312(9):477-481.*

Two-year-old sweet chestnut seedlings were grown in constantly ventilated tunnels at ambient (350 vpm) or double (700 vpm) CO2 concentration during a full growing season. End-of-night dark respiration of aerial parts was measured in each CO2 concentration throughout the growing season. Dark respiration rate of enriched plants showed a net decrease as compared to control plants during the first half of the growing season. This difference decreased with time and became negligible in the fall. Atmospheric CO2 concentration acted instantaneously on the respiration rate: when doubled, it decreased control plant respiration and when decreased, it enhanced CO2 enriched plant respiration. The explanation of these findings remains hypothetical. It is concluded that the rise in carbon dioxide level of the atmosphere will affect the carbon balance of young trees not only through an increase in net photosynthesis during the day, but also at night by reducing respiratory losses.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, LEAF

603
Elkohen, A., H. Rouhier, and M. Mousseau. 1992. Changes in dry-weight and nitrogen partitioning induced by elevated co2 depend on soil nutrient availability in sweet chestnut (castanea-sativa mill). *Annales Des Sciences Forestieres 49(2):83-90.*

The effect of 2 levels of atmospheric carbon dioxide (ambient, ie 350 ppm, and double, ie 700 ppm) and 2 contrasting levels of mineral nutrition on dry weight, nitrogen accumulation and partitioning were examined in 2-year-old chestnut seedlings (Castanea sativa Mill), grown in pots outdoors throughout the vegetative season. Fertilization had a pronounced effect on dry weight accumulation, tree height, leaf area, and plant nitrogen content. Carbon dioxide enrichment significantly increased total biomass by about 20%, both on fertilized and on unfertilized forest soil. However, the partitioning of biomass was very different: on the unfertilized soil, only the root biomass was increased, leading to an increase in the root: shoot ratio. Contrastingly, on fertilized soil only stem biomass and diameter but not height were increased. Carbon dioxide enrichment significantly reduced the nitrogen concentration in all organs, irrespective of the nutrient availability. However, the biomass increase made up for this reduction in such a way that the total nitrogen pool per tree remained unchanged.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, FORESTS, GROWTH, PLANTS, QUERCUS-ALBA, ROOT, SEEDLINGS

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Elkohen, A., L. Venet, and M. Mousseau. 1993. Growth and photosynthesis of 2 deciduous forest species at elevated carbon-dioxide. *Functional Ecology 7(4):480-486.*

1. Two-year-old sweet chestnut (Castanea sativa) and beech (Fagus sylvatica) seedlings were grown in large pots of forest soil, at ambient (+/-350 mul l-1) and double (700 mul l-1) atmospheric CO2 Concentration in constantly ventilated.mini- green-houses during an entire growing season. 2. CO2 enrichment caused very different changes in these two temperate deciduous species. A 20% dry weight enhancement was obtained for sweet chestnut, and a 60% enhancement in beech. This greater effect of elevated CO2 in beech was the result of a significant increase of net photosynthesis of the seedlings occurring during the whole season. However, in sweet chestnut, this increase in photosynthesis lasted only a few weeks and then an acclimation process took place. 3. No effect of increased CO2 could be found on sweet chestnut leaf area or leaf number, while a significant effect was found with beech, in which total leaf area per plant increased, owing to a greater number of growth flushes, of progressively larger leaves. 4. The partitioning of the biomass increase due to elevated CO2 was very different in the two species. All additional dry matter was allocated to the roots in sweet chestnut, while it was partitioned equally amongst all organs of the beech seedling. 5. The reactions to elevated CO2 of different tree species is discussed in relation to their specific growth strategy.

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Ellert, B.H., and H.H. Janzen. 1999. Short-term influence of tillage on CO2 fluxes from a semi-arid soil on the Canadian Prairies. *Soil & Tillage Research 50(1):21-32.*

The flux of CO2 from soil determines the extent to which carbon (C) deposited as plant litter is retained in the soil. Retention of soil C is beneficial for soil physical, chemical and biological properties, and is essential if soils are to be used as a repository of C to mitigate atmospheric CO2 increases. Although tillage is assumed to have a major influence on soil C retention, the extent to which tillage enhances the transfer of soil C to the atmosphere is uncertain. We assessed the short-term (50 h) influence of tillage on CO2 fluxes from Chernozemic soils under a two-year wheat (Triticum aestivum L.)-summerfallow rotation in a semi-arid region of the Canadian Prairie, The tillage effect and its persistence were assessed by using a portable CO2 analyzer to record several temporal series of CO2 fluxes, along undisturbed and tilled transects, at successive time intervals (from -0.5 to 50 h) after a single pass with a heavy-duty cultivator. Immediately after tillage, CO2 fluxes along the tilled transects increased from 2 to 4-fold above pre-tillage fluxes, but the increases were short-lived and fluxes along undisturbed and tilled transects were again similar within 24 h of cultivation. Total amounts of CO2 released by a tillage operation were quantified by: 1. linear interpolations among successive fluxes along tilled and undisturbed transects, and 2. by fitting a model to successive differences between fluxes along the transects. Both methods estimated the amounts of tillage-susceptible CO2 to be in the range of 3.6-7.2 kg C ha(-1). The

tillage-induced flush of CO2 was attributed mainly to enhanced transport of CO2 already in the soil, but enhanced production of CO2 by heterotrophic soil organisms also may have contributed to the flush. Regardless of the sources of CO2 released by single tillage operations, amounts of tillage-susceptible soil C were minor; even 10 passes with a cultivator would account for less than 5% of annual soil CO2 emissions or crop residue production in these cropping systems. Our study suggested that the short- term influence of tillage on the transfer of soil C to atmospheric CO2 is small under semi-arid conditions like those in southern Alberta, Canada.

KEYWORDS: CARBON-DIOXIDE FLUX, COVER, CROPPING SYSTEMS, EVOLUTION, LIGHT FRACTION, MICROORGANISMS, ORGANIC-MATTER, RESPIRATION

606

Ellis, R.H., P.Q. Craufurd, R.J. Summerfield, and E.H. Roberts. 1995. Linear relations between carbon-dioxide concentration and rate - of development towards flowering in sorghum, cowpea and soybean. *Annals of Botany 75(2):193-198.*

Negative linear relations were detected ($P < 0.005$) between the rate of progress from sowing to panicle initiation and CO2 concentration (210-720 mu mol CO2 mol(-1) air) for two genotypes of sorghum [Sorghum bicolor (L.) Moench]. Relations between CO2 concentration and the rate of progress from sewing to first flowering were also negative in soyabean [Glycine max (L). Merrill] ($P < 0.025$), but positive in cowpea [Vigna unguiculata (L.) Walp.] ($P < 0.025$), albeit that in both grain legumes sensitivity was much less than in sorghum. Thus CO2 elevation does not delay flowering in all short-day species. The considerable effect of CO2 concentration on times to panicle initiation resulted in large differences among the sorghum plants at this developmental stage; with increase in CO2 concentration, plants were taller with slightly more leaves and more pronounced apical extension. At the same time after sowing however, sorghum plants were heavier ($P < 0.05$) at 210 than at 360 mu mol CO2 mol(-1) air. In contrast, relations between the dry masses of the soyabean and cowpea plants and CO2 concentration were positive and curvilinear ($P < 0.05$). It is suggested that the impact of global environmental change could be severe for sorghum production in the semi-arid tropics.

KEYWORDS: BICOLOR, CLIMATE, CO2- ENRICHMENT, ELEVATED CO2, FLORAL INITIATION, GROWTH, TEMPERATURE, VIGNA UNGUICULATA L, YIELD

607

Ellsworth, D.S. 1999. CO2 enrichment in a maturing pine forest: are CO2 exchange and water status in the canopy affected? *Plant, Cell and Environment 22(5):461-472.*

Elevated CO2 is expected to reduce forest water use as a result of CO2-induced stomatal closure, which has implications for ecosystem-scale phenomena controlled by water availability. Leaf-level CO2 and H2O exchange responses and plant and soil water relations were examined in a maturing loblolly pine (Pinus taeda L,) stand in a free-air CO2 enrichment (FACE) experiment in North Carolina, USA to test if these parameters were affected by elevated CO2, Current-year foliage in the canopy was continuously exposed to elevated CO2 (ambient CO2 + 200 mu mol mol(-1)) in free-air during needle growth and development for lip to 400 d. Photosynthesis in upper canopy foliage was stimulated by 50-60% by elevated CO2 compared with ambient controls. This enhancement was similar in current-year, ambient-grown foliage temporarily measured at elevated CO2 compared with long-term elevated CO2 grown foliage, Significant photosynthetic enhancement by CO2 was maintained over a range of conditions except during peak drought. There was no evidence of water savings in elevated CO2 plots in FACE compared to ambient plots under drought and non-drought conditions. This was supported by evidence from three independent measures. First, stomatal conductance was not significantly different in elevated CO2 versus ambient trees of P. taeda, Calculations of time-integrated c(i)/c(a) ratios from analysis of foliar delta(13)C showed that these ratios were maintained in foliage under elevated CO2. Second, soil moisture was not significantly different between ambient and elevated CO2 plots during drought. Third, pre-dawn and mid-day leaf water potentials were also unaffected by the seasonal CO2 exposure, as were tissue osmotic potentials and turgor loss points. Together the results strongly support the hypothesis that maturing P. taeda trees have low stomatal responsiveness to elevated CO2. Elevated CO2 effects on water relations in loblolly pine-dominated forest ecosystems may be absent or small apart from those mediated by leaf area. Large photosynthetic enhancements in the upper canopy of P. taeda by elevated CO2 indicate that this maturing forest may have a large carbon sequestration capacity with limiting water supply.

KEYWORDS: DROUGHT, ELEVATED CARBON-DIOXIDE, GROWTH, INCREASING ATMOSPHERIC CO2, LEAF GAS-EXCHANGE, LOBLOLLY-PINE, NET PHOTOSYNTHESIS, RESPONSES, SEEDLINGS, STOMATAL CONDUCTANCE

608

Ellsworth, D.S., R. Oren, C. Huang, N. Phillips, and G.R. Hendrey. 1995. Leaf and canopy responses to elevated co2 in a pine forest under free-air co2 enrichment. *Oecologia 104(2):139-146.*

Physiological responses to elevated CO2 at the leaf and canopy- level were studied in an intact pine (Pinus taeda) forest ecosystem exposed to elevated CO2 using a free-air CO2 enrichment (FACE) technique. Normalized canopy water-use of trees exposed to elevated CO2 over an 8-day exposure period was similar to that of trees exposed to current ambient CO2 under sunny conditions. During a portion of the exposure period when sky conditions were cloudy, CO2-exposed trees showed minor (less than or equal to 7%) but significant reductions in relative sap flux density compared to trees under ambient CO2 conditions. Short-term (minutes) direct stomatal responses to elevated CO2 were also relatively weak (approximate to 5% reduction in stomatal aperture in response to high CO2 concentrations). We observed no evidence of adjustment in stomatal conductance in foliage grown under elevated CO2 for nearly 80 days compared to foliage grown under current ambient CO2 so intrinsic leaf water-use efficiency at elevated CO2 was enhanced primarily by direct responses of photosynthesis to CO2. We did not detect statistical differences in parameters from photosynthetic responses to intercellular CO2 (A(net)-C-i curves) for Pinus taeda foliage grown under elevated CO2 (550 mu mol mol(-1)) for 50-80 days compared to those for foliage grown under current ambient CO2 from similar-sized reference trees nearby. In both cases, leaf net photosynthetic rate at 550 mu mol mol(-1) CO2 was enhanced by approximately 65% compared to the rate at ambient CO2 (350 mu mol mol(-1)). A similar level of enhancement under elevated CO2 was observed for daily photosynthesis under field conditions on a sunny day. While enhancement of photosynthesis by elevated CO2 during the study period appears to be primarily attributable to direct photosynthetic responses to CO2 in the pine forest, longer-term CO2 responses and feedbacks remain to be evaluated.

KEYWORDS: AREA, CARBON-DIOXIDE ENRICHMENT, CONDUCTANCE, GAS-EXCHANGE, GROWTH, PHOTOSYNTHESIS, RISING CO2, SEEDLINGS, TREES, WATER-STRESS

609

Ellsworth, D.S., R. Oren, C. Huang, N. Phillips, and G.R. Hendrey. 1996. Leaf and canopy responses to elevated CO2 in a pine forest under free-air CO2 enrichment (vol 104, pg 139, 1995). *Oecologia*

106(3):416.

610
ElMaayar, M., B. Singh, P. Andre, C.R. Bryant, and J.P. Thouez. 1997. The effects of climatic change and CO2 fertilisation on agriculture in Quebec. *Agricultural and Forest Meteorology 85(3-4):193-208.*

The agricultural sector forms an important part of the economy of Quebec. The risk of global increase of atmospheric CO2 concentration and associated climatic change and their influence on agriculture need to be assessed. Although many studies have been conducted on the effect of climate change on agriculture in various parts of the world, fewer studies have focused on the combined effects of climatic change and CO2 fertilisation on agriculture. This study, using the outputs of the Canadian Climate Centre (CCC) general circulation model coupled with the Food and Agricultural Organization (FAG) crop model, attempts to assess the response of agricultural productivity to both direct (or fertilisation) and indirect (or climatic) effects of increased atmospheric CO2 concentration, for a variety of crops including C-3 and C-4 cereals, legumes, vegetables and special crops grown in Quebec. It appears that C-4 cereal (corn and sorghum) crops would benefit by climate change but would be least favoured by CO2 fertilisation effect. (C) 1997 Published by Elsevier Science B.V.

KEYWORDS: CARBON DIOXIDE, CROP, DRY-WEIGHT, ENRICHMENT, GROWTH, SCENARIO, TEMPERATURE, UNITED-STATES, WHEAT, YIELD

611
Elmeskaoui, A., J.P. Damont, M.J. Poulin, Y. Piche, and Y. Desjardins. 1995. A tripartite culture system for endomycorrhizal inoculation of micropropagated strawberry plantlets in-vitro. *Mycorrhiza 5(5):313-319.*

The objective of the current investigation was to develop a reliable method to obtain vesicular-arbuscular mycorrhizae (VAM) in micropropagated plantlets and to determine their influence on growth, An in vitro system for culturing the VA mycorrhizal fungus Glomus intraradices with Ri T-DNA- transformed carrot roots or nontransformed tomato roots was used in this study as a potential active source of inoculum for the colonization of micropropagated plantlets. After root induction, micropropagated plantlets grown on cellulose plugs (sorbarod) were placed in contact with the primary mycorrhizae in growth chambers enriched with 5000 ppm CO2 and fed with a minimal medium. After 20 days of tripartite culture, all plantlets placed in contact with the primary symbiosis were colonized by the VAM fungus. As inoculum source, 30-day-old VA mycorrhizal transformed carrot roots had a substantially higher infection potential than 5-, 10- or 20-day-old VAM. Colonized plantlets had more extensive root systems and better shoot growth than control plants. The VAM symbiosis reduced the plantlet osmotic potential. This response may be a useful pre- adaptation for plantlets during transfer to the acclimatization stage.

KEYWORDS: ASPARAGUS, FUNGI, GROWTH, INFECTION, INVITRO, PROPAGATION, SYMBIOSIS, TRANSPORT, VA-MYCORRHIZAL, VESICULAR-ARBUSCULAR MYCORRHIZAE

612
Endo, M., and I. Ikushima. 1997. Effects of CO2 enrichment on yields and preservability of cut flowers in Phalaenopsis. *Journal of the Japanese Society for Horticultural Science 66(1):169-174.*

The effect of CO2 enrichment on Phalaenopsis cut flower production was examined for 30 months throughout five flowering cycles. The plant was cultured in three greenhouses with different CO2 levels of (A) : control, daily mean of ambient air = 438 ppm; (B) : 700 ppm; and (C) : 1000 ppm. 1. The fresh weight of cut flowers, the numbers of inflorescence and flowers per 20 plants varied, depending on the CO2 concentration for each flowering cycle. 2. The preservability (vase life) of cut flowers always improved under higher CO2 levels. Organic acid contents of plants were also higher under higher CO2 levels. The malic acid content in the flowers was higher than in the younger leaf and flower stalk at 1:00 PM and 10:00 PM; and it was also higher in the younger leaf than in the flower stalk at 10:00 PM, but lower at 1:00 PM. The pH value of plants was always lower at higher ambient CO2 levels, and lower in the younger leaf and flower stalk at 1:00 PM than at 10:00 PM, wheras at those same times the sugar content at the higher ambient CO2 levels reached its maximum.

KEYWORDS: LEAF, PHOTOSYNTHESIS

613
Endo, M., and I. Ikusima. 1997. Effects of CO2 enrichment by complete combustion of liquid petroleum gas on growth of Doritaenopsis. *Journal of the Japanese Society for Horticultural Science 66(1):163-168.*

The effects of increasing ambient CO2 levels on the growth of developing Doritaenopsis plants in a greenhouse were studied for 840 days. Leaf area, dry weight, and content of total carbon and total nitrogen in dry matter were measured every three months, and the time course of the relative growth rate (RGR) was investigated. Leaf area and dry weight increased with increasing CO2 concentration from 438 ppm to 946 ppm in the atmosphere. In an initial growth stage when plants were transplanted from flasks to pots, RGR increased as the CO2 level increased. RGR during a later vegetative growth stage was not affected by the CO2 concentration, and its value was 0.006/day. The value of RGR was less than that of the other C- 3, C-4, and CAM plants.

KEYWORDS: LIGHT, PLANTS, RESPONSES

614
Enoch, H.Z., and J.M. Olesen. 1993. Plant-response to irrigation with water enriched with carbon- dioxide. *New Phytologist 125(2):249-258.*

The influence of irrigation with CO2-enriched water on plant development and yield is reviewed. The reason for irrigation with CO2-enriched water was - in most cases - to increase yield. The present evaluation considers results from over a hundred studies performed since the first experiment in 1866. Special emphasis is given to the comparison of 85 experiments made by Mitscherlich in 1910 with 358 irrigation experiments made in the last 80 years. In a statistical analysis of these experiments, the measured plant parameter (often growth and/or gas exchange rates) showed a highly significant mean increase of 2.9 % in plants irrigated with CO2-enriched water as compared with control. Evidence of five mechanisms was found. The subterranean carbon dioxide concentration influences: (a) the rate of nitrification and hence of nitrogen availability; (b) the rate of weathering and pH, and hence the availability of other plant nutrients; (c) the CO2 uptake via roots into the transpiration stream, contributing to the rate of leaf photosynthesis; (d) the hormone levels in the plant; and (e) the rate of pesticide decomposition in soils. After examining the available evidence we found that (a) and (b) in some experiments are important to plant growth, since they change the physiochemical environment of the roots. On the other hand, while (c) could theoretically contribute up to 5% of plant carbon assimilation, it usually contributes less than 1%, while (d) contributes most of the observed effects of CO2-enriched water on plants. In addition, pesticide decomposition in soils can be delayed by supra- or sub-optimal CO2 concentrations.

KEYWORDS: ETHYLENE, GASEOUS CO2 TRANSPORT, GROWTH, ROOT ENVIRONMENT, SEEDLINGS, SOIL, TUBERIZATION

615

Entry, J.A., G.B. Runion, S.A. Prior, R.J. Mitchell, and H.H. Rogers. 1998. Influence of CO2 enrichment and nitrogen fertilization on tissue chemistry and carbon allocation in longleaf pine seedlings. *Plant and Soil 200(1):3-11.*

One-year old, nursery-grown longleaf pine (Pinus palustris Mill.) seedlings were grown in 45-L pots containing a coarse sandy medium and were exposed to two concentrations of atmospheric CO2 (365 or 720 mu mol(-1)) and two levels of nitrogen (N) fertility (40 or 400 kg N ha(-1) yr(-1)) within open top chambers for 20 months. At harvest, needles, stems, coarse roots, and fine roots were separated and weighed. Subsamples of each tissue were frozen in liquid N, lyophilized at -50 degrees C, and ground to pass a 0.2 mm sieve. Tissue samples were analyzed for carbon (C), N, nonpolar extractives (fats, waxes, and oils = FWO), nonstructural carbohydrates (total sugars and starch), and structural carbohydrates (cellulose, lignin, and tannins). Increased dry weights of each tissue were observed under elevated CO2 and with high N; however, main effects of CO2 were significant only on belowground tissues. The high N fertility tended to result in increased partitioning of biomass aboveground, resulting in significantly lower root to shoot ratios. Elevated CO2 did not affect biomass allocation among tissues. Both atmospheric CO2 and N fertility tended to affect concentration of C compounds in belowground, more than aboveground, tissues. Elevated CO2 resulted in lower concentrations of starch, cellulose, and lignin, but increased concentrations of FWO in root tissues. High N fertility increased the concentration of starch, cellulose, and tannins, but resulted in lower concentrations of lignin and FWO in roots. Differences between CO2 concentrations tended to occur only with high N fertility. Atmospheric CO2 did not affect allocation patterns for any compound; however the high N treatment tended to result in a lower percentage of sugars, cellulose, and lignin belowground.

KEYWORDS: ALLELOCHEMICALS, COTTON PLANTS, DIOXIDE, ELEVATED ATMOSPHERIC CO2, GROWTH, PLANT-RESPONSES, PRODUCTIVITY, RESPIRATORY RESPONSES, ROOTS, SOIL

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Epron, D., E. Dreyer, C. Picon, and J.M. Guehl. 1994. Relationship between co2-dependent o-2 evolution and photosystem-II activity in oak (quercus-petraea) trees grown in the field and in seedlings grown in ambient or elevated co2. *Tree Physiology 14(7-9):725-733.*

The light-response of the apparent quantum yield of photosynthetic O2 evolution (PHI(O2)) under non- photorespiratory conditions was measured together with the photochemical efficiency Of PS II (DELTAF/F(m)'), the photochemical efficiency of open PS II reaction centers (F(v)'/F(m)') and the photochemical fluorescence quenching (q(p)) of leaf disks punched from oak leaves of seedlings grown in ambient (350 mumol mol-1) or elevated (700 mumol mol- 1) CO2 in a greenhouse, and from sunlit leaves of mature oak trees (Quercus petraea (Matt.) Liebl.). There were marked differences between seedlings and trees. In seedlings, CO2 concentration during growth did not modify the light response of photosynthesis or PS II activity. There was a single linear relationship between PHI(O2) and DELTAF/F(m)' in seedling leaves that was independent of the CO2 concentration imposed during growth. In contrast, this relationship was curvilinear in sunlit leaves of adult trees. In seedling leaves, the decrease in q(p) (i.e., the proportion of open PS II reaction centers) largely accounted for the decrease in DELTAF/F(m)', whereas the decrease in DELTAF/F(m)' in sunlit leaves of mature oak trees was dependent on both q(p) and F(v)'/F(m)'.

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Epron, D., D. Godard, G. Cornic, and B. Genty. 1995. Limitation of net co2 assimilation rate by internal resistances to co2 transfer in the leaves of 2 tree species (fagus- sylvatica L and castanea-sativa mill). *Plant, Cell and Environment 18(1):43-51.*

Using a combination of gas-exchange and chlorophyll fluorescence measurements, low apparent CO2/O-2 specificity factors (1300 mol mol(-1)) were estimated for the leaves of two deciduous tree species (Fagus sylvatica and Castanea sativa), These low values contrasted with those estimated for two herbaceous species and were ascribed to a drop in the CO2 mole fraction between the intercellular airspace (C-i) and the catalytic site of Rubisco (C-c) due to internal resistances to CO2 transfer, C-c was calculated assuming a specificity of Rubisco value of 2560 mol mol(-1). The drop between C-i and C-c was used to calculate the internal conductance for CO2 (g(i)), A good correlation between mean values of net CO2 assimilation rate (A) and g(i) was observed within a set of data obtained using 13 woody plant species, including our own data, We report that the relative limitation of A, which can be ascribed to internal resistances to CO2 transfer, was 24-30%, High internal resistances to CO2 transfer may explain the low apparent maximal rates of carboxylation and electron transport of some woody plant species calculated from A/C-i curves.

KEYWORDS: CHLOROPHYLL FLUORESCENCE, ELEVATED CO2, GAS-EXCHANGE, MESOPHYLL CONDUCTANCE, PHOTOSYNTHETIC ELECTRON-TRANSPORT, PLANTS, RESPIRATION, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, SPECIFICITY FACTOR, STOMATAL CONDUCTANCE

618

Epron, D., R. Liozon, and M. Mousseau. 1996. Effects of elevated CO2 concentration on leaf characteristics and photosynthetic capacity of beech (Fagus sylvatica) during the growing season. *Tree Physiology 16(4):425-432.*

Two-year-old beech (Fagus sylvatica L.) saplings were planted directly in the ground at high density (100 per m(2)), in an experimental design that realistically mimicked field conditions, and grown for two years in air containing CO2 at either ambient or an elevated (ambient + 350 ppm) concentration. Plant dry mass and leaf area were increased by a two-year exposure to elevated CO2. The saplings produced physiologically distinct types of sun leaves associated with the first and second growth flushes. Leaves of the second flush had a higher leaf mass per unit area and less chlorophyll per unit area, per unit dry mass and per unit nitrogen than leaves of the first flush. Chlorophyll content expressed per unit nitrogen decreased over time in plants grown in elevated CO2, which suggests that, in elevated CO2, less nitrogen was invested in machinery of the photosynthetic light reactions. In early summer, the photosynthetic capacity measured at saturating irradiance and CO2 was slightly but not significantly higher in saplings grown in elevated CO2 than in saplings grown in ambient CO2. However, a decrease in photosynthetic capacity was observed after July in leaves of saplings grown in CO2-enriched air. The results demonstrate that photosynthetic acclimation to elevated CO2 can occur in field-grown saplings in late summer, at the time of growth cessation.

KEYWORDS: ACCLIMATION, CARBON DIOXIDE, CHLOROPHYLL, ENRICHMENT, GAS-EXCHANGE, GROWTH, LEAVES, RESPONSES, SEEDLINGS, SHADE PLANTS

619

Erhardt, A., and H.P. Rusterholz. 1997. Effects of elevated CO2 on flowering phenology and nectar production. *Acta Oecologica-International Journal of Ecology 18(3):249-253.*

Effects of elevated CO2 on flowering phenology and nectar production were studied in five important nectar plants of calcareous grasslands, i.e. Lotus corniculatus, Trifolium pratense, Betonica officinalis, Scabiosa columbaria ia and Centaurea jacea. Glasshouse experiments showed that flowering probability was significantly enhanced in C. jacea. B. officinalis flowered earlier and L. corniculatus produced more flowers under elevated CO2. In contrast, the number of flowers decreased in T. pratense. The amount of nectar produced per flower was not affected in the investigated legumes (T. pratense, L. corniculatus), but was significantly reduced in the other forbs. Elevated CO2 did not significantly affect nectarsugar concentration and sugar composition. However, S. columbaria and C: jacea produced significantly less total sugar per flower under elevated CO2. The nectar amino acid concentration remained unaffected in all investigated plant species whereas the total of amino acids produced per flower was significantly reduced in all nan-legumes. In addition, the amino acid composition changed significantly in all investigated species except for C. jacea. The observed effects are unexpected and are a potential threat to flower visitors such as most butterflies which have no alternative food resources except nectar. Changes in nectar production due to elevated CO2 could also generally have detrimental effects on the interactions of flowers and their pollinators.

620

Erickson, D.J. 1999. Nitrogen deposition, terrestrial carbon uptake and changes in the seasonal cycle of atmospheric CO2. *Geophysical Research Letters 26(21):3313-3316.*

Observational evidence indicates an increasing trend in the amplitude of the seasonal cycle of atmospheric CO2 over the last several decades. Here, the influence of nitrogen deposition on the seasonal cycle of atmospheric CO2 is investigated using a global carbon cycle model embedded in a 3- D general circulation model. We employ a recently published estimate of the enhancement of carbon dioxide uptake induced by the atmospheric deposition of NOy and NHx. We partition the carbon sink related to nitrogen deposition over the seasonal cycle of CO2 uptake. The modeled increase in the amplitude of the seasonal cycle of CO2 in the Northern Hemisphere related to the simulated nitrogen deposition alone is 25%-50% of observed. At Mauna Loa the increased amplitude in the CO2 seasonal cycle due to nitrogen deposition is 50-90% of that observed. The subtle interaction between 3-D atmospheric transport, atmospheric nitrogen deposition, and seasonal CO2 uptake results in significant changes in the amplitude of the seasonal cycle of atmospheric CO2. The magnitude of these nitrogen deposition-induced changes in the atmospheric behavior of CO2 is comparable to other processes that are thought to influence global carbon cycle dynamics.

KEYWORDS: DIOXIDE, EXCHANGE, GROWTH, MODEL, SINK

621

Ericsson, T. 1995. Growth and shoot - root ratio of seedlings in relation to nutrient availability. *Plant and Soil 169:205-214.*

The influence of mineral nutrient availability, light intensity and CO2 on growth and shoot:root ratio in young plants is reviewed. Special emphasis in this evaluation is given to data from laboratory experiments with small Betula pendula plants, in which the concept of steady-state nutrition has been applied. Three distinctly different dry matter allocation patterns were observed when growth was limited by the availability of mineral nutrients: 1, Root growth was favoured when N, P or S were the major growth constraints. 2, The opposite pattern obtained when K, Mg and Mn restricted growth. 3, Shortage of Ca, Fe and Zn had almost no effect on the shoot:root ratio. The light regime had no effect on dry matter allocation except at very low photon flux densities (< 6.5 mol m(-2) day(-1)), in which a small decrease in the root fraction was observed. Shortage of CO2 on the other hand, strongly decreased root development, while an increase of the atmospheric CO2 concentration had no influence on dry matter partitioning. An increased allocation of dry matter to below- ground parts was associated with an increased amount of starch in the tissues. Depletion of the carbohydrate stores occurred under all conditions in which root development was inhibited. It is concluded that the internal balance between labile nitrogen and carbon in the root and the shoot system determines how dry matter is being partitioned in the plant. The consistency of this statement with literature data and existing models for shoot:root regulation is examined.

KEYWORDS: ASSIMILATION, BETULA-PENDULA ROTH, BIRCH SEEDLINGS, ELEVATED CO2, NITROGEN STRESS, PHOTON FLUX-DENSITY, PHOTOSYNTHESIS, PLANT NUTRITION, TRANSLOCATION, WHEAT TRITICUM- AESTIVUM

622

Ershova, A.N., and V.A. Khripach. 1996. Effect of epibrassinolide on lipid peroxidation in Pisum sativum at normal aeration and under oxygen deficiency. *Russian Journal of Plant Physiology 43(6):750-752.*

The effect of epibrassinolide on oxidative lipid degradation in pea seedlings was studied at normal aeration and in oxygen- deprived and CO2-enriched media. The content of various products of lipid peroxidation (POL), including the primary derivatives (conjugated dienoic acids) and end products (malonyl dialdehyde, MDA), was shown to decrease in seedlings treated with epibrassinolide (10 mg/l). Epibrassinolide inhibited POL in pea seedlings more strongly than kinetin. These effects became even more pronounced in plants under hypoxia or in the CO2-enriched medium. The content of conjugated dienes declined by 13 and 21% at hypoxia and in the CO2-medium compared to their content in air-grown seedlings, whereas the content of MDA was 38 and 26% below the level in the untreated plants, respectively. We presume that as a protector, epibrassinolide can inhibit the oxidative degradation of lipids in biological membranes and prevent the disruption of membrane structures. Thus it increases the tolerance of plants to deleterious factors.

623

Esler, K.J., P.W. Rundel, and P. Vorster. 1999. Biogeography of prostrate-leaved geophytes in semi-arid South Africa: hypotheses on functionality. *Plant Ecology 142(1-2):105-120.*

Nowhere is the species diversity of geophytes greater than in the five mediterranean-climate ecosystems of the world. Of these, the Cape mediterranean zone of South Africa is the most speciose. While the relative diversity and importance of geophytes of all of the other four mediterranean regions of the world drops off sharply as one moves into adjacent winter- rainfall desert regions, geophytes in the semi-arid to arid Succulent Karoo (including Namaqualand) remain a very important component of the flora, both in terms of abundance and diversity (comprising 13 to 29% of the regional floras in this region). Apart from species richness, there are also a number of interesting geophyte growth forms in this region. One unusual growth form is geophytes with flattened leaves that lie prostrate on the soil surface. At least eight families (Amaryllidaceae, Colchicaceae, Eriospermaceae, Geraniaceae, Hyacinthaceae, Iridaceae, Orchidaceae and Oxalidaceae) exhibit this growth form. While this growth form is relatively common in many geophyte lineages in the Succulent Karoo biome and the Cape mediterranean zone (Fynbos biome), and occurs infrequently through the summer-rainfall temperate regions of Africa, it is virtually absent in other regions worldwide. A null hypothesis is that the prostrate leaved trait is a neutral characteristic, however biogeographical data do not support this. A neutral trait would be unlikely to show such a clear

pattern of distribution. Several alternative hypotheses on the adaptive significance of this growth form are discussed. These include: avoidance of herbivory, reduction in competition from neighbors, creation of a CO2 enriched environment below the leaves, reduction of water loss around the roots, reduction of water loss through transpiration, precipitation of dew on the leaves and maintenance of optimal leaf temperatures for growth.

KEYWORDS: ALLOCATION, BIOMASS, FLORA, LOWLAND COASTAL FYNBOS, SUBSPECIES PUBESCENS

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Estiarte, M., J. Penuelas, B.A. Kimball, D.L. Hendrix, P.J. Pinter, G.W. Wall, R.L. LaMorte, and D.J. Hunsaker. 1999. Free-air CO2 enrichment of wheat: leaf flavonoid concentration throughout the growth cycle. *Physiologia Plantarum 105(3):423-433.*

To test the predictions that plants will have a larger flavonoid concentration in a future world with a CO2-enriched atmosphere, wheat (Triticum aestivum L. cv. Yecora Rojo) was grown in a field experiment using FACE (free-air CO2 enrichment) technology under two levels of atmospheric CO2 concentration: ambient (370 pmol mol(-1)) and enriched (550 pmol mol(-1)), and under two levels of irrigation: well-watered (100% replacement of potential evapotranspiration) and half-watered. We also studied the effects of CO2 on the concentration of total non-structural carbohydrates (TNC) and nitrogen (N), two parameters hypothesized to be linked to flavonoid metabolism. Throughout the growth cycle the concentration of isoorientin, the most abundant flavonoid, decreased by 62% (from an average of 12.5 mg g(-1) on day of year (DOY) 41 to an average of 4.8 mg g(-1) on DOY 123), whereas the concentration of tricin, another characteristic flavone, increased by two orders of magnitude (from an average of 0.007 mg g(-1) of isoorientin equivalents on DOY 41 to an average of 0.6 mg g(-1) of isoorientin equivalents on DIOY 123). Although flavonoid concentration was dependent on growth stage, the effects of treatments on phenology did not invalidate the comparisons between treatments. CO2-enriched plants had higher flavonoid concentrations (14% more isoorientin, an average of 7.0 mg g(-1) for ambient CO2 vs an average of 8.0 mg g(-1) for enriched CO2), higher TNC concentrations and lower N concentrations in upper canopy leaves throughout the growth cycle. Well-irrigated plants had higher flavonoid concentrations (11% more isoorientin, an average of 7.1 mg g(-1) for half watered vs an average of 7.9 mg g(-1) for well-watered) throughout the growth cycle, whereas the effect of irrigation treatments on TNC and N was more variable. These results are in accordance with the hypotheses that higher carbon availability promoted by CO2-enrichment provides carbon that can be invested in carbon-based secondary compounds such as flavonoids. The rise in atmospheric CO2 may thus indirectly affect wheat-pest relations, alter the pathogen predisposition and improve the UV-B protection by changing flavonoid concentrations.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CHEMICAL-COMPOSITION, ELEVATED CO2, LEAVES, N-AVAILABILITY, NITROGEN, NUTRIENT BALANCE, SOURCE-SINK RELATIONS, UV-B, WATER-USE

625

Estiarte, M., J. Penuelas, B.A. Kimball, S.B. Idso, R.L. Lamorte, P.J. Pinter, G.W. Wall, and R.L. Garcia. 1994. Elevated co2 effects on stomatal density of wheat and sour orange trees. *Journal of Experimental Botany 45(280):1665-1668.*

No significant differences were found in stomatal densities or stomatal indices of wheat or sour orange trees grown at high CO2 concentrations in two different CO2 enrichment systems (Free-Air CO2 enrichment for wheat and Open-Top Chambers for orange trees). These results are in accordance with most of the previous results obtained in short-term experimental studies which suggest that plants do not acclimate to increasing CO2 concentration by changing stomatal density within a single generation.

KEYWORDS: ANATOMY, ENRICHMENT, GROWTH

626

Ewert, F., and H. Pleijel. 1999. Phenological development, leaf emergence, tillering and leaf area index, and duration of spring wheat across Europe in response to CO2 and ozone. *European Journal of Agronomy 10(3-4):171-184.*

Phenological development, leaf emergence, tillering and leaf area index (LAI), and duration (LAD) of spring wheat cv. Minaret, grown in open-top chambers at different sites throughout Europe for up to 3 years at each site, were investigated in response to elevated CO2 (ambient CO2 x2) and ozone (ambient ozone x1.5) concentrations. Phenological development varied among experiments and was partly explained by differences in temperature among sites and years. There was a weak positive relationship between the thermal rate of development and the mean daylength for the period from emergence to anthesis. Main stems produced on average 7.7 leaves with little variation among experiments. Variation was higher for the thermal rate of leaf emergence, which was partly explained by differences in the rate of change of daylength at plant emergence among seasons. Phenological development, rate of leaf emergence and final leaf number were not affected by CO2 and ozone exposure. Responses of tillering and LAI to CO2 and ozone exposure were significant only in some experiments. However, the direction of responses was consistent for most experiments. The number of tillers and ears per plant, respectively, was increased as a result of CO2 enrichment by about 13% at the beginning of stem elongation (DC31), at anthesis and at maturity. Exposure to ozone had no effect on tillering. LAI was increased as a result of CO2 elevation by about 11% at DC31 and by about 14% at anthesis. Ozone exposure reduced LAI at anthesis by about 9%. No such effect was observed at DC31. There were very few interactive effects of CO2 and ozone on tillering and LAI. Variations in tillering and LAI, and their responses to CO2 and ozone exposure, were partly explained by single linear relationships considering differences in plant density, tiller density and the duration of developmental phases among experiments. Consideration of temperature and incident photosynthetically active radiation in this analysis did not reduce the unexplained variation. There was a negative effect of ozone exposure on leaf area duration at most sites. Direct effects of elevated CO2 concentration on leaf senescence, both positive and negative, were observed in some experiments. There was evidence in several experiments that elevated CO2 concentration ameliorated the negative effect of ozone on leaf area duration. It was concluded from these results that an analysis of the interactive effects of climate, CO2 and ozone on canopy development requires reference to the physiological processes involved.

KEYWORDS: CARBON-DIOXIDE ENRICHMENT, CROPS, ELEVATED CO2, GRAIN QUALITY, GROWTH, TEMPERATURE, TOP FIELD CHAMBERS, TRITICUM-AESTIVUM L, WINTER-WHEAT, YIELD COMPONENTS

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Ewert, F., M. van Oijen, and J.R. Porter. 1999. Simulation of growth and development processes of spring wheat in response to CO2 and ozone for different sites and years in Europe using mechanistic crop simulation models. *European Journal of Agronomy 10(3-4):231-247.*

The response of crop growth and yield to CO2 and ozone is known to depend on climatic conditions and is difficult to quantify due to the complexity of the processes involved. Two modified mechanistic crop

simulation models (AFRCWHEAT2-O3 and LINTULCC), which differ in the levels of mechanistic detail, were used to simulate the effects of CO2 (ambient, ambient x2) and ozone (ambient, ambient x1.5) on growth and developmental processes of spring wheat in response to climatic conditions. Simulations were analysed using data from the ESPACE-wheat project in which spring wheat cv. Minaret was grown in open-top chambers at nine sites throughout Europe and for up to 3 years at each site. Both models closely predicted phenological development and the average measured biomass at maturity. However, intermediate growth variables such as biomass and leaf area index (LAI) at anthesis, seasonal accumulated photosynthetically active radiation intercepted by the crop (Sigma IPAR), the average seasonal light use efficiency (LUE) and the light saturated rate of flag leaf photosynthesis (A(sat)) were predicted differently and less accurately by the two models. The effect of CO2 on the final biomass was underestimated by AFRCWHEAT2-O3 due to its poor simulation of the effect of CO2 on tillering, and LAI.LINTULCC overestimated the response of biomass production to changes in CO2 level due to an overprediction of the effect of CO2 on LUE. The measured effect of ozone exposure on final biomass was predicted closely by the two models. The models also simulated the observed interactive effect of CO2 and ozone on biomass production. However, the effects of ozone on LAI, Sigma IPAR and A(sat) were simulated differently by the models and less accurately with LINTULCC for the ozone effects on LAI and Sigma IPAR. Predictions of the variation between sites and years of growth and development parameters and of their responses to CO2 and ozone were poor for both AFRCWHEAT2-O3 and LINTULCC. It was concluded that other factors than those considered in the models such as chamber design and soil properties may have affected the growth and development of cv. Minaret. An analysis of the relationships between growth parameters calculated from the simulations supported this conclusion. In order to apply models for global change impact assessment studies, the difficulties in simulating biomass production in response to CO2 need to be considered. We suggest that the simulation of leaf area dynamics deserves particular attention in this regard.

KEYWORDS: AIR, CLIMATE, EXPOSURE, OPEN-TOP CHAMBERS, PHOTOSYNTHESIS, PLANTS, PRODUCTIVITY, TRITICUM-AESTIVUM, WINTER-WHEAT, YIELD

628
Fajer, E.D. 1989. The effects of enriched CO2 atmospheres on plant-insect herbivore interactions- growth-responses of larvae of the specialist butterfly, Junonia coenia (lepidoptera, nymphalidae). *Oecologia 81(4):514-520.*

629
Fajer, E.D., M.D. Bowers, and F.A. Bazzaz. 1991. The effects of enriched CO2 atmospheres on the buckeye butterfly, Junonia coenia. *Ecology 72(2):751-754.*

KEYWORDS: CARBON-DIOXIDE ATMOSPHERES, CLIMATE, LEPIDOPTERA, NOCTUIDAE

630
Fajer, E.D., M.D. Bowers, and F.A. Bazzaz. 1991. Performance and allocation patterns of the perennial herb, Plantago lanceolata, in response to simulated herbivory and elevated CO2 environments. *Oecologia 87(1):37-42.*

We tested the prediction that plants grown in elevated CO2 environments are better able to compensate for biomass lost to herbivory than plants grown in ambient CO2 environments. The herbaceous perennial Plantago lanceolata (Plantaginaceae) was grown in either near ambient (380 ppm) or enriched (700 ppm) CO2 atmospheres, and then after 4 weeks, plants experienced either 1) no defoliation; 2) every fourth leaf removed by cutting; or 3) every other leaf removed by cutting. Plants were harvested at week 13 (9 weeks after simulated herbivory treatments). Vegetative and reproductive weights were compared, and seeds were counted, weighed, and germinated to assess viability. Plants grown in enriched CO2 environments had significantly greater shoot weights, leaf areas, and root weights, yet had significantly lower reproductive weights (i.e. stalks + spikes + seeds) and produced fewer seeds, than plants grown in ambient CO2 environments. Relative biomass allocation patterns further illustrated differences in plant responses to enriched CO2 atmospheres: enriched CO2-grown plants only allocated 10% of their carbon resources to reproduction whereas ambient CO2-grown plants allocated over 20%. Effects of simulated herbivory on plant performance were much less dramatic than those induced by enriched CO2 atmospheres. Leaf area removal did not reduce shoot weights or reproductive weights of plants in either CO2 treatment relative to control plants. However, plants from both CO2 treatments experienced reductions in root weights with leaf area removal, indicating that plants compensated for lost above-ground tissues, and maintained comparable levels of reproductive output and seed viability, at the expense of root growth.

KEYWORDS: GROWTH

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Fajer, E.D., M.D. Bowers, and F.A. Bazzaz. 1992. The effect of nutrients and enriched co2 environments on production of carbon-based allelochemicals in plantago - a test of the carbon nutrient balance hypothesis. *The American Naturalist 140(4):707-723.*

In a test of the carbon/nutrient (C/N) balance hypothesis, we grew the perennial herb Plantago lanceolata in different CO2 and nutrient environments and then (1) measured the total allocation to shoots, roots, and reproductive parts and (2) quantified aucubin, catalpol, and verbascoside contents of replicate plants of six genotypes. Plants grown under low- nutrient conditions do have higher concentrations of carbon-based allelochemicals than plants grown under high-nutrient conditions. However, in contrast to the C/N balance hypothesis, plants grown in elevated (700-mu-L.L-1) CO2 conditions had similar, or lower, concentrations of carbon-based allelochemicals than plants grown in ambient (350-mu-L.L-1) CO2 conditions. We suggest that augmented substrate concentrations (i.e., excess carbohydrates) are a necessary but insufficient trigger for increased secondary metabolism; instead, hormonal and/or direct physical cues (such as light) may be essential to synthesize or activate the appropriate enzyme systems. Moreover, although plant genotype significantly affected plant growth, reproduction, and chemistry, we never observed significant genotype-by-CO2 interactions for these factors, which suggests that changing CO2 environments may not improve the fitness of certain genotypes over others.

KEYWORDS: CHEMICAL DEFENSE, DIOXIDE ATMOSPHERES, EXPERIMENTAL ECOLOGICAL GENETICS, HETEROTHECA-SUBAXILLARIS, INSECT HERBIVORE INTERACTIONS, JUNONIA-COENIA, LANCEOLATA L, LIMITING CONDITIONS, REPRODUCTIVE EFFORT, VOLATILE LEAF TERPENES

632
Falge, E., R.J. Ryel, M. Alsheimer, and J.D. Tenhunen. 1997. Effects of stand structure and physiology on forest gas exchange: a simulation study for Norway spruce. *Trees-Structure and Function 11(7):436-448.*

The process-based simulation model STAND-FLUX describes canopy water vapor and carbon dioxide exchange based on rates calculated for

individual trees and as affected by local gradients in photon flux density (PFD), atmospheric humidity, atmospheric carbon dioxide concentration, and air temperature. Direct, diffuse, and reflected PFD incident on foliage elements within compartments of individual trees (defined by vertical layers and a series of concentric cylinders centered on the trunk) is calculated for a 3-dimensional matrix of points. Foliage element gas exchange rates are based on estimates of carboxylation, RuBP regeneration, and respiratory capacities as well as the correlated behavior found between stomatal conductance and assimilation rate. Because of the difficulties associated with effective sampling and description of spatial variation in structure and leaf level gas exchange parameters for trees comprising the forest canopy, the significance for canopy water and carbon dioxide exchange of varied representations of tree foliage distribution and of physiology is examined. The additional interactive effects encountered due to changes in tree density and, thus, spatial aggregation or disaggregation of foliage is also studied. The analysis is conducted within the context of observed structural and physiological variation encountered in Norway spruce (Picea abies) stands in the Fichtelgebirge region of central Germany. Potentials for simplifying the three-dimensional canopy gas exchange model without sizable influence on canopy flux rates were small. A relatively large number of sample points within the tree crowns is necessary to obtain consistent calculations of flux rates because of the nonlinear relationship between PFD and net photosynthesis. Transpiration and net photosynthesis for stands with a low leaf area index (LAI) may be obtained from single tree estimates for each tree class weighted by class frequency, while 30 or more trees per class in differing relation to neighboring trees may be necessary to calculate reliable estimates of net photosynthesis in canopies with high LAI. The complexity in structure assumed for modeled trees was important, especially when overall canopy foliage area was either high or low due to spatial heterogeneity in clumping, e.g., potential canopy overlaps or side-lighting. Effects were greater for calculated net photosynthesis than for transpiration, reflecting higher sensitivity of net photosynthesis to differences in light distribution within individual trees. Accuracy in estimates of physiological parameters is equally important, and these characteristics have profound effects on estimated canopy gas exchange rates. While one-dimensional representations of canopy structure or approximations of tree physiological characteristics from other canopies or species may often be necessary in assessing vegetation/atmosphere exchanges, especially in the study of water balance of landscapes or regions, STANDFLUX provides a tool that can aid in evaluating the limitations of these simpler approaches.

KEYWORDS: CANOPY, CONDUCTANCE, DECIDUOUS FOREST, ELEVATED CO2, LEAF, MODEL, PHOTOSYNTHESIS, SCALING CARBON-DIOXIDE, TUSSOCK GRASSES, WATER-VAPOR EXCHANGE

633

Falloon, P.D., P. Smith, J.U. Smith, J. Szabo, K. Coleman, and S. Marshall. 1998. Regional estimates of carbon sequestration potential: linking the Rothamsted Carbon Model to GIS databases. *Biology and Fertility of Soils 27(3):236-241.*

Soil organic matter (SOM) represents a major pool of carbon within the biosphere. It is estimated at about 1400 Pg globally, which is roughly twice that in atmospheric CO2. The soil can act as both a source and a sink for carbon and nutrients, Changes in agricultural land use and climate can lead to changes in the amount of carbon held in soils, thus, affecting the fluxes of CO2 to and from the atmosphere. Some agricultural management practices will lead to a net sequestration of carbon in the soil. Regional estimates of the carbon sequestration potential of these practices are crucial if policy makers are to plan future land uses to reduce national CO, emissions. In Europe, carbon sequestration potential has previously been estimated using data from the Global Change and Terrestrial Ecosystems Soil Organic Matter Network (GCTE SOMNET). Linear relationships between management practices and yearly changes in soil organic carbon were developed and used to estimate changes in the total carbon stock of European soils. To refine these semi-quantitative estimates, the local soil type, meteorological conditions and land use must also be taken into account. To this end, we have modified the Rothamsted Carbon Model, so that it can be used in a predictive manner. with SOMNET data. The data is then adjusted for local conditions using Geographical Information Systems databases. In this paper, we describe how these developments call be used to estimate carbon sequestration at the regional level using a dynamic simulation model linked to spatially explicit data. Some calculations of the potential effects of afforestation on soil carbon stocks in Central Hungary provide a simple example of the system in use.

KEYWORDS: CLIMATE, CO2, SOILS, STORAGE

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Fangmeier, A., L. De Temmerman, L. Mortensen, K. Kemp, J. Burke, R. Mitchell, M. van Oijen, and H.J. Weigel. 1999. Effects on nutrients and on grain quality in spring wheat crops grown under elevated CO2 concentrations and stress conditions in the European, multiple-site experiment 'ESPACE-wheat'. *European Journal of Agronomy 10(3-4):215-229.*

Nutrient element concentrations and grain quality were assessed in spring wheat grown under elevated CO2 concentrations and contrasting levels of tropospheric ozone at different nitrogen supply rates at several European sites. Carbon dioxide enrichment proved to affect nutrient concentrations in a complex manner, In green leaves, all elements (with exception of phosphorus and iron) decreased. In contrast, effects on the element composition of grains were restricted to reductions in nitrogen, calcium, sulphur and iron. Ozone exposure resulted in no significant effects on nutrient element concentrations in different tissues in the overall analysis. The nitrogen demand of green tissues was reduced due to CO2 enrichment as shown by reductions in the critical leaf nitrogen concentration and also enhanced nitrogen use efficiency. Reductions in the content of ribulose-bisphosphate carboxylase/oxygenase and repression of the photorespiratory pathway and reduced nitrogen allocation to enzymes driving the photosynthetic carbon oxidation cycle were chiefly responsible for this effect. Thus, nitrogen acquisition by the crop did not match carbon acquisition under CO2 enrichment, Since crop nitrogen uptake from the soil was already completed at anthesis, nitrogen allocated to the grain after anthesis originated from vegetative poors-causing grain nitrogen concentrations to decrease under CO2 enrichment (on average by 15% when CO2 concentrations increased from 360 to 680 mu mol mol(-1)). Correspondingly, grain quality was reduced by CO2 enrichment. The Zeleny value, Hagberg value and dry/wet gluten content decreased significantly with increasing [CO2]. Despite the beneficial impact of CO2 enrichment on growth and yield of C-3 cereal crops, declines in flour quality due to reduced nitrogen content are likely in a future, [CO2]-rich world.

KEYWORDS: AMBIENT AIR, CLIMATE CHANGE, LITTER QUALITY, MINERAL NUTRITION, NORWAY SPRUCE, RISING ATMOSPHERIC CO2, SPRUCE PICEA-ABIES, TOP FIELD CHAMBERS, TRITICUM-AESTIVUM L, TROPOSPHERIC OZONE

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Fangmeier, A., U. Gruters, U. Hertstein, A. SandhageHofmann, B. Vermehren, and H.J. Jager. 1996. Effects of elevated CO2, nitrogen supply and tropospheric ozone on spring wheat .1. Growth and yield. *Environmental Pollution 91(3):381-390.*

Spring wheat (Triticum aestivum L. cv. Minaret) was exposed to three CO2 levels, in combination with two nitrogen fertilizer levels and two

levels of tropospheric ozone, from sowing to ripening in open-top chambers. Three additional nitrogen fertilizer treatments were carried out at the lowest and the highest CO2 level, respectively. Plants were harvested at growth stages 31, 65 and 93 and separated into up to eight fractions to gain information about biomass partitioning. CO2 enrichment (263 mu l litre(-1) above ambient levels) drastically increased biomass of organs serving as long-term carbohydrate pools. Peduncle weight increased by 92%, stem weight by 73% and flag leaf sheath weight by 59% at growth stage 65. Average increase in shoot biomass due to CO2 enrichment amounted to 51% at growth stage 65 and 36% at final harvest. Average yield increase was 34%. Elevated nitrogen application was most effective on biomass of green tissues. Yield was increased by 30% when nitrogen application was increased from 150 to 270 kg N ha(-1). Significant interactions were observed between CO2 enrichment and nitrogen application. Yield increase due to CO2 ranged from 23% at 120 kg N to 47% at 330 kg N. Triticum aestivum cv. Minaret was not very responsive to ozone at 1.5 times ambient levels. 1000 grain weight was slightly decreased, which was compensated by an increased number of grains.

KEYWORDS: CARBOHYDRATE, CARBON DIOXIDE, DRY-MATTER, NUTRITION, RESPONSES, STEMS, STORAGE, STRESS, TEMPERATURE, WINTER-WHEAT

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Fangmeier, A., U. Gruters, P. Hogy, B. Vermehren, and H.J. Jager. 1997. Effects of elevated CO2 nitrogen supply and tropospheric ozone on spring wheat .2. Nutrients (N, P, K, S, Ca, Mg, Fe, Mn, Zn). *Environmental Pollution 96(1):43-59.*

CO2 enrichment is expected to alter leaf demand for nitrogen and phosphorus in plant species with C-3 carbon dioxide fixation pathway, thus possibly causing nutrient imbalances in the tissues and disturbance of distribution and redistribution patterns within the plants. To test the influence of CO2 enrichment and elevated tropospheric ozone in combination with different nitrogen supply, spring wheat (Tritium aestivum L. cv. Minaret) was exposed to three levels of CO2 (361, 523, and 639 mu l liter(-1), 24 h mean from sowing to final harvest), two levels of ozone (28.4 and 51.3 nl litre(-1)) and two levels of nitrogen supply (150 and 270 kg ha(-1)) in a full-factorial design in open-top field chambers. Additional fertilization experiments (120, 210, and 330 kg N ha(-1)) were carried out at low and high CO2 levels. Macronutrients (N, P, K, S, Ca, Mg) and three micronutrients (Mn, Fe, Zn) were analysed in samples obtained at three different developmental stages: beginning of shoot elongation, anthesis, and ripening. At each harvest, plant samples were separated into different organs (green and senescent leaves, stem sections, ears, grains). According to analyses of tissue concentrations at the beginning of shoot elongation, the plants were sufficiently equipped with nutrients. Elevated ozone levels neither affected tissue concentrations nor shoot uptake of the nutrients. CO2 and nitrogen treatments affected nutrient uptake, distribution and redistribution in a complex manner. CO2 enrichment increased nitrogen-use efficiency and caused a lower demand for nitrogen in green tissues which was reflected in a decrease of critical nitrogen concentrations, lower leaf nitrogen concentrations and lower nitrogen pools in the leaves. Since grain nitrogen uptake during grain filling depended completely on redistribution from vegetative pools in green tissues, grain nitrogen concentrations fell considerably with severe implications for grain quality. Ca, S, Mg and Zn in green tissues were influenced by CO2 enrichment in a similar manner to nitrogen. Phosphorus concentrations in green tissues, on the other hand, were not, or only slightly, affected by elevated CO2. In stems, 'dilution' of all nutrients except manganese was observed, caused by the huge accumulation of water soluble carbohydrates, mainly fructans, in these tissues under CO2 enrichment. Whole shoot uptake was either remarkably increased (K, Mn, P, Mg), nearly unaffected (N, S, Fe, Zn) or decreased (Ca) under CO2 enrichment. Thus, nutrient cycling in plant-soil systems is expected to be altered under CO2 enrichment. (C) 1997 Elsevier Science Ltd.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, CARBOHYDRATE, CARBON DIOXIDE, GROWTH-RESPONSE, MINERAL NUTRITION, PHOTOSYNTHESIS, SOURCE-SINK RELATIONS, STRESS, VEGETATION

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Fangmeier, A., U. Gruters, B. Vermehren, and H.J. Jager. 1996. Responses of some cereal cultivars to CO2 enrichment and tropospheric ozone at different levels of nitrogen supply. *Journal of Applied Botany-Angewandte Botanik 70(1-2):12-18.*

Two cultivars of spring wheat (Triticum aestivum L. cv. 'Nandu' and cv. 'Minaret') and one cultivar of spring barley (Hordeum vulgare L. cv. 'Alexis') were exposed to CO2 enrichment (concentrations ranging from 363 to 650 mu l l(-1)), ozone (ambient and 1.7 times ambient levels) at different levels of nitrogen nutrition in open-top field chambers from sowing to maturity. CO2 increased grain yield and shoot biomass, barley showing the smallest response and wheat 'Nandu' being most responsive. The cultivars were rather insensitive to ozone, however, a decrease of thousand grain weight was observed in one of the wheat cultivars ('Minaret') at high ozone levels. In this cultivar, interactions between CO2 and ozone were observed. Elevated CO2 appeared to be protective against impairments caused by ozone. CO2 and nitrogen supply strongly interacted. CO2 fertilizing effects on grain yield of wheat 'Minaret' ranged from 22.9 % at 120 kg N ha(-1) to 47.4 % at 330 kg N ha(-1). Increase in grain yield by CO2 was accompanied with a decrease of grain nitrogen content. Grain yield increase and grain nitrogen content depression exactly compensated each other and led to constant amounts of nitrogen stored in the grains on an area unit basis independent from the applied CO2 concentration. The grain quality, assessed as nitrogen content, was severely decreased by CO2 enrichment. The regressions obtained from the data suggest that nearly twice the nitrogen supply will be required to maintain the nitrogen content in grains at the same level if CO2 concentrations rise from the current 363 mu l l(-1) (seasonal mean 1994) to 650 mu l l(-1).

KEYWORDS: CARBON DIOXIDE, ELEVATED CO2, GROWTH, OPEN-AIR FUMIGATION, PHOTOSYNTHESIS, TOP FIELD CHAMBERS, TRITICUM-AESTIVUM L, VEGETATION, WINTER-WHEAT, YIELD

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Farage, P.K., I.F. McKee, and S.P. Long. 1998. Does a low nitrogen supply necessarily lead to acclimation of photosynthesis to elevated CO2? *Plant Physiology 118(2):573-580.*

Long-term exposure of plants to elevated partial pressures of CO, (pCO(2)) often depresses photosynthetic capacity. The mechanistic basis for this photosynthetic acclimation may involve accumulation of carbohydrate and may be promoted by nutrient limitation. However, our current knowledge is inadequate for making reliable predictions concerning the onset and extent of acclimation. Many studies have sought to investigate the effects of N supply but the methodologies used generally do not allow separation of the direct effects of limited N availability from those caused by a N dilution effect due to accelerated growth at elevated pCO(2). To dissociate these interactions, wheat (Triticum aestivum L.) was grown hydroponically and N was added in direct proportion to plant growth. Photosynthesis did not acclimate to elevated pCO(2) even when growth was restricted by a low-N relative addition rate. Ribulose-l, 5-bisphosphate carboxylase/oxygenase activity and quantity were maintained, there was no evidence for triose phosphate limitation of photosynthesis, and tissue N content remained within the range recorded for healthy wheat plants. In contrast, wheat grown in sand culture with N supplied at a fixed concentration suffered

photosynthetic acclimation at elevated pCO(2) in a low-N treatment. This was accompanied by a significant reduction in the quantity of active ribulose-l, 5- bisphosphate carboxylase/oxygenase and leaf N content.

KEYWORDS: C-3 PLANTS, CARBON, ENRICHMENT, GROWTH, PERSPECTIVE, PRODUCTIVITY, RESPONSES, RISING ATMOSPHERIC CO2, TREES, WHEAT

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Faria, T., M. Vaz, P. Schwanz, A. Polle, J.S. Pereira, and M.M. Chaves. 1999. Responses of photosynthetic and defence systems to high temperature stress in Quercus suber L-seedlings crown under elevated CO2. *Plant Biology 1(3):365-371.*

Growth in elevated CO2 led to an increase in biomass production per plant as a result of enhanced carbon uptake and lower rates of respiration, compared to ambient CO2-grown plants. No down-regulation of photosynthesis was found after six months of growth under elevated CO2. Photosynthetic rates at 15 degrees C or 35 degrees C were also higher in elevated than in ambient CO2-grown plants, when measured at their respective CO2 growth condition. Stomata of elevated CO2-grown plants were less responsive to temperature as compared to ambient CO2 plants. The after effect of a heat-shock treatment (4 h at 45 degrees C in a chamber with 80% of relative humidity and 800-1000 mu mol m(-2) s(-1) photon flux density) on A(max) was less in elevated than in ambient CO2-grown plants. At the photochemical level, the negative effect of the heat-shock treatment was slightly more pronounced in ambient than in elevated CO2-grown plants. A greater tolerance to oxidative stress caused by high temperatures in elevated CO2-grown plants, in comparison to ambient CO2 plants, is suggested by the increase in superoxide dismutase activity, after 1 h at 45 degrees C, as well as its relatively high activity after 2 and 4 h of the heat shock in the elevated CO2-grown plants in contrast with the decrease to residual levels of superoxide dismutase activity in ambient CO2-grown plants immediately after 1 h at 45 degrees C. The observed increase in catalase after 1 h at 45 degrees C in both ambient and elevated CO2-grown plants, can be ascribed to the higher rates of photorespiration and respiration under this high temperature.

KEYWORDS: ACCLIMATION, ANTIOXIDATIVE ENZYMES, CARBON DIOXIDE, CHLOROPHYLL FLUORESCENCE, DOWN-REGULATION, PHOTOSYSTEM, PICEA-ABIES L, PLANTS, RISING ATMOSPHERIC CO2, SUPEROXIDE-DISMUTASE

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Faria, T., D. Wilkins, R.T. Besford, M. Vaz, J.S. Pereira, and M.M. Chaves. 1996. Growth at elevated CO2 leads to down-regulation of photosynthesis and altered response to high temperature in Quercus suber L seedlings. *Journal of Experimental Botany 47(304):1755-1761.*

The effects of growth at elevated CO2 on the response to high temperatures in terms of carbon assimilation (net photosynthesis, stomatal conductance, amount and activity of Rubisco, and concentrations of total soluble sugars and starch) and of photochemistry (for example, the efficiency of excitation energy captured by open photosystem II reaction centres) were studied in cork oak (Quercus suber L.). Plants grown in elevated CO2 (700 ppm) showed a down-regulation of photosynthesis and had lower amounts and activity of Rubisco than plants grown at ambient CO2 (350 ppm), after 14 months in the greenhouse. At that time plants were subjected to a heat- shock treatment (4 h at 45 degrees C in a chamber with 80% relative humidity and 800-1000 mu mol m(-2) s(-1) photon flux density). Growth in a CO2-enriched atmosphere seems to protect cork oak leaves from the short-term effects of high temperature. Elevated CO2 plants had positive net carbon uptake rates during the heat shock treatment whereas plants grown at ambient CO2 showed negative rates. Moreover, recovery was faster in high CO2-grown plants which, after 30 min at 25 degrees C, exhibited higher net carbon uptake rates and lower decreases in photosynthetic capacity (A(max) as well as in the efficiency of excitation energy captured by open photosystem II reaction centres (F-v/F-m) than plants grown at ambient CO2. The stomata of elevated CO2 plants were also less responsive when exposed to high temperature.

KEYWORDS: ACCLIMATION, CHLOROPHYLL FLUORESCENCE, ENZYMES, EXPRESSION, GENES, LEAVES, MECHANISM, PROTEINS, RUBISCO, TREES

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Farnsworth, E.J., and F.A. Bazzaz. 1995. Inter-generic and intra-generic differences in growth, reproduction, and fitness of 9 herbaceous annual species grown in elevated co2 environments. *Oecologia 104(4):454-466.*

In assessing the capacity of plants to adapt to rapidly changing global climate, we must elucidate the impacts of elevated carbon dioxide on reproduction, fitness and evolution. We investigated how elevated CO2 influenced reproduction and growth of plants exhibiting a range of floral morphologies, the implications of shifts in allocation for fitness in these species, and whether related taxa would show similar patterns of response. Three herbaceous, annual species each of the genera Polygonum, Ipomoea, and Cassia were grown under 350 or 700 ppm CO2. Vegetative growth and reproductive output were measured non-destructively throughout the full life span, and vegetative biomass was quantified for a subsample of plants in a harvest at first flowering. Viability and germination studies of seed progeny were conducted to characterize fitness precisely. Early vegetative growth was often enhanced in high- CO2 grown plants of Polygonum and Cassia (but not Ipomoea). However, early vegetative growth was not a strong predictor of subsequent reproduction. Phenology and production of floral buds, flowers, unripe and abscised fruits differed between CO2 treatments, and genera differed in their reproductive and fitness responses to elevated CO2. Polygonum and Cassia species showed accelerated, enhanced reproduction, while Ipomoea species generally declined in reproductive output in elevated CO2. Seed "quality" and fitness (in terms of viability and percentage germination) were not always directly correlated with quantity produced, indicating that output alone may not reliably indicate fitness or evolutionary potential. Species within genera typically responded more consistently to CO2 than unrelated species. Cluster analyses were performed separately on suites of vegetative and reproductive characters. Some species assorted within genera when these reproductive responses were considered, but vegetative responses did not reflect taxonomic affinity in these plants. Congeners may respond similarly in terms of reproductive output under global change, but fitness and prognoses of population persistence and evolutionary performance can be inferred only rarely from examination of vegetative characters alone.

KEYWORDS: ALLOCATION, AMBIENT, CARBON DIOXIDE, CASSIA-FASCICULATA, ENRICHMENT, FECUNDITY, INTRASPECIFIC VARIATION, OVULE ABORTION, PLANTS, SEED PRODUCTION

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Farnsworth, E.J., A.M. Ellison, and W.K. Gong. 1996. Elevated CO2 alters anatomy, physiology, growth, and reproduction of red mangrove (Rhizophora mangle L). *Oecologia 108(4):599-609.*

Mangroves, woody halophytes restricted to protected tropical coasts, form some of the most productive ecosystems in the world, but their capacity to act as a carbon source or sink under climate change is unknown. Their ability to adjust growth or to function as potential carbon sinks under conditions of rising atmospheric CO2 during global

change may affect global carbon cycling, but as yet has not been investigated experimentally. Halophyte responses to CO2 doubling may be constrained by the need to use carbon conservatively under water-limited conditions, but data are lacking to issue general predictions. We describe the growth, architecture, biomass allocation, anatomy, and photosynthetic physiology of the predominant neotropical mangrove tree, Rhizophora mangle L., grown solitarily in ambient (350 mu ll(-1)) and double-ambient (700 mu ll(-1)) CO2 concentrations for over 1 year. Mangrove seedlings exhibited significantly increased biomass, total stem length, branching activity, and total leaf area in elevated CO2. Enhanced total plant biomass under high CO2 was associated with higher root:shoot ratios, relative growth rates, and net assimilation rates, but few allometric shifts were attributable to CO2 treatment independent of plant size. Maximal photosynthetic rates were enhanced among high-CO2 plants while stomatal conductances were lower, but the magnitude of the treatment difference declined over time, and high-CO2 seedlings showed a lower P-max at 700 mu ll(-1) CO2 than low-CO2 plants transferred to 700 mu ll(-1) CO2: possible evidence of downregulation. The relative thicknesses of leaf cell layers were not affected by treatment. Stomatal density decreased as epidermal cells enlarged in elevated CO2. Foliar chlorophyll, nitrogen, and sodium concentrations were lower in high CO2. Mangroves grown in high CO2 were reproductive after only 1 year of growth (fully 2 years before they typically reproduce in the field), produced aerial roots, and showed extensive lignification of the main stem; hence, elevated CO2 appeared to accelerate maturation as well as growth. Data from this long- term study suggest that certain mangrove growth characters will change flexibly as atmospheric CO2 increases, and accord with responses previously shown in Rhizophora apiculata. Such results must be integrated with data from sea-level rise studies to yield predictions of mangrove performance under changing climate.

KEYWORDS: ATMOSPHERIC CO2, AVICENNIA-MARINA, CARBON DIOXIDE, CARIBBEAN REGION, CLIMATE CHANGE, ECOSYSTEM COLLAPSE, ESTUARINE MARSH, HOLOCENE ANALOGS, INTERSPECIFIC VARIATION, SEA-LEVEL RISE

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Farrar, J.F., and M.L. Williams. 1991. The effects of increased atmospheric carbon-dioxide and temperature on carbon partitioning, source-sink relations and respiration. *Plant, Cell and Environment 14(8):819-830.*

Herbaceous C3 plants grown in elevated CO2 show increases in carbon assimilation and carbohydrate accumulation (particularly starch) within source leaves. Although changes in the partitioning of biomass between root and shoot occur, the proportion of this extra assimilate made available for sink growth is not known. Root:shoot ratios tend to increase for CO2-enriched herbaceous plants and decrease for CO2-enriched trees. Root:shoot ratios for cereals tend to remain constant. In contrast, elevated temperatures decrease carbohydrate accumulation within source and sink regions of a plant and decrease root:shoot ratios. Allometric analysis of at least two species showing changes in root:shoot ratios due to elevated CO2 show no alteration in the whole-plant partitioning of biomass. Little information is available for interactions between temperature and CO2. Cold-adapted plants show little response to elevated levels of CO2, with some species showing a decline in biomass accumulation. In general though, increasing temperature will increase sucrose synthesis, transport and utilization for CO2-enriched plants and decrease carbohydrate accumulation within the leaf. Literature reports are discussed in relation to the hypothesis that sucrose is a major factor in the control of plant carbon partitioning. A model is presented in support.

KEYWORDS: ABSCISIC- ACID, CARBOHYDRATE CONTENT, CO2-ENRICHMENT, DARK RESPIRATION, ELEVATED CO2, PHASEOLUS-VULGARIS, PLANT GROWTH, POTATO-TUBERS, SOYBEAN PHYSIOLOGY, SUGAR-BEET

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Favis-Mortlock, D.T., and S.J.T. Guerra. 1999. The implications of general circulation model estimates of rainfall for future erosion: a case study from Brazil. *Catena 37(3-4):329-354.*

One consequence of global change will be shifts in the probability of occurrence of soil erosion by water. This could have serious consequences for those areas of the world which are present-day 'hotspots' for erosion. By means of a case study, this paper suggests an approach to quantifying the change in risk of serious erosion for sites in such areas. The case study focuses on future erosion under intensive soya bean cultivation in the Mate Grosso area of Brazil. On the area's highly erodible latosols, current erosion problems are severe. Scenarios of change future climate change are taken from general circulation models (GCMs) and used to perturb current- climate weather data. These are input to an erosion model (water erosion prediction project (WEPP)-CO2), together with local knowledge regarding current and probable future land use, in order to estimate future changes in erosion rates. WEPP- simulated average annual sediment yield increases in one of the scenarios and decreases in the other two, reflecting the range of uncertainty in predictions of future rainfall. Using the 'best-guess' climate scenario from the UK Meteorological Office's HADCM2 GCM, the increase in mean annual sediment yield is 27%. Increases are disproportionately greater in wetter years. Average rates for individual months increase by over 100%. Erosion increases most on those parts of the hillslope profile which are currently hardest-hit by erosion. At present, an annual sediment yield of 5 t ha(-1) is currently exceeded in about 1 year in 2. The HADCM2 simulations suggest that an equal or greater rate will occur in about 70% of years by around 2050. A rate of at least 10 t ha(-1) yr(-1) is currently exceeded in about 1 year in 5. The HADCM2 simulations suggest that this will rise, to about 1 year in 4.

KEYWORDS: ADJUSTMENTS, CLIMATE CHANGE, ELEVATED CO2, FARMER SCENARIO, PRESENT TECHNOLOGY, RESPONSES, SIMULATIONS, SOIL-EROSION, SOUTH-DOWNS, WHEAT YIELD

645

Fearnside, P.M. 1999. Plantation forestry in Brazil: the potential impacts of climatic change. *Biomass & Bioenergy 16(2):91-102.*

Most climatic changes predicted to occur in Brazil would reduce yields of silvicultural plantations, mainly through increased frequency and severity of droughts brought on by global warming and by reduction of water vapor sources in Amazonia caused by deforestation. Some additional negative effects could result from changes in temperature, and positive effects could result from CO2 enrichment. The net effects would be negative, forcing the country to expand plantations onto less-productive land, requiring increased plantation area land consequent economic losses) out of proportion to the climatic change itself. These impacts would affect carbon sequestration and storage consequences of any plans for subsidizing silviculture as a global warming mitigation option. Climate change can be expected to increase the area of plantations needed to supply projected internal demand for and exports of end products from Brazil. June-July-August (dry season) precipitation reductions indicated by simulations reported by the Intergovernmental Panel on Climate Change (IPCC) correspond to rainfall declines in this critical season of approximately 34% in Amazonia, 39% in Southern Brazil and 61% in the Northeast. As an example, if rainfall in Brazilian plantation areas (most of which are now in Southern Brazil) were to decline by 50%, the area needed in 2050 would expand by an estimated 38% over the constant climate case, bringing the total plantation area to 4.5 times the 1991 area. These large areas of additional plantations imply substantial social and environmental impacts. Further addition of

plantation area as a global warming response option would augment these impacts, indicating the need for caution in evaluating carbon sequestration proposals. (C) 1999 Elsevier Science Ltd. All rights reserved.

KEYWORDS: AMAZON BASIN, CARBON

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Feng, X.H., and S. Epstein. 1996. Climatic trends from isotopic records of tree rings: The past 100-200 years. *Climatic Change 33(4):551-562.*

There has been a great deal of discussion about global warming from accumulation of anthropogenic greenhouse gases in the atmosphere (Houghton et al., 1990). Relatively less attention has been paid to spatial and/or temporal climatic variations that may be associated with a warmer climate (Rind et al., 1989) or with anthropogenic activities (Schneider, 1994). In this article; we show that an increase in climatic variability may have started. Fourteen isotopic time series of tree rings are presented. These trees were randomly collected from world- wide locations and cover time periods of 120 to over 200 years. The isotopic records show increasing delta D values that suggest a consistent and progressive warming occurred in the 19th century in all locations where the trees were sampled. The rate of warming is greater at relatively cold locations than at warm locations with two exceptions. The records also suggest greater climatic variations both temporally and spatially in the 20th century than in the 19th century.

KEYWORDS: ATMOSPHERIC CO2, CELLULOSE, D-H RATIO, D/H RATIOS, ENRICHMENT, LEAF WATER, NON-EXCHANGEABLE HYDROGEN, NORTH-AMERICA, PRECIPITATION, VARIABILITY

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Ferguson, S.A. 1997. A climate-change scenario for the Columbia River basin. *Usda Forest Service Pacific Northwest Research Station Research Paper (499):CP1-CP&.*

This work describes the method used to generate a climate- change scenario for the Columbia River basin. The scenario considers climate patterns that may change if the atmospheric concentration of carbon dioxide (CO2), or its greenhouse gas equivalent, were to double over pre-Industrial Revolution values. Given the current rate of increase in atmospheric CO2 concentration, doubling could occur within the next 50 to 100 years. The Columbia River basin is in a transition climate zone between predominating maritime to the west, arctic to the north, and continental to the east. Consequently, it is difficult to characterize through means and averages. Therefore, many of the current stochastic methods for developing climate-change scenarios cannot directly apply to the basin. To circumvent this problem, a composite approach was taken to generate a climate scenario that considers knowledge of current regional climate controls, available output from general circulation and regional climate models, and observed changes in climate. The resulting climate-change scenario suggests that precipitation could increase substantially during winter (+20 to +50 percent) and moderately during spring and autumn (+5 to +35 percent). A slight decrease (0 to -5 percent) in summer precipitation is possible, except for the southeastern portions of the basin that may experience an increase in convective precipitation (+5 percent). Low- elevation (<1 kilometer) temperatures throughout the year may increase 1 to 3 degrees C, with greatest increases during winter. This amount of temperature change is possible because of an expected loss of low-elevation snow cover. At high elevations, increased cloud cover could cause average temperatures to decrease during winter but be synchronized with possible warming at low elevations during summer. The diurnal range of temperature could decrease, especially in summer and autumn.

KEYWORDS: INCOMPLETE, MODEL, PRECIPITATION, TEMPERATURE, UNITED-STATES

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Fernandez, M.D., A. Pieters, C. Donoso, W. Tezara, M. Azkue, C. Herrera, E. Rengifo, and A. Herrera. 1998. Effects of a natural source of very high CO2 concentration on the leaf gas exchange, xylem water potential and stomatal characteristics of plants of Spatiphylum cannifolium and Bauhinia multinervia. *New Phytologist 138(4):689-697.*

The effect of a very high CO2 mole fraction (27 000-35 000 mu mol mol(-1)) on photosynthesis and water relations was studied during the dry and the rainy season in plants of Spatiphylum cannifolium (Dryand.) Schott and Bauhinia multinervia (H.B.K.) DC. growing near natural cold CO2 springs. Xylem water potential in plants of both species was lowered by drought, high CO2 growth-concentration decreasing it further in S. cannifolium. In plants of both species growing under high CO2 concentration photosynthetic rates measured at a CO2 mole fraction of 1000 mu mol mol(-1) were higher than in plants growing at ambient CO2 mole fraction and measured at 350 mu mol mol(-1). The response was the result of a direct effect of CO2 on the photosynthetic machinery. Changes in carboxylation efficiency in response to high CO2 were found during the rainy season, with an increase in S. cannifolium and a decrease in B. multinervia; a significant interaction between growth CO2 concentration and season in B. multinervia resulted from significant effects of both factors. An increase in intrinsic water-use efficiency due to high CO2 was determined in both species by an increase in photosynthetic rate as well as a decrease in leaf conductance. In high-CO2 plants of S. cannifolium a 71 % decrease in stomatal density and 73 % in stomatal index suggested that CO2 affected stomatal initiation, whereas in B. multinervia an 85 % decrease in stomatal index and a 72 % decrease in stomatal density indicated that CO2 influenced stomatal initiation as well as epidermal cell expansion. Our results indicate that very high CO2 concentrations did not inhibit photosynthesis in these species, and that growth under high CO2 allowed plants to attain carbon balances higher than those of plants growing under low CO2. This was particularly so during the dry season, since the photosynthetic rates at the corresponding ambient concentration were higher in plants nearer the springs, and carboxylation efficiency and some stomatal characteristics of both species apparently acclimated to high CO2, but patterns were not consistent and bore no obvious relationship to photosynthetic capacity.

KEYWORDS: ATMOSPHERIC CO2, BIOMASS ALLOCATION, DENSITY, ELEVATED CARBON-DIOXIDE, ENRICHMENT, GROWTH, LEAVES, PHOTOSYNTHESIS, SCIRPUS- OLNEYI, USE EFFICIENCY

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FerrarioMery, S., M.C. Thibaud, T. Betsche, M.H. Valadier, and C.H. Foyer. 1997. Modulation of carbon and nitrogen metabolism, and of nitrate reductase, in untransformed and transformed Nicotiana plumbaginifolia during CO2 enrichment of plants grown in pots and in hydroponic culture. *Planta 202(4):510-521.*

Transformed plants of Nicotiana plumbaginifolia Viv. constitutively expressing nitrate reductase (35S-NR) or beta- glucuronidase (35S-GUS) and untransformed controls were grown for two weeks in a CO2-enriched atmosphere. Whereas CO2 enrichment (1000 mu l. 1(-1)) resulted in an increase in the carbon (C) to nitrogen (N) ratio of both the tobacco lines grown in pots with vermiculite, the C/N ratio was only slightly modified when plants were grown in hydroponic culture in high CO2 compared to those grown in air. Constitutive nitrate reductase (NR) expression per se did not change the C/N ratio of the shoots or roots. Biomass accumulation was similar in both types of plant when hydroponic or pot-grown material, grown in air or high CO2, were

compared. Shoot dry matter accumulation was primarily related to the presence of stored carbohydrate (starch and sucrose) in the leaves. In the pot- grown tobacco, growth at elevated CO2 levels caused a concomitant decrease in the N content of the leaves involving losses in NO3- and amino contrast, the N content and composition were similar in all plants grown in hydroponic culture. The 35S-NR plants grown in air had higher foliar maximum extractable NR activities and increased glutamine levels (on a chlorophyll or protein basis) than the untransformed controls. These increases were maintained following CO2 enrichment when the plants were grown in hydroponic culture, suggesting that an increased flux through nitrogen assimilation was possible in the 35S-NR plants. Under CO2 enrichment the NR activation state in the leaves was similar in all plants. When the 35S-NR plants were grown in pots, however, foliar NR activity and glutamine content fell in the 35S-NR transformants to levels similar to those of the untransformed controls. The differences in NR activity between untransformed and 35S-NR leaves were much less pronounced in the hydroponic than in the pst-grown material but the difference in total extractable NR activity was more marked following CO2 enrichment. Foliar NR message levels were decreased by CO2 enrichment in all growth conditions but this was much more pronounced in pot-grown material than in that grown hydroponically. Since beta-glucuronidase (GUS) activity and message levels in 35S-GUS plants grown under the same conditions of CO2 enrichment (to test the effects of CO2 enrichment on the activity of the 35S promoter) were found to be constant, we conclude that NR message turnover was specifically accelerated in the 35S-NR plants as well as in the untransformed controls as a result of CO2 enrichment. The molecular and metabolic signals involved in increased NR message and protein turnover are not known but possible effecters include NO3-, glutamine and asparagine. We conclude that plants grown in hydroponic culture have greater access to N than those grown in pots. Regardless of the culture method, CO2 enrichment has a direct effect on NR mRNA stability.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, CONSTITUTIVE EXPRESSION, DIOXIDE ENRICHMENT, ETIOLATED BARLEY LEAVES, GENE-EXPRESSION, GLUTAMINE-SYNTHETASE, LIGHT, PHOTOSYNTHESIS, TOMATO

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Ferris, R., I. Nijs, T. Behaeghe, and I. Impens. 1996. Contrasting CO2 and temperature effects on leaf growth of perennial ryegrass in spring and summer. *Journal of Experimental Botany 47(301):1033-1043.*

The effects of increased atmospheric carbon dioxide (CO2) of 700 mu mol mol(-1) and increased air temperature of +4 degrees C were examined in Lolium perenne L. cv. Vigor, growing in semi-controlled greenhouses, Leaf growth, segmental elongation rates (SER), water relations, cell wall (tensiometric) extensibility (%P) and epidermal cell lengths (ECL) were measured in expanding leaves in spring and summer. In elevated CO2, shoot dry weight (SDW) increased in mid-summer, In both seasons, SDW decreased in elevated air temperatures with this reduction being greater in summer as compared to spring, Specific leaf area (SLA) decreased in elevated CO2 and in CO2 x temperature in both seasons, In spring, increased leaf extension and SER in elevated CO2 were linked with increased ECL, %P and final leaf size whilst in summer all were reduced, In high temperature, leaf extension, SER, %P and final leaf size were reduced in both seasons. In elevated CO2 x temperature, leaf extension, SER, %P, and ECL increased in spring, but final leaf size remained unaltered, whilst in summer all decreased. Mid-morning water potential did not differ with CO2 or temperature treatments. Leaf turgor pressure increased in elevated CO2 in spring and remained similar to the control in summer whilst solute potential decreased in spring and increased in summer, Contrasting seasonal growth responses of L. perenne in response to elevated CO2 and temperature suggests pasture management may change in the future, The grazing season may be prolonged, but whole season productivity may become more variable than today.

KEYWORDS: CARBON-DIOXIDE CONCENTRATION, CELL-GROWTH, DIVERSE ALTITUDINAL RANGES, ELEVATED CO2, EXPANSION, GROWING LEAVES, LOLIUM-TEMULENTUM, PLANT GROWTH, RESPONSES, WATER RELATIONS

651

Ferris, R., I. Nijs, T. Behaeghe, and I. Impens. 1996. Elevated CO2 and temperature have different effects on leaf anatomy of perennial ryegrass in spring and summer. *Annals of Botany 78(4):489-497.*

Mature second leaves of Lolium perenne L. cv. Vigor, were sampled in a spring and summer regrowth period. Effects of CO2 enrichment and increased air temperature on stomatal density, stomatal index, guard cell length, epidermal cell density, epidermal cell length and mesophyll cell area were examined for different positions on the leaf and seasons of growth. Leaf stomatal density was smaller in spring but greater in summer in elevated CO2 and higher in both seasons in elevated temperature and in elevated CO2 x temperature relative to the respective controls. In spring, leaf stomatal index was reduced in elevated CO2 but in summer it varied with position on the leaf. In elevated temperature, stomatal index in both seasons was lower at the tip/middle of the leaf but slightly higher at the base. In elevated CO2 x temperature, stomatal index varied with position on the leaf and between seasons. Leaf epidermal cell density was higher in all treatments relative to controls except in elevated CO2 (spring) and elevated CO2 x temperature (summer), it was reduced at the leaf base. In all treatments, stomatal density and epidermal cell density declined from leaf tip to base, whilst guard cell length showed an inverse relationship, increasing towards the base. Leaf epidermal cell length and mesophyll cell area increased in elevated CO2 in spring and decreased in summer. In elevated CO2 x temperature leaf epidermal cell length remained unaltered in spring compared to the control but decreased in summer. Stomatal conductance was lower in all treatments except in summer in elevated CO2 it was higher than in the ambient CO2. These contrasting responses in anatomy to elevated CO2 and temperature provide information that might account. for differences in seasonal leaf area development observed in L. perenne under the same conditions. (C) 1996 Annals of Botany Company

KEYWORDS: ATMOSPHERIC CO2, CARBON-DIOXIDE CONCENTRATION, ENRICHMENT, GAS-EXCHANGE, GROWTH, LEAVES, POPLAR CLONES, RESPONSES, STOMATAL DENSITY, WATER

652

Ferris, R., and G. Taylor. 1993. Contrasting effects of elevated co2 on the root and shoot growth of 4 native herbs commonly found in chalk grassland. *New Phytologist 125(4):855-866.*

The aim of this study was to investigate the impact of ambient (345 mu l l(-1)) and elevated (590 mu l l(-1)) CO2 on the root and shoot growth of four native chalk grassland herbs: Sanguisorba minor Scop. (salad burnet), Lotus corniculatus L. (birdsfoot trefoil), Anthyllis vulneraria L. (kidney vetch) and Plantage media L. (hoary plantain). Elevated CO2 had contrasting effects on both shoot and root growth of the four species studied. Both leaf expansion and production were stimulated by elevated CO2 for S. minor, L. corniculatus and P. media, whilst for A. vulneraria, only leaflet shape appeared to be altered by elevated CO2, with the production of broader leaflets, compared with those produced in ambient CO2. After 100 d shoot biomass was enhanced in elevated CO2 for S. minor and L. corniculatus, whilst there was no effect of elevated CO2 on shoot biomass for A. vulneraria or P. media. Contrasting effects of CO2 were also apparent for measurements of specific leaf area (SLA), which

increased for L. corniculatus, decreased for A. vulneraria and remained unaltered for S. minor and P. media in elevated compared with ambient CO2. Elevated CO2 also had contrasting effects on both the growth and morphology of roots. The accumulation of root biomass was stimulated following exposure to elevated CO2 for S. minor and L. corniculatus whilst there was no effect on root biomass for A. vulneraria or P. media. Root length was measured on three occasions during the 100 d and revealed that exposure to elevated CO2 promoted root extension in S. minor, L. corniculatus and P. media, but not in A. vulneraria. Specific root length (SRL, length per unit dry weight) was increased in elevated CO2 for one species, P. media, whilst the root to shoot ratio of all four species remained unchanged by CO2. These results show that four native herbs differ in their response to CO2, suggesting that the structure of this plant community may be altered in the future.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CARBON-DIOXIDE, COMMUNITIES, ECOSYSTEMS, ENRICHMENT, LEAF ANATOMY, PHOTOSYNTHESIS, RESPONSES, SOURCE-SINK RELATIONS, TEMPERATURE

653

Ferris, R., and G. Taylor. 1994. Elevated co2, water relations and biophysics of leaf extension in 4 chalk grassland herbs. *New Phytologist 127(2):297-307.*

Diurnal measurements of leaf or leaflet extension, water relations and cell wall extensibility (phi) were made on young growing leaves of four chalk downland herbs (Sanguisorba minor Scop., Lotus corniculatus L., Anthyllis vulneraria L. and Plantago media L.) growing in controlled environment cabinets and exposed to either ambient or elevated CO2. This study revealed differences in the effect of CO2 and the control of leaf growth between the four species. Leaf extension rate (LER) increased significantly at night (average over 8 h) in elevated CO2 for S. minor, A. vulneraria and P. media with a significant increase over the first 4 h of darkness for S. mines, L. corniculatus and P. media, whilst for S. minor and P. media average day-time LER (over 16 h) also increased significantly in elevated CO2 as compared with ambient CO2. Water potential (Psi), solute potential (Psi(s)), turgor pressure (P), yield turgor (Y) and the effective turgor for growth (Pe) were measured using psychrometers. Solute potentials of S. minor, A. vulneraria acid P. media decreased significantly following exposure to elevated CO2 with a significant reduction in Psi(s) during the day in A. vulneraria. Turgor pressure increased significantly in elevated CO2 as compared with ambient CO2 in A. vulneraria but there was no effect of elevated CO2 on P in the other species. No effects of CO2 on Psi, Y or Pe were observed. Leaf cell wall extensibility (phi) increased significantly in leaves of S. minor, L. corniculatus and P. media exposed to elevated CO2, whereas in A. vulneraria, there was no effect of CO2 on extensibility. These results suggest that the mechanism by which elevated CO2 promotes leaf growth differs between species since in S. minor, L. corniculatus and P. media, CO2 promoted growth through an influence on cell wall properties, whilst in A. vulneraria, higher values of P explain the increased leaf growth in elevated CO2 for this species.

KEYWORDS: EXPANSION, LEAVES, PHOTOSYNTHESIS, PLANT-CELL GROWTH, PRODUCTIVITY, SALIX-VIMINALIS, TEMPERATURE, WALL EXTENSIBILITY, XYLOGLUCAN ENDOTRANSGLYCOSYLASE, YIELD TURGOR

654

Ferris, R., and G. Taylor. 1994. Increased root-growth in elevated co2 - a biophysical analysis of root cell elongation. *Journal of Experimental Botany 45(280):1603-1612.*

A biophysical analysis of root expansion was conducted in four chalk downland herbs (Sanguisorba minor Scop., Lotus corniculatus L., Anthyllis vulneraria L. and Plantago media L.) exposed to either ambient or elevated CO, in controlled environment cabinets. Measurements of fine (F) and extra-fine (EF) root extension rate (RER), water relations, and cell wall tensiometric extensibility revealed differences in the diurnal pattern of root growth between species. After 35 d of exposure to elevated CO2, RER of both F and EF roots increased significantly in darkness and on illumination for S. minor, whilst for A. vulneraria (EF roots only) and L. corniculatus a significant increase occurred at night whereas for P. media a significant increase occurred during the day. Cells measured in the zone of elongation were longer in all species exposed to elevated CO2. Water potential (Psi), solute potential (Psi(s)), turgor pressure (P), yield turgor (Y) and effective turgor (Pe) were measured by stress-relaxation of excised root tips placed in psychrometers. Solute potentials decreased significantly for all species following exposure to elevated CO2. In S. minor and L. corniculatus, P and Pe, respectively, were higher in elevated CO2. No significant effects of CO2 on Y were observed (not shown). Root cell wall tensiometric extensibility, measured as % plasticity, increased in all species exposed to elevated CO2. These results suggest that root growth is enhanced following increased cell expansion and that increased P and cell wall tensiometric extensibility are both important for root growth in elevated CO2.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, LEAF GROWTH, MAIZE ROOTS, PLANTS, PRESSURE PROBE, TURGOR, WALL EXTENSIBILITY, WATER RELATIONS, XYLOGLUCAN ENDOTRANSGLYCOSYLASE, YIELD THRESHOLD

655

Ferris, R., and G. Taylor. 1994. Stomatal characteristics of 4 native herbs following exposure to elevated co2. *Annals of Botany 73(4):447-453.*

KEYWORDS: ALLIUM, CARBON DIOXIDE, CELLS, DENSITY, ENRICHMENT, GROWTH, INCREASES, LEAF ANATOMY, NUMBERS, POPLAR CLONES

656

Ferris, R., and G. Taylor. 1995. Contrasting effects of elevated CO2 and water deficit on two native herbs. *New Phytologist 131(4):491-501.*

This study investigated the effects of carbon dioxide (CO2) enrichment and soil water deficit on the water use efficiency (WUE) and growth of Sanguisorba minor Scop. (salad burnet) and Anthyllis vulneraria L. (kidney vetch), growing in controlled environments. Instantaneous WUE (IWUE) increased in both species in elevated CO2, with a higher average increase in unwatered (UW) A. vulneraria over the drying cycle. Total plant WUE of A. vulneraria increased in elevated CO2 and under water deficit: the UW plants in elevated CO2 had higher WUE and reduced water loss. By contrast, thee was only an effect of water supply on S. minor: total plant WUE increased and water loss decreased in the UW plants in both CO2 treatments. Total apparent root length (ARL) of both species increased with CO2 enrichment and in UW S. minor total ARL was increased. By contrast, for A. vulneraria, total ARL of UW plants increased in ambient CO2, but decreased in elevated CO2 as compared with well-watered (WW) plants. Shoot dry weight (SDW) and root dry weight increased in both species (WW and UW) with CO2 enrichment. For UW S. minor, SDW decreased relative to WW plants in both CO2 treatments. By contrast, ANOVA showed no significant effect of water supply on SDW of A. vulneraria. Leaflet length increased in both species in elevated CO2 and decreased following drought. Cell wall tensiometric extensibility (%P) increased in expanding leaves of S. minor in elevated CO2 and for both species %P decreased in the UW plants as compared with those WW. Leaf water potential (Psi) of both species was lower in growing leaves of WW plants in elevated CO2. Water deficit reduced the Psi of growing leaves in both CO2 treatments.

The different responses of these species suggest that in a drier, enriched CO2 environment survival in a community might depend on their ability to maintain growth at the same time as conserving water.

KEYWORDS: BETULA, CARBON DIOXIDE, DROUGHT, ENRICHMENT, GROWTH, LIMITED CONDITIONS, SEEDLINGS, STRESS, USE EFFICIENCY, YIELD

657

Ferris, R., T.R. Wheeler, R.H. Ellis, and P. Hadley. 1999. Seed yield after environmental stress in soybean grown under elevated CO2. *Crop Science 39(3):710-718.*

Episodes of high temperature and drought are predicted to occur more frequently under conditions of future climate change, This study investigated whether an episode of high air temperature (HT + 15 degrees C), water deficit (WD), or both (HTWD), for 8 d, had the same effects on the yield of soybean [Glycine max (L.) Merrill, cv. Fiskeby V] grown under either ambient (aCO(2); 360 mu mol mol(-1) CO2) or elevated (eCO(2); 700 mu mol mol(-1) CO2) CO2 concentrations. Plants were grown in a glasshouse at either aCO(2) or at eCO(2) until 52 d after sowing (DAS). The 8-d stress treatments were then imposed before the plants were returned to their original environments. Across harvests, total biomass was 41% greater under eCO(2) than under aCO(2) but reduced by HT, WD, and HTWD under both CO2 concentrations, The relative response of total biomass to HT,WD, and HTWD episodes was the same for plants grown under either aCO(2) or eCO(2). At maturity, seed dry weight and number per plant under eCO(2) were increased by an average of 32 and 22%, respectively, compared with aCO(2). The same parameters were reduced after HTWD by 29 and 30%, respectively, in aCO(2) and eCO(2), Seed filling was earlier under HT and HTWD The rate of change in harvest index was unaltered by CO2 while under HTWD, it decreased. Seed number explained 85% of the variation in yield, but yield was also related linearly to photosynthesis during seed filling, suggesting both are important determinants of yields under stress.

KEYWORDS: CARBON DIOXIDE, CLIMATIC VARIABILITY, CROP YIELDS, LONG-TERM, LUPINUS-ANGUSTIFOLIUS L, PHOTOSYNTHESIS, PRODUCTIVITY, RESPONSES, TRANSIENT HIGH-TEMPERATURES, WATER-STRESS

658

Ferris, R., T.R. Wheeler, P. Hadley, and R.H. Ellis. 1998. Recovery of photosynthesis after environmental stress in soybean grown under elevated CO2. *Crop Science 38(4):948-955.*

Episodes of high temperature and water deficit may be more frequent under predicted future climates of warmer mean temperatures and elevated CO2. This study investigated whether the effects of an episode of high sir temperature (HT, 43 degrees C as a daily maximum), water deficit (WD), or both, had the same effect on the recovery of photosynthesis and on leaf water relations of soybean [Glycine max (L.) Merr., cv. Fiskeby V] grown at ambient CO2 (aCO(2)) or elevated CO2 (eCO(2)). An 8-d period of HT, WD, or both (HTWD) were imposed during early seed filling of soybean grown in glasshouses at either 362 or 685 mu mol mol(-1) CO2. Photosynthesis (Amax), stomatal conductance (g(s)), and water relations were measured in fully expanded upper-canopy leaves. Immediately after the 8-d treatments at 60 d after sowing (DAS), Amax was reduced by 31, 48, and 64% in aCO(2) and by 28, 39, and 49% in eCO(2) under HT, WD, and HTWD, respectively, but no significant interactions were detected. At 60 DAS, g(s) was reduced by WD and HTWD in aCO(2) but not by HT while there was little change in g(s) by WD, HT, and HTWD under eCO(2). Amar fully recovered under WD in eCO(2) by 66 DAS, while Amax remained reduced under WD in aCO(2). Under each CO2 concentration, almost full recovery of Amar occurred under HT by 75 DAS but under HTWD Amar never attained control values. At 60 DAS, early morning leaf water potential (Psi) was lower after HT, WD, and HTWD and Amax was a negative function of Psi, at each CO2 concentration. The results suggest that full recovery of Amax from WD was only possible under eCO(2), because at aCO(2), immediately after the stress episode, Psi was below the threshold for chloroplast damage.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CLIMATIC VARIABILITY, CROP YIELDS, ENRICHMENT, GAS-EXCHANGE, LEAF WATER POTENTIALS, PERENNIAL RYEGRASS, PLANTS, RESPONSES, TEMPERATURE

659

Field, C.B. 1994. Carbon-cycle - arctic chill for co2 uptake. *Nature 371(6497):472-473.*

KEYWORDS: AMBIENT, ATMOSPHERIC CO2, ELEVATED CO2, TUSSOCK TUNDRA

660

Field, C.B., F.S. Chapin, P.A. Matson, and H.A. Mooney. 1992. Responses of terrestrial ecosystems to the changing atmosphere - a resource-based approach. *Annual Review of Ecology and Systematics 23:201-235.*

KEYWORDS: ALASKAN TUSSOCK TUNDRA, ALPINE LIFE ZONE, CARBON NUTRIENT BALANCE, ELEVATED CO2 CONCENTRATIONS, HARDWOOD LEAF LITTER, L KARST STANDS, NITROGEN-USE EFFICIENCY, SOURCE-SINK RELATIONS, TEMPERATE FOREST ECOSYSTEMS, WATER-USE EFFICIENCY

661

Field, C.B., R.B. Jackson, and H.A. Mooney. 1995. Stomatal responses to increased co2 - implications from the plant to the global-scale. *Plant, Cell and Environment 18(10):1214-1225.*

Increased atmospheric CO2 Often but not always leads to large decreases in leaf conductance, Decreased leaf conductance has important implications for a number of components of CO2 responses, from the plant to the global scale, All of the factors that are sensitive to a change in soil moisture, either amount or timing, may be affected by increased CO2. The list of potentially sensitive processes includes soil evaporation, run- off, decomposition, and physiological adjustments of plants, as well as factors such as canopy development and the composition of the plant and microbial communities, Experimental evidence concerning ecosystem-scale consequences of the effects of CO2 on water use is only beginning to accumulate, but the initial indication is that, in water-limited areas, the effects of CO2- induced changes in leaf conductance are comparable in importance to those of CO2-induced changes in photosynthesis, Above the leaf scale, a number of processes interact to modulate the response of canopy or regional evapotranspiration to increased CO2. While some components of these processes tend to amplify the sensitivity of evapotranspiration to altered leaf conductance, the most likely overall pattern is one in which the responses of canopy and regional evapotranspiration are substantially smaller than the responses of canopy conductance, The effects of increased CO2 on canopy evapotranspiration are likely to be smallest in aerodynamically smooth canopies with high leaf conductances, Under these circumstances, which are largely restricted to agriculture, decreases in evapotranspiration may be only one-fourth as large as decreases in canopy conductance, Decreased canopy conductances over large regions may lead to altered climate, including increased temperature and decreased precipitation, The simulation experiments to date predict small effects globally, but these could be important regionally, especially

in combination with radiative (greenhouse) effects of increased CO2.

KEYWORDS: ATMOSPHERIC CO2, CONDUCTANCE, ELEVATED CARBON-DIOXIDE, GAS-EXCHANGE, GROWTH, LEAF-AREA, PHOTOSYNTHESIS, SCIRPUS- OLNEYI, TRANSPIRATION, WATER-STRESS

662
Field, C.B., C.P. Lund, N.R. Chiariello, and B.E. Mortimer. 1997. CO2 effects on the water budget of grassland microcosm communities. *Global Change Biology 3(3):197-206.*

Experimental grassland ecosystems, in microcosms 0.2 m in diameter and with a 0.95 m soil column, varied in their responses to elevated partial pressure of CO2 (pCO(2)) and altered moisture inputs. Ecosystems on moderately fertile sandstone soil and with a typical mix of moderately fast- growing sandstone species, responded to elevated pCO(2) with decreases in mid-season evapotranspiration of nearly 50%. This pattern reversed at the end of the growing season, and sandstone ecosystems under elevated pCO(2) continued active transpiration farther into the summer drought. The sandstone ecosystems appeared to convert mid-season water conservation into increased late-season growth. Effects of increased pCO(2) on ecosystem evapotranspiration were much smaller in ecosystems with very infertile serpentine soil and a diverse mixture of slow-growing serpentine species.

KEYWORDS: AMBIENT, COTTON, ELEVATED CO2, ENRICHMENT, EVAPOTRANSPIRATION, INCREASES, RESPONSES, SIMULATIONS, STOMATAL CONDUCTANCE, TRANSPIRATION

663
Field, C.D. 1995. Impact of expected climate-change on mangroves. *Hydrobiologia 295(1-3):75-81.*

There is a consensus of scientific opinion that the activities of man will cause a significant change in the global climate over the next hundred years. The rising level of carbon dioxide and other industrial gases in the atmosphere may lead to global warming with an accompanying rise in sea-level. Mangrove ecosystems grow in the intertidal zones in tropical and sub- tropical regions and are likely to be early indicators of the effects of climate change. The best estimates of predicted climate change in the literature are presented. It is suggested that a rise in mean sea-level may be the most important factor influencing the future distribution of mangroves but that the effect will vary dramatically depending on the local rate of sea-level rise and the availability of sediment to support reestablishment of the mangroves. The predicted rise in mean air temperature will probably be of little consequence to the development of mangroves in general but it may mean that the presence of mangroves will move further north and south, though this will depend on a number of additional factors. The effect of enhanced atmospheric CO2 on the growth of mangroves is unknown at this time but that there is some evidence that not all species of mangroves will respond similarly. The socio- economic impacts of the effects of climate change on mangrove ecosystems may include increased risk of flooding, increased erosion of coast lines, saline intrusion and increased storm surges.

KEYWORDS: AVICENNIA-MARINA, ELEVATED CO2, GREY MANGROVE, GROWTH, PLANT-RESPONSES, SALINITY, SEA-LEVEL, STOMATAL RESPONSES

664
Fierro, A., N. Tremblay, and A. Gosselin. 1994. Supplemental carbon-dioxide and light improved tomato and pepper seedling growth and yield. *Hortscience 29(3):152-154.*

The experiment was conducted to determine the effects of CO2 enrichment (900 mul.liter-1, 8 hours/day) in combination with supplementary lighting of 100 mumol.s-1.m-2 (16-h photoperiod) on tomato (Lycopersicon esculentum Mill.) and sweet pepper (Capsicum annuum L.) seedling growth in the greenhouse and subsequent yield in the field. Enrichment with CO2 and supplementary lighting for almost-equal-to 3 weeks before transplanting increased accumulation of dry matter in shoots by almost-equal-to 50% compared with the control, while root dry weight increased 49% for tomato and 62% for pepper. Early yields increased by almost-equal-to 15% and 11% for tomato and pepper, respectively.

KEYWORDS: CO2, NITROGEN- FERTILIZATION, VEGETABLE TRANSPLANT PRODUCTION

665
Figueira, A., and J. Janick. 1994. Optimizing carbon-dioxide and light levels during in-vitro culture of theobroma-cacao. *Journal of the American Society for Horticultural Science 119(4):865-871.*

In vitro culture of axillary cotyledonary shoots of Theobroma cacao L. (cacao) under increasing CO2 concentration from ambient to 24,000 ppm (culture tube levels) significantly increased total shoot elongation, number of leaves, leaf area per explant, and shoot dry and fresh weight. Although light was necessary for the CO2 response, the effect of various photon fluxes was not significant for the measured growth parameters. Net photosynthesis estimated on the basis of CO2 depletion in culture tubes increased 3.5 times from 463 to 2639 ppm CO2, and increased 1.5 times from 2639 to 14,849 ppm CO2, but declined from 14,849 to 24,015 ppm CO2. Ethylene concentration in culture vessels increased under enriched CO2 conditions. Depletion of nutrients (fructose, K, Ca, Mg, and P) from the medium was increased under enriched CO2 conditions.

KEYWORDS: AMELONADO, CO2- ENRICHMENT, GROWTH, PLANTLETS, SHOOT PROLIFERATION, STRAWBERRY, TISSUE

666
Figueira, A., A. Whipkey, and J. Janick. 1991. Increased co2 and light promote invitro shoot growth and development of theobroma-cacao. *Journal of the American Society for Horticultural Science 116(3):585-589.*

Axillary shoots of cacao (Theobroma cacao L.), induced in vitro with cytokinins (BA or TDZ), elongated and produced leaves only in the presence of cotyledons and/or roots. Detached axillary shoots, which do not grow in vitro under conventional tissue culture protocols, rooted with auxin and developed normally in vivo. Detached axillary shoots from cotyledonary nodes and single-node cuttings from mature plants were induced to elongate and produce normal leaves in the presence of 20,000 ppm CO2 and a photosynthetic photon flux density (PPFD) of 150 to 200-mu-mol.s-1.m-2. Subcultured nodal cuttings continued to elongate and produce leaves under elevated CO2 and light levels, and some formed roots. Subculture of microcuttings under CO2 enrichment could be the basis for a rapid system of micropropagation for cacao. Chemical names used: N- (phenylmethyl)-1H-purin-6-amine (BA); 1H-indole-3-butyric acid (IBA); alpha-naphthaleneacetic acid (NAA); thidiazuron (TDZ).

KEYWORDS: CULTIVATED INVITRO, L VAR AMELONADO, PROLIFERATION, PROPAGATION, TISSUES

667
Finlayson, S.A., and D.M. Reid. 1996. The effect of CO2 On ethylene evolution and elongation rate in roots of sunflower (Helianthus annuus)

seedlings. *Physiologia Plantarum 98(4):875-881.*

Both carbon dioxide and ethylene can affect the rate of root elongation. Carbon dioxide can also promote ethylene biosynthesis by enhancing the activity of 1-aminocylopropane-1- carboxylic acid (ACC) oxidase. Since the amount of CO2 in the soil air, and in the atmosphere surrounding roots held in enclosed containers, is known to vary widely, we investigated the effects of varying CO2 concentrations on ethylene production by excised and intact sunflower roots (Helianthus annuus L. cv. Dahlgren 131). Seedlings were germinated in an aeroponic system in which the roots hung freely in a chamber and were misted with nutrient solution. This allowed for treatment, manipulation and harvest of undamaged and minimally disturbed roots. While exposure of excised roots to 0.5% CO2 could produce a small increase in ethylene production (compared to roots in ambient CO2), CO2 concentrations of 2% and above always inhibited ethylene evolution. This inhibition of ethylene production by CO2 was attributed to a reduction in the availability of ACC; however, elevated CO2 had no effect on ACC oxidase activity. ACC levels in excised roots were depressed by CO2 at a concentration of 2% (as compared to ambient CO2), but n-malonyl-ACC (MACC) levels were not affected. Treating intact roots with 2% CO2 inhibited elongation by over 50%. Maximum inhibition of elongation occurred 1 h after the CO2 treatment began, but elongation rates returned to untreated values by 6 h. Supplying these same intact roots with 2% CO2 did not alter ethylene evolution. Thus, in excised sunflower roots 2% CO2 treatment reduces ethylene evolution by lowering the availability of ACC. Intact seedlings respond differently in that 2% CO2 does not affect ethylene production in roots. These intact roots also temporarily exhibit a significantly reduced rate of elongation in response to 2% CO2.

KEYWORDS: 1-AMINOCYCLOPROPANE-1-CARBOXYLATE OXIDASE, ACC OXIDASE, ACTIVATION, CARBON DIOXIDE, FORMING ENZYME, GROWTH, PLANTS, RESPIRATION, SOIL O2, WATER

668

Firbank, L.G., A.R. Watkinson, L.R. Norton, and T.W. Ashenden. 1995. Plant-populations and global environmental-change - the effects of different temperature, carbon-dioxide and nutrient regimes on density-dependence in populations of vulpia-ciliata. *Functional Ecology 9(3):432-441.*

1. Monocultures of Vulpia ciliata spp. ambigua were subjected to a range of temperatures, CO2, nutrient and density regimes in a factorial design housed within solar-domes. Temperature treatments were imposed at ambient and +3 degrees C levels, CO2 at ambient and +340 ppm, and there were three levels of nutrients and eight levels of densities ranging from 156 to 31250 seeds m(-2). The abiotic treatments were imposed after emergence. 2. There was little mortality and this was unrelated to the treatments. Plants grew more quickly at the high temperature, high nutrient and low density regimes, and flowering was earlier at the high temperature regime. 3. At seed set, biomass per plant and seed production per plant were analysed by analysis of variance and by fitting mean yield- density models expanded to account for different environmental conditions. Biomass and fecundity were greatest at high temperature, high nutrient and low density regimes. Allocation of biomass to shoots was greater at the high temperatures, as were seed number/shoot biomass ratios. Any effects of CO2 were negligible. The parameter b describing the nature of the relationship between seed production per plant and density was always less than unity but was greater at the higher temperature regime. The response to density was therefore undercompensating in all conditions, implying that populations would display monotonic damping to equilibrium densities. 4. Under proposed future environmental regimes, V. ciliata has the capacity for more rapid population growth from low levels and for a northwards range shift. However, if open ground is not maintained, its habitat may become dominated by species that are more competitive or that have a higher rate of increase.

KEYWORDS: BRECKLAND, CLIMATE, CO2- ENRICHMENT, ELEVATED CO2, FASCICULATA, GROWTH-RESPONSES, PHYSIOLOGY, SIMULATION, SINGLE-SPECIES POPULATIONS, SOURCE-SINK RELATIONS

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Fischer, B.U., M. Frehner, T. Hebeisen, S. Zanetti, F. Stadelmann, A. Luscher, U.A. Hartwig, G.R. Hendrey, H. Blum, and J. Nosberger. 1997. Source-sink relations in Lolium perenne L. as reflected by carbohydrate concentrations in leaves and pseudo-stems during regrowth in a free air carbon dioxide enrichment (FACE) experiment. *Plant, Cell and Environment 20(7):945-952.*

The effect of an elevated partial pressure of CO2 (P-CO2) on carbohydrate concentrations in source leaves and pseudostems (stubble) of Lolium perenne L., (perennial ryegrass) during regrowth was studied in a regularly defoliated grass sward in the field, The free air carbon dioxide enrichment (FACE) technology enabled natural environmental conditions to be provided, Two levels of nitrogen (N) supply were used to modulate potential plant growth. Carbohydrate concentrations in source leaves were increased at elevated P-CO2, particularly at low N supply, Elevated leaf carbohydrate concentrations were related to an increased structural carbon (C) to N ratio and thus reflected an increased C availability together with a N- dependent sink limitation, Immediately after defoliation, apparent assimilate export rates (differences in the carbohydrate concentrations of young source leaves measured in the evening and on the following morning) showed a greater increase at elevated p(CO2) than at ambient p(CO2); however, replenishment of carbohydrate reserves was not accelerated Distinct, treatment-dependent carbohydrate concentrations in pseudo-stems suggested an increasing degree of C-sink limitation from the treatment at ambient p(CO2) with high N supply to that at elevated P-CO2 With low N supply. During two growing seasons, no evidence of a substantial change in the response of the carbohydrate source in L. perenne to elevated p(CO2) was found, Our results support the view that the response of L. perenne to elevated p(CO2) is restricted by a C- sink limitation, which is particularly severe at low N supply.

KEYWORDS: ELEVATED CO2, GROWTH, LEAF, PASTURE TURVES, PLANTS, RESPIRATION, RYEGRASS, SIMULATED SEASONAL-CHANGES, TEMPERATURE, TRIFOLIUM- REPENS

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Fischer, M., D. Matthies, and B. Schmid. 1997. Responses of rare calcareous grassland plants to elevated CO2: a field experiment with Gentianella germanica and Gentiana cruciata. *Journal of Ecology 85(5):681-691.*

1 Endangered plant species may be particularly vulnerable to global change. We investigated differences in the behaviour of the rare calcareous grassland species Gentiana cruciata and Gentianella germanica under ambient (360 mu l l(-1)) and elevated CO2 (600 mu l l(-1)) in a field experiment. 2 Rosettes of G. germanica and C. cruciata were planted into grassland plots with 29 other plant species. Each of the 30 rosettes of G. germanica in a plot represented a different maternal seed family, whereas G. cruciata was grown from a mixture of seeds from one field site. After overwintering, eight of the 12 plots were equipped with open-top chambers, four of which were run at ambient and four at elevated CO2 concentrations; the remaining four plots were left without chambers. 3 CO2 concentration did not significantly affect growth and survival of G. cruciata. Rosette diameter increased by 70% over 1 year. 4 Overall only 13.6% of transplanted G. germanica survived for 1 year. Elevated CO2 reduced survival by 57% (this reduction was

only marginally significant due to large variation between plots) and seed set by 46%. Both these effects appeared to be mediated by competition from other species since survival and seed set were negatively correlated with total plot biomass at the time of fastest growth in June 1994 and at the time of fruit set in October, respectively. Compared with plots under ambient CO2, population growth rate (based on survival and reproduction) was reduced by 56% under elevated CO2. 5 There were no significant effects of elevated CO2 on leaf characters in either species. 6 The sugar concentration of the nectar of G. germanica was increased by 36% under elevated CO2 but its composition remained unchanged. 7 Significant interactions between the effects of seed family and CO2 concentration on demographic parameters in G. germanica indicated large genetic variation in the response to elevated CO2, which represents evolutionary potential. Although predictions based on mean responses are therefore unreliable, the majority of genotypes reacted negatively to elevated CO2, suggesting that competitive exclusion and extinction of G. germanica would occur at many sites before populations could adapt to increased concentrations of CO2.

KEYWORDS: ATMOSPHERIC CO2, BIOMASS PRODUCTION, CHALK GRASSLANDS, CLOVER TRIFOLIUM-REPENS, GROWTH, PERFORMANCE, RYEGRASS LOLIUM-PERENNE, SHORT-LIVED FORBS, TEMPERATURE, WHITE CLOVER

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Fiscus, E.L., and C.D. Reid. 1995. Pollutant ozone does not affect stomatal limitation to photosynthesis in soybean in ambient or elevated co2. *Plant Physiology 108(2):63.*

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Fiscus, E.L., C.D. Reid, J.E. Miller, and A.S. Heagle. 1997. Elevated CO2 reduces O-3 flux and O-3-induced yield losses in soybeans: Possible implications for elevated CO2 studies. *Journal of Experimental Botany 48(307):307-313.*

Soybeans were grown for three seasons in open-top field chambers to determine (1) whether elevated CO2 (360 Versus 700 mu mol mol(-1)) alleviates some of the yield loss due to pollutant O-3, (2) whether the partial stomatal closure resulting froth chronic O-3 exposure (charcoal-filtered air versus 1.5 x ambient concentrations) is a cause or result of decreased photosynthesis, and (3) possible implications of CO2/O-3 interactions to climate change studies using elevated CO2. Leaf conductance was reduced by elevated CO2, regardless of O-3 level, or by exposure to O-3 alone. AS a result of these effects on conductance, high CO2 reduced estimated midday O-3 flux into the leaf by an average of 50% in charcoal-filtered air and 35% in the high O-3 treatment. However, while exposure to O-3 reduced seed yields by 41% at ambient CO2 levels, the yield reduction was completely ameliorated by elevated CO2. The threshold midday O-3 flux for yield loss appears to be 20-30 nmol m(-2) s(-1) in this study. Although elevated CO2 increased total biomass production, it did not increase seed yields. A/C- i curves show a large reduction in the stomatal limitation to photosynthesis due to elevated CO2, but no effect of O-3. These data demonstrate that (1) reduced conductance due to O-3 is the result, and not the cause, of reduced photosynthesis, (2) 700 mu mol mol(-1) CO2 can completely ameliorate yield losses due to O-3 within the limits of these experiments, and (3) some reports of increased yields under elevated CO2 treatments may, at least in part, reflect the amelioration of unrecognized suppression of yield by O-3 or other stresses.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, B RADIATION, CONDUCTANCE, ENRICHMENT, GROWTH, LEAF RESPIRATION, OZONE, PHOTOSYNTHESIS, POLLUTANTS, WATER DEFICIT

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Fitter, A.H., J.D. Graves, J. Wolfenden, G.K. Self, T.K. Brown, D. Bogie, and T.A. Mansfield. 1997. Root production and turnover and carbon budgets of two contrasting grasslands under ambient and elevated atmospheric carbon dioxide concentrations. *New Phytologist 137(2):247-255.*

Monoliths of two contrasting vegetation types, a species-rich grassland on a brown earth soil over limestone and a species- poor community on a peaty gley, were transferred to solardomes and grown under ambient (350 mu l l(-1)) and elevated (600 mu l l(-1)) CO2 for 2 yr. Shoot biomass was unaltered but root biomass increased by 40-50% under elevated CO2. Root production was increased by elevated CO2 in the peat soil, measured both as instantaneous and cumulative rates, but only the latter measure was increased in the limestone soil. Root growth was stimulated more at 6 cm depth than at 10 cm in the limestone soil. Turnover was faster under elevated CO2 in the peat soil, but there was only a small effect on turnover in the limestone soil. Elevated CO, reduced nitrogen concentration in roots and might have increased mycorrhizal colonization. Respiration rate was correlated with N concentration, and was therefore lower in roots grown at elevated CO2. Estimates of the C budget of the two communities, based upon root production and on net C uptake, suggest that C sequestration in the peat soil increases by c. 0.2 kg C m(-2) yr(-1) (= 2 t ha yr(-1)) under elevated CO2.

KEYWORDS: BIOMASS, CO2- ENRICHMENT, GROWTH, STORAGE

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Fitter, A.H., G.K. Self, J. Wolfenden, M.M.I. vanVuuren, T.K. Brown, L. Williamson, J.D. Graves, and D. Robinson. 1996. Root production and mortality under elevated atmospheric carbon dioxide. *Plant and Soil 187(2):299-306.*

An essential component of an understanding of carbon flux is the quantification of movement through the root carbon pool. Although estimates have been made using radiocarbon, the use of minirhizotrons provides a direct measurement of rates of root birth and death. We have measured root demographic parameters under a semi-natural grassland and for wheat. The grassland was studied along a natural altitudinal gradient in northern England, and similar turf from the site was grown in elevated CO2 in solardomes. Root biomass was enhanced under elevated CO2. Root birth and death rates were both increased to a similar extent in elevated CO2, so that the throughput of carbon was greater than in ambient CO2, but root half-lives were shorter under elevated CO2 only under a Juncus/Nardus sward on a peaty gley soil, and not under a Festuca turf on a brown earth soil. In a separate experiment, wheat also responded to elevated CO2 by increased root production, and there was a marked shift towards surface rooting: root development at a depth of 80-85 cm was both reduced and delayed. In conjunction with published results for trees, these data suggest that the impact of elevated CO2 will be system- dependent, affecting the spatio-temporal pattern of root growth in some ecosystems and the rate of turnover in others. Turrnover is also sensitive to temperature, soil fertility and other environmental variables, all of which are likely to change in tandem with atmospheric CO2 concentrations. Differences in turnover and time and location of rhizodeposition may have a large effect on rates of carbon cycling.

KEYWORDS: CO2- ENRICHMENT, FORESTS, GRASSES, GROWTH, PATTERNS, RESPONSES, TURNOVER

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Flagella, Z., R.G. Campanile, M.C. Stoppelli, A. De Caro, and N. Di Fonzo. 1998. Drought tolerance of photosynthetic electron transport under CO2-enriched and normal air in cereal species. *Physiologia*

Plantarum 104(4):753-759.

The quantum yield of photosynthetic electron transport (Phi PSII), evaluated by means of chlorophyll (Chl) fluorescence analysis, has proven to be a useful screening test for drought tolerance in durum wheat (Triticum durum Desf.). To explore the potential of this parameter further in detecting drought- tolerant genotypes, three cereal species were studied; Phi PSII measurements were carried out under two different gas mixtures, at three points of the induction curve (to obtain the maximal Phi PSII and both the transient and steady-state actual Phi PSII), and at three different water stress levels (moderate, severe and drastic). The species investigated were durum and bread wheat (Triticum aestivum L.) and barley (Hordeum vulgare L.); two cultivars per species, characterized by different levels of drought tolerance, were tested. The two gas mixtures used were normal air (21% O-2, 0.035% CO2 in N-2) to monitor the whole photosynthetic process under physiological conditions, and CO2 enriched-low O-2 air (1% O-2, 5% CO2 in N- 2) to monitor Phi PSII reduction under stress mainly related to Calvin cycle activity. When Phi PSII related to both assimilatory and non-assimilatory metabolism was evaluated, the cultivar differences observed under normal air were more representative of the agronomic performance upon drought stress than under high CO2-low O-2 air. Maximal Phi PSII showed no difference among either cultivars, gas mixtures or stress levels, the efficiency of excitation capture being highly resistant to drought. The Phi PSII evaluated during the transient yielded predictable values in respect of drought tolerance for durum wheat and barley cultivars, highlighting the key role of regulatory processes such as the Mehler peroxidase reaction and possibly also cyclic electron transport, in preventing overreduction under stress. The results clearly show that when Chi fluorescence analysis is used as a parameter in plant breeding, different experimental conditions should be used depending on the physiological mechanism that is bred or selected for.

KEYWORDS: CARBON ASSIMILATION, CHLOROPHYLL FLUORESCENCE, CULTIVARS, DURUM-WHEAT, EFFICIENCIES, LIGHT, PHOTOINHIBITION, PHOTOSYSTEM, QUANTUM YIELD, WATER

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Flanagan, L.B., S.L. Phillips, J.R. Ehleringer, J. Lloyd, and G.D. Farquhar. 1994. Effect of changes in leaf water oxygen isotopic composition on discrimination against (coo)-o-18-o-16 during photosynthetic gas-exchange. *Australian Journal of Plant Physiology 21(2):221-234.*

Photosynthetic gas exchange measurements were combined with measurements of the carbon and oxygen stable isotopic composition of CO2 after it passed over a leaf of Phaseolus vulgaris or Senecio spp. plants held in a controlled environment chamber. Calculations were then made of discrimination by the leaf against (CO2)-C-13 and (COO)-O-18-O- 16. Leaves were maintained at different vapour pressure gradients in order to generate a range of leaf water O-18/O-16 ratios. The O-18 content of leaf water increased when plants were exposed to higher vapour pressure deficits. The observed (COO)-O-18-O-16 discrimination values also increased with an increase in the leaf-air vapour pressure gradient and the associated change in leaf water 18/(OO)-O-16 values. In addition, the observed (COO)-O-18-O-16 discrimination values were strongly correlated with values predicted by a mechanistic model of isotopic fractionation.

KEYWORDS: CARBONIC-ANHYDRASE, CO2 DIFFUSION, DEUTERIUM, ENRICHMENT, HYDROGEN, LEAVES, O-18, PLANTS, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE, STABLE OXYGEN

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Flexas, J., M. Badger, W.S. Chow, H. Medrano, and C.B. Osmond. 1999. Analysis of the relative increase in photosynthetic O-2 uptake when photosynthesis in grapevine leaves is inhibited following low night temperatures and/or water stress. *Plant Physiology 121(2):675-684.*

We found similarities between the effects of low night temperatures (5 degrees C-10 degrees C) and slowly imposed water stress on photosynthesis in grapevine (Vitis vinifera L.) leaves. Exposure of plants growing outdoors to successive chilling nights caused light- and CO2 saturated photosynthetic O-2 evolution to decline to zero within 5 d. Plants recovered after four warm nights. These photosynthetic responses were confirmed in potted plants, even when roots were heated. The inhibitory effects of chilling were greater after a period of illumination, probably because transpiration induced higher water deficit. Stomatal closure only accounted for part of the inhibition of photosynthesis. Fluorescence measurements showed no evidence of photoinhibition, but nonphotochemical quenching increased in stressed plants. The most characteristic response to both stresses was an increase in the ratio of electron transport to net O-2 evolution, even at high external CO2 concentrations. Oxygen isotope exchange revealed that this imbalance was due to increased O-2 uptake, which probably has two components: photorespiration and the Mehler reaction. Chilling- and drought-induced water stress enhanced both O-2 uptake processes, and both processes maintained relatively high rates of electron flow as CO2 exchange approached zero in stressed leaves. Presumably, high electron transport associated with O-2 uptake processes also maintained a high Delta pH, thus affording photoprotection.

KEYWORDS: CHLOROPHYLL FLUORESCENCE, CO2 ASSIMILATION, ELECTRON-TRANSPORT, LIGHT, MEHLER-PEROXIDASE REACTION, OXYGEN- EXCHANGE, PHOTOINHIBITION, PLANTS, QUANTUM YIELD, VITIS-VINIFERA L

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Foley, J.A., S. Levis, I.C. Prentice, D. Pollard, and S.L. Thompson. 1998. Coupling dynamic models of climate and vegetation. *Global Change Biology 4(5):561-579.*

Numerous studies have underscored the importance of terrestrial ecosystems as an integral component of the Earth's climate system. This realization has already led to efforts to link simple equilibrium vegetation models with Atmospheric General Circulation Models through iterative coupling procedures. While these linked models have pointed to several possible climate- vegetation feedback mechanisms, they have been limited by two shortcomings: (i) they only consider the equilibrium response of vegetation to shifting climatic conditions and therefore cannot be used to explore transient interactions between climate and vegetation; and (ii) the representations of vegetation processes and land-atmosphere exchange processes are still treated by two separate models and, as a result, may contain physical or ecological inconsistencies. Here we present, as a proof concept, a more tightly integrated framework for simulating global climate and vegetation interactions. The prototype coupled model consists of the GENESIS (version 2) Atmospheric General Circulation Model and the IBIS (version 1) Dynamic Global Vegetation Model. The two models are directly coupled through a common treatment of land surface and ecophysiological processes, which is used to calculate the energy, water, carbon, and momentum fluxes between vegetation, soils, and the atmosphere. On one side of the interface, GENESIS simulates the physics and general circulation of the atmosphere. On the other side, IBIS predicts transient changes in the vegetation structure through changes in the carbon balance and competition among plants within terrestrial ecosystems. As an initial test of this modelling framework, we perform a 30 year simulation in which the coupled model is supplied with modern CO2 concentrations, observed ocean temperatures, and modern insolation. In this exploratory study, we run the GENESIS atmospheric model at relatively coarse horizontal resolution (4.50

latitude by 7.5 degrees longitude) and IBIS at moderate resolution (2 degrees latitude by 2 degrees longitude). We initialize the models with globally uniform climatic conditions and the modern distribution of potential vegetation cover. While the simulation does not fully reach equilibrium by the end of the run, several general features of the coupled model behaviour emerge. We compare the results of the coupled model against the observed patterns of modern climate. The model correctly simulates the basic zonal distribution of temperature and precipitation, but several important regional biases remain. In particular, there is a significant warm bias in the high northern latitudes, and cooler than observed conditions over the Himalayas, central South America, and north-central Africa. In terms of precipitation, the model simulates drier than observed conditions in much of South America, equatorial Africa and Indonesia, with wetter than observed conditions in northern Africa and China. Comparing the model results against observed patterns of vegetation coves shows that the general placement of forests and grasslands is roughly captured by the model. In addition, the model simulates a roughly correct separation of evergreen and deciduous forests in the tropical, temperate and boreal zones. However, the general patterns of global vegetation cover are only approximately correct: there are still significant regional biases in the simulation. In particular, forest cover is not simulated correctly in large portions of central Canada and southern South America, and grasslands extend too far into northern Africa. These preliminary results demonstrate the feasibility of coupling climate models with fully dynamic representations of the terrestrial biosphere. Continued development of fully coupled climate-vegetation models will facilitate the exploration of a broad range of global change issues, including the potential role of vegetation feedbacks within the climate system, and the impact of climate variability and transient climate change on the terrestrial biosphere.

KEYWORDS: ATMOSPHERIC CO2, GENERAL-CIRCULATION MODELS, LEAF, PHOTOSYNTHESIS, PLANT FUNCTIONAL TYPES, SENSITIVITY, STOMATAL CONDUCTANCE, TERRESTRIAL BIOSPHERE, TRANSFER SCHEME LSX, TRANSPIRATION

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Fonseca, F., C.G. Bowsher, and I. Stulen. 1997. Impact of elevated atmospheric CO2 on nitrate reductase transcription and activity in leaves and roots of Plantago major. *Physiologia Plantarum 100(4):940-948.*

Vegetative plants of an inbred line, A4, of Plantage major ssp. pleiosperma (L.) Pilger were grown at 350 mu l 1(-1) or at elevated (700 mu l l(-1)) CO2 in non-limiting nutrient solution with nitrate. Both the relative growth rate (RGR) and the root to total plant weight ratio (RWR) were increased by elevated CO2. However, the stimulation of both RGR and RWR was transient and did not last longer than 8 days. To investigate the physiological mechanisms involved in this stimulation, related changes in C/N metabolism were examined. In the roots soluble sugar concentration increased during the transient period of RGR stimulation (up to 23%), as did the root respiration rate. Changes in nitrogen metabolism were also restricted to this period and consisted of an increase in (1) in vivo and in vitro root nitrate reductase (EC 1.6.6.1) activity, (2) in vitro leaf nitrate reductase activity, (3) leaf and root nitrate reductase mRNA and (4) reduced nitrogen concentration in the roots. The elevated CO2-related signal for the increase in nitrate reductase transcript levels in the roots is discussed in terms of the increased availability of soluble sugars. The results suggest that the short-term enhancement of root carbon and nitrogen metabolism may be responsible for the transient effect of elevated CO, on whole plant RGR.

KEYWORDS: ASSIMILATION, CARBOHYDRATE CONTENT, CARBON DIOXIDE, EXPRESSION, GROWTH, MAIZE, METABOLISM, NITRITE-REDUCTASE, PHOTOSYNTHESIS, RAPID MODULATION

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Fonseca, F., J. DenHertog, and I. Stulen. 1996. The response of Plantago major ssp pleiosperma to elevated CO2 is modulated by the formation of secondary shoots. *New Phytologist 133(4):627-635.*

The effect of elevated CO2 on the relative growth rate (RGR) of Plantago major ssp. pleiosperma was studied during the vegetative stage, in relation to plant development, by growing plants at 350 mu l l(-1) or at 700 mu l l(-1) CO2 in non- limiting nutrient solution with nitrate. To minimize interference by the accumulation of non-structural carbohydrates in the interpretation of results, RGR was expressed on a f. wt basis (RGR(FW)), as were all plant weight ratios. Stimulation of the RGR(FW) Of the whole plant by elevated CO2 was transient, and did not last longer than 8 d. At the same time a transient increase in root weight ratio (RWR) was observed. In order to investigate whether the transient effect of elevated CO2 on RGR(FW) was size-dependent, the data were plotted versus total f. wt (log(e) transformed). The transient period of stimulation of RGR(FW) and of RWR by elevated CO2 was still found, but in both CO2 treatments RGR(FW) decreased after a certain plant size had been reached. This size coincided with the stage at which secondary shoots started to develop, and was reached earlier in plants grown at elevated CO2. The RGR of these secondary shoots (RGR(see)) was Still increased when the period of whole plant stimulation of RGR(FW) had ended, indicating that the development of these new sinks took priority over a continuation of the stimulation of RWR. It is hypothesized that in this Plantago subspecies the response of the RGR(FW) of the whole plants to elevated CO2 is modulated by the formation of secondary shoots. Apparently, partitioning of the extra soluble carbohydrates at elevated CO2 to this tissue takes precedence over partitioning to the roots. resulting in a cessation of stimulation of plant RGR(FW) by elevated CO2.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CARBON-DIOXIDE, COTTON, ENRICHMENT, PHOTOSYNTHESIS, PHYSIOLOGY, RELATIVE GROWTH-RATE, RESPIRATION, SEEDLINGS, TEMPERATURE

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Fordham, M., J.D. Barnes, I. Bettarini, A. Polle, N. Slee, C. Raines, F. Miglietta, and A. Raschi. 1997. The impact of elevated CO2 on growth and photosynthesis in Agrostis canina L ssp monteluccii adapted to contrasting atmospheric CO2 concentrations. *Oecologia 110(2):169-178.*

The aim of this study was to characterise growth and photosynthetic capacity in plants adapted to long-term contrasting atmospheric CO2 concentrations (C-a). Seeds of Agrostis canina L. ssp. monteluccii were collected from a natural CO2 transect in central-western Italy and plants grown in controlled environment chambers at both ambient and elevated CO2 (350 and 700 mu mol mol(-1)) in nutrient-rich soil. Seasonal mean C-a at the source of the plant material ranged from 610 to 451 mu mol CO2 mol(-1), derived from C-4 leaf stable carbon isotope discrimination (delta(13)C). Under chamber conditions, CO2 enrichment stimulated the growth of all populations. However, plants originating from elevated C-a exhibited higher initial relative growth rates (RGRs) irrespective of chamber CO2 concentrations and a positive relationship was found between RGR and C-a at the seed source. Seed weight was positively correlated with C-a, but differences in seed weight were found to explain no more than 34% of the variation in RGRs at elevated CO2. Longer-term experiments (over 98 days) on two populations originating from the extremes of the transect (451 and 610 mu mol CO2 mol(-1)) indicated that differences in growth between populations were maintained when plants were grown at both 350 and 700 mu mol CO2 mol(-1). Analysis of leaf material revealed an increase in the cell wall fraction (CWF) in plants grown at elevated CO2, with plants originating from high C-a exhibiting constitutively lower levels but a variable response in terms of the degree of lignification. In vivo gas exchange measurements revealed

no significant differences in light and CO2 saturated rates of photosynthesis and carboxylation efficiency between populations or with CO2 treatment. Moreover, SDS-PAGE/LISA quantification of leaf ribulose bisphosphate carboxylase/oxygenase (Rubisco) showed no difference in Rubisco content between populations or CO2 treatments. These findings suggest that long-term adaptation to growth at elevated CO2 may be associated with a potential for increased growth, but this does not appear to be linked with differences in the intrinsic capacity for photosynthesis.

KEYWORDS: ACCLIMATION, CARBOXYLASE, ECOSYSTEMS, EFFICIENCY, ENRICHMENT, ENVIRONMENT, PLANTS, PROTEINS, RESPONSES, WHEAT

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Fournioux, J.C., and R. Bessis. 1993. Use of carbon-dioxide enrichment to obtain adult morphology of grapevine invitro. *Plant Cell Tissue and Organ Culture 33(1):51-57.*

A procedure has been developed for in vitro propagation of Vitis vinifera 'Pinot noir' from lateral-bud cuttings under high CO2 concentration (1200 mumol mol-1). Because of inhibition of rooting by CO2, this procedure requires a rooting pre-culture of explants on medium with sucrose before the CO2- enriched culture on sucrose-free medium. Shoot growth was enhanced by CO2 enrichment as a result of both a higher rate of leaf production and greater internode elongation. Leaf expansion and tendril growth were promoted and better rooting was obtained. The more significant effect of CO2 enrichment was to promote adult morphology with, in particular, the tendril pattern. Thus, for the first time, grapevine plants have been produced in vitro without typical juvenile characteristics. CO2 enrichment appears to be an interesting process to improve the in vitro propagation of grapevines.

KEYWORDS: CULTURE, MORPHOGENESIS, VITIS-VINIFERA L

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Fowler, D., J.N. Cape, M. Coyle, C. Flechard, J. Kuylenstierna, K. Hicks, D. Derwent, C. Johnson, and D. Stevenson. 1999. The global exposure of forests to air pollutants. *Water, Air, and Soil Pollution 116(1-2):5-32.*

The tall, aerodynamically rough surfaces of forests provide for the efficient exchange of heat and momentum between terrestrial surfaces and the atmosphere. The same properties of forests also provide for large potential rates of deposition of pollutant gases, aerosols and cloud droplets. For some reactive pollutant gases, including SO2, HNO3 and NH3, rates of deposition may be large and substantially larger than onto shorter vegetation and is the cause of the so called "filtering effect" of forest canopies. Pollutant inputs to moorland and forest have been compared using measured ambient concentrations from an unpolluted site in southern Scotland and a more polluted site in south eastern Germany. The inputs of S and N to forest at the Scottish site exceed moorland by 16% and 31% respectively with inputs of 7.3 kg S ha(-1) y and 10.6 kg N ha(-1) y(-1). At the continental site inputs to the forest were 43% and 48% larger than over moorland for S and N deposition with totals of 53.6 kg S ha(-1) y(-1) and 69.5 kg N ha(-)1 y(-)1 respectively. The inputs of acidity to global forests show that in 1985 most of the areas receiving > 1 kg H+ ha(-1) y(-1) as S are in the temperate latitudes, with 8% of total global forest exceeding this threshold. By 2050, 17% of global forest will be receiving > 1 kg H-1 ha(-1) as S and most of the increase is in tropical and sub-tropical countries. Forests throughout the world are also exposed to elevated concentrations of ozone. Taking 60 ppb O-3 as a concentration likely to be phytotoxic to sensitive forest species, a global model has been used to simulate the global exposure of forests to potentially phytotoxic O-3 concentrations for the years 1860, 1950, 1970, 1990 and 2100. The model shows no exposure to concentrations in excess of 60 ppb in 1860, and of the 6% of global forest exposed to concentrations > 60 ppb in 1950, 75% were in temperate latitudes and 25% in the tropics. By 1990 24% of global forest is exposed to O-3 concentrates > 60 ppb, and this increases to almost 50% of global forest by 2100. While the uncertainty in the future pollution climate of global forest is considerable, the likely impact of O-3 and acid deposition is even more difficult to assess because of interactions between these pollutants and substantial changes in ambient CO2 concentration, N deposition and climate over the same period, but the effects are unlikely to be beneficial overall.

KEYWORDS: ATMOSPHERIC AMMONIA, DIOXIDE, DRY DEPOSITION, EXCHANGE, MOORLAND, NITROGEN, POLLUTION, TEMPERATE, TROPOSPHERIC OZONE, VEGETATED SURFACES

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Franchito, S.H., V.B. Rao, and R.R. da Silva. 1998. A parameterization of radiative fluxes suitable for use in a statistical-dynamical model. *Meteorology and Atmospheric Physics 69(1-2):23-38.*

A parameterization of shortwave and longwave radiation fluxes derived from detailed radiative transfer models is included in a global primitive equation statistical-dynamical model (SDM) with two bulk atmospheric layers. The model is validated comparing the model simulations with the observed mean annual and seasonal zonally averaged climate. The results show that the simulation of the shortwave and longwave radiation fluxes matches well with the observations. The SDM variables such as surface and 500hPa temperatures, zonal winds at 250hPa and 750 hPa, vertical velocity at 500 hPa and precipitation are also in good agreement with the observations. A comparison between the results obtained with the present SDM and those with the previous version of the model indicates that the model results improved when the parameterization of the radiative fluxes based on detailed radiative transfer models are included into the SDM. The SDM is used to investigate its response to the greenhouse effect. Sensitivity experiments regarding the doubling of CO2 and the changing of the cloud amount and height an performed. In the case 2xCO(2) the model results are consistent with those obtained from GCMs, showing a warming of the climate system. An enhancement of the greenhouse effect is also noted when the cloud layer is higher. However, an increase of the cloud amount in all the latitude belts provokes an increase of the surface temperature near poles and a decrease in all the other regions. This suggests that the greenhouse effect overcomes the albedo effect in the polar latitudes and the opposite occurs in other regions. In all the experiments the changes in the surface temperature an larger near poles, mainly in the Southern Hemisphere.

KEYWORDS: CLIMATE MODEL, CO2, EARTH, ENERGY-BALANCE, GENERAL-CIRCULATION MODEL, MACROCLIMATE, SEASONAL CYCLE, SENSITIVITY, SOLAR RADIATION, SURFACE-TEMPERATURE

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Franck, V.M., B.A. Hungate, F.S. Chapin, and C.B. Field. 1997. Decomposition of litter produced under elevated CO2: Dependence on plant species and nutrient supply. *Biogeochemistry 36(3):223-237.*

We investigated the effect of CO2 concentration and soil nutrient availability during growth on the subsequent decomposition and nitrogen (N) release from litter of four annual grasses that differ in resource requirements and native habitat. Vulpia microstachys is a native grass found on California serpentine soils, whereas Avena fatua, Bromus hordaceus, and Lolium multiflorum are introduced grasses restricted to more fertile sandstone soils (Hobbs & Mooney 1991). Growth in elevated CO2 altered litter C:N ratio, decomposition, and N release, but the direction and magnitude of the changes differed among plant species and nutrient treatments, Elevated CO2 had relatively

modest effects on C:N ratio of litter, increasing this ratio in Lolium roots (and shoots at high nutrients), but decreasing C:N ratio in Avena shoots. Growth of plants under elevated CO2 decreased the decomposition rate of Vulpia litter, but increased decomposition of Avena litter from the high-nutrient treatment. The impact of elevated CO2 on N loss from litter also differed among species, with Vulpia litter from high-CO2 plants releasing N more slowly than ambient-CO2 litter, whereas growth under elevated CO2 caused increased N loss from Avena litter. CO2 effects on N release in Lolium and Bromus depended on the nutrient regime in which plants were grown. There was no overall relationship between litter C:N ratio and decomposition rate or N release across species and treatments. Based on our study and the literature, we conclude chat the effects of elevated CO2 on decomposition and N release from litter are highly species-specific. These results do not support the hypothesis that CO2 effects on litter quality consistently lead to decreased nutrient availability in nutrient-limited ecosystems exposed to elevated CO2.

KEYWORDS: ATMOSPHERIC CO2, DIOXIDE, ENRICHMENT, GLOBAL CARBON-CYCLE, GROWTH, LEAF LITTER, NITROGEN, QUALITY, RESPONSES, SERPENTINE GRASSLAND

686

Frank, A.B., and A. Bauer. 1996. Temperature, nitrogen, and carbon dioxide effects on spring wheat development and spikelet numbers. *Crop Science 36(3):659-665.*

Spring wheat (Triticum aestivum L.) responds favorably to elevated atmospheric carbon dioxide concentration ([CO2]) at optimum temperatures. Predictions are for air temperatures to increase as global [CO2] increases. Since spring wheat grain yields generally decline as temperature increases, there is a need to understand the effects of both [CO2] and temperature on spring wheat growth, development, and yield potential. Objectives were to evaluate combinations of [CO2], air temperature, and applied N levels on leaf and apex development, spike components, tiller numbers, dry matter, plant height, and water use in spring wheat. 'Amidon' spring wheat was grown in controlled environment chambers at all combinations of 350, 650, and 950 mu L L(-1) [CO2], 0, 100, and 300 kg N ha(-1), and 14/18 degrees C and 22/26 degrees C night/day air temperatures. Temperature affected the Haun stage by growth degree-days (GDD) relationship more than N or [CO2]. The phyllochron in GDD was greater for plants grown at 22/26 degrees C (433 GDD) than at 14/18 degrees C (345 GDD). The Haun stage at apex double ridge and terminal spikelet increased as applied N and [CO2] increased. Fertile spikelet numbers increased as [CO2] and N level increased at 14/18 degrees C, but at 22/26 degrees C, spikelets increased as N increased and decreased as [CO2] increased. Fertile spikelets were greatest at 14/18 degrees C and 650 mu L L(-1) [CO2]. Results suggest that at elevated [CO2] and adequate soil water, air temperature is more important than [CO2] in controlling grain yield potential. Because wheat yield potential at higher temperatures decreased as [CO2] increased, a northly shift in the spring wheat growing areas may occur if global temperatures increased in concert with [CO2].

KEYWORDS: AIR-TEMPERATURE, CO2-ENRICHMENT, GROWTH, PHYSIOLOGY, PLANTS, RATES, RESPONSES, SOIL-WATER, WINTER-WHEAT, YIELD

687

Fredeen, A.L., and C.B. Field. 1995. Contrasting leaf and ecosystem co2 and h2o exchange in avena- fatua monoculture - growth at ambient and elevated co2. *Photosynthesis Research 43(3):263-271.*

Elevated CO2 (ambient + 35 Pa) increased shoot dry mass production in Avena fatua by similar to 68% at maturity. This increase in shoot biomass was paralleled by an 81% increase in average net CO2 uptake (A) per unit of leaf area and a 65% increase in average A at the 'ecosystem' level per unit of ground area. Elevated CO2 also increased 'ecosystem' A per unit of biomass. However, the products of total leaf area and light- saturated leaf A divided by the ground surface area over time appeared to lie on a single response curve for both CO2 treatments. The approximate slope of the response suggests that the integrated light saturated capacity for leaf photosynthesis is similar to 10-fold greater than the 'ecosystem' rate. 'Ecosystem' respiration (night) per unit of ground area, which includes soil and plant respiration, ranged from -20 (at day 19) to -18 (at day 40) mu mol m(-2) s(-1) for both elevated and ambient CO2 Avena. 'Ecosystem' below-ground respiration at the time of seedling emergence was similar to -10 mu mol m(-2) s(- 1), while that occuring after shoot removal at the termination of the experiment ranged from -5 to -6 mu mol m(-2) s(-1). Hence, no significant differences between elevated and ambient CO2 treatments were found in any respiration measure on a ground area basis, though 'ecosystem' respiration on a shoot biomass basis was clearly reduced by elevated CO2. Significant differences existed between leaf and 'ecosystem' water flux. In general, leaf transpiration (E) decreased over the course of the experiment, possibly in response to leaf aging, while 'ecosystem' rates of evapotranspiration (ET) remained constant, probably because falling leaf rates were offset by an increasing total leaf biomass. Transpiration was lower in plants grown at elevated CO2, though variation was high because of variability in leaf age and ambient light conditions and differences were not significant. In contrast, 'ecosystem' evapotranspiration (ET) was significantly decreased by elevated CO2 on 5 out of 8 measurement dates. Photosynthetic water use efficiencies (A/E at the leaf level, A/ET at the 'ecosystem' level) were increased by elevated CO2. Increases were due to both increased A at leaf and 'ecosystem' level and decreased leaf E and 'ecosystem' ET.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, LIMITATION, NUTRIENTS, PHOTOSYNTHESIS, PLANTS, RESPONSES, WATER-USE EFFICIENCY

688

Fredeen, A.L., G.W. Koch, and C.B. Field. 1995. Effects of atmospheric CO2 enrichment on ecosystem CO2 exchange in a nutrient and water limited grassland. *Journal of Biogeography 22(2-3):215-219.*

We have completed 3 years of a study aimed at understanding the impact of elevated atmospheric CO2 on ecosystem properties of annual grasslands at the Jasper Ridge Biological Preserve, Stanford, CA, U.S.A. Measurements of net ecosystem CO2 uptake were made on intact grassland (on serpentine and sandstone derived soils grown in open-top chambers since December 1991). We measured CO2 exchange in the field with transparent Teflon- lined acrylic chambers coupled to an open gas exchange system. Net ecosystem CO2 uptake for both the high productivity sandstone and the low productivity serpentine grassland communities ranged from 2 to 11 mu mol m(-2) ground s(-1) in 1992 and 1993, similar to rates obtained with eddy covariance techniques on the sandstone and serpentine grasslands at Jasper Ridge in a previous study. There was a significant effect of elevated CO2 on net ecosystem CO2 uptake rate (40-48% increase in 1992 and 17-117% increase in 1993: ANOVA P = 0.018). Although elevated CO2 consistently enhanced net ecosystem CO2 uptake at the growth CO2 concentrations, acclimation occurred such that elevated CO2-grown ecosystems had reduced rates of CO2 uptake relative to ambient CO2-grown ecosystems at either ambient or elevated CO2 measurement concentrations of CO2. The reduction in ecosystem level photosynthetic capacity in elevated CO2 treatments was accompanied by decreased foliar ribulose-bis-phosphate carboxylase (rubisco) activity on a weight basis in the species dominant in both grassland communities. Decreases in rubisco activity resulted largely from increases in leaf mass per area in elevated CO2 plants. In general, net ecosystem CO2 uptake was positively correlated with peak biomass. However, the data suggest that biomass yield for a

given level of net ecosystem CO2 uptake may be lower in elevated CO2 chambers, especially in the higher productivity sandstone community.

KEYWORDS: AVAILABILITY, CARBON DIOXIDE, ELEVATED CO2, NITROGEN, PHOTOSYNTHESIS, RESPONSES

689

Fredeen, A.L., G.W. Koch, and C.B. Field. 1998. Influence of fertilization and atmospheric CO2 enrichment on ecosystem CO2 and H2O exchanges in single- and multiple-species grassland microcosms. *Environmental and Experimental Botany 40(2):147-157.*

This paper reports on measurements of net CO2 and H2O exchange from single- and multiple-species microcosms composed of California annual grassland species grown at either ambient or elevated (ambient + 36 Pa) CO2. Microcosms consisted of grassland species grown in PVC tubes (similar to 0.95 m deep x 0.2 m diameter) containing similar to 45 kg of either serpentine or sandstone derived soil or parent material in open-top enclosures under ambient meteorological conditions. Half of the microcosms were left unfertilized (low nutrient) while the other half received an intermediate level of a slow- release (N,P,K) fertilizer (high nutrient). Gas exchange was performed by sealing individual microcosms within a transparent chamber (on clear sunny days) and coupling this to an open gas- exchange system. In fertilized single-species microcosms, elevated CO2 consistently enhanced net 'ecosystem' CO2 exchange (NCE) on a ground area basis in both early and late spring. Among unfertilized single-species microcosms, no significant trends or differences were observed in NCE between those grown at ambient versus elevated CO2. The NCE in sandstone and serpentine multiple-species microcosms was monitored seasonally over a majority of the 1993-1994 growing season. Rates were largely unaffected by growth CO2 or fertilization until after mid-February, 1994. Water-use efficiency (WUE = NCE/evapotranspiration (ET)) was generally enhanced by elevated CO2, but this was primarily a result of enhancements in NCE as opposed to decreases in ET. Enhancements in NCE by elevated CO2 in fertilized single-species microcosms at the growth-CO2, concentration were partially explained by higher above-ground biomass in elevated CO2 microcosms. However, ecosystem-level 'acclimation' occurred such that microcosms grown at elevated CO2 consistently had lower NCE than ambient CO2 treatments at a single measurement CO2 concentration (ambient or elevated). The reduction in apparent ecosystem-level photosynthetic capacity in elevated CO2 microcosms was accompanied by decreases in foliar Rubisco activity, such that NCE measured at ambient CO2 was highly correlated (r = 0.98) with foliar Rubisco activity across the three single-species microcosms in which it was measured.

KEYWORDS: ALPINE GRASSLAND, AVAILABILITY, CARBON DIOXIDE, ELEVATED CO2, GROWTH-RESPONSES, NITROGEN, PHOTOSYNTHESIS, PLANTS, USE EFFICIENCY, WATER-LIMITED GRASSLAND

690

Fredeen, A.L., J.T. Randerson, N.M. Holbrook, and C.B. Field. 1997. Elevated atmospheric CO2 increases water availability in a water-limited grassland ecosystem. *Journal of the American Water Resources Association 33(5):1033-1039.*

Californian annual grassland on sandstone (moderately fertile) and serpentine (very infertile) soils at the Jasper Ridge Biological Preserve, Stanford, California, were exposed to ambient or elevated (ambient + 36 Pa CO2) atmospheric CO2 in open-top chambers since December 1991. We measured ecosystem evapotranspiration with open gas-exchange systems, and soil moisture with time-domain reflectometry (TDR) over 0-15 cm (serpentine) and 0-30 cm (sandstone) depths, at times of peak above ground physiological activity. Evapotranspiration decreased by 12 to 63 percent under elevated CO2 in three consecutive years in the sandstone ecosystem ($p = 0.053$, $p = 0.162$, $p = 0.082$ in 1992, 1993, and 1994, respectively). In correspondence with decreased evapotranspiration, late-season soil moisture reserves in the sandstone were extended temporally by 10 +/- 3 days in 1993 and by 28 +/- 11 days in 1994. The effect of elevated CO2 on soil moisture was greater in the drier spring of 1994 (419 mm annual rainfall) than in 1993 (905 mm annual rainfall). In the serpentine ecosystem, evapotranspiration and soil moisture reserves were not clearly affected by elevated CO2. Soil water may be conserved in drought-affected ecosystems exposed to elevated CO2, but the amount of conservation appears to depend on the relative importance of transpiration and soil evaporation in controlling water flux.

KEYWORDS: AMBIENT, ELECTROMAGNETIC DETERMINATION, EVAPORATION, EXCHANGE, PATTERNS, PLANT, RESPONSES, SCALE, STOMATAL CONTROL, TRANSPIRATION

691

Frederick, J.R., D.M. Alm, J.D. Hesketh, and F.E. Below. 1990. Overcoming drought-induced decreases in soybean leaf photosynthesis by measuring with co2-enriched air. *Photosynthesis Research 25(1):49-57.*

692

Frederick, K.D. 1993. Climate-change impacts on water-resources and possible responses in the mink region. *Climatic Change 24(1-2):83-115.*

The capacity to supply both instream and offstream water uses under alternative climate conditions and likely future changes in population, technology, and water-using practices are examined through an adaptation of the framework developed in the Second National Water Assessment. Two measures of the adequacy of water supplies - the availability of renewable supplies to provide for withdrawal and instream uses and the relation between desired instream flows and current streamflows - are used to examine the impact of the 1931-1940 analog climate (with and without CO2 enrichment) on Missouri, Iowa, Nebraska, and Kansas (MINK). The impacts of the analog climate on water supplies are estimated from actual streamflow data and estimates of the differences in reservoir evaporation under the 1931-1940 analog and the 1951-1980 control climates. A modification of the Erosion Productivity Inventory Calculator (EPIC) model is used to estimate the impacts of the analog climate (with and without CO2 enrichment) on irrigation water use. Water, which is already a scarce resource in the MINK region, would become much scarcer if the climate of the 1930s were to become the norm. Mean assessed total streamflow would drop to 69% of the control climate level for the Missouri River Basin, 71% for the Upper Mississippi, and 93% for the Arkansas. Even in the absence of climate change, MINK will have less water in the year 2030 than it does today because groundwater stocks are being depleted and increased upstream diversions would reduce surface flows into these states. Irrigation and instream uses such as navigation, hydroelectric power production, recreation, and fish and wildlife habitat would be most adversely, impacted by the climate-induced changes in water supplies.

693

Freeman, C., R. Baxter, J.F. Farrar, S.E. Jones, S. Plum, T.W. Ashendon, and C. Stirling. 1998. Could competition between plants and microbes regulate plant nutrition and atmospheric CO2 concentrations? *The Science of the Total Environment 220(2-3):181-184.*

It has been proposed that under high CO2, soil microbes may outcompete plants for access to inorganic nutrients, leading to a negative feedback to the fertilising effects of that CO2. However, tests of the hypothesis using radioisotope tracers indicate that, in the competition for inorganic nutrients, higher CO2 concentrations may actually favour the plants rather than the microflora. The relatively lower microbial metabolism could, however, have an indirect adverse effect on plant nutrition by restricting nutrient cycling in soils, and has the potential to induce negative feedback to rising atmospheric CO2 concentrations.

KEYWORDS: DISSOLVED ORGANIC-MATTER, ELEVATED CARBON-DIOXIDE

694

Frehner, M., A. Luscher, T. Hebeisen, S. Zanetti, F. Schubiger, and M. Scalet. 1997. Effects of elevated partial pressure of carbon dioxide and season of the year on forage quality and cyanide concentration of Trifolium repens L. from a FACE experiment. *Acta Oecologica-International Journal of Ecology 18(3):297-304.*

Differently managed (cutting frequency and N fertilization) Trifolium repens monocultures were grown at 60 Pa and 35 Pa of pCO(2) (partial pressure of CO2) in a Free Air Carbon dioxide Enrichment (FACE) array. The concentrations of cyanide, digestible organic matter, crude protein and net energy for lactation were measured at different harvests throughout the growing season. The average cyanide concentrations differed significantly in the years and the seasons within the year; however, the concentrations were not affected by CO2. Digestible organic matter, crude protein and net energy for lactation differed significantly with the seasons of the year and cutting frequencies. While digestible organic matter and net energy for lactation were not affected by elevated pCO(2), the concentration of crude protein decreased from 288 g kg(-1) at ambient to 251 g kg(-1) at elevated pCO(2). Since the crude protein concentration in herbage from Trifolium monocultures was very high even at elevated CO2, it is suggested that this decrease in crude protein concentration does not negatively affect forage quality. We conclude that, in Trifolium herbage, the seasons of the year and management practices are more decisive for forage quality than changes in pCO(2). We shall discuss how forage quality and cyanide intake by ruminants may, however, be affected by CO2-induced shifts in the proportion of species in mixed plant communities.

KEYWORDS: ECOSYSTEM, HERBIVORE INTERACTIONS, INSECT HERBIVORE, NITROGEN, PHOTOSYNTHESIS, PLANTS, RESPONSES, RISING CO2, ROOT FRACTION, TEMPERATURE

695

Frick, J., S.S. Nielsen, and C.A. Mitchell. 1994. Yield and seed oil content response of dwarf, rapid-cycling brassica to nitrogen treatments, planting density, and carbon- dioxide enrichment. *Journal of the American Society for Horticultural Science 119(6):1137-1143.*

Effects of N level (15 to 30 mM), time of N increase (14 to 28 days after planting), and planting density (1163 to 2093 plants/m(2)) were determined for crop yield responses of dwarf, rapid-cycling brassica (Brassica napus L., CrGC 5-2, Genome: ACaacc). Crops were grown in solid-matrix hydroponic systems and under controlled-environment conditions, including nonsupplemented (ambient) or elevated CO2 concentrations (998 +/- 12 mumol mol(-1)). The highest seed yield rate obtained (4.4 g.m(-2).day(-1)) occurred with the lowest N level (15 mM) applied at the latest treatment time (day 28). In all trials, CO2 enrichment reduced seed yield rate and harvest index by delaying the onset of flowering and senescence and stimulating vegetative shoot growth. The highest shoot biomass accumulation rate (55.5 g.m-2.day(-1)) occurred with the highest N level (30 mM) applied at the earliest time (day 14). Seed oil content was not significantly affected by CO2 enrichment. Maximum seed oil content (30% to 34%, dry weight basis) was obtained using the lowest N level (15 mM) initiated at the latest treatment time (day 28). In general, an increase in seed oil content was accompanied by a decrease in seed protein. Seed carbohydrate, moisture, and ash contents did not vary significantly in response to experimental treatments. Effects of N level and time of N increase were consistently significant for most crop responses. Planting density was significant only under elevated CO2 conditions.

KEYWORDS: AUTUMN, GROWTH, NAPUS, OILSEED RAPE, SIZE

696

Friedlingstein, P., I. Fung, E. Holland, J. John, G. Brasseur, D. Erickson, and D. Schimel. 1995. On the contribution of co2 fertilization to the missing biospheric sink. *Global Biogeochemical Cycles 9(4):541-556.*

A gridded biospheric carbon model is used to investigate the impact of the atmospheric CO2 increase on terrestrial carbon storage. The analysis shows that the calculated CO2 fertilization sink is dependent not just on the mathematical formulation of the "beta factor" but also on the relative controls of net primary productivity (NPP), carbon residence times, and resource availability. The modeled evolution of the biosphere for the period 1850-1990 shows an increasing lag between NPP and the heterotrophic respiration. The time evolution of the modeled biospheric sink (i.e., difference between enhanced NPP and enhanced respiration) does not match that obtained by deconvolution of the ice core CO2 time series. Agreement between the two is reasonable for the first half of the period, but during the recent decades the deconvoluted CO2 increase is much too fast to be explained by the CO2 fertilization effect only. Therefore other mechanisms than CO2 fertilization should also contribute to the missing sink. Our results suggest that about two thirds to three fourths of the 1850-1990 integrated missing sink is due to the CO2 greening of the biosphere. The remainder may be due to the increased level of nitrogen deposition starting around 1950.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CLIMATE, DECOMPOSITION DYNAMICS, ECOSYSTEMS, ELEVATED CO2, MODEL, NITROGEN, RESPONSES, SIMULATION, TROPICAL DEFORESTATION

697

Friedlingstein, P., G. Joel, C.B. Field, and I.Y. Fung. 1999. Toward an allocation scheme for global terrestrial carbon models. *Global Change Biology 5(7):755-770.*

The distribution of assimilated carbon among the plant parts has a profound effect on plant growth, and at a larger scale, on terrestrial biogeochemistry. Although important progress has been made in modelling photosynthesis, less effort has been spent on understanding the carbon allocation, especially at large spatial scales. Whereas several individual-level models of plant growth include an allocation scheme, most global terrestrial models still assume constant allocation of net primary production (NPP) among plant parts, without any environmental coupling. Here, we use the CASA biosphere model as a platform for exploring a new global allocation scheme that estimates allocation of photosynthesis products among leaves, stems, and roots depending on resource availability. The philosophy underlying the model is that-allocation patterns result from evolved responses that adjust carbon investments to facilitate capture of the most limiting resources, i.e. light, water, and mineral nitrogen. In addition, we allow allocation of NPP to vary in response to changes in atmospheric CO2. The relative magnitudes of changes in NPP and resource-use efficiency control the response of root:shoot allocation. For ambient CO2, the model produces realistic changes in above- ground allocation along productivity

gradients. In comparison to the CASA standard estimate using fixed allocation ratios, the new allocation scheme tends to favour root allocation, leading to a 10% lower global biomass. Elevated CO2, which alters the balance between growth and available resources, generally leads to reduced water stress and consequently, decreased root:shoot ratio. The major exception is forest ecosystems, where increased nitrogen stress induces a larger root allocation.

KEYWORDS: ATMOSPHERIC CO2 CONCENTRATION, BIOMASS ALLOCATION, BIOSPHERE-MODEL, INTERNAL NITROGEN CONCENTRATION, LONG-TERM ELEVATION, NET PRIMARY PRODUCTION, PARTITIONING MODEL, PLANT-RESPONSES, SHOOT RATIOS, SURFACE PARAMETERIZATION SIB2

698

Friend, A.D., and P.M. Cox. 1995. Modeling the effects of atmospheric co2 on vegetation atmosphere interactions. *Agricultural and Forest Meteorology 73(3-4):285-295.*

The effect of doubling atmospheric CO2 concentration (C-a) on climate and vegetation is investigated using a combined climate-vegetation model. The vegetation model predicts the response of leaf area index, canopy transpiration (E(T)) and whole-plant carbon balance to changes in climate, soil moisture, and atmospheric CO2 forcing. This model has been embedded in the UK Meteorological Office Single Column Model (SCM), which provides the climate feedback to the vegetation. The vegetation model uses an optimisation approach to predict stomatal resistance, a biochemical model to predict photosynthesis and a simple carbon balance model to predict leaf area. Respiration is calculated as a function of leaf area and vegetation height. Clouds are assumed to be radiatively passive in the SCM to avoid unrealistic feedbacks. Simulations were performed with the fully interactive vegetation-climate model for an Amazon location with the present-day value of C-a (1 x CO2), and twice this value (2 x CO2). In addition, two other types of simulation were performed at both CO2 concentrations: one in which the vegetation component was forced only with 1 x CO2, and one using a fixed surface resistance. The latter case is equivalent to simulations using most current general circulation models. In all the simulations, increased atmospheric CO2 caused an increase in surface temperature owing to increased radiative forcing. With a fixed resistance, mean E(T) was increased by 5.6% and sensible heat flux was reduced by 3.8%. The fully interactive model had significant effects on the response of both climate and productivity to C-a. Increased C-a caused stomatal closure, which resulted in a reduction in mean E(T) Of 25%. The effect of C-a on E(T) was amplified by the positive feedback resulting from the effect of increased air humidity deficit on stomatal resistance.

KEYWORDS: CARBON DIOXIDE, ELEVATED CO2, FIELD, PHOTOSYNTHESIS, SEEDLINGS, STOMATAL CONDUCTANCE, TRANSPIRATION

699

Fritschi, F.B., K.J. Boote, L.E. Sollenberger, and L.H. Allen. 1999. Carbon dioxide and temperature effects on forage establishment: tissue composition and nutritive value. *Global Change Biology 5(7):743-753.*

Atmospheric CO2 concentration ([CO2]) and temperature are likely to increase in the future and may change plant growth and composition characteristics. Rhizoma peanut (Arachis glabrata Benth.) and bahiagrass (Paspalum notatum Flugge) were grown on a natural field soil in temperature-gradient greenhouses to evaluate the effects of elevated [CO2] and temperature on tissue composition and digestibility during the establishment year. Carbon dioxide levels were maintained at 365 (ambient) and 640 mu L CO2 L-1 air. The temperature- gradient greenhouses were regulated to obtain air temperature sectors of 0.2, 1.5, 2.9, and 4.5 degrees C above ambient. Samples were taken of previously undefoliated herbage at 57, 86, 121, 148, and 217 days after planting and entire plots were harvested at 218 days after planting. Elevated [CO2] increased total nonstructural carbohydrate concentration in rhizoma peanut leaves by almost 50%. Rhizoma peanut leaf N concentration was 6% lower at elevated than at ambient [CO2]. The N concentration in new rhizomes of rhizoma peanut was increased by high [CO2], while the N concentration in bahiagrass was not affected by temperature or [CO2]. No effects of [CO2] and temperature were found on neutral detergent fibre in rhizoma peanut leaves or stems; however, elevated [CO2] increased neutral detergent fibre in bahiagrass leaves. Only at season end was in vitro organic matter digestion of rhizoma peanut higher at ambient (623 g kg(-1)) than at elevated [CO2] (609 g kg(-1)). Elevated [CO2] had a greater effect on tissue composition of rhizoma peanut than of bahiagrass. These data suggest that elevated temperature and CO2-induced changes in chemical composition of forage species adapted to humid subtropics will be relatively small, particularly for C4 species.

KEYWORDS: DECIDUOUS TREES, ELEVATED ATMOSPHERIC CO2, GAS-EXCHANGE, GRACILIS C-4, INSECT PERFORMANCE, LEAF, NITROGEN, PASCOPYRUM-SMITHII C-3, PLANT, ROOT FRACTION

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Fritschi, F.B., K.J. Boote, L.E. Sollenberger, L.H. Allen, and T.R. Sinclair. 1999. Carbon dioxide and temperature effects on forage establishment: photosynthesis and biomass production. *Global Change Biology 5(4):441-453.*

Concerns about climatic change have stimulated interest in the response of plants to increasing CO2 concentration ([CO2]), temperature, and their possible interactions. The purpose of this study was to determine the effects of elevated [CO2] and air temperature on photosynthesis, development, and biomass production of rhizoma peanut (Arachis glabrata Benth.) and bahiagrass (Paspalum notatum Flugge) during the establishment year. Forages were grown in four temperature-gradient greenhouses on a natural Grossarenic Paleudult soil profile at temperatures of 0.2, 1.5, 2.9, and 4.5 degrees C above ambient, and at [CO2] of 365 and 640 mu L CO2 L-1 air. Elevated [CO2] accelerated establishment and ground cover of both species. Leaf and canopy photosynthesis of both species increased at elevated [CO2], with greater increases in rhizoma peanut than bahiagrass. Averaged across five sampling dates, total biomass production of rhizoma peanut and bahiagrass responded to elevated [CO2] with a 52 and 9% increase, respectively. Increasing temperature enhanced biomass production of bahiagrass but not rhizoma peanut. Forage yield at the end of the growing season in CO2-enriched treatments was increased over that in ambient [CO2] treatments (385 vs. 318 g m(-2) for rhizoma peanut and 376 vs. 321 g m(-2) for bahiagrass). Overall, the enhancement of rhizoma peanut under elevated [CO2] was greater than that of bahiagrass; however, bahiagrass responded more positively to increasing temperature.

KEYWORDS: AIR CO-2 ENRICHMENT, CLIMATE, ELEVATED ATMOSPHERIC CO2, GRACILIS C-4, GROWTH, LEAF GAS-EXCHANGE, LEAVES, LOLIUM, PASCOPYRUM-SMITHII C-3, RESPONSES

701

Fujii, N., M. Watanabe, Y. Watanabe, and N. Shimada. 1994. Relationship between oxalate synthesis and glycolate cycle in spinach. *Journal of the Japanese Society for Horticultural Science 62(4):789-794.*

The relationship between oxalate synthesis and glycolate pathway in spinach (Spinacia oleracea L. cv. Sunlight) was studied by exposing

seedling to 1,000 PPM CO2-enriched atmosphere. It was observed that CO2-enrichment increased the content of ascorbic acid but decreased that of oxalate. It was presumed that reducing the rate of glycolate synthesis would reduce the content of oxalate. Mature leaves of spinach grown under normal conditions, were fed with [2-C-14] glycolate and [1-C-14] ascorbic acid to compare their contribution as a precursor of oxalate. Using the values of the C-14 distribution to oxalate, photorespiratory glycolate metabolic rate and the turnover rate of ascorbic acid, the rate of oxalate synthesis was calculated. It was observed that glycolate was more efficient as a precursor of oxalate synthesis than it was for ascorbic acid. From these results, we postulate that the oxalate synthesis is closely related to the glycolate cycle.

KEYWORDS: CALCIUM

702

Gahrooee, F.R. 1998. Impacts of elevated atmospheric CO2 on litter quality, litter decomposability and nitrogen turnover rate of two oak species in a Mediterranean forest ecosystem. *Global Change Biology 4(6):667-677.*

Elevated CO2 may affect litter quality of plants, and subsequently C and N cycling in terrestrial ecosystems, but changes in litter quality associated with elevated CO2 are poorly known. Abscised leaf litter of two oak species (Quercus cerris L. and a. pubescens Willd.) exposed to long-term elevated CO2 around a natural CO2 spring in Tuscany (Italy) was used to study the impact of increasing concentration of atmospheric CO2 on litter quality and C and N turnover rates in a Mediterranean-type ecosystem. Litter samples were collected in an area with elevated CO2 (>500 ppm) and in an area with ambient CO2 concentration (360 ppm). Leaf samples were analysed for concentrations of total C, N, lignin, cellulose, acid detergent residue (ADR) and polyphenol. The decomposition rate of litter was studied using a litter bag experiment (12 months) and laboratory incubations (3 months). In the laboratory incubations, N mineralization in litter samples was measured as well (125 days). Litter quality was expressed in terms of chemical composition and element ratios. None of the litter quality parameters was affected by elevated CO2 for the two Quercus species. Remaining mass in a. cerris and Q. pubescens litter from elevated CO2 was similar to that from ambient conditions. C mineralization in Q. pubescens litter from elevated CO2 was lower than that from ambient CO2, but the difference was insignificant. This effect was not observed for Q. cerris. N mineralization was higher from litter grown at elevated CO2, but this difference disappeared at the end of the incubation. Litter of a. pubescens had a higher quality than Q. cerris, and indeed mineralized more rapidly in the laboratory, but not under field conditions.

KEYWORDS: CARBON DIOXIDE, CLIMATE CHANGE, DECOMPOSITION, GROWTH, LEAF LITTER, PHOTOSYNTHESIS, RESPIRATION, RESPONSES, SOIL, TERRESTRIAL ECOSYSTEMS

703

Gallardo, A., and J. Merino. 1998. Soil nitrogen dynamics in response to carbon increase in a Mediterranean shrubland of SW Spain. *Soil Biology and Biochemistry 30(10-11):1349-1358.*

Most models predict that high atmospheric CO2 concentrations will lead to an increase in the C-to-N ratio of litter production in terrestrial ecosystems. The effect of an increase in the soil C-to-N ratio on the nitrogen dynamics in a Mediterranean shrubland was simulated by mixing with the lifter layer wood shavings with a high C-to-N ratio. Samples of mineral soil, taken subsequently eight times during 404 d, were analyzed for total C, total N, total soil carbohydrates, potential net N mineralization, potential net nitrification and microbial biomass-N. We found significant increases in the concentration of total carbohydrates, C-to-N ratio and microbial biomass N in amended soils during the experiment, while potential net N mineralization rate and net nitrification rate significantly decreased; amounts of available nitrogen (NH4+-N + NO3-N) were unaffected by the amendment treatment. However, by the end of the experiment, no significant differences between amended and control soil samples were found. The total carbohydrates-to-K2SO4-extractable total-N ratio was the best predictor of both net mineralization rate and microbial biomass N, showing that the available C-to- available-N ratio is a better indicator of N dynamics than the total C to total N ratio. Our results support the hypothesis that increasing C availability in soils leads to a decrease in N availability for plants through the immobilization of N in microbial biomass and to an increase in the temporal heterogeneity of soil properties in a Mediterranean shrubland.

KEYWORDS: ANNUAL GRASSLAND, DIOXIDE, ECOSYSTEMS, ELEVATED ATMOSPHERIC CO2, MICROBIAL BIOMASS, MINERAL-SOIL, NITRIFICATION, OLD-GROWTH FOREST, PLANTS, TALLGRASS PRAIRIE

704

Galtier, N., C.H. Foyer, E. Murchie, R. Alred, P. Quick, T.A. Voelker, C. Thepenier, G. Lasceve, and T. Betsche. 1995. Effects of light and atmospheric carbon-dioxide enrichment on photosynthesis and carbon partitioning in the leaves of tomato (lycopersicon-esculentum L) plants over-expressing sucrose- phosphate synthase. *Journal of Experimental Botany 46:1335-1344.*

Photosynthetic carbon assimilation, carbon partitioning and foliar carbon budgets were measured in the leaves of transformed tomato plants expressing a maize sucrose-phosphate synthase (SPS) gene in addition to the native enzyme, and in untransformed controls. The maize SPS gene was expressed under control of either the promoter of the small subunit of ribulose 1,5-bisphosphate carboxylase (rbcS promoter; lines 2, 9 and 18) or the 35S promoter from cauliflower mosaic virus (CaMV promoter; line 13). The rate of sucrose synthesis was increased relative to that of starch and sucrose/starch ratios were higher throughout the photoperiod in the leaves of all plants expressing high SPS activity. The leaf carbon budget over the day/night cycle in air at low irradiance (180 mu mol photon m(- 2) s(-1)) was similar in all plants. Net photosynthesis measured in air and at elevated CO2 (800-1500 mu l I-1) on whole plants grown in air at 400 mu mol m(-2) s(-1) irradiance was significantly increased in the high SPS expressors compared to the untransformed controls and was highest where SPS activity was greatest. At high CO2 the stimulation of photosynthesis was more pronounced, We conclude that SPS activity is a major point of control of photosynthesis particularly under saturating light and CO2.

KEYWORDS: ACCLIMATION, BIOSYNTHESIS, CARBOHYDRATE, ELEVATED CO2, GROWTH, INHIBITION, PHASEOLUS-VULGARIS L, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, SPINACH LEAVES, STARCH

705

Gao, K., Y. Aruga, K. Asada, T. Ishihara, T. Akano, and M. Kiyohara. 1991. Enhanced growth of the red alga porphyra-yezoensis ueda in high co2 concentrations. *Journal of Applied Phycology 3(4):355-362.*

Leafy thalli of the red alga Porphyra yezoensis Ueda, initiated from conchospores released from free-living conchocelis, were cultured using aeration with high CO2. It was found that the higher the CO2 concentration, the faster the growth of the thalli. Aeration with elevated CO2 lowered pH in dark, but raised pH remarkably in light with the thalli, because the photosynthetic conversion of HCO3- to OH- and CO2 proceeded much faster than the dissociation of hydrated CO2 releasing

H+. Photosynthesis of the alga was found to be enhanced in the seawater of elevated dissolved inorganic carbon (DIC, CO2 + HC O3- + CO3-). It is concluded that the increased pH in the light resulted in the increase of DIC in the culture media, thus enhancing photosynthesis and growth. The relevance of the results to removal of atmospheric CO2 by marine algae is discussed.

KEYWORDS: ASSIMILATION, CHONDRUS-CRISPUS, DIATOM, INORGANIC-CARBON UPTAKE, MARINE MACROALGAE, PHAEOPHYTA, PHOTOSYNTHESIS, PLANTS, TRANSPORT, WATER

706
Gao, K., Y. Aruga, K. Asada, T. Ishihara, T. Akano, and M. Kiyohara. 1993. Calcification in the articulated coralline alga corallina-pilulifera, with special reference to the effect of elevated co2 concentration. *Marine Biology 117(1):129-132.*

Calcification in Corallina pilulifera Postels et Ruprecht displayed diurnal variations in aerated (350 ppm CO2) culture media, with faster rates during the light than during the dark period. Addition of CO2 (air + 1250 ppm) inhibited calcification. This was attributable to the decreased pH resulting from CO2 addition. Both photosynthesis and calcification were enhanced in seawater, with elevated dissolved inorganic carbon concentrations at a constant pH of 8.2.

KEYWORDS: CAULERPALES, CHLOROPHYCEAE, GROWTH, HALIMEDA, MARINE PLANTS, PHOTOSYNTHESIS, RESPIRATION

707
Gao, K., Y. Aruga, K. Asada, and M. Kiyohara. 1993. Influence of enhanced co2 on growth and photosynthesis of the red algae gracilaria sp and g-chilensis. *Journal of Applied Phycology 5(6):563-571.*

The influence of elevated CO2 concentrations on growth and photosynthesis of Gracilaria sp. and G. chilensis was investigated in order to procure information on the effective utilization of CO2. Growth of both was enhanced by CO2 enrichment (air + 650 ppm CO2, air + 1250 ppm CO2), the enhancement being greater in Gracilaria sp. Both species increased uptake of NO, with CO, enrichment. Photosynthetic inorganic carbon uptake was depressed in G. chilensis by pre- culture (15 days) with CO2 enrichment, but little affected in Gracilaria sp. Mass spectrometric analysis showed that O-2 uptake was higher in the light than in the dark for both species and in both cases was higher in Gracilaria sp. The higher growth enhancement in Gracilaria sp. was attributed to greater depression of photorespiration by the enrichment of CO2 in culture.

KEYWORDS: ANHYDRASE, INORGANIC CARBON, MARINE MACROALGAE, PHYSIOLOGY

708
Gao, Q., and M. Yu. 1998. A model of regional vegetation dynamics and its application to the study of Northeast China Transect (NECT) responses to global change. *Global Biogeochemical Cycles 12(2):329-344.*

We developed a dynamic regional vegetation model to address problems of responses of regional vegetation to elevated ambient CO2 and climatic change. The model takes into consideration both local ecosystem processes within a patch or grid cell, such as plant growth and death, and mass and energy flow, such as plant migration, across adjacent grid cells. The model is able to couple vegetation structure dynamics and primary production processes. The normalized differential vegetation index from meteorological satellite AVHRR was used to parameterize the model. Plant migration rates were derived based on effective seedling distribution around parent plants. The model was applied to Northeast China Transect at a spatial resolution of 10 min latitude by 10 min longitude per grid cell and a temporal resolution of 1 month. The results indicated that with doubled CO2 concentration, a 20% increase in precipitation and a 4 degrees C increase in temperature, the model predicted that net primary productivity (NPP) of Larix forests, conifer-broadleaf mixed forests, Aneurolepidium chinense steppes, Stipa grandis steppes, and wetland and salty meadows would decrease by 15% to 20%. However, NPP of deciduous broadleaf forests, woodland and shrubs, Stipa baicalensis meadow steppes, and desert grasslands would increase by 20% to 115%, as predicted by the model for the same climatic scenario. The average NPP of natural vegetation over the whole transect would decrease slightly, largely because of the compensation between the positive effects of increased CO2 and precipitation and the negative effect of increased evapotranspiration induced by increased temperature.

KEYWORDS: BIOMASS, CLIMATE, FOREST ECOSYSTEM PROCESSES, GENERAL-MODEL, NET PRIMARY PRODUCTIVITY, PHOTOSYNTHESIS, SATELLITE, SENSITIVITY, SIMULATION, TERRESTRIAL BIOSPHERE

709
Gao, Q., and X.S. Zhang. 1997. A simulation study of responses of the northeast China transect to elevated CO2 and climate change. *Ecological Applications 7(2):470-483.*

The spatiotemporal variations of vegetation biomass of the ecological transect in northeast China were simulated. Slate variables of the model included green biomass and nongreen biomass of 12 vegetation categories and water contents of three soil layers. The simulated monthly green biomass was converted into NDVI, or Normalized Differential Vegetation Index of AVHRR (Advanced Very High Resolution Radiometry). A comparison between the modeled and the observed NDVI was made at 10' spatial resolution, Atmospheric CO2 concentration and montiiiy precipitation were used as two driving variables for global change simulation. Effects of precipitation increments on percentage sunshine, relative humidity, radiation, evapotranspiration, and eventually soil water and plant growth, were considered, Two levers of CO2 concentration (present, doubled) and seven levels of precipitation increments (0, 0.05, 0.1, 0.15, 0.2, 0.25, and 0.30) were prescribed for a total of 14 simulation runs. A steady-state solution was obtained for each simulation run. The results of simulation showed that with the present climate conditions, doubling atmospheric CO2 concentration led approximately to a 20.3% increase in green biomass, 11.0% increase in nongreen biomass, 19,0% increase in green NPP, 12.8% increase in nongreen NPP, and 24.9% increase in overall average NPP at steady state, These increases go, respectively, to 32.9, 13.9, 30.0, 20.1, and 23.4% when a 30% precipitation increase was superimposed on the doubled CO2 concentration.

KEYWORDS: FORESTS, LEAF-AREA INDEX, MODEL, PHOTOSYNTHESIS, PRODUCTIVITY, SATELLITE, VEGETATION

710
Garbutt, K., W.E. Williams, and F.A. Bazzaz. 1990. Analysis of the differential response of 5 annuals to elevated CO2 during growth. *Ecology 71(3):1185-1194.*

711
Garcia, J.M. 1993. Effect of co2 in fruit storage atmosphere on olive oil quality. *Grasas Y Aceites 44(3):169-174.*

Olive fruits (Olea europaea, cv. "Picual") were stored at 5- degrees-C and

four different atmospheres (% CO2/% O2/%N2: 0/21/78: 5/20/75; 10/19/71 and 20/17/63). At 5-degrees-C the enrichment of the fruit storage atmosphere with concentrations of CO2 above 5% resulted in a linear increase of the acidity of extracted oils after 60 days of fruit storage time. This fact showed a strong relationship with the appearence of fruit decay. Simple refrigeration of fruits at 5-degrees-C for 60 days was sufficient to mantain the commercial quality of "virgin extra" in oil extracted from them. Oils obtained from fruits stored at 5-degrees-C in CO2 enriched atmospheres showed lower peroxide index and UV absorbance (270 nm), but developed off-flavor. Therefore, greater-than-or-equal-to 5% CO2 concentrations in storage atmosphere of olive fruits for oil production at 5-degrees-C must be avoided.

712

Garcia, J.M., and J. Streif. 1993. Quality and storage potential of pear .1. Influence of ca- storage and ulo-storage conditions. *Gartenbauwissenschaft 58(1):36-41.*

In a CA experiment the storage potential of different pear cultivars was investigated, especially the behaviour of the fruits against elevated CO2 concentrations and/or ultra low oxygen (ULO).The following CA combinations were tested: < 1 % CO2 + 3 % O2; 3 % CO2 + 3 % O2; < 1 % CO2 + 1 % O2; 3 % CO2 + 1 % O2, and refrigerated storage at -1-degrees-C 'Packham's Triumph' showed the best storage potential of all tested cultivars followed by 'Conference' and 'Doyenne' du Comice. The keepability of 'General Leclerc' was only slightly improved by CA conditions compared with cold stored pears. CA storage of 'Alexander Lucas' and 'Bristol Cross' didn't show an obvious advantage because of high CO2 damages. Therefore, CO2 concentrations in CA storage of these two cultivars should be < 1 %. 'Conference' and 'General Leclerc' tolerate up to 2 % CO2, 'Doyenne du Comice' and 'Packham's Triumph' up to 3 % CO2. ULO conditions amplified the CO2 damages in the CO2 sensitive cultivars, but improved the keepability of 'Doyenne du Comice' and 'Packham's Triumph'.

713

Garcia, R.L., S.B. Idso, and B.A. Kimball. 1994. Net photosynthesis as a function of carbon-dioxide concentration in pine trees grown at ambient and elevated co2. *Environmental and Experimental Botany 34(3):337-341.*

Pinus eldarica seedlings were grown in a field of Avondale loam at Phoenix, Arizona within transparent open-top enclosures maintained for 15 months at mean CO2 concentrations of 402 and 788 mu l 1(-1), after which whole-tree net photosynthetic rates were measured at a number of CO2 concentrations ranging from ambient (360 mu l 1(-1)) to 3000 mu l 1(-1). Rates of the low- CO2-treatment trees saturated at approximately five times their ambient-concentration value; while rates of the high-CO2- treatment trees rose linearly across the entire CO2 range investigated to more than 10 times their value al 360 mu l 1(- 1). These findings suggest that long-term exposure to elevated CO2 can increase the ability of trees with unrestricted root systems to respond positively to still higher CO2 concentrations.

KEYWORDS: ACCLIMATION, ENRICHMENT, PLANTS, RESPIRATION

714

Garcia, R.L., S.B. Idso, G.W. Wall, and B.A. Kimball. 1994. Changes in net photosynthesis and growth of pinus-eldarica seedlings in response to atmospheric co2 enrichment. *Plant, Cell and Environment 17(8):971-978.*

Pinus eldarica L. trees, rooted in the natural soil of an agricultural field at Phoenix, Arizona, were grown from the seedling stage in clear-plastic-wall open-top enclosures maintained at four different atmospheric CO2 concentrations for 15 months. Light response functions were determined for one tree from each treatment by means of whole-tree net CO2 exchange measurements at the end of this period, after which rates of carbon assimilation of an ambient-treatment tree were measured across a range of atmospheric COP concentrations. The first of these data sets incorporates the consequences of both the CO2-induced enhancement of net photosynthesis per unit needle area and the CO2-induced enhancement of needle area itself (due primarily to the production of more needles), whereas the second data set reflects only the first of these effects. Hence the division of the normalized results of the first data set by the normalized results of the second set yields a representation of the increase in whole-tree net photosynthesis due to enhanced needle production caused by atmospheric CO2 enrichment. In the solitary trees we studied, the relative contribution of this effect increased rapidly with the CO2 concentration of the air to increase whole-tree net photosynthesis by nearly 50% at a CO2 concentration approximately 300 mu mol mol(-1) above ambient.

KEYWORDS: AMBIENT, CARBON DIOXIDE, ELEVATED CO2, FIELD, LIGHT, PRODUCTIVITY, SCIRPUS- OLNEYI, SOUR ORANGE TREES, TEMPERATURE, YIELD

715

Garcia, R.L., S.P. Long, G.W. Wall, C.P. Osborne, B.A. Kimball, G.Y. Nie, P.J. Pinter, R.L. Lamorte, and F. Wechsung. 1998. Photosynthesis and conductance of spring-wheat leaves: field response to continuous free-air atmospheric CO2 enrichment. *Plant, Cell and Environment 21(7):659-669.*

Spring wheat was grown from emergence to grain maturity in two partial pressures of CO2 (pCO(2)): ambient air of nominally 37 Pa and air enriched with CO2 to 55 Pa using a free-air CO2 enrichment (FACE) apparatus. This experiment was the first of its kind to be conducted within a cereal field without the modifications or disturbance of microclimate and rooting environment that accompanied previous studies, It provided a unique opportunity to examine the hypothesis that continuous exposure of wheat to elevated pCO(2) will lead to acclimatory loss of photosynthetic capacity. The diurnal courses of photosynthesis and conductance for upper canopy leaves were followed throughout the development of the crop and compared to model-predicted rates of photosynthesis. The seasonal average of midday photosynthesis rates was 28% greater in plants exposed to elevated pCO(2) than in contols and the seasonal average of the daily integrals of photosynthesis was 21% greater in elevated pCO(2) than in ambient air. The mean conductance at midday was reduced by 36%. The observed enhancement of photosynthesis in elevated pCO(2) agreed closely with that predicted from a mechanistic biochemical model that assumed no acclimation of photosynthetic capacity. Measured values fell below predicted only in the flag leaves in the mid afternoon before the onset of grain-filling and over the whole diurnal course at the end of grain-filling. The loss of enhancement at this final stage was attributed to the earlier senescence of flag leaves in elevated pCO(2). In contrast to some controlled-environment and field-enclosure studies, this field-scale study of wheat using free-air CO2 enrichment found little evidence of acclimatory loss of photosynthetic capacity with growth in elevated pCO(2) and a significant and substantial increase in leaf photosynthesis throughout the life of the crop.

KEYWORDS: ACCLIMATION, CAPACITY, CARBON-DIOXIDE ENRICHMENT, ELEVATED CO2, GROWTH, LEAF, PRODUCTIVITY, PROTEINS, WATER-USE EFFICIENCY, WINTER-WHEAT

716

Garcia-Ibilcieta, D., and J.C. Pushnik. 1997. Differential gene displays from Pinus ponderosa seedlings experiencing elevated CO2 stress. *Faseb Journal 11(9):A1104.*

717

Gardner, S.D.L., G. Taylor, and C. Bosac. 1995. Leaf growth of hybrid poplar following exposure to elevated co2. *New Phytologist 131(1):81-90.*

Leaf extension was stimulated following exposure of three interamerican hybrid poplar clones (Populus trichocarpa x P. deltoides); 'Unal', 'Boelare', and 'Beaupre' and a euramerican clone 'Primo' (Populus nigra x P. deltoides) to elevated CO2 in controlled environment chambers. For all three interamerican clones the evidence suggests that this was the result of increased leaf cell expansion associated with enhanced cell wall extensibility (WEx), measured as tensiometric increases in cell wall plasticity. For the interamerican clone 'Boelare', there was also a significant increase in cell wall elasticity following exposure to elevated CO2 (P less than or equal to 0.001). The effect of elevated CO2 in stimulating cell wall extensibility was confirmed in a detailed spatial analysis of extensibility made across the lamina of expanding leaves of the clone 'Boelare'. For two of the interamerican hybrids, 'Unal' and 'Beaupre', both leaf cell water potential (psi) and turgor pressure (P) were lower in elevated than in ambient CO2 By contrast, no significant effects on the cell wall properties or leaf water relations for the euramerican hybrid 'Primo' were observed following exposure to elevated CO2, suggesting that the mechanism for increased leaf extension in elevated CO2 differed, depending on clone. The cumulative total length of leaves of 'Boelare' grown in elevated CO2 was significantly increased (P less than or equal to 0.05) and since leaf number was not significantly increased in any inter-american clone it is hypothesized that final leaf size was stimulated in elevated CO2 for these clones. By contrast, there was no significant effect of CO2 on cumulative total leaf length for the euramerican clone 'Primo', but leaf number was significantly increased by elevated CO2. The measurements suggest that total tree leaf area was stimulated for a range of poplar hybrids exposed to elevated CO2. Given the short rotation of a coppiced crop, it is likely that increased leaf areas will result in enhanced stemwood production when hybrid poplars are grown in the CO2 concentrations predicted for the next century.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, BIOPHYSICS, ENRICHMENT, FORESTS, PLANT-CELL GROWTH, SALIX-VIMINALIS, SEEDLINGS, WALL EXTENSIBILITY, WATER-LIMITED CONDITIONS, YIELD

718

Gary, C., N. Bertin, J.S. Frossard, and J. Le Bot. 1998. High mineral contents explain the low construction cost of leaves, stems and fruits of tomato plants. *Journal of Experimental Botany 49(318):49-57.*

The construction cost of plant tissues is used in crop models to convert the products of photosynthesis into biomass. As for other greenhouse crops, tomato tissues are specific in that they have a high mineral content. The consequences of this accumulation of minerals on the construction cost of the tissues and the possible interactions with the physiological age of the organs and with the CO2 concentration in the atmosphere was examined. For that purpose, three methods of estimating the construction cost were used and compared. Large quantities of minerals accumulated in the tissues of tomato plants (ranging from 0.05 in fruits to 0.26 g g(-1) DM in leaves). The subsequent dilution of the organic matter explained why the estimated construction cost of the dry matter (organic matter + minerals) was fairly low in comparison to that of other crop species. The construction cost was higher in fruits than in vegetative organs, partly because of a lower mineral content. It decreased by 7-12% from top to bottom of the canopy, following the increase in the physiological age of the tissues. This ontogenic drift was partly explained by the accumulation of minerals in the older organs. In the conditions of CO2 enrichment of a commercial greenhouse, no effect of CO2 concentration on the mineral content and on the construction cost of tissues was observed. Such a variability of the construction cost of tomato plant tissues due to the accumulation of minerals or to the ontogeny questions the use of standard values in crop models.

KEYWORDS: CARBON CONTENT, COMBUSTION, CROP, DARK RESPIRATION, EFFICIENCY, ELEVATED CO2, GRAIN-SORGHUM, GREENHOUSE TOMATO, GROWTH, TEMPERATURE

719

Gay, A.P., and B. Hauck. 1994. Acclimation of lolium-temulentum to enhanced carbon-dioxide concentration. *Journal of Experimental Botany 45(277):1133-1141.*

Acclimation of single plants of Lolium temulentum to changing [CO2] was studied on plants grown in controlled environments at 20 degrees C with an 8 h photoperiod. In the first experiment plants were grown at 135 mu mol m(-2) s(-1) photosynthetic photon flux density (PPFD) at m s 415 mu l l(-1) or 550 mu l l(-1) [CO2] with some plants transferred from the lower to the higher [CO2] at emergence of leaf 4. In the second experiment plants were grown at 135 and 500 mu mol m(-2) s(-1) PPFD at 345 and 575 mu l l(-1) [CO2]. High [CO2] during growth had little effect on stomatal density, total soluble proteins, chlorophyll a content, amount of Rubisco or cytochrome f. However, increasing [CO2] during measurement increased photosynthetic rates, particularly in high light. Plants grown in the higher [CO2] had greater leaf extension, leaf and plant growth rates in low but not in high light. The results are discussed in relation to the limitation of growth by sink capacity and the modifications in the plant which allow the storage of extra assimilates at high [CO2].

KEYWORDS: ATMOSPHERIC CO2, ELEVATED CO2, FESTUCA-PRATENSIS, GROWTH, LEAF, LEAVES, PERENNIAL RYEGRASS, PHOTOSYNTHESIS, PROTEINS, STOMATAL DENSITY

720

Gebauer, R.L.E., J.F. Reynolds, and B.R. Strain. 1996. Allometric relations and growth in Pinus taeda: The effect of elevated CO2 and changing N availability. *New Phytologist 134(1):85-93.*

Loblolly pine (Pinus taeda L.) seedlings were grown for 138 d at two CO2 partial pressures (35 and 70 Pa CO2) and four N solution concentrations (0.5, 1.5, 3.5 and 6.5 mM NH4NO3). Allometric regression analysis was used to determine whether patterns of biomass allocation among functionally distinct plant-parts were directly controlled by CO2 and N availability or whether differences between treatments were the result of size-dependent changes in allocation. Both CO2 and N availability affected growth of loblolly pine. Growth stimulation by CO2 at nonlimiting N solution concentrations (3.5 and 6.5 mM NH4NO3) was c. 90%. At the lowest N solution concentration (0.5 mM NH4NO3), total plant biomass was still enhanced by 35% under elevated CO2. Relative growth rates were highly correlated with net assimilation rates, whereas leaf mass ratio remained unchanged under the wide range of CO2 and N solution concentrations. When differences in plant size were adjusted apparent CO2 effects on biomass allocation among different plant parts disappeared, indicating that CO2 only indirectly affected allocation through accelerated growth. N availability, by contrast, had a direct effect on biomass allocation, but primarily at the lowest N solution concentration (0.5 mM NH4NO3). Loblolly pine compensated for N limitation by increasing specific lateral root length and proportional biomass allocation to the lateral root system. The results emphasize the significance of distinguishing size-dependent effects on biomass allocation from functional adjustments

made in direct response to changing resource availability.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, ENRICHMENT, LOBLOLLY-PINE, NITROGEN CONCENTRATION, PHOTOSYNTHESIS, ROOT LENGTH, SEEDLINGS, SHOOT, WOODY-PLANTS

721

Gebauer, R.L.E., B.R. Strain, and J.P. Reynolds. 1998. The effect of elevated CO2 and N availability on tissue concentrations and whole plant pools of carbon-based secondary compounds in loblolly pine (Pinus taeda). *Oecologia 113(1):29-36.*

We examined the extent to which carbon investment into secondary compounds in loblolly pine (Pinus taeda L.) is changed by the interactive effect of elevated CO2 and N availability and whether differences among treatments are the result of size-dependent changes. Seedlings were grown for 138 days at two CO2 partial pressures (35 and 70 Pa CO2) and four N solution concentrations (0.5, 1.5, 3.5, and 6.5 mmol l(-1) NO3NH4) and concentrations of total phenolics and condensed tannins were determined four times during plant development in primary and fascicular needles, stems and lateral and tap roots. Concentrations of total phenolics in lateral roots and condensed tannins in tap roots were relatively high regardless of treatment. In the smallest seedlings secondary compound concentrations were relatively high and decreased in the initial growth phase. Thereafter condensed tannins accumulated strongly during plant maturation in all plant parts except in lateral roots, where concentrations did not change. Concentrations of total phenolics continued to decrease in lateral roots while they remained constant in all other plant parts. At the final harvest plants grown at elevated CO2 or low N availability showed increased concentrations of condensed tannins in aboveground parts. The CO2 effect, however, disappeared when size differences were adjusted for, indicating that CO2 only indirectly affected concentrations of condensed tannins through accelerating growth. Concentrations of total phenolics increased directly in response to low N availability and elevated CO2 in primary and fascicular needles and in lateral roots, which is consistent with predictions of the carbon-nutrient balance (CNB) hypothesis. The CNB hypothesis is also supported by the strong positive correlations between soluble sugar and total phenolics and between starch and condensed tannins. The results suggest that predictions of the CNB hypothesis could be improved if developmentally induced changes of secondary compounds were included.

KEYWORDS: DECOMPOSITION, DEFENSE, GROWTH, HERBIVORY, METABOLISM, NITROGEN, NUTRIENT BALANCE, PAPER BIRCH, PERFORMANCE, PHENOLIC-COMPOUNDS

722

Gedroc, J.J., K.D.M. McConnaughay, and J.S. Coleman. 1996. Plasticity in root shoot partitioning: Optimal, ontogenetic, or both? *Functional Ecology 10(1):44-50.*

1. We tested whether plants increase root,shoot ratios to compensate for limitations of below-ground resources in a manner consistent with optimal partitioning theory or whether the relative production of roots and shoots is controlled by species-specific developmental patterns. Individuals of two annual plant species, Abutilon theophrasti and Chenopodium album, were grown from seed in controlled greenhouse conditions under high- or low-nutrient regimes. Mid-way through the experiment, a sub-set of low-nutrient-grown plants were given high nutrient availability and a sub-set of high-nutrient-grown plants were transferred to a low nutrient environment. 2. Under continuous nutrient regimes: (1) high-nutrient-grown plants of both species grew faster and had a lower root:shoot ratio than low-nutrient-grown plants, consistent with optimal partitioning theory; (2) both species exhibited a substantial amount of ontogenetic drift as root:shoot ratios decreased through ontogeny (subsequent to an initial increase in R/S shortly after germination); (3) allometric analyses revealed that increased allocation to roots occurred very early in ontogeny for both species, after which the relative growth of shoots exceeded that of roots in low-nutrient-grown plants compared to their high nutrient-grown counterparts - a result inconsistent with optimal partitioning theory. 3. Under temporally varying nutrient regimes: (1) growth substantially increased in low-nutrient-grown plants that were switched to a high-nutrient environment without a change in root:shoot partitioning; (2) there was no change in growth or partitioning when plants were switched from a high- to a low-nutrient regime. 4. We conclude that, for these annual species, root/shoot partitioning is partially consistent with optimal partitioning theory but that is also highly ontogenetically constrained. This constraint is evident both in substantive ontogenetic drift in partitioning and in the period during development that plasticity in partitioning can be expressed.

KEYWORDS: CARBON DIOXIDE, CONSEQUENCES, ELEVATED CO2, FRAGMENTATION, GROWTH, NITROGEN CONCENTRATION, PERFORMANCE, PLANT, SIZE, SPACE

723

Geethakumari, V.L., and K. Shivashankar. 1991. Studies on organic amendment and CO2 enrichment in ragi soybean intercropping systems. *Indian Journal of Agronomy 36(2):202-206.*

Organic amendment comprising of ragi husk and FYM mixed in 1:1 ratio by weight promoted organic carbon content and available P status of the soil. A level of 4 t/ha of organic amendment promoted the uptake of N significantly by both ragi and soybean. Availability of P and K were also favourably influenced. Uptake of nutrients by soybean was promoted by CO2 enrichment. Available P status was higher in intercropped ragi and soybean as compared to pure crops but nutrient uptake was higher by pure crops.

724

Geiger, M., V. Haake, F. Ludewig, U. Sonnewald, and M. Stitt. 1999. The nitrate and ammonium nitrate supply have a major influence on the response of photosynthesis, carbon metabolism, nitrogen metabolism and growth to elevated carbon dioxide in tobacco. *Plant, Cell and Environment 22(10):1177-1199.*

The effect of elevated [CO2] on biomass, nitrate, ammonium, amino acids, protein, nitrate reductase activity, carbohydrates, photosynthesis, the activities of Rubisco and Sig other Calvin cycle enzymes, and transcripts for Rubisco small subunit, Rubisco activase, chlorophyll a binding protein, NADP-glyceraldehyde-3-phosphate dehydrogenase, aldolase, transketolase, plastid fructose-1,6-bisphosphatase and ADP-glucose pyrophosphorylase was investigated in tobacco growing an 2, 6 and 20 mM nitrate and 1, 3 and 10 mM ammonium nitate. (i) The growth stimulation in elevated [CO2] was attenuated in intermediate and abolished in low nitrogen. (ii) Elevated [CO2] led to a decline of nitrate, ammonium, amino acids especially glutamine, and protein in low nitrogen and a dramatic decrease in intermediate nitrogen, but not in high nitrogen. (iii) Elevated [CO2] led to a decrease of nitrate reductase activity in low, intermediate and high ammonium nitrate and in intermediate nitrate, but not in high nitrate, (iii) At low nitrogen, starch increased relative to sugars. Elevated [CO2] exaggerated this shift. ADP-glucose pyrophosphorylase transcript increased in low nitrogen, and in elevated [CO2]. (iv) In high nitrogen, sugars rose in elevated [CO2], but there was no acclimation of photosynthetic rate, only a small decrease of Rubisco and no decrease of other Calvin cycle enzymes and no decrease of the corresponding transcripts. In lower nitrogen, there was a marked acclimation of photosynthetic rate and a general decrease of Calvin cycle enzymes, even though sugar levels did not increase. The

decreased activities were due to a general decrease of leaf protein. The corresponding transcripts did not decrease except at very low nitrogen. (v) It is concluded that many of the effects of elevated [CO2] on nitrate metabolism, photosynthate allocation, photosynthetic acclimation and growth are due to a shift in nitrogen status.

KEYWORDS: ADP-GLUCOSE PYROPHOSPHORYLASE, ATMOSPHERIC CO2 ENRICHMENT, GAS-EXCHANGE, LOBLOLLY-PINE, MINERAL NUTRITION, PINUS-TAEDA, PLANT GROWTH, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, SOUR ORANGE TREES, TAEDA L SEEDLINGS

725

Geiger, M., P. Walch-Liu, C. Engels, J. Harnecker, E.D. Schulze, F. Ludewig, U. Sonnewald, W.R. Scheible, and M. Stitt. 1998. Enhanced carbon dioxide leads to a modified diurnal rhythm of nitrate reductase activity in older plants, and a large stimulation of nitrate reductase activity and higher levels of amino acids in young tobacco plants. *Plant, Cell and Environment 21(3):253-268.*

Higher rates of nitrate assimilation are required to support faster growth in enhanced carbon dioxide. To investigate how this is achieved, tobacco plants were grown on high nitrate and high light in ambient and enhanced (700 mu mol mol(-1)) carbon dioxide. Surprisingly, enhanced carbon dioxide did not increase leaf nitrate reductase (MR) activity in the middle of the photoperiod. Possible reasons for this anomalous result were investigated. (a) Measurements of biomass, nitrate, amino acids and glutamine in plants fertilized once and twice daily with 12 mol m(-3) nitrate showed that enhanced carbon dioxide did not lead to a nitrate limitation in these plants. (b) Enhanced carbon dioxide modified the diurnal regulation of NR activity in source leaves. The transcript for nia declined during the light period in a similar manner in ambient and enhanced carbon dioxide. The decline of the transcript correlated with a decrease of nitrate in the leaf, and was temporarily reversed after re-irrigating with nitrate in the second part of the photoperiod. The decline of the transcript was not correlated with changes of sugars or glutamine. NR activity and protein decline in the second part of the photoperiod, and NR is inactivated in the dark in ambient carbon dioxide. The decline of NR activity was smaller and dark inactivation was partially reversed in enhanced carbon dioxide, indicating that post- transcriptional or post-translational regulation of NR has been modified. The increased activation and stability of NR in enhanced carbon dioxide was correlated with higher sugars and lower glutamine in the leaves. (c) Enhanced carbon dioxide led to increased levels of the minor amino acids in leaves. (d) Enhanced carbon dioxide led to a large decrease of glycine and a small decrease of serine in leaves of mature plants. The glycine:serine ratio decreased in source leaves of older plants and seedlings. The consequences of a lower rate of photorespiration for the levels of glutamine and the regulation of nitrogen metabolism are discussed. (e) Enhanced carbon dioxide also modified the diurnal regulation of NR in roots. The nia transcript increased after nitrate fertilization in the early and the second part of the photoperiod. The response of the transcript was not accentuated in enhanced carbon dioxide. NR activity declined slightly during the photoperiod in ambient carbon dioxide, whereas it increased 2-fold in enhanced carbon dioxide. The increase of root NR activity in enhanced carbon dioxide was preceded by a transient increase of sugars, and was followed by a decline of sugars, a faster decrease of nitrate than in ambient carbon dioxide, and an increase of nitrite in the roots. (f) To interpret the physiological significance of these changes-in nitrate metabolism, they were compared with the current growth rate of the plants. (g) In 4-5-week-old plants, the current rate of growth was similar in ambient and enhanced carbon dioxide (approximate to 0.4 g(-1) d(-1)). Enhanced carbon dioxide only led to small changes of NR activity, nitrate decreased, and overall amino acids were not significantly increased. (h) Young seedlings had a high growth rate (0.5 g(-1) d(-1)) in ambient carbon dioxide, that was increased by another 20% in enhanced carbon dioxide. Enhanced carbon dioxide led to larger increases of NR activity and NR activation, a 2-3-fold increase of glutamine, a 50% increase of glutamate, and a 2-3-fold increase in minor amino acids. It also led to a higher nitrate level. It is argued that enhanced carbon dioxide leads to a very effective stimulation of nitrate uptake, nitrate assimilation and amino acid synthesis in seedlings. This will play an important role in allowing faster growth rates in enhanced carbon dioxide at this stage.

KEYWORDS: ATMOSPHERIC CO2 CONCENTRATION, ELEVATED CO2, ENRICHMENT, GROWTH, MINERAL NUTRITION, NITRITE-REDUCTASE, NITROGEN, POSTTRANSLATIONAL REGULATION, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, SINK REGULATION

726

GenoudGourichon, C., H. Sallanon, and A. Coudret. 1996. Effects of sucrose, agar, irradiance and CO2 concentration during the rooting phase on the acclimation of Rosa hybrida plantlets to ex vitro conditions. *Photosynthetica 32(2):263-270.*

Plantlets of Rosa hybrida cv. Deladel Madame Delbard were grown in vitro under different CO2 concentrations and irradiances, The medium was solid or liquid with or without sucrose, Morphological (shoot length, leaf number, leaf area, root number and root length) and photosynthetic parameters (photosynthesis/irradiance curves and phosphoenolpyruvate carboxylase and ribulose-1,5-bisphosphate carboxylase/oxygenase activities) were measured. Sucrose was necessary for root formation but not for root initiation, Culture in sucrose-free and liquid medium, under CO2 enrichment and high photosynthetic photon flux density increased the photosynthetic abilities and improved acclimation of plantlets to ex vitro conditions even if these plants had no roots after the rooting initiation phase.

KEYWORDS: CULTURED INVITRO, PHOTOSYNTHESIS

727

George, V., D. Cantin, D. Gerant, and P. Dizengremel. 1997. Long-term effects of elevated CO2 concentration on respiratory enzymes and dark respiration in pedunculate oak leaves. *Plant Physiology 114(3):657.*

728

George, V., D. Gerant, and P. Dizengremel. 1996. Photosynthesis, Rubisco activity and mitochondrial malate oxidation in pedunculate oak (Quercus robur L) seedlings grown under present and elevated atmospheric CO2 concentrations. *Annales Des Sciences Forestieres 53(2-3):469-474.*

Pedunculate oak seedlings were grown at 350 and 700 mu L/L CO2 in controlled chambers. After 130 days at elevated CO2, the biomass of the whole plant did not significantly increase. Photosynthesis, Rubisco activity, mitochondrial malate oxidation, carbohydrates and nitrogen contents were examined in the fourth growth flush. At 700 mu L/L CO2, the leaf net photosynthetic rate was 220% higher than at 350 mu L/L CO2. The decreased activity of Rubisco was accompanied by an accumulation of sucrose and glucose. The decreased oxidative capacity of crude leaf mitochondria from elevated CO2 plants was driven by the lower nitrogen and protein contents rather than by the higher carbohydrates contents in the leaves. Nevertheless, direct effects of elevated CO2 on the respiratory biochemistry cannot be excluded.

KEYWORDS: RESPIRATION, TREES

729

Gesch, R.W., K.J. Boote, J.C.V. Vu, L.H. Allen, and G. Bowes. 1998. Changes in growth CO2 result in rapid adjustments of ribulose- 1,5-bisphosphate carboxylase/oxygenase small subunit gene expression in expanding and mature leaves of rice. *Plant Physiology 118(2):521-529.*

The accumulation of soluble carbohydrates resulting from growth under elevated CO2 may potentially signal the repression of gene activity for the small subunit of ribulose-1,5- bisphosphate carboxylase/oxygenase (rbcS). To test this hypothesis we grew rice (Oryza sativa L.) under ambient (350 mu L L-1) and high (700 mu L L-1) CO2 in outdoor, sunlit, environment-controlled chambers and performed a cross-switching of growth CO2 concentration at the late-vegetative phase. Within 24 h, plants switched to high CO2 showed a 15% and 23% decrease in rbcS mRNA, whereas plants switched to ambient CO2 increased 27% and 11% in expanding and mature leaves, respectively. Ribulose-1,5-bisphosphate carboxylase/oxygenase total activity and protein content 8 d after the switch increased up to 27% and 20%, respectively, in plants switched to ambient CO2, but changed very little in plants switched to high CO2. Plants maintained at high CO2 showed greater carbohydrate pool sizes and lower rbcS transcript levels than plants kept at ambient CO2. However, after switching growth CO2 concentration, there was not a simple correlation between carbohydrate and rbcS transcript levels. We conclude that although carbohydrates may be important in the regulation of rbcS expression, changes in total pool size alone could not predict the rapid changes in expression that we observed.

KEYWORDS: ACCLIMATION, ACCUMULATION, ATMOSPHERIC CARBON-DIOXIDE, ELEVATED CO2, HIGHER-PLANTS, MECHANISM, PHOTOSYNTHESIS, RUBISCO, SOURCE-SINK RELATIONS, TEMPERATURE

730

Ghannoum, O., and J.P. Conroy. 1998. Nitrogen deficiency precludes a growth response to CO2 enrichment in C-3 and C-4 Panicum grasses. *Australian Journal of Plant Physiology 25(5):627-636.*

We investigated the interaction of nitrogen (N) supply and CO2 enrichment on the growth and photosynthesis of Panicum laxum (C-3), P. coloratum (C-4) and P. antidotale (C-4). Plants were grown at ambient CO2 partial pressures (p(a)) of either 36 (low) or 71 (high) Pa, in potted soil supplied with 0 (low) or 60 (high) mg N kg(-1) soil week(-1). Elevated CO2 enhanced total plant dry mass of all three species by approximately 28% under high N supply, but had no effect on biomass accumulation under N deficiency. CO2 enrichment resulted in reductions of CO2 assimilation rates (A; measured at comparable p(a)) of P. laxum, indicating acclimation of photosynthesis. This acclimation, which was more pronounced under N stress, was unrelated to changes in leaf N or non-structural carbohydrate concentrations, because neither were affected by CO2 enrichment. In the C-4 grasses grown at low N, A were fully saturated at the current ambient p(a), whereas at high N, A increased slightly when CO2 was raised to 71 Pa. N deficiency reduced the initial slope of the CO2 response curve of A in P. antidotale, and this effect was more pronounced at high CO2. In conclusion, the preclusion of a growth response to CO2 enrichment by N deficiency was correlated with a strong inhibition of A in the C-3 species, and the saturation of A at below current atmospheric p(a) in C-4 species.

KEYWORDS: ACCLIMATION, CARBON DIOXIDE, CARBOXYLASE, DRY-MATTER, ELEVATED CO2, NUTRITION, PHOTOSYNTHESIS, RESPIRATION, SOURCE-SINK RELATIONS, TEMPERATURE

731

Ghannoum, O., K. Siebke, S. Von Caemmerer, and J.P. Conroy. 1998. The photosynthesis of young Panicum C-4 leaves is not C-3-like. *Plant, Cell and Environment 21(11):1123-1131.*

Evidence is presented contrary to the suggestion that C-4 plants grow larger at elevated CO2 because the C-4 pathway of young C-4 leaves has C-3-like characteristics, making their photosynthesis O-2 sensitive and responsive to high CO2, We combined PAM fluorescence with gas exchange measurements to examine the O-2 dependence of photosynthesis in young and mature leaves of Panicum antidotale (C-4, NADP-ME) and P. coloratum (C4, NAD-ME), at an intercellular CO2 concentration of 5 Pa. P. laxum (C-3) was used for comparison, The young C, leaves had COL and light response curves typical of C-4 photosynthesis. When the O-2 concentration was gradually increased between 2 and 40%, CO2 assimilation rates (A) of both mature and young C-4 leaves were little affected, while the ratio of the quantum yield of photosystem II to that of CO2 assimilation (Phi(PSII)/Phi(CO2)) increased more in young (up to 31%) than mature (up to 10%) C-4 leaves. A of C-3 leaves decreased by 1.3 and Phi(PSII)/Phi(CO2) increased by 9-fold, over the same range of O-2 concentrations. Larger increases in electron transport requirements in young, relative to mature, C-4 leaves at low CO2 are indicative of greater O-2 sensitivity of photorespiration, Photosynthesis modelling showed that young C-4 leaves have lower bundle sheath CO2 concentration, brought about by higher bundle sheath conductance relative to the activity of the C-4 and C-3 cycles and/or lower ratio of activities of the C-4 to C-3 cycles.

KEYWORDS: ATMOSPHERIC CO2 ENRICHMENT, CARBON ASSIMILATION, CHLOROPHYLL FLUORESCENCE, DEVELOPING MAIZE LEAVES, ELECTRON-TRANSPORT, GENE-EXPRESSION, IRRADIANCE, LEAF DEVELOPMENT, PHOTOSYSTEM, QUANTUM YIELD

732

Ghannoum, O., S. vonCaemmerer, E.W.R. Barlow, and J.P. Conroy. 1996. Effect of CO2 enrichment on growth, morphology and gas exchange of a C-3 (Panicum laxum) and a C-4 (Panicum antidotale) grass grown at two irradiance levels. *Plant Physiology 111(2):211.*

733

Ghannoum, O., S. vonCaemmerer, E.W.R. Barlow, and J.P. Conroy. 1997. The effect of CO2 enrichment and irradiance on the growth, morphology and gas exchange of a C-3 (Panicum laxum) and a C-4 (Panicum antidotale) grass. *Australian Journal of Plant Physiology 24(2):227-237.*

The effect of CO2 enrichment and irradiance on the growth and gas exchange of two tropical grasses, Panicum laxum (C-3) and Panicum antidotale (C-4) were investigated. The two species were grown at either 350 (low) or 700 (high) mu L L-1 CO2 concentration, under 40% (low) or 100% (high) of direct sunlight and supplied with ample water and nutrition. Elevated CO2 enhanced plant dry weight at both irradiances in the C-3 species (1.41-fold and 1.71-fold increase at low and high light, respectively) but only at high light in the C-4 species (1.28 fold increase). CO2 enrichment had no effect on the dry weight of P. antidotale, when stem development was suppressed by growth under artificial lighting. When measured at the CO2 concentration at which they were grown, assimilation rates were similar in the low and high CO2 grown plants, for both species. However, when measurements made at low CO2 were compared, CO2 assimilation rates of the high light, high CO2 grown C-3 and C- 4 species were lower than those of their low CO2 grown counterparts. High CO2 strongly reduced the stomatal conductance of both species, while it affected the Rubisco content (30% decrease) of the high light C-3 species only. This work shows clearly that C-4 species can respond to CO2 enrichment under favourable growth conditions, and that acclimation to elevated CO2 in pasture grasses does not necessarily involve accumulation of non-structural

carbohydrates or reduction of total N or soluble proteins in source leaves.

KEYWORDS: ACCLIMATION, ASSIMILATION, CARBON DIOXIDE, ELEVATED ATMOSPHERIC CO2, NITROGEN-USE EFFICIENCY, PARTIAL-PRESSURE, PHOTOSYNTHETIC CAPACITY, PLANTS, RESPONSES, TEMPERATURE

734
Ghannoum, O., S. vonCaemmerer, E.W.R. Barlow, and J.P. Conroy. 1997. The effect of CO2 enrichment and irradiance on the growth, morphology and gas exchange of a C-3 (Panicum laxum) and a C-4 (Panicum antidotale) grass (vol 24, pg 227, 1997). *Australian Journal of Plant Physiology 24(3):U2.*

735
Gifford, R.M. 1992. Implications of the globally increasing atmospheric CO2 concentration and temperature for the Australian terrestrial carbon budget - integration using a simple-model. *Australian Journal of Botany 40(4-5):527-543.*

A simple continentally aggregated model of the Australian terrestrial carbon budget (CQUESTA) integrates information on CO2 and temperature effects and is applied to evaluating whether vegetation is absorbing anthropogenic CO2. Information from the literature is used to parameterise CQUESTA. A standard set of parameters is adopted for exploratory purposes. Historical information is used to describe the average CO2 concentration and temperature over the southern hemisphere from 1750 AD to the present. From the present to 2050 AD the 'business-as-usual' scenario described by the Intergovernmental Panel on Climate Change (IPCC) is applied. The standard parameterisation of the model suggests that the changing CO2 concentration and temperature regime since 1750 AD has been causing continuous net sequestration of carbon into Australian live vegetation and soils. The present modelled rate of net sequestration is of a similar magnitude to CO2 emissions from continental fossil fuel burning and land clearing combined. The rate of sequestration is predicted to continue to increase until 2050 AD and beyond if atmospheric CO2 concentration and temperature continue to increase. However, there remains considerable experimental uncertainty about the correct parameterisation of the model. The findings have implications for policies on greenhouse effect gas emissions.

KEYWORDS: ACCLIMATION, DIOXIDE, DYNAMICS, ELEVATED CO2, GROWTH, NITROGEN, PHOTOSYNTHESIS, SOIL, TUSSOCK TUNDRA, WATER

736
Gifford, R.M. 1994. The global carbon-cycle - a viewpoint on the missing sink. *Australian Journal of Plant Physiology 21(1):1-15.*

Atmospheric carbon budgets that ignore the possibility of terrestrial ecosystem responses to global atmospheric change do not balance; there is a 'missing sink' of about 0.4 - 4 Gt C yr(-1). This paper argues a case that mechanistically it is well within the bounds of possibility that increasing carbon storage in vegetation and soils in response to the globally increasing CO2 concentration, temperature and nitrogen deposition can account for the missing C sink. Global warming conditions considered alone would be unlikely to cause most ecosystems to emit CO2, because the N mineralised by any enhanced soil organic matter decomposition would be largely taken up by plants and reconverted into organic matter having a much higher C:N ratio than that in the soil. Models of the global terrestrial C cycle indicate that an extra 0.5 - 4 Gt C yr(-1) could well be being stored in soils and vegetation today in response to the CO2 fertilising effect, having regard for the interactions with growth restricting water, light and nitrogen levels. To obtain direct proof as to whether that this is happening or not is a major challenge.

KEYWORDS: BIOSPHERE, BUDGET, CLIMATE, DIOXIDE, ECOSYSTEMS, ELEVATED CO2, INCREASING ATMOSPHERIC CO2, PLANT GROWTH, RESPONSES, TEMPERATURE

737
Gifford, R.M. 1995. Whole plant respiration and photosynthesis of wheat under increased CO2 concentration and temperature: Long-term vs short-term distinctions for modelling. *Global Change Biology 1(6):385-396.*

Short- and long-term effects of elevated CO2 concentration and temperature on whole plant respiratory relationships are examined for wheat grown at four constant temperatures and at two CO2 concentrations. Whole plant CO2 exchange was measured on a 24 h basis and measurement conditions varied both to observe short-term effects and to determine the growth respiration coefficient (r(g))r dry weight maintenance coefficient (r(g)), basal (i.e. dark acclimated) respiration coefficient (r(b)), and 24 h respiration:photosynthesis ratio (R:P). There was no response of r(b) to short-term variation in CO2 concentration. For plants with adequate N-supply, r(g) was unaffected by the growth-CO2 despite a 10% reduction in the plant's N concentration (%N). However, r(m) was decreased 13%, and r(b) was decreased 20% by growth in elevated CO2 concentration relative to ambient. Nevertheless, R:P was not affected by growth in elevated CO2. Whole plant respiration responded to short-term variation of + 5 degrees C around the growth temperature with low sensitivity (Q(10) = 1.8 at 15 degrees C, 1.3 at 30 degrees C). The shape of the response of whole plant respiration to growth temperature was different from that of the short term response, being a slanted S-shape declining between 25 and 30 degrees C. While r(m) increased, r(g) decreased when growth temperature increased between 15 and 20 degrees C. Above 20 degrees C r(m) became temperature insensitive while r(g) increased with growth temperature. Despite these complex component responses, R:P increased only from 0.40 to 0.43 between 15 degrees and 30 degrees C growth temperatures. Giving the plants a step increase in temperature caused a transient increase in R:P which recovered to the pre- transient value in 3 days. It is concluded that use of a constant R:P with respect to average temperature and CO2 concentration may be a more simple and accurate way to model the responses of wheat crop respiration to 'climate change' than the more complex and mechanistically dubious functional analysis into growth and maintenance components.

KEYWORDS: ELEVATED CO2, GROWTH

738
Gifford, R.M., J.L. Lutze, and D. Barrett. 1996. Global atmospheric change effects on terrestrial carbon sequestration: Exploration with a global C- and N-cycle model (CQUESTN). *Plant and Soil 187(2):369-387.*

A model of the interacting global carbon and nitrogen cycles (CQUESTN) is developed to explore the possible history of C-sequestration into the terrestrial biosphere in response to the global increases (past and possible future) in atmospheric CO2 concentration, temperature and N-deposition. The model is based on published estimates of pre-industrial C and N pools and fluxes into vegetation, litter and soil compartments. It was found necessary to assign low estimates of N pools and fluxes to be compatible with the more firmly established C-cycle data. Net primary production was made responsive to phytomass N level, and to CO2 and temperature deviation from preindustrial values with sensitivities covering the ranges in the

literature. Biological N-fixation could be made either unresponsive to soil C:N ratio, or could act to tend to restore the preindustrial C:N of humus with different N-fixation intensities. As for all such simulation models, uncertainties in both data and functional relationships render it more useful for qualitative evaluation than for quantitative prediction. With the N-fixation response turned off, the historic CO2 increase led to standard-model sequestration into terrestrial ecosystems in 1995AD of 1.8 Ct C yr(-1). With N-fixation restoring humus C:N strongly, C sequestration was 3 Ct yr(-1) in 1995. In both cases C:N of phytomass and litter increased with time and these increases were plausible when compared with experimental data on CO2 effects. The temperature increase also caused net C sequestration in the model biosphere because decrease in soil organic matter was more than offset by the increase in phytomass deriving from the extra N mineralised. For temperature increase to reduce system C pool size, the biosphere "leakiness" to N would have to increase substantially with temperature. Assuming a constant N-loss coefficient, the historic temperature increase alone caused standard-model net C sequestration to be about 0.6 Gt C in 1995. Given the disparity of plant and microbial C:N, the modelled impact of anthropogenic N-deposition on C- sequestration depends substantially on whether the deposited N is initially taken up by plants or by soil microorganisms. Assuming the latter, standard-model net sequestration in 1995 was 0.2 Ct C in 1995 from the N-deposition effect alone. Combining the effects of the historic courses of CO2, temperature and N-deposition, the standard-model gave C- sequestration of 3.5 Ct in 1995. This involved an assumed weak response of biological N-fixation to the increased carbon status of the ecosystem. For N-fixation to track ecosystem C- fixation in the long term however, more phosphorus must enter the biological cycle. New experimental evidence shows that plants in elevated CO2 have the capacity to mobilize more phosphorus from so-called "unavailable" sources using mechanisms involving exudation of organic acids and phosphatases.

KEYWORDS: BIOSPHERE, CO2 CONCENTRATION, ELEVATED CO2, LITTER DECOMPOSITION, NITROGEN, ORGANIC-ACIDS, PLANT, SOIL, STORAGE, TEMPERATURE-DEPENDENCE

739

Gil, M.I., D.M. Holcroft, and A.A. Kader. 1997. Changes in strawberry anthocyanins and other polyphenols in response to carbon dioxide treatments. *Journal of Agricultural and Food Chemistry 45(5):1662-1667.*

Carbon dioxide-enriched atmospheres are used to reduce the incidence and severity of decay and to extend the postharvest life of strawberries. The influence of CO2 on the postharvest quality parameters of strawberries, particularly the stability of anthocyanins and other phenolic compounds, was investigated. Freshly harvested strawberries were placed in jars ventilated continuously with air or air enriched with 10%, 20%, or 40% CO2 at 5 degrees C for 10 days. Samples were taken initially, and after 5 and 10 days of storage, and color (L* a* b* color space), pH, TA, TSS, and firmness were measured. Anthocyanins and other phenolics were analyzed by HPLC. Elevated CO2 degraded internal color while air-treated fruit remained red. Internal and external tissues differed in composition and concentration of phenolic compounds. CO2 had a minimal effect on the anthocyanin content of external tissues but induced a remarkable decrease in anthocyanin content of internal tissues. Factors, such as pH and copigmentation, that could explain this degradation are discussed.

KEYWORDS: COLOR, FIRMNESS, FRUITS, JUICE, MODIFIED ATMOSPHERES, QUALITY

740

Gilmanov, T.G., and W.C. Oechel. 1995. New estimates of organic matter reserves and net primary productivity of the North American tundra ecosystems. *Journal of Biogeography 22(4-5):723-741.*

The reserves and fluxes of carbon in ecosystems of the circumpolar tundra biome should be among the most responsive to climatic change, including their transformation from a CO2 sink to a CO2 source with respect to the atmosphere. To estimate accurately the significance of Arctic tundra to global carbon stocks and balances, quantitative geographically referenced estimates of the masses and fluxes of carbon are needed. Although new empirically based estimates of reserves and productivity were recently obtained for the Eurasian part of the tundra biome using GIS technology, the figures currently used for carbon reserves and productivity of the North American tundra ecosystems are based on earlier expert estimates or large scale models based on data primarily for non-tundra areas. To obtain new more empirically based estimates of the reserves and fluxes of carbon in North American tundra ecosystems a set of records of North American tundra ecosystems was obtained from the Global Arctic/Alpine Climate/Soil/Plant Productivity Data Base (Global Change Research Group, San Diego State University). This data base contains phytomass, productivity, climatic and soil characteristics for nearly fifty tundra-type ecosystems studied during the past 30 years in Alaska and Northern Canada. This information was used to interpolate the necessary data for all the tundra cells (1 X 1 degree) of the simple GIS, based on the Global Vegetation Map and the FAO/UNESCO Soil Map of the World. By integrating the corresponding maps of phytomass and productivity the quantitative estimates of the reserves and. productivity fluxes of organic matter in tundra ecosystems of North America and Greenland (4.12 x 10(6) km(2) total area) were obtained: 2.26 Gt above-ground phytomass, 4.99 Gt total phytomass, 91.3 Gt soil organic matter of the active layer; 0.56 Gt/yr above- ground net primary production; 0.98 Gt/yrotal net primary production. As an alternative means of determining the productivity totals for North American tundra ecosystems, the phenomenological model of the form: NPP=f(T,H,G), relating net primary production of tundra ecosystems to climatic, soil and vegetation factors, was applied to the GIS layers of mean annual temperature (T), soil organic matter content (H), and above-ground phytomass density (G) to produce a map of modelled NPP estimates for North American tundra ecosystems. The subroutine of spatial integration of the local production estimates takes into account geographical changes in the landscape composition (proportions of the zonal, meadow, mire and aquatic ecosystem types) and results in totals of 0.58 Gt/yr for above-ground and 1.16 Gt/yr for total net primary production of tundra ecosystems of North America and Greenland.

KEYWORDS: ACCUMULATION, ALASKA, ARCTIC TUNDRA, BIOMASS, CLIMATE, NUTRIENT, PLANT, SOIL PROPERTIES, VEGETATION TYPES

741

Gimenez, C., V.J. Mitchell, and D.W. Lawlor. 1992. Regulation of photosynthetic rate of 2 sunflower hybrids under water-stress. *Plant Physiology 98(2):516-524.*

The effect of short-term water stress on photosynthesis of two sunflower hybrids (Helianthus annuus L. cv Sungro-380 and cv SH-3622), differing in productivity under field conditions, was measured. The rate of CO2 assimilation of young, mature leaves of SH-3622 under well-watered conditions was approximately 30% greater than that of Sungro-380 in bright light and elevated CO2; the carboxylation efficiency was also larger. Growth at large photon flux increased assimilation rates of both hybrids. The changes in leaf composition, including cell numbers and sizes, chlorophyll content, and amounts of total soluble and ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) protein, and in Rubisco activity and amount of ribulose-1,5- bisphosphate (RuBP) were determined to assess the factors regulating the differences in assimilation of the hybrids at high and low water potentials. The amounts of chlorophyll, soluble protein, Rubisco protein and the initial activity of

Rubisco and its activation state did not differ significantly between hybrids. However, unstressed leaves of SH-3622 had more, smaller cells per unit area and 60% more RuBP per unit leaf area than that of Sungro-380. Water stress developing over 4 days decreased the assimilation of both hybrids similarly. Changes in the amounts of chlorophyll, soluble and Rubisco protein, and Rubisco activity and activation state were small and were not sufficient to explain the decrease in photosynthesis; neither was decreased stomatal conductance (or stomatal "patchiness"). Reduction of photosynthesis per unit leaf area from 25 to 5 micromoles CO2 per square meter per second in both hybrids was caused by a decrease in the amount of RuBP from approximately 130 to 40 micromoles per square meter in SH-3622 and from 80 to 40 micromoles per square meter in Sungro. Differences between hybrids and their response to water stress is discussed in relation to control of RuBP regeneration.

KEYWORDS: BISPHOSPHATE CARBOXYLASE ACTIVITY, C-3, INHIBITION, LEAVES, OXYGENASE, PLANTS, POTENTIALS, PROTEIN, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE, WHEAT GENOTYPES

742

Giordano, M., J.S. Davis, and G. Bowes. 1994. Organic-carbon release by dunaliella-salina (chlorophyta) under different growth-conditions of co2, nitrogen, and salinity. *Journal of Phycology 30(2):249-257.*

Two strains of Dunaliella salina (Dunal) Teod., UTEX 1644 and UTEX 200, were cultured under different growth regimes, including 10 mM NO3- or NH4+, 1.5 or 3.0 M NaCl, and low (0.035%) or high (5%) CO2 in air. The release of C-14-labeled dissolved organic carbon (DOC), expressed as a rate and as a percentage of photo synthetic (CO2)-C-14, assimilation, was subsequently determined. The percentage of DOC released was inversely related to cell density in the assay medium, but photosynthesis on a per-cell basis was not. Release of DOC was low, in the range of 1-5% of photosynthesis, but during acclimation to growth on NH4+, it rose to 11%. The presence of NH4+ rather than NO3- in the growth medium increased the rate of release by both strains, but the percentage release was stimulated only in UTEX 200 cells, because their photosynthetic ra te was depressed by NH4+. For UTEX 1644, high, as compared to low, CO2-grown cells, had somewhat higher rates a nd percentages of DOC release, but release from UTEX 200 cells was unaffected by the growth-CO2. The rate of DOC release by high CO2-grown cells was not enhanced at a low concentration of dissolved inorganic carbon, indicating that the released material did not originate from the photorespiratory pathway. The effects of NaCl on DOC release varied with strain a nd growth conditions. For UTEX 200, the cells in NO3-, but not NH4+, exhibited a doubling or more in percentage Of release with a doubling in NaCl concentration, irrespective of growth-CO2. With UTEX 1644 the low CO2-grown cells showed the greatest enhancement in 3.0 M NaCl. Organic matter accumulated on the external surface of the cell membrane and constituted a well- defined cell-coat, which was more dense in NH4+ than in NO3-- grown cells. Microtubules, which may play a role in maintaining cell shape, were observed just below the plasma membrane. From a practical viewpoint, the presence of organic material in the hypersaline ponds of salt-works is detrimental to salt production. When D. salina cells become abundant in such ponds, the attendant, continuous release of DOC may make a significant contribution to the problem.

KEYWORDS: BIOCULATA, COAT, EXCRETION, GREEN-ALGA, HEALTHY CELLS, INTRACELLULAR GLYCEROL, MARINE-PHYTOPLANKTON, METABOLISM, TEMPERATURE, TERTIOLECTA

743

Gleadow, R.M., W.J. Foley, and I.E. Woodrow. 1998. Enhanced CO2 alters the relationship between photosynthesis and defence in cyanogenic Eucalyptus cladocalyx F. Muell. *Plant, Cell and Environment 21(1):12-22.*

The effect of elevated CO2 and different levels of nitrogen on the partitioning of nitrogen between photosynthesis and a constitutive nitrogen-based secondary metabolite (the cyanogenic glycoside prunasin) was examined in Eucalyptus cladocalyx. Our hypothesis was that the expected increase in photosynthetic nitrogen-use efficiency of plants grown at elevated CO2 concentrations would lead to an effective reallocation of available nitrogen from photosynthesis to prunasin, Seedlings were grown at two concentrations of CO2 and nitrogen, and the proportion of leaf nitrogen allocated to photosynthesis, ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco), protein and prunasin compared, Up to 20% of leaf nitrogen was allocated to the cyanogenic glycoside, although this proportion varied with leaf age, position and growth conditions, Leaf prunasin concentration,vas strongly affected by nitrogen supply, but did not increase, on a dry weight basis, in the leaves from the elevated CO2 treatments, However, the proportion of nitrogen allocated to prunasin increased significantly, in spite of a decreasing pool of leaf nitrogen, in the plants grown at elevated concentrations of CO2. There was less protein in leaves of plants grown at elevated CO2 in both nitrogen treatments, while the concentration of active sites of Rubisco only decreased in plants from the low-nitrogen treatment. These changes in leaf chemistry may have significant implications in terms of the palatability of foliage and defence against herbivores.

KEYWORDS: ACCLIMATION, C-3 PLANTS, CARBON NUTRIENT BALANCE, ELEVATED ATMOSPHERIC CO2, GAS-EXCHANGE, GROWTH, HERBIVORE INTERACTIONS, NITROGEN, RISING CO2, TOMATO PLANTS

744

Glenn, D.M., and W.V. Welker. 1997. Effects of rhizosphere carbon dioxide on the nutrition and growth of peach trees. *Hortscience 32(7):1197-1199.*

Our objectives in this study were to measure the effects of low levels of root system carbon dioxide on peach tree growth (Prunus persica L. Batsch) and nutrient uptake. Using soil and hydroponic systems, we found that increased root CO2: 1) increased root growth without increasing shoot growth, 2) increased leaf P concentration, 3) decreased leaf N concentration, and 4) reduced water use relative to air injection or no treatment.

KEYWORDS: ATMOSPHERIC CO2 ENRICHMENT, INORGANIC CARBON, METABOLISM, PLANTS, RESPIRATION, RESPONSES, ROOT-GROWTH, SEEDLINGS, SOIL, WATER

745

Gloser, J., and M. Bartak. 1994. Net photosynthesis, growth-rate and biomass allocation in a rhizomatous grass calamagrostis-epigejos grown at elevated co2 concentration. *Photosynthetica 30(1):143-150.*

Young plants of Calamagrostis epigejos (L.) Roth were grown in controlled environments with two regimes of CO2 in the air: normal (350 cm(3) m(-3)) and elevated (700 cm(3) m(-3)). The relative growth rate of plants grown at elevated CO2 was increased by about 20 % in comparison with control plants cultivated at ambient CO2 concentration. Partitioning of assimilates into roots (+ rhizomes) and shoots was the same in both treatments. Slightly lower values of specific leaf area, leaf mass ratio and leaf area ratio were found in the plants grown at elevated CO2. The net photosynthetic rate (P-N) was measured gasometrically in plants from both treatments at 350 and 700 cm(3) m(-3) CO2 in the leaf chamber. There were no significant differences between plants grown at either CO2 concentration in their responses to radiation and CO2 conditions during measurements, i.e., no regulation of photosynthetic

processes in response to elevated CO2 was detectable. P-N at saturating irradiance and maximum apparent quantum yield of photosynthesis were always considerably higher at doubled CO2 concentration during measurements.

KEYWORDS: CARBON DIOXIDE, ECOSYSTEMS, PLANTS, PRODUCTIVITY, RESPIRATION, RESPONSES, TEMPERATURE

746

Godbold, D.L., and G.M. Berntson. 1997. Elevated atmospheric CO2 concentration changes ectomycorrhizal morphotype assemblages in Betula papyrifera. *Tree Physiology 17(5):347-350.*

Ectomycorrhizae are extremely diverse, with different species of fungi having very different physiologies and morphologies that, in turn, confer a range of different benefits to the host plant. To test the hypothesis that elevated CO2 leads to changes in the assemblage of ectomycorrhizae associated with trees, we examined the number and frequency of ectomycorrhizal morphotypes colonizing roots of Betula papyrifera Marsh. saplings grown at an ambient or elevated (700 ppm) atmospheric CO2 concentration for 24 weeks. Elevated CO2 resulted in significant changes in the composition of the ectomycorrhizal assemblage toward morphotypes with a higher incidence of emanating hyphae and rhizomorphs. We conclude that B. papyrifera saplings will be able to support a more costly mycorrhization in future elevated-CO2 atmospheres.

KEYWORDS: CARBON DIOXIDE, FUNGI, GROWTH, INFECTION, MYCELIUM, PINE, RESPONSES, ROOTS, SEEDLINGS

747

Godbold, D.L., G.M. Berntson, and F.A. Bazzaz. 1997. Growth and mycorrhizal colonization of three North American tree species under elevated atmospheric CO2. *New Phytologist 137(3):433-440.*

We investigated the effect of elevated CO2 on the growth and mycorrhizal colonization of three tree species native to north- eastern American forests (Betula papyrifera Marsh., Pinus strobus L. and Tsuga canadensis L. Carr). Saplings of the tree species were collected from Harvard Forest, Massachusetts, and grown in forest soil under ambient (c. 375 ppm) and elevated (700 ppm) atmospheric CO2 concentrations for 27-35 wk. In all three species there was a trend to increasing whole-plant, total-root and fine-root biomass in elevated CO2, and a significant increase in the degree of ectomycorrhizal colonization in B. papyrifera and P. strobus, but not in T. canadensis. However, in T. canadensis the degree of colonization with arbuscular mycorrhizas increased significantly. In both the ambient and elevated environments, on the roots of B. papyrifera and P. strobus 12 distinct ectomycorrhizal morphotypes were identified. Distinct changes in the ectomycorrhizal morphotype assemblage of B. papyrifera were observed under CO2 enrichment. This change resulted in an increase in the frequency of ectomycorrhizas with a higher incidence of emanating hyphae and rhizomorphs, and resulted in a higher density of fungal hyphae in a root exclusion chamber.

KEYWORDS: CARBON DIOXIDE, ECTOMYCORRHIZAL PLANTS, ENRICHMENT, FUNGI, LOBLOLLY-PINE, NUTRIENT, RESPONSES, ROOTS, SEEDLINGS, VEGETATIVE MYCELIUM

748

Goettel, M.S., G.M. Duke, and D.W. Goerzen. 1997. Pathogenicity of Ascosphaera larvis to larvae of the alfalfa leafcutting bee, Megachile rotundata. *Canadian Entomologist 129(6):1059-1065.*

Laboratory assays and field surveys showed that Ascosphaera larvis (Bissett) is a pathogen of alfalfa leafcutting bee larvae, capable of causing high mortality in commercial populations. In one population over 21% of bees were found to be infected by A. larvis. However, overall levels of the disease are low and it is unlikely that this pathogen poses an immediate threat to commercial leafcutting bee populations in Canada. The LD50 was determined to be 1.9 x 10(5) spores/bee. Elevated levels of CO2 are required for in vitro spore germination. The disease can easily be diagnosed within bee cells by X-ray radiography, thereby enabling disease levels to be monitored using conventional methods utilized by the industry to monitor leafcutting bee quality.

KEYWORDS: CHALKBROOD

749

Goldewijk, K.K., J.G. Vanminnen, G.J.J. Kreileman, M. Vloedbeld, and R. Leemans. 1994. Simulating the carbon flux between the terrestrial environment and the atmosphere. *Water, Air, and Soil Pollution 76(1-2):199-230.*

A Terrestrial C Cycle model that is incorporated in the Integrated Model to Assess the Greenhouse Effect (IMAGE 2.0) is described. The model is a geographically explicit implementation of a model that simulates the major C fluxes in different compartments of the terrestrial biosphere and between the biosphere and the atmosphere. Climatic parameters, land cover and atmospheric C concentrations determine the result of the dynamic C simulations. The impact of changing land cover patterns, caused by anthropogenic activities (shifting agriculture, de- and afforestation) and climatic change are modeled implicitly. Feedback processes such as CO2 fertilization and temperature effects on photosynthesis, respiration and decomposition are modeled explicitly. The major innovation of this approach is that the consequences of climate change are taken into account instantly and that their results can be quantified on a global medium-resolution grid. The objectives of this paper are to describe the C cycle model in detail, present the linkages with other parts of the IMAGE 2.0 framework, and give an array of different simulations to validate and test the robustness of this modeling approach. The computed global net primary production (NPP) for the terrestrial biosphere in 1990 was 60.6 Gt C a-1, with a global net ecosystem production (NEP) of 2.4 Gt C a-1. The simulated C flux as result from land cover changes was 1.1 Gt C a-1, so that the terrestrial biosphere in 1990 acted as a C sink of 1.3 Gt C a-1. Global phytomass amounted 567.5 Gt C and the dead biomass pool was 1517.7 Gt C. IMAGE 2.0 simulated for the period 1970 - 2050 a global average temperature increase of 1.6-degrees-C and a global average precipitation increase of 0.1 mm/day. The CO2 concentration in 2050 was 522.2 ppm. The computed NPP for the year 2050 is 82.5 Gt C a-1, with a NEP of 8.1 Gt C a-1. Projected land cover changes result in a C flux of 0.9 Gt C a-1, so that the terrestrial biosphere will be a strong sink of 7.2 Gt C a-1. The amount of phytomass hardly changed (600.7 Gt C) but the distribution over the different regions had. Dead biomass increased significantly to 1667.2 Gt C.

KEYWORDS: BIOSPHERE, CO2 CONCENTRATIONS, ELEVATED CO2, FEEDBACK PROCESSES, GLOBAL CHANGE, LAND-USE, MANAGED FORESTS, MODEL, STORAGE, WATER-USE EFFICIENCY

750

Gong, H., S. Nilsen, and J.F. Allen. 1993. Photoinhibition of photosynthesis invivo - involvement of multiple sites in a photodamage process under co2-free and o2- free conditions. *Biochimica Et Biophysica Acta 1142(1-2):115-122.*

Intact Lemna gibba plants were illuminated by photoinhibitory light in air, in air minus O2, in air minus CO2, and in pure N2. In pure N2, the degree of photoinhibition increased 3-5- times compared with that in air.

This high degree of photoinhibition is described as photodamage. Photodamage was found to constitute a syndrome, that is, it is due to inactivation of multiple sites. These sites include RC II component(s) from P680 to Q(A); the Q(B)-Site; and a component of PS I. In photodamage, the donor side of PS II and PS II excitation energy transfer remain unimpaired, but the size of the PS I antenna seems to decrease. Photodamage is distinguishable from photoinactivation. Photoinactivation occurred in air and could be attributed to inhibition of electron transport from Q(A)- to Q(B). During photoinactivation the D1 protein of RC II became degraded faster than the detectable inhibition of Q(B) reduction. The photoinhibition- induced rise in F0 occurred only during the process of photodamage but not during that of photoinactivation, and was a secondary event which arose as a consequence of photodamage. Atmospheric O2 alleviated photodamage but increased photoinactivation. The light-induced Dl degradation and inhibition of Q(A) to Q(B) electron transfer were enhanced in vivo not only by O2 but also by depletion of CO2.

KEYWORDS: ANAEROBIC CONDITIONS, CHLAMYDOMONAS-REINHARDTII, CHLOROPHYLL FLUORESCENCE, D1 PROTEIN, DEGRADATION, ENERGY-DISTRIBUTION, ISOLATED-CHLOROPLASTS, MECHANISM, PHOTOSYSTEM, REACTION CENTERS

751

GonzalezMeler, M.A., M. RibasCarbo, J.N. Siedow, and B.G. Drake. 1996. Direct inhibition of plant mitochondrial respiration by elevated CO2. *Plant Physiology 112(3):1349-1355.*

Doubling the concentration of atmospheric CO2 often inhibits plant respiration, but the mechanistic basis of this effect is unknown. We investigated the direct effects of increasing the concentration of CO2 by 360 mu L L(-1) above ambient on O-2 uptake in isolated mitochondria from soybean (Glycine max L. cv Ransom) cotyledons. Increasing the CO2 concentration inhibited the oxidation of succinate, external NADH, and succinate and external NADH combined. The inhibition was greater when mitochondria were preincubated for 10 min in the presence of the elevated CO2 concentration prior to the measurement of O-2 uptake. Elevated CO2 concentration inhibited the salicylhydroxamic acid-resistant cytochrome pathway, but had no direct effect on the cyanide-resistant alternative pathway. We also investigated the direct effects of elevated CO2 concentration on the activities of cytochrome c oxidase and succinate dehydrogenase (SDH) and found that the activity of both enzymes was inhibited. The kinetics of inhibition of cytochrome c oxidase were time-dependent. The level of SDH inhibition depended on the concentration of succinate in the reaction mixture. Direct inhibition of respiration by elevated CO2 in plants and intact tissues may be due at least in part to the inhibition of cytochrome c oxidase and SDH.

KEYWORDS: ATMOSPHERIC CO2, CARBON-DIOXIDE EFFLUX, DARK RESPIRATION, GROWTH, LEAF RESPIRATION, PATHWAYS, PEAR FRUIT, ROOT RESPIRATION, SHORT- TERM, SOIL

752

Gonzalez-Meler, M.A., and J.N. Siedow. 1999. Direct inhibition of mitochondrial respiratory enzymes by elevated CO2: does it matter at the tissue or whole-plant level? *Tree Physiology 19(4-5):253-259.*

On average, a doubling in current atmospheric [CO2] results in a 15 to 20% direct inhibition of respiration, although the variability associated with this value is large within and among species. Direct effects of CO2 on respiration may also be relevant to tree canopies because of dynamic fluctuations between nighttime and daytime [CO2] throughout the growing season. The mechanism by which CO2 inhibits respiration is not known. A doubling of ambient [CO2] inhibits the activity of the mitochondrial enzymes, cytochrome c oxidase and succinate dehydrogenase. If inhibition of these enzymes is the only factor involved in the direct inhibition of respiration, the overall inhibition of specific respiration will be proportional to the control that such enzymes exert on the overall respiratory rate. We analyzed the effects of [CO2] on respiration in an attempt to scale the direct effects of CO2 on respiratory enzymes to the whole-plant level. Sensitivity analysis showed that inhibition of mitochondrial enzymes by doubling current atmospheric [CO2] does not explain entirely the CO2 inhibition of tissue or whole-plant respiration. We conclude that CO2-dependent suppression of respiratory enzymatic activity will be minimal when cytochrome c oxidase inhibition is scaled up from the mitochondria to the whole tree and that the primary mechanism for the direct inhibitory effect remains to be identified.

KEYWORDS: ATMOSPHERIC CO2, CARBOHYDRATE STATUS, CARBON-DIOXIDE CONCENTRATIONS, DARK RESPIRATION, GROWTH, LEAF RESPIRATION, PHOTOSYNTHESIS, RESPONSES, ROOT RESPIRATION, SHORT- TERM

753

Goodale, C.L., J.D. Aber, and E.P. Farrell. 1998. Predicting the relative sensitivity of forest production in Ireland to site quality and climate change. *Climate Research 10(1):51-67.*

Most model-based predictions of climate change effects on forest ecosystems have used either potential or static descriptions of vegetation and site, removing the effects of direct management or land use. In this paper we use a previously developed and validated model of carbon and water balances in forest ecosystems (PnET-II) to assess the relative sensitivity of forest production in Ireland to predicted climate change and to ambient variability in site quality. After validating the model against measured productivity for 2 sets of stands, we ran the model using existing variation in site quality, represented as differences in foliar N concentration, and also for predicted changes in climate and atmospheric CO2. Resulting variations in productivity were compared with those due to potential errors in the specification of input parameters and to variation in current ambient climate across the region. The effects on net primary production (NPP) and wood production of either ambient variation in climate or predicted changes in temperature, precipitation and CO2 are quite small (0 to 30%) relative to the effects of ambient variability in site quality (up to 400%). The range of possible variation in other user-specified physiological parameters resulted in changes of less than 10% in model predictions. We conclude that site-specific conditions and management practices result in a range of forest productivity that is much greater than any likely to be induced by climate change or CO2 enrichment. We also suggest that it is essential to understand and map spatial variability in site quality, as well as to understand how the productive capacity of landscapes will change in response to management and pollution loading, if we are to predict the actual role that climate change will play in altering forest productivity and global biogeochemistry.

KEYWORDS: BIOMASS DISTRIBUTION, GENERAL-CIRCULATION MODEL, LEAF CO2 EXCHANGE, NET PRIMARY PRODUCTION, PACIFIC NORTHWEST, PHOTOSYNTHESIS- NITROGEN RELATIONS, PICEA-SITCHENSIS, SITCHENSIS BONG CARR, STOMATAL CONDUCTANCE, WATER-USE EFFICIENCY

754

Goodfellow, J., D. Eamus, and G. Duff. 1997. Diurnal and seasonal changes in the impact of CO2 enrichment on assimilation, stomatal conductance and growth in a long-term study of Mangifera indica in the wet-dry tropics of Australia. *Tree Physiology 17(5):291-299.*

We studied assimilation, stomatal conductance and growth of Mangifera indica L. saplings during long-term exposure to a CO2-enriched

atmosphere in the seasonally wet-dry tropics of northern Australia. Grafted saplings of M. indica were planted in the ground in four air-conditioned, sunlit, plastic-covered chambers and exposed to CO2 at the ambient or an elevated (700 mu mol mol(-1)) concentration for 28 months. Light-saturating assimilation (A(max)), stomatal conductance (g(s)), apparent quantum yield (phi), biomass and leaf area were measured periodically. After 28 months, the CO2 treatments were changed in all four chambers from ambient to the elevated concentration or vice versa, and A(max) and g(s) were remeasured during a two-week exposure to the new regime. Throughout the 28-month period of exposure, A(max) and apparent quantum yield of leaves in the elevated CO2 treatment were enhanced, whereas stomatal conductance and stomatal density of leaves were reduced. The relative impacts of atmospheric CO2 enrichment on assimilation and stomatal conductance were significantly larger in the dry season than in the wet season. Total tree biomass was substantially increased in response to atmospheric CO2 enrichment throughout the experimental period, but total canopy area did not differ between CO2 treatments at either the first or the last harvest. During the two-week period following the change in CO2 concentration, A(max) of plants grown in ambient air but measured in CO2-enriched air was significantly larger than that of trees grown and measured in CO2-enriched air. There was no difference in A(max) between trees grown and measured in ambient air compared to trees grown in CO2-enriched air but measured in ambient air. No evidence of down-regulation of assimilation in response to atmospheric CO2 enrichment was observed when rates of assimilation were compared at a common intercellular CO2 concentration. Reduced stomatal conductance in response to atmospheric CO2 enrichment was attributed to a decline in both stomatal aperture and stomatal density.

KEYWORDS: CARBON DIOXIDE, ELEVATED ATMOSPHERIC CO2, FIELD, FOLIAR GAS-EXCHANGE, LEAF, MARANTHES-CORYMBOSA, NET PHOTOSYNTHESIS, PHOTOSYNTHETIC RESPONSE, PLANTS, TREES

755

Goodfellow, J.E., D. Eamus, and G.A. Duff. 1997. The impact of CO2 enrichment on assimilation, stomatal conductance and growth in a long-term study of Mangifera indica in the wet-dry tropics of Australia. *Plant Physiology 114(3):480.*

756

Gordon, D.C., M.M.I. VanVuuren, B. Marshall, and D. Robinson. 1995. Plant growth chambers for the simultaneous control of soil and air temperatures, and of atmospheric carbon dioxide concentration. *Global Change Biology 1(6):455-464.*

Many facilities for growing plants at elevated atmospheric concentrations of CO2 ([CO2]) neglect the control of temperature, especially of the soil. Soil and root temperatures in conventional, free-standing pots often exceed those which would occur in the field at a given air temperature. A plant growth facility is described in which atmospheric CO2 can be maintained at different concentrations while soil and air temperatures mimic spatial and temporal patterns seen in the field. It consists of glasshouse-located chambers in which [CO2] is monitored by an infra-red gas analyser and maintained by injection of CO2 from a cylinder. Air is cooled by a heat exchange unit. Plants grow in soil in 1.2 m long containers that are surrounded by cooling coils and thermal insulation. Both [CO2] and temperature are controlled by customized software. Air temperature is programmed to follow a sine function of diurnal time. Soil temperature at a depth of 0.55 m is programmed to be constant. Temperature at 0.1 m depth varies as a damped, lagged function of air temperature; that at 1.0 m as a similar function of the 0.55 m temperature. [CO2] is maintained within 20 mu mol mol(-1) of target concentrations during daylight. A feature of the system is that plant material is labelled with a C-13 enrichment different from that of carbon in soil organic matter. The operation of the system is illustrated with data collected in an experiment with spring wheat (Triticum aestivum L., cv Tonic) grown at ambient [CO2] and at [CO2] 350 mu mol mol(-1) greater than ambient.

KEYWORDS: CO2

757

Gordon, H.B., P.H. Whetton, A.B. Pittock, A.M. Fowler, and M.R. Haylock. 1992. Simulated changes in daily rainfall intensity due to the enhanced greenhouse-effect - implications for extreme rainfall events. *Climate Dynamics 8(2):83-102.*

In this study we present rainfall results from equilibrium 1 x - and 2 x CO2 experiments with the CSIRO 4-level general circulation model. The 1 X CO2 results are discussed in relation to observed climate. Discussion of the 2 x CO2 results focuses upon changes in convective and non-convective rainfall as simulated in the model, and the consequences these changes have for simulated daily rainfall intensity and the frequency of heavy rainfall events. In doing this analysis, we recognize the significant shortcomings of GCM simulations of precipitation processes. However, because of the potential significance of any changes in heavy rainfall events as a result of the enhanced greenhouse effect, we believe a first examination of relevant GCM rainfall results is warranted. Generally, the model results show a marked increase in rainfall originating from penetrative convection and, in the mid- latitudes, a decline in large-scale (non-convective) rainfall. It is argued that these changes in rainfall type are a consequence of the increased moisture holding capacity of the warmer atmosphere simulated for 2 x CO2 conditions. Related to changes in rainfall type, rainfall intensity (rain per rain day) increases in the model for most regions of the globe. Increases extend even to regions where total rainfall decreases. Indeed, the greater intensity of daily rainfall is a much clearer response of the model to increased greenhouse gases than the changes in total rainfall. We also find a decrease in the number of rainy days in the middle latitudes of both the Northern and Southern Hemispheres. To further elucidate these results daily rainfall frequency distributions are examined globally and for four selected regions of interest. In all regions the frequency of high rainfall events increases, and the return period of such events decreases markedly. If realistic, the findings have potentially serious practical implications in terms of an increased frequency and severity of floods in most regions. However, we discuss various important sources of uncertainty in the results presented, and indicate the need for rainfall intensity results to be examined in enhanced greenhouse experiments with other GCMs.

KEYWORDS: CLIMATE VARIABILITY, CO2, GENERAL-CIRCULATION MODEL, OCEAN, TEMPERATURE, WATER-VAPOR

758

Gorissen, A. 1996. Elevated CO2 evokes quantitative and qualitative changes in carbon dynamics in a plant/soil system: Mechanisms and implications. *Plant and Soil 187(2):289-298.*

It is hypothesized that carbon storage in soil will increase under an elevated atmospheric CO2 concentration due to a combination of an increased net CO2 uptake, a shift in carbon allocation pattern in the plant/soil system and a decreased decomposition rate of plant residues. An overview of several studies, performed in our laboratory, on the effects of elevated CO2 on net carbon uptake, allocation to the soil and decomposition of roots is given to test this hypothesis. The studies included wheat, ryegrass and Douglas-fir and comprised both short-term and long-term studies. Total dry weight of the plants increased up to 62%, but depended on nutrient availability. These results were supported by the data on net (CO2)-C-14 uptake. A shift in C-14-carbon

distribution from shoots to roots was found in perennial species, although this depended on nutrient availability. The decomposition experiments showed that roots cultivated at 700 mu L L-1 CO2 were decomposed more slowly than those cultivated at 350 mu L L-1 CO2. Even after two growing seasons differences up to 13% were observed, although this was found to be dependent on the nitrogen level at which the roots were grown. Both an increased carbon allocation to the soil due to an increased carbon uptake, whether or not combined with a shift in distribution pattern, and a decreased decomposition of root residues will enhance the possibilities of carbon sequestration in soil, thus supporting our hypothesis. However, nutrient availability and the response of the soil microbial biomass (size and activity) play a major role in the processes involved and require attention to clarify plant/soil responses in the long term with regard to sustained stimulation of carbon input into soils and the decomposability of roots and rhizodeposition. Soil texture will also have a strong effect on decomposition rates as a result of differences in the protecting capacity for organic matter. More detailed information on these changes is needed for a proper use of models simulating soil carbon dynamics in the long term.

KEYWORDS: ATMOSPHERIC CO2, DECOMPOSITION, FINE ROOTS, LEAF LITTER, MICROBIAL BIOMASS, NITROGEN, ORGANIC-MATTER, ROOT-DERIVED MATERIAL, SOIL SYSTEM, TURNOVER

759

Gorissen, A., P.J. Kuikman, and H. Vandebeek. 1995. Carbon allocation and water-use in juvenile douglas-fir under elevated co2. *New Phytologist 129(2):275-282.*

In this study the impact of an elevated CO2 level on allocation of assimilates and water use efficiency of Douglas fir [Pseudotsuga menziesii (Mirb.) France] was investigated. Juvenile Douglas firs were exposed to a long-term treatment at 350 and 700 pi l(-1) CO2 for 14 months and subsequently crosswise transferred to phytotrons for a short-term treatment with 350 and 700 mu l l(-1) CO2 for 4 wk in an atmosphere continuously labelled with (CO2)-C-14. No interactive effects on total net uptake of (CO2)-C-14 between long-term treatment and short-term treatment were observed. The short-term treatment with 700 mu l l(-1) CO2 increased the total net uptake of (CO2)-C-14 by 22%, compared with the 350 mu l l(-1) CO2 treatment. The long-term pretreatment did not affect the total net uptake, suggesting that photosynthetic acclimation had not occurred. However, expressed per unit of needle mass a 14% reduction was observed in the trees pretreated at 700 mu l l(-1) CO2. This was not because of a reduced sink strength of the root system. This reduced uptake per unit of needle mass after long-term treatment may have implications for carbon storage in forest ecosystems. The results showed that an initial growth stimulation can eventually be annulled by developing physiological or morphological adaptions. (CO2)-C-14 the root/soil respiration increased in the short-term treatment with 700 mu l l(-1) CO2, indicating a stimulated use of current carbon compounds either by roots or microorganisms. The water use efficiency during the short-term treatment with 700 mu l l(-1) CO2 increased by 32%, but was not affected by the long- term pretreatment. Water use per unit needle mass during the short-term treatment was decreased both by the short-term treatment and by the long-term pretreatment by about 15%. Some of the observed effects appeared to be persistent, such as decreased water use per unit needle mass, whereas others, stimulation of total net (CO2)-C-14 uptake and water use efficiency, were transient.

KEYWORDS: BLACK SPRUCE SEEDLINGS, DIOXIDE, ECOSYSTEMS, ENRICHMENT, GROWTH, LIQUIDAMBAR-STYRACIFLUA, PHOTOSYNTHETIC ACCLIMATION, PINUS-TAEDA SEEDLINGS, RESPONSES, ROOT-DERIVED MATERIAL

760

Gorissen, A., P.J. Kuikman, J.H. vanGinkel, H. vandeBeek, and A.G. Jansen. 1996. ESPAS - An advanced phytotron for measuring carbon dynamics in a whole plant-soil system. *Plant and Soil 179(1):81-87.*

The use of carbon isotopes as tracers is essential for measuring carbon flows in an intact whole plant-soil system. Here, we describe an Experimental Soil Plant Atmosphere System (ESPAS) to perform pulse-labelling and steady-state labelling experiments with (CO2)-C-13 and (CO2)-C-14. The ESPAS facility is an environmental research tool that is used to measure the carbon fluxes from the atmosphere to the roots and into the soil and the microbial biomass and to study decomposition of plant residues and soil organic matter. The influence of environmental conditions in the atmosphere or in soil on the carbon allocation and turnover in the plant-soil ecosystem can be quantified. The design and the technical description of the phytotrons is presented and evidence is provided that the phytotrons are equivalent. For this purpose, Triticum aestivum plants were cultivated in the phytotrons for 39 days and shoot growth, root growth and water use were compared. No significant differences were observed for plant growth and water use. As an example of the practical application of the equipment, an experiment with elevated atmospheric CO2 is presented. Data are given on the uptake of C-14 under ambient (350 mu L L(-1)) and elevated (700 mu L L(-1)CO(2) in Lolium perenne and Festuca arundinacea and the distribution of C-14 among different plant- soil compartments i.e. shoot, root, root-soil respiration, and soil. We conclude that these phytotrons yield detailed information on gross carbon flows in a whole plant-soil system that can not be obtained without sensitive carbon tracers. Such data are important for proper calibration of simulation models on soil organic matter.

KEYWORDS: DIOXIDE, DOUGLAS-FIR, OZONE, RHIZOSPHERE, ROOT-DERIVED MATERIAL, TRANSLOCATION, TURNOVER, WHEAT

761

Gorissen, A., J.H. Vanginkel, J.J.B. Keurentjes, and J.A. Vanveen. 1995. Grass root decomposition is retarded when grass has been grown under elevated co2. *Soil Biology and Biochemistry 27(1):117-120.*

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, CYCLE, INCREASE, LEAF LITTER, NITROGEN, SOIL

762

Gorny, J.R., and A.A. Kader. 1996. Controlled-atmosphere suppression of ACC synthase and ACC oxidase in 'Golden Delicious' apples during long-term cold storage. *Journal of the American Society for Horticultural Science 121(4):751-755.*

Preclimacteric 'Golden Delicious' apples (Malus domestica Borkh.) were stored at 0 degrees C in: air; air + 5% CO2; 2% O- 2 + 98% N-2; or 2% O-2 + 5% CO2 + 93% N-2, and sampled monthly for 4 months to investigate the mechanism(s) by which reduced O-2 and/or elevated CO2 atmospheres inhibit C2H4 biosynthesis. Ethylene biosynthesis rates and in vitro ACS activity were closely correlated in all treatments, while in vitro ACO activity significantly increased over time regardless of the treatment. Only a small amount of C2H4 biosynthesis inhibition by lowered O-2 and/or elevated CO2 atmospheres could be accounted for by suppressed induction of ACO activity, Western blot analysis demonstrated that apples held for 2 months in lowered O-2 and/or elevated CO2 atmospheres had significantly reduced abundance of ACO protein, compared to fruit held in air. Northern blot analysis of ACS and ACO transcript abundance revealed that reduced O-2 and/or elevated CO2 atmospheres delay induction and reduce the abundance of both transcripts, Reduced O-2 and/or elevated CO2 atmospheres reduce

C2H4 biosynthesis by delaying and suppressing expression of ACS at the transcriptional level and by reducing the abundance of active ACO protein. Chemical names used: 1-aminocyclopropane-1- carboxylic acid (ACC), ACC synthase (ACS), ACC oxidase (ACO), ethylene (C2H4), S-adenosylmethionine (AdoMet).

KEYWORDS: 1-AMINOCYCLOPROPANE-1-CARBOXYLIC ACID, ETHYLENE PRODUCTION, EXPRESSION, FRUIT, PROTEIN, PURIFICATION

763
Gorny, J.R., and A.A. Kader. 1996. Regulation of ethylene biosynthesis in climacteric apple fruit by elevated CO2 and reduced O-2 atmospheres. *Postharvest Biology and Technology 9(3):311-323.*

Autocatalytic (System II) C2H4 biosynthesis in climacteric 'Golden Delicious' apples (Malus domestica Borkh) was effectively inhibited at 20 degrees C by atmospheres of 20% CO2-enriched air (17% O-2 + 63% N-2) or 0.25% O-2 (balance N- 2). In vitro 1-aminocyclopropane-1-carboxylic acid (ACC) synthase (ACC-S) activity of apples held in atmospheres of air + 20% CO2 or 0.25% O-2 was significantly inhibited when compared to apples kept in air, and correlated well with fruit C2H4 production rates. In vivo and in vitro ACC oxidase (ACC-O) activity of fruit held in atmospheres of air, air + 20% CO2 or 0.25% O-2 were similar when the assays were performed under standard assay conditions (i.e., in vivo assay performed in air, in vitro assay performed in air + 6% CO2). However, if the in vivo or in vitro ACC-O enzyme activity assays were performed in an atmosphere of 0.25% O-2, ACC-O catalytic competency and activity were significantly reduced. When the in vivo or in vitro ACC-O enzyme activity assays were performed in an atmosphere of air + 20% CO2, ACC-O enzyme activity was actually stimulated. These data indicate that elevated levels of CO2 do not inhibit ACC-O catalytic competency. Western blot analysis revealed that ACC-O protein abundance was not significantly affected by any of the treatments tested, and only the 0.25% O- 2 atmosphere significantly inhibited ACC-O activity. ACC-S activity was significantly reduced by atmospheres of air + 20% CO2 or 0.25% O-2 but not via direct inhibition of ACC-S catalytic competency.

KEYWORDS: 1-AMINOCYCLOPROPANE-1-CARBOXYLIC ACID, CARBON DIOXIDE, OXIDASE, PH, PURIFICATION, SYNTHASE

764
Gorny, J.R., and A.A. Kader. 1997. Low oxygen and elevated carbon dioxide atmospheres inhibit ethylene biosynthesis in preclimacteric and climacteric apple fruit. *Journal of the American Society for Horticultural Science 122(4):542-546.*

Autocatalytic C2H4 biosynthesis in preclimacteric apple fruit (Malus domestica Borkh, 'Golden Delicious') was prevented by storage in atmospheres of 20% CO2-enriched air (17% O-2+ 63% N- 2) or 0.25% O-2 (balance N-2). In preclimacteric fruit, both treatments inhibited C2H4 biosynthesis by suppressing expression of ACC synthase (ACC-S) at the mRNA level. ACC oxidase (ACC-O) mRNA abundance and in vitro enzyme activity also were impaired by these treatments. However, the conversion of ACC to C2H4 never became the rate limiting step in C2H4 biosynthesis, C2H4 biosynthesis also was effectively inhibited in climacteric apple fruit kept in air + 20% CO2 or 0.25% O-2. Climacteric apples also exhibited suppressed expression of ACC- S at the mRNA level, while ACC-O transcript abundance, enzyme activity, and protein abundance mere reduced only slightly. ACC-S is the key regulatory enzyme of C2H4 biosynthesis and is the major site at which elevated CO2 and reduced O-2 atmospheres inhibit C2H4 biosynthesis, irrespective of fruit physiological maturity. Chemical names used: 1-aminocyclopropane-1-carboxcylic acid (ACC).

KEYWORDS: 1-AMINOCYCLOPROPANE-1-CARBOXYLIC ACID, EXPRESSION, OXIDASE, PROPYLENE, PROTEIN, PURIFICATION, SYNTHASE, TOMATO

765
Goudriaan, J. 1992. Where goes the carbon-dioxide - the role of vegetation. *Recherche 23(243):597.*

KEYWORDS: AGRICULTURAL YIELD, ASSEMBLAGE, CO2-ENRICHMENT, PLANT, SOYBEAN LEAVES

766
Gouk, S.S., J. He, and C.S. Hew. 1999. Changes in photosynthetic capability and carbohydrate production in an epiphytic CAM orchid plantlet exposed to super-elevated CO2. *Environmental and Experimental Botany 41(3):219-230.*

The effects on growth in super-elevated (1%) CO2 in terms of photosynthetic capability and carbohydrate production were studied in an epiphytic CAM (Crassulacean acid metabolism) orchid plantlet, Mokara Yellow (Arachmis hookeriana x Ascocenda Madame Kenny). The growth of the plantlets was greatly enhanced after growing for 3 months at 1% CO2 compared with the control plantlets (0.035% CO2). CO2 enrichment produced more than a 2- fold increase in dry matter production. The enhanced root growth at 1% CO2 led to a higher root:shoot ratio. Plantlets grown at super-elevated CO2 had higher F-v/F-m values, a higher photochemical quenching (q(P)) and a relatively lower non- photochemical quenching (q(N)). CO2 at 1% appeared to enhance the utilization of captured light energy in the orchid plantlets. CO2 enrichment also increased contents of soluble sugars (glucose and sucrose) and starch in the orchid plantlets. The extra starch formed under 1% CO, did not cause a disruption of the chloroplasts. Chlorophyll content was higher and a clear granal stacking was evident in young leaves and roots of plantlets grown at 1% CO2. An extensive thylakoid system was observed in the young leaf chloroplasts of the CO2- enriched plantlets indicating an improved development of the photosynthetic apparatus when compared to that of the control plantlets. The increased photosynthetic capacity and enhanced growth of the epiphytic roots under CO, enrichment would facilitate the generation of more photoassimilates and acquisition of essential resources, thereby increasing the survival rate of orchid plantlets under stressful field conditions.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CHLOROPHYLL FLUORESCENCE, CULTURE, ENRICHMENT, GROWTH, INVITRO, RESPONSES, ROOTS, STRAWBERRY PLANTLETS, ULTRASTRUCTURE

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Gouk, S.S., J.W.H. Yong, and C.S. Hew. 1997. Effects of super-elevated CO2 on the growth and carboxylating enzymes in an epiphytic CAM orchid plantlet. *Journal of Plant Physiology 151(2):129-136.*

Responses of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) and phosphoenolpyruvate carboxylase (PEPCase) to super-elevated CO2 were determined along with dry mass production, chlorophyll, soluble protein and nocturnal malate increases (NMI) for an epiphytic Crassulacean acid metabolism (CAM) orchid plantlet, Mokara Yellow. After S-month culture period, the total dry mass under super-elevated CO2 was 170% higher than the plantlets grown in 0.03% CO2; young leaf dry mass was 4-fold higher while the root dry mass increased 278% and 344% under 1% and 5% CO2 respectively. Higher root:shoot ratio was observed under super-elevated CO2; 0.22 in 0.03% CO2, 0.32 in 1% CO2 and 0.38 in 5% CO2. The averaged increase in total young leaf area was 244% and 373% under 1% and 5% CO2 respectively Leaf

chlorophyll expressed per unit fresh weight was reduced under 5% CO2 but it increased 19% and 67% in old and young leaves of 3-month plantlets under 1% CO2. The root chlorophyll content increased 108% and 154% under 1%;, and 5% CO2 respectively. Soluble protein in young leaves increased 32% under 1% CO2 and 75% under 5% CO2, while the increase in root protein varied from 36% to 100%. The activities of Rubisco and PEPCase el:pressed per unit protein were reduced under super- elevated CO2, particularly in 5% CO2, the decreases ranged from 12% to 90% in Rubisco and 27% to 90% in PEPCase. Nevertheless, the leaf Rubisco:PEPCase ratio increased 110% to 362% under super-elevated CO2. Increased NMI, ranged from 23% to 182% under super-elevated CO2, contributed to the increased dry matter accumulation in Mokara plantlets. Throughout the S-month culture period, the CO2-enriched plantlets showed enhanced growth particularly under 1% CO2 in terms of biomass production, chlorophyll, soluble protein and NMI despite a concomitant decrease in the activities of the carboxylating enzymes.

KEYWORDS: CARBON DIOXIDE, CRASSULACEAN ACID METABOLISM, ENRICHMENT, INVITRO, OPUNTIA FICUS INDICA, PHOTOSYNTHESIS, STRAWBERRY PLANTLETS, SUCROSE, TEMPERATURE, TISSUE-CULTURE

768

Goulart, B.L., P.E. Hammer, K.B. Evensen, W. Janisiewicz, and F. Takeda. 1992. Pyrrolnitrin, captan + benomyl, and high co2 enhance raspberry shelf-life at 0C or 18C. *Journal of the American Society for Horticultural Science 117(2):265-270.*

The effects of preharvest applications of pyrrolnitrin (a biologically derived fungicide) on postharvest longevity of 'Bristol' black raspberry (Rubus occidentalis L.) and 'Heritage' red raspberry [R. idaeus L. var. strigosus (Michx.) Maxim] were evaluated at two storage temperatures. Preharvest fungicide treatments were 200 mg pyrrolnitrin/liter, a standard fungicide treatment (captan + benomyl or iprodione) or a distilled water control applied 1 day before first harvest. Black raspberries were stored at 18 or 0 +/- 1C in air or 20% CO2. Red raspberries were stored at the same temperatures in air only. Pyrrolnitrin-treated berries often had less gray mold (Botrytis cinerea Pers. ex Fr.) in storage than the control but more than berries treated with the standard fungicides. Storage in a modified atmosphere of 20% CO2 greatly improved postharvest quality of black raspberries at both storage temperatures by reducing gray mold development. The combination of standard fungicide or pyrrolnitrin, high CO2, and low temperature resulted in more than 2 weeks of storage with less than 5% disease on black raspberries; however, discoloration limited marketability after almost- equal-to 8 days under these conditions. Chemical names used: 3-chloro-4-(2'-nitro-3'-chlorophenyl)-pyrrole (pyrrolnitrin); N-trichloromethylthio-4-cyclohexene-1,2-dicarboximide (captan); methyl 1-(butylcarbamoyl)-2-benzimidazolecarbamate) (benomyl); 3-(3,5-dichlorophenyl)-N-(1-methylethyl)-2,4-dioxo-1-imidazolidinecarboxamide (Rovral, iprodione).

KEYWORDS: STRAWBERRIES

769

Graham, E.A., and P.S. Nobel. 1996. Long-term effects of a doubled atmospheric CO2 concentration on the CAM species Agave deserti. *Journal of Experimental Botany 47(294):61-69.*

To examine the effects of a doubled atmospheric CO2 concentration and other aspects of global climate change on a common CAM species native to the Sonoran Desert, Agave deserti was grown under 370 and 750 mu mol CO2 mol(-1) air and gas exchange was measured under various environmental conditions. Doubling the CO2 concentration increased daily net CO2 uptake by 49% throughout the 17 months and decreased daily transpiration by 24%, leading to a 110% increase in water-use efficiency, Under the doubled CO2 concentration, the activity of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) was 11% lower, phosphoenolpyruvate carboxylase was 34% lower, and the activated:total ratio for Rubisco was 25% greater than under the current CO2 concentration. Less leaf epicuticular wax occurred on plants under the doubled CO2 concentration, which decreased the reflectance of photosynthetic photon flux (PPF); the chlorophyll content per unit leaf area was also less, The enhancement of daily net CO2 uptake by doubling the CO2 concentration increased when the PPF was decreased below 25 mol m(-2) d(-1), when water was withheld, and when day/night temperatures were below 17/12 degrees C, More leaves, each with a greater surface area, were produced per plant under the doubled CO2 concentration. The combination of increased total leaf surface area and increased daily net CO2 uptake led to an 88% stimulation of dry mass accumulation under the doubled CO2 concentration, A rising atmospheric CO2 concentration, together with accompanying changes in temperature, precipitation, and PPF, should increase growth and productivity of native populations of A. deserti.

KEYWORDS: CROP RESPONSES, ELEVATED CARBON-DIOXIDE, ENRICHMENT, ENVIRONMENTAL PHYSIOLOGY, EPICUTICULAR WAX LOAD, GROWTH, PHOTOSYNTHESIS, PLANT, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE, RISING CO2

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Grams, T.E.E., S. Anegg, K.H. Haberle, C. Langebartels, and R. Matyssek. 1999. Interactions of chronic exposure to elevated CO2 and O-3 levels in the photosynthetic light and dark reactions of European beech (Fagus sylvatica). *New Phytologist 144(1):95-107.*

Young trees of European beech (Fagus sylvatica) acclimated for one growing season to ambient (c. 367 mu l l(-1)) or elevated CO2 levels (c. 660 mu l l(-1)) were exposed during the subsequent year to combinations of the same CO2 regimes and ambient or twice-ambient ozone (O-3) levels (generated from the database of a rural site). By the end of June, before the development of macroscopic leaf injury, the raised O-3 levels had not affected the light and dark reactions of photosynthesis. However, acclimation to elevated CO2 had resulted in lowered chlorophyll and nitrogen concentrations, whereas photosynthetic performance, examined over a wide range of parameters from light and dark reactions, remained unchanged or showed only slight reductions (e.g. apparent electron transport rate, ETR; apparent quantum yield of CO2 gas exchange, Phi(CO2); apparent carboxylation efficiency, CE; and photosynthetic capacity at light and CO2 saturation, PC). In August, after the appearance of leaf necroses, plants grown under ambient CO2 and twice-ambient O-3 conditions declined in both the photosynthetic light reactions (optimum electron quantum yield, Fv/F-m, non-photochemical energy quenching, NPQ, reduction state of Q(A), apparent electron quantum yield, Phi(PSI)I, maximum electron transport rates) and the dark reactions as reflected by CE, Phi(CO2), as well as the maximum CO2 uptake rate (i.e. PC). CE, Phi(CO2) and PC were reduced by c. 75, 40 and 75%, respectively, relative to plants exposed to ambient CO2 and O-3 levels. By contrast, plants exposed to twice-ambient O-3 and elevated CO2 levels maintained a photosynthetic performance similar to individuals grown either under ambient CO2 and ambient O-3, or elevated CO2 and ambient O-3 conditions. The long-term exposure to elevated CO2 therefore tended to counteract adverse chronic effects of enhanced O-3 levels on photosynthesis. Possible reasons for this compensatory effect in F. sylvatica are discussed.

KEYWORDS: ATMOSPHERIC CO2, BETULA-PENDULA, CARBON DIOXIDE, CHLOROPHYLL FLUORESCENCE, LEAF GAS-EXCHANGE, LOW OZONE CONCENTRATIONS, NORWAY SPRUCE, PHOTOSYSTEM, SPRUCE PICEA-ABIES, TROPOSPHERIC OZONE

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Grams, T.E.E., and R. Matyssek. 1999. Elevated CO2 counteracts the limitation by chronic ozone exposure on photosynthesis in Fagus sylvatica L.: Comparison between chlorophyll fluorescence and leaf gas exchange. *Phyton-Annales Rei Botanicae 39(4):31-39.*

The interaction of elevated CO2 and enhanced chronic ozone (O- 3) impact was analysed throughout the growing season in the photosynthetic response (chlorophyll fluorescence and leaf gas exchange) of beech saplings (Fagus sylvatica) which had been acclimated to CO2 supply during the year prior to the experiment. Both light and dark reactions (i.e. electron transport rate and photosynthetic capacity) of plants grown at ambient CO2 and twice-ambient O-3 concentrations were distinctly reduced by August. The O-3-induced decline was counteracted by elevated CO2 supply (i.e. ambient +300 ppm). Plants grown at high CO2 supply and ambient or twice-ambient O- 3 concentrations displayed a photosynthetic performance similar to plants exposed to ambient CO2 and O-3 conditions. Responses in chlorophyll fluorescence were found to be consistent with those in leaf gas exchange.

KEYWORDS: BEECH, CARBON DIOXIDE, GROWTH, LEAVES, NORWAY SPRUCE, O-3, RESPONSES, SPRING WHEAT, TROPOSPHERIC OZONE, YIELD

772

Grant, R.F. 1998. Simulation in ecosys of root growth response to contrasting soil water and nitrogen. *Ecological Modelling 107(2-3):237-264.*

If mathematical models of plant growth are to perform reliably under diverse conditions of soil and climate, then the effects of these conditions on root growth must be represented. A mathematical model of root and mycorrhizal growth is proposed to represent the effects of soil and climate on growth using the hypothesis that a functional equilibrium exists among root axes and shoot branches. In this model access to growth resources (C, N, P, water) by different axes or branches depends upon (1) proximity of the axis or branch to the point of resource acquisition, and (2) the rate at which resources are consumed by the axis or branch in relation to that by other axes or branches. This model was coupled to a plant growth model as part of the ecosystem simulation model ecosys, and its sensitivity to changes in model parameters and soil boundary conditions was tested. Simulated root growth was less sensitive to changes in soil water and nitrogen than was simulated shoot growth. This lower sensitivity allowed the model to simulate changes in root,shoot ratios with changes in soil water and nitrogen that were consistent with those commonly reported in the literature. Changes in soil water also caused changes in vertical distributions of root length density to be simulated that were also consistent with those reported. Changes in root,shoot partitioning and in root density distributions allowed improved access by plants in the model to limiting growth resources. The root model was parameterized from basic root growth studies conducted independently of the model, and without reference to site-specific patterns of seasonal root growth. Consequently the model is likely to be of general value in the simulation of root growth under diverse soil conditions, although such generality needs to be established through further testing under different soils, climates and crops. The precision of some of the model parameters is uncertain and the sensitivity of the model to this uncertainty is discussed.

KEYWORDS: AIR CO-2 ENRICHMENT, CARBON DIOXIDE, FACE EXPERIMENT, MODEL, MYCORRHIZAL FUNGI, PHOSPHORUS, PLANTS, SHOOT DEVELOPMENT, WINTER-WHEAT, ZEA-MAYS

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Grant, R.F., T.A. Black, G. den Hartog, J.A. Berry, H.H. Neumann, P.D. Blanken, P.C. Yang, C. Russell, and I.A. Nalder. 1999. Diurnal and annual exchanges of mass and energy between an aspen-hazelnut forest and the atmosphere: Testing the mathematical model Ecosys with data from the BOREAS experiment. *Journal of Geophysical Research-Atmospheres 104(D22):27699-27717.*

There is much uncertainty about the net carbon (C) exchange of boreal forest ecosystems, although this exchange may be an important part of global C dynamics. To resolve this uncertainty, net C exchange has been measured at several sites in the boreal forest of Canada as part of the Boreal Ecosystem- Atmosphere Study (BOREAS). One of these sites is the Southern Old Aspen site at which diurnal CO2 and energy (radiation, latent, and sensible heat) fluxes were measured during 1994 using eddy correlation techniques at different positions within a mixed 70 year old aspen-hazelnut forest. These measurements were used to test a complex ecosystem model "ecosys" in which mass and energy exchanges between terrestrial ecosystems and the atmosphere are simulated hourly under diverse conditions of soil, management, and climate. These simulations explained between 70% and 80% of diurnal variation in ecosystem CO2 and energy fluxes measured during three 1 week intervals in late April, early June, and mid-July. Total annual CO2 fluxes indicated that during 1994, aspen was a net sink of 540 (modeled) versus 670 (measured) g C m(-2) yr(-1), while hazelnut plus soil were a net source of 472 (modeled) versus 540 (measured) g C m(-2) yr(-1). The aspen-hazelnut forest at the BOREAS site was therefore estimated to be a net sink of about 68 (modeled) versus 130 (measured) g C m(-2) yr(-1) during 1994. Long-term simulations indicated that this sink may be larger during cooler years and smaller during warmer years because C fixation in the model was less sensitive to temperature than respiration. These simulations also indicated that the magnitude of this sink declines with forest age because respiration increases with respect to fixation as standing phytomass grows. Confidence in the predictive capabilities of ecosystem models at decadal or centennial timescales is improved by well-constrained tests of these models at hourly timescales.

KEYWORDS: BLACK SPRUCE, CO2- ENRICHMENT, ELEVATED CARBON-DIOXIDE, JACK PINE, NITROUS-OXIDE, PHOSPHORUS UPTAKE, ROOT-GROWTH, SIMULATION-MODEL, SOIL ORGANIC MATTER, TREMBLING ASPEN

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Grant, R.F., R.L. Garcia, P.J. Pinter, D. Hunsaker, G.W. Wall, B.A. Kimball, and R.L. LaMorte. 1995. Interaction between atmospheric CO2 concentration and water deficit on gas exchange and crop growth: Testing of ecosys with data from the Free Air CO2 Enrichment (FACE) experiment. *Global Change Biology 1(6):443-454.*

Soil water deficits are likely to influence the response of crop growth and yield to changes in atmospheric CO2 concentrations (C-a), but the extent of this influence is uncertain. To study the interaction of water deficits and C-a on crop growth, the ecosystem simulation model ecosys was tested with data for diurnal gas exchange and seasonal wheat growth measured during 1993 under high and low irrigation at C- a = 370 and 550 mu mol mol(-1) in the Free Air CO2 Enrichment (FACE) experiment near Phoenix, AZ. The model, supported by the data from canopy gas exchange enclosures, indicated that under high irrigation canopy conductance (g(c)) at C-a = 550 mu mol mol(-1) was reduced to about 0.75 that at C-a = 370 mu mol mol(-1), but that under low irrigation, g(c) was reduced less. Consequently when C-a was increased from 370 to 550 mu mol mol(-1), canopy transpiration was reduced less, and net CO2 fixation was increased more, under low irrigation than under high irrigation. The simulated effects of C-a and irrigation on diurnal gas exchange were also apparent on seasonal water use and grain yield. Simulated vs. measured seasonal water use by wheat under high irrigation was reduced by 6% vs. 4% at C-a = 550 vs. 370 mu mol mol(-1), but that under low irrigation was increased by 3% vs. 5%. Simulated

vs. measured grain yield of wheat under high irrigation was increased by 16% vs. 8%, but that under low irrigation was increased by 38% vs. 21%. In ecosys, the interaction between C-a and irrigation on diurnal gas exchange, and hence on seasonal crop growth and water use, was attributed to a convergence of simulated g(c) towards common values under both C-a as canopy turgor declined. This convergence caused transpiration to decrease comparatively less, but CO2 fixation to increase comparatively more, under high vs. low C-a. Convergence of g(c) was in turn attributed to improved turgor maintenance under elevated C-a caused by greater storage C concentrations in the leaves, and by greater rooting density in the soil.

KEYWORDS: BIOCHEMICAL-MODEL, CANOPY PHOTOSYNTHESIS, CARBOXYLASE-OXYGENASE, ELEVATED CARBON-DIOXIDE, MAIZE, ROOT-GROWTH, SIMULATION-MODEL, SOYBEAN LEAVES, TEMPERATURE, WINTER-WHEAT

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Grant, R.F., B.A. Kimball, P.J. Pinter, G.W. Wall, R.L. Garcia, R.L. Lamorte, and D.J. Hunsaker. 1995. Carbon-dioxide effects on crop energy-balance - testing ecosys with a free-air co2 enrichment (face) experiment. *Agronomy Journal 87(3):446-457.*

Elevated CO2 concentrations (C-e) have been observed to decrease short-term plant water use under controlled conditions by increasing stomatal resistance. The extent to which this decrease occurs over a growing season in the held is uncertain, however, because stomatal resistance is only one of many mechanisms that control water use. In this study, we tested the ecosystem simulation model ecosys, which reproduces an hourly energy balance through soil-vegetation systems under defined atmospheric boundary renditions, using energy exchange data measured as part of the Free-Air CO2 Enrichment (FACE) experiment at C-e = 550 vs. 370 mu mol mol(-1). The model reproduced reductions in measured upward latent heat fluxes that varied from -10 to +40 W m(-2), depending on atmospheric conditions. In the model, the primary effect of elevated C-e on latent heat fluxes was through canopy stomatal conductance. This effect was largely offset by secondary effects through canopy temperature that enabled the model to reproduce measured changes in sensible heat fluxes. The total effect simulated by ecosys of C-e = 550 vs. 370 mu mol mol(-1) on evapotranspiration during the entire PACE experiment was a reduction of 7%. This reduction compares with one of 11% estimated from accumulated daily measurements of latent heat flux. In the model, the different effects of C-e on plant water use depend on atmosphere and soil boundary conditions, and are highly dynamic. Consequently the simulated C-e-water use relationship is likely to be site-specific. The use of models such as ecosys allows site-specific boundary conditions to be considered in the study of C-e effects on plant growth and water use.

KEYWORDS: BIOCHEMICAL-MODEL, CANOPY PHOTOSYNTHESIS, EXPERIMENTAL- VERIFICATION, OSMOTIC ADJUSTMENT, PLANT GROWTH, ROOT-GROWTH, SIMULATION-MODEL, SOIL COMPACTION, STOMATAL CONDUCTANCE, WATER-USE EFFICIENCY

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Grant, R.F., G.W. Wall, B.A. Kimball, K.F.A. Frumau, P.J. Pinter, D.J. Hunsaker, and R.L. Lamorte. 1999. Crop water relations under different CO2 and irrigation: testing of ecosys with the free air CO2 enrichment (FACE) experiment. *Agricultural and Forest Meteorology 95(1):27-51.*

Increases in crop growth under elevated atmospheric CO2 concentration (C-A) have frequently been observed to be greater under water-limited versus non-limited conditions. Crop simulation models used in climate change studies should be capable of reproducing such changes in growth response to C-A with changes in environmental conditions. We propose that changes with soil water status in crop growth response to C-A can be simulated if stomatal resistance is considered to vary directly with air-leaf C-A gradient, inversely with leaf carboxylation rate, and exponentially with leaf turgor. Resistance simulated in this way increases with C-A relatively less, and CO2 fixation increases with C-A relatively more, under water-limited versus non-limited conditions. As part of the ecosystem model ecosys, this simulation technique caused changes in leaf conductance and CO2 fixation, and in canopy water potential, temperature and energy balance in a modelling experiment that were consistent with changes measured under 355 versus 550 mu mol mol(-1) C-A and low versus high irrigation in a free air CO2 enrichment (FACE) experiment on wheat. Changes with C-A in simulated crop water relations allowed the model to reproduce under 550 mu mol mol(-1) C-A and low versus high irrigation a measured increase of 20 versus 10% in seasonal wheat biomass, and a measured decrease of 2 versus 5% in seasonal evapotranspiration, The basic nature of the processes simulated in this model is intended to enable its use under a wide range of soil, management and climate conditions.

KEYWORDS: ATMOSPHERIC CO2, CARBON-DIOXIDE ENRICHMENT, ENERGY-BALANCE, EXPERIMENTAL-VERIFICATION, GAS-EXCHANGE, ROOT-GROWTH, SIMULATION-MODEL, SOIL TEMPERATURE, STOMATAL CONDUCTANCE, USE EFFICIENCY

777

Grant, W.J.R., H.M. Fan, W.J.S. Downton, and B.R. Loveys. 1992. Effects of co2 enrichment on the physiology and propagation of 2 australian ornamental plants, chamelaucium-uncinatum (schauer) X chamelaucium-floriferum (ms) and correa- schlechtendalii (behr). *Scientia Horticulturae 52(4):337-342.*

Root formation on both Chamelaucium and Correa cuttings maintained at high humidity in an enclosed fog tunnel was significantly enhanced when ambient CO2 was increased from 350 to 800 mubar. CO2 enrichment resulted in decreased transpiration and increased water potential of cuttings implying an effect of CO2 on stomatal conductance. CO2 enrichment led to increased starch levels in cuttings of both species probably by raising the intercellular partial pressure of CO2. Increased starch content with CO2 enrichment was able to account for 70-90% of the dry weight increase in Correa, but only for 10-30% of the dry weight increase in Chamelaucium. It is suggested that the stimulation of rooting associated with CO2 enrichment probably derives from the improved water relations of the cuttings rather than from increased carbohydrate levels.

KEYWORDS: CUTTINGS

778

Grant, W.J.R., and B.R. Loveys. 1996. Controlling rootstock sprouts of Agonis flexuosa (Willd) Sweet at ambient and elevated CO2 by multiple applications of low concentration NAA. *Australian Journal of Experimental Agriculture 36(5):619-624.*

A method for grafting variegated scion material to green leafed Agonis flexuosa (Willd.) Sweet stock was developed to overcome the difficulty of striking cuttings. However sprouting of both seedling and cutting-grown A. flexuosa rootstocks was a significant problem. Microwedge grafting of actively growing leafy scions and stocks in fog at 32/22 degrees C gave 90-100% success and scion bud activity was stimulated within 2 weeks. Weekly or fortnightly spray applications of 100 mg NAA/L (napthaleneacetic acid), starting at the time of grafting, gave effective sprout control whereas a single pregraft spray of 200 mg NAA/L was not effective. CO2 enrichment of the fog environment was

investigated as a means of enhancing scion growth. CO2 at 80 kPa increased scion dry weight (DW), leaf and branch numbers, but had no effect on rootstock sprout or stem DW or sprout numbers. Optimum NAA concentrations for rootstock sprout suppression under elevated CO2 with fog, were 50-100 mg/L, which were not deleterious to scion shoot length, when sprayed on the stock portion only. Stock sprout numbers, scion leaf and branch numbers were negatively correlated with NAA concentration. Sprout growth at 100 mg NAA/L was about 5% of control sprout growth. Concentrations greater than or equal to 200 mg NAA/L caused leaf tip necrosis and excess stem callusing. Scion growth was inversely related to the degree of resprouting in control treatments.

KEYWORDS: ENRICHMENT, GROWTH, TREES

779

Grashoff, C., P. Dijkstra, S. Nonhebel, A.H.C.M. Schapendonk, and S.C. VandeGeijn. 1995. Effects of climate change on productivity of cereals and legumes; model evaluation of observed year-to-year variability of the CO2 response. *Global Change Biology 1(6):417-428.*

The effect of elevated [CO2] on the productivity of spring wheat, winter wheat and faba bean was studied in experiments in climatized crop enclosures in the Wageningen Rhizolab in 1991- 93. Simulation models for crop growth were used to explore possible causes for the observed differences in the CO2 response. Measurements of the canopy gas exchange (CO2 and water vapour) were made continuously from emergence until harvest. At an external [CO2] of 700 mu mol mol(-1), Maximum Canopy CO2 Exchange Rate (CCFRmax) at canopy closure was stimulated by 51% for spring wheat and by 71% for faba bean. At the end of the growing season, above ground biomass increase at 700 mu mol mol(-1) was 58% (faba bean), 35% (spring wheat) and 19% (winter wheat) and the harvest index did not change. For model exploration, weather data sets for the period 1975-88 and 1991-93 were used, assuming adequate water supply and [CO2] at 350 and 700 mu mol mol(-1). For spring wheat the simulated responses (35-50%) were at the upper end of the experimental results. In agreement with experiments, simulations showed smaller responses for winter wheat and larger responses for faba bean. Further model explorations showed that this differential effect in the CO2 response may not be primarily due to fundamental physiological differences between the crops, but may be at least partly due to differences in the daily air temperatures during comparable stages of growth of these crops. Simulations also showed that variations between years in CO2 response can be largely explained by differences in weather conditions (especially temperature) between growing seasons.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, DRY-MATTER, ELEVATED CO2, GROWTH, PATTERN, PHOTOSYNTHESIS, VICIA-FABA L, WHEAT, YIELD VARIABILITY

780

Graumlich, L.J. 1991. Sub-alpine tree growth, climate, and increasing CO2 - an assessment of recent growth trends. *Ecology 72(1):1-11.*

LaMarche et al. (1984) hypothesized that recent trends of increasing ring widths in subalpine conifers may be due to the fertilizing effects of increased atmospheric CO2. Five tree- ring series from foxtail pine (Pinus balfouriana), lodgepole pine (P. murrayana), and western juniper (Juniperus occidentalis) collected in the Sierra Nevada, California, were analyzed to determine if the temporal and spatial patterns of recent growth were consistent with the hypothesized CO2-induced growth enhancement. Specifically, I address the following questions: (1) Can growth trends be explained solely in terms of climatic variation? (2) Are recent growth trends unusual with respect to long-term growth records? For three of the five sites, 20th-century growth variation can be adequately modeled as a function of climatic variation. For the remaining two sites, trends in the residuals from the growth/climate models indicate systematic underestimation of growth during the past decade that could be interpreted as either CO2 fertilization or as a response to extreme climatic events during the mid 1970s. At all five sites, current growth levels have been equalled or exceeded during some preindustrial periods. Taken together, these results do not indicate that CO2-induced growth enhancement is occurring among subalpine conifers in the Sierra Nevada. While the results presented here offer no support for the hypothesized CO2 fertilization effect, they do provide insights into the response of subalpine conifers to climatic variation. Response surfaces demonstrate that precipitation during previous winter and temperature during the current summer interact in controlling growth and that the response can be nonlinear. Although maximum growth rates occur under conditions of high winter precipitation and warm summers for all three species, substantial species-to-species variation occurs in the response to these two variables.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CALIFORNIA, FORESTS, PINE, RESPONSES, SIERRA NEVADA

781

Graybill, D.A., and S.B. Idso. 1993. Detecting the aerial fertilization effect of atmospheric co2 enrichment in tree-ring chronologies. *Global Biogeochemical Cycles 7(1):81-95.*

The growth-promoting effects of the historical increase in the air's CO2 content are not yet evident in tree-ring records where yearly biomass additions are apportioned among all plant parts. When almost all new biomass goes into cambial enlargement, however, a growth increase of 60% or more is observed over the past two centuries. As a result, calibration of tree-ring records of this nature with instrumental climate records may not be feasible because of such growth changes. However, climate signals prior to about the mid-19th century may yet be discovered by calibrating such tree-ring series with independently derived proxy climate records for those times.

KEYWORDS: CARBON DIOXIDE, ELEVATED CO2, FOREST, GROWTH TRENDS, PAST 2 CENTURIES, PHOTOSYNTHETIC ACCLIMATION, SOUR ORANGE TREES

782

Grayston, S.J., C.D. Campbell, J.L. Lutze, and R.M. Gifford. 1998. Impact of elevated CO2 on the metabolic diversity of microbial communities in N-limited grass swards. *Plant and Soil 203(2):289-300.*

The impact of elevated atmospheric CO2 on qualitative and quantitative changes in rhizosphere carbon flow will have important consequences for nutrient cycling and storage in soil, through the effect on the activity, biomass size and composition of soil microbial communities. We hypothesized that microbial communities from the rhizosphere of Danthonia richardsonii, a native C3 Australian grass, growing at ambient and twice ambient CO2 and varying rates of low N application (20, 60, 180 kg N ha(-1)) will be different as a consequence of qualitative and quantitative change in rhizosphere carbon flow. We used the Biolog(TM) system to construct sole carbon source utilisation profiles of these communities from the rhizosphere of D. richardsonii. Biolog(TM) GN and MT plates, the latter to which more ecologically relevant root exudate carbon sources were added, were used to characterise the communities. Microbial communities from the rhizosphere of D. richardsonii grown for four years at twice ambient CO2 had significantly greater utilisation of all carbon sources except those with a low C:N ratio (neutral and acidic amino acids, amides, N-heterocycles, long chain aliphatic acids) than communities from plants grown at ambient CO2. This indicates a change in microbial community composition suggesting that under elevated CO2 compounds with a higher C:N ratio were exuded. Enumeration of microorganisms, using

plate counts, indicated that there was a preferential stimulation of fungal growth at elevated CO2 and confirmed that bacterial metabolic activity (C utilisation rates), not population size (counts), were stimulated by additional C flow at elevated CO2. Nitrogen was an additional rate-limiting factor for microbial growth in soil and had a significant impact on the microbial response to elevated CO2. Microbial populations were higher in the rhizosphere of plants receiving the highest N application, but the communities receiving the lowest N application were most active. These results have important implications for carbon turnover and storage in soils where changes in soil microbial community structure and stimulation of the activity of microorganisms which prefer to grow on rhizodeposits may lead to a decrease in the composition of organic matter and result in an accumulation of soil carbon.

KEYWORDS: ATMOSPHERIC CO2, C SOURCE UTILIZATION, CARBON-SOURCE UTILIZATION, DIOXIDE, ENRICHMENT, GROWTH, NITROGEN, PLANT-RESPONSES, RHIZOSPHERE, SOIL

783

Greaves, A.J., and J.G. Buwalda. 1996. Observations of diurnal decline of photosynthetic gas exchange in kiwifruit and the effect of external CO2 concentration. *New Zealand Journal of Crop and Horticultural Science 24(4):361-369.*

The prevalence of diurnal decline of photosynthesis in field- grown kiwifruit (Actinidia deliciosa (A. Chev.) C.F. Liang et A.R. Ferguson var. deliciosa 'Hayward') and the effects of elevated CO2 concentration during decline were studied. During the seasonal period from soon after fruit set to harvest, marked diurnal reductions of photosynthesis rate were found that could not be correlated with levels of photosynthetically active radiation (PAR), temperature, and transpiration. Declines of photosynthesis were observed only on clear days characterised by benign environmental conditions other than sustained irradiance at saturating or near saturating levels. Elevation of CO2 concentration to 200 mu mol/mol above ambient during photosynthesis decline overcame the decline effect, allowing photosynthesis to track irradiance levels throughout the day. Possible mechanisms generating the diurnal decline and the alleviation by elevation of CO2 concentration are discussed.

KEYWORDS: ACTINIDIA-DELICIOSA VINES, C-3 PLANTS, CAPACITY, DEPRESSION, FIELD, GROWTH, LEAVES, RADIATION

784

Greer, D.H., W.A. Laing, and B.D. Campbell. 1995. Photosynthetic responses of 13 pasture species to elevated co2 and temperature. *Australian Journal of Plant Physiology 22(5):713-722.*

Thirteen common pasture species, (eleven C-3 and two C-4), were grown in controlled environments at 12/7, 18/13 and 28/23 degrees C and at 350 and 700 ppm CO2 to evaluate the effects of elevated CO2 on their photosynthetic responses. Photosynthesis was measured at the growth temperatures and at both 350 and 700 ppm CO2. In C-3 species, short-term (within minutes) increases in CO2 had the greatest effect on photosynthesis, with an average of 50-60% higher rates in plants exposed to 700 ppm CO2 at each temperature. However, there was a continuum of response between the C-3 species whereas C-4 species were unaffected by short-term changes in CO2 There was also a long-term (4-8 weeks) response to high CO2, with an average of about 40-50% higher rates of photosynthesis, with some response by C-4 species. Both short- and long-term responses were negatively correlated with the photosynthetic rate of each species at 350 ppm CO2 and all species were less efficient at converting photosynthate to dry matter at elevated CO2. These data show clearly that photosynthesis of these cool temperate pasture species can respond to elevated CO2, especially at low temperatures. This will have consequences for predicting the potential effects of climate change, accompanied by rising CO2, on pasture ecosystems.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CARBON-DIOXIDE, ENVIRONMENTS, GROWTH, PERENNIAL RYEGRASS, PRODUCTIVITY, RESPIRATION, SOURCE-SINK RELATIONS, WHITE CLOVER, YIELD

785

Gregor, H.D. 1992. The potential role of temperate forests as sinks for co2 - examples from the german environmental-policy against global warming. *Water, Air, and Soil Pollution 64(1-2):197-212.*

Among industrialized nations Germany ranks fourth in CO2 emissions. Most of these originate from the use of fossil fuels. Based on reports of a parliamentary study commission, established in 1987, and other expert groups in Germany this article adresses possible environmental effects of increasing atmospheric CO2, the sink potential of temperate forests and the influence of forest damage on this potential. A strategy for a 25 to 30% or 250 to 300 X 10(6) t yr-1 CO2 emissions reduction by 2005 (which Germany has itself committed to) is described in which measures to enhance C sequestration by forests play an important role. Expansion of forest area, a further increase of C storage by appropriate management and the restoration and protection of forest health impaired by air pollution would result in an additional storage of 17 to 20 x 10(6) t yr-1 of CO2, equaling 6 to 8% of the reduction target.

786

Gregory, K.M. 1996. Are paleoclimate estimates biased by foliar physiognomic responses to increased atmospheric CO2? *Palaeogeography Palaeoclimatology Palaeoecology 124(1-2):39-51.*

Physiognomic analysis of fossil angiosperm leaves has provided an important quantitative database of Tertiary terrestrial paleoclimate. However, atmospheric CO2 level, a critical control on plant growth, may have been higher in the Tertiary. It is thus crucial to investigate whether elevated CO2 affects leaf physiognomy. In this study, leaves were collected from white oak (Quercus alba L.) seedlings grown in open-top growth chambers at Oak Ridge National Laboratory. The only physiognomic change noted is an increase in length to width ratio with increasing CO2. In the literature, leaf size has been observed to increase, decrease or remain unchanged for woody C-3 species grown in elevated CO2. Typically, one sees more variation due to microsite or phenotype than due to CO2 level. By applying these observed physiognomic trends to two fossil floras, it is argued that estimates of mean annual temperature and growing season precipitation may be biased on the order of 1 degrees C and 20 cm, respectively. These are relatively small effects, as the values are similar to the standard errors of the regression models used to estimate paleoclimate. The lack of data, the variability of response to CO2 associated with microsite and phenotype, and the question of whether observed short-term trends with elevated CO2 are sustained make it impossible to propose a correction factor. Adequate sample size and sampling of several sites are the best way to attempt to compensate for CO2 effects on a given fossil flora until response to CO2 is better understood.

KEYWORDS: CARBON-DIOXIDE ENRICHMENT, ELEVATED CO2, GAS-EXCHANGE, LEAF ANATOMY, LEAVES, LIRIODENDRON-TULIPIFERA L, NORTH-AMERICA, SEEDLINGS, TREE GROWTH, WATER-USE

787

Gregory, P.J., J.A. Palta, and G.R. Batts. 1996. Root systems and root:mass ratio - Carbon allocation under current and projected atmospheric conditions in arable crops. *Plant and Soil 187(2):221-228.*

Roots of annual crop plants are a major sink for carbon particularly during early, vegetative growth when up to one- half of all assimilated carbon may be translocated belowground. Flowering marks a particularly important change in resource allocation, especially in determinate species, with considerably less allocation to roots and, depending on environmental conditions, there may be insufficient for maintenance. Studies with C-14 indicate the rapid transfer belowground of assimilates with typically 50% translocated in young cereal plants of which 50% is respired; exudation/rhizodeposition is generally <5% of the fixed carbon. Root:total plant mass decreases through the season and is affected by soil and atmospheric conditions. Limited water availability increased the allocation of C-13 to roots of wheat grown in columns so that at booting 0.38 of shoot C (ignoring shoot respiration) was belowground compared to 0.31 in well- watered plants. Elevated CO2 (700 mu mol CO2 mol(-1) air) increased the proportion of root:total mass by 55% compared with normal concentration, while increasing the air temperature by a mean of 3 degrees C decreased the proportion from 0.093 in the cool treatment to 0.055 in the warm treatment.

KEYWORDS: CO2- ENRICHMENT, DUPLEX SOIL, FIELD CONDITIONS, GRAIN-SORGHUM, PLANT-RESPONSES, SHOOT GROWTH, SOWING DATE, VULGARE L CULTIVARS, WATER-USE, WINTER-WHEAT

788

Grieb, B., U. Gross, E. Pleschka, B. Arnholdtschmitt, and K.H. Neumann. 1994. Embryogenesis of photoautotrophic cell-cultures of daucus- carota L. *Plant Cell Tissue and Organ Culture 38(2-3):115-122.*

In this paper photoautotrophic carrot (Daucus carota L.) suspension cultures are described which are able to produce somatic embryos. The development of somatic embryos, however, requires a sucrose supplement. Although an elevation of the CO2 concentration up to 2.3% results in the same level of dry weight production as with sucrose in the medium, somatic embryos could not be observed. Results on the influence of sucrose on some aspects of the photosynthetic apparatus of cultured cells are discussed.

KEYWORDS: CARROT, EMBRYOS, PHOTOSYNTHESIS, SOMATIC EMBRYOGENESIS, STORAGE PROTEINS, SUSPENSION

789

Gries, C., B.A. Kimball, and S.B. Idso. 1993. Nutrient-uptake during the course of a year by sour orange trees growing in ambient and elevated atmospheric carbon- dioxide concentrations. *Journal of Plant Nutrition 16(1):129-147.*

During the third year of a long-term carbon dioxide (CO2) enrichment study, macro- and micro-nutrient concentrations in leaves and roots of sour orange trees were analyzed. Data for yearly courses of the macronutrients Ca, Mg, N, P, K, Na, and S and the micronutrients B, Cu, Fe, Mn, and Zn are presented. Significantly higher concentrations of N, K, Ca, and Mn were found in leaves of the control trees. The degree of difference varied seasonally: the greatest differences occured in summer, whereas essentially no differences were found in spring and winter.

KEYWORDS: CO2- ENRICHMENT, GROWTH, NITROGEN, PLANTS, RESPONSES, SEEDLINGS, YIELD

790

Griffin, K.L., J.T. Ball, and B.R. Strain. 1996. Direct and indirect effects of elevated CO2 on whole-shoot respiration in ponderosa pine seedlings. *Tree Physiology 16(1-2):33-41.*

We determined the short-term direct and longterm indirect effects of CO2 on apparent dark respiration (CO2 efflux in the dark) in ponderosa pine (Pinus ponderosa Dougl. ex Laws.) seedlings grown in 35 or 70 Pa CO2 partial pressure for 163 days in naturally lit, controlled-environment chambers. Two soil N treatments (7 and 107 ppm total N, low-N and high-N treatments, respectively) were imposed by watering half the plants every 2 weeks with 15/15/18 fertilizer (N,P,K) and the other half with demineralized water. Direct effects of ambient CO2 partial pressure on apparent dark respiration were measured during short-term manipulations (from minutes to hours) of the CO2 environment surrounding the aboveground portion of individual seedlings. Shea-term increases in the ambient CO2 partial pressure consistently resulted in significant decreases in CO2 efflux of seedling in all treatments. Efflux of CO2 decreased by 3 to 13% when measurement CO2 partial pressure was increased from 35 to 70 Pa, and by 8 to 46% over the entire measurement range from 0 to 100 Pa. No significant interactions between the indirect effects of growth CO2 partial pressure and the direct effects of the measurement CO2 partial pressure were found. Seedlings grown in the high-N treatment were significantly less sensitive to short-term changes in CO2 partial pressures than seedlings grown in the low-N treatment. Apparent respiration tended to decrease in seedlings grown in elevated CO2, but the decrease was not significant. Nitrogen had a large effect on CO2 efflux, increasing apparent respiration more than twofold on both a leaf area and a leaf or shoot mass basis. Both the direct and indirect effects of elevated CO2 were correlated with change's in the C/N ratio. A model of cumulative CO2 efflux for a 160-day period demonstrated that, despite a 49% increase in total plant biomass, seedlings grown in the high-N + high-CO2 treatment lost only 2% more carbon than seedlings grown in the high-N + low-CO2 treatment, suggesting increased carbon use efficiency in plants grown in elevated CO2. We conclude that small changes in instantaneous CO2 efflux, such as those observed in ponderosa pine seedlings, could scale to large changes in carbon sequestration.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, ECOSYSTEMS, GROWTH, LEAVES, PARTIAL-PRESSURE, PHOTOSYNTHESIS, PLANTS, TEMPERATURE, TREES

791

Griffin, K.L., M.A. Bashkin, R.B. Thomas, and B.R. Strain. 1997. Interactive effects of soil nitrogen and atmospheric carbon dioxide on root/rhizosphere carbon dioxide efflux from loblolly and ponderosa pine seedlings. *Plant and Soil 190(1):11-18.*

We measured CO2 efflux from intact root/rhizosphere systems of 155 day old loblolly (Pinus taeda L.) and ponderosa (Pinus ponderosa Dougl, ex Laws.) pine seedlings in order to study the effects of elevated atmospheric CO2 on the below-ground carbon balance of coniferous tree seedlings. Seedlings were grown in sterilized sand culture, watered daily with either 1, 3.5 or 7 mM NH4+, and maintained in an atmosphere of either 35 or 70 Pa CO2. Carbon dioxide efflux (mu mol CO2 plant(-1) s(-1)) from the root/rhizosphere system of both species significantly increased when seedlings were grown in elevated CO2, primarily due to large increases in root mass. Specific CO2 efflux (mu mol CO2 g root(-1) s(-1)) responded to CO2 only under conditions of adequate soil nitrogen availability (3.5 mM). Under these conditions, CO2 efflux rates from loblolly pine increased 70% from 0.0089 to 0.0151 mu mol g(-1) s(-1) with elevated CO2 while ponderosa pine responded with a 59% decrease, from 0.0187 to 0.0077 mu mol g(-1) s(-1). Although below ground CO2 efflux from seedlings grown in either sub- optimal (I mM) or supra-optimal (7 mM) nitrogen availability did not respond to CO2, there was a significant nitrogen treatment effect. Seedlings grown in supra-optimal soil nitrogen had significantly increased specific CO2 efflux rates, and significantly lower total biomass compared to either of the other two nitrogen treatments. These results indicate that carbon losses from the root/rhizosphere systems are responsive to environmental

resource availability, that the magnitude and direction of these responses are species dependent, and may lead to significantly different effects on whole plant carbon balance of these two forest tree species.

KEYWORDS: ECOSYSTEMS, ELEVATED CO2, ENRICHMENT, FEEDBACK, GROWTH, PLANT, RESPONSES, RHIZOSPHERE, ROOT RESPIRATION, TAEDA L SEEDLINGS

792

Griffin, K.L., and Y.Q. Luo. 1999. Sensitivity and acclimation of Glycine max (L.) Merr. leaf gas exchange to CO2 partial pressure. *Environmental and Experimental Botany 42(2):141-153.*

Theoretical studies suggest that partitioning leaf photosynthetic responses to CO2 partial pressures into two components, sensitivity and acclimation, facilitates both scaling-up photosynthetic responses and predicting global terrestrial carbon influx. Here, we experimentally examine these two components by growing soybean (Glycine max) in two CO2 partial pressures, 35 and 70 Pa, and making a suite of ecophysiological measurements on expanding and fully expanded leaves. These CO2 treatments resulted in a variety of acclimation responses, including changes in net photosynthetic rate and capacity, stomatal conductance, transpiration, and respiration. These responses were strongly dependent on leaf age. Despite the wide variety of acclimation responses, the experimentally derived photosynthetic sensitivity did not vary with CO2 treatments or leaf age. In addition, the photosynthetic sensitivity to ambient CO2 partial pressure was consistent with the sensitivity to intercellular CO2 partial pressure, indicating little effect of stomatal conductance on photosynthetic sensitivity. This study supports the theoretical conclusion that photosynthetic sensitivity is independent of growth environment and leaf age, as well as photosynthetic acclimation, even though the latter varies with both environmental and developmental factors. Accordingly, photosynthetic sensitivity may be directly extrapolated from leaf to globe to predict the increment in terrestrial carbon influx stimulated by the yearly increase in atmospheric CO2, whereas the acclimation component must be used to adjust the overall global estimate. (C) 1999 Elsevier Science B.V. All rights reserved.

KEYWORDS: ASSIMILATION, ATMOSPHERIC CARBON-DIOXIDE, C-3 PLANTS, CONDUCTANCE, ELEVATED CO2, LONG-TERM EXPOSURE, PHASEOLUS-VULGARIS L, PHOTOSYNTHETIC ACCLIMATION, TEMPERATURE, WATER-STRESS

793

Griffin, K.L., P.D. Ross, D.A. Sims, Y. Luo, J.R. Seemann, C.A. Fox, and J.T. Ball. 1996. EcoCELLs: Tools for mesocosm scale measurements of gas exchange. *Plant, Cell and Environment 19(10):1210-1221.*

We describe the use of a unique plant growth facility, which has as its centerpiece four 'EcoCELLs', or 5x7 m mesocosms designed as open-flow, mass-balance systems for the measurement of carbon, water and trace gas fluxes. This system is unique in that it was conceived specifically to bridge the gap between measurement scales during long-term experiments examining the function and development of model ecosystems. There are several advantages to using EcoCELLs, including (i) the same theory of operation as leaf level gas exchange systems, but with continuous operation at a much larger scale; (ii) the ability to independently evaluate canopy-level and ecosystem models; (iii) simultaneous manipulation of environmental factors and measurement of system-level responses, and (iv) maximum access to, and manipulation of, a large rooting volume. In addition to discussing the theory, construction and relative merits of EcoCELLs, we describe the calibration and use of the EcoCELLs during a 'proof of concept' experiment, This experiment involved growing soybeans under two ambient CO2 concentrations (similar to 360 and 710 mu mol mol(-1)). During this experiment, we asked 'How accurate is the simplest model that can be used to scale from leaf-level to canopy-level responses?' in order to illustrate the utility of the EcoCELLs in validating canopy-scale models.

KEYWORDS: ARCTIC TUNDRA, ATMOSPHERIC CARBON-DIOXIDE, BRANCH BAG, CLIMATE CHANGE, ELEVATED CO2, FIELD, OPEN-TOP CHAMBERS, PLANT-RESPONSES, TRACE GASES, TUSSOCK TUNDRA

794

Griffin, K.L., and J.R. Seemann. 1996. Plants, CO2 and photosynthesis in the 21st century. *Chemistry & Biology 3(4):245-254.*

Human activity in the last 200 years has led to a marked increase in the level of CO2 in the atmosphere. Plants sense increases in CO2 levels and initially respond with an increase in photosynthetic rate, which may then slow as the plant adapts. This increase in photosynthetic rate may account in part for the 'disappearance' of an estimated 1.8 gigatons of carbon per year.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, CLIMATE CHANGE, ELEVATED CO2, GAS-EXCHANGE, LONG-TERM EXPOSURE, METABOLITE LEVELS, PHASEOLUS-VULGARIS L, RIBULOSE BISPHOSPHATE CARBOXYLASE, TUSSOCK TUNDRA

795

Griffin, K.L., D.A. Sims, and J.R. Seemann. 1999. Altered night-time CO2 concentration affects the growth, physiology and biochemistry of soybean. *Plant, Cell and Environment 22(1):91-99.*

Soybean plants (Glycine max (L.) Merr. c. v. Williams) were grown in CO2 controlled, natural-light growth chambers under one of four atmospheric CO2 concentrations ([CO2]): (1) 250 mu mol mol(-1) 24 h d(-1) [250/250]; (2) 1000 mu mol mol(-1) 24 h d(-1) [1000/1000]; (3) 250 mu mol mol(-1) during daylight hours and 1000 mmol mol(-1) during nighttime hours [250/1000] or (4) 1000 mu mol mol(-1) during daylight hours and 250 mmol mol(-1) during night-time hours [1000/250]. During the vegetative growth phase few physiological differences were observed between plants exposed to a constant 24 h [CO2] (250/250 and 1000/1000) and those that were switched to a higher or lower [CO2] at night (250/1000 and 1000/250), suggesting that the primary physiological responses of plants to growth in elevated [CO2] is apparently a response to daytime [CO2] only. However, by the end of the reproductive growth phase, major differences were observed. Plants grown in the 1000/250 regime, when compared with those in the 1000/1000 regime, had significantly more leaf area and leaf mass, 27% more total plant dry mass, but only 18% of the fruit mass. After 12 weeks of growth these plants also had 19% higher respiration rates and 32% lower photosynthetic rates than the 1000/1000 plants. As a result the ratio of carbon gain to carbon loss was reduced significantly in the plants exposed to the reduced night-time [CO2]. Plants grown in the opposite switching environment, 250/1000 versus 250/250, showed no major differences in biomass accumulation or allocation with the exception of a significant increase in the amount of leaf mass per unit area. Physiologically, those plants exposed to elevated night-time [CO2] had 21% lower respiration rates, 14% lower photosynthetic rates and a significant increase in the ratio of carbon gain to carbon loss, again when compared with the 250/250 plants. Biochemical differences also were found. Ribulose-1,5-bisphosphate carboxylase/ oxygenase concentrations decreased in the 250/1000 treatment compared with the 250/250 plants, and phosphoenolpyruvate carboxylase activity decreased in the 1000/250 compared with the 1000/1000 plants. Glucose, fructose and to a lesser extent sucrose concentrations also were reduced in the 1000/250 treatment compared with the 1000/1000 plants. These results

indicate that experimental protocols that do not maintain elevated CO2 levels 24 h d(-1) can have significant effects on plant biomass, carbon allocation and physiology, at least for fast-growing annual crop plants. Furthermore, the results suggest some plant processes other than photosynthesis are sensitive to [CO2] and under ecologically relevant conditions, such as high night-time [CO2], whole plant carbon balance can be affected.

KEYWORDS: CARBON-DIOXIDE CONCENTRATION, DARK RESPIRATION, ELEVATED ATMOSPHERIC CO2, HIGH AMBIENT CO2, MAX L MERR, PHOSPHOENOLPYRUVATE CARBOXYLASE, PHOTOSYNTHESIS, PLANTS, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, SHORT- TERM

796

Griffin, K.L., R.B. Thomas, and B.R. Strain. 1993. Effects of nitrogen supply and elevated carbon-dioxide on construction cost in leaves of pinus-taeda (L) seedlings. *Oecologia 95(4):575-580.*

Seedlings of loblolly pine (Pinus taeda L.) were grown under varying conditions of soil nitrogen and atmospheric carbon dioxide availability to investigate the interactive effects of these resources on the energetic requirements for leaf growth. Increasing the ambient CO2 partial pressure from 35 to 65 Pa increased seedling growth only when soil nitrogen was high. Biomass increased by 55% and photosynthesis increased by 13% after 100 days of CO2 enrichment. Leaves from seedlings grown in high soil nitrogen were 7.0% more expensive on a g glucose g-1 dry mass basis to produce than those grown in low nitrogen, while elevated CO2 decreased leaf cost by 3.5%. Nitrogen and CO2 availability had an interactive effect on leaf construction cost expressed on an area basis, reflecting source-sink interactions. When both resources were abundant, leaf construction cost on an area basis was relatively high (81.8 +/- 3.0 g glucose m-2) compared to leaves from high nitrogen, low CO2 seedlings (56.3 +/- 3.0 g glucose m-2) and low nitrogen, low CO2 seedlings (67.1 +/- 2.7 g glucose m-2). Leaf construction cost appears to respond to alterations in the utilization of photoassimilates mediated by resource availability.

KEYWORDS: ACCLIMATION, ALLOCATION, ATMOSPHERIC CO2 ENRICHMENT, CHLOROPHYLL CONTENT, GROWTH, LONG-TERM EXPOSURE, MAINTENANCE RESPIRATION, PHOTOSYNTHETIC INHIBITION, RESPONSES, WATER

797

Griffin, K.L., W.E. Winner, and B.R. Strain. 1995. Growth and dry-matter partitioning in loblolly and ponderosa pine-seedlings in response to carbon and nitrogen availability. *New Phytologist 129(4):547-556.*

We grew loblolly pine (Pinus taeda L.) and ponderosa pine (Pinus ponderosa Dougl. ex Laws.) seedlings in a factorial experiment with two CO2 partial pressures (35 and 70 Pa) and two nitrogen treatments (1.0 and 3.5 mM NH4+) for one growing season in a 'common garden' experiment designed to examine the extent that dry matter and nitrogen accumulation and partitioning are environmentally controlled. Ponderosa pine seedlings grown in 35 Pa CO2 and 3.5 mM NH4+ showed symptoms of nitrogen toxicity, characterized by greatly reduced growth, and moderately reduced total plant N. With the exception of this treatment combination, there were no significant differences between species in total plant dry matter or total plant nitrogen, suggesting that responses of growth to environmental conditions were stronger than heritable responses. There were however large differences in dry matter and N partitioning between the two species. Increases in leaf mass were largest in loblolly pine, whilst ponderosa pine tended to have higher root:shoot (R:S) ratios. R:S ratio of loblolly increased in response to C availability and decreased in response to N availability, whilst R: S ratio of ponderosa pine was much less responsive to resource availability. Total plant N varied with N supply, and N partitioning was related to plant growth and carbon partitioning. Carbon and N were interactive, such that an increase in the accumulation of either resource was always accompanied by an increase in the other. Over several seasons the different patterns of resource acquisition and biomass allocation that we observed in a uniform environment could potentially result in different growth rates at most resource levels. In the first season, contrary to our expectations, heritable differences in growth rate did not appear.

KEYWORDS: ATMOSPHERIC CO2, DIFFERENT IRRADIANCE LEVELS, DIOXIDE, ECOSYSTEMS, ENRICHMENT, FORESTS, LIQUIDAMBAR- STYRACIFLUA, NITRATE, TAEDA SEEDLINGS, WATER-STRESS

798

Griffin, K.L., W.E. Winner, and B.R. Strain. 1996. Construction cost of loblolly and ponderosa pine leaves grown with varying carbon and nitrogen availability. *Plant, Cell and Environment 19(6):729-739.*

We grew loblolly and ponderosa pine seedlings in a factorial experiment with two CO2 partial pressures (35 and 70 Pa), and two nitrogen treatments (1 . 0 and 3 . 5 mol m(-3) NH4+), for one growing season to examine the effects of carbon and nitrogen availability on leaf construction cost, Growth in elevated CO2 reduced leaf nitrogen concentrations by 17 to 40%, and increased C:N by 22 to 68%. Elevated N availability increased leaf N concentrations and decreased C:N, Non-structural carbohydrates increased in high-CO2-grown loblolly seedlings, except in fascicles from low N, and in ponderosa primary and fascicle leaves grown in high N, In loblolly, increases in starch were nearly 2-fold greater than the increases in soluble sugars, In ponderosa, only the soluble sugars were affected by CO2. Leaf construction cost (g glucose g(-1) dm) varied by 9 . 3% across all treatments, All of the variation in loblolly leaf construction cost could be explained by changes in non-structural carbohydrates. A model of the response of construction cost to changes in the mass of different biochemical fractions suggests that the remainder of the variation in ponderosa, not explained by non-structural carbohydrates, is probably attributable to changes in lignin, phenolic or protein concentrations.

KEYWORDS: ALLOCATION, BIOMASS, DIOXIDE, ENERGY, NUTRIENTS, PLANTS, SEEDLINGS, TAEDA

799

Griffiths, B.S., K. Ritz, N. Ebblewhite, and G. Dobson. 1999. Soil microbial community structure: Effects of substrate loading rates. *Soil Biology and Biochemistry 31(1):145-153.*

A fuller understanding of the interactions which affect rhizosphere microbial community structure requires experimental manipulation of the individual components of that interaction (e.g. amount and composition of exudate, soil moisture and soil nutrient status). We describe an experiment where a synthetic root exudate was applied continuously to a soil held at constant water potential. The solution contained compounds characteristic of root exudates (fructose, glucose, sucrose, succinic acid, malic acid, arginine, serine and cysteine), which were added at a range of concentrations. After 14 d of such substrate addition, a central portion of soil, known to be influenced by the added substrate, was removed for analysis. Microbial community structure of this central core was determined by the broad-scale measurements; community DNA hybridisation and %G + C profiling, and phospholipid-fatty acid analysis (PLFA). The trend was that microbial community structure changed consistently as substrate loading increased, and that fungi dominated over bacteria at high substrate loading rates. The DNA and the PLFA analyses both indicated that there was a coherent gradient of changes with increased substrate loading. This may have arisen as a consequence of the competitive ability of soil microorganisms being

dependent on the quantity of available substrate. (C) 1998 Elsevier Science Ltd. All rights reserved.

KEYWORDS: BACTERIOPLANKTON, BIOMASS, CARBON, DNA HYBRIDIZATION, ELEVATED ATMOSPHERIC CO2, FATTY-ACIDS, GLUCOSE, MASS- SPECTROMETRY, PROFILES, RHIZOSPHERE

800

Griffiths, B.S., K. Ritz, N. Ebblewhite, E. Paterson, and K. Killham. 1998. Ryegrass rhizosphere microbial community structure under elevated carbon dioxide concentrations, with observations on wheat rhizosphere. *Soil Biology and Biochemistry 30(3):315-321.*

The structure of microbial communities in the rhizospheres of ryegrass and wheat, growing at an elevated atmospheric CO2 concentration, was investigated using broad-scale DNA techniques. Community DNA hybridisation and %G + C base profiling by thermal denaturation assess changes at the whole microbial community level. DNA analysis of the rhizosphere of ryegrass grown in soil microcosms for 28 or 42 d, showed only minor differences between plants grown at 450 or 720 mu l CO2 l(-1). In a second experiment with ryegrass, 5 of 10 replicate microcosms were pulse labelled with (CO2)-C-14 and 5 simultaneously sampled for DNA analysis. Carbon partitioning below ground showed changes due to the elevated CO2, notably an increased proportion of fi?ted carbon in non-microbial biomass residue in the rhizosphere. There was again no effect of elevated CO2 on rhizosphere microbial community structure. Community DNA hybridisation indicated that the rhizosphere communities under ambient and elevated CO2 were 86% similar (unlikely to be a biologically relevant change), with indistinguishable %G + C profiles. Wheat was grown to maturity (129 d) in a different soil microcosm design, and rhizosphere microbial communities from plants grown at 350 and 700 mu l CO2 l(-1) were identical according to the DNA analyses. In these experiments rhizosphere microbial community structure at the broad scale was unaffected by the interactions occurring below ground as a result of elevated concentrations of CO2. (C) 1998 Elsevier Science Ltd. All rights reserved.

KEYWORDS: ATMOSPHERIC CO2 CONCENTRATION, DNA HYBRIDIZATION, ENRICHMENT, FEEDBACK, GROWTH, HYBRIDIZATION TECHNIQUE, POPULATIONS, RESPONSES, ROOTS, SOIL

801

Grime, J.P., K. Thompson, R. Hunt, J.G. Hodgson, J.H.C. Cornelissen, I.H. Rorison, G.A.F. Hendry, T.W. Ashenden, A.P. Askew, S.R. Band, R.E. Booth, C.C. Bossard, B.D. Campbell, J.E.L. Cooper, A.W. Davison, P.L. Gupta, W. Hall, D.W. Hand, M.A. Hannah, S.H. Hillier, D.J. Hodkinson, A. Jalili, Z. Liu, J.M.L. Mackey, N. Matthews, M.A. Mowforth, A.M. Neal, R.J. Reader, K. Reiling, W. RossFraser, R.E. Spencer, F. Sutton, D.E. Tasker, P.C. Thorpe, and J. Whitehouse. 1997. Integrated screening validates primary axes of specialisation in plants. *Oikos 79(2):259-281.*

Standardised procedures have been used to measure 67 traits in 43 common plants of the British flora. This paper provides an interpretation of the most consistent patterns in the resulting matrix by means of correlation, ordination and classification analyses. Only a weak coupling was observed between attributes of the regenerative and established phases of the life history. However, within each phase, attributes were strongly aggregated into sets and a high proportion of the variation between species coincided with a single axis. Attributes of the established phase displayed remarkably consistent trends, with a strong 'Axis 1' being identified by three different multivariate methods. There was a marked correlation between foliar concentrations of N, P, K, Ca and Mg, high concentrations of which coincided with the capacity for rapid growth in productive conditions and an inability to sustain yield under limiting supplies of nutrients. A diverse array of other traits, less immediately involving mineral nutrients, were also entrained in Axis 1; these included life history, root and shoot foraging, the morphology, longevity, tensile strength and palatability of leaves, and the decomposition rate of leaf litter. This pattern occurred in both monocotyledons and dicotyledons and appeared to reflect a tradeoff between attributes conferring an ability for high rates of resource acquisition in productive habitats and those responsible for retention of resource capital in unproductive conditions. The second axis of variation evident in the established phase was related to phylogeny and distinguished between monocotyledons and dicotyledons on the basis of a diverse set of traits including genome size, cell size, root and shoot foraging characteristics and vascular tissues. A third axis was detected in which ephemerals and perennials were separated by differences in attributes such as breeding system, leaf decomposition rate and a set of traits reflecting the small stature of many short-lived plants. In the regenerative phase, the leading axis was clearly related to the widely recognised tradeoff between seed size and seed number and was consistent with current understanding of seed banks, and with modern theories explaining species coexistence in terms of complementary responses to temporal and spatial variation in vegetation gap dynamics. The data provide strong evidence of functional integration between evolutionary specialisations in root and shoot and support Donald's unified theory of competitive ability. The data are not consistent with theories of functional types based upon evolutionary tradeoffs in allocation between root and shoot. We suggest that the evidence assembled here and elsewhere in the current literature points to the existence of primary functional types, including those recognised by Ramenskii and Grime. These functional types can be reconciled with the individuality of plant ecologies in the field and provide an effective basis For interpretation and prediction at various scales from the plant community to regional floras. There are particular opportunities for prediction of successional trajectories, the role of herbivores in vegetation succession and the response of vegetation to eutrophication and extreme climatic events. It is also suggested that aspects of this investigation may provide a Darwinian underpinning for Odum's theory of ecosystem maturation.

KEYWORDS: ALLOCATION, CO2- ENRICHMENT, COMPETITION, ECOLOGICAL STRATEGIES, GERMINATION CHARACTERISTICS, LIFE-HISTORY STRATEGIES, LOCAL FLORA, RELATIVE GROWTH-RATE, SUCCESSION, VEGETATION

802

Grimm, A.G., and J. Fuhrer. 1992. The response of spring wheat (triticum-aestivum L) to ozone at higher elevations .1. Measurement of ozone and carbon-dioxide fluxes in open-top field chambers. *New Phytologist 121(2):201-210.*

The flux of O3 was determined in open-top chambers (OTC) used to investigate its effect on spring wheat (Triticum aestivum L., cv. Albis) in 1989 and 1990. The experimental site was located at 900 m above sea level at Zimmerwald, near Bern (Switzerland). The aims were to evaluate the use of OTCs for O3 flux measurements under field conditions, to assess the role of stomata in controlling the O3 fluxes, and to establish a quantitative relationship between radiation-weighted O3 concentrations and O3 flux. Measurements were carried out from full expansion of flag leaves until the onset of senescence. Ozone flux was determined by mass balance using the concentrations of O3 measured at the inlet and outlet of the OTC. The CO2 exchange rate was corrected for soil-borne CO2 and used as a reference. Measurements of temperature, photosynthetically active radiation (PAR), saturated water vapour pressure deficit (SVPD), and boundary layer conductance were used to describe the microclimate inside OTCs. In the warmer microclimate in 1989, the plant canopy was characterized by a smaller leaf area index (LAI) than in 1990, while the fluxes of O3 and CO2 during daytime were generally larger in 1989. The diurnal patterns of

fluxes of O3 and CO2 in OTCs supplied with unfiltered air were similar. It is estimated that O3 absorption via the stomata contributed 50-70 % of its total flux. Identical relationships between leaf conductance for O3 measured by porometry and leaf conductance calculated from O3 flux were found in both years, but measured leaf conductance during daytime was generally smaller in 1990 than in 1989. The results indicate that stomatal conductance largely controlled O3 flux, and that the canopy structure has an influence on the overall conductance of the canopy. Different linear functions were obtained for the relationship between radiation-weighted O3 concentration and O3 flux, using data from OTCs supplied with either charcoal-filtered air, unfiltered air or unfiltered air enriched with O3 (two levels). These relationships form the basis for the calculation of mean O3 fluxes which can be used as an exposure index in the exposure-response analysis.

KEYWORDS: ABIES L KARST, BARLEY, CROP YIELD, DEPOSITION, GAS-EXCHANGE, INJURY, PHOTOSYNTHESIS, RESISTANCES, SITCHENSIS BONG CARR, TRANSPIRATION

803

Grimmer, C., T. Bachfischer, and E. Komor. 1999. Carbohydrate partitioning into starch in leaves of Ricinus communis L-grown under elevated CO2 is controlled by sucrose. *Plant, Cell and Environment 22(10):1275-1280.*

Ricinus communis plants were grown. under normal (350 ppm) and elevated (700 ppm) CO2 atmosphere and the growth and carbohydrate status of leaf 2 (first leaf above the pair of primary leaves) was studied. Elevated carbon dioxide stimulated the growth of leaves 1.7-fold. The glucose and fructose concentrations exhibited the same diurnal rhythm under both growth conditions. The sucrose concentrations stayed relatively constant and at 700 ppm were one-third higher than at 350 ppm. The starch content increased steadily during the day and disappeared overnight at 350 ppm CO2, but remained partially in plants at 700 ppm CO2, Consequently at 700 ppm CO2, the leaves accumulated starch continuously over their life time, The rate of starch synthesis was correlated to the activity of ADP- glucose pyrophosphorylase, which was related to the sucrose concentration in the leaf, It is concluded that sucrose controls the expression of ADP-glucose pyrophosphorylase, leading to a shift of carbohydrate partitioning into starch when more sucrose is produced than consumed or exported, a situation which is especially pertinent at elevated CO2, These results show that the previously experimentally observed transscriptional regulation of starch synthesis by sucrose occurs in vivo in the daily life of a leaf.

KEYWORDS: ADP-GLUCOSE PYROPHOSPHORYLASE, CARBON DIOXIDE, GENES, PLANTS, POTATO, TUBERS

804

Grimmer, C., and E. Komor. 1999. Assimilate export by leaves of Ricinus communis L. growing under normal and elevated carbon dioxide concentrations: the same rate during the day, a different rate at night. *Planta 209(3):275-281.*

Castor bean (Ricinus communis L.) plants were grown for 5-7 weeks in a controlled environment at 350 mu l l(-1) or 700 mu l l(-1) CO2. Carbon assimilation, assimilate deposition, dark respiration and assimilate mobilization were measured in leaves 2, 3 and 4 (counted from the base of the plant), and a balance sheet of carbon input and export was elaborated for both CO2 concentrations. Carbon dioxide assimilation was nearly constant over the illumination period, with only a slight depression occurring at the end of the day in mature source leaves, not in young source leaves, Assimilation was ca. 40% higher at 700 mu l l(-1) than at 350 mu l l(-1) CO2. The source leaves increased steadily in weight per unit area during the first 3 weeks, more at 700 mu l l(-1) than at 350 mu l l(-1) CO2. On top of an irreversible weight increase, there was a large gain in dry weight during the day, which was reversed during the night. This reversible weight gain was constant over the life time of the leaf and ca. 80% higher at 700 mu l l(-1) than at 350 yl l(-1). Most of it was due to carbohydrates. The carbon content (as a percentage) was not altered by the CO2 treatment. Respiration was 25% higher in high-CO2 plants when based on leaf area, but the same when based on dry weight. The rate of carbon export via the phloem was the same during the daytime in plants grown at 350 mu l l(-1) and 700 mu l l(-1) CO2. During the night the low-CO2 plants had only 50% of the daytime export rate, in contrast to the high-CO2 plants which maintained the high export rate. It was concluded that the phloem loading system is saturated during the daytime in both CO2 regimes, whereas during the night the assimilate supply is reduced in plants in the normal CO2 concentration. Two-thirds of the carbon exported from the leaves was permanently incorporated as plant dry matter in the residual plant parts. This "assimilation efficiency" was the same for both CO2 regimes. It is speculated that under 350 mu l l(-1) CO2 the growing Ricinus plant operates at sink limitation during the day and at source limitation during the night.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, GROWTH, PHOTOSYNTHESIS, PLANTS, STARCH, SUCROSE

805

Grobbelaar, N., W.M. Chou, and T.C. Huang. 1992. Effect of co2, o2, dcmu, fccp, and dl-glyceraldehyde on the nitrogenase activity of synechococcus rf-1. *Botanical Bulletin of Academia Sinica 33(2):167-174.*

Elevated atmospheric CO2 concentrations drastically inhibit nitrogenase activity of the unicellular Synechococcus RF-1 but stimulate photosynthetic CO2 assimilation. The inhibitory effect on nitrogenase activity is stronger in the light than in the dark. During three hours, 1% CO2 in air can reduce nitrogenase activity in the light by about 50% compared to that in unenriched air. The inhibitory effect of elevated CO2 concentrations on nitrogenase activity persists for many hours after the organism has been returned to air not enriched with CO2. The nitrogenase activity of heterocystous cyanobacteria, generally, does not appear to be affected by 5% CO2 in the air. DCMU strongly enhanced nitrogenase activity and inhibited the assimilation of CO2 by Synechococcus RF-1 in the light, and elevated atmospheric O2 concentrations reduced the nitrogenase activity, especially in the dark. DL-glyceraldehyde at a concentration of 19.4 mM strongly inhibited nitrogenase activity, dark respiration, and photosynthesis. FCCP had no effect on dark respiration but depressed nitrogenase activity and photosynthesis of Synechococcus RF-1. The inhibitory effect of FCCP on nitrogenase activity was stronger in the dark than in the light.

KEYWORDS: BLUE GREEN ALGA, DINITROGEN, LIGHT, PHOTOSYNTHESIS, RHYTHM

806

Grodzinski, B. 1992. Plant nutrition and growth-regulation by co2 enrichment. *BioScience 42(7):517-525.*

KEYWORDS: ABSCISIC- ACID, ACCLIMATION, ATMOSPHERIC CO2, CARBONIC-ANHYDRASE, CARBOXYLASE, ETHYLENE, EXCHANGE, PHOTOSYNTHESIS, STOMATAL DENSITY, WHOLE PLANT

807

Grodzinski, B., J.R. Jiao, and E.D. Leonardos. 1998. Estimating photosynthesis and concurrent export rates in C-3 and C-4 species at ambient and elevated CO2. *Plant Physiology 117(1):207-215.*

The ability of 21 C-3 and C-4 monocot and dicot species to rapidly export newly fixed C in the light at both ambient and enriched CO2 levels was compared. Photosynthesis and concurrent export rates were estimated during isotopic equilibrium of the transport sugars using a steady-state (CO2)-C-14-labeling procedure. At ambient CO2 photosynthesis and export rates for C-3 species were 5 to 15 and 1 to 10 mu mol C m(-2) s(-1), respectively, and 20 to 30 and 15 to 22 mu mol C m(-2) s(-1), respectively, for C-4 species. A linear regression plot of export on photosynthesis rate of all species had a correlation coefficient of 0.87. When concurrent export was expressed as a percentage of photosynthesis, several C-3 dicots that produced transport sugars other than Suc had high efflux rates relative to photosynthesis, comparable to those of C-4 species. At high CO2 photosynthetic and export rates were only slightly altered in C, species, and photosynthesis increased but export rates did not in all C(3)species. The C-3 species that had high efflux rates relative to photosynthesis at ambient CO2 exported at rates comparable to those of C-4 species on both an absolute basis and as a percentage of photosynthesis. At ambient CO2 there were strong linear relationships between photosynthesis, sugar synthesis, and concurrent export. However, at high CO2 the relationships between photosynthesis and export rate and between sugar synthesis and export rate were not as strong because sugars and starch were accumulated.

KEYWORDS: HIGHER-PLANTS, LEAF, LEAVES, SALVIA-SPLENDENS, STARCH, STEADY-STATE PHOTOSYNTHESIS, SUCROSE, TEMPERATURE

808

Grodzinski, B., L. Woodrow, E.D. Leonardos, M. Dixon, and M.J. Tsujita. UNKNOWN YEAR. Plant responses to short- and long-term exposures to high carbon dioxide levels in closed environments. *Natural and Artificial Ecosystems :203-211.*

When higher plants are exposed to elevated levels of CO2 for both short- and long-term periods photosynthetic C-gain and photoassimilate export from leaves are generally increased. Water use efficiency is increased on a leaf area basis. During long-term exposures, photosynthesis rates on leaf and whole plant bases are altered in a species specific manner. The most common pattern in C-3 plants is an enhanced rate of whole plant photosynthesis in a well irradiated canopy. Nevertheless, in some herbaceous species prolonged exposure to high CO2 results in remobilization of nitrogenous reserves (i.e., leaf protein degradation) and reduced rates of mature leaf photosynthesis when assayed at ambient CO2 and O-2 levels. Both short- and long-term exposures to those CO2 levels (i.e., 100 to 2,000 mu l.l(-1)) which modify photosynthesis and export, also modify both endogenous ethylene gas (C2H4) release, and substrate, 1- aminocyclopropane-1-carboxylic acid (ACC), saturated C2H4 release rates from irradiated leaves. Photosynthetically active canopy leaves contribute most of the C2H4 released from the canopy. Prolonged growth at high CO2 results in a persistent increase in the rate of endogenous C2H4 release from leaves which can, only in part, be attributed to the increase of the endogenous pools of C2H4 pathway intermediates (e.g., methionine, M-ACC, and ACC). The capacity for increasing the rate of C2H4 release in response to short-term exposures to varying CO2 levels does not decline after prolonged growth at high CO2. When leaves, whole plants, and model canopies of tomato plants are exposed to exogenous C2H4 a reduction in the rate of photosynthesis can, in each case, be attributed to the classical effects of C2H4 on plant development and morphology. The effect of C2H4 on CO2 gas exchange of plant canopies is shown to be dependent on the canopy leaf area index.

KEYWORDS: INCOMPLETE, ACCLIMATION, ATMOSPHERIC CO2, ETHYLENE RELEASE, GAS-EXCHANGE, LEAVES, LYCOPERSICON-ESCULENTUM MILL, PHOTOSYNTHESIS, TOMATO, XANTHIUM-STRUMARIUM L, ZEA-MAYS

809

Groninger, J.W., K.H. Johnsen, J.R. Seiler, R.E. Will, D.S. Ellsworth, and C.A. Maier. 1999. Elevated carbon dioxide in the atmosphere - What might it mean for loblolly pine plantation forestry? *Journal of Forestry 97(7):4-10.*

Research with loblolly pine suggests that projected increases iii atmospheric CO2 concentration will accelerate early growth and could result in shouter rotation length, reduced time until first commercial thinning, higher optimal planting density, and possibly higher maximum stocking level in managed stands. We discuss some of the physiological processes and stand dynamics that underlie these changes, as well as silvicultural strategies that may serve to ensure sustainability of intensively managed forest systems in the face of increasing CO2 and possible climate change.

KEYWORDS: CO2 CONCENTRATIONS, GAS-EXCHANGE, GROWTH, NET PHOTOSYNTHESIS, PHOTOSYNTHETIC CAPACITY, ROOT RESTRICTION, SEEDLINGS, STOMATAL CONDUCTANCE, TAEDA TREES, WATER

810

Groninger, J.W., J.R. Seiler, S.M. Zedaker, and P.C. Berrang. 1995. Effects of elevated co2, water-stress, and nitrogen level on competitive interactions of simulated loblolly-pine and sweetgum stands. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 25(7):1077-1083.*

Loblolly pine (Pinus taeda L.) and sweetgum (Liquidambar styraciflua L.) were grown in mixed stands and in monocultures at 2.54 X 2.54 cm spacing in controlled-environment chambers. Treatments consisted of present (ambient) and projected future (ambient + 400 ppm) carbon dioxide (CO2) concentrations, drought-stressed, and well-watered conditions, and low (20 kg N/ha) and high (474 kg N/ha) nitrogen application rates. After two accelerated growing cycles, total biomass of both species was significantly greater under elevated CO2. No significant interactions between CO2 concentration and water availability, nitrogen availability, or stand type were observed. Competitive interactions between loblolly pine and sweetgum were strongly influenced by water availability, but not CO2 concentration. Assessment of species response to CO2 was dependent upon growth in monoculture or mixture. Under low water availability, data from monocultures suggested that sweetgum had a stronger growth response to elevated CO2 concentrations than loblolly pine. In contrast, results from mixed-species stands showed that the competitive status of loblolly pine and sweetgum did not change under the high CO2 concentration. These results underscore the value of growing co-occurring species in mixed stands under varying levels of multiple resources for the determination of relative performance under future environments.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, FIELD, GROWTH, INTERFERENCE, LIQUIDAMBAR- STYRACIFLUA, PLANTS, RESPONSES, TAEDA SEEDLINGS

811

Groninger, J.W., J.R. Seiler, S.M. Zedaker, and P.C. Berrang. 1996. Effects of CO2 concentration and water availability on growth and gas exchange in greenhouse-grown miniature stands of Loblolly Pine and Red Maple. *Functional Ecology 10(6):708-716.*

1. The study assesses the effects of atmospheric CO2 concentration and water availability on stand development and photosynthetic characteristics of Loblolly Pine (Pinus taeda) and Red Maple (Acer rubrum). Miniature stands of these species were grown from seed in monoculture and in a 50:50 replacement mixture for two accelerated growing seasons. 2. Both species had greater biomass under the higher

levels of CO2 and water availability. Biomass of Loblolly Pine seedlings in mixed stands exceeded that in monocultures, while the opposite was true for Red Maple. No significant treatment interactions were detected for total biomass. Significant main effects for water and stand type were detected for stem height of Loblolly Pine. CO2, water and stand type interactions were observed for height of Red Maple. 3. Net photosynthetic rates were measured on miniature stand canopies and constituent seedlings from these stands. Both species exhibited higher photosynthetic rates under elevated CO2. However, expression of photosynthesis on a leaf mass or soil area basis affected conclusions regarding the role of water availability on stand-level response to elevated CO2.

KEYWORDS: ATMOSPHERIC CO2, BEECH STANDS, ELEVATED CARBON-DIOXIDE, ENRICHMENT, INTERFERENCE INTERACTIONS, LIQUIDAMBAR- STYRACIFLUA, RESPONSES, STRESS, TAEDA SEEDLINGS, TREE SEEDLINGS

812

Groninger, J.W., J.R. Seiler, S.M. Zedaker, and P.C. Berrang. 1996. Photosynthetic response of loblolly pine and sweetgum seedling stands to elevated carbon dioxide, water stress, and nitrogen level. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 26(1):95-102.*

Seedling stands of loblolly pine (Pinus taeda L.) and sweetgum (Liquidambar styraciflua L.) were grown in monoculture or mixed stands for two growing cycles in controlled-environment chambers. Treatments consisted of ambient (408 ppm) and elevated (806 ppm) CO2 concentrations, water-stressed and well- watered conditions, and low (20 kg N/ha) and high (215 kg N/ha) nitrogen application rates. Photosynthesis rates were measured under ambient and elevated cuvette CO2 concentrations for both whole stands and individual seedlings from these stands. Significant interactions between CO2 and water suggested that elevated CO2 concentration compensated for low water availability in individually measured loblolly pine and in whole seedling stands regardless of stand type. Expressing photosynthesis on a soil area versus a leaf-mass basis influenced the photosynthetic rankings of the three stand types relative to one another. Net photosynthetic rates per unit leaf mass were 390 and 880% higher in individually measured seedlings than in whole monoculture stands for loblolly pine and sweetgum, respectively. Lower photosynthetic contributions from lower canopy leaves in whole seedling stands compared with the upper canopy leaves used in individual-seedling measurements were thought to be responsible for lower photosynthetic rates in seedling stands. These results suggest that photosynthetic response is influenced by canopy dynamics that are unaccounted for by individual-seedling measurements of photosynthesis. Differences in photosynthetic response between loblolly pine and sweetgum stands and individuals are thought to be largely due to species-specific differences in canopy light extinction characteristics.

KEYWORDS: CO2- ENRICHMENT, FORESTS, GAS-EXCHANGE, GROWTH, LIQUIDAMBAR- STYRACIFLUA, RUBISCO, TAEDA SEEDLINGS

813

Gross, U., F. Gilles, L. Bender, P. Berghofer, and K.H. Neumann. 1993. The influence of sucrose and an elevated co2 concentration on photosynthesis of photoautotrophic peanut (arachis-hypogaea L) cell-cultures. *Plant Cell Tissue and Organ Culture 33(2):143-150.*

Using photoautotrophic cells of Arachis hypogaea (L.) growing at ambient CO2, it was shown that exogenous sucrose supplied to the liquid medium reduced (CO2)-C-14 fixation (supplied as NaH (CO3)-C-14) . This was mostly due to a reduced labelling in P-esters, and to a lesser extent, in the serine/glycine moiety. However, radioactivity in the neutral sugar fraction was increased upon supplement of exogenous sucrose. The reduced labelling of P-esters and serine/glycine agrees with a lower concentration and specific activity of Rubisco in the sucrose supplied treatments as compared to the control. Following a transfer into a sugar free nutrient medium the concentration and activity of Rubisco is increased. The concentration of PEPCase was not influenced by sucrose application, although its specific activity was increased. At elevated CO2 concentration (2.34% v/v) the Rubisco concentration and specific activity was at the same level as in the control (0.03% V/V CO2). However, the concentration and the specific activity of PEPCase was increased and dry weight increase was about 8-9-fold higher than at ambient CO2.

KEYWORDS: ENZYME, FLAGELLATE CHLOROGONIUM-ELONGATUM, LEAVES, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE, SUBUNITS

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Grossman, S., T. Kartschall, B.A. Kimball, D.J. Hunsaker, R.L. LaMorte, R.L. Garcia, G.W. Wall, and P.J. Pinter. 1995. Simulated responses of energy and water fluxes to ambient atmosphere and free-air carbon dioxide enrichment in wheat. *Journal of Biogeography 22(4-5):601-609.*

Increased ambient carbon dioxide has been associated with CO2-induced stomatal closure which affects growth and evapotranspiration of crop canopies. This results in changes of the energy balance components of the soil-plant-atmosphere system. The agroecosystem wheat model DEMETER was linked to a soil-vegetation-atmosphere-transfer module which includes the energy balance of the crop canopy and the energy balance of the soil surface. Thus, it was possible to calculate evapotranspiration, canopy temperature and the changed ratio of sensible and latent heat fluxes in response to elevated atmospheric CO2 concentrations. The free-air carbon dioxide enrichment (FACE) technique provided a largely undisturbed regime for atmospheric exchange. During the FACE wheat experiment at Maricopa in 1992-93, the effects of elevated atmospheric CO2 concentrations on energy balance and evapotranspiration of the wheat canopy at about 350-370 mu mol/mol (control) and 550 mu mol/mol (FACE) were investigated. The recorded data were used for model validation. Diurnal trends of all energy balance components and the canopy temperature were simulated for FACE and control conditions using hourly weather data. Results were compared with the observed data on 16 March 1993. Simulated cumulative seasonal evapotranspiration was found in good accordance to the observed one. Consistent with observations, the simulations suggest that there was a small reduction in evapotranspiration of about 4%. Of course, with the observed increases in growth, there were even larger increases in water use efficiency.

KEYWORDS: TEMPERATURE

815

Grossman-Clarke, S., B.A. Kimball, D.J. Hunsaker, S.P. Long, R.L. Garcia, T. Kartschall, G.W. Wall, P.J. Printer, F. Wechsung, and R.L. LaMorte. 1999. Effects of elevated atmospheric CO2 on canopy transpiration in senescent spring wheat. *Agricultural and Forest Meteorology 93(2):95-109.*

The seasonal course of canopy transpiration and the diurnal courses of latent heat flux of a spring wheat crop were simulated for atmospheric CO2 concentrations of 370 and 550 mu mol mol(-1). The hourly weather data, soil parameters and the irrigation and fertilizer treatments of the Free-Air Carbon Dioxide Enrichment wheat experiment in Arizona (1992-1993) were used to drive the model. The simulation results were tested against field measurements with special emphasis on the period

between anthesis and maturity. A model integrating leaf photosynthesis and stomatal conductance was scaled to canopy level in order to be used in the wheat growth model. The simulated intercellular CO2 concentration, C-i, was determined from the ratio of C-i to the CO2 concentration at the leaf surface, C-s, the leaf-to-air specific humidity deficit and a possibly unfulfilled transpiration demand, After anthesis, the measured assimilation rates of the flag leaves decreased more rapidly than their stomatal conductances, leading to a rise in the C-i/C-s ratio. In order to describe this observation, an empirical model approach was developed which took into account the leaf nitrogen content for the calculation of the C-i/C-s ratio. Simulation results obtained with the new model version were in good agreement with the measurements. If changes in the C-i/C-s ratio in accordance with the decrease in leaf nitrogen content during leaf senescence were not considered in the model, simulations revealed an underestimation of the daily canopy transpiration of up to 20% and a decrease in simulated seasonal canopy transpiration by 10%. The measured reduction in the seasonal sum of canopy transpiration and soil evaporation owing to CO2 enrichment, in comparison, was only about 5%.

KEYWORDS: AMBIENT ATMOSPHERE, C-3 PLANTS, CARBON-DIOXIDE ENRICHMENT, LEAF, LEAVES, MODEL, NITROGEN, PHOTOSYNTHESIS, STOMATAL CONDUCTANCE, WATER-USE

816

Grotenhuis, T.P., and B. Bugbee. 1997. Super-optimal CO2 reduces seed yield but not vegetative growth in wheat. *Crop Science 37(4):1215-1222.*

Although terrestrial atmospheric CO2 levels will not reach 1000 mu mol mol(-1) (0.1%) for decades, CO2 levels in growth chambers and greenhouses routinely exceed that concentration. CO2 levels in life support systems in space can exceed 10 000 mu mol mol(-1)(1%). Numerous studies have examined CO2 effects up to 1000 mu mol mol(-1), but biochemical measurements indicate that the beneficial effects of CO2 can continue beyond this concentration. We studied the effects of near-optimal (approximate to 1200 mu mol mol(-1)) and super-optimal CO2 levels (2400 mu mol mol(-1)) on yield of two cultivars of hydroponically grown wheat (Triticum aestivum L.) in 12 trials in growth chambers. Increasing CO2 from sub-optimal to near- optimal (350-1200 mu mol mol(-1)) increased vegetative growth by 25% and seed yield by 15% in both cultivars. Yield increases were primarily the result of an increased number of heads per square meter. Further elevation of CO2 to 2500 mu mol mol(-1) reduced seed yield by 22% ($P < 0.001$) in cv. Veery-10 and by 15% ($P < 0.001$) in cv. USU-Apogee. Super-optimal CO2 did not decrease the number of heads per square meter, but reduced seeds per head by 10% and mass per seed by 11%. The toxic effect of CO2 was similar over a range of light levels from half to full sunlight. Subsequent trials revealed that super- optimal CO2 during the interval between 2 wk before and after anthesis mimicked the effect of constant super-optimal CO2. Furthermore, near-optimal CO2 during the same interval mimicked the effect of constant near-optimal CO2. Nutrient concentration of leaves and heads was not affected by CO2. These results suggest that super optimal CO2 inhibits some process that occurs near the time of seed set resulting in decreased seed set, seed mass, and yield.

KEYWORDS: CARBON DIOXIDE, EFFICIENCY, ENRICHMENT, ETHYLENE BIOSYNTHESIS, GAS-EXCHANGE, INTACT SUNFLOWER PLANTS, LEAVES, LIGHT, PHOTOSYNTHETIC ACCLIMATION, RESPIRATION

817

Grotenhuis, T., J. Reuveni, and B. Bugbee. UNKNOWN YEAR. Super-optimal CO2 reduces wheat yield in growth chamber and greenhouse environments. *Life Sciences: Life Support Systems Studies-I :1901-1904.*

Seven growth chamber trials (six replicate trials using 0.035, 0.12, and 0.25 % CO2 in air and one trial using 0.12, 0.80, and 2.0% CO2 in air) and three replicate greenhouse trials (0.035, 0.10, 0.18, 0.26, 0.50, and 1.0% CO2 in air) compare the effects of super-optimal CO2 on the seed yield, harvest index, and vegetative growth rate of wheat (Triticum aestivum L. cvs. USU-Apogee and Veery-10). Plants in the growth chamber trials were grown hydroponically under fluorescent lamps, while the greenhouse trials were grown under sunlight and high pressure sodium lamps and in soilless media. Plants in the greenhouse trials responded similarly to those in the growth chamber trials; maximum yields occurred near 0.10 and 0.12 % CO2 and decreased significantly thereafter. This research indicates that the toxic effects of elevated CO2 are not specific to only one environment and has important implications for the design of bio-regenerative life support systems in space, and for the future of terrestrial agriculture.

KEYWORDS: INCOMPLETE, ETHYLENE

818

Grulke, N.E., J.L. Hom, and S.W. Roberts. 1993. Physiological adjustment of 2 full-sib families of ponderosa pine to elevated co2. *Tree Physiology 12(4):391-401.*

Seeds from two full-sib families of ponderosa pine (Pinus ponderosa) with known differences in growth rates were germinated and grown in an ambient (350 mul l-1) or elevated (700 mul l-1) CO2 concentration. Gas exchange at both ambient and elevated CO2 concentrations was measured 1, 6,39, and 112 days after the seed coat was shed. Initial stimulation of CO2 exchange rate (CER) by elevated CO2 was large (> 100%). On Day 1, CER of seedlings grown in elevated CO2 and measured at ambient CO2 was significantly lower than the CER of seedlings grown and measured at ambient CO2, indicating physiological adjustment of the seedlings exposed to elevated CO2. Physiological acclimation to elevated CO2 was complete by Day 39 when there was no significant difference in CER between seedlings grown and measured at ambient CO2 and seedlings grown and measured at elevated CO2. After 4 months, the light response of seedlings in the two treatments was determined at both ambient and elevated CO2. Light compensation point, CER at light saturation, and apparent quantum efficiency of seedlings grown and measured at ambient CO2 were not significantly different from those of seedlings grown and measured at elevated CO2. With a short-term increase in CO2, CER at light saturation (5.16 +/- 0.52 versus 3.13 +/- 0.30 mumol CO2 m-2 s- 1) and apparent quantum efficiency (0.082 +/- 0.011 versus 0.045 +/- 0.003 mumol CO2 mumol-1 quanta) were significantly increased. Leaf C/N ratio was significantly increased in the elevated CO2 treatment. There were few significant differences between families for any response to elevated CO2. Under the experimental conditions, high growth rate was not correlated with a greater response to elevated CO2.

819

Grulke, N.E., G.H. Riechers, W.C. Oechel, U. Hjelm, and C. Jaeger. 1990. Carbon balance in tussock tundra under ambient and elevated atmospheric CO2. *Oecologia 83(4):485-494.*

820

Gruters, U. 1999. On the role of wheat stem reserves when source-sink balance is disturbed by elevated CO2. *Journal of Applied Botany-Angewandte Botanik 73(1-2):55-62.*

Spring wheat (Triticum aestivum L. cv. Minaret) was exposed to 360 and 680 mu mol mol(-1) CO2 in open top chambers during the vegetation periods of 1994/1995. In 1994 fractionated harvests were carried out at weekly intervals from the onset of stem elongation,. At final harvest CO, enhanced aboveground biomass and yield by 49.7 and 43.2%, respectively. From all plant organs stem dry weights showed the largest increases under doubled CO2, whereas leaf-blade dry weights increased only slightly. Since stems are known as sites of intermediary carbohydrate-storage, carbohydrate composition was analysed in the internodes of the main stem. Carbohydrates were determined as fructans, sucrose and reducing sugars. CO2 stimulated the amounts per organ of all components, but fructans showed the largest increases. Fructan accumulation lasted about one week longer and remobilisation was faster under elevated CO2. The results are consistent with current knowledge, that temporary storage pools accomodate source photosynthate supply to sink demand and suggested a predominant role of the intermediary stem reserves, when source-sink relations are changed under elevated CO2. The contribution of the main stem reserves to the main stem yield was also enhanced by elevated CO2 (6.1-8.7% compared to 10.0-14.2%). In 1995 growth and yield increase due to elevated CO2 (50.6 and 53%) was comparable to 1994. A functional growth analysis of the stem dry weight was carried out in this year. There was only a slightly longer accumulation phase in response to elevated CO2. Combined stem reserves contributed 12-18% to the final grain yield thereby contradicting, the suggestions based on the results of the year 1994.

KEYWORDS: FRUCTAN ACCUMULATION, GROWTH, PLANTS, SPRING WHEAT, TEMPERATURE, YIELD

821

Guak, S., D.M. Olsyzk, L.H. Fuchigami, and D.T. Tingey. 1998. Effects of elevated CO2 and temperature on cold hardiness and spring bud burst and growth in Douglas-fir (Pseudotsuga menziesii). *Tree Physiology 18(10):671-679.*

We examined effects of elevated CO2 and temperature on cold hardiness and bud burst of Douglas-fir (Pseudotsuga menziesii (Mirb.) France) seedlings. Two-year-old seedlings were grown for 2.5 years in semi-closed, sunlit chambers at either ambient or elevated (ambient + approximate to 4 degrees C) air temperature in the presence of an ambient or elevated (ambient + approximate to 200 ppm) CO2 concentration. The elevated temperature treatment delayed needle cold hardening in the autumn and slowed dehardening in the spring. At maximum hardiness, trees in the elevated temperature treatment were less hardy by about 7 degrees C than trees in the ambient temperature treatment. In general, trees exposed to elevated CO2 were slightly less hardy during hardening and dehardening than trees exposed to ambient CO2. For trees in the elevated temperature treatments, date to 30% burst of branch terminal buds was advanced by about 6 and 15 days in the presence of elevated CO2 and ambient CO2, respectively. After bud burst started, however, the rate of increase in % bud burst was slower in the elevated temperature treatments than in the ambient temperature treatments. Time of bud burst was more synchronous and bud burst was completed within a shorter period in trees at ambient temperature (with and without elevated CO2) than in trees at elevated temperature. Exposure to elevated temperature reduced final % bud burst of both leader and branch terminal buds and reduced growth of the leader shoot. We conclude that climatic warming will influence the physiological processes of dormancy and cold hardiness development in Douglas-fir growing in the relatively mild temperate region of western Oregon, reducing bud burst and shoot growth.

KEYWORDS: BUDBURST, DORMANCY, FROST DAMAGE, PICEA-SITCHENSIS, PROBABILITY, RISK, TREES

822

Guehl, J.M., C. Picon, G. Aussenac, and P. Gross. 1994. Interactive effects of elevated co2 and soil drought on growth and transpiration efficiency and its determinants in 2 european forest tree species. *Tree Physiology 14(7-9):707-724.*

The responses of growth and transpiration efficiency (W = biomass accumulation/water consumption) to ambient and elevated atmospheric CO2 concentrations (350 and 700 mumol mol-1, respectively) were investigated under optimal nutrient supply in well-watered and in drought conditions in two temperate- forest tree species: Quercus petraea Liebl. and Pinus pinaster Ait. Under well-watered conditions, doubling the CO2 concentration for one growing season increased biomass growth by 138% in Q. petraea and by 63% in P. pinaster. In contrast, under drought conditions, elevated CO2 increased biomass growth by only 47% in Q. petraea and had no significant effect on biomass growth in P. pinaster. Transpiration efficiency was higher in Q. petraea than in P. pinaster in all treatments. This difference was linked (i) to lower carbon isotope discrimination (DELTA), and thus lower values of the intercellular/ambient CO2 concentration (c(i)/c(a)) ratio, in Q. petraea, (ii) to lower values of leaf mass ratio (LMR, leaf mass/whole plant mass), which we suggest was positively related to the proportion of daytime carbon fixation lost by respiration (PHI), in Q. petraea, and (iii) to slightly lower C concentrations in Q. petraea than in P. pinaster. The CO2- promoted increase in W was higher in Q. petraea (+80%) than in P. pinaster (+50%), and the difference was associated with a more pronounced decrease in PHI in response to elevated CO2 in Q. petraea than in P. pinaster, which could be linked with the N dilution effect observed in Q. petraea. Because PHI also directly affects growth, the CO2-induced enhancement of PHI in Q. petraea is a crucial determinant of the growth stimulation observed in this species. Leaf gas exchange regulation was not the only factor involved in the responses of growth and W to elevated CO2 and drought, other physiological processes that have crucial roles include carbon and N allocation and respiration.

823

Gunderson, C.A., R.J. Norby, and S.D. Wullschleger. 1993. Foliar gas-exchange responses of 2 deciduous hardwoods during 3 years of growth in elevated co2 - no loss of photosynthetic enhancement. *Plant, Cell and Environment 16(7):797-807.*

Responses of photosynthesis and stomatal conductance were monitored throughout a 3-year field exposure of Liriodendron tulipifera (yellow-poplar) and Quercus alba (white oak) to elevated concentrations of atmospheric CO2. Exposure to atmospheres enriched with +150 and +300 mumol mol-1 CO2 increased net photosynthesis by 12-144% over the course of the study. Net photosynthesis was consistently higher at +300 than at +150 mumol mol-1 CO2. The effect Of CO2 enrichment on stomatal conductance was limited, but instantaneous leaf-level water use efficiency increased significantly. No decrease in the responsiveness of photosynthesis to CO2 enrichment over time was detected, and the responses were consistent throughout the canopy and across successive growth flushes and seasons. The relationships between internal CO2 concentration and photosynthesis (e.g. photosynthetic capacity and carboxylation efficiency) were not altered by growth at elevated concentrations of CO2. No alteration in the timing of leaf senescence or abscission was detected, suggesting that the seasonal duration of effective gas-exchange was unaffected by CO2 treatment. These results are consistent with data previously reported for these species in controlled-environment studies, and suggest that leaf-level photosynthesis does not down-regulate in these species as a result of acclimation to CO2 enrichment in the field. This sustained enhancement of photosynthesis provides the opportunity for increased growth and carbon storage by trees as the atmospheric concentration of CO2 rises, but many additional factors interact in determining whole-plant and forest responses to global change.

KEYWORDS: ATMOSPHERIC CO2, CARBON-DIOXIDE ENRICHMENT, CO2-ENRICHED ATMOSPHERES, LEAVES, LIRIODENDRON-TULIPIFERA L, LONG-TERM EXPOSURE, SCIRPUS- OLNEYI, SEEDLINGS, TUSSOCK TUNDRA, WATER-USE

824

Gunderson, C.A., and S.D. Wullschleger. 1994. Photosynthetic acclimation in trees to rising atmospheric co2 - a broader perspective. *Photosynthesis Research 39(3):369-388.*

Analysis of leaf-level photosynthetic responses of 39 tree species grown in elevated concentrations of atmospheric CO2 indicated an average photosynthetic enhancement of 44% when measured at the growth [CO2]. When photosynthesis was measured at a common ambient [CO2], photosynthesis of plants grown at elevated [CO2] was reduced, on average, 21% relative to ambient-grown trees, but variability was high. The evidence linking photosynthetic acclimation in trees with changes at the biochemical level is examined, along with anatomical and morphological changes in trees that impact leaf- and canopy- level photosynthetic response to CO2 enrichment. Nutrient limitations and variations in sink strength appear to influence photosynthetic acclimation, but the evidence in trees for one predominant factor controlling acclimation is lacking. Regardless of the mechanisms that underlie photosynthetic acclimation, it is doubtful that this response will be complete. A new focus on adjustments to rising [CO2] at canopy, stand, and forest scales is needed to predict ecosystem response to a changing environment.

KEYWORDS: CASTANEA-SATIVA MILL, ELEVATED CARBON-DIOXIDE, GAS-EXCHANGE, PHOSPHORUS DEFICIENCY, PINUS-RADIATA, PLANT-RESPONSES, POPLAR CLONES, RADIATA D-DON, STOMATAL CONDUCTANCE, WATER-STRESS

825

Gunn, S., S.J. Bailey, and J.F. Farrar. 1999. Partitioning of dry mass and leaf area within plants of three species grown at elevated CO2. *Functional Ecology 13:3-11.*

1. We tested the hypothesis that the net partitioning of dry mass and dry mass:area relationships is unaltered when plants are grown at elevated atmospheric CO2 concentrations. 2. The total dry mass of Dactylis glomerata, Bellis perennis and Trifolium repens was higher for plants in 700 compared to 350 mu mol CO2 mol(-1) when grown hydroponically in controlled- environment cabinets. 3. Shoot:root ratios were higher and leaf area ratios and specific leaf areas lower in all species grown at elevated CO2. Leaf mass ratio was higher in plants of B. perennis and D. glomerata grown at elevated CO2. 4. Whilst these data suggest that CO2 alters the net partitioning of dry mass and dry mass:leaf area relationships, allometric comparisons of the components of dry mass and leaf area suggest at most a small effect of CO2. CO2 changed only two of a total of 12 allometric coefficients we calculated for the three species: v relating shoot to root dry mass was higher in D. glomerata, whilst v relating leaf area to total dry mass was lower in T. repens. 5. CO2 alone has very little effect on partitioning when the size of the plant is taken into account.

KEYWORDS: ALLOCATION, ATMOSPHERIC CARBON-DIOXIDE, COMMUNITIES, CROP RESPONSES, ENRICHMENT, MATTER, NITROGEN, RESPIRATION, ROOT, TEMPERATURE

826

GunthardtGoerg, M.S. 1997. Leaf and shoot formation of young spruce and beech exposed to elevated CO2. *Acta Oecologica-International Journal of Ecology 18(3):335-341.*

Sixteen open-top chambers (divided into two halves each containing either calcareous or acidic soil) were supplied in four combinations with either 366 or 550 mu l CO2 L-1, and either 2.5 or 25 kg N ha-(1) y(-1) (ammonium nitrate by irrigation). The development of young spruce (Picea abies) and beech (Fagus sylvatica) trees planted in the chambers together with understory plants will be studied over four years. The presented data are preliminary results from the first year of this experiment and refer to 64 spruce and 64 beech trees from two different Swiss spruce and beech provenances; two trees each per soil type, sampled in July and September in each chamber. Specific current-year spruce nee die length (length/dry mass) was reduced by elevated CO2 due to an increase in dry mass. Beech specific leaf area was only temporarily reduced in July. Elevated CO2 induced an earlier autumnal leaf discoloration. Total current-year shoot length per spruce and total number of leaves per beech tree were not influenced by the first year treatment with elevated CO2. N deposition had no effect on these parameters, but soil type influenced spruce needle colour Spruce, in contrast to beech, may therefore profit from elevated CO2 (when other resources are unlimited) by increasing shoot and needle dry mass.

KEYWORDS: ACCLIMATION, GROWTH, PLANT-RESPONSES, PRODUCTIVITY, TREES

827

Guy, M., G. Granoth, and J. Gale. 1990. Cultivation of Lemna gibba under desert conditions .2. the effect of raised winter temperature, CO2 enrichment and shading on productivity. *Biomass 23(1):1-11.*

828

GwynnJones, D., J.A. Lee, and T.V. Callaghan. 1997. Effects of enhanced UV-B radiation and elevated carbon dioxide concentrations on a sub-Arctic forest heath ecosystem. *Plant Ecology 128(1-2):242-249.*

An experiment is described which studies the effects of enhanced UV-B radiation (simulating a 15% reduction in the Ozone layer) and elevated atmospheric concentrations of CO2 (600 ppm) on the dwarf shrub layer of a sub-arctic forest heath ecosystem at Abisko, North Sweden. The experimental treatments were first applied in 1993, and have covered most of the snow- free season (late May to early September) 1993-1995. Effects of the treatments on the four dwarf shrub species have been recorded largely using non-destructive measures (Vaccinium uliginosum, Vaccinium myrtillus - deciduous species and Vaccinium vitis-idaea and Empetrum hermaphroditum - evergreen species). Effects of the treatments on stem growth and leaf thickness have so far been small, although CO2 treatments initially stimulated stem extension in Vaccinium myrtillus 1993 and depressed growth in V. vitis idaea in 1994 and E. hermaphroditum during 1995. UV-B treatments stimulated fruit production in V. myrtillus in both 1994 and 1995, but there was no effect on reproductive phenology. There were also marked effects of UV-B treatments on insect herbivory in the deciduous dwarf shrubs; with leaf area loss being greater than the control in the UV-B treatment in V. myrtillus and less in V. uliginosum. The results point to the possibility of important effects of the treatments on physiological and chemical processes within the plants. The ecological results of such effects may not be immediately apparent, but may be far reaching, pointing to the need for long-term in situ experimentation in predicting the effects of these global change variables.

KEYWORDS: CO2, DWARF SHRUBS, GROWTH, PEA, PLANTS, RESPONSES, ULTRAVIOLET-RADIATION

829

Habash, D.Z., M.A.J. Parry, S. Parmar, M.J. Paul, S. Driscoll, J. Knight, J.C. Gray, and D.W. Lawlor. 1996. The regulation of

component processes of photosynthesis in transgenic tobacco with decreased phosphoribulokinase activity. *Photosynthesis Research 49(2):159-167.*

Tobacco plants (Nicotiana tabacum L.) transformed with an inverted cDNA encoding ribulose 5-phosphate kinase (phosphoribulokinase,PRK;EC 2.7.1.19) were employed to study the in vivo relationship between photosynthetic electron transport and the partitioning of electron transport products to major carbon metabolism sinks under conditions of elevated ATP concentrations and limited ribulose 1,5-bisphosphate (RuBP) regeneration. Simultaneous measurements of room temperature chlorophyll fluorescence and CO2 gas exchange were conducted on intact leaves. Under ambient CO2 concentrations and light intensities above those at which the plants were grown, transformants with only 5% of PRK activity showed 'down-regulation' of PS II activity and electron transport in response to a decrease in net carbon assimilation when compared to wild-type. This was manifested as a decline in the efficiency of PS II electron transport (Phi(PS II)), an increase in dissipation of excess absorbed light in the antennae of PS II and a decline in : total linear electron transport (J(1)), electron transport dedicated to carbon assimilation (J(A)) and electron transport allocated to photorespiration (J(L)). The transformants showed no alteration in the Rubisco specificity factor measured in vitro and calculated in vivo but had a relatively smaller ratio of RuBP oxygenation to carboxylation rates (v(o)/v(c)), due to a higher CO2 concentration at the carboxylation site (C-c). The relationship between Phi(PS II) and Phi(CO2) was similar in transformants and wild-type under photorespiratory conditions demonstrating no change in the intrinsic relationship between PS II function and carbon assimilation, however, a novel result of this study is that this similar relationship occurred at different values of quantum flux, J(1), J(A), J(L) and v(o)/v(c) in the transformant. For both wild-type and transformants, an assessment was made of the possible presence of a third major sink for electron transport products, beside RuBP oxygenation and carboxylation, the data provided no evidence for such a sink.

KEYWORDS: CHLOROPHYLL FLUORESCENCE, DROUGHT STRESS, ELECTRON-TRANSPORT, GAS-EXCHANGE, LEAVES, NET CO2 ASSIMILATION, PHOTORESPIRATION, REDUCTION, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, RUBISCO

830

Habash, D.Z., M.J. Paul, M.A.J. Parry, A.J. Keys, and D.W. Lawlor. 1995. Increased capacity for photosynthesis in wheat grown at elevated co2 - the relationship between electron-transport and carbon metabolism. *Planta 197(3):482-489.*

Spring wheat (Triticum aestivum L.) was grown under optimal nutrition for six weeks at 700 and 350 mu mol . mol(-1) CO2 and simultaneous measurements of photosystem-II (PSII) chlorophyll fluorescence and gas exchange were conducted on intact attached leaves. Plants grown at elevated CO2 had double the concentration of CO2 at the carboxylation site (C-c) despite a lowered stomatal (g(s)) and mesophyll (g(m)) conductance compared with ambient-grown plants. Plants grown at elevated CO2 had a higher relative quantum yield of PSII electron transport (Phi(PSII)) and a higher relative quantum yield of CO2 fixation (Phi CO2). The higher Phi(PSII) was due to a larger proportion of open PSII centres, estimated by the coefficient of photochemical quenching of fluorescence (q(p)), with no change in the efficiency of light harvesting and energy transduction by open PSII centres (F'(v)/F'(m)). Analysis of the relationship between Phi(PSII) and Phi(CO2) conducted under various CO2 and O-2 concentrations showed that the higher Phi(CO2) for a given Phi(PSII) in leaves developed under elevated CO2 was similar to that obtained in leaves upon a partial reduction in photorespiration. Calculation of the allocation of photosynthetic electron-transport products to CO2 and O-2 showed that for leaves developed in elevated CO2, there was an increase in both total linear electron flow and electron flow to CO2 and a decrease in electron flow to O-2. Plants developed under elevated CO, showed positive acclimation manifested by a higher Phi(CO2) when measured under ambient CO2 and higher assimilation rates in A/C-i curves. Initial and to tal activity of ribulose-1,5- bisphosphate carboxylase- oxygenase (Rubisco EC 4.1.1.39) measured in vitro increased by 16 and 15% respectively in leaves from plants grown in elevated CO2, which was in agreement with a 15% higher in vivo carboxylation efficiency. It is concluded that growth of spring wheat at elevated CO2 enhances photosynthesis due to a change in the balance of component processes manifested as an increased capacity for carbon fixation, total electron transport and Rubisco activity, and a concomitant partial reduction of photorespiration.

KEYWORDS: CARBOXYLASE, CHLOROPHYLL FLUORESCENCE, FIELD, GAS-EXCHANGE, LEAVES, PHYSIOLOGY, QUANTUM YIELD, STRESS

831

Hadley, P., G.R. Batts, R.H. Ellis, J.I.L. Morison, S. Pearson, and T.R. Wheeler. 1995. Temperature-gradient chambers for research on global environment change .2. a twin-wall tunnel system for low- stature, field-grown crops using a split heat-pump. *Plant, Cell and Environment 18(9):1055-1063.*

A temperature gradient chamber (TGC) is described which enables elevated CO2 concentrations and a dynamic temperature gradient to be imposed on field crops throughout their life cycle under standard husbandry. Air is circulated through two double-walled polyethylene-covered tunnels connected to a split heat pump system to give a near-linear temperature gradient along each tunnel, Solar energy gain along each tunnel and exchange with outer tunnel air flow contribute to the temperature gradient and also produce diurnal and seasonal temperature fluctuations corresponding to ambient conditions, Mean temperature gradients of between 3 and 5 degrees C have been recorded throughout the growing seasons of crops of lettuce, carrot, cauliflower and winter wheat, Elevated or present CO2 concentrations are maintained in each of two pairs of tunnels throughout the cropping season using pure CO2 injected through motorized needle valves. This system can realistically simulate aspects of the effects of projected future environmental change on crop growth, development and yield, and in particular the possible interaction of the effects of increased CO2 and temperature.

KEYWORDS: CO2

832

Hager, C., G. Wurth, and G.H. Kohlmaier. 1999. Biomass of forest stands under climatic change: a German case study with the Frankfurt biosphere model (FBM). *Tellus Series B-Chemical and Physical Meteorology 51(2):385-401.*

In this contribution, we perform a case study of the German forests. We couple the Frankfurt biosphere model (FBM) with a model of the age class development (AGEDYN). The coupled model is applied to simulate the temporal development of carbon pools in German forests under the influence of climate change taking into account changes in the age class structure. In the base case, the growth of forest stands is simulated using a temporally averaged climate dataset, being representative for the contemporary climate conditions. To assess the sensitivity of forest growth to changes in environmental conditions, the FBM is run in several scenarios. In these simulations the effects both of climate change and of the direct effect of increased levels of atmospheric CO2 on photosynthesis (CO2 fertilization) on forest growth are assessed. In another simulation run with the FBM both effects - climate change and CO2 fertilization are combined. In simulations under present day's

climate conditions a good agreement is gained between simulation results and statistical data of the present standing stock carbon density of Germany's forests. A pure climate change leads to a decrease of the annual increments as well as to the climax standing stocks. The negative effect of climate change alone is overcompensated by enhanced photosynthesis in the simulations with combined climate change and CO2 fertilization. In the transient case, the coupled model is used in two scenarios describing first a continuation of present day's climate conditions and second a transient climate change from present conditions (1990) to 2 x CO2 conditions in 2090. Here, the simulations indicate that changes in the forest's age class structure can have a stronger influence on the future carbon balance of the forests in the considered region than the combined effect of climate change and CO2 fertilization.

KEYWORDS: ATMOSPHERE, BOREAL FORESTS, CARBON DYNAMICS, CO2, EXCHANGE, GLOBAL VEGETATION, PRODUCTIVITY, RESPONSES, TERRESTRIAL ECOSYSTEMS

833

Hakala, K. 1998. Growth and yield potential of spring wheat in a simulated changed climate with increased CO2 and higher temperature. *European Journal of Agronomy 9(1):41-52.*

The effects of climatic change on the growth, yield and nitrogen content of spring wheat (Triticum aestivum L., cv. Polkka) were studied from 1992 to 1994. The crop was sown directly in the field, at a normal sowing density. Leaf canopies were exposed to CO2 concentrations of 700 mu l l(-1) and temperatures 3 degrees C higher than ambient throughout the growing season. CO2 concentrations were elevated in open-top chambers 3m in diameter. Temperatures were elevated in an automatically controlled greenhouse built over the experimental field. To simulate conditions predicted for a future warmer climate, the wheat crop was sown 2-3 weeks earlier in the elevated temperature (future warmer climate) than in the ambient temperature treatment (present climate). In the elevated temperature experiment, the average temperatures and development rates were not increased during the period from sowing to anthesis, but from anthesis to maturity, both temperatures and development rates were increased. The small increase in the development rate after anthesis at elevated temperatures in 1992 and 1994 did not affect the grain weight, but the considerable increase in development rate in 1993 was accompanied by a decrease in grain weight. CO2 enrichment had no effect on development rate. The total biomass at harvest was significantly higher in CO2 enrichment in both temperature treatments. Although the mean increase in grain yield was not significant, the yields tended to be higher in CO2 enrichment. The magnitude of the increase in biomass and grain yield in CO2 enrichment ranged from about 5 to 60%. The increase in yield was mainly attributed to an increase in the number of ear- bearing shoots m(-2). Seed number per main shoot and seed weight were in general not increased with CO2 enrichment unless these were exceptionally low in the ambient CO2 conditions (in 1993). The harvest index was decreased at elevated temperatures, but there was no significant effect of CO2 enrichment. There was a small (7%) but significant decrease in the nitrogen content of the grain in CO2 enrichment at ambient temperatures. (C) 1998 Elsevier Science B.V.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, DRY-MATTER, ELEVATED CO2, ENRICHMENT, FIELD, NITROGEN, PHOTOSYNTHESIS, PLANT GROWTH, RESPONSES

834

Hakala, K., and T. Mela. 1996. The effects of prolonged exposure to elevated temperatures and elevated CO2 levels on the growth, yield and dry matter partitioning of field-sown meadow fescue. *Agricultural and Food Science in Finland 5(3):285-298.*

Field-sown meadow fescue (Festuca pratensis, cv. Kalevi) stands were exposed to elevated temperatures (+3 degrees C) and elevated CO2 (700 ppm) levels in two experiments conducted in 1992-1993 (experiment 1) and in 1994-1995 (experiment 2). Total aboveground yield was, on average, 38% higher at elevated than at ambient temperatures. At ambient temperatures elevated CO2 increased the number of tillers by 63% in 1992, 24% in 1993, 90% in 1994 and 14% in 1995. At elevated temperatures, the increase in tiller number in elevated CO2 was seen only in the first growing seasons after sowing. The total yield in a growing season was about 10% higher in elevated CO2 in experiment 1. In experiment 2 the yield was more than 20% higher in elevated CO2 at elevated temperatures, whereas at ambient temperatures the rise in CO2 level had no effect on the yield; the root biomass, however, increased by more than 30%. In elevated CO2 at ambient temperatures the root biomass also increased in experiment 1, but at elevated temperatures there was no consistent change. The soluble carbohydrate content of above-ground biomass was 5-48% higher in elevated CO2 at most of the measuring times during the growing season, but the nitrogen content did not show a clear decrease. The reasons for the lack of a marked increase in biomass in elevated CO2 despite a 40-60% increase in photosynthesis are discussed.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, CARBON-DIOXIDE CONCENTRATION, ENRICHMENT, GAS-EXCHANGE, LOLIUM-PERENNE, NITROGEN, PERENNIAL RYEGRASS, PHOTOSYNTHESIS, RESPONSES

835

Hakala, K., T. Mela, H. Laurila, and T. Kaukoranta. 1996. Arrangement of experiments for simulating the effects of elevated temperatures and elevated CO2 levels on field-sown crops in Finland. *Agricultural and Food Science in Finland 5(1):25-47.*

The experimental plants: spring wheat, winter wheat, spring barley, meadow fescue, potato, strawberry and black currant were sown or planted directly in the field, part of which was covered by an automatically controlled greenhouse to elevate the temperature by 3 degrees C. The temperature of the other part of the field (open field) was not elevated, but the field was covered with the same plastic film as the greenhouse to achieve radiation and rainfall conditions comparable to those in the greenhouse. To elevate the CO2 concentrations, four open top chambers (OTC) were built for the greenhouse, and four for the open field. Two of these, both in the greenhouse and in the open field, were supplied with pure CO2 to elevate their CO2 level to 700 ppm. The temperatures inside the greenhouse followed accurately the desired level. The relative humidity was somewhat higher in the greenhouse and in the OTC:s than in the open field, especially after the modifications in the ventilation of the greenhouse and in the OTC:s in 1994. Because the OTC:s were large (3 m in diameter), the temperatures inside them differed very little from the surrounding air temperature. The short-term variation in the CO2 concentrations in the OTC:s with elevated CO2 was, however, quite high. The control of the CO2 concentrations improved each year from 1992 to 1994, as the CO2 supplying system was modified. The effects of the experimental conditions on plant growth and phenology are discussed.

KEYWORDS: PHOTOSYNTHESIS, PLANTS

836

Hall, D.O., D.S. Ojima, W.J. Parton, and J.M.O. Scurlock. 1995. Response of temperate and tropical grasslands to CO2 and climate change. *Journal of Biogeography 22(2-3):537-547.*

Under a recent SCOPE collaborative project, longterm data from eleven tropical and temperate grassland sites were used (a) to validate the CENTURY model of plant-soil ecosystems and (b) to model climate

change and CO2 effects for thirty-one temperate and tropical grassland sites, representing seven ecoregions of the world. Model calibration and testing showed that soil carbon and nitrogen dynamics can be well simulated for the grassland biome worldwide, over a wide range of climate and soil types. The interannual response of above ground biomass and plant residue to variation in climate resulted in a good correspondence between simulated and observed dynamics on a monthly basis. These results are useful for analysis and description of grassland carbon dynamics, and as a reference point for testing predictions of net primary production (NPP) and biomass dynamics from levels of more physiologically based models. Prediction of plant and soil organic matter C and N dynamics requires knowledge of climate, soil texture, N inputs and fire and grazing patterns. CENTURY simulations of climate change and CO2 effects showed increased NPP for climate change alone, except in cold desert steppe regions, and CO2 increased production everywhere. Climate changes, predominantly a warming of these ecosystems, caused soil carbon to decrease overall, especially in cold desert and temperate steppes. Increased production due to elevated CO2 tended to ameliorate soil carbon losses and tropical savannas were actually soil carbon sinks. Climate change alone projected a carbon loss of 3-4 Pg after 50 years, and 1-2 Pg for the combined climate change and CO2 simulated effects. We analysed the dynamic response of some of the major CENTURY output parameters (e.g. NPP, soil organic matter, N mineralization and decomposition) for their sensitivity to climate change and increasing CO2 for one of the two general circulation models (GFHI scenario). This analysis was limited to a subset of five well-known study sites, representing five of the seven ecoregions.

KEYWORDS: BIOMASS, CARBON, CONIFEROUS FORESTS, DECOMPOSITION, DYNAMICS, MODEL, PRODUCTIVITY, SOIL

837

Hall, D.O., and J.M.O. Scurlock. 1991. Climate change and productivity of natural grasslands. *Annals of Botany 67:49-55.*

KEYWORDS: BIOSPHERE, CARBON, DYNAMICS, ELEVATED CO2, ESTUARINE MARSH, NITROGEN, PLANTS

838

Hall, F.G. 1999. Introduction to special section: BOREAS in 1999: Experiment and science overview. *Journal of Geophysical Research-Atmospheres 104(D22):27627-27639.*

The goal of BOREAS is to improve our understanding of the interactions between the boreal forest biome and the atmosphere in order to clarify their roles in global change. This overview briefly reviews the science background and motivations for the Boreal Ecosystem-Atmosphere Study (BOREAS). The findings of the 27 papers in this journal special issue are reviewed. Important scientific results of the project to date are summarized, and future research directions are identified.

KEYWORDS: ATMOSPHERE INTERACTIONS, BALANCE, CARBON DIOXIDE, CO2, FOREST, HIGH-LATITUDES, LAND-ATMOSPHERE, MODEL, NORTHERN, WATER

839

Hall, J.M., E. Paterson, and K. Killham. 1998. The effect of elevated CO2 concentration and soil pH on the relationship between plant growth and rhizosphere denitrification potential. *Global Change Biology 4(2):209-216.*

The effect of CO2 concentration on plant growth and the size of the rhizosphere denitrifier population was investigated for ryegrass grown at 3 different soil pH values (pH 4.3, 5.9 and 7.0). Soil microcosms were planted with ryegrass and maintained under constant growth conditions at either ambient (450ppm) or elevated (720ppm) CO2 concentration. At harvest, the rhizosphere soil was collected and subjected to a potential denitrification assay to provide an estimate of the size of the denitrifier population present. Ryegrass dry matter production varied across the pH range studied and contrary to other studies, elevated CO2 concentration did not consistently increase growth. Plant growth was reduced by approximate to 35% and 23% at pH 4.3 and pH 5.9, respectively, under elevated CO2 concentration. At pH 7.0, however, plant growth was increased by approximate to 45% under elevated CO2. Potential denitrification rates within the rhizosphere followed a similar pattern to plant growth in the different treatments, suggesting that plant growth and the size of denitrifier population within the rhizosphere are coupled. This study investigates the relationship between plant growth and rhizosphere denitrification potential, thereby providing an estimate of the size of the denitrifier population under increased CO2 concentration and soil pH.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, ENRICHMENT, FIELD, FLOW, LOLIUM-PERENNE, MICROBIAL BIOMASS, NITROGEN, PHOTOSYNTHESIS, RESPONSES, ROOTS

840

Halloy, S.R.P., and A.F. Mark. 1996. Comparative leaf morphology spectra of plant communities in New Zealand, the Andes and the European Alps. *Journal of the Royal Society of New Zealand 26(1):41-78.*

Leaf morphology of native vegetation tias often been interpreted as a sensitive indicator of environmental conditions, presumably as a result of natural selection. If environmental pressures act as a selective force on community leaf morphology, then we would expect a high degree of similarity in similar environments, regardless of biogeographic origin of the flora. A comparative study of full regional floras of alpine vascular plants was undertaken to test the sensitivity of leaf morphology to macro-environmental conditions. Five alpine sites and one lowland (control) site were selected in southern New Zealand spanning 1.5 degrees latitude and 2323 m. Three sites with equivalent alpine environments were selected in South America across a 60 degrees latitudinal and 4200 m altitudinal span with subtropical forest used as a control. A further alpine site from the European Alps was included as an outlier. Twenty leaf parameters were obtained for 2143 taxonomic entities x sites. Both the mean and the frequency distribution of leaf size and shape parameters were distinctive for each locality. Several morphological trends were found. Means of New Zealand contiguous low-alpine and high-alpine site pairs differed in. length -33%, width -14%, length/width -20%, leaf area -44%, entire margin -2% (variable), coriaceousness -18%, folded +22%, pubescence +40%. At higher elevations, leaves become smaller but rounder, considerably softer, are more often folded into crypts or similar structures and are more often pubescent. These changes corresponded to reductions of 2-3 degrees C in mean annual air temperature, c. 10% in mean minimum relative humidity and 7% in CO2 partial pressure. Despite the biogeographic and environmental differences, New Zealand and South American low-alpine sites were consistently similar in their morphological parameters and consistently different from high-alpine sites (except in Tierra del Fuego). High alpine sites were also consistently similar across the Pacific. Several parameters were found to have multimodal frequency distributions that were not significantly different in widely separate localities with different floras. The results suggest that plant community morphology is an emergent property, the magnitude of which is environmentally constrained.

KEYWORDS: ALPINE LIFE ZONE, ALTITUDINAL VARIATION, ANATOMY, CLIMATE, CONDUCTANCE, FLORA, FOSSILS, LATITUDINAL GRADIENT, RADIATION, SIZE

841

Ham, J.M., C.E. Owensby, and P.I. Coyne. 1993. Technique for measuring air-flow and carbon-dioxide flux in large, open-top chambers. *Journal of Environmental Quality 22(4):759-766.*

Open-Top Chambers (OTCs) are commonly used to evaluate the effect of CO2, O3, and other trace gases on vegetation. A study was conducted to develop and test a new technique for measuring forced air flow and net CO2 flux from OTCs. Experiments were performed with a 4.5-m diam. OTC that had a sealed floor and a specialized air delivery system. Air flow through the chamber was computed with the Bernoulli equation using measurements of the pressure differential between the air delivery ducts and the chamber interior. An independent measurement of air flow was made simultaneously to calibrate and verify the accuracy of the Bernoulli relationship. The CO2 flux density was calculated as the product of chamber air flow and the difference in CO2 concentration between the air entering and exhausting from the OTC (C(in) - C(out)). Accuracy of the system was evaluated by releasing CO2 within the OTC at known rates to emulate respiration from the field surface. Data were collected with OTCs at ambient and elevated CO2 (almost-equal-to 700 mumol mol-1). Results showed that the Bernoulli equation, with a flow coefficient of 0.7, accurately measured air flow in the OTC to within +/- 5% regardless of flow rate and air duct geometry. Experiments in ambient OTCs showed that CO2 flux density (mumol m-2 s-1), computed from 2-min averages of air flow and C(in) - C(out), was typically within +/- 10% of actual flux, provided that the exit air velocity at the top of the OTC was greater than 0.6 m s-1. Obtaining the same level of accuracy in CO2- enriched OTCs, however, required a critical exit velocity near 1.2 m s-1 to minimize the incursion of ambient air and prevent contamination of the exit gas sample. When flux data were integrated over time to estimate daily CO2 flux (mumol m-2 d- 1), actual and measured values agreed to within +/- 2% for both ambient and CO2-enriched chambers, suggesting that accurate measurements of daily net C exchange are possible with this technique.

KEYWORDS: CO2, EXCHANGE, FIELD CHAMBERS, WIND-TUNNEL

842

Ham, J.M., C.E. Owensby, P.I. Coyne, and D.J. Bremer. 1995. Fluxes of co2 and water-vapor from a prairie ecosystem exposed to ambient and elevated atmospheric co2. *Agricultural and Forest Meteorology 77(1-2):73-93.*

Increasing concentrations of atmospheric CO2 may alter the carbon and water relations of prairie ecosystems. A C-4- dominated tallgrass prairie near Manhattan, KS, was exposed to 2x ambient CO2 concentrations using 4.5 m-diameter open-top chambers. Whole-chamber net CO2 exchange (NCE) and evapotranspiration (ET) were continuously monitored in CO2- enriched and ambient (no enrichment) plots over a 34-d period encompassing the time of peak biomass in July and August, 1993. Soil-surface CO2 fluxes were measured with a portable surface chamber, and sap flow (water transport in xylem) in individual grass culms was monitored with heat balance techniques. Environmental measurements were used to determine the effect of CO2 on the surface energy balance and canopy resistances to vapor flux. In 1993, frequent rainfall kept soil water near field capacity and minimized plant water stress. Over the 34-d measurement period, average daily NCE (canopy photosynthesis - soil and canopy respiration) was 9.3 g CO2 m(-2) in the ambient treatment and 11.4 g CO2 m(-2) under CO2 enrichment. However, differences in NCE were caused mainly by delayed senescence in the CO2-enriched plots at the end of the growing season. At earlier stages of growth, elevated CO2 had no effect on NCE. Soil-surface CO2 fluxes typically ranged from 0.4 to 0.66 mg CO2 m(-2) s(-1), but were slightly greater in the CO2-enriched chambers. CO2 enrichment reduced daily ET by 22%, reduced sap flow by 18%, and increased canopy resistance to vapor flux by 24 s m(-1). Greater NCE and lower ET resulted in higher daytime water use efficiency (WUE) under CO2 enrichment vs. ambient (9.84 vs. 7.26 g CO2 kg(-1) H2O). However, record high precipitation during the 1993 season moderated the effect of WUE on plant growth, and elevated CO2 had no effect on peak aboveground biomass. CO2-induced stomatal closure also affected the energy balance of the surface by reducing latent heat flux (LE), thereby causing a consequent change in sensible heat flux (H). The daytime Bowen ratio (H/LE) for the study period was near zero for the ambient treatment and 0.21 under CO2 enrichment.

KEYWORDS: CANOPY PHOTOSYNTHESIS, CARBON DIOXIDE, CROP, EXCHANGE, FLOW, RESPONSES

843

Hamerlynck, E.P., C.A. McAllister, A.K. Knapp, J.M. Ham, and C.E. Owensby. 1997. Photosynthetic gas exchange and water relation responses of three tallgrass prairie species to elevated carbon dioxide and moderate drought. *International Journal of Plant Science 158(5):608-616.*

Undisturbed tallgrass prairie was exposed to ambient and elevated (twice-ambient) levels of atmospheric CO, and experimental dry periods. Seasonal and diurnal midday leaf water potential (Psi(leaf)), net photosynthesis (A(net)), and stomatal conductance (g(s)) responses of three tallgrass prairie growth forms-a C-4 grass, Andropogon gerardii; a broad- leaved woody C, shrub, Symphiocarpos orbiculatus; and a C-3 perennial forb, Salvia pitcheri-were assessed. Psi(leaf) in A. gerardii and S, orbiculatus was higher under elevated CO2, regardless of soil moisture, while Psi(leaf) in S. pitcheri responded only to drought. Elevated CO2 always stimulated A(net) in the C-3 species, while A. gerardii A(net) increased only under dry conditions. However, A(net) under elevated CO2 in the C-3 species declined with drought but not in the C,grass, Under wet conditions, g(s) reduced in elevated CO2 for all species. During dry periods, g, at elevated CO, was sometimes higher than in ambient CO2. Our results support claims that elevated CO2 will stimulate tallgrass prairie productivity during dry periods and possibly reduce temporal and spatial variability in productivity in these grasslands.

KEYWORDS: AMBIENT, ATMOSPHERIC CO2, BIOMASS PRODUCTION, BOUTELOUA-GRACILIS, C-4 GRASS, GRASS ANDROPOGON-GERARDII, NITROGEN, PASCOPYRUM-SMITHII, SOIL MOISTURE, TOPOGRAPHIC POSITION

844

Hanba, Y.T., E. Wada, M. Osaki, and T. Nakamura. 1996. Growth and delta C-13 responses to increasing atmospheric carbon dioxide concentrations for several crop species. *Isotopes in Environmental and Health Studies 32(1):41-54.*

The responses of plant growth and carbon isotope discrimination (Delta) to elevated atmospheric CO2 concentrations for several crop species (lettuce: Lactuca sativa L.; corn: Zea mays L. var. P3540; wheat: Triticum aestivum L. var Haruyutaka; and soybean: Glycine max (L). Merr. var. Kitamusume) were investigated. Shoot relative growth rate was used to indicate plant growth, and delta(13)C value of leaf materials in corn (C4 species) was used to calculate Delta for C3 species. Plant growth was stimulated by enriched CO2, while Delta remained almost constant as CO2 concentration changed. Delta showed interspecific difference, and the plant species of larger Delta had larger relative growth rates. Relative growth rates of the plants of larger Delta were stimulated by CO2 enrichment more than those of the plants of smaller Delta. We propose that plant Delta could be a possible parameter to assess the interspecific difference of plant response to the increasing atmospheric CO2 concentrations.

KEYWORDS: CO2 CONCENTRATIONS, COOL-SEASON GRASSES,

ELEVATED CO2, ENVIRONMENTS, GAS-EXCHANGE, ISOTOPE DISCRIMINATION, PHOTOSYNTHESIS, PLANTS, SPRING WHEAT, WATER-USE EFFICIENCY

845
Hand, D.W., J.W. Wilson, and B. Acock. 1993. Effects of light and co2 on net photosynthetic rates of stands of aubergine and amaranthus. *Annals of Botany 71(3):209-216.*

KEYWORDS: CARBON DIOXIDE, CROP PHOTOSYNTHESIS, ENRICHMENT, ENVIRONMENT, PLANT GROWTH, RESPONSES

846
Handel, M.D., and J.S. Risbey. 1992. An annotated-bibliography on the greenhouse-effect and climate change. *Climatic Change 21(2):97-253.*

The literature on climate change from an enhanced greenhouse effect is large and growing rapidly. The problems considered are increasingly interdisciplinary. For these reasons many workers will find useful pointers to the literature in the fields interacting with, but outside of, their own. We present here an annotated bibliography on issues relating to changes in the concentrations of Earth's greenhouse gases. The areas covered include theory and numerical modelling of climate change; cycles involving carbon dioxide and other radiatively important trace gases; observations of climate change and the problems associated with those observations; paleoclimatology as it relates to previous changes in the greenhouse gases; the impacts on and interactions with managed and natural ecosystems from climate change; policy issues related to climate change and to the limitation of climate change; history of the study of the greenhouse effect; and some other causes of climate change. Selection of papers has been made to facilitate rapid introduction to most of the important issues and findings in an area. Over 600 articles, reports, and books are discussed.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, DOUBLED CO2 CLIMATE, EARTHS RADIATION BUDGET, GENERAL-CIRCULATION MODEL, GLOBAL CLIMATE, NORTH-ATLANTIC OCEAN, RISING SEA-LEVEL, SURFACE AIR-TEMPERATURE, TRACE GASES, VOSTOK ICE-CORE

847
Hanninen, H. 1995. Effects of climatic-change on trees from cool and temperate regions - an ecophysiological approach to modeling of bud burst phenology. *Canadian Journal of Botany-Revue Canadienne De Botanique 73(2):183-199.*

A framework is presented for meddling bud burst phenology of trees from the cool and temperate regions. Three ecophysiological aspects affecting the timing of bud burst are considered: (i) effects of environmental factors on the rest status of the bud, (ii) effect of rest status on the ability for bud burst, and (iii) direct effect of air temperature on the rate of development towards bud burst. Any model for bud burst phenology can be presented within the framework with three submodels, each of them addressing one of the corresponding three ecophysiological aspects. A total of 96 hypothetical models were synthesized by combining submodels presented in the literature. The models were tested in two experiments with saplings of Pinus sylvestris L. growing in experimental chambers at their natural site in eastern Finland. In the first experiment, air temperature and (or) concentration of atmospheric CO2 was elevated. Elevation of the air temperature hastened bud burst, whereas elevation of the concentration of CO2 did not affect it. Several models accurately predicted the timing of bud burst for natural conditions but too early for bud burst at the elevated temperatures. This finding suggests that (i) the risk of a premature bud burst with subsequent frost damage, as a result of climatic warming, was overestimated in a recent simulation study, and (ii) bud burst observations in natural conditions alone are not sufficient for the testing of these mechanistic models. Several models did predict the timing of bud burst accurately for all treatments, but none of them obtained sufficiently strong support from the findings to stand out as superior or uniquely correct. In the second experiment a photoperiod submodel for rest break was tested by exposing the saplings to short-day conditions. The short-day treatment had only a minor effect on the timing of bud burst. These results demonstrated the importance of the concept of model realism: the accuracy of a model can be lost in new conditions (e.g., global warming), unless the model correctly addresses the essential ecophysiological aspects of the regulation of timing of bud burst.

KEYWORDS: BUDBURST, CORNUS-SERICEA L, DORMANCY RELEASE, DOUGLAS-FIR, FLUSHING TEMPERATURE, FROST DAMAGE, PHOTOPERIOD, PLANTS, SEEDLINGS, THERMAL TIME

848
Hanson, J.D., B.B. Baker, and R.M. Bourdon. 1993. Comparison of the effects of different climate change scenarios on rangeland livestock production. *Agricultural Systems 41(4):487-502.*

The effect of climate change on plant and livestock production in the Great Plains of North America is an important issue. The purpose of this study was to modify an existing rangeland ecosystem model and to simulate a cow/calf production system under different climate scenarios. The project required the capability of simulating rangeland livestock production under different ambient CO2 concentrations, temperatures and precipitation patterns. Climate change scenarios were created from three general circulation models (GCMs): GISS (Goddard Institute for Space Studies model), GFDL (Geophysical Fluid Dynamic Laboratory model), and UKMO (United Kingdom Meteorological Office model). Results from the GCMs were used to modify the climate record for a site in northeastern Colorado. Concomitantly, modifications were made to the SPUR model to help predict the effect of predicted climate change on selected variables of the range/livestock ecosystem. Simulation runs showed that predicted climate change will affect plant and animal production for rangelands. Changes in production were more closely related to changes in temperature and precipitation than to enhanced [CO2] alone. The effect of climate change on livestock production was very complex and results were dependent on the particular GCM scenario being simulated.

KEYWORDS: BIOMASS, MODEL

849
Hao, X.M., B.A. Hale, and D.P. Ormrod. 1997. The effects of ultraviolet-B radiation and carbon dioxide on growth and photosynthesis of tomato. *Canadian Journal of Botany-Revue Canadienne De Botanique 75(2):213-219.*

Tomato (Lycopersicon esculentum Mill.) plants were exposed, in controlled environments with 2.7 Wi(m(2).day) background ultraviolet-B (UV-B) radiation from fluorescent and incandescent lamps, to ambient (380 mu L.L-1) or elevated (600 mu L.L-1) CO2 combined with a total of 7.2 or 13.1 kJ/(m(2).day) UV-B radiation to determine effects on growth and photosynthesis. Ten consecutive days of exposure to the higher level of UV-B significantly reduced total and stem dry weight, leaf area, and plant height compared with the lower level. Only leaf area and plant height were significantly reduced after 19 consecutive days of exposure. To investigate whether plants recover from UV-B damage, the UV-B exposures were halted for 3 days after 19 days of UV-B exposure and then restarted for a further 2 days. The largest reduction in plant growth was found after 3 days with no UV-B followed by 2 days of the higher level of UV-B. Plants did not recover from UV-B damage during

the 3 days with background UV-B. Significant CO(2)xUV-B interactions were detected on stem dry weight after 10 consecutive days of the higher level of UV-B and on total dry weight, leaf dry weight, stem dry weight, and plant height after 3 days with no UV-B followed by 2 days of the higher level of UV-B. The higher dose of enhanced UV-B resulted in more severe damage at 600 mu L.L-1 CO than at ambient CO2. The higher level of UV-B did not affect the leaf net photosynthesis rate on a leaf area basis, although this UV-B level may have inhibited tomato growth through reducing the photosynthetic area. UV-absorbing compounds in leaves in the highest UV-B radiation level for 19 days were greater than for leaves with the lower dose. These UV-absorbing compounds in the higher UV-B dose diminished more than in the lower dose plants during the 3 days without UV-B. The UV-absorbing compounds maintained by plants exposed to the highest level of UV-B radiation may have protected plants from UV-B damage, particularly between 10 and 19 consecutive days of exposure.

KEYWORDS: CO2, EXPOSURE, IRRADIATION, MUTANTS, N,N-DIMETHYLFORMAMIDE, OZONE, PLANTS, QUALITY, RICE, YIELD

850
Hao, Y.Y., and R.E. Brackett. 1993. Influence of modified atmosphere on growth of vegetable spoilage bacteria in media. *Journal of Food Protection 56(3):223-228.*

Six gas mixtures (CO2/O2/N2: 0/5/95, 0/10/90, 5/10/85, 5/20/75, 10/5/85, and 10/20/70) and air were used to investigate the effect of modified atmosphere (MA) on growth of four vegetable spoilage bacteria. In addition, we determined the ability of the MA which most inhibited spoilage bacteria to reduce spoilage in bell peppers inoculated with the respective bacteria. In general, MA did not significantly affect growth of the bacteria tested. Growth of Erwinia, Pseudomonas, Xanthomonas, and Pepper # 15 (a pectinolytic Pseudomonas) at 10 and 20-degrees-C was not significantly affected regardless of gas mixtures. At 5-degrees-C, growth of Erwinia, Xanthomonas, and Pepper # 15 was slightly reduced by some gas mixtures (CO2/O2/N2: 0/5/95, 0/10/90, and 10/5/85; 10/5/85; 0/5/95 and 10/5/85, respectively). Modified atmosphere containing 10% CO2, 5% O2, and 85% N2 did not reduce the ability of bacteria tested to grow at elevated concentrations of sodium chloride. In addition, this MA composition did not change the percentage of bell peppers spoiled by test bacteria inoculated. However, overall visual quality was enhanced by MA.

KEYWORDS: BACILLUS-CEREUS, CARBON DIOXIDE, CO2, MARKET QUALITY, MINIMALLY PROCESSED FRUITS, PSEUDOMONAS- FLUORESCENS, SHELF-LIFE, STORAGE LIFE, STORED BROCCOLI, ZUCCHINI SQUASH

851
Harley, P.C., R.B. Thomas, J.F. Reynolds, and B.R. Strain. 1992. Modeling photosynthesis of cotton grown in elevated co2. *Plant, Cell and Environment 15(3):271-282.*

Cotton plants were grown in CO2-controlled growth chambers in atmospheres of either 35 or 65 Pa CO2. A widely accepted model of C3 leaf photosynthesis was parameterized for leaves from both CO2 treatments using non-linear least squares regression techniques, but in order to achieve reasonable fits, it was necessary to include a phosphate limitation resulting from inadequate triose phosphate utilization. Despite the accumulation of large amounts of starch (> 50 g m-2) in the high CO2 plants, the photosynthetic characteristics of leaves in both treatments were similar, although the maximum rate of Rubisco activity (Vc(max)), estimated from A versus C(i) response curves measured at 29-degrees-C, was almost-equal-to 10% lower in leaves from plants grown in high CO2. The relationship between key model parameters and total leaf N was linear, the only difference between CO2 treatments being a slight reduction in the slope of the line relating Vc(max) to leaf N in plants grown at high CO2, Stomatal conductance of leaves of plants grown and measured at 65 Pa CO2 was approximately 32% lower than that of plants grown and measured at 35 Pa. Because photosynthetic capacity of leaves grown in high CO2 was only slightly less than that of leaves grown in 35Pa CO2, net photosynthesis measured at the growth CO2, light and temperature conditions was approximately 25% greater in leaves of plants grown in high CO2, despite the reduction in leaf conductance. Greater assimilation rate was one factor allowing plants grown in high CO2 to incorporate 30% more biomass during the first 36 d of growth.

KEYWORDS: C-3 PLANTS, CARBON DIOXIDE, DEPENDENCE, ENRICHMENT, GAS-EXCHANGE, LEAVES, LIMITATIONS, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE, SPECIFICITY, TEMPERATURE

852
Harrison, K., W. Broecker, and G. Bonani. 1993. A strategy for estimating the impact of co2 fertilization on soil carbon storage. *Global Biogeochemical Cycles 7(1):69-80.*

As soils are a likely candidate for the so-called missing carbon sink, we explore the possible impact of CO2 fertilization on the global humus inventory. For any given greening-induced enhancement of plant growth, the increase in soil carbon inventory will depend on the spectrum of turnover times with respect to oxidation. Here we develop estimates of carbon turnover rates based on soil radiocarbon measurements.

KEYWORDS: BOMB-PRODUCED C-14, DIOXIDE, DISTRIBUTIONS, DYNAMICS, ORGANIC-MATTER, RADIOCARBON, SIMULATIONS, TURNOVER, WORLD OCEAN MODEL, ZEALAND

853
Harrison, P.A., and R.E. Butterfield. 1996. Effects of climate change on Europe-wide winter wheat and sunflower productivity. *Climate Research 7(3):225-241.*

Spatially explicit crop models were developed from mechanistic principles to investigate the regional impacts of climate change. The approach highlights the spatial variability of crop responses to altered environmental conditions. The mechanistic nature of the models allows some confidence to be placed in the results that are produced under climate change scenarios. Two crop models have been constructed and applied across a large European region: EuroWheat (winter wheat) and EuroSunfl (sunflower). Model results were compared with observed phenology and yield across a variety of scales and found to capture the current spatial variability in wheat and sunflower productivity. Climate change scenarios from both equilibrium and transient general circulation model experiments were applied to each crop model. Wheat yields are predicted to increase throughout Europe for all climate change scenarios. Conversely, water-limited sunflower yields decrease in most regions and scenarios. More positive effects are predicted for winter wheat than sunflower due to a lower sensitivity to increased temperature and a higher sensitivity to elevated concentrations of CO2. The lowest yield increases for wheat and the largest yield decreases for sunflower are found in western Europe, whilst the most positive responses for both crops occur in central and eastern Europe. Predictions for southern Europe are highly sensitive both within the region and between the scenarios. The old generation of equilibrium climate change scenarios gives the worst predictions (lowest yield increases or highest yield decreases). More beneficial responses are observed for the new generation of transient scenarios for both wheat and sunflower. Area averaged results for Europe, based on the United Kingdom Meterorological Office transient experiment (UKTR), indicate a rate of increase in winter wheat yields of 0.2 t ha(-1) decade(-1) up to the 2020s

and 0.36 t ha(-1) decade(-1) beyond. Smaller changes are predicted for sunflower: a rate of decrease of 0.05 t ha(-1) decade(-1) up to the 2020s followed by an increase of 0.05 t ha(-1) decade(-1).

KEYWORDS: CO2 CONCENTRATION, GRADUAL CHANGES, GROWTH, INCREASING CARBON-DIOXIDE, OCEAN-ATMOSPHERE MODEL, PHENOLOGY, SIMULATION-MODEL, TEMPERATURE, TRANSIENT RESPONSES, WATER

854

Hartz, T.K., A. Baameur, and D.B. Holt. 1991. Carbon-dioxide enrichment of high-value crops under tunnel culture. *Journal of the American Society for Horticultural Science 116(6):970-973.*

The feasibility of field-scale CO2 enrichment of vegetable crops grown under tunnel culture was studied with cucumber (Cucumis sativus L. cv. Dasher II, summer squash (Cucurbita pepo L. cv. Gold Bar), and tomato (Lycopersicon esculentum Mill. cv. Bingo) grown under polyethylene tunnels. The drip irrigation system was used to uniformly deliver a CO2-enriched air stream independent of irrigation. Carbon dioxide was maintained between 700 and 1000-mu-l.liter-1 during daylight hours. Enrichment began immediately after crop establishment and continued for almost-equal-to 4 weeks. At the end of the treatment phase, enrichment had significantly increased plant dry weight in the 2 years of tests. This growth advantage continued through harvest, with enriched cucumber, squash, and tomato plots yielding 30%, 20%, and 32% more fruit, respectively, in 1989. In 1990, cucumber and squash yields were increased 20%, and 16%, respectively. As performed, the expense of CO2 enrichment represented less than a 10% increase in total preharvest costs. A similar test was conducted on fall-planted strawberries (Fragaria X ananassa Duch. cvs. Irvine and Chandler). Carbon dioxide enrichment under tunnel culture modestly increased 'Irvine' yields but did not affect 'Chandler'.

KEYWORDS: CO2, GROWTH, POTATO PLANTS, RESPONSES, ROOT ZONE

855

Harvey, L.D.D. 1996. Development of a risk-hedging CO2-emission policy .2. Risks associated with measures to limit emissions, synthesis, and conclusions. *Climatic Change 34(1):41-71.*

This paper is Part II of a two-part series in which the risks associated with unrestrained greenhouse-gas emissions, and with measures to limit emissions, are reviewed. A sustained limitation of global CO2 emissions requires global population stabilization, a reduction in per capita emissions in the developed world, and a limitation of the increase in per capita emissions in the developing world. Reducing or limiting per capita emissions requires a major effort to improve the efficiency with which energy is transformed and used; urban development which minimizes the need for the private automobile and facilitates district heating, cooling, and cogeneration systems; and accelerated development of renewable energy. The following risks associated with these efforts to limit CO2 emissions are reviewed here: (i) resources might be diverted from other urgent needs; (ii) economic growth might be reduced; (iii) reduction measures might cost more than expected; (iv) early action might cost more than later action; (v) reduction measures might have undesired side effects; (vi) reduction measures might require heavy-handed government intervention; and (vii) reduction measures might not work. With gradual implementation of a diversified portfolio of measures, these risks can be greatly reduced. Net risk is further reduced by the fact that a number of non-climatic benefits would result from measures to limit CO2 emissions. Based on the review of risks associated with measures to limit emissions here, and the review of the risks associated with unrestrained emissions presented in Part I, it is concluded that a reasonable near- term (20-30 year) risk hedging strategy is one which seeks to stabilize global fossil CO2 emissions at the present (early 1990's) level. This in turn implies an emission reduction of 26% for industrialized countries as a whole and 40-50% for Canada and the USA if developing country emissions are to increase by no more than 60%, which in itself would require major assistance from the industrialized countries. The effectiveness of global CO2-emission stabilization in slowing down the buildup of atmospheric CO2 is enhanced by the fact that the airborne fraction (ratio of annual atmospheric CO2 increase to total annual anthropogenic emissions) decreases if emissions are stabilized, whereas it increases if emissions continue to grow exponentially. The framework and conclusions presented here are critically compared with so-called optimization frameworks.

KEYWORDS: CO2 EMISSIONS, CONSERVATION, ELECTRICITY, ENERGY EFFICIENCY, FUTURE, GLOBAL CLIMATE-CHANGE, GREENHOUSE, PERSPECTIVES, REDUCTION, UNITED-STATES

856

Harwood, K.G., J.S. Gillon, A. Roberts, and H. Griffiths. 1999. Determinants of isotopic coupling of CO2 and water vapour within a Quercus petraea forest canopy. *Oecologia 119(1):109-119.*

Concentration and isotopic composition (delta(13)C and delta(18)O) of ambient CO2 and water vapour were determined within a Quercus petraea canopy, Northumberland, UK. From continuous measurements made across a 36-h period from three heights within the forest canopy, we generated mixing lines (Keeling plots) for delta(a) (CO2)-C-13, delta(a) (COO)-O-18-O- 16 and delta(a) (H2O)-O-18, to derive the isotopic composition of the signal being released from forest to atmosphere. These were compared directly with measurements of different respective pools within the forest system, i.e. delta(13)C of organic matter input for delta(a) (CO2)-C-13 delta(18)O Of exchangeable water for delta(a) (COO)-O-18-O-16 and transpired water vapour for delta(a) (H2O)-O-18. [CO2] and delta(a) (CO2)- C-13 showed strong coupling, where the released CO2 was, on average, 4 per mil enriched compared to the organic matter of plant material in the system? suggesting either fractionation of organic material before eventual release as soil-respired CO2, or temporal differences in ecosystem discrimination. delta(a) (COO)-O-18-O-16 was less well coupled to [CO2], probably due to the heterogeneity and transient nature of water pools (soil, leaf and moss) within the forest. Similarly, delta(a) (H2O)-O-18 was less coupled to [H2O], again reflecting the transient nature of water transpired to the forest, seen as uncoupling during times of large changes in vapour pressure deficit. The delta(18)O of transpired water vapour, inferred from both mixing lines at the canopy scale and direct measurement at the leaf level, approximated that of source water, confirming that an isotopic steady state held for the forest integrated over the daily cycle. This demonstrates that isotopic coupling of CO2 and water vapour within a forest canopy will depend on absolute differences in the isotopic composition of the respective pools involved in exchange and on the stability of each of these pools with time.

KEYWORDS: 3-DIMENSIONAL SYNTHESIS, ATMOSPHERIC CO2, CARBON DIOXIDE, DISCRIMINATION, LEAF WATER, O-18 CONTENT, RAIN-FOREST, RESPIRED CO2, SPATIAL VARIATIONS, STABLE OXYGEN

857

Haszpra, L. 1999. On the representativeness of carbon dioxide measurements. *Journal of Geophysical Research-Atmospheres 104(D21):26953-26960.*

On the basis of the measurements at two monitoring sites located close to each other (220 km) in plain regions in Hungary, the representativeness of low-elevation continental CO2 measurements is

estimated. It is shown that under such conditions only the measurements carried out in the early afternoon hours can be considered as regionally representative for the CO2 content of the planetary boundary layer (PBL). Filtering the data in this way, it is calculated that the characteristic CO2 mixing ratio in the PBL may be about 2.5 ppm higher over this part of Europe than at the Mauna Loa Observatory (National Oceanic and Atmospheric Administration), Hawaii.

KEYWORDS: ATMOSPHERIC CO2, BUDGET, LATITUDINAL DISTRIBUTION, MODEL, OCEANIC UPTAKE, SINKS

858

Hattenschwiler, S., S. Buhler, and C. Korner. 1999. Quality, decomposition and isopod consumption of tree litter produced under elevated CO2. *Oikos 85(2):271-281.*

Rising atmospheric CO2 is expected to alter plant tissue quality which in turn could affect litter quality, decomposition, and carbon and nutrient turnover. We tested this hypothesis using leaf litter of beech (Fagus sylvatica) and branchlets (wood + bark) of spruce (Picea abies) produced under contrasting CO2 concentrations in model ecosystems. Both types of litter produced under elevated CO2 had significantly lower N concentrations, but showed no CO2-related differences in carbon and lignin concentrations. Decomposition rates (mass loss) assessed in a natural temperate forest were significantly slower in litter produced at high CO2. However, this effect became stronger in beech leaves but gradually disappeared in spruce branchlets over the 331-d exposure period. Irrespective of CO2 treatment beech leaf litter lost 16% of its initial N content. Spruce branchlets produced at low CO2 lost 50% of their initial N content, and those produced at high CO2 lost 26%. Two isopod species representing native macro-decomposers consumed 36% more of the high CO2-produced beech litter than they did of low CO2-produced beech litter. Only small, and non- significant increases in consumption of high CO2-produced spruce branchlets were observed. Isopods feeding on high CO, litter also produced more feces than those feeding litter from low CO2. Our results indicate that CO2-induced litter quality changes influence only certain stages of decomposition. and that these stages differ between different litter types. Inhibitory effects of elevated CO2, however, may be compensated by the positive feed-back of intensified "litter processing" of low quality litter by macro-decomposers. Consequently, the entire cycle of litter production and decomposition must be included in the analysis of the potential effects of rising CO2 on litter decomposition. This includes both micro- and macro- decomposer specific effects.

KEYWORDS: ATMOSPHERIC CO2, FOREST LITTER, HARDWOOD LEAF LITTER, LEAVES, LIGNIN CONTENT, NEEDLE LITTER, NITROGEN DYNAMICS, RATES, SPRUCE MODEL-ECOSYSTEMS, TERRESTRIAL ISOPODS

859

Hattenschwiler, S., and C. Korner. 1996. Effects of elevated CO2 and increased nitrogen deposition on photosynthesis and growth of understory plants in spruce model ecosystems. *Oecologia 106(2):172-180.*

We studied the effects of-atmospheric CO, enrichment (280, 420 and 560 mu l CO2 l(-1)) and increased N deposition (0.30 and 90 kg ha(-1) year(-1)) on the spruce-forest understory species Oxalis acetosella, Homogyne alpina and Rubus hirtus. Clones of these species formed the ground cover in nine 0.7 m(2) model ecosystems with 5-year-old Picea abies trees (leaf area index of approx. 2.2). Communities grew on natural forest soil in a simulated montane climate. Independently of N deposition, the rate of light-saturated net photosynthesis of leaves grown and measured at 420 mu l CO2 l(-1) was higher in Oxalis and in Homogyne, but was not significantly different in Rubus compared to leaves grown and measured at the pre-industrial CO2 concentration of 280 mu l l(-1). Remark ably, further CO2 enrichment to 560 mu l l(-1) caused no additional increase of CO2 uptake. With increasing CO2 supply concentrations of non- structural carbohydrates in leaves increased and N concentrations decreased in all species, whereas N deposition had no significant effect on these traits. Above-ground biomass and leaf area production were not significantly affected by elevated CO2 in the more vigorously growing species O. acetosella and R. hirtus, but the "slow growing" H. alpina produced almost twice as much biomass and 50% more leaf area per plant under 420 mu l CO2 l(-1) compared to 280 mu l l(-1) (again no further stimulation at 560 mu l l(-1)). In contrast, increased N addition stimulated growth in Oxalis and Rubus but had no effect on Homogyne. in Oxalis (only) biomass per plant was positively correlated with microhabitat quantum flux density at low CO2, but not at high CO2 indicating carbon saturation. On the other hand, the less shade-tolerant Homogyne profited from CO2 enrichment at all understory light levels facilitating its spread into more shady micro-habitats under elevated CO2. These species-specific responses to CO2 and N deposition will affect community structure. The non-linear responses to elevated CO2 of several of the traits studied here suggest that the largest responses to rising atmospheric CO2 are under way now or have already occurred and possible future responses to further increases in CO2 concentration are likely to be much smaller in these understory species.

KEYWORDS: ATMOSPHERIC DEPOSITION, CARBON, DECIDUOUS FOREST, HERB, LEAVES, LIGHT, RESPONSES, VEGETATION

860

Hattenschwiler, S., and C. Korner. 1996. System-level adjustments to elevated CO2 in model spruce ecosystems. *Global Change Biology 2(4):377-387.*

Atmospheric carbon dioxide enrichment and increasing nitrogen deposition are often predicted to increase forest productivity based on currently available data for isolated forest tree seedlings or their leaves. However, it is highly uncertain whether such seedling responses will scale to the stand level. Therefore, we studied the effects of increasing CO2 (280, 420 and 560 mu L L(-1)) and increasing rates of wet N deposition (0, 30 and 90 kg ha(-1) y(-1)) on whole stands of 4-year-old spruce trees (Picea abies). One tree from each of six clones, together with two herbaceous understory species, were established in each of nine 0.7 m(2) model ecosystems in nutrient poor forest soil and grown in a simulated montane climate for two years. Shoot level light-saturated net photosynthesis measured at growth CO2 concentrations increased with increasing CO2, as well as with increasing N deposition. However, predawn shoot respiration was unaffected by treatments. When measured at a common CO2 concentration of 420 mu L L(-1) 37% down-regulation of photosynthesis was observed in plants grown at 560 mu L CO2 L(-1). Length growth of shoots and stem diameter were not affected by CO2 or N deposition. Bud burst was delayed, leaf area index (LAI) was lower, needle litter fall increased and soil CO2 efflux increased with increasing CO2. N deposition had no effect on these traits. At the ecosystem level the rate of net CO2 exchange was not significantly different between CO2 and N treatments. Most of the responses to CO2 studied here were non-linear with the most significant differences between 280 and 420 mu L CO2 L(-1) and relatively small changes between 420 and 560 mu L CO2 L(-1). Our results suggest that the lack of above-ground growth responses to elevated CO2 is due to the combined effects of physiological down-regulation of photosynthesis at the leaf level, allometric adjustment at the canopy level (reduced LAI), and increasing strength of below-ground carbon sinks. The non- linearity of treatment effects further suggests that major responses of coniferous forests to atmospheric CO2 enrichment might already be under way and that future responses may be comparatively smaller.

KEYWORDS: AIR-POLLUTION, ATMOSPHERIC CO2, CARBON

DIOXIDE, COMMUNITIES, DECIDUOUS FOREST, GLOBAL CHANGE, PLANT GROWTH, RESPONSES, SEEDLINGS, TREES

861
Hattenschwiler, S., and C. Korner. 1997. Annual CO2 budget of spruce model ecosystems in the third year of exposure to elevated CO2. *Acta Oecologica-International Journal of Ecology 18(3):319-325.*

Clones of 4-year-old spruce trees (Picea abies) were grown in competition in model ecosystems with nutrient-poor natural forest soil and natural understory vegetation and were exposed to three CO, concentrations (280, 420 and 560 mu mol mol(-1)) for three years. Diurnal net ecosystem CO2 uptake (NECd), nocturnal net ecosystem CO2 loss (NECn) and soil CO2 efflux were measured repeatedly in the third year of CO2 exposure and were used to estimate an annual ecosystem CO2 budget. The CO2 induced stimulation of NECd varied over the year with no measurable stimulation in spring and fall but a high mid-season CO2 stimulation. Respiratory losses of whole ecosystems and soil CO2 efflux alone were both progressively increased with increasing CO2, thus counteracting the CO2 stimulation of photosynthesis per unit ground area. Consequently, the annual net ecosystem CO2 uptake was only moderately and non-linearly stimulated by CO2 (+8% = 84 g C m(-2) a(-1) at 420 and +9% = 90 g C m(-2) a(-1) at 560 compared to 280 mu mol CO2 mol(-1)). We conclude that the rising atmospheric CO2 concentration may lead to an increase in annual net ecosystem carbon gain of rather nutrient-poor spruce communities. Our results further suggest that CO2 fertilization effects may be greatest under current CO2 concentration and that relative increases of net ecosystem CO2 uptake will become relatively smaller as atmospheric CO2 will continue to rise.

KEYWORDS: ALPINE GRASSLAND, CARBON DIOXIDE, CYCLE, RESPONSES

862
Hattenschwiler, S., and C. Korner. 1997. Growth of autotrophic and root-hemiparasitic understory plants under elevated CO2 and increased N deposition. *Acta Oecologica-International Journal of Ecology 18(3):327-333.*

Effects of atmospheric CO2 enrichment (280, 420 and 560 mu mol CO2 mol(-1)) and increased N deposition (0, 30 and 90 kg ha(-1) a(-1)) on Oxalis acetosella, Homogyne alpina, and Melampyrum sylvaticum, growing in model ecosystems beneath spruce stands, were studied. Aboveground biomass in the less-shade-tolerant Homogyne and in the annual hemiparasite Melampyrum was strongly increased with increasing CO2, but not in the more shade- adapted Oxalis. In contrast, increased N deposition stimulated growth in Oxalis, but had no effect on Homogyne and Melampyrum. Due to spruce canopy closure Homogyne,le became light limited and its survivorship was strongly correlated with spruce canopy LAI in the second year of the experiment. Our results suggest, that elevated CO2 facilitates the expansion of Hamogyne into less favourable micro-habitats (deeper shade) and that increasing N deposition enables more vigorously growing species like Oxalis to increase in abundance. Growth of the hemiparasite Melampyrum was stimulated indirectly by increased heterotrophic carbon supply (carbon isotope data) from the host (Picea abies), and thus, this species may also increase in abundance with increasing CO2. However, possible indirect effects (canopy feedbacks) make predictions of long-term understory development difficult.

KEYWORDS: CARBON, ECOSYSTEMS

863
Hattenschwiler, S., and C. Korner. 1998. Biomass allocation and canopy development in spruce model ecosystems under elevated CO2 and increased N deposition. *Oecologia 113(1):104-114.*

Ecosystem-level experiments on the effects of atmospheric CO2 enrichment and N deposition on forest trees are urgently needed. Here we present data for nine model ecosystems of spruce (Picea abies) on natural nutrient-poor montane forest soil (0.7 m(2) of ground and 350 kg weight). Each system was composed of six 7-year-old (at harvest) trees each representing a different genotype, and a herbaceous understory layer (three species). The model ecosystems were exposed to three different CO2 concentrations (280, 420, 560 mu l l(-1)) and three different rates of wet N deposition (0, 30, 90 kg ha(-1) year(- 1)) in a simulated annual course of Swiss montane climate for 3 years. The total ecosystem biomass was not affected by CO2 concentration, but increased with increasing N deposition. However, biomass allocation to roots increased with increasing CO2 leading to significantly lower leaf mass ratios (LMRs) and leaf area ratios (LARs) in trees grown at elevated CO2. In contrast to CO2 enrichment, N deposition increased biomass allocation to the aboveground plant parts, and thus LMR and LAR were higher with increasing N deposition. We observed no CO2 x N interactions on growth, biomass production, or allocation, and there were also no genotype x treatment interactions. The final leaf area index (LAI) of the spruce canopies was 19% smaller at 420 and 27% smaller at 560 than that measured at 280 mu l CO2 l(-1), but was not significantly altered by increasing N deposition. Lower LAIs at elevated CO2 largely resulted from shorter branches (less needles per individual tree) and partially from increased needle litterfall. Independently of N deposition, total aboveground N content in the spruce communities declined with increasing CO2 (-18% at 420 and -31% at 560 compared to 280 mu l CO2 l(-1)). N deposition had the opposite effect on total above ground N content (+18% at 30 and +52% at 90 compared to 0 kg N ha(-1) year(-1)). Our results suggest that under competitive conditions on natural forest soil, atmospheric CO2 enrichment may not lead to higher ecosystem biomass production, but N deposition is likely to do so. The reduction in LAI under elevated CO2 suggests allometric down-regulation of photosynthetic carbon uptake at the canopy level. The strong decline in the tree nitrogen mass per unit ground area in response to elevated CO2 may indicate CO2- induced reductions of soil N availability.

KEYWORDS: AIR-POLLUTION, ATMOSPHERIC CO2, CARBON DIOXIDE, COMPENSATORY RESPONSES, GLOBAL CHANGE, LEAF-AREA, MINERAL NUTRITION, NITROGEN DEPOSITION, NORWAY SPRUCE, TERRESTRIAL ECOSYSTEMS

864
Hattenschwiler, S., F. Miglietta, A. Raschi, and C. Korner. 1997. Morphological adjustments of mature Quercus ilex trees to elevated CO2. *Acta Oecologica-International Journal of Ecology 18(3):361-365.*

It is still not known whether mature forest trees. respond to increasing atmospheric CO2 concentrations in similar ways as seedlings do. Mature Mediterranean oaks (Quercus ilex) growing in a CO2 enriched atmosphere around natural CO2 vents since the seedling stage showed a moderate, age dependent increase in stem biomass production, but had significantly lower biomass of 6-year-old branches, decreased branching, and lower leaf area per unit branch biomass, compared to control trees at a nearby unenriched site. Our data indicate that trees in natural forest stands morphologically adjust to increasing CO2 and reduce CO2 induced initial growth stimulations. Allometric adjustments such as reduction in leaf area may be regarded as a "down- regulation" of canopy photosynthesis and may be an effective mechanism for saving water.

KEYWORDS: ENRICHMENT, GROWTH, SEEDLINGS

865

Hattenschwiler, S., F. Miglietta, A. Raschi, and C. Korner. 1997. Thirty years of in situ tree growth under elevated CO2: a model for future forest responses? *Global Change Biology 3(5):463-471.*

Rising concentrations of atmospheric carbon dioxide have been predicted to stimulate the growth of forest trees. However, long-term effects on trees growing to maturity and to canopy closure while exposed to elevated CO2 have never been examined. We compared tree ring chronologies of Mediterranean Quercus ilex which have been continuously exposed to elevated CO2 (around 650 mu mol mol(-1)) since they were seedlings, near two separate natural CO2 springs with those from trees at nearby ambient-CO2 'control' sites. Trees grown under high CO2 for 30 years (1964-93) showed a 12% greater final radial stem width than those growing at the ambient-CO2 control sites. However, this stimulation was largely due to responses when trees were young. By the time trees were 25-30 y old the annual difference in tree ring width between low and high CO2 grown trees had disappeared. At any given tree age, elevated CO2 had a relatively greater positive effect on tree ring width in years with a dry spring compared to years with more rainfall between April and May. This indicates a beneficial effect of elevated CO2 on tree water relations under drought stress. Our data suggest that the early regeneration phase of forest stands can be accelerated in CO2-enriched atmospheres and that maximum biomass per land area may be reached sooner than under lower CO2 concentrations. In our study, high CO2 grown Q. ilex trees reached the same stem basal area at the age of 26 y as control trees at 29 y,i.e. three years earlier (faster turnover of carbon?). Reliable predictions of the future development of forests need to account for the variable responses of trees over their entire lifetime. Such responses to elevated CO2 can presently only be assessed at such unique field sites.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, CHRONOLOGIES, CLIMATE, ECOSYSTEMS, PLANTS, PRODUCTIVITY, RING-WIDTH, VEGETATION

866
Hattenschwiler, S., and C. Schafellner. 1999. Opposing effects of elevated CO2 and N deposition on Lymantria monacha larvae feeding on spruce trees. *Oecologia 118(2):210-217.*

The effects of elevated atmospheric CO and increased wet N deposition on leaf quality and insect herbivory were evaluated in nine model ecosystems composed of 7-year-old spruce trees (Picea abies) and three understorey species established on natural forest soil. Each model ecosystem was grown in a simulated montane climate, and was exposed to one of three CO2 concentrations (280, 420, and 560 mu l l(-1)) and to one of three levels of N deposition (0, 30, and 90 kg ha(-1) year(-1)) for 3 years. In the 3rd year of the experiment second to third instars of the nun moth (Lymantria monacha) were allowed to feed directly on current-year needles of top canopy branches of each tree for 13 days. Specific leaf area (SLA), water content, and N concentration decreased in needles exposed to elevated CO2, whereas the concentrations of starch, condensed tannins, and total phenolics increased. Increased N deposition had no significant effect on SLA, and water content, but the concentrations of starch, condensed tannins, and total phenolics decreased, and sugar and N concentrations increased. Despite higher relative consumption rates (RCRs) larvae consumed 33% less N per unit larval biomass and per day at the two high CO2 treatments, compared to those feeding on 280 mu l l(-1)-needles, but they maintained similar N accumulation rates due to increased N utilization efficiencies (NUE). However, over the 12-day experimental period larvae gained less N overall and reached a 35% lower biomass in the two high-CO2 treatments compared to those at 280 mu l l(-1). The effects of increased N deposition on needle quality and insect performance were generally opposite to those of CO enrichment, but were lower in magnitude. We conclude that altered needle quality in response to elevated CO2 will impair the growth and development of L. monacha larvae. Increasing N deposition may mitigate these effects, which could lead to altered insect herbivore distributions depending on regional patterns of N deposition.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, DECIDUOUS TREES, FOLIAGE, FOOD PLANTS, GROWTH, INSECT HERBIVORE INTERACTIONS, NITROGEN, PERFORMANCE, RESPONSES

867
Hattenschwiler, S., F.H. Schweingruber, and C. Korner. 1996. Tree ring responses to elevated CO2 and increased N deposition in Picea abies. *Plant, Cell and Environment 19(12):1369-1378.*

Four- to seven-year-old spruce trees (Picea abies) were exposed to three CO2 concentrations (280, 420 and 560 cm(3) m(-3)) and three rates of wet N deposition (0, 30 and 90 kg ha(-1) year(- 1)) for 3 years in a simulated montane forest climate, Six trees from each of six clones were grown in competition in each of nine 100 x 70 x 36 cm model ecosystems with nutrient-poor natural forest soil, Stem discs were analysed using X-ray densitometry, The radial stem increment was not affected by [CO2] but increased with increasing rates of N deposition, Wood density was increased by [CO2], but decreased by N deposition, Woodstarch concentration increased, and wood nitrogen concentration decreased with increasing [CO2], but neither was affected by N deposition, The lignin concentration in wood was affected by neither [CO2] nor N deposition, Our results suggest that, under natural growth conditions, rising atmospheric [CO2] will not lead to enhanced radial stem growth of spruce, but atmospheric N deposition will, and in some regions is probably already doing so, Elevated [CO2], however, will lead to denser wood unless this effect is compensated by massive atmospheric N deposition, It can be speculated that greater wood density under elevated [CO2] may alter the mechanical properties of wood, and higher ratios of C/N and lignin/N in wood grown at elevated [CO2] may affect nutrient cycles of forest ecosystems.

KEYWORDS: CARBON DIOXIDE, CHRONOLOGIES, COMMUNITIES, DECOMPOSITION, FOREST, GROWTH, NORTH-AMERICA, PLANTS, RISING ATMOSPHERIC CO2, SUMMER TEMPERATURES

868
Hatton, T.J., J. Walker, W.R. Dawes, and F.X. Dunin. 1992. Simulations of hydroecological responses to elevated CO2 at the catchment scale. *Australian Journal of Botany 40(4-5):679-696.*

A spatially explicit hydroecological landscape model of water, carbon and energy balances (Topog-IRM) is described. The landscape is envisaged as a catchment forested with a single stratum comprising Eucalyptus maculata trees. The model was used to simulate the direct effects of a 2X elevation in atmospheric carbon dioxide at two levels of nitrogen on catchment water yield, soil moisture status and tree growth, Experimental results used to parameterise the model are detailed. Key features of the model are (1) an ability to scale hydrological processes at the catchment scale in three dimensions, and (2) a means to integrate multiple factors/stresses on plant growth. The effects of CO2 on catchment hydrology (water yield or soil moisture content) and forest growth (expressed as leaf area index, LAI) were modelled for a 2-year period, and contrasted with the effects of added nitrogen. Results were expressed as totals for the catchment or spatially distributed across the catchment. For the total catchment, water yield increased in the order: high CO2 with low N, high CO2 with high N, ambient CO2 with low N, ambient CO2 with high N. LAI increased from 3.3 to 5.7 in the order: ambient CO2 with low N, ambient CO2 with high N, high CO2 with low N, high CO2 with high N. These results agree with previous data. New findings are: (1) with elevated CO2 a new equilibrium in transpiration is established in which leaf area increases offset decreases in stomatal

conductance; (2) the addition of nitrogen increases transpiration without any indication of a new equilibrium being reached during the simulated period; (3) the spatial distribution of soil moisture changes, presenting a new resource base for spatial changes to species composition and growth rates. The major hydroecological responses to elevated CO2 are seen as increased maximum upper canopy leaf area, increased litter inputs, especially at times of drought (hence changed fire regimes), changes in the composition of the understorey (hence litter composition, soil microfauna, and the spatial expression of biological diversity) and a slight increase in water yield.

KEYWORDS: ASSIMILATION, CARBON BALANCE, CLIMATE CHANGE, FOREST ECOSYSTEM PROCESSES, GENERAL-MODEL, LEAF CONDUCTANCE, PARTIAL-PRESSURE, PHOTOSYNTHESIS, REGIONAL APPLICATIONS, TRANSPIRATION

869

Hausler, R.E., P.J. Lea, and R.C. Leegood. 1994. Control of photosynthesis in barley leaves with reduced activities of glutamine-synthetase or glutamate synthase .2. Control of electron-transport and co2 assimilation. *Planta 194(3):418-435.*

Heterozygous plants of barley (Hordeum vulgare L. cv. Maris Mink) with activities of chloroplastic glutamine synthetase (GS) between 47% and 97% of the wild-type and ferredoxin- dependent glutamate synthase (Fd-GOGAT) activities down to 63% of the wild-type have been used to study the control of photosynthetic fluxes. Rates of CO2 assimilation measured over a range of intercellular CO2 concentrations and photon flux densities (PFDs) were little different in the wild-type and a mutant with 47% GS, although total activities of ribulose-1, 5- bisphosphate carboxylase/oxygenase (Rubisco) decreased by about 20% with a decrease in GS to 50% of the wild-type. The quantum efficiencies of photosystem II electron transport (Phi PSII) and CO2 assimilation (Phi CO2) were determined. Phi PSII was lower than expected in mutants with 50% less GS under conditions which enhance the photorespiratory flux, but were identical to the wildtype under non-photorespiratory conditions, suggesting that at high rates of photorespiration the electron requirement for net CO2 assimilation declines in plants with decreased GS. This discrepancy in the electron requirement between the wild-type and the 47% GS mutant was enhanced at high temperatures and low CO2, conditions which favour oxygenation by Rubisco. Photochemical and non- photochemical chlorophyll a fluorescence quenching as well as the quantum efficiency of excitation-energy capture by open photosystem II reaction centres were differentially affected in mutants with less GS relative to the wild-type when CO2 was lowered or the PFD was varied. The quantum efficiencies of electron transport in photosystems I and II were closely correlated under a range of PFDs and CO2 concentrations, confirming that the rate of linear electron transport was much lower in plants with less GS. It is shown that GS exerts considerable control (flux control coefficients between 0.5 and 1.0) on the electron requirement for CO2 assimilation at high fluxes of photorespiration relative to CO2 assimilation. Apart from the control of GS on protein and Rubisco contents, GS in the wild-type has also some direct positive control on CO2 assimilation. However, negative control on CO2 assimilation was found in mutants with 50% less GS. These data, taken with the data on electron requirements for CO2 assimilation, suggest that CO2-fixing processes other than that catalysed by Rubisco, such as carboxylation of phosphoenolpyruvate, or an inhibition of photorespiration (e.g. glycine decarboxylation), may contribute to the observed CO2 exchange and photosystem II electron transport in plants with less GS. In the 63%-Fd-GOGAT mutant, rates of CO2 assimilation were appreciably lower than in the wild-type under a range of PFDs and CO2 concentrations, which largely reflected lower contents of Rubisco in the Fd- GOGAT mutants. Assimilation of CO2 was inhibited appreciably at high CO2 concentrations. There was little difference in the electron requirement for CO2 assimilation between the wild-type and mutants with less Fd-GOGAT, although there were indications that a triose-phosphate/glycerate-3-phosphate shuttle or cyclic electron transport operates to balance ATP generation and NADP reduction. The latter was supported by a curvilinear relationship of photosystem I and II electron transport in the 63% Fd-GOGAT mutant. A positive control is exerted by Fd-GOGAT on the amounts of protein and Rubisco and on CO2 assimilation.

KEYWORDS: CHLOROPHYLL FLUORESCENCE, GAS-EXCHANGE, LIGHT, PHOTOSYSTEM, QUANTUM YIELDS, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, SERINE, SPECIFICITY, SPINACH-CHLOROPLASTS, TOBACCO-LEAVES

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Havstrom, M., T.V. Callaghan, and S. Jonasson. 1993. Differential growth-responses of cassiope-tetragona, an arctic dwarf-shrub, to environmental perturbations among 3 contrasting high sites and sub-arctic sites. *Oikos 66(3):389-402.*

Three populations of Cassiope tetragona (Ericaceae) were subjected to in situ environmental perturbations simulating predictions of global warming. The populations were selected to represent different parts of the range of the species, one growing in a high arctic coastal heath at Ny-Alesund (Svalbard, northern part of the species' range), one at a subarctic fellfield at 1150 m a.s.l. at Abisko, Swedish Lapland, and one in a subarctic tree-line heath at 450 m a.s.l. at Abisko, southern part of the species' range. The manipulations included nutrient addition, shading and two levels of temperature enhancement using passive greenhouses. The micrometeorological effects of the shading treatment was similar to that of a mountain birch canopy and the temperature enhancement treatments had the desired effect to increase the average air temperature by 2-4-degrees-C. Greenhouses which had a gap between the soil and the greenhouse plastic were particularly successful in creating the desired climatic perturbation without causing extreme maximum temperatures or other unwanted side-effects. The environmental manipulations caused strikingly different responses in the vegetative growth pattern of main shoots of C. tetragona among the three populations: at the subarctic tree-line heath, nutrient addition caused a substantial increase in growth, whereas it was the temperature enhancement treatments that caused increases, although smaller, at the subarctic fellfield and the high arctic heath sites. At the high arctic site, we also found growth reduced in response to shading, but at the subarctic sites, and particularly at the tree-line heath site, shading caused a marked etiolation of the shoots. Hence, different factors seem to produce very different responses in the vegetative growth of C. tetragona in different parts of its geographical range. We conclude that competition for nutrients and light are the main limiting factors for the growth of Cassiope tetragona near the lower distributional limit (LODIL) of the species, but that temperature is the main limiting factor in the northern parts of its range, and at high altitudes in the southern parts of its range. We also suggest that the direct effect of predicted future climatic warming on the growth of Cassiope tetragona will increase towards the north, whereas a possible indirect effect of increasing nutrient availability following a temperature increase will be the main effect in the southern and lower parts of its range. These responses could, however, be modified by shading from other species responding to environmental change by increased growth.

KEYWORDS: CLIMATIC CHANGE, ELEVATED CO2 CONCENTRATIONS, GREENHOUSE, PLANT- COMMUNITIES, TUSSOCK TUNDRA

871

Haxeltine, A., and I.C. Prentice. 1996. A general model for the light-use efficiency of primary production. *Functional Ecology 10(5):551-561.*

1. Net primary production (NPP) by terrestrial ecosystems appears to be proportional to absorbed photosynthetically active radiation (APAR) on a seasonal and annual basis. This observation has been used in 'diagnostic' models that estimate NPP from remotely sensed vegetation indices. In 'prognostic' process-based models carbon fluxes are more commonly integrated with respect to leaf area index assuming invariant leaf photosynthetic parameters. This approach does not lead to a proportional relationship between NPP and APAR. However, leaf nitrogen content and Rubisco activity are known to vary seasonally and with canopy position, and there is evidence that this variation takes place in such a way as to nearly optimize total canopy net photosynthesis. 2. Using standard formulations for the instantaneous response of leaf net photosynthesis to APAR, we show that the optimized canopy net photosynthesis is proportional to APAR. This theory leads to reasonable values for the maximum (unstressed) light-use efficiency of gross and net primary production of C-3 plants at current ambient CO2, comparable with empirical estimates for agricultural crops and forest plantations. 3. By relating the standard formulations to the Collatz-Farquhar model of photosynthesis, we show that a range of observed physiological responses to temperature and CO2 can be understood as consequences of the optimization. These responses include the CO2 fertilization response and stomatal closure in C-3 plants, the increase of leaf N concentration with decreasing growing season temperature, and the downward acclimation of leaf respiration and N content with increasing ambient CO2. The theory provides a way to integrate diverse experimental observations into a general framework for modelling terrestrial primary production.

KEYWORDS: ATMOSPHERIC CO2, CARBON GAIN, CLIMATE CHANGE, CO2 CONCENTRATIONS, DAILY CANOPY PHOTOSYNTHESIS, ELEVATED CO2, LEAF NITROGEN DISTRIBUTION, PLANTS, SOLAR RADIATION, STOMATAL CONDUCTANCE

872

Hdider, C., L.P. Vezina, and Y. Desjardins. 1994. Short-term studies of (no3-)-n-15 and (nh4+)-n-15 uptake by micropropagated strawberry shoots cultured with or without co2 enrichment. *Plant Cell Tissue and Organ Culture 37(2):185-191.*

The uptake of (NO3-)-N-15 and (NH4+)-N-15 has been examined in 5-,10- and 28-day-old micropropagated strawberry (Fragaria x ananassa Duch. cv. Kent) shoots rooted in one-half strength Murashige and Skoog (MS) liquid medium on cellulose plugs (Sorbarods). The results indicated that the plantlets absorbed both NO3- and NH4+ during the culture with a greater uptake of NH4+ at 5 days of culture. Furthermore, a pronounced reduction in NO3- and NH4+ uptake at 10 and 28 days of culture Ras observed within 6 h of the short-term uptake study. This reduction could be explained by the low CO2 concentration in test tubes during the photoperiod, since no reduction in nitrogen uptake occurred in the CO2 enriched condition. The results are interpreted as an indication of the important role for photosynthetic CO2 fixation in the process of nitrogen uptake by the plantlets during the rooting stage.

KEYWORDS: GROWTH, INVITRO, NITROGEN, PLANTLETS

873

He, P., K.P. Bader, A. Radunz, U. Kahmann, G.H. Ruppel, and G.H. Schmid. 1998. Gas exchange characteristics in leaves of the Euphorbiacea Aleurites montana as consequence of growth under 700 ppm CO2 in air - A study on photosynthesis and photorespiration in the Chinese tung-oil tree. *Zeitschrift Fur Naturforschung C-A Journal of Biosciences 53(3-4):151-158.*

Three months old plants of the Chinese tung-oil tree Aleurites montana (Euphorbiaceae) were cultivated for 4 months in air containing 700 ppm CO2. These plants, which grow substantially better in the CO2-enriched atmosphere, were analyzed by mass spectrometry for photosynthesis and photorespiration together with control plants grown all the lime in normal (350 ppm CO2) air. Thereafter part of the plants was subjected for two weeks to 0.3 ppm SO2 in the atmosphere and again analyzed for photosynthesis and photorespiration. Aleurites montana exhibits a strongly CO2-dependent photosynthesis which partially explains the observed stimulatory effect of 700 ppm CO2 on growth of the plant. In control plants grown in normal air, photorespiration measured simultaneously with photosynthesis via the uptake of O-18(2) in the light, is much lower than in C-3-plants like tobacco (He et at, 1995, Z. Naturforsch. 50c, 781-788). In Aleurites grown in 700 ppm CO2, however, photorespiration is completely absent in contrast to tobacco when grown under 700 ppm CO2. In tobacco, photorespiration is not inhibited to the extent of the in vitro experiments in which plants grown at 350 ppm CO2 are measured under the increased CO2 content of 700 ppm. Gas exchange measurements carried out by mass spectrometry show that the ratio of O-2 evolved to CO2 fixed is about 0.5. Apparently, part of the CO2 fixed is channelled into a metabolic path without concomitant O-2-evolution. Although the plant has no succulent appearance (its leaves somehow resemble maple leaves) apparently a Crassulacean type metabolism is performed. When Aleurites plants grown all the time in normal air with 350 ppm, are exposed for two weeks to 0.3 ppm SO2 the treatment completely inhibits this CO2-fixing portion which is tentatively attributed to a Crassulacean type of metabolism. This is demonstrated by a normal C-3-type ratio O-2 evolved/CO2 fixed of 1. When Aleurites plants, grown for 4 months in a CO2- enriched atmosphere of 700 ppm CO2, are subjected for two weeks to 0.3 ppm SO2, the features of control plants show up again. When these plants are tested under 350 ppm CO2 the Crassulacean type CO2-fixation apparently is not inhibited by SO2. Photorespiration, although low is present in the same activity as in the controls. Seemingly, an increased level of CO2 in air tends to alleviate the impact of the SO2 at least in the Chinese lung-oil tree.

KEYWORDS: LIGHT, RATES, TOBACCO MUTANTS

874

He, P., K.P. Bader, A. Radunz, and G.H. Schmid. 1995. Consequences of high CO2-concentrations in air on growth and gas-exchange rates in tobacco mutants. *Zeitschrift Fur Naturforschung C-A Journal of Biosciences 50(11-12):781-788.*

Wild type tobacco N. tabacum var. John William's Broadleaf and the tobacco aurea mutant Su/su were permanently grown under 700 ppm CO2 in air. In comparison to plants grown under 350 ppm CO2 in air but under otherwise identical conditions growth was substantially enhanced. Gas exchange measurements carried out by mass spectrometry show that the rate of photosynthesis in the wild type and in the mutant is increased by more than 100%. The photorespiratory rate in the wild type measured;as O-18(2)- uptake in the light in the "700 ppm CO2-plants" is not reduced to the extent expected or deduced from experiments in which the 350 ppm system responds under in vitro conditions to 700 ppm CO2. An analysis of the induction kinetics of room temperature fluorescence kinetics of the adapted (700 ppm CO2) system and the control system (350 ppm CO2) under various CO2-partial pressures shows that permanent growth under the elevated CO2-partial pressure leads to a structural modification of the photosynthetic apparatus.

KEYWORDS: AUREA MUTANT, LIGHT, PARAMETERS, PHOTOSYNTHESIS, RESPIRATION

875

He, P., A. Radunz, K.P. Bader, and G.H. Schmid. 1996. Influence of CO2 and SO2 on growth and structure of photosystem II of the Chinese

tung-oil tree Aleurites montana. *Zeitschrift Fur Naturforschung C-A Journal of Biosciences 51(7-8):441-453.*

Three months old plants of the Chinese tung-oil tree Alenrites montana were cultivated for 4 months in air containing an increased amount of 700 ppm CO2. During the exposure to 700 ppm CO2 the plants exhibited a considerably stronger growth (30- 40%) in comparison to the control plants (grown in normal air). In these CO2-plants during the entire analyzing period the amount of soluble proteins, of soluble sugars and the chlorophyll content were lower than in control plants. The protein content, referred to leaf area, increased during this time in both plant types by approx. 50% but with a different time course. The increase is faster in CO2-plants compared to control plants, and ends up with similar values in both plants after 4 months. No difference is seen between sun and shade leaves. The chlorophyll content in both sun and shade leaves is 20% lower in CO2-plants. Whereas the chlorophyll content in sun leaves stays constant during development, it has increased in shade leaves by 20% at the end of the 4 months period. The content of soluble sugars is lower in CO2-plants compared to control plants. The difference is bigger in sun leaves than in shade leaves. The ribulose 1.5-bisphosphate carboxylase/oxygenase content almost doubles within the experimentation period, but seems to be subject to large variations. CO2-plants contain in general less ribulose 1.5- bisphosphate carboxylase/oxygenase than control plants. The content of coupling factor of photophosphorylation is 20% lower in CO2-plants when compared to control plants and remains during development more constant in CO2-plants. The molecular structure of the photosystem II-complex undergoes under the influence of the increased CO2-content a quantitative modification. The light harvesting complex (LHCP) and the extrinsic peptide with the molecular mass of 33 kDa increase in CO2-plants. Gassing with SO2 (0.3 ppm in air) leads to a strong damage of the plants. The damaging influence is already seen after 6 days and leads to a partial leaf-shedding of the tree. In the visually still intact remaining leaves the chlorophyll content referred to unit leaf area decreases by 63%, that of soluble sugars by 65%, the content of soluble proteins and that of Rubisco decrease by 26% and 36% respectively. The light harvesting complex and the chlorophyll-binding peptides (43 and 47 kDa) increase whereas the extrinsic peptides decrease. It looks as if the simultaneous application of SO2 (0.3 ppm) and increased CO2 (700 ppm) releaves the damaging effect of SO2. Plant growth does not exhibit a difference in comparison to control plants. Soluble proteins and chlorophyll increase by 27% and 33% and the ribulose 1.5-bisphosphate carboxylase/oxygenase content as well as that of soluble sugars increases by 18 respectively 14%. The peptide composition of photosystem II shows a quantitative modification. The LHCP increases and the chlorophyll-binding peptides and the peptides with a molecular mass smaller than 24 kDa are reduced. The quantity of extrinsic peptides appears unchanged. Ribulose 1,5- bisphosphate carboxylase/oxygenase and the CF1-complex of Aleurites are immunochemically only partially identical to the corresponding enzymes of Nicotiana tabacum as demonstrated by tandem-cross-immune electrophoresis.

KEYWORDS: ACCLIMATION, ELEVATED CO2, LEAVES, NICOTIANA-TABACUM, ORGANIZATION, PHOTOSYNTHETIC APPARATUS, RUBISCO, SHADE PLANTS, SUN, THYLAKOID MEMBRANES

876

He, X.Q., Y.H. Lin, J.X. Lin, and Y.X. Hu. 1998. Relationship between stomatal density and the changes of atmospheric CO2 concentrations. *Chinese Science Bulletin 43(11):928-930.*

The relationship between the stomatal density of five woody plants endemic to China, i.e. Eucommia ulmoides, Quercus liaotungensis, Q. glandulifera var. brevipetiolata, Cyclocarya paliurus and Ficus heteromorpha, and the atmospheric CO2 concentrations was studied by observations on leaves of the herbarium-stored specimens(1920s-1990s). The results showed that the stomatal density in Eucommia ulmoides, Quercus liaotungensis and Q. glandulifera var. brevipetiolata decreased significantly in response to the elevated atmospheric CO2 concentrations, while in Cyclocarya paliurus it decreased slightly and in Ficus heteromorpha there were no responses.

KEYWORDS: INCREASE, NUMBERS

877

He, Y., X.S. Yang, D.R. Miller, G.R. Hendrey, K.F. Lewin, and J. Nagy. 1996. Effects of face system operation on the micrometeorology of a loblolly pine stand. *Transactions of the Asae 39(4):1551-1556.*

The effects of the gas injection operation on air movement in the loblolly pine stand at the Duke Forest prototype BNL-FACE User Facility were investigated The micrometeorological conditions were measured using three-dimensional sonic anemometers in the center of the FACE ring at two heights, one just above the canopy (median height of the canopy = 9 m) at 11.6 m and another at 6.8 m above the ground where the canopy war the most dense. While the micrometeorological parameters were sampled continuously at 10 Hz, the gas injection system was turned alternatively on and off every 5 min for about 100 h. The analyses indicated that the system operation had little effect on the micrometeorology processes above the canopy. There were small magnitude but detectable changes in some of the micrometeorological parameters within the canopy, primarily during stable atmospheric conditions, in response to this 5-min alternation. The gas injection operation created a slightly diverging windfield in the top half of the canopy in the enclosed stand A slight dampening of the vertical wind and air temperature fluctuations was detected No detectable effects on the mean, or accumulated, heat and momentum fluxes at the measurement locations were found. in general, the system was shown to cause minimal disturbances to the natural environment compared to traditional carbon dioxide (CO2) enrichment facilities and it provides a better alternative for long-term ecological studies.

KEYWORDS: CO2- ENRICHMENT

878

He, Z.L., S. von Caemmerer, G.S. Hudson, G.D. Price, M.R. Badger, and T.J. Andrews. 1997. Ribulose-1,5-bisphosphate carboxylase/oxygenase activase deficiency delays senescence of ribulose-1,5-bisphosphate carboxylase/oxygenase but progressively impairs its catalysis during tobacco leaf development. *Plant Physiology 115(4):1569-1580.*

Transgenic tobacco (Nicotiana tabacum L. cv W38) plants with an antisense gene directed against the mRNA of ribulose-1,5- biphosphate carboxylase/oxygenase (Rubisco) activase grew more slowly than wild-type plants in a CO2-enriched atmosphere, but eventually attained the same height and number of leaves. Compared with the wild type, the anti-activase plants had reduced CO2 assimilation rates, normal contents of chlorophyll and soluble leaf protein, and much higher Rubisco contents, particularly in older leaves. Activase deficiency greatly delayed the usual developmental decline in Rubisco content seen in wild-type leaves. This effect was much less obvious in another transgenic tobacco with an antisense gene directed against chloroplast-located glyceraldehyde-3-phosphate dehydrogenase, which also had reduced photosynthetic rates and delayed development. Although Rubisco carbamylation was reduced in the anti-activase plants, the reduction was not sufficient to explain the reduced photosynthetic rate of older anti-activase leaves. Instead, up to a 10-fold reduction in the catalytic turnover rate of carbamylated Rubisco in vivo appeared to be the main cause. Slower catalytic turnover by carbamylated Rubisco was particularly obvious in high-CO2-grown leaves but was also detectable in air-grown leaves. Rubisco activity measured immediately after rapid

extraction of anti- activase leaves was not much less than that predicted from its degree of carbamylation, ruling out slow release of an inhibitor from carbamylated sites as a major cause of the phenomenon. Nor could substrate scarcity or product inhibition account for the impairment. We conclude that activase must have a role in vivo, direct or indirect, in promoting the activity of carbamylated Rubisco in addition to its role in promoting carbamylation.

KEYWORDS: 1,5-BISPHOSPHATE CARBOXYLASE, CARBAMYLATION, GAS-EXCHANGE, GENE-EXPRESSION, INHIBITION, LEAVES, OXYGENASE, PHOTOSYNTHESIS, RIBULOSE BISPHOSPHATE CARBOXYLASE, RUBISCO ACTIVASE

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Heagle, A.S., F.L. Booker, J.E. Miller, W.A. Pursley, and L.A. Stefanski. 1999. Influence of daily carbon dioxide exposure duration and root environment on soybean response to elevated carbon dioxide. *Journal of Environmental Quality 28(2):666-675.*

Little is known about effects of daily CO2 enrichment duration and root environment on plant response to elevated CO2. Two experiments were performed,vith Essex soybean (Glycine max L, Merr,) in open-top field chambers to address these questions. In one experiment, effects of 12 and 24 h d(-1) exposures to double-ambient CO2 were compared for plants grown in 14 L pots that were either insulated to moderate soil temperature or not insulated. Although never significant statistically, trends at some growth stages suggested that nighttime CO2 enrichment contributed to growth and yield. Plants grew and yielded more in insulated than noninsulated pots, but there were no significant CO2 enrichment X insulation interactions. In the second experiment, response to approximately 1.3, 1.6, and 1.9 times ambient CO2 was compared for plants grown in the ground or 14 L pots. Enhancement of photosynthesis, growth, and yield by CO2 enrichment was similar in pots and in the ground. Linear responses to different CO2 concentrations were significant for all yield components in both root environments, whereas quadratic responses were significant for plants in pots but not for plants in the ground. Tests of proportionality of response for yield components shelved no evidence of significant differences between plants in pots and in the ground except weight per 100 seeds. Seed yield enhancement at 1.9 times ambient CO2 was 36% for plants in pots and 33% for plants in the ground. Overall, proportional response of soybean to CO2 enrichment was relatively uniform in spite of large differences in baseline growth and yield.

KEYWORDS: ATMOSPHERIC CO2 ENRICHMENT, CHAMBERS, ENHANCEMENT, FIELD, GROWTH, OZONE, PHOTOSYNTHETIC ACCLIMATION, PLANT-RESPONSES, YIELD RESPONSE

880

Heagle, A.S., R.L. Brandenburg, J.C. Burns, and J.E. Miller. 1994. Ozone and carbon-dioxide effects on spider-mites in white clover and peanut. *Journal of Environmental Quality 23(6):1168-1176.*

Effects of O-3 and/or elevated CO2 on two-spotted spider mites (Tetranychus urticae Koch) grown on an On-sensitive and an O-3-resistant clone of white clover (Trifolium repens L.) were measured in greenhouse and field experiments. Peanut (Arachis hypogeae L.) 'NC-9' was used in one greenhouse study with O-3. In field studies, O-3 treatments were charcoal filtered air (CF), nonfiltered air (NF), and two NF treatments with On added for 12 h d(-1) at proportions of approximate to 1.25 and 1.50 times the ambient O-3 concentration. In greenhouse studies, constant amounts of O-3 were added to CF for 6 h d(-1) to achieve mean concentrations ranging from 5 to 100 nL L(-1). For the greenhouse O-3 X CO2 experiment, CO2 concentrations were ambient and approximately twice-ambient for 24 h d(-1). Plants were exposed to O-3 and/or CO2 for approximate to 7 d before infestation with mites; daily exposures continued for 14 to 28 d to allow reproduction for at least two generations. Leaves were sampled to count eggs, larvae, nymphs, and adults. Ozone caused more chlorosis and necrosis on the O-3-sensitive clover clone (NC-S) than on the Oa-resistant clone (NC-R). Carbon dioxide enrichment increased shoot growth of both clones by approximate to 33%. Statistical analyses indicated significant O-3 effects in some experiments and nonsignificant O-3 effects in others. A trend toward increased mite populations with increased O-3 occurred, however, on NC-S in all trials. No consistent trends occurred with NC-R. With peanut, a significant linear increase in mite population occurred with increased O-3. Carbon dioxide enrichment increased the rate of population increase on both clover clones, but more so on NC-R. At 22 to 28 d after infestation, the total population in the twice-ambient CO2 treatment was 65% greater than in the ambient treatment for NC-R and 22% greater than in the ambient treatment for NC-S. There were no statistically significant interactive effects between CO2 and O-3 On mite population growth. The apparent clone effects on mite population response to O-3 and CO2 strongly suggest that responses were mediated through the host plants.

KEYWORDS: ALTERED FEEDING PREFERENCE, AMBIENT AIR-POLLUTION, APHID INFESTATION, BEETLE EPILACHNA-VARIVESTIS, GROWTH, HERBIVORE INTERACTIONS, HOST PLANTS, INSECT HERBIVORE, RESPONSES, TOP FIELD CHAMBERS

881

Heagle, A.S., J.E. Miller, and F.L. Booker. 1998. Influence of ozone stress on soybean response to carbon dioxide enrichment: I. Foliar properties. *Crop Science 38(1):113-121.*

Tropospheric O-3 can cause foliar injury, decreased growth, and decreased yield, whereas CO2 enrichment generally causes opposite effects. Little is known about plant response to mixtures of O-3 and CO2. Open-top field chambers were ere used to determine if foliar responses of soybean [Glycine max (L.) Merr.] to CO2 enrichment are affected by O-3 stress and vice versa. Plants were grown in 14-L pots and exposed to four CO2 and three O-3 concentrations in 12 combinations. The CO2 treatments were ambient (366 mu L L-1) and three treatments with CO2 added for 24 h d(-1) at approximately 1.3, 1.6, and 2.0 times ambient. The O-3 treatments were charcoal-filtered air (CF), nonfiltered air (NF), and NF with O-3 added for 12 h d(-1) (NF+), resulting in seasonal concentrations of approximately 20, 46, and 75 nL L-1. Foliar effects of CO2 enrichment were dependent on the amount of stress caused by O-3 In the CF treatment, plants were not stressed by O-3, and CO2 enrichment caused chlorosis and decreased chlorophyll. In the IVF and NF+ treatments, plants were stressed by O-3, and CO2 enrichment suppressed chlorosis and increased chlorophyll. Ozone decreased specific leaf weight, increased foliar N and C, and decreased C/N ratios, whereas CO2 caused opposite responses for these measures. Ozone increased foliar S and B but did not affect P or K concentrations. Conversely, CO2 enrichment suppressed foliar S, B, P, and K concentrations. These interactions between O-3 and CO2 emphasize a need to consider the amount of plant stress caused by O-3 in studies to measure effects of CO2 enrichment.

KEYWORDS: AGRICULTURAL CROPS, ASSESSING IMPACTS, ATMOSPHERIC CO2 ENRICHMENT, CHLOROPHYLL CONTENT, ELEVATED CO2, EXCHANGE-RATE, GAS-EXCHANGE, GROWTH, NITROGEN NUTRITION, PLANT-RESPONSES

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Heagle, A.S., J.E. Miller, F.L. Booker, and W.A. Pursley. 1999. Ozone stress, carbon dioxide enrichment, and nitrogen fertility interactions in cotton. *Crop Science 39(3):731-741.*

Ozone (O-3) in the troposphere can cause plant stress leading to foliar injury and suppressed growth and yield, whereas elevated CO2 generally enhances growth and yield. Numerous studies have been performed to determine effects of O-3 and CO2 separately, but relatively few have been performed to determine if O-3 can affect plant response to CO2 or vice versa. Open-top field chambers were used to determine if such interactions occur for cotton (Gossypium hirsutum L.), which is relatively sensitive to O-3. Nitrogen nutrition is especially important in cotton production so N nutrition was included as an experimental factor. Plants were grown in 14-L pots at low, medium, and high soil N levels and exposed to three CO2 and two or three O-3 treatments in all combinations during two seasons. The CO2 treatments were ambient (370 mu L L-1) and two treatments with CO2 added for 24 h d(-1) at approximately 1.5 and 2.0 Limes ambient. In 1995, the O-3 treatments were charcoal filtered air (CP), and nonfiltered air (NF) with O-3 added for 12 h d(-1) (NF+). In 1996, a NF treatment was also included to represent ambient O-3 conditions. The CF, NF, and NF+ treatments resulted in seasonal O-3 concentrations of approximately 23, 51, and 75 nL L-1. Carbon dioxide enrichment generally stimulated growth and yield whereas O-3 exposure suppressed growth. and yield. Stimulation induced by CO2 increased as O-3 stress increased. For example, in 1995 at medium N, the percentage increase in yield caused by doubling CO2 in CF air was 0%, but was 52% in NF+ air. Comparable values for 1996 were 23% in CF air and 140% in NF+ air. These interactions occurred for a range of soil N levels, and were probably caused by CO2-induced prevention of O-3 stress. The results emphasize the need to consider O-3 x CO2 interactions to ensure correct interpretation of cause-effect relationships in CO2 enrichment studies with crops that are sensitive to O-3.

KEYWORDS: ATMOSPHERIC CO2, CHAMBERS, ELEVATED CO2, FACE, GROWTH, INJURY, PLANT-RESPONSES, SOIL MOISTURE, SOYBEAN RESPONSE, YIELD RESPONSE

883

Heagle, A.S., J.E. Miller, and W.A. Pursley. 1998. Influence of ozone stress on soybean response to carbon dioxide enrichment: III. Yield and seed quality. *Crop Science 38(1):128-134.*

Ozone in the troposphere can cause plant stress, whereas elevated CO2 generally causes positive responses. Little is known of how these gases interact to affect plant response. Interactive effects on yield and seed quality of soybean [Glycine max (L.) Merr.] grown in 14-L pots were measured in open-top field chambers. Essex was tested in 1993, and Essex, Holladay, and NK 6955 were tested in 1994. Plants were exposed from emergence to maturity to four CO2 levels (ambient and 1.3, 1.6, and 2.0 times ambient) and three O-3 levels (0.4, 0.9, and 1.5 times ambient) in 12 combinations. Increasing O-3 suppressed growth and yield, whereas CO2 enrichment stimulated growth and yield. Carbon dioxide-induced stimulation was greater for plants stressed by O-3 than for non stressed plants. For example, CO2 at 2.0 times ambient increased 2-yr mean seed yield of Essex by 16, 24, and 81% at O-3 levels of O.4, 0.9, and 1.5 times ambient, respectively. Effects of O-3 and CO2 on seed oil content were variable with numerous cultivar differences. Seed protein content was never affected. Elevated O-3 suppressed oleic acid content in seeds, whereas CO2 increased it; the nature of the O-3 x CO2 interaction for oleic acid was similar to that observed for most yield measures. Carbon dioxide-induced stimulation of plants stressed by O-3 was apparently caused partly by amelioration of O-3 stress. Interactions between O-3 and CO2 must be considered for proper interpretation of cause-effect relationships in CO2 enrichment studies.

KEYWORDS: CHAMBERS, CO2, FIELD, GROWTH, O-3

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Heagle, A.S., J.E. Miller, D.E. Sherrill, and J.O. Rawlings. 1993. Effects of ozone and carbon-dioxide mixtures on 2 clones of white clover. *New Phytologist 123(4):751-762.*

The effects of mixtures of ozone and carbon dioxide on growth and physiology of an O3-sensitive (NC-S) and an O3-resistant (NC-R) clone of white clover (Trifolium repens L.) were determined. The experiment was performed in a greenhouse with O3 treatments of 5 and 82 nl l-1 (ppb) for 6 h d-1 and CO2 treatments of 380 (ambient), 490,600, and 710 mul l-1 (ppm) for 24 h d-1. Enrichment with CO2 decreased foliar gas exchange (measured as stomatal resistance) of NC-R more than that of NC- S whereas O3 decreased gas exchange of NC-S more than that of NC-R. Ozone caused extensive foliar injury of NC-S but caused only slight injury of NC-R. CO2 enrichment suppressed O3- induced foliar injury of NC-S as measured after 4 wk of exposure, but this effect diminished after 8 wk of exposure. CO2 enrichment decreased the relative chlorophyll content (mug of chlorophyll mg-1 of leaf tissue sampled) but not the total chlorophyll (total chlorophyll in the leaves sampled). There were no O3 x CO2 interactions for foliar chlorophyll. High concentrations of CO2 caused reddening of new leaves near the end of the 8 wk exposure period. CO2 enrichment decreased foliar concentrations of N, P, K, S, Cu, B, and Fe, increased foliar concentrations of Mn, but did not affect Zn, Ca, or Mg. Ozone exposure did not modify the CO2 effects on foliar nutrient concentration. Ozone decreased growth of NC-S but not NC-R while CO2 enrichment stimulated growth of both clones. The highest CO2 concentration appeared to decrease the effects of O3 on growth of NC-S. However, except for a transitory effect on foliar injury, there was no evidence that CO2, at concentrations less than the highest used in this study, will protect white clover from the effects of tropospheric O3.

KEYWORDS: AGRICULTURAL CROPS, ASSESSING IMPACTS, ATMOSPHERIC CO2 ENRICHMENT, ELEVATED CO2, GROWTH, LADINO CLOVER, LOLIUM-PERENNE L, MANAGED MODEL-ECOSYSTEMS, TALL FESCUE PASTURE, WATER-USE

885

Heath, J. 1998. Stomata of trees growing in CO2-enriched air show reduced sensitivity to vapour pressure deficit and drought. *Plant, Cell and Environment 21(11):1077-1088.*

Stomatal conductance (g(s)) and photosynthetic rate (A) mere measured in young beech (Fagus sylvatica), chestnut (Castanea sativa) and oak (Quercus robur) growing in ambient or CO2- enriched air. In oak, g(s) was consistently reduced in elevated CO2, However, in beech and chestnut, the stomata of trees growing in elevated CO2 failed to close normally in response to increased leaf-to-air vapour pressure deficit (LAVPD). Consequently, while g(s) was reduced in elevated CO2 on days with low LAVPD, on warm sunny days (with correspondingly high LAVPD) g(s) was unchanged or even slightly higher in elevated CO2. Furthermore, during drought, g(s) of beech and chestnut was unresponsive to [CO2], over a wide range of ambient LAVPD, whereas in oak g(s) was reduced by an average of 50% in elevated CO2. Stimulation of A by elevated CO2 in beech and chestnut was restricted to days with high irradiance, and was greatest in beech during drought. Hence, most of the additional carbon gain in elevated CO2 was made at the expense of water economy, at precisely those times (drought, high evaporative demand) when mater conservation was most important. Such effects could have serious consequences for drought tolerance, growth and, ultimately, survival as atmospheric [CO2] increases.

KEYWORDS: ABSCISIC- ACID, ATMOSPHERIC CO2, ELEVATED CARBON-DIOXIDE, FAGUS-SYLVATICA, GUARD-CELL, HYDRAULIC CONDUCTANCE, LEAF GAS- EXCHANGE, RESPONSES, SIGNAL-TRANSDUCTION, WATER-LOSS REGULATION

886

Heath, J., and G. Kerstiens. 1997. Effects of elevated CO2 on leaf gas exchange in beech and oak at two levels of nutrient supply: Consequences for sensitivity to drought in beech. *Plant, Cell and Environment 20(1):57-67.*

Beech (Fagus sylvatica L.) and pedunculate oak (Quercus robur L,) were grown from seed for two whole seasons at two CO, concentrations (ambient and ambient + 250 mu mol mol(-1)) with two levels of soil nutrient supply, Measurements of net leaf photosynthetic rate (A) and stomatal conductance (g(s)) of well-watered plants were taken over both seasons; a drought treatment was applied in the middle of the second growing season to a separate sample of beech drawn from the same population, The net leaf photosynthetic rate of well-watered plants was stimulated in elevated CO2 by an average of 75% in beech and 33% in oak; the effect continued through both growing seasons at both nutrient levels, There were no interactive effects of CO2 concentration and nutrient level on A or g(s) in beech or oak, Stomatal conductance was reduced in elevated CO2 by an average of 34% in oak, but in beech there were no significant reductions in g(s) except under cloudy conditions (-22% in elevated CO2), During drought, there was no effect of CO2 concentration on g(s) in beech grown with high nutrients, but for beech grown with low nutrients, g(s) was significantly higher in elevated CO2, causing more rapid soil drying, With high nutrient supply, soil drying was more rapid at elevated CO2 due to increased leaf area, It appears that beech may substantially increase whole-plant water consumption in elevated CO2, especially under conditions of high temperature and irradiance when damage due to high evaporative demand is most likely to occur, thereby putting itself at risk during periods of drought.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, FAGUS-SYLVATICA L, FOREST, GROWTH, PHOTOSYNTHESIS, PLANTS, RESPONSES, SEEDLINGS, WATER-USE EFFICIENCY

887

Heath, J., G. Kerstiens, and M.T. Tyree. 1997. Stem hydraulic conductance of European beech (Fagus sylvatica L.) and pedunculate oak (Quercus robur L.) grown in elevated CO2. *Journal of Experimental Botany 48(312):1487-1489.*

Over two seasons in c. 600 ppm CO2, oak had lower stomatal conductance in CO2-enriched compared to ambient air, Beech showed no response to CO2 concentration on sunny days, Mirroring this pattern, exposure to elevated CO2 reduced whole- shoot hydraulic conductance per unit leaf area in oak, but not in beech.

KEYWORDS: CARBON DIOXIDE, DROUGHT, PLANTS, SEEDLINGS, WATER-USE

888

Hebeisen, T., A. Luscher, and J. Nosberger. 1997. Effects of elevated atmospheric CO2 and nitrogen fertilisation on yield of Trifolium repens and Lolium perenne. *Acta Oecologica-International Journal of Ecology 18(3):277-284.*

Trifolium repens L. and Lolium perenne L. were grown in monocultures and bi-species mixture in a Free Air Carbon Dioxide Enrichment (FACE) experiment at elevated (60 Pa) and ambient (35 Pa) CO2 partial pressure (pCO(2)) for two years. The effects of nitrogen fertilisation (10 and 42 g N m(-2) a(- 1) in 1993; 14 and 56 g N m(-2) a(-1) in 1994) on the growth response to pCO, were investigated in frequently defoliated (7 cuts in 1993; 8 cuts in 1994) swards. The yield of Trifolium in monocultures increased by 22% when grown at elevated pCO(2). In contrast, the yield of Lolium monocultures was not affected (2%) by elevated pCO(2), whereas Lolium increased its root mass considerably. The consequence of these interspecific differences in the CO2 response was an increase in the proportion of Trifolium in the mixed swards from 39% at ambient to 50% at elevated pCO(2). However, the proportion of the species was more strongly affected by N fertilisation than by elevated pCO(2). Based on these 2' results, we conclude that the species proportion in managed grassland may change as the CO2 concentration increases. However, an adapted management may, at least partially, counteract such CO2 induced changes in the proportion of the species.

KEYWORDS: CARBON, ENRICHMENT, GRASSLAND, GROWTH, RYEGRASS, WHITE CLOVER

889

Hebeisen, T., A. Luscher, S. Zanetti, B.U. Fischer, U.A. Hartwig, M. Frehner, G.R. Hendrey, H. Blum, and J. Nosberger. 1997. Growth response of Trifolium repens L and Lolium perenne L as monocultures and bi-species mixture to free air CO2 enrichment and management. *Global Change Biology 3(2):149-160.*

Trifolium repens L. and Lolium perenne L. were grown in monocultures and bi-species mixture in a Free Air Carbon Dioxide Enrichment (FACE) experiment at elevated (60 Pa) and ambient (35 Pa) CO2 partial pressure (pCO(2)) for three years. The effects of defoliation frequencies (4 and 7 cuts in 1993; 4 and 8 cuts in 1994/95) and nitrogen fertilization (10 and 42 g m(-2) y(-1) N in 1993; 14 and 56 g m(-2) y(-1) in 1994/95) on the growth response to pCO(2) were investigated. There were significant interspecific differences in the CO2 responses during the first two years, while in the third growing season, these interspecific differences disappeared. Yield of T. repens in monocultures increased in the first two years by 20% when grown at elevated pCO(2). This CO2 response was independent of defoliation frequency and nitrogen fertilization. In the third year, the CO2 response of T. repens declined to 11%. In contrast, yield of L. perenne monocultures increased by only 7% on average over three years at elevated pCO(2). The yield response of L. perenne to CO2 changed according to defoliation frequency and nitrogen fertilization, mainly in the second and third year. The ratio of root/yield of L. perenne increased under elevated pCO(2), low N fertilizer rate, and frequent defoliation, but it remained unchanged in T. repens. We suggest that the more abundant root growth of L. perenne was related to increased N limitation under elevated pCO(2). The consequence of these interspecific differences in the CO2 response was a higher proportion of T. repens in the mixed swards at elevated pCO(2). This was evident in all combinations of defoliation and nitrogen treatments. However, the proportion of the species was more strongly affected by N fertilization and defoliation frequency than by elevated pCO(2). Based on these results, we conclude that the species proportion in managed grassland may change as the CO2 concentration increases. However, an adapted management could, at least partially, counteract such CO2 induced changes in the proportion of the species. Since the availability of mineral N in the soil may be important for the species' responses to elevated pCO(2), more long-term studies, particularly of processes in the soil, are required to predict the entire ecosystem response.

KEYWORDS: ATMOSPHERIC CO2, CARBON-DIOXIDE CONCENTRATION, ELEVATED CO2, GRASS, MINERAL NUTRITION, NITROGEN-FERTILIZER, ROOT-GROWTH, RYEGRASS, TALLGRASS PRAIRIE, WHITE CLOVER

890

Hedges, L.V., J. Gurevitch, and P.S. Curtis. 1999. The meta-analysis of response ratios in experimental ecology. *Ecology 80(4):1150-1156.*

Meta-analysis provides formal statistical techniques for summarizing the results of independent experiments and is increasingly being used in ecology. The response ratio (the ratio of mean outcome in the experimental group to that in the control group) and closely related measures of proportionate change are often used as measures of effect

magnitude in ecology. Using these metrics for meta-analysis requires knowledge of their statistical properties, but these have not been previously derived. We give the approximate sampling distribution of the log response ratio, discuss why it is a particularly useful metric for many applications in ecology, and demonstrate how to use it in meta-analysis. The meta- analysis of response-ratio data is illustrated using experimental data on the effects of increased atmospheric CO2 on plant biomass responses.

KEYWORDS: CO2, METAANALYSIS

891

Heifetz, P.B., A. Lers, D.H. Turpin, N.W. Gillham, J.E. Boynton, and C.B. Osmond. 1997. dr and spr/sr mutations of Chlamydomonas reinhardtii affecting D1 protein function and synthesis define two independent steps leading to chronic photoinhibition and confer differential fitness. *Plant, Cell and Environment 20(9):1145-1157.*

The effects of introduced chloroplast gene mutations affecting D1 synthesis, turnover and function on photosynthesis, growth and competitive ability were examined in autotrophic cultures of Chlamydomonas reinhardtii (Chlorophyta) adapted to low or high irradiance. Few discernible effects were evident when the mutants were grown in low light (LL, 70 mu mol m(-2) s(-1)). The herbicide-resistant psbA mutation Ser(264) --> Ala (dr) slowed electron transfer and accelerated D1 degradation in cells grown under high light (HL, 600 mu mol m(-2) s(-1)). The maximum rate of light- and CO2-saturated photosynthesis, cell growth rate and competitive ability in the dr mutant were reduced compared to wild type under HL. However, the wild-type rate of D1 synthesis in dr was adequate to compensate for accelerated D1 degradation. 16S rRNA mutations conferring resistance to streptomycin and spectinomycin (spr/sr) that altered chloroplast ribosome structure and assembly were used to inhibit chloroplast protein synthesis. In spr/sr cells grown under HL, D1 synthesis was reduced by 40-60% compared to wild type and D1 degradation was accelerated, leading to a 4-fold reduction in D1 pool size. The reduced D1 levels were accompanied by an elevation of F-o and a decline in F-v/F-m, quantum yield and maximum rate of CO2-saturated photosynthesis. Chemostat experiments showed that the growth rate and competitive ability of spr/sr were reduced against both wild type and dr.

KEYWORDS: 32-KILODALTON PROTEIN, CHLOROPHYLL FLUORESCENCE, CHLOROPLAST, LIGHT-INTENSITY, PHALARIS-PARADOXA, PHOTOSYNTHESIS, PHOTOSYSTEM, RIBOSOMAL-RNA GENES, TRIAZINE RESISTANCE, ULVA-ROTUNDATA

892

Heilman, J.L., D.R. Cobos, F.A. Heinsch, C.S. Campbell, and K.J. McInnes. 1999. Tower-based conditional sampling for measuring ecosystem-scale carbon dioxide exchange in coastal wetlands. *Estuaries 22(3A):584-591.*

Long-term measurements of CO2 exchange between coastal wetlands and the atmosphere are necessary to improve our understanding of the role these ecosystems play in the global carbon cycle, and the response of these systems to environmental change. We conducted research to adapt and evaluate tower-based conditional sampling as a method for measuring net CO2 exchange (NCE) at the ecosystem scale on a continuous basis. With conditional sampling, NCE is determined from the product of the standard deviation of vertical wind velocity, the difference in CO2 concentration between updrafts and downdrafts in the constant flux portion of the boundary layer above the surface, and an empirical coefficient. We constructed a system that used a sonic anemometer to measure vertical wind velocity (w) and control a high-speed three-way valve that diverted air from updrafts and down,drafts into separate sample lines, depending on the direction of w. An infrared gas analyzer was used to measure the concentration difference. The conditional sampling system was installed and tested in a marsh in the Nueces River Delta near Corpus Christi, Texas, as part of a long-term study of effects of freshwater inflow on CO2 flux. System accuracy was evaluated by comparing conditional sampling measurements of water vapor flux with independent estimates obtained with the Bowen ratio method. Average daily flux estimates for the two methods agreed to within 13%. Measurements showed that freshwater inflow due to flooding of the Nueces River increased NCE by increasing CO2 assimilation and decreasing CO2 efflux. Over a 65-d period, daily NCE varied from a maximum gain of 0.16 mol CO2 m(-2) d(-1) during flooding to a maximum loss of - 0.14 mol CO2 m(-2) d(-1) when the marsh dried. Our study showed that conditional sampling was well suited for quantifying CO2 exchange in coastal wetlands on a diel, daily, and seasonal basis.

KEYWORDS: ATMOSPHERIC CO2 CONCENTRATION, CANOPY PHOTOSYNTHESIS, CHESAPEAKE BAY, CROP, ELEVATED CO2, FIELD, FLUX MEASUREMENT, SEQUESTRATION, USE EFFICIENCY, WATER

893

Heineke, D., F. Kauder, W. Frommer, C. Kuhn, B. Gillissen, F. Ludewig, and U. Sonnewald. 1999. Application of transgenic plants in understanding responses to atmospheric change. *Plant, Cell and Environment 22(6):623-628.*

Acclimation of plants to an increase in atmospheric carbon dioxide concentration is a well described phenomenon, It is characterized by an increase in leaf carbohydrates and a degradation of ribulose 1,5-bisphosphate carboxylase protein (Rubisco) leading in the long term to a lower rate of CO2 assimilation than expected from the kinetic constants of Rubisco, This article summarizes studies with transgenic plants grown in elevated pCO(2) which are modified in their capacity of CO2 fixation, of sucrose and starch synthesis, of triosephosphate and sucrose transport and of sink metabolism of sucrose, These studies show that a feedback accumulation of carbohydrates in leaves play only a minor role in acclimation, because leaf starch synthesis functions as an efficient buffer for photoassimilates. There is some evidence that in elevated pCO(2), plants grow faster and senescence is induced earlier.

KEYWORDS: ANTISENSE REPRESSION, ELEVATED CO2, EXPRESSION, INHIBITION, PHOTOSYNTHETIC ACCLIMATION, POTATO PLANTS, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, TOBACCO, TRIOSE-PHOSPHATE TRANSLOCATOR, YEAST- DERIVED INVERTASE

894

Heissner, A. 1996. A simple model of greenhouse climate for short term control of temperature, air humidity, and CO2 concentration. *Gartenbauwissenschaft 61(6):289-300.*

A simple greenhouse climate model was designed for short term control of temperature, air humidity, and CO2 concentration. The model is based on the balances of thermal energy, water vapour, and carbon dioxide and is represented by a system of three nonlinear differential equations of the first order. The reaction of the canopy is taken into consideration through empirical models of CO2 gas exchange and transpiration of tomato plants. Model inputs are the meteorological conditions in the open (temperature, air humidity, CO2 concentration, global radiation, and wind velocity), the temperature of the ground surface in the greenhouse, and the temperature on the greenhouse cover as well as four control variables (heating, ventilation, CO2 enrichment, and moistening of the air). Measurements were carried out in two greenhouses with glass and plastic film cover under conditions of ventilation to estimate model quantities and to test the suitability of the

model fort prognosis. By means of simulations possibilities for the comparison of control strategies were demonstrated.

KEYWORDS: SYSTEM, TRANSPIRATION

895

Hemming, J.D.C., and R.L. Lindroth. 1999. Effects of light and nutrient availability on aspen: Growth, phytochemistry, and insect performance. *Journal of Chemical Ecology 25(7):1687-1714.*

This study explored the effect of resource availability on plant phytochemical composition within the framework of carbon- nutrient balance (CNB) theory. We grew quaking aspen (Populus tremuloides) under two levels of light and three levels of nutrient availability and measured photosynthesis, productivity, and foliar chemistry [water, total nonstructural carbohydrates (TNC), condensed tannins, and phenolic glycosides]. Gypsy moths (Lymantria dispar) and forest tent caterpillars (Malacosoma disstria) were reared on foliage from each of the treatments to determine effects on insect performance. Photosynthetic rates increased under high light, but were not influenced by nutrient availability. Tree growth increased in response to both the direct and interactive effects of light and nutrient availability. Increasing light reduced foliar nitrogen, while increasing nutrient availability increased foliar nitrogen. TNC levels were elevated under high light conditions, but were not influenced by nutrient availability. Starch and condensed tannins responded to changes in resource availability in a manner consistent with CNB theory; levels were highest under conditions where tree growth was limited more than photosynthesis (i.e., high light-low nutrient availability). Concentrations of phenolic glycosides, however, were only moderately influenced by resource availability. In general, insect performance varied relatively little among treatments. Both species performed most poorly on the high light-low nutrient availability treatment. Because phenolic glycosides are the primary factor determining aspen quality for these insects, and because levels of these compounds were minimally affected by the treatments, the limited response of the insects was not surprising. Thus, the ability of CNB theory to accurately predict allocation to defense compounds depends on the response of specific allelochemicals to changes in resource availability. Moreover, whether allelochemicals serve to defend the plant depends on the response of insects to specific allelochemicals. Finally, in contrast to predictions of CNB theory, we found substantial allocation to storage and defense compounds under conditions in which growth was carbon-limited (e.g., low light), suggesting a cost to defense in terms of reduced growth.

KEYWORDS: BETULA-PENDULA ROTH, CLONAL VARIATION, ELEVATED ATMOSPHERIC CO2, FOLIAR CHEMISTRY, FOREST TENT CATERPILLARS, HARDWOOD SEEDLINGS, MINERAL NUTRITION, NO3 AVAILABILITY, POPULUS-TREMULOIDES MICHX, SUCCESSIONAL STATUS

896

Hendrey, G.R. 1992. Global greenhouse studies - need for a new approach to ecosystem manipulation. *Critical Reviews in Plant Sciences 11(2-3):61-74.*

KEYWORDS: BALANCE, CARBON DIOXIDE, ELEVATED ATMOSPHERIC CO2, ENRICHMENT, FIELD, GROWTH, PHOTOSYNTHESIS, RESPONSES, TEMPERATURE, TUSSOCK TUNDRA

897

Hendrey, G.R., D.S. Ellsworth, K.F. Lewin, and J. Nagy. 1999. A free-air enrichment system for exposing tall forest vegetation to elevated atmospheric CO2. *Global Change Biology 5(3):293-309.*

A free-air CO2 enrichment (FACE) system was designed to permit the experimental exposure of tall vegetation such as stands of forest trees to elevated atmospheric CO2 concentrations ([CO2](a)) without enclosures that alter tree microenvironment. We describe a prototype FACE system currently in operation in forest plots in a maturing loblolly pine(Pinus taeda L.) stand in North Carolina, USA. The system uses feedback control technology to control [CO2] in a 26 m diameter forest plot that is over 10 m tall, while monitoring the 3D plot volume to characterize the whole-stand CO2 regime achieved during enrichment. in the second summer season of operation of the FACE system, atmospheric CO2 enrichment was conducted in the forest during all daylight hours for 96.7% of the scheduled running time from 23 May to 14 October with a preset target [CO2] of 550 mu mol mol(-1), approximate to 200 mu mol mol(-1) above ambient [CO2]. The system provided spatial and temporal control of [CO2] similar to that reported for open-top chambers over trees, but without enclosing the vegetation. The daily average daytime [CO2] within the upper forest canopy at the centre of the FACE plot was 552 +/- 9 mu mol mol-l (mean +/- SD). The FACE system maintained I-minute average [CO2] to within +/- 110 mu mol mol(-1) of the target [CO2] for 92% of the operating time. Deviations of [CO2] outside of this range were short-lived (most lasting < 60 s) and rare, with fewer than 4 excursion events of a minute or longer per day. Acceptable spatial control of [CO2] by the system was achieved,,with over 90% of the entire canopy volume within +/- 10% of the target [CO2] over the exposure season. CO2 consumption by the FACE system was much higher than for open- top chambers on an absolute basis, but similar to that of open- top chambers and branch bag chambers on a per unit volume basis. CO2 consumption by the FACE system was strongly related to windspeed, averaging 50 g CO2 m(-3) h(-1) for thestand for an average windspeed of 1.5 m s(-1) during summer. The [CO2] control results show that the free-air approach is a tractable way to study long-term and short-term alterations in trace gases, even within entire tall forest ecosystems. The FACE approach permits the study of a wide range of forest stand and ecosystem processes under manipulated [CO2](a) that were previously impossible or intractable to study in true forest ecosystems.

KEYWORDS: CARBON-DIOXIDE CONCENTRATION, FACE, FIELD CROPS, GROWTH, OPEN-TOP CHAMBERS, PHOTOSYNTHESIS, PINE PINUS- TAEDA, SHORT- TERM, STOMATAL CONDUCTANCE, TEMPERATE TREES

898

Hendrey, G.R., and B.A. Kimball. 1994. The face program. *Agricultural and Forest Meteorology 70(1-4):3-14.*

A large, cooperative, integrated experimental program utilizing free-air CO2 enrichment (FACE) is being conducted to expose plants to elevated concentrations of CO2. The goals are to evaluate the effects of increasing atmospheric CO2 on plants and ecosystems and, in the long run, to contribute to the evaluation of terrestrial plant feedback regulation on the rate of change of CO2 in the atmosphere. Having no walls, the FACE system allows plants to be grown under realistic microclimate and CO2 conditions expected to prevail in the mid-twenty-first century. Data obtained under such conditions are needed for validation of models being developed to predict the effects of increasing CO2 and changing climate variables on plants, ecosystems, agricultural productivity and water resources. Setup costs for the FACE systems used in these experiments are similar to the costs of field chamber systems. Although annual operating costs are about three times the cost of field chambers, FACE plots are relatively large, leading to an economy of scale, so that per unit of treated plant material, FACE systems are the least expensive approach for well- integrated field experiments. These features have provided an incentive to conduct comprehensive FACE experiments with many cooperating scientists working together to measure numerous plant, soil and micrometeorological parameters, as described in the collection of papers in this special issue of 'Agricultural

and Forest Meterology'.

KEYWORDS: AIR CO-2 ENRICHMENT, ATMOSPHERIC CARBON-DIOXIDE, ECOSYSTEMS, ELEVATED CO2, EXPOSURE, FIELD, OPEN-TOP CHAMBER, PHOTOSYNTHESIS, POPULATIONS, VEGETATION

899

Hendrey, G.R., K.F. Lewin, and J. Nagy. 1993. Free air carbon-dioxide enrichment - development, progress, results. *Vegetatio 104:17-31.*

Credible predictions of climate change depend in part on predictions of future CO2 concentrations in the atmosphere. Terrestrial plants are a large sink for atmospheric CO2 and the sink rate is influenced by the atmospheric CO2 concentration. Reliable field experiments are needed to evaluate how terrestrial plants will adjust to increasing CO2 and thereby influence the rate of change of atmospheric CO2. Brookhaven National Laboratory (BNL) has developed a unique Free-Air CO2 Enrichment (FACE) system for a cooperative research program sponsored by the U.S. Department of Energy and U.S. Department of Agriculture, currently operating as the FACE User Facility at the Maricopa Agricultural Center (MAC) of the University of Arizona. The BNL FACE system is a tool for studying the effects of CO2 enrichment on vegetation and natural ecosystems, and the exchange of carbon between the biosphere and the atmosphere, in open-air settings without any containment. The FACE system provides stable control of CO2 at 550 ppm +/- 10%, based on 1- min averages, over 90% of the time. In 1990, this level of control was achieved over an area as large as 380 m2, at an annual operating cost of $668 m-2. During two field seasons of enrichment with cotton (Gossypium hirsutum) as the test plant, enrichment to 550 ppm CO2 resulted in significant increases in photosynthesis and biomass of leaves, stems and roots, reduced evapotranspiration, and changes in root morphology. In addition, soil respiration increased and evapotranspiration decreased.

KEYWORDS: FIELD CROPS, FUMIGATION, POLLUTION, SYSTEM

900

Hendrey, G.R., S.P. Long, I.F. McKee, and N.R. Baker. 1997. Can photosynthesis respond to short-term fluctuations in atmospheric carbon dioxide? *Photosynthesis Research 51(3):179-184.*

Rapid and irregular variations of atmospheric CO2 concentrations (c(a)) occur in nature but are often very much more pronounced and frequent when artificially enriching CO2 concentrations in simulating the future atmosphere. Therefore, there is the danger that plant responses at elevated CO2 in fumigation experiments might reflect the increased Frequency and amplitude of fluctuation in concentration as well as the increase in average concentration. Tests were conducted to determine whether the photosynthetic process could sense such fluctuations in c(a). Instantaneous chlorophyll fluorescence (F-t) was monitored for wheat leaves (Triticum aestivum cv. Hereward) exposed to c(a) oscillating symmetrically by 225 mu mol mol(-1) about a c(a) set point concentration of 575 or 650 mu mol mol(-1). No F-t response was detected to half-cycle step changes in c(a) lasting less than two seconds, but at half- cycles of two seconds or longer, the response of F-t was pronounced. In order to determine the in vivo linear electron transport rate (J) the O-2 concentration was maintained at 21 mmol mol(-1) to eliminate photorespiration. J which is directly proportional to the rate of CO2 uptake under these conditions, was not significantly changed at half-cycles of 30 s or less but was decreased by half-cycles of 60 s or longer. It was inferred that if duration of an oscillation is less than 1 minute and is symmetrical with respect to mean CO2 concentration, then there is no effect on current carbon uptake, but oscillations of 1 minute or more decrease photosynthetic CO2 uptake in wheat.

KEYWORDS: ELECTRON-TRANSPORT, LEAVES, MESOPHYLL CONDUCTANCE, ZEA-MAYS

901

Hendrix, D.L., J.R. Mauney, B.A. Kimball, K. Lewin, J. Nagy, and G.R. Hendrey. 1994. Influence of elevated co2 and mild water-stress on nonstructural carbohydrates in field-grown cotton tissues. *Agricultural and Forest Meteorology 70(1-4):153-162.*

Root, stem and leaf tissues, from cotton plants exposed to CO2 at ambient (370 mumol mol-1 (control)) or elevated (550 mumol mol-1 (FACE; free-air carbon dioxide enrichment)) levels in the field during the 1990 and 1991 growing seasons, were analyzed for nonstructural carbohydrates (glucose, fructose, sucrose and starch). Besides the FACE treatment, these plants were also exposed to two irrigation levels: 100% and 67% replacement of evapotranspiration. FACE had a greater effect upon cotton plant nonstructural carbohydrates than did irrigation treatments. Leaf carbohydrate content was increased by FACE, but this increase was much more pronounced in the stems and roots. Starch and soluble sugars in leaves in FACE plots tended to be consistently greater than in control leaves, without much change in carbohydrate content during the growing season. In contrast, root and stem, starch and soluble sugar pools were strongly increased by FACE and fluctuated strongly during the growing season. In both seasons, stem and taproot nonstructural carbohydrate content passed through a minimum during periods of heavy boll set. The fluctuations in stem and root carbohydrate content were therefore probably caused by the varying metabolic demands of the developing plant. These results suggest that a significant effect of CO2 enrichment on starch-accumulating plants is an increase of nonstructural carbohydrate, especially starch, in nonleaf storage pools. This buildup occurs somewhat independently of the water status of the plant, and these enlarged pools can be drawn upon by the growing plant to maintain growth during periods of high metabolic demand.

KEYWORDS: ATMOSPHERIC CO2, CO2, ENRICHMENT, EXPORT, PLANT GROWTH, TEMPERATURE, TUSSOCK TUNDRA, YIELD

902

Hendry, M.J., C.A. Mendoza, R.A. Kirkland, and J.R. Lawrence. 1999. Quantification of transient CO2 production in a sandy unsaturated zone. *Water Resources Research 35(7):2189-2198.*

Temporal and spatial respiration rates were determined in a 5.7-m thick, sandy, unsaturated zone over a 550-day period using measured CO2 concentrations, CO2 fluxes to the atmosphere, moisture contents, and temperatures. Cyclical patterns in CO2 concentrations were measured in duplicate nests of nine gas samplers. Maximum CO2 gas concentrations occurred during the summer (0.85-1.22%), and minimum concentrations occurred during the winter (0.04-0.24%). CO2 gas concentrations decreased with increasing depth during the summer and increased with depth during the winter. A one-dimensional finite element model was developed to quantify transient respiration rates through the unsaturated zone. The model was calibrated to the measured CO2 concentrations. Temperature and moisture content variations were represented with an analytical expression and linear interpolation of field-measured values, respectively, in the model. Simulation results provided very good approximations to the field-measured CO2 concentrations, but predicted CO2 fluxes to the atmosphere were higher than measured. Respiration rates ranged from 5 mu g C g(-1) d(-1) in the soil horizon during the summer to about <10(-4) mu g C g(-1) d(-1) in unsaturated sections of the C horizon. A sensitivity analysis showed that the respiration rates in the C horizon must be <10(-3) mu g C g(-1) d(-1) and that the majority of the elevated CO2 concentrations in this thick unsaturated zone are the result of respiration in the soil horizon. Overall, roots contribute about 75% of the CO2 in the summer months. O-2 gas, microbial analyses, and the distribution of root biomass supported this conclusion. These

observations also imply that although microorganisms are present in subsurface environments their in situ activity in this sandy unsaturated zone may be very low.

KEYWORDS: AQUIFER, ATMOSPHERE, BIODEGRADATION, CARBON DIOXIDE, FIELD CONDITIONS, FOREST, MICROBIAL ACTIVITY, SOIL RESPIRATION, TEMPERATURES, TRANSPORT

903

Henning, F.P., C.W. Wood, H.H. Rogers, G.B. Runion, and S.A. Prior. 1996. Composition and decomposition of soybean and sorghum tissues grown under elevated atmospheric carbon dioxide. *Journal of Environmental Quality 25(4):822-827.*

It has been hypothesized that changes in both quantity and quality of plant residue inputs to soils as atmospheric carbon dioxide (CO2) concentration increases may alter carbon (C) and nitrogen (N) turnover rates and pool sizes, We determined the effect of elevated atmospheric CO2 on plant tissue quality, and flow modifications in tissue quality affect C and N mineralization. Soybean [C-3; Glycine max (L.) Merr. cv. Stonewall] and sorghum [C-4; Sorghum bicolor (L.) Moen, cv. Savanna 5] were grown under elevated (704.96 +/- 0.33 mu mol CO2 mol(-1)) and ambient (357.44 +/- 0.12 mu mol CO2 mol(-1)) atmospheric CO2 in open-top chambers, Leaf and stem tissues were separated from harvested plants and analyzed for C, N, lignin, and cellulose. Tissues were applied to Norfolk loamy sand (fine-loamy, siliceous, thermic Typic Kandiudult) and aerobically incubated for 70-d to determine C and N mineralization, C turnover, relative N mineralization, and C/N mineralized. Elevated CO2 had no effect on plant residue C concentration, but N concentration of soybean leaves and stems and sorghum stems was reduced; however, CO2 enrichment increased C/N ratio and lignin concentration for only sorghum stems and soybean leaves, respectively. Source of plant residue (i.e., produced under either elevated or ambient CO2) had no impact on soil C turnover, relative N mineralization, cumulative C and N mineralization, and C/N mineralized, These data suggest that increasing atmospheric CO2 will have little effect on composition or decomposition of field crop residues. Thus, since CO2 enrichment results in increased photosynthetic C fixation, the possibility exists For increased soil C storage under field crops in an elevated CO2 world.

KEYWORDS: CO2 LEVELS, DYNAMICS, NITROGEN, ORGANIC-MATTER, RESPONSES, SYSTEMS

904

Herbert, D.A., E.B. Rastetter, G.R. Shaver, and G.I. Agren. 1999. Effects of plant growth characteristics on biogeochemistry and community composition in a changing climate. *Ecosystems 2(4):367-382.*

Vegetation growth characteristics influence ecosystem biogeochemistry and must be incorporated in models used to project biogeochemical responses to climate variations. We used a multiple-element limitation model (MEL) to examine how variations in nutrient use efficiency (NUE) and net primary production to biomass ratio (nPBR) affect changes in ecosystem C stocks after an increase in temperature and atmospheric CO2. nPBR influences the initial rates of response, but the magnitude and direction of long-term responses are determined NUE. MEL was used to simulate responses to climate change in communities composed of two species differing in nPBR and/or NUE. When only nPBR differed between the species, the high-nPBR species outgrew the low-nPBR species early in the simulations, but the shift in dominance was transitory because of secondary N limitations. High-NUE and were therefore favored under elevated CO2. Increased temperature stimulated N release from soil organic matter (SOM) and therefore favored low-NUE species. The combined release from C and N limitation under the combination of increased temperature and elevated CO2 favored high-NUE species. High C:N litter from high-NUE species limited the N-supply rate from SOM, which favors the dominance of the high-NUE species in the short term. However, in the long term increased litter production resulted in SOM accumulation, which reestablished a N supply rate favorable to the reestablishment and dominance of the low-NUE species. Conditions then reverted to a state favorable to the high-NUE species.

KEYWORDS: ALASKAN TUNDRA, BIOLOGICAL INVASION, CARBON STORAGE, GLOBAL CHANGE, MYRICA-FAYA, NITROGEN, RESPONSES, TERRESTRIAL ECOSYSTEMS, TROPICAL FORESTS, VEGETATION TYPES

905

Herbst, M., and G. Hormann. 1998. Predicting effects of temperature increase on the water balance of beech forest - An application of the 'KAUSHA' model. *Climatic Change 40(3-4):683-698.*

The water balance model 'KAUSHA' (Halldin, 1989) was applied to a 100-year-old beech (Fagus sylvatica L.) forest in northern Germany. Overall, a satisfying agreement between modelled evapotranspiration values and independent micrometeorological measurements (Bowen ratio energy balance method) could be observed, although for rainy days KAUSHA showed a tendency to overestimate evapotranspiration. The model was used to predict the effects of a climate warming on the water budgets of the forest. It is shown that a temperature increase of 2 degrees C due to a rising CO2 content of the atmosphere will not change the yearly totals of evapotranspiration significantly, but could have serious effects on the soil water balance during the vegetation period. Because under climate change conditions a higher amount of the available soil water has already been evaporated in winter and spring, soil water content will limit the transpiration of the trees from July to September much more strongly. Therefore, the yield of beech forest might also suffer from drought effects. It can be concluded that a better knowledge of the seasonal distribution of rainfall under climate change conditions is indispensable for predicting effects of rising temperatures and CO2 concentrations on ecosystems.

KEYWORDS: CLIMATE-CHANGE SCENARIOS, CO2- ENRICHMENT, ECOSYSTEMS, ELEVATED CARBON-DIOXIDE, EVAPOTRANSPIRATION, GROWTH, OCEAN-ATMOSPHERE MODEL, RESPONSES, SCOTS PINE, SIMULATION

906

Herrick, J.D., and R.B. Thomas. 1999. Effects of CO2 enrichment on the photosynthetic light response of sun and shade leaves of canopy sweetgum trees (Liquidambar styraciflua) in a forest ecosystem. *Tree Physiology 19(12):779-786.*

To investigate whether sun and shade leaves respond differently to CO2 enrichment, we examined photosynthetic light response of sun and shade leaves in canopy sweetgum (Liquidambar styraciflua L.) trees growing at ambient and elevated (ambient + 200 mu l l(-1)) atmospheric CO2 in the Brookhaven National Laboratory/Duke University Free Air CO2 Enrichment (FACE) experiment. The sweetgum trees were naturally established in a 15-year-old forest dominated by loblolly pine (Pinus taeda L.). Measurements were made in early June and late August 1997 during the first full year of CO2 fumigation in the Duke Forest FACE experiment. Sun leaves had a 68% greater leaf mass per unit area, 63% more leaf N per unit leaf area, 27% more chlorophyll per unit leaf area and 77% greater light-saturated photosynthetic rates than shade leaves. Elevated CO2 strongly stimulated light-saturated photosynthesis of sun and shade leaves in June and August; however, the relative photosynthetic enhancement by elevated CO2 for sun leaves was mon than double the relative enhancement of shade leaves. Elevated CO2

stimulated apparent quantum yield by 30%. but there was no interaction between CO2 and leaf position. Daytime leaf-level carbon gain extrapolated from photosynthetic light response curves indicated that sun leaves were enhanced 98% by elevated CO2, whereas shade leaves were enhanced 41%. Elevated CO2 did not significantly affect leaf N per unit area in sun or shade leaves during either measurement period. Thus, the greater CO2 enhancement of light-saturated photosynthesis in sun leaves than in shade leaves was probably a result of a greater amount of nitrogen per unit leaf area in sun leaves. A full understanding of the effects of increasing atmospheric CO2 concentrations on forest ecosystems must take account of the complex nature of the light environment through the canopy and how light interacts with CO2 to affect photosynthesis.

KEYWORDS: ATMOSPHERIC CO2, DECIDUOUS FOREST, DIFFERENT IRRADIANCE LEVELS, ELEVATED CARBON-DIOXIDE, GAS-EXCHANGE, LOBLOLLY-PINE, LONG-TERM ELEVATION, NITROGEN LEVEL, PINUS-TAEDA SEEDLINGS, WATER-STRESS

907

Herrmann, B., and U. Feller. 1998. CO2, light and temperature influence senescence and protein degradation in wheat leaf segments. *Physiologia Plantarum 103(3):320-326.*

Effects of environmental conditions influencing photosynthesis and photorespiration on senescence and net protein degradation were investigated in segments from the first leaf of young wheat (Triticum aestivum cv. Arina) plants. The segments were floated on H2O at 25, 30 or 35 degrees C in continuous light (PAR: 50 or 150 mu mol m(-2) s(-1)) in ambient air and in CO2- depleted air. Stromal enzymes, including phosphoglycolate phosphatase, glutamine synthetase, ferredoxin-dependent glutamate synthase, phosphoribulokinase, and the peroxisomal enzyme, glycolate oxidase, were detected by SDS-PAGE followed by immunoblotting with specific antibodies. In general, the net degradation of proteins and chlorophylls was delayed in CO2- depleted air. However, little effect of CO2 on protein degradation was observed at 25 degrees C under the lower level of irradiance. The senescence retardation by the removal of CO2 was most pronounced at 30 degrees C and at the higher irradiance. The stromal enzymes declined in a coordinated manner. Immunoreactive fragments from the degraded polypeptides were in most cases not detectable. However, an insolubilized fragment of glycolate oxidase accumulated in vivo, especially at 25 degrees C in the presence of CO2. Detection of this fragment was minimal after incubation at 30 degrees C and completely absent on blots from segments kept at 35 degrees C. In CO2-depleted air, the fragment was only weakly detectable after incubation at 25 degrees C. The results from these investigations indicate that environmental conditions that influence photosynthesis may interfere with senescence and protein catabolism in wheat leaves.

KEYWORDS: ACCLIMATION, ACCUMULATION, CALVIN-CYCLE, DETACHED LEAVES, ELEVATED CO2, EXPRESSION, GLUTAMINE-SYNTHETASE, LIMITING CO2, PHOTOSYNTHESIS, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE

908

Hertstein, U., J. Colls, F. Ewert, and M. van Oijen. 1999. Climatic conditions and concentrations of carbon dioxide and air pollutants during 'ESPACE-wheat' experiments. *European Journal of Agronomy 10(3-4):163-169.*

A major objective of the ESPACE-wheat programme was to perform by means of open-top chambers (OTCs) 'standardised' experimental investigations of spring wheat responses to increased atmospheric CO2 and O-3 concentrations and to other environmental stresses at different locations in Europe, representing a broad range of different climatic conditions. From 1994 to 1996 a total number of 25 OTC experiments were carried out. In addition, four growth chamber experiments focusing on key physiological processes of wheat growth in CO2- enriched air were performed. According to the specific needs for subsequent modelling purposes, environmental data were collected during experiments, i.e. air temperature, global radiation, humidity and trace gas concentrations. In the present paper results of these measurements are summarised. It was shown, that the OTC-experiments covered a considerable range of growing season mean-air-temperatures (13.0-23.4 degrees C) and global irradiances (10.8-18.1 MJ m(-2) d(-1)), the most important driving variables for crop growth simulation models. Mean concentrations of CO2 and O-3 in ambient air and in different treatments illustrated the observed variability of trace gas exposures between different experiments. Implications for subsequent analyses of biological response data are discussed.

909

Hertstein, U., A. Fangmeier, and H.J. Jager. 1996. ESPACE-wheat (European Stress Physiology and Climate Experiment-project 1: Wheat): Objectives, general approach, and first results. *Journal of Applied Botany-Angewandte Botanik 70(5-6):172-180.*

The "European Stress Physiology and Climate Experiment - project 1: wheat" (acronym: ESPACE-wheat) is funded by the EU since 1994. In the present paper the projects goals, the general methodological approach, and a summary of the experimental work performed in 1994 and 1995 are described. Main objectives of the project are 1) to investigate experimentally the sensitivity of wheat growth, development and productivity to changes in CO2 concentration, climatic variables and other physiological stresses, 2) to use experimental data for extension, improvement and validation of process-based wheat growth simulation models, and 3) to use models for assessments of the influences on crops of climatic change, increasing CO2 concentration and additional physiological stresses in Europe. Most experimental investigations are being performed by means of open-top chambers (OTC's) according to a common standard protocol to meet specific data requirements for model construction and validation. ESPACE-wheat OTC-experiments in 1994 and 1995 are summarized and the principal methods of data evaluation are presented by analyzing responses of grain yield and aboveground biomass of spring wheat, cv. Minaret, to CO2 enrichment and other factors varied in experiments at different sites. The mean observed CO2-doubling responses was about 1.4, i.e. grain yield and biomass production were increased by about 40% compared to growth in ambient CO2 concentration. However, there was a large variability of responses between sites and years. Results are discussed with respect to modeling attempts.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, CROP RESPONSES, IMPACTS, OZONE, PLANTS, VEGETATION

910

Hew, C.S., S.E. Hin, J.W.H. Yong, S.S. Gouk, and M. Tanaka. 1995. In-vitro co2 enrichment of cam orchid plantlets. *Journal of Horticultural Science 70(5):721-736.*

Increased growth of an in vitro-propagated CAM orchid hybrid Mokara 'White' was obtained using a novel method of COP enrichment in an optimized photoautotrophic open system compared with the conventional closed system of culture. The optimization process for the open system involved the manipulation of external CO2 concentrations (0.03%, 1% and 10%), sucrose requirements, light intensities (80 and 200 mu mol m(-2) s(-1)) and the venting of headspace ethylene from the culture vessels. The physiological basis for increased growth in these CAM orchid plantlets after three months was attributed to the direct

effects of elevated CO2 resulting in higher CAM activity for the plantlets and to the elevated CO2 present in the system which might interact with the ethylene present thereby reducing the inhibition of growth of plantlets due to ethylene.

KEYWORDS: FIXATION, GROWTH, INVITRO

911

Heyworth, C.J., G.R. Iason, V. Temperton, P.G. Jarvis, and A.J. Duncan. 1998. The effect of elevated CO2 concentration and nutrient supply on carbon-based plant secondary metabolites in Pinus sylvestris L. *Oecologia 115(3):344-350.*

This study investigated changes in carbon-based plant secondary metabolite concentrations in the needles of Pinus sylvestris saplings, in response to longterm elevation of atmospheric CO?, at two rates of nutrient supply. Experimental trees were grown for 3 years in eight open-top chambers (OTCs), four of which were maintained at ambient (similar to 350 mu mol mol(-1)) and four at elevated (700 mu mol mol(-1)) CO2 concentrations, plus four open air control plots. Within each of these treatments, plants received either high (7.0 g N m(-2) year(-1) added) or low (no nutrients added) races of nutrient supply for two years. Needles from lateral branches were analysed chemically for concentrations of condensed tannins and monoterpenes. Biochemical determinations of cellulase digestibility and protein precipitating capacity of their phenolic extracts were made because of their potential of importance in ecological interactions between pine and other organisms including herbivores and decomposers. Elevated CO2 concentration caused an increase ($P < 0.05$) in dry mass per needle, tree height and the concentration of the monoterpene alpha-pinene, but there were no direct effects of CO2 concentration on any of the other chemical measurements made. High nutrient availability increased cellulase digestibility of pine needles. There was a significant negative effect of the OTCs on protein precipitating capacity of the needle extracts in comparison to the open-air controls. Results suggest that predicted changes in atmospheric CO2 concentration will be insufficient to produce large changes in the concentration of condensed tannins and monoterpenes in Scots pine. Processes which are influenced by these compounds, such as decomposition and herbivore food selection; along with their effects on ecosystem functioning, are therefore unlikely to be directly affected through changes in these secondary metabolites.

KEYWORDS: ALLELOCHEMICALS, ATMOSPHERIC CO2, BALANCE, CONTORTA, DIOXIDE CONCENTRATION, ECOSYSTEMS, FERTILIZATION, PERFORMANCE, RESPONSES, TANNIN

912

Hibberd, J.M., P. Richardson, R. Whitbread, and J.F. Farrar. 1996. Effects of leaf age, basal meristem and infection with powdery mildew on photosynthesis in barley grown in 700 mu mol mol(-1) CO2. *New Phytologist 134(2):317-325.*

The rate of net photosynthesis in the second leaf of barley was higher in 700 than 350 mu mol mol(-1) CO2 when measured in the CO2 concentration in which the plants were grown, but the magnitude of this difference decreased as the leaf aged. Infection by powdery mildew accelerated the decline in net photosynthesis of leaves grown in either 350 or 700 mu mol mol(-1) CO2. A/C-i curves allowed the reduction in net photosynthesis of plants exposed to 700 mu mol mol(-1) CO2 or after infection by powdery mildew to be related to changes in the carboxylation efficiency or in the regeneration of ribulose 1,5-bisphosphate. The carboxylation efficiency declined in plants exposed to 700 mu mol mol(-1) CO2. In plants infected with powdery mildew, the reduction in net photosynthesis was associated with both reduced carboxylation efficiency and reduced ability to regenerate ribulose 1,5-bisphosphate. Reduced carboxylation efficiency of the second leaf of plants grown in 700 mu mol mol(-1) CO2 was not associated with a reduction in the concentration of rubisco within the leaf. In contrast to the presence of a close exogenous sink, leaf age had large effects on the acclimation of photosynthesis to 700 mu mol mol(-1) CO2.

KEYWORDS: ACCLIMATION, BROWN RUST, CARBON DIOXIDE, GAS-EXCHANGE, LEAVES, PROTEIN, RIBULOSE BISPHOSPHATE CARBOXYLASE, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, STOMATAL CONDUCTANCE, TOMATO PLANTS

913

Hibberd, J.M., R. Whitbread, and J.F. Farrar. 1996. Carbohydrate metabolism in source leaves of barley grown in 700 mu mol mol(-1) CO2 and infected with powdery mildew. *New Phytologist 133(4):659-671.*

Soluble carbohydrate accumulated faster in second leaf blades of barley when plants were grown in 700 mu mol mol(-1) CO2 rather than 350 mu mol mol(-1) CO2. Infection of the second leaf blade by powdery mildew had no effect on the concentration of soluble carbohydrate until 6 d after inoculation when it was lower than in controls. The accumulation of soluble carbohydrate in the second leaf of uninfected plants grown in 700 mu mol mol(-1) CO2 was due largely to earlier and faster accumulation of fructan. TLC showed that the series of fructan was not different in plants grown in 700 mu mol mu mol(-1) CO2 relative to plants grown in 350 mu mol mol(-1) CO2, neither did infection by powdery mildew affect the series of fructan present in the second leaf blade. The rate constant for phloem loading obtained by compartmental analysis of C-14 efflux from the leaf blade was not reduced in plants grown in 700 mu mol mol(-1) CO2, indicating that carbohydrate accumulation was not caused by reduced ability of the leaf to export carbon.

KEYWORDS: CARBON, COMPARTMENTAL ANALYSIS, ELEVATED CO2, FLUXES, FRUCTAN ACCUMULATION, LEAF BLADES, PLANTS, STARCH, SUCROSE

914

Hibberd, J.M., R. Whitbread, and J.F. Farrar. 1996. Effect of 700 mu mol mol(-1) CO2 and infection with powdery mildew on the growth and carbon partitioning of barley. *New Phytologist 134(2):309-315.*

The dry weight of barley plants in 700 mu mol mol(-1) CO2 was increased by 19 d after planting relative to plants grown in 350 mu mol mol(-1) CO2. Infection of the second leaf by powdery mildew led to reduced growth rates in both 350 and 700 mu mol mol(-1) CO2, but the reduction in growth was transitory in 350 mu mol mol(-1) CO2. Neither the alIometric coefficient k between shoot and root, nor the leaf weight ratio, was altered by growth in 700 mu mol mol(-1) CO2 or by infection with powdery mildew. The number of tillers produced increased per plant but not per unit d. wt in 700 mu mol mol(-1) CO2. The growth response of barley to increased concentrations of CO2 and/or to infection with powdery mildew was not associated with alterations in net carbon partitioning, so a change in the ratio of photosynthetic to non-photosynthetic tissue, contributed to neither the growth response of barley to 700 mu mol mol(-1) CO2 nor to infection with powdery mildew. The increase in the growth rate of barley in 700 mu mol mol(-1) CO2 and the reduction in the growth rate after infection occurred at the same time as increased and reduced rates of net photosynthesis respectively.

KEYWORDS: DIOXIDE, ELEVATED CO2, PHOTOSYNTHESIS, ROOT, RUST, TEMPERATURE

915
Hibberd, J.M., R. Whitbread, and J.F. Farrar. 1996. Effect of elevated concentrations of CO2 on infection of barley by Erysiphe graminis. *Physiological and Molecular Plant Pathology 48(1):37-53.*

Although there was no difference in the percentage of powdery mildew conidia that germinated on the second leaf of barley plants grown in either 350 or 700 ppm CO2, the percentage of conidia that progressed to produce colonies was lower in plants grown in 700 than in 350 ppm CO2. The lower percentage of conidia producing hyphae in 700 ppm CO2 was due to a higher proportion of the spores being arrested at the appressorial stage. The reduction in penetration of spores in 700 ppm CO2 was due neither to 700 ppm CO2 per se, nor to ontogenetic changes in the host tissue. Removing the epicuticular waxes from the surface of the leaf had no effect on the development of conidia on the surface of leaves in 350 or 700 ppm CO2, showing that increased epicuticular waxes were not causing the increased resistance to primary penetration of powdery mildew in 700 ppm CO2. We relate reduced rates of primary penetration in barley grown in 700 ppm CO2 to higher rates of net photosynthesis allowing increased mobilisation of resources into resistance including the production of papillae and accumulation of silicon at the sites of appressorial penetration. Established colonies of powdery mildew grew faster in 700 ppm CO2 than in 350 ppm CO2, coincident with accumulation of host carbohydrate in the source leaf.

KEYWORDS: AGE, CARBON DIOXIDE, GERMLING DEVELOPMENT, INSOLUBLE SILICON, LEAVES, POWDERY MILDEW, PRIMARY PENETRATION, RESISTANCE, SPRING BARLEY, WHEAT

916
Hibbs, D.E., S.S. Chan, M. Castellano, and C.H. Niu. 1995. Response of red alder seedlings to co2 enrichment and water- stress. *New Phytologist 129(4):569-577.*

Red alder (Alnus rubra Bong.) is a nitrogen-fixing pioneer tree species of the Pacific Northwest of North America. We investigated the response of different seed sources of red alder to elevated atmospheric CO2 and to varied levels of water stress. Seeds were stratified, germinated and grown for up to 147 d under ambient (350 mu l l(-1)) or elevated (700 mu l l(- 1)) CO2. There were no significant interactions of seed source latitude with either treatment, although seedlings from more northerly sources were larger. Elevated CO2 and low moisture stress resulted in larger plants with more leaf area; effects of the two factors appeared additive. Effects of both factors on biomass allocation, including root:shoot ratios, were small or nonsignificant. Elevated CO2 decreased specific nitrogenase activity and generally increased photosynthesis (A) and stomatal conductance (g). The ratio A:g, potential water use efficiency, also increased when plants were under water stress. Elevated CO2 appears to improve drought tolerance in red alder. Overall, these results indicate that red alder would benefit in total plant growth from increased ambient CO2 and could tolerate changes in precipitation.

KEYWORDS: ALLOCATION, ALNUS-RUBRA, ATMOSPHERIC CARBON-DIOXIDE, ELEVATED CO2, GROWTH, NODULATION

917
Hikosaka, K. 1997. Modelling optimal temperature acclimation of the photosynthetic apparatus in C-3 plants with respect to nitrogen use. *Annals of Botany 80(6):721-730.*

A new hypothesis for temperature acclimation by the photosynthetic apparatus is presented. An optimization model is developed to examined effects of changes in the organization of photosynthetic components on leaf photosynthesis under various growth temperatures where the photosynthetic apparatus is not damaged. In this model, photosynthetic rate is limited either by the capacity of ribulose bisphosphate carboxylase (RuBPCase) to consume ribulose bisphosphate (RuBP), or by the capacity of RuBP regeneration. For temperature dependence of the RuBPCase activity, data from Spinacia oleracea L., which have a temperature optimum of 30 degrees C, are used. For temperature dependence of the capacity of RuBP regeneration, two contrasting curves that have temperature optima of 30 degrees C (Eucalyptus pauciflora Sieb. ex Spreng) and 40 degrees C (Larrea divaricata Cav.) are applied. The temperature dependence of each process is fixed for respective species, but the rate of each process varies with changes in the amounts of components. The cost of proteins, in terms of nitrogen, required to carry out each process is calculated when nitrogen is partitioned differently among photosynthetic components. The optimal nitrogen partitioning that maximizes daily photosynthesis at a given temperature is obtained. The predicted temperature optimum of the photosynthetic rate in Larrea divaricata exhibits large shifts with changes in target temperature, while shifts are negligible in Eucalyptus pauciflora. It is suggested that the shift in temperature optimum of photosynthetic rate is large when the temperature dependences of the capacities of RuBPCase and RuBP regeneration differ from each other. (C) 1997 Annals of Botany Company.

KEYWORDS: CO2/O2 SPECIFICITY, DESERT SHRUB, ELECTRON-TRANSPORT, ELEVATED CO2, GAS-EXCHANGE, GROWTH TEMPERATURE, INTACT LEAVES, LARREA- DIVARICATA, NERIUM-OLEANDER, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE

918
Hikosaka, K., and T. Hirose. 1998. Leaf and canopy photosynthesis of C-3 plants at elevated CO2 in relation to optimal partitioning of nitrogen among photosynthetic components: theoretical prediction. *Ecological Modelling 106(2-3):247-259.*

Effects of changes in the organization of photosynthetic components on leaf photosynthesis under contrasting atmospheric CO2 conditions (35 and 70 Pa) are evaluated using an optimization model, in which the photosynthetic rate is limited either by the capacity of ribulose bisphosphate carboxylase (RuBPCase) to consume ribulose bisphosphate (RuBP) or by the capacity of RuBP regeneration. The nitrogen cost of photosynthetic components to carry out each process is calculated for the optimal partitioning of nitrogen among the components. The model predicts that nitrogen allocation to the components carrying out RuBP regeneration should be increased with reduction in allocation to RuBPCase to maximize daily photosynthesis at 70 Pa CO2. Al a temperature of 25 degrees C, doubling the current CO2 level increases daily photosynthesis by 60% with optimal reallocation of the nitrogen partitioning while the increase without reallocation of nitrogen is 40%. However, at lower growth irradiance, the advantage in daily photosynthesis due to the reallocation decreases with increasing nitrogen content. The ratio of photosynthesis at 70 Pa to that at 35 Pa increases with increasing temperature. The effects of CO2 levels on photosynthesis of a canopy in which nitrogen is optimally allocated among leaf layers are also examined. At 25 degrees C, canopy photosynthesis at the doubled CO2 level is predicted to increase 60 and 40% with and without the optimization of nitrogen partitioning among photosynthetic components, respectively. Doubling the CO2 level does not affect the optimal nitrogen distribution among leaf layers in the canopy irrespective of optimization of nitrogen partitioning among photosynthetic components.

KEYWORDS: ACCLIMATION, ALLOCATION, ASSIMILATION, ATMOSPHERIC CO2, LEAVES, LIMITATIONS, MODEL, RESPECT, SYSTEM, TEMPERATURE

919
Hilbert, D.W., A. Larigauderie, and J.F. Reynolds. 1991. The influence of carbon-dioxide and daily photon-flux density on optimal leaf nitrogen concentration and root - shoot ratio. *Annals of Botany 68(4):365-376.*

KEYWORDS: ALLOCATION, CO2- ENRICHMENT, GROWTH, LEAVES, LIGHT, PHOTOSYNTHETIC CHARACTERISTICS, SEEDLINGS, SHADE PLANTS, STOMATAL CONDUCTANCE, USE EFFICIENCY

920
Hileman, D.R., N.C. Bhattacharya, P.P. Ghosh, P.K. Biswas, K.F. Lewin, and G.R. Hendrey. 1992. Responses of photosynthesis and stomatal conductance to elevated carbon-dioxide in field-grown cotton. *Critical Reviews in Plant Sciences 11(2-3):227-231.*

KEYWORDS: BEHAVIOR, CO2- ENRICHMENT, NITROGEN DEFICIENCY, PLANTS, SORGHUM, SUNFLOWER, WATER RELATIONS

921
Hileman, D.R., G. Huluka, P.K. Kenjige, N. Sinha, N.C. Bhattacharya, P.K. Biswas, K.F. Lewin, J. Nagy, and G.R. Hendrey. 1994. Canopy photosynthesis and transpiration of field-grown cotton exposed to free-air co2 enrichment (face) and differential irrigation. *Agricultural and Forest Meteorology 70(1-4):189-207.*

Growth, yield and leaf photosynthetic rates of cotton (Gossypium hirsutum L.) all respond strongly to CO2 enrichment, but the gas exchange of whole cotton canopies grown under elevated CO2 has not been investigated. We compared the effects of CO2 enrichment on both single-leaf and whole-canopy photosynthetic rates in cotton. We also determined whole- canopy photosynthetic and transpiration rates in cotton in response to CO2 enrichment and differential irrigation. Field-grown cotton was exposed to either 550 mumol mol-1 of CO2 using the free-air carbon dioxide enrichment (FACE) system or to 370 mumol mol-1 in control plots. In the second year of the experiment, half of each plot received reduced levels of irrigation. Rates of photosynthesis and stomatal conductance of single leaves were determined using a portable photosynthesis system and a portable steady-state porometer, respectively. Rates of whole-canopy photosynthesis and transpiration were determined using a custom-built chamber (about 1 m x 1 m). Midday net photosynthesis rates of both leaves and canopies were 19-41% higher in the CO2-enriched plots than in control plots. The CO2 effect on leaf photosynthesis was greatest in July, whereas the CO2 effect on canopy photosynthesis was greatest in June and decreased thereafter as mutual shading of leaves and the amount of non-photosynthetic biomass increased. Midday stomatal conductance values of leaves were 13-44% greater in control plants than in CO2-enriched plants. Except for late in the second season, canopy transpiration rates were not affected by the CO2 treatment because the decrease in stomatal conductance was offset by an increase in plant size. Differential irrigation led to no significant differences in either canopy photosynthesis or transpiration, possibly because differential irrigation was applied only during the second half of the season. It appears that cotton crops grown in a future, higher-CO2 climate may have increased photosynthetic rates, but water requirements may not be reduced.

KEYWORDS: CARBON DIOXIDE, ELEVATED CO2, LEAF, NITROGEN DEFICIENCY, PLANTS, RESPONSES, STOMATAL CONDUCTANCE, STRESS, WATER-USE EFFICIENCY, YIELD

922
Hirose, T., D.D. Ackerly, M.B. Traw, and F.A. Bazzaz. 1996. Effects of CO2 elevation on canopy development in the stands of two co-occurring annuals. *Oecologia 108(2):215-223.*

Elevated CO2 may increase dry mass production of canopies directly through increasing net assimilation rate of leaves and also indirectly through increasing leaf area index (LAI). We studied the effects of CO2 elevation on canopy productivity and development in monospecific and mixed (1:1) stands of two co- occurring C-3 annual species, Abutilon theophrasti and Ambrosia artemisiifolia. The stands were established in the glasshouse with two CO2 levels (360 and 700 mu l/l) under natural light conditions. The planting density was 100 per m(2) and LAI increased up to 2.6 in 53 days of growth. Root competition was excluded by growing each plant in an individual pot. However, interference was apparent in the amount of photons absorbed by the plants and in photon absorption per unit leaf area. Greater photon absorption by Abutilon in the mixed stand was due to different canopy structures: Abutilon distributed leaves in the upper layers in the canopy while Ambrosia distributed leaves more to the lower layers. CO2 elevation did not affect the relative performance and light interception of the two species in mixed stands. Total aboveground dry mass was significantly increased with CO2 elevation, while no significant effects on leaf area development were observed. CO2 elevation increased dry mass production by 30-50%, which was mediated by 35-38% increase in the net assimilation rate (NAR) and 37-60% increase in the nitrogen use efficiency (NUE, net assimilation rate per unit leaf nitrogen). Since there was a strong overall correlation between LAI and aboveground nitrogen and no significant difference was found in the regression of LAI against aboveground nitrogen between the two CO2 levels, we hypothesized that leaf area development was controlled by the amount of nitrogen taken up from the soil. This hypothesis suggests that the increased LAI with CO2 elevation observed by several authors might be due to increased uptake of nitrogen with increased root growth.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CARBON-DIOXIDE, C-4 ANNUALS, GAS-EXCHANGE, GROWTH, LEAF, NITROGEN CONCENTRATION, PHOTOSYNTHESIS, TEMPERATURE, TUSSOCK TUNDRA

923
Hirose, T., D.D. Ackerly, M.B. Traw, D. Ramseier, and F.A. Bazzaz. 1997. CO2 elevation, canopy photosynthesis, and optimal leaf area index. *Ecology 78(8):2339-2350.*

We studied the effects of CO2 elevation on leaf and canopy photosynthesis and optimal leaf area index (LAI) for stands of the annual species Abutilon theophrasti and Ambrosia artemisiifolia. Leaf photosynthesis was modeled as a function of photosynthetic photon flux density (PPFD) and nitrogen content per unit leaf area (N-L). There was a curvilinear relationship between the light-saturated rates of leaf photosynthesis (P-max) and N-L. CO2 elevation significantly increased P-max as a function of N, in both species. Dark respiration (R-d) was linearly correlated with N-L. CO2 elevation slightly but significantly increased R-d in Abutilon, while it had no significant effect on R-d in Ambrosia. The initial slope of a light-response curve was determined from quantum yield (phi(abs)) multiplied by leaf absorptance and then calibrated against N-L. Daily canopy photosynthesis, calculated by integration of leaf photosynthesis with the actual distribution of leaf area, leaf N, and PPFD within a canopy, showed fairly good agreement with the canopy photosynthesis estimated from growth analysis. CO2 elevation increased canopy photosynthesis by 30-50%. Based on the leaf photosynthesis model for Abutilon, we calculated daily canopy photosynthesis for a given LAI and N availability, in which N was assumed to be distributed optimally within a leaf canopy to maximize daily canopy photosynthesis. An optimal LAI to maximize daily canopy photosynthesis was obtained for each level of N availability and this optimum increased with increasing N availability. Contrary to the often predicted increase in LAI with CO2 elevation, the optimum LAI did not

increase at high CO2 when N availability was limited. Two factors were suggested to be involved in counteracting the increase in LAI in a high-CO2 world. One is the higher phi(abs) of plants grown in elevated CO2, which makes leaves in the canopy more N limited, favors higher N-L and thus lowers optimal LAI. The other is the higher R-d in elevated CO2, which leads to higher light compensation points, and lowers optimal LAI.

KEYWORDS: ANNUALS, C-3, CARBON-DIOXIDE CONCENTRATION, ECOSYSTEMS, GAS-EXCHANGE, GROWTH, NITROGEN DISTRIBUTION, RESPIRATION, RESPONSES, TEMPERATURE

924

Hirose, T., and F.A. Bazzaz. 1998. Trade-off between light- and nitrogen-use efficiency in canopy photosynthesis. *Annals of Botany 82(2):195-202.*

If the light-use efficiency (LUE) of species in a canopy is constant, canopy photosynthesis (CP) is proportional to the number of photons (Phi) absorbed by the canopy (CP = LUE x Phi). Likewise, if nitrogen-use efficiency (NUE) is constant, canopy photosynthesis is proportional to the amount of total leaf nitrogen (LN) (CP = NUE x LN). We applied these concepts to monospecific and mixed (1:1) stands of annuals (Abutilon theophrasti and Ambrosia artemisiifolia) at two stages, established in an ambient (360 mu l l(-1)) or elevated (700 mu l l(-1)) CO2 atmosphere. In both CO2 concentrations, across the two species, daily canopy photosynthesis gave strong linear regressions with zero intercepts both against the number of absorbed photons and against total leaf nitrogen in the canopy. Doubling CO2 increased LUE by 20-80 % and NUE by 20-100 %. LUE tended to be higher in Ambrosia than in Abutilon, and also higher in the later stage of canopy development than in the younger stage. Interference by Abutilon increased the LUE of Ambrosia. On the other hand, NUE tended to be higher in Abutilon than in Ambrosia, and to be higher in younger than in later stages. Interference by Abutilon decreased the NUE of Ambrosia. Thus, there are trade-offs (negative correlations) between LUE and NUE, which result from differences in leaf nitrogen per unit leaf area and from differences in leaf area development in the canopy. LUE increased with increasing leaf nitrogen concentration, while NUE increased with increasing light availability in the canopy. (C) 1998 Annals of Botany Company.

KEYWORDS: ABSORPTION, ALLOCATION, AREA, C-3 PLANTS, CARBON GAIN, CO2 ELEVATION, LEAF NITROGEN, LEAVES, MODEL, RADIATION

925

Hirschel, G., C. Korner, and J.A. Arnone. 1997. Will rising atmospheric CO2 affect leaf litter quality and in situ decomposition rates in native plant communities? *Oecologia 110(3):387-392.*

Though field data for naturally senesced leaf litter are rare, it is commonly assumed that rising atmospheric CO2 concentrations will reduce leaf litter quality and decomposition rates in terrestrial ecosystems and that this will lead to decreased rates of nutrient cycling and increased carbon sequestration in native ecosystems. We generally found that the quality of naturally senesced leaf litter (i.e. concentrations of C, N and lignin; C:N, lignin:N) of a variety of native plant species produced in alpine, temperate and tropical communities maintained at elevated CO2 (600-680 mu l(- 1)) was not significantly different from that produced in similar communities maintained at current ambient CO2 concentrations (340-355 mu l l(-1)). When this litter was allowed to decompose in situ in a humid tropical forest in Panama (Cecropia peltata, Elettaria cardamomum, and Ficus benjamina, 130 days exposure) and in a lowland temperate calcareous grassland in Switzerland (Carex flacca and a graminoid species mixture; 261 days exposure), decomposition rates of litter produced under ambient and elevated CO2 did not differ significantly. The one exception to this pattern occurred in the high alpine sedge, Carex curvula, growing in the Swiss Alps. Decomposition of litter produced in situ under elevated CO2 was significantly slower than that of litter produced under ambient CO2 (14% vs. 21% of the initial litter mass had decomposed over a 61-day exposure period, respectively). Overall, our results indicate that relatively little or no change in leaf litter quality can be expected in plant communities growing under soil fertilities common in many native ecosystems as atmospheric CO2 concentrations continue to rise. Even in situations where small reductions in litter quality do occur, these may not necessarily lead to significantly slower rates of decomposition. Hence in many native species in situ litter decomposition rates, and the time course of decomposition, may remain relatively unaffected by rising CO2.

KEYWORDS: BIOMASS, CARBON DIOXIDE, DYNAMICS, ECOSYSTEMS, ELEVATED CO2, FOREST, GRASSLAND, NITROGEN, PRODUCTIVITY, RESPONSES

926

Hobbie, J.E., B.L. Kwiatkowski, E.B. Rastetter, D.A. Walker, and R.B. McKane. 1998. Carbon cycling in the Kuparuk basin: Plant production, carbon storage, and sensitivity to future changes. *Journal of Geophysical Research-Atmospheres 103(D22):29065-29073.*

The Marine Biological Laboratory General Ecosystem Model was calibrated for an arctic tussock tundra system using data from long-term observations and experiments at Toolik Lake, Alaska. These experiments include the effects of changes in temperature, light, CO2, and nutrients, so the model could be applied to five regions comprising the entire Kuparuk River basin. Met primary production, averaged for the entire basin, was 92 g C m(-2) yr(-1). A 150 year simulation of carbon storage under a doubling of CO2 (slow ramp-up) and a temperature increase of 3.5 degrees C gave an estimate of +400 g C m(-2) when soil moisture increased and +500 g C m(-2) when soil moisture decreased. Drier soils stimulated decomposition producing an increase in nitrogen availability; the increased N led to increased net primary production. If this result is applicable to other arctic ecosystems, then it is unlikely that warming will enhance carbon loss to the atmosphere to further enhance warming.

KEYWORDS: ARCTIC TUNDRA, BALANCE, CLIMATE CHANGE, CO2, DIOXIDE, GLOBAL CHANGE, MODEL, RESPONSES, TERRESTRIAL ECOSYSTEMS

927

Hocking, P.J., and C.P. Meyer. 1991. Carbon-dioxide enrichment decreases critical nitrate and nitrogen concentrations in wheat. *Journal of Plant Nutrition 14(6):571-584.*

Atmospheric carbon dioxide (CO2) levels are increasing. In a glasshouse experiment with wheat grown at 5 levels of nitrate (NO3) supply, CO2 enrichment (1500 cm3/m3) substantially decreased critical concentrations of NO3-N and total-N in stem bases and leaves. For example, critical NO3-N concentrations in stem bases at Feekes Stages 1.5, 5, and 10.3, were 4.5, 2.0, and 2.0 mg/g dry wt, respectively, for CO2-enriched plants, compared with 7.5, 6.2 and 6.4 mg/g dry wt, respectively, for control plants grown at the ambient level of CO2. However, concentrations of NO3-N in the rooting medium required to produce maximum dry matter accumulation by CO2-enriched plants were similar to those of control plants at the three growth stages. Critical concentrations of NO3-N and total-N declined with time in stem bases and leaves of plants grown at both ambient and elevated CO2 levels, but the decline was greater for CO2-enriched plants. It was concluded that diagnostic criteria based on current critical N concentrations may

become invalid as the atmospheric level of CO2 increases.

KEYWORDS: AVAILABILITY, CO2- ENRICHMENT, DEFICIENCY, DRY-MATTER, GROWTH, NUTRITION, SOIL, SPRING WHEAT, YIELD

928
Hocking, P.J., and C.P. Meyer. 1991. Effects of CO2 enrichment and nitrogen stress on growth, and partitioning of dry-matter and nitrogen in wheat and maize. *Australian Journal of Plant Physiology 18(4):339-356.*

Atmospheric CO2 levels are increasing, but little is known about how this will affect tissue concentrations and the partitioning of agriculturally important nutrients such as nitrogen (N) within crop plants. To investigate this, a glasshouse experiment was conducted in which wheat, a C3 species, and maize, a C4 species, were grown for 8 weeks at high CO2 (1500 cm3 m-3) on N supplies ranging from deficient (0.5 mol m-3) to more than adequate for maximum growth (25 mol m-3). Wheat responded to both CO2 enrichment and N supply; maize responded only to N supply. CO2-enriched wheat produced about twice the dry matter of control plants at all levels of N supply. Tiller and ear numbers were increased by CO2 enrichment irrespective of N supply. Enriched wheat plants had a lower Leaf Area Ratio but higher Net Assimilation Rate and Relative Growth Rate than control plants. There was no effect of CO2 enrichment on specific leaf weight. The enriched plants had lower shoot to root dry matter ratios than thecontrols at 6 mol m-3 N and higher. Shoot to root dry matter ratios of both wheat and maize increased with increasing N supply. CO2-enriched wheat plants accumulated more N than the controls but the proportional increase in N content was not as great as that in dry matter, with the result that concentrations of total-N and nitrate-N were lower in all organs of enriched plants, including ears. Nitrate reductase activity was lower in enriched than in control wheat plants. N-use efficiency by wheat was increased by CO2 enrichment. From a practical point of view, the study indicates that critical total-N and NO3-N concentrations used to diagnose the N status of wheat will need to be reassessed as global CO2 levels increase. Elevated CO2 may also reduce the protein content of grain and thus the baking quality of hard wheats.

KEYWORDS: CARBON-DIOXIDE CONCENTRATION, MINERAL NUTRITION, NITRATE, NUTRIENT CONCENTRATION, PHOSPHORUS, PHOTOSYNTHESIS, PLANT GROWTH, USE EFFICIENCY, WATER, YIELD

929
Hoddinott, J., and R. Scott. 1996. The influence of light quality and carbon dioxide enrichment on the growth and physiology of seedlings of three conifer species .1. Growth responses. *Canadian Journal of Botany-Revue Canadienne De Botanique 74(3):383-390.*

Plant growth responds to light quality, as evaluated by the red/far-red (R/FR) quantum flux ratio, and to the level of CO2. Pinus banksiana, Picea mariana and Picea glauca seedlings were raised at 350, 700, or 1050 at mu L . L(-1) CO2 and high or low R/FR ratios and growth was measured over a 16-week growth period. Far-red rich light enhanced the whole plant and height relative growth rates of Pinus banksiana. The three species showed species specific responses in plant organ relative growth rates and partitioning ratios. On the basis of their biomass partitioning the species would be ranked Pinus banksiana < Picea mariana < Picea glauca for shade tolerance. In commercial operations, seedlings grown for outplanting are selected, in part, on the basis of plant form as described by the stem height/diameter ratio. More desirable ratios were obtained at ambient CO2 concentrations for Pinus banksiana and Picea mariana in red rich light and for Picea glauca in far-red rich light.

KEYWORDS: ATMOSPHERIC CO2 ENRICHMENT, BLACK SPRUCE SEEDLINGS, FORESTS, NATURAL- ENVIRONMENT, PHYTOCHROME

930
Hoddinott, J., and R. Scott. 1996. The influence of light quality and carbon dioxide enrichment on the growth and physiology of seedlings of three conifer species .2. Physiological responses. *Canadian Journal of Botany-Revue Canadienne De Botanique 74(3):391-402.*

Pinus banksiana, Picea mariana, and Picea glauca were grown at 350, 700, or 1050 mu L . L(-1) CO2 and either high or low red/far-red quantum flux ratios. After a 16-week, long day growth period, seedlings were subjected sequentially to short daylengths, then short days with low temperatures. Various physiological parameters were determined at the end of each treatment phase to monitor how those treatments influenced the onset of seedling dormancy. After the long day treatments, high ratios increased the total chlorophyll content and reduced the original level of chlorophyll fluorescence and the shoot total nonstructural carbohydrate content in very shade-intolerant Pinus banksiana. In shade-tolerant Picea mariana, high CO2 levels caused the main effects on these parameters while neither light quality or CO2 had significant effects on them in shade-tolerant Picea glauca. Short days and low temperature induced a proportional increase in the partitioning of total nonstructural carbohydrate to the roots in all species and produced other species and treatment-specific responses.

KEYWORDS: ATMOSPHERIC CO2 ENRICHMENT, BLACK SPRUCE SEEDLINGS, CHLOROPHYLL FLUORESCENCE, FORESTS, FROST HARDINESS, PHOTOSYNTHESIS, PHYTOCHROME, PINUS-RADIATA, PLANTS, TEMPERATURE

931
Hodge, A. 1996. Impact of elevated CO2 on mycorrhizal associations and implications for plant growth. *Biology and Fertility of Soils 23(4):388-398.*

The impact of increasing concentrations of atmospheric CO2 upon plant physiology has been widely investigated. Plant, and in particular root, growth is nearly always enhanced as a direct consequence of CO2 enrichment, with C-3 species generally more responsive than C-4 species. Such alterations in plant productivity will have consequence for below-ground processes and increased carbon allocation to the roots may favour symbiotic relationships. This paper discusses the current information available for the consequences of these changes upon mycorrhizal relationships. Generally mycorrhizal plants grown under CO2 enrichment show enhanced phosphorus uptake but nitrogen uptake is unaffected. This increased nutrient uptake is not correlated with increased mycorrhizal colonization of the roots. Similarly root exudation does not increase under CO2 enrichment but qualitative differences have yet to be assessed. However, it is predicted that total rhizodeposition of materials will increase as will litter inputs, although mineral and biochemical alterations to these plant derived inputs may occur. The consequences of such changes within the rhizosphere are discussed and future research priorities identified.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, BOUTELOUA-GRACILIS, CASTANEA-SATIVA MILL, ECTOMYCORRHIZAL FUNGI, GAS-EXCHANGE, GLOMUS-MOSSEAE, NUTRIENT-UPTAKE, PHOTOSYNTHETIC ACCLIMATION, SEEDLING GROWTH, WOODY-PLANTS

932
Hodge, A., and P. Millard. 1998. Effect of elevated CO2 on carbon partitioning and exudate release from Plantago lanceolata seedlings.

Physiologia Plantarum 103(2):280-286.

Plantago lanceolata L. seedlings were grown in sand microcosm units over a 43-day experimental period under two CO2 regimes (800 or 400 mu mol mol(-1)) to investigate the effect of elevated atmospheric CO2 concentration on carbon partitioning and exudate release. Total organic carbon (TOC) content of the collected exudate material was measured throughout the experimental period. After 42 days growth the seedlings were labelled with [C-14]-CO2 and the fate of the label within the plant and its release by the roots monitored. Elevated CO2 significantly (P less than or equal to 0.001) enhanced shoot, root and total dry matter production although the R:S ratio was unaltered, suggesting no alteration in press carbon partitioning. The cumulative release of TOC (in mg C) over 0-42 days was unaltered by CO2 treatment however, when expressed as a percentage of net assimilated C, ambient-grown plants released a significantly (P less than or equal to 0.001) higher percentage from their roots compared to elevated CO2-grown plants (i.e. 8 vs 3%). The distribution of C-14-label was markedly altered by CO2 treatment with significantly (P less than or equal to 0.001) greater per cent label partitioned to the roots under elevated CO2. This indicates increased partitioning of recent assimilate belowground under elevated CO2 treatment although there was no significant difference in the percentage of C-14-label released by the roots. Comparison of plant C budgets based on C-14-pulse-chase methodology and TOC measurements is discussed.

KEYWORDS: ATMOSPHERIC CO2, ENRICHMENT, FLOW, GROWTH, MAIZE, RESPONSES, RHIZOSPHERE, ROOT EXUDATION, SOIL BIOTA, ZEA MAYS L

933

Hodge, A., E. Paterson, S.J. Grayston, C.D. Campbell, B.G. Ord, and K. Killham. 1998. Characterisation and microbial utilisation of exudate material from the rhizosphere of Lolium perenne grown under CO2 enrichment. *Soil Biology and Biochemistry 30(8-9):1033-1043.*

The effects of elevated atmospheric CO2 concentration on alterations, both qualitatively and quantitatively, of exuded compounds from the roots of Lolium perenne seedlings were investigated by growing plants in a sterilised sand microcosm unit. In addition, the effect of CO2 treatment on carbon substrate utilisation of microbial populations extracted from the rhizosphere of L. perenne seedlings grown in soil microcosm units was examined and alterations on microbial activity and diversity assessed using a commercially-available redox-based sole C source utilisation test (Biolog(R)) including additional exudate compounds. Both types of microcosm units (sand and soil) were maintained at specific growth conditions under two CO2 regimes (450 and 720 mu mol mol(-1)). Growth of L. perenne seedlings from both types of microcosm units was enhanced under elevated atmospheric CO2 although the root-to-shoot ratios were not significantly altered, indicating no gross change in dry matter partitioning. Cumulative total organic carbon (TOC) release in the exudate material over the duration of the experiment was significantly (P less than or equal to 0.05) higher from ambient-grown seedlings despite a significant (P less than or equal to 0.05) increase in the dry weight of roots of the elevated CO2 grown seedlings as determined at harvest. Over the individual sampling periods TOC release was significantly (P less than or equal to 0.05) higher from elevated CO2 grown seedlings on only one occasion (21 d). Qualitative differences, measured between d 1-6 and 14-18, also occurred with elevated CO2 treatment decreasing the amount of phenolic acids and total sugars at the latter sampling period compared to ambient CO2 seedlings. Total numbers of bacteria were significantly (P less than or equal to 0.05) decreased under elevated CO2 although culturable numbers significantly (P less than or equal to 0.05) increased. This increase in culturable microorganisms may explain the faster carbon source utilisation rates of the elevated CO2 treatment. No change in morphotypes of microbial colonies were observed suggesting a quantitative difference due to elevated CO2 treatment only.

KEYWORDS: BIOMASS, CARBON DIOXIDE, COMMUNITIES, ELEVATED ATMOSPHERIC CO2, NITROGEN, PLANT-RESPONSES, ROOTS, SEEDLINGS, SOIL BIOTA, ZEA MAYS L

934

Hoen, H.F., and B. Solberg. 1994. Potential and economic-efficiency of carbon sequestration in forest biomass through silvicultural management. *Forest Science 40(3):429-451.*

This paper has two main objectives: First, to discuss in principle some vital methodological issues which have to be considered when analyzing bow preferable measures in forestry are to decrease the atmospheric concentration of greenhouse gases (GHGs). Economic evaluation of the flow of carbon in and out of the atmosphere is discussed, related particularly to two important problems: (1) the determination of the utility of reducing the quantity of CO2 in the atmosphere at a given point in time; and (2) the intertemporal evaluation of a flow of atmospheric CO2 reductions. The marginal cost, measured as the change in net present value, is proposed as a proper measure for ranking of alternative projects. Secondly, a case study is reported. The case study is based on forest-level optimization with a model estimating carbon flows related to forest biomass growth and decay, linked to a long-range forest management planning (LFMP) model. Alternative stand treatment schedules are simulated, and the forest management problem is solved by linear programming in a model I type LFMP model for the county of Buskerud, with a forest area of 574,000 ha. The potential for increasing the net carbon sequestration related to timber production by changes in the forest management over a time period of 30 yr is studied. A total of 253 stand treatment schedules was calculated for the 40 stand types, allowing for the following stand treatment options, (1) continued growth, (2) release thinnings of young growth, (3) thinning, (4) fertilization, (5) clear felling, (6) clear felling with retention of seed trees, and (7) planting or natural regeneration depending on the felling regime. The study shows that there is a significant potential for increasing the present value of the flow of net CO2 fixations (NPV(CO2)) by changing the forest management on the productive forest area of Buskerud. Compared with the NPV(CO2) obtained when the net present value of the timber cash flow (NPV(NOK)) for the area is maximized (BASE problem), an increase between 8.4%-17.9% in NPV(CO2) can be obtained. The potential for increasing the NPV(CO2) depends on the real rate of discount. The corresponding decrease in the NPV(NOK) lies between 8.1% and 14.9%. The results further indicate that a large proportion of the increase in NPV(CO2) can be obtained by changes in forest management at a moderate marginal cost. If we assume that 80% of the maximum potential increase in NPV(CO2) is obtained, this gives a yearly increase (30-yr annuity) in net CO2 fixation in the range from 145,000 to 250,000 tons (depending on the real rate of discount and assumptions about fertilization) by changing the management of the 574,000 ha of productive forestland in Buskerud, compared to the current forest management practice (BASE problem). Obtaining 80% of the maximum potential increase in NPV(CO2) imposes a decrease in the NPV(NOK) in the range of 22% to 65% of the total potential difference in NPV(NOK) between the BASE problem and the NPV(CO2) maximizing problem. The annual decrease (30-yr annuity) in NPV(NOK) corresponding to the 80% of the maximum potential NPV(CO2) increase, is ranging between 7.6 and 25 million NOK. The results indicate that at a RRD of 4%, 5%, and 7% p.a., 80% of the increase in NPV(CO2) can be reached at a marginal cost (shadow price) below 150 NOK (21/US$) per ton NPV(CO2). Measured per ton C, the corresponding marginal cost is 551 NOK (79 US$) per ton C. For RRDs at 3% p.a. and 2% p.a., the marginal costs are significantly higher, but relaxing the NPV(CO2) constraint to 60% of the total increase brings the marginal costs down and below half of this level (59 NOK or 8 US$ per ton NPV(CO2)) for 3% p.a. and to a comparable level (182 NOK or 26

US$ per ton NPV(CO2)) for 2% p.a. These results are related to changes in the management of the forested area in even-aged stands and do not take into account measures such as afforestation of marginal agricultural land or changes of tree species. Fertilization, avoiding release thinning in young growth, and changes in clear felling priorities were the most cost-efficient changes in stand treatment management in order to increase the net CO2 fixation.

KEYWORDS: ELEVATED CO2, RESPONSES

935

Hogan, K.P., I. Fleck, R. Bungard, J.M. Cheeseman, and D. Whitehead. 1997. Effect of elevated CO2 on the utilization of light energy in Nothofagus fusca and Pinus radiata. *Journal of Experimental Botany 48(311):1289-1297.*

Red beech (Nothofagus fusca (Hook. F.) Oerst.; Fagaceae) and radiata pine (Pinus radiata D. non; Pinaceae) were grown for 16 months in large open-top chambers at ambient (37 Pa) and elevated (66 Pa) atmospheric partial pressure of CO2, and in control plots (no chamber). Summer-time measurements showed that photosynthetic capacity was similar at elevated CO2 (light and CO2-saturated value of 17.2 mu mol m(-2) s(-1) for beech, 13.5 mu mol m(-2) s(-1) for pine), plants grown at ambient CO2 (beech 21.0 mu mol m(-2) s(-1), pine 14.9 mu mol m(-2) s(-1)) or control plants grown without chambers (beech 23.2 mu mol m(- 2) s(-1), pine 12.9 mu mol m(-2) s(-1)). However, the higher CO2 partial pressure had a direct effect on photosynthetic rate, such that under their respective growth conditions, photosynthesis for the elevated CO2 treatment (measured at 70 Pa CO2 partial pressure: beech 14.1 mu mol m(-2) s(-1) pine 10.3) was greater than in ambient (measured at 35 Pa CO2: beech 9.7 mu mol m(-2) s(-1), pine 7.0 mu mol m(-2) s(-1)) or control plants (beech 10.3 mu mol m(-2) s(-1), pine 7.2 mu mol m(-2) s(-1)). Measurements of chlorophyll fluorescence revealed no evidence of photodamage in any treatment for either species. the quantity of the photoprotective xanthophyll cycle pigments and their degree of de-epoxidation at midday did not differ among treatments for either species. The photochemical efficiency of photosystem II (yield) was lower in control plants than in chamber-grown plants, and was higher in chamber plants at ambient than at elevated CO2. These results suggest that at lower (ambient) CO2 partial pressure, beech plants may have dissipated excess energy by a mechanism that does not involve the xanthophyll cycle pigments.

KEYWORDS: CARBON METABOLISM, CAROTENOIDS, CHLOROPHYLL FLUORESCENCE, ELECTRON-TRANSPORT, INHIBITION, PHOTOINHIBITION, PHOTOSYNTHESIS, PLANTS, RESPONSES, TEMPERATURE

936

Hogan, K.P., A.P. Smith, and L.H. Ziska. 1991. Potential effects of elevated CO2 and changes in temperature on tropical plants. *Plant, Cell and Environment 14(8):763-778.*

Very little attention has been directed at the responses of tropical plants to increases in global atmospheric CO2 concentrations and the potential climatic changes. The available data, from greenhouse and laboratory studies, indicate that the photosynthesis, growth and water use efficiency of tropical plants can increase at higher CO2 Concentrations. However, under field conditions abiotic (light, water or nutrients) or biotic (competition or herbivory) factors might limit these responses. In general, elevated atmospheric CO2 concentrations seem to increase plant tolerance to stress, including low water availability, high or low temperature, and photoinhibition. Thus, some species may be able to extend their ranges into physically less favourable sites, and biological interactions may become relatively more important in determining the distribution and abundance of species. Tropical plants may be more narrowly adapted to prevailing temperature regimes than are temperate plants, so expected changes in temperature might be relatively more important in the tropics. Reduced transpiration due to decreased stomatal conductance could modify the effects of water stress as a cue for vegetative or reproductive phenology of plants of seasonal tropical areas. The available information suggests that changes in atmospheric CO2 concentrations could affect processes as varied as plant/herbivore interactions, decomposition and nutrient cycling, local and geographic distributions of species and community types, and ecosystem productivity. However, data on tropical plants are few, and there seem to be no published tropical studies carried out in the field. Immediate steps should be undertaken to reduce our ignorance of this critical area.

KEYWORDS: AMAZON DEFORESTATION, ATMOSPHERIC CO2, CLIMATE CHANGE, COSTA-RICA, GLOBAL CARBON-CYCLE, INSECT HERBIVORE, PHOTOSYNTHETIC RESPONSES, RAIN-FOREST, ULTRAVIOLET-B RADIATION, WATER RELATIONS

937

Hogan, K.P., D. Whitehead, J. Kallarackal, J.G. Buwalda, J. Meekings, and G.N.D. Rogers. 1996. Photosynthetic activity of leaves of Pinus radiata and Nothofagus fusca after 1 year of growth at elevated CO2. *Australian Journal of Plant Physiology 23(5):623-630.*

Radiata pine (Pinus radiata D.Don) and red beech (Nothofagus fused (Hook.f.) Oerst.) were grown for over 1 year at elevated (ELEV, 64 Pa) and ambient (AMB, 38 Pa) CO2 partial pressure in open-top chambers. Springtime measurements of overwintering leaves showed that light- and CO2-saturated photosynthetic rates (A,,) of pine leaves were similar for the two treatments (AMB: 6.7 +/- 1.08 mu mol m(-2) s(-1), mean +/- 1 s.e.; ELEV: 6.6 +/- 0.47) but, for beech leaves, A(max) was greater for AMB plants (8.8 +/- 0.90 mu mol m(-2) s(-1)) than for ELEV plants (6.10 +/- 0.71). Summertime measurements of leaves grown that spring showed that for pine, A(max) was similar in the two CO2 treatments (AMB 14.9 mu mol m(-2) s(-1) +/- 0.80; ELEV: 13.5 +/- 1.9) while, for beech, A(max) was higher in AMB plants (21.0 +/- 1.1) than in ELEV plants (17.2 +/- 1.9), although the difference was not statistically significant. These results indicate downregulation of photosynthetic capacity of beech but not pine. V-cmax did not differ between treatments within species, suggesting that there was no acclimation of rubisco activity. Triose phosphate utilisation limitation may have contributed to the downregulation of A(max) in beech. For pine, photosynthesis at treatment CO2 partial pressures was greater in ELEV plants in both spring and summer. For beech measured at treatment CO2 partial pressures, photosynthesis was greater in ELEV plants in summer, but was similar between treatments in the springtime.

KEYWORDS: ACCLIMATION, ASSIMILATION, ATMOSPHERIC CO2, C-3 PLANTS, CARBON DIOXIDE, ENHANCEMENT, LIMITATIONS, LOBLOLLY-PINE, NUTRITION, SENESCENCE

938

Holbrook, G.P., J. Hansen, K. Wallick, and T.M. Zinnen. 1993. Starch accumulation during hydroponic growth of spinach and basil plants under carbon-dioxide enrichment. *Environmental and Experimental Botany 33(2):313-321.*

The effects of CO2 enrichment, photoperiod duration, and inorganic phosphate levels on growth and starch accumulation by spinach and basil plants were studied in a commercial hydroponic facility. During a 3-week growth period, both species exhibited increased whole-plant fresh weight as a result of an increase in atmospheric CO2 concentration from 400 to 1500 mul/l. However, basil leaves exhibited a 1.5- to 2-fold greater increase in specific leaf weight (SLW), and accumulated starch to much greater levels than did leaves of spinach. At 1500 mul CO2/l, starch accounted for up to 38% of SLW with basil compared to < 10%

of SLW with spinach. The maximum ratio of starch/chlorophyll was 55.0 in basil leaves vs 8.0 in spinach leaves. High ratio values were associated with the appearance of chlorotic symptoms in leaves of basil grown under CO2 enrichment (WALLICK and ZINNEN (1990) Plant Disease 74, 171-173), whereas spinach did not exhibit chlorosis. Increasing inorganic phosphate concentrations from 0.7 to 1.8 mM in the hydroponic medium did not appreciably affect leaf starch accumulation in either species. Starch accumulation in basil leaves was not consistently related to the duration of the photoperiod. However, photoperiod-induced changes in leaf starch levels were much greater in basil than spinach. The results clearly indicate that different horticultural crops can show diverse responses to CO2 enrichment, and thus highlight the need to develop individual growth strategies to optimize production quality of each species.

KEYWORDS: ACCLIMATION, ACTIVATION, ATMOSPHERES, CO2-ENRICHMENT, CROP RESPONSES, LEAVES, PHOTOSYNTHESIS, SUCROSE PHOSPHATE SYNTHASE, TOMATO, YIELD

939

Holcroft, D.M., M.I. Gil, and A.A. Kader. 1998. Effect of carbon dioxide on anthocyanins, phenylalanine ammonia lyase and glucosyltransferase in the arils of stored pomegranates. *Journal of the American Society for Horticultural Science 123(1):136-140.*

Wonderful' Pomegranates (Punica granatum L.) were placed in jars ventilated continuously with air or air enriched with 10 or 20 kPa CO2 at 10 degrees C for 6 weeks. Samples were taken initially and after 1, 2, 4, and 6 weeks, and postharvest quality attributes were measured. The arils of the pomegranates stored in air were deeper red than the initial controls and than those stored in CO2-enriched atmospheres. This increased color was associated with increased anthocyanin concentration. Arils from fruit stored in air enriched with 10 kPa CO2 had a lower anthocyanin concentration than air-stored fruit, and atmospheres enriched with 20 kPa CO2 had even lower levels, possibly from suppressed anthocyanin biosynthesis. Anthocyanin concentration correlated well with the activity of phenylalanine ammonia lyase but not with glucosyltransferase activity. Moderate CO2 atmospheres (10 kPa) prolong the storage life and maintain quality of pomegranates, including adequate red color intensity of the arils.

KEYWORDS: APPLE, ATMOSPHERE, BIOSYNTHESIS, CO2, CULTIVARS, LETTUCE TISSUE, PHENOLICS, PIGMENTATION, STORAGE, STRAWBERRY FRUIT

940

Holcroft, D.M., and A.A. Kader. 1999. Carbon dioxide-induced changes in color and anthocyanin synthesis of stored strawberry fruit. *Hortscience 34(7):1244-1248.*

Anthocyanin concentrations increased in both external and internal tissues of 'Selva' strawberries (Fragaria xananassa Duch.) stored in air at 5 degrees C for 10 days, but the increase was lower in fruit stored in air enriched with 10 or 20 kPa CO2. Flesh red color was less intense in CO2 storage than in air storage. Activities of phenylalanine ammonia lyase (PAL) and UDP glucose : flavonoid glucosyltransferase (GT) decreased during storage, with decreases being greater in both external and internal tissues of strawberry fruit stored in air + 20 kPa CO2 than in those kept in air. Activities of both PAL and GT in external tissues of strawberries stored in air + 10 kPa CO2 were similar to those in fruit stored in air, while enzyme activities in internal tissues more closely resembled those from fruit stored in air +20 kPa CO2. Phenolic compounds increased during storage but were not affected by the storage atmosphere. The pH increased and titratable acidity decreased during storage; these effects were enhanced in internal tissues by the CO2 treatments, and may in turn have influenced anthocyanin expression.

KEYWORDS: BIOSYNTHESIS, CULTIVARS, PHENYLALANINE AMMONIA-LYASE

941

Holland, E.A., A.R. Townsend, and P.M. Vitousek. 1995. Variability in temperature regulation of co2 fluxes and n mineralization from 5 hawaiian soils - implications for a changing climate. *Global Change Biology 1(2):115-123.*

We examined the possibility that microbial adaptation to temperature could affect rates of CO2, N2O and CH4 release from soils. Laboratory incubations were used to determine the functional relationship between temperature and CO2, N2O and CH4 fluxes for five soils collected across an elevational range in Hawaii. Initial rates of CO2 production and net N mineralization increased exponentially from 15 degrees C to 55 degrees C; initial rates of CH4 and N2O release were more complex. No optimum temperature (in which rates decline at higher and lower temperatures) was apparent for any of the gases, but respiration declined with time at higher temperatures, suggesting rapid depletion of readily available substrate. Mean Q(10)s for respiration varied from 1.4 to 2.0, a typical range for tropical soils. The functional relationship between CO2 production and temperature was consistent among all five soils, despite the substantial differences in mean annual temperature, soils, and land-use among the sites. Temperature responses of N2O and CH4 fluxes did not follow simple Q(10) relationships suggesting that temperature functions developed for CO2 release from heterotrophic respiration cannot be simply extrapolated. Expanding this study to tropical heterotrophic respiration, the flux is more sensitive to changes in Q(10) than to changes in temperature on a per unit basis: the partial derivative with respect to temperature is 2.4 Gt C . degrees C- 1, with respect to Q(10) it is 3.5 Gt C . Q(10) unit(-1). Therefore, what appears to be minor variability might still produce substantial uncertainty in regional estimates of gas exchange.

KEYWORDS: ATMOSPHERE, CARBON DIOXIDE, EMISSIONS, GRASSLANDS, MODEL, VEGETATION

942

Hollander, B., and H. Krug. 1991. Effects of high CO2 concentrations on vegetable species .1. Symptoms, ranges of injuries, and reactions of species. *Gartenbauwissenschaft 56(5):193-205.*

To test the reactions of various vegetable species to high CO2-concentrations, the plants were treated with 1-3% technical CO2 day and night for 10-42 days in growth chambers (table 1). The development of CO2 injury symptoms as well as growth rates were noted and measured. With exception of spinach and sweet pepper, which showed no symptoms in the range tested, CO2 injuries occurred in the form of morphological alterations (epinastic and hyponastic rolling of the leaves, crisping, reduction and thickening of the leaf lamina), chlorosis (marginal or in areas between the veins), necrosis, wilting, drying up and browning ot the veins (kohlrabi). The symptoms mentioned varied between the species and between the cultivars. The injuries occurred at young leaves only (beans), at older leaves (kohlrabi) or at all leaves (fig. 1-5, table 6). Moreover, high CO2-concentrations caused a remarkable reduction of growth (fig. 6). Ensuring favourable growth conditions the cold-season species tolerated concentrations of 1% CO2 for 4-6 weeks showing only week (radish var. niger, kohlrabi, corn salad) or no significant growth reductions (radish, var. sativus, lettuce). Light injuries and morphological alterations were identifiable after 2-3 weeks. Higher concentrations caused stronger growth reductions, injuries appeared after 1 week using 2% CO2 and after 2-3 days using 3% CO2. The warm-season species tested reacted more sensitive. Cucumbers tolerated 1% CO2 for 2-3 weeks, using 2% CO2 wilting and driving injuries occurred already after 1 day table 2). In case of disturbances of the water status of the plants by transplanting, top dressing or sharp decrease of air

humidity cucumber wilted with 1% CO2 already after a few days. Equal reactions were observed with radish, var. sativus. With tomatoes strong injuries of the leaves causing leaf death were observed after 7 days with 1% CO2 and after 5 days with 2% CO2. Bush beans reacted by a distinct reduction of leaf area growth and by chlorotic discolorations.

KEYWORDS: ACCLIMATION, CARBON DIOXIDE, ENRICHMENT, MONOECIOUS CUCUMBERS, PHARBITIS, PLANT GROWTH

943

Hollander, B., and H. Krug. 1992. Effects of high co2-concentrations on vegetable species .2. Growth, co2-gas-exchange and stomata resistance. *Gartenbauwissenschaft 57(1):32-43.*

In the climatic conditions tested the growth of young cucumber plants (3-7 leaf stage) was slightly promoted as well by day as by continuous enrichment with 5000-mu-l/l CO2 compared to the control (400-mu-l/l CO2). A definite effect of enrichment during the night was not evident. The analysis of the growth components and gas exchange measurements revealed, that CO2 enrichment during the day as well as during day and night increased net assimilation rate and dark respiration distinctly. Enrichment during the night showed no effect on net assimilation rate and increased dark respiration only slightly. The specific leaf area was strongly reduced by the high CO2 concentration, but leaf weight ratio was rarely changed. By these morphogenetic effects growth promotion by an increased net assimilation rate was diminished. Continuous CO2 enrichment to cucumber plants with CO2 concentrations greater- than-or-equal-to 1000-mu-l/l decreased stomata resistance. This effect increased with higher CO2 concentrations and longer treatments. The stomata remained open even at night and at low air humidity. Also with CO2 enrichment up to 5000-mu-l/l during the day or during the night only the stomata remained wider open than in the control plants. The reaction of stomata to high CO2-concentrations is reversible. The regeneration proceeds all the faster as lower the proceeding concentration and shorter the exposition. The actions of high CO2-concentrations on stomata movement of cucumbers were confirmed with other species.

KEYWORDS: CARBON-DIOXIDE CONCENTRATION, CO2-ENRICHMENT, DARK RESPIRATION, DRY-MATTER PRODUCTION, LEAVES, PHOTOSYNTHETIC RATE, PLANT GROWTH, RESPONSES, TRANSPIRATION, VICIA-FABA

944

Homma, K., H. Nakagawa, T. Horie, H. Ohnishi, H.Y. Kim, and M. Ohnishi. 1999. Energy budget and transpiration characteristics of rice grown under elevated CO2 and high temperature conditions as determined by remotely sensed canopy temperatures. *Japanese Journal of Crop Science 68(1):137-145.*

The effects of elevated CO2 concentration and high temperatures on transpiration and gaseous diffusive resistances of rice canopy were investigated. Akihikari and IR36 cultivars were grown under two CO2 concentrations ([CO2], 365 and 700 mu L L- 1) X three temperatures (29.8, 30.4 and 32.5 degrees C on average over the experimental period), created by two Temperature Gradient Chambers. From 2 August (panicle initiation) to 22 August (booting), measurements were made of dry and wet bulb temperatures, canopy surface temperatures (T- c) and net radiation along with evapotranspiration (E) measurements by microlysimeters. Aerodynamic resistance (r(a)), obtained from the measured E and microclimate data, showed a fairly constant value (11.7 s m(-1). Then, r(a), T-c and microclimates data were substituted into energy budget equations to obtain E and canopy resistance (r(c)). In all plots, calculated E was in good agreement with measurement by lysimeters, and r(c) reached minimum values (r(c,min)) at solar radiation above 500 W m(-2). Elevated [CO2] at the lowest temperature plot increased r(c,min) by 40-49% and T-c by 1.4- 1.6 degrees C and it reduced E by 14-16% of those under ambient CO2 conditions. With the rising growth temperature, these effects of elevated [CO2] drastically decreased. The observed r(c,min) responses to temperature and [CO2] seemed to have reflected a long-term acclimation of rice to these environments. These results indicate that anticipated global warming significantly reduces the advantageous effects of elevated [CO2] on plant water use.

KEYWORDS: CARBON DIOXIDE

945

Hopkins, D.W., J.A. Chudek, E.A. Webster, and D. Barraclough. 1997. Following the decomposition of ryegrass labelled with C-13 and N-15 in soil by solid-state nuclear magnetic resonance spectroscopy. *European Journal of Soil Science 48(4):623-631.*

Investigating the biogeochemistry of plant material decomposition in soil has been restricted by difficulties extracting and identifying organic compounds. In this study the decomposition of C-13- and N-15-labelled Lolium perenne leaves mixed with mineral soil has been investigated over 224 days of incubation under laboratory conditions. Decomposition was followed using short-term rates of CO2 evolution, the amounts of C-13 and N-15 remaining were determined by mass spectrometry, and C-13 and N-15 solid-state nuclear magnetic resonance (NMR) spectroscopy was used to characterize chemically the plant material as it decomposed. After 224 days 48% of the added C-13 had been lost with a rapid period of CO2 evolution over the first 56 days. The fraction of cross- polarization magic angle spinning (CP MAS) C-13 NMR spectra represented by O-alkyl-C signal probably in carbohydrates (chemical shift, 60-90 p.p.m.) declined from 60 to 20% of the spectrum (chemical shift, 0-200 p.p.m.) over 224 days. The rate of decline of the total C-13 exceeded that of the 60-90 p.p.m. signal during the first 56 days and was similar thereafter. The fraction of the CP MAS C-13 NMR spectra represented by the alkyl- and methyl-C (chemical shift, 10-45 p.p.m.) signal increased from 5 to 14% over the first 14 days and was 19% after 224 days. CP MAS C-13 NMR of C-13- and N-15-L. perenne contained in 100-mu m aperture mesh bags incubated in the soil for 56 days indicated that the remaining material was mainly carbohydrate but there was an increase in the alkyl-and methyl- C associated with the bag's contents. After 224 days incubation of the labelled C-13- and N-15-L. perenne mixed with the soil, 40% of the added N-15 had been lost. Throughout the incubation there was only one signal centred around 100 p.p.m, detectable in the CP MAS N-15 NMR spectra. This signal corresponded to amide N-15 in peptides and may have been of plant or microbial origin or both. Although there had been substantial interaction between the added N-15 and the soil microorganisms, the associated redistribution of N-15 from plant to microbial tissues occurred within the amide region. The feasibility of following some of the component processes of plant material decomposition in soil using NMR has been demonstrated in this study and evidence that microbial synthesis contributes to the increase in alkyl- and methyl-C content of soil during decomposition has been represented.

KEYWORDS: CPMAS, ELEVATED CO2, IMMOBILIZATION, MICROBIAL BIOMASS, MINERALIZATION, NMR-SPECTROSCOPY, ORGANIC-MATTER, PARTICLE-SIZE, PLANT- MATERIAL, WHOLE SOILS

946

Horie, T., H. Nakagawa, J. Nakano, K. Hamotani, and H.Y. Kim. 1995. Temperature-gradient chambers for research on global environment change .3. a system designed for rice in kyoto, japan. *Plant, Cell and Environment 18(9):1064-1069.*

Synthesis and validation of crop models for assessment of of the impact

of elevated atmospheric CO2 concentration and anticipated global warming on crop production require crop response data obtained under field-like conditions, The temperature gradient chamber (TGC) with the facility for CO2 enrichment allows the creation of various CO2 and temperature regimes for crops over the entire growth period with relatively inexpensive construction and running costs, The TGC develops a temperature gradient along its longitudinal axis using solar energy during the day and heating at night while maintaining the natural diurnal cycle, The temperature gradient and the CO2 concentration in the TGC are regulated by computer control of the air ventilation rate through the TGC and of the CO2 release rate, Longitudinal gradients of CO2 concentration and water vapour pressure deficit of air in the TGC were generally less than 5% and +/-0.2 kPa, respectively. A CO2 enrichment experiment on rice in the TGC showed that a doubling of the CO2 concentration markedly enhanced crop dry matter production, Temperature had less effect on dry matter production, although panicle dry weight was greatly decreased at higher temperature as a result of high-temperature-induced sterility of rice spikelets, Since rice spikelets are most sensitive to high temperature at the moment of flowering, and their flowering habit is highly synchronized with the diurnal courses of environmental conditions, the TGC is a useful tool in understanding rice responses to changes in atmosphere and temperature.

KEYWORDS: CARBON DIOXIDE, RESPONSES

947
Horn, M.E., and J.M. Widholm. 1994. Photoautotrophic growth of soybean cells in suspension-culture .3. Characterization of carbon fixation products under high and low co2 levels. *Plant Cell Tissue and Organ Culture 39(3):239-244.*

A photoautotrophic soybean suspension culture (SB-P) was used to study CO2 assimilation while exposed to elevated or ambient CO2 levels. These studies showed that under elevated CO2 (5% v/v) malate is the dominant fixation product, strongly suggesting that phosphoenolpyruvate carboxylase (PEPCase) is the primary enzyme involved in carbon fixation in these cells under their normal growth conditions. Citrate and [aspartate + glutamate] were also significant fixation products during fifteen minutes of exposure to (CO2)-C-14. During the ten minute unlabeled CO2 chase however, C-14-malate continued to increase while citrate and [aspartate + glutamate] declined. Fixation of (CO2)-C-14 under ambient CO2 levels (0.037%) showed a very different product pattern as 3-phosphoglycerate was very high in the first one to two minutes followed by increases in [serine + glycine] and [aspartate + glutamate]. Hexose phosphates were also quite high initially but then declined relatively rapidly. Thus, the carbon fixation pattern at ambient CO2 levels resembles somewhat that seen in C3 leaf cells while that seen at elevated CO2 levels more closely resembles that of a C-4 plant. The initial fixation product of C-3 plants, 3-PGA, was never detectable under high CO2 conditions. These data suggest that an in vitro photoautotrophic system would be suitable for studying carbon fixation physiology during photosynthetic and non- photosynthetic growth.

KEYWORDS: CHENOPODIUM-RUBRUM, METABOLISM, PHOTOSYNTHESIS

948
Hostetler, S.W., and F. Giorgi. 1995. Effects of a 2-times-co2 climate on 2 large lake systems - pyramid lake, nevada, and yellowstone lake, wyoming. *Global and Planetary Change 10(1-4):43-54.*

The possible effects of trace-gas induced climatic changes on Pyramid and Yellowstone Lakes are assessed using a model of lake temperature. The model is driven by 3 1/2 years of hourly meteorological data obtained directly from the output of doubled-CO2 experiments (2 x CO2) conducted with a regional climate model nested in a general circulation model. The regional atmospheric model is the climate version of the National Center for Atmospheric Research/Pennsylvania State University mesoscale model, MM4. Average annual surface temperature of Pyramid Lake for the 2 X CO2 climate is 15.5 +/- 5.4 degrees C (+/- 1 sigma), 2.8 degrees C higher than the control. Annual overturn of the lake ceases as a result of these higher temperatures for the 2 x CO2 climate. Evaporation increases from 1400 mm yr(-1) in the control to 1595 mm yr(-1) in the 2 X CO2 simulation, but net water supplied to the Pyramid Lake basin increases from -6 mm yr(-1) in the control to +27 mm yr(-1) in the 2 x CO2 simulation due to increased precipitation. For the open water periods, the average annual surface temperature of Yellowstone Lake is 13.2 +/- 5.1 degrees C for the 2 x CO2 climate, a temperature 1.6 degrees C higher than the control. The annual duration of ice cover on the lake is 152 days in the 2 X CO2 simulation, a reduction of 44 days relative to the control, Warming of the lake for the 2 x CO2 climate is mostly confined to the near-surface. Simulated spring overturn for the 2 X CO2 climate occurs earlier in the year and fall overturn later than in the control. Evaporation increases from 544 mm yr(-1) to 600 mm yr(-1) in the 2 X CO2 simulation, but net water supplied to the Yellowstone Lake basin increases from +373 mm yr(-1) in the control to +619 mm yr(-1) due to increased precipitation. The effects of these climatic changes suggest possible deterioration of water quality and productivity in Pyramid Lake and possible enhancement of productivity in Yellowstone Lake.

KEYWORDS: EVAPORATION, FISH, MODEL, POTENTIAL CHANGES, SIMULATION, THERMAL HABITAT

949
Houghton, R.A. 1996. Converting terrestrial ecosystems from sources to sinks of carbon. *Ambio 25(4):267-272.*

It may be possible to sequester carbon in forests and forest products, but to date global trends in land management have resulted in a release of terrestrial carbon to the atmosphere. Over 100 PgC were released between 1850 and 1980, and during the 1980s global changes in land use (predominantly deforestation) caused a net release of 1.6 PgC yr(-1), about 25% of the total emissions of carbon dioxide from human activities and about 15% of the enhanced radiative forcing. Management practices that could change this release of terrestrial carbon to an accumulation include (i) a halt to deforestation; (ii) an expansion in the land area of forests; (iii) an increase in the stocks of carbon in existing forests; (iv) more efficient harvest and greater use of wood in long-lasting products; and (v) the substitution of wood fuels for fossil fuels. However, the rate of global warming needs management as well. Unless the warming is gradual enough to avoid widespread mortality of forests, the additional releases of carbon caused by the warming itself, through increased respiration, decay, and fires, may cancel the intended effects of forest management.

KEYWORDS: CLIMATE, CO2, DEFORESTATION, DIOXIDE, FLUX, LAND-USE CHANGE, SEQUESTRATION, TRANSIENT-RESPONSE, TROPICAL FORESTS, VEGETATION

950
Houpis, J.L.J., P.D. Anderson, J.C. Pushnik, and D.J. Anschel. 1999. Among-provenance variability of gas exchange and growth in response to long-term elevated CO2 exposure. *Water, Air, and Soil Pollution 116(1-2):403-412.*

Genetic variability can have profound effects on the interpretation of results from elevated CO2 studies, and future forest management decisions. Information on which varieties are best suited to future atmospheric conditions is needed to develop future forest management practices. A large-scale screening study of the effects of elevated CO2

on 15 half- sibling sources of genetically superior ponderosa pine (Pinus ponderosa Dougl ex P. Laws.) is presented. These sources represent multiple elevations and latitudes throughout California. Among-provenance variability in the effects of elevated CO2 on gas exchange and growth, and their correlation with geographic origin were investigated in ponderosa pine seedlings subjected to ambient or elevated CO2 concentrations (525 mu mol mol(-1) CO2, and 700 mu mol mol(-1) CO2) for more than two years in open-top chambers. Substantial among- provenance variability in growth response to elevated CO2 was evident, with 8 sources demonstrating no significant growth response to elevated CO2 while 7 sources responded positively. For all sources, elevated CO2 increased photosynthesis (ranging from 19% increase at 525 mu mol mol(-1) CO2 to 49% increase at 700 mu mol mol(-1) CO2). A modest correlation existed between geographic origin and above ground growth response to elevated CO2.

KEYWORDS: ATMOSPHERIC CO2, BIOMASS ALLOCATION, CARBON DIOXIDE, CLIMATE CHANGE, ENRICHMENT, FAMILIES, LEAVES, PHOTOSYNTHESIS, PLANT-RESPONSES, PONDEROSA PINE

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Houpis, J.L.J., J. Pushnik, D. Anschel, P. Anderson, and R. Demaree. 1995. Intraspecific variability of photosynthetic traits of pinus- ponderosa subjected to long-term exposure to elevated co2. *Plant Physiology 108(2):62.*

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Howden, S.M., G.M. McKeon, L. Walker, J.O. Carter, J.P. Conroy, K.A. Day, W.B. Hall, A.J. Ash, and O. Ghannoum. 1999. Global change impacts on native pastures in south-east Queensland, Australia. *Environmental Modelling & Software 14(4):307-316.*

Increases in atmospheric concentrations of greenhouse gases such as carbon dioxide (CO2) are likely to impact on grazing industries through direct effects on plant growth and through possible changes in climate. Assessment of the likely direction and magnitude of these impacts requires development of appropriate modelling capacities linked with experimental work. This paper documents the adaptation of an existing soil- pasture-livestock model, GRASP, to simulate system responses to changes in CO2. The adapted model is then used to compare these responses under current climate and CO2 conditions with four possible future scenarios: (1) doubled CO2; (2) doubled CO2 and increased temperature; (3) as in the previous scenario but with a drier climate; and (4) as in (2) but with a wetter climate. These studies suggest that CO2 changes alone are likely to have beneficial effects, with increased pasture growth, increased and less variable liveweight gain, and increased ground cover. However, subsoil drainage is likely to increase. Growth responses to CO2 are likely to be greater in drier years than in wetter years partly due to nitrogen limitations in the soils of the region. Increases in temperature in combination with CO2 further increased animal production due to the increased number of growing days in the cooler months. The increased rainfall scenario had few additional positive effects but further increased subsoil drainage. In contrast, the drier scenario had reduced plant and animal production when compared with current conditions even though seasonal transpiration efficiency was increased by 20% due to increased CO2.

KEYWORDS: ATMOSPHERIC CO2, BOUTELOUA-GRACILIS C-4, CLIMATE, ELEVATED CARBON-DIOXIDE, GAS-EXCHANGE, GRASS, GROWTH, PASCOPYRUM-SMITHII C-3, RESPONSES, WATER-USE

953

Hu, S.J., M.K. Firestone, and F.S. Chapin. 1998. Elevated atmospheric CO2 and soil biota. *Science 281(5376):518.*

954

Hu, S.J., M.K. Firestone, and F.S. Chapin. 1999. Soil microbial feedbacks to atmospheric CO2 enrichment. *Trends in Ecology and Evolution 14(11):433-437.*

Increased atmospheric CO2 concentration often stimulates plant photosynthesis, enhances carbon (C) allocation belowground, increases plant nutrient uptake and improves the efficiency of plant water use. Recent studies suggest that microbial responses to CO2-induced alterations in soil C, water and nutrient availability play an important role in determining ecosystem feedback to CO2 elevation. However, to date, most of the published results have been obtained from short-term experiments or from studies using high-nutrient or disturbed soils. Information on microbial responses to CO2-induced changes in natural and/or mature ecosystems with nutrient limitations is critical to predict changes in terrestrial ecosystem C storage under future CO2 scenarios.

KEYWORDS: DECOMPOSITION RATES, ELEVATED CARBON-DIOXIDE, LITTER QUALITY, MODEL ECOSYSTEM, N-AVAILABILITY, NITROGEN CYCLES, ORGANIC-MATTER, TALLGRASS PRAIRIE, TERRESTRIAL ECOSYSTEMS, WHITE CLOVER

955

Huang, B.R., J.W. Johnson, and D.S. NeSmith. 1997. Responses to root-zone CO2 enrichment and hypoxia of wheat genotypes differing in waterlogging tolerance. *Crop Science 37(2):464-468.*

Knowledge of wheat (Triticum aestivum L.) responses to CO2 and O-2 in the root environment could improve understanding of the mechanisms of waterlogging tolerance and thus help develop waterlogging-tolerant wheat plants. This experiment was designed to investigate the responses to elevated CO2 and hypoxia of two wheat genotypes, Bayles and Savannah, which differ in waterlogging tolerance. Plants were grown in a growth chamber in nutrient solutions. Nutrient solutions were bubbled with ambient air (control), N-2 containing 5 kPa O-2 and ambient CO2 (hypoxia), N-2 containing 10 kPa CO2 and ambient O- 2 (high CO2, ambient O-2), and N-2 containing 10 kPa CO2 and 5 kPa O-2 (high CO2, low O-2). Hypoxia alone had adverse effects on net photosynthesis (P-n), stomatal conductance (g(s)), water relations, leaf chlorophyll (chi) content, and shoot and root growth. The effects were greater for waterlogging-sensitive Bayles. When compared with the aerated control, the combination of elevated CO2 and hypoxia caused significant reductions in P- n, g(s), leaf water potential, and leaf chi content for Bayles, and in shoot and root growth for both Bayles and Savannah. Photosynthetic rate and leaf chi content of Savannah were increased when roots of hypoxic plants were exposed to elevated CO2, but this was not true for Bayles. Root-zone CO2 enrichment at ambient O-2 had no significant effects on shoot growth, but reduced root growth In both genotypes. The results showed that CO2 enrichment under root hypoxia can alleviate some negative effects of hypoxia on P-n, leaf chl content, and shoot growth, the effect being larger for waterlogging-tolerant Savannah.

KEYWORDS: AERENCHYMA, O2, RESPIRATION, SOIL CARBON-DIOXIDE, TOMATO PLANTS, TRANSPORT, WATER RELATIONS

956

Huang, Y.S., F.A. Street-Perrott, R.A. Perrot, P. Metzger, and G. Eglinton. 1999. Glacial-interglacial environmental changes inferred

from molecular and compound-specific delta C-13 analyses of sediments from Sacred Lake, Mt. Kenya. *Geochimica et Cosmochimica Acta 63(9):1383-1404.*

Molecular Stratigraphic analyses, including lipid distributions and compound-specific delta(13)C measurements, have been performed at 15 levels in a sediment core from Sacred Lake, Mt. Kenya, a high-altitude (2350 m a.s.l.) freshwater lake with a record extending from the last glacial (>40,000 cal. yr BP) through the present interglacial; Terrestrial and aquatic organic-matter sources were independently assessed using source-specific biomarkers. delta(13)C values of long-chain n- alkyl lipids from terrestrial higher plants exhibit large glacial to interglacial shifts: those from the last glacial maximum (LGM) (-20 to -18 parts per thousand) indicate a terrestrial vegetation dominated by C-4 grasses or sedges, whereas those from the early Holocene (-34 to -27 parts per thousand) reflect recolonization of the catchment area by C-3 plants, consistent with a rapid rise in the upper treeline. Specific algal biomarkers, including five unsaturated hydrocarbons of novel structure ascribed to the microalga Botryococcus braunii, were abundant, as confirmed by scanning electronic microscopy (SEM). An extreme delta(13)C shift of over 25 parts per thousand is displayed by the algal biomarkers, an elevated value of -5.1 parts per thousand at the last glacial maximum (LGM) contrasting with a minimum value of -30.3 parts per thousand at the beginning of the Holocene. A major change in the molecular distributions of the algal biomarkers parallels this large delta(13)C shift, with acyclic isoprenoid hydrocarbons dominating the last glacial and cyclic isoprenoid hydrocarbons the Holocene. The low atmospheric partial pressure of CO2 (pCO(2)) at the LGM would favour photosynthetic organisms possessing CO2-concentrating mechanisms, including terrestrial C-4 grasses and freshwater green algae. Hence, glacial/interglacial changes in pCO(2), and in the CO2:O-2 ratio in particular, had a significant impact on both terrestrial and aquatic ecosystems on Mt. Kenya, in addition to the effects of climate and local environmental factors. Copyright (C) 1999 Elsevier Science Ltd.

KEYWORDS: ALGA BOTRYOCOCCUS-BRAUNII, ATMOSPHERIC CO2, C-4 GRASSES, CARBON-ISOTOPE FRACTIONATION, DIOXIDE METABOLISMS, FRESH- WATER PLANTS, MOUNT KENYA, N-ALKANES, ORGANIC-MATTER, VEGETATION CHANGE

957

Hufton, C.A., R.T. Besford, and A.R. Wellburn. 1996. Effects of NO (+NO2) pollution on growth, nitrate reductase activities and associated protein contents in glasshouse lettuce grown hydroponically in winter with CO2 enrichment. *New Phytologist 133(3):495-501.*

Winter hydroponic growth of several lettuce cultivars under glass showed considerable inhibition (up to 47%) of growth after 6 wk exposure to concentrations of NO (+ NO2; 450 nl l(- 1) in total) typical of emissions from propane burners used for direct heating and CO2 enrichment. After a further 4 wk under similar conditions, however, these growth depressions were replaced by a swing into benefit so that, by harvest, pollutant-exposed lettuces were bigger and had faster assimilation rates than those growing in clean CO2-enriched air. This adaptation may partly be explained by enhanced use of NO2-derived N by lettuce leaves, a consequence of increased nitrate reductase (NaR) activities and amounts of associated NaR proteins, despite adequate nitrate also being available in the hydroponic fluid. Rates of NaR activity in the roots, by contrast, were depressed by NO (+ NO2) pollution. NaR activities were highest in early afternoon in clean or polluted air but these daily patterns did not coincide with the content of NaR-associated proteins determined by ELISA. Other mechanisms of modulating NaR activity must therefore be responsible.

KEYWORDS: DIOXIDE, EXPRESSION, GENES, LIGHT-DARK MODULATION, LONG-TERM EXPOSURES, NITRITE-REDUCTASE, NITROGEN- METABOLISM, OXIDES, PLANTS, TOMATO

958

Hughes, L., and F.A. Bazzaz. 1997. Effect of elevated CO2 on interactions between the western flower thrips, Frankliniella occidentalis (Thysanoptera: Thripidae) and the common milkweed, Asclepias syriaca. *Oecologia 109(2):286-290.*

We measured the effect of elevated CO2 on populations of the western flower thrips, Frankliniella occidentalis and on the amount of leaf damage inflicted by the thrips to one of its host plants, the common milkweed, Asclepias syriaca. Plants grown at elevated CO2 had significantly greater aboveground biomass and C:N ratios, and significantly reduced percentage nitrogen. The number of thrips per plant was not affected by CO2 treatment, but the density of thrips (numbers per gram aboveground biomass), was significantly reduced at high CO2. Consumption by thrips, expressed as the amount of damaged leaf area per capita, was significantly greater at high CO2, and the amount of leaf area damaged by thrips was increased by 33%. However overall leaf area at elevated CO2 increased by 62%, more than compensating for the increase in thrips consumption. The net outcome was that plants at elevated CO2 had 3.6 times more undamaged leaf area available for photosynthesis than plants at ambient CO2, even though they had only 1.6 times the overall amount of leaf area. This study highlights the need for measuring the effects of herbivory at the whole-plant level and also the importance of taking herbivory into account when predicting plant responses to elevated CO2.

KEYWORDS: CARBON-DIOXIDE ATMOSPHERES, CHAMBERS, GROWTH, INSECT HERBIVORE INTERACTIONS, LEPIDOPTERA, NOCTUIDAE, PAPER BIRCH, PERFORMANCE, PLANTS, RESPONSES

959

Huluka, G., D.R. Hileman, P.K. Biswas, K.F. Lewin, J. Nagy, and G.R. Hendrey. 1994. Effects of elevated co2 and water-stress on mineral concentration of cotton. *Agricultural and Forest Meteorology 70(1-4):141-152.*

Projected increases in atmospheric CO2 concentrations may alter mineral and protein levels in plant tissues, systematically affecting growth, nutrient cycling and utilization, residue decomposition, and insect-plant interactions in the future. The free-air CO2 enrichment (FACE) system provided an opportunity to monitor seasonal trends in nutrient status and crude protein content of cotton (Gossypium hirsutum L. cv. Deltapine 77) grown in a natural field setting without the limitations often imposed by growth chambers or reduced rooting volumes. In 1990, plants were exposed to two levels of atmospheric CO2 (FACE, almost-equal-to 550 mumol mol-1 and CONTROL, almost-equal-to 370 mumol mol-1) and two irrigation regimes (100% and 75% replacement of evapotranspiration) beginning in early July. Cotton leaves, stem, and roots were sampled at different times during the season and analyzed for C, N, Ca, K, Mg, P, Cu, Fe, Mn, Zn, B, Mo, Si and protein. The N and protein concentrations of leaves, stems and roots were significantly lower in FACE plants than in CONTROL plants, but C:N ratios were higher for the FACE plants than the CONTROL plants. Some other elements were significantly affected by CO2 enrichment, but not for all dates and all plant tissues. There were no significant effects in any of the data because of the irrigation treatment or the irrigation-CO2 interaction. Reductions in tissue N and protein concentrations and the increases in the C:N with CO2 enrichment have important implications for agricultural and natural systems and demand additional research.

KEYWORDS: ACCLIMATION, CARBON DIOXIDE, DRY-MATTER, ENRICHMENT, GROWTH, LEPIDOPTERA, NITROGEN, NUTRIENT CONCENTRATIONS, PLANTS, STARCH

960

Humphries, S.W., and S.P. Long. 1995. Wimovac - a software package for modeling the dynamics of plant leaf and canopy photosynthesis. *Computer Applications in the Biosciences 11(4):361-371.*

The ability to predict net carbon exchange and production of vegetation in response to predicted atmospheric and climate change is critical to assessing the potential impacts of these changes. Mathematical models provide an important tool in the study of whole plant, canopy and ecosystem responses to global environmental change. Because this requires prediction beyond experience, mechanistic rather than empirical models are needed. The uniformity and strong understanding of the photosynthetic process, which is the primary point of response of plant production to global atmospheric change, provides a basis for such an approach. Existing modelling systems have been developed primarily for expert modellers and have not been easily accessible to experimentalists, managers and students. Here we describe a modular modelling system operating within Winnows to provide this access. WIMOVAC (Windows Intuitive Model of Vegetation response to Atmosphere and Climate Change) is designed to facilitate the modelling of various aspects of plant photosynthesis with particular emphasis on the effects of global climate change. WIMOVAC has been designed to run on IBM PC-compatible computers running Microsoft Windows. The package allows the sophisticated control of the simulation processes for photosynthesis through a standardized Windows user interface and provides automatically formatted results as either tabulated data or as a range of customizable graphs. WIMOVAC has been written in Microsoft Visual Basic, to facilitate the rapid development of user-friendly modules within the familiar Windows framework, while allowing a structured development. The highly interactive nature of controls adopted by WIMOVAC makes it suitable for research, management and educational purposes.

KEYWORDS: C-3, CARBON DIOXIDE, ELEVATED CO2, RESPONSES, YIELD

961

Hungate, B.A., J. Canadell, and F.S. Chapin. 1996. Plant species mediate changes in soil microbial N in response to elevated CO2. *Ecology 77(8):2505-2515.*

The effect of elevated CO2 on plant-microbial interactions and nitrogen (N) cycling is critical to predicting plant growth responses to elevated CO2, because plant growth is often N- limited. We investigated whether the effects of elevated CO2 on plant-microbial N dynamics differed among six annual plant species: three European grasses that have invaded California grasslands, and one grass and two forbs native to California serpentine grassland. Elevated CO2 altered plant N pools and (NH4+)-N-15 uptake, but the direction and magnitude of the changes were species dependent. The introduced grasses showed increased plant N pools and (NH4+)-N-15 uptake, whereas the native species showed smaller increases or even decreases in plant N pools and N-15(4)+ uptake. Under nutrient enrichment, soil microbial N and (NH4+)-N-15 uptake differed among soils with different plant species, but they were not affected by elevated CO2. At low nutrients, elevated CO2 altered soil microbial N and (NH4+)-N-15 uptake, but the direction and magnitude of the changes were species dependent. The changes in soil microbial N were positively correlated with changes in the plant N pool, suggesting that there was no trade-off in N uptake between plants and microbes. These results also suggest that plant species composition will partly determine the direction of changes in soil N cycling in response to elevated CO2.

KEYWORDS: ANNUAL GRASSLAND, ATMOSPHERIC CO2, CARBON DIOXIDE, DECOMPOSITION, DYNAMICS, ECOSYSTEMS, FOREST, GROWTH, LEAF LITTER, NITROGEN CYCLES

962

Hungate, B.A., F.S. Chapin, H. Zhong, E.A. Holland, and C.B. Field. 1997. Stimulation of grassland nitrogen cycling under carbon dioxide enrichment. *Oecologia 109(1):149-153.*

Nitrogen (N) limits plant growth in many terrestrial ecosystems, potentially constraining terrestrial ecosystem response to elevated CO2. In this study, elevated CO2 stimulated gross N mineralization and plant N uptake in two annual grasslands. In contrast to other studies that have invoked increased C input to soil as the mechanism altering soil N cycling in response to elevated CO2, increased soil moisture, due to decreased plant transpiration in elevated CO2, best explains the changes we observed. This study suggests that atmospheric CO2 concentration may influence ecosystem biogeochemistry through plant control of soil moisture.

KEYWORDS: ATMOSPHERIC CO2, BACTERIA, ECOSYSTEMS, FEEDBACK, MINERALIZATION, NITRATE, NITRIFICATION, PLANT, RESPONSES, SOILS

963

Hungate, B.A., P. Dijkstra, D.W. Johnson, C.R. Hinkle, and B.G. Drake. 1999. Elevated CO2 increases nitrogen fixation and decreases soil nitrogen mineralization in Florida scrub oak. *Global Change Biology 5(7):781-789.*

We report changes in nitrogen cycling in Florida scrub oak in response to elevated atmospheric CO2 during the first 14 months of experimental treatment. Elevated CO2 stimulated above-ground growth, nitrogen mass, and root nodule production of the nitrogen-fixing vine, Galactia elliottii Nuttall. During this period, elevated CO2 reduced rates of gross nitrogen mineralization in soil, and resulted in lower recovery of nitrate on resin lysimeters. Elevated CO2 did not alter nitrogen in the soil microbial biomass, but increased the specific rate of ammonium immobilization (NH4+ immobilized per unit microbial N) measured over a 24-h period. Increased carbon input to soil through greater root growth combined with a decrease in the quality of that carbon in elevated CO2 best explains these changes. These results demonstrate that atmospheric CO2 concentration influences both the internal cycling of nitrogen (mineralization, immobilization, and nitrification) as well as the processes that regulate total ecosystem nitrogen mass (nitrogen fixation and nitrate leaching) in Florida coastal scrub oak. If these changes in nitrogen cycling are sustained, they could cause long-term feedbacks to the growth responses of plants to elevated CO2. Greater nitrogen fixation and reduced leaching could stimulate nitrogen-limited plant growth by increasing the mass of labile nitrogen in the ecosystem. By contrast, reduced nitrogen mineralization and increased immobilization will restrict the supply rate of plant-available nitrogen, potentially reducing plant growth. Thus, the net feedback to plant growth will depend on the balance of these effects through time.

KEYWORDS: ANNUAL GRASSLAND, ATMOSPHERIC CO2, CARBON-DIOXIDE ENRICHMENT, GROWTH-RESPONSE, LONG-TERM, PLANTS, ROOT NODULE ACTIVITY, SYMBIOTIC N-2 FIXATION, TRIFOLIUM- REPENS, WHITE CLOVER

964

Hungate, B.A., E.A. Holland, R.B. Jackson, F.S. Chapin, H.A. Mooney, and C.B. Field. 1997. The fate of carbon in grasslands under carbon dioxide enrichment. *Nature 388(6642):576-579.*

The concentration of carbon dioxide (CO2) in the Earth's atmosphere is rising rapidly(1), with the potential to alter many ecosystem processes. Elevated CO2 often stimulates photosynthesis(2), creating the possibility that the terrestrial biosphere will sequester carbon in response to rising atmospheric CO2 concentration, partly offsetting emissions from fossil-

fuel combustion, cement manufacture, and deforestation(3,4). However, the responses of intact ecosystems to elevated CO2 concentration, particularly the below-ground responses, are not well understood. Here we present an annual budget focusing on below-ground carbon cycling for two grassland ecosystems exposed to elevated CO2 concentrations. Three years of experimental CO2 doubling increased ecosystem carbon uptake, but greatly increased carbon partitioning to rapidly cycling carbon pools below ground, This provides an explanation for the imbalance observed in numerous CO2 experiments, where the carbon increment from increased photosynthesis is greater than the increments in ecosystem carbon stocks. The shift in ecosystem carbon partitioning suggests that elevated CO2 concentration causes a greater increase in carbon cycling than in carbon storage in grasslands.

KEYWORDS: ATMOSPHERIC CO2 ENRICHMENT, BUDGET, GROWTH, IMPACT, NITROGEN, PHOTOSYNTHESIS, RESPONSES, ROOT, TERRESTRIAL ECOSYSTEMS, WATER

965

Hungate, B.A., R.B. Jackson, C.B. Field, and F.S. Chapin. 1996. Detecting changes in soil carbon in CO2 enrichment experiments. *Plant and Soil 187(2):135-145.*

After four growing seasons, elevated CO did not significantly alter surface soil C pools in two intact annual grasslands. However, soil C pools in these systems are large compared to the likely changes caused by elevated CO2. We calculated statistical power to detect changes in soil C, using an approach applicable to all elevated CO2 experiments. The distinctive isotopic signature of the fossil-fuel-derived CO2 added to the elevated CO2 treatment provides a C tracer to determine the rate of incorporation of newly-fixed C into soil. This rate constrains the size of the possible effect of elevated CO2 on soil C, Even after four years of treatment, statistical power to detect plausible changes in soil C under elevated CO2 is quite low. Analysis of other elevated CO2 experiments in the literature indicates that either CO2 does not affect soil C content, or that reported CO2 effects on soil C are too large to be a simple consequence of increased plant carbon inputs, suggesting that other mechanisms are involved, or that the differences are due to chance. Determining the effects of elevated CO2 on total soil C and long-term C storage requires more powerful experimental techniques or experiments of longer duration.

KEYWORDS: AMBIENT, BIOMASS PRODUCTION, DYNAMICS, ELEVATED CO2, GRASSLAND, NITROGEN, PLANTS, RESPONSES, TALLGRASS PRAIRIE, TEMPERATURE

966

Hungate, B.A., T.E. Jordan, R.B. Jackson, and B.G. Drake. 1997. Atmospheric nitrogen deposition. *Science 275(5301):739-740.*

KEYWORDS: CARBON DIOXIDE, CO2- ENRICHMENT, GROWTH, PISUM-SATIVUM, PLANTS

967

Hungate, B.A., C.P. Lund, H.L. Pearson, and F.S. Chapin. 1997. Elevated CO2 and nutrient addition alter soil N cycling and N trace gas fluxes with early season wet-up in a California annual grassland. *Biogeochemistry 37(2):89-109.*

We examined the effects of growth carbon dioxide (CO2) concentration and soil nutrient availability on nitrogen (N) transformations and N trace gas fluxes in California grassland microcosms during early-season wet-up, a time when rates of N transformation and N trace gas flux are high. After plant senescence and summer drought, we simulated the first fall rains and examined N cycling. Growth at elevated CO2 increased root production and root carbon:nitrogen ratio, Under nutrient enrichment, elevated CO2 increased microbial N immobilization during wet-up, leading to a 43% reduction in gross nitrification and a 55% reduction in NO emission from soil. Elevated CO2 increased microbial N immobilization at ambient nutrients, but did not alter nitrification or NO emission. Elevated CO2 did not alter soil emission of N2O at either nutrient level. Addition of NPK fertilizer (1:1:1) stimulated N mineralization and nitrification, leading to increased N2O and NO emission from soil, The results of our study support a mechanistic model in which elevated CO2 alters soil N cycling and NO emission: increased root production and increased C:N ratio in elevated CO2 stimulate N immobilization, thereby decreasing nitrification and associated NO emission when nutrients are abundant. This model is consistent with OUT basic understanding of how C availability influences soil N cycling and thus may apply to many terrestrial ecosystems.

KEYWORDS: DECOMPOSITION, DRY SOIL, EMISSIONS, FOREST, LITTER QUALITY, MICROBIAL BIOMASS, NITRIC-OXIDE, NITROGEN

968

Hunsaker, D.J., G.R. Hendrey, B.A. Kimball, K.F. Lewin, J.R. Mauney, and J. Nagy. 1994. Cotton evapotranspiration under field conditions with co2 enrichment and variable soil-moisture regimes. *Agricultural and Forest Meteorology 70(1-4):247-258.*

The CO2 concentration of the atmosphere is predicted to double by the next century, and this is expected to increase significantly the growth and yield of many important agricultural crops. One consequence of larger and more vigorous plants may be increased crop evapotranspiration (ET) and irrigation water requirements. The objective of this work was to determine ET of cotton (Gossypium hirsutum L. cv. 'Deltapine 77') grown under ambient (about 370 mumol mol-1) and enriched (550 mumol mol-1) CO2 concentrations for both well- watered and water-stress irrigation managements. Studies were conducted in 1990 and 1991 within a large, drip-irrigated cotton field in central Arizona. Cotton ET was measured during the growing seasons using a soil water balance, based on neutron gauge soil water measurements. ET, for periods from 7 to 14 days, was not significantly different between ambient and enriched CO2 treatments at the 0.05 probability level, and the total seasonal ET for the CO2 treatments varied by 2% or less in either year. However, water-stress treatments, which were initiated on 3 July (day of year (DOY) 184) in 1990 and on 20 May (DOY 128) in 1991, had significantly lower ($P < 0.05$) ET than well-watered treatments starting at the end of July in 1990 and in early July in 1991 when the plants were about 75-90 days old. The result that CO2 enrichment to 550 mumol mol-1 did not significantly change the ET of cotton was consistent with the results of co-investigators who measured ET in the same experiments using stem flow gauges and an energy balance. This result implies that irrigation water use would not have to be increased to produce cotton in a future high-CO2 world. However, if a concomitant change in climate occurs, such as global warming, cotton evapotranspiration may change in response to the changed weather condition.

KEYWORDS: CARBON DIOXIDE, WATER-USE, YIELD

969

Hunsaker, D.J., B.A. Kimball, P.J. Pinter, R.L. LaMorte, and G.W. Wall. 1996. Carbon dioxide enrichment and irrigation effects on wheat evapotranspiration and water use efficiency. *Transactions of the Asae 39(4):1345-1355.*

Evapotranspiration (ET) and water use efficiency were evaluated for two spring wheat crops, grown in a drip-irrigated field under ambient (about 370 mu mol mol(-1)) and enriched (550 mu mol mol(-1)) carbon dioxide

(CO2) concentrations during the 1992-1993, and 1993-1994, Free-Air CO Enrichment (FACE) experiments in central Arizona. CO2-enriched (FACE) and ambient CO2 (CONTROL) treatments were replicated in four circular plots, 25 m in diameter, and well-watered (WET) and water- stressed (DRY) irrigation treatments were imposed on one-half of each plot. Wheat ET, measured over discrete time periods of several days by a soil water balance, was significantly higher for WET than DRY irrigation treatments after the first week in March in both years. Differences in ET between CO2 treatments during the season were generally small, although there was a consistent trend towards decreased ET for the FACE over CONTROL under the well-watered irrigation regime. The two-year average reduction in seasonal ET owing to the FACE treatment was about 5% under WET irrigation and was consistent with the results from two parallel investigations that used an energy balance and sap flow measurements. Under the DRY irrigation treatment, seasonal ET was 5 and 0.9% higher for the FACE treatment in the first and second years, respectively. Water use efficiency (grain yield per unit seasonal ET) was significantly higher for FACE treatments; 15 and 24% higher than CONTROL under DRY irrigation, and 13 and 18% higher than CONTROL under WET irrigation. The results indicate that irrigation requirements for fully irrigated wheat may be slightly lower in the future high-CO2 environment.

KEYWORDS: CO2- ENRICHMENT, COTTON, FACILITY, FIELD, TRANSPIRATION, YIELD

970

Hunt, H.W., E.T. Elliott, J.K. Detling, J.A. Morgan, and D.X. Chen. 1996. Responses of a C-3 and a C-4 perennial grass to elevated CO2 and temperature under different water regimes. *Global Change Biology 2(1):35-47.*

An experiment was carried out to determine the effects of elevated CO2, elevated temperatures, and altered water regimes in native shortgrass steppe. Intact soil cores dominated by Bouteloua gracilis, a C-4 perennial grass, or Pascopyrum smithii, a C-3 perennial grass, were placed in growth chambers with 350 or 700 mu L L(-1) atmospheric CO2, and under either normal or elevated temperatures. The normal regime mimicked field patterns of diurnal and seasonal temperatures, and the high-temperature regime was 4 degrees C warmer. Water was supplied at three different levels in a seasonal pattern similar to that observed in the field. Total biomass after two growing seasons was 19% greater under elevated CO2, with no significant difference between the C-3 and C-4 grass. The effect of elevated CO2 on biomass was greatest at the intermediate water level. The positive effect of elevated CO2 on shoot biomass was greater at normal temperatures in B. gracilis, and greater at elevated temperatures in P. smithii. Neither root-to-shoot ratio nor production of seed heads was affected by elevated CO2. Plant tissue N and soil inorganic N concentrations were lower under elevated CO2, but no more so in the C-3 than the C-4 plant. Elevated CO2 appeared to increase plant N limitation, but there was no strong evidence for an increase in N limitation or a decrease in the size of the CO2 effect from the first to the second growing season. Autumn samples of large roots plus crowns, the perennial organs, had 11% greater total N under elevated CO2, in spite of greater N limitation.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, ECOSYSTEMS, GROWTH-RESPONSE, NITROGEN CONCENTRATION, PHOTOSYNTHESIS, RISING CO2, ROOT, SHORTGRASS PRAIRIE, TALLGRASS PRAIRIE, TUSSOCK TUNDRA

971

Hunt, H.W., J.A. Morgan, and J.J. Read. 1998. Simulating growth and root-shoot partitioning in prairie grasses under elevated atmospheric CO2 and water stress. *Annals of Botany 81(4):489-501.*

We constructed a model simulating growth, shoot-root partitioning, plant nitrogen (N) concentration and total nonstructural carbohydrates in perennial grasses. Carbon (C) allocation was based on the concept of a functional balance between root and shoot growth, which responded to variable plant C and N supplies. Interactions between the plant and environment were made explicit by way of variables for soil water and soil inorganic N. The model was fitted to data on the growth of two species of perennial grass subjected to elevated atmospheric CO2 and water stress treatments. The model exhibited complex feedbacks between plant and environment, and the indirect effects of CO2 and water treatments on soil water and soil inorganic N supplies were important in interpreting observed plant responses. Growth was surprisingly insensitive to shoot-root partitioning in the model, apparently because of the limited soil N supply, which weakened the expected positive relationship between root growth and total N uptake. Alternative models for the regulation of allocation between shoots and roots were objectively compared by using optimization to find the least squares fit of each model to the data. Regulation by various combinations of C and N uptake rates, C and N substrate concentrations, and shoot and root biomass gave nearly equivalent fits to the data, apparently because these variables were correlated with each other. A partitioning function that maximized growth predicted too high a root to shoot ratio, suggesting that partitioning did not serve to maximize growth under the conditions of the experiment (C) 1998 Annals of Botany Company.

KEYWORDS: ALLOCATION, C-4 PLANTS, CARBON, CLIMATE CHANGE, MODEL, NITROGEN, PLANT GROWTH, RESPONSES, SHORTGRASS PRAIRIE, SOIL

972

Hunt, H.W., M.J. Trlica, E.F. Redente, J.C. Moore, J.K. Detling, T.G.F. Kittel, D.E. Walter, M.C. Fowler, D.A. Klein, and E.T. Elliott. 1991. Simulation-model for the effects of climate change on temperate grassland ecosystems. *Ecological Modelling 53(3-4):205-246.*

We studied the responses of temperate grasslands to climate change using a grassland ecosystem model which simulates seasonal dynamics of shoots, roots, soil water, mycorrhizal fungi, saprophytic microbes, soil fauna, inorganic nitrogen, plant residues and soil organic matter. Forty-year simulations were made for several climate change scenarios. The model was driven with observed weather and with combinations of elevated atmospheric CO2, elevated temperature, and either increased or decreased precipitation. Precipitation and CO2 level accounted for most of the variation among climate change treatments in the responses of soil, plants, animals and microbes. Elevated temperature extended the growing season but depressed photosynthesis in the summer, with little net effect on annual primary production. Doubling CO2 (1) caused persistent increases in primary production, in spite of greater nitrogen limitation, and (2) led to greater storage of carbon in plant residues and soil organic matter. The increased carbon storage was not great enough to keep pace with the present rate of increase in atmospheric CO2.

KEYWORDS: ATMOSPHERIC CO2 ENRICHMENT, BIOMASS DYNAMICS, BLUE-GRAMA, BOUTELOUA-GRACILIS, CARBON DIOXIDE, CRESTED WHEATGRASS, ELEVATED CO2, NATIVE SHORTGRASS ECOSYSTEM, SOIL-WATER, USE EFFICIENCY

973

Hunt, R., and G.M. Constable. 1993. Multifactorial growth-responses in holcus-lanatus - optima and limiting factors. *Annals of Botany 71(4):357-368.*

KEYWORDS: CO2- ENRICHMENT, INTEGRATED ANALYSIS, LIGHT INTERCEPTION, LOCAL FLORA, PLANT GROWTH, TEMPERATURE, WEIGHT, WHEAT, YIELD

974

Hunt, R., and J.H.C. Cornelissen. 1997. Components of relative growth rate and their interrelations in 59 temperate plant species. *New Phytologist 135(3):395-417.*

Three groups of species (21 herbaceous monocotyledons, 22 herbaceous dicotyledons and 16 woody dicotyledons), including representatives of a wide range of natural habitats and life forms in inland Britain, were grown in the seedling phase in a resource-rich controlled environment and assessed over a 14-day period (21 d in the case of woody species). Mean values of relative growth rate (RGR), Unit leaf rate (ULR), leaf area ratio (LAR), leaf weight fraction (LWF), specific leaf area (SLA), and the root-shoot allometric coefficient were derived. In herbaceous species, the grand mean RGR was 0.20 d(-1), comparable to values previously recorded. For woody species, the mean was 0.09 d(-1). An existing assumption linking high RGR to high allocation to photosynthetic biomass was upheld by comparisons made between groups. Within groups, however, no pattern of this kind could be demonstrated. When photosynthetically active radiation was increased from 125 to 250 mu mol m(-2) s(-1), ULR was increased almost pro rata. The parallel response in RGR was only slight, being offset by considerable reductions in LAR. The apparent mean quantum yield for photosynthesis in herbaceous species (whole-plant d. wt basis) was 0.60 g mol(-1). There was no significant dependence of RGR on ULR in any of the three groups of species, although the absolute magnitude of ULR declined in the order: herbaceous monocotyledons > herbaceous dicotyledons > woody dicotyledons. In all three groups, RGR was strongly dependent upon LAR but no differences emerged in absolute scale of LAR. The absolute scale of mean LWF decreased from herbaceous to woody species, but the dependence of LAR on LWF strengthened. Groups showed no systematic differences in magnitude of SLA, but the correlation of LAR with SLA was strong throughout. Multiple regression showed that the leading determinants of RGR were ULR and SLA in herbaceous species and LWF in woody species. Principal components analyses (PCA) on each of the three groups explained at least 77% of variation and agreed closely with an optimal (non-hierarchical) classification. Only six cluster 'types' were recognized out of the 16 theoretically possible combinations of 'high' or 'low' values of the four growth parameters. Strong evidence of evolutionary trade-offs emerged, most strikingly in that high RGR was never seen in combination with low SLA. The morphological/physiological types identified by an all-groups PCA separated woody from the herbaceous species, but dicotyledons were almost congruent with the monocotyledons. The non-growth-analytical attributes most strongly correlated with mean RGR were percentage yield at a low level of mineral nutrients, leaf nitrogen concentration, and seed weight. It was concluded that mean RGR plays a central role in the identification of pathways of evolutionary specialization in herbaceous species.

KEYWORDS: ALLOCATION PATTERNS, CARBON DIOXIDE, CHEMICAL-COMPOSITION, CO2- ENRICHMENT, EMERGENT MACROPHYTES, GRASS, LEAF, ROOT, SEED, STRATEGIES

975

Hunt, R., D.W. Hand, M.A. Hannah, and A.M. Neal. 1991. Response to CO2 enrichment in 27 herbaceous species. *Functional Ecology 5(3):410-421.*

CO2-enrichment experiments were performed on 25 British native species of widely differing ecology. Two crops, one C3 (sunflower) and one C4 (maize), were also included. The background regime involved full-light, glasshouse conditions, non-limiting supplies of water and mineral nutrients and a daytime mean temperature of 18-degrees-C. Four CO2 treatments were maintained at nominal concentrations of 350, 500, 650 or 800 v.p.m. over a 56-day period. Hyperbolic functions were fitted to yield vs CO2 concentration. The functions were then used to generate predictions of Q540/350 (the quotient of present yield under the CO2 regime predicted for the year 2050) and Q700/350 (the quotient of present yield predicted for a doubling of ambient CO2 concentration). Values of Q540/350 for whole-plant dry weight ranged from below 1.01 to 1.49, the upper values being at least similar in magnitude to those already observed in C3 crops. The mean value of whole-plant Q700/350 for 11 species of near-competitive strategy was 1.43. Four species of stress-tolerant or ruderal strategy had a mean Q700/350 of only 1.05. High CO2 responsiveness was common only within the competitive strategy and its close relations. The fitted Q540/350 for species of the pure strategy was 1.38. In the centre of the strategic range the fitted value was 1.12, and at the far extreme, the value for species of ruderal or stress-tolerant strategy was only 1.03.

976

Hunt, R., D.W. Hand, M.A. Hannah, and A.M. Neal. 1993. Further responses to co2 enrichment in british herbaceous species. *Functional Ecology 7(6):661-668.*

1. CO2-enrichment experiments have been performed on 15 British herbaceous species of widely differing ecology The conditions of growth were very similar to those used in a previous study and involved full-light glasshouse conditions, non-Limiting supplies of water and mineral nutrients and a daytime mean temperature of 18 degrees C. Four CO2 treatments were maintained (350, 500, 650 or 800 vpm) over periods of 49 or 52 days. 2. Hyperbolic functions were fitted to yield vs CO2 concentration. The functions were used to generate predictions of Q(540/350) (the quotient of the 'present' yield which is predicted for the CO2 regime expected by the year 2050) and Q(700/350) (the quotient predicted for a doubling of the present ambient CO2 concentration). Values of Q(540/350) for whole-plant dry weight ranged from below 1.00 to 1.19. The mean Value of whole-plant Q(700/350) for eight species of 'competitive' functional type was 1.13. Six species of 'stress-tolerant' or 'ruderal' type had a mean Q(700/350) Of only 1.07. 3. The new data support and amplify an earlier conclusion that high CO2 responsiveness is normal only within the competitive functional type (or 'strategy') and its close relations. A simplified and more broadly based general prediction now gives a fitted percentage increase after approximately 7 weeks' growth of 27% for species of broadly competitive strategy In the centre of the range of functional types the fitted values now range from 13 to 20%, and at the far extremes, the value for species of either the ruderal or the stress-tolerant type is now 6%. The gradient of this response is statistically significant, but less steep than that previously reported.

977

Hunt, R., D.W. Hand, M.A. Hannah, and A.M. Neal. 1995. Temporal and nutritional influences on the response to elevated co2 in selected british grasses. *Annals of Botany 75(2):207-216.*

To investigate the duration of the CO2 response and its interaction with mineral nutrition, CO2-enrichment experiments were performed on four British grasses of differing ecology and functional type: Arrhenatherum elatius (L.) Beauv., Festuca ovina L., Festuca rubra L. and Poa annua L. Naturally-lit, glasshouse cabinets were used, with a non-limiting water supply and a daytime mean temperature of 18 degrees C. Two CO2 treatments were maintained at nominal concentrations of 350 and 700 vpm and were combined factorially with two levels of balanced mineral nutrition at conductivities of 0.1 and 1 mS cm(-1). Harvests took place at planting-out, and at 16, 37 and 58 d thereafter. Fitted curves were used to derive instantaneous values of total dry weight, relative growth rate (RGR), shoot weight fraction (SWF) and unit shoot rate (USR) for all combinations of species, CO2 level, nutrient level and time of harvesting. At the higher nutrient level there was a reasonably close

agreement with previous estimates of the CO2 response in the four species. The response, if any, most often arose from an increase in USR being accompanied by a less than proportionate decline in SWF. Responses were sustained throughout the period studied. At the lower nutrient level, all species showed a CO2 response initially, but this declined at a rate which was inversely related to the CO2-responsiveness of the species at the higher nutrient level. The underlying ontogenetic drift appeared to be markedly towards adjustment in SWF and away from that of USR. However, this drift was retarded, suspended or even reversed by low-nutrient conditions and/or by high CO2 responsiveness in the species itself.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, GROWTH-ANALYSIS, NITROGEN, PLANT GROWTH, RATIO, ROOT, SEEDLINGS, SHOOT, TREES

978

Huntley, B. 1995. Plant-species response to climate-change - implications for the conservation of european birds. *Ibis 137:S127-S138.*

Wildlife conservation faces new and extreme challenges in adapting to the accelerating dynamics of a world responding to global change, The Quaternary record shows that migration has been the usual response of organisms to environmental change, This record also reveals that forecast future climate changes are of a magnitude and in a direction unprecedented in recent earth history: the rate of these changes is likely also to surpass that of any comparable change during the last 2.4 million years, The relationship between a species' geographical distribution and present climate may be modelled by a surface representing the probability of encountering that species under given combinations of climate conditions, This 'climate response surface' then may be used to simulate potential future distributions of the species in response to forecast climate scenarios, Such simulations reveal the magnitude of the impacts of these forecast climate changes. Although to date this approach has been applied in Europe only to plants, it promises to be valuable also for other groups of organisms, including birds. Some bird species, however, may respond more directly to either habitat structure or presence of specific food plants; such factors may be incorporated into the models when required, The magnitude of likely vegetation changes necessitates a global approach to conservation if there is to be any hope of long-term success, Successful conservation of global biodiversity will depend upon conservation of the global environment and limitation of the human population much more than upon parochial efforts to conserve locally rare organisms or habitats.

KEYWORDS: CO2, COMMUNITIES, GRADIENTS, MIGRATION, MODEL, NORTH-AMERICA, POLLEN, SURFACES

979

Huntley, B., P.M. Berry, W. Cramer, and A.P. McDonald. 1995. Modelling present and potential future ranges of some European higher plants using climate response surfaces. *Journal of Biogeography 22(6):967-1001.*

It is hypothesized that the principal features of higher plant distributions at continental scales are determined by the macroclimate. Bioclimate data have been computed on a 50 km grid across Europe. Along with published maps of higher plant distributions based upon the same grid, these data have been used to derive climate response surfaces that model the relationship between a species' distribution and the present climate. Eight species representative of a variety of phytogeographic patterns have been investigated. The results support the hypothesis that the European distributions of all eight species are principally determined by macroclimate and illustrate the nature of the climatic constraints upon each species. Simulated future distributions in equilibrium with 2 x CO2 climate scenarios derived from two alternative GCMs show that all of the species are likely to experience major shifts in their potential range if such climatic changes take place. Some species may suffer substantial range and population reductions and others may face the threat of extinction. The rate of the forecast climate changes is such that few, if any, species may be able to maintain their ranges in equilibrium with the changing climate. In consequence, the transient impacts upon ecosystems will be varied but often may lead to a period of dominance by opportunist, early-successional species. Our simulations of potential ranges take no account of such factors as photoperiod or the direct effects of CO2, both of which may substantially alter the realized future equilibrium.

KEYWORDS: BRITISH-ISLES, GRADIENTS, MIGRATION, NORTH-AMERICA, POLLEN, REGRESSION, SPECIES RESPONSE, TILIA-CORDATA, VEGETATION

980

Hurry, V., M. Tobiaeson, S. Kromer, P. Gardestrom, and G. Oquist. 1995. Mitochondria contribute to increased photosynthetic capacity of leaves of winter rye (secale-cereale L) following cold- hardening. *Plant, Cell and Environment 18(1):69-76.*

Cold-hardening of winter rye (Secale cereale L. cv. Musketeer) increased dark respiration from -2.2 to -3.9 mu mol O-2 m(- 2)s(-1) and doubled light- and CO2-saturated photosynthesis at 20 degrees C from 18.1 to 37.0 mu mol O-2 m(-2) s(-1). We added oligomycin at a concentration that specifically inhibits oxidative phosphorylation to see whether the observed increase in dark respiration reflected an increase in respiration in the light, and whether this contributed to the enhanced photosynthesis of cold-hardened leaves, Oligomycin inhibited light- and CO2-saturated rates of photosynthesis in non- hardened and cold-hardened leaves by 14 and 25%, respectively, and decreased photochemical quenching of chlorophyll a fluorescence to a greater degree in cold-hardened than in non- hardened leaves, These data indicate an increase both in the rate of respiration in the light, and in the importance of respiration to photosynthesis following cold-hardening, Analysis of metabolite pools indicated that oligomycin inhibited photosynthesis by limiting regeneration of ribulose- 1,5-bisphosphate, This limitation was particularly severe in cold-hardened leaves, and the resulting low 3-phosphoglycerate pools led to a feed-forward inhibition of sucrose-phosphate synthase activity, Thus, it does not appear that oxidative phosphorylation supports the increase in photosynthetic O-2 evolution following cold-hardening by increasing the availability of cytosolic ATP, The data instead support the hypothesis that the mitochondria function in the light by using the reducing equivalents generated by nan-cyclic photosynthetic electron transport.

KEYWORDS: ACCUMULATION, BARLEY HORDEUM-VULGARE, LOW-TEMPERATURE, METABOLISM, OXIDATIVE-PHOSPHORYLATION, PROTOPLASTS, RESPIRATION, SUCROSE PHOSPHATE SYNTHASE, TERM PHOTOINHIBITION, WHEAT

981

Hussain, M.W., L.H. Allen, and G. Bowes. 1999. Up-regulation of sucrose phosphate synthase in rice grown under elevated CO2 and temperature. *Photosynthesis Research 60(2-3):199-208.*

Rice (Oryza sativa L. cv. IR-30) was grown season-long in outdoor, controlled-environment chambers at 33 Pa CO2 with day/night/paddy-water temperatures of 28/21/25 degrees C, and at 66 Pa CO2 with five different day/night/paddy-water temperature regimes (25/18/21, 28/21/25, 31/24/28, 34/27/31 and 37/30/34 degrees C). Sucrose phosphate synthase (SPS) activities in leaf extracts at 21, 48 and 81 days after planting (DAP) were assayed under saturating and selective (limiting) conditions. Diel SPS activity data indicated that rice SPS was light regulated; with up to 2.2-fold higher rates during the day.

Throughout the growth season, leaf SPS activities were up-regulated in the CO2-enriched plants, averaging 20 and 12% higher than in ambient-CO2 grown plants in selective and saturating assays, respectively. Similarly, SPS activities increased 2.4% for each 1 degrees C rise in growth temperature from 25 to 34 degrees C, but decreased 11.5% at 37 degrees C. Leaf sucrose content was higher, and mirrored SPS activity better, than starch, although starch was more responsive to CO2 treatment. Leaf sucrose and starch contents were significantly higher throughout the season in plants at elevated CO2, but the N content averaged 6.5% lower. Increasing growth temperatures from 25 to 37 degrees C caused a linear decrease (62%) in leaf starch content, but not in sucrose. Consequently, the starch:sucrose ratio declined with growth temperature. The data are consistent with the hypothesis that the up-regulation of leaf SPS may be an acclimation response of rice to optimize the utilization and export of organic-C with the increased rates of inorganic-C fixation in elevated CO2 or temperature growth regimes.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, CARBON-DIOXIDE CONCENTRATION, GENE-EXPRESSION, LEAVES, METABOLISM, PHASEOLUS-VULGARIS, PHOTOSYNTHESIS, PLANT GROWTH, RESPONSES

982

Hutchin, P.R., M.C. Press, J.A. Lee, and T.W. Ashenden. 1995. Elevated concentrations of co2 may double methane emissions from mires. *Global Change Biology 1(2):125-128.*

The potential impact of an increase in methane emissions from natural wetlands on climate change models could be very large. We report a profound increase in methane emissions from cores of mire peat and vegetation as a direct result of increasing the CO2 concentration from 355 to 550 mu mol mol(-1) (a 60% increase). Increased CH4 fluxes were observed throughout the four month period of study. Seasonal variation in CH4 flux, consistent with that seen in the field, was observed under both ambient and elevated CO2. Under ambient CO2 methane fluxes rose from 0.02 mu mol m(-2) s(-1) in May to 0.11 mu mol m(-2) s(-3) in July before declining again in August. Under elevated CO2, methane fluxes were at least 100% greater throughout the experiment, rising from 0.05 mu mol m(-2) s(-1) in May to a peak of 0.27 mu mol m(-2) s(-1) in July. The stimulation of CH4 emissions was accompanied by a 100% increase in rates of photosynthesis from 4.6 (+/- 0.3) under ambient CO2 to 9.3 (+/- 0.7) mu mol m(-2) s(-1). Root and shoot biomass were unaffected.

KEYWORDS: PADDY FIELDS, RICE PADDY, SOIL TEMPERATURE, TUNDRA, WETLANDS

983

Hutjes, R.W.A., P. Kabat, S.W. Running, W.J. Shuttleworth, C. Field, B. Bass, M.A.F.D. Dias, R. Avissar, A. Becker, M. Claussen, A.J. Dolman, R.A. Feddes, M. Fosberg, Y. Fukushima, J.H.C. Gash, L. Guenni, H. Hoff, P.G. Jarvis, I. Kayane, A.N. Krenke, C. Liu, M. Meybeck, C.A. Nobre, L. Oyebande, A. Pitman, R.A. Pielke, M. Raupach, B. Saugier, E.D. Schulze, P.J. Sellers, J.D. Tenhunen, R. Valentini, R.L. Victoria, and C.J. Vorosmarty. 1998. Biospheric aspects of the hydrological cycle - Preface. *Journal of Hydrology 213(1-4):1-21.*

The Core Project Biospheric Aspects of the Hydrological Cycle (BAHC) of the International Geosphere Biosphere Programme (IGBP) addresses the biospheric aspects of the hydrological cycle through experiments and modelling of energy, water, carbon dioxide and sediment fluxes in the soil-vegetation- atmosphere system at a variety of spatial and temporal scales. Active regulation of water, energy and carbon dioxide fluxes by the vegetation make it an important factor in regulating the Earth's hydrological cycle and in the formation of the climate. Consequently, human induced conversion of vegetation cover is an important driver for climate change. A number of recent studies, discussed in this paper, emphasise the importance of the terrestrial biosphere for the climate system. Initially, these studies demonstrate the influence of the land surface on tropical weather and climate, revealing the mechanisms, acting at various scales, that connect increasing temperatures and decreasing rainfall to large-scale deforestation and other forms of land degradation. More recently, the significance of the land surface processes for water cycle and for weather and climate in temperate and boreal zones was demonstrated. In addition the terrestrial biosphere plays a significant role in the carbon dioxide fluxes and in global carbon balance. Recent work suggests that many ecosystems both in the tropics and in temperate zones may act as a substantial sink for carbon dioxide, though the temporal variability of this sink strength is yet unclear. Further, carbon dioxide uptake and evaporation by vegetation are intrinsically coupled leading to Links and feedbacks between land surface and climate that are hardly explored yet. Earth's vegetation cover and its changes owing to human impact have a profound influence on a lateral redistribution of water and transported constituents, such as nutrients and sediments, and acts therefore as an important moderator of Earth's biogeochemical cycles. In the BAHC science programme, the importance of studying the influence of climate and human activities on mobilisation and river-borne transport of constituents is explicitly articulated. The terrestrial water and associated material cycles are studied as highly dynamic in space and time, and reflect a complex interplay among climatic forcing, topography, land cover and vegetation dynamics. Despite a large progress in our understanding of how the terrestrial biosphere interacts with Earth's and climate system and with the terrestrial part of its hydrological cycle, a number of basic issues still remain unresolved. Limited to the scope of BAHC, the paper briefly assesses the present status and identifies the most important outstanding issues, which require further research. Two, arguably most important outstanding issues are identified: a limited understanding of natural variability, especially with respect to seasonal to inter-annual cycles, and of a complex ecosystem behaviour resulting from multiple feedbacks and multiple coupled biogeochemical cycles within the overall climate system. This leads to two major challenges for the future science agenda related to global change research. First, there is a need for a strong multidisciplinary integration of research efforts in both modelling and experiments, the latter extending to inter- annual timescales. Second, the ever increasing complexity in characterisation and modelling of the climate system, which is mainly owing to incorporation of the biosphere's and human feedbacks, may call for a new approach in global change impact studies. Methodologies need to be developed to identify risks to, and vulnerability of environmental systems, taking into account all important interactions between atmospheric, ecological and hydrological processes at relevant scales. With respect to the influence of climate and human activities on mobilisation and river-borne transport of constituents, the main issues for the future are related to declining availability and quality of ground data for quantity and quality of water discharge. Such assessments presented in this paper, in combination with community wide science evaluation, has lead to an update of the science agenda for BAHC, a summary of which is provided in the appendix.

KEYWORDS: ATMOSPHERIC CO2, CLIMATIC IMPACTS, DROUGHT, FIELD EXPERIMENT, FLUXES, GENERAL-CIRCULATION MODEL, SCALING CHARACTERISTICS, SEMI-ARID REGIONS, TERRESTRIAL ECOSYSTEMS, VEGETATION

984

Huxman, K.A., S.D. Smith, and D.S. Neuman. 1999. Root hydraulic conductivity of Larrea tridentata and Helianthus annuus under elevated CO2. *Plant, Cell and Environment 22(3):325-330.*

While investigations into shoot responses to elevated atmospheric CO2

are extensive, few studies have focused on how an elevated atmospheric CO2 environment might impact root functions such as water uptake and transport. Knowledge of functional root responses may be particularly important in ecosystems where water is limiting if predictions about global climate change are true. In this study we investigated the effect of elevated CO2 on the root hydraulic conductivity (L-p) of a C-3 perennial, Lawea tridentata, and a C-3 annual, Helianthus annuus. The plants were grown in a glasshouse under ambient (360 mu mol mol(-1)) and elevated (700 mu mol mol(-1)) CO2. The L-p through intact root systems was measured using a hydrostatic pressure-induced flow system. Leaf gas exchange was also determined for both species and leaf water potential (psi(leaf)) was determined in L, tridentata, The L-p of L, tridentata roots was unchanged by an elevated CO2 growth environment. Stomatal conductance (g(s)) and transpiration (E) decreased and photosynthetic rate (A(net)) and psi(leaf) increased in L, tridentata, There were no changes in biomass, leaf area, stem diameter or root : shoot (R : S) ratio for L, tridentata. In H, annuus, elevated CO2 induced a nearly two- fold decrease in root L-p. There was no effect of growth under elevated CO2 on A(net), g(s), E, above- and below-ground dry mass, R : S ratio, leaf area, root length or stem diameter in this species. The results demonstrate that rising atmospheric CO2 can impact water uptake and transport in roots in a species-specific manner. Possible mechanisms for the observed decrease in root L-p in H, annuus under elevated CO2 are currently under investigation and may relate to either axial or radial components of root L-p.

KEYWORDS: ANATOMY, C-3, CARBON-DIOXIDE CONCENTRATION, CONDUCTANCE, ENRICHMENT, ENVIRONMENT, GROWTH, PLANTS, RESPONSES, WHEAT

985

Huxman, T.E., E.P. Hamerlynck, D.N. Jordan, K.J. Salsman, and S.D. Smith. 1998. The effects of parental CO2 environment on seed quality and subsequent seedling performance in Bromus rubens. *Oecologia 114(2):202-208.*

Seeds were collected and compared from parent plants of Bromus rubens L. (Poaceae), an exotic Mojave Desert annual grass, grown in ambient (360 mu mol mol(-1)) and elevated (700 mu mol mol(-1)) CO2 to determine if parental CO2 growth conditions affected seed quality. Performance of seeds developed on the above plants was evaluated to determine the influence of parental CO2 growth conditions on germination, growth rate, and leaf production, Seeds of B. rubens developed oil parents grown in elevated CO2 had a larger pericarp surface area, higher C:N ratio, and less total mass than ambient-developed seeds, Parental CO2 environment did not have an effect on germination percentage or mean germination timer as determined by radicle emergence. Seedlings from elevated-CO2-developed seeds had a reduced relative growth rate and achieved smaller final mass over the same growth period. Elevated-CO2-developed seeds had smaller seed reset-yes than ambient seeds, as determined by growing seedlings in sterile media and monitoring senescence. It appears that increased seed C:N ratios associated with plants grown under elevated CO2 may have a major effect on seed quality (morphology, nutrition) and seedling performance (e.g., growth rate and leaf production). Since the invasive success of B. rubens is primarily due to its ability to rapidly germinate, increase leaf area and maintain a relatively high growth rate compared to native annuals and perennial grasses, reductions in seed duality and seedling performance in elevated CO2 may have significant impacts on future community composition in the Mojave Desert.

KEYWORDS: ALLOCATION, ELEVATED CO2, ENRICHMENT, GERMINATION, GRASSLAND, GROWTH, PLANTS, RESPONSES

986

Huxman, T.E., E.P. Hamerlynck, M.E. Loik, and S.D. Smith. 1998. Gas exchange and chlorophyll fluorescence responses of three south-western Yucca species to elevated CO2 and high temperature. *Plant, Cell and Environment 21(12):1275-1283.*

The ability of seedlings to tolerate temperature extremes is important in determining the distribution of perennial plants in the arid south-western USA, and the manner in which elevated CO2 impacts the ability of plants to tolerate high temperatures is relatively unknown, Whereas the effects of chronic high temperature (30-38 degrees C) and elevated CO2 are comparatively well understood, little research has assessed plant performance in elevated CO2 during extreme (> 45 degrees C) temperature events, We exposed three species of Yucca to 360 and 700 mu mol CO, mol(-1) for 8 months, then 9 d of high temperature (up to 53 degrees C) to evaluate the impacts of elevated CO2 on the potential for photosynthetic function during external high temperature. Seedlings of a coastal C-3 species (Yucca whipplei), a desert C-3 species (Yucca brevifolia), and a desert CAM species (Yucca schidigera), were used to test for differences among functional groups. In general, Yuccas exposed to elevated CO2 showed decreases in carboxylation efficiency as compared with plants grown at ambient before the initiation of high temperature, The coastal species (Y. whipplei) showed significant reductions (33%) in CO2 saturated maximum assimilation rate (A(max)), but the desert species (Y. brevifolia and Y. schidigera) showed no such reductions in A(max). Stomatal conductance was lower in elevated CO2 as compared with ambient throughout the temperature event; however, there were species-specific differences over time. Elevated CO2 enhanced photosynthesis in Y. whipplei at high temperatures for a period of 4 d, but not for Y. brevifolia or Y. schidigera, Elevated CO2 offset photoinhibition (measured as F-v/F-m) in Y. whipplei as compared with ambient CO2, depending on exposure time to high temperature. Stable F-v/F-m in Y. whipplei occurred in parallel with increases in the quantum yield of photosystem II (Phi PSII) at high temperatures in elevated CO2. The value of Phi PSII remained constant or decreased with increasing temperature in all other treatment and species combinations, This suggests that the reductions in F-v/F-m resulted from thermal energy dissipation in the pigment bed for Y. brevifolia and Y. schidigera, The greater efficiency of photosystem II in Y. whipplei helped to maintain photosynthetic function at high temperatures in elevated CO2. These patterns are in contrast to the hypothesis that high temperatures in elevated CO2 would increase the potential for photoinhibition, Our results suggest that elevated CO2 may offset high-temperature stress in coastal Yucca, but not in those species native to drier systems, Therefore, in the case of Y. whipplei, elevated CO2 may allow plants to survive extreme temperature events, potentially relaxing the effects of high temperature on the establishment in novel habitats.

KEYWORDS: ACCLIMATION, AGAVE-DESERTI, ATMOSPHERIC CO2, AVAILABILITY, BREVIFOLIA, GROWTH, PHOTOSYNTHESIS, PHYSIOLOGY, PLANTS, STRESS

987

Huxman, T.E., E.P. Hamerlynck, B.D. Moore, S.D. Smith, D.N. Jordan, S.F. Zitzer, R.S. Nowak, J.S. Coleman, and J.R. Seemann. 1998. Photosynthetic down-regulation in Larrea tridentata exposed to elevated atmospheric CO2: interaction with drought under glasshouse and field (FACE) exposure. *Plant, Cell and Environment 21(11):1153-1161.*

The photosynthetic response of Larrea tridentata Cav,, an evergreen Mojave Desert shrub, to elevated atmospheric CO2 and drought was examined to assist in the understanding of how plants from water-limited ecosystems will respond to rising CO2, We hypothesized that photosynthetic down-regulation would disappear during periods of water Limitation, and would, therefore, likely be a seasonally transient event. To test this we measured photosynthetic, water relations and fluorescence responses during periods of increased and decreased mater

availability in two different treatment implementations: (1) from seedlings exposed to 360, 550, and 700 mu mol mol(-1) CO2 in a glasshouse; and (2) from intact adults exposed to 360 and 550 mu mol mol(-1) CO2 at the Nevada Desert FACE (Free Air CO2 Enrichment) Facility. FACE and glasshouse wed-watered Larrea significantly down-regulated photosynthesis at elevated CO2, reducing maximum photosynthetic rate (A(max)), carboxylation efficiency (CE), and Rubisco catalytic sites, whereas droughted Larrea showed a differing response depending on treatment technique. A(max) and CE were lower in droughted Larrea compared with well-watered plants, and CO2 had no effect on these reduced photosynthetic parameters. However, Rubisco catalytic sites decreased in droughted Larrea at elevated CO2. Operating C-i increased at elevated CO2 in droughted plants, resulting in greater photosynthetic rates at elevated CO2 as compared with ambient CO2. In well-watered plants, the changes in operating C-i, CE andA(max) resulted in similar photosynthetic rates across CO2 treatments. Our results suggest that drought can diminish photosynthetic down-regulation to elevated CO2 in Larrea, resulting in seasonally transient patterns of enhanced carbon gain. These results suggest that water status may ultimately control the photosynthetic response of desert systems to rising CO2.

KEYWORDS: ACCLIMATION, CARBON DIOXIDE, DESERT, ECOSYSTEMS, GAS-EXCHANGE, GROWTH, INTACT LEAVES, RESPONSES, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE, TEMPERATURE

988

Hymus, G.J., D.S. Ellsworth, N.R. Baker, and S.P. Long. 1999. Does free-air carbon dioxide enrichment affect photochemical energy use by evergreen trees in different seasons? A chlorophyll fluorescence study of mature loblolly pine. *Plant Physiology 120(4):1183-1191.*

Previous studies of the effects of growth at elevated CO2 on energy partitioning in the photosynthetic apparatus have produced conflicting results. The hypothesis was developed and tested that elevated CO2 increases photochemical energy use when there is a high demand for assimilates and decreases usage when demand is low. Modulated chlorophyll a fluorescence and leaf gas exchange were measured on needles at the top of a mature, 12-m loblolly pine (Pinus taeda L.) forest. Trees were exposed to ambient CO2 or ambient plus 20 Pa CO2 using free-air CO2 enrichment. During April and August, periods of shoot growth, light-saturated photosynthesis and linear electron transport were increased by elevated CO2. In November, when growth had ceased but temperatures were still moderate, CO2 treatment had no significant effect on linear electron transport. In February, when low temperatures were likely to inhibit translocation, CO2 treatment caused a significant decrease in linear electron transport. This coincided with a slower recovery of the maximum photosystem II efficiency on transfer of needles to the shade, indicating that growth in elevated CO2 induced a more persistent photoinhibition. Both the summer increase and the winter decrease in linear electron transport in elevated CO2 resulted from a change in photochemical quenching, not in the efficiency of energy transfer within the photosystem II antenna. There was no evidence of any effect of CO2 on photochemical energy sinks other than carbon metabolism. Our results suggest that elevated CO2 may increase the effects of winter stress on evergreen foliage.

KEYWORDS: ANTIOXIDATIVE ENZYMES, ASSIMILATION, ELEVATED CO2, LEAVES, LONG-TERM EXPOSURE, NET PHOTOSYNTHESIS, PHOTOSYNTHETIC ELECTRON-TRANSPORT, PHOTOSYSTEM-II ACTIVITY, QUANTUM YIELD, RISING ATMOSPHERIC CO2

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Hyodo, H., C. Hashimoto, S. Morozumi, W.Z. Hu, and K. Tanaka. 1993. Characterization and induction of the activity of 1-aminocyclopropane-1-carboxylate oxidase in the wounded mesocarp tissue of cucurbita-maxima. *Plant and Cell Physiology 34(5):667-671.*

1-Aminocyclopropane-1-carboxylate (ACC) oxidase (ethylene- forming enzyme) was isolated from wounded mesocarp tissue of Cucurbita maxima (winter squash) fruit, and its enzymatic properties were investigated. The enzyme required Fe2+ and ascorbate for its activity as well as ACC and O2 as substrates. The in vitro enzyme activity was enhanced by CO2. The apparent K(m) value for ACC was 175 muM under atmospheric conditions. The enzyme activity was inhibited by sulfhydryl inhibitors and divalent cations such as Co2+, Cu2+, and Zn2+. ACC oxidase activity was induced at a rapid rate by wounding in parallel with an increase in the rate of ethylene production. The exposure of excised discs of mesocarp to 2,5-norbornadiene (NBD), an inhibitor of ethylene action, strongly suppressed induction of the enzyme, and the application of ethylene significantly accelerated the induction of the activity of ACC oxidase in the wounded mesocarp tissue. These results suggests that endogenous ethylene produced in response to wounding may function in promoting the induction of ACC oxidase.

KEYWORDS: ACID SYNTHASE, APPLE FRUIT, BIOSYNTHESIS, CANTALOUPE, CONVERSION, ETHYLENE-FORMING ENZYME, WINTER SQUASH FRUIT

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Idso, C.D., S.B. Idso, and R.C. Balling. 1998. The urban CO2 dome of Phoenix, Arizona. *Physical Geography 19(2):95-108.*

Air temperatures, relative humidities, and atmospheric carbon dioxide concentrations were measured at a height of 2 m at approximate 1.6-km intervals prior to sunrise and in the middle of the afternoon on five days in January along a number of different transects through the extended metropolitan area of Phoenix, Arizona. Spatially interpolated maps of the data indicate the presence of an "urban CO2 dome" that reaches concentrations as high as 555 ppmv in the city center and decreases to a value of approximately 370 ppmv on the outskirts of the city at this time of year. Pre-dawn CO2 values inside the dome are considerably higher than mid-afternoon values, suggesting that solar-induced convective mixing and the photosynthetic uptake of CO2 by urban vegetation may play significant roles in diurnally redistributing the anthropogenically produced CO2 that, together with that produced by plant respiration, accumulates near the ground during the night and early morning hours. Temperature and relative humidity appear to have little influence on either the concentration or location of the CO2 dome, but variations in wind speed and direction at times may disrupt the pattern that develops under normally fair conditions. The high CO2 concentrations within the dome may help to ameliorate the deleterious effects of urban air pollution on vegetation growing within the city. Together with the urban heat island phenomenon, they may also provide a natural laboratory for studying the effects of contemporaneous warming and atmospheric CO2 enrichment within the context of predicted future global change.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, ELEVATED CO2, HEAT-ISLAND, NET PHOTOSYNTHESIS, PLANT-RESPONSES, RURAL TRANSECT, SULFUR-DIOXIDE, TEMPORAL ANALYSIS, WATER-USE, YIELD

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Idso, K.E., and S.B. Idso. 1994. Plant-responses to atmospheric co2 enrichment in the face of environmental constraints - a review of the past 10 years research. *Agricultural and Forest Meteorology 69(3-4):153-203.*

This paper presents a detailed analysis of several hundred plant carbon