

responses of forests to future global change scenarios will be speculative until mature tree responses to CO₂ enrichment and the effects of temperature on terrestrial sources and sinks of CO₂ can be determined.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, ELEVATED CO₂, GAS-EXCHANGE, INTERIOR ALASKA, RESPIRATION, ROOT-GROWTH, SEEDLINGS, SOIL-NITROGEN MINERALIZATION, TEMPERATURE, TREES

1418

MacDonald, N.W., D.L. Randlett, and D.R. Zak. 1999. Soil warming and carbon loss from a lake states spodosol. *Soil Science Society of America Journal* 63(1):211-218.

Elevated soil temperatures may increase C loss from soils by accelerating microbial respiration and dissolved organic C leaching. We evaluated the effect of elevated soil temperatures on C losses from a forest Spodosol by incubating soil cores from surface (Oa + A + E) and subsurface (Bhs) horizons at two seasonal temperature regimes. One regime simulated the normal course of soil temperatures in northern lower Michigan, and the other simulated soil temperatures representing an amount of warming that might occur under some global warming theory calculations. We measured the amounts of CO₂-C respired and dissolved organic C leached from the soil cores during a 33-wk period. Microbial respiration rates, after adjustment for variation in initial rates, were significantly increased by soil warming and were greater in surface than in subsurface horizons. Warming significantly increased cumulative C respired, with greater losses from surface soils (greater than or equal to 50 mg C g⁻¹ C) as compared with subsurface soils (less than or equal to 25 mg C g⁻¹ C). Mean quantities of dissolved organic C leached, ranging from 2.3 to 3.2 mg C g⁻¹ C, did not differ significantly by soil horizon or temperature regime. Increased microbial respiration in surface soil horizons was the process most responsive to soil warming in the Spodosol samples we examined. Whether this is a short-term effect that would disappear once pools of labile C are exhausted, or represents a long-term response to soil warming, remains uncertain.

KEYWORDS: AIR- POLLUTION GRADIENT, CLIMATE CHANGE, DECIDUOUS FOREST, DISSOLVED ORGANIC-CARBON, MICROBIAL RESPIRATION, NET NITROGEN, NITROGEN MINERALIZATION, NORTHERN HARDWOOD FORESTS, TEMPERATURE, TRACE GAS FLUXES

1419

Mackay, R.M., and M.A.K. Khalil. 1995. Doubled CO₂ experiments with the global-change-research-center 2-dimensional statistical dynamical climate model. *Journal of Geophysical Research-Atmospheres* 100(D10):21127-21135.

The zonally averaged response of the Global Change Research Center two-dimensional (2-D) statistical dynamical climate model (GCRC 2-D SDCM) to a doubling of atmospheric carbon dioxide (350 parts per million by volume (ppmv) to 700 ppmv) is reported. The model solves the two-dimensional primitive equations in finite difference form (mass continuity, Newton's second law, and the first law of thermodynamics) for the prognostic variables: zonal mean density, zonal mean zonal velocity, zonal mean meridional velocity, and zonal mean temperature on a grid that has 18 nodes in latitude and 9 vertical nodes (plus the surface). The equation of state, $p = \rho RT$, and an assumed hydrostatic atmosphere, $\Delta p = -\rho g \Delta z$, are used to diagnostically calculate the zonal mean pressure and vertical velocity for each grid node, and the moisture balance equation is used to estimate the precipitation rate. The model includes seasonal variations in solar intensity, including the effects of eccentricity, and has observed land and ocean fractions set for each zone. Seasonally varying values of cloud amounts, relative

humidity profiles, ozone, and sea ice are all prescribed in the model. Equator to pole ocean heat transport is simulated in the model by turbulent diffusion. The change in global mean annual surface air temperature due to a doubling of atmospheric CO₂ in the 2-D model is 1.61 K, which is close to that simulated by the one-dimensional (1-D) radiative convective model (RCM) which is at the heart of the 2-D model radiation code (1.67 K for the moist adiabatic lapse rate assumption in 1-D RCM). We find that the change in temperature structure of the model atmosphere has many of the characteristics common to General Circulation Models, including amplified warming at the poles and the upper tropical troposphere, and stratospheric cooling. Because of the potential importance of atmospheric circulation feedbacks on climate change, we have also investigated the response of the zonal wind field to a doubling of CO₂ and have found distinct patterns of change that are related to the change in temperature structure. In addition, we find that both the global mean kinetic energy and simulated Hadley circulation increase when CO₂ is doubled. The increase in mean kinetic energy is a result of the increase in upper level meridional temperature gradients simulated by the model. It is stressed that changes in atmospheric dynamics associated with increased carbon dioxide may also be very important to the final steady state distribution of such greenhouse gases as ozone and water vapor. Hence further research in this regard is warranted.

KEYWORDS: GENERAL-CIRCULATION, IMPACT, PARAMETERIZATION

1420

Mackowiak, C.L., and R.M. Wheeler. 1996. Growth and stomatal behavior of hydroponically cultured potato (*Solanum tuberosum* L) at elevated and super-elevated CO₂. *Journal of Plant Physiology* 149(1-2):205-210.

Potato cultivars Denali and Norland were grown in a controlled environment under low irradiance and CO₂ partial pressures of 50, 100, 500, and 1000 Pa. The highest CO₂ partial pressures, 500 and 1000 Pa, reduced tuber yield when compared to 100 Pa CO₂. Upper canopy stomatal conductance was greatest at the higher CO₂ partial pressures (500 and 1000 Pa) for both cultivars, and conductance of Denali was consistently higher than Norland. Stomatal conductance tended to decline sooner with plant age at 50 and 100 Pa CO₂ than at 500 and 1000 Pa. Water uptake was also greatest at the higher CO₂ partial pressures, which resulted in lowest water-use efficiencies at 500 and 1000 Pa. These observations suggest that stomatal function under very high CO₂ partial pressures (500-1000 Pa) does not follow known patterns observed at moderate partial pressures (50-100 Pa). Although there is little concern about CO₂ partial pressures reaching extreme levels in the natural environment, this information should be useful for controlled environments or space life support systems (e.g. space vehicles or habitats), where CO₂ partial pressures of 500-1000 Pa are common.

KEYWORDS: ALLOCATION, EXCHANGE, INDIVIDUAL TUBERS, LIFE SUPPORT SYSTEMS, PHOTOPERIODS, PHOTOSYNTHATE, SPACE, TEMPERATURE

1421

Madsen, T.V. 1993. Growth and photosynthetic acclimation by *Ranunculus-aquaticus* L in response to inorganic carbon availability. *New Phytologist* 125(4):707-715.

Relative growth rates of *Ranunculus aquatilis* L. were measured in the laboratory at dissolved inorganic carbon (DIC) concentrations between 0.2 and 5.2 mM at air-equilibrium CO₂ (16 μM) and also at 0.55 mM DIC with elevated CO₂ (350 μM). For plants grown at air-equilibrium CO₂, growth was limited by inorganic carbon below 1.6 mM DIC and

the apparent half saturation constant was 0.5 mM. The growth rate at elevated CO₂ was 50% higher than the carbon saturated rates obtained at high DIC concentrations and air-equilibrium CO₂, where HCO₃⁻ is dominant. This difference is suggested to be caused by differences in uptake mechanisms for CO₂ and HCO₃⁻. Uptake of CO₂ is a diffusive process, whereas HCO₃⁻ use is an active process which involves uptake/transport systems in the cell membranes. The plants acclimated to the DIC regime for growth by reductions in carboxylation efficiency and bicarbonate affinity, but enhanced photosynthetic capacity at elevated DIC. Within the range of concentrations used, the acclimation to CO₂ and HCO₃⁻ was quantitatively similar, except for the HCO₃⁻ uptake capacity which increased at high DIC and air-equilibrium CO₂ but declined at elevated CO₂. Dark respiration was unaffected by inorganic carbon per se, but increased with growth rate. Maintenance respiration was constant among treatments. It is concluded that inorganic carbon, apart from being the primary substrate for photosynthesis, has secondary growth regulatory effects which affect the photosynthetic apparatus of the plants.

KEYWORDS: AFFINITY, BICARBONATE, CO₂, DIFFERENTIAL ABILITY, ENVIRONMENTAL-FACTORS, FRESH-WATER MACROPHYTES, LIGHT, PH, PLANTS, STREAMS

1422

Madsen, T.V., S.C. Maberly, and G. Bowes. 1996. Photosynthetic acclimation of submersed angiosperms to CO₂ and HCO₃⁻. *Aquatic Botany* 53(1-2):15-30.

Photosynthetic acclimation after growth under a factorial combination of three concentrations of CO₂ (1, 16 and 910 μ M) and two concentrations of HCO₃⁻ (0.2 and 1.5 mM) was measured for *Callitriche cophocarpa* Sendt., *Elodea canadensis* L.C. Rich. and *Ranunculus peltatus* Schrank. *Callitriche cophocarpa* was restricted to CO₂ as a carbon source while the other two species also used HCO₃⁻. None of the species showed C-4-like photosynthesis as evidenced by low activities of phosphoenolpyruvate carboxylase. Carbon exchange characteristics and biochemical capacities were down-regulated in response to increasing inorganic carbon during growth. In all three species, P-max initial slope of net photosynthesis versus [CO₂], rubisco activity, protein content and chlorophyll content decreased, and CO₂ compensation concentration increased with increased inorganic carbon. In addition, for the two HCO₃⁻ users, the rate of HCO₃⁻-dependent photosynthesis at zero [CO₂] and 1.5 mM HCO₃⁻ decreased with inorganic carbon. The response to increased [GO₂] was greater than that to increased [HCO₃⁻]. Morphological acclimation to inorganic carbon was evident in all species. The root/shoot ratio increased with increasing [CO₂] but was unaffected by [HCO₃⁻]. The specific leaf area declined with carbon availability in *Callitriche* and *Ranunculus*, whereas no change was observed in *Elodea*. There was a significant positive correlation between various carbon exchange characteristics and between these and the chlorophyll content and rubisco activity, suggesting that carbon exchange, light capture and carbon fixation are regulated in parallel in response to carbon availability. The general down-regulation response shown by these aquatic plants to elevated inorganic carbon resembles the response of some terrestrial C-3 species to elevated CO₂.

KEYWORDS: AQUATIC MACROPHYTES, BICARBONATE, CARBON DIOXIDE, FRESH-WATER MACROPHYTES, GROWTH, LIGHT, PLANTS

1423

Madsen, T.V., H.B.A. Prins, and G. Bowe. 1997. Will elevated CO₂ affect aquatic plants? *Plant Physiology* 114(3):21001.

1424

Madsen, T.V., K. Sandjensen, and S. Beer. 1993. Comparison of photosynthetic performance and carboxylation capacity in a range of aquatic macrophytes of different growth forms. *Aquatic Botany* 44(4):373-384.

Photosynthesis, carbon extraction capacity and ribulose-1,5-bisphosphate carboxylase/oxygenase (RUBISCO) activity were determined for 35 species of submerged aquatic macrophytes differing with respect to taxonomy, growth form and habitat. Photosynthetic rates per unit of chlorophyll and dry weight at ambient CO₂ concentrations (about 15 μ M) as well as carbon extraction capacity increased among plant groups in the order: isoetids, amphibious species, elodeids with no apparent HCO₃⁻ use, elodeids with HCO₃⁻ use, marine angiosperms and marine macroalgae. Photosynthetic rates at elevated CO₂ concentrations (300-350 μ M) showed the same pattern but smaller differences among the groups. Only for some of the marine macroalgae did photosynthesis at ambient CO₂ approach photosynthesis at elevated CO₂. Species with high carbon extraction capacity, presumably based on active HCO₃⁻ use, usually had low RUBISCO activity, low chlorophyll content and low surface to volume ratio. The opposite pattern was found among species with low carbon extraction capacity. The low chlorophyll content and high chlorophyll specific photosynthesis of species with high carbon transport capability (i.e. particularly the marine algae), suggest that running costs associated with inorganic carbon assimilation are reduced when a CO₂ concentrating system operates.

KEYWORDS: CO₂, FRESH-WATER MACROPHYTES, INORGANIC CARBON, MARINE, PLANTS, ROOTS

1425

Maevskaya, S.N., T.F. Andreeva, S.Y. Voevodskaya, and N.N. Cherkanova. 1990. Effect of elevated CO₂ concentration on photosynthesis and nitrogen-metabolism of mustard plants. *Soviet Plant Physiology* 37(5):687-692.

We investigated the effect of prolonged (8- to 10-day) influence of elevated atmospheric CO₂ content (0.14%) on the photosynthetic rate and nitrogen metabolism in mustard plants (*Brassica juncea* L.). The photosynthetic rate and intensity of nitrogen metabolism in leaves of mustard plants in the vegetative phase of growth are higher under conditions of elevated atmospheric CO₂ concentration than in leaves of plants that developed under conditions of normal CO₂ content in the atmosphere. Intensification of nitrogen metabolism occurred mainly due to increase of NR activity. Activity of GS and GO increased to a lesser extent. Significant changes were detected in the rates of synthesis of separate amino acids. Thus, formation of alanine and aspartic acid increased by 84 and 40%, respectively, but the rates of glycine and serine synthesis declined. The excess of amino acids (alanine and aspartic acid) is evacuated from the metabolic pool into vacuoles, with the result that a normal metabolic pool of amino acids is preserved. A state of homeostasis is preserved, protein and chlorophyll synthesis is not disturbed, and growth and biomass accumulation intensify in plants under conditions of elevated CO₂ concentration.

KEYWORDS: CARBON-DIOXIDE ENRICHMENT, GROWTH, WHEAT

1426

Magan, N., and E.S. Baxter. 1996. Effect of increased CO₂ concentration and temperature on the phyllosphere mycoflora of winter wheat flag leaves during ripening. *Annals of Applied Biology* 129(2):189-195.

The impact of elevated carbon dioxide (CO₂, 600/700 μ mol mol⁻¹) and temperature (+ 4 degrees C) on phyllosphere fungi colonising flag leaves of mini crops of winter wheat cv. Mercia between anthesis and

harvest was determined in a computer- controlled environment facility in 1993 and 1994. In both years the total fungal populations (cm²) leaf) were found to have increased due to exposure to either elevated CO₂ and elevated CO₂ + temperature treatments. This was mainly due to significant increases in populations of *Cladosporium* spp. (*C. cladosporioides* and *C. herbarum*) on the flag leaves during ripening. Other phyllosphere component species such as white and pink yeasts were not markedly affected by treatments. The range of fungal species found in such controlled environment chambers was narrower than that commonly found on flag leaves of field grown crops. Common and important colonisers of leaves and ripening ears such as *Aureobasidium pullulans*, *Epicoccum nigrum* and *Fusarium* spp. were seldom isolated.

KEYWORDS: FUNGI, GROWTH, OPEN-AIR FUMIGATION, OZONE, SULFUR-DIOXIDE, YIELD

1427

Maillard, P., E. Deleens, F. Castell, and F.A. Daudet. 1999. Source-sink relationships for carbon and nitrogen during early growth of *Juglans regia* L. seedlings: analysis at two elevated CO₂ concentrations. *Annals of Forest Science* 56(1):59-69.

Assimilation and allocation of carbon (C) and nitrogen (N) were studied in seedlings (*Juglans regia* L.) grown for 55 days under controlled conditions (22 degrees C, 12 h, 90 % relative humidity [RH]) using two CO₂ concentrations (550 and 800 μ mol L⁻¹ CO₂). C and N decrease in seeds was unaltered by CO₂. At the end of seed contribution (day 35), C and N accumulation in seedlings was favoured under 800 μ mol L⁻¹ [CO₂], resulting in an increase of about +50 % for C and +35 % for N. Growth enhancement was larger in roots than in shoot, resulting in a higher root:shoot ratio (R:S = 0.62) with respect to 550 μ mol L⁻¹ CO₂ (R:S = 0.40) at day 55. These results were due, in order, to: 1) a shoot respiration temporarily depressed by [CO₂], 2) a reduction by 46 % of the root + soil respiration, 3) a stimulation by 14 % of the C assimilation and 1) an increased uptake and assimilation of N coming from the rooting medium. An increased use of N originated from the seed was observed in leaves and lateral roots, suggesting optimisation of distribution of stored N pools by seedlings. These changes finally gave rise to an increased C:N ratio for taproot (+27 %), roots (+20 %), stem (+28 %), and leaves (+12 %), suggesting a N dilution in the tissues. ((C) Inra/Elsevier, Paris.).

KEYWORDS: ALLOCATION, ATMOSPHERIC CO₂, AUTOTROPHY, DIOXIDE, ENRICHMENT, QUERCUS-ROBUR SEEDLINGS, RESPIRATION, TERM, WALNUT SEEDLINGS, WOODY-PLANTS

1428

Majeau, N., and J.R. Coleman. 1996. Effect of CO₂ concentration on carbonic anhydrase and ribulose-1,5-bisphosphate carboxylase/oxygenase expression in pea. *Plant Physiology* 112(2):569-574.

The effect of external CO₂ concentration on the expression of carbonic anhydrase (CA) and ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) was examined in pea (*Pisum sativum* cv Little Marvel) leaves. Enzyme activities and their transcript levels were reduced in plants grown at 1000 μ mol L⁻¹ CO₂ compared with plants grown in ambient air. Growth at 160 μ mol L⁻¹ CO₂ also appeared to reduce steady-state transcript levels for *rbcs*, the gene encoding the small subunit of Rubisco, and for *ca*, the gene encoding CA; however, *rbcs* transcripts were reduced to a greater extent at this concentration. Rubisco activity was slightly lower in plants grown at 160 μ mol L⁻¹ CO₂, and CA activity was significantly higher than that observed in air-grown plants. Transfer of plants from 1000 μ mol L⁻¹ to air levels of CO₂ resulted in a rapid increase in both *ca* and *rbcs* transcript abundance in fully expanded leaves, followed by an increase in enzyme activity. Plants transferred

from air to high-CO₂ concentrations appeared to modulate transcript abundance and enzyme activity less quickly. Foliar carbohydrate levels were also examined in plants grown continuously at high and ambient CO₂, and following changes in growth conditions that rapidly altered *ca* and *rbcs* transcript abundance and enzyme activities.

KEYWORDS: ACCLIMATION, ANTISENSE RNA, ATMOSPHERIC CO₂, CHLAMYDOMONAS-REINHARDTII, ELEVATED CO₂, GAS-EXCHANGE, MECHANISM, PHOTOSYNTHESIS, TOMATO PLANTS, TRANSGENIC TOBACCO PLANTS

1429

Makino, A. 1994. Biochemistry of C₃-photosynthesis in high CO₂. *Journal of Plant Research* 107(1085):79-84.

The short-term responses of C₃ photosynthesis to high CO₂ are described first. Regulation of photosynthesis in the short term is determined by interaction among the capacities of light harvesting, electron transport, ribulose-1,5-bisphosphate carboxylase (Rubisco) and orthophosphate (Pi) regeneration during starch and sucrose synthesis. Photosynthesis under high CO₂ conditions is limited by either electron transport or Pi regeneration capacities, and Rubisco is deactivated to maintain a balance between each step in the photosynthetic pathway. Subsequently, the long-term effects on photosynthesis are discussed. Long-term CO₂ enhancement leads to carbohydrate accumulation. Accumulation of carbohydrates is not associated with a Pi-regeneration limitation on photosynthesis, and this limitation is apparently removed during long-term exposure to high CO₂. Enhanced CO₂ does not affect Rubisco content and electron transport capacity for a given leaf-nitrogen content. In addition, the deactivated Rubisco immediately after exposure to high CO₂ does not recover during the subsequent prolonged exposure. Such evidence may indicate that plants do not necessarily have an ideal acclimation response to high CO₂ at the biochemical level.

KEYWORDS: C-3 PLANTS, CARBON-DIOXIDE ENRICHMENT, DRY-MATTER PRODUCTION, ELECTRON-TRANSPORT, ELEVATED CO₂, GAS-EXCHANGE, LONG-TERM EXPOSURE, PHASEOLUS-VULGARIS L, RIBULOSE BISPHOSPHATE CARBOXYLASE, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE

1430

Makino, A., M. Harada, T. Sato, H. Nakano, and T. Mae. 1997. Growth and N allocation in rice plants under CO₂ enrichment. *Plant Physiology* 115(1):199-203.

The effects of CO₂ enrichment on growth and N allocation of rice (*Oryza sativa* L.) were examined. The plants were grown hydroponically in growth chambers with a 14-h photoperiod (1000 μ mol quanta m⁻² s⁻¹) and a day/night temperature of 25/20 degrees C. From the 28th to 70th d after germination, the plants were exposed to two CO₂ partial pressures, namely 36 and 100 Pa. The CO₂ enrichment increased the final biomass, but this was caused by a stimulation of the growth rate during the first week of the exposure to elevated CO₂ partial pressures. The disappearance of the initial stimulation of the growth rate was associated with a decreased leaf area ratio. Furthermore, CO₂ enrichment decreased the investment of N in the leaf blades, whereas the N allocation into the leaf sheaths and roots increased. Thus, the decrease in leaf N content by CO₂ enrichment was not due to dilution of N caused by a relative increase in the plant biomass but was due to the change in N allocation at the whole-plant level. We conclude that the growth responses of rice to CO₂ enrichment are mainly controlled by leaf area expansion and N allocation into leaf blades at the whole-plant level.

KEYWORDS: ELEVATED CO₂, LEAF-AREA, NITROGEN-USE, PARTIAL-PRESSURE, PHOTOSYNTHESIS, RIBULOSE-1;5-

1431

Makino, A., and T. Mae. 1999. Photosynthesis and plant growth at elevated levels of CO₂. *Plant and Cell Physiology* 40(10):999-1006.

In this review, we discuss the effects of elevated CO₂ levels on photosynthesis in relation to the whole plant growth in terrestrial higher C-3 plants. Short-term CO₂ enrichment stimulates the rate of photosynthesis. Plant mass is also enhanced by CO₂ enrichment. However, the effects of long-term CO₂ enrichment on photosynthesis are variable. Generally, the prolonged exposure to CO₂ enrichment reduces the initial stimulation of photosynthesis in many species, and frequently suppresses photosynthesis. These responses are attributed to secondary responses related to either excess carbohydrate accumulation or decreased N content rather than direct responses to CO₂. Accumulation of carbohydrates in leaves may lead to the repression of photosynthetic gene expression and excess starch seems to hinder CO₂ diffusion. Therefore, the species which have the sink organs for carbohydrate accumulation do not show the suppression of photosynthesis. The suppression of photosynthesis by CO₂ enrichment is always associated with decreases in leaf N and Rubisco contents. These decreases are not due to dilution of N caused by a relative increase in the plant mass but are the result of a decrease in N allocation to leaves at the level of the whole plant, and the decrease in Rubisco content is not selective. Leaf senescence and plant development are also accelerated by CO₂ enrichment. However, they are independent of each other in some species. Thus, various responses to CO₂ observed at the level of a single leaf result from manifold responses at the level of the whole plant grown under conditions of CO₂ enrichment.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, C-3 PLANTS, ELECTRON-TRANSPORT, GAS-EXCHANGE, LONG-TERM EXPOSURE, NITROGEN ALLOCATION, PHASEOLUS-VULGARIS L, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE, RICE LEAVES, WHEAT LEAVES

1432

Makino, A., H. Nakano, T. Mae, T. Shimada, M. Matsuoka, K. Shimamoto, M.M. Tokutomi, and N. Yamamoto. 1997. Rubisco and N allocation in rice under elevated CO₂. Optimization of Rubisco content by antisense rbc S. *Plant Physiology* 114(3):1091.

1433

Makino, A., T. Shimada, S. Takumi, K. Kaneko, M. Matsuoka, K. Shimamoto, H. Nakano, M. MiyaoTokutomi, T. Mae, and N. Yamamoto. 1997. Does decrease in ribulose-1,5-bisphosphate carboxylase by antisense RbcS lead to a higher N-use efficiency of photosynthesis under conditions of saturating CO₂ and light in rice plants? *Plant Physiology* 114(2):483-491.

Rice (*Oryza sativa* L.) plants with decreased ribulose-1,5- bisphosphate carboxylase (Rubisco) were obtained by transformation with the rice rbcS antisense gene under the control of the rice rbcS promoter. The primary transformants were screened for the Rubisco to leaf N ratio, and the transformant with 65% wild-type Rubisco was selected as a plant set with optimal Rubisco content at saturating CO₂ partial pressures for photosynthesis under conditions of high irradiance and 25 degrees C. This optimal Rubisco content was estimated from the amounts and kinetic constants of Rubisco and the gas-exchange data. The R-1 selfed progeny of the selected transformant were grown hydroponically with different N concentrations. Rubisco content in the R-1 population was distributed into two groups: 56 plants had about 65% wild-type Rubisco,

whereas 23 plants were very similar to the wild type. Although the plants with decreased Rubisco showed 20% lower rates of light-saturated photosynthesis in normal air (36 Pa CO₂), they had 5 to 15% higher rates of photosynthesis in elevated partial pressures of CO₂ (100-115 Pa CO₂) than the wild-type plants for a given leaf N content. We conclude that the rice plants with 65% wild-type Rubisco show a higher N-use efficiency of photosynthesis under conditions of saturating CO₂ and high irradiance.

KEYWORDS: C-3 PLANTS, ELEVATED CO₂, GAS-EXCHANGE, INTACT LEAVES, NITROGEN NUTRITION, PHASEOLUS-VULGARIS L, RIBULOSE 1;5-BISPHOSPHATE, SMALL-SUBUNIT, SUCROSE SYNTHESIS ENZYMES, TRANSGENIC TOBACCO

1434

Makino, Y., K. Iwasaki, and T. Hirata. 1996. A theoretical model for oxygen consumption in fresh produce under an atmosphere with carbon dioxide. *Journal of Agricultural Engineering Research* 65(3):193-203.

A practical model for fresh produce, which includes the effect of the depression of respiration caused by CO₂, is proposed on the basis of the modified Langmuir adsorption theory. The O₂ consumption rates for several kinds of fresh produce under atmospheric conditions with enhanced CO₂ were measured and the data was analysed using the proposed model. The rate parameters of the model for estimating respiration of fresh produce were determined, and the model was found to be adaptable for describing the O₂ consumption in terms of the depression by CO₂. Mathematical analysis of a modified atmosphere packaging (MAP) system for shredded cabbage and broccoli was carried out using the proposed rate equation and the basic mass balance. The simulated results agreed well with the experimental data. The proposed O₂ consumption model is considered to be useful for the design of MAP systems under the atmospheric condition with CO₂ gas. (C) 1996 Silsoe Research Institute

KEYWORDS: CO₂, FRUITS, GAS-EXCHANGE, O₂, PACKAGE, PRINCIPLES, QUALITY, RESPIRATION, VEGETABLES

1435

Malanson, G.P. 1993. Comment on modeling ecological response to climatic-change. *Climatic Change* 23(2):95-109.

Researchers have developed many computer simulation models to project ecological responses to climatic change. Three general types of models are examined: transfer functions, stand models, and physiological models. Criteria for evaluation are, first, ability to represent observed and theoretical responses to climatic change i.e., geographical migration, individualistic responses, and disequilibrium or inertia, and second, ability to provide useful information on biological diversity and impacts on society. Because of their roots in ecological interactions at the species level, stand models best meet these criteria at present, but physiological models have greater potential, given unlimited computing power.

KEYWORDS: ATMOSPHERIC CO₂ ENRICHMENT, CARBON DIOXIDE, COMPUTER-AIDED RECONSTRUCTION, EASTERN NORTH-AMERICA, ELEVATED CO₂, FOREST ECOSYSTEM PROCESSES, GRASSLAND ECOSYSTEMS, GREAT-PLAINS, INCREASING CO₂, QUATERNARY LANDSCAPE DYNAMICS

1436

Malhi, Y., D.D. Baldocchi, and P.G. Jarvis. 1999. The carbon balance of tropical, temperate and boreal forests. *Plant, Cell and Environment* 22(6):715-740.

Forest biomes are major reserves for terrestrial carbon, and major components of global primary productivity. The carbon balance of forests is determined by a number of component processes of carbon acquisition and carbon loss, and a small shift in the magnitude of these processes would have a large impact on the global carbon cycle. In this paper, we discuss the climatic influences on the carbon dynamics of boreal, temperate and tropical forests by presenting a new synthesis of micrometeorological, ecophysiological and forestry data, concentrating on three case-study sites. Historical changes in the carbon balance of each biome are also reviewed, and the evidence for a carbon sink in each forest biome and its likely behaviour under future global change are discussed. We conclude that there have been significant advances in determining the carbon balance of forests, but there are still critical uncertainties remaining, particularly in the behaviour of soil carbon stocks.

KEYWORDS: ATMOSPHERIC CO₂ CONCENTRATIONS, DECIDUOUS FOREST, INTERANNUAL CLIMATE VARIABILITY, LAND-USE CHANGE, LAST GLACIAL MAXIMUM, LONG-TERM MEASUREMENTS, NET PRIMARY PRODUCTION, RAIN-FOREST, TERRESTRIAL ECOSYSTEMS, WATER-VAPOR EXCHANGE

1437

Malmstrom, C.M., and C.B. Field. 1997. Virus-induced differences in the response of oat plants to elevated carbon dioxide. *Plant, Cell and Environment* 20(2):178-188.

Disease is an integral element of agricultural and natural systems, but the roles pathogens play in determining ecosystem response to elevated CO₂ have rarely been examined. To investigate whether disease can alter the response of plants to CO₂, we examined the effects of doubled CO₂ (approximate to 700 $\mu\text{mol mol}^{-1}$) on *Avena sativa* infected with barley yellow dwarf virus (BYDV), a common pathogen of cereals and grasses. Oats infected with BYDV showed a significantly greater biomass response to CO₂ enrichment than did healthy plants. Root mass of diseased plants increased by 37-60% with CO₂ enrichment, but was largely unaffected in healthy plants. CO₂ enrichment increased midday leaf-level photosynthesis and instantaneous water use efficiency by 34 and 93% in healthy plants and by 48 and 174% in infected plants. Foliar carbohydrates increased with both CO₂ enrichment and BYDV infection, but the two factors affected individual peaks dissimilarly. CO₂ enrichment may alter the epidemiology of BYDV by increasing the persistence of infected plants.

KEYWORDS: ACCUMULATION, ATMOSPHERIC CO₂, BARLEY YELLOW DWARF, CARBOHYDRATE-COMPOSITION, CO₂ CONCENTRATION, GROWTH, METABOLISM, SUGAR-BEET LEAVES, TRANSGENIC TOBACCO PLANTS, WHEAT

1438

Malmstrom, C.M., M.V. Thompson, G.P. Juday, S.O. Los, J.T. Randerson, and C.B. Field. 1997. Interannual variation in global-scale net primary production: Testing model estimates. *Global Biogeochemical Cycles* 11(3):367-392.

Testing estimates of year-to-year variation in global net primary production (NPP) poses some challenges. Large-scale, multiyear records of production are not readily available for natural systems but are for agricultural systems. We use records of agricultural yields at selected sites to test NPP estimates produced by CASA, a global-scale production model driven by both meteorological data and the satellite-derived normalized difference vegetation index (NDVI). We also test estimates produced by the Miami model, which has underlain several analyses of biosphere response to interannual changes in climate. In addition, we test estimates against tree ring data for one boreal site for which data from both coniferous and deciduous species were available. The agricultural

tests demonstrate that CASA can reasonably estimate interannual variation in production. The Miami model estimates variation more poorly. However, differences in NDVI-processing algorithms substantially affect CASA's estimates of interannual variation. Of the four versions tested, the FASIR NDVI most closely reproduced yield data and showed the least correlation with changes in equatorial crossing time of the National Oceanic and Atmospheric Administration satellites. One issue raised is the source of the positive trends evident in CASA's NDVI-based estimates of global NPP. The existence of these trends is consistent with potential stimulation of terrestrial production by factors such as CO₂ enrichment, N fertilization, or temperature warming, but the magnitude of the global trends seen is significantly greater than suggested by constraints imposed by atmospheric fluxes.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, AVHRR DATA, CALIBRATION, DATA SET, DIFFERENCE VEGETATION INDEX, GROSS PRIMARY PRODUCTIVITY, HIGH-RESOLUTION RADIOMETER, SATELLITE DATA, TEMPERATURE, VARIABILITY

1439

Manderscheid, R., J. Bender, H.J. Jager, and H.J. Weigel. 1995. Effects of season long CO₂ enrichment on cereals. 2. Nutrient concentrations and grain quality. *Agriculture Ecosystems & Environment* 54(3):175-185.

Two cultivars each of spring wheat (*Triticum aestivum* L., cv. Star and cv. Turbo) and spring barley (*Hordeum vulgare* L., cv. Alexis and cv. Arena) were exposed season-long to ambient (384 p.p.m.) and above ambient CO₂ concentrations (551, 718 p.p.m.) in open-top chambers. Plant samples were taken at the booting stage and at maturity. Concentrations (grams per gram dry weight) of macro (Ca, K, Mg, N, P, S) and micronutrients (Fe, Mn, Zn) were measured in stems, leaves, ears and grains, and the amino acid composition of the grain protein was determined. For most nutrients studied the sequence and size of the response of the four cereal plants to the CO₂ enrichment was cv. Arena < cv. Alexis < cv. Turbo < cv. Star. The CO₂ enrichment usually produced a decrease in nutrient concentrations, which was already detectable at the booting stage and was further enhanced until plant maturity. Nutrient concentrations of straw were more affected than those of grains. The decrease in concentration was greatest for N followed by Mg, Ca and K, and the maximum decrease as compared with ambient CO₂ amounted to 43%, 35%, 33% and 21% for straw, and 30%, 13%, 28% and - 6% for grains. Concentrations of micronutrients were also found to be partially decreased by about 10-30%. At 718 p.p.m. CO₂ grain protein concentrations were 96% (cv. Arena), 85% (cv. Alexis), 72% (cv. Turbo) and 70% (cv. Star) of the ambient CO₂ value, however, the index of essential amino acids was increased. Overall, the CO₂ enrichment did not decrease the nutrient harvest index of all nutrients except of sulphur. Nutrient use efficiency increased by high CO₂ levels for cv. Star and cv. Turbo and decreased for cv. Arena.

KEYWORDS: ATMOSPHERIC CO₂, CARBOHYDRATE, CARBON-DIOXIDE ENRICHMENT, DRY-MATTER, ELEVATED CO₂, GROWTH, NITROGEN CONCENTRATIONS, PHYSIOLOGY, RESPONSES, WINTER-WHEAT

1440

Manderscheid, R., J. Bender, U. Schenk, and H.J. Weigel. 1997. Response of biomass and nitrogen yield of white clover to radiation and atmospheric CO₂ concentration. *Environmental and Experimental Botany* 38(2):131-143.

The objectives of the present study were to test (i) whether the effect of season-long CO₂ enrichment on plant dry matter production of white clover (*Trifolium repens* cv. Karina) depends on the temperature or can solely be explained by changes in radiation use efficiency, and (ii)

whether the atmospheric CO₂ concentration affects the relationship between tissue %N and plant biomass. Plants were grown in pots with adequate nutrient and water supply and were exposed to ambient and above ambient CO₂ concentrations (approximately + 80 ppm, + 160 ppm, + 280 ppm) in open-top chambers for two seasons. Nitrogen fertilizer was given only before the experiment started to promote N-2 fixation. Plants were clipped to a height of 5 cm, when the canopy had reached a height of about 20 cm and when the CO₂ effect had not been diminished due to self-shading of the leaves. Photon exposure (400-700 nm) measured above the canopy was linearly related to the above ground biomass, the leaf area index and the nitrogen yield ($r(2) > 0.94$). The slopes of the curves depended on the CO₂ concentration. Since most of the radiation (>90%) was absorbed by the foliage, the slopes were used to calculate the CO₂ effect on the radiation use efficiency of biomass production, which is shown to increase curvilinearly between 380 and 660 ppm CO₂ from 2.7 g MJ⁻¹ to 3.9 g MJ⁻¹. CO₂ enrichment increased above ground biomass by increasing the leaf number, the individual leaf weight and the leaf area; specific leaf weight was not affected. The relative CO₂ response varied between harvests; there was a slight but not significant positive relationship with mean daytime temperature. At the beginning of the season, plant nitrogen concentration in the above ground biomass was decreased by CO₂ enrichment. However, at later growth stages, when the plants depended solely on N-2 fixation, nitrogen concentration was found to be increased when the nitrogen concentration value was adjusted for the decrease due to the higher biomass of the plants exposed to elevated CO₂. (C) 1997 Elsevier Science B.V.

KEYWORDS: CARBON DIOXIDE, ELEVATED CO₂, LOLIUM-PERENNE, OPEN-TOP CHAMBERS, PASTURE TURVES, PERENNIAL RYEGRASS, PLANT-RESPONSES, SIMULATED SEASONAL-CHANGES, TRIFOLIUM-REPENS L, USE EFFICIENCY

1441

Manderscheid, R., and H.J. Weigel. 1995. Do increasing atmospheric CO₂ concentrations contribute to yield increases of German crops. *Journal of Agronomy and Crop Science-Zeitschrift für Acker und Pflanzenbau* 175(2):73-82.

The global atmospheric CO₂-concentration is increasing and there has been an increase in Germany of about 30 ppm from 340 ppm to 370 ppm CO₂ during the last two decades. The hectare yield of many crops has also increased during this time period. The objective of the present study was to estimate whether the past and future change in the atmospheric composition significantly contributes to the increase in hectare yield. Different crop species (beans, *Phaseolus vulgaris*, cv Pfalzer Juni; spring barley, *Hordeum vulgare* L., cvs. Alexis and Arena; spring wheat, *Triticum aestivum* L., cvs. Star and Turbo; maize, *Zea mays* L., cvs. Bonny and Boss) were grown at ambient (372 ppm) and at slightly elevated CO₂-concentrations (459 ppm and 539 ppm) in open-top chambers and the effect of the different CO₂-concentrations on the growth and yield of the plants was measured. The past and future CO₂-effect was estimated from the slope of a linear CO₂-yield curve (percentage increase in yield per ppm CO₂, 100 % at 370 ppm) fitted to the data and those from previous studies on wheat and maize. The percentage increase in yield per ppm CO₂ is insignificant for beans, of borderline significance for silage maize (0.06 % per ppm), and 0.35 % per ppm and 0.26 % per ppm for barley and wheat, respectively. The CO₂-elevation primarily decreases the tiller dieback of the cereals. Considering the increase in CO₂ of 30 ppm and in the hectare yield of 25 % (barley) and 28 % (wheat) from 1970 to 1990, the contribution of CO₂ to the increase in the agricultural production is estimated to be one fourth up to one half of the increase in hectare yield of spring cereals. Given a recent yearly increase of 2 ppm the future CO₂-related increase in hectare yield is estimated to be about 0.5-0.7 % per year.

KEYWORDS: CARBON DIOXIDE, ELEVATED CO₂, ENRICHMENT,

GROWTH, PHASEOLUS-VULGARIS, PLANTS, RESPONSES, WHEAT

1442

Manderscheid, R., and H.J. Weigel. 1997. Photosynthetic and growth responses of old and modern spring wheat cultivars to atmospheric CO₂ enrichment. *Agriculture Ecosystems & Environment* 64(1):65-73.

Cultivars of spring wheat (*Triticum aestivum* L.) introduced between 1890 and 1988 were cultivated in pots under optimal growth conditions and exposed during the whole growing season to normal (379 p.p.m.) and elevated CO₂ concentrations (689 p.p.m.) in open-top chambers. CO₂ effects were measured at anthesis on flag leaf composition (chlorophyll and protein) and photosynthetic parameters, and at maturity on plant growth and yield. CO₂ enrichment did not affect light saturated rate of photosynthesis measured at 400 p.p.m. CO₂ or protein, total chlorophyll and dry weight content per unit leaf area. However, single flag leaf area and fresh weight per leaf area were increased by CO₂. This increase was possibly responsible for a significant decrease in the chlorophyll a/b ratio. Under normal atmospheric CO₂ concentration, the total above-ground biomass, stem weight and height, and ear number were negatively correlated with the year of cultivar release. Despite no evidence of CO₂ acclimation, i.e. changes in flag leaf composition, CO₂ enrichment resulted in a greater growth stimulation of the older than the modern cultivars. This was due to a greater CO₂ effect on those growth components that were altered during plant breeding of wheat in the past, i.e. stem weight and height, and ear number. The average CO₂-related increase in biomass and grain yield amounted to ca 46% and 28% for the three old (1890-1943) and three modern cultivars (1965- 1988), respectively. Differences in yield response to CO₂ enrichment between old and modern cultivars could be mainly explained by changes in ear number. (C) 1997 Elsevier Science B.V.

KEYWORDS: CARBON DIOXIDE, COMPONENTS, ELEVATED CO₂, IMPROVEMENT, LEAVES, PLANTS, TEMPERATURE, VARIETIES, WINTER-WHEAT, YIELD

1443

Manninen, P., J. Pakarinen, and H. Kallio. 1997. Large-scale supercritical carbon dioxide extraction and supercritical carbon dioxide countercurrent extraction of cloudberry seed oil. *Journal of Agricultural and Food Chemistry* 45(7):2533-2538.

Dried press residue of cloudberry [*Rubus chamaemorus* (Rosaceae)] was extracted with carbon dioxide at pressures of 90-300 bar and at a temperature of 40 or 60 degrees C using a pilot-scale or a production-scale plant. The yield of the extract at the highest pressure was approximately 15% less than that obtained with Soxhlet extraction using diethyl ether as solvent. The extracts were either solids or viscous oils depending on the amount of neutral lipids, which increased with increasing pressure. No significant differences in the composition of the major constituent fatty acids in any of the extracts were found. The color of the extracts was clearly dependent on the amount of carotenes, which consisted mainly of beta-carotene. The content of carotenes in the extracts did not increase at pressures higher than 150 bar. The amount of tocopherols in the extracts obtained at highest pressure was found to be approximately 3 times less than that at lower pressures. Countercurrent CO₂ extraction of the cloudberry oil extracted at 300 bar and 40 degrees C resulted in enrichment of tocopherols in the extracts and a decrease in the amount of carotenes. The concentrations of tocopherols and carotenes in all of the CO₂ extracts, the countercurrent extracts, and the raffinates were found to be clearly higher than those in the edible part of fresh cloudberry reported by other authors.

1444

Mansfield, J.L., P.S. Curtis, D.R. Zak, and K.S. Pregitzer. 1999. Genotypic variation for condensed tannin production in trembling aspen (*Populus tremuloides*, Salicaceae) under elevated CO₂ and in high- and low-fertility soil. *American Journal of Botany* 86(8):1154-1159.

The carbon/nutrient balance hypothesis suggests that leaf carbon to nitrogen ratios influence the synthesis of secondary compounds such as condensed tannins. We studied the effects of rising atmospheric carbon dioxide on carbon to nitrogen ratios and tannin production. Six genotypes of *Populus tremuloides* were grown under elevated and ambient CO₂ partial pressure and high- and low-fertility soil in field open-top chambers in northern lower Michigan, USA. During the second year of exposure, leaves were harvested three times (June, August, and September) and analyzed for condensed tannin concentration. The carbon/nutrient balance hypothesis was supported overall, with significantly greater leaf tannin concentration at high CO₂ and low soil fertility compared to ambient CO₂ and high soil fertility. However, some genotypes increased tannin concentration at elevated compared to ambient CO₂, while others showed no CO₂ response. Performance of lepidopteran leaf miner (*Phyllonorycter tremuloidiella*) larvae feeding on these plants varied across genotypes, CO₂, and fertility treatments. These results suggest that with rising atmospheric CO₂, plant secondary compound production may vary within species. This could have consequences for plant-herbivore and plant-microbe interactions and for the evolutionary response of this species to global climate change.

KEYWORDS: ATMOSPHERIC CO₂, CARBON NUTRIENT BALANCE, CLONAL VARIATION, FOLIAR CHEMISTRY, FOREST TENT CATERPILLARS, GYPSY MOTHS, INSECT HERBIVORE, PERFORMANCE, RAPHANUS-RAPHANISTRUM, WILD RADISH

1445

Mansfield, T.A. 1998. Stomata and plant water relations: does air pollution create problems? *Environmental Pollution* 101(1):1-11.

Small changes in the gaseous composition of the atmosphere have many different impacts on terrestrial plants. Some of the most important involve changes in stomatal control of leaf conductance. Evolution has provided highly complex mechanisms by which stomata respond to a wide range of environmental factors to balance the conflicting priorities of carbon gain for photosynthesis and water conservation. These mechanisms involve direct responses of the guard cells to aspects of the aerial environment, and hormonal communication within the plant enabling conductance to be adjusted according to soil moisture status. Various aspects of these delicately balanced mechanisms can be disturbed by air pollutants. Impairment of the regulation of plant water use by SO₂ and O₃ has been known for some years, but there are still many obstacles to our understanding of the variations in response between species, or even between genotypes of the same species. A surprising outcome of some recent studies is the suggestion that CO₂ pollution may disrupt the control of water relations in some species because their stomata do not close sufficiently in CO₂-enriched air. It has often been taken for granted that the elevation of atmospheric CO₂ would lead to economies in water use by plant canopies, but the underlying assumptions are now being seriously questioned. (C) 1998 Elsevier Science Ltd. All rights reserved.

KEYWORDS: ABIES L. KARST, ABSCISIC-ACID, CARBON DIOXIDE, CYTOSOLIC-FREE CALCIUM, ELEVATED CO₂, FAGUS-SYLVAICA L, FOLIAR GAS-EXCHANGE, NORWAY SPRUCE, PICEA-ABIES, SOIL-MOISTURE STRESS

1446

Marek, L.F., and M.H. Spalding. 1991. Changes in photorespiratory enzyme-activity in response to limiting CO₂ in *Chlamydomonas reinhardtii*. *Plant Physiology* 97(1):420-425.

The activity of two photorespiratory enzymes, phosphoglycolate phosphatase (PGPase) and glycolate dehydrogenase (glycolate DH), changes when CO₂-enriched wild-type (WT) *Chlamydomonas reinhardtii* cells are transferred to air levels of CO₂. Adaptation to air levels of CO₂ by *Chlamydomonas* involves induction of a CO₂-concentrating mechanism (CCM) which increases the internal inorganic carbon concentration and suppresses oxygenase activity of ribulose-1,5-bisphosphate carboxylase/oxygenase. PGPase in cell extracts shows a transient increase in activity that reaches a maximum 3 to 5 hours after transfer and then declines to the original level within 48 hours. The decline in PGPase activity begins at about the time that physiological evidence indicates the CCM is approaching maximal activity. Glycolate DH activity in 24 hour air-adapted WT cells is double that seen in CO₂-enriched cells. Unlike WT, the high-CO₂-requiring mutant, *cia-5*, does not respond to limiting CO₂ conditions: it does not induce any known aspects of the CCM and it does not show changes in PGPase or glycolate DH activities. Other known mutants of the CCM show patterns of PGPase and glycolate DH activity after transfer to limiting CO₂ which are different from WT and *cia-5* but which are consistent with changes in activity being initiated by the same factor that induces the CCM, although secondary regulation must also be involved.

KEYWORDS: ADAPTATION, CONCENTRATING MECHANISM, DEFICIENT, EXCHANGE, EXCRETION, GLYCOLATE DEHYDROGENASE, MUTANT, PHOTOSYNTHESIS

1447

Marek, M.V., and J. Kalina. 1996. Comparison of two experimental approaches used in the investigations of the long-term effects of elevated CO₂ concentration. *Photosynthetica* 32(1):129-133.

Two experimental devices used in the investigations of the long-term effects of elevated CO₂ were compared from the point of view of occurrence of downregulation of photosynthesis. The comparison was made on the basis of net photosynthetic rate/internal CO₂ concentration (P-N/C-i) response and effective quantum yield of photosystem 2 (PS2), respectively. In branch bags, the needles of Norway spruce showed no down regulation of photosynthetic capacity. However, in open top chambers decreases in maximal P-N (32%), carboxylation efficiency (28%) and potential photochemical efficiency of PS2 (8%), and the quantum yield (up to 50%) were detected.

KEYWORDS: EXPOSURE, PLANTS

1448

Marek, M.V., J. Kalina, and M. Matoušková. 1995. Response of photosynthetic carbon assimilation of Norway spruce exposed to long-term elevation of CO₂ concentration. *Photosynthetica* 31(2):209-220.

Young (12 years old) Norway spruce (*Picea abies* [L.] Karst.) trees were exposed to ambient CO₂ or ambient + 350 $\mu\text{mol}(\text{CO}_2) \text{mol}^{-1}$ continuously over 2 growing seasons in open-top chambers, under field conditions of a mountain stand. Comprehensive analysis of CO₂ assimilation was performed after 4 and 22 weeks of the second growing season to evaluate the influence of elevated atmospheric CO₂. A combination of gas exchange and a mathematical model of ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBPCO) activity was used. After 4 weeks of exposure no statistically significant stimulation of the radiant energy and CO₂ saturated rate of CO₂ uptake (P-Nsat) by the elevated CO₂ concentration was found. Yet after 24 weeks a statistically significant depression of P-Nsat (38%) and carboxylation efficiency (32%) was observed. Depression of photosynthetic activity by elevated CO₂ resulted from a decrease in the RuBPCO carboxylation rate. The electron transport rate was also modified similarly to the rate of RuBP formation. An accompanying decrease in nitrogen content of the needles (by 12%) together with an increase in total saccharides (by 34%) was observed.

after 24 weeks of exposure to enhanced CO₂.

KEYWORDS: ACCLIMATION, ACTIVATION, ATMOSPHERIC CO₂, DIOXIDE CONCENTRATION, ENRICHMENT, GAS-EXCHANGE, GROWTH, INHIBITION, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE, TEMPERATURE

1449

Marek, M.V., M. Sprtova, and J. Kalina. 1997. The photosynthetic irradiance-response of Norway spruce exposed to a long-term elevation of CO₂ concentration. *Photosynthetica* 33(2):259-268.

During an open-top chamber experiment performed in a mountain stand of young (12-year-old) Norway spruce (*Picea abies* [L.] Karst.), the trees were exposed to one of two CO₂ concentrations (ambient CO₂, AC, or AC + 350 $\mu\text{mol mol}^{-1}$) = elevated CO₂, EC) continuously over three growing seasons. To evaluate the EC influence, measurements of the relations between the rate of net CO₂ uptake (P-N) and incidental photosynthetically active photon flux density (PPFD), as well as the content of photosynthetic pigments and chlorophyll (Chl) a fluorescence were taken in the third growing season. The short-term response to EC was evident mainly on ribulose-1,5- biphosphate carboxylase/oxygenase kinetics without any significant change to the utilization of radiant energy. The long-term effect of EC was responsible for a decrease in P-N, Content of Chl a + b, F-v/F-m ratio, quantum yield of fluorescence, and photochemical quenching. Changes of stoichiometry between the electron transport, Calvin cycle and the end-product synthesis were confirmed for responses to the longterm import of EC and led to a definition of the photosynthetic acclimation to EC an Norway spruce.

KEYWORDS: ACCLIMATION, ASSIMILATION, ATMOSPHERIC CO₂, CARBON DIOXIDE, CHLOROPHYLL FLUORESCENCE, ENRICHMENT, GROWTH, INHIBITION, LEAVES, LIGHT-RESPONSE

1450

Margolis, H.A., and M.G. Ryan. 1997. A physiological basis for biosphere-atmosphere interactions in the boreal forest: an overview. *Tree Physiology* 17(8-9):491-499.

Interdisciplinary field experiments for global change research are large, intensive efforts that study the controls on fluxes of carbon, water, trace gases, and energy between terrestrial ecosystems and the atmosphere at a range of spatial scales. Forest ecophysiology can make significant contributions to such efforts by measuring, interpreting, and modeling these fluxes for the individual components of forest ecosystems and then integrating the results into holistic ecosystem process models. The Boreal Ecosystem-Atmosphere Study (BOREAS) was undertaken because of the importance of the boreal forest biome to various global change issues. The study was conducted from 1993 to 1996 at sites in Saskatchewan and Manitoba, Canada. Results have shown that physiological processes of plants in the boreal forest can have large-scale consequences. For example, the composition of tree species strongly influences flux rates, with deciduous species having much higher carbon and water fluxes than coniferous species. Additionally, physiological limitations to transpiration in boreal conifers, even when soil water is abundant, reduces latent heat flux and increases sensible heat flux over large regions. This physiological control of transpiration can increase the depth of the atmospheric boundary layer on warm spring days to a level similar to that found in desert biomes. This special issue features 10 articles that address various aspects of the physiological basis of biosphere-atmosphere interactions in the boreal forest. The articles emphasize the environmental controls on water flux, carbon flux, and ecosystem productivity.

KEYWORDS: CARBON DIOXIDE, CLIMATIC CHANGE, CO₂,

EASTERN SIBERIA, ECOSYSTEM, EXCHANGE, FIELD EXPERIMENT FIVE, MODELS, RADIATION, REFLECTANCE

1451

Margolis, H.A., and L.P. Vezina. 1990. Atmospheric CO₂ enrichment and the development of frost hardiness in containerized black spruce seedlings. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 20(9):1392-1398.

1452

Marilley, L., U.A. Hartwig, and M. Aragno. 1999. Influence of an elevated atmospheric CO₂ content on soil and rhizosphere bacterial communities beneath *Lolium perenne* and *Trifolium repens* under field conditions. *Microbial Ecology* 38(1):39-49.

The increase in atmospheric CO₂ content alters C-3 plant photosynthetic rate, leading to changes in rhizodeposition and other root activities. This may influence the activity, the biomass, and the structure of soil and rhizosphere microbial communities and therefore the nutrient cycling rates and the plant growth. The present paper focuses on bacterial numbers and on community structure. The rhizospheres of two grassland plants, *Lolium perenne* (ryegrass) and *Trifolium repens* (white clover), were divided into three fractions: the bulk soil, the rhizospheric soil, and the rhizoplaneendorrhizosphere. The elevated atmospheric CO₂ content increased the most probable numbers of heterotrophic bacteria in the rhizosphere of *L. perenne*. However, this effect lasted only at the beginning of the vegetation period for *T. repens*. Community structure was assessed after isolation of DNA, PCR amplification, and construction of cloned 16S rDNA libraries. Amplified ribosomal DNA restriction analysis (ARDRA) and colony hybridization with an oligonucleotide probe designed to detect *Pseudomonas* spp. showed under elevated atmospheric CO₂ content an increased dominance of pseudomonads in the rhizosphere of *L. perenne* and a decreased dominance in the rhizosphere of *T. repens*. This work provides evidence for a CO₂-induced alteration in the structure of the rhizosphere bacterial populations, suggesting a possible alteration of the plant-growth-promoting- rhizobacterial (PGPR) effect.

KEYWORDS: 16S RDNA, CARBON DIOXIDE, DIVERSITY, ENRICHMENT, GROWTH, NITROGEN CYCLES, PSEUDOMONAS, RIBOSOMAL-RNA GENES, ROOTS, SYMBIOTIC N-2 FIXATION

1453

Marino, B.D.V., T.R. Mahato, J.W. Druitt, L. Leight, G.H. Lin, R.M. Russell, and F.N. Tubiello. 1999. The agricultural biome of Biosphere 2: Structure, composition and function. *Ecological Engineering* 13(1-4):199-234.

The agricultural mesocosm of Biosphere 2, known as the Intensive Agricultural Biome (IAB), provided food for the inhabitants of the facility during two periods of material closure between 1991 and 1994 (Mission I, September 26, 1991 to September 26, 1993, eight-person crew; Mission II, March 6, 1994 to September 17, 1994, seven-person crew). The design and operation of the mesocosm and preliminary results for food production of the IAB are described for both periods. The overall rate of crop production for the 0.22 ha area (soil depth of 1 m; soil and atmospheric volumes of approximately 2000 m³ and 38000 m³), respectively) sustained both crews. Overall production rates in Biosphere 2 exceeded those characteristic of fertile agricultural land in the most efficient agrarian communities, despite comparatively lower light levels, lack of insect pollinators and unusually dense insect pests. Crop yields were markedly higher for Mission II than for Mission I due, in part, to experience and improvements based on the first closure. The health of the Biospherians is briefly discussed in the context of a low-

calorie (1800-2200 kcal day⁻¹) per person for Mission I and 2200-2400 kcal day⁻¹ for Mission II), nutrient-dense diet characteristic of the Biosphere 2 food paradigm. High productivity and biodiversity were due to many factors including high resolution climate control, hyper-intensive agricultural practices, selection and planting of food crops adapted to humid, tropical and sub-tropical conditions, nutrient recycling, intensive pest management, and the superambient levels of atmospheric CO₂ (concentrations up to 4500 ppmv were reported during the 1991 to 1994 occupations). Radiation use efficiency (RUE) for wheat for both periods and a post-Mission II planting were comparable to RUEs observed in other experimental elevated CO₂ settings such as Controlled Ecological Life Support-Systems (CELSS) and Free Air CO₂ Enrichment studies (FACE) even though yields were comparatively lower due to low light levels. Integrated management of pests, soil conditions and agricultural practices were key factors in the sustainability of the IAB resulting in minimization of plant loss due to insect herbivory, nematode infestation and reduction in the quality of IAB soils. The use of soils rather than hydroponic systems for the IAB had significant consequences for CO₂, N₂O and O₂ concentrations in the Biosphere 2 atmosphere and rendered primary regeneration technologies ineffective over the periods of closure. The initial high organic carbon content of the IAB soils prescribed by the designers proved to be the largest single source of CO₂ and the largest sink for O₂. The choice of a soil-based compared to a hydroponic-based agricultural system contributed to the accumulation of N₂O to levels as high as 300 times current ambient levels (approximately 310 ppbv). The IAB of Biosphere 2 has the potential; with system improvement, to be a high-yielding, self-sustaining agricultural mesocosm suited for a variety of research endeavors. (C) 1999 Elsevier Science B.V. All rights reserved.

KEYWORDS: CELSS, CO₂, ENVIRONMENT, LIFE-SUPPORT, PERFORMANCE, PLANT GROWTH, PRODUCTIVITY, SOILS, SYSTEMS, WHEAT

1454

Mark, U., and M. Tevini. 1997. Effects of solar ultraviolet-B radiation, temperature and CO₂ on growth and physiology of sunflower and maize seedlings. *Plant Ecology* 128(1-2):224-234.

The effects of solar UV-B radiation, in combination with elevated temperature (4 degrees C) and CO₂ (680 mu L L⁻¹) concentration, on sunflower and maize seedlings were studied from May to August in 1991 at the research station Quinta de Sao Pedro in Portugal (38.7 degrees N). The ambient solar radiation of Portugal was reduced to levels of Central European latitudes by using the ozone filter technique. This radiation served as control, while the ambient solar radiation of Portugal was to simulate intense UV-B treatment (+30%). All plants were grown up to 18 days in 4 climate controlled growth chambers simulating a daily course of temperature with T-max=28 degrees C or 32 degrees C, resp., and ambient CO₂ concentrations (340 mu L L⁻¹); in one chamber the CO₂ concentration was twice as high (680 mu L L⁻¹). Under intense UV-B and at 28 degrees C (T-max) all growth parameters (height, leaf area, fresh and dry weight, stem elongation rate, relative growth rate) of sunflower and maize seedlings were reduced down to 35% as compared to controls. An increase in growing temperature by 4 degrees C, alone or in combination with doubled CO₂, compensated or even overcompensated the UV-B effect so that the treated plants were comparable to controls. Chlorophyll content, on a leaf area basis, increased under intense UV-B radiation. This increase was compensated by lower leaf areas, resulting in comparable chlorophyll contents. Similar to growth, also the net photosynthetic rates of sunflower and maize seedlings were reduced down to 29% by intense UV-B calculated on a chlorophyll basis. This reduction was compensated by an increased temperature. Doubling of CO₂ concentration had effects only on sunflower seedlings in which the photosynthetic rates were higher than in the controls. Dark respiration rates of the seedlings were not

influenced by any experimental condition. Transpiration and water use efficiency (wue) were not influenced by intense UV-B. Higher temperatures led to higher transpiration rates and lower water use efficiencies, resp. Doubling of CO₂ reduced the transpiration rate drastically while for wue maximum values were recorded.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CROP PLANTS, DARK RESPIRATION, ENRICHMENT, GAS-EXCHANGE, HIGHER-PLANTS, NET PHOTOSYNTHESIS, PHOTOSYNTHETIC CHARACTERISTICS, PHOTOSYSTEM, WHEAT

1455

Markkola, A.M., A. Ohtonen, U. AhonenJonnarth, and R. Ohtonen. 1996. Scots pine responses to CO₂ enrichment .1. Ectomycorrhizal fungi and soil fauna. *Environmental Pollution* 94(3):309-316.

Ectomycorrhizal Scots pine seedlings were grown in unfertilized forest soil at ambient and double (ca 700 ppm) atmospheric concentrations of CO₂. The biomass of seedlings and fungal biomass both in the roots and in the soil and the numbers of certain groups of soil animals were measured under summer conditions and after an artificial winter acclimation period. No biomass parameter showed any significant change due to CO₂ elevation. Increases were found during the winter acclimation period in total and fine root biomasses, fungal biomass in the soil and total fungal biomass both in the roots and in the soil, while the ratio of needle biomass:fungal biomass and the shoot:root ratio decreased. The N concentration in previous-year needles was lower in the double CO₂ environment than with ambient CO₂. Enchytraeids almost disappeared in the double CO₂ environment during winter acclimation, while the numbers of nematodes increased at the same time in both treatments. (C) 1997 Elsevier Science Ltd.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, BIOMASS, ELEVATED CO₂, GAS-EXCHANGE, MYCORRHIZAL COLONIZATION, PLANTS, POLLUTION GRADIENT, ROOTS, SEEDLING GROWTH, SOURCE-SINK RELATIONS

1456

Marks, S., and K. Clay. 1990. Effects of CO₂ enrichment, nutrient addition, and fungal endophyte-infection on the growth of 2 grasses. *Oecologia* 84(2):207-214.

1457

Marks, S., and D.E. Lincoln. 1996. Antiherbivore defense mutualism under elevated carbon dioxide levels: A fungal endophyte and grass. *Environmental Entomology* 25(3):618-623.

Previous studies have shown that insects commonly consume more when fed leaf tissue grown under CO₂ enrichment, but with few negative effects on growth. However, lepidopteran larvae fed tissue infected with Balansiae fungal endophytes (which produce toxic alkaloids) typically eat less but also suffer negative effects on growth and survival. This study was carried out to understand how these 2 factors may interact to affect larval consumption and growth in fall armyworm, *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae). Infected and uninfected ramets of a single genotype of tall fescue, *Festuca arundinacea* Schreb., were grown under CO₂ concentrations of 400 and 700 mu l CO₂/liter of air. Relative consumption of leaf tissue by larvae was 32% greater in the high CO₂ treatment compared with leaves grown under low CO₂ concentrations, but was not influenced by infection. As expected, larvae had significantly decreased relative growth rates when fed infected tissue, with their growth rates somewhat increased under high CO₂ levels. Increased CO₂ level and infection both led to significantly reduced efficiency of conversion of ingested food. These 2

factors also interacted so that the lowest efficiency of conversion of ingested food was seen when both infection and an enriched atmospheric CO₂ environment were present. As global atmospheric CO₂ levels continue to increase, it appears that fungal endophytes will continue to be important in turfgrasses as protection against insect herbivores and may lead to increased fitness for infected plant genotypes.

KEYWORDS: ATMOSPHERIC CO₂ ENRICHMENT, INFECTED TALL FESCUE, INSECT HERBIVORE INTERACTIONS, LEPIDOPTERA, PERENNIAL RYEGRASS, PERFORMANCE, PLANT, QUERCUS-ALBA, RESPONSES, SEEDLING GROWTH

1458

Maroco, J.P., G.E. Edwards, and M.S.B. Ku. 1999. Photosynthetic acclimation of maize to growth under elevated levels of carbon dioxide. *Planta* 210(1):115-125.

The effects of elevated CO₂ concentrations on the photochemistry, biochemistry and physiology of C-4 photosynthesis were studied in maize (*Zea mays* L.). Plants were grown at ambient (350 $\mu\text{mol L}^{-1}$) or ca. 3 times ambient (1100 $\mu\text{mol L}^{-1}$) CO₂ levels under high light conditions in a greenhouse for 30 d. Relative to plants grown at ambient CO₂ levels, plants grown under elevated CO₂ accumulated ca. 20% more biomass and 23% more leaf area. When measured at the CO₂ concentration of growth, mature leaves of high-CO₂-grown plants had higher light-saturated rates of photosynthesis (ca. 15%), lower stomatal conductance (71%), higher water-use efficiency (225%) and higher dark respiration rates (100%). High-CO₂-grown plants had lower carboxylation efficiencies (23%), measured under limiting CO₂, and lower leaf protein contents (22%). Activities of a number of C-3 and C-4 cycle enzymes decreased on a leaf-area basis in the high-CO₂-grown plants by 5-30%, with NADP-malate dehydrogenase exhibiting the greatest decrease. In contrast, activities of fructose 1,6-bisphosphatase and ADP-glucose pyrophosphorylase increased significantly under elevated CO₂ condition (8% and 36%, respectively). These data show that the C-4 plant maize may benefit from elevated CO₂ through acclimation in the capacities of certain photosynthetic enzymes. The increased capacity to synthesize sucrose and starch, and to utilize these endproducts of photosynthesis to produce extra energy by respiration, may contribute to the enhanced growth of maize under elevated CO₂.

KEYWORDS: ATMOSPHERIC CO₂, C-4, CARBOHYDRATE, ENRICHMENT, GAS-EXCHANGE, GENE-EXPRESSION, HIGH CO₂ CONCENTRATIONS, LEAVES, PLANT GROWTH, WATER-USE

1459

Marshall, J.D., and R.A. Monserud. 1996. Homeostatic gas-exchange parameters inferred from C-13/C-12 in tree rings of conifers. *Oecologia* 105(1):13-21.

The CO₂ concentration of the atmosphere has increased by almost 30% in the past two centuries, with most of the increase (> 5 Pa) during the past 60 years. Controlled environment studies of crop plants dependent on the C-3 photosynthetic pathway indicate that an increase of this magnitude would enhance net photosynthesis, reduce stomatal conductance, and increase the difference in CO₂ concentration across the stomata, i.e., CO₂ concentration outside the leaf to that within (c(a)-c(i)). Here we report evidence, based on stable isotope composition of tree rings from three species of field-grown, native conifer trees; that the trees have indeed responded. However, rather than increasing c(a)-c(i), intercellular CO₂ concentrations have shifted upward to match the rise in atmospheric concentrations, holding c(a)-c(i) constant. No differences were detected among Douglas-fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*), or western white pine (*Pinus monticola*). The values of c(a)-c(i) were inferred from stable carbon isotope ratio ($\delta^{13}\text{C}$) of tree ring holocellulose adjusted for the 0.6- 2.6 parts per

thousand difference between holocellulose and whole sapwood. The cellulose extraction removed contaminants deposited in the tree ring after it formed and the adjustment corrected for the enrichment of cellulose relative to whole tissue. The whole sapwood values were then adjusted for published estimates of past atmospheric $\delta^{13}\text{C}$ and CO₂ concentrations. To avoid confounding tree age with CO₂, cellulose deposited by saplings in the inner rings of trees when the mature trees were saplings, between 1910-1929 and 1941-1970: thus saplings were compared to saplings. In a separate analysis, the juvenile effect, which describes the tendency for $\delta^{13}\text{C}$ to increase in the first decades of a tree's life, was quantified independent of source CO₂ effects. This study provides evidence that conifers have undergone adjustments in the intercellular CO₂ concentration that have maintained c(a)-c(i) constant. Based on these results and others, we suggest that c(a)-c(i) which has also been referred to as the intrinsic water-use efficiency, should be considered a homeostatic gas-exchange set point for these conifer species.

KEYWORDS: ATMOSPHERIC CO₂ CONCENTRATION, CARBON ISOTOPE DISCRIMINATION, DIOXIDE CONCENTRATION, DOUGLAS-FIR, ELEVATED CO₂, GROWTH, LEAVES, PARTIAL-PRESSURE, PHOTOSYNTHESIS, WATER-USE EFFICIENCY

1460

Martin, C.A., J.C. Stutz, B.A. Kimball, S.B. Idso, and D.H. Akey. 1995. Growth and topological changes of citrus-limon (L) burm f eureka in response to high-temperatures and elevated atmospheric carbon-dioxide. *Journal of the American Society for Horticultural Science* 120(6):1025-1031.

Growth and topological indices of 'Eureka' lemon were measured after 6 months in well-watered and well-fertilized conditions and factorial combinations of moderate (29/21C day/night) or high (42/32C day/night) temperatures and ambient (350 to 380 $\mu\text{mol} \cdot \text{mol}^{-1}$) or elevated (constant 680 $\mu\text{mol} \cdot \text{mol}^{-1}$) CO₂. In high temperatures, plants were smaller and had higher levels of leaf chlorophyll alpha than in moderate temperatures. Moreover, plants in high temperatures and elevated CO₂ had about 15% higher levels of leaf chlorophyll alpha than those in high temperatures and ambient CO₂. In high temperatures, plant growth in elevated CO₂ was about 87% more than in ambient CO₂. Thus, high CO₂ reduced the negative effect of high temperature on shoot growth. In moderate temperatures, plant growth in elevated CO₂ was only about 21% more than in ambient CO₂. Irrespective of temperature treatments, shoot branch architecture in elevated CO₂ was more hierarchical than those in ambient CO₂. Specific shoot extension, a topological measure of branch frequency, was not affected by elevated CO₂ in moderate temperatures, but was increased by elevated CO₂ enrichment in high temperatures-an indication of decreased branch frequency and increased apical dominance. In moderate temperatures, plants in elevated CO₂ had fibrous root branch patterns that were less hierarchical than at ambient CO₂. The lengths of exterior and interior fibrous roots between branch points and the length of second-degree adventitious lateral branches were increased >50% by high temperatures compared with moderate temperatures. Root length between branch points was not affected by CO₂ levels.

KEYWORDS: ARCHITECTURAL ANALYSIS, CARBOXYLASE, CO₂ CONCENTRATIONS, ENRICHMENT, GAS-EXCHANGE, PHOTOSYNTHESIS, PLANT-ROOT SYSTEMS, PRODUCTIVITY, RESPIRATION, SEEDLINGS

1461

Martin, P. 1992. Exe: a climatically sensitive model to study climate change and co₂ enhancement effects on forests. *Australian Journal of Botany* 40(4-5):717-735.

Vegetation plays a significant role in determining the local and regional hydrology of ice-free continental surfaces and the dynamics of the atmosphere above it. Vegetation also influences the global climate directly by affecting atmospheric chemistry. In particular, it partially controls the carbon cycle. In turn, vegetation is influenced by climate and changes in the ambient concentration of CO₂. This may have important consequences for agriculture and natural resource exploitation. A formal recognition of atmosphere/biosphere interrelationships is crucial but insufficient. Systematic investigations of the interactions between climate, plant physiology and ecology are badly needed. In this spirit, this paper presents the results of numerical simulations performed with the Energy, water and momentum exchange, and Ecological dynamics (EXE) model at a local scale over periods of 400-800 (simulation) years. EXE constitutes a first attempt to couple a physiologically based water budget and an explicit treatment of ecological dynamics. In principle, EXE could be forced by the output of an atmospheric general circulation model (GCM). Within this context, the paper demonstrates through the examples it analyses that both potential stomatal response to CO₂ and the possible range of changes in atmospheric relative humidity are likely major factors in determining the ecosystem response to greenhouse warming. Consequently, they should be considered in future studies of this kind. The paper also provides explanations regarding the movement of ecotones, defined as the transition zones between different vegetation assemblages. Taking the North American forest/prairie boundary as a case study, the analysis of the results shows how, in a greenhouse warmed world, St Paul, MN, might look like North Platte, NE. Finally, building on the previous example by using two different models, this study illustrates that results can be strongly model dependent and encourages extreme caution in their interpretation.

KEYWORDS: AMAZONIAN RAINFOREST, SIMPLE BIOSPHERE MODEL

1462

Martin, P.H., and A.B. Guenther. 1995. Insights into the dynamics of forest succession and non-methane hydrocarbon trace gas emissions. *Journal of Biogeography* 22(2-3):493-499.

Natural biogenic non-methane hydrocarbon (NMHC) emissions significantly influence the concentrations of free hydroxyl and peroxy radicals, carbon monoxide and tropospheric ozone. Present concerns with air pollution and the global carbon balance call for a better understanding of the respective roles of climate dynamics and vegetation succession in determining NMHC emissions. This constitutes the focus of the present paper. The approach consists in coupling the Energy, Water and Momentum Exchange and Ecological Dynamics model, a climatically sensitive, physically based gap phase forest dynamics model, and NMHC trace gas emission algorithms to assess possible changes in NMHC emissions from forests under stationary and changing climatic conditions. In summary, it is possible to follow the temporal evolution of foliar emissions over centuries using a vegetation dynamics model coupled with an NMHC emissions module. Significant changes in isoprene and terpene emissions can take place as vegetation succession occurs under stationary climatic conditions and as climatic perturbations of the type and magnitude foreseen for global change alter the local microclimate. As illustrated by two examples, emissions may decrease or increase depending on the local climate and vegetation. The respective actions of changes in species absolute and relative abundance and changes in temperature interact very non-linearly making changes in emissions difficult to predict. None the less, coupled models of the kind described here may provide useful insights into the direction of such changes.

KEYWORDS: CARBON, CLIMATE, CO₂, MODEL

1463

Martinez, I., M.I. Orus, and E. Marco. 1997. Carboxysome structure and function in a mutant of *Synechococcus* that requires high levels of CO₂ for growth. *Plant Physiology and Biochemistry* 35(2):137-146.

The high CO₂-requiring mutant N1 of *Synechococcus* sp. PCC 7942 possesses aberrant carboxysomes and is unable to utilize the internal inorganic carbon pool for photosynthesis. Normal carboxysomal carbonic anhydrase (EC 4.2.1.1) and ribulose 1,5 biphosphate carboxylase/oxygenase (EC 4.1.1.39) activities were obtained under saturated substrate concentrations, but limiting concentrations of inorganic carbon resulted in a lower Rubisco activity compared to the wild type. The polypeptidic pattern of carboxysome-enriched fractions showed no differences between wild type and mutant N1, suggesting that the putative gene product inactivated in the mutant does not constitute a polypeptide of the carboxysome shell, but could play an important role in the process of carboxysome assembly. Data obtained are discussed in relation to the proposed quantitative model of the inorganic carbon concentrating mechanism of cyanobacteria.

KEYWORDS: CONCENTRATING MECHANISM, CYANOBACTERIA, GENE, INORGANIC CARBON FLUXES, PCC7942, PHOTOSYNTHESIS, REGION, RIBULOSE-1,5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, SP STRAIN PCC-7942, THIOBACILLUS-NEAPOLITANUS

1464

Martins, A., A. Casimiro, and M.S. Pais. 1997. Influence of mycorrhization on physiological parameters of micropropagated *Castanea sativa* Mill. plants. *Mycorrhiza* 7(3):161-165.

Mycorrhizal micropropagated *Castanea sativa* plants were studied in terms of growth and physiological parameters following in vitro mycorrhization with *Pisolithus tinctorius*. Mycorrhization enhanced growth of micropropagated chestnut plants, increased their protein content and photosynthetic rates, decreased the respiratory rates and CO₂ compensation point, RuBisCO activity was not significantly different in mycorrhizal and control plants, although there was an increase in the amount of RuBisCO in the former. Mycorrhization increased plant biomass and improved plants physiological status, thus enhancing the acclimatization process.

KEYWORDS: CARBON BALANCE, DOUGLAS-FIR, FUNGI, GROWTH, LEAVES, NITROGEN, PHOSPHORUS, PHOTOSYNTHESIS, SEEDLINGS, WILLOW ECTOMYCORRHIZAS

1465

Martos, J.M.G. 1993. Effect of CO₂ in storage atmosphere on mill olive fruit physiology. *Grasas Y Aceites* 44(2):81-84.

Olive fruits (*Olea europaea*) used for oil production 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 storage atmosphere with greater-than-or-equal-to 5% CO₂ concentrations produced a proportional increase of the physiological disorder occurring in stored fruits. This occurrence had a strong relationship with the appearance of fruit decay. Simple refrigeration at 5- degrees-C was sufficient to maintain the same degree of ripening of olive fruits for 60 days. However, a longer period of storage at 5-degrees-C originated a remarkable incidence of chilling injuries in the fruits.

1466

Masle, J. 1992. Will plant performance on soils prone to drought or with

high mechanical impedance to root penetration be improved under elevated atmospheric CO₂ concentration? *Australian Journal of Botany* 40(4-5):491-500.

Plants growing on dry soils or on soils with high mechanical resistance to root penetration grow more slowly and exhibit lower stomatal conductance than those growing on moist and loose soils. In most situations in nature where edaphic stresses develop rather slowly (compared to stresses imposed in most pot experiments conducted under controlled conditions), photosynthesis is mainly reduced via stomatal effects rather than via changes in mesophyll capacity for photosynthesis. Elevated CO₂ will induce an increase in the internal partial pressure of CO₂, despite stomatal conductance being lowered even further. Photosynthesis will therefore be improved, and leaf turgor will be increased. It is widely thought that growth on dry or hard soils is not carbon limited because levels of soluble carbohydrates in the leaves and root cells are increased. It is shown in this paper that growth on soil with high mechanical resistance does respond to elevated CO₂. However, this response is smaller than expected from the increase of carbon assimilation rate because: (a) carbon partitioning is altered so that supplementary carbohydrates are preferentially allocated to the roots; (b) leaf growth sensitivity to internal availability of sugars is lower than in plants growing on loose soils. These alterations of 'sink activity' and carbon partitioning are mediated by unknown signalling factor(s) induced in the roots. It is not known whether the root factors acting in droughted plants are of the same nature. In both droughted and impeded plants the interacting effects of these factors and of ambient CO₂ levels are likely to result in improved transpiration efficiency. More experiments are needed in this area, however, especially to ascertain the relative contribution of changes in growth patterns versus changes in the patterns of water use. In conclusion, the importance of identifying the nature of the sink limitations induced by root signals is emphasised. It is a fundamental area of research to be developed not only for assessing growth responses to rising CO₂ under edaphic stress, but likely also for reconciling conflicting responses of field-grown and pot-grown plants.

KEYWORDS: *ABSCISIC-ACID, CARBON DIOXIDE, DRYING SOIL, GROWTH, LEAVES, PHASEOLUS-VULGARIS L, PHOTOSYNTHETIC CAPACITY, STOMATAL CONDUCTANCE, WATER-STRESS, WHEAT SEEDLINGS*

1467

Masle, J., G.S. Hudson, and M.R. Badger. 1993. Effects of ambient CO₂ concentration on growth and nitrogen use in tobacco (*Nicotiana tabacum*) plants transformed with an antisense gene to the small-subunit of ribulose-1,5-bisphosphate carboxylase oxygenase. *Plant Physiology* 103(4):1075-1088.

Growth of the R1 progeny of a tobacco plant (*Nicotiana tabacum*) transformed with an antisense gene to the small subunit of ribulose-1,5-carboxylase/oxygenase (Rubisco) was analyzed under 330 and 930 mbar of CO₂, at an irradiance of 1000 μmol quanta m⁻² s⁻¹. Rubisco activity was reduced to 30 to 50% and 13 to 18% of that in the wild type when one and two copies of the antisense gene, respectively, were present in the genome, whereas null plants and wild-type plants had similar phenotypes. At 330 mbar of CO₂ all antisense plants were smaller than the wild type. There was no indication that Rubisco is present in excess in the wild type with respect to growth under high light. Raising ambient CO₂ pressure to 930 mbar caused plants with one copy of the DNA transferred from plasmid to plant genome to achieve the same size as the wild type at 330 mbar, but plants with two copies remained smaller. Differences in final size were due mostly to early differences in relative rate of leaf area expansion (m² m⁻² d⁻¹) or of biomass accumulation (g g⁻¹ d⁻¹): within less than 2 weeks after germination relative growth rates reached a steady-state value similar for all plants. Plants with greater carboxylation rates were characterized by a higher ratio of leaf carbon to leaf area, and at later stages, they were

characterized also by a relatively greater allocation of structural and nonstructural carbon to roots versus leaves. However, these changes per se did not appear to be causing the long-term insensitivity of relative growth rates to variations in carboxylation rate. Nor was this insensitivity due to feedback inhibition of photosynthesis in leaves grown at high partial pressure of CO₂ in the air (p(a)) or with high Rubisco activity, even when the amount of starch approached 40% of leaf dry weight. We propose that other intrinsic rate-limiting processes that are independent of carbohydrate supply were involved. Under plentiful nitrogen supply, reduction in the amount of nitrogen invested in Rubisco was more than compensated for by an increase in leaf nitrate. Nitrogen content of organic matter, excluding Rubisco, was unaffected by the antisense gene. In contrast, it was systematically lower at elevated p(a) than at normal p(a). Combined with the positive effects of p(a) on growth, this resulted in the single-dose antisense plants growing as fast at 930 mbar of CO₂ as the wild-type plants at 330 mbar of CO₂ but at a lower organic nitrogen cost.

KEYWORDS: *CARBON DIOXIDE, ELEVATED CO₂, IMPACT, LEAVES, LIGHT, PARTIAL-PRESSURE, PHOTOSYNTHETIC ACCLIMATION, RBCS, RIBULOSE BISPHOSPHATE CARBOXYLASE, WHEAT SEEDLINGS*

1468

Matamala, R., and B.G. Drake. 1999. The influence of atmospheric CO₂ enrichment on plant-soil nitrogen interactions in a wetland plant community on the Chesapeake Bay. *Plant and Soil* 210(1):93-101.

We investigated plant and soil nitrogen pools and soil processes in monospecific stands of the C-3 sedge *Scirpus olneyi* and the C-4 grass *Spartina patens* grown in the field in open top chambers in a brackish marsh on the Chesapeake Bay. Stands of *S. olneyi* responded to eight years of elevated CO₂, by increased rates of net ecosystem gas exchange and a large stimulation of net ecosystem production. We conducted our study in the summer of 1994 and 1995 when soil cores were collected and aboveground biomass was estimated. Nitrogen concentration in elevated CO₂ treatments was reduced 15% in stems of *S. olneyi* and 8% in the upper 10 cm of the soil profile. While total plant nitrogen per unit of land area remained the same between treatments, total soil nitrogen showed a non-significant tendency to decrease in the upper 10 cm of the soil profile in elevated CO₂ both years of study. A significant decrease in soil bulk density largely contributed to the observed decrease in soil nitrogen. Exchangeable nitrogen and potential denitrification rates were also reduced in elevated CO₂, but net nitrogen mineralization was unchanged by elevated CO₂ treatment in *S. olneyi* both years. Plants and soils in a pure stand of the C-4 grass, *S. patens*, showed none of these effects of elevated CO₂ treatment. Our data provides evidence of changes in nitrogen dynamics of an ecosystem exposed to elevated CO₂ for eight years; however due to the variability in these data, we cannot say if or how these changes are likely to impact the effect of rising CO₂ on primary production or carbon accumulation in this ecosystem in the future.

KEYWORDS: *CARBON-DIOXIDE ENRICHMENT, DECOMPOSITION, DENITRIFICATION, ELEVATED CO₂, ESTUARINE MARSH, GAS FLUXES, LEAF LITTER, LOLIUM-PERENNE, PHOTOSYNTHESIS, SCIRPUS-OLNEYI*

1469

Mathooko, F.M. 1996. Regulation of ethylene biosynthesis in higher plants by carbon dioxide. *Postharvest Biology and Technology* 7(1-2):1-26.

Elevated CO₂ levels used with or without reduced O₂ levels regulate many biochemical and physiological processes in higher plants, among them ethylene biosynthesis. The mode of action of elevated CO₂ in the

regulation of ethylene biosynthesis is still a subject of much debate. Various hypotheses have been put forward to explain its model(s) of action and most of them have pointed out that CO₂ regulates ethylene biosynthesis, at least in part, by counteracting ethylene action. This is thought to be mainly through the regulation of 1-aminocyclopropane-1-carboxylate (ACC) synthase, presumably the rate-limiting enzyme in the ethylene biosynthetic pathway, and in some instances ACC oxidase. The present review brings together recent developments on the biochemical, physiological and molecular bases for the regulation by CO₂ of ethylene biosynthesis in higher plants. The mode of activation of ACC oxidase by CO₂ is also discussed.

KEYWORDS: CUCURBITA-MAXIMA, ENCODING 1-AMINOCYCLOPROPANE-1-CARBOXYLATE SYNTHASE, FORMING ENZYME, GENES, LEAF-DISKS, LIGHT INHIBITION, MESSENGER-RNA, POSTHARVEST PHYSIOLOGY, TOMATO FRUITS, WOUND ETHYLENE

1470

Mathooko, F.M. 1996. Regulation of respiratory metabolism in fruits and vegetables by carbon dioxide. *Postharvest Biology and Technology* 9(3):247-264.

The respiratory rate of fruits and vegetables can be used as an indicator for designing storage conditions to maximize the longevity of these commodities. One postharvest technique that has been used to prolong the storage life of some of these commodities is the use of a controlled atmosphere. The modulation of respiratory metabolism of such commodities held in controlled atmospheres containing reduced oxygen and/or elevated carbon dioxide levels has been thought of as the primary reason for the beneficial effects on the commodities. However, the mechanism by which elevated carbon dioxide influences the regulation of respiratory metabolism is still obscure and several hypotheses have been proposed for its mode(s) of action. The regulation may be directed towards the glycolytic pathway, the fermentative metabolism, the tricarboxylic acid cycle or the electron transport system, presumably through its influence on the synthesis, degradation, inactivation and/or activation of the respective enzymes. It may also be through the antagonistic effects of carbon dioxide on ethylene action as well as its influence on secondary metabolism through an alteration in cell pH. This article discusses the recent developments on the biochemical and physiological fronts as well as the possible mode(s) of action of elevated carbon dioxide in the regulation of respiratory metabolism in fruits and vegetables.

KEYWORDS: ALCOHOL-DEHYDROGENASE, BARTLETT PEARS, CO₂-ENRICHED ATMOSPHERES, CONTROLLED ATMOSPHERES, ELEVATED CO₂ CONCENTRATIONS, FRUCTOSE 2;6-BISPHOSPHATE, INDUCTION, OXYGEN, QUALITY, STORAGE

1471

Mathooko, F.M., Y. Kubo, A. Inaba, and R. Nakamura. 1995. Characterization of the regulation of ethylene biosynthesis in tomato fruit by carbon-dioxide and diazocyclopentadiene. *Postharvest Biology and Technology* 5(3):221-233.

The regulation of ethylene biosynthesis by CO₂ and diazocyclopentadiene (DACP), both inhibitors of ethylene action, was investigated in tomato (*Lycopersicon esculentum* Mill. cv. 'Momotaro') fruit held at 25 degrees C. When the tomato fruit at the pink stage of ripeness were treated with 20% CO₂ (+ 20% O₂ + 60% N₂) or DACP, ethylene production by the fruit was rapidly decreased. The inhibition of ethylene production resulted primarily, if not solely, from the suppression of the activities of both 1-aminocyclopropane-1-carboxylic acid (ACC) synthase and ACC oxidase. The inhibition of ACC synthase activity subsequently led to low levels of ACC. CO₂ treatment further

inhibited ACC conjugation into 1-(malonylamino)cyclopropane-1-carboxylic acid (MACC). By contrast, DACP-treated fruit maintained slightly higher levels of MACC relative to the control fruit. When the fruit were transferred from the CO₂-enriched atmosphere to air, ethylene production, ACC and MACC contents and the activities of ACC synthase and ACC oxidase increased gradually to the control level after 24 h, while these values, except for MACC content, remained low in DACP-treated fruit throughout the experimental period. These results indicate that CO₂ and DACP regulate ethylene production in tomato fruit by inhibiting ACC synthase and ACC oxidase activities and further support the hypothesis that the autocatalytic signal associated with ethylene action during fruit ripening stimulates the activities of both enzymes.

KEYWORDS: 1-AMINOCYCLOPROPANE-1-CARBOXYLIC ACID, ASSAY, CAPABILITY, CONTROLLED ATMOSPHERES, DACP, PRECLIMACTERIC TOMATO, SYNTHASE

1472

Mathooko, F.M., Y. Kubo, A. Inaba, and R. Nakamura. 1995. Induction of ethylene biosynthesis and polyamine accumulation in cucumber fruit in response to carbon-dioxide stress. *Postharvest Biology and Technology* 5(1-2):51-65.

Carbon dioxide stress-induced ethylene biosynthesis, respiration and polyamine accumulation in cucumber fruit (*Cucumis sativus* L. cv. Sharp-1) held at 25 degrees C was investigated. Control fruit produced little ethylene and the respiration rate decreased with increase in incubation time while polyamine levels decreased. Elevated CO₂ induced ethylene production, respiration and polyamine accumulation. Putrescine and spermidine levels increased in response to CO₂ treatment, whereas spermine levels were not significantly affected. No cadaverine was detected in all treatments. The increase in ethylene production paralleled increases in 1-aminocyclopropane-1-carboxylic acid (ACC) and the activities of both ACC synthase and in vitro ACC oxidase. Infiltration of the fruit with aminooxyacetic acid, a potent inhibitor of the conversion of S-adenosylmethionine (AdoMet) to ACC completely blocked CO₂ stress-induced ethylene production. Similarly, cycloheximide, an inhibitor of nucleocytoplasmic protein synthesis effectively blocked CO₂ stress induction of polyamine accumulation, ethylene production, ACC formation and the development of ACC synthase. Withdrawal of CO₂ gas caused cessation of increases in ethylene production, respiration, ACC, putrescine and the activities of ACC synthase and ACC oxidase, but caused increase in spermidine and spermine levels. These data indicate that CO₂ induces de novo synthesis of ACC synthase thereby causing accumulation of ACC and increase in ethylene production and suggest that the conversion of AdoMet to ACC is the rate-limiting step in CO₂ stress-induced ethylene biosynthesis. The induction, however, requires continuous presence of the stimulus. The results also suggest that protein synthesis might be required for the CO₂ stress induction of polyamine biosynthesis. The results further suggest that in cucumber fruit under CO₂ stress, at least, the ethylene and polyamine biosynthetic pathways are not competitive.

KEYWORDS: 1-AMINOCYCLOPROPANE-1-CARBOXYLIC ACID, ACTIVATION, C₂H₄ PRODUCTION, CHILLING INJURY, ELICITOR, OXIDASE, PUTRESCINE, SATIVUS L, SPERMIDINE, STORAGE

1473

Mathooko, F.M., M.W. Mwaniki, A. Nakatsuka, S. Shiomi, Y. Kubo, A. Inaba, and R. Nakamura. 1999. Expression characteristics of CS-ACS1, CS-ACS2 and CS-ACS3, three members of the 1-aminocyclopropane-1-carboxylate synthase gene family in cucumber (*Cucumis sativus* L.) fruit under carbon dioxide stress. *Plant and Cell Physiology* 40(2):164-172.

Fire investigated the expression pattern of three 1-aminocyclopropane-1-carboxylate (ACC) synthase genes, CS-ACS1, CS-ACS2 and CS-ACS3 in cucumber (*Cucumis sativus* L.) fruit under CO₂ stress. CO₂ stress-induced ethylene production paralleled the accumulation of only CS-ACS1 transcripts which disappeared upon withdrawal of CO₂. Cycloheximide inhibited the CO₂ stress-induced ethylene production but superinduced the accumulation of CS-ACS1 transcript. At higher concentrations, cycloheximide also induced the accumulation of CS-ACS2 and CS-ACS3 transcripts. In the presence of CO₂ and cycloheximide, the accumulation of CS-ACS2 transcript occurred within 1h, disappeared after 3h and increased greatly upon withdrawal of CO₂. Inhibitors of protein kinase and types 1 and 2A protein phosphatases which inhibited and stimulated, respectively, CO₂ stress-induced ethylene production had little effect on the expression of these genes. The results presented here identify CS-ACS1 as the main ACC synthase gene responsible for the increased ethylene biosynthesis in cucumber fruit under CO₂ stress and suggest that this gene is a primary response gene and its expression is under negative control since it is expressed by treatment with cycloheximide. The results further suggest that the regulation of CO₂ stress-induced ethylene biosynthesis by reversible protein phosphorylation does not result from enhanced ACC synthase transcription.

KEYWORDS: ACID SYNTHASE, ARABIDOPSIS-THALIANA, BINDING PROTEIN, ESCHERICHIA-COLI, ETHYLENE BIOSYNTHESIS, INDOLEACETIC-ACID, MUNG BEAN HYPOCOTYLS, PROTEIN-PHOSPHORYLATION, STRUCTURAL CHARACTERIZATION, TOMATO LYCOPERSICON-ESCULENTUM

1474

Mathooko, F.M., T. Sotokawa, Y. Kubo, A. Inaba, and R. Nakamura. 1993. Retention of freshness in fig fruit by CO₂-enriched atmosphere treatment or modified atmosphere packaging under ambient-temperature. *Journal of the Japanese Society for Horticultural Science* 62(3):661-667.

At 20-degrees-C, freshness retention of figs (*Ficus carica* L. cv. Masui Dauphine) by CO₂-enriched atmosphere treatment or modified atmosphere packaging were studied in an attempt to reduce deterioration during transportation. CO₂-enriched atmosphere treatment inhibited ethylene production, delayed the incidence of mold growth and promoted ethanol production. Majority of the figs exposed to 60% or 80% CO₂ for 2 days were still marketable 1 day after transfer to air at 20-degrees-C. Based on mold growth, figs stored in air and in unperforated polyethylene bags deteriorated slightly faster than those stored in perforated bags. A gas mixture of 80% CO₂ + 20% O₂ or 100% CO₂ introduced into the polyethylene bags before sealing were more effective in the control of mold growth compared to air or 100% N₂ and equally effective in reducing ethylene accumulation as 100% N₂. The results suggest that postharvest deterioration of figs can be reduced by either CO₂-enriched atmosphere treatment or through modified atmosphere packaging.

KEYWORDS: LIFE, O₂, QUALITY, RESPIRATION, STORAGE, STRAWBERRIES

1475

Matsueda, H., and H.Y. Inoue. 1999. Aircraft measurements of trace gases between Japan and Singapore in October of 1993, 1996, and 1997. *Geophysical Research Letters* 26(16):2413-2416.

Carbon dioxide (CO₂) methane (CH₄), and carbon monoxide (CO) mixing ratios were measured in discrete air samples from aircraft between Japan and Singapore in October. The mixing ratios of all trace gases at 9-12 km were enhanced over the South China Sea in 1997 compared with those in 1993 and 1996. Vertical distributions of all trace

gases over Singapore in 1997 also showed largely elevated mixing ratios at all altitudes. These distributions indicate a wide outflow of trace gases from intense biomass burning in the southeast Asia regions in the very strong El Nino year. The enhanced trace gases showed a strong linear correlation between CH₄ and CO, and between CO and CO₂, with the regression slopes of 0.051 Delta CH(4)ppb/Delta COppb and 0.089 (Delta COppb/Delta CO(2)ppb). The emission ratios are characteristic of fires with relatively lower combustion efficiency from the tropical rain forest and peat lands in Kalimantan and Sumatra of Indonesia.

KEYWORDS: AFRICAN SAVANNA ECOSYSTEMS, BRAZIL, CARBON-MONOXIDE, DRY SEASON, EMISSIONS, FIRES, METHANE, SOUTHERN AFRICA, UPPER TROPOSPHERE, WESTERN AFRICA

1476

Matsui, T., O.S. Namuco, L.H. Ziska, and T. Horie. 1997. Effects of high temperature and CO₂ concentration on spikelet sterility in indica rice. *Field Crops Research* 51(3):213-219.

The effects of increasing temperature and CO₂ concentration on floral sterility were examined for rice (cv. IR 72) using open-top chambers located at the International Rice Research Institute in Los Banes, Philippines. The field-based open-top chamber system was used to simulate four different environments: ambient temperature and CO₂ concentration (control); ambient temperature, ambient +300 mu l l(-1) CO₂; ambient +4 degrees C temperature, ambient CO₂ concentration; ambient +4 degrees C temperature, ambient + 300 mu l l(-1) CO₂. High temperature during flowering resulted in increased pollen sterility with the degree of sterility exacerbated if rice was exposed to both high temperature and increased CO₂ concentration. The critical air temperature for spikelet sterility (as determined from the number of germinated pollen grains on the stigma) was reduced by ca 1 degrees C at elevated concentrations of carbon dioxide. We speculate that this downward shift in critical temperature may be due to the observed increase in air temperature within the canopy at high CO₂ concentrations. This increase in air temperature, in turn, may be related to stomatal closure and reduced transpirational cooling in an elevated CO₂ environment. Data from this experiment indicate that increasing CO₂ concentration could limit rice yield if average air temperature increased simultaneously.

KEYWORDS: CARBON-DIOXIDE ENRICHMENT, GROWTH, RESPONSES, YIELD

1477

Matthies, D., and P. Egli. 1999. Response of a root hemiparasite to elevated CO₂ depends on host type and soil nutrients. *Oecologia* 120(1):156-161.

Although elevated CO₂ may affect various forms of ecological interactions, the effect of elevated CO₂ on interactions between parasitic plants and their hosts has received little attention. We examined the effect of elevated CO₂ (590 mu l l(-1)) at two nutrient (NPK) levels on the interactions of the facultative root hemiparasite *Rhinanthus alectorolophus* with two of its hosts, the grass *Lolium perenne* and the legume *Medicago sativa*. To study possible effects on parasite mediation of competition between hosts, the parasite was grown with each host separately and with both hosts simultaneously. In addition, all combinations of hosts were grown without the parasite. Both the parasite and the host plants responded to elevated CO₂ with increased growth, but only at high nutrient levels. The CO₂ response of the hemiparasite was stronger than that of the hosts, but depended on the host species available. With *L. perenne* and *M. sativa* simultaneously available as hosts, the biomass of the parasite grown at elevated CO₂ was 5.7 times that of parasites grown at ambient CO₂. Nitrogen concentration in the parasites was not influenced by the treatments and was not related to

parasite biomass. The presence of the parasite strongly reduced both the biomass of the hosts and total productivity of the system. This effect was much stronger at low than at high nutrient levels, but was not influenced by CO₂ level. Elevated CO₂ did not influence the competitive balance between the two different hosts grown in mixture. The results of this study support the hypothesis that hemiparasites may influence community structure and suggest that these effects are robust to changes in CO₂ concentration.

KEYWORDS: ATMOSPHERIC CO₂, CARBON DIOXIDE, COMPETITION, GROWTH, PARASITIC PLANT, PERFORMANCE, TRIFOLIUM-REPENS

1478

Matysiak, B., and J. Nowak. 1994. Carbon-dioxide and light effects on photosynthesis, transpiration and ex-vitro growth of homalomena emerald gem plantlets. *Scientia Horticulturae* 57(4):353-358.

Micropropagated plantlets of Homalomena cultivar 'Emerald Gem' were grown ex vitro at two CO₂ concentrations (350 and 1200 μmol mol⁻¹) and two light levels (50 and 150 μmol m⁻² s⁻¹ photosynthetic photon flux density (PPFD)). Plants grown at 1200 μmol mol⁻¹ CO₂ and at 150 μmol m⁻² s⁻¹ PPFD accumulated dry weight of shoots and roots three and two times higher, respectively, and had a leaf area 2.4 times higher than that of plants grown at 350 μmol mol⁻¹ CO₂ and 50 μmol m⁻² s⁻¹ PPFD. These plants also had the highest rate of photosynthesis. Carbon dioxide enrichment was more effective than supplementary light to increase plant growth. The CO₂ assimilation rate, photorespiration, transpiration and stomatal conductance to water vapour were strongly promoted by light at 150 μmol m⁻² s⁻¹, irrespective of CO₂ concentration. CO₂ enrichment enhanced the CO₂ assimilation rate and quantum efficiency but decreased the rate of transpiration at 50 μmol m⁻² s⁻¹ PPFD and stomatal conductance to water vapour at 50 and 150 μmol m⁻² s⁻¹ PPFD.

KEYWORDS: CULTURE

1479

Matysiak, B., and J. Nowak. 1998. Acclimatization and the growth of Ficus benjamina microcuttings as affected by carbon dioxide concentration. *Journal of Horticultural Science & Biotechnology* 73(2):185-188.

The influence of CO₂ concentrations (350 and 1200 μmol mol⁻¹) on the growth of Ficus benjamina microcuttings cv. Golden King and cv. Natasja, was investigated with reference to light levels (50 and 150 μmol m⁻² s⁻¹ PPFD, Photosynthetic Photon Flux Density) and the nutrient solution concentrations (0.7, 1.4, 2.1 and 2.8 mS cm⁻¹ EC, electrical conductivity). Plants grown in peat + perlite at 1,200 μmol mol⁻¹ CO₂ concentration and simultaneously at high PPFD level (150 μmol m⁻² s⁻¹) had the highest shoot and root fresh weights and the highest leaf area. Elevation of CO₂ concentration at low level of PPFD did not affect the growth of F. benjamina. Survival of F. benjamina microcuttings cultivated in rockwool was low (65-90%) and the growth rate was slow, irrespective of nutrient solution concentration. CO₂ enrichment increased survival and accelerated the growth of these microcuttings. The best growth of F. benjamina microcuttings cultivated in rockwool was at 1,200 μmol mol⁻¹ CO₂ and the highest level of electrical conductivity (EC) 2.8 mS cm⁻¹.

KEYWORDS: ENRICHMENT, INVITRO, PHOTOSYNTHESIS, PLANTLETS, TRANSPIRATION

1480

Mauney, J.R., B.A. Kimball, P.J. Pinter, R.L. Lamorte, K.F. Lewin,

J. Nagy, and G.R. Hendrey. 1994. Growth and yield of cotton in response to a free-air carbon-dioxide enrichment (face) environment. *Agricultural and Forest Meteorology* 70(1-4):49-67.

To quantify the growth and yield responses to CO₂ enrichment in an open field setting, free-air CO₂ enrichment (FACE) technology was used to expose a cotton (*Gossypium hirsutum* L.) crop to 550 μmol mol⁻¹ CO₂ throughout the growing seasons of 1989, 1990 and 1991 in fields near Maricopa, Arizona. In 1990 and 1991 a water stress treatment was also imposed. Response data for all years were consistent, and the data for 1991 were the least compromised by unusual weather or equipment failures. In that season the biomass was increased 37% by the 48% increase in CO₂ concentration. Harvestable yield was increased 43%. The increase in biomass and yield was attributed to increased early leaf area, more profuse flowering and a longer period of fruit retention. The FACE treatment increased water-use efficiency (WUE) to the same amount in the well-irrigated plots as in the water-stressed plots. The increase in WUE was due to the increase in biomass production rather than a reduction of consumptive use.

1481

Mavrogianopoulos, G.N., J. Spanakis, and P. Tsikalas. 1999. Effect of carbon dioxide enrichment and salinity on photosynthesis and yield in melon. *Scientia Horticulturae* 79(1-2):51-63.

Melon (*Cucumis melo* L. Cv Parnon) grown in rockwool culture in the greenhouse was CO₂ enriched, for 5 h every morning, at 400, 800 and 1200 μmol mol⁻¹ and trickle-irrigated with nutrient solutions amended with 0, 25 and 50 mM NaCl. High CO₂ level increased fruit yield, the increase being greater in unsalinated plants than in salinated. With total shoot fresh weight, the increase was greater in salinated plants. CO₂ enrichment also increased leaf growth and the chlorophyll content of the measured leaves. Addition of NaCl in the nutrient solution caused significant reduction in total yield, the reduction being greater at higher concentrations of CO₂. At 25 mM NaCl, the decrease in yield resulted mainly from the smaller fruit size, but at 50 mM yield reduction was due both to smaller fruit size and to fewer fruits per plant. Addition of NaCl caused significant reduction in total shoot fresh weight in all cases, the reduction being greater at the lower level of CO₂. Salinity also, significantly reduced leaf surface irrespective of CO₂ level. Chlorophyll content was reduced by NaCl mainly at the level of 50 mM NaCl. A stronger correlation was found between salinity and shoot fresh weight, plant height and leaf surface area, than salinity and yield and other characteristics. Measurements of gas exchange showed that, for the above mentioned CO₂ and NaCl concentrations, net assimilation was affected by CO₂ to a greater degree than by salinity. Stomatal conductance was most affected by salinity at a concentration of 50 mM NaCl. (C) 1999 Elsevier Science B.V. All rights reserved.

KEYWORDS: CO₂- ENRICHMENT, FRUIT-QUALITY, GROWTH REDUCTION, ION CONCENTRATION, LEAF TISSUE, MUSKMELON, NaCl, PLANTS, SALT TOLERANCE, STOMATAL CONDUCTANCE

1482

Mayeux, H.S., H.B. Johnson, H.W. Polley, M.J. Dumesnil, and G.A. Spanel. 1993. A controlled environment chamber for growing plants across a subambient CO₂ gradient. *Functional Ecology* 7(1):125-133.

1. An elongated, controlled environment chamber is described in which a continuous, reproducible gradient of subambient CO₂ Concentration ([CO₂]) is maintained during daylight hours to assess plant responses to past increases in atmospheric [CO₂]. 2. The [CO₂] of air moved unidirectionally through the 37-6-m long chamber by a blower is progressively depleted by photosynthesis of plants growing in the

chamber. 3. Plant top- growth is contained in a transparent film tunnel which rests upon an enclosed soil volume that is 45 cm wide and 76 cm deep. 4. The desired minimum concentration to which CO₂ is depleted at the end of the chamber, usually 150 or 200 $\mu\text{mol l}^{-1}$, is maintained by varying the blower speed with a micrologger program dependent upon real-time sensing Of [CO₂] and light intensity. 5. Dewpoint and dry bulb temperatures are also controlled by a micrologger- and computer-monitored air- conditioning system.

1483

Mayeux, H.S., H.B. Johnson, H.W. Polley, and S.R. Malone. 1997. Yield of wheat across a subambient carbon dioxide gradient. *Global Change Biology* 3(3):269-278.

Yields and yield components of two cultivars of day-neutral spring wheat (*Triticum aestivum* L.) were assessed along a gradient of daytime carbon dioxide (CO₂) concentrations from about 200 to near 350 $\mu\text{mol CO}_2$ (mol air^{-1}) in a 38 m-long controlled environment chamber. The range in CO₂ concentration studied approximates that of Earth's atmosphere since the last ice age. This 75% rise in CO₂ concentration increased grain yields more than 200% under well-watered conditions and by 80- 150% when wheat was grown without additions of water during the last half of the 100-day growing season. The 27% increase in CO₂ from the pre-industrial level of 150 years ago (275 $\mu\text{mol mol}^{-1}$) to near the current concentration (350 $\mu\text{mol mol}^{-1}$) increased grain yields of 'Yaqui 54' and 'Seri M82' spring wheats by 55% and 53%, respectively, under well-watered conditions. Yield increased because of greater numbers of grains per spike, rather than heavier grains or numbers of spikes per plant. Water use increased little with CO₂ concentration, resulting in improved water use efficiency as CO₂ rose. Data suggest that rising CO₂ concentration contributed to the substantial increase in average wheat yields in the U.S. during recent decades.

KEYWORDS: ALLOCATION, ATMOSPHERIC CO₂, BP, DRY-MATTER, ENRICHMENT, EXCHANGE, GROWTH, INCREASING CO₂, PHOTOSYNTHESIS, RECORD

1484

Mayr, C., M. Miller, and H. Insam. 1999. Elevated CO₂ alters community-level physiological profiles and enzyme activities in alpine grassland. *Journal of Microbiological Methods* 36(1-2):35-43.

Plots of an alpine grassland in the Swiss Alps were treated with elevated (680 $\mu\text{mol l}^{-1}$) and ambient CO₂ (355 $\mu\text{mol l}^{-1}$) in open top chambers (OTC). Several plots were also treated with NPK-fertilizer. Community level physiological profiles (CLPPs) of the soil bacteria were examined by Biolog GN microplates and enzyme activities were determined through the release of methylumbelliferyl (MUF) and methylcoumarin (MC) from MUF- or MC-labelled substrates. A canonical discriminant analysis (CDA) followed by multivariate analysis of variance showed a significant effect of elevated CO₂ on the CLPPs both under fertilized and unfertilized conditions. Further, the installation of the OTCs caused significant shifts in the CLPPs (chamber effect). Of the four enzyme activities tested, the beta-D-cellobiohydrolase (CELase) and N-acetyl-beta-D- glucosaminidase (NAGase) activity were enhanced under elevated CO₂. L-Leucin-7-aminopeptidase (APEase) activity decreased, when the plots received fertilizer. beta-D-Glucosidase (GLUase) remained unaffected. The results suggest effects of elevated CO₂ on specific microbial activities even under low mineral nutrient conditions and when bulk parameters like microbial biomass or respiration, which have been investigated on the same site, remain unaffected. The observed medium-term changes point at possible long-term consequences for the ecosystem that may not be specified yet. (C) 1999 Elsevier Science B.V. All rights reserved.

KEYWORDS: ATMOSPHERIC CO₂, CARBON-DIOXIDE CONCENTRATIONS, ENRICHMENT, LITTER DECOMPOSITION, MICROBIAL COMMUNITIES, MYCORRHIZAL COLONIZATION, PINE SEEDLINGS, RESPONSES, RHIZOSPHERE, SOIL

1485

Maytin, C.E., M.F. Acevedo, R. Jaimez, R. Addressen, M.A. Harwell, A. Robock, and A. Azocar. 1995. Potential effects of global climatic-change on the phenology and yield of maize in venezuela. *Climatic Change* 29(2):189-211.

Simulated impacts of global and regional climate change, induced by an enhanced greenhouse effect and by Amazonian deforestation, on the phenology and yield of two grain corn cultivars in Venezuela (CENIAP PB-8 and OBREGON) are reported. Three sires were selected: Turen, Barinas and Yaritagua, representing two important agricultural regions in the country. The CERES-Maize model, a mechanistic process-based model, in the Decision Support System for Agrotechnology Transfer (DSSAT) was used for the crop simulations. These simulations assume non-limiting nutrients, no pest damage and no damage from excess water; therefore, the results indicate only the difference between baseline and perturbed climatic conditions, when other conditions remain the same. Four greenhouse-induced global climate change scenarios, covering different sensitivity levels, and one deforestation-induced regional climate change scenario were used. The greenhouse scenarios assume increased air temperature, increased rainfall and decreased incoming solar radiation, as derived from atmospheric GCMs for doubled CO₂ conditions. The deforestation scenarios assume increased air temperature, increased incoming solar radiation and decreased rainfall, as predicted by coupled atmosphere- biosphere models for extensive deforestation of a portion of the Amazon basin. Two baseline climate years for each site were selected, one year with average precipitation and another with lower than average rainfall. Scenarios associated with the greenhouse effect cause a decrease in yield of both cultivars at all three sites, while the deforestation scenarios produce small changes. Sensitivity tests revealed the reasons for these responses. Increasing temperatures, especially daily maximum temperatures, reduce yield by reducing the duration of the phenological phases of both cultivars, as expected from CERES- Maize. The reduction of the duration of the kernel filling phase has the largest effect on yield. Increases of precipitation associated with greenhouse warming have no effects on yield, because these sites already have adequate precipitation; however, the crop model used here does not simulate potential negative effects of excess water, which could have important consequences in terms of soil erosion and nutrient leaching. Increases in solar radiation increased yields, according to the non-saturating light response of the photosynthesis rate: of a C-4 plant like corn, compensating for reduced yields from increased temperatures in deforestation scenarios. In the greenhouse scenarios, reduced insolation (due to increased cloud cover) and increased temperatures combine to reduce yields; a combination of temperature increase with a reduction in solar radiation produces fewer and lighter kernels.

KEYWORDS: CROP RESPONSE, MODEL, NITROGEN, SIMULATION

1486

Mbata, G.N., and C. Reichmuth. 1996. The comparative effectiveness of different modified atmospheres for the disinfestation of Bambarra groundnuts, *Vigna subterranea* (L) Verde, infested by *Callosobruchus subinnotatus* (Pic) (Coleoptera:Bruchidae). *Journal of Stored Products Research* 32(1):45-51.

Four atmospheres containing high levels of carbon dioxide (CO₂) and different quantities of oxygen (0, 2.0, 3.7, 5.1%) were investigated for their toxicity to *Callosobruchus subinnotatus* (Pic), The quantity of oxygen contained in atmospheres influenced the disinfestation levels in

bambarra groundnuts infested by *C. subinnotatus*. The different developmental stages had varying susceptibilities to the atmospheres. Atmospheres containing low concentrations of oxygen (2.0, 3.7%) enhanced the mortality of adults. The anoxic atmosphere of 100% CO₂ was more toxic to eggs, larvae, and pupae than the other atmospheres. There was a progressive decrease in toxicity as the quantity of oxygen in the inert atmospheres increased. Copyright (C) 1996 Elsevier Science Ltd

1487

McConnaughay, K.D.M., S.L. Bassow, G.M. Berntson, and F.A. Bazzaz. 1996. Leaf senescence and decline of end-of-season gas exchange in five temperate deciduous tree species grown in elevated CO₂ concentrations. *Global Change Biology* 2(1):25-33.

We measured rates of leaf senescence and leaf level gas exchange during autumnal senescence for seedlings of five temperate forest tree species under current and elevated atmospheric CO₂ concentrations and low- and high-nutrient regimes. Relative indices of whole canopy carbon gain, water loss and water use efficiency through the senescent period were calculated based on a simple integrative model combining gas exchange per unit leaf area and standing canopy area per unit time. Seedlings grown under elevated [CO₂] generally had smaller canopies than their current [CO₂]-grown counterparts throughout most of the senescent period. This was a result of smaller pre-senescent canopies or accelerated rates of leaf drop. Leaf-level photosynthetic rates were higher under elevated [CO₂] for grey birch canopies and for low-nutrient red maple and high-nutrient ash canopies, but declined rapidly to values below those of their current [CO₂] counterparts by midway through the senescent period. CO₂ enrichment reduced photosynthetic rates for the remaining species throughout some or all of the senescent period. As a result of smaller canopy sizes and reduced photosynthetic rates, elevated [CO₂]-grown seedlings had lower indices of whole canopy end-of-season carbon gain with few exceptions. Leaf level transpiration rates were highly variable during autumnal senescence, and neither [CO₂] nor nutrient regime had consistent effects on water loss per unit leaf area or integrated whole canopy water loss throughout the senescent period. Indices of whole canopy, end-of-season estimates of water use efficiency, however, were consistently lower under CO₂ enrichment, with few exceptions. These results suggest that whole canopy end-of-season gas exchange may be altered significantly in an elevated [CO₂] world, resulting in reduced carbon gain and water use efficiency for many temperate forest tree seedlings. Seedling growth and survivorship, and ultimately temperate forest regeneration, could be reduced in CO₂-enriched forests of the future.

KEYWORDS: ECOSYSTEMS, ENRICHMENT, LIGHT, NITROGEN, PLANTS, RESPONSES, SEEDLINGS

1488

McConnaughay, K.D.M., G.M. Berntson, and F.A. Bazzaz. 1993. Limitations to CO₂-induced growth enhancement in pot studies. *Oecologia* 94(4):550-557.

Recently, it has been suggested that small pots may reduce or eliminate plant responses to enriched CO₂ atmospheres due to root restriction. While smaller pot volumes provide less physical space available for root growth, they also provide less nutrients. Reduced nutrient availability alone may reduce growth enhancement under elevated CO₂. To investigate the relative importance of limited physical rooting space separate from and in conjunction with soil nutrients, we grew plants at ambient and double-ambient CO₂ levels in growth containers of varied volume, shape, nutrient concentration, and total nutrient content. Two species (*Abutilon theophrasti*, a C₃ dicot with a deep tap root and *Setaria faberii*, a C₄ monocot with a shallow diffuse root system) were

selected for their contrasting physiology and root architecture. Shoot demography was determined weekly and biomass was determined after eight and ten weeks of growth. Increasing total nutrients, either by increasing nutrient concentration or by increasing pot size, increased plant growth. Further, increasing pot size while maintaining equal total nutrients per pot resulted in increased total biomass for both species. CO₂-induced growth and reproductive yield enhancements were greatest in pots with high nutrient concentrations, regardless of total nutrient content or pot size, and were also mediated by the shape of the pot. CO₂-induced growth and reproductive yield enhancements were unaffected by pot size (growth) or were greater in small pots (reproductive yield), regardless of total nutrient content, contrary to predictions based on earlier studies. These results suggest that several aspects of growth conditions within pots may influence the CO₂ responses of plants; pot size, pot shape, the concentration and total amount of nutrient additions to pots may lead to over- or underestimates of the CO₂ responses of real-world plants.

KEYWORDS: ATMOSPHERIC CO₂, COMMUNITIES, ECOSYSTEMS, ELEVATED CARBON-DIOXIDE, PHOTOSYNTHETIC ACCLIMATION, PRODUCTIVITY, RESPONSES, RESTRICTION, ROOT-GROWTH, TUSsock TUNDRA

1489

McConnaughay, K.D.M., and J.S. Coleman. 1999. Biomass allocation in plants: Ontogeny or optimality? A test along three resource gradients. *Ecology* 80(8):2581-2593.

We examined biomass allocation patterns throughout the entire vegetative growth phase for three species of annual plants along three separate gradients of resource availability to determine whether observed patterns of allocational plasticity are consistent with optimal partitioning theory. Individuals of the annual plant species *Abutilon theophrasti*, *Chenopodium album*, and *Polygonum pensylvanicum* were grown from locally field-gathered seed in controlled greenhouse conditions across gradients of light, nutrients, and water. Frequent harvests were used to determine the growth and allocation (root vs. shoot, and leaf area vs. biomass) responses of these plants over a 57-d period. Growth analysis revealed that each species displayed significant plasticity in growth rates and substantial amounts of ontogenetic drift in root: shoot biomass ratios and ratios of leaf area to biomass across each of the three resource gradients. Ontogenetically controlled comparisons of root : shoot and leaf area ratios across light and nutrient gradients were generally consistent with predictions based on optimal partitioning theory; allocation to roots decreased and leaf area increased under low light and high nutrient conditions. These trends were confirmed, though were less dramatic, in allometric plots of biomass allocation throughout ontogeny. These species did not alter biomass allocation (beyond ontogenetic drift) in response to the broadly varying water regimes. Furthermore, many of the observed differences in biomass allocation were limited to a given time during growth and development. We conclude that, for these rapidly growing annual species, plasticity in biomass allocation patterns is only partially consistent with optimal partitioning theory, and that these plastic responses are ontogenetically constrained. Further, while these species did adjust biomass allocation patterns in response to light and nutrient availability, they did not adjust biomass allocation in response to water availability, despite dramatic plasticity in growth rates along all three resource gradients. Our results support a developmentally explicit model of plasticity in biomass allocation in response to limiting resources.

KEYWORDS: ELEVATED CO₂, GROWTH, INTERNAL NITROGEN CONCENTRATION, LIGHT-INTENSITY, MODEL, PLASTICITY, RESPONSES, ROOT, SHOOT RATIOS, WILD RADISH

1490

McConnaughey, K.D.M., A.B. Nicotra, and F.A. Bazzaz. 1996. Rooting volume, nutrient availability, and CO₂-induced growth enhancements in temperate forest tree seedlings. *Ecological Applications* 6(2):619-627.

We examined growth and allocation responses to CO₂ enrichment for three species of co-occurring temperate forest tree seedlings grown in pots of varying rooting volumes and nutrient supply. Under both current and projected future CO₂ atmospheres, tree seedling growth was substantially greater with greater total nutrient supply (either due to increased nutrient addition rate or increased rooting volume) for all species. Increasing rooting volume alone, holding total nutrient supply constant, increased growth for gray and yellow birch and decreased growth for red maple. Root/shoot ratios were less and specific leaf masses were greater for plants grown in smaller pots, suggesting that the smaller pots did restrict root growth with consequences for whole-plant carbon allocation. After 12 wk of growth at light levels simulating those found in small gaps in temperate forests, each species exhibited growth, allocational and/or architectural differences due to increased CO₂. Of 11 traits measured, 9 were significantly altered by CO₂ regime. Gray birch responded in architectural and allocational parameters only; total carbon accumulation after 12 wk of growth was not affected by CO₂ regime. Red maple and especially yellow birch grew larger in elevated CO₂, and were less responsive in architectural and allocational parameters than gray birch. Increasing N concentration did not increase CO₂-induced growth enhancements, except for increased leaf production in gray birch. In fact, CO₂-induced increases in branch production were greatest at low nutrient concentration. Pot size had no effect on CO₂-induced growth responses, except that CO₂-induced enhancement in branch production was greater in smaller pots. With few exceptions, conditions within pots did not influence responses to elevated CO₂, despite the many growth and architectural responses manifested by these tree seedlings in response to CO₂, nutrient regime, and pot size.

KEYWORDS: AMBIENT, CO₂ LEVELS, COMMUNITIES, ECOSYSTEMS, ELEVATED CARBON-DIOXIDE, LIGHT, PHOTOSYNTHETIC ACCLIMATION, PLANTS, RESPONSES, RESTRICTION

1491

McDonald, E.P., J. Agrell, and R.L. Lindroth. 1999. CO₂ and light effects on deciduous trees: growth, foliar chemistry, and insect performance. *Oecologia* 119(3):389-399.

This study examined the effects of CO₂ and light availability on sapling growth and foliar chemistry, and consequences for insect performance. Quaking aspen (*Populus tremuloides* Michx.), paper birch (*Betula papyrifera* Marsh.), and sugar maple (*Acer saccharum* Marsh.) were grown in controlled environment greenhouses under ambient or elevated CO₂ (38.7 and 69.6 Pa), and low or high light availability (375 and 855 $\mu\text{mol m}^{-2} \text{s}^{-1}$). Because CO₂ and light are both required for carbon assimilation, the levels of these two resources are expected to have strong interactive effects on tree growth and secondary metabolism. Results from this study support that prediction, indicating that the relative effect of rising atmospheric CO₂ concentrations on the growth and secondary metabolism of deciduous trees may be dependent on light environment. Trees in ambient CO₂-low light environments had substantial levels of phytochemicals despite low growth rates; the concept of basal secondary metabolism is proposed to explain allocation to secondary metabolites under growth-limiting conditions. Differences between CO₂ and light effects on the responses of growth and secondary metabolite levels suggest that relative allocation is not dependent solely on the amount of carbon assimilated. The relative growth rates and indices of feeding efficiency for gypsy moth (*Lymantria dispar* L.) larvae fed foliage from the experimental treatments showed no significant interactive effects of light and CO₂, although some main effects and many host species interactions were significant. Gypsy moth

performance was negatively correlated with CO₂- and light-induced increases in the phenolic glycoside content of aspen foliage. Insects were not strongly affected, however, by treatment differences in the nutritional and secondary chemical components of birch and maple.

KEYWORDS: BIRCH BETULA, CARBON NUTRIENT BALANCE, ELEVATED ATMOSPHERIC CO₂, FOREST TENT CATERpillARS, GYPSY-MOTH, NO₃ AVAILABILITY, PHENOLIC GLYCOSIDES, QUAKING ASPEN, SECONDARY METABOLITES, TERRESTRIAL ECOSYSTEMS

1492

McElwain, J.C. 1998. Do fossil plants signal palaeoatmospheric CO₂ concentration in the geological past? *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* 353(1365):83-95.

Fossil, subfossil, and herbarium leaves have been shown to provide a morphological signal of the atmospheric carbon dioxide (CO₂) environment in which they developed by means of their stomatal density and index. An inverse relationship between stomatal density/index and atmospheric CO₂ concentration has been documented for all the studies to date concerning fossil and subfossil material. Furthermore, this relationship has been demonstrated experimentally by growing plants under elevated and reduced CO₂ concentrations. To date, the mechanism that controls the stomatal density response to atmospheric CO₂ concentration remains unknown. However, stomatal parameters of fossil plants have been successfully used as a proxy indicator of palaeo-CO₂ levels. This paper presents new estimates of palaeoatmospheric CO₂ concentrations for the Middle Eocene (Lutetian), based on the stomatal ratios of fossil Lauraceae species from Bournemouth in England. Estimates of atmospheric CO₂ concentrations derived from stomatal data from plants of the Early Devonian, Late Carboniferous, Early Permian and Middle Jurassic ages are reviewed in the light of new data. Semi-quantitative palaeo-CO₂ estimates based on the stomatal ratio (a ratio of the stomatal index of a fossil plant to that of a selected nearest living equivalent) have in the past relied on the use of a Carboniferous standard. The application of a new standard based on the present-day CO₂ level is reported here for comparison. The resultant ranges of palaeo-CO₂ estimates made from standardized fossil stomatal ratio data are in good agreement with both carbon isotopic data from terrestrial and marine sources and long-term carbon cycle modelling estimates for all the time periods studied. These data indicate elevated atmospheric CO₂ concentrations during the Early Devonian, Middle Jurassic and Middle Eocene, and reduced concentrations during the Late Carboniferous and Early Permian. Such data are important in demonstrating the long-term responses of plants to changing CO₂ concentrations and in contributing to the database needed for general circulation model climatic analogues.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CLIMATE, ENVIRONMENTAL-CHANGE, EOCENE, INCREASE, INDEX, OAK LEAVES, ORGANIC-MATTER, RECORD, STOMATAL DENSITY

1493

McElwain, J.C., and W.G. Chaloner. 1995. Stomatal density and index of fossil plants track atmospheric carbon-dioxide in the paleozoic. *Annals of Botany* 76(4):389-395.

It has been demonstrated that the leaves of a range of forest tree species have responded to the rising concentration of atmospheric CO₂ over the last 200 years by a decrease in both stomatal density and stomatal index. This response has also been demonstrated experimentally by growing plants under elevated CO₂ concentrations. Investigation of Quaternary fossil leaves has shown a corresponding stomatal response to changing CO₂ concentrations through a glacial-interglacial cycle, as revealed by ice core data. Tertiary leaves show a similar pattern of stomatal density change, using palynological evidence of palaeo-temperature as a proxy

measure of CO₂ concentration. The present work extends this approach into the Palaeozoic fossil plant record. The stomatal density and index of Early Devonian, Carboniferous and Early Permian plants has been investigated, to test for any relationship that they may show with the changes in atmospheric CO₂ concentration, derived from physical evidence, over that period. Observed changes in the stomatal data give support to the suggestion from physical evidence, that atmospheric CO₂ concentrations fell from an Early Devonian high of 10-12 times its present value, to one comparable to that of the present day by the end of the Carboniferous. These results suggest that stomatal density of fossil leaves has potential value for assessing changes in atmospheric CO₂ concentration through geological time. (C) 1995 Annals of Botany Company

KEYWORDS: CO₂- ENRICHMENT

1494

McElwain, J.C., and W.G. Chaloner. 1996. The fossil cuticle as a skeletal record of environmental change. *Palaios* 11(4):376-388.

The plant cuticle with its stomatal pores represents an important interface between the plant and its surrounding environment. The potential of cuticular features such as cuticle thickness, stomatal density, stomatal index and stomatal ratio to signal the environment in which they grew and developed have been reviewed. In particular new stomatal data from three Yorkshire Middle Jurassic species, *Brachyphyllum crucis* Kendall, *Brachyphyllum mamillare* Lindley and Hutton and *Ginkgo huttonii* (Sternberg) Heer, have been compared with those of two selected nearest living equivalent (NLE) species *Athrotaxis cupressoides* and *Ginkgo biloba*, in an attempt to deduce the atmospheric carbon dioxide concentration from that time. It appears that the development of a thick cuticle can represent an adaptation to more than one kind of environmental constraint and evidently is a feature of certain taxonomic groups. It was concluded therefore that cuticle thickness, taken on its own was nor a suitable palaeo-ecological indicator. In contrast however stomatal parameters of fossil plants seem to have great potential as palaeo-atmospheric indicators of carbon dioxide and in this sense as "skeletal evidence of palaeo-ecological change." The stomatal density and index results of the Jurassic species were significantly lower ($P < 0.0001$) than those of their selected NLE species, therefore indicating elevated atmospheric CO₂ concentrations for the Middle Jurassic. In addition the stomatal ratios of the Jurassic species were in agreement with those of previous Devonian and Carboniferous stomatal ratio results. These results are consistent with the evidence from carbon cycle modelling and carbon isotopic data which infer elevated atmospheric CO₂ concentrations during the Middle Jurassic of 4 to 5 times and 6 to 10 times the present atmospheric level respectively.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CO₂-ENRICHMENT, CYCLE, EVOLUTION, LEAF, LEAVES, PLANT, RESPONSES, STOMATAL DENSITY, TEMPERATURE

1495

McGuire, A.D., L.A. Joyce, D.W. Kicklighter, J.M. Melillo, G. Esser, and C.J. Vorosmarty. 1993. Productivity response of climatic temperate forests to elevated- temperature and carbon-dioxide - a north-american comparison between 2 global-models. *Climatic Change* 24(4):287-310.

We assess the appropriateness of using regression- and process- based approaches for predicting biogeochemical responses of ecosystems to global change. We applied a regression-based model, the Osnabruck Model (OBM), and a process-based model, the Terrestrial Ecosystem Model (TEM), to the historical range of temperate forests in North America in a factorial experiment with three levels of temperature (+0-degrees-C, +2-degrees-C, and +5-degrees-C) and two levels of CO₂

(350 ppmv and 700 ppmv) at a spatial resolution of 0.5-degrees latitude by 0.5-degrees longitude. For contemporary climate (+0-degrees-C, 350 ppmv), OBM and TEM estimate the total net primary productivity (NPP) for temperate forests in North America to be 2.250 and 2.602 x 10(15) g C . yr⁻¹, respectively. Although the continental predictions for contemporary climate are similar, the responses of NPP to altered changes qualitatively differ; at +0-degrees-C and 700 PPMV CO₂, OBM and TEM predict median increases in NPP of 12.5% and 2.5%, respectively. The response of NPP to elevated temperature agrees most between the models in northern areas of moist temperate forest, but disagrees in southern areas and in regions of dry temperate forest. In all regions, the response to CO₂ is qualitatively different between the models. These differences occur, in part, because TEM includes known feedbacks between temperature and ecosystem processes that affect N availability, photosynthesis, respiration, and soil moisture. Also, it may not be appropriate to extrapolate regression-based models for climatic conditions that are not now experienced by ecosystems. The results of this study suggest that the process-based approach is able to progress beyond the limitations of the regression-based approach for predicting biogeochemical responses to global change.

KEYWORDS: CO₂- ENRICHMENT, DRY-MATTER, GRASSLAND BIOGEOCHEMISTRY, GREAT-PLAINS, GROWTH, NITROGEN, PHOTOSYNTHESIS, SIMULATION, TERRESTRIAL ECOSYSTEMS, VEGETATION

1496

McGuire, A.D., J.M. Melillo, and L.A. Joyce. 1995. The role of nitrogen in the response of forest net primary production to elevated atmospheric carbon-dioxide. *Annual Review of Ecology and Systematics* 26:473-503.

We review experimental studies to evaluate how the nitrogen cycle influences the response of forest net primary production (NPP) to elevated CO₂. The studies in our survey report that at the tissue level, elevated CO₂ reduces leaf nitrogen concentration an average 21%, but that it has a smaller effect on nitrogen concentrations in stems and fine roots. In contrast, higher soil nitrogen availability generally increases leaf nitrogen concentration. Among studies that manipulate both soil nitrogen availability and atmospheric CO₂, photosynthetic response depends on a linear relationship with the response of leaf nitrogen concentration and the amount of change in atmospheric CO₂ concentration. Although elevated CO₂ often results in reduced tissue respiration rate per unit biomass, the link to changes in tissue nitrogen concentration is not well studied.

KEYWORDS: BETULA-PENDULA ROTH, CASTANEA-SATIVA MILL, CHENOPODIUM-ALBUM L, CO₂- ENRICHMENT, GROWTH-RESPONSE, LIRIODENDRON-TULIPIFERA L, LOBLOLLY-PINE SEEDLINGS, QUERCUS-ALBA, USE EFFICIENCY, WATER-STRESS

1497

McGuire, A.D., J.M. Melillo, D.W. Kicklighter, and L.A. Joyce. 1995. Equilibrium responses of soil carbon to climate change: Empirical and process-based estimates. *Journal of Biogeography* 22(4-5):785-796.

We use a new version of the Terrestrial Ecosystem Model (TEM), which has been parameterized to control for reactive soil organic carbon (SOC) across climatic gradients, to evaluate the sensitivity of SOC to a 1 degrees C warming in both empirical and process-based analyses. In the empirical analyses we use the steady state SOC estimates of TEM to derive SOC-response equations that depend on temperature and volumetric soil moisture, and extrapolate them across the terrestrial biosphere at 0.5 degrees spatial resolution. For contemporary climate and atmospheric CO₂, mean annual temperature explains 34.8% of the variance in the natural logarithm of TEM-estimated SOC. Because the

inclusion of mean annual volumetric soil moisture in the regression explains an additional 19.6%, a soil moisture term in an equation of SOC response should improve estimates. For a 1 degrees C warming, the globally derived empirical model estimates a terrestrial SOC loss of 22.6 10(15) g (Pg), with 77.9% of the loss in extra-tropical ecosystems. To explore whether loss estimates of SOC are affected by the spatial scale at which the response equations are derived, we derive equations for each of the eighteen ecosystems considered in this study. The sensitivity of terrestrial SOC estimated by summing the losses predicted by each of the ecosystem empirical models is greater (27.9 Pg per degrees C) than that estimated by the global empirical model; the 12.2 Pg loss (43.7%) in tropical ecosystems suggests that they may be more sensitive to warming. The global process-based loss of SOC estimated by TEM in response to a 1 degrees C warming (26.3 Pg) is similar to the sum of the ecosystem empirical losses, but the 13.6 Pg loss (51.7%) in extra-tropical ecosystems suggests that they may be slightly less sensitive to warming. For the modelling of SOC responses, these results suggest that soil moisture is useful to incorporate in empirical models of SOC response and that globally derived empirical models may conceal regional sensitivity of SOC to warming. The analyses in this study suggest that the maximum loss of SOC to the atmosphere per degrees C warming is less than 2% of the terrestrial soil carbon inventory. Because the NPP response to elevated CO₂ has the potential to compensate for this loss, the scenario of warming enhancing soil carbon loss to further enhance warming is unlikely in the absence of land use or changes in vegetation distribution.

KEYWORDS: CO₂, DIOXIDE, ECOSYSTEMS, GRASSLAND BIOGEOCHEMISTRY, GREAT-PLAINS, PRODUCTIVITY, SPATIAL VARIABILITY, STORAGE, TEMPERATURE, WORLD

1498

McGuire, A.D., J.M. Melillo, D.W. Kicklighter, Y.D. Pan, X.M. Xiao, J. Helfrich, B. Moore, C.J. Vorosmarty, and A.L. Schloss. 1997. Equilibrium responses of global net primary production and carbon storage to doubled atmospheric carbon dioxide: Sensitivity to changes in vegetation nitrogen concentration. *Global Biogeochemical Cycles* 11(2):173-189.

We ran the terrestrial ecosystem model (TEM) for the globe at 0.5 degrees resolution for atmospheric CO₂ concentrations of 340 and 680 parts per million by volume (ppmv) to evaluate global and regional responses of net primary production (NPP) and carbon storage to elevated CO₂ for their sensitivity to changes in vegetation nitrogen concentration. At 340 ppmv, TEM estimated global NPP of 49.0 10(15) g (Pg) C yr(-1) and global total carbon storage of 1701.8 Pg C; the estimate of total carbon storage does not include the carbon content of inert soil organic matter. For the reference simulation in which doubled atmospheric CO₂ was accompanied with no change in vegetation nitrogen concentration, global NPP increased 4.1 Pg C yr(-1) (8.3%), and global total carbon storage increased 114.2 Pg C. To examine sensitivity in the global responses of NPP and carbon storage to decreases in the nitrogen concentration of vegetation, we compared doubled CO₂ responses of the reference TEM to simulations in which the vegetation nitrogen concentration was reduced without influencing decomposition dynamics ("lower N" simulations) and to simulations in which reductions in vegetation nitrogen concentration influence decomposition dynamics ("lower N+D" simulations). We conducted three lower N simulations and three lower N+D simulations in which we reduced the nitrogen concentration of vegetation by 7.5, 15.0, and 22.5%. In the lower N simulations, the response of global NPP to doubled atmospheric CO₂ increased approximately 2 Pg C yr(-1) for each incremental 7.5% reduction in vegetation nitrogen concentration, and vegetation carbon increased approximately an additional 40 Pg C, and soil carbon increased an additional 30 Pg C, for a total carbon storage increase of approximately 70 Pg C. In the lower N+D simulations, the responses of NPP and vegetation carbon storage were

relatively insensitive to differences in the reduction of nitrogen concentration, but soil carbon storage showed a large change. The insensitivity of NPP in the N+D simulations occurred because potential enhancements in NPP associated with reduced vegetation nitrogen concentration were approximately offset by lower nitrogen availability associated with the decomposition dynamics of reduced litter nitrogen concentration. For each 7.5% reduction in vegetation nitrogen concentration, soil carbon increased approximately an additional 60 Pg C, while vegetation carbon storage increased by only approximately 5 Pg C. As the reduction in vegetation nitrogen concentration gets greater in the lower N+D simulations, more of the additional carbon storage tends to become concentrated in the north temperate- boreal region in comparison to the tropics. Other studies with TEM show that elevated CO₂ more than offsets the effects of climate change to cause increased carbon storage. The results of this study indicate that carbon storage would be enhanced by the influence of changes in plant nitrogen concentration on carbon assimilation and decomposition rates. Thus changes in vegetation nitrogen concentration may have important implications for the ability of the terrestrial biosphere to mitigate increases in the atmospheric concentration of CO₂ and climate changes associated with the increases.

KEYWORDS: C-4 PLANTS, CHENOPODIUM-ALBUM L, CO₂ CONCENTRATION, FORESTS, GROWTH-RESPONSE, LEAF NITROGEN, PHOTOSYNTHESIS, PLANT GROWTH, USE EFFICIENCY, WATER

1499

McHale, P.J., M.J. Mitchell, and F.P. Bowles. 1998. Soil warming in a northern hardwood forest: trace gas fluxes and leaf litter decomposition. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 28(9):1365-1372.

The response of trace gas fluxes (CO₂ CH₄ and N₂) and litter decomposition to increased soil temperature was evaluated in a northern hardwood forest. Four experimental plots (10 x 10 m) had heating cables installed within the forest floor. Temperatures at 5 cm were increased 2.5, 5.0, or 7.5 degrees C in individual heated plots during the field season in 1993 and 1994. The fourth plot was a cabled, nonheated reference. Trace gas fluxes were monitored using closed chambers. Soil moisture was monitored using tensiometers and time domain reflectometry. Changes in leaf litter decomposition were quantified using litter bags for American beech (*Fagus grandifolia* Ehrh.) and sugar maple (*Acer saccharum* Marsh.) litter. Fluxes of CO₂ increased exponentially with increased soil temperatures within treatments and were higher in heated plots than in the reference plot. Temperature coefficients (Q₁₀) and mass remaining of American beech leaf litter decreased with the level of heating, suggesting a nonlinear microbial response to elevated temperatures. Soil water content exhibited the most influence on CH₄ and N₂O flux in the second season. The experimental manipulations showed the importance of evaluating the influence of soil temperature coupled with effects of N and moisture availability.

KEYWORDS: CLIMATE CHANGE, FIELD, METHANE, NITROUS-OXIDE, RESPONSES, TEMPERATE

1500

McIntyre, M., and B. McNeil. 1998. Morphogenetic and biochemical effects of dissolved carbon dioxide on filamentous fungi in submerged cultivation. *Applied Microbiology and Biotechnology* 50(3):291-298.

The inhibitory effects of elevated CO₂ in submerged fermentation processes involving bacteria and yeasts have been extensively examined. However, until recently, there have been few similar studies involving filamentous fungi, despite the economic importance of this group of organisms. Many of the investigations that have been carried out have

involved inappropriate simulation methods and, as a result, may have overestimated the morphogenetic and biochemical effects of elevated CO₂ on filamentous fungi. Recent studies, involving continuous culture of *Aspergillus niger* and the use of computerised image analysis systems, have allowed a more detailed and accurate description of elevated CO₂ inhibition and quantification of the subtler morphogenetic effects. A critical evaluation of the various experimental methods that have been used to simulate, at laboratory scale, what is assumed to occur in large-scale bioreactors is necessary. The review of simulation methods employed has much broader relevance to many other microbial and cell culture systems, emphasising the need to think about the appropriateness and relevance of experimental design.

KEYWORDS: *ASPERGILLUS-NIGER A60, CHRYSOGENUM, CO₂, CONTINUOUS CULTURES, EVOLUTION RATE, IMAGE-ANALYSIS, MICROORGANISMS, MORPHOLOGY, PENICILLIN FERMENTATIONS, YEAST GROWTH*

1501

McKane, R.B., E.B. Rastetter, J.M. Melillo, G.R. Shaver, C.S. Hopkins, D.N. Fernandes, D.L. Skole, and W.H. Chomentowski. 1995. Effects of global change on carbon storage in tropical forests of south-america. *Global Biogeochemical Cycles* 9(3):329-350.

We used a process-based model of ecosystem biogeochemistry (MEL-GEM) to evaluate the effects of global change on carbon (C) storage in mature tropical forest ecosystems in the Amazon Basin of Brazil. We first derived a single parameterization of the model that was consistent with all the C stock and turnover data from three intensively studied sites within the Amazon Basin that differed in temperature, rainfall, and cloudiness. The range in temperature, soil moisture, and photosynthetically active radiation (PAR) among these sites is about as large as the anticipated changes in these variables in the tropics under CO₂-induced climate change. We then tested the parameterized model by predicting C stocks along a 2400-km transect in the Amazon Basin. Comparison of predicted and measured vegetation and soil C stocks along this transect suggests that the model provides a reasonable approximation of how climatic and hydrologic factors regulate present-day C stocks within the Amazon Basin. Finally, we used the model to predict and analyze changes in ecosystem C stocks under projected changes in atmospheric CO₂ and climate. The central hypothesis of this exercise is that changes in ecosystem C storage in response to climate and CO₂ will interact strongly with changes in other element cycles, particularly the nitrogen (N) and phosphorus (P) cycles. We conclude that C storage will increase in Amazonian forests as a result of (1) redistribution of nutrients from soil (with low C:nutrient ratios) to vegetation (with high C:nutrient ratios), (2) increases in the C:nutrient ratio of vegetation and soil, and (3) increased sequestration of external nutrient inputs by the ecosystem. Our analyses suggest that C:nutrient interactions will constrain increases in C storage to a maximum of 63 Mg/ha during the next 200 years, or about 16% above present-day stocks. However, it is impossible to predict how much smaller the actual increase in C storage will be until more is known about the controls on soil P availability. On the basis of these analyses, we identify several topics for further research in the moist tropics that must be addressed to resolve these uncertainties.

KEYWORDS: *AMAZON BASIN, CLIMATE CHANGE, CYCLE, DIOXIDE, MODEL, NUTRIENT DYNAMICS, PRODUCTIVITY, RESPONSES, SOILS, TERRESTRIAL ECOSYSTEMS*

1502

McKane, R.B., E.B. Rastetter, G.R. Shaver, K.J. Nadelhoffer, A.E. Giblin, J.A. Laundre, and F.S. Chapin. 1997. Climatic effects on tundra carbon storage inferred from experimental data and a model. *Ecology* 78(4):1170-1187.

We used a process-based model of ecosystem carbon (C) and nitrogen (N) dynamics, MEL-GEM (Marine Biological Laboratory General Ecosystem Model), to integrate and analyze the results of several experiments that examined the response of arctic tussock tundra to manipulations of CO₂, temperature, light, and soil nutrients. The experiments manipulated these variables over 3- to 9-yr periods and were intended to simulate anticipated changes in the arctic environment. Our objective was to use the model to extend the analysis of the experimental data so that unmeasured changes in ecosystem C storage and the underlying mechanisms controlling those changes could be estimated and compared. Using an inverse calibration method, we derived a single parameter set for the model that closely simulated the measured responses of tussock tundra to all of the experimental treatments. This parameterization allowed us to infer confidence limits for ecosystem components and processes that were not directly measured in the experiments. Thus, we used the model to estimate changes in ecosystem C storage by inferring key soil processes within the constraints imposed by measured components of the ecosystem C budget. Because tussock tundra is strongly N limited, we hypothesized that changes in ecosystem C storage in response to the experimental treatments would be constrained by several key aspects of C-N interactions: (1) changes in the amount of N in the ecosystem, (2) changes in the C:N ratios of vegetation and soil, and (3) redistribution of N between soil (with a low C:N ratio) and vegetation (with a high C:N ratio). The model results reveal widely differing patterns of change in C-N interactions and constraints on change in ecosystem C storage among treatments. For example, after 9 yr the elevated CO₂ (2 x ambient) treatment and the N fertilized (10 g N.m⁻² yr⁻¹) treatment increased ecosystem C stocks by 1.4 and 2.9%, respectively. Whereas the increase in the CO₂ treatment was due solely to an increase in the C:N ratios of vegetation and soil, the increase in the fertilized treatment was due to increased ecosystem N content and a shift of N from soil to vegetation. In contrast, the greenhouse (3.5 degrees C above ambient) and shade (one-half ambient light) treatments decreased ecosystem C stocks by 1.9 and 2.7%, respectively. The primary reason for the net C losses in these treatments was an increase in respiration relative to photosynthesis, with a consequent decrease in the ecosystem C:N ratio. However, when we simulated the elevated temperatures in the greenhouse treatment without the confounding effects of decreased light intensity (an artifact of the greenhouse structures), there was a long-term increase in ecosystem C stocks because of increased photosynthetic response to the temperature-induced shift of N from soil to vegetation. If our simulated changes in ecosystem C storage are extrapolated for the approximate to 43 Pg C contained in arctic tundras globally, the maximum net gain or loss (approximate to 0.3% per yr) from tundra would be equivalent to 0.13 Pg C/yr. Although fluxes of this magnitude would have a relatively minor impact on current changes in atmospheric CO₂, the long-term impact on tundra C stores could be significant. The synthesis and insights provided by the model should make it possible to extrapolate into the future with a better understanding of the processes governing long-term changes in tundra C storage.

KEYWORDS: *ALASKAN TUSSOCK TUNDRA, ARCTIC TUNDRA, CO₂, ERIOPHORUM VAGINATUM, GLOBAL CHANGE, ORGANIC-MATTER, PLANT GROWTH, TERRESTRIAL ECOSYSTEMS, VEGETATION TYPES, VERTICAL-DISTRIBUTION*

1503

McKee, I.F., J.F. Bullimore, and S.P. Long. 1997. Will elevated CO₂ concentrations protect the yield of wheat from O₃-3 damage? *Plant, Cell and Environment* 20(1):77-84.

This study investigated the interacting effects of carbon dioxide and ozone concentrations on the growth and yield of spring wheat (*Triticum aestivum* L, cv, Wembley). Plants were exposed from time of sowing to harvest to reciprocal combinations of two carbon dioxide and two ozone treatments: [CO₂] at 350 or 700 μmol mol⁻¹, and [O₃] at <5 or 60

nmol mol⁻¹), Records of leaf emergence, leaf duration and tillering were taken throughout leaf development, At harvest, biomass, yield and partitioning were analysed. Our data showed that elevated [CO₂] fully protected against the detrimental effect of elevated [O₃] on biomass, but not yield.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, EXCHANGE, EXPOSURE, GRAIN QUALITY, GROWTH, OZONE, PHOTOSYNTHESIS, RESPONSES, SPRING WHEAT

1504

McKee, I.F., M. Eiblmeier, and A. Polle. 1997. Enhanced ozone-tolerance in wheat grown at an elevated CO₂ concentration: ozone exclusion and detoxification. *New Phytologist* 137(2):275-284.

Elevated [CO₂] has been shown to protect photosynthesis and growth of wheat against moderately elevated [O₃]. To investigate the role of ozone exclusion and detoxification in this protection, spring wheat (*Triticum aestivum* L. cv. Wembley) was grown from seed, in controlled-environment chambers, under reciprocal combinations of [CO₂] at 350 or 700 $\mu\text{mol mol}^{-1}$ and [O₃] peaking at < 5 or 60 nmol mol⁻¹, respectively. Cumulative ozone dose to the mesophyll and antioxidant status were determined throughout flag leaf development. Catalase activity correlated with rates of photorespiration and declined in response to elevated [CO₂] and/or [O₃]. Superoxide dismutase activity was not significantly affected by either condition. Neither ascorbate nor glutathione content was enhanced by elevated [CO₂]. In wheat, at moderately elevated [O₃], our results show that stomatal exclusion plays a major role in the protective effect of elevated [CO₂] against O₃ damage.

KEYWORDS: ATMOSPHERIC CO₂, BEAN-LEAVES, CARBON DIOXIDE, HYDROGEN- PEROXIDE, PHASEOLUS-VULGARIS L, PHOTOSYNTHESIS, PICEA-ABIES L, RESPONSES, SUPEROXIDE-DISMUTASE, TRANSGENIC TOBACCO

1505

McKee, I.F., P.K. Farage, and S.P. Long. 1995. The interactive effects of elevated CO₂ and O₃ concentration on photosynthesis in spring wheat. *Photosynthesis Research* 45(2):111-119.

This study investigated the interacting effects of carbon dioxide and ozone on photosynthetic physiology in the flag leaves of spring wheat (*Triticum aestivum* L. cv. Wembley), at three stages of development. Plants were exposed throughout their development to reciprocal combinations of two carbon dioxide and two ozone treatments: [CO₂] at 350 or 700 $\mu\text{mol mol}^{-1}$, [O₃] at < 5 or 60 nmol mol⁻¹. Gas exchange analysis, coupled spectrophotometric assay for RuBisCO activity, and SDS-PAGE, were used to examine the relative importance of pollutant effects on i) stomatal conductance, ii) quantum yield, and iii) RuBisCO activity, activation, and concentration. Independently, both elevated [CO₂] and elevated [O₃] caused a loss of RuBisCO protein and V_{cmax}. In combination, elevated [CO₂] partially protected against the deleterious effects of ozone. It did this partly by reducing stomatal conductance, and thereby reducing the effective ozone dose. Elevated [O₃] caused stomatal closure largely via its effect on photoassimilation.

KEYWORDS: ATMOSPHERIC CO₂, EXPOSURE, FIELD, NET PHOTOSYNTHESIS, OXYGENASE, OZONE STRESS, PLANTS, RIBULOSE BISPHOSPHATE CARBOXYLASE, TEMPERATURE, TRITICUM-AESTIVUM L

1506

McKee, I.F., P.K. Farage, and S.P. Long. 1995. The interactive effects of elevated CO₂ and O₃ concentration on photosynthesis in spring

wheat (vol 45, pg 111, 1995). *Photosynthesis Research* 46(3):479.

1507

McKee, I.F., and F.I. Woodward. 1994. CO₂ enrichment responses of wheat - interactions with temperature, nitrate and phosphate. *New Phytologist* 127(3):447-453.

Rising levels of atmospheric CO₂, climate change, and fertilizer pollution provide the ecological imperative for investigating the interaction between plant responses to atmospheric CO₂ concentration, temperature and nutrient supply. In this study spring wheat (*Triticum aestivum* L. cv. Wembley) was grown at 40, 50, 60 and 70 Pa atmospheric CO₂ pressure and three experiments were conducted to investigate interactions between growth responses to the CO₂ treatment and: (i) temperature (24/16 degrees C vs. 18/10 degrees C - day/night), (ii) nutrient solution nitrate concentration (2.5, 5, 10 and 15 mM Ca(NO₃)₂·4H₂O), and (iii) phosphate concentration (0.025 and 0.5 mM KH₂PO₄). Dry mass and root/shoot ratio increased with CO₂ level at the higher temperature. These responses were reversed at the lower temperature. The increase in yield with CO₂ enhancement was limited by low rates of nutrient supply in both absolute and relative terms. In the elevated CO₂ treatments, the shoot nitrogen concentration was reduced, as was the proportional allocation to the uppermost leaves. These results are discussed with respect to possible physiological mechanisms and potential for improved crop performance in a future, elevated CO₂ world.

KEYWORDS: AIR- TEMPERATURE, CARBON DIOXIDE, DIFFERENT IRRADIANCES, DRY-MATTER, ELEVATED CO₂, PLANT GROWTH, SPRING WHEAT, STOMATAL CONDUCTANCE, WATER-USE, WINTER-WHEAT

1508

McKee, I.F., and F.I. Woodward. 1994. The effect of growth at elevated CO₂ concentrations on photosynthesis in wheat. *Plant, Cell and Environment* 17(7):853-859.

Rising levels of atmospheric CO₂ will have profound, direct effects on plant carbon metabolism. In this study we used gas exchange measurements, models describing the instantaneous response of leaf net CO₂ assimilation rate (A) to intercellular CO₂ partial pressure (C_i), in vitro enzyme activity assay, and carbohydrate assay in order to investigate the photosynthetic responses of wheat (*Triticum aestivum* L., cv. Wembley) to growth under elevated partial pressures of atmospheric CO₂ (C_a). At flag leaf ligule emergence, the modelled, in vivo, maximum carboxylation velocity for RuBisCO was significantly lower in plants grown at elevated C_a than in plants grown at ambient C_a (70 Pa compared with 40 Pa). By 12 d after ligule emergence, no significant difference in this parameter was detectable. At ligule emergence, plants grown at elevated C_a exhibited reduced in vitro initial activities and activation states of RuBisCO. At their respective growth C_i values, the photosynthesis of 40-Pa-grown plants was sensitive to p(O₂) and to p(CO₂), whereas that of 70-Pa-grown plants was insensitive. Both sucrose and starch accumulated more rapidly in the leaves of plants grown at 70 Pa. At flag leaf ligule emergence, modelled non-photorespiratory respiration in the light (R(d)) was significantly higher in 70-Pa-grown plants than in 40-Pa-grown plants. By 12 d after ligule emergence no significant differences in R(d) were detectable.

KEYWORDS: ANTISENSE RBCS, ATMOSPHERIC CO₂, CALVIN CYCLE ENZYMES, CARBON DIOXIDE, DARK RESPIRATION, GAS-EXCHANGE, LEAVES, RIBULOSE BISPHOSPHATE CARBOXYLASE, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, RUBISCO ACTIVITY

1509

McKeehen, J.D., D.J. Smart, C.L. Mackowiak, R.M. Wheeler, and S.S. Nielsen. UNKNOWN YEAR. Effect of CO₂ levels on nutrient content of lettuce and radish. *Natural and Artificial Ecosystems* :85-92.

Atmospheric carbon-dioxide enrichment is known to affect the yield of lettuce and radish grown in controlled environments, but little is known about CO₂ enrichment effects on the chemical composition of lettuce and radish. These crops are useful model systems for a Controlled Ecological Life-Support System (CELSS), largely because of their relatively short production cycles. Lettuce (*Lactuca sativa* L.) cultivar 'Waldmann's Green' and radish (*Raphanus sativus* L.) cultivar 'Giant White Globe' were grown both in the field and in controlled environments, where hydroponic nutrient solution, light, and temperature were regulated, and where CO₂ levels were controlled at 400, 1000, 5000, or 10,000 ppm. Plants were harvested at maturity, dried, and analyzed for proximate composition (protein, fat, ash, and carbohydrate), total nitrogen (N), nitrate N, free sugars, starch, total dietary fiber, and minerals. Total N, protein N, nonprotein N (NPN), and nitrate N generally increased for radish roots and lettuce leaves when grown under growth chamber conditions compared to field conditions. The nitrate-N level of lettuce leaves, as a percentage of total NPN, decreased with increasing levels of CO₂ enrichment. The ash content of radish roots and of radish and lettuce leaves decreased with increasing levels of CO₂ enrichment. The levels of certain minerals differed between field- and chamber-grown materials, including changes in the calcium (Ca) and phosphorus (P) contents of radish roots and lettuce leaves, resulting in reduced Ca/P ratio for chamber-grown materials. The free-sugar contents were similar between the field and chamber-grown lettuce leaves, but total dietary fiber content was much higher in the field-grown plant material. The starch content of growth-chamber lettuce increased with CO₂ level.

KEYWORDS: INCOMPLETE, CARBOHYDRATE, GROWTH, NITRATE, NITRITE

1510

McLaughlin, S., and K. Percy. 1999. Forest health in North America: Some perspectives on actual and potential roles of climate and air pollution. *Water, Air, and Soil Pollution* 116(1-2):151-197.

The perceived health of forest ecosystems over large temporal and spatial scales can be strongly influenced by the frames of reference chosen to evaluate both forest condition and the functional integrity of sustaining forest processes. North American forests are diverse in range, species composition, past disturbance history, and current management practices. Therefore the implications of changes in environmental stress from atmospheric pollution and/or global climate change on health of these forests will vary widely across the landscape. Forest health surveys that focus on the average forest condition may do a credible job of representing the near-term trends in economic value while failing to detect fundamental changes in the processes by which these values are sustained over the longer term. Indications of increased levels of environmental stress on forest growth and nutrient cycles are currently apparent in several forest types in North America. Measurements of forest ecophysiological responses to air pollutants in integrated case studies with four forest types (southern pine, western pine, high elevation red spruce, and northeastern hardwoods) indicate that ambient levels of ozone and/or acidic deposition can alter basic processes of water, carbon, and nutrient allocation by forest trees. These changes then provide a mechanistic basis for pollutant stress to enhance a wider range of natural stresses that also affect and are affected by these resources. Future climatic changes may ameliorate (+ CO₂) or exacerbate (+ temperature, + UV-B) these effects. Current projections of forest responses to global climate change do not consider important physiological changes induced by air pollutants that may amplify climatic stresses. These include reduced rooting mass, depth, and

function, increased respiration, and reduced water use efficiency. Monitoring and understanding the relative roles of natural and anthropogenic stress in influencing future forest health will require programs that are structured to evaluate responses at appropriate frequencies across gradients in both forest resources and the stresses that influence them. Such programs must also be accompanied by supplemental process-oriented and pattern-oriented investigations that more thoroughly test cause and effect relationships among stresses and responses of both forests and the biogeochemical cycles that sustain them.

KEYWORDS: ABIES L KARST, ACIDIC DEPOSITION, FOLIAR NUTRIENT STATUS, LOBLOLLY-PINE SEEDLINGS, NITROGEN DEPOSITION, PICEA-ABIES, QUEBEC APPALACHIANS, RED SPRUCE SAPLINGS, SOUTHEASTERN UNITED-STATES, SUGAR MAPLE DIEBACK

1511

McMaster, G.S., D.R. LeCain, J.A. Morgan, L. Aiguo, and D.L. Hendrix. 1999. Elevated CO₂ increases wheat CER, leaf and tiller development, and shoot and root growth. *Journal of Agronomy and Crop Science-Zeitschrift Fur Acker Und Pflanzenbau* 183(2):119-128.

Whole-plant responses to elevated CO₂ throughout the life cycle are needed to understand future impacts of elevated atmospheric CO₂. In this study, *Triticum aestivum* L. leaf carbon exchange rates (CER) and carbohydrates, growth, and development were examined at the tillering, booting, and grain-filling stages in growth chambers with CO₂ concentrations of 350 (ambient) or 700 (high) $\mu\text{mol mol}^{-1}$. Single-leaf CER values measured on plants grown at high CO₂ were 50% greater than those measured on plants grown at ambient CO₂ for all growth stages, with no photosynthetic acclimation observed at high CO₂. Leaves grown in high CO₂ had more starch and simple sugars at tillering and booting, and more starch at grain-filling, than those grown in ambient CO₂. CER and carbohydrate levels were positively correlated with leaf appearance rates and tillering (especially third-, fourth- and fifth-order tillers). Elevated CO₂ slightly delayed tiller appearance, but accelerated tiller development after appearance. Although high CO₂ increased leaf appearance rates, final leaf number/culm was not effected because growth stages were reached slightly sooner. Greater plant biomass was related to greater tillering. Doubling CO₂ significantly increased both shoot and root dry weight, but decreased the shoot to root ratio. High CO₂ plants had more spikes plant⁻¹ and spikelets spike⁻¹, but a similar number of fertile spikelets spike⁻¹. Elevated CO₂ resulted in greater shoot, root and spike production and quicker canopy development by increasing leaf and tiller appearance rates and phenology.

KEYWORDS: ACCLIMATION, CARBON DIOXIDE, ENRICHMENT, EXCHANGE, NITROGEN, PHOTOSYNTHESIS, SPRING WHEAT, VEGETATIVE DEVELOPMENT, WINTER-WHEAT, YIELD

1512

McMaster, H.J. 1999. The potential impact of global warming on hail losses to winter cereal crops in New South Wales. *Climatic Change* 43(2):455-476.

This study was undertaken to determine the impact of potential global warming on the magnitude of hail losses to winter cereal crops within two areas situated on the western slopes of New South Wales, Australia. A model relating historical crop hail losses to climatic variables was developed for each area. These models included seasonal measures of vertical instability, low-level moisture and the height of the freezing level. In both areas, windshear was not found to be an important factor influencing seasonal crop hail losses. The two crop hail loss models were then used in conjunction with upper-air climatic data from three single

mixed-layer global climate models (GCMs). Each GCM was run for 1 x CO₂ conditions and for 2 x CO₂ conditions. The enhanced greenhouse effect on climatic variables was taken to be the difference between their values for these two runs. Changes to climatic variables were then translated directly into changes in the percentage value of the winter cereal crop lost due to hail. In both areas, the three GCMs agreed concerning the direction of change in each of the variables used in the crop hail loss model. GCM simulations of the greenhouse effect resulted in a decline in winter cereal crop hail losses, with the exception of one GCM simulation at one location where losses increased slightly. None of the changes due to the enhanced greenhouse effect, however, were significant owing to a large observed seasonal variability of crop hail losses. Also, the simulated seasonal variability of crop hail losses did not change significantly due to the enhanced greenhouse effect. These results depended on two important assumptions. Firstly, it was assumed that the dominant relationships between climatic variables and crop hail losses in the past would remain the same in a future climate. Secondly, it was assumed that the single mixed-layer GCMs used in the study were correctly predicting climate change under enhanced greenhouse conditions.

KEYWORDS: CLIMATE CHANGE, EL-NINO, MODEL, RAINFALL, SIMULATED CONVECTIVE STORMS, TEMPERATURE

1513

McMurtrie, R.E., and H.N. Comins. 1996. The temporal response of forest ecosystems to doubled atmospheric CO₂ concentration. *Global Change Biology* 2(1):49-57.

Vegetation responses to high [CO₂] include both direct photosynthetic effects and indirect effects associated with various plant and soil feedbacks. Synthesis of these direct and indirect effects requires ecosystem process models describing the cycling of carbon and essential mineral nutrients through plants and soils. Here we use the ecosystem model G'DAY to investigate responses to an instantaneous doubling of [CO₂]. The analysis indicates that the magnitude and even direction of the growth response to high [CO₂] can vary widely on different timescales, because responses on different timescales are determined by different ecosystem-level feedbacks and hence by different sets of key model parameters. Of particular importance are parameters describing the flexibility of plant and soil nitrogen to carbon (N:C) ratios; large responses occur if N:C ratios decline significantly at high [CO₂], with little or no response if N:C ratios are inflexible. According to G'DAY, the CO₂-response changes over time because responses on longer timescales are dictated by the N:C ratios of less rapidly cycled organic matter.

KEYWORDS: CARBON, CLIMATE, DECOMPOSITION, DYNAMICS, ELEVATED CO₂, LEAF LITTER, NITROGEN, NUTRIENT, PRODUCTIVITY, TERRESTRIAL ECOSYSTEMS

1514

McMurtrie, R.E., H.N. Comins, M.U.F. Kirschbaum, and Y.P. Wang. 1992. Modifying existing forest growth-models to take account of effects of elevated CO₂. *Australian Journal of Botany* 40(4-5):657-677.

Most published process models of the growth of forest stands are concerned predominantly with either tree physiology or nutrient cycling, concentrating respectively on photosynthetic carbon gain and allocation, or on decomposition and nutrient uptake processes. Mechanistic formulations of direct CO₂ effects on photosynthesis have been incorporated in some physiology-based models, whereas modifications incorporating direct CO₂ effects in nutrient-driven models have usually been more empirical. Physiology-based models predict considerable CO₂-fertiliser effects, while nutrient driven models tend to be less

sensitive to elevated ambient CO₂ concentration (C(a)). This paper describes how effects of elevated C(a) can be incorporated in these various types of forest growth models. The magnitude of the simulated response to elevated C(a) varies markedly depending on a particular model's spatial and temporal resolution and on which processes are incorporated. Two physiology-based models of forest canopy processes (MAESTRO and BIOMASS) and a plant-soil model (G'DAY) are considered here. MAESTRO and BIOMASS incorporate mechanistic descriptions of the biochemical basis of photosynthesis by C3 plants, while G'DAY contains a simplified formulation but includes soil processes. All three models are used to simulate the response to an instantaneous doubling of C(a). Simulations of MAESTRO and BIOMASS show that on a clear day total canopy photosynthesis is temperature-dependent with increases of approximately 10, 45 and 70% at 10, 25 and 40-degrees-C respectively. A simulation for a stand of *Pinus radiata* growing with abundant water and nutrients and mean annual day-time temperature of 14.8-degrees-C shows an increase of 25% in annual canopy photosynthesis. On nutrient-limited sites plant responses to elevated C(a) are constrained by feedbacks associated with rates of decomposition and nutrient cycling. According to the G'DAY model, which incorporates these feedbacks, an instantaneous doubling of C(a) leads to a 27% initial productivity increase lasting less than a decade and a more modest increase of 8% sustained in the long term.

KEYWORDS: C-4 PLANTS, EUCALYPTUS-PAUCIFLORA, LEAF NITROGEN, PAR ABSORPTION, PHOTOSYNTHESIS, PRODUCTIVITY, QUANTUM YIELD, SITKA SPRUCE, TEMPERATURE, TERRESTRIAL ECOSYSTEMS

1515

McMurtrie, R.E., and Y.P. Wang. 1993. Mathematical-models of the photosynthetic response of tree stands to rising CO₂ concentrations and temperatures. *Plant, Cell and Environment* 16(1):1-13.

Two published models of canopy photosynthesis, MAESTRO and BIOMASS, are simulated to examine the response of tree stands to increasing ambient concentrations of carbon dioxide (C(a)) and temperatures. The models employ the same equations to describe leaf gas exchange, but differ considerably in the level of detail employed to represent canopy structure and radiation environment. Daily rates of canopy photosynthesis simulated by the two models agree to within 10% across a range of CO₂ concentrations and temperatures. A doubling of C(a) leads to modest increases of simulated daily canopy photosynthesis at low temperatures (10% increase at 10-degrees-C), but larger increases at higher temperatures (60% increase at 30-degrees-C). The temperature and CO₂ dependencies of canopy photosynthesis are interpreted in terms of simulated contributions by quantum-saturated and non-saturated foliage. Simulations are presented for periods ranging from a diurnal cycle to several years. Annual canopy photosynthesis simulated by BIOMASS for trees experiencing no water stress is linearly related to simulated annual absorbed photosynthetically active radiation, with light utilization coefficients for carbon of $\epsilon = 1.66$ and 2.07 g MJ^{-1} derived for C(a) of 350 and 700 $\mu\text{mol mol}^{-1}$, respectively.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, C-3, CARBOXYLASE-OXYGENASE, CLIMATE CHANGE, ELEVATED CO₂, GAS-EXCHANGE, PAR ABSORPTION, RESPIRATION, SITKA SPRUCE, TUSsock TUNDRA

1516

Medlyn, B.E. 1996. Interactive effects of atmospheric carbon dioxide and leaf nitrogen concentration on canopy light use efficiency: A modeling analysis. *Tree Physiology* 16(1-2):201-209.

Potential increases in plant productivity in response to increasing atmospheric CO₂ concentration are likely to be constrained by nutrient

limitations. However, the interactive effects of nitrogen nutrition and CO₂ concentration on growth are difficult to define because both factors affect several aspects of growth, including photosynthesis, respiration, and leaf area. By expressing growth as a product of light intercepted and light use efficiency (epsilon), it is possible to decouple the effects of nutrient availability and CO₂ concentration on photosynthetic rates from their effects on other aspects of plant growth. I used measured responses of leaf photosynthesis to leaf nitrogen (N) content and CO₂ concentration to parameterize a model of canopy radiation absorption and photosynthesis, and then used the model to estimate the response of E to elevated CO₂ concentration for *Pinus radiata* D. Don, *Nothofagus fusca* (Hook. f.) Orst. and *Eucalyptus grandis* W. Hill ex Maiden. Down-regulation of photosynthesis at elevated CO₂ was represented as a reduction in either leaf N content or leaf Rubisco activity. The response of epsilon to elevated CO₂, which differed among the three species, was analyzed in terms of the underlying relationships between leaf photosynthesis and leaf N content. The response was independent of leaf N content when photosynthesis was down-regulated to the same extent at low and high leaf N content. Interactive effects of N availability and CO₂ on growth are thus likely to be the result of either differences in down-regulation of photosynthesis at low and high N availability or interactive effects of CO₂ and N availability on other aspects of plant growth.

KEYWORDS: C-3 PLANTS, CO₂ CONCENTRATIONS, ELEVATED CO₂, ENRICHMENT, FERTILIZATION, GROWTH, LEAVES, MINERAL NUTRITION, PHOTOSYNTHETIC CAPACITY, PINUS-RADIATA

1517

Medlyn, B.E. 1996. The optimal allocation of nitrogen within the C-3 photosynthetic system at elevated CO₂. *Australian Journal of Plant Physiology* 23(5):593-603.

The distribution of nitrogen among compounds involved in photosynthesis varies in response to changes in environmental conditions such as photon flux density. However, the extent to which the nitrogen distribution within leaves adjusts in response to increased atmospheric CO₂ is unclear. A model was used to determine the nitrogen distribution which maximises photosynthesis under realistic light regimes at both current and elevated levels of CO₂, and a comparison was made with observed leaf nitrogen distributions reported in the literature. The model accurately predicted the distribution of nitrogen within the photosynthetic system for leaves grown at current levels of CO₂, except at very high leaf nitrogen contents. The model predicted that, under a doubling of CO₂ concentration from its current level, the ratio of electron transport capacity to Rubisco activity (J(max):V-cmax) should increase by 40%. In contrast, measurements of J(max):V-cmax taken from the literature show a slight but non-significant increase in response to an increase in CO₂. The discrepancy between predicted and observed J(max):V-cmax suggests that leaf nitrogen distribution does not acclimate optimally to elevated CO₂. Alternatively, the discrepancy may be due to effects of CO₂ which the model fails to take into account, such as a possible decrease in the conductance to CO₂ transfer between the intercellular spaces and the sites of carboxylation at elevated CO₂.

KEYWORDS: CANOPY PHOTOSYNTHESIS, CARBON DIOXIDE, DIFFERENT IRRADIANCES, GAS-EXCHANGE, HIGH ATMOSPHERIC CO₂, LEAF NITROGEN, PHOTON FLUX-DENSITY, RIBULOSE BIPHOSPHATE CARBOXYLASE, RIBULOSE-1;5-BIPHOSPHATE CARBOXYLASE-OXYGENASE, TRANSGENIC TOBACCO

1518

Medlyn, B.E., and P.G. Jarvis. 1999. Design and use of a database of

model parameters from elevated [CO₂] experiments. *Ecological Modelling* 124(1):69-83.

This paper describes a new approach for linking experiments and models: a searchable database of model parameter values obtained directly from experiments. The experiments were carried out as part of a major European project studying the long-term effects of elevated [CO₂] on European forest species. To ensure that the information obtained from these experiments was fully utilised in the modelling component of the project, a database was used to store and synthesise experimental data. Key features of the database include: (1) Data is stored as model parameters rather than raw experimental data, which aids transfer of information from experiments to models. (2) Extensive meta-data is stored, which is crucial for correct interpretation of parameter values. (3) The database has a relational structure, which facilitates data retrieval. In this paper, we document the structure of the database. The structure is flexible and generic and could easily be adapted to suit other fields of research. We illustrate the use of the database with examples from the project. (C) 1999 Elsevier Science B.V. All rights reserved.

KEYWORDS: SCOTS PINE

1519

Megonigal, J.P., and W.H. Schlesinger. 1997. Enhanced CH₄ emissions from a wetland soil exposed to elevated CO₂. *Biogeochemistry* 37(1):77-88.

Methane emissions from wetland soils are generally a positive function of plant size and primary productivity, and may be expected to increase due to enhanced rates of plant growth in a future atmosphere of elevated CO₂. We performed two experiments with *Orontium aquaticum*, a common emergent aquatic macrophyte in temperate and sub-tropical wetlands, to determine if enhanced rates of photosynthesis in elevated CO₂ atmospheres would increase CH₄ emissions from wetland soils. *O. aquaticum* was grown from seed in soil cores under ambient and elevated (ca. 2-times ambient) concentrations of CO₂ in an initial glasshouse study lasting 3 months and then a growth chamber study lasting 6 months. Photosynthetic rates were 54 to 71% higher under elevated CO₂ than ambient CO₂, but plant biomass was not significantly different at the end of the experiment. In each case, CH₄ emissions were higher under elevated than ambient CO₂ levels after 2 to 4 months of treatment, suggesting a close coupling between photosynthesis and methanogenesis in our plant-soil system. Methane emissions in the growth chamber study increased by 136%. We observed a significant decrease in transpiration rates under elevated CO₂ in the growth chamber study, and speculate that elevated CO₂ may also stimulate CH₄ emissions by increasing the extent and duration of flooding in some wetland ecosystems. Elevated CO₂ may dramatically increase CH₄ emissions from wetlands, a source that currently accounts for 40% of global emissions.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO₂, CARBON DIOXIDE, ECOSYSTEM, FLUXES, METHANE EMISSIONS, PERSPECTIVE, REDOX, TEMPERATURE, WATER-TABLE

1520

Meheriuk, M. 1990. Effects of diphenylamine, gibberellic-acid, daminozide, calcium, high CO₂ and elevated-temperatures on quality of stored bartlett pears. *Canadian Journal of Plant Science* 70(3):887-892.

1521

Meier, M., and J. Fuhrer. 1997. Effect of elevated CO₂ on orchard grass and red clover grown in mixture at two levels of nitrogen or water

supply. *Environmental and Experimental Botany* 38(3):251-262.

A mixture of orchard grass (*Dactylis glomerata* L.) and red clover (*Trifolium pratense* L.) was grown in microcosms at either ambient (40 Pa) or elevated CO₂ (78 Pa) and supplied with two levels of nitrogen (N) or two levels of irrigation. The aim was to study how reduced N or water supply affect the CO₂ response of shoot and root growth, in relationship to changes in the plant C/N ratio. Plant growth was monitored non-destructively, and shoot dry mass was determined after 41 days (first growth period) and after 67 days (second growth period). Stubble and root dry mass, and C/N ratios in roots and shoots were measured only after regrowth. Elevated CO₂ continuously stimulated growth of the mixture, and increased the shoot biomass in the absence of N or water limitations without changing the shoot/root dry weight ratio, nor the C/N ratio. The CO₂-effect on orchard grass tended to be stronger than the effect on red clover, and was more pronounced during the first as compared to the second growth period. At low N, yield of red clover showed the stronger CO₂ response, whereas with reduced water supply the relative CO₂-stimulation of shoot biomass in orchard grass was more pronounced. Both low-N and reduced water supply decreased shoot, root, and stubble biomass, decreased the shoot/root ratio, and increased the C/N ratio. Elevated CO₂ reduced negative effects of limited N or water supply on shoot growth, but the positive CO₂ effect at low N declined with time. The interaction between CO₂ and N was most pronounced for stubble mass, whereas the interaction between CO₂ and reduced water supply was only significant for root mass. It is concluded that changes in shoot/root ratio are mainly caused by low N and reduced water supply via changes in the N-status of the plant, and that elevated CO₂ has little effect on the shoot/root ratio, but tends to reduce negative effects of limiting N and water on growth. (C) 1997 Published by Elsevier Science B.V.

KEYWORDS: ATMOSPHERIC CO₂, CARBON DIOXIDE, DRY-MATTER, ENRICHMENT, MANAGED MODEL-ECOSYSTEMS, PLANT-RESPONSE, RYEGRASS *LOLIUM-PERENNE*, STRESS, *TRIFOLIUM-REPENS* L, WHITE CLOVER

1522

Meier, M., M. Saurer, C. Haldemann, and J. Fuhrer. 1997. Effect of elevated CO₂ on the carbon balance of a grass-clover mixture. *Acta Oecologica-International Journal of Ecology* 18(3):313-317.

Experiments were carried out to investigate the effect of elevated CO₂ (780 $\mu\text{mol mol}^{-1}$) on the C-balance and carbon release from the roots of a mixture of *Dactylis glomerata* and *Trifolium pratense*. The plants were grown for 67 days in a growth chamber with controlled watering and fertilisation, with an intermediate harvest after 41 days. Elevated CO₂ increased total net uptake of carbon (C) by about 30% by the end of regrowth. Total net C-uptake and the amount of C recovered in the second harvest were balanced at both CO₂ concentrations, and the root: shoot ratio was not affected by elevated CO₂. C-13-allocation to roots, and C-13 released into the root environment were measured following pulse-labelling with (CO₂)- C-13 at the end of regrowth. Relative to the amount of C-13 taken up by the shoot, C-13 allocation to roots was 1.6%, and C-13 released from roots was only 0.4%. No significant difference in these proportions was observed at elevated CO₂, but in absolute terms, plants grown at elevated CO₂ released more C-13 from the roots.

1523

Meinander, O., S. Somersalo, T. Holopainen, and R.J. Strasser. 1996. Scots pines after exposure to elevated ozone and carbon dioxide probed by reflectance spectra and chlorophylla fluorescence transients. *Journal of Plant Physiology* 148(1-2):229-236.

Natural Scots pines have been exposed to filtered air, ambient air and air with elevated O₃ or/and CO₂ in open top chambers. The trees showed no differences in their optical responses prior to the fumigations. After the fumigation period of three months the plants were in good health. The position of the maximum derivative of the green light reflectance in carbon dioxide fumigated pines was shifted from the control pines inflection point, by approximately 4 nm towards shorter wavelengths. The position of the red edge derivative maximum showed no significant changes. By fluorescence techniques (as OJIP - fast fluorescence transients) nearly no change was found in the quantum yield for electron transport ($\phi(o)$ or excitation energy trapping $\phi(Po)$). However, the estimated activities as absorption, trapping or electron transport per cross-section increased considerably for all samples with elevated O₃ or CO₂. This increased activity seems to be due to an increased antenna size in O₃ treated samples. At elevated CO₂ the antenna size is decreased whereas the density of reaction centers per cross-section increased. This means that two different stress-adaptation mechanisms can lead to a similar macroscopic phenomenon like e.g. an increased metabolic activity.

KEYWORDS: FOREST DECLINE

1524

Melack, J.M., J. Dozier, C.R. Goldman, D. Greenland, A.M. Milner, and R.J. Naiman. 1997. Effects of climate change on inland waters of the Pacific Coastal Mountains and Western Great Basin of North America. *Hydrological Processes* 11(8):971-992.

The region designated as the Pacific Coastal Mountains and Western Great Basin extends from southern Alaska (64 degrees N) to southern California (34 degrees N) and ranges in altitude from sea level to 6200 m. Orographic effects combine with moisture-laden frontal systems originating in the Pacific Ocean to produce areas of very high precipitation on western slopes and dry basins of internal drainage on eastern flanks of the mountains. In the southern half of the region most of the runoff occurs during winter or spring, while in the northern part most occurs in summer, especially in glaciated basins. Analyses of long-term climatic and hydrological records, combined with palaeoclimatic reconstructions and simulations of future climates, are used as the basis for likely scenarios of climatic variations. The predicted hydrological response in northern California to a climate with doubled CO₂ and higher temperatures is a decrease in the amount of precipitation falling as snow, and substantially increased runoff during winter and less in late spring and summer. One consequence of the predicted earlier runoff is higher salinity in summer and autumn in San Francisco Bay. In saline lakes, the incidence of meromixis and the associated reduction in nutrient supply and algal abundance is expected to vary significantly as runoff fluctuates. In subalpine lakes, global warming will probably lead to increased productivity. Lacustrine productivity can also be altered by changes in wind regimes, drought-enhanced forest fires and maximal or minimal snowpacks associated with atmospheric anomalies such as El Niño-Southern Oscillation (ENSO) events. Reduced stream temperature from increased contributions of glacial meltwater and decreased channel stability from changed runoff patterns and altered sediment loads has the potential to reduce the diversity of zoobenthic communities in predominately glacier-fed rivers. Climatic warming is likely to result in reduced growth and survival of sockeye salmon in freshwater, which would, in turn, increase marine mortality. Further research activities should include expanded studies at high elevations and of glacier mass balances and glacial runoff, applications of remote sensing to monitor changes, further refinement of regional climatic models to improve forecasts of future conditions and continued analyses of long-term physical, chemical and biological data to help understand responses to future climates. (C) 1997 by John Wiley & Sons, Ltd.

KEYWORDS: HYDROLOGIC SENSITIVITIES, HYPERSALINE MONO-LAKE, INTERANNUAL FLUCTUATIONS, PRECIPITATION

1525

Melillo, J.M., J. Borchers, J. Chaney, H. Fisher, S. Fox, A. Haxeltine, A. Janetos, D.W. Kicklighter, T.G.F. Kittel, A.D. McGuire, R. McKeown, R. Neilson, R. Nemani, D.S. Ojima, T. Painter, Y. Pan, W.J. Parton, L. Pierce, L. Pitelka, C. Prentice, B. Rizzo, N.A. Rosenbloom, S. Running, D.S. Schimel, S. Sitch, T. Smith, and I. Woodward. 1995. Vegetation ecosystem modeling and analysis project - comparing biogeography and biogeochemistry models in a continental-scale study of terrestrial ecosystem responses to climate-change and CO₂ doubling. *Global Biogeochemical Cycles* 9(4):407-437.

We compare the simulations of three biogeography models (BIOME2, Dynamic Global Phytogeography Model (DOLY), and Mapped Atmosphere-Plant Soil System (MAPSS)) and three biogeochemistry models (BIOME-BGC (BioGeochemistry Cycles), CENTURY, and Terrestrial Ecosystem Model (TEM)) for the conterminous United States under contemporary conditions of atmospheric CO₂ and climate. We also compare the simulations of these models under doubled CO₂ and a range of climate scenarios. For contemporary conditions, the biogeography models successfully simulate the geographic distribution of major vegetation types and have similar estimates of area for forests (42 to 46% of the conterminous United States), grasslands (17 to 27%), savannas (15 to 25%), and shrublands (14 to 18%). The biogeochemistry models estimate similar continental-scale net primary production (NPP; 3125 to 3772 x 10¹² gC yr⁻¹) and total carbon storage (108 to 118 x 10¹⁵ gC) for contemporary conditions. Among the scenarios of doubled CO₂ and associated equilibrium climates produced by the three general circulation models (Oregon State University (OSU), Geophysical Fluid Dynamics Laboratory (GFDL), and United Kingdom Meteorological Office (UKMO)), all three biogeography models show both gains and losses of total forest area depending on the scenario (between 38 and 53% of conterminous United States area). The only consistent gains in forest area with all three models (BIOME2, DOLY, and MAPSS) were under the GFDL scenario due to large increases in precipitation. MAPSS lost forest area under UKMO, DOLY under OSU, and BIOME2 under both UKMO and OSU. The variability in forest area estimates occurs because the hydrologic cycles of the biogeography models have different sensitivities to increases in temperature and CO₂. However, in general, the biogeography models produced broadly similar results when incorporating both climate change and elevated CO₂ concentrations. For these scenarios, the NPP estimated by the biogeochemistry models increases between 2% (BIOME-BGC with UKMO climate) and 35% (TEM with UKMO climate). Changes in total carbon storage range from losses of 33% (BIOME-BGC with UKMO climate) to gains of 16% (TEM with OSU climate). The CENTURY responses of NPP and carbon storage are positive and intermediate to the responses of BIOME-BGC and TEM. The variability in carbon cycle responses occurs because the hydrologic and nitrogen cycles of the biogeochemistry models have different sensitivities to increases in temperature and CO₂. When the biogeochemistry models are run with the vegetation distributions of the biogeography models, NPP ranges from no response (BIOME-BGC with all three biogeography model vegetations for UKMO climate) to increases of 40% (TEM with MAPSS vegetation for OSU climate). The total carbon storage response ranges from a decrease of 39% (BIOME-BGC with MAPSS vegetation for UKMO climate) to an increase of 32% (TEM with MAPSS vegetation for OSU and GFDL climates). The UKMO responses of BIOME-BGC with MAPSS vegetation are primarily caused by decreases in forested area and temperature-induced water stress. The OSU and GFDL responses of TEM with MAPSS vegetations are primarily caused by forest expansion and temperature-enhanced nitrogen cycling.

KEYWORDS: BALANCE, EXCHANGE, FOREST, GENERAL-MODEL,

1526

Melillo, J.M., R.A. Houghton, D.W. Kicklighter, and A.D. McGuire. 1996. Tropical deforestation and the global carbon budget. *Annual Review of Energy and the Environment* 21:293-310.

The CO₂ concentration of the atmosphere has increased by almost 30% since 1800. This increase is due largely to two factors: the combustion of fossil fuel and deforestation to create croplands and pastures. Deforestation results in a net flux of carbon to the atmosphere because forests contain 20-50 times more carbon per unit area than agricultural lands. In recent decades, the tropics have been the primary region of deforestation. The annual rate of CO₂ released due to tropical deforestation during the early 1990s has been estimated at between 1.2 and 2.3 gigatons C. The range represents uncertainties about both the rates of deforestation and the amounts of carbon stored in different types of tropical forests at the time of cutting. An evaluation of the role of tropical regions in the global carbon budget must include both the carbon flux to the atmosphere due to deforestation and carbon accumulation, if any, in intact forests. In the early 1990s, the release of CO₂ from tropical deforestation appears to have been mostly offset by CO₂ uptake occurring elsewhere in the tropics, according to an analysis of recent trends in the atmospheric concentrations of O-2 and N-2. Interannual variations in climate and/or CO₂ fertilization may have been responsible for the CO₂ uptake in intact forests. These mechanisms are consistent with site-specific measurements of net carbon fluxes between tropical forests and the atmosphere, and with regional and global simulations using process-based biogeochemistry models.

KEYWORDS: ABANDONED PASTURES, ATMOSPHERIC CARBON, BURN AGRICULTURE, EASTERN AMAZONIA, LAND-USE CHANGE, ORGANIC-CARBON, RAIN-FOREST, SATELLITE DATA, SIZE-FRACTIONS, UPPER RIO NEGRO

1527

Melillo, J.M., A.D. McGuire, D.W. Kicklighter, B. Moore, C.J. Vorosmarty, and A.L. Schloss. 1993. Global climate-change and terrestrial net primary production. *Nature* 363(6426):234-240.

A process-based model was used to estimate global patterns of net primary production and soil nitrogen cycling for contemporary climate conditions and current atmospheric CO₂ concentration. Over half of the global annual net primary production was estimated to occur in the tropics, with most of the production attributable to tropical evergreen forest. The effects of CO₂ doubling and associated climate changes were also explored. The responses in tropical and dry temperate ecosystems were dominated by CO₂, but those in northern and moist temperate ecosystems reflected the effects of temperature on nitrogen availability.

KEYWORDS: ALLOCATION, CO₂-ENRICHMENT, ELEVATED CO₂, FORESTS, GROWTH, LIMITATION, NITROGEN, NUTRITION, RESPONSES, SENSITIVITY

1528

Melkonian, J., S.J. Riha, and D.S. Wilks. 1998. Simulation of elevated CO₂ effects on daily net canopy carbon assimilation and crop yield. *Agricultural Systems* 58(1):87-106.

Three formulations for estimating the impact of elevated CO₂ on daily net canopy carbon assimilation (A) are compared. The formulations are all physiologically based but vary in the detail with which A is represented. When implemented in two crop models, all formulations

predict increased yield under elevated CO₂, with the formulation incorporating the most detailed representation of A predicting the smallest yield increase. In the crop model with more complex representations of growth and yield, and where increased photoassimilates under elevated CO₂ are allowed to affect processes such as leaf area development, yield predictions under elevated CO₂ can be substantially greater than the predicted increase in A for each formulation. These results indicate that the representation of A and assumptions regarding adaptation to elevated CO₂ of A, crop growth and carbon partitioning will have large impacts on simulation model predictions of crop yields at elevated CO₂. (C) 1998 Elsevier Science Ltd. All rights reserved.

KEYWORDS: CLIMATE CHANGE, DIOXIDE, GROWTH, MODEL, RADIATION, SPRING WHEAT, TEMPERATURE

1529

Menard, C., and B. Dansereau. 1992. Influence of photosynthetic photon flux-density and planting scheme on growth and development of cultivar royalty roses. *Scientia Horticulturae* 50(3):197-207.

The influence of photosynthetic photon flux density (PPFD) and planting scheme on growth, development, yield and quality of RosaXhybrida cultivar 'Royalty' was investigated. Three planting schemes (two, three, and four parallel rows) and three light treatments (ambient light and ambient light Plus supplemental lighting with either 50 or 100-mu-mol s⁻¹ m⁻² PPFD (high pressure sodium lamps) were studied. Generally, supplementary PPFD enhanced the vegetative and reproductive growth of the plants compared to plants grown in ambient light conditions. Marketable yield per plant was increased significantly by 79% (P<0.05) for the crop period from 1 January to 24 March 1988 when a PPFD of 50-mu-mol s⁻¹ m⁻² was added to ambient light conditions. Carbon dioxide enrichment increased yield by 113% when a PPFD of 50-mu-mol s⁻¹ m⁻² was added to ambient light during the crop period of 1 January to 24 March, 1989. The number of flowers per plant in the superior classes (commercial classification: 'Select' and 'No. 1') was enhanced for this period compared with the same period the previous year when no supplemental carbon dioxide was provided. Generally the planting scheme of two parallel rows gave the best overall results.

KEYWORDS: GREENHOUSE ROSES, SUPPLEMENTARY

1530

Miao, S.L. 1995. Acorn mass and seedling growth in quercus-rubra in response to elevated co₂. *Journal of Vegetation Science* 6(5):697-700.

In order to explore whether seed size affects plant response to elevated CO₂ plants grown from red oak (*Quercus rubra* L.) acorns were studied for differences in their first year response to CO₂ concentrations of 350 and 700 ul/l. Overall, at final harvest, total biomass of plants grown in elevated CO₂ were 47 % larger than that of plants grown in ambient CO₂. There were significant interactions between CO₂ treatments and initial acorn mass for total biomass, as well as for root, leaf, and stem biomass. Although total biomass increased with increasing initial acorn mass for both high and ambient CO₂ plants, high CO₂ plants exhibited a greater increase than ambient CO₂ plants, as indicated by a steeper slope in high CO₂ plants. However, CO₂ levels did not affect biomass partitioning traits, such as root/shoot ratio, leaf, stem, and root weight ratios, and leaf area ratio. These results suggest that variation in seed size or initial plant size can cause intraspecific variation in response to elevated CO₂.

1531

Miao, S.L., P.M. Wayne, and F.A. Bazzaz. 1992. Elevated co-2

differentially alters the responses of cooccurring birch and maple seedlings to a moisture gradient. *Oecologia* 90(2):300-304.

To determine the effects of elevated CO₂ and soil moisture status on growth and niche characteristics of birch and maple seedlings, gray birch (*Betula populifolia*) and red maple (*Acer rubrum*) were experimentally raised along a soil moisture gradient ranging from extreme drought to flooded conditions at both ambient and elevated atmospheric CO₂ levels. The magnitude of growth enhancement due to CO₂ was largely contingent on soil moisture conditions, but differently so for maple than for birch seedlings. Red maple showed greatest CO₂ enhancements under moderately moist soil conditions, whereas gray birch showed greatest enhancements under moderately dry soil conditions. Additionally, CO₂ had a relatively greater ameliorating effect in flooded conditions for red maple than for gray birch, whereas the reverse pattern was true for these species under extreme drought conditions. For both species, elevated CO₂ resulted in a reduction in niche breadths on the moisture gradient; 5% for gray birch and 23% for red maple. Species niche overlap (proportional overall) was also lower at elevated CO₂ (0.98 to 0.88:11%). This study highlights the utility of of experiments crossing CO₂ levels with gradients of other resources as effective tools for elucidating the potential consequences of elevated CO₂ on species distributions and potential interactions in natural communities.

KEYWORDS: CARBON DIOXIDE, CO₂- ENRICHMENT, GROWTH-RESPONSES, LIQUIDAMBAR- STYRACIFLUA, PINUS-TAEDA SEEDLINGS, WATER-STRESS

1532

Micallef, B.J., K.A. Haskins, P.J. Vanderveer, K.S. Roh, C.K. Shewmaker, and T.D. Sharkey. 1995. Altered photosynthesis, flowering, and fruiting in transgenic tomato plants that have an increased capacity for sucrose synthesis. *Planta* 196(2):327-334.

Photosynthesis, leaf assimilate partitioning, flowering, and fruiting were examined in two lines of *Lycopersicon esculentum* Mill. transformed with a gene coding for sucrose-phosphate esculentum (SPS) (EC 2.3.1.14) from *Zea mays* L. expressed from a tobacco ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) small subunit promoter. Plants were grown at either 35 or 65 Pa CO₂ and high light (1000 mu mol photons . m⁻². s⁻¹). Limiting and maximum SPS activities were significantly greater (up to 12 times) in the leaves of SPS-transformed lines for all treatments. Partitioning of carbon into sucrose increased 50% for the SPS transformants. Intact leaves of the control lines exhibited CO₂-insensitivity of photosynthesis at high CO₂ levels, whereas the SPS transformants did not exhibit CO₂-insensitivity. The O₂-sensitivity of photosynthesis was also greater for the SPS-transformed lines compared to the untransformed control when measured at 65 Pa CO₂. These data indicate that the SPS transformants had a reduced limitation on photosynthesis imposed by end-product synthesis. Growth at 65 Pa CO₂ resulted in reduced photosynthetic capacity for control lines but not for SPS-transformed lines. When grown at 65 Pa CO₂, SPS transformed lines had a 20% greater photosynthetic rate than controls when measured at 65 Pa CO₂ and a 35% greater rate when measured at 105 Pa CO₂. Photosynthetic rates were not different between lines when grown at 35 Pa CO₂. The time to 50% blossoming was reduced and the total number of inflorescences was significantly greater for the SPS transformants when grown at either 35 or 65 Pa CO₂. At 35 Pa CO₂, the total fruit number of the SPS transformants was up to 1.5 times that of the controls, the fruit matured earlier, and there was up to a 32% increase in total fruit dry weight. Fruit yield was not significantly different between the lines when grown at 65 Pa CO₂. Therefore, there was not a strict relationship between yield and leaf photosynthesis rate. Flowering and fruit development of the SPS-transformed lines grown at 35 Pa CO₂ showed similar trends to the controls grown at 65 Pa CO₂. Incidences of bios som-end rot were also reduced in the SPS-transformed lines. These data indicate that altering starch/sucrose partitioning by increasing the

capacity for sucrose synthesis can affect acclimation to elevated CO₂ partial pressure and flowering and fruiting in tomato.

KEYWORDS: ACCLIMATION, CO₂- ENRICHMENT, ELEVATED CO₂, GAS-EXCHANGE, GROWTH, LEAVES, PHASEOLUS-VULGARIS, PHOSPHATE SYNTHASE, TEMPERATURE, YIELD

1533

Micallef, B.J., P.J. Vanderveer, and T.D. Sharkey. 1996. Responses to elevated CO₂ of *Flaveria linearis* plants having a reduced activity of cytosolic fructose-1,6-bisphosphatase. *Plant, Cell and Environment* 19(1):10-16.

Wide variation exists in the growth responses of C-3 plants to elevated CO₂ levels. To investigate the role of photosynthetic feedback in this phenomenon, photosynthetic parameters and growth were measured for lines of *Flaveria linearis* with low, intermediate or high cytosolic fructose-1,6-bisphosphatase (cytFBPase) activity when grown at either 35 or 65 Pa CO₂. The effects of pot size on the responses of these lines to elevated CO₂ were also examined. Photosynthesis and growth of plants with low cytFBPase activity were less responsive to elevated CO₂, and these plants had a reduced maximum potential for photosynthesis and growth. Plants with intermediate cytFBPase activity also showed a lower relative growth enhancement when grown at 65 Pa CO₂. There was a significant pot size effect on photosynthesis and growth for line 85-1 (high cytFBPase). This effect was greatest for Line 85-1 when grown at 35 Pa CO₂, since these plants showed the greatest downward acclimation of photosynthesis when grown in small pots. There was a minimal pot size effect for line 84-9 (low cytFBPase), and this could be partly attributed to the reduced CO₂ sensitivity of this line. It is proposed that the capacity for sucrose synthesis in C-3 plants is partly responsible for their wide variation in CO₂ responsiveness.

KEYWORDS: MUTANT, PHOTOSYNTHETIC ACCLIMATION

1534

Michaels, P.J. 1993. Benign greenhouse. *Research & Exploration* 9(2):222-233.

Several lines of evidence are emerging that suggest that the "popular vision" of global warming-major agricultural damage, disastrous sea-level rise, and ecological disequilibrium-is flawed. The popular vision is driven primarily by the prospect of enhanced daytime warming, particularly in summer. What has been observed is a warming that is beneath the projections that support the popular vision, and a warming that has occurred virtually all during the night in the Northern Hemisphere. In the Southern Hemisphere there is also evidence of disproportionate night warming. Several sources of data indicate that this night warming has been caused by an increase in cloudiness that could be a consequence of the greenhouse enhancement itself. The results of the night warming-longer growing seasons, little change in moisture stress, and a possible increase in ice volume-are opposite to the popular vision of climatic change.

KEYWORDS: ATMOSPHERE, CLIMATE CHANGE, CO₂, GENERAL-CIRCULATION MODEL, SUNSHINE, UNITED-STATES

1535

Midgley, G.F., W.D. Stock, and J.M. Juritz. 1995. Effects of elevated CO₂ on Cape Fynbos species adapted to soils of different nutrient status: Nutrient- and CO₂-responsiveness. *Journal of Biogeography* 22(2-3):185-191.

The combined effects of elevated atmospheric CO₂ and nutrient supply rate on plant biomass accumulation were determined for four

Leucadendron species (Proteaceae) of the mediterranean climate Fynbos Biome, South Africa. Juvenile individuals were grown for 6 months in experiments comprising 2X2 factorial combinations of substrate nutrient supply rate and atmospheric CO₂ concentration in open-top chambers in a greenhouse. The four selected Leucadendron species included one pair of species common on extremely nutrient-poor acid sands (typical of the Fynbos Biome), and another pair associated with more nutrient rich substrates (rare in the Fynbos Biome). Plant biomass accumulation data were analysed to explore the determinants of plant CO₂ responsiveness, particularly the role of plant sink strength characteristics. Results lead us to speculate that the nitrogen:phosphorus supply ratio may have limited plant CO₂ responsiveness in three of the four species under conditions of higher nutrient supply rate. Intrinsic plant growth characteristics, possibly related to the relative ability of the species to generate sinks, may ultimately have limited the capacity of all species to respond to elevated CO₂.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, MOUNTAIN FYNBOS, NUTRITION, PHOSPHORUS, PHOTOSYNTHETIC ACCLIMATION, PLANT GROWTH, PROTEACEAE, RESPONSES, SINK STRENGTH

1536

Midgley, G.F., S.J.E. Wand, and N.W. Pammenter. 1999. Nutrient and genotypic effects on CO₂-responsiveness: Photosynthetic regulation in Leucadendron species of a nutrient-poor environment. *Journal of Experimental Botany* 50(333):533-542.

Four South African Leucadendron congeners with divergent soil N and P preferences were grown as juveniles at contrasting nutrient concentrations at ambient (350 $\mu\text{mol mol}^{-1}$) and elevated (700 $\mu\text{mol mol}^{-1}$) atmospheric CO₂ levels. Photosynthetic parameters were related to leaf nutrient and carbohydrate status to reveal controls of carbon uptake rate. In all species, elevated CO₂ depressed both the maximum Rubisco catalytic activity (V_c, V_{max}, by 19-44%) and maximum electron transport rate (J_{max}) by 13-39%, indicating significant photosynthetic acclimation of both measures. Even so, all species had increased maximum light-saturated rate of net CO₂ uptake (A_{max}) at the elevated growth CO₂ level, due to higher intercellular CO₂ concentration (c_i). Leaf nitrogen concentration was central to photosynthetic performance, correlating with A_{max}, V_c, V_{max} and J_{max}. V_c, V_{max} and J_{max} were linearly cc-correlated, revealing a relatively invariable J_{max}:V_c, V_{max} ratio, probably due to N resource optimization between light harvesting (RuBP regeneration) and carboxylation. Leaf total non-structural carbohydrate concentration (primarily starch) increased in high CO₂, and was correlated with the reduction in V_c, V_{max} and J_{max}. Apparent feedback control of V_c, V_{max} and J_{max} was thus surprisingly consistent across all species, and may regulate carbon exchange in response to end-product fluctuation. If so, elevated CO₂ may have emulated an excess end-product condition, triggering both V_c, V_{max} and J_{max} down-regulation. In Leucadendron, a general physiological mechanism seems to control excess carbohydrate formation, and photosynthetic responsiveness to elevated CO₂, independently of genotype and nutrient concentration. This mechanism may underlie photosynthetic acclimation to source:sink imbalances resulting from such diverse conditions as elevated CO₂, low sink strength, low carbohydrate export, and nutrient limitation.

KEYWORDS: ACCLIMATION, ARABIDOPSIS-THALIANA, CARBOHYDRATE-METABOLISM, ELEVATED ATMOSPHERIC CO₂, ENRICHMENT, LEAF NITROGEN, PHOTON FLUX- DENSITY, PLANT-RESPONSES, SOUTH-AFRICA, TEMPERATURE

1537

Miglietta, F., I. Bettarini, A. Raschi, C. Korner, and F.P. Vaccari.

1998. Isotope discrimination and photosynthesis of vegetation growing in the Bossoleto CO₂ spring. *Chemosphere* 36(4-5):771-776.

The Bossoleto CO₂ spring emits CO₂ which has a stable carbon isotopic ratio ($\delta^{13}\text{C} = -8$ parts per thousand). We determined $\delta^{13}\text{C}$ on leaves of several individual species growing in Bossoleto and in a nearby control site at ambient CO₂. $\delta^{13}\text{C}$ was 6% more negative in leaves of species collected from the grassland community of Bossoleto, indicating increased discrimination (Δ) against the heavy carbon isotope. No such changes were found in ruderal species growing in the same spring, suggesting that photosynthetic capacity was much less affected. Δ was substantially increased under elevated CO₂ in leaves of *Quercus pubescens* but not in *Quercus ilex*, which also did not show any increase in non-structural carbohydrates. Gas-exchange measurements made on *Plantago lanceolata*, supported the view that photosynthetic capacity is decreased in plants grown under elevated CO₂ and on poor soils. (C) 1998 Elsevier Science Ltd.

KEYWORDS: CARBON

1538

Miglietta, F., A. Giuntoli, and M. Bindi. 1996. The effect of free air carbon dioxide enrichment (FACE) and soil nitrogen availability on the photosynthetic capacity of wheat. *Photosynthesis Research* 47(3):281-290.

A simple system for free air carbon dioxide enrichment (FACE) was recently developed and it is here briefly described. Such a MiniFACE system allowed the elevation of CO₂ concentration of small field plots avoiding the occurrence of large spatial and temporal fluctuations. A CO₂ enrichment field experiment was conducted in Italy in the season 1993-1994 with wheat (cv. Super-dwarf Mercia). A randomized experimental design was used with the treatment combination CO₂ x soil N, replicated twice. Gas exchange measurements showed that photosynthetic capacity was significantly decreased in plants exposed to elevated CO₂ and grown under nitrogen deficiency. Photosynthetic acclimation was, in this case, due to the occurrence of reduced rates of rubP saturated and rubP regeneration limited photosynthesis. Gas exchange measurements did not instead reveal any significant effect of elevated CO₂ on the photosynthetic capacity of leaves of plants well fertilized with nitrogen, in spite of a transitory negative effect on rubP regeneration limited photosynthesis that was detected to occur in the central part of a day with high irradiance. It is concluded that the levels of nitrogen fertilization will play a substantial role in modulating CO₂ fertilization effects on growth and yields of wheat crops under the scenario of future climate change.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO₂ CONCENTRATIONS, C-3 PLANTS, CARBOXYLASE-OXYGENASE, ELEVATED CO₂, LEAVES, PLANT GROWTH, SOURCE-SINK RELATIONS, TEMPERATURE, WINTER-WHEAT

1539

Miglietta, F., M. Lanini, M. Bindi, and V. Magliulo. 1997. Free air CO₂ enrichment of potato (*Solanum tuberosum*, L.): design and performance of the CO₂-fumigation system. *Global Change Biology* 3(5):417-427.

Free Air CO₂ Enrichment (FACE) systems are used to fumigate unconfined field plots with CO₂. As these installations can treat a sufficiently large area without interfering with natural climatic conditions, they are considered important tools for global change research worldwide. However, there is general consensus that elevated capital costs of existing FACE systems as well as high running costs may prevent their application at the required level of scale. A new and small FACE system that was designed to reduce both capital costs and

CO₂ use, is described in this paper. Due to its intermediate size (8 m diameter) between the smaller Mini-FACE systems that were developed in Italy and the larger systems designed by the Brookhaven National Laboratory in the USA, it was named Mid-FACE. The Mid-FACE was at first developed as a prototype and then used to enrich field grown potato crops in a CO₂ concentration gradient experimental design. Technical details of a Mid-FACE prototype and of the operational set-up are presented in this paper together with performance data in terms of temporal and spatial control of CO₂ concentrations within the experimental area.

KEYWORDS: CARBON DIOXIDE, COTTON, EXPOSURE, FACE SYSTEM, FACILITY, TRACE GASES, WHEAT

1540

Miglietta, F., V. Magliulo, M. Bindi, L. Cerio, F.P. Vaccari, V. Loduca, and A. Peressotti. 1998. Free air CO₂ enrichment of potato (*Solanum tuberosum* L.): development, growth and yield. *Global Change Biology* 4(2):163-172.

A FACE (Free Air CO₂ Enrichment) experiment was carried out on Potato (*Solanum tuberosum* L., cv. Primura) in 1995 in Italy. Three FACE rings were used to fumigate circular field plots of 8 m diameter while two rings were used as controls at ambient CO₂ concentrations. Four CO₂ exposure levels were used in the rings (ambient, 460, 560 and 660 $\mu\text{mol mol}^{-1}$). Phenology and crop development, canopy surface temperature, above- and below-ground biomass were monitored during the growing season. Crop phenology was affected by elevated CO₂, as the date of flowering was progressively anticipated in the 660, 560, 460 $\mu\text{mol mol}^{-1}$ treatments. Crop development was not affected significantly as plant height, leaf area and the number of leaves per plant were the same in the four treatments. Elevated atmospheric CO₂ levels had, instead, a significant effect on the accumulation of total nonstructural carbohydrates (TNC = soluble sugars + starch) in the leaves during a sunny day. Specific leaf area was decreased under elevated CO₂ with a response that paralleled that of TNC concentrations. This reflected the occurrence of a progressive increase of photosynthetic rates and carbon assimilation in plants exposed to increasingly higher levels of atmospheric CO₂. Tuber growth and final tuber yield were also stimulated by rising CO₂ levels. When calculated by regression of tuber yield vs. the imposed levels of CO₂ concentration, yield stimulation was as large as 10% every 100 $\mu\text{mol mol}^{-1}$ increase, which translated into over 40% enhancement in yield under 660 $\mu\text{mol mol}^{-1}$. This was related to a higher number of tubers rather than greater mean tuber mass or size. Leaf senescence was accelerated under elevated CO₂ and a linear relationship was found between atmospheric CO₂ levels and leaf reflectance measured at 0.55 μm wavelength. We conclude that significant CO₂ stimulation of yield has to be expected for potato under future climate scenarios, and that crop phenology will be affected as well.

KEYWORDS: CARBON DIOXIDE, CLIMATE CHANGE, COTTON, ELEVATED CO₂, IRRADIANCE, LEAVES, PLANTS, TEMPERATURE, WHEAT, WORLD

1541

Miglietta, F., and A. Raschi. 1993. Studying the effect of elevated CO₂ in the open in a naturally enriched environment in central Italy. *Vegetatio* 104:391-400.

A gas vents area was recently localized in Central Italy. The gas emitted from the vents is composed by 92% of carbon dioxide and this produces an anomaly in the composition of the atmosphere over an area of about 2 ha. Atmospheric carbon dioxide concentration was measured by means of an infrared gas analyzer and diffusion tubes in several points and for some days within the area. Measurements revealed that the site can be

at least divided into three sub-areas having increasing CO₂ concentration in the air. A preliminary analysis of natural vegetation in the area was conducted by counting stomatal and epidermal cells number and measuring guard cell size on leaves of several oak trees growing both near and far away from the vents. This analysis suggested that elevated CO₂ may have reduced the size of guard cells leaving stomatal density and stomatal index unaltered.

KEYWORDS: CARBON DIOXIDE, GROWTH, INCREASES, NUMBERS, STOMATAL DENSITY

1542

Miglietta, F., A. Raschi, I. Bettarini, R. Resti, and F. Selvi. 1993. Natural CO₂ springs in Italy - a resource for examining long-term response of vegetation to rising atmospheric CO₂ concentrations. *Plant, Cell and Environment* 16(7):873-878.

It is estimated that more than 100 geothermal CO₂ springs exist in central-western Italy. Eight springs were selected in which the atmospheric CO₂ concentrations were consistently observed to be above the current atmospheric average of 354 μmol mol⁻¹. CO₂ concentration measurements at some of the springs are reported. The springs are described, and their major topographic and vegetational features are reported. Preliminary observations made on natural vegetation growing around the gas vents are then illustrated. An azonal pattern of vegetation distribution occurs around every CO₂ spring regardless of soil type and phytoclimatic areas. This is composed of pioneer populations of a Northern Eurasian species (*Agrostis canina* L.) which is often associated with *Scirpus lacustris* L. The potential of these sites for studying the long-term response of vegetation to rising atmospheric CO₂ concentrations is discussed.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, GROWTH, INCREASES, NUMBERS, STOMATAL DENSITY

1543

Miglietta, F., A. Raschi, R. Resti, and M. Badiani. 1993. Growth and ontomorphogenesis of soybean (*Glycine max* Merrill) in an open, naturally CO₂-enriched environment. *Plant, Cell and Environment* 16(8):909-918.

Springs emitting carbon dioxide are frequent in Central Italy and provide a way of testing the response of plants to CO₂ enrichment under natural conditions. Results of a CO₂ enrichment experiment on soybean at a CO₂ spring (Solfatara) are presented. The experimental site is characterized by significant anomalies in atmospheric CO₂ concentration produced by a large number of vents emitting almost pure CO₂ (93%) plus small amounts of hydrogen sulphide, methane, nitrogen and oxygen. Within the gas vent area, plants were grown at three sub-areas whose mean CO₂ concentrations during daytime were 350, 652 and 2370 μmol mol⁻¹, respectively. Weekly harvests were made to measure biomass growth, leaf area and ontogenetic development. Biomass growth rate and seed yield were enhanced by elevated CO₂. In particular, ontomorphogenetic development was affected by elevated CO₂ with high levels of CO₂ increasing the total number of main stem leaf nodes and the area of the main stem trifoliolate leaves. Biochemical analysis of plant tissue suggested that there was no effect of the small amounts of H₂S on the response to CO₂ enrichment. Non-protein sulphhydryl compounds did not accumulate in leaf tissues and the overall capacity of leaf extracts to oxidize exogenously added NADH was not decreased. The limitations and advantages of experimenting with crop plants at elevated CO₂ in the open and in the proximity of carbon dioxide springs are discussed.

KEYWORDS: CANOPY, CARBON-DIOXIDE ENRICHMENT, CO₂ CONCENTRATION, FIELD, INDEX, LEAVES, PHOTOSYNTHESIS,

PLANTS, SULFUR, TEMPERATURE

1544

Miglietta, F., M. Tanasescu, and A. Marica. 1995. The expected effects of climate change on wheat development. *Global Change Biology* 1(6):407-415.

Air temperature and the atmospheric concentrations of carbon dioxide are expected to rise. These two factors have a great potential to affect development, growth and yield of crops, including wheat. Rising air temperature may affect wheat development more than rising atmospheric CO₂ as there is not yet evidence that elevated CO₂ concentrations can directly induce changes in wheat development. In winter wheat, temperature has a complex effect on development due to its strong interaction with vernalization and photoperiod. In this paper, potential effects of rising temperature on the development of winter wheat from sowing to heading are considered in the light of this complex controlling mechanism. Data from a large series of field trials made in Romania is analysed at first and, subsequently, the IATA-Wheat Phenology model is used to calculate the impact of air warming on wheat development under different climate change scenarios. Data from the field trials showed very clearly the occurrence of a complex temperature/photoperiod/vernalization interaction for field sown crops and demonstrated that the photoperiodic and vernalization responses have a key role in controlling the duration of the emergence-heading period. Temperature plays, instead, a central role in controlling seed germination and crop emergence as well as leaf initiation and leaf appearance rate. The results of model analysis showed very well that the impact of an even or uneven distribution of warming effects may be very different. In the first case, the model predicted that the duration of the vegetative period was at least partly reduced in some years. In the second case, the model suggested that if warming will be more pronounced in winter than in spring, as predicted for some areas of the world by General Circulation Models, we may expect an increase in the duration of the vegetative phase of growth. On the contrary, in case of a spring warming but unchanged winter temperatures, we may expect a substantial decrease in the duration of the vegetative period.

KEYWORDS: FIELD, GROWTH, MODEL, NUMBER, PHOTOPERIOD, SPRING WHEAT, VERNALIZATION, WATER

1545

Mikkelsen, T.N., and H. Ropoulsen. 1994. Exposure of Norway spruce to ozone increases the sensitivity of current year needles to photoinhibition and desiccation. *New Phytologist* 128(1):153-163.

Physiological effects of ozone exposure over three consecutive growing seasons on current year needles of Norway spruce were studied in open-top chambers, during daily fumigation cycles in the summer, and after the termination of ozone fumigation in autumn 1990. The trees were exposed to two levels of ozone: charcoal filtered air and non-filtered air to which 30 nl l⁻¹ of ozone was added in three consecutive years from 1988 to 1990, daily from May to September (8 hours a day). Photosynthesis, stomatal conductance, transpiration and chlorophyll fluorescence were studied on selected days. Significant decreases in net photosynthesis and chlorophyll fluorescence (F_v/F_m) were found during periods with co-occurrence of high ozone concentrations and high light intensities, indicating interactions between effects of ozone and photoinhibition. After termination of fumigation enhanced rates of photosynthesis were seen in the trees which had been exposed to ozone. A significant decrease in F_v/F_m was found for twigs from ozone treated trees when exposed to severe desiccation.

KEYWORDS: ABIES L. KARST, AIR-POLLUTANTS, BISPHOSPHATE CARBOXYLASE OXYGENASE, CHLOROPHYLL FLUORESCENCE-KINETICS, CO₂ ASSIMILATION, GAS-EXCHANGE, LONG-TERM

EXPOSURE, NET PHOTOSYNTHESIS, NONSTOMATAL LIMITATION, OPEN-TOP CHAMBERS

1546

Miller, A., C.H. Tsai, D. Hemphill, M. Endres, S. Rodermel, and M. Spalding. 1997. Elevated CO₂ effects during leaf ontogeny - A new perspective on acclimation. *Plant Physiology* 115(3):1195-1200.

For many plants growth in elevated CO₂ leads to reduced rates of photosynthesis. To examine the role that leaf ontogeny plays in the acclimation response, we monitored photosynthesis and some related parameters at short intervals throughout the ontogenetic development of tobacco (*Nicotiana tabacum* L.) leaves under ambient (350 μ L L⁻¹) and high (950 μ L L⁻¹) CO₂ conditions. The pattern of photosynthetic rate over time was similar between the two treatments and consistent with the expected pattern for a typical dicot leaf. However, the photosynthesis pattern in high-CO₂-grown tobacco was shifted temporally to an earlier maximum and subsequent senescent decline. Ribulose-1,5-biphosphate carboxylase/oxygenase activity appeared to be the main factor regulating photosynthetic rates in both treatments. Therefore, we propose a new model for interpreting the acclimation response. Lowered photosynthetic rates observed during acclimation appear to be the result of a shift in the timing of the normal photosynthetic stages of leaf ontogeny to an earlier onset of the natural decline in photosynthetic rates associated with senescence.

KEYWORDS: ATMOSPHERIC CO₂, GAS-EXCHANGE, GROWTH, PHOTOSYNTHETIC ACCLIMATION, PROTEINS, TOMATO PLANTS, TRANSFORMED TOBACCO

1547

Miller, C., and D.L. Urban. 1999. Forest pattern, fire, and climatic change in the Sierra Nevada. *Ecosystems* 2(1):76-87.

In the Sierra Nevada, distributions of forest tree species are largely controlled by the soil-moisture balance. Changes in temperature or precipitation as a result of increased greenhouse gas concentrations could lead to changes in species distributions. In addition, climatic change could increase the frequency and severity of wildfires. We used a forest gap model developed for Sierra Nevada forests to investigate the potential sensitivity of these forests to climatic change, including a changing fire regime. Fuel moisture influences the fire regime and couples fire to climate. Fires are also affected by fuel loads, which accumulate according to forest structure and composition. These model features were used to investigate the complex interactions between climate, fire, and forest dynamics. Eight hypothetical climate-change scenarios were simulated, including two general circulation model (GCM) predictions of a 2 x CO₂ world. The response of forest structure, species composition, and the fire regime to these changes in the climate were examined at four sites across an elevation gradient. Impacts on woody biomass and species composition as a result of climatic change were site specific and depended on the environmental constraints of a site and the environmental tolerances of the tree species simulated. Climatic change altered the fire regime both directly and indirectly. Fire frequency responded directly to climate's influence on fuel moisture, whereas fire extent was affected by changes that occurred in either woody biomass or species composition. The influence of species composition on fuel-bed bulk density was particularly important. Future fires in the Sierra Nevada could be both more frequent and of greater spatial extent if GCM predictions prove true.

KEYWORDS: AGE, HISTORY, LANDSCAPES, PROCESS MODEL, SENSITIVITY, VEGETATION

1548

Miller, J.B., D. Yakir, J.W.C. White, and P.P. Tans. 1999. Measurement of O-18/O-16 in the soil-atmosphere CO₂ flux. *Global Biogeochemical Cycles* 13(3):761-774.

Measurements of O-18 in atmospheric CO₂ can be used to trace gross photosynthetic and respiratory CO₂ fluxes between the atmosphere and the terrestrial biosphere. However, this requires knowledge of the O-18 signatures attributable to the fluxes from soil and leaves. Newly developed methods were employed to measure the O-18 of soil-respired CO₂ and depth profiles of near-surface soil CO₂ in order to evaluate the factors influencing isotopic soil-atmosphere CO₂ exchange. The O-18 soil-respired CO₂ varied predominantly as a function of the O-18 of soil water which, in turn, changed with soil drying and with seasonal variations in source water. The O-18 of soil-respired CO₂ corresponds to full isotopic equilibrium with soil water at a depth ranging between 5 and 15 cm. The O-18 of respired CO₂, in reality, results from a weighted average of partial equilibria over a range of depths. Soil water isotopic enrichment of up to 10 parts per thousand in the top 5 cm did not appear to strongly influence the isotopic composition of the respired CO₂. We demonstrate that during measurements "invasion" of atmospheric CO₂ (the diffusion of ambient CO₂ into the soil, followed by partial equilibration and retrodiffusion) must be considered to accurately calculate the O-18 of the soil-respired CO₂. The impact of invasion in natural settings is also considered. We also have determined the effective kinetic fractionation of CO₂ diffusion out of the soil to be 7.2 +/- 0.3 parts per thousand. High-resolution (1 cm) depth profiles of O-18 of near-surface (top 10 cm) soil CO₂ were carried out by gas chromatography-isotope ratio mass spectrometry (IRMS). This novel technique allowed us to observe the competitive diffusion-equilibration process near the soil surface and to test simulations by a diffusion and equilibration model of the soil CO₂ O-18 content.

KEYWORDS: CARBON DIOXIDE, DELTA O 18, DIRECT EQUILIBRATION, EXCHANGE, ISOTOPIC COMPOSITION, LEAF WATER, O-18, OXYGEN, SURFACE, VEGETATION

1549

Miller, J.E., A.S. Heagle, and W.A. Pursley. 1998. Influence of ozone stress on soybean response to carbon dioxide enrichment: II. Biomass and development. *Crop Science* 38(1):122-128.

Previous research has shown that elevated CO₂ concentrations can increase plant growth, whereas the air pollutant O-3 is phytotoxic. Because elevated concentrations of these gases will co-occur, the objective of our experiment was to determine if estimates of plant growth response to future levels of CO₂ and O-3 require experiments to test the gases in combination. Soybean plants [*Glycine max* (L.) Merr. cv. Essex] were exposed in open-top chambers to combinations of O-3 and CO₂ from plant emergence through physiological maturity. Ozone treatments were charcoal-filtered air (CF), nonfiltered air (NF), and NF with O-3 added for 12 h d⁻¹ (NF+) (seasonal mean 12 h d⁻¹) O-3 concentrations of 20, 50, or 79 nL L⁻¹, respectively). Carbon dioxide exposures were for 24 h d⁻¹ giving seasonal mean 12 h d⁻¹) concentrations of 370, 482, 599, or 713 μ L L⁻¹. Over the season, elevated CO₂ usually stimulated growth and O-3 suppressed growth. Elevated CO₂ usually increased partitioning of biomass to branches, decreased partitioning to pods, increased specific leaf weight, and decreased leaf area ratio. Ozone suppressed leaf and root weight ratios, increased pod weight ratios, and decreased specific leaf weight. Toward the end of the season, both O-3 and CO₂ accelerated reproductive development. Elevated CO₂ moderated suppression of growth by O-3, and the highest CO₂ concentration completely ameliorated O-3 effects on main stem biomass, root biomass, and leaf area. Ozone, however, limited some positive growth responses to CO₂, especially at less than a doubling of CO₂ concentrations. These results indicate that in order to understand the future impacts of atmospheric gases such as elevated CO₂ and O-3 on crop growth, their combined effects should be

determined.

KEYWORDS: ATMOSPHERIC CO₂, CHAMBERS, GROWTH, PLANT-RESPONSES

1550

Mishra, R.S., M.Z. Abidin, and D.C. Uprety. 1999. Interactive effects of elevated CO₂ and moisture stress on the photosynthesis, water relation and growth of Brassica species. *Journal of Agronomy and Crop Science-Zeitschrift Fur Acker Und Pflanzenbau* 182(4):223-229.

Interactive effects of elevated CO₂ and moisture stress on photosynthesis, growth and water relation of Brassica species were studied using open top chamber technology. Brassica species responded to the elevated CO₂ significantly under moisture stress condition. The adverse effect of moisture stress on the photosynthesis and plant water components were minimized by elevated levels of CO₂. Drought susceptible species of *B. campestris* and *B. nigra* responded better to elevated CO₂ compared to drought tolerant Brassica species such as *B. carinata* and *B. juncea*. The plant water potential significantly improved by elevated CO₂ coupled with higher stomatal resistance and root growth.

KEYWORDS: ATMOSPHERIC CO₂, DEFICITS, LEAF-AREA, SEEDLINGS, WHEAT, YIELD

1551

Mitchell, C.A., C.H. Chun, W.E. Brandt, and S.S. Nielsen. 1997. Environmental modification of yield and nutrient composition of 'Waldmann's Green' leaf lettuce. *Journal of Food Quality* 20(1):73-80.

Leaf number, dry weight, and nutrient composition of *Lactuca sativa* L. cv. 'Waldmann's Green' leaves were compared following 9 days of treatment in a controlled environment room under various combinations of photosynthetic photon flux (PPF:350 vs 800 $\mu\text{mol m}^{-2} \text{s}^{-1}$), atmospheric CO₂ level (ambient vs 1500 $\mu\text{mol mol}^{-1}$), and single-strength (1X:15 mM) vs double-strength (2X:30 mM) nitrogen (N) as NO₃⁻ alone or as NH₄⁺ + NO₃⁻ (1:5 molar ratio). CO₂ enrichment greatly enhanced leaf number under all PPF and N conditions, but increased leaf dry weight only at high PPF. Conditions favoring high photosynthesis enhanced leaf starch content 3-fold, and protein content increased as much as 64% with 2X NH₄⁺+NO₃⁻. Free sugar content was 6 to 9% of leaf dry weight for all treatment combinations, while fat was 1.5 to 3.5%. Ash content varied from 15 to 20% of leaf dry weight. Modified controlled environments can be used to enhance the nutritional content as well as the yield of crops to be used for life support in space-deployed, self-sustaining human habitats. Leaf lettuce is a useful model crop for demonstrating the potential of nutritional value added by environmental manipulation.

KEYWORDS: GROWTH, LIGHT, MANIPULATION, TISSUE

1552

Mitchell, J.F.B. 1990. Greenhouse warming - is the midholocene a good analog. *Journal of Climate* 3(11):1177-1192.

The mid-Holocene period (from approximately 9000 to 6000 years before present) is often suggested as an analogue for enhanced greenhouse warming. The changes in net radiative forcing at the top of atmosphere are very different; increases in greenhouse gases producing a small annual mean warming of little seasonal or latitudinal variation, whereas during the Holocene the annual mean did not change but there were large seasonal and latitudinal variations. Two climate model experiments, one in which CO₂ amounts are doubled and the other in which the value of the earth's orbital parameters are altered to those

appropriate to 9000 years before present (BP), are compared. Any similarity in the simulated response is found to be limited to the northern continents and, even there, the mechanisms producing the changes differ between the two experiments. Assuming that the gross behavior of the model is realistic, the Holocene is not a good analogue for a "greenhouse" warming. Furthermore, as the mechanisms operating in the two experiments are different, a model which produces a realistic simulation for the mid-Holocene and present climate need not necessarily produce a reliable simulation of greenhouse warming. However, a comparison of simulated climates for the mid-Holocene and that reconstructed from paleoclimatic data may help to constrain the existing range of subgridscale parametrizations used in climate models.

1553

Mitchell, K.A., P.V. Bolstad, and J.M. Vose. 1999. Interspecific and environmentally induced variation in foliar dark respiration among eighteen southeastern deciduous tree species. *Tree Physiology* 19(13):861-870.

We measured variations in leaf dark respiration rate (R_d) and leaf nitrogen (N) across species, canopy light environment, and elevation for 18 co-occurring deciduous hardwood species in the southern Appalachian mountains of western North Carolina. Our overall objective was to estimate leaf respiration rates under typical conditions and to determine how they varied within and among species. Mean dark respiration rate at 20 degrees C (R_d-mass, $\mu\text{mol CO}_2 (\text{kg leaf dry mass})^{-1} \text{s}^{-1}$) for all 18 species was 7.31 $\mu\text{mol kg}^{-1} \text{s}^{-1}$. Mean R_d-mass of individual species varied from 5.17 $\mu\text{mol kg}^{-1} \text{s}^{-1}$ for *Quercus coccinea* Muenchh, to 8.25 $\mu\text{mol kg}^{-1} \text{s}^{-1}$ for *Liriodendron tulipifera* L. Dark respiration rate varied by leaf canopy position and was higher in leaves collected from high-light environments. When expressed on an area basis, dark respiration rate (R_d-area, $\mu\text{mol CO}_2 (\text{kg leaf dry area})^{-1} \text{s}^{-1}$) showed a strong linear relationship with the predictor variables leaf nitrogen (N-area, g N (m leaf area)⁻²) and leaf structure (LMA, g leaf dry mass (m leaf area)⁻²) ($r^2 = 0.62$). This covariance was largely a result of changes in leaf structure with canopy position; smaller thicker leaves occur at upper canopy positions in high-light environments. Mass-based expression of leaf nitrogen and dark respiration rate showed that nitrogen concentration (N-mass, mg N (g leaf dry mass)⁻¹) was only moderately predictive of variation in R_d-mass for all leaves pooled ($r^2 = 0.11$), within species, or among species. We found distinct elevational trends, with both R_d-mass and N-mass higher in trees originating from high-elevation, cooler growth environments. Consideration of interspecies differences, vertical gradients in canopy light environment, and elevation, may improve our ability to scale leaf respiration to the canopy in forest process models.

KEYWORDS: ACCLIMATION, BOREAL FOREST ECOSYSTEMS, CANOPY, CARBON GAIN, GROWTH, LEAF LIFE-SPAN, MAINTENANCE RESPIRATION, PHOTOSYNTHESIS- NITROGEN RELATIONS, PLANT, TEMPERATURE

1554

Mitchell, R.A.C., C.R. Black, S. Burkart, J.I. Burke, A. Donnelly, L. de Temmerman, A. Fangmeier, B.J. Mulholland, J.C. Theobald, and M. van Oijen. 1999. Photosynthetic responses in spring wheat grown under elevated CO₂ concentrations and stress conditions in the European, multiple-site experiment 'ESPACE-wheat'. *European Journal of Agronomy* 10(3-4):205-214.

Spring wheat cv. Minaret crop stands were grown under ambient and elevated CO₂ concentrations at seven sites in Germany, Ireland, the UK, Belgium and the Netherlands. Six of the sites used open-top chambers and one used a controlled environment mimicking field conditions. The

effect of elevated CO₂ for a range of N application regimes, O₃ concentrations, and growth temperatures on flag leaf photosynthesis was studied. Before anthesis, flag leaf photosynthesis was stimulated about 50% by 650 compared with 350 μmol mol⁻¹ CO₂ at all sites, regardless of other treatments. Furthermore, there was no evidence of a decrease in photosynthetic capacity of flag leaves due to growth at elevated CO₂ before anthesis, even for low N treatments. However, photosynthetic capacity, particularly carboxylation capacity, of flag leaves was usually decreased by growth at elevated CO₂ after anthesis, especially in low N treatments. Acclimation of photosynthesis to elevated CO₂ therefore appears to occur only slowly, consistent with a response to changes in sink-source relationships, rather than a direct response. Effect of elevated CO₂ on stomatal conductance was much more variable between sites and treatments, but on average was decreased by similar to 10% at 650 compared with 350 μmol mol⁻¹ CO₂. Carboxylation capacity of flag leaves was decreased by growth at elevated O₃ both before and after anthesis, regardless of CO₂ concentration. (C) 1999 Elsevier Science B.V. All rights reserved.

KEYWORDS: PLANTS, PRODUCTIVITY, PROTEINS, RISING ATMOSPHERIC CO₂, TEMPERATURE

1555

Mitchell, R.A.C., C.L. Gibbard, V.J. Mitchell, and D.W. Lawlor. 1996. Effects of shading in different developmental phases on biomass and grain yield of winter wheat at ambient and elevated CO₂. *Plant, Cell and Environment* 19(5):615-621.

Winter wheat (*Triticum aestivum* cv. Mercia) was grown in a controlled-environment facility under simulated field conditions at ambient (360 μmol mol⁻¹) and elevated (690 μmol mol⁻¹) CO₂ concentrations. Some of the plants were shaded to mimic cloudy conditions during three periods of about 20 d duration between terminal spikelet and start of grain-fill, giving 16 treatments in all. Elevated CO₂ increased grain yield by about 20%, while shading in any period decreased yield, with the greatest effect in the last period, encompassing anthesis. No interactions between these effects were significant for grain yield, but there were complex interactions for mean grain size. Observed effects of shading and elevated CO₂ on biomass production were well predicted by a simulation model. Observed effects of treatments on yield could be related to effects on biomass using a simple model which assumes that yield is proportional to biomass production, with coefficients of 0.42 (g grain yield g⁻¹ biomass) for the first two periods and 0.74 for the last period. Wheat models should therefore include developmental changes in sensitivity of yield to biomass production, but biomass changes induced by different CO₂ concentrations or light environments can be treated as having equivalent effects on grain yield.

KEYWORDS: CROPS, GROWTH, MODEL, NITROGEN, NUMBER, SOLAR RADIATION, SPRING WHEAT, TEMPERATURE

1556

Mitchell, R.A.C., D.W. Lawlor, V.J. Mitchell, C.L. Gibbard, E.M. White, and J.R. Porter. 1995. Effects of elevated CO₂ concentration and increased temperature on winter-wheat - test of arcwheat1 simulation-model. *Plant, Cell and Environment* 18(7):736-748.

Winter wheat (*Triticum aestivum* L., cv. Mercia) was grown in a controlled-environment facility at two CO₂ concentrations (targets 350 and 700 μmol mol⁻¹), and two temperature regimes (tracking ambient and ambient + 4 degrees C). Observations of phenology, canopy growth, dry matter production and grain yield were used to test the ARCWHEAT1 simulation model. Dry-matter production and grain yield were increased at elevated CO₂ concentration (27 and 39%, respectively) and reduced at increased temperature (-16 and -35%, respectively). ARCWHEAT1 substantially underestimated canopy

growth for all treatments. However, differences in the facility environment from field conditions over the winter, indicated by the unusually rapid canopy growth observed in this period, meant that empirical model relationships were being used outside the conditions for which they were developed. The ARCWHEAT1 productivity submodel, given observed green area indices as inputs, overestimated the effect of CO₂ on productivity. An alternative, more mechanistic submodel of productivity, based on the SUCROS87 and Farquhar and von Caemmerer models, simulated observed crop biomass very closely. When these productivity simulations were inputted into the ARCWHEAT1 partitioning and grain-fill submodels, grain yield was predicted poorly, mainly as a result of the assumption that the number of grains is proportional to total growth during a short preanthesis phase. While yield was not correlated with growth in this phase, it was correlated with growth in longer preanthesis phases, indicating that ARCWHEAT1 could be improved by taking into account the contribution of earlier growth in determining yield.

KEYWORDS: CROPS, GENES, GROWTH, NUMBER, PHOTOSYNTHESIS, RBCS, SOLAR RADIATION, SPRING WHEAT, YIELD

1557

Mitchell, R.A.C., V.J. Mitchell, S.P. Driscoll, J. Franklin, and D.W. Lawlor. 1993. Effects of increased CO₂ concentration and temperature on growth and yield of winter-wheat at 2 levels of nitrogen application. *Plant, Cell and Environment* 16(5):521-529.

Winter wheat (*Triticum aestivum* L., cv. Mercia) was grown in chambers under light and temperature conditions similar to the UK field environment for the 1990/1991 growing season at two levels each of atmospheric CO₂ concentration (seasonal means: 361 and 692 μmol mol⁻¹), temperature (tracking ambient and ambient +4-degrees-C) and nitrogen application (equivalent to 87 and 489 kg ha⁻¹ total N applied). Total dry matter productivity through the season, the maximum number of shoots and final ear number were stimulated by CO₂ enrichment at both levels of the temperature and N treatments. At high N, there was a CO₂-induced stimulation of grain yield (+15%) similar to that for total crop dry mass (+12%), and there was no significant interaction with temperature. This contrasts with other studies, where positive interactions between the effects of increases in temperature and CO₂ have been found. Temperature had a direct, negative effect on yield at both levels of the N and CO₂ treatments. This could be explained by the temperature-dependent shortening of the phenological stages, and therefore, the time available for accumulating resources for grain formation. At high N, there was also a reduction in grain set at ambient +4-degrees-C temperature, but the overall negative effect of warmer temperature was greater on the number of grains (-37%) than on yield (-18%), due to a compensating increase in average grain mass. At low N, despite increasing total crop dry mass and the number of ears, elevated CO₂ did not increase grain yield and caused a significant decrease under ambient temperature conditions. This can be explained in terms of a stimulation of early vegetative growth by CO₂ enrichment leading to a reduction in the amount of N available later for the formation and filling of grain.

KEYWORDS: CARBON DIOXIDE, DRY-MATTER, ENRICHMENT, PHOTOSYNTHESIS, PLANT GROWTH, PRODUCTIVITY, RADIATION, RESPIRATION, SEED YIELD, STRESS

1558

Mitchell, R.J., G.B. Runion, S.A. Prior, H.H. Rogers, J.S. Amthor, and F.P. Henning. 1995. Effects of nitrogen on pinus-palustris foliar respiratory responses to elevated atmospheric CO₂ concentration. *Journal of Experimental Botany* 46(291):1561-1567.

Indirect effects of atmospheric CO₂ concentration [CO₂], on longleaf pine (*Pinus palustris* Mill.) foliage respiration were studied by growing trees in a factorial arrangement of low and high [CO₂] (369 and 729 $\mu\text{mol CO}_2 \text{ mol}^{-1}$) and low and high N (40 and 400 $\text{kg ha}^{-1} \text{ yr}^{-1}$). Direct effects of [CO₂] on leaf respiration were tested by measuring respiration rates of foliage from all treatments at two CO₂ levels (360 and 720 $\mu\text{mol CO}_2 \text{ mol}^{-1}$) at the time of measurement. Elevated CO₂ did not directly or indirectly affect leaf respiration when expressed on a leaf area or mass basis, but a significant increase in respiration per unit leaf N was observed in trees grown in elevated [CO₂] (indirect response to elevated [CO₂]). The lack of a [CO₂] effect on respiration, when analysed on an area or mass basis, may have resulted from combined effects of [CO₂] on factors that increase respiration (e.g. greater availability of non-structural carbohydrates stimulating growth and carbon export from leaves) and on factors that decrease respiration (e.g. lower N concentration leading to lower construction costs and maintenance requirements). Thus, [CO₂] affected factors that influence respiration, but in opposing ways.

KEYWORDS: CARBOHYDRATE STATUS, CARBON DIOXIDE, CASTANEA-SATIVA MILL, CLIMATE CHANGE, CONSTRUCTION COST, DARK RESPIRATION, GROWTH, LEAF RESPIRATION, PLANT RESPIRATION, TREE SEEDLINGS

1559

Mitra, A., P.S. Bhattacharya, S. Dey, S.K. Sawarkar, and B.C. Bhattacharyya. 1998. Photoautotrophic in vitro culture of *Chrysanthemum* under CO₂ enrichment. *Biotechnology Techniques* 12(4):335-337.

Photoautotrophic culture of *Chrysanthemum* was established under CO₂ enrichment (2% v/v). The shoot length and number of leaves were almost equal (2.7 cm and 14 respectively) both under photoautotrophic and photomixotrophic cultures, recorded after four weeks of incubation. Similarly, average dry mass of the plantlets were comparable (31 and 28 mg respectively) under both conditions. The number of branches and internode length which influence the number of propagule potential for mass propagation, were also identical. Nevertheless, photoautotrophic cultivation minimized the risk of contamination in cultures, which in turn will reduce the production cost.

KEYWORDS: INVITRO

1560

Mitra, A., S. Dey, and S.K. Sawarkar. 1998. Photoautotrophic in vitro multiplication of the orchid *Dendrobium* under CO₂ enrichment. *Biologia Plantarum* 41(1):145-148.

An attempt to reduce the production cost on tissue cultured plants, photoautotrophic culture of a high value orchid *Dendrobium* was established under CO₂-enriched conditions. The shoot length and the number of leaves were almost equal in plantlets grown on medium with 2% sucrose or without sucrose and under normal or enhanced (40 $\mu\text{mol m}^{-2} \text{ s}^{-1}$) CO₂ concentration, whereas the fresh and dry masses were higher in cultures grown in sucrose containing media or under CO₂ enrichment. Development of roots was observed only on media without sucrose, but CO₂ enrichment did not have significant effects on in vitro rootings.

KEYWORDS: CULTURE, GROWTH, INVITRO

1561

Mitsuda, H. 1999. Toward solutions for food crisis in the 21st century - From basic research to development of innovative food technologies. *Proceedings of the Japan Academy Series B-Physical and Biological Sciences* 75(8):246-253.

The population explosion in the 21st century will have a severe impact on the problems associated with food supply and the environment. Even at present, the shortage of food protein resources is an acute problem. Effective countermeasures to cope with the ever worsening shortage of protein resources in the next century are absolutely essential. We have developed methods to produce and isolate single cell proteins in an ample yield. We have also found that among food grains rice has the highest protein content, and have found that the protein in the grain is present in discrete particles, for which we coined the name "protein bodies". Rice protein has a relatively good balance of essential amino acids, and hence a relatively high nutritional value. We were able to increase the nutritional value further by fortifying it with L-lysine by a novel soaking method. New methods of food preservation will be important to cope with the 21st century food problems, because a large amount of food is lost either on the farm or during storage, to microorganisms, rodents and insects. We developed the carbon dioxide exchange method (CEM), in which food is stored under CO₂ in hermetically sealed containers (called Hibernation Rice), CO₂ is reversibly adsorbed to, and desorbed from the amino groups of food proteins. We also developed underwater and underground food storage methods earlier (1967-72), to take advantage of constant low temperatures in these conditions. Based on these studies, large scale storage methods in 200 kg steel drums in CO₂ have been developed on an industrial scale which is operated on a commercial base. Methylbromide destroys the ozone layer, and will be banned completely from use for food presentation or any other purposes. Storage under CO₂ is far superior to methylbromide because CO₂ completely eliminates the rice weevil and other insects, has no toxicity or public health problems, and is economical. CO₂ is a very effective synergist when used with the pasteurization gas, ozone, to sterilize foods against the virulent pathogenic strain of *E. coli*, O-157 and black pepper which are known to be contaminated with bacteria. The use of CO₂ may add to an already high production of CO₂ from other sources, such as combustion of fossil fuels. Effective measures to prevent leakage of CO₂ are needed. We are striving for an innovative idea to prevent the escape of CO₂ and the consequential warming of the earth.

1562

Miyachi, S., J. Burger, K. Kotzabasis, J. Thielmann, and H. Senger. 1996. Photosynthetic characteristics of three strains of cyanobacteria grown under low- or high-CO₂ conditions. *Zeitschrift Fur Naturforschung C-A Journal of Biosciences* 51(1-2):40-46.

Quantum requirements of photosynthetic oxygen evolution at 679 nm, fluorescence emission spectra at liquid nitrogen temperature (77 K) and fluorescence induction kinetics in the presence of DCMU, were measured in the cyanobacteria *Anabaena variabilis* M3, *Anabaena variabilis* ATCC 29413 and *Anacystis nidulans* R2, each grown under low- or high-CO₂ conditions. Low- CO₂ grown cells of the cyanobacteria showed a higher quantum requirement of photosynthetic oxygen evolution and a higher ratio of F-710-740 to F-680-700 fluorescence and a lower variable fluorescence in the presence of DCMU than high-CO₂ grown cells. These findings indicate a change in excitation energy distribution in favour of photosystem I. The result might be an enhancement in ATP formation caused by cyclic electron flow which in turn provokes dissolved inorganic carbon (DIG) accumulation in these low-CO₂ grown cells.

KEYWORDS: ANACYSTIS-NIDULANS, CHLOROPHYLL FLUORESCENCE, CHLOROPLASTS, CO₂ CONCENTRATION, FIXATION, INDUCTION, INORGANIC CARBON, LIGHT, PHOTOSYSTEM- 2, SYSTEM

1563

Miyashita, Y., Y. Kitaya, C. Kubota, and T. Kozai. 1996.

Photoautotrophic growth of potato plantlets as affected by explant leaf area, fresh weight and stem length. *Scientia Horticulturae* 65(2-3):199-202.

Photoautotrophic growth in vitro of potato (*Solanum tuberosum* L. cv. Benimaru) explants varied with their initial leaf area and stem length. Photoautotrophic growth was much greater in leafy than in leafless explants. Variability in photoautotrophic growth was smallest in the explants with the greatest leaf area. The results indicated that use of explants with a large leaf area is important to maximize photoautotrophic growth and to minimize variation in photoautotrophic growth of explants in vitro.

1564

Mjwara, J.M., C.E.J. Botha, and S.E. Radloff. 1996. Photosynthesis, growth and nutrient changes in non-nodulated *Phaseolus vulgaris* grown under atmospheric and elevated carbon dioxide conditions. *Physiologia Plantarum* 97(4):754-763.

The response of *Phaseolus vulgaris* L. cv. Contender grown under controlled environment at either ambient or elevated (360 and 700 $\mu\text{mol mol}^{-1}$, respectively) CO_2 concentrations ($[\text{CO}_2]$), was monitored from 10 days after germination (DAG) until the onset of senescence. Elevated CO_2 had a pronounced effect on total plant height (TPH), leaf area (LA), leaf dry weight (LD), total plant biomass (TB) accumulation and specific leaf area (SLA). All of these were significantly increased under elevated carbon dioxide with the exception of SLA which was significantly reduced. Other than high initial growth rates in CO_2 -enriched plants, relative growth rates remained relatively unchanged throughout the growth period. While the trends in growth parameters were clearly different between $[\text{CO}_2]$, some physiological processes were largely transient, in particular, net assimilation rate (NAR) and foliar nutrient concentrations of N, Mg and Cu. CO_2 enrichment significantly increased NAR, but from 20 DAG, a steady decline to almost similar levels to those measured in plants grown under ambient CO_2 occurred. A similar trend was observed for leaf N content where the loss of leaf nitrogen in CO_2 -enriched plants after 20 DAG, was significantly greater than that observed for ambient- CO_2 plants. Under enhanced CO_2 , the foliar concentrations of K and Mn were increased significantly whilst P, Ca, Fe and Zn were reduced significantly. Changes in Mg and Cu concentrations were insignificant. In addition, high CO_2 grown plants exhibited a pronounced leaf discoloration or chlorosis, coupled with a significant reduction in leaf longevity.

KEYWORDS: ACCLIMATION, CO_2 - ENRICHMENT, LIGHT, MINERAL NUTRITION, NITROGEN, PLANTS, SEEDLINGS, TEMPERATURE, TOMATO, WATER-USE EFFICIENCY

1565

Mo, G., D. Nie, M.B. Kirkham, H. He, L.K. Ballou, F.W. Caldwell, and E.T. Kanemasu. 1992. Root and shoot weight in a tallgrass prairie under elevated carbon-dioxide. *Environmental and Experimental Botany* 32(3):193-201.

The atmospheric concentration of carbon dioxide (CO_2) is increasing and knowing how this will affect native vegetation is important. The objective of this study was to determine the effect of elevated CO_2 on root growth in a tallgrass prairie kept at a high water level (73 cm of water in a 200 cm soil profile) and a low water level (66 cm of water in 200 cm). Sixteen cylindrical plastic chambers were placed on the prairie to maintain two levels of CO_2 (ambient or twice ambient). At the end of two seasons' exposure to the different treatments, dry weight and length of roots in the 0-40 cm depth were determined. Shoot growth also was measured to determine shoot: root ratios. The CO_2 and water treatments had no significant effect on root dry weight in the 0-40 cm depth. In the

0-10 cm depth, doubled CO_2 reduced dry weight and length of roots of plants grown under the high water level by 47 and 31 %, respectively. Warm-season, C4 grasses had the highest shoot dry weight, which was greatest under the high water, ambient CO_2 treatment. The shoot: root ratio did not change with treatment.

KEYWORDS: C-3, CO_2 , COMMUNITIES, ENRICHMENT, GROWTH, RESPONSES, SOIL, WATER-USE, YIELD

1566

Mohanraju, R., B.S. Rajagopal, and L. Daniels. 1997. Isolation and characterization of a methanogenic bacterium from mangrove sediments. *Journal of Marine Biotechnology* 5(2-3):147-152.

A methanogenic bacterium was enriched with trimethylamine and isolated from mangrove sediments. The isolate was a non-spore-forming regular to slightly irregular coccus (0.4-1 mm in diameter). The isolate required sodium chloride for growth with maximal methanogenesis at 420 mM NaCl at 30 degrees C. The optimal growth temperature was 30-35 degrees C with maximal methane production at 30 degrees C. The maximum growth rate was between pH 6.6 and 7.2 with maximum methane production at pH 6.8. The growth requirement of sulfide was 10-15 mM with maximum methane production at 10 mM at 30 degrees C. Mono-, di-, and trimethylamine or methanol were substrates for the methanogen; sodium acetate and H-2: CO_2 were not. The DNA base content is consistent with the type descriptions of *Methanococoides methylutens*, a methylotrophic methanogen isolated from submarine sediments. The isolate was found to utilize methylamines that are found in mangroves without having to compete with sulfate-reducing bacteria for H-2.

KEYWORDS: BETAINE, CHOLINE, CO-CULTURE, METABOLISM, METHANOSARCINA-BARKERI, METHYLATED AMINES, SP-NOV, SULFATE REDUCTION, TRIMETHYLAMINE

1567

Mohapatra, P.K. 1990. CO_2 enrichment and physiology of inflorescence development in wheat. *Photosynthetica* 24(1):9-15.

1568

Monje, O., and B. Bugbee. 1998. Adaptation to high CO_2 concentration in an optimal environment: radiation capture, canopy quantum yield and carbon use efficiency. *Plant, Cell and Environment* 21(3):315-324.

The effect of elevated $[\text{CO}_2]$ on wheat (*Triticum aestivum* L, Veery 10) productivity was examined by analysing radiation capture, canopy quantum yield, canopy carbon use efficiency, harvest index and daily C gain. Canopies were grown at either 330 or 1200 $\mu\text{mol mol}^{-1}$ $[\text{CO}_2]$ in controlled environments, where root and shoot C fluxes were monitored continuously from emergence to harvest. A rapidly circulating hydroponic solution supplied nutrients, water and root zone oxygen. At harvest, dry mass predicted from gas exchange data was 102.8 +/- 4.7% of the observed dry mass in six trials. Neither radiation capture efficiency nor carbon use efficiency were affected by elevated $[\text{CO}_2]$, but yield increased by 13% due to a sustained increase in canopy quantum yield. CO_2 enrichment increased root mass, tiller number and seed mass. Harvest index and chlorophyll concentration were unchanged, but CO_2 enrichment increased average life cycle net photosynthesis (13%, $P < 0.05$) and root respiration (24%, $P < 0.05$). These data indicate that plant communities adapt to CO_2 enrichment through changes in C allocation. Elevated $[\text{CO}_2]$ increases sink strength in optimal environments, resulting in sustained increases in photosynthetic capacity, canopy quantum yield and daily C gain

throughout the life cycle.

KEYWORDS: DARK RESPIRATION, DIOXIDE CONCENTRATION, ELEVATED CO₂, LEAVES, PHOTOSYNTHETIC ACCLIMATION, PHYSIOLOGY, RESPONSES, SOURCE-SINK RELATIONS, TEMPERATURE, WHEAT

1569

Monz, C.A., H.W. Hunt, F.B. Reeves, and E.T. Elliott. 1994. The response of mycorrhizal colonization to elevated CO₂ and climate-change in *Paspopyrum-smithii* and *bouteloua-gracilis*. *Plant and Soil* 165(1):75-80.

Large intact soil cores of nearly pure stands of *Paspopyrum smithii* (western wheatgrass, C-3) and *Bouteloua gracilis* (blue grama, C-4) were extracted from the Central Plains Experimental Range in northeastern Colorado, USA and transferred to controlled environment chambers. Cores were exposed to a variety of water, temperature and CO₂ regimes for a total of four annual growth cycles. Root subsamples were harvested after the completion of the second and fourth growth cycles at a time corresponding to late winter, and were examined microscopically for the presence of mycorrhizae. After two growth cycles in the growth chambers, 54% of the root length was colonized in *P. smithii*, compared to 35% in blue grama. Field control plants had significantly lower colonization. Elevation of CO₂ increased mycorrhizal colonization in *B. gracilis* by 46% but had no effect in *P. smithii*. Temperatures 4 degrees C higher than normal decreased colonization in *P. smithii* by 15%. Increased annual precipitation decreased colonization in both species. Simulated climate change conditions of elevated CO₂, elevated temperature and lowered precipitation decreased colonization in *P. smithii* but had less effect on *B. gracilis*. After four growth cycles in *P. smithii*, trends of treatments remained similar, but overall colonization rate decreased.

KEYWORDS: C-3, ECOSYSTEMS, GROWTH

1570

Mooney, H.A. 1991. Biological response to climate change - an agenda for research. *Ecological Applications* 1(2):112-117.

Our knowledge of the structure and functioning of terrestrial ecosystems on a global scale is not developed to a sufficient degree to understand - much less predict - the consequences of climate change either on the systems themselves or on subsequent atmospheric interactions. In many regards we have lagged behind the atmospheric scientists, and to a certain degree the oceanographers, in establishing a global understanding of the dynamics of our respective systems. This is due in part to the inherently greater complexity of biotic systems, but also to the lack of appropriate tools to measure regional biotic processes. These tools are now becoming available and with them a better understanding of terrestrial and atmospheric interactions. Even as these capabilities become a reality we must be realistic in recognizing that we have so far to go along the road to understanding that useful predictive capacity may elude us for a long time to come. What we now need to do is act on the recommendations that have been emerging over the past few years and develop a global program to document more precisely the distribution, structure, and quantity of the earth's biotic systems, their principal functional properties, and - most difficult of all - their changing nature. In order to do this we will have to: (1) perfect some of the emerging new tools for assessing these properties, (2) fill some of the gaps in our knowledge about the relevant processes, and (3) establish an international network of long-term observations and large-scale ecosystem manipulations. We have been aware of these needs and shortcomings for some time and we must move from plans to concerted international action.

KEYWORDS: ELEVATED CO₂, PLANTS

1571

Mooney, H.A., B.G. Drake, R.J. Luxmoore, W.C. Oechel, and L.F. Pitelka. 1991. Predicting ecosystem responses to elevated CO₂ concentrations. *BioScience* 41(2):96-104.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CLIMATE CHANGE, ESTUARINE MARSH, GROWTH-RESPONSES, LONG-TERM EXPOSURE, NUTRIENT-UPTAKE, PHOSPHORUS DEFICIENCY, PHOTOSYNTHETIC INHIBITION, PINUS-RADIATA, WATER-STRESS

1572

Mooney, H.A., and G.W. Koch. 1994. The impact of rising CO₂ concentrations on the terrestrial biosphere. *Ambio* 23(1):74-76.

Large advances have been made in linking terrestrial biospheric and atmospheric processes in real time. Further, it is now possible to model the potential response of the Earth's primary productivity to the changing climate and to changes in atmospheric CO₂ concentration. We still have limited information, however, on the total responses of ecosystems to enhanced CO₂ because of the complex web of possible interactions. What is needed are experiments on whole ecosystems under enhanced CO₂ in which all of the potential interactions and feedbacks can be monitored, including plant-microbe, plant-herbivore, and plant-atmosphere interactions. A global network of experiments in the major biomes of the world is being developed within the International Geosphere-Biosphere Programme (IGBP) to resolve questions related to the implications of a changed pattern of biomass distribution in the biosphere.

KEYWORDS: CARBON DIOXIDE, COMMUNITIES, ECOSYSTEMS, ELEVATED CO₂, GROWTH, RESPONSES

1573

Moore, B.D., S.H. Cheng, J. Rice, and J.R. Seemann. 1998. Sucrose cycling, Rubisco expression, and prediction of photosynthetic acclimation to elevated atmospheric CO₂. *Plant, Cell and Environment* 21(9):905-915.

Photosynthetic acclimation to elevated CO₂ cannot presently be predicted due to our limited understanding of the molecular mechanisms and metabolic signals that regulate photosynthetic gene expression. We have examined acclimation by comparing changes in the leaf content of RuBP carboxylase/oxygenase (Rubisco) with changes in the transcripts of Rubisco subunit genes and with leaf carbohydrate metabolism. When grown at 1000 mm³ dm⁻³ CO₂, 12 of 16 crop species at peak vegetative growth had a 15-44% decrease in leaf Rubisco protein, but with no specific association with changes in transcript levels measured at midday. Species with only modest reductions in Rubisco content (10-20%) often had a large reduction in Rubisco small subunit gene mRNAs (> 30%), with no reduction in large subunit gene mRNAs. However, species with a very large reduction in Rubisco content generally had only small reductions in transcript mRNAs. Photosynthetic acclimation also was not specifically associated with a change in the level of any particular carbohydrate measured at midday. However, a threshold relationship was found between the reduction in Rubisco content at high CO₂ and absolute levels of soluble acid invertase activity measured in plants grown at ambient or high CO₂. This relationship was valid for 15 of the 16 species examined. There also occurred a similar, albeit less robust, threshold relationship between the leaf hexose/sucrose ratio at high CO₂ and a reduced photosynthetic capacity greater than or equal to 20%. These data indicate that carbohydrate repression of photosynthetic gene expression at elevated CO₂ may involve leaf

sucrose cycling through acid invertase and hexokinase.

KEYWORDS: CARBON CATABOLITE REPRESSION, CARBOXYLASE SMALL-SUBUNIT, GAS-EXCHANGE, GENE-EXPRESSION, GROWTH, HIGHER-PLANTS, LEAF DEVELOPMENT, MECHANISM, POTATO-TUBERS, RIBULOSE-1,5-BISPHOSPHATE CARBOXYLASE

1574

Moore, B.D., D.E. Palmquist, and J.R. Seemann. 1997. Influence of plant growth at high CO₂ concentrations on leaf content of ribulose-1,5-bisphosphate carboxylase/oxygenase and intracellular distribution of soluble carbohydrates in tobacco, snapdragon, and parsley. *Plant Physiology* 115(1):241-248.

We have examined the possible role of leaf cytosolic hexoses and the expression of mannitol metabolism as mechanisms that may affect the repression of photosynthetic capacity when plants are grown at 1000 versus 380 $\mu\text{L L}^{-1}$ CO₂. In plants grown at high CO₂, leaf ribulose-1,5-bisphosphate carboxylase/oxygenase content declined by greater than or equal to 20% in tobacco (*Nicotiana glauca*) but was not affected in the mannitol-producing species snapdragon (*Antirrhinum majus*) and parsley (*Petroselinum hortense*). In the three species mesophyll glucose and fructose at midday occurred almost entirely in the vacuole (>99%), irrespective of growth CO₂ levels. The estimated cytosolic concentrations of glucose and fructose were less than or equal to 100 μM . In the three species grown at high CO₂, total leaf carbohydrates increased 60 to 100%, but mannitol metabolism did not function as an overflow mechanism for the increased accumulation of carbohydrate. In both snapdragon and parsley grown at ambient or high CO₂, mannitol occurred in the chloroplast and cytosol at estimated midday concentrations of 0.1 M or more each. The compartmentation of leaf hexoses and the metabolism of alternate carbohydrates are further considered in relation to photosynthetic acclimation to high levels of CO₂.

KEYWORDS: CARBON FLOW, CELERY LEAVES, ELEVATED CO₂, GAS-EXCHANGE, MANNITOL, METABOLITE LEVELS, PHOTOSYNTHESIS, SPINACH LEAVES, SUCROSE ACCUMULATION, TRANSGENIC TOBACCO

1575

Moore, T.R., N.T. Roulet, and J.M. Waddington. 1998. Uncertainty in predicting the effect of climatic change on the carbon cycling of Canadian peatlands. *Climatic Change* 40(2):229-245.

Northern peatlands play an important role globally in the cycling of C, through the exchange of CO₂ with the atmosphere, the emission of CH₄, the production and export of dissolved organic carbon (DOC) and the storage of C. Under 2 x CO₂ GCM scenarios, most Canadian peatlands will be exposed to increases in mean annual temperature ranging between 2 and 6 degrees C and increases in mean annual precipitation of 0 to 15 %, with the most pronounced changes occurring during the winter. The increase in CO₂ uptake by plants, through warmer temperatures and elevated atmospheric CO₂, is likely to be offset by increased soil respiration rates in response to warmer soils and lowered water tables. CH₄ emissions are likely to decrease in most peatlands because of lowered water tables, except where the peat surface adjusts to fluctuating water tables, and in permafrost, where the collapse of dry plateau and palsas will lead to increased CH₄ emission. There likely will be little change in DOC production, but DOC export to water bodies will decrease as runoff decreases. The storage of C in peatlands is sensitive to all C cycle components and is difficult to predict. The challenge is to develop quantitative models capable of making these predictions for different peatlands. We present some qualitative responses, with levels of uncertainty. There will be, however, as much variation in response to climatic change within a peatland as there will be among peatland

regions.

KEYWORDS: ATMOSPHERE, BALANCE, CO₂ FLUXES, CONTINENTAL WESTERN CANADA, DISCONTINUOUS PERMAFROST, DISSOLVED ORGANIC-CARBON, METHANE EMISSIONS, POOR FEN, TEMPORAL VARIABILITY, WETLANDS

1576

Moore, T.R., J.A. Trofymow, B. Taylor, C. Prescott, C. Camire, L. Duschene, J. Fyles, L. Kozak, M. Kranabetter, I. Morrison, M. Siltanen, S. Smith, B. Titus, S. Visser, R. Wein, and S. Zoltai. 1999. Litter decomposition rates in Canadian forests. *Global Change Biology* 5(1):75-82.

The effect of litter quality and climate on the rate of decomposition of plant tissues was examined by the measurement of mass remaining after 3 years' exposure of 11 litter types placed at 18 forest sites across Canada. Amongst sites, mass remaining was strongly related to mean annual temperature and precipitation and amongst litter types the ratio of Klason lignin to nitrogen in the initial tissue was the most important litter quality variable. When combined into a multiple regression, mean annual temperature, mean annual precipitation and Klason lignin:nitrogen ratio explained 73% of the variance in mass remaining for all sites and tissues. Using three doubled CO₂ GCM climate change scenarios for four Canadian regions, these relationships were used to predict increases in decomposition rate of 4-7% of contemporary rates (based on mass remaining after 3 years), because of increased temperature and precipitation. This increase may be partially offset by evidence that plants growing under elevated atmospheric CO₂ concentrations produce litter with high lignin:nitrogen ratios which slows the rate of decomposition, but this change will be small compared to the increased rate of decomposition derived from climatic changes.

KEYWORDS: CARBON DIOXIDE, CLIMATE CHANGE, DECAY-RATES, ELEVATED ATMOSPHERIC CO₂, LEAF LITTER, LIGNIN CONTROL, MASS-LOSS, NUTRIENT-UP TAKE, TERM DECOMPOSITION, TERRESTRIAL ECOSYSTEMS

1577

Moorhead, D.L., and A.E. Linkins. 1997. Elevated CO₂ alters belowground exoenzyme activities in tussock tundra. *Plant and Soil* 189(2):321-329.

A three-year exposure to a CO₂ concentration of 680 $\mu\text{mol mol}^{-1}$ altered the enzymic characteristics of root surfaces, associated ectomycorrhizae, and in soils surrounding roots in a tussock tundra ecosystem of north Alaska, USA. At elevated CO₂, phosphatase activity was higher on *Eriophorum vaginatum* root surfaces, ectomycorrhizal rhizomorphs and mantles associated with *Betula nana* roots, and in Oe and Oi soil horizons associated with plant roots. Also, endocellulase and exocellulase activities at elevated CO₂ were higher in ectomycorrhizal rhizomorphs and lower in Oe and Oi soil horizons associated with roots. These results suggest that arctic plants respond to raised CO₂ by increasing activities associated with nutrient acquisition, e.g. higher phosphatase activities on surfaces of roots and ectomycorrhizae, and greater cellulase activity in ectomycorrhizae. Changes in enzyme activities of surrounding soils are consistent with an increase in carbon exudation from plant roots, which would be expected to inhibit cellulase activities and stimulate phosphatase activities of soil microflora. These data were used to modify existing simulation models describing tussock phosphatase activities and litter decay. Model projections suggest that observed increases in phosphatase activities at 680 $\mu\text{mol mol}^{-1}$ CO₂, could augment total annual phosphorus release within tussocks by more than 40%, at present levels of root and ectomycorrhizae biomass. This includes a nearly three- fold increase in potential phosphatase activity of *E. vaginatum* roots, per unit of surface area. Observed

reductions in cellulase activities could diminish cellulose turnover by 45% in soils within rooting zones, which could substantially increase mineral nitrogen availability in soils due to lowered microbial immobilization.

KEYWORDS: ATMOSPHERIC CO₂, BACTERIAL-POPULATIONS, CARBON DIOXIDE, CELLULASE ACTIVITY, DECOMPOSING LEAF LITTER, ERIOPHORUM VAGINATUM, FREEZE-THAW CYCLES, MICROBIAL ACTIVITY, MODELING SYNTHESIS, PHOSPHATASE-ACTIVITIES

1578

Moorhead, D.L., R.L. Sinsabaugh, A.E. Linkins, and J.F. Reynolds. 1996. Decomposition processes: Modelling approaches and applications. *The Science of the Total Environment* 183(1-2):137-149.

Decomposition is a fundamental ecosystem process, strongly influencing ecosystem dynamics through the release of organically bound nutrients. Decomposition is also a complex phenomenon that can be modified by changes in the characteristics of the decaying materials or prevailing environmental conditions. For these reasons, the impacts of local, regional or global environmental changes on the quality and turnover of dead organic matter are of considerable interest. However, realistic limits to the complexity, as well as temporal and spatial scales, of experimental studies restrict their usefulness in extrapolating long-term or large-scale results of simultaneous environmental changes. Alternatively, many simulation models have been constructed to gain insight to potential impacts of anthropogenic activities. Because structure and approach determine the strengths and limitations of a model, they must be considered when applying one to a problem or otherwise interpreting model behaviour. There are two basically different types of models: (1) empirical models generally ignore underlying processes when describing system behaviour, while (2) mechanistic models reproduce system behaviour by simulating underlying processes. The former models are usually accurate within the range of conditions for which they are constructed but tend to be unreliable when extended beyond these limits. In contrast, application of a mechanistic model to novel conditions assumes only that the underlying mechanisms behave in a consistent manner. In this paper, we examine models developed at different levels of resolution to simulate various aspects of decomposition and nutrient cycling and how they have been used to assess potential impacts of environmental changes on terrestrial ecosystems.

KEYWORDS: BACTERIAL-POPULATIONS, CLIMATE CHANGE, ELEVATED ATMOSPHERIC CO₂, LIGNIN CONTROL, LITTER DECOMPOSITION, LONG-TERM RESPONSE, MODELING SYNTHESIS, ORGANIC-MATTER, TERRESTRIAL ECOSYSTEMS, TUSsock TUNDRA

1579

Morcuende, R., P. Perez, R. MartinezCarrasco, I.M. DelMolino, and L.S. DeLaPuente. 1996. Long- and short-term responses of leaf carbohydrate levels and photosynthesis to decreased sink demand in soybean. *Plant, Cell and Environment* 19(8):976-982.

Axillary buds and the apical portion of shoots of soybean [*Glycine max* (L.) Merr. cultivar Turchina] plants were trimmed to investigate long-term regulation of photosynthesis by sink demand at ambient CO₂ and 22 degrees C. Also, in intact and trimmed shoots, the CO₂ level was increased to 660 $\mu\text{mol mol}^{-1}$ and temperature was lowered to 5 degrees C to examine the superimposed short-term responses of photosynthesis to low sink demand. Under growth conditions, trimming the shoots increased leaf photosynthesis and the levels of sucrose, glucose-6-phosphate (G6P) and 3-phosphoglycerate (PGA), as well as the G6P/fructose-6-phosphate (F6P) and sucrose/starch ratios, while it decreased the level of starch and the triose-phosphate (glyceraldehyde 3-

phosphate and dihydroxyacetone phosphate, TP)/PGA ratio. Photosynthesis enhancement was accompanied by increased chlorophyll contents and ribulose-1,5-bisphosphate carboxylase oxygenase (Rubisco) activity. Sink removal consistently increased photosynthesis measured under a variety of conditions (growth CO₂ or a short-term change to 660 $\mu\text{mol mol}^{-1}$ CO₂; growth temperature or a short-term change to 5 degrees C), except when low temperature was combined with ambient CO₂; the increase in photosynthesis was higher under short-term elevated CO₂ than at ambient CO₂. In contrast with its effect at ambient CO₂, shoot trimming increased the levels of TP and ribulose-1,5-bisphosphate (RuBP) and the TP/PGA ratio under high-CO₂ conditions.

KEYWORDS: CARBON ASSIMILATION, CARBOXYLASE, ELEVATED CO₂, METABOLISM, PLANTS, RIBULOSE 1;5-BISPHOSPHATE, SPINACH LEAVES, SUCROSE PHOSPHATE SYNTHASE, TEMPERATURE, WHEAT

1580

Morgan, J.A., H.W. Hunt, C.A. Monz, and D.R. Lecain. 1994. Consequences of growth at 2 carbon-dioxide concentrations and 2 temperatures for leaf gas-exchange in *Pascopyrum smithii* (C-3) and *Bouteloua gracilis* (C-4). *Plant, Cell and Environment* 17(9):1023-1033.

Continually rising atmospheric CO₂ concentrations and possible climatic change may cause significant changes in plant communities. This study was undertaken to investigate gas exchange in two important grass species of the short-grass steppe, *Pascopyrum smithii* (western wheatgrass), C-3, and *Bouteloua gracilis* (blue grama), C4, grown at different CO₂ concentrations and temperatures. Intact soil cores containing each species were extracted from grasslands in north-eastern Colorado, USA, placed in growth chambers, and grown at combinations of two CO₂ concentrations (350 and 700 $\mu\text{mol mol}^{-1}$) and two temperature regimes (field average and elevated by 4 degrees C). Leaf gas exchange was measured during the second, third and fourth growth seasons. All plants exhibited higher leaf CO₂ assimilation rates (A) with increasing measurement CO₂ concentration, with greater responses being observed in the cool-season C-3 species *P. smithii*. Changes in the shape of intercellular CO₂ response curves of A for both species indicated photosynthetic acclimation to the different growth environments. The photosynthetic capacity of *P. smithii* leaves tended to be reduced in plants grown at high CO₂ concentrations, although A for plants grown and measured at 700 $\mu\text{mol mol}^{-1}$ CO₂ was 41% greater than that in plants grown and measured at 350 $\mu\text{mol mol}^{-1}$ CO₂. Low leaf N concentration may have contributed to photosynthetic acclimation to CO₂. A severe reduction in photosynthetic capacity was exhibited in *P. smithii* plants grown long-term at elevated temperatures. As a result, the potential response of photosynthesis to CO₂ enrichment was reduced in *P. smithii* plants grown long-term at the higher temperature.

KEYWORDS: ATMOSPHERIC CO₂ CONCENTRATIONS, ECOSYSTEMS, ELEVATED CO₂, ENRICHMENT, GRASS, PHOTOSYNTHETIC ACCLIMATION, PLANTS, PRAIRIE, PRODUCTIVITY, RESPONSES

1581

Morgan, J.A., W.G. Knight, L.M. Dudley, and H.W. Hunt. 1994. Enhanced root-system C-sink activity, water relations and aspects of nutrient acquisition in mycotrophic *Bouteloua gracilis* subjected to CO₂ enrichment. *Plant and Soil* 165(1):139-146.

In order to better elucidate fixed-C partitioning, nutrient acquisition and water relations of prairie grasses under elevated [CO₂], we grew the C-4 grass *Bouteloua gracilis* (H.B.K.) lag ex Steud. from seed in soil-packed, column- lysimeters in two growth chambers maintained at current

ambient [CO₂] (350 μ L L⁻¹) and twice enriched [CO₂] (700 μ L L⁻¹). Once established, plants were deficit irrigated; growth chamber conditions were maintained at day/night temperatures of 25/16 degrees C, relative humidities of 35%/90% and a 14-hour photoperiod to simulate summer conditions on the shortgrass steppe in eastern Colorado. After 11 weeks of growth, plants grown under CO₂ enrichment had produced 35% and 65% greater total and root biomass, respectively, and had twice the level of vesicular-arbuscular mycorrhizal (VAM) infection (19.8% versus 10.8%) as plants grown under current ambient [CO₂]. The CO₂-enriched plants also exhibited greater leaf water potentials and higher plant water use efficiencies. Plant N uptake was reduced by CO₂ enrichment, while P uptake appeared little influenced by CO₂ regime. Under the conditions of the experiment, CO₂ enrichment increased root biomass and VAM infection via stimulated growth and adjustments in C partitioning below-ground.

KEYWORDS: COMMUNITIES, ELEVATED CARBON-DIOXIDE, GROWTH, NITROGEN, PHOSPHORUS, PHOTOSYNTHESIS, PLANTS, QUERCUS-ALBA, SOIL, STRESS

1582

Morgan, J.A., D.R. LeCain, J.J. Read, H.W. Hunt, and W.G. Knight. 1998. Photosynthetic pathway and ontogeny affect water relations and the impact of CO₂ on *Bouteloua gracilis* (C-4) and *Pascopyrum smithii* (C-3). *Oecologia* 114(4):483-493.

The eastern Colorado shortgrass steppe is dominated by the C-4 grass, *Bouteloua gracilis*, but contains a mixture of C-3 grasses as well, including *Pascopyrum smithii*. Although the ecology of this region has been extensively studied, there is little information on how increasing atmospheric CO₂ will affect it. This growth chamber study investigated gas exchange, water relations, growth, and biomass and carbohydrate partitioning in *B. gracilis* and *P. gracilis* grown under present ambient and elevated CO₂ concentrations of 350 μ L L⁻¹ and 700 μ L L⁻¹, respectively, and two deficit irrigation regimes. The experiment was conducted in soil-packed columns planted to either species over a 2-month period under summer-like conditions and with no fertilizer additions. Our objective was to better understand how these species and the functional groups they represent will respond in future CO₂-enriched environments. Leaf CO₂ assimilation (A(n)), transpiration use efficiency (TUE, or A(n)/transpiration), plant growth, and whole-plant water use efficiency (WUE, or plant biomass production/water evapotranspired) of both species were greater at elevated CO₂, although responses were more pronounced for *P. smithii*. Elevated CO₂ enhanced photosynthesis, TUE, and growth in both species through higher soil water content (SWC) and leaf water potentials (Psi) and stimulation of photosynthesis. Consumptive water use was greater and TUE less for *P. smithii* than *B. gracilis* during early growth when soil water was more available. Declining SWC with time was associated with a steadily increased sequestering of total non-structural carbohydrates (TNCs), storage carbohydrates (primarily fructans for *P. Smithii*) and biomass in belowground organs of *P. smithii*, but not *B. gracilis*. The root:shoot ratio of *P. smithii* also increased at elevated CO₂ while the root:shoot ratio of *B. gracilis* was unresponsive to CO₂. These partitioning responses may be the consequence of different ontogenetic strategies of a cool-season and warm-season grass entering a warm, dry summer period; the cool-season *P. smithii* responds by sequestering TNCs belowground in preparation for summer dormancy, while resource partitioning of the warm-season *B. gracilis* remains unaltered. One consequence of greater partitioning of resources into *P. smithii* belowground organs in the present study was maintenance of higher Psi and A(n) rates. This, along with differences in photosynthetic pathway, may have accounted for the greater responsiveness of *P. smithii* to CO₂ enrichment compared to *B. gracilis*.

KEYWORDS: AGROPYRON-SMITHII, CARBON DIOXIDE, ELEVATED CO₂, GAS-EXCHANGE, GRASS, LEAF, NICHE

SEPARATION, PRAIRIE ECOSYSTEM, RESPONSES, USE EFFICIENCY

1583

Moriguchi, T., and R.J. Romani. 1995. Mitochondrial self-restoration as an index to the capacity of avocado fruit to sustain atmospheric stress at 2 climacteric states. *Journal of the American Society for Horticultural Science* 120(4):643-649.

A strong association is implicit between mitochondrial function and the energy demands of cells responding to stress. Yet, the dynamics of this organelle-cellular dependency have been difficult to resolve. This study examines a new diagnostic parameter namely, mitochondrial maintenance and self-restoration as exhibited by the course of respiratory functions (States 3 and 4 respiratory rates, respiratory control) of mitochondria extracted during and after exposure of intact 'Hass' avocado (*Persea americana*) fruit to different stress atmospheres: anoxia (100% N₂) or high (25% and 75%) CO₂ for varying durations. Comparisons are made with direct exposure of the mitochondria themselves to similar atmospheres. In general, exposure of the fruit to CO₂ rich atmospheres enhanced the capacity of their mitochondria to restore energy-linked functions whereas anoxia caused irreparable damage. The physiological (climacteric) state of the fruit also affected the stress capacity of the mitochondria contained therein, anaerobiosis being more harmful to mitochondria in riper fruit. In contrast to their effects *in vivo*, *in vitro* anoxia appeared to sustain mitochondrial energy-linked functions, whereas high CO₂ was clearly harmful. These and other observations are discussed in the context of mitochondrial self-restoration or homeostasis and its relevance to postharvest stress-atmosphere storage for purposes such as pathogen suppression or insect control.

1584

Morin, F., M. Andre, and T. Betsche. 1992. Growth-kinetics, carbohydrate, and leaf phosphate content of clover (*trifolium-subterraneum* L) after transfer to a high CO₂ atmosphere or to high light and ambient air. *Plant Physiology* 99(1):89-95.

Intact air-grown (photosynthetic photon flux density, 400 microeinsteins per square meter per second) clover plants (*Trifolium subterraneum* L.) were transferred to high CO₂ (4000 microliters CO₂ per liter; photosynthetic photon flux density, 400 microeinsteins per square meter per second) or to high light (340 microliters CO₂ per liter; photosynthetic photon flux density, 800 microeinsteins per square meter per second) to similarly stimulate photosynthetic net CO₂ uptake. The daily increment of net CO₂ uptake declined transiently in high CO₂, but not in high light, below the values in air/standard light. After about 3 days in high CO₂, the daily increment of net CO₂ uptake increased but did not reach the high light values. Nightly CO₂ release increased immediately in high light, whereas there was a 3-day lag phase in high CO₂. During this time, starch accumulated to a high level, and leaf deterioration was observed only in high CO₂. After 12 days, starch was two- to threefold higher in high CO₂ than in high light, whereas sucrose was similar. Leaf carbohydrates were determined during the first and fourth day in high CO₂. Starch increased rapidly throughout the day. Early in the day, sucrose was low and similar in high CO₂ and ambient air (same light). Later, sucrose increased considerably in high CO₂. The findings that (a) much more photosynthetic carbon was partitioned into the leaf starch pool in high CO₂ than in high light, although net CO₂ uptake was similar, and that (b) rapid starch formation occurred in high CO₂ even when leaf sucrose was only slightly elevated suggest that low sink capacity was not the main constraint in high CO₂. It is proposed that carbon partitioning between starch (chloroplast) and sucrose (cytosol) was perturbed by high CO₂ because of the lack of photorespiration. Total phosphate pools were determined in leaves.

Concentrations based on fresh weight of orthophosphate, soluble esterified phosphate, and total phosphate markedly declined during 13 days of exposure of the plants to high CO₂ but changed little in high light/ambient air. During this time, the ratio of orthophosphate to soluble esterified phosphate decreased considerably in high CO₂ and increased slightly in high light/ambient air. It appears that phosphate uptake and growth were similarly stimulated by high light, whereas the coordination was weak in high CO₂.

KEYWORDS: ACCLIMATION, CARBON METABOLISM, CHLOROPLASTS, DIOXIDE, ENRICHMENT, LEAVES, LIMITATION, PHOTOSYNTHESIS, SUCROSE, TRANSPORT

1585

Morison, J.I.L. 1993. Response of plants to CO₂ under water limited conditions. *Vegetatio* 104:193-209.

The influence of increased atmospheric CO₂ on the interaction between plant growth and water use is proving to be one of the most profound impacts of the anthropogenic 'Greenhouse Effect'. This paper illustrates the interaction between CO₂ and water in plant growth at a range of scales. Most published work has concentrated on water use efficiency, especially at shorter time scales, and has shown large increases of leaf water use efficiency with increased CO₂. However, the magnitude of the effect is variable, and does not consistently agree with predictions from simple leaf gas exchange considerations. The longer the time scales considered, the less the information and the more the uncertainty in the response to CO₂, because of the additional factors that have to be considered, such as changes in leaf area, respiration of non-photosynthetic tissues and soil evaporation. The need for more detailed studies of the interactions between plant evaporation, water supply, water status and growth is stressed, as increased CO₂ can affect all of these either directly, or indirectly through feedbacks with leaf gas exchange, carbon partitioning, leaf growth, canopy development and root growth.

KEYWORDS: ATMOSPHERIC CO₂, CARBON-DIOXIDE ENRICHMENT, ELEVATED CO₂, GAS-EXCHANGE, LIQUIDAMBAR-STYRACIFLUA, PINUS-TAEDA SEEDLINGS, ROOT-GROWTH, STOMATAL CONDUCTANCE, USE EFFICIENCY, WINTER-WHEAT

1586

Morison, J.I.L. 1998. Stomatal response to increased CO₂ concentration. *Journal of Experimental Botany* 49:443-452.

The stomatal response to CO₂ is important in understanding stomatal physiology, and important in understanding vegetation-atmosphere exchanges at all scales from the individual plant up to global vegetation. Despite the long history of experiments on stomatal responses to CO₂ there are still considerable uncertainties in both these tasks. The difficulty in understanding differences in stomatal conductance between plants grown for any length of time in different CO₂ atmospheres is stressed because of the many other possible changes in the plants' carbohydrate, nutrient and water relations. The other key issues that are highlighted are: whether stomata acclimate to CO₂ either in parallel with any mesophyll photosynthetic acclimation or independently of changes in the mesophyll; whether stomata on different leaf surfaces respond to CO₂ similarly; and whether reported changes in stomatal frequency are important to leaf gas exchange. The need for direct examination of stomatal sensitivity of plants grown in different CO₂ concentrations is stressed.

KEYWORDS: ATMOSPHERIC CO₂, CONDUCTANCE, ELEVATED CARBON-DIOXIDE, GAS-EXCHANGE, GROWTH, LEAVES, PHASEOLUS-VULGARIS L, PHOTOSYNTHESIS, TEMPERATURE, WATER-USE EFFICIENCY

1587

Morison, J.I.L., and D.W. Lawlor. 1999. Interactions between increasing CO₂ concentration and temperature on plant growth. *Plant, Cell and Environment* 22(6):659-682.

The global environment is changing with increasing temperature and atmospheric carbon dioxide concentration, [CO₂]. Because these two factors are concomitant, and the global [CO₂] rise will affect all biomes across the full global range of temperatures, it is essential to review the theory and observations on effects of temperature and [CO₂] interactions on plant carbon balance, growth, development, biomass accumulation and yield. Although there are sound theoretical reasons for expecting a larger stimulation of net CO₂ assimilation rates by increased [CO₂] at higher temperatures, this does not necessarily mean that the pattern of biomass and yield responses to increasing [CO₂] and temperature is determined by this response. This paper reviews the interactions between the effects of [CO₂] and temperature on plants. There is little unequivocal evidence for large differences in response to [CO₂] at different temperatures, as studies are confounded by the different responses of species adapted and acclimated to different temperatures, and the interspecific differences in growth form and development pattern. We conclude by stressing the importance of initiation and expansion of meristems and organs and the balance between assimilate supply and sink activity in determining the growth response to increasing [CO₂] and temperature.

KEYWORDS: ATMOSPHERIC CO₂, CARBON-DIOXIDE CONCENTRATION, ELEVATED CO₂, GLOBAL ENVIRONMENT CHANGE, LONG-TERM, NATURAL-POPULATIONS, OPEN-TOP CHAMBERS, TRITICUM-AESTIVUM L, WATER-USE, WINTER-WHEAT

1588

Morokuma, M., M. Yajima, and S. Yonemura. 1996. Effects of elevated CO₂ concentration and warming on growth and yield of rice. *Japanese Journal of Crop Science* 65(2):222-228.

Effects of combined treatments of CO₂ (400, 660, 1200 ppm) and air temperature (outdoor tracking, outdoor+2 degrees C) on growth and yield of rice (*Oryza sativa* L. cv. Nipponbare) grown in growth chambers under natural sunlight were investigated. The effects of container size (tank, 3.5 l pot) on growth and yield were also examined. Plants were grown under simulated paddyfield conditions. Growth parameters under the elevated CO₂ and temperature conditions were promoted at the maximum tiller number stage but not at the heading stage, without appreciable difference in such parameters. In the 660HT plot, dry weight increased about 30% at both stages compared with the 400NT plot. In the 1200HT plot, it increased more than that of the 660HT plot at the maximum tiller number stage but at the heading stage, the degree of promotion was decreased substantially. Dry matter distribution to leaf blades was reduced, and the nitrogen ratio in leaf blades were low in plants grown in both 660HT and 1200HT plants. In the 1200HT plot, the yield was remarkably reduced probably due to the high temperature sterility. Potted, limited-root-space plants grew smaller above-ground parts than did tank plants (less limited), without any difference in root production. From these results, the production processes of rice crop are discussed in terms of climate conditions predicted for the future.

KEYWORDS: ACCLIMATION, CARBON-DIOXIDE CONCENTRATION, RESPONSES, TEMPERATURE

1589

Morse, S.R., and F.A. Bazzaz. 1994. Elevated CO₂ and temperature alter recruitment and size hierarchies in C-3 and C-4 annuals. *Ecology* 75(4):966-975.

In order to understand the implications of changes in global CO₂ concentrations and temperature for the growth and fitness of individual plants, performance must be investigated in relation to the performance of other plants within a population. In this study we examined patterns of recruitment, mortality, and size structure of monospecific stands in response to ambient (400 µmol/L) and elevated CO₂ concentrations (700 µmol/L) across three temperature regimes; 18 degrees, 28 degrees, and 38 degrees C. We created experimental populations of two annual plants that differ in their photosynthetic pathway and water use patterns: *Abutilon theophrasti* (C-3) and *Amaranthus retroflexus* (C-4). The effects of CO₂, temperature, and their interactions on population structure were complex and species dependent. For both species increasing temperature resulted in higher germination and faster initial growth rates. These initial temperature responses increased the intensity and role of competition in determining stand size and structure. Postemergence responses to elevated CO₂ differed markedly between the two species. For *Abutilon*, the C-3 species, self-thinning and the mean biomass of the survivors increased under elevated CO₂. For *Amaranthus*, survivorship, but not growth, increased under elevated CO₂ conditions. We attribute differences in response between species not only to photosynthetic pathway, but also to differences in the onset of competition mediated through differences in plant form and in resource uptake and deployment. The patterns of stand development in response to CO₂ and temperature suggest that the effects of changing CO₂ and temperature may be understood within mechanistically based models of resource use. Temperature regulates the rate of resource use and the onset of interference among plants, while CO₂ functions both as a resource and a resource regulator. Although mortality was concentrated later in stand development for *Abutilon* than *Amaranthus*, overall patterns of stand size and structure were similar for both species; mortality and size inequalities increased with increasing temperature and CO₂. Because size is often correlated with fecundity, an increase in size hierarchies in response to elevated CO₂, in conjunction with a decrease in survivorship, may result in a smaller effective population size. Our ability to predict changes in effective population size due to changing size hierarchies alone, however, should also consider developmental shifts in response to elevated CO₂ that may result in, as in this study, a decrease in the minimum size at the onset of flowering.

KEYWORDS: COMPETITION, DENSITY, ENRICHMENT, FITNESS, GROWTH, MONOCULTURES, PLANT-POPULATIONS, STANDS, VARIABILITY

1590

Morse, S.R., P. Wayne, S.L. Miao, and F.A. Bazzaz. 1993. Elevated CO₂ and drought alter tissue water relations of birch (*Betula populifolia* marsh) seedlings. *Oecologia* 95(4):599-602.

The effect of increasing atmospheric CO₂ concentrations on tissue water relations was examined in *Betula populifolia*, a common pioneer tree species of the northeastern U.S. deciduous forests. Components of tissue water relations were estimated from pressure volume curves of tree seedlings grown in either ambient (350 µmol l⁻¹) or elevated CO₂ (700 µmol l⁻¹), and both mesic and xeric water regimes. Both CO₂ and water treatment had significant effects on osmotic potential at full hydration, apoplasmic fractions, and tissue elastic moduli. Under xeric conditions and ambient CO₂ concentrations, plants showed a decrease in osmotic potentials of 0.15 MPa and an increase in tissue elastic moduli at full hydration of 1.5 MPa. The decrease in elasticity may enable plants to improve the soil-plant water potential gradient given a small change in water content, while lower osmotic potentials shift the zero turgor loss point to lower water potentials. Under elevated CO₂, plants in xeric conditions had osmotic potentials 0.2 MPa lower than mesic plants and decreased elastic moduli at full hydration. The increase in tissue elasticity at elevated CO₂ enabled the xeric plants to maintain positive turgor pressures at lower water potentials and tissue water contents. Surprisingly, the elevated CO₂ plants under mesic conditions had the

most inelastic tissues. We propose that this inelasticity may enable plants to generate a favorable water potential gradient from the soil to the plant despite the low stomatal conductances observed under elevated CO₂ conditions.

KEYWORDS: ANATOMY, CARBON-DIOXIDE ENRICHMENT, GROWTH, LIQUIDAMBAR-STYRACIFLUA, MORPHOLOGY, PINUS-TAEDA SEEDLINGS, PLANTS, PRESSURE, STRESS, WHEAT

1591

Mortensen, L.M. 1992. Diurnal photosynthesis and transpiration of *Ficus benjamina* L. as affected by length of photoperiod, CO₂ concentration and light level. *Acta Agriculturae Scandinavica Section B-Soil and Plant Science* 42(2):100-105.

The diurnal net photosynthesis of *Ficus benjamina* L., cultivar Cleo, was studied at different daylengths (12, 18 and 24 h day⁻¹), photosynthetic photon flux densities (40 and 120 µmol m⁻² s⁻¹ PPFD) and CO₂ concentrations (350 and 700 µmol mol⁻¹). Net photosynthesis increased to a maximum after 5-6 and 6-7 h of light at 12 and 18 h day⁻¹ photoperiods, respectively, followed by a decrease towards the end of the photoperiod. At a photoperiod of 18 h day⁻¹ similar diurnal curves were found at 350 and 700 µmol mol⁻¹ CO₂, and at 40 and 120 µmol m⁻² s⁻¹ PPFD. Five days after the photoperiod was changed from 18 to a 24 h day⁻¹ the diurnal rhythm disappeared. Transpiration followed the same diurnal rhythm as that for photosynthesis. The water-use efficiency was enhanced by raising the CO₂ concentration. A decrease in the CO₂ concentration from 700 to 350 µmol mol⁻¹ after six days at high CO₂ first significantly decreased the photosynthesis, but three days later it reached the same level as that at high CO₂.

KEYWORDS: BEAN-PLANTS, CARBON-DIOXIDE CONCENTRATIONS, EXCHANGE, GROWTH, INHIBITION, LEAVES, RESPONSES

1592

Mortensen, L.M. 1992. Effects of ozone concentration on growth of tomato at various light, air humidity and carbon-dioxide levels. *Scientia Horticulturae* 49(1-2):17-24.

The effect of ozone (O₃) concentration on the growth of *Lycopersicon esculentum* was studied at different photosynthetic photon flux densities (PPFD), relative air humidities (RH) and carbon dioxide (CO₂) concentrations. Increasing the O₃ concentration from < 10 to 85 nl l⁻¹ for 6 h per day reduced the shoot dry weight 35% at 70% RH and 62% at 90% RH. Increasing the PPFD from 100 to 350 µmol m⁻² s⁻¹ significantly reduced the effect of O₃ in one of two experiments. The most pronounced interaction between RH, PPFD and O₃ was found on plant height. High O₃ levels generally decreased plant height at low PPFD and had no, or a stimulating, effect at high PPFD. Raising the RH from 70 to 90% significantly increased the negative effect of O₃ on height. Increasing the O₃ concentration from < 10 to 65 nl l⁻¹ significantly decreased plant height at low CO₂ concentration (300-340 µmol l⁻¹), but small effects were found at high CO₂ concentration (700-800 µmol l⁻¹).

KEYWORDS: LEAVES, SUMMER CO₂ ENRICHMENT, TEMPERATURES, TRANSPIRATION, YIELD

1593

Mortensen, L.M. 1994. Effects of carbon-dioxide concentration on assimilate partitioning, photosynthesis and transpiration of *Betula-pendula* roth and *Picea-abies* (L) karst seedlings at 2 temperatures. *Acta Agriculturae Scandinavica Section B-Soil and Plant Science* 44(3):164-169.

Seedlings of *Betula pendula* Roth. and *Picea abies* (L.) Karst. were grown at 350 and 700 $\mu\text{mol mol}^{-1}$ CO_2 for 35 or 45 days at 15 and 20 degrees C in eight growth chambers. The mean photosynthetic flux was 15-22 $\mu\text{mol m}^{-2}$ day^{-1} . The mean relative growth rate was increased by 7% in *Betula* and by 10% in *Picea* at the highest CO_2 concentration. This corresponded to an increase in the total plant dry weight of 20 and 19%, respectively. The shoot:root and leaf:stem ratios were unaffected by the CO_2 concentration in both species. High CO_2 levels increased the stem diameter and the number of lateral shoots in *Betula*. Increasing the temperature did not affect the assimilate partitioning between leaf stem and root in *Betula*, but the needle:stem ratio decreased in *Picea*. Elevated CO_2 concentration increased the number of lateral shoots in *Betula* more at 15 than at 20 degrees C, however, the total weight of the lateral shoots was not affected. With this exception the effect of CO_2 was generally the same at both temperatures. Measurements of the CO_2 exchange rates indicated that a slight acclimation to high CO_2 had taken place at the end of the experimental period in the two species. Elevated CO_2 slightly decreased the transpiration rate of *Betula*.

KEYWORDS: ATMOSPHERIC CO_2 , ENRICHMENT, GROWTH, LIGHT, PLANTS, RESPONSES, TREES, WATER-USE

1594

Mortensen, L.M. 1994. Effects of day-night temperature-variations on growth, morphogenesis and flowering of *Kalanchoe blossfeldiana* V poelln at different CO_2 concentrations, daylengths and photon flux densities. *Scientia Horticulturae* 59(3-4):233-241.

Growth and flowering of *Kalanchoe blossfeldiana* were studied at two temperature treatments (constant, CT; day lower than night temperature, negative DIF) in combination with two CO_2 concentrations (360 and 900 $\mu\text{mol mol}^{-1}$), two daylengths (DL; 12 and 18 h) and two photosynthetic photon flux densities (PPFD; 85 and 130 $\mu\text{mol m}^{-2}$ s^{-1}). In addition to the two temperature treatments, a 2-h low temperature pulse (DROP) was included in combination with short days and low CO_2 levels. The experiment was conducted in 18 growth chambers with artificial light only. The plant dry weight at saleable stage was the same at the different temperature treatments irrespective of CO_2 concentration, DL or PPFD. The dry weight was similarly (31- 40%) increased by CO_2 enrichment, or increasing DL or PPFD. Total plant height was slightly, but consistently increased by negative DIF relative to CT, irrespective of the level of the other climate factors. The DROP treatment in short DL increased the height relative to both negative DIF and CT. Negative DIF delayed flowering by 2-4 days at 360 $\mu\text{mol mol}^{-1}$ CO_2 , but promoted it by 2-4 days at 900 $\mu\text{mol mol}^{-1}$ CO_2 . Fresh weight of flowers was unaffected by temperature treatments irrespective of DL and PPFD. It was concluded that the best plant quality was obtained at constant temperature throughout day and night irrespective of the level of the other climate factors.

1595

Mortensen, L.M. 1994. Effects of elevated CO_2 concentrations on growth and yield of 8 vegetable species in a cool climate. *Scientia Horticulturae* 58(3):177-185.

The effects of elevated CO_2 concentrations on the yield of *Allium cepa* (onion), *Allium ampeloprasum* (leek), *Apium graveolens* var. dulce (celery), *Apium graveolens* var. rapaceum (celery root), *Brassica pekinensis* (chinese cabbage), *Daucus carota* (carrot), *Lactuca sativa* (lettuce) and *Petroselinum crispum* (parsley) grown in containers, were studied in six 9-M2 large field plots surrounded by 1.8-m high plastic foil walls ('field chambers'). Three of the chambers were supplied with pure CO_2 gas through perforated tubes. Increasing the CO_2 concentration from ambient (355 $\mu\text{mol mol}^{-1}$) to 800-900 $\mu\text{mol mol}^{-1}$

increased the yield (fresh weight) by 23% in onion (two cultivars) and by 8% in carrot (three cultivars). The dry weight based yield increase was 18% in lettuce (three cultivars), 19% in carrot and 17% in parsley (one cultivar). The yields of leek (two cultivars), chinese cabbage (three cultivars), celery (one cultivar) and celery root (one cultivar) were not significantly affected by the CO_2 concentration. Generally, no 'chamber effect' was found on the yields of the different species.

KEYWORDS: CROP, ENRICHMENT, PLANTS, RESPONSES

1596

Mortensen, L.M. 1994. The influence of carbon-dioxide or ozone concentration on growth and assimilate partitioning in seedlings of 9 conifers. *Acta Agriculturae Scandinavica Section B-Soil and Plant Science* 44(3):157-163.

Seedlings of nine different conifers were exposed to 355 and 730 $\mu\text{mol mol}^{-1}$ CO_2 , or low ($< 15 \text{ nmol mol}^{-1}$) and elevated O-3 concentration (70 nmol mol^{-1}) for 81-116 days. The experiments were conducted in growth chambers placed in a greenhouse. Increased CO_2 concentration enhanced the mean relative growth rate (RGR) and total plant dry weight by 4 and 33% in *Larix leptolepis*, by 4 and 38% in *Larix sibirica*, by 7 and 47% in *Picea glauca* and by 3 and 16% in *Picea sitchensis*, respectively. The growth rates and dry weights of *Pinus contorta*, *Pinus mugo* and *Pseudotsuga menziesii* were not significantly affected. Carbon dioxide enrichment enhanced RGR of two provenances of *Picea abies* by 4 and 6%, respectively, while a third provenance was unaffected. In *Pinus sylvestris*, only the RGR of one of three provenances was stimulated by CO_2 enrichment (4%). After two growth seasons CO_2 enrichment enhanced RGR and total plant dry weight by 11 and 35% in *Picea abies* and by 12 and 36% in *Pinus sylvestris*, respectively. Elevated CO_2 decreased the shoot:root ratio in *Larix leptolepis*, and decreased the needle:stem ratio in *Picea glauca*, but increased it in *Pseudotsuga menziesii*. Elevated O-3 significantly decreased the plant dry weight in *Picea sitchensis*, *Pseudotsuga menziesii* and in one of three provenances of *Pinus sylvestris*, while the other species and provenances were unaffected. Increased O-3 concentration increased the shoot:root dry weight ratio in one of three *Picea abies* provenances, in all three *Pinus sylvestris* provenances and in *Pinus contorta*. The needle:stem ratio was enhanced by O-3 in seven of the nine species. The O-3 exposure caused chlorosis of needles in all species except *Pseudotsuga menziesii*.

KEYWORDS: CO_2 - ENRICHMENT, PHOTOSYNTHESIS, SOUR ORANGE TREES

1597

Mortensen, L.M. 1995. Diurnal carbon-dioxide exchange-rates of greenhouse roses under artificial-light as compared with daylight conditions in summer. *Acta Agriculturae Scandinavica Section B-Soil and Plant Science* 45(2):148-152.

Carbon dioxide exchange rates (CER) of greenhouse roses (cut flowers) were measured under daylight conditions in a greenhouse in July, and under artificial light only (300 $\mu\text{mol m}^{-2}$ s^{-1}) PPFD in 18 h day^{-1}) at two CO_2 concentrations (350 and 700 $\mu\text{mol mol}^{-1}$). The daily CER varied considerably from day to day owing to the large variation in solar radiation. Light saturation of CER seemed not to be reached even on clear days, and a light dose (PAP = number of photosynthetic active photons) produced by variable light over one week in summer gave the same total CER as a similar PAP produced by a constant PPFD. CER at constant PPFD increased rapidly during the first two hours of the photoperiod, followed by a slight increase during the subsequent hours, before CER slightly decreased towards the end of the photoperiod. Raising the CO_2 concentration significantly increased CER during the entire photoperiod, and by 32% as a mean for the whole photoperiod.

Elevated CO₂ decreased the night respiration of the plants by 30%. As a total of the light and dark period, CO₂ enrichment increased CER by 38%.

KEYWORDS: CO₂- ENRICHMENT, GROWTH

1598

Mortensen, L.M. 1995. Effect of carbon-dioxide concentration on biomass production and partitioning in betula-pubescons ehrh seedlings at different ozone and temperature regimes. *Environmental Pollution* 87(3):337-343.

Seedlings of *Betula pubescens* were grown at two CO₂ concentrations, in combination with either two O₃ concentrations or two air temperatures, during 34-35 days at 24 h day⁻¹ photoperiod in growth chambers placed in a greenhouse. Increasing the CO₂ concentration from 350 to 560 μmol mol⁻¹ at 17-degrees-C air temperature increased the dry weight of the main leaves, main stem, branches and root. The mean relative growth rate (RGR) was increased 10% by CO₂ enrichment, while increasing the O₃ concentration from 7 to 62 nmol mol⁻¹ decreased the RGR by 9%. The relative biomass distribution between the different plant components was not significantly affected by the CO₂ concentration irrespective of the O₃ concentration. No significant interactions between CO₂ and O₃ concentration were found except on leaf size, which was stimulated more by elevated CO₂ concentration at high, compared to low, O₃ levels. In another experiment, elevated CO₂ (700 μmol mol⁻¹) significantly increased the dry weight of the different plant components, and more at 20-degrees-C than at 15-degrees-C. Raising the CO₂ concentration increased the RGR by 5 and 10% at 15 and 20-degrees-C, respectively. CO₂ enrichment increased the branch dry weight relatively more than the dry weight of the other plant parts. Increasing the CO₂ concentration or temperature increased the plant height and stem diameter, however, no interactions between CO₂ and temperature were found.

KEYWORDS: CO₂, GROWTH, O-3, PHOTOSYNTHESIS

1599

Mortensen, L.M. 1997. Effects of carbon dioxide concentrations on three grass species grown in mixture in two soil types at different ozone concentrations or temperatures. *Acta Agriculturae Scandinavica Section B-Soil and Plant Science* 47(1):14-19.

A seed mixture of *Phleum pratense* L., *Lolium perenne* L. and *Festuca pratensis* Huds. was grown in sphagnum peat or sandy soil in six growth chambers placed in a greenhouse compartment. Two different experiments were performed. Increasing the CO₂ concentration from 375 to 740 μmol mol⁻¹ increased the total dry weight of the grass mixture by about 30%, while an increase in the O-3 concentration from < 10 to 50 nmol mol⁻¹ decreased the dry weight by 18% as a mean in both experiments. The relative dry weights of the three species were not significantly affected by elevated CO₂ concentrations at low O-3, while *Lolium* increased its relative dry weight at high O-3 concentrations at low CO₂ on the expenditure of *Phleum* dry weight. CO₂ enrichment counteracted some of this O-3 effect. No significant interaction between CO₂ concentration and temperature (14 and 19 degrees C mean temperature) was found with respect to the dry weights of the three species. The soil type had generally no influence on the effect of CO₂ and O-3. However, plant growth was significantly slower in sandy soil than in peat.

KEYWORDS: ELEVATED CO₂, LIGHT, NITROGEN, O-3, PASTURE, PERENNIAL RYEGRASS, PLANT-RESPONSES, WHEAT, WHITE CLOVER

1600

Mortensen, L.M. 1998. Effects of elevated CO₂ concentration on growth of *Betula pubescens* Ehrh. in different climatic conditions. *Scandinavian Journal of Forest Research* 13(2):197-203.

Seedlings of *Betula pubescens* Ehrh. (mountain birch) were grown at ambient and elevated CO₂ concentrations in environment- controlled growth chambers, and in chambers or wind tunnels in the field. In the two preliminary experiments in a controlled environment, CO₂ enrichment increased the dry weights of six birch provenances grown at a daily mean temperature (MT) of 17 degrees C and 15 provenances grown at 12.5 degrees C MT by 27 and 7%, respectively. In more realistic conditions in field chambers (13.9 degrees C MT), the shoot dry weight of plants grown for 65 days was not significantly affected by the elevated CO₂ concentration. In a parallel experiment, CO₂ enrichment increased the shoot dry weight by 36% in both unheated (14.7 degrees C MT) and heated (18.1 degrees C MT) wind tunnels. In a final experiment over two seasons in open- top chambers at 850 m a.s.l., elevated CO₂ concentrations increased the root (42%) but not the shoot dry weight. The results are discussed in relation to variable climatic conditions.

KEYWORDS: AIR- TEMPERATURE, ATMOSPHERIC CO₂, CARBON-DIOXIDE CONCENTRATION, CARBOXYLASE, ENRICHMENT, LEAVES, PENDULA ROTH, PHOTOSYNTHESIS, PLANT-RESPONSES, SEEDLINGS

1601

Mortensen, L.M. 1999. Effects of different carbon dioxide and ozone concentrations on shoot growth of *Phleum pratense* L. and *Betula pubescens* Ehrh. as influenced by day length and irradiance. *Acta Agriculturae Scandinavica Section B-Soil and Plant Science* 49(1):50-56.

Seedlings of *Phleum pratense* L. (timothy) and *Betula pubescens* Ehrh. (mountain birch) were grown for 37 or 42 days at all combinations of two CO₂ concentrations (350 and 700 μmol mol⁻¹), two O-3 concentrations (13 and 59 nmol mol⁻¹) in 8 h day⁻¹), two day lengths (17 and 24 h DL) and two levels of supplementary lighting (150 and 210 μmol m⁻² s⁻¹) photosynthetic photon flux, PPF) in 16 growth chambers placed in a greenhouse. Elevated CO₂ concentration increased the mean shoot dry weight by 47% in timothy and by 39% in birch. No significant interactions were found between CO₂ and O-3, DL or PPF with respect to shoot dry weight in the two species. The number of shoots in timothy was generally enhanced by CO₂ enrichment. The number of branches in birch was strongly enhanced by elevated CO₂ at 17 but not at 24 h DL, and the ratio of the fresh weight of branches to main shoot was significantly increased irrespective of DL. Increasing the O-3 concentration caused visible leaf injuries both in timothy (chlorosis/necrosis) and in birch (yellow stipples/brown spots), while the shoot weight was not significantly affected. The number of O-3-induced injuries in timothy was decreased by increasing the CO₂ concentration or the total irradiance (increasing DL and/or PPF). The number of injuries in birch was slightly decreased by increasing PPF; however, CO₂ enrichment had no effect.

KEYWORDS: CLOVER, ELEVATED CO₂ CONCENTRATION, ENRICHMENT, PENDULA ROTH, PHOTOSYNTHESIS, PLANTS, RESPONSES, SEEDLINGS, TEMPERATURE

1602

Mortensen, L.M. 1999. Foliar injuries caused by ozone in *Betula pubescens* Ehrh. and *Phleum pratense* L. as influenced by climatic conditions before and during O-3 exposure. *Acta Agriculturae Scandinavica Section B-Soil and Plant Science* 49(1):44-49.

Seedlings of *Betula pubescens* Ehrh. (mountain birch) and *Phleum pratense* L. (timothy) were grown for 42 days under full light or 50% shade in the field at 12 degrees C, and at comparable photosynthetic active radiation (PAR) levels in a greenhouse at 18 degrees C. Plants from the four pretreatments were exposed to 78 nmol mol⁻¹ (ppb) O₃ (8 h day⁻¹) under two temperatures (15 and 25 degrees C), two relative air humidities (50 and 80% RH) or two CO₂ concentrations (400 and 750 μmol mol⁻¹) during 7 days. The accumulated O₃ dose over 40 nmol mol⁻¹ O₃ (AOT40) was 2.6 μmol mol⁻¹-hours (ppm-h). Decreasing the temperature during exposure significantly increased the amount of injury induced by O₃ in leaves of birch (yellow mottling/bronzing) as well as timothy (chlorosis/necrosis). Increasing the air humidity or decreasing the CO₂ concentration strongly enhanced the injuries caused by O₃ in timothy, but not in birch. In general, both birch and timothy plants grown in the greenhouse and in the field had the same O₃ sensitivity. However, decreasing the PAR level during the pretreatment enhanced leaf injury in birch but not in timothy. At the most sensitive exposure climate, 15 degrees C/80% RH, leaf injury developed at an AOT40 of 0.7-0.9 ppm-h in both species.

KEYWORDS: CARBON-DIOXIDE CONCENTRATION, GROWTH, HUMIDITY, PENDULA ROTH, PHOTOSYNTHESIS, RESPIRATION, SEEDLINGS, TEMPERATURE, TRANSPIRATION

1603

Mortensen, L.M., and R. Moe. 1992. Effects of CO₂ enrichment and different day/night temperature combinations on growth and flowering of *Rosa* L. and *Kalanchoe blossfeldiana* V. *Scientia Horticulturae* 51(1-2):145-153.

The effects of increasing the CO₂ concentration from 350 to 700-μmol⁻¹ on growth and flowering of *Rosa* L. and *Kalanchoe blossfeldiana* at four different day/night temperature combinations (20/20-degrees-C, 23/14-degrees-C and 17/26- degrees-C day/night, and 20/20-degrees-C with 2 h at 14- degrees-C in the morning) were studied in 16 growth chambers. An increase in the CO₂ concentration resulted in enhanced total dry weight, stem: leaf fresh weight ratio, flower fresh weight, length and diameter of the rose shoot, while the number of days until flowering was not affected. With the 17/26-degrees-C treatment, rose shoots were 3-4 cm shorter, and with the 23/14- degrees-C treatment flowering occurred about 2 days earlier than with the other temperature treatments. The results were the same for *Rosa* cultivars 'Frisco' and 'Kiss'. No significant interactions between CO₂ and temperature were found. Plant dry weight and fresh weight of flowers in *Kalanchoe* were generally enhanced by CO₂ enrichment. The effects of CO₂ on dry weight, plant height and flower stem length were greater with the 23/14-degrees-C treatment compared with the effects of the other temperature treatments. A constant temperature (20/20- degrees-C) and the 23/14-degrees-C treatments gave the shortest and tallest plants, respectively.

1604

Mortensen, L.M., and A. Saebo. 1996. The effect of elevated CO₂ concentration on growth of *Phleum pratense* L. in different parts of the growth season. *Acta Agriculturae Scandinavica Section B-Soil and Plant Science* 46(2):128-134.

Seedlings of *Phleum pratense* L. (timothy) of the same age were grown in five sequential four-week periods during one growth season (May 5-September 23) at low (380 μmol mol⁻¹) and high (650 μmol mol⁻¹) CO₂ concentration. The experiment was performed in 10 × 9 m² field plots surrounded by plastic foil walls ("field chambers") in the relatively cool climate (10- 13 degrees C mean temperature) of the west coast of Norway (59 degrees N latitude). Raising the CO₂ concentration generally decreased the height of the grass (8-23%), especially at the beginning and end of the growth season. The number of shoots was

significantly increased (13-42%) by CO₂ enrichment in all growth periods except the last. Elevated CO₂ did not influence the above-ground biomass (dry weight) in the first (May) and last (September) period, but increased it by 14-51% in the intervening periods (June-August). Positive effects of CO₂ enrichment on plant biomass were correlated with positive effects on the number of shoots. Elevated CO₂ concentrations resulted in 25-64% denser plant biomass (dry weight per unit air volume) in the different growth periods. In general, a positive "chamber effect" on plant height and dry weight was found in spite of the small air temperature differences between the insides and the outsides of the chambers. A greenhouse experiment showed that wind speeds above 3 m s⁻¹ strongly decreased height and dry weight of timothy seedlings. The reduced wind speeds inside the chambers could therefore explain the "chamber effects" found.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, PLANT-RESPONSES, TEMPERATURE

1605

Mosier, A.R. 1998. Soil processes and global change. *Biology and Fertility of Soils* 27(3):221-229.

Contributors to the Intergovernmental Panel on Climate Change (IPCC) generally agree that increases in the atmospheric concentration of greenhouse trace gases (i.e., CO₂, CH₄, N₂O, O₃) since preindustrial times, about the year 1750, have led to changes in the earth's climate. During the past 250 years the atmospheric concentrations of CO₂, CH₄, and N₂O have increased by 30, 145, and 15%, respectively. A doubling of preindustrial CO₂ concentrations by the end of the twenty-first century is expected to raise global mean surface temperature by about 2 degrees C and increase the frequency of severe weather events. These increases are attributed mainly to fossil fuel use, land-use change, and agriculture. Soils and climate changes are related by bidirectional interactions. Soil processes directly affect climatic changes through the production and consumption of CO₂, CH₄, and N₂O and, indirectly, through the production and consumption of NH₃, NO, and CO. Although CO₂ is primarily produced through fossil fuel combustion, land-use changes, conversion of forest and grasslands to agriculture, have contributed significantly to atmospheric increase of CO₂. Changes in land use and management can also result in the net uptake, sequestration, of atmospheric CO₂. CH₄ and N₂O are produced (30% and 70%, respectively) in the soil, and soil processes will likely regulate future changes in the atmospheric concentration of these gases. The soil-atmosphere exchange of CO₂, CH₄, and N₂O are interrelated, and changes in one cycle can impact changes in the N cycle and resulting soil-atmosphere exchange of N₂O. Conversely, N addition increases C sequestration. On the other hand, soil processes are influenced by climatic change through imposed changes in soil temperature, soil water, and nutrient competition. Increasing concentrations of atmospheric CO₂ alters plant response to environmental parameters and frequently results in increased efficiency in use of N and water. In annual crops increased CO₂ generally leads to increased crop productivity. In natural systems, the long-term impact of increased CO₂ on ecosystem sustainability is not known. These changes may also result in altered CO₂, CH₄, and N₂O exchange with the soil. Because of large temporal and spatial variability in the soil-atmosphere exchange of trace gases, the measurement of the absolute amount and prediction of the changes of these fluxes, as they are impacted by global change on regional and global scales, is still difficult. In recent years, however, much progress has been made in decreasing the uncertainty of field scale flux measurements, and efforts are being directed to large scale field and modeling programs. This paper briefly relates soil process and issues akin to the soil-atmosphere exchange of CO₂, CH₄, and N₂O. The impact of climate change, particularly increasing atmospheric CO₂ concentrations, on soil processes is also briefly discussed.

KEYWORDS: CARBON DIOXIDE, CULTIVATION,

1606

Mousseau, M. 1993. Effects of elevated CO₂ on growth, photosynthesis and respiration of sweet chestnut (*Castanea-sativa* Mill). *Vegetatio* 104:413-419.

Two year old sweet chestnut seedlings (*Castanea sativa* Mill) were grown in pots at ambient (350 $\mu\text{mol}\cdot\text{mol}^{-1}$) and double (700 $\mu\text{mol}\cdot\text{mol}^{-1}$) atmospheric CO₂ concentration in constantly ventilated greenhouses during entire growing seasons. CO₂ enrichment caused either no significant change or a decrease in shoot growth response, depending on yearly weather condition either reduced or unchanged under elevated CO₂. However, when grown under controlled conditions in a growth chamber, leaf area was enlarged with elevated CO₂. The CO₂ exchanges of whole plants were measured during the growing season. In elevated CO₂, net photosynthetic rate was maximum in May and then decreased, reaching the level of the control at the end of the season. End of night dark respiration of enriched plants was significantly lower than that of control plants; this difference decreased with time and became negligible in the fall. The original CO₂ level acted instantaneously on the respiration rate: a double concentration in CO₂ decreased the respiration of control plants and a reduced concentration enhanced the respiration of enriched plants. The carbon balance of a chestnut seedling may then be modified in elevated CO₂ by increased carbon inputs and decreased carbon outputs.

KEYWORDS: ACCLIMATION, CARBON DIOXIDE, DARK RESPIRATION, ENRICHMENT, FORESTS, HIGH ATMOSPHERIC CO₂, SEEDLINGS, TREES

1607

Mousseau, M., and B. Saugier. 1992. The direct effect of increased CO₂ on gas-exchange and growth of forest tree species. *Journal of Experimental Botany* 43(253):1121-1130.

CO₂ enrichment of the atmosphere is now well documented and its effect on the growth of world forests is being questioned by the scientific community. The direct effects of increased CO₂ on tree species are reviewed: the different experimental approaches are described, as well as the principal results already obtained. Short-term experiments have shown an increased photosynthetic rate, as predicted by leaf models. In longer experiments this increase is reduced after a few weeks or months by mechanisms that remain to be found. Elevated CO₂ seems to decrease the dark respiration rate, but the results are still controversial. Biomass partitioning in elevated CO₂ is clearly related to the mineral supply of the trees: An increase in root investment in elevated CO₂ is related to a poor mineral status. The mineral content of trees grown in elevated CO₂ is generally lowered compared to controls. No general rule has yet been found for the effect of increased CO₂ on leaf area development. The paper emphasizes large areas of ignorance: the reasons for the different responses of different species, which may be related to their developmental strategies, are largely ignored. Much experimental effort is needed to parameterize all the physiological processes which are susceptible to change with an increase in atmospheric CO₂, leading to a change in forest tree growth.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CASTANEA-SATIVA MILL, DARK RESPIRATION, ENRICHMENT, LEAF, NUTRIENT-UP TAKE, PLANTS, RESPONSES, SEEDLINGS, SHORT-TERM

1608

Moya, T.B., L.H. Ziska, O.S. Namuco, and D. Olszyk. 1998. Growth

dynamics and genotypic variation in tropical, field-grown paddy rice (*Oryza sativa* L.) in response to increasing carbon dioxide and temperature. *Global Change Biology* 4(6):645-656.

While previous studies have examined the growth and yield response of rice to continued increases in CO₂ concentration and potential increases in air temperature, little work has focused on the long-term response of tropical paddy rice (i.e. the bulk of world rice production) in situ, or genotypic differences among cultivars in response to increasing CO₂ and/or temperature. At the International Rice Research Institute, rice (cv IR72) was grown from germination until maturity for 4 field seasons, the 1994 and 1995 wet and the 1995 and 1996 dry seasons at three different CO₂ concentrations (ambient, ambient + 200 and ambient + 300 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO₂) and two air temperatures (ambient and ambient + 4 degrees C) using open-top field chambers placed within a paddy site. Overall, enhanced levels of CO₂ alone resulted in significant increases in total biomass at maturity and increased seed yield with the relative degree of enhancement consistent over growing seasons across both temperatures. Enhanced levels of temperature alone resulted in decreases or no change in total biomass and decreased seed yield at maturity across both CO₂ levels. In general, simultaneous increases in air temperature as well as CO₂ concentration offset the stimulation of biomass and grain yield compared to the effect of CO₂ concentration alone. For either the 1995 wet and 1996 dry seasons, additional cultivars (N-22, NPT1 and NPT2) were grown in conjunction with IR72 at the same CO₂ and temperature treatments. Among the cultivars tested, N-22 showed the greatest relative response of both yield and biomass to increasing CO₂, while NPT2 showed no response and IR72 was intermediate. For all cultivars, however, the combination of increasing CO₂ concentration and air temperature resulted in reduced grain yield and declining harvest index compared to increased CO₂ alone. Data from these experiments indicate that (a) rice growth and yield can respond positively under tropical paddy conditions to elevated CO₂, but that simultaneous exposure to elevated temperature may negate the CO₂ response to grain yield; and, (b) sufficient intraspecific variation exists among cultivars for future selection of rice cultivars which may, potentially, convert greater amounts of CO₂ into harvestable yield.

KEYWORDS: CO₂-ENRICHMENT, YIELD

1609

Msudoe, N.N.A. 1990. 2 mutants of *Arabidopsis thaliana* that become chlorotic in atmospheres enriched with CO₂. *Plant, Cell and Environment* 13(6):575-580.

1610

Mtolera, M.S.P., J. Collen, M. Pedersen, and A.K. Semesi. 1995. Destructive hydrogen peroxide production in *Eucheuma denticulatum* (Rhodophyta) during stress caused by elevated pH, high light intensities and competition with other species. *European Journal of Phycology* 30(4):289-297.

Growth of *Eucheuma denticulatum* was studied in the field and in laboratory experiments. Field co-cultivation of *E. denticulatum* with the green alga *Ulva reticulata* or the seagrass *Thalassia* sp, reduced daily growth rate (DGR) of a Tanzanian and a Philippine strain of *E. denticulatum* by 10-100% and 10-55%, respectively, depending upon the type of water current: a unidirectional water current produced the best growth. Laboratory co-cultivation of a Tanzanian strain of *E. denticulatum* with *U. reticulata* also reduced DGR (to 8% of the control) and nitrate-nitrogen uptake rate (to < 30% of the control) of *E. denticulatum* and, moreover, it increased epiphytism of a red filamentous alga on *E. denticulatum*. *E. denticulatum* monoculture at pH 8.6 +/- 0.5 or at photosynthetic photon flux densities (PPFDs) higher than its growth optimum (350 +/- 50 $\mu\text{mol photons m}^{-2}\text{s}^{-1}$) also

increased epiphytism. The lack of a competitive mechanism for inorganic carbon uptake in *Eucheuma* may have contributed to its reduced growth during co-cultivation. During co-cultivation, elevated pH regimes (pH > 8.5) were created around the *Eucheuma* thalli as a result of photosynthesis, thus decreasing the concentration of CO₂ in the seawater to values around 1 μM. As *Eucheuma* depends mainly on the CO₂ in the seawater for its growth a higher pH can cause CO₂ limitation by decreasing CO₂ concentration. Hydrogen peroxide (H₂O₂) production from the Tanzanian strain was also determined by luminol-dependent chemiluminescence. H₂O₂ production was found to increase with increased pH and PPFD (probably as a result of oxidative stress). Preincubation of plants with catalase for 5 min before addition of luminol prevented chemiluminescence, confirming H₂O₂ as the substrate of the luminol reaction. We suggest that the inefficiency of E, denticulatum in HCO₃⁻ utilisation contributes to its poor growth during field coexistence with seagrasses or *Ulva* sp. and that carbon deficiency induces H₂O₂ production in E, denticulatum.

KEYWORDS: GROWTH, HYPERSENSITIVE REACTION, INORGANIC CARBON, *KAPPAPHYCUS-ALVAREZII*, LIPID-PEROXIDATION, METABOLISM, OXYGEN, PHOTOSYNTHESIS, RED SEAWEEDS, *ULVA-FASCIATA*

1611

Muchow, R.C., and T.R. Sinclair. 1991. Water deficit effects on maize yields modeled under current and greenhouse climates. *Agronomy Journal* 83(6):1052-1059.

The availability of water imposes one of the major limits on rainfed maize (*Zea mays* L.) productivity. This analysis was undertaken in an attempt to quantify the effects of limited water on maize growth and yield by extending a simple, mechanistic model in which temperature regulates crop development and intercepted solar radiation is used to calculate crop biomass accumulation. A soil water budget was incorporated into the model by accounting for inputs from rainfall and irrigation, and water use by soil evaporation and crop transpiration. The response functions of leaf area development and crop gas exchange to the soil water budget were developed from experimental studies. The model was used to interpret a range of field experiments using observed daily values of temperature, solar radiation, and rainfall or irrigation, where water deficits of varying durations developed at different stages of growth. The relative simplicity of the model and its robustness in simulating maize yields under a range of water-availability conditions allows the model to be readily used for studies of crop performance under alternate conditions. One such study, presented here, was a yield assessment for rainfed maize under possible "greenhouse" climates where temperature and atmospheric CO₂ concentration were increased. An increase in temperature combined with decreased rainfall lowered grain yield, although the increase in crop water use efficiency associated with elevated CO₂ concentration, ameliorated the response to the greenhouse climate. Grain yields for the greenhouse climates as compared to current conditions increased, or decreased only slightly, except when the greenhouse climate was assumed to result in severely decreased rainfall.

KEYWORDS: ARID TROPICAL ENVIRONMENT, COMPONENTS, EVAPORATION, FIELD, NITROGEN LIMITATIONS, PEARL-MILLET, SOIL, SORGHUM, SOYBEAN GRAIN PRODUCTION, WHEAT

1612

Mudrik, V.A., A.K. Romanova, B.N. Ivanov, N.S. Novichkova, and V.A. Polyakova. 1997. Effect of increased CO₂ concentration on growth, photosynthesis, and composition of *Pisum sativum* L plants. *Russian Journal of Plant Physiology* 44(2):141-146.

Pisum sativum L.) plants grown for 3 weeks at 0.03 (control plants)

or 0.5% CO₂ (CO₂-plants) concentration were used to study the effects of increased CO₂ concentration on plant growth, CO₂ exchange, morphological pattern, and the content of carbohydrates and protein in plant leaves. The fresh and dry weights, the ratio of plant dry weight to the total area of its leaves and stipules, and the root/shoot dry weight ratio were 150, 42, and 24%, respectively, higher in the CO₂- plants. Protein content was similar in the leaves of CO₂- exposed and control plants, whereas the content of sugars and starch was significantly higher in the leaves of the CO₂- plants. The rate of CO₂ exchange per plant measured at 0.5% CO₂ in plants grown under this carbon dioxide concentration was 1.8 times higher than in control plants grown and measured at a low CO₂ concentration. Within the range of the studied CO₂ concentrations, the net photosynthesis measured at 0.5% CO₂ in the plants previously grown at this level of CO₂ content in the air was enhanced only due to the rise in CO₂ concentration used by plants as a substrate for carboxylation. However, in the CO₂-plants, the rate of photosynthesis measured at 0.03 and 0.5% CO₂ and calculated per dry weight unit was lower than that in the control plants. The causes of limitations imposed on photosynthesis at a higher CO₂ concentration are discussed. It is proposed that accumulation of sugars induced a nonstomatal limitation of photosynthesis in the CO₂-plants. An increase in the root/shoot ratio indicates some changes in the hormonal status of plants under the influence of a high CO₂ concentration.

KEYWORDS: CARBON DIOXIDE, CHLOROPLAST

1613

Muellerdombois, D. 1992. Potential effects of the increase in carbon-dioxide and climate change on the dynamics of vegetation. *Water, Air, and Soil Pollution* 64(1-2):61-79.

The continued CO₂ loading of the atmosphere appears to be responsible for inducing three new force factors controlling dynamic changes in the world's vegetation. They come from (1) enhanced fertilization with the single most important plant nutrient, (2) the widely expected global temperature increase, and (3) aggravated weather disturbances. Increased CO₂ absorption may enhance plant growth but it may also increase soil-nutrient limitations. It surely will enhance the metabolism of forest trees similarly as global warming will enhance plant metabolism, but both factors may also shorten the lifespan of perennial plants. Increased weather disturbances can be expected to produce new physiological stresses on the standing vegetation, particularly on habitats with poor soils. Since wide-spread forest decline has been reported from both the Atlantic and Pacific region, it seems possible that the roughly synchronic mass mortality of trees during the past two decades is related to the global increase in CO₂. The paper gives an overview of forest decline and dieback as known from past and present research and suggests how the changing atmospheric environment may interact in this widely observed contemporary Phenomenon of vegetation dynamics.

KEYWORDS: CANOPY DIEBACK, DECLINE, ECOSYSTEMS, EL-NINO, FORESTS, ISLANDS, MORTALITY, NEW-ZEALAND, SENESCENCE, STAND-LEVEL DIEBACK

1614

Mulchi, C., B. Rudorff, E. Lee, R. Rowland, and R. Pausch. 1995. Morphological responses among crop species to full-season exposures to enhanced concentrations of atmospheric CO₂ and O₃. *Water, Air, and Soil Pollution* 85(3):1379-1386.

Field studies using open-top chambers were conducted at USDA- BARC involving the growth of soybeans ('89 & '90), wheat ('91 & '92), and corn ('91), under increased concentrations of atmospheric CO₂ and O₃. Treatment responses were compared in all cases to plants grown in charcoal-filtered (CF) air (seasonal 7-h mean = 25 ± 3 n mol O₃ mol(-1)) having 350 or 500 μmol CO₂ mol(-1). Elevated seasonal O₃

levels for the soybean, wheat, and corn studies averaged 72.2 +/- 4, 62.7 +/- 2, and 70.2 n mol O-3 mol(-1), respectively. Results presented were obtained for plants grown in silt loam soil under well-watered conditions. Grain yield increases in response to elevated CO₂ in the absence of O-3 stress averaged 9.0, 12.0, and 1.0% for soybean, wheat, and corn, respectively. Reductions in grain yields in response to the elevated O-3 treatments at 350 mu mol CO₂ mol(-1) averaged 20.0, 29.0 and 13.0% for soybean, wheat, and corn, respectively. Reductions in grain yields in response to elevated O-3 at 500 mu mol CO₂ mol(-1) averaged 20.0, 8.0, and 7.0% for soybean, wheat, and corn, respectively. Dry biomass and harvest index in wheat were significantly reduced by O-3 stress at 350 mu mol mol(-1) CO₂ but not at 500 u mol mol(-1) CO₂. Seed weight 1000(-1) for soybeans and wheat was significantly increased by CO₂ enrichment and decreased by O-3 stress. Seed weight 1000(-1) in corn was increased by O-3 stress suggesting that O-3 affected pollination resulting in fewer kernels per ear.

KEYWORDS: CARBON DIOXIDE

1615

Mulholland, B.J., J. Craigon, C.R. Black, J.J. Colls, J. Atherton, and G. Landon. 1997. Effects of elevated carbon dioxide and ozone on the growth and yield of spring wheat (*Triticum aestivum* L.). *Journal of Experimental Botany* 48(306):113-122.

Spring wheat cv. Minaret was grown under three carbon dioxide (CO₂) and two ozone (O-3) concentrations from seedling emergence to maturity in open-top chambers. Under elevated CO₂ concentrations, the green leaf area index of the main shoot was increased, largely due to an increase in green leaf area duration. Biomass increased linearly in response to increasing CO₂ (ambient, 550 and 680 ppm). At anthesis, stem and ear dry weights and plant height were increased by up to 174%, 5% and 9 cm, respectively, and biomass at maturity was 23% greater in the 680 ppm treatment as compared to the ambient control. Grain numbers per spikelet and per ear were increased by 0.2 and 5 grains, respectively, and this, coupled with a higher number of ears bearing tillers, increased grain yield by up to 33%. Exposure to a 7 h daily mean O-3 concentration of 60 ppb induced premature leaf senescence during early vegetative growth (leaves 1-7) under ambient CO₂ concentrations. Damage to the main shoot and possible seedling mortality during the first 3 weeks of exposure altered canopy structure and increased the proportion of tillers 1 and 2 which survived to produce ears at maturity was increased; as a result, grain yield was not significantly affected. In contrast to the older leaves, the flag leaf (leaf 8) sustained no visible O-3 damage, and mean grain yield per ear was not affected. Interactions between elevated CO₂ and O-3 influenced the severity of visible leaf damage (leaves 1-7), with elevated CO₂ apparently protecting against O-3-induced premature senescence during early vegetative growth. The data suggest that the flag leaf of Minaret, a major source of assimilate during grain fill, may be relatively insensitive to O-3 exposure. Possible mechanisms involved in damage and/or recovery are discussed.

KEYWORDS: CEREALS, CO₂-ENRICHMENT, DRY-WEIGHT, GRAIN QUALITY, IMPACTS, NITROGEN, O-3, PHOTOSYNTHESIS, PLANT-RESPONSES, VEGETATION

1616

Mulholland, B.J., J. Craigon, C.R. Black, J.J. Colls, J. Atherton, and G. Landon. 1997. Impact of elevated atmospheric CO₂ and O-3 on gas exchange and chlorophyll content in spring wheat (*Triticum aestivum* L.). *Journal of Experimental Botany* 48(315):1853-1863.

Stands of spring wheat grown in open-top chambers (OTCs) were used to assess the individual and interactive effects of season-long exposure to elevated atmospheric carbon dioxide (CO₂) and ozone (O-3) on the photosynthetic and gas exchange properties of leaves of differing age

and position within the canopy. The observed effects were related to estimated ozone fluxes to individual leaves. Foliar chlorophyll content was unaffected by elevated CO₂, but photosynthesis under saturating irradiances was increased by up to 100% at 680 mu mol mol(-1) CO₂ relative to the ambient CO₂ control; instantaneous water use efficiency was improved by a combination of increased photosynthesis and reduced transpiration. Exposure to a seasonal mean O-3 concentration (7 h d(-1)) of 84 nmol mol(-1) under ambient CO₂ accelerated leaf senescence following full expansion, at which time chlorophyll content was unaffected. Stomatal regulation of pollutant uptake was limited since estimated O-3 fluxes to individual leaves were not reduced by elevated atmospheric CO₂. A common feature of O-3-treated leaves under ambient CO₂ was an initial stimulation of photosynthesis and stomatal conductance for up to 4 d and 10 d, respectively, after full leaf expansion, but thereafter both variables declined rapidly. The O-3-induced decline in chlorophyll content was less rapid under elevated CO₂ and photosynthesis was increased relative to the ambient CO₂ treatment. A/C-i analyses suggested that an increase in the amount of in vivo active RuBisCO may be involved in mitigating O-3-induced damage to leaves. The results obtained suggest that elevated atmospheric CO₂ has an important role in restricting the damaging effects of O-3 on photosynthetic activity during the vegetative growth of spring wheat, and that additional direct effects on reproductive development were responsible for the substantial reductions in grain yield obtained at final harvest, against which elevated CO₂ provided little or no protection.

KEYWORDS: AIR-POLLUTANTS, BISPHTHOSPHATE CARBOXYLASE OXYGENASE, BRASSICA-NAPUS L, CARBON DIOXIDE, NET PHOTOSYNTHESIS, PHOTOSYNTHETIC ACCLIMATION, PLANT-RESPONSES, REPRODUCTIVE DEVELOPMENT, VICIA-FABA L, WATER-USE EFFICIENCY

1617

Mulholland, B.J., J. Craigon, C.R. Black, J.J. Colls, J. Atherton, and G. Landon. 1998. Effects of elevated CO₂ and O-3 on the rate and duration of grain growth and harvest index in spring wheat (*Triticum aestivum* L.). *Global Change Biology* 4(6):627-635.

Wheat (*Triticum aestivum* L.) cv. Minaret was grown in open-top chambers (OTCs) in 1995 and 1996 under three carbon dioxide (CO₂) and two ozone (O-3) levels. Plants were harvested regularly between anthesis and maturity to examine the rate of grain growth (dG/dt; mg d(-1)) and the rate of increase in harvest index (dHI/dt; % d(-1)). The duration of grain filling was not affected by elevated CO₂ or O-3, but was 12 days shorter in 1995, when the daily mean temperature was over 3 degrees C higher than in 1996. Season-long exposure to elevated CO₂ (680 mu mol mol(-1)) significantly increased the rate of grain growth in both years and mean grain weight at maturity (MGW) was up to 11% higher than in the chambered ambient air control (chAA; 383 mu mol mol(-1)). However, the increase in final yield obtained under elevated CO₂ relative to the chAA control in 1996 resulted primarily from a 27% increase in grain number per unit ground area. dG/dt was significantly reduced by elevated O-3 under ambient CO₂ conditions in 1995, but final grain yield was not affected because of a concurrent increase in grain number. Neither dG/dt nor dHI/dt were affected by the higher mean O-3 concentrations applied in 1996 (77 vs. 66 nmol mol(-1)); the differing effects of O-3 on grain growth in 1995 and 1996 observed in both the ambient and elevated CO₂ treatments may reflect the contrasting temperature environments experienced. Grain yield was nevertheless reduced under elevated O-3 in 1996, primarily because of a substantial decrease in grain number. The data obtained show that, although exposure to elevated CO₂ and O-3 individually or in combination may affect both dG/dt and dHI/dt, the presence of elevated CO₂ does not protect against substantial O-3-induced yield losses resulting from its direct deleterious impact on reproductive processes. The implications of these results for food production under future climatic conditions are considered.

KEYWORDS: BRASSICA-NAPUS L, CARBON DIOXIDE, CHRONIC OZONE, ENRICHMENT, IMPACT, QUALITY, RED WINTER-WHEAT, REPRODUCTIVE DEVELOPMENT, TEMPERATURE, YIELD

1618

Mulholland, B.J., J. Craigon, C.R. Black, J.J. Colls, J. Atherton, and G. Landon. 1998. Growth, light interception and yield responses of spring wheat (*Triticum aestivum* L.) grown under elevated CO₂ and O-3 in open-top chambers. *Global Change Biology* 4(2):121-130.

Spring wheat cv. Minaret was grown to maturity under three carbon dioxide (CO₂) and two ozone (O-3) concentrations in open-top chambers (OTC). Green leaf area index (LAI) was increased by elevated CO₂ under ambient O-3 conditions as a direct result of increases in tillering, rather than individual leaf areas. Yellow LAI was also greater in the 550 and 680 $\mu\text{mol mol}^{-1}$ CO₂ treatments than in the chambered ambient control; individual leaves on the main shoot senesced more rapidly under 550 $\mu\text{mol mol}^{-1}$ CO₂, but senescence was delayed at 680 $\mu\text{mol mol}^{-1}$ CO₂. Fractional light interception (f) during the vegetative period was up to 26% greater under 680 $\mu\text{mol mol}^{-1}$ CO₂ than in the control treatment, but seasonal accumulated intercepted radiation was only increased by 8%. As a result of greater carbon assimilation during canopy development, plants grown under elevated CO₂ were taller at anthesis and stem and ear biomass were 27 and 16% greater than in control plants. At maturity, yield was 30% greater in the 680 $\mu\text{mol mol}^{-1}$ CO₂ treatment, due to a combination of increases in the number of ears per m⁻², grain number per ear and individual grain weight (IGW). Exposure to a seasonal mean (7 h d⁻¹) of 84 nmol mol^{-1} O-3 under ambient CO₂ decreased green LAI and increased yellow LAI, thereby reducing both f and accumulated intercepted radiation by approximate to 16%. Individual leaves senesced completely 7- 28 days earlier than in control plants. At anthesis, the plants were shorter than controls and exhibited reductions in stem and ear biomass of 15 and 23%. Grain yield at maturity was decreased by 30% due to a combination of reductions in ear number m⁻², the numbers of grains per spikelet and per ear and IGW. The presence of elevated CO₂ reduced the rate of O-3- induced leaf senescence and resulted in the maintenance of a higher green LAI during vegetative growth under ambient CO₂ conditions. Grain yields at maturity were nevertheless lower than those obtained in the corresponding elevated CO₂ treatments in the absence of elevated O-3. Thus, although the presence of elevated CO₂ reduced the damaging impact of ozone on radiation interception and vegetative growth, substantial yield losses were nevertheless induced. These data suggest that spring wheat may be susceptible to O-3-induced injury during anthesis irrespective of the atmospheric CO₂ concentration. Possible deleterious mechanisms operating through effects on pollen viability, seed set and the duration of grain filling are discussed.

KEYWORDS: BRASSICA-NAPUS L, CARBON DIOXIDE, DRY-MATTER, ENRICHMENT, FIELD CHAMBERS, GRAIN QUALITY, OZONE, PHOTOSYNTHESIS, REPRODUCTIVE DEVELOPMENT, WINTER-WHEAT

1619

Muller, C., W. Reuter, W. Wehrmeyer, H. Dau, and H. Senger. 1993. Adaptation of the photosynthetic apparatus of *Anacystis nidulans* to irradiance and CO₂-concentration. *Botanica Acta* 106(6):480-487.

Homocontinuous cultures of the cyanobacterium *Anacystis nidulans* (syn. *Synechococcus* sp. PCC 6301) were grown at white light intensities of 2 and 20 W/M², and supplied with 0.03 and 3 % CO₂ enriched air. The mutual influence of these growth factors on the development of the photosynthetic apparatus was studied by analyses of the pigment content, by low temperature absorbance and fluorescence spectroscopy, by analyses of oxygen evolution light-saturation curves,

and by SDS PAGE of isolated phycobilisomes. The two growth factors, light and CO₂, distinctly affect the absorption cross section of the photosynthetic apparatus, which is expressed by its pigment pattern, excitation energy distribution and capacity. In response to low CO₂ concentrations, the phycocyanin/allophycocyanin ratios were lower and one linker polypeptide L(R)30, of the phycobilisomes was no longer detectable in SDS PAGE. Apparently, low CO₂ adaptation results in shorter phycobilisome rods. Specifically, upon adaptation to low light intensities, the chlorophyll and the phycocyanin content on a per cell basis increase by about 50 % suggesting a parallel increase in the amount of phycobilisomes and photosystem core-complexes. Low light adaptation and low CO₂ adaptation both cause a shift of the excitation energy distribution in favor of photosystem I. Variations in the content of the "anchor" polypeptides L(CM)60 and L(CM)75 are possibly related to changes in the excitation energy transfer from phycobilisomes to the photosystem II and photosystem I core-complexes.

KEYWORDS: ACCLIMATION, ALGA, ANABAENA, CYANOBACTERIA, LIGHT-INTENSITY, MASTIGOCLADUS-LAMINOSUS, MICROCYSTIS- AERUGINOSA, ORGANIZATION, PHYCOBILISOME STRUCTURE, REACTION CENTERS

1620

Muller, J. 1993. Dry-matter production, CO₂ exchange, carbohydrate and nitrogen- content of winter-wheat at elevated CO₂ concentration and drought stress. *Journal of Agronomy and Crop Science-Zeitschrift Fur Acker Und Pflanzenbau* 171(4):217-235.

Methods of mathematical modelling and simulation are being used to an increasing degree in estimating the effects of rising atmospheric CO₂ concentration and changing climatic conditions on agricultural ecosystems. In this context, detailed knowledge is required about the possible effects on crop growth and physiological processes. To this aim, the influence of an elevated CO₂ concentration and of drought stress on dry matter production, CO₂ exchange, and on carbohydrate and nitrogen content was studied in two winter wheat varieties from shooting to milk ripeness. Elevated CO₂ concentration leads to a compensation of drought stress and at optimal water supply to an increase of vegetative dry matter and of yield to the fourfold value. This effects were caused by enhanced growth of secondary tillers which were reduced in plants cultivated at atmospheric CO₂ concentration. Analogous effects in the development of ear organs were influenced additionally by competitive interactions between the developing organs. The content and the mass of ethanol soluble carbohydrates in leaves and stems were increased after the CO₂ treatment and exhausted more completely during the grain filling period after drought stress. Plants cultivated from shooting to milk ripeness at elevated CO₂ concentration showed a reduced response of net photosynthesis rate to increasing CO₂ concentration by comparison with untreated plants.

KEYWORDS: CARBON-DIOXIDE ENRICHMENT, CROP RESPONSES, DIFFERENT IRRADIANCES, ENVIRONMENTS, LEAVES, PHOTOSYNTHESIS, PLANT GROWTH, SPRING WHEAT, WATER-USE, YIELD

1621

Muller, M., D. Grill, and H. Guttenberger. 1994. The effects of interactions between ozone and CO₂ on the chromosomes of Norway spruce root-meristems. *Phyton-Annales Rei Botanicae* 34(2):321-335.

A Norway spruce (*Picea abies* (L.) Karsten) test system was used to study the immediate and after effects of increased ozone or elevated CO₂ or both, on root tip chromosomes. Five-year-old potted spruce trees were exposed in environmental chambers to elevated concentrations of ozone (0.1 cm³m⁻³) for the study of an immediate effect and to elevated concentrations of carbon dioxide (750 cm³m⁻³) and ozone (0.08 cm³m⁻³)

3) as single variables or in combination and then transferred to a field for the observation of an after effect. Elevated ozone caused an increased number of chromosomal abnormalities directly after finishing the fumigation and also 21 months later. Elevated CO₂ more likely induced a decrease rather than an increase in the number of chromosomal aberrations. The most common abnormalities were chromosome stickiness, in the form of connections, clumped metaphases and amorphous chromatin masses. An increased number of chromosomal aberrations especially chromosome stickiness reflects highly toxic effects, usually of an irreversible type leading to cell death.

1622

Munoz, M.T., P. Aguado, N. Ortega, M.I. Escibano, and C. Merodio. 1999. Regulation of ethylene and polyamine synthesis by elevated carbon dioxide in cherimoya fruit stored at ripening and chilling temperatures. *Australian Journal of Plant Physiology* 26(3):201-209.

In this study we focused on the effect of high CO₂ level (20%) on ethylene and polyamine biosynthesis in cherimoya (*Annona cherimola* Mill.) fruits stored at ripening (20 degrees C) and chilling (6 degrees C) temperatures. At ripening temperature, CO₂ inhibited ethylene production, but 1-aminocyclopropane-1-carboxylate (ACC) oxidase activity was similar to that in ripe control fruits. CO₂ treatment led to a decline in putrescine (Put) and a major accumulation of spermidine (Spd) and spermine (Spm) without any effect on arginine decarboxylase (ADC) activity. These results confirm the preferential transformation of Put to Spd and Spm in CO₂-treated fruits. At chilling temperature, the increase in ACC oxidase activity was inhibited and the V-max of ADC increased. A combination of chilling temperature storage and high CO₂ level led to suppression of basal ethylene production while ACC oxidase activity remained unchanged. In addition, fruits held at these conditions had higher polyamine titres than the untreated control. We propose that, in CO₂-treated fruits, the absence of autocatalytic or basal ethylene production, depending on the temperature, may be due to deviation of the S-adenosylmethionine (SAM) pool towards polyamine synthesis, primarily Spd and Spm.

KEYWORDS: 1-AMINOCYCLOPROPANE-1-CARBOXYLIC ACID, ACC SYNTHASE, ACCUMULATION, ARGININE DECARBOXYLASE, BIOSYNTHESIS, PEA-SEEDLINGS, SENESCENCE, SPERMIDINE, TOMATO FRUIT, ZUCCHINI SQUASH

1623

Munoz, M.T., M.I. Escibano, and C. Merodio. 1997. Ethanol metabolism in cherimoya fruit during storage at ambient and under high CO₂ atmospheres. *Journal of Horticultural Science* 72(3):363-370.

Cherimoya fruits (*Annona cherimola*, Mill.) were kept in 20% O₂ + 20% CO₂ for UP to 3 d at 20 degrees C and then transferred to air to study the effect of high CO₂ levels on fermentation enzymes, ethanol and acetaldehyde content and ripening evolution. Ethanol and acetaldehyde content increased during ripening in air mainly associated with the first respiration peak. At the end of the short-term high CO₂ treatment, cherimoya fruit had a lower aerobic respiration rate while concentrations of acetaldehyde and ethanol were greatly increased compared with those of air-control fruit. The activation of fermentation pathway by high CO₂ atmosphere is mainly due to an enhancement in pyruvate decarboxylase (PDC) activity. High CO₂ treatment prevented the ripening process but, after transfer to air a decrease in fermentation metabolism was recorded and fruit was able to ripen, showing a typical decrease in tissue pH.

KEYWORDS: ACETALDEHYDE, ALCOHOL-DEHYDROGENASE, ETHYLENE PRODUCTION, MILL, PEAR, PLANTS, PYRUVATE

DECARBOXYLASE, RESPIRATION

1624

Murage, E.N., N. Watashiro, and M. Masuda. 1996. Leaf chlorosis and carbon metabolism of eggplant in response to continuous light and carbon dioxide. *Scientia Horticulturae* 67(1-2):27-37.

Leaf chlorosis and carbon metabolism were examined in the youngest fully expanded leaves of eggplants (*Solanum melongena* L. cultivar 'Senryo') grown starting from the third true leaf stage (acropetally) under 12-h and 24-h (continuous) light periods for 6 days, and under continuous illumination with either 0, 6 or 12 h of carbon dioxide (CO₂)-free air per day for 10 days at a photosynthetic photon flux density (PPFD) of 100 $\mu\text{mol m}^{-2} \text{s}^{-1}$. The amount of (CO₂)-C-13 assimilated under continuous light was lower on Day 3 and declined even further on Day 6. On the contrary, starch accumulation and the levels of glucose and fructose were highest under continuous illumination and were at their maximum on the fourth day. However, no difference was observed in the amount of leaf sucrose formed in the 12- and 24-h light treatments. Leaves of plants continuously lit developed leaf chlorosis starting from the fourth day. Growing plants with 12 h of CO₂-free air per day drastically reduced the amounts of starch and sugar accumulated in the leaves, inhibited the development of chlorosis and enhanced the chlorophyll content. With either the 6 or 0 h of CO₂-free air per day, the plants grew better but the leaves accumulated large amounts of starch and sugars and finally developed mild and severe chlorosis, respectively. The results strongly implicated the involvement of carbon metabolism in the predisposition of leaf chlorosis observed under continuous light.

KEYWORDS: MAGNESIUM, PHOSPHATE SYNTHASE ACTIVITY, PHOTOPERIOD, PHOTOSYNTHETIC PERIOD DURATION, PLANTS, POTASSIUM, RHYTHMS, SOYBEAN LEAVES, STARCH

1625

Murakami, A., S.J. Kim, and Y. Fujita. 1997. Changes in photosystem stoichiometry in response to environmental conditions for cell growth observed with the cyanophyte *Synechocystis* PCC 6714. *Plant and Cell Physiology* 38(4):392-397.

Changes in photosystem stoichiometry in response to shift of environments for cell growth other than light regime were studied with the cyanophyte *Synechocystis* PCC 6714 in relation to the change induced by light-quality shift. Following two environment-shifts were examined: the shift of molecular form of inorganic carbon source for photosynthesis from CO₂ to HCO₃⁻ (CO₂ stress) and the increase in salinity of the medium with NaCl (0.5 M) (Na⁺ stress). Both CO₂ and Na⁺ stresses induced the increase in PSI abundance resulting in a higher PSI/PSII stoichiometry. CO₂ stress was found to elevate simultaneously Cyt c oxidase activity (V-max). The feature was the same as that caused by light-quality shift from preferential excitation of PSI to PSII (light stress) though the enhancement by either stress was smaller than that by light stress. Under our experimental conditions, PSI/PSII stoichiometry appeared to increase at a fairly constant rate to the basal level even when the basal level had been differently determined by the light-quality. Enhancing rates for PSI/PSII stoichiometry and for Cyt c oxidase activity were also similar to each other. Since the two stresses affect the thylakoid electron transport similarly to the shift of light-quality, we interpreted our results as follows: three environmental stresses, CO₂, Na⁺, and light stresses, cause changes in electron turnover capacity of PSI and Cyt c oxidase under a similar, probably a common, mechanism for monitoring redox state of thylakoid electron transport system.

KEYWORDS: ANACYSTIS-NIDULANS, COMPLEX, CYANOBACTERIAL PHOTOSYNTHETIC SYSTEM, CYTOCHROME-OXIDASE, ELECTRON-TRANSPORT COMPOSITION, II LIGHT,

1626

Murchie, E.H., and P. Horton. 1997. Acclimation of photosynthesis to irradiance and spectral quality in British plant species: Chlorophyll content, photosynthetic capacity and habitat preference. *Plant, Cell and Environment* 20(4):438-448.

Twenty-two common British angiosperms were examined for their ability to acclimate photosynthetically to sun and shade conditions. Plants were grown under low irradiance, far-red enriched light (50 $\mu\text{mol m}^{-2} \text{s}^{-1}$), selected to mimic as closely as possible natural canopy shade, and moderately high light of insufficient irradiance to induce photoinhibitory or photoprotective responses (300 $\mu\text{mol m}^{-2} \text{s}^{-1}$). Light- and CO_2 -saturated photosynthetic rates of $\text{m}^2 \text{s}^{-1}$ oxygen evolution (P_{max}) and chlorophyll content were measured. Large variation was found in both parameters, and two 'strategies' for long-term acclimation were identified: firstly a change in chlorophyll per unit leaf area which was found to correlate positively with photosynthetic capacity, and secondly changes in chlorophyll a/b ratio and P_{max} , indicative of alterations at the chloroplast level, which were not associated with a change in chlorophyll content per unit leaf area. Combinations of these two strategies may occur, giving rise to the observed diversity in photosynthetic acclimation. The extent and nature of photosynthetic acclimation were compared with an index of shade association, calculated from the association each species has with woodland. It was found that the greatest flexibility for change at the chloroplast level was found in those species possessing an intermediate shade association, whilst acclimation in 'sun' species proceeded by a change in chlorophyll content; obligate shade species showed little capacity for acclimation at either the chloroplast or leaf level. A framework for explaining the variation between plant species in leaf-level photosynthetic capacity, in relation to the natural light environment, is presented. This is the first time the potential for light acclimation of photosynthesis in different plant species has been satisfactorily linked to habitat distribution.

KEYWORDS: ARABIDOPSIS-THALIANA, COMPONENTS, ELECTRON-TRANSPORT, GROWTH-CONDITIONS, LEAVES, LIGHT ENVIRONMENT, PEA-CHLOROPLASTS, PHOTOSYSTEM, SHADE PLANTS, THYLAKOID MEMBRANES

1627

Murchie, E.H., C. Sarrobert, P. Contard, T. Betsche, C.H. Foyer, and N. Galtier. 1999. Overexpression of sucrose-phosphate synthase in tomato plants grown with CO_2 enrichment leads to decreased foliar carbohydrate accumulation relative to untransformed controls. *Plant Physiology and Biochemistry* 37(4):251-260.

Tomato plants expressing the maize sucrose-phosphate synthase (SPS) cDNA under the control of the promoter of the small subunit of ribulose-1,5-bisphosphate carboxylase oxygenase (rbcS) promoter were grown 5 weeks in air (450 $\mu\text{mol m}^{-2} \text{s}^{-1}$ irradiance, 350 ppm CO_2) and then either maintained in air or exposed to CO_2 enrichment (1 000 ppm CO_2) for 8 d. A linear relationship between the foliar sucrose to starch ratio and maximal extractable SPS activity was found both in air and high CO_2 . Starch accumulation was dramatically increased in all plants subjected to CO_2 enrichment but the CO_2 -dependent increase in foliar starch accumulation was much lower in the leaves of the SPS transformants than in those of the untransformed controls in the same conditions. Maximal extractable ribulose-1,5-bisphosphate carboxylase/oxygenase activity was reduced by growth at high CO_2 to a similar extent in both plant types. The carbon/nitrogen ratios were similar in both plant lines in both growth conditions after 20 d exposure to high CO_2 . A small (5 %) increase in carbon export capacity was observed at high CO_2 in the leaves of transformed plants compared to leaves from untransformed controls. Increased foliar SPS activity did not, however,

prevent acclimation of photosynthesis in plants grown with long-term CO_2 enrichment. (C) Elsevier, Paris.

KEYWORDS: ACCLIMATION, CARBON, ELEVATED CO_2 , EXPRESSION, GENES, METABOLISM, NITROGEN, PHOTOSYNTHESIS, SINK REGULATION, TRANSCRIPT LEVELS

1628

Murphy, K.P., J.M. Santamaria, W.J. Davies, and P.J. Lumsden. 1998. Ventilation of culture vessels. I. Increased growth in vitro and survival ex vitro of Delphinium. *Journal of Horticultural Science & Biotechnology* 73(6):725-729.

Inclusion of small circular apertures covered with filters in the sides of plastic culture vessels led to a small but significant increase in the multiplication rate of Delphinium cultured in vitro and greater survival following transfer ex vitro. Filters had no effect on the multiplication rate and survival of Hosta. In vessels with apertures there was a large increase in the rate of water loss, but relative humidity was greater than 95% in both intact vessels and in vessels with filters. It is suggested that in vessels with apertures there was an increase in the flow of water vapour from the vessel atmosphere to the external atmosphere, due to a reduced diffusive resistance. The improved performance of Delphinium plants could have resulted from an increase in transpiration and movement of water (and therefore some nutrients) through the plants.

KEYWORDS: AERATION, CARBON DIOXIDE, CO_2 -ENRICHMENT, ETHYLENE, INVITRO, PLANTLETS, REDUCED HUMIDITY, RESISTANCE

1629

Murray, D.R. 1995. Plant-responses to carbon-dioxide. *American Journal of Botany* 82(5):690-697.

The average atmospheric concentration of CO_2 will probably double before the end of next century. Many of the consequences for plant growth can and should be determined now. In this review the effects of $[\text{CO}_2]$ on a variety of plant processes are summarized: stomatal opening and closing; stomatal density; respiration; root morphogenesis; and flowering. The effects of growth under elevated $[\text{CO}_2]$ on crop yield and seed composition are also discussed. Adverse effects on the composition of C-3 cereal grains are clearly indicated.

KEYWORDS: DARK RESPIRATION, DRY-MATTER, ELEVATED ATMOSPHERIC CO_2 , GROWTH, GUARD-CELLS, PERENNIAL RYEGRASS, STOMATAL DENSITY, WATER-USE EFFICIENCY, WHITE CLOVER, ZOSTERA-CAPRICORN

1630

Murray, M.B., I.D. Leith, and P.G. Jarvis. 1996. The effect of long term CO_2 enrichment on the growth, biomass partitioning and mineral nutrition of Sitka spruce (*Picea sitchensis* (Bong) Carr). *Trees-Structure and Function* 10(6):393-402.

Sitka spruce [*Picea sitchensis* (Pong.) Carr.] seedlings were grown for 3 years in an outside control plot or in ambient (similar to 355 $\mu\text{mol mol}^{-1}$) or elevated (ambient + 350 $\mu\text{mol mol}^{-1}$) atmospheric CO_2 environments, within open top chambers (OTCs) at the Institute of Terrestrial Ecology, Edinburgh. Sequential harvests were carried out at the end of each growing season and throughout the 1991 growing season, five in all. Plants grown in elevated CO_2 had, (i) 35 and 10% larger root/shoot ratios at the end of the first and third season, respectively, (ii) significantly higher summer leader extension relative growth rates, which declined more rapidly in early autumn than ambient grown plants, (iii) after three growing seasons a significantly increased

mean annual relative growth rate, (iv) consistently lower foliar nutrient concentrations, and (v) after two growing seasons smaller total projected needle areas. Plants grown inside OTCs were taller, heavier and had a smaller root/shoot ratio than those grown outside the chambers. There was no effect of CO₂ concentration on Sitka spruce leaf characteristics, although leaf area ratio, specific leaf area and leaf weight ratio all fell throughout the course of the 3 year experiment.

KEYWORDS: ALLOCATION, BETULA-PENDULA ROTH, CARBON DIOXIDE, CASTANEA-SATIVA MILL, ELEVATED ATMOSPHERIC CO₂, NITROGEN, NUTRIENTS, PLANT-RESPONSES, SEEDLINGS, TREES

1631

Murray, M.B., R.I. Smith, I.D. Leith, D. Fowler, H.S.J. Lee, A.D. Friend, and P.G. Jarvis. 1994. Effects of elevated CO₂, nutrition and climatic warming on bud phenology in Sitka spruce (*Picea sitchensis*) and their impact on the risk of frost damage. *Tree Physiology* 14(7-9):691-706.

Effects of elevated CO₂, clone and plant nutrition on bud dormancy of Sitka spruce (*Picea sitchensis* (Bong.) Carr.) were examined. Sitka spruce seedlings were fumigated with ambient or elevated (ambient + 350 μmol mol⁻¹) concentrations of CO₂ in open-top chambers for three growing seasons. In 1991 and 1992, elevated CO₂ delayed bud burst in the spring and advanced bud set in the autumn. The effect of the open-top chamber on the thermal requirement for bud burst was greater than the effect of elevated CO₂ (50 and 30 day degrees (D(d)), respectively). In a second study, four clones of Sitka spruce taken from two provenances, at 43 and 54-degrees-N, were fumigated with ambient or elevated CO₂. There was a large natural variation in the timing of bud burst and bud set among the clones. Elevated CO₂ had no effect on bud dormancy of the Skidegate a clone, but it reduced the growing season of the North Bend b clone by 20 days. In a third study, Sitka spruce seedlings growing in ambient or elevated CO₂, were supplied with one of three nutrient regimes, low (0.1 x potential), medium (0.5 x potential) or high (2.0 x potential), using a method and solution based on the Ingstad technique. Elevated CO₂ did not affect bud dormancy in the high-nutrient treatment, but it reduced the growing season of plants in the low-nutrient treatment by 22 days. Increasing plant nutrient supply lengthened the growing season, plants flushed earlier in the spring and set bud later in the autumn. The effects of elevated CO₂ plus a 0, 2 or 4-degrees-C climatic warming on the timing of bud burst and the subsequent risk of frost damage were assessed using a simulation model and meteorological data from three sites, Edinburgh, Braemar and Masset. The model predicted that (i) doubling the CO₂ concentration in the absence of climatic warming, will delay the onset of bud burst at all three sites, (ii) climatic warming in ambient CO₂ will hasten bud burst and (iii) climatic warming in elevated CO₂ will hasten bud burst at Edinburgh and Braemar but to a lesser extent than climatic warming alone. At Masset, a 4-degrees-C warming was required to advance the date of bud burst of seedlings in the elevated CO₂ treatment. At all three sites, elevated CO₂ and climatic warming increased the mean daily temperature on the date of bud burst, thus reducing the risk of subsequent frost damage.

1632

Murthy, R., and P.M. Dougherty. 1997. Effect of carbon dioxide, fertilization and irrigation on loblolly pine branch morphology. *Trees-Structure and Function* 11(8):485-493.

Foliage and wood parameters of branches of 12-year-old loblolly pine (*Pinus taeda* L.) trees were characterized after 21 months of exposure to fertilizer, irrigation and elevated CO₂ treatments. Branches of loblolly pine trees were enclosed in plastic chambers and exposed to ambient,

ambient +175 and ambient +350 μmol mol⁻¹ CO₂ concentrations. Measurements of foliage and wood at the fascicle, flush and branch levels were made at the end of the 21 month study period. The +350 CO₂ treatment did not significantly increase fascicle radius or length but did increase the number of fascicles on the first flush. Fertilization significantly increased fascicle radius and length, while irrigation significantly increased number of fascicles and flush length of first flush. The +350 CO₂ treatment also significantly increased flush length of the first flush. Significant interaction of fertilization and irrigation with CO₂ was observed for fascicle length. Significant interactions of fertilization and irrigation were also observed for flush length, number of fascicles and fascicle length. Observed increases in fascicle radius, fascicle length, number of fascicles and flush length may have been responsible for the significantly higher flush leaf area observed for the all three treatments. Also, a combination of fertilization and irrigation increased leaf area by 82% compared to that in the control when averaged across CO₂ treatments. At the branch level +350 CO₂ treatment significantly increased shoot length but not the number of flushes on the branch. In general with the exception of bark density and total number of needle scales, neither fertilization nor irrigation had any significant effect on other branch level parameters. Results from this study indicate that with 'global change' an increase in CO₂ alone may increase leaf area via an increase in flush length and number of fascicles. Combining increases in CO₂ with fertilization and irrigation could greatly enhance leaf area which when coupled to observed increases in net photosynthesis as a result of elevated CO₂ could greatly increase productivity of loblolly pine trees.

KEYWORDS: ATMOSPHERIC CO₂ ENRICHMENT, ELEVATED CO₂, GROWTH-RESPONSES, LEAF-AREA, LIQUIDAMBAR-STYRACIFLUA, MINERAL NUTRITION, SEASONS, SPRUCE SEEDLINGS, TAEDA SEEDLINGS, WATER-STRESS

1633

Murthy, R., P.M. Dougherty, S.J. Zarnoch, and H.L. Allen. 1996. Effects of carbon dioxide, fertilization, and irrigation on photosynthetic capacity of loblolly pine trees. *Tree Physiology* 16(6):537-546.

Branches of nine-year-old loblolly pine trees grown in a 2 x 2 factorial combination of fertilization and irrigation were exposed for 11 months to ambient, ambient + 175, or ambient + 350 μmol mol⁻¹ CO₂. Rates of light-saturated net photosynthesis (A(max)), maximum stomatal conductance to water vapor (g(max)), and foliar nitrogen concentration (% dry mass) were assessed monthly from April 1993 until September 1993 on 1992 foliage (one-year-old) and from July 1993 to March 1994 on 1993 foliage (current-year). Rates of A(max) of foliage in the ambient + 175 CO₂ treatment and ambient + 350 were 32-47 and 83-91% greater, respectively, than that of foliage in the ambient CO₂ treatment. There was a statistically significant interaction between CO₂ treatment and fertilization or irrigation treatment on A(max) on only one measurement date for each age class of foliage. Light-saturated stomatal conductance to water vapor (g(max)) was significantly affected by CO₂ treatment on only four measurement dates. Light-saturated g(max) in winter was only 42% of summer g(max) even though soil water during winter was near field capacity and evaporative demand was low. Fertilization increased foliar N concentration by 30% over the study period when averaged across CO₂ treatments. During the study period, the ambient + 350 CO₂ treatment decreased average foliar N concentration of one-year-old foliage in the control, irrigated, fertilized and irrigated + fertilized plots by 5, 6.4, 9.6 and 11%, respectively, compared with one-year-old foliage in the corresponding ambient CO₂ treatments. The percent increase in A(max) due to CO₂ enrichment was similar in all irrigation and fertilization treatments and the effect persisted throughout the 11-month study period for both one-year-old and current-year foliage.

KEYWORDS: ATMOSPHERIC CO₂ CONCENTRATIONS, ELEVATED

CO₂, ENRICHMENT, GAS-EXCHANGE, GROWTH, NUTRITION, RESPONSES, SEEDLINGS, SOUR ORANGE TREES, WATER

1634

Murthy, R., S.J. Zarnoch, and P.M. Dougherty. 1997. Seasonal trends of light-saturated net photosynthesis and stomatal conductance of loblolly pine trees grown in contrasting environments of nutrition, water and carbon dioxide. *Plant, Cell and Environment* 20(5):558-568.

Repeated measures analysis was used to evaluate the effect of long-term CO₂ enhancement on seasonal trends of light-saturated rates of net photosynthesis (A(sat)) and stomatal conductance to water vapour (g(sat)) of 9-year-old loblolly pine (*Pinus taeda* L.) trees grown in a 2 x 2 factorial experimental design of nutrition and water. A significant interaction effect of CO₂ and nutrition on mean A(sat) was observed for juvenile foliage. Also, juvenile foliage exposed to + 350 $\mu\text{mol mol}^{-1}$ CO₂ had a higher rate of increase of A(sat) between late summer and early autumn. This would lead to a greater potential for recharging carbohydrate reserves for winter. Mature foliage was affected by CO₂, water and nutrient treatments in two ways. First, A(sat) was significantly increased as a result of elevated CO₂ in January, a period when stomatal conductance was only 47% of the maximum observed rate. Secondly, the rate of increase of A(sat) from winter to early spring was accelerated as a result of both nutrient + water and + 350 $\mu\text{mol mol}^{-1}$ CO₂ treatments. This accelerated response resulted in a greater potential for photosynthate production during the period when growth initiation occurred. Nutrient, water or carbon dioxide treatments did not significantly alter trends in g(sat) for mature or juvenile foliage. A significant nutrition x CO₂ interaction was observed for the mature foliage, suggesting that g(sat) increased with increasing CO₂ and nutrition. These results may have important consequences for the determination of the water use efficiency of loblolly pine. In spite of low g(sat) in the winter to early spring period, there was a substantial gain in A(sat) attributable to elevated CO₂ concentrations.

KEYWORDS: ATMOSPHERIC CO₂, BRANCH BAG, DIFFERENT IRRADIANCE LEVELS, ELEVATED CO₂, ENRICHMENT, FOLIAR GAS-EXCHANGE, LEAF, LIQUIDAMBAR- STYRACIFLUA, RESPONSES, TAEDA SEEDLINGS

1635

Muschak, M., L. Willmitzer, and J. Fisahn. 1999. Gas-exchange analysis of chloroplastic fructose-1,6-bisphosphatase antisense potatoes at different air humidities and at elevated CO₂. *Planta* 209(1):104-111.

Gas-exchange measurements were performed to analyze the leaf conductances and assimilation rates of potato (*Solanum tuberosum* L. cv. Desiree) plants expressing an antisense construct against chloroplastic fructose-1,6-bisphosphatase (FBPase, EC 3.1.3.11) in response to increasing photon flux densities, different relative air humidities and elevated CO₂ concentrations. Assimilation rates (A) and transpiration rates (E) were observed during a stepwise increase of photon flux density. These experiments were carried out under atmospheric conditions and in air containing 500 $\mu\text{mol mol}^{-1}$ CO₂. In both gas atmospheres, two levels of relative air humidity (60-70% and 70-80%) were applied in different sets of measurements. Intercellular CO₂ concentration, leaf conductance, air-to-leaf vapour pressure deficit, and instantaneous water-use efficiency (A/E) were determined. As expected, assimilation rates of the FBPase antisense plants were significantly reduced as compared to the wild type. Saturation of assimilation rates in transgenic plants occurred at a photon flux density of 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$, whereas saturation in wild type plants was observed at 600 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Elevated ambient CO₂ levels did not effect assimilation rates of transgenic plants. At 70-80% relative humidity and atmospheric CO₂ concentration the FBPase antisense plants had significantly higher leaf conductances than wild-

type plants while no difference emerged at 60-70%. These differences in leaf conductance vanished at elevated levels of ambient CO₂. Stomatal response to different relative air humidities was not affected by mesophyll photosynthetic activity. It is suggested that the regulation of stomatal opening upon changes in photon flux density is merely mediated by a signal transmitted from mesophyll cells, whereas the intercellular CO₂ concentration plays a minor role in this kind of stomatal response. The results are discussed with respect to stomatal control by environmental parameters and mesophyll photosynthesis.

KEYWORDS: ABCISIC- ACID, CARBON DIOXIDE, GROWTH, GUARD-CELLS, HIGHER-PLANTS, PHOTOSYNTHESIS, STOMATAL RESPONSES, VICIA-FABA L, VIOLAXANTHIN CYCLE, ZEAXANTHIN

1636

Musil, C.F., G.F. Midgley, and S.J.E. Wand. 1999. Carry-over of enhanced ultraviolet-B exposure effects to successive generations of a desert annual: interaction with atmospheric CO₂ and nutrient supply. *Global Change Biology* 5(3):311-329.

The performance of fifth generation offspring of a desert annual (*Dimorphotheca sinuata* DC.) were compared in the absence of UV-B, under variable atmospheric CO₂ and nutrient supply after four consecutive generations of concurrent exposure of their progenitors to UV-B at ambient (seasonal range: 2.55-8.85 $\text{kJ m}^{-2} \text{d}^{-1}$) and enhanced (seasonal range: 4.70-11.41 $\text{kJ m}^{-2} \text{d}^{-1}$) levels. Offspring of progenitors grown under elevated UV-B exhibited a diminished photosynthetic rate, a consequence of a reduced leaf density, and diminished foliar levels of carotenoids, polyphenolics and anthocyanins. Conversely nonstructural carbohydrate and chlorophyll b levels were increased. Altered physiology was accompanied by reduced apical dominance and earlier flowering, features generally considered under photomorphogenic control, increased branching and inflorescence production and greater partitioning of biomass to reproductive structures, but diminished seed production. Many of these changes were magnified under nutrient limitation and intensified under atmospheric CO₂ enriched conditions. The latter disagrees with current opinion that elevated CO₂ may reduce detrimental UVB effects, at least over the long-term. Observed correlations between seed production and polyphenolic, especially anthocyanin, levels in offspring, and indications of diminished lignification (thinner leaves, less robust stems and fewer lignified seeds set) all pointed to the involvement of the phenylpropanoid pathway in seed formation and plant structural development and its disruption during long-term UV-B exposure. Comparisons with earlier generations revealed trends with cumulative generations of enhanced UVB exposure of increasing chlorophyll b and nonstructural carbohydrates, decreasing polyphenolics and biomass allocation to vegetative structures, and diminishing seed production despite increasing biomass allocation to reproductive structures. Notwithstanding some physiological compensation (increased chlorophyll b), the accumulation and persistence of these ostensibly inherited changes in physiological and reproductive performance suggest a greater impact of elevated UV-B on vegetation, primary production and regeneration over the long-term than presently envisaged.

KEYWORDS: CARBON-DIOXIDE ENRICHMENT, CHLOROPHYLL CONTENT, ELEVATED CO₂, ELEVATIONAL GRADIENT, ETIOLATING TOMATO SEEDLINGS, HYPOCOTYL ELONGATION, PHOTON FLUX- DENSITY, POLYMORPHIC DIASPORES, TERRESTRIAL ECOSYSTEMS, UV-B

1637

Myers, D.A., R.B. Thomas, and E.H. Delucia. 1999. Photosynthetic capacity of loblolly pine (*Pinus taeda* L.) trees during the first year of carbon dioxide enrichment in a forest ecosystem. *Plant, Cell and Environment* 22(5):473-481.

Our objective was to assess the photosynthetic responses of loblolly pine trees (*Pinus taeda* L.) during the first full growth season (1997) at the Brookhaven National Lab/Duke University Free Air CO₂ Enrichment (FACE) experiment. Gas exchange, fluorescence characteristics, and leaf biochemistry of ambient CO₂ (control) needles and ambient + 20 Pa CO₂ (elevated) needles were examined five times during the year. The enhancement of photosynthesis by elevated CO₂ in mature loblolly pine trees varied across the season and was influenced by abiotic and biotic factors. Photosynthetic enhancement by elevated CO₂ was strongly correlated with leaf temperature. The magnitude of photosynthetic enhancement was zero in March but was as great as 52% later in the season. In March, reduced sink demand and lower temperatures resulted in lower net photosynthesis, lower carboxylation rates and higher excess energy dissipation from the elevated CO₂ needles than from control needles. The greatest photosynthetic enhancement by CO₂ enrichment was observed in July during a period of high temperature and low precipitation, and in September during recovery from this period of low precipitation. In July, loblolly pine trees in the control rings exhibited lower net photosynthetic rates, lower maximum rates of photosynthesis at saturating CO₂ and light, lower values of carboxylation and electron transport rates (modelled from A-C-i curves), lower total Rubisco activity, and lower photochemical quenching of fluorescence in comparison to other measurement periods. During this period of low precipitation trees in the elevated CO₂ rings exhibited reduced net photosynthesis and photochemical quenching of fluorescence, but there was little effect on light- and CO₂-saturated rates of photosynthesis, modelled rates of carboxylation or electron transport, or Rubisco activity. These first-year data will be used to compare with similar measurements from subsequent years of the FACE experiment in order to determine whether photosynthetic acclimation to CO₂ occurs in these canopy loblolly pine trees growing in a forest ecosystem.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO₂, C-3 PLANTS, ELEVATED CO₂, GAS-EXCHANGE, LEAF, LEAVES, NET PHOTOSYNTHESIS, STOMATAL CONDUCTANCE, TEMPERATURE

1638

Myers, R.E., D.E. Deyton, and C.E. Sams. 1996. Applying soybean oil to dormant peach trees alters internal atmosphere, reduces respiration, delays bloom, and thins flower buds. *Journal of the American Society for Horticultural Science* 121(1):96-100.

Dormant 'Georgia Belle' peach [*Prunus persica* (L.) Batsch.] trees were sprayed in early February 1992 with single applications of 0%, 2.5%, 5.0%, 10.0%, or 20.0% (v/v) crude soybean oil. 'Redhaven' trees were sprayed in February 1993 with single applications of 0%, 2.5%, 5.0%, 10.0%, or 15% degummed soybean oil. Additional treatments of two applications of 2.5% or 5.0% oil were included each year. Both crude and degummed soybean oil treatments interfered with escape of respiratory CO₂ from shoots and increased internal CO₂ concentrations in shoots for up to 8 days compared to untreated trees. Respiration rates, relative to controls, were decreased for 8 days following treatment, indicating a feedback inhibition of respiration by the elevated CO₂. Thus, an internal controlled atmosphere condition was created. Ethylene evolution was elevated for 28 days after treatment. Flower bud development was delayed by treating trees with 5% crude or degummed soybean oil. Trees treated with 10% crude or degummed soybean oil bloomed 6 days later than untreated trees. Repeated sprays of one half concentration delayed bloom an additional four days in 1992, but <1 day in 1993 compared to a single spray of the same total concentration. Application of soybean oil caused bud damage and reduced flower bud density (number of flower buds/cm branch length) at anthesis. In a trial comparing petroleum oil and degummed soybean oil, yields of trees treated with 6% or 9% soybean oil were 17% greater than the untreated trees and 29% more than petroleum treated trees. These results suggest that applying soybean oil delays date of peach bloom and may be used as a bloom thinner.

1639

Nadelhoffer, K.J., B.A. Emmett, P. Gundersen, O.J. Kjonaas, C.J. Koopmans, P. Schleppi, A. Tietema, and R.F. Wright. 1999. Nitrogen deposition makes a minor contribution to carbon sequestration in temperate forests. *Nature* 398(6723):145-148.

Humans have altered global nitrogen cycling such that more atmospheric N₂ is being converted ('fixed') into biologically reactive forms by anthropogenic activities than by all natural processes combined(1). In particular, nitrogen oxides emitted during fuel combustion and ammonia volatilized as a result of intensive agriculture have increased atmospheric nitrogen inputs (mostly NO₃ and NH₄) to temperate forests in the Northern Hemisphere(2-4). Because tree growth in northern temperate regions is typically nitrogen-limited(5), increased nitrogen deposition could have the effect of attenuating rising atmospheric CO₂ by stimulating the accumulation of forest biomass. Forest inventories indicate that the carbon contents of northern forests have increased concurrently with nitrogen deposition since the 1950s(6-8). In addition, variations in atmospheric CO₂ indicate a globally significant carbon sink in northern mid-latitude forest regions(9-12). It is unclear, however, whether elevated nitrogen deposition or other factors are the primary cause of carbon sequestration in northern forests. Here we use evidence from N-15-tracer studies in nine forests to show that elevated nitrogen deposition is unlikely to be a major contributor to the putative CO₂ sink in forested northern temperate regions.

KEYWORDS: ADDITIONS, BIOSPHERE, CO₂, CYCLE, MAINE, NITRATE, SINK, STORAGE, TERRESTRIAL ECOSYSTEMS, USA

1640

Naeem, S., L.J. Thompson, S.P. Lawler, J.H. Lawton, and R.M. Woodfin. 1995. Empirical-evidence that declining species-diversity may alter the performance of terrestrial ecosystems. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* 347(1321):249-262.

We examined experimentally the association between species diversity and ecosystem processes in a series of terrestrial mesocosms. We developed and maintained 14 mesocosms whose biota were assembled from a single pool of plant and animal species and whose environmental conditions were identically controlled. Each community contained four trophic levels: primary producers (annual herbs), consumers (herbivorous molluscs and phloem sucking insects), secondary consumers (parasitoids) and decomposers (earthworms, Collembola and microbes). All mesocosms received the same diurnal pattern of light, temperature, relative humidity and water. The initial volume of soil, soil structure, composition, nutrient content and inocula of both soil microbes and nematodes were also identical among replicates. The only experimentally manipulated factor was the number of plant and animal species within each trophic level. High, medium and low diversity communities had nine, 15 or 31 plant and animal species, respectively. We measured five ecosystem processes as response variables in these mesocosms over the course of 206 days: (i) community respiration; (ii) productivity; (iii) decomposition; (iv) nutrient retention; and (v) water retention. The manipulation of diversity produced communities that differed significantly in their ecosystem processes. Our results provide the first evidence (obtained by a direct manipulation of diversity under controlled environmental conditions) that ecosystem processes may be affected by loss of diversity.

KEYWORDS: BIODIVERSITY, CO₂, ELEVATED CARBON-DIOXIDE

1641

Nagy, J., K.F. Lewin, G.R. Hendrey, E. Hassinger, and R. Lamorte.

1994. FACE facility CO₂ concentration control and CO₂ use in 1990 and 1991. *Agricultural and Forest Meteorology* 70(1-4):31-48.

CO₂ treatment level control and CO₂ use are reported for free-air carbon dioxide enrichment (FACE) facility operations at the University of Arizona's Maricopa Agricultural Center in 1990 and 1991. These are required for evaluation of the validity of biological experiments conducted in four replicates of paired experimental and control plots in a large cotton field and the cost-effectiveness of the plant fumigation facility. Gas concentration was controlled to 550 μmol mol⁻¹ at the center of each experimental plot, just above the canopy. In both years, season-long (April-September) average CO₂ levels during treatment hours (05:00-19:00 h Mountain Standard Time) were 550 μmol mol⁻¹ measured at treatment plot centers when the facility was operating. Including downtime, the season average was 548 μmol mol⁻¹ in 1991. In 1990, the season averages for the four elevated CO₂ treatments varied from 522 to 544 μmol mol⁻¹, owing to extended periods of downtime after lightning damage. Ambient CO₂ concentration during treatment was 370 μmol mol⁻¹. Instantaneous measurements of CO₂ concentration were within 10% of the target concentration of 550 μmol mol⁻¹ more than 65% of the time when the facility was operating, and 1 min averages were within 10% of the target concentration for 90% of the time. The long-term average of CO₂ concentration measured over the 20 m diameter experimental area of one array at the height of the canopy was in the range 550-580 μmol mol⁻¹ during July 1991, with the higher values near the edges. In 1991, CO₂ demand averaged 1250 kg per array per 14 h treatment day, or 4 kg m⁻² of fumigated plant canopy. The FACE facility provided good temporal and spatial control of CO₂ concentration and was a cost-effective method for large-scale field evaluations of the biological effects of CO₂.

KEYWORDS: FIELD CROPS, SYSTEM

1642

Naidu, S.L., and E.H. DeLucia. 1999. First-year growth response of trees in an intact forest exposed to elevated CO₂. *Global Change Biology* 5(5):609-613.

Although elevated atmospheric CO₂ has been shown to increase growth of tree seedlings and saplings, the response of intact forest ecosystems and established trees is unclear. We report results from the first large-scale experimental system designed to study the effects of elevated CO₂ on an intact forest with the full complement of species interactions and environmental stresses. During the first year of exposure to approximate 1.5 x ambient CO₂, canopy loblolly pine (*Pinus taeda*, L.) trees increased basal area growth rate by 24% but understorey trees of loblolly pine, sweetgum (*Liquidambar styraciflua* L.), and red maple (*Acer rubrum* L.) did not respond. Winged elm (*Ulmus alata* Michx.) had a marginally significant increase in growth rate (P=0.069). These data suggest that this ecosystem has the capacity to respond immediately to a step increase in atmospheric CO₂; however, as exposure time increases, nutrient limitations may reduce this initial growth stimulation.

KEYWORDS: ATMOSPHERIC CO₂, AVAILABILITY, CARBON DIOXIDE, GAS-EXCHANGE, LOBLOLLY-PINE, NITROGEN, PHOTOSYNTHESIS, PLANTS, SEEDLINGS, TAEDA

1643

Naidu, S.L., J.H. Sullivan, A.H. Teramura, and E.H. DeLucia. 1993. The effects of ultraviolet-B radiation on photosynthesis of different aged needles in field-grown loblolly-pine. *Tree Physiology* 12(2):151-162.

We examined the effect of supplemental UV-B radiation (290-320 nm) on photosynthetic characteristics of different aged needles of 3-year-old, field-grown loblolly pine (*Pinus taeda* L.). Needles in four age classes were examined: I, most recently fully expanded, year 3; II, first flush,

year 3; III, final flush, year 2; and IV, oldest needles still present, year 2. Enhanced UV-B radiation caused a statistically significant decrease (6%) in the ratio of variable to maximum fluorescence (F(v)/F(m)) following dark adaptation only in needles from the youngest age class, suggesting transient damage to photosynthesis. However, no effects of enhanced UV-B radiation on other instantaneous measures of photosynthesis, including maximum photosynthesis, apparent quantum yield and dark respiration, were seen for needles of any age. Foliar nitrogen concentration was unaffected by UV-B treatment. However, the C-13/C-12 carbon isotope ratios (delta C-13-a time integrated measure of photosynthetic function) of needles in age classes II and IV were 3% (P < 0.01) and 2% (P < 0.05) more negative, respectively, in treated plants than in control plants. Exposure to enhanced UV-B radiation caused a 20% decrease in total biomass and a 4% (P < 0.05), 25% (P < 0.01), and 9% (P < 0.01) decrease in needle length of needles in age classes I, II, and IV, respectively. The observed decreases in delta C-13, and F(v)/F(m) of the needles in the youngest needle age class suggest subtle damage to photosynthesis, although overall growth reductions were probably a result of decreased total leaf surface rather than decreased photosynthetic capacity. Needles of age class IV had lower light- and CO₂-saturated maximum photosynthetic rates (39%), lower dark respiration (34%), lower light saturation points (37%), lower foliar nitrogen concentration (28%), and lower delta C-13 (14%) values than needles of age class I. Apparent quantum yield and F(v)/F(m) did not change with needle age. The observed changes in photosynthesis and foliage chemical composition with needle age are consistent with previous studies of coniferous trees and may represent adaptations of older needles to shaded conditions within the canopy.

1644

Nakadai, T., H. Koizumi, Y. Usami, M. Satoh, and T. Oikawa. 1993. Examination of the method for measuring soil respiration in cultivated land - effect of carbon-dioxide concentration on soil respiration. *Ecological Research* 8(1):65-71.

An acceleration of soil respiration with decreasing CO₂ concentration was suggested in the field measurements. The result supports that obtained in laboratory experiments in our previous study. The CO₂ concentrations in a chamber of the alkali absorption method (the AA-method) were about 150-250 parts/10(6) lower than that in the atmosphere (about 350 parts/10(6)), while those observed in the open-flow IRGA method (the OF-method) were nearly equal to the soil surface CO₂ levels. The AA-method at such low CO₂ levels in the chamber appears to overestimate the soil respiration. Our results showed that the rates obtained by the AA-method were about twice as large as those by the OF-method in field and laboratory measurements. This finding has important consequences with respect to the validity of the existing data obtained by the AA-method and the estimation of changes in the terrestrial carbon flow with elevated CO₂ concentrations.

KEYWORDS: DYNAMICS, ECOSYSTEMS, EVOLUTION, GRASSLAND, LITTER, STORAGE, TEMPERATURE

1645

Nakamura, T., M. Osaki, T. Koike, Y.T. Hanba, E. Wada, and T. Tadano. 1997. Effect of CO₂ enrichment on carbon and nitrogen interaction in wheat and soybean. *Soil Science and Plant Nutrition* 43(4):789-798.

Effect of CO₂ enrichment on the carbon-nitrogen balance in whole plant and the acclimation of photosynthesis was studied in wheat (spring wheat) and soybean (A62-1 [nodulated] and A62-2 [non-nodulated]) with a combination of two nitrogen application rates (0 g N land area m(-2) and 30 g N land area m(-2)) and two temperature treatments (30/20 degrees C (day/night) and 26/16 degrees C). Results were as

follows. 1. Carbon (dry matter)-nitrogen balance of whole plant throughout growth was remarkably different between wheat and soybean, as follows: 1) in wheat, the relationship between the amount of dry matter (DMt) and amount of nitrogen absorbed (Nt) in whole plant was expressed by an exponential regression, in which the regression coefficient was affected by only the nitrogen application rate, and not by CO₂ and temperature treatments, and 2) in soybean the DMt-Nt relationship was basically expressed by a linear regression, in which the regression coefficient was only slightly affected by the nitrogen treatment (at ON, DMt-Nt balance finally converged to a linear regression). Thus, carbon-nitrogen interaction in wheat was strongly affected by the underground environment (nitrogen nutrition), but not by the above ground environment (CO₂ enrichment and temperature), while that in soybean was less affected by both under and above ground environments, 2. The photosynthetic response curve to CO₂ concentration in wheat and soybean was less affected by the CO₂ enrichment treatment, while that in wheat and soybean (A62-2) was affected by the nitrogen treatment, indicating that nitrogen nutrition is a more important factor for the regulation of photosynthesis regardless of the CO₂ enrichment, 3. Carbon isotope discrimination (d) in soybean was similar to that in wheat under ambient CO₂, while lower than that in wheat under CO₂ enrichment, suggesting that the carbon metabolism is considerably different between wheat and soybean under the CO₂ enrichment conditions.

KEYWORDS: ACCLIMATION, DIOXIDE CONCENTRATION, ELEVATED ATMOSPHERIC CO₂, FIELD CROPS, GAS-EXCHANGE, GROWTH, LONG-TERM EXPOSURE, PHOTOSYNTHETIC INHIBITION, PLANTS, RIBULOSE BIPHOSPHATE CARBOXYLASE

1646

Nakano, H., A. Makino, and T. Mae. 1997. The effect of elevated partial pressures of CO₂ on the relationship between photosynthetic capacity and N content in rice leaves. *Plant Physiology* 115(1):191-198.

The effects of growth CO₂ levels on the photosynthetic rates; the amounts of ribulose-1,5-bisphosphate carboxylase (Rubisco), chlorophyll (Chl), and cytochrome f; sucrose phosphate synthase activity; and total N content were examined in young, fully expanded leaves of rice (*Oryza sativa* L.). The plants were grown hydroponically under two CO₂ partial pressures of 36 and 100 Pa at three N concentrations. The light-saturated photosynthesis at 36 Pa CO₂ was lower in the plants grown in 100 Pa CO₂ than those grown in 36 Pa CO₂. Similarly, the amounts of Rubisco, Chl, and total N were decreased in the leaves of the plants grown in 100 Pa CO₂. However, regression analysis showed no differences between the two CO₂ treatments in the relationship between photosynthesis and total N or in the relationship between Rubisco and Chl and total N. Although a relative decrease in Rubisco to cytochrome f for sucrose phosphate synthase was found in the plants grown in 100 Pa CO₂, this was the result of a decrease in total N content by CO₂ enrichment. The activation state of Rubisco was also unaffected by growth CO₂ levels. Thus, decreases in the photosynthetic capacity of the plants grown in 100 Pa CO₂ could be simply accounted for by a decrease in the absolute amount of leaf N.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, C-3 PLANTS, ELECTRON-TRANSPORT, GAS-EXCHANGE, LONG-TERM EXPOSURE, NITROGEN NUTRITION, PHASEOLUS-VULGARIS L, RIBULOSE-1;5-BIPHOSPHATE CARBOXYLASE, SOYBEAN LEAVES, SUCROSE SYNTHESIS ENZYMES

1647

Nakayama, F.S., G. Huluka, B.A. Kimball, K.F. Lewin, J. Nagy, and G.R. Hendrey. 1994. Soil carbon-dioxide fluxes in natural and CO₂-enriched systems. *Agricultural and Forest Meteorology* 70(1-4):131-140.

Carbon dioxide fluxes between the soil and atmosphere were determined on the 1991 free-air carbon dioxide enrichment (FACE) experiment at the Maricopa Agricultural Center, Maricopa, Arizona. The study was conducted on drip-irrigated cotton in conjunction with other physical and physiological measurements. Fluxes were measured with a 1.6 l closed-chamber static sampling system. The main treatment for the open-air release study had two levels of CO₂-ambient air with CO₂ concentration of approximately 370 μmol mol⁻¹ (control) and CO₂-enriched air with CO₂ concentration of approximately 550 μmol mol⁻¹ (FACE). The enrichment was made over the daylight hours (05:00-19:00 h). Two quantities of water application, 'wet' (1050 mm) and 'dry' (790 mm), were superimposed on the two CO₂ levels. The observed soil CO₂ fluxes ranged from 2 to 8 μmol m⁻² s⁻¹ over the cultivation period. The CO₂ fluxes were significantly higher in the FACE than in the control plots, and also higher for the wet than for the dry irrigation level. In addition, an interaction between CO₂ and water levels was present. The CO₂ enrichment effect on soil CO₂ flux remained for approximately 4 weeks after the enrichment was ended. A detailed study on the procedure for determining flux indicated that some of the random and inconsistent flux values observed in the field could be attributed to a high CO₂ concentration present in the first of the two gas samples taken to estimate flux.

KEYWORDS: RESPIRATION

1648

Nakazawa, T., S. Murayama, M. Toi, M. Ishizawa, K. Otonashi, S. Aoki, and S. Yamamoto. 1997. Temporal variations of the CO₂ concentration and its carbon and oxygen isotopic ratios in a temperate forest in the central part of the main island of Japan. *Tellus Series B-Chemical and Physical Meteorology* 49(4):364-381.

Using discrete air sampling, values of delta(13)C and delta(18)O in atmospheric CO₂, as well as its concentration, were measured in a forest in the central part of the main island of Japan during the period from June 1994 to June 1996 to examine the biospheric contribution to their temporal variations. delta(13)C shows a prominent diurnal variation with high values in the daytime and low values in the nighttime, especially during the warm season. delta(13)C also vary seasonally, showing a maximum in summer and a minimum in spring. The diurnal and seasonal variations of delta(13)C are opposite in phase with those of the CO₂ concentration. The rate of change in delta(13)C with respect to the CO₂ concentration is found to be approximately -0.05 parts per thousand/ppmv. This suggests that the diurnal and seasonal variations of the CO₂ concentration are produced primarily by diurnally- and seasonally-dependent photosynthetic-respiratory processes of the biosphere near the observation site, respectively. In the warm season, delta(18)O also increases in the daytime and decreased in the nighttime, which is similar to the diurnal variation of delta(13)C, but opposite to that of the CO₂ concentration. The diurnal delta(18)O variation is thought to be caused by the release of isotopically heavy CO₂ during photosynthesis, and light CO₂ during respiration. However, an interpretation of the seasonal delta(18)O variation is found to be much more difficult than those of delta(13)C and the CO₂ concentration. This is likely due to complicated combinations of different seasonally varying fluxes of biospheric CO₂ into the atmosphere, as well as to various weather-dependent factors governing the delta(18)O composition in CO₂.

KEYWORDS: ABUNDANCE, ATMOSPHERIC WATER-VAPOR, DIOXIDE, ENRICHMENT, EXCHANGE, LEAF WATER, PACIFIC-OCEAN, REGION, SECULAR VARIATIONS, VEGETATION

1649

Napolitano, R., and M.P. Juarez. 1997. Entomopathogenous fungi degrade epicuticular hydrocarbons of *Triatoma infestans*. *Archives of*

Studies were undertaken to analyze the ability of entomopathogenous fungi to degrade insect hydrocarbons. Strains of *Beauveria bassiana* and *Metarhizium anisopliae* pathogenic to the blood-sucking bug *Triatoma infestans* were grown on hydrocarbon and non-hydrocarbon insect lipid extracts and on synthetic hydrocarbon-enriched media as the sole carbon source. Entomopathogenous fungi were shown to utilize hydrocarbons as the only carbon source for their growth. Insect-derived hydrocarbons served more efficiently as metabolic fuel rather than synthetic compounds of similar structure. [^3H]-Pentacosane, [$^{11,12}\text{-H-}^3$]-1,1-dimethylnonacosane, and [^{14}C]-hexadecane were catabolized into different amounts of polar lipids, free fatty acids, and acylglycerols. In experiments using the branched alkane, labeled hydrocarbons of different chain length than the precursor were also synthesized. Evidence of complete catabolism was obtained by a significant release of (CO_2)- ^{14}C from [^{14}C]-hexadecane. (CO_2)- ^{14}C production might be used as a simple method to compare hydrocarbon utilization by fungal strains. These data demonstrate that entomopathogenous fungi are able to transform a variety of hydrocarbon structures into different lipid products, part of which may be subsequently utilized for energy production and for the biosynthesis of cellular components. These data are the first evidence of hydrocarbon catabolism and synthesis in entomopathogenous fungi. (C) 1997 Academic Press.

KEYWORDS: ALKANES, INTEGUMENT, LIPIDS, NONHEME IRON PROTEIN, OMEGA-HYDROXYLASE, PSEUDOMONAS-OLEOVORANS

1650

Navarro, C., C. Teisson, F. Cote, and J. Ganry. 1994. Effects of light-intensity and CO_2 concentration on growth of banana plants (*Musa* spp., cultivar petite-naine) in-vitro and subsequent growth following acclimatization. *Scientia Horticulturae* 60(1-2):41-54.

The development of micropropagated banana plants during the in vitro growth phase prior to acclimatization was studied both in tight vessels under two different photosynthetic photon flux densities (PPFD of 30 and 240 $\mu\text{mol m}^{-2} \text{s}^{-1}$) and in continuously flushed vessels under three atmospheric CO_2 concentrations (0.034, 0.24 and 4.0%) at 240 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD. In tight vessels at low PPFD, the CO_2 originating from dark respiration was partially fixed during the light period, indicating photosynthetic activity by the plants in vitro. At high PPFD, CO_2 originating from dark respiration was rapidly fixed in the early hours of the light period and CO_2 concentration became the limiting factor for photosynthetic activity. Plants in vitro grown under high PPFD accumulated 2.3 times the dry matter achieved by plants in low PPFD. However, this developmental advantage acquired in vitro was not maintained ex vitro at the end of the acclimatization phase (on a leaf area basis). In continuously flushed vessels, treatments with 0.24% and 4.0% CO_2 -enriched atmospheres enhanced dry matter accumulation in vitro by 1.6 and 2.3 times, respectively, as compared to a 0.034% CO_2 treatment. Twenty days after transfer ex vitro, the development of plants (on a leaf area basis) from these CO_2 treatments was no longer significantly different. The relative growth rate ex vitro was lower for plants cultured in a CO_2 -enriched atmosphere in vitro than for those cultured at 0.034% CO_2 .

KEYWORDS: AERATION, CARBON DIOXIDE, CULTURES, ENRICHMENT, INVITRO, RASPBERRY, SOIL, STRAWBERRY

1651

Navas, M.L. 1998. Individual species performance and response of multispecific communities to elevated CO_2 : a review. *Functional Ecology* 12(5):721-727.

KEYWORDS: ATMOSPHERIC CO_2 , BIOMASS CARBON, CARBON DIOXIDE, COMPETITION, GROWTH-RESPONSES, PERENNIAL RYEGRASS, PLANT-POPULATIONS, POPULATION-DYNAMICS, SIZE HIERARCHIES, WHITE CLOVER

1652

Navas, M.L., E. Garnier, M.P. Austin, and R.M. Gifford. 1999. Effect of competition on the responses of grasses and legumes to elevated atmospheric CO_2 along a nitrogen gradient: differences between isolated plants, monocultures and multi-species mixtures. *New Phytologist* 143(2):323-331.

The responses to CO_2 of perennial grasses (*Danthonia richardsonii* and *Phalaris aquatica*) and legumes (*Lotus pedunculatus* and *Trifolium repens*) were compared under controlled conditions for isolated plants, monoculture stands and mixed-species stands along a N gradient to test whether: plant-plant interactions between species in mixed stands changed with concentration of CO_2 ; responses to CO_2 of species in mixtures could be related to their responses as single stands; responses of mixtures to CO_2 could be related to the responses of individual species to CO_2 and to competition. Plants were grown for 60 d in sand, using nutrient solutions (six nitrate concentrations from 0.25 to 16 mM NO_3), at ambient (c. 357 $\mu\text{mol l}^{-1}$) or elevated CO_2 (c. 712 $\mu\text{mol l}^{-1}$). Species dominance in the mixtures depended more on the range of N than of CO_2 concentration provided: *T. repens* and *L. pedunculatus* dominated at low concentrations of N; *L. pedunculatus* and *P. aquatica* performed better at high concentrations. Responses of species in mixtures to CO_2 were related to their responses in monocultures but not to those of isolated plants. Species biomass proportions in mixtures under ambient CO_2 determined the outcome of mixture responses to CO_2 more than of individual species responses to CO_2 . These results emphasize the influence of plant-plant interactions on community responses to CO_2 , since mixture behaviour under elevated CO_2 could not be scaled-up from responses by isolated plants in this experiment.

KEYWORDS: ANNUALS, BIOMASS, COMMUNITY, ENRICHMENT, FACE, GRASSLAND, GROWTH, LIGHT, SEASONS

1653

Navas, M.L., J.L. Guillermin, J. Fabreguettes, and J. Roy. 1995. The influence of elevated CO_2 on community structure, biomass and carbon balance of mediterranean old-field microcosms. *Global Change Biology* 1(5):325-335.

We studied the effects of a doubling of atmospheric CO_2 concentration on intact monoliths of Mediterranean grassland in growth chambers where climatic field conditions were simulated. During the six month growing season, changes in community structure were monitored by quantifying species richness and cover. The CO_2 exchange of microcosms was measured continuously and the resulting quantity and quality of biomass were evaluated. Species richness and cover did not respond to elevated CO_2 . After one month of treatment, CO_2 exchange measured during the day did not differ between CO_2 levels but the night respiration was two-fold higher under elevated CO_2 . Stimulations of both day and night CO_2 flux by short-term CO_2 enrichment were recorded several times during the growing season. These results suggest that despite some downward adjustment of photosynthesis, net canopy photosynthesis was stimulated by elevated CO_2 , but this stimulation was compensated for by an increased respiration. The 20% stimulation of final phytomass under elevated CO_2 was not significant: it resulted from unchanged live plant matter but a significant, 100% increase in litter accumulation. These results suggest that in low-productivity Mediterranean herbaceous systems, the greatest effect of CO_2 is not on the storage of carbon in biomass but on the turnover of the carbon in the plants.

KEYWORDS: AMBIENT, ATMOSPHERIC CO₂, C-3, DIOXIDE, ECOSYSTEM, ESTUARINE MARSH, GLOBAL CLIMATE-CHANGE, GROWTH, PLANTS, TUSSOCK TUNDRA

1654

Navas, M.L., L. Sonie, J. Richarte, and J. Roy. 1997. The influence of elevated CO₂ on species phenology, growth and reproduction in a Mediterranean old-field community. *Global Change Biology* 3(6):523-530.

We studied the effects on the phenology, growth and reproduction of 19 Mediterranean species, of elevating the atmospheric CO₂ concentration ([CO₂]) to twice-ambient. Intact monoliths were taken from an old-field and put, during a six month growing season, into growth chambers in which external climatic conditions were mimicked and [CO₂] was regulated. Fruit set time was significantly changed in six species under elevated [CO₂] and leaf and branch senescence accelerated in most species. Grasses had fewer leaves and legumes were more branched at peak production under elevated [CO₂] than under ambient. Plant seed number was not significantly changed under elevated [CO₂], whereas the reproductive effort of grasses was significantly depressed. Reproductive and vegetative characteristics showed related responses to [CO₂], as species with enhanced biomass had a hastened fruit set time, a higher number of fruits per plant and a higher reproductive biomass under elevated [CO₂] than under ambient conditions, while species with depressed biomass had a delayed fruit set time, a lower number of fruits per plant and a lower reproductive biomass. Our results also show a high interspecific variability in [CO₂] response, but some trends emerged at the family level: the production of vegetative and reproductive modules were depressed in grasses and slightly stimulated in legumes.

KEYWORDS: ALLOCATION, ALPINE GRASSLAND, ATMOSPHERIC CO₂, CARBON-DIOXIDE ENRICHMENT, DENSITY, DYNAMICS, PLANT GROWTH, RESPONSES, TEMPERATURE, YIELD

1655

Nederhoff, E.M. 1992. Effects of CO₂ on greenhouse grown eggplant (*Solanum melongena* L.). 1. Leaf conductance. *Journal of Horticultural Science* 67(6):795-803.

Leaf conductance of eggplant (*Solanum melongena* L., cv. Cosmos) was measured comparatively in two glasshouse compartments, with continuously low or high CO₂ (on average 415 or 685 $\mu\text{mol mol}^{-1}$, respectively). Measurements were carried out on eight days between February and June 1991 in an early planted crop. A regression equation was fitted to the data to account for the effects of PAR, air humidity and CO₂ on leaf conductance. Calculations with this equation demonstrated that leaf conductance was reduced by 10.2% per 100 $\mu\text{mol mol}^{-1}$ increase in CO₂, which is a three to four times stronger response than in other fruit vegetable crops. When, on some occasional days, CO₂ was kept equal in the two compartments, leaf conductance was not different, indicating that stomatal behaviour had not adapted to long lasting CO₂ conditions. The rate of crop transpiration, as estimated with the Penman-Monteith combination equation, was reduced by elevated CO₂ by only a few percent on average and by about 15% in a period of some weeks in spring.

KEYWORDS: ABSCISIC- ACID, AIR HUMIDITY, CROPS, ENRICHMENT, LEAVES, RESPONSES, WATER-STRESS

1656

Nederhoff, E.M., and R. Degraaf. 1993. Effects of CO₂ on leaf conductance and canopy transpiration of greenhouse-grown cucumber and tomato. *Journal of Horticultural Science* 68(6):925-937.

The effects of carbon dioxide (CO₂) on stomatal opening and canopy transpiration were investigated in cucumber (*Cucumis sativus* L., cv. Jessica) and tomato (*Lycopersicon esculentum* Mill., cv. Calypso). Stomatal opening (i.e. leaf conductance, g) was measured with a porometer, and canopy transpiration rate (E) with weighing lysimeters on intact plants in large greenhouses. Regression analysis was applied to account for the effects of radiation, air humidity, leaf temperature and CO₂ on g. The effect of CO₂ on E, which is primarily through g and secondarily through adjusted air humidity, was investigated by combining the regression equation for g with the Penman-Monteith equation for E. The relative effect of CO₂, as calculated with the fitted regression equations, was a decrease of about 4% in g for cucumber and of about 3% for tomato, per 100 $\mu\text{mol mol}^{-1}$ increase in CO₂, in the range of about 300 to 1200 $\mu\text{mol mol}^{-1}$ CO₂. The effect of CO₂ on E was smaller than on g and the extent of the effect depended on the conditions, mainly ventilation rate. The ratio K (relative change in calculated E divided by relative change in calculated g) was estimated at less than 0.2, except at low radiation. In reality, K will be even lower, because feedback mechanisms enforce the reduction in g and counteract the reduction in E. So the reduction of the transpiration rate of greenhouse cucumber and tomato caused by moderate CO₂ enrichment is small and mostly negligible, except under low light conditions.

KEYWORDS: CROPS, RADIATION, RESISTANCES

1657

Nederhoff, E.M., A.N.M. Dekoning, and A.A. Rijdsdijk. 1992. Leaf deformation and fruit production of glasshouse grown tomato (*Lycopersicon-esculentum* mill) as affected by CO₂ plant-density and pruning. *Journal of Horticultural Science* 67(3):411-420.

During summer, glasshouse grown tomato plants (*Lycopersicon esculentum* Mill.) often demonstrate leaf deformation, reduced leaf area (short leaves) and low Specific Leaf Area (SLA), sometimes accompanied by higher dry matter content of leaves and stems and higher leaf starch content. This so-called "Short Leaves Syndrome" (SLS), which decreases the production capacity, was investigated with emphasis on the effects of CO₂ concentration. As a working hypothesis it was postulated that SLS is indirectly caused by an oversupply of assimilates relative to the sink capacity. An experiment was conducted between 10 May and 31 July 1990 in 12 glasshouse compartments. The sink/source ratio was varied by maintaining two levels of CO₂, multifactorially combined with two plant densities and three pruning treatments. CO₂ enrichment and wider planting enhanced SLS and decreased leaf area and SLA of upper leaves. Leaf pruning and fruit pruning, however, did not give clear effects on vegetative characteristics, although the impact on the sink/source ratio was of the same order of magnitude. As a mechanism for these effects, we suggest that SLS is caused by calcium deficiency in the apex, a condition more severe when much phloem sap (with low calcium content) is available, i.e. when the sink/source ratio is lower. Stronger effects of CO₂ and plant density than of pruning on the incidence of SLS, may be due to local effects of sink/source relationships or to involvement of other processes, like transpiration. In crops with little SLS-symptoms, CO₂ enrichment increased the weight of fruits grown during the treatment period by 31%, whereas in crops with severe SLS, CO₂ enrichment aggravated SLS and had no significant effect on fruit production. CO₂ enrichment in summer is beneficial if SLS is prevented, which can be achieved by maintaining a higher plant density or, in an early crop, an extra shoot on the plants in spring and summer.

KEYWORDS: CALCIUM, CO₂- ENRICHMENT, DRY-MATTER

1658

Nederhoff, E.M., A.A. Rijdsdijk, and R. Degraaf. 1992. Leaf conductance and rate of crop transpiration of greenhouse grown sweet-

pepper (*capsicum-annuum-L*) as affected by carbon- dioxide. *Scientia Horticulturae* 52(4):283-301.

The effects of carbon dioxide concentration (CO₂) in the range 300-1100 $\mu\text{mol mol}^{-1}$ on leaf conductance (g) and rate of crop transpiration (E) of sweet pepper (*Capsicum annuum L.*) were investigated in spring 1990. In two greenhouse compartments (154 m²) that were simultaneously exposed to different CO₂ levels, leaf conductance of the upper leaves was measured with a steady state diffusion porometer and crop transpiration rates were measured with three weighing lysimeters per greenhouse compartment. Multiple regression equations, describing the effects of photosynthetic active radiation (PAR), vapour pressure deficit (VPD)-leaf-air, CO₂ and optionally leaf temperature on g, were fitted to the measured data. The fitted regression curves demonstrated that 100 $\mu\text{mol mol}^{-1}$ increase in CO₂ reduced g by about 3%, at any level of CO₂, VPD and PAR, if VPD and PAR would remain constant. Measured rates of crop transpiration were highly correlated to radiation and were in reasonable accordance with the Penman-Monteith combination equation. With this equation it was estimated that a 10% decrease in g would reduce E by 1.5-3% at high levels of g (high radiation) and by 4-7% at low g (dark weather), at least if VPD would remain constant. In a greenhouse-crop system, however, owing to thermal and hydrologic feedbacks, an increase in CO₂ leads to a considerable increase in VPD-leaf-air. This enforces the effect of CO₂ on g and counteracts the effect of CO₂ on E, because the driving force for transpiration is enhanced. Thus, in general the apparent response of g to changes in CO₂ is far greater than the mentioned percentage, whereas the apparent response of E is relatively small.

KEYWORDS: CO₂, LEAVES, RESISTANCES

1659

Neilson, R.P., and R.J. Drapek. 1998. Potentially complex biosphere responses to transient global warming. *Global Change Biology* 4(5):505-521.

Feedback interactions between terrestrial vegetation and climate could alter predictions of the responses of both systems to a doubling of atmospheric CO₂. Most previous analyses of biosphere responses to global warming have used output from equilibrium simulations of current and future climate, as compared to more recently available transient GCM simulations. We compared the vegetation responses to these two different classes of GCM simulation (equilibrium and transient) using an equilibrium vegetation distribution model, MAPSS. Average climatologies were extracted from the transient GCM simulations for current and doubled (2 x) CO₂ concentrations (taken to be 2070-2099) for use by the equilibrium vegetation model. However, the 2 x CO₂ climates extracted from the transient GCM simulations were not in equilibrium, having attained only about 65% of their eventual 2 x CO₂ equilibrium temperature change. Most of the differences in global vegetation response appeared to be related to a very different simulated change in the pole to tropic temperature gradient. Also, the transient scenarios produced much larger increases of precipitation in temperate latitudes, commensurate with a minimum in the latitudinal temperature change. Thus, the (equilibrium) global vegetation response, under the transient scenarios, tends more to a greening than a decline in vegetation density, as often previously simulated. It may be that much of the world could become greener during the early phases of global warming, only to reverse in later, more equilibrated stages. However, whether or not the world's vegetation experiences large drought-induced declines or perhaps large vegetation expansions in early stages could be determined by the degree to which elevated CO₂ will actually benefit natural vegetation, an issue still under debate. There may occur oscillations, perhaps on long timescales, between greener and drier phases, due to different frequency responses of the coupled ocean-atmosphere-biosphere interactions. Such oscillations would likely, of themselves, impart further reverberations to

the coupled Earth System.

KEYWORDS: ATMOSPHERE, BOREAL FOREST, CO₂, FEEDBACKS, HOLOCENE, MODEL, REGIONAL CLIMATE, SENSITIVITY, TROPICAL DEFORESTATION, VEGETATION

1660

Nemry, B., L. Francois, J.C. Gerard, A. Bondeau, and M. Heimann. 1999. Comparing global models of terrestrial net primary productivity (NPP): analysis of the seasonal atmospheric CO₂ signal. *Global Change Biology* 5:65-76.

Eight terrestrial biospheric models (TBMs) calculating the monthly distributions of both net primary productivity (NPP) and soil heterotrophic respiration (R-H) in the Potsdam NPP Model Intercomparison workshop are used to simulate seasonal patterns of atmospheric CO₂ concentration. For each model, we used net ecosystem productivity (NEP=NPP-R-H) as the source function in the TM2 atmospheric transport model from the Max- Planck Institute for Meteorology. Comparing the simulated concentration fields with detrended measurements from 25 monitoring stations spread over the world, we found that the decreasing seasonal amplitude from north to south is rather well reproduced by all the models, though the amplitudes are slightly too low in the north. The agreement between the simulated and observed seasonality is good in the northern hemisphere, but poor in the southern hemisphere, even when the ocean is accounted for. Based on a Fourier analysis of the calculated zonal atmospheric signals, tropical NEP plays a key role in the seasonal cycle of the atmospheric CO₂ in the whole southern hemisphere. The relatively poor match between measured and predicted atmospheric CO₂ in this hemisphere suggests problems with all the models. The simulation of water relations, a dominant regulator of NEP in the tropics, is a leading candidate for the source of these problems.

KEYWORDS: CARBON DIOXIDE, CYCLE, EXCHANGE, LAND BIOSPHERE, TRANSPORT, VEGETATION

1661

Newberry, R.M., and J. Wolfenden. 1996. Effects of elevated CO₂ and nutrient supply on the seasonal growth and morphology of *Agrostis capillaris*. *New Phytologist* 132(3):403-411.

Responses to elevated CO₂ have been studied using an upland grass species, *Agrostis capillaris* L. The plants were grown in sand culture with a range of N, P and K concentrations, in 'Solardome' growth chambers with either ambient air or a CO₂ concentration of 250 $\mu\text{mol mol}^{-1}$ above ambient. The interactive effects of high CO₂ and nutrient supply on plant growth and morphology were monitored throughout the growing season. *A. capillaris* exhibited positive growth responses to enhanced CO₂, even at limiting supplies of N and P. Moreover, greater shoot mass at elevated CO₂ was attributed to disproportionate increases in leaf and tiller number, resulting in an increase in the average leaf number per tiller. However, total leaf area remained unaffected, indicating that leaf size was reduced. There was no evidence of any acclimation in the growth response of *A. capillaris* to additional CO₂, even in N and P-stressed plants. On the contrary, a stimulation in leaf production was observed later in the growing season. A consistent interaction was observed between N and P concentrations, whereby the response to one element was greater at higher concentrations of the other. In addition, there were indications of competition among the three elements for uptake at the root. These findings indicate the importance of multifactorial nutrient experiments in developing an understanding of the complex relationships during CO₂ enrichment.

KEYWORDS: CARBON DIOXIDE, CROP RESPONSES,

1662

Newbery, R.M., J. Wolfenden, T.A. Mansfield, and A.F. Harrison. 1995. Nitrogen, phosphorus and potassium uptake and demand in *agrostis-capillaris* - the influence of elevated CO₂ and nutrient supply. *New Phytologist* 130(4):565-574.

Responses to elevated CO₂ have been studied using *Agrostis capillaris* L., an upland grass which is abundant on nutrient-poor soils. Plants were grown in sand culture with a wide range of nitrogen, phosphorus and potassium concentrations, and the impact of CO₂ on the demand for nutrients was determined using isotopic root bioassays. Plants grown with the smallest concentrations of N and P showed typical foliar symptoms associated with deficiency of these elements. However, even when supplies of N and P were limiting to growth, additional CO₂ (250 ppm above ambient) influenced neither total N nor total P in above-ground tissues, nor nutrient demands as indicated by the bioassay. The estimates of the demand of the plants for K from the Rb-86 bioassay indicated an appreciable increase when plants were raised in elevated CO₂. For plants of the same size with the same nutrient supply, those grown in elevated CO₂ consistently displayed an increased internal demand for K. Uptake of K was not, however, enhanced by elevated CO₂ even in non-limiting conditions and it might therefore be limited by a factor other than K supply. The overall conclusion from the experiments is that when *A. capillaris* is grown in elevated CO₂, uptake of N, P and K fails to increase proportionally with dry mass. This was true even when nutrient supplies were adequate, and it appears that nutrient-use-efficiency might increase to enable the plants to maintain growth in elevated CO₂.

KEYWORDS: ALLOCATION, AVAILABILITY, CARBON DIOXIDE, DRY-MATTER, ENRICHMENT, GROWTH, LIMITATION, NUTRITION, PHOTOSYNTHESIS, PLANTS

1663

Newman, J.A., D.J. Gibson, E. Hickam, M. Lorenz, E. Adams, L. Bybee, and R. Thompson. 1999. Elevated carbon dioxide results in smaller populations of the bird cherry-oat aphid *Rhopalosiphum padi*. *Ecological Entomology* 24(4):486-489.

KEYWORDS: ACCLIMATION, ALLOCATION, ATMOSPHERIC CO₂, CO₂-ENRICHMENT, HOMOPTERA, INFECTION, INSECT HERBIVORE, PLANTS, RESPONSES, SAGEBRUSH

1664

Newton, P.C.D. 1991. Direct effects of increasing carbon-dioxide on pasture plants and communities. *New Zealand Journal of Agricultural Research* 34(1):1-24.

The atmospheric carbon dioxide (CO₂) level is rising and is expected to double during the next century. This paper reviews information on the responses of pasture species and communities to elevated CO₂. Data for some further non-arable species are included where relevant. The effect of CO₂ on yield and on morphological and physiological characteristics are considered together with aspects of particular relevance to pasture, for example, herbivory, plant community relationships, and experimental methods for the exposure of pasture to elevated CO₂. At the plant level, physiological responses to CO₂ include enhanced net photosynthesis and reduced stomatal conductance; morphological changes include greater leaf areas, shoot production, and root:shoot ratios. Little is known about community responses or about plant-herbivore dynamics at elevated CO₂. Changes in herbage quality, tissue turnover, and botanical composition may be expected but confirmation of these responses will

only be possible when data are available from long-term studies of grazed pasture at elevated CO₂.

KEYWORDS: ATMOSPHERIC CO₂ CONCENTRATION, CLOVER TRIFOLIUM-REPENS, ELEVATED CO₂, GAS-EXCHANGE, LOLIUM-PERENNE, OLD-FIELD PERENNIALS, ORDERED DEVELOPMENT, PHOTOSYNTHETIC RESPONSE, WATER-USE, WHITE CLOVER

1665

Newton, P.C.D., C.C. Bell, and H. Clark. 1996. Carbon dioxide emissions from mineral springs in Northland and the potential of these sites for studying the effects of elevated carbon dioxide on pastures. *New Zealand Journal of Agricultural Research* 39(1):33-40.

Sites in Northland with mineral springs were examined for their potential as experimental areas to study the effects of elevated carbon dioxide (CO₂) on grassland. A suitable site was defined as having: (1) grassland species; (2) cold springs; (3) high levels of gas flow; and (4) high concentrations of CO₂. Two sites were selected for detailed study-Hakanoa Springs near Kamo and Waiare Spring near Kaeo. At Hakanoa, the vegetation was scrubby but at least 10 grassland species were present. Two vents released large volumes of CO₂ resulting in concentrations at 10 cm above ground level that ranged from 5000 μ l/litre near the vent to 400 μ l/litre 10 m downwind. At Waiare, the spring was situated in a grazed grass paddock that contained 10 grass species as well as *Trifolium repens* and *Lotus* spp. There was little enrichment of CO₂ above the canopy but high concentrations were measured at mid-canopy height with a maximum value exceeding 2000 μ l/litre. Because of the nature of the enrichment within, but not above the canopy, it appeared that the enrichment was from the soil. This was confirmed by measurements of soil CO₂ efflux that were consistently very high (greater than 9.9 g CO₂/m² per h in some instances). The springs have existed for decades and the sites offer the potential to study plant material that has been exposed to elevated CO₂ for very long periods.

KEYWORDS: CO₂ CONCENTRATIONS, COMMUNITIES, ENVIRONMENT, ESTUARINE MARSH, GROWTH

1666

Newton, P.C.D., H. Clark, C.C. Bell, and E.M. Glasgow. 1996. Interaction of soil moisture and elevated CO₂ on the above-ground growth rate, root length density and gas exchange of turves from temperate pasture. *Journal of Experimental Botany* 47(299):771-779.

Interactions between water availability and elevated atmospheric CO₂ concentrations have the potential to be important factors in determining future forage supply from temperate pastures. Using large turves from an established pasture, the response of these communities at 350 or 700 μ l(-l) CO₂ to a soil moisture deficit and to recovery from the deficit in comparison to turves that were well-watered throughout was measured. Prior to this experiment the turves had been exposed to the CO₂ treatments for 324 d. Net CO₂ exchange continued at elevated CO₂ even when the volumetric soil moisture content was less than 0.10 m³ m(-3) soil; at the same moisture deficit gas exchange at ambient CO₂ was zero. The additional carbon fixed by the elevated CO₂ turves was primarily allocated below-ground as shown by the maintenance of root length density at the same level as in well-watered turves. When the dry turves were rewatered there was compensatory growth at ambient CO₂ so that the above-ground growth rate exceeded that of turves that had not experienced a moisture deficit. At the start of this experiment, the turves that were growing at 700 μ l(-l) CO₂ had a greater proportion of legume (principally white clover, *Trifolium repens* L.) in the harvested herbage. There was a trend for the legume content at elevated CO₂ to be reduced under a soil moisture deficit. The results indicate different strategies in response to soil moisture deficits depending on the CO₂

concentration, At ambient CO₂, growth stopped, but plants were able to respond strongly on rewatering; while at elevated CO₂ growth continued (particularly belowground), but no additional growth was evident on rewatering. Ecosystem gas exchange measurements taken at the end of the experiment (after 429 d of exposure to CO₂) showed 33% more CO₂ was fixed at elevated CO₂ with only a small (12%) and nonsignificant downward regulation.

KEYWORDS: ATMOSPHERIC CO₂, CANOPY PHOTOSYNTHESIS, CARBON DIOXIDE, COMPETITION, ENRICHMENT, LOLIUM-PERENNE, PLANT GROWTH, RESPONSES, SEEDLINGS, WATER-USE

1667

Newton, P.C.D., H. Clark, C.C. Bell, E.M. Glasgow, and B.D. Campbell. 1994. Effects of elevated CO₂ and simulated seasonal-changes in temperature on the species composition and growth-rates of pasture turves. *Annals of Botany* 73(1):53-59.

KEYWORDS: ANNUALS, ATMOSPHERIC CARBON-DIOXIDE, COMMUNITIES, ECOSYSTEM, ENRICHMENT, NITROGEN, PERENNIAL RYEGRASS, PLANT GROWTH, RESPIRATION, WHITE CLOVER

1668

Newton, P.C.D., H. Clark, C.C. Bell, E.M. Glasgow, K.R. Tate, D.J. Ross, G.W. Yeates, and S. Saggarr. 1995. Plant growth and soil processes in temperate grassland communities at elevated CO₂. *Journal of Biogeography* 22(2-3):235-240.

Turves of a Mollic Psammaquent soil were used in controlled environment rooms to examine the response of managed temperate pasture communities to 350, 525 or 700 p.p.m. CO₂. Yield of herbage (regrowth over 3-week intervals) increased only slightly with higher CO₂; however, the botanical composition was markedly different. At elevated CO₂ *Paspalum dilatatum* (C4) and *Lolium perenne* (C3) declined as a proportion of harvested yield despite a stimulation of single leaf photosynthesis that was comparable to that found in *Trifolium repens*, a species that increased in abundance. Changes in species composition were largely a consequence of CO₂-induced differences in axillary bud activity. Net primary productivity below-ground was stimulated by CO₂. Soil CO₂-C production was greater in elevated CO₂ treatments, and was consistent with a greater input of herbage and root mass and/or metabolites and of more readily decomposable material. Levels of microbial biomass were unchanged, but enchytraeids were more abundant at elevated CO₂. Tracking of (CO₂)-C-14 into the various C pools also indicated a more rapid turnover of C at elevated CO₂ but no change in pool sizes. No consistent effects on net mineralization of N were observed.

KEYWORDS: ATMOSPHERIC CO₂, CARBON DIOXIDE, FEEDBACK, NITROGEN

1669

Nguyen, Q.T., T. Kozai, G. Niu, and U.V. Nguyen. 1998. Photosynthetic characteristics of coffee (*Coffea arabusta*) plantlets in vitro in response to different CO₂ concentrations and light intensities. *Plant Cell Tissue and Organ Culture* 55(2):133-139.

The photosynthetic characteristics of coffee (*Coffea arabusta*) plantlets cultured in vitro in response to different CO₂ concentrations inside the culture vessel and photosynthetic photon flux (PPF) were investigated preliminarily. The estimation of net photosynthetic rate (P-n) of coffee plantlets involved three methods: (1) estimating time courses of actual P-n in situ based on measuring CO₂ concentrations inside and outside

the vessel during a 45-day period, (2) estimating P-n in situ at different CO₂ concentrations and PPFs using the above measuring approach for 10-day and 30-day old in vitro plantlets, and (3) estimating P-n of a single leaf at different CO₂ concentrations and PPFs by using a portable photosynthesis measurement system for 45-day old in vitro coffee plantlets. The results showed that coffee plantlets in vitro had relatively high photosynthetic ability and that the P-n increased with the increase in CO₂ concentration inside the vessel. The CO₂ saturation point of in vitro coffee plantlets was high (4500-5000 μmol mol⁻¹); on the other hand, the PPF saturation point was not so high as compared to some other species, though it increased with increasing CO₂ concentration inside the vessel.

KEYWORDS: INVITRO

1670

Nicolas, M.E., R. Munns, A.B. Samarakoon, and R.M. Gifford. 1993. Elevated CO₂ improves the growth of wheat under salinity. *Australian Journal of Plant Physiology* 20(3):349-360.

Wheat plants (*Triticum aestivum* cv. Matong and *T. durum* cv. Modoc) were grown at ambient and elevated CO₂ (350 μmol m⁻³ above ambient) in soil with or without 150 mol m⁻³ NaCl for 6 weeks. The increase in dry matter, leaf area and tillering under high CO₂ was relatively greater under saline than non-saline conditions for both cultivars. Tillering was the primary component of growth affected by both salinity and high CO₂. Salinity greatly reduced tillering and high CO₂ partly reversed the effects of salinity. High CO₂ increased dry matter accumulation of the salt-sensitive Modoc to a greater extent (+104%) than that of the more salt-tolerant Matong (+73%) in the salt treatment. Transpiration rates were greatly reduced by salinity for both cultivars. Under high CO₂, increased leaf areas compensated for reduced transpiration rates per unit leaf area (i.e. greater stomatal closure), and total transpiration was little affected by CO₂ level within each treatment. The more salt-tolerant Matong showed greater stomatal closure and higher transpiration efficiencies than the salt-sensitive Modoc under salinity. High CO₂ reduced transpiration rate (per unit dry weight) by 40 to 50%, but did not significantly change the rate of sodium accumulation (per unit dry weight), indicating that salt uptake was largely independent of water uptake, and that high CO₂ did not increase growth by reducing the salt load. Our results suggest that high CO₂ increased growth by stimulating the development of tiller buds that would otherwise have been inhibited.

KEYWORDS: ATMOSPHERIC CO₂, BARLEY, CARBON DIOXIDE, CL CONCENTRATIONS, DRY-WEIGHT, ENRICHMENT, LEAF-AREA, NaCl-TREATED PLANTS, PHOTOSYNTHESIS, WATER-STRESS

1671

Nicolussi, K., S. Bortenschlager, and C. Korner. 1995. Increase in tree-ring width in sub-alpine *Pinus cembra* from the central alps that may be CO₂-related. *Trees-Structure and Function* 9(4):181-189.

It has been suggested many times that elevated atmospheric CO₂ levels should stimulate radial increment of stem growth. However, interpretation of dendrochronologies with respect to a CO₂ signal is a difficult task, since a multitude of environmental and tree factors influence the growth of stems. Here we provide a data set from subalpine stone pine which covers the period from 1750 to 1988, and from which growth rings of the 80- to 90-year age class were analysed. The most common climatological effects are taken into consideration. We found a steady and significant increase of mean ring width for the considered age class from approximately 1 mm per year in the middle of the last century to about 1.4 mm per year at present. Selected periods of equal mean summer temperatures in the last century and in more recent decades still yield a mean stimulation of about 25% for which atmospheric CO₂ enrichment appears to be the most plausible

explanation. The recent dramatic increase of atmospheric N-deposition could confound this interpretation, but chronologies of the last 2 decades during which wet and dry deposition of N-compounds showed the most dramatic increase exhibit no deviation from the long term trend. In contrast to the so far conflicting evidence of tree-ring responses to atmospheric changes the clear signal obtained here may be explained as follows: (1) stone pine produces little late season wood and moisture is never a limiting factor (particularly not in the early season); (2) comparatively good climatic records permitted the selection of thermally comparable periods; (3) trees grew under little spatial competition, (4) cores were collected well below the upper altitudinal range-limit of stone pine, leaving enough physiological leeway under episodic climatic stress, but (5) trees grew at altitudes high enough so that the reduction of the partial pressure of CO₂ could be expected to cause CO₂ to become relatively more limiting than at low elevations.

1672

Nie, D., H. He, M.B. Kirkham, and E.T. Kanemasu. 1992. Photosynthesis of a C3 grass and a C4 grass under elevated CO₂. *Photosynthetica* 26(2):189-198.

The net photosynthetic rate (P(N)), intercellular CO₂ concentration (C(i)), transpiration rate (E), stomatal resistance (r(s)), and water potential (PSI(W)) of a C3 grass (Kentucky bluegrass, *Poa pratensis* L.) and a C4 grass (big bluestem, *Andropogon gerardii* Vitman) growing in the spring in a tallgrass prairie under two levels of CO₂ (ambient and twice ambient) were compared. Elevated CO₂ (HC) increased P(N) of Kentucky bluegrass (C3) by 47.0 % but did not affect P(N) of big bluestem (C4). HC increased C(i) of both grasses by about the same amount (is-approximately-equal-to cm³ m⁻³), but reduced E (and parallelly increased r(s)) of big bluestem more than those of Kentucky bluegrass. HC increased PSI(W) of both grasses by about 30 %. Kentucky bluegrass had a lower PSI(W) than big bluestem, but HC increased PSI(W) of Kentucky bluegrass to values more similar to those of big bluestem under ambient CO₂ (LC). Hence a high PSI(W), resulting from HC, was necessary for a high P(N).

KEYWORDS: ANNUALS, ATMOSPHERIC CO₂, C-3, CARBON DIOXIDE, CLIMATE CHANGE, COMPETITION, ECOSYSTEMS, GROWTH, PLANTS

1673

Nie, D., H. He, G. Mo, M.B. Kirkham, and E.T. Kanemasu. 1992. Canopy photosynthesis and evapotranspiration of rangeland plants under doubled carbon-dioxide in closed-top chambers. *Agricultural and Forest Meteorology* 61(3-4):205-217.

It is important to know how the increasing atmospheric concentration of carbon dioxide (CO₂) will affect growth of agricultural plants. The objective of this study was to determine the effect of elevated CO₂ on canopy photosynthetic rate of prairie (rangeland) plants growing under natural field conditions. The dominant plants were warm-season grasses with the C4 type of photosynthesis. Sixteen closed-top, cylindrical, plastic chambers (1.5 m in diameter; 1.8 m tall) were placed on the prairie to maintain two levels of CO₂ (ambient and twice ambient) over a full growing season in 1990. The soil (silty clay loam) was kept at a high water (field capacity) or a low water level (no water added). Carbon dioxide concentration, air temperature, net radiation, canopy photosynthetic rate, and canopy evapotranspiration rate were measured in the 16 chambers on 49 sunny days during the season. The target value for high-CO₂ chambers was 720 cm³ CO₂ m⁻³; the measured mean concentrations varied from 710.8 to 720.1 cm³ CO₂ m⁻³. For chambers with ambient CO₂, the chamber-to-chamber variation was minor, with mean values ranging from 350.8 to 356.0 cm³ CO₂ m⁻³. Daytime air temperatures at 100 cm aboveground in the chambered plots averaged

2.7-degrees-C warmer than outside. Early in the season, net radiation was usually similar among chambers with the different CO₂ and water treatments, but late in the season, differences occurred among chambers, possibly because of the amount of tall grasses that shaded the radiometers. Under the high-water treatment, canopy photosynthesis of plants grown with doubled and ambient CO₂ averaged 41.8 μmol m⁻² s⁻¹ and 44.5 μmol m⁻² s⁻¹, respectively. These results are consistent with previous findings, which showed that the photosynthetic rate of C4 plants on rangeland was not augmented when the CO₂ concentration was increased. Under the low-water treatment, photosynthesis of plants grown with doubled CO₂ was slightly more (36.9 μmol m⁻² s⁻¹) than that of plants grown with ambient CO₂ (31.7 μmol m⁻² s⁻¹). This observation is in agreement with other results, which have shown that high CO₂ alleviates water-stress effects on plants. Elevated CO₂ reduced canopy evapotranspiration rate by 18 and 8%, under the high- and low-water levels, respectively. The results suggested that, as the CO₂ concentration in the atmosphere increases, water lost from rangelands will be reduced.

KEYWORDS: AMBIENT, WATER-USE

1674

Nie, D., M.B. Kirkham, L.K. Ballou, D.J. Lawlor, and E.T. Kanemasu. 1992. Changes in prairie vegetation under elevated carbon-dioxide levels and 2 soil-moisture regimes. *Journal of Vegetation Science* 3(5):673-678.

It is important to know how increasing levels of atmospheric CO₂ will affect native vegetation. The objective of this study was to determine the effect of elevated CO₂ concentrations on species composition in a tallgrass prairie kept at a high water level (730 mm of water in a 2000 mm soil profile) and a low water level (660 mm of water in 2000 mm). 16 cylindrical plastic chambers were placed on the prairie to maintain two levels of CO₂ (ambient or twice ambient) during two growing seasons in 1989 and 1990. Frequency of species was determined on 25 July 1989 and on 5 and 10 October 1990. At the beginning of the study, *Poa pratensis* (Kentucky bluegrass), the dominant C3 species, had the highest frequency of 43.3%, but decreased with time. However, at the end of the experiment and under the high soil-water level, there were more *P. pratensis* plants in the elevated CO₂ treatment (frequency: 13.5%) than in the ambient CO₂ treatment (1.0%). Under the low soil water regime, the reverse occurred (frequencies: 3.6 % and 11.0 % for high and low CO₂, respectively). The frequency of major C4 plants, *Andropogon gerardii* (big bluestem), *A. scoparius* (little bluestem) and *Sorghastrum nutans* (Indian grass) was not affected by CO₂. However, water did affect their frequency. Under low water, the frequency of *A. gerardii* decreased between 1989 and 1990. Under both soil moisture levels, the frequencies of *S. nutans* and *A. scoparius* increased. At the end of the study, Indian grass grown with high water had the highest frequency of all species on the prairie (frequency at the end of the study in October, 1990, of 44.4% and 47.4% for the high and low CO₂ levels, respectively). Unlike Indian grass, little bluestem grew better under low water conditions than under high water conditions. These results suggest that, if the climate becomes drier, *A. scoparius* will flourish more than *S. nutans* or *A. gerardii*, and *P. pratensis* may die out. Elevated CO₂ might not increase survival of C3 plants under dry conditions, if temperatures are too high for them.

1675

Nie, G.Y., D.L. Hendrix, S.P. Long, and A.N. Webber. 1995. The effect of elevated CO₂ concentration throughout the growth of a wheat crop in the field on the expression of photosynthetic genes in relation to carbohydrate accumulation. *Plant Physiology* 108(2):92.

1676

Nie, G.Y., D.L. Hendrix, A.N. Webber, B.A. Kimball, and S.P. Long. 1995. Increased accumulation of carbohydrates and decreased photosynthetic gene transcript levels in wheat grown at an elevated CO₂ concentration in the field. *Plant Physiology* 108(3):975-983.

Repression of photosynthetic genes by increased soluble carbohydrate concentrations may explain acclimation of photosynthesis to elevated CO₂ concentration. This hypothesis was examined in a field crop of spring wheat (*Triticum aestivum* L.) grown at both ambient (approximately 360 $\mu\text{mol mol}^{-1}$) and elevated (550 $\mu\text{mol mol}^{-1}$) atmospheric CO₂ concentrations using free-air CO₂ enrichment at Maricopa, Arizona. The correspondence of steady-state levels of mRNA transcripts (coding for the 83-kD photosystem I apoprotein, sedoheptulose-1,7-bisphosphatase, phosphoribulokinase, phosphoglycerokinase, and the large and small subunits of ribulose-1,5-bisphosphate carboxylase/oxygenase) with leaf carbohydrate concentrations (glucose-6-phosphate, glucose, fructose, sucrose, fructans, and starch) was examined at different stages of crop and leaf development and through the diurnal cycle. Overall only a weak correspondence between increased soluble carbohydrate concentrations and decreased levels for nuclear gene transcripts was found. The difference in soluble carbohydrate concentration between leaves grown at elevated and current ambient CO₂ concentrations diminished with crop development, whereas the difference in transcript levels increased. In the flag leaf, soluble carbohydrate concentrations declined markedly with the onset of grain filling; yet transcript levels also declined. The results suggest that, whereas the hypothesis may hold well in model laboratory systems, many other factors modified its significance in this field wheat crop.

KEYWORDS: ACCLIMATION, CARBON DIOXIDE, EXPRESSION, HIGH ATMOSPHERIC CO₂, LEAVES, LONG-TERM EXPOSURE, MESSENGER-RNA, NUCLEAR, RIBULOSE-1,5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, STARCH

1677

Nie, G.Y., S.P. Long, R.L. Garcia, B.A. Kimball, R.L. Lamorte, P.J. Pinter, G.W. Wall, and A.N. Webber. 1995. Effects of free-air CO₂ enrichment on the development of the photosynthetic apparatus in wheat, as indicated by changes in leaf proteins. *Plant, Cell and Environment* 18(8):855-864.

A spring wheat crop was grown at ambient and elevated (550 $\mu\text{mol mol}^{-1}$) CO₂ concentrations under free-air CO₂ enrichment (FACE) in the field. Four experimental blocks, each comprising 21-m-diameter FACE and control experimental areas, were used. CO₂ elevation was maintained day and night from crop emergence to final grain harvest. This experiment provided a unique opportunity to examine the hypothesis that CO₂ elevation in the field would lead to acclimatory changes within the photosynthetic apparatus under open field conditions and to assess whether acclimation was affected by crop developmental stage, leaf ontogeny and leaf age. Change in the photosynthetic apparatus was assessed by measuring changes in the composition of total leaf and thylakoid polypeptides separated by SDS-PAGE. For leaves at completion of emergence of the blade, growth at the elevated CO₂ concentration had no apparent effect on the amount of any of the major proteins of the photosynthetic apparatus regardless of the leaf examined. Leaf 5 on the main stem was in full sunlight at emergence, but then became shaded progressively as 3-4 further leaves formed above with continued development of the crop. By 35 d following completion of blade emergence, leaf 5 was in shade. At this point, the chlorophyll *a*/*b* ratio had declined by 26% both in plants grown at the control CO₂ concentration and in those grown at the elevated CO₂ concentration, which is indicative of shade acclimation. The ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) content declined by 45% in the control leaves, but by 60% in the leaves grown at the elevated CO₂

concentration. The light-harvesting complex of photosystem II (LHCII) and the chlorophyll content showed no decrease and no difference between treatments, indicating that the decrease in Rubisco was not an effect of earlier senescence in the leaves at the elevated CO₂ concentration. Following completion of the emergence of the flag-leaf blade, the elevated-CO₂ treatment inhibited the further accumulation of Rubisco which was apparent in control leaves over the subsequent 14 d. From this point onwards, the flag leaves from both treatments showed a loss of Rubisco, which was far more pronounced in the elevated-CO₂ treatment, so that by 36 d the Rubisco content of these leaves was just 70% of that of the controls and by 52 d it was only 20%. At 36 d, there was no decline in chlorophyll, LHCII or the chloroplast ATPase coupling factor (CFI) in the elevated CO₂ concentration treatment relative to the control. By 52 d, all of these proteins showed a significant decline relative to the control. This indicates that the decreased concentration of Rubisco at this final stage probably reflected earlier senescence in the elevated-CO₂ treatment, but that this was preceded by a CO₂-concentration-dependent decline in Rubisco.

KEYWORDS: ACCLIMATION, CARBON-DIOXIDE CONCENTRATION, ELEVATED CO₂, GROWTH, HIGH ATMOSPHERIC CO₂, LEAVES, RESPONSES, RIBULOSE-1,5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, SENESCENCE, TEMPERATURES

1678

Nie, G.Y., S.P. Long, and A. Webber. 1993. The effect of nitrogen supply on down-regulation of photosynthesis in spring wheat grown in an elevated CO₂ concentration. *Plant Physiology* 102(1):138.

1679

Nielsen, M.V. 1995. Photosynthetic characteristics of the coccolithophorid *emiliania-huxleyi* (prymnesiophyceae) exposed to elevated concentrations of dissolved inorganic carbon. *Journal of Phycology* 31(5):715-719.

Light-saturated photosynthesis (P-max) of *Emiliania huxleyi* (Lohmann) Hay et Mohler is known to be carbon-limited at natural concentrations of dissolved inorganic carbon (DIC). In the present study, light-limited and light-saturated photosynthetic rates of *E. huxleyi* were studied at three concentrations of DIC (2.4, 7.4, and 12.4 mM) for high-calcite (C-in/C-tot = 0.48) and low-calcite (C-in/C-tot = 0.08) cells of the same strain. The photosynthetic efficiency (α) and the maximum quantum yield ($\Phi(\text{max})$) increased by more than a factor of 2 from the lowest to the highest DIC level. P-max, α , and $\Phi(\text{max})$ were always higher for the high-calcite than for the low-calcite cells at identical DIC levels. This may indicate that the calcification process acts as an extra supplier of CO₂ for photosynthesis making the CO₂ shortage at natural DIC levels a little smaller for high-calcite than for low-calcite *E. huxleyi*. A dependency of $\Phi(\text{max})$ on DIC has not previously been shown for marine phytoplankton. $\Phi(\text{max})$ is a key parameter in recent biooptical models of phytoplankton productivity, and the results from the present study are therefore important for modeling the productivity of *E. huxleyi*.

KEYWORDS: ALGAE, CALCIFICATION, DIATOMS, DIOXIDE, GROWTH, LIGHT, LOHMANN KAMPTNER, PHYTOPLANKTON

1680

Niewiadomska, E., C. Gaucher-Veilleux, N. Chevrier, Y. Mauffette, and P. Dizengremel. 1999. Elevated CO₂ does not provide protection against ozone considering the activity of several antioxidant enzymes in the leaves of sugar maple. *Journal of Plant Physiology* 155(1):70-77.

Seedlings of sugar maple (*Acer saccharum* Marsch.) were exposed for 46 days to 700 ppm of CO₂, 200 ppb of ozone, and 700 ppm of CO₂ + 200 ppb of ozone. A significant increase in the activity of H₂O₂ scavenging enzymes, i.e. ascorbate peroxidase [EC 1.11.1.11] and catalase [EC 1.11.1.6], was measured due to the action of O₃. This increase was rather negatively affected by elevated CO₂. A tendency of decreased activity of glutathione reductase [EC 1.6.4.2] and superoxide dismutase [EC 1.15.1.1] due to the action of O₃ was detected. Elevated CO₂ does not provide enhanced tolerance to oxidative stress in the seedlings of sugar maple. Changes in the activity of antioxidant enzymes were more pronounced in the young leaves (developed during the experiment) than in the old leaves (developed before starting the experiment). Stimulation of chloroplastic FeSOD by elevated CO₂ was observed, indicating oxidative stress in chloroplasts evoked by elevated CO₂ level. This effect did not result in enhanced protection against the detrimental effect of ozone, most probably due to compartmentation of CO₂ and O₃ effects within the cell.

KEYWORDS: ASCORBATE PEROXIDASE, CARBON DIOXIDE, ENHANCED OZONE, GLUTATHIONE-REDUCTASE, HYDROGEN-PEROXIDE, NORWAY SPRUCE, PICEA-ABIES, PLANTS, STRESS RESPONSES, TOBACCO

1681

Niinemets, U., J.D. Tenhunen, N.R. Cantá, M.M. Chaves, T. Faria, J.S. Pereira, and J.F. Reynolds. 1999. Interactive effects of nitrogen and phosphorus on the acclimation potential of foliage photosynthetic properties of cork oak, *Quercus suber*, to elevated atmospheric CO₂ concentrations. *Global Change Biology* 5(4):455-470.

Leaf gas-exchange and chemical composition were investigated in seedlings of *Quercus suber* L. grown for 21 months either at elevated (700 $\mu\text{mol mol}^{-1}$) or normal (350 $\mu\text{mol mol}^{-1}$) ambient atmospheric CO₂ concentrations, [CO₂], in a sandy nutrient-poor soil with either 'high' N (0.3 mol N m⁻³ in the irrigation solution) or with 'low' N (0.05 mol N m⁻³) and with a constant suboptimal concentration of the other macro- and micronutrients. Although elevated [CO₂] yielded the greatest total plant biomass in 'high' nitrogen treatment, it resulted in lower leaf nutrient concentrations in all cases, independent of the nutrient addition regime, and in greater nonstructural carbohydrate concentrations. By contrast, nitrogen treatment did not affect foliar N concentrations, but resulted in lower phosphorus concentrations, suggesting that under lower N, P use-efficiency in foliar biomass production was lower. Phosphorus deficiency was evident in all treatments, as photosynthesis became CO₂ insensitive at intercellular CO₂ concentrations larger than approximate to 300 $\mu\text{mol mol}^{-1}$, and net assimilation rates measured at an ambient [CO₂] of 350 $\mu\text{mol mol}^{-1}$ or at 700 $\mu\text{mol mol}^{-1}$ were not significantly different. Moreover, there was a positive correlation of foliar P with maximum Rubisco (Ribulose-1,5-bisphosphate carboxylase/oxygenase) carboxylase activity (V_{cmax}), which potentially limits photosynthesis at low [CO₂], and the capacities of photosynthetic electron transport (J_{max}) and phosphate utilization (P_{max}), which are potentially limiting at high [CO₂]. None of these potential limits was correlated with foliar nitrogen concentration, indicating that photosynthetic N use-efficiency was directly dependent on foliar P availability. Though the tendencies were towards lower capacities of potential limitations of photosynthesis in high [CO₂] grown specimens, the effects were statistically insignificant, because of (i) large within-treatment variability related to foliar P, and (ii) small decreases in P/N ratio with increasing [CO₂], resulting in balanced changes in other foliar compounds potentially limiting carbon acquisition. The results of the current study indicate that under P-deficiency, the down-regulation of excess biochemical capacities proceeds in a similar manner in leaves grown under normal and elevated [CO₂], and also that foliar P/N ratios for optimum photosynthesis are likely to increase with increasing growth CO₂ concentrations.

KEYWORDS: C-3 PLANTS, CARBON DIOXIDE, ELECTRON-TRANSPORT, LEAF GAS- EXCHANGE, NUTRIENT CONCENTRATIONS, PHASEOLUS-VULGARIS L, PHOSPHATE CONCENTRATION, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE, STOMATAL CONDUCTANCE, WATER-USE EFFICIENCY

1682

Nijs, I., T. Behaeghe, and I. Impens. 1995. Leaf nitrogen content as a predictor of photosynthetic capacity in ambient and global change conditions. *Journal of Biogeography* 22(2-3):177-183.

Leaf assimilation capacity in *Lolium perenne*, grown in elevated CO₂ level (700 $\mu\text{mol mol}^{-1}$) and/or increased air temperature (ambient + 4 degrees C) could be predicted from leaf N content expressed on an area basis, although the linear relationships between maximum carboxylation rate (V_{cmax}) and leaf N depended on treatment. The model, based on Farquhar, Von Caemmerer & Berry (1980) showed negative long-term effects of increased air temperature on V_{cmax} and J_{max} while longterm exposure to increased CO₂ level affected only V_{cmax}. Acclimation responses to these global changes therefore could not be explained by changes in N-content alone, but also in terms of changes in photosynthetic nitrogen use efficiency. Stimulation of photosynthesis by elevated CO₂ was not affected by reduction of leaf N in leaves developed in ambient air temperature, while part of the CO₂ benefit was lost in leaves developed in increased air temperature. This suggests that N-deficient ecosystems maintain the potential to respond to elevated CO₂ concentration, unless other processes than the primary carbon metabolism become limiting at low N supply. Similar to nitrogen content, changes in photon flux density did not change the CO₂ benefit either, unless a transition occurred from one limiting process to another (electron transport to carboxylation or vice versa). Hypotheses on interaction between CO₂ level, nitrogen status of the leaf and light intensity are formulated to support these findings.

KEYWORDS: ASSIMILATION, C-3 PLANTS, CANOPY PHOTOSYNTHESIS, CO₂- ENRICHMENT, ELEVATED CO₂, GROWTH-RESPONSE, LEAVES, LIGHT, PLANT GROWTH, TEMPERATURE

1683

Nijs, I., R. Ferris, H. Blum, G. Hendrey, and I. Impens. 1997. Stomatal regulation in a changing climate: a field study using Free Air Temperature Increase (FATI) and Free Air CO₂ enrichment (FACE). *Plant, Cell and Environment* 20(8):1041-1050.

This study investigates effects of climate warming (+2.5 degrees C above ambient) and elevated CO₂ concentration (600 $\mu\text{mol mol}^{-1}$) on the stomatal functioning and the water relations of *Lolium perenne*, using Free Air Temperature Increase (FATI) and Free Air CO₂ Enrichment (FACE). Compared to growth at ambient temperature, whole-season temperature increase reduced leaf stomatal conductance, but only at the top of the canopy (-14.6 and -8.8% at ambient and elevated CO₂, respectively). However, because higher canopy temperature raised the leaf-to-air vapour pressure difference, leaf transpiration rate increased (+28% at ambient and +48% at elevated CO₂) and instantaneous leaf water use efficiency, derived from short-term measurements of assimilation and transpiration rate, declined (-11% at ambient and -13% at elevated CO₂). Nevertheless, at the stand level, growth at +2.5 degrees C reduced transpiration due to fewer tillers per plant and a smaller leaf area per tiller. This sparser vegetation was also more closely coupled to the atmosphere and maintained a drier internal microclimate. To assess whether the stomatal behaviour observed in this experiment could be explained by prevailing concepts of stomatal functioning, three models were applied (Cowan 1977; Ball,

Woodrow & Berry 1987; Leuning 1995), The latter model accounted for the highest proportion of variability in the data (58%) and was insensitive to CO₂ and temperature regime, which suggests that the principles of stomatal regulation are not affected by changes in CO₂ or climate.

KEYWORDS: CARBON DIOXIDE, COTTON, ELEVATED CO₂, GROWTH, LEAF, LOLIUM-PERENNE, PERENNIAL RYEGRASS, PHOTOSYNTHESIS, TRANSPIRATION, WATER RELATIONS

1684

Nijs, I., and I. Impens. 1993. Effects of long-term elevated atmospheric carbon-dioxide on lolium-perenne and trifolium-repens, using a simple photosynthesis model. *Vegetatio* 104:421-431.

Changes in gross canopy photosynthetic rate (PGc), produced by long-term exposure to an elevated atmospheric CO₂ level (626 +/- 50 μmol mol⁻¹), were modelled for *Lolium perenne* L. cv. Vigor and *Trifolium repens* L. cv. Blanca, using a simple photosynthesis model, based on biochemical and physiological information (leaf gross CO₂ uptake in saturating light, P(max), and leaf quantum efficiency, alpha) and structural vegetation parameters (leaf area index, LAI, canopy extinction coefficient, k, leaf transmission, M). Correction of PGc for leaf respiration allowed comparison with previously measured canopy net CO₂ exchange rates, with the average divergence from model prediction amounting to about 6%. Sensitivity analysis showed that for a three-week old canopy, the PGc increase in high CO₂ could be attributed largely to changes in P(max) and alpha, while differences in canopy architecture were no longer important for the PGc-stimulation (which they were in the early growth stages). As a consequence of this increasing LAI with canopy age, the gain of daytime CO₂ uptake is progressively eroded by the increasing burden of canopy respiration in high-CO₂ grown *Lolium perenne*. Modelling canopy photosynthesis in different regrowth stages after cutting (one week, two weeks,...), revealed that the difference in a 24-h CO₂ balance between the ambient and the high CO₂ treatment is reduced with regrowth time and completely disappears after 6 weeks.

KEYWORDS: CO₂

1685

Nijs, I., and I. Impens. 1996. Effects of elevated CO₂ concentration and climate-warming on photosynthesis during winter in *Lolium perenne*. *Journal of Experimental Botany* 47(300):915-924.

Long-term effects of atmospheric carbon dioxide concentration (ambient or 700 μmol mol⁻¹) and air temperature (simulation of field conditions or +4 degrees C) on leaf photosynthetic rate were examined in *Lolium perenne* L. cv. Vigor, exposed to natural illumination during winter. Photosynthetic capacity was compared over a range of air temperatures and photon flux densities of photosynthetically active radiation which were representative of winter climate (5-15 degrees C and 0-500 μmol m⁻² s⁻¹), with CO₂ level during measurement similar to that during the experimental period. Long-term exposure to increased air temperature reduced leaf CO₂ fixation capacity by 23% (averaged over all measurement conditions), resulting from a decline in light-saturated uptake rate, but not in incident-light quantum efficiency. CO₂-stimulation was largely absent in plants grown in ambient temperature, but pronounced in plants grown under +4 degrees C, where it compensated for two-thirds of the 23% drop. This enhancing effect of elevated CO₂ level on leaf CO₂ uptake rate observed in the warmer treatment, was strongly dependent on measurement temperature, increasing from 5% at 5 degrees C, to up to 32% at 15 degrees C. Measurements of chlorophyll fluorescence and dry matter corresponded with the observed changes in assimilation capacity, which could not be attributed to a deteriorated nitrogen status of the leaves as there was a

similar N content on an area basis. Several hypotheses are considered to explain the observed CO₂-temperature interactions.

KEYWORDS: AIR-TEMPERATURE, ASSIMILATION, CARBON-DIOXIDE CONCENTRATION, LEAF, LEAVES, LIMITATION, NITROGEN, PLANTS, PRODUCTIVITY, QUANTUM YIELD

1686

Nijs, I., and I. Impens. 1997. An analysis of the balance between root and shoot activity in *Lolium perenne* cv Melvina. Effects of CO₂ concentration and air temperature. *New Phytologist* 135(1):81-91.

This study investigated the mechanisms which control the partitioning between roots and shoots in plants subjected to changes in environment. Two types of analyses were used: firstly, an examination of the cost and revenue associated with investment in different plant parts, and secondly, a test of the principle of functional equilibrium between roots and shoots, i.e. whether root dry matter x root specific activity balances shoot dry matter x shoot specific activity. Measurements were made on individual plants of *Lolium perenne* in sunlit controlled environments, grown from germination to canopy closure under optimal nitrogen supply. At the final harvest, increased air temperature (+4 degrees C above ambient) reduced whole-plant dry matter by 12% relative to the control, whereas elevated CO₂ mole fraction (700 μmol mol⁻¹) led to a 38% gain. The combined treatment yielded an intermediate result (+19%). Plants grown at +4 degrees C maintained balanced activity between roots and shoots throughout the experimental period, irrespective of CO₂ concentration. This required enhanced allocation to roots in young plants to compensate for a strong negative effect of higher temperature on root specific activity, which suggests that plants conserve balanced activity by adjusting dry matter partitioning. The extra cost involved with the adjustment at +4 degrees C significantly enhanced the cost:revenue ratio of plant investment. In ambient temperature, the balance between roots and shoots departed from equilibrium, slightly at ambient but substantially at elevated CO₂: the plants accumulated excess carbon relative to nitrogen, and this imbalance increased with plant age. At elevated CO₂, the cost:revenue ratio increased in young plants but this was later reversed owing to loss of root specific activity, which explains the gradually declining CO₂ stimulation with time. The strategies in equilibrating root and shoot functioning observed in the different treatments are discussed in the light of whole plant performance.

KEYWORDS: ALLOCATION, BIOMASS, CARBON DIOXIDE, ENRICHMENT, LEAF, MODEL, NITROGEN CONCENTRATION, OPTIMIZATION, PHOTOSYNTHESIS, RESPONSES

1687

Nijs, I., I. Impens, and P. Vanhecke. 1992. Diurnal changes in the response of canopy photosynthetic rate to elevated CO₂ in a coupled temperature-light environment. *Photosynthesis Research* 32(2):121-130.

The relative increase with elevated CO₂ of canopy CO₂ uptake rate (A), derived from continuous measurements during the day, was examined in full-cover vegetative *Lolium perenne* canopies after 17 days of regrowth. The stands were grown at ambient (358 +/- 50-μmol mol⁻¹) and increased (626 +/- 50-μmol mol⁻¹) CO₂ concentration in sunlit growth chambers. Over the entire range of temperature and light conditions (which were strongly coupled and increased simultaneously), A was on average twice as large in high compared to ambient CO₂. This response (called M = A in high CO₂/A in ambient CO₂) could not be explained by changes in canopy conductance for CO₂ diffusion (GC). In spite of interaction and strong coupling between temperature and light intensity, there was evidence that temperature rather than light determined M. Further, high CO₂ treatment was found to alleviate the afternoon depression in A observed in ambient CO₂. A temperature

optimum shift or/and a larger carbohydrate sink capacity through altered root/shoot ratio are proposed in explanation.

KEYWORDS: AIR- TEMPERATURE, CARBON-DIOXIDE CONCENTRATION, GROWTH, PLANTS, YIELD

1688

Nijs, I., F. Kockelbergh, H. Teughels, H. Blum, G. Hendrey, and I. Impens. 1996. Free air temperature increase (FATI): A new tool to study global warming effects on plants in the field. *Plant, Cell and Environment* 19(4):495-502.

A new technique, called Free Air Temperature Increase (FATI), was developed to artificially induce increased canopy temperature in field conditions without the use of enclosures. This acronym was chosen in analogy with FACE (Free Air CO₂ Enrichment), a technique which produces elevated CO₂ concentrations [CO₂] in open field conditions. The FATI system simulates global warming in small ecosystems of limited height, using infrared heaters from which all radiation below 800 nm is removed by selective cut-off filters to avoid undesirable photomorphogenetic effects. An electronic control circuit tracks the ambient canopy temperature in an unheated reference plot with thermocouples, and modulates the radiant energy from the lamps to produce a 2.5 degrees C increment in the canopy temperature of an associated heated plot (continuously day and night). This pre-set target differential is relatively constant over time due to the fast response of the lamps and the use of a proportional action controller (the standard deviation of this increment was <1 degrees C in a 3 week field study with 1007 measurements). Furthermore, the increase in leaf temperature does not depend on the vertical position within the canopy or on the height of the stand. Possible applications and alternative designs are discussed.

KEYWORDS: CARBON DIOXIDE, CO₂, ENVIRONMENT, GROWTH, LIGHT, PHOTOSYNTHESIS

1689

Nijs, I., H. Teughels, H. Blum, G. Hendrey, and I. Impens. 1996. Simulation of climate change with infrared heaters reduces the productivity of *Lolium perenne* L in summer. *Environmental and Experimental Botany* 36(3):271-280.

Field-grown perennial ryegrass was subjected to climate warming and elevated CO₂ concentration during summer in free air conditions (no enclosure of the vegetation). Increased foliage temperature (2.5 degrees C above fluctuating ambient) was induced by heating the stand with infrared radiation sources, modulated by an electronic control device (FATI, Free Air Temperature Increase). Enhanced CO₂ was produced by a FACE system (Free Air CO₂ Enrichment). Exposure to simulated climate warming drastically reduced above-ground harvestable dry matter (52% loss). The nitrogen allocated to the leaf fraction was thus concentrated into less dry matter, which enhanced the nitrogen concentration on a mass basis (+17%) but also per unit leaf area (+47%). As a consequence, CO₂ assimilation rates were not affected in these slower growing plants in the +2.5 degrees C treatment, and the photochemical efficiency of non-cyclic electron transport of photosystem II was also unaffected. Although the plants were grown in the field without root restrictions, long-term exposure to elevated CO₂ concentration induced noticeable acclimation of the photosynthetic apparatus (40% loss of fixation potential), which largely outweighed the direct stimulation in this summer period. Part of the reduced rates could be attributed to lower N concentration on a leaf area basis. The results are compared with responses of this species in sunlit conditioned greenhouses, which indicates that experiments in enclosures may underestimate effects in the field. This also emphasizes the need to validate other plant responses to climate warming and CO₂ enrichment

in free air conditions.

KEYWORDS: ACCLIMATION, ELEVATED CO₂, GROWTH, NITROGEN, PLANTS, TEMPERATURE, TISSUE

1690

Niklaus, P.A. 1998. Effects of elevated atmospheric CO₂ on soil microbiota in calcareous grassland. *Global Change Biology* 4(4):451-458.

Microbial responses to three years of CO₂ enrichment (600 μ mol L⁻¹) in the field were investigated in calcareous grassland. Microbial biomass carbon (C) and soil organic C and nitrogen (N) were not significantly influenced by elevated CO₂. Microbial C:N ratios significantly decreased under elevated CO₂ (-15%, P = 0.01) and microbial N increased by +18% (P = 0.04). Soil basal respiration was significantly increased on one out of 7 sampling dates (+14%, P = 0.03; December of the third year of treatment), whereas the metabolic quotient for CO₂ (qCO₂) = basal respiration/microbial C did not exhibit any significant differences between CO₂ treatments. Also no responses of microbial activity and biomass were found in a complementary greenhouse study where intact grassland turfs taken from the field site were factorially treated with elevated CO₂ and phosphorus (P) fertilizer (1 g P m⁻² y⁻¹). Previously reported C balance calculations showed that in the ecosystem investigated growing season soil C inputs were strongly enhanced under elevated CO₂. It is hypothesized that the absence of microbial responses to these enhanced soil C fluxes originated from mineral nutrient limitations of microbial processes. Laboratory incubations showed that short-term microbial growth (one week) was strongly limited by N availability, whereas P was not limiting in this soil. The absence of large effects of elevated CO₂ on microbial activity or biomass in such nutrient-poor natural ecosystems is in marked contrast to previously published large and short-term microbial responses to CO₂ enrichment which were found in fertilized or disturbed systems. It is speculated that the absence of such responses in undisturbed natural ecosystems in which mineral nutrient cycles have equilibrated over longer periods of time is caused by mineral nutrient limitations which are ineffective in disturbed or fertilized systems and that therefore microbial responses to elevated CO₂ must be studied in natural, undisturbed systems.

KEYWORDS: BIOMASS, CARBON DIOXIDE, CYCLE, ECOSYSTEM, FEEDBACK, NITROGEN, PLANT, RESPONSES, SYSTEM, TUNDRA

1691

Niklaus, P.A., and C. Korner. 1996. Responses of soil microbiota of a late successional alpine grassland to long term CO₂ enrichment. *Plant and Soil* 184(2):219-229.

We investigated microbial responses in a late successional sedge-dominated alpine grassland to four seasons of CO₂ enrichment. Part of the plots received fertilizer equivalent to 4.5 g N m⁻² a⁻¹. Soil basal respiration (R(mic)), the metabolic quotient for CO₂ (qCO₂) = R(mic)/C-mic, microbial C and N (C-mic and N-mic) as well as total soil organic C and N showed no response to CO₂ enrichment alone. However, when the CO₂ treatment was combined with fertilizer addition R(mic) and qCO₂ were statistically significantly higher under elevated CO₂ than under ambient conditions (+57% and +71%, respectively). Fertilizer addition increased microbial N pools by 17%, but this was not influenced by elevated CO₂. Microbial C was neither affected by elevated CO₂ nor fertilizer. The lack of a CO₂-effect in unfertilized plots was surprising in the light of our evidence (based on C balance) that enhanced soil C inputs must have occurred under elevated CO₂ regardless of fertilizer treatment. Based on these data and other published work we suggest that microbial responses to elevated CO₂ in such stable, late-successional ecosystems are limited by the availability

of mineral nutrients and that results obtained with fertile or heavily disturbed substrates are unsuitable to predict future microbial responses to elevated CO₂ in natural systems. However, when nutrient limitation is removed (e.g. by wet nitrogen deposition) microbes make use of the additional carbon introduced into the soil system. We believe that the response of natural ecosystems to elevated CO₂ must be studied in situ in natural, undisturbed systems.

KEYWORDS: ATMOSPHERIC CO₂, BIOMASS, CARBON DIOXIDE, ELEVATED CO₂, FEEDBACK, FLOW, NITROGEN

1692

Niklaus, P.A., P.W. Leadley, J. Stocklin, and C. Korner. 1998. Nutrient relations in calcareous grassland under elevated CO₂. *Oecologia* 116(1-2):67-75.

Plant nutrient responses to 4 years of CO₂ enrichment were investigated in situ in calcareous grassland. Beginning in year 2, plant aboveground C:N ratios were increased by 9% to 22% at elevated CO₂ ($P < 0.01$), depending on year. Total amounts of N removed in biomass harvests during the first 4 years were not affected by elevated CO₂ (19.9 +/- 1.3 and 21.1 +/- 1.3 g N m⁻²) at ambient and elevated CO₂, indicating that the observed plant biomass increases were solely attained by dilution of nutrients. Total aboveground P and tissue N:P ratios also were not altered by CO₂ enrichment (12.5 +/- 2 g N g⁻¹ P in both treatments). In contrast to non-legumes (>98% of community aboveground biomass), legume C/N was not reduced at elevated CO₂ and legume N:P was slightly increased. We attribute the less reduced N concentration in legumes at elevated CO₂ to the fact that virtually all legume N originated from symbiotic N₂ fixation (%N_{dfa} approximate to 90%), and thus legume growth was not limited by soil N. While total plant N was not affected by elevated CO₂, microbial N pools increased by +18% under CO₂ enrichment ($P = 0.04$) and plant available soil N decreased. Hence, there was a net increase in the overall biotic N pool, largely due increases in the microbial N pool. In order to assess the effects of legumes for ecosystem CO₂ responses and to estimate the degree to which plant growth was P-limited, two greenhouse experiments were conducted, using firstly undisturbed grassland monoliths from the field site, and secondly designed 'microcosm' communities on natural soil. Half the microcosms were planted with legumes and half were planted without. Both monoliths and microcosms were exposed to elevated CO₂ and P fertilization in a factored design. After two seasons, plant N pools in both unfertilized monoliths and microcosm communities were unaffected by CO₂ enrichment, similar to what was found in the field. However, when P was added total plant N pools increased at elevated CO₂. This community-level effect originated almost solely from legume stimulation. The results suggest a complex interaction between atmospheric CO₂ concentrations, N and P supply. Overall ecosystem productivity is N-limited, whereas CO₂ effects on legume growth and their N₂ fixation are limited by P.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CLOVER TRIFOLIUM-REPENS, ENRICHMENT, LOLIUM-PERENNE L, MANAGED MODEL-ECOSYSTEMS, NITROGEN-FIXATION, RESPONSES, TALLGRASS PRAIRIE, WHITE CLOVER, WOODY-PLANTS

1693

Niklaus, P.A., D. Spinnler, and C. Korner. 1998. Soil moisture dynamics of calcareous grassland under elevated CO₂. *Oecologia* 117(1-2):201-208.

Water relations of nutrient-poor calcareous grassland under long-term CO₂ enrichment were investigated. Understanding CO₂ effects on soil moisture is critical because productivity in these grasslands is water limited. In general, leaf conductance was reduced at elevated CO₂, but

responses strongly depended on date and species. Evapotranspiration (measured as H₂O gas exchange) revealed only small, non-significant reductions at elevated CO₂, indicating that leaf conductance effects were strongly buffered by leaf boundary layer and canopy conductance (leaf area index was not or only marginally increased under elevated CO₂). However, these minute and non-significant responses of water vapour loss accumulated over time and resulted in significantly higher soil moisture in CO₂-enriched plots (gravimetric spot measurements and continuous readings using a network of time-domain reflectometry probes). Differences strongly depended on date, with the smallest effects when soil moisture was very high (after heavy precipitation) and effects were largest at intermediate soil moisture. Elevated CO₂ also affected diurnal soil moisture courses and rewetting of soils after precipitation. We conclude that ecosystem-level controls of the water balance (including soil feedbacks) overshadow by far the physiological effects observed at the leaf level. Indirect effects of CO₂ enrichment mediated by trends in soil moisture will have far-ranging consequences on plant species composition, soil bacterial and faunal activity as well as on soil physical structure and may indirectly also affect hydrology and trace gas emissions and atmospheric chemistry.

KEYWORDS: ATMOSPHERIC CO₂, CARBON, FLUXES, GROWTH, PLANT, RESPONSES, STOMATAL CONDUCTANCE, WATER-USE EFFICIENCY

1694

Nikolaidis, N.P., H.L. Hu, and C. Ecsedy. 1994. Effects of climatic variability on the hydrologic response of a fresh-water watershed. *Aquatic Sciences* 56(2):161-178.

A generalized watershed model was used to evaluate the effects of global climate changes on the hydrologic responses of freshwater ecosystems. The Enhanced Trickle Down (ETD) model was applied to W-3 watershed located near Danville, Vermont. Eight years of field data was used to perform model calibration and verification and the results were presented in Nikolaidis et al., (1993). Results from the Goddard Institute for Space Studies (GISS) and the Geophysical Fluid Dynamics Laboratory (GFDL) general circulation models which simulated the doubling of present day atmospheric CO₂ scenarios were used to perform the hydrologic simulations for the W-3 watershed. The results indicate that the W-3 watershed will experience increases in annual evapotranspiration and decreases in annual outflow and soil moisture. Stochastic models that simulate collective statistical properties of meteorological time series were developed to generate data to drive the ETD model in a Monte- Carlo fashion for quantification of the uncertainty in the model predictions due to input time series. This coupled deterministic and stochastic model was used to generate probable scenarios of future hydrology of the W-3 watershed. The predicted evapotranspiration and soil moisture under doubling present day atmospheric CO₂ scenarios exceed the present day uncertainty due to input time series by a factor greater than 2. The results indicate that the hydrologic response of the W-3 watershed will be significantly different than its present day response. The Enhanced Trickle Down model can be used to evaluate land surface feedbacks and assessing water quantity management in the event of climate change.

KEYWORDS: ACIDIFICATION, CALIFORNIA, DEPOSITION, MODELS, RESOURCES, RIVER BASIN

1695

Nilsen, E.T., P.W. Rundel, and M.R. Sharifi. 1996. Diurnal gas exchange characteristics of two stem photosynthesizing legumes in relation to the climate at two contrasting sites in the California desert. *Flora* 191(2):105-116.

The diurnal and seasonal patterns of climate, shoot water potential, stem

photosynthesis (Pn), stem conductance, and stem intercellular CO₂ were measured for two legume shrubs in the southern California desert at two elevations at four seasons of the year. One species (*Senna armata*), is restricted to the Mojave desert and was studied at 950 m elevation, while the other species (*Caesalpinia virgata*) is endemic to the Sonoran desert and was studied at 180 m elevation. The Sonoran desert site was characterized by higher temperatures, higher vapor pressure deficits, and more consistent solar radiation than the Mojave desert site. During the summer, the differences between the microclimates of the two sites were maximal. Both species have high predawn and midday shoot water potentials compared with other desert species, most likely because they have vertical stem orientation and low stem conductance. Stem Pn was positive all year, but Pn(max) decreased for *C. virgata* during the summer. Stem temperature, and its impact on vapor pressure deficit, was the most important regulator of stem photosynthesis. Although there were large changes in stem Pn between winter and summer, there was little change in intercellular CO₂ among seasons inferring no change in water use efficiency. Stem Pn most likely provides most of the carbon gain for both species because leaves are small and ephemeral, and stems are present and actively gaining carbon all year.

KEYWORDS: *ERIOGONUM-INFLATUM, LEAF, MORPHOLOGY, STOMATAL CONDUCTANCE*

1696

Ning, B., Y. Kubo, A. Inaba, and R. Nakamura. 1997. Physiological responses of Chinese pear 'Yali' fruit to CO₂-enriched and/or O₂-reduced atmospheres. *Journal of the Japanese Society for Horticultural Science* 66(3-4):613-620.

Respiration and ethylene production rates of Chinese pear 'Yali' fruit (*Pyrus ussuriensis* Maxim. var. *sinensis* Kikuchi) stored in CO₂-enriched and/or O₂-reduced atmospheres. In addition, several types of polyethylene film packaging were also applied to the long-term storage of 'Yali' fruit. 1. Oxygen uptake and ethylene production in 'Yali' fruit at 20 degrees C decreased with increasing CO₂ concentration up to 40%. Ethylene production under 60% CO₂ was markedly inhibited, whereas O₂ uptake was promoted; a physiological disorder in the flesh developed. 2. Under the same storage condition, oxygen uptake and ethylene production consistently decreased with decreasing O₂ concentration. However, when O₂ was decreased to less than 5%, CO₂ output exceeded O₂ uptake, suggesting that anaerobic respiration was occurring. 3. Respiration was inhibited in fruit kept at 10 or 20 degrees C under 5% CO₂ + 3% O₂ during the first 4 days of storage and then increased suddenly thereafter accompanied by the development of a physiological disorder. 4. The storage life of the fruit packed in a film with soda lime at 10 degrees C, in which O₂ became to about 8%, was prolonged by about a month, as compared to that of those packed in a perforated bag. The gas concentration higher than 5% CO₂ and/or lower than 5% O₂ within a plastic bag caused an accumulation of ethanol and the development of disorder in flesh, thus shortening storage life of fruit. Our results suggest that 'Yali' fruit is sensitive to both CO₂-enriched and O₂-reduced atmospheres, and that 2% CO₂ and 8% O₂ are about optimal for its long-term storage.

KEYWORDS: *1-AMINOCYCLOPROPANE-1-CARBOXYLIC ACID, ETHYLENE, QUALITY*

1697

Ning, L., B.E. Petersen, G.E. Edwards, L.S. Daley, and J.B. Callis. 1997. Recovery of digital information stored in living plant leaf photosynthetic apparatus as fluorescence signals. *Applied Spectroscopy* 51(1):1-9.

A CCD (charge-coupled device)-equipped, imaging spectroscopic instrument is discussed that can be reversible and rapidly reconfigured

to image photosynthetic fluorescence, allowing two-dimensional spatial estimates of fluorescence quantum yield (Y'). Y' images of leaf areas with immediately functional photosynthetic apparatus appear smooth and uniform and are much less affected by variations in chlorophyll content and light path through the leaf. However, areas of the leaf where the photosynthetic apparatus has different light history, pathology, or other damage generate different Y' value images. This characteristic allowed storage and recovery of images from leaves. Extending this finding, we prepared binary data coding for the value of pi to 99 decimal places (100 digits), on living leaves. The images containing the binary codes for these digits can be "read" by eye, because the human brain interprets visual data with great skill. However, it was necessary to enhance the images to facilitate instrument "reading". A program was developed to enhance the images and "read" the data images with no errors. The photosynthetic mechanism involved (nonphotochemical quenching), the role of leaf age and germplasm variation, and the potential applications of this finding in terms of bioelectronics are discussed.

KEYWORDS: *CHLOROPHYLL-A FLUORESCENCE, CO2 ASSIMILATION, COMPLEX, LEAVES, MUTANTS, PHOTOCURRENTS, PHOTOSYSTEM, PLATINIZED CHLOROPLASTS, SPECTRA, TRANSIENT*

1698

Nitschelm, J.J., A. Luscher, U.A. Hartwig, and C. VanKessel. 1997. Using stable isotopes to determine soil carbon input differences under ambient and elevated atmospheric CO₂ conditions. *Global Change Biology* 3(5):411-416.

Quantitative estimates of soil C input under ambient (35 Pa) and elevated (60 Pa) CO₂-partial pressure (pCO₂) were determined in a Free-Air Carbon dioxide Enrichment (FACE) experiment. To facilitate C-13-tracing, *Trifolium repens* L. was grown in a soil with an initial delta(13)C distinct by at least 5 parts per thousand from the delta(13)C of *T. repens* grown under ambient or elevated pCO₂. A shift in delta(13)C of the soil organic C was detected after one growing season. Calculated new soil C inputs in soil under ambient and elevated pCO₂ were 2 and 3 t ha⁻¹, respectively. Our findings suggest that under elevated CO₂ conditions, soil C sequestration may be altered by changes in plant biomass production and quality.

KEYWORDS: *C-13 NATURAL ABUNDANCE, DIOXIDE ENRICHMENT, DYNAMICS, LITTER QUALITY, NITROGEN, ORGANIC-MATTER, PERENNIAL RYEGRASS, PLANTS, TALLGRASS PRAIRIE, WHITE CLOVER*

1699

Niu, G., T. Kozai, M. Hayashi, and M. Tateno. 1997. Time course simulations of CO₂ concentration and net photosynthetic rates of potato plantlets cultured under different lighting cycles. *Transactions of the Asae* 40(6):1711-1718.

Potato (*Solanum tuberosum* L. cv. Benimaru) plantlets were cultured under four lighting cycles with the same ratio of photo/dark period (16 h/8 h, 4 h/2 h, 1 h/0.5 h, and 0.25 h/0.125 h) photoautotrophically (without sugar in the medium) and photomixotrophically (with sugar in the medium) in vitro for 28 days. Simulations of time courses of CO₂ concentration in the vessel (C-i) for plantlets cultured photoautotrophically, and photomixotrophically and dry weight accumulations of the plantlets cultured photoautotrophically were conducted using the same model and parameter values as those in Niu and Kozai (1997). While underestimation and overestimation of the time courses of C-i in some treatments were observed the simulated values of C-i and the dry weight accumulation of the plantlets generally agreed with the measured values. The simulated responses of net photosynthetic

rate of the plantlets to C-i indicated that in the early, culture period, plantlets have higher photosynthetic ability under photoautotrophic than under photomixotrophic culture conditions. The quantitative relationship between daily net photosynthetic rate (daily net production) and vessel ventilation rate per plantlet was simulated under various CO₂ levels outside the vessel for given sizes of potato plantlets cultured in vitro photoautotrophically, to aid appropriate CO₂ enrichment and vessel design in commercial micropropagation systems.

KEYWORDS: ENRICHMENT, GROWTH, INVITRO

1700

Nobel, P.S. 1991. Environmental productivity indexes and productivity for *Opuntia ficus-indica* under current and elevated atmospheric CO₂ levels. *Plant, Cell and Environment* 14(7):637-646.

The productivity of the prickly-pear cactus *Opuntia ficus-indica*, which is cultivated worldwide for its fruits and stem segments, was predicted based on the responses of its net CO₂ uptake to soil water status, air temperature and photosynthetic photon flux density (PPFD). Each of these environmental factors was represented by an index with a maximum value of unity when that factor was not limiting net CO₂ uptake over a 24-h period. The water index, the temperature index, and the PPFD index were determined for 87 sites in the contiguous United States using data from 189 weather stations and for 148 sites worldwide using data from 1464 weather stations. The product of these three indices, the environmental productivity index (EPI), was used to predict the productivity of *O. ficus-indica* under current climatic conditions and under those accompanying a possible increase in the atmospheric CO₂ level to 650- μ -mol mol⁻¹. Sites with temperatures always above -10-degrees-C and hence suitable for prickly-pear cultivation numbered 37 in the United States and 110 worldwide; such sites increased by 43 and 5%, respectively, for the global warming accompanying the elevated CO₂. Productivity of *O. ficus-indica* was at least 15 tonnes dry weight hectare⁻¹ year⁻¹, comparable to that of many agronomic crops, for 20 sites with temperatures always above -10-degrees-C in the contiguous United States and for 12 such sites worldwide under current climatic conditions; such sites increased by 85 and 117%, respectively, under the elevated CO₂ condition, mainly because of direct effects of the atmospheric CO₂ level on net CO₂ uptake. In summary, simulations based on EPI indicate that *O. ficus-indica* may presently be advantageously cultivated over a substantial fraction of the earth's surface, such regions increasing markedly with a future doubling in atmospheric CO₂ levels.

KEYWORDS: AGAVE-DESERTI, PAR INTERCEPTION, PREDICTIONS, RESPONSES, TEMPERATURE, UNITED-STATES, WATER

1701

Nobel, P.S. 1996. Responses of some North American CAM plants to freezing temperatures and doubled CO₂ concentrations: Implications of global climate change for extending cultivation. *Journal of Arid Environments* 34(2):187-196.

Environmental influences on the cultivation of Crassulacean acid metabolism (CAM) plants, which are especially well adapted to arid regions with limited rainfall, were evaluated with respect to two aspects of global climate change. Cellular uptake of a vital stain, which occurs in living cells only, was halved at -6+/-1 degrees C for the cultivated CAM species *Agave salmiana*, *Opuntia ficus indica* and *Stenocereus queretaroensis* growing at day/night air temperatures of 30 degrees C/20 degrees C compared with -12 degrees C for the wild species *Opuntia humifusa*. When plants were grown at reduced temperatures of 10 degrees C/0 degrees C, stain uptake was halved at about -8 degrees C for the cultivated species but at -24 degrees C for *O. humifusa*. The greater

low-temperature sensitivity and the lesser low-temperature acclimation of the cultivated species severely limit the regions where they can presently be grown, but such regions will expand as air temperatures rise accompanying global climate change. When the atmospheric CO₂ concentration was doubled from the current ambient value of 360 μ mol mol⁻¹ to 720 μ mol mol⁻¹, net CO₂ uptake over 24-h periods increased 36% for *A. salmiana* and *S. queretaroensis*; about one-third of the increase resulted from higher net CO₂ uptake rates in the last 4 h of daytime and two-thirds from higher rates during the first 8 h of the night. The doubled atmospheric CO₂ concentration predicted to occur before the end of the twenty-first century will increase CO₂ uptake and hence biomass productivity of such CAM species, further expanding the regions where they may be profitably cultivated. (C) 1996 Academic Press Limited.

KEYWORDS: AGAVE-VILMORINIANA, ATMOSPHERIC CO₂, CACTACEAE, ELEVATED CARBON-DIOXIDE, FRUIT CROP, GROWTH, OPUNTIA FICUS INDICA, PRODUCTIVITY, TOLERANCE, UNITED-STATES

1702

Nobel, P.S. 1996. Shading, osmoticum, and hormone effects on organ development for detached cladodes of *Opuntia ficus-indica*. *International Journal of Plant Science* 157(6):722-728.

To help understand what conditions lead to the development of new organs on shoots of *Opuntia ficus-indica*, a widely cultivated prickly pear cactus, detached cladodes were kept in a glasshouse and were shaded, exposed to full sunlight, or exposed to full sunlight and injected with various osmotica and hormones. Daughter cladodes emerged more slowly on cladodes detached in January (mean time of 12.6 wk) than in May (4.2 wk). In the field, new organ development was more rapid and more fruits were produced compared with cladodes detached in January and kept in a glasshouse. Shading by 94% essentially eliminated the development of daughter cladodes for cladodes harvested in both seasons over the 18-wk observation period. Daughter cladodes had a lower percentage dry mass and a higher water potential than the detached cladodes on which they developed, suggesting that water entered them primarily via the phloem. Compared with detached cladodes injected weekly with 1% of the cladode fresh mass of water for 6 wk, injection of 1.5 M sucrose accelerated daughter cladode development by 1.4 wk 750 mM KCl by 3.0 wk, and 750 mM KNO₃ by 4.8 wk. Injection of 20 μ M gibberellic acid (GA(3) and GA(4)) virtually eliminated the development of daughter cladodes. Injection of 800 μ M indole-3-acetic acid accelerated cladode development by 3.1 wk and 800 μ M kinetin by 4.0 wk, both resulting in a greater biomass for the new organs. Thus production of daughter cladodes by detached cladodes of *O. ficus-indica* was enhanced by a higher tissue osmotic pressure, indole-acetic acid, and kinetin and was inhibited by shading and gibberellic acid.

KEYWORDS: CACTACEAE, CACTUS, CO₂, FRUIT-DEVELOPMENT, GIBBERELIC-ACID, GROWTH, METABOLISM, PHOTOPERIOD, PLANTS, TIME

1703

Nobel, P.S., M.Y. Cui, and A.A. Israel. 1994. Light, chlorophyll, carboxylase activity and CO₂ fixation at various depths in the chlorenchyma of *Opuntia ficus-indica* (L) miller under current and elevated CO₂. *New Phytologist* 128(2):315-322.

Mature cladodes of *Opuntia ficus-indica* (L.) Miller have a thick chlorenchyma (about 4 mm) with a relatively high chlorophyll content (0.65 g m⁻²), suggesting that light may be greatly attenuated and hence CO₂ fixation negligible in the inner part of this tissue. Indeed, blue light (400-470 nm) and red light (670-685 nm) were 99 % attenuated in the

outer 2 mm of the chlorenchyma when the cladodes developed under both current and elevated CO₂ concentrations. Nevertheless, the nocturnal acidity increase and C-14 accumulation following a brief exposure to (CO₂)-C-14 night decreased only 22 to 47 % for a layer 2-3 mm deep in the chlorenchyma of this CAM plant. Under a particular growth CO₂, the activities of both ribulose- 1,5-bisphosphate carboxylase/oxygenase and phosphoenolpyruvate carboxylase were similar for each of the outer three 1-mm-thick layers of the chlorenchyma. Therefore, although the light level and total chlorophyll decreased sharply with depth and the chlorophyll a/b ratio also decreased, substantial CO₂ fixation apparently occurs throughout most of the chlorenchyma. When *O. ficus-indica* was grown under 720 $\mu\text{mol CO}_2 \text{ mol}^{-1}$, the chlorenchyma was 20 % thicker but contained 11 % less chlorophyll and had a lower absorptance than under the current CO₂ concentration (370 μmol^{-1}). Greater nocturnal acidity increases and C-14 accumulation following exposure to (CO₂)-C- 14 at night occurred at the doubled CO₂ concentration despite 29-39% reductions in the activities of the two carboxylating enzymes, the lower absorptance, and a 24 % increase in the cladode reflectance from 400 to 700 nm.

KEYWORDS: CRASSULACEAN ACID METABOLISM, ENVIRONMENT, GRADIENTS, LEAF, LEAVES, PALISADE TISSUE, PHOTOSYNTHETIC PROPERTIES, PLANTS, REFLECTANCE, TRANSMITTANCE

1704

Nobel, P.S., M.Y. Cui, P.M. Miller, and Y.Q. Luo. 1994. Influences of soil volume and an elevated CO₂ level on growth and CO₂ exchange for the crassulacean acid metabolism plant *Opuntia ficus-indica*. *Physiologia Plantarum* 90(1):173-180.

Effects of the current (38 Pa) and an elevated (74 Pa) CO₂ partial pressure on root and shoot areas, biomass accumulation and daily net CO₂ exchange were determined for *Opuntia ficus-indica* (L.) Miller, a highly productive Crassulacean acid metabolism species cultivated worldwide. Plants were grown in environmentally controlled rooms for 18 weeks in pots of three soil volumes (2 600, 6 500 and 26 000 cm³), the smallest of which was intended to restrict root growth. For plants in the medium-sized soil volume, basal cladodes tended to be thicker and areas of main and lateral roots tended to be greater as the CO₂ level was doubled. Daughter cladodes tended to be initiated sooner at the current compared with the elevated CO₂ level but total areas were similar by 10 weeks. At 10 weeks, daily net CO₂ uptake for the three soil volumes averaged 24% higher for plants growing under elevated compared with current CO₂ levels. but at 18 weeks only 3% enhancement in uptake occurred. Dry weight gain was enhanced 24% by elevated CO₂ during the first 10 weeks but only 8% over 18 weeks. Increasing the soil volume 10-fold led to a greater stimulation of daily net CO₂ uptake and biomass production than did doubling the CO₂ level. At 18 weeks, root biomass doubled and shoot biomass nearly doubled as the soil volume was increased 10-fold; the effects of soil volume tended to be greater for elevated CO₂. The amount of cladode nitrogen per unit dry weight decreased as the CO₂ level was raised and increased as soil volume increased, the latter suggesting that the effects of soil volume could be due to nitrogen limitations.

KEYWORDS: AGAVE-VILMORINIANA, ATMOSPHERIC CARBON-DIOXIDE, BIOMASS, NITROGEN, PHOTOSYNTHETIC ACCLIMATION, PRODUCTIVITY, RESPONSES, SOURCE-SINK RELATIONS, TEMPERATURE, TERM

1705

Nobel, P.S., and V.G. Decortazar. 1991. Growth and predicted productivity of *Opuntia ficus-indica* for current and elevated carbon-dioxide. *Agronomy Journal* 83(1):224-230.

Opuntia ficus-indica (L.) Mill., a prickly pear cactus cultivated worldwide for its fruits and stem segments, can have an annual dry weight productivity exceeding that of many crops. Using a recently introduced environmental productivity index (EPI), the influences of water status, temperature, and photosynthetically active radiation (PAR) on its productivity can be predicted. This investigation calculated the water index, the temperature index, and the PAR index, whose product equals EPI, for 169 sites distributed approximately uniformly across the contiguous USA for present climatic conditions as well as for those associated with an elevated CO₂ concentration of 650- $\mu\text{L L}^{-1}$. The effect of elevated CO₂ on growth of *O. ficus-indica* was directly measured, and low temperature limitations on productivity were considered. The dry weight gain of *O. ficus-indica* during 6 mo in an environmental growth chamber was 23% greater at 650 compared with 350- $\mu\text{L L}^{-1}$ CO₂ and increased as the duration of the wet period increased, in agreement with predictions of the water index (the fraction of maximal net CO₂ uptake during a 24-h period for the prevailing plant water status). For closely spaced plants that lead to a high productivity per unit ground area, EPI averaged about 0.10, except in desert regions where the water index lowered EPI, in the far North or South and at high elevations where the temperature index lowered EPI, and in the Northeast and Northwest where the PAR index lowered EPI. The predicted annual dry weight productivity for *O. ficus-indica* was 12.8 Mg ha⁻¹ yr⁻¹ under current conditions, and 16.3 Mg ha⁻¹ yr⁻¹ under those associated with 650- $\mu\text{L L}^{-1}$ CO₂. Both productivities are relatively high compared with other agronomic plants. The percentage of sites where temperatures fall below - 15-degrees- C at least once during the 10 years simulated, which would be lethal to most prickly pear cacti, was reduced from 49 to 18% by the general warming expected to accompany an approximate doubling of the atmospheric CO₂ concentration.

KEYWORDS: CACTUS, CO₂, DESERT, PAR INTERCEPTION, PLANT, RESPONSES

1706

Nobel, P.S., and A.A. Israel. 1994. Cladode development, environmental responses of CO₂ uptake, and productivity for *Opuntia ficus-indica* under elevated CO₂. *Journal of Experimental Botany* 45(272):295-303.

Opuntia ficus-indica, an extremely productive CAM plant cultivated in many countries, was exposed to 36, 52, and 72-73 Pa CO₂ in field plots and open-top chambers. Initiation of new cladodes (stem segments) was monitored until the canopy closed, after which bimonthly harvests maintained the plants for one year at a cladode area per unit ground area that is optimal for biomass production. Doubling the CO₂ partial pressure slightly increased the number of first-order daughter cladodes growing on the basal (planted) cladodes after 3 months and nearly doubled the number and area of second-order cladodes. When the CO₂ level was doubled, cladodes were 5% thicker after a few months and 11 to 16% thicker after one year. Although the productivity enhancement by elevated CO₂ tended to decrease during the year, the annual above-ground dry-mass gain was 37 to 40% higher when the CO₂ level was doubled, reaching 65 tons hectare⁻¹ year⁻¹ in a field plot. Well-watered cladodes at day/night air temperatures of 25 degrees C/15 degrees C and a total daily photosynthetic photon flux (PPF) of 15 mol m⁻² d⁻¹ in controlled environment chambers had 74% more net CO₂ uptake over 24 h at 73 Pa than at 37 Pa CO₂. With doubled CO₂, the percentage enhancement of net CO₂ uptake increased as the PPF was lowered, as the temperature was raised, and during drought. Using an environmental productivity index based on such factors, net CO₂ uptake and hence productivity of *O. ficus-indica* can be predicted for elevated CO₂ levels and other variations accompanying global climate change.

KEYWORDS: ATMOSPHERIC CO₂, CARBON DIOXIDE, ENRICHMENT, GROWTH, PHOTOSYNTHETIC ACCLIMATION,

PHYSIOLOGICAL-RESPONSES, PREDICTION, PRICKLY PEAR CACTUS, RISING CO₂, TEMPERATURE

1707

Nobel, P.S., A.A. Israel, and N. Wang. 1996. Growth, CO₂ uptake, and responses of the carboxylating enzymes to inorganic carbon in two highly productive CAM species at current and doubled CO₂ concentrations. *Plant, Cell and Environment* 19(5):585-592.

In *Agave salmiana* Otto ex Salm. var. *salmiana* grown for 41/2 months in open-top chambers, 55% more leaves unfolded and 52% more fresh mass was produced at 730 than at 370 $\mu\text{mol CO}_2 \text{ mol}^{-1}$. A doubling of the CO₂ concentration also stimulated growth in another highly productive CAM species, *Opuntia ficus-indica* (L.) Miller, leading to earlier initiation and 37% more daughter cladodes. Substantial net CO₂ uptake occurred earlier in the afternoon and lasted longer through the night for *A. salmiana* at 730 than at 370 $\mu\text{mol CO}_2 \text{ mol}^{-1}$, resulting in 59% more total daily net CO₂ uptake. The Michaelis constant (HCO₃⁻) for PEPCase was 15% lower for *A. salmiana* and 44% lower for *O. ficus-indica* when the CO₂ concentration was doubled; the percentage of Rubisco in the activated state in vivo was on average 64% higher at the doubled CO₂ concentration. Thus the substantial increases in net CO₂ uptake and biomass production that occurred in these two CAM species when the ambient CO₂ concentration was doubled resulted mainly from higher inorganic carbon levels for their carboxylating enzymes, a greater substrate affinity for PEPCase, and a greater percentage of Rubisco in the activated state.

KEYWORDS: AGAVE-VILMORINIANA, CRASSULACEAN ACID METABOLISM, DIOXIDE, ELEVATED CO₂, PHOTOSYNTHESIS, PLANTS, TERM, WATER-STRESS

1708

Noble, R., K.F. Jensen, B.S. Ruff, and K. Loats. 1992. Response of *Acer saccharum* seedlings to elevated carbon-dioxide and ozone. *Ohio Journal of Science* 92(3):60-62.

Newly germinated seedlings of *Acer saccharum* were grown in atmospheres of elevated carbon dioxide (CO₂) or ozone (O₃) for 85 days. Net photosynthesis measured on initial leaves and recently formed leaves tended (though not always statistically significant) to increase with an increase in CO₂. Biomass measured at the end of the study also increased with and increase in CO₂. Ozone at 0.15 ppm did not have a significant impact on either net photosynthesis or growth; however, with O₃-treatment, biomass increased at elevated CO₂ levels.

KEYWORDS: CO₂, GROWTH, VEGETATION

1709

Noctor, G., A.C.M. Arisi, L. Jouanin, and C.H. Foyer. 1999. Photorespiratory glycine enhances glutathione accumulation in both the chloroplastic and cytosolic compartments. *Journal of Experimental Botany* 50(336):1157-1167.

Transformed poplars overexpressing gamma-glutamylcysteine synthetase (gamma-ECS) in the chloroplast (Lggs) were used to investigate chloroplastic biosynthesis of glutathione (GSH). In Lggs leaves, GSH contents were enhanced by up to 3.7-fold. In general, the highest GSH contents were observed in lines with highest gamma-glutamylcysteine (gamma-EC) contents. These lines had relatively low glycine. In darkness, foliar GSH decreased and gamma-EC increased. Illumination of pre-darkened Lggs in air resulted in a 5-fold decrease in the gamma-EC:GSH ratio. This light-induced decrease was largely abolished if leaves were illuminated at high CO₂. Consequently, the gamma-EC:GSH ratio of illuminated leaves was much higher at high CO₂ than

in air. At high CO₂ total foliar amino acids were higher, but glycine and serine were lower, than in air. These results suggest that photorespiratory glycine is used in chloroplastic GSH synthesis. Despite this, net CO₂ fixation was similar in Lggs to untransformed poplars. Pre-illuminated leaf discs from Lggs, and poplars overexpressing gamma-ECS in the cytosol (ggs), were incubated in darkness with a range of metabolites. After 15 h, discs from both types of transformant incubated on water had accumulated high levels of gamma-EC and showed marked increases in the $\gamma\text{-EC:GSH}$ ratio. Feeding glycine, serine, glycollate or phosphoserine, attenuated the dark-induced changes in the gamma-EC:GSH ratio, whereas 3-phosphoglycerate (PGA), phosphoenolpyruvate, glycerate, and hydroxypyruvate did not. Glycine produced from glycollate was therefore required for maximal GSH accumulation in both the chloroplastic and cytosolic compartment. Production of glycine from PGA failed to meet the demand of increased GSH synthetic capacity.

KEYWORDS: ARABIDOPSIS-THALIANA, DEFICIENT MUTANT, EXCESS SULFUR, FOLIAR GLUTATHIONE, GAMMA-GLUTAMYL-CYSTEINE SYNTHETASE, LEAF PEROXISOMES, METABOLITE CONCENTRATIONS, SERINE, SPINACH LEAVES, SUBCELLULAR VOLUMES

1710

Nonhebel, S. 1996. Effects of temperature rise and increase in CO₂ concentration on simulated wheat yields in Europe. *Climatic Change* 34(1):73-90.

A crop-growth-simulation model based on SUCROS87 was used to study effects of temperature rise and increase of atmospheric CO₂ concentration on wheat yields in several regions in Europe. The model simulated potential and water-limited crop production (growth with ample supply of nutrients and in the absence of damage by pests, diseases and weeds). Historic daily weather data from 13 sites in Western Europe were used as starting point. For potential production (optimal water) a 3 degrees C temperature rise led to a yield decline due to a shortening of the growing period on all locations. Doubling of the CO₂ concentration caused an increase in yield of 40% due to higher assimilation rates. It was found that effects of higher temperature and higher CO₂ concentration were nearly additive and the combination of both led to a yield increase of 1-2 ton ha⁻¹. A very small CO₂-temperature interaction was found: the effect of doubled CO₂ concentration on crop yield was larger at higher temperatures. The inter-annual yield variability was hardly affected. When water was limiting crop-production effects of temperature rise and higher CO₂ levels were different than for the potential production. Rise in temperature led to a smaller yield reduction, doubled CO₂ concentration to a larger yield increase and combination of both led to a large yield increase (3 ton ha⁻¹) in comparison with yields simulated for the present situation. Both rise in temperature and increase in the CO₂ concentration reduced water requirements of the crop. Water shortages became smaller, leading to a reduction in inter-annual variability. It is concluded that when no major changes in precipitation pattern occur a climate change will not affect wheat yields since negative effects of higher temperatures are compensated by positive effects of CO₂ enrichment.

KEYWORDS: AGRICULTURE, ATMOSPHERIC CO₂, CO₂-INDUCED CLIMATIC-CHANGE, GROWTH, MODELS

1711

Norby, R.J. 1994. Issues and perspectives for investigating root responses to elevated atmospheric carbon-dioxide. *Plant and Soil* 165(1):9-20.

A thorough assessment of how plants and ecosystems will respond to increasing concentrations of atmospheric CO₂ requires that the

responses of root systems and associated belowground processes be understood. Static measures of root-to-shoot ratio have not been satisfactory for describing the integrated responses of plants to CO₂-enriched atmospheres, but research with a process orientation has suggested that elevated CO₂ can stimulate root growth or root activity and provide a positive feedback on plant growth. There are, however, critical questions concerning the relevance of root data from short-term studies with potted plants when scaling to questions about plants in the field. Data on root responses to CO₂ enrichment in the field are fragmentary, but they allow us to more clearly define research questions for further investigation. Three perspectives for analyzing the significance of root responses as a component of the overall response of the terrestrial biosphere to increasing atmospheric CO₂ are suggested: (1) roots as a platform for nutrient acquisition and a mediator of whole-plant response to CO₂; (2) carbon storage in roots as a component of whole-plant carbon storage; and (3) effects of CO₂ enrichment on root turnover and the implications for carbon storage as soil organic matter. The relative importance of these different perspectives will vary depending on the ecosystem of interest and the larger-scale issues being considered.

KEYWORDS: CLIMATE CHANGE, CO₂- ENRICHMENT, FINE ROOTS, FORESTED ECOSYSTEMS, GROWTH, MINERAL NUTRITION, ORGANIC-MATTER, PARTIAL-PRESSURE, SOUR ORANGE TREES

1712

Norby, R.J. 1996. Oaks in a high-CO₂ world. *Annales Des Sciences Forestieres* 53(2-3):413-429.

The concentration of carbon dioxide in the atmosphere is one environmental factor that is certain to influence the physiology and productivity of oak trees everywhere. Direct assessment of the impact of increasing CO₂ is very difficult, however, because of the long-term nature of CO₂ effects and the myriad potential interactions between CO₂ and other environmental factors that can influence the physiological and ecological relationships of oaks. The CO₂ responses of at least 11 *Quercus* species have been investigated, primarily in experiments with seedlings. The growth response varies considerably among these experiments, and there appears to be no basis for differentiating the response of oaks as a group from those of other woody plants. The more important challenge is to find a basis for addressing questions about the responses of oak forest ecosystems from experimental data on individual seedlings and saplings. A series of experiments with white oak (*Quercus alba* L) seedlings and saplings was focused toward larger-scale questions, such as whether N limitations would preclude growth responses to elevated CO₂ and whether short-term physiological responses could be sustained over longer time scales. These experiments suggested three issues that are particularly important for addressing forest responses: leaf area dynamics, fine root production, and biotic interactions. By focusing seedling and sapling experiments toward these issues, we gain insight into the important processes that will influence ecosystem response and, at least in a qualitative sense, the sensitivity of those processes to elevated CO₂.

KEYWORDS: ATMOSPHERIC CO₂ ENRICHMENT, CARBON DIOXIDE, ELEVATED CO₂, FOREST, GROWTH, LEAVES, QUERCUS-ALBA, RESPONSES, STOMATAL DENSITY, TREE SEEDLINGS

1713

Norby, R.J. 1998. Nitrogen deposition: a component of global change analyses. *New Phytologist* 139(1):189-200.

The global cycles of carbon and nitrogen are being perturbed by human activities that increase the transfer from large pools of non-reactive

forms of the elements to reactive forms that are essential to the functioning of the terrestrial biosphere. The cycles are closely linked at all scales, and global change analyses must consider C and N cycles together. The increasing amount of N originating from fossil fuel combustion and deposited to terrestrial ecosystems as nitrogen oxides could increase the capacity of ecosystems to sequester C, thereby removing some of the excess carbon dioxide from the atmosphere and slowing the development of greenhouse warming. Several global and ecosystem models have calculated the amount of C sequestration that can be attributed to N deposition, based on assumptions about the allocation of N among ecosystem components with different C:N ratios. They support the premise that, since industrialization began, N deposition has been responsible for an increasing terrestrial C sink, but there is great uncertainty whether ecosystems will continue to retain exogenous N. Whether terrestrial ecosystems continue to sequester additional C will depend in part on their response to increasing concentrations of atmospheric carbon dioxide, widely thought to be constrained by limited N availability. Ecosystem models generally support the conclusion that responses to increasing concentrations of carbon dioxide will be greater, and the range of possible responses will be wider, in ecosystems where increased N inputs originate as atmospheric deposition. The interactions between N deposition and increasing carbon dioxide concentrations could be altered considerably, however, by additional factors, including N saturation of ecosystems, changes in community composition, and climate change. Nitrogen deposition is also linked to global change issues through the volatile losses of nitrous oxide, which is a potent greenhouse gas, and the role of nitrogen oxides in the production of tropospheric ozone, which could interact with plant responses to elevated carbon dioxide. Any consideration of the role of N deposition in global change issues must also balance the projected responses against the serious detrimental impact of excess N on the environment.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CO₂ CONCENTRATION, ELEVATED CO₂, FOREST ECOSYSTEMS, LEAF-AREA, LOBLOLLY-PINE, PHOTOSYNTHESIS, PRODUCTIVITY, RESPONSES, TERRESTRIAL ECOSYSTEMS

1714

Norby, R.J., and M.F. Cotrufo. 1998. Global change - A question of litter quality. *Nature* 396(6706):17-18.

KEYWORDS: DECOMPOSITION, ELEVATED CO₂

1715

Norby, R.J., N.T. Edwards, J.S. Riggs, C.H. Abner, S.D. Wullschlegel, and C.A. Gunderson. 1997. Temperature-controlled open-top chambers for global change research. *Global Change Biology* 3(3):259-267.

To enable experiments on the interactive effects of elevated atmospheric CO₂ and increased air temperature on physiological processes in trees to be carried out, we altered the standard design of open-top chambers by replacing blowers with evaporative coolers and in-line heaters, with a feedback control system to maintain ambient or elevated air temperatures within the chambers. Ambient and elevated (+ 4 degrees C) temperature regimes were attained consistently and reliably throughout the growing season, with high reproducibility between chambers. From May through December the average of nearly 300,000 temperature measurements was 18.5 degrees C in ambient air, 18.9 +/- 0.6 degrees C in six ambient chambers, and 22.4 +/- 0.9 degrees C in six elevated temperature chambers. The difference in soil temperature between ambient and elevated chambers was 1.2 degrees C. Absolute humidity (vapour pressure) in the chambers was higher than that of ambient air, but it was generally similar between temperature treatments. Vapour pressure deficit therefore was higher in elevated temperature

chambers than in ambient chambers, and this difference is considered an inseparable part of the temperature treatment. The addition of a temperature control system to open-top chambers removes what has been an important flaw in this important tool for global change research.

KEYWORDS: AIR-POLLUTION, BIOMASS PRODUCTION, ELEVATED CO₂, FIELD, PLANT-RESPONSES, SEEDLINGS

1716

Norby, R.J., C.A. Gunderson, S.D. Wullschleger, E.G. Oneill, and M.K. McCracken. 1992. Productivity and compensatory responses of yellow-poplar trees in elevated CO₂. *Nature* 357(6376):322-324.

INCREASED forest growth in response to globally rising CO₂ concentrations could provide an additional sink for the excess carbon added to the atmosphere from fossil fuels 1,2. The response of trees to increased CO₂, however, can be expected to be modified by the interactions of other environmental resources and stresses, higher-order ecological interactions and internal feedbacks inherent in the growth of large, perennial organisms 3,4. To test whether short-term stimulation of tree growth by elevated CO₂ can be sustained without inputs from other environmental resources, we grew yellow-poplar (*Liriodendron tulipifera* L.) saplings for most of three growing seasons with continuous exposure to ambient or elevated concentrations of atmospheric CO₂. Despite a sustained increase in leaf-level photosynthesis and lower rates of foliar respiration in CO₂-enriched trees, whole-plant carbon storage did not increase. The absence of a significant growth response is explained by changes in carbon allocation patterns, specifically a relative decrease in leaf production and an increase in fine root production. Although these compensatory responses reduced the potential increase in carbon storage in increased CO₂ concentrations, they also favour the efficient use of resources over the longer term.

1717

Norby, R.J., and E.G. Oneill. 1991. Leaf-area compensation and nutrient interactions in CO₂-enriched seedlings of yellow-poplar (*Liriodendron tulipifera* L.). *New Phytologist* 117(4):515-528.

The responses of yellow-poplar (*Liriodendron tulipifera* L.) seedlings to elevated levels of atmospheric CO₂ were investigated to identify attributes governing growth and physiological responses to CO₂. Based on the pattern of leaf initiation and nutrient requirements of the species, it was predicted that (1) CO₂ enrichment would enhance growth of yellow-poplar seedlings both through accelerated leaf area production and through higher rates of carbon assimilation per unit leaf area; and (2) growth enhancement of yellow-poplar by CO₂ enrichment would be reduced by nutrient limitations. The hypotheses were tested in an experiment in which yellow-poplar plants were grown from seed for 24 weeks in controlled-environment chambers. The experimental design comprised three atmospheric CO₂ concentrations (371, 493, and 787 cm³ m⁻³), two levels of mineral nutrients (unfertilized or weekly additions of complete nutrient solution), and three harvests (6, 12, and 24 weeks). Plant growth rate, water use, foliar gas exchange, component dry weights, and nutrient contents were measured. Both hypotheses were rejected. Whole-plant dry weight increased similarly with CO₂ enrichment in plants provided with additional mineral nutrients and in unfertilized plants, although the fertilized plants grew 10-fold larger. The increase in dry weight resulting from elevated CO₂ occurred only in root systems. Although leaves were produced continuously during the experiment, leaf area was slightly reduced in elevated CO₂, and the whole-plant growth response was wholly attributable to an increase in carbon assimilation per unit leaf area. Although the compensation between photosynthesis and leaf area reduced the potential growth response to CO₂, the reduction in leaf area ratio was associated with a significant increase in water-use efficiency. This unexpected result

demonstrated the importance of feedbacks and interactions between resources in shaping the response of a plant to CO₂.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CONDUCTANCE, DROUGHT, ENRICHMENT, GROWTH-RESPONSES, HIGH CO₂, PHOSPHORUS DEFICIENCY, PINUS-RADIATA, STRESS, WATER-USE EFFICIENCY

1718

Norby, R.J., S.D. Wullschleger, C.A. Gunderson, D.W. Johnson, and R. Ceulemans. 1999. Tree responses to rising CO₂ in field experiments: implications for the future forest. *Plant, Cell and Environment* 22(6):683-714.

The need to assess the role of forests in the global cycling of carbon and how that role will change as the atmospheric concentration of CO₂ increases has spawned many experiments over a range of scales. Experiments using open-top chambers have been established at many sites to test whether the short-term responses of tree seedlings described in controlled environments would be sustained over several growing seasons under field conditions. Here we review the results of those experiments, using the framework of the interacting cycles of carbon, water and nutrients, because that is the framework of the ecosystem models that are being used to address the decades-long response of forests. Our analysis suggests that most of what was learned in seedling studies was qualitatively correct. The evidence from field-grown trees suggests a continued and consistent stimulation of photosynthesis of about 60% for a 300 p.p.m. increase in [CO₂], and there is little evidence of the long-term loss of sensitivity to CO₂ that was suggested by earlier experiments with tree seedlings in pots. Despite the importance of respiration to a tree's carbon budget, no strong scientific consensus has yet emerged concerning the potential direct or acclimation response of woody plant respiration to CO₂ enrichment. The relative effect of CO₂ on above-ground dry mass was highly variable and greater than that indicated by most syntheses of seedling studies. Effects of CO₂ concentration on static measures of response are confounded with the acceleration of ontogeny observed in elevated CO₂. The trees in these open-top chamber experiments were in an exponential growth phase, and the large growth responses to elevated CO₂ resulted from the compound interest associated with an increasing leaf area. This effect cannot be expected to persist in a closed-canopy forest where growth potential is constrained by a steady-state leaf area index. A more robust and informative measure of tree growth in these experiments is the annual increment in wood mass per unit leaf area, which increased 27% in elevated CO₂. There is no support for the conclusion from many studies of seedlings that root-to-shoot ratio is increased by elevated CO₂; the production of fine roots may be enhanced, but it is not clear that this response would persist in a forest. Foliar nitrogen concentrations were lower in CO₂-enriched trees, but to a lesser extent than was indicated in seedling studies and only when expressed on a leaf mass basis. The prediction that leaf litter C/N ratio would increase was not supported in field experiments. Also contrasting with seedling studies, there is little evidence from the field studies that stomatal conductance is consistently affected by CO₂; however, this is a topic that demands more study. Experiments with trees in open-top chambers under field conditions have provided data on longer-term, larger-scale responses of trees to elevated CO₂ under field conditions, confirmed some of the conclusions from previous seedling studies, and challenged other conclusions. There remain important obstacles to using these experimental results to predict forest responses to rising CO₂, but the studies are valuable nonetheless for guiding ecosystem model development and revealing the critical questions that must be addressed in new larger-scale CO₂ experiments.

KEYWORDS: CARBON-DIOXIDE CONCENTRATION, ELEVATED ATMOSPHERIC CO₂, GLOBAL CLIMATE MODEL, LIRIODENDRON-TULIPIFERA L, LONG-TERM ELEVATION, NET PRIMARY PRODUCTION, PONDEROSA PINE-SEEDLINGS, SOIL-N-

1719

Norby, R.J., S.D. Wullschlegel, C.A. Gunderson, and C.T. Nietch. 1995. Increased growth efficiency of quercus-alba trees in a CO₂-enriched atmosphere. *New Phytologist* 131(1):91-97.

Forests have a prominent role in the global carbon cycle, but their response to a changing atmosphere cannot be measured directly. Experimental observations of small trees in CO₂-enriched atmospheres must be interpreted carefully if they are to be relevant to the potential responses of forest trees. We grew white oak (*Quercus alba* L.) saplings for four complete growing seasons in open-top chambers with different partial pressures of atmospheric CO₂. White oak saplings produced 58% more dry mass in 50 Pa CO₂ and 135% more in 65 Pa, compared with plants in ambient (35 Pa) CO₂. Although this result might suggest a substantial potential for increased carbon storage in forests, the large difference in growth rate could be attributed to a stimulation of growth very early in the experiment. There was not a sustained effect of CO₂ on relative growth rate after the first year, and the increased absolute growth rate could persist only so long as leaf area could increase, a condition that would not occur indefinitely in a forest. Nevertheless, annual stem wood production per unit area (growth efficiency) was 37% greater in elevated CO₂. This increase in growth efficiency, a response that is consistent across diverse studies, implies a potential increase in carbon sequestration by forests, subject to critical assumptions about forest canopy development in a CO₂-enriched atmosphere.

KEYWORDS: CARBON DIOXIDE, CO₂-ENRICHMENT, ELEVATED CO₂, FORESTS, RESPONSES, SEEDLINGS, SOIL

1720

Norris, T.S., and B.J. Bailey. 1996. Use of simulation analysis to improve the design of open-top chambers. *Agricultural and Forest Meteorology* 78(3-4):259-275.

A greenhouse climate simulation model, employing linked first-order integral and differential equations, was adapted to predict the microclimate within carbon-dioxide-enriched open-top chambers (OTCs) suitable for climate change research. The simulation model was validated using experimental measurements from a prototype OTC test rig constructed at Silsoe Research Institute; this model was then used to investigate the effect of employing a controlled combination of air recirculation and ventilation on carbon dioxide consumption for a chamber containing wheat plants. Control criteria for a controlled-ventilation OTC were investigated using the simulation and verified experimentally; results showed that a 2 degrees C temperature excess limit within the chamber could be achieved in practice for a chamber exhibiting minimal wind incursion through the open-top, provided that a mechanical ventilation rate of 6 air changes minute⁻¹ was provided during periods of peak solar flux. Furthermore, the simulation suggested that, by applying controlled ventilation and recirculation to OTCs, it is feasible to reduce the daily consumption of enrichment gas to achieve 560 $\mu\text{mol mol}^{-1}$ concentration within a 3 m-diameter and 3 m-high chamber located at an exposed site to 15 kg in comparison to the estimated 100 kg required when continuous ventilation is employed.

KEYWORDS: CO₂ CONCENTRATION, FIELD CHAMBERS, GAS-EXCHANGE, OZONE

1721

North, G.B., T.L. Moore, and P.S. Nobel. 1995. Cladode development for *Opuntia ficus-indica* (Cactaceae) under current and doubled CO₂ concentrations. *American Journal of Botany* 82(2):159-166.

Morphological and anatomical changes for first-order daughter cladodes (flattened stem segments) of a prickly pear cactus, *Opuntia ficus-indica*, were monitored to determine the effects of a doubled atmospheric CO₂ concentration on their development and mature form. For daughter cladodes developing in controlled environment chambers for 60 d, maximal elongation rates were similar under a photosynthetic photon flux density (PPFD) of 6 mol m⁻² d⁻¹ and a CO₂ concentration of 370 $\mu\text{l liter}^{-1}$, an increased PPFD (10 mol m⁻² d⁻¹), and an increased PPFD and a doubled CO₂ concentration. These maximal rates, however, occurred at 20, 15, and 12 d, respectively. The maximal relative growth rate under the doubled CO₂ concentration was about twice that under the other conditions. For cladodes at 60 d as well as after 4 and 16 mo in open-top chambers, doubling the CO₂ concentration had no effect on final length or width. At 4 mo, cladodes under doubled CO₂ were 27% thicker, perhaps allowing the earlier production of second-order daughter cladodes. The chlorenchyma was then 31% thicker and composed of longer cells. At 16 mo, the difference in cladode thickness diminished, but the chlorenchyma remained thicker under doubled CO₂, which may contribute to greater net CO₂ uptake for *O. ficus-indica* under elevated CO₂ concentrations. Two other persistent differences were a 20% lower stomatal frequency and a 30% thicker cuticle with more epicuticular wax for cladodes under doubled CO₂, both of which may help reduce transpirational water loss.

KEYWORDS: ANATOMY, CRASSULACEAN ACID METABOLISM, ELEVATED CO₂, ENRICHMENT, EPICUTICULAR WAX, GROWTH, LEAVES, MORPHOLOGY, POLYACANTHA CACTACEAE, RESPONSES

1722

Norton, L.R., L.G. Firbank, and H. Blum. 1999. Effects of free-air CO₂ Enrichment (FACE) on experimental grassland communities. *Functional Ecology* 13:38-44.

1. Experimental grassland communities (turves) were exposed to elevated (60 Pa) and ambient (35 Pa) CO₂ partial pressures (pCO₂) in a Free-air Carbon Dioxide Enrichment (FACE) experiment between 30 March 1995 and 4 July 1996. The vegetation was cut once during the experiment prior to the final harvest (harvest 2). 2. No significant treatment effects on total plant biomass at the whole turf level were detected, although biomass was typically about 25% higher under fumigation in year 1 and about 15% higher in year 2, 3. Biomass for two of the six sown species was significantly higher at harvest 2 than at harvest 1. There were no significant differences between individual species biomass under the two CO₂ treatments at either harvest 1 or 2 or in terms of overall cumulative biomass. However, in four of the five sown species in both years biomass tended to be higher in the fumigated than in the control rings (*Cerastium holosteoides*, *Phleum pratense*, *Plantago lanceolata* and *Poa trivialis*). In contrast, *Lolium perenne* showed increased biomass under the control treatment relative to the fumigated treatment in both years. Owing to the high variance both within and between rings for each of the two treatments the statistical power of most, but not all, of the analyses carried out was poor. 4. The relative proportions of each species in the turves under fumigated and control treatments was broadly similar after the first summer, with differences in the second year being mainly owing to the negative response of *L. perenne* to CO₂ fumigation.

KEYWORDS: ALPINE GRASSLAND, COMPETITION, ELEVATED CO₂, GROWTH, LOLIUM-PERENNE, PHLEUM-PRATENSE, PLANTS, RESPONSES, TREES, TRIFOLIUM-REPENS L

1723

Norton, L.R., L.G. Firbank, A.J. Gray, and A.R. Watkinson. 1999. Responses to elevated temperature and CO₂ in the perennial grass *Agrostis curtisii* in relation to population origin. *Functional Ecology*

1. Evolutionary responses to climate change will depend on the presence of heritable variation within species populations for traits that increase fitness under the changing conditions. Patterns of ecotypic differentiation in relation to latitude in some species suggest that such variation exists in relation to temperature responses. Response to elevated CO₂, whether heritable or not, is not expected to be related to latitudinal or climatic differences within temperate regions. 2. To test these ideas, seeds were collected from 10 populations of the outbreeding perennial grass *Agrostis curtisii* across its range in Europe from south Wales to Portugal. Plants were grown under ambient and elevated temperature and CO₂ conditions, in a factorial design, in solardomes; two half sibs from each population were planted in separate pots in each of the two replicate domes with each combination of treatments. One half sib was harvested at the end of the first summer, the second at the end of the second summer. 3. Survival was uniformly high and flowering uniformly low across treatments and populations. 4. Responses to temperature and CO₂ treatments varied over time for almost all populations. Treatment effects were not significant on plants harvested in year 1, although there was a trend towards higher shoot biomass under the elevated temperature and CO₂ treatment. In year 2 shoot biomass was significantly higher under the elevated temperature treatment across all populations and there was a strong trend towards decreased biomass under elevated CO₂. 5. There were no significant correlations of plant response to either CO₂ or temperature with climate at origin. 6. These results warn of the dangers of extrapolating evolutionary plant responses to CO₂ from short-term experiments.

KEYWORDS: BIOMASS, CARBON, ENRICHMENT, ENVIRONMENTS, GROWTH, INTRASPECIFIC VARIATION, PHOTOSYNTHESIS, PLANT-RESPONSES

1724

Norton, L.R., L.G. Firbank, and A.R. Watkinson. 1995. Ecotypic differentiation of response to enhanced CO₂ and temperature levels in *Arabidopsis thaliana*. *Oecologia* 104(3):394-396.

Five ecotypes of *Arabidopsis thaliana*, from widely dispersed origins, were grown under combinations of ambient and elevated atmospheric CO₂ concentrations and ambient and elevated temperatures within solardomes. Total above-ground plant biomass was measured when the majority of plants across all ecotypes and treatments had formed seed pods. There were substantial differences in biomass between the ecotypes across all treatments. Temperature had no effect on biomass whilst CO₂ had a significant effect both alone and in interaction with ecotype. The CO₂ x ecotype interaction was mostly due to the enhancement of a single ecotype from the Cape Verde Islands.

KEYWORDS: ENRICHMENT

1725

Nosberger, J., and B. Campbell. 1997. Interactions between elevated CO₂ and water supply in grasslands - an introduction. *Global Change Biology* 3(3):175.

1726

Novero, R., D.H. Smith, F.D. Moore, J.F. Shanahan, and R. Dandria. 1991. Field-grown tomato response to carbonated water application. *Agronomy Journal* 83(5):911-916.

Direct release of CO₂ gas to achieve a cost-effective method of atmospheric CO₂ enrichment has not been proven feasible under field conditions. We hypothesized that greater efficiency of application would

occur by applying CO₂ via carbonated water and that application would also result in beneficial modifications of the soil environment. Our objectives were to evaluate crop, soil, and atmospheric CO₂ responses to application of carbonated water under pressure through a drip irrigation system. Studies were conducted under mulched and unmulched conditions in 1988 using tomato (*Lycopersicon esculentum* Mill.). In 1989, carbonated water was applied at approximately 2-, 4-, and 6-d intervals to determine the effect of irrigation frequency. In 1988, a positive yield response of 9% was obtained in the presence of mulch. No response was observed in open beds. Fruit yields were increased at all three irrigation frequencies in 1989, with increases in fresh-market and total fruit yields averaging 16.4 and 15.9%, respectively. Atmospheric enrichment was observed during carbonated water application, but residual enrichment between irrigations was difficult to detect. Significant increase in soil-air CO₂ from carbonated water application was noted throughout the intervals between successive irrigation events. Carbonated water application also decreased soil pH for periods of up to 5 d after irrigation and increased apparent uptake of P, K, Ca, Mg, Zn, Fe, Mn, Cu, and B. Based on the limited duration of enrichment relative to the entire growing season for any of the carbonated water treatments, the yield responses observed could not be attributed solely to atmospheric enrichment. Thus, we conclude that yield increases resulted from the combined effects of limited atmospheric CO₂ enrichment and soil environment modifications leading to improved nutrient uptake.

KEYWORDS: ATMOSPHERIC CO₂, COTTON, DIOXIDE

1727

Nowak, E.J., and C.E. Martin. 1995. Effect of elevated CO₂ on nocturnal malate accumulation in the CAM species *Tillandsia ionantha* and *Crassula arborescens*. *Photosynthetica* 31(3):441-444.

The effect of elevated CO₂ on overnight malate accumulation in the CAM epiphyte *Tillandsia ionantha* and the CAM terrestrial species *Crassula arborescens* was compared. Both species showed an increase in nocturnal accumulation of malate with increasing CO₂ concentrations. This study is the first to show an increase in nighttime malate accumulation with increasing levels of CO₂ at near-ambient concentrations in a CAM plant. The results indicate that some CAM plants can respond to increasing levels of CO₂ in the atmosphere, potentially leading to an increase in productivity.

KEYWORDS: ACID METABOLISM, GROWTH, KALANCHOE-DAIGREMONTIANA, OPUNTIA FICUS INDICA, PLANTS

1728

Nunes, M.A., J.D.C. Ramalho, and M.A. Dias. 1993. Effect of nitrogen supply on the photosynthetic performance of leaves from coffee plants exposed to bright light. *Journal of Experimental Botany* 44(262):893-899.

Although *Coffea arabica* L. grows naturally in shaded habitats, it can be cultivated under high light intensity, but not without severe photoinhibition mainly during the period of transfer from the nursery into the field. The present work examines some of the changes in the photosynthetic performance induced by exposure to high light and the possibility of using enhanced nitrogen levels to overcome photoinhibition. For that purpose, young plants of *Coffea arabica* L. (cv. Catuai) grown in a shaded greenhouse were treated with 0, 1 and 2 mmol of nitrogen and 4 weeks later exposed to full solar irradiation, outside. Visible damage due to exposure to full sunlight appeared within 2 d in all plants, resulting in a reduced photosynthetic leaf area and drastic shedding of leaves in the unfertilized plants. These effects were considerably less in plants with the highest N dose. After 130 d of exposure, there was 100% mortality in plants receiving no extra

nitrogen, compared with 30% in the plants treated with 2 mmol nitrogen. Photosynthesis rates, leaf conductance and transpiration presented minimum values after 4 d of light stress. Large changes in the photosynthetic capacity (measured at high CO₂ concentration and high light intensity), quantum efficiency and fluorescence yield (F(v)/F(m)) indicate that net photosynthesis rate in the air had been reduced by both stomatal closure and by changes at the photochemical level. All indicators show that N-fertilized plants were less affected by photoinhibition.

KEYWORDS: ANACYSTIS-NIDULANS, BARLEY LEAVES, CHLOROPHYLL FLUORESCENCE, CO₂ ASSIMILATION, PHOTONHIBITION, RECOVERY, SOLANUM-DULCAMA, TEMPERATURE, WATER RELATIONS, WILLOW LEAVES

1729

Nungesser, M.K., L.A. Joyce, and A.D. McGuire. 1999. Effects of spatial aggregation on predictions of forest climate change response. *Climate Research* 11(2):109-124.

We investigated the influence of spatial aggregation on modeled forest responses to climate change by applying the process-based Terrestrial Ecosystem Model (TEM) to a fine resolution spatial grid (100 km(2)) and to a coarse resolution spatial grid (2500 km(2)). Three climate scenarios were simulated: baseline (present) climate with ambient CO₂ and 2 future climates derived from the general circulation models OSU and GFDL-Q with elevated atmospheric CO₂. For baseline climate, the aggregation error of the national (U.S.) study area was very small, -0.4%. Forest-level aggregation error ranged from -1.6 to 11.8%, with the largest aggregation error occurring in boreal forest types. Coarse grid resolution inputs underestimated production for boreal and forested boreal wetland forests and overestimated net primary production (NPP) for temperate conifer, temperate deciduous, and temperate forested wetland forests. Aggregation error for coarse grid cells ranged between -25.6 and 27.3%. Aggregation errors were especially large in transition regions between temperate and boreal forest types. An analysis that homogenized inputs for the 10 km grid cells within a 50 km grid indicated that aggregation of forest types and air temperature from fine to coarse grid cells contributed most to the spatial aggregation error. The aggregation error for the OSU climate was similar to the GFDL-Q climate and both results were similar to the aggregation error of the baseline climate in magnitude, sign, and spatial pattern. While aggregation error was similar across the baseline, GFDL-Q and OSU scenarios, NPP response to the GFDL-Q and OSU climates increased 13 to 30% above the baseline NPP. Within each climate scenario, the estimated NPP response to climate change differed by less than 1% between the coarse and fine resolutions. Except for transition regions and regions with substantial variability in air temperature, our simulations indicate that the use of 0.5 degrees resolution provides an acceptable level of aggregation error at the 3 scales of analysis in this study. Improvements could be made by focusing computational intensity in heterogeneous regions and avoid computational intensity in regions that are relatively homogeneous with respect to vegetation and air temperature.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CO₂ EXCHANGE, EQUILIBRIUM RESPONSES, FRANKFURT BIOSPHERE MODEL, NET PRIMARY PRODUCTION, PRECIPITATION, SCALE, TERRESTRIAL ECOSYSTEMS, VARIABILITY, VEGETATION

1730

Nussbaumer, U., J. Ascher, A. Kraft, and H. Insam. 1997. Litter decomposition of a tropical understory species (*Ctenanthe lubbersiana*) grown under ambient and elevated CO₂. *Acta Oecologica-International Journal of Ecology* 18(3):377-381.

A CO₂ evolution and a dissolved organic carbon (DOC)-die-away test were used to determine the inherent decomposability of plant litter of *Ctenanthe lubbersiana* grown under ambient (340 ppm) and elevated CO₂ (610 ppm). The CO₂ evolution of leaf litter in a 10 day decomposition assay was retarded by 7% (P = 0.046). In the DOG-die-away test, the decomposition of a leaf litter hot water extract was retarded by 8% (P = 0.039). The decomposition of the solid litter fraction was retarded by 16% (P = 0.101). The decomposition rate of petioles was not affected by elevated CO₂. Despite the differences were small, the results suggest possible effects on ecosystem C cycling.

KEYWORDS: ATMOSPHERIC CO₂, BIOMASS, CARBON, COMMUNITIES, QUALITY, SOIL

1731

Obenland, D.M., L.H. Aug, and R.E. Rij. 1994. Timing and control of methanethiol emission from broccoli florets induced by atmospheric modification. *Journal of Horticultural Science* 69(6):1061-1065.

Storage of broccoli (*Brassica oleracea* L., Italica Group) under conditions of low O₂ concentration extends its shelf life. Excessively low O₂, however, leads to the formation of an offensive odour which is primarily due to the emission of methanethiol. In this study, we investigated the initial induction and control of methanethiol production of broccoli florets exposed to various levels of O₂ and CO₂ over short-term periods of 10 h or less. Lowering the O₂ concentration surrounding the broccoli florets by continuously flowing N₂ through the sample containers acted to initiate the production of methanethiol within 1 h after the O₂ concentration had reached 0.5%. After initiation the rate of production showed a slow but steady increase during the 10 h of experimentation. In contrast, introduction of O₂ into the sample containers while the broccoli florets were actively producing methanethiol led to a rapid 79% drop in the amount of methanethiol detected within 15 min, followed by a complete absence of methanethiol within another 15 min. Resumption of N₂ flow acted to reinitiate methanethiol production, with the initiation requiring a lesser amount of time than that required for the initial induction of methanethiol production. Experiments with elevated CO₂ concentrations of up to 26.5% determined that CO₂ is an inhibitor of methanethiol production.

KEYWORDS: STORAGE

1732

Oechel, W.C., S. Cowles, N. Grulke, S.J. Hastings, B. Lawrence, T. Prudhomme, G. Riechers, B. Strain, D. Tissue, and G. Vourlitis. 1994. Transient nature of CO₂ fertilization in arctic tundra. *Nature* 371(6497):500-503.

THERE has been much debate about the effect of increased atmospheric CO₂ concentrations on plant net primary production(1,3) and on net ecosystem CO₂ flux(3-10). Apparently conflicting experimental findings could be the result of differences in genetic potential(11-15) and resource availability(16-20), different experimental conditions(21-24) and the fact that many studies have focused on individual components of the system(2,21,25-27) rather than the whole ecosystem. Here we present results of an in situ experiment on the response of an intact native ecosystem to elevated CO₂. An undisturbed patch of tussock tundra at Toolik Lake, Alaska, was enclosed in greenhouses in which the CO₂ level, moisture and temperature could be controlled(28), and was subjected to ambient (340 p.p.m.) and elevated (680 p.p.m.) levels of CO₂ and temperature (+4 degrees C). Air humidity, precipitation and soil water table were maintained at ambient control levels. For a doubled CO₂ level alone, complete homeostasis of the CO₂ flux was re-established within three years, whereas the regions exposed to a combination of higher temperatures and doubled CO₂ showed persistent fertilization effect on net ecosystem carbon sequestration over this time.

This difference may be due to enhanced sink activity from the direct effects of higher temperatures on growth (16,29-33) and to indirect effects from enhanced nutrient supply caused by increased mineralization (10,11,19,27,34). These results indicate that the responses of native ecosystems to elevated CO₂ may not always be positive, and are unlikely to be straightforward. Clearly, CO₂ fertilization effects must always be considered in the context of genetic limitation, resource availability and other such factors.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, BIOMASS PRODUCTION, CLIMATE CHANGE, ELEVATED CO₂, MINERAL NUTRITION, PHOTOSYNTHETIC ACCLIMATION, SOIL TEMPERATURE, TRANSGENIC TOBACCO PLANTS, TUSSOCK TUNDRA, UNMANAGED ECOSYSTEMS

1733

Oechel, W.C., G. Riechers, W.T. Lawrence, T.J. Prudhomme, N. Grulke, and S.J. Hastings. 1992. CO₂ in an automated, null-balance system for studying the effects of elevated CO₂ and global climate change on unmanaged ecosystems. *Functional Ecology* 6(1):86-100.

An automated, CO₂-controlled, long-term greenhouse system ('CO₂LT') has been developed to provide replicated in situ ecosystem-level manipulation of atmospheric CO₂ concentration and temperature for intact plots of tussock tundra, and to measure the instantaneous ecosystem-level CO₂ exchange rates within each of the plots under the treatments imposed. This is a computer-controlled, closed, null-balance greenhouse system consisting of 12 chambers with individual control of CO₂ concentration and temperature. Carbon dioxide can be maintained in each chamber at concentrations from well below ambient (150-200- μ -l-l-1) to more than 900- μ -l-l-1. Air temperature can be fixed, set to track ambient, or can track ambient temperature with a specified offset allowing studies of the interaction of CO₂ and temperature. Despite the complications involved in tracking a naturally fluctuating environment, the CO₂LT system performs very well. Temperatures in individual chambers average within 1-degree-C of ambient or target temperatures over a 24-h period and carbon dioxide concentration control rivals that of laboratory-based, control-environment systems. Photon flux density within the chambers is within 93% of ambient values. Comparison to unenclosed tundra indicates minimal chamber effects on depth of thaw, air, leaf, or soil temperatures, or net ecosystem CO₂ flux. Chamber effects are generally small, and the experimental design allows separation and interpretation of treatment effects despite any unavoidable chamber effects. Both diurnal and seasonal patterns of net ecosystem CO₂ flux can be accurately tracked with this system. Field measurements indicate net ecosystem CO₂ loss under current environmental conditions, a possible response to recent climate change. Field measurements also indicate initial enhancement of net ecosystem CO₂ uptake with elevated atmospheric CO₂. Photosynthetic adjustment to elevated CO₂ lowers ecosystem response to that of ambient chambers by mid-season. Also indicated is the possibility of delayed senescence of photosynthetic capacity at elevated CO₂.

1734

Oechel, W.C., and G.L. Vourlitis. 1994. The effects of climate-change on land atmosphere feedbacks in arctic tundra regions. *Trends in Ecology and Evolution* 9(9):324-329.

Recently reported high-latitude warming has the potential to affect arctic ecosystem structure and function in the short and long term. Arctic ecosystems are known sources of atmospheric CH₄, and recent CO₂ flux measurements indicate that these ecosystems are now, at least regionally, net sources of atmospheric CO₂. It appears that over the short term (decades to centuries), arctic ecosystems may represent a positive feedback on global atmospheric CO₂ concentrations and associated

greenhouse gas-induced climate change. In addition, short-term feedbacks may be large enough to affect both local and global surface temperatures. Over the long term, changes in the structure, function and composition of arctic ecosystems may increase C accumulation relatively more than the amount lost, thus restoring the sink status of arctic ecosystems.

KEYWORDS: ACID PEAT, ALASKAN TUNDRA, BALANCE, CARBON DIOXIDE, ECOSYSTEMS, ELEVATED CO₂, EMISSIONS, METHANE, TEMPERATURE, TUSSOCK TUNDRA

1735

Oechel, W.C., G.L. Vourlitis, S. Brooks, T.L. Crawford, and E. Dumas. 1998. Intercomparison among chamber, tower, and aircraft net CO₂ and energy fluxes measured during the Arctic System Science Land-Atmosphere-Ice Interactions (ARCSS-LAI) Flux Study. *Journal of Geophysical Research-Atmospheres* 103(D22):28993-29003.

Measurements of net ecosystem CO₂ exchange (NEE) and energy balance were made using chamber-, tower-, and aircraft-based measurement techniques in Alaskan arctic tundra ecosystems during the 1994-1995 growing seasons (June-August). One of our objectives was to quantify the interrelationships between the NEE and the energy balance measurements made from different sampling techniques. Qualitative and quantitative intercomparisons revealed that on average the correspondence between the mass and energy fluxes measured by these sampling methods was good despite potential spatial and temporal mismatches in sampling scale. Quantitative comparisons using least squares linear regression analyses with the tower-based measurements of NEE as the independent variable indicate that the chamber- and aircraft-based NEE measurements were generally lower relative to the tower-based measurements (slope = 0.76-0.86). Similarly, tower-aircraft comparisons of latent (L-e) and sensible (H) heat exchange indicated that the aircraft-based measurements were lower than the tower-based measurements (slope = 0.72-0.80). Qualitative comparisons, however, indicate that the correspondence among the chamber-, tower-, and aircraft-measured fluxes varied both seasonally and interannually, suggesting the lack of a consistent bias between the sampling techniques. The results suggest that differences observed between the chamber, tower, and aircraft flux measurements were primarily due to the failure to account for the spatial distribution of surface types in the tower and aircraft sampling footprint, problems involved in the comparison of temporal and spatial averages, and temporal (e.g., seasonal and interannual) variance in rates of mass and energy flux for a given point. Other potential sources of variance include the underestimation of nocturnal NEE by the tower-based eddy covariance system, and the periodic occurrence of an elevated CO₂ plume in the atmosphere over the Prudhoe Bay oil field. Even with these potential sources of variation, the results reveal that the various methods give comparable estimates of NEE and energy flux within a range of temporal or spatial variability.

KEYWORDS: ALASKA, BROOKS-RANGE, CARBON DIOXIDE, CLIMATE CHANGE, EDDY-COVARIANCE, HEAT, OPEN-PATH, TUNDRA ECOSYSTEMS, VAPOR, WATER

1736

Oechel, W.C., G.L. Vourlitis, S.J. Hastings, R.P. Ault, and P. Bryant. 1998. The effects of water table manipulation and elevated temperature on the net CO₂ flux of wet sedge tundra ecosystems. *Global Change Biology* 4(1):77-90.

lit situ manipulations were conducted in a naturally drained lake on the arctic coastal plain near Prudhoe Bay, Alaska (70 degrees 21.98' N, 148 degrees 33.72' W) to assess the potential shortterm effects of decreased water table and elevated temperature on net ecosystem CO₂ flux. The

experiments were conducted over a 2-year period, and during that time, water table depth of drained plots was maintained on average 7 cm lower than the ambient water table, and surface temperatures of plots exposed to elevated temperature were increased on average 0.5 degrees C. Water table drainage, and to a lesser extent elevated temperature, resulted in significant increases in ecosystem respiration (ER) rates, and only small and variable changes in gross ecosystem productivity (GEP). As a result, drained plots were net sources of approximate to 40 gC m(-2) season(-1) over both years of manipulation, while control plots were net sinks of atmospheric CO₂ of about 10 gC m(-2) season(-1) (growing season length was an estimated 125 days). Control plots exposed to elevated temperatures accumulated slightly more carbon than control plots exposed to ambient temperatures. The direct effects of elevated temperature on net CO₂ flux, ER, and GEP were small, however, elevated temperature appeared to interact with drainage to exacerbate the amount of net carbon loss. These data suggest that many currently saturated or nearly saturated wet sedge ecosystems of the north slope of Alaska may become significant sources of CO₂ to the atmosphere if climate change predictions of increased evapotranspiration and reduced soil water status are realized. There is ample evidence that this may be already occurring in arctic Alaska, as a change in net carbon balance has been observed for both tussock and wet-sedge tundra ecosystems over the last 2-3 decades, which coincides with a recent increase in surface temperature and an associated decrease in soil water content. In contrast, if precipitation increases relatively more than evapotranspiration, then increases in soil moisture content will likely result in greater carbon accumulation.

KEYWORDS: ALASKA, ARCTIC TUNDRA, ATMOSPHERE, BROOKS-RANGE, CARBON DIOXIDE, CLIMATE CHANGE, METHANE FLUXES, SOILS, TUSSOCK TUNDRA, VEGETATION

1737

Oechel, W.C., G.L. Vourlitis, S.J. Hastings, and S.A. Bochkarev. 1995. Change in arctic CO₂ flux over 2 decades - effects of climate-change at barrow, Alaska. *Ecological Applications* 5(3):846-855.

A significant difference in net ecosystem carbon balance of wet sedge ecosystems in the Barrow, Alaska region was observed between CO₂ flux measurements obtained during the International Biological Program in 1971 and measurements made during the 1991-1992 growing seasons. Currently, high-center polygons are net sources of CO₂ to the atmosphere of approximate to 14 gC . m(-2). yr(-1), while low-center polygons are losing approximate to 3.6 gC . m(-2). yr(-1), and ice wedge habitats are accumulating 4.0 gC . m(-2). yr(-1). On average, moist meadow habitats characteristic of the IBP-II site are currently sources of approximate to 1.3 gC . m(-2). yr(-1) to the atmosphere compared to the reported accumulation of approximate to 25 gC . m(-2). yr(-1) determined in 1971. This difference in ecosystem function over the last two decades may be due to the recently reported increase in surface temperatures resulting in decreases in the soil moisture status. These results point to the importance of long-term research sites and databases for determining the potential effects of climate change on ecosystem function.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, BALANCE, ECOSYSTEMS, GROWTH, NUTRIENT, PERMAFROST, SOIL, TEMPERATURE, TUNDRA, WATER

1738

Oeschger, H. 1992. Atmospheric CO₂ - global change and regulation mechanisms. *Berichte Der Bunsen-Gesellschaft-Physical Chemistry Chemical Physics* 96(3):252-257.

For the estimate of the distribution in the carbon system of the CO₂ emitted into the atmosphere due to human activities, the exchange of

carbon between atmosphere and ocean, and between atmosphere and biosphere needs to be considered. Information on this spreading of excess CO₂ can be obtained from measurements of a.o. CO₂, C-13/C-12, C-14/C in the atmosphere, of natural and nuclear weapon produced C-14 in the ocean and in the biota and of other natural or anthropogenic tracers. - Based essentially on such information, models for the CO₂ uptake by the carbon system have been developed which are capable of reproducing the result of the drop in the rate of increase of CO₂ emissions from 4.5% to 2% per year following the oil-embargo in 1973. - Of special interest regarding the understanding of the carbon cycle and its role in controlling the climate of the Earth are the observations in polar ice cores covering the past 160.000 years, corresponding to one and a half glaciation cycles. They show variations of atmospheric CO₂, CH₄, and N₂O parallel to the climatic variations. Measurements of C-13/C-12 in shells of foraminifera support the hypothesis that these CO₂ changes are caused by changes in the ocean's biological pump, i.e. the flux of detrital organic carbon from the surface to the deep ocean, which affects the total inorganic carbon in the surface ocean and the partial pressure of CO₂.

KEYWORDS: ICE CORE, RECORD

1739

Ogasawara, N., H. Inden, and T. Asahira. 1996. Effects of lighting cycle on *Caladium* plantlets grown under ventilated and airtight culture vessels in relation to net daily CO₂ uptakes. *Journal of the Japanese Society for Horticultural Science* 65(1):129-134.

Caladium plantlets were cultured in vitro under a long lighting cycle (16 hr light/8 hr dark) and a short lighting cycle (2 hr light/1 hr dark). When gas exchange between the inside and outside of the culture vessel was allowed, the short lighting cycle enhanced growth, but when the culture vessel was airtight, the lighting cycle had no effect on growth. The estimated net daily CO₂ uptake under the short lighting cycle is greater than that under the long lighting cycle only when gas exchange occurs between the inside and outside of the vessel. These results demonstrate that the enhancement of growth by the short lighting cycle is due to an increase in the amount of available CO₂ resulting from the reduced escape of CO₂ from the vessel.

KEYWORDS: INVITRO

1740

Ojala, A., P. Kankaala, J. Haapamaki, and T. Tulonen. 1995. Immediate responses of photosynthesis and dark respiration of late summer stands of *Equisetum fluviatile* L to increasing concentrations of atmospheric CO₂. *Journal of Applied Botany-Angewandte Botanik* 69(5-6):169-176.

Short-term responses of net photosynthesis, apparent dark respiration and gross photosynthesis of *Equisetum fluviatile* to increasing concentrations of atmospheric CO₂ were studied by using transplanted stands of natural origin. Three transplantations with biomasses of 274, 407, and 401 g dry weight m(-2) were established six weeks before the measurements in late August. Net photosynthesis and apparent dark respiration was measured from the change of CO₂ concentration inside polycarbonate chambers with diameter of 0.455 m and volume of 0.207 m(3). Altogether 50 experiments for determination of CO₂ influx rates and 24 for efflux rates were run without any pre-treatment to higher CO₂ and each of them lasted 20-30 min. The response of net photosynthesis of *E. fluviatile* to CO₂ enrichment was less clear than the response to temperature or irradiance. Nevertheless, the stands showed an increase of ca. 25 % in net photosynthesis when the CO₂ concentration in air was increased from ambient to 500-600 ppm. When the CO₂ concentration was > 600 ppm the increase was ca. 60 %. A multilinear regression model combining solar radiation, temperature and CO₂ concentration

could only explain 46.4 % of the variation in the observed rates of net photosynthesis. The apparent dark respiration was positively correlated with temperature but inversely related to CO₂ concentration. When the CO₂ concentration was doubled from ambient the stands of *E. fluviatile* reduced their apparent dark respiration by ca. 50 %. Under higher CO₂ concentration *E. fluviatile* appeared more effective than in the ambient concentration, as the production lost through respiration decreased. When the concentration of atmospheric CO₂ was < 500 ppm, 57.5 % of gross production was respired whereas above 500 ppm of CO₂ the corresponding proportion was only 34.2 %. As the enrichment with CO₂ resulted in decreased respiration rates and it was known from long-term growth and photosynthesis experiments that neither shoot growth in length in *E. fluviatile* is stimulated by higher CO₂ concentrations nor do the stands show down-regulation of photosynthesis after several weeks of CO₂ enrichment, it was concluded that the extra carbon fixed was allocated to storage through growth of below-ground biomass.

KEYWORDS: AQUATIC MACROPHYTES, CARBON DIOXIDE, COMMUNITIES, ENRICHMENT, GROWTH, LAKE PAAJARVI, PLANTS, SHORT- TERM, SOUTHERN FINLAND, WATER HYACINTH

1741

Ojima, D.S., W.J. Parton, D.S. Schimel, J.M.O. Scurlock, and T.G.F. Kittel. 1993. Modeling the effects of climatic and CO₂ changes on grassland storage of soil-C. *Water, Air, and Soil Pollution* 70(1-4):643-657.

We present results from analyses of the sensitivity of global grassland ecosystems to modified climate and atmospheric CO₂ levels. We assess 31 grassland sites from around the world under two different General Circulation Models (GCM) double CO₂ climates. These grasslands are representative of mostly naturally occurring ecosystems, however, in many regions of the world, grasslands have been greatly modified by recent land use changes. In this paper we focus on the ecosystem dynamics of natural grasslands. The climate change results indicate that simulated soil C losses occur in all but one grassland ecoregion, ranging from 0 to 14% of current soil C levels for the surface 20 cm. The Eurasian grasslands lost the greatest amount of soil C (approximately 1200 g C m⁻²) and the other temperate grasslands losses ranged from 0 to 1000 g C m⁻², averaging approximately 350 g C m⁻². The tropical grasslands and savannas lost the least amount of soil C per unit area ranging from no change to 300 g C m⁻² losses, averaging approximately 70 g C m⁻². plant production varies according to modifications in rainfall under the altered climate and to altered nitrogen mineralization rates. The two GCM's differed in predictions of rainfall with a doubling of CO₂, and these differences are reflected in plant production. Soil decomposition rates responded most predictably to changes in temperature. Direct CO₂ enhancement effects on decomposition and plant production tended to reduce the net impact of climate alterations alone.

KEYWORDS: TERRESTRIAL

1742

Olaizola, M., E.O. Duerr, and D.W. Freeman. 1991. Effect of CO₂ enhancement in an outdoor algal production system using tetraselmis. *Journal of Applied Phycology* 3(4):363-366.

One of the objectives of microalgal culture is to provide reliable production technology for important live aquaculture feed organisms. Presented here are the results of experiments designed to provide a better understanding of the relationship between inorganic carbon availability and algal production. Our results suggest that through additions of CO₂ gas we were able to maintain sufficient dissolved carbon to stabilize outdoor algal cultures. Increases in the rate of addition of CO₂ increased levels of dissolved CO₂, total dissolved inorganic carbon (SIGMA-

CO₂), and decreased pH in the growth medium. This translated into improved buffering capacity of the culture medium and higher growth rate. A minimum of 2.4 mM SIGMA-CO₂ was found necessary to maintain a maximal growth rate of 0.7 doublings/day. We also found that the increased productivity more than offsets the cost of adding the CO₂.

1743

Olesniewicz, K.S., and R.B. Thomas. 1999. Effects of mycorrhizal colonization on biomass production and nitrogen fixation of black locust (*Robinia pseudoacacia*) seedlings grown under elevated atmospheric carbon dioxide. *New Phytologist* 142(1):133-140.

Interactive effects of elevated atmospheric CO₂ and arbuscular mycorrhizal (AM) fungi on biomass production and N-2 fixation were investigated using black locust (*Robinia pseudoacacia*). Seedlings were grown in growth chambers maintained at either 350 μmol mol⁻¹ or 710 μmol mol⁻¹ CO₂. Seedlings were inoculated with *Rhizobium* spp. and were grown with or without AM fungi. The N-15 isotope dilution method was used to determine N source partitioning between N, fixation and inorganic fertilizer uptake. Elevated atmospheric CO₂ significantly increased the percentage of fine roots that were colonized by AM fungi. Mycorrhizal seedlings grown under elevated CO₂ had the greatest overall plant biomass production, nodulation, N and P content, and root N absorption. Additionally, elevated CO₂ levels enhanced nodule and root mass production, as well as N, fixation rates, of nonmycorrhizal seedlings. However, the relative response of biomass production to CO₂ enrichment was greater in non-mycorrhizal seedlings than in mycorrhizal seedlings. This study provides strong evidence that arbuscular mycorrhizal fungi play an important role in the extent to which plant nutrition of symbiotic N-2-fixing tree species is affected by enriched atmospheric CO₂.

KEYWORDS: BOUTELOUA-GRACILIS, CLIMATE CHANGE, CO₂-ENRICHMENT, EXTERNAL HYPHAE, GLOMUS-RHIZOBIUM SYMBIOSIS, N-UPTAKE, N₂ FIXATION, PHOSPHATE NUTRITION, SOIL N, TRIFOLIUM-SUBTERRANEUM L

1744

Olszyk, D.M., H.G.S. Centeno, L.H. Ziska, J.S. Kern, and R.B. Matthews. 1999. Global climate change, rice productivity and methane emissions: comparison of simulated and experimental results. *Agricultural and Forest Meteorology* 97(2):87-101.

Irrigated rice production is a major food source for a large portion of the world's population, and a major anthropogenic source of the greenhouse gas methane (CH₄). Potential impacts of global climate change [elevated carbon dioxide (CO₂) and/or elevated temperature] on rice can be predicted with simulation models, but experiments are necessary to determine how well these models mimic the responses of the field crop. This paper compares grain yield, biomass, and methane emissions from experiments at the international Rice Research Institute (IRRI) at Los Banos, the Philippines, with potential responses based on simulations using the ORYZA1 process model and the climate data from those experiments. Yield and biomass were compared for the 1995 and 1996 dry seasons (DS) and the 1994 wet season (WS). Emissions of CH₄ from rice fields were evaluated for the 1995 WS and 1996 DS. Simulated and experimental responses (adjusted for effects of the open-top chambers on plant growth) differed with climate change scenario, response parameter, and season. Under current climate conditions (ambient CO₂ and ambient temperature), simulated grain yield was 14% lower than the adjusted experimental grain yield in the 1996 DS, but was 17 and 37% higher than experimental grain yield in the 1995 DS and 1994 WS, respectively. With current climate, simulations underestimated experimental aboveground, belowground, and total biomass. The

simulated CH₄ emissions were the same as the experimental emissions, assuming CH₄ emissions were 2.9% of the simulated total biomass carbon. With elevated CO₂ and ambient temperature, simulations predicted greater increases (compared with current climate) in grain yield, aboveground biomass, and total biomass, but generally smaller increases in belowground biomass and CH₄ emissions than the significant (at $p < 0.05$) increases that were found experimentally. With ambient CO₂ and elevated temperature, both simulations and experiments generally showed either no change or a decrease in grain yield and biomass, but none of the responses in the experiments were statistically significant. Simulated ambient CO₂ and elevated temperature resulted in a smaller decrease in CH₄ emissions than the significant decrease found in the experiments. For both elevated CO₂ and elevated temperature, simulated grain yield increased in all three seasons, whereas there were no significant effects on experimental grain yield. The simulations predicted smaller increases in belowground biomass and CH₄ emissions with elevated CO₂ and elevated temperature than the significant increases in the experiments. To better correspond to experimental results, this study suggested that current simulation models could be improved in terms of effects of temperature on grain yield and use of belowground biomass to estimate CH₄ emissions. (C) 1999 Elsevier Science B.V. All rights reserved.

KEYWORDS: CO₂, GROWTH, IMPACT, INCREASING CARBON-DIOXIDE, ORYZA-SATIVA, PADDYRICE, PLANTS, TEMPERATURE, TROPICAL RICE, YIELD

1745

Olszyk, D.M., and C. Wise. 1997. Interactive effects of elevated CO₂ and O-3 on rice and flacca tomato. *Agriculture Ecosystems & Environment* 66(1):1-10.

Atmospheric concentrations of both carbon dioxide (CO₂) and ozone (O-3) are increasing, with potentially dramatic effects on plants. This study was conducted to determine interactive effects of CO₂ and O-3 on rice (*Oryza sativa* L. cv. IR 74) and a 'wilty' mutant of tomato (*Lycopersicon esculentum* Mill. flacca). Plants were grown from seed in a glasshouse and exposed for 28 days to ambient or elevated CO₂ (approximate to 400 or 700 $\mu\text{mol mol}^{-1}$ CO₂) and/or ambient or elevated O-3 (peak/valley pattern of exposure with cumulative totals of approximate to 1 or 44 $\mu\text{mol l}^{-1}$ h). Elevated CO₂ alleviated O-3-associated decreases in allocation of biomass to roots, as indicated by a decreased root:shoot ratio ($p < 0.05$), and also reduced injury from O-3 as indicated by leaf greenness readings for one experiment ($p < 0.05$). By itself, elevated CO₂ resulted in increases in total plant and individual organ (root, leaf, stem) dry weights and root:shoot ratio and elevated O-3 resulted in increases in main culm leaf number and a decrease in stem dry weight ($p < 0.05$). Elevated CO₂ had no significant effect on the tendency for O-3-induced biomass reductions of flacca tomato. For flacca, elevated CO₂ alone increased shoot and root biomass ($p < 0.05$), and elevated O-3 alone tended to decrease biomass for both parameters, but only at $p = 0.09$ and 0.11, respectively. This study was preliminary, as the environmental conditions in these experiments may have altered O-3 and CO₂ responses of the plants. However, these results provided additional evidence that elevated CO₂ inhibits adverse effects of O-3 on plants, and that the interactive response may be mediated by stomata. (C) 1997 Elsevier Science B.V.

KEYWORDS: AIR- POLLUTANTS, B RADIATION, BIOMASS, CARBON-DIOXIDE CONCENTRATION, CHRONIC OZONE, EXPOSURE, GROWTH, REGIMES, RESPONSES, SEEDLINGS

1746

Olszyk, D., C. Wise, E. VanEss, M. Apple, and D. Tingey. 1998. Phenology and growth of shoots, needles, and buds of Douglas- fir seedlings with elevated CO₂ and (or) temperature. *Canadian Journal of*

Botany-Revue Canadienne De Botanique 76(12):1991-2001.

Increased atmospheric CO₂ and global warming may affect overall tree growth, but impacts of these combined stresses are largely unknown in terms of multiple growing season impacts on specific flushes. Thus, the effects of ambient or elevated CO₂ (approximately 200 $\mu\text{mol mol}^{-1}$) above ambient) and ambient or elevated temperature (approximately 4 degrees C above ambient) were evaluated for both main and second (lammas) flushes of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) France). Established seedlings were grown for three full growing seasons in outdoor, sunlit chambers, which maintained diel and seasonal variation in climate. A reconstructed forest soil was used with a seasonal wet and dry cycle and without added fertilizer. Compared with ambient CO₂ elevated CO₂ had no impact on overall phenology and growth of terminal shoots, needles, or buds. In contrast, compared with ambient temperature, elevated temperature resulted in higher shoot and needle growth rates early in the season; reduced final terminal shoot length; and either reduced, increased, or unchanged final needle length, depending on season. Initiation of the lammas flush was delayed and (or) decreased at elevated temperature. Leading terminal bud break and growth occurred earlier; however, resting bud length was reduced, and bud width tended to increase with elevated temperature. Thus, at least during early seedling growth, elevated temperatures may reduce both main- and lammas- flush growth, thereby altering tree productivity, whereas elevated CO₂ may have little effect on main or lammas growth at either the current or elevated temperature.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, BURST, HARDINESS, PINE, RESPONSES, SEASONALITY, TREES, WOODY- PLANTS

1747

Olszyk, D., C. Wise, E. VanEss, and D. Tingey. 1998. Elevated temperature but not elevated CO₂ affects long-term patterns of stem diameter and height of Douglas-fir seedlings. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 28(7):1046-1054.

Global climatic change may impact forest productivity, but data are lacking on potential effects of elevated CO₂ and temperature on tree growth. We determined changes in shoot growth for Douglas-fir (*Pseudotsuga menziesii* (Mirb.) France) seedlings exposed to ambient or elevated CO₂ (+approximate to 179 $\mu\text{mol mol}^{-1}$), and ambient or elevated temperature (+approximate to 3.5 degrees C). Seedlings were grown for 4 years (three complete growing seasons) in outdoor, sunlit chambers. In each season, height growth was initiated earlier and, in two seasons, ceased earlier for elevated compared with ambient temperature trees. Elevated temperature reduced intermediate and final plant heights. Stem diameter growth began earlier each season at the elevated compared with the ambient temperature, but temperature had no effect on final stem diameter. Elevated temperature tended to reduce leaf ($p = 0.07$) but not woody biomass. Elevated CO₂ had no significant effects on stem diameter, height, and leaf or woody biomass, and there were no significant CO₂ x temperature interactions. Thus, elevated temperatures (but not elevated CO₂) associated with climate change may decrease seedling canopy growth as indicated by reduced height and leaf biomass but have little or no effect on overall woody growth as indicated by stem diameter and woody biomass.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, BIOMASS ALLOCATION, CLIMATE CHANGE, FORESTS, GROWTH, PONDEROSA PINE

1748

Oltchev, A., A. Ibrom, K. Morgenstern, H. Kreilein, and G. Gravenhorst. 1999. Evaluation of the response of a spruce forest

ecosystem on climatic changes: Results of modelling experiments. *Physics and Chemistry of the Earth Part B-Hydrology Oceans and Atmosphere* 24(1-2):103-110.

The physical and chemical environment of forests will change in the future. How forests will react to new conditions is not known yet. In order to get an idea of the sensitivity of present forests to possible atmospheric changes, it is helpful to investigate the physiological response of forest ecosystem to a change of key environmental parameters. In order to estimate the response of a mountain spruce forest to different atmospheric conditions during the summer a six-layer non-steady-state SVAT model (SLODSVAT) was used. Eight scenarios were used for modelling energy and mass exchange during an eleven day summer period, combining different combinations of microclimatic conditions. All atmospheric scenarios were examined for three various CO₂ mixing ratio levels: 350ppm (current condition), 450ppm and 550ppm. A scenario "0" assuming the current climatic features at different CO₂ contents was considered as well. Structural and physiological adaptation of the forest to the new atmospheric conditions were not taken into account. For all scenarios the modelling results show increased net CO₂ flux into the forest with increasing ambient CO₂ concentration. Maximum net CO₂ uptake was simulated for dry climate scenarios. Transpiration and evapotranspiration rates had similar trends independently of the ambient CO₂ concentration used: at cold and wet conditions they decreased, while at warm and dry conditions transpiration and evapotranspiration rates increased. The influence of CO₂ concentrations on transpiration rates is of minor importance if compared to changes of temperature, water vapour pressure, cloud amount and atmospheric precipitation as considered in this investigation. (C) 1998 Elsevier Science Ltd. All rights reserved.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CO₂-ENRICHMENT, PINE

1749

Ommen, O.E., A. Donnelly, S. Vanhoutvin, M. van Oijen, and R. Manderscheid. 1999. Chlorophyll content of spring wheat flag leaves grown under elevated CO₂ concentrations and other environmental stresses within the 'ESPACE-wheat' project. *European Journal of Agronomy* 10(3-4):197-203.

Spring wheat cv. Minaret was grown in open-top chambers at four sites across Europe. The effect of different treatments (CO₂ enrichment, O-3 fumigation, drought stress and temperature) on the chlorophyll content of the flag leaf was investigated using the MINOLTA SPAD-502 meter. Under optimum growth conditions the maximum chlorophyll content, which was reached at anthesis, was consistent among the sites ranging from 460 to 500 mg chlorophyll m⁻². No significant effect of elevated CO₂ or O-3 was observed at anthesis. Leaf senescence, indicated by the chlorophyll breakdown after anthesis, was relatively constant in the control chambers. Under control conditions, thermal time until 50% chlorophyll loss was reached was 600 degrees C day. Elevated CO₂ caused a faster decline in chlorophyll content (thermal time until 50% chlorophyll loss was reduced to 500-580 degrees C day) indicating a faster rate of plant development at two experimental sites. The effect of ozone on chlorophyll content depended on the time and dose of O-3 exposure. During grain filling, high O-3 concentrations induced premature senescence of the flag leaves (up to -130 degrees C day). This deleterious effect was mitigated by elevated CO₂. Drought stress led to faster chlorophyll breakdown irrespective of CO₂ treatment. (C) 1999 Elsevier Science B.V. All rights reserved.

KEYWORDS: ATMOSPHERIC CO₂, CARBON DIOXIDE, GAS-EXCHANGE, OPEN-TOP CHAMBERS, OZONE, PHOTOSYNTHESIS, TRITICUM-AESTIVUM L, WATER-STRESS, WINTER-WHEAT, YIELD

1750

Oneill, E.G. 1994. Responses of soil biota to elevated atmospheric carbon-dioxide. *Plant and Soil* 165(1):55-65.

Increasing concentrations of atmospheric CO₂ could have dramatic effects upon terrestrial ecosystems including changes in ecosystem structure, nutrient cycling rates, net primary production, C source-sink relationships and successional patterns. All of these potential changes will be constrained to some degree by below ground processes and mediated by responses of soil biota to indirect effects of CO₂ enrichment. A review of our current state of knowledge regarding responses of soil biota is presented, covering responses of mycorrhizae, N-fixing bacteria and actinomycetes, soil microbiota, plant pathogens, and soil fauna. Emphasis will be placed on consequences to biota of increasing C input through the rhizosphere and resulting feedbacks to above ground systems. Rising CO₂ may also result in altered nutrient concentrations of plant litter, potentially changing decomposition rates through indirect effects upon decomposer communities. Thus, this review will also cover current information on decomposition of litter produced at elevated CO₂.

KEYWORDS: CO₂- ENRICHMENT, DOUGLAS-FIR ECOSYSTEM, DYNAMICS, INDUCED NITROGEN MINERALIZATION, MYCORRHIZAL, PISUM-SATIVUM, QUERCUS-ALBA, RHIZOSPHERE, ROOT, SEEDLING GROWTH

1751

Ong, B.L., C.K.K. Koh, and Y.C. Wee. 1998. Effects of CO₂ on growth and photosynthesis of *Pyrrosia piloselloides* (L.) Price gametophytes. *Photosynthetica* 35(1):21-27.

The effects of CO₂ concentration on spore germination, growth, and net photosynthetic rate (P-N) Of gametophytes of a tropical epiphytic fern, *Pyrrosia piloselloides*, were investigated over a 100-d period. Increasing CO₂ concentration stimulated spore germination and enhanced gametophytic growth. The appearance of sexual organs and formation of sporophytes were accelerated with higher CO₂ during growth. Radiant energy saturated P-N and dark respiration rate also increased with increasing CO₂ concentrations during growth.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CARBON-DIOXIDE, CROP RESPONSES, ECOSYSTEMS, ELEVATED CO₂, ENRICHMENT, LEAF AGE, RESPIRATION, SEEDLINGS, STOMATAL CONDUCTANCE

1752

Ormrod, D.P., V.M. Lesser, D.M. Olszyk, and D.T. Tingey. 1999. Elevated temperature and carbon dioxide affect chlorophylls and carotenoids in douglas-fir seedlings. *International Journal of Plant Science* 160(3):529-534.

The objective of this study was to determine whether increased temperature and CO₂ concentration would decrease or increase the concentrations of foliar pigments in 5-yr-old seedlings of Douglas-fir *Pseudotsuga menziesii* [Mirb.] France var. *menziesii*. Seedlings were grown for 3 yr in sunlit, controlled environment chambers under ambient conditions or with a 179 μmol L⁻¹ elevation of CO₂ and/or a 3.5 degrees C elevation of temperature. Current- and previous-year needles were extracted with methanol for determination of chlorophylls and b, total carotenoids, and UV-absorbing compounds. Interactive effects of elevated temperature and CO₂ on the measured responses were not significant. Current-year needles from the elevated CO₂ treatment had the lowest chlorophyll and carotenoid concentrations, whereas needles of both age classes in the elevated temperature treatment had the highest concentrations of chlorophylls; current-year needles had the highest carotenoid concentration at elevated temperature. Neither temperature

nor CO₂ affected the concentrations of UV-absorbing compounds or needle fresh mass significantly. Chlorophyll a was correlated with carotenoids across all treatments ($r = 0.75-0.89$) in both needle age classes and with chlorophyll b in most treatments.

KEYWORDS: *ATMOSPHERIC CO₂ ENRICHMENT, AVAILABILITY, B RADIATION, LEAVES, LIGHT, PACIFIC NORTHWEST, PHOTOSYNTHESIS, PLANT GROWTH, SCOTS PINE, UV-B*

1753

Osborne, C.P., B.G. Drake, J. LaRoche, and S.P. Long. 1997. Does long-term elevation of CO₂ concentration increase photosynthesis in forest floor vegetation? Indian strawberry in a Maryland forest (vol 114, pg 337, 1997). *Plant Physiology* 114(4):1571.

As the partial pressure of CO₂ (pCO₂) in the atmosphere rises, photorespiratory loss of carbon in C-3 photosynthesis will diminish and the net efficiency of light-limited photosynthetic carbon uptake should rise. We tested this expectation for Indian strawberry (*Duchesnea indica*) growing on a Maryland forest floor. Open-top chambers were used to elevate the pCO₂ of a forest floor habitat to 67 Pa and were paired with control chambers providing an ambient pCO₂ of 38 Pa. After 3.5 years, *D. indica* leaves grown and measured in the elevated pCO₂ showed a significantly greater maximum quantum efficiency of net photosynthesis (by 22%) and a lower light compensation point (by 42%) than leaves grown and measured in the control chambers. The quantum efficiency to minimize photorespiration, measured in 1% O₂, was the same for controls and plants grown at elevated pCO₂. This showed that the maximum efficiency of light-energy transduction into assimilated carbon was not altered by acclimation and that the increase in light-limited photosynthesis at elevated pCO₂ was simply a function of the decrease in photorespiration. Acclimation did decrease the ribulose-1,5-bisphosphate carboxylase/oxygenase and light-harvesting chlorophyll protein content of the leaf by more than 30%. These changes were associated with a decreased capacity for light-saturated, but not light-limited, photosynthesis. Even so, leaves of *D. indica* grown and measured at elevated pCO₂ showed greater light-saturated photosynthetic rates than leaves grown and measured at the current atmospheric pCO₂. In situ measurements under natural forest floor lighting showed large increases in leaf photosynthesis at elevated pCO₂, relative to controls, in both summer and fall. The increase in efficiency of light-limited photosynthesis with elevated pCO₂ allowed positive net photosynthetic carbon uptake on days and at locations on the forest floor that light fluxes were insufficient for positive net photosynthesis in the current atmospheric pCO₂.

1754

Osborne, C.P., B.G. Drake, J. LaRoche, and S.P. Long. 1997. Does long-term elevation of CO₂ concentration increase photosynthesis in forest floor vegetation? Indiana strawberry in a Maryland forest. *Plant Physiology* 114(1):337-344.

As the partial pressure of CO₂ (pCO₂) in the atmosphere rises, photorespiratory loss of carbon in C-3 photosynthesis will diminish and the net efficiency of light-limited photosynthetic carbon uptake should rise. We tested this expectation for Indiana strawberry (*Duchesnea indica*) growing on a Maryland forest floor. Open-top chambers were used to elevate the pCO₂ of a forest floor habitat to 67 Pa and were paired with control chambers providing an ambient pCO₂ of 38 Pa. After 3.5 years, *D. indica* leaves grown and measured in the elevated pCO₂ showed a significantly greater maximum quantum efficiency of net photosynthesis (by 22%) and a lower light compensation point (by 42%) than leaves grown and measured in the control chambers. The quantum efficiency to minimize photorespiration, measured in 1% O₂, was the same for controls and plants grown at elevated pCO₂. This

showed that the maximum efficiency of light-energy transduction into assimilated carbon was not altered by acclimation and that the increase in light-limited photosynthesis at elevated pCO₂ was simply a function of the decrease in photorespiration. Acclimation did decrease the ribulose-1,5-bisphosphate carboxylase/oxygenase and light-harvesting chlorophyll protein content of the leaf by more than 30%. These changes were associated with a decreased capacity for light-saturated, but not light-limited, photosynthesis. Even so, leaves of *D. indica* grown and measured at elevated pCO₂ showed greater light-saturated photosynthetic rates than leaves grown and measured at the current atmospheric pCO₂. In situ measurements under natural forest floor lighting showed large increases in leaf photosynthesis at elevated pCO₂, relative to controls, in both summer and fall. The increase in efficiency of light-limited photosynthesis with elevated pCO₂ allowed positive net photosynthetic carbon uptake on days and at locations on the forest floor that light fluxes were insufficient for positive net photosynthesis in the current atmospheric pCO₂.

KEYWORDS: *ACCLIMATION, ATMOSPHERIC CO₂, CARBON DIOXIDE, EXPRESSION, GROWTH, NITROGEN, PROTEINS, QUANTUM YIELD, RUBISCO, VASCULAR PLANTS*

1755

Osborne, C.P., J. LaRoche, R.L. Garcia, B.A. Kimball, G.W. Wall, P.J. Pinter, R.L. LaMorte, G.R. Hendrey, and S.P. Long. 1998. Does leaf position within a canopy affect acclimation of photosynthesis to elevated CO₂? Analysis of a wheat crop under free-air CO₂ enrichment. *Plant Physiology* 117(3):1037-1045.

Previous studies of photosynthetic acclimation to elevated CO₂ have focused on the most recently expanded, sunlit leaves in the canopy. We examined acclimation in a vertical profile of leaves through a canopy of wheat (*Triticum aestivum* L.). The crop was grown at an elevated CO₂ partial pressure of 55 Pa within a replicated field experiment using free-air CO₂ enrichment. Gas exchange was used to estimate in vivo carboxylation capacity and the maximum rate of ribulose-1,5-bisphosphate-limited photosynthesis. Net photosynthetic CO₂ uptake was measured for leaves in situ within the canopy. Leaf contents of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco), light-harvesting-complex (LHC) proteins, and total N were determined. Elevated CO₂ did not affect carboxylation capacity in the most recently expanded leaves but led to a decrease in lower, shaded leaves during grain development. Despite this acclimation, in situ photosynthetic CO₂ uptake remained higher under elevated CO₂. Acclimation at elevated CO₂ was accompanied by decreases in both Rubisco and total leaf N contents and an increase in LHC content. Elevated CO₂ led to a larger increase in LHC/Rubisco in lower canopy leaves than in the uppermost leaf. Acclimation of leaf photosynthesis to elevated CO₂ therefore depended on both vertical position within the canopy and the developmental stage.

KEYWORDS: *APPARATUS, ATMOSPHERIC CO₂, CARBON-DIOXIDE ENRICHMENT, FIELD, GAS-EXCHANGE, GROWTH, NITROGEN, PERSPECTIVE, PLANTS, REDISTRIBUTION*

1756

Osborne, J.L., C.S. Awmack, S.J. Clark, I.H. Williams, and V.C. Mills. 1997. Nectar and flower production in *Vicia faba* L (field bean) at ambient and elevated carbon dioxide. *Apidologie* 28(1):43-55.

Atmospheric CO₂ has been predicted to double by the year 2100. Elevated CO₂ causes an increase in photosynthetic rate and extra assimilate is allocated to plant growth, seed and fruit production. Increased investment in flowers may have implications for pollination in entomophilous plants. Floral nectar standing crop, flower production and longevity were examined in *Vicia faba*, field bean, at ambient and

elevated CO₂. Nectar standing crop did not differ significantly between treatments but plants grown at elevated CO₂ produced approximately 25% more flowers per plant and these lived 17% longer than those grown at ambient CO₂. A plant grown at elevated CO₂ may thus produce more nectar in total and, together with its increased floral display, may be more attractive to pollinators, but pollen flow will not necessarily be improved.

KEYWORDS: CO₂, FLORAL NECTARY, HONEY BEES, MODIFIED STOMATA, PLANTS, TEMPERATURE

1757

Osorio, J., M.L. Osorio, M.M. Chaves, and J.S. Pereira. 1998. Water deficits are more important in delaying growth than in changing patterns of carbon allocation in *Eucalyptus globulus*. *Tree Physiology* 18(6):363-373.

Potted cuttings of three *Eucalyptus globulus* Labill, clones (AR3, CN44, MP11) were either well watered or subjected to one of two soil water deficit regimes for six months in a greenhouse. Reductions in lateral branching, leaf production and leaf expansion were the leading contributors to the large differences observed in biomass production between well-watered and water-stressed plants. Although no significant differences among clones were observed in dry matter accumulation or in the magnitude of the response to soil water deficits, sensitivity of lateral branching, leaf initiation and whole-plant foliage to water stress was significantly lower in CN44 than in AR3 and MP11. When the confounding effect of differences in plant size resulting from the different watering regimes was removed, allometric analysis indicated that the genotypes differed in biomass allocation patterns. In addition to a drought-induced reduction in leaf number, water deficits also resulted in smaller leaves because leaf expansion was inhibited during dehydration events. Resumption of leaf expansion following stress relief occurred in all of the clones, but was particularly evident in severely stressed plants of Clone AR3, possibly as a result of the osmotic adjustment observed in this genotype.

KEYWORDS: AREA, DISCRIMINATION, DROUGHT, ELEVATED CO₂, LEAF GROWTH, NITROGEN, OSMOTIC ADJUSTMENT, PHOTOSYNTHESIS, SEEDLINGS, SOIL-MOISTURE STRESS

1758

Ottosen, C.O. 1994. Net photosynthesis of *Schefflera arboricola* hayata clones at different CO₂ concentration and photosynthetic flux densities. *Acta Agriculturae Scandinavica Section B-Soil and Plant Science* 44(4):248-250.

KEYWORDS: CO₂, ENRICHMENT, FICUS-BENJAMINA, GROWTH, LEAVES

1759

Overdieck, D. 1993. Effects of atmospheric CO₂ enrichment on CO₂ exchange-rates of beech stands in small model-ecosystems. *Water, Air, and Soil Pollution* 70(1-4):259-277.

CO₂ enrichment experiments were performed during two vegetation periods on young beech stands in four closed mini-greenhouses. The houses were climatized according to the outside microclimate (+/- 0.5-degrees-C, +/- 15 % rel. air humidity, wind speed approximately to outside in the range of 0.5 - 2.5 m s⁻¹, max. 17 % PAR reduction). The model ecosystems - consisting of 36 young beech (2.5 yr-old) in a soil block of 0.38 m³ and an air volume of 0.64 m³ - were exposed to CO₂ concentrations of the unchanged ambient air (350 +/- 34 ppmv, control) and of 700 ppmv (698 +/- 10 ppmv). Plant growth parameters were measured non destructively and at the end of the 1st season samples were

taken for weighing the phytomass. CO₂ gas exchange of the stands taken as a whole were continuously measured with two entire mini-greenhouses and, in addition, a compact mini-cuvette system (CMS 400, Walz) was used for measuring dark respiration and CO₂ net assimilation rates of single leaves in both stands. Under the influence of the additional CO₂ supply stem diameter (2 cm above the first lateral roots) was increased by 13.5 %, stem height by 27.4 %, and the number of leaves/tree by 33 % at the end of the 2nd season. The number of buds was not significantly different and the effect on mean area per leaf was insignificant. Leaf area index was by 1.4 units greater. All dry weights of the main organs were increased after the 1st season: leaf 60 %, stem 34 %, bud 54 %. Roots < 2 mm phi weighed 1.5-fold more and roots > 2 mm phi 1.7-fold more under elevated CO₂. CO₂ gas exchange of two systems was measured. Whole system CO₂ losses during night as well as photosynthetic CO₂ gains during days were greater at 700 ppmv than in the control system. However, if one balances CO₂ gains with CO₂ losses over a period of five days in August both model-ecosystems taken as a whole were sinks for CO₂. During this selected time period of 5 days at the peak of the season the beech stand at 350 ppmv was the greater sink. At 350 ppmv CO₂ (control) the average leaf respiration for 20-degrees-C amounted to 0.31 +/- 0.18 and at 700 ppmv to 0.57 +/- 0.42 mumol CO₂ m⁻² s⁻¹ (n = 35/40, t = 3.48, alpha < 0.05), and correlated positively with leaf temperature. At light saturation the mean net assimilation rate was 4.48 mumol m⁻² (leaf area) s⁻¹ in the control and 6.21 mumol m⁻² s⁻¹ at the high CO₂ concentration corresponding with an enhancement factor of 1.39 for the selected time period. Results from the whole stand and from single leaf measurements are compared by means of mathematical modelling procedures in order to quantify CO₂ enrichment effects on beech model ecosystems.

KEYWORDS: ELEVATED CARBON-DIOXIDE, FIELD, GAS-EXCHANGE, PLANTS, QUERCUS-ALBA, SEEDLING GROWTH, VEGETATION

1760

Overdieck, D. 1993. Elevated CO₂ and the mineral-content of herbaceous and woody- plants. *Vegetatio* 104:403-411.

The CO₂ enrichment effects (300-650 mumol mol⁻¹) on mineral concentration (N, P, K, Ca, Mg, Mn, Fe, Zn), absolute total mineral contents per individual and of whole stands of four herbaceous (*Trifolium repens* L., *Trifolium pratense* L., *Lolium perenne* L., *Festuca pratensis* HUDS.) and two woody species (*Acer pseudo-platanus* L., *Fagus sylvatica* L.) were investigated. In general, the mineral concentration of the plant tissues decreased (all six species: N > Ca > K > Mg) with the exception of P. Mn and Fe were only determined for the tree species. Both decreased in concentration (Mn > Fe). Zn was only analysed for *Trifolium pratense* and *Festuca pratensis* and decreased significantly in the grass. Despite of decreases in concentrations of as much as 20 % in some cases there were increases in absolute amounts per individual and, therefore, in the whole vegetation up to 25 % because of the enhanced dry matter accumulation at elevated CO₂ supply.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CLOVER TRIFOLIUM-REPENS, ENRICHMENT, GAS-EXCHANGE, GROWTH, LOLIUM-PERENNE L, MANAGED MODEL-ECOSYSTEMS, NUTRIENT-UPTAKE, RYEGRASS, WHITE CLOVER

1761

Overdieck, D. 1996. CO₂ gas exchange and mass production during germination of radish at elevated atmospheric CO₂ concentration. *Journal of Applied Botany-Angewandte Botanik* 70(5-6):205-210.

The influence of elevated CO₂ concentration (similar to 700 mu mol mol⁻¹) on dry mass accumulation and CO₂ net assimilation of

germinating *Raphanus sativus* L.-seeds was investigated during growth over 10 days at low light during the day (16 h, photosynthetic photon flux density (PPFD): 20-70 $\mu\text{mol m}^{-2}\text{s}^{-1}$) and at darkness (8 h). Investigations at similar to 360 (unchanged ambient air) and at similar to 400 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ served as controls. At germination and development in a WALZ- mini-cuvette (part of CMS 400) with constant microclimatic conditions (20 degrees C, PPFD during day: 20-60 $\mu\text{mol m}^{-2} \text{ s}^{-1}$), vapor pressure deficit: similar to 0.5 kPa dry mass decreased by 14% in the course of the experiment without measurable influence of CO_2 concentration. In a subsequent experiment with continuous CO_2 gas exchange measurements on groups of 10 germinating radishes over 10 days at similar to 360 ($n = 6$) and at similar to 700 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ ($n = 5$) and, except for PPFD (70 $\mu\text{mol m}^{-2} \text{ s}^{-1}$), under unchanged microclimatic conditions no measurable CO_2 effect on dark respiration ($R(d)$) could be found. In light and in both CO_2 treatments maximum respiration was reached at day 3 or 4; whereas during darkness its level remained unchanged until the 10(th) day. At 700 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ during the day compensation of respiratory CO_2 losses by photosynthetic gains was reached one day earlier than in the control. CO_2 net assimilation during the light phase of the 10(th) day was enhanced by the elevated CO_2 supply by a factor of 2.2 relative to the control. Results of CO_2 gas exchange measurements on groups of 10 germinating radish seeds taken day by day from phytotron chambers with the same microclimatic conditions as before (similar to 400 and similar to 700 $\mu\text{mol CO}_2 \text{ mol}^{-1}$, $n = 3/\text{day}$ and CO_2 concentration) again showed no CO_2 effect on dark respiration; however, a positive effect on CO_2 net assimilation clearly occurred once more in light (with an enhancement factor after 10 days of similar to 1.5). The mean dry mass balance - calculated by means of all CO_2 gas exchange rates and the C-content [%] of seeds and seedlings of the last experiment - resulted after 10 days in a photosynthetically not yet compensated loss of 8.7% from the starting seed dry mass at 400 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ and of only 3.3% at 700 $\mu\text{mol CO}_2 \text{ mol}^{-1}$. The reported positive CO_2 effect on growth and net production of radish reported in literature could, therefore, be explained at least in the germinating phase by enhanced CO_2 net assimilation with unchanging CO_2 losses by simultaneous dark respiration.

KEYWORDS: CARBON-DIOXIDE EFFLUX, DARK RESPIRATION, ENRICHMENT, GROWTH, INHIBITION, PLANTS, TEMPERATURE

1762

Overdieck, D., and M. Forstreuter. 1994. Evapotranspiration of beech stands and transpiration of beech leaves subject to atmospheric CO_2 enrichment. *Tree Physiology* 14(7-9):997-1003.

Beech trees (*Fagus sylvatica* L.) show reduced stomatal conductance and increased leaf area index in response to increased atmospheric CO_2 concentration. To determine whether the reduction in stomatal conductance results in lower stand evapotranspiration, we compared transpiration on a leaf-area basis and stand evapotranspiration on a ground-area basis in young European beech trees growing in greenhouses at ambient (360 \pm 34 $\mu\text{mol mol}^{-1}$) and elevated (698 \pm 10 $\mu\text{mol mol}^{-1}$) CO_2 concentrations. Trees were grown in homogenized natural soil at constant soil water supply for two growing seasons. At light saturation, leaf transpiration rates were, on average, 18% lower in the elevated CO_2 treatment than in the ambient CO_2 treatment. Mean transpiration coefficients (transpiration/net CO_2 uptake) of leaves were 179 and 110 in the ambient and elevated CO_2 treatments, respectively, indicating improved water use efficiency in trees in the elevated CO_2 treatment. Total leaf conductance was decreased by 32% at light saturation. The elevated CO_2 treatment resulted in a 14% reduction in stand evapotranspiration. In both CO_2 treatments, evapotranspiration increased linearly at a rate of 0.2 kg $\text{H}_2\text{O m}^{-2} \text{ day}^{-1}$ for each 1-degree-C rise in air temperature between 14 and 25-degree-C. We conclude that, under Central European conditions, water losses from deciduous forest stands will be reduced by a doubling

of tropospheric CO_2 concentration.

1763

Owensby, C.E. 1993. Potential impacts of elevated CO_2 and aboveground and belowground litter quality of a tallgrass prairie. *Water, Air, and Soil Pollution* 70(1-4):413-424.

Increased atmospheric CO_2 will likely impact the productivity of arid and semiarid ecosystems through increased C, N, and water use efficiencies at the individual plant level. Tallgrass prairie has had increased above- and belowground biomass production under elevated CO_2 , primarily due to increased water use efficiency. There is an apparent decreased N requirement to sustain increased productivity in CO_2 -enriched tallgrass prairie, and C:N ratios of plant litter above and below ground have increased. The tallgrass prairie ecosystem level response to elevated CO_2 on the C cycle could potentially increase C storage. Reduced litter quality associated with elevated CO_2 in tallgrass prairie has the potential to reduce decomposition rates, and ruminant digestion rate of plant biomass apparently has been lowered. Reduced intake by ruminants would shunt more of the plant biomass directly into the detrital food chain, thereby slowing decomposition further. The potential impact is for increased C to be retained as soil organic matter in the tallgrass prairie.

KEYWORDS: CARBON-DIOXIDE ENRICHMENT, COMMUNITIES, DECOMPOSITION, ESTUARINE MARSH, GRASSLAND ECOSYSTEMS, GROWTH, NITROGEN, PHOTOSYNTHETIC ACCLIMATION, PLANTS, RESPONSES

1764

Owensby, C.E., L.M. Auen, and P.I. Coyne. 1994. Biomass production in a nitrogen-fertilized, tallgrass prairie ecosystem exposed to ambient and elevated levels of CO_2 . *Plant and Soil* 165(1):105-113.

Increased biomass production in terrestrial ecosystems with elevated atmospheric CO_2 may be constrained by nutrient limitations as a result of increased requirement or reduced availability caused by reduced turnover rates of nutrients. To determine the short-term impact of nitrogen (N) fertilization on plant biomass production under elevated CO_2 , we compared the response of N-fertilized tallgrass prairie at ambient and twice-ambient CO_2 levels over a 2-year period. Native tallgrass prairie plots (4.5 m diameter) were exposed continuously (24 h) to ambient and twice-ambient CO_2 from 1 April to 26 October. We compared our results to an unfertilized companion experiment on the same research site. Above- and belowground biomass production and leaf area of fertilized plots were greater with elevated than ambient CO_2 in both years. The increase in biomass at high CO_2 occurred mainly aboveground in 1991, a dry year, and belowground in 1990, a wet year. Nitrogen concentration was lower in plants exposed to elevated CO_2 , but total standing crop N was greater at high CO_2 . Increased root biomass under elevated CO_2 apparently increased N uptake. The biomass production response to elevated CO_2 was much greater on N-fertilized than unfertilized prairie, particularly in the dry year. We conclude that biomass production response to elevated CO_2 was suppressed by N limitation in years with below-normal precipitation. Reduced N concentration in above- and belowground biomass could slow microbial degradation of soil organic matter and surface litter, thereby exacerbating N limitation in the long term.

KEYWORDS: CARBON DIOXIDE, COMMUNITIES, DYNAMICS, ENRICHMENT, ESTUARINE MARSH, GROWTH, PLANTS, RESPONSES

1765

Owensby, C.E., P.I. Coyne, and L.M. Auen. 1993. Nitrogen and phosphorus dynamics of a tallgrass prairie ecosystem exposed to elevated carbon-dioxide. *Plant, Cell and Environment* 16(7):843-850.

A tallgrass prairie ecosystem was exposed to ambient and twice-ambient CO₂ concentrations in open-top chambers and compared to unchambered ambient CO₂ during the entire growing season from 1989 through 1991. Dominant species were *Andropogon gerardii* (C4), *A. scoparius* (C4), *Sorghastrum nutans* (C4) and *Poa pratensis* (C3). Nitrogen and phosphorus concentrations in *A. gerardii*, *P. pratensis* and dicotyledonous herbs above ground biomass were estimated by periodic sampling throughout the growing season in 1989 and 1990. In 1991, N and P concentrations in peak biomass were estimated by an early August harvest. N and P concentrations in root production as a function of treatment were estimated using root ingrowth bags that remained in place throughout the growing season. Total N and P in above- and belowground biomass were calculated as products of concentration and peak biomass by species groups. N concentration in *A. gerardii* and dicotyledonous herb aboveground biomass was lower and total N higher in elevated CO₂ plots than in ambient CO₂ plots. N concentration in *P. pratensis* aboveground biomass was lower in elevated CO₂ plots than in ambient, but total N did not differ among treatments in 2 out of 3 years. In 1990, N concentration in root ingrowth bag biomass was lower and total N greater in elevated CO₂ than in ambient CO₂ plots. Root ingrowth bag biomass N concentration did not differ among treatments in 1991, but total N was greater in elevated CO₂ plots than in ambient CO₂ plots. P concentration was lower under elevated CO₂ compared to ambient in 1989, but did not differ substantially among treatments in 1990 or 1991. In all years, total P in aboveground *A. gerardii* and root ingrowth bag biomass was greater under elevated CO₂ than ambient. P concentration and total P in *P. pratensis* was similar among treatments.

KEYWORDS: ATMOSPHERIC CO₂, C-3, COMMUNITIES, ENRICHMENT, ESTUARINE MARSH, GROWTH, INSECT HERBIVORE, MYCORRHIZAL FUNGI, PLANTS, TEMPERATURE

1766

Owensby, C.E., P.I. Coyne, J.M. Ham, L.M. Auen, and A.K. Knapp. 1993. Biomass production in a tallgrass prairie ecosystem exposed to ambient and elevated CO₂. *Ecological Applications* 3(4):644-653.

Responses to elevated CO₂ have not been measured for natural grassland ecosystems. Global carbon budgets will likely be affected by changes in biomass production and allocation in the major terrestrial ecosystems. Whether ecosystems sequester or release excess carbon to the atmosphere will partly determine the extent and rate that atmospheric CO₂ concentration rises. Elevated CO₂ also may change plant community species composition and water status. We determined above- and belowground biomass production, plant community species composition, and measured and modeled water status of a tallgrass prairie ecosystem in Kansas exposed to ambient and twice-ambient CO₂ concentrations in open-top chambers during the entire growing season from 1989 through 1991. Dominant species were *Andropogon gerardii*, *A. scoparius*, and *Sorghastrum nutans* (C-4 metabolism) and *Poa pratensis* (C-3). Aboveground biomass and leaf area were estimated by periodic sampling throughout the growing season in 1989 and 1990. In 1991, peak biomass and leaf area were estimated by an early August harvest. Relative root production among treatments was estimated using root ingrowth bags which remained in place throughout the growing season. Latent heat flux was simulated with and without water stress. Botanical composition was estimated annually. Compared to ambient CO₂ levels, elevated CO₂ increased production of C-4 grass species, but not of C-3 grass species. Species composition of C-4 grasses did not change, but *Poa pratensis* (C-3) declined, and C-3 forbs increased in the stand with elevated CO₂ compared to ambient. Open-top chambers appeared to reduce latent heat flux and increase water-use efficiency similar to the elevated CO₂ treatment when water stress was not severe,

but under severe water stress, the chamber effect on water-use efficiency was limited. In natural ecosystems with periodic moisture stress, increased water-use efficiency under elevated CO₂ apparently would have a greater impact on productivity irrespective of photosynthetic pathway.

KEYWORDS: BALANCE, BLUESTEM, CARBON DIOXIDE, COMMUNITIES, ESTUARINE MARSH, GAS-EXCHANGE, GROWTH, PHOTOSYNTHESIS, RESPONSES, WATER-USE EFFICIENCY

1767

Owensby, C.E., J.M. Ham, A.K. Knapp, and L.M. Auen. 1999. Biomass production and species composition change in a tallgrass prairie ecosystem after long-term exposure to elevated atmospheric CO₂. *Global Change Biology* 5(5):497-506.

To determine the long-term impact of elevated CO₂ on primary production of native tallgrass prairie, we compared the responses of tallgrass prairie at ambient and twice-ambient atmospheric CO₂ levels over an 8-year period. Plots in open-top chambers (4.5 m diameter) were exposed continuously (24 h) to ambient and elevated CO₂ from early April to late October each year. Unchambered plots were monitored also. Aboveground peak biomass was determined by clipping each year in early August, and root growth was estimated by harvesting roots from root ingrowth bags. Plant community composition was censused each year in early June. In the last 2 years of the study, subplots were clipped on 1 June or 1 July, and regrowth was harvested on 1 October. Volumetric soil water content of the 0-100 cm soil layer was determined using neutron scattering, and was generally higher in elevated CO₂ plots than ambient. Peak aboveground biomass was greater on elevated CO₂ plots than ambient CO₂ plots with or without chambers during years with significant plant water stress. Above-ground regrowth biomass was greater under elevated CO₂ than under ambient CO₂ in a year with late-season water stress, but did not differ in a wetter year. Root ingrowth biomass was also greater in elevated CO₂ plots than ambient CO₂ plots when water stress occurred during the growing season. The basal cover and relative amount of warm-season perennial grasses (C4) in the stand changed little during the 8-year period, but basal cover and relative amount of cool-season perennial grasses (C3) in the stand declined in the elevated CO₂ plots and in ambient CO₂ plots with chambers. Forbs (C3) and members of the Cyperaceae (C3) increased in basal cover and relative amount in the stand at elevated compared to ambient CO₂. Greater biomass production under elevated CO₂ in C4-dominated grasslands may lead to a greater carbon sequestration by those ecosystems and reduce peak atmospheric CO₂ concentrations in the future.

KEYWORDS: AMBIENT, C-4 GRASS, CARBON DIOXIDE, COMPETITIVE INTERACTIONS, DECOMPOSITION, LEAF LITTER, NITROGEN, RESPONSES, TERRESTRIAL ECOSYSTEMS, WATER RELATIONS

1768

Owensby, C.E., J.M. Ham, A.K. Knapp, D. Bremer, and L.M. Auen. 1997. Water vapour fluxes and their impact under elevated CO₂ in a C4-tallgrass prairie. *Global Change Biology* 3(3):189-195.

We measured leaf-level stomatal conductance, xylem pressure potential, and stomate number and size as well as whole plant sag now and canopy-level water vapour fluxes in a C4-tallgrass prairie in Kansas exposed to ambient and elevated CO₂. Stomatal conductance was reduced by as much as 50% under elevated CO₂ compared to ambient. In addition, there was a reduction in stomate number of the C4 grass, *Andropogon gerardii* Vitman, and the C3 dicot herb, *Salvia pitcheri* Torr., under elevated CO₂ compared to ambient. The result was an improved water status for plants exposed to elevated CO₂ which was

reflected by a less negative xylem pressure potential compared to plants exposed to ambient CO₂. Sap flow rates were 20 to 30% lower for plants exposed to elevated CO₂ than for those exposed to ambient CO₂. At the canopy level, evapotranspiration was reduced by 22% under elevated CO₂. The reduced water use by the plant canopy under elevated CO₂ extended the photosynthetically-active period when water became limiting in the ecosystem. The result was an increased above- and belowground biomass production in years when water stress was frequent.

KEYWORDS: AMBIENT, ATMOSPHERIC CO₂, C-4 GRASS, CARBON DIOXIDE, CHAMBER, ECOSYSTEMS, FLOW, INCREASE, RESPONSES, STOMATAL DENSITY

1769

Pacala, S.W., and D.H. Deutschman. 1995. Details that matter: The spatial distribution of individual trees maintains forest ecosystem function. *Oikos* 74(3):357-365.

This paper shows that the processes controlling tree-scale spatial heterogeneity in forests have large effects on system-level properties such as standing crop, and on community-level properties such as successional species turnover. A "mean field" version of the forest simulation model SORTIE is developed in which horizontal spatial heterogeneity is eliminated while vertical structure is retained. The mean-field model maintains only approximately one half the standing crop and loses successional diversity approximately twice as fast as the full spatial model. Data from natural stands support the spatial model. A partial differential equation limit of the mean-field simulator is also derived. The results are set in the context of ongoing efforts to develop models intended to predict the biosphere's response to global change. The importance of processes governing fine-scale spatial heterogeneity implies that biospheric models will agree with nature only if they are phenomenological (e.g. fitted to data) at large scale, or if spatial scaling rules are discovered that allow one to derive system-level properties from individual-level processes.

KEYWORDS: CO₂, MODEL, RESPONSES

1770

Pachepsky, L.B., and B. Acock. 1996. An adequate model of photosynthesis. 2. Dependence of parameters on environmental factors. *Agricultural Systems* 50(2):227-238.

Models of photosynthesis are commonly written as functions of light, temperature and CO₂ concentration ([CO₂]). In an ideal model, the parameter values would be independent of these environmental factors. However, there is no ideal photosynthesis model, so it is necessary to know how the parameters vary in response to the environment. Three of the most popular models of photosynthesis were fitted to experimental data for tomato plants, including light response curves measured at temperatures of 18, 25 and 32 degrees C and [CO₂] of 100, 350, 700 and 1000 ppm. Statistical analysis of parameter values allowed us to find their dependencies on environmental factors. Light utilization efficiency proved to be constant at ambient and elevated [CO₂]. Values of alpha at 100 mu l l(-1) [CO₂] were approximately half of those at 350, 700 and 1000 mu l l(-1) [CO₂]. Leaf conductance for CO₂ transfer tau depended on temperature as well as on [CO₂]. Two other parameters, one connected with respiration, R and Farquhar's 'curvature factor' theta, were both linearly dependent on temperature.

KEYWORDS: C-3, CO₂, LIGHT, O₂, PLANTS, TEMPERATURE

1771

Pachepsky, L.B., and B. Acock. 1996. A model 2DLEAF of leaf gas

exchange: Development, validation, and ecological application. *Ecological Modelling* 93(1-3):1-18.

A two-dimensional model (2DLEAF) of leaf photosynthesis and transpiration has been developed that explicitly accounts for gas diffusion through the boundary layer and the intercellular space as well as for stomatal regulation. The model has been validated for tomato. It was used to study the effect of stomatal density on photosynthesis and transpiration rate. It has been demonstrated by varying stomatal density in the model that the stomatal density measured on tomato leaves provides the maximal photosynthesis rate for both 300 and 600 mu l l(-1) [CO₂]. The transpiration rate varied in direct proportion to stomatal density at all values of stomatal aperture, but transpiration efficiency (photosynthesis rate/transpiration rate) was higher at 600 mu l l(-1) [CO₂] with a normal stomatal density than at 300 mu l l(-1) [CO₂] with a stomatal density reduced 25%. Such calculations with 2DLEAF can be useful for analysis of contradicting data presented in publications on possible changes in stomatal density in a future high [CO₂] atmosphere.

KEYWORDS: CONDUCTANCE, DENSITY, ELEVATED CO₂, INCREASES, LEAVES, NUMBERS, PHOTOSYNTHESIS, TRANSPORT

1772

Pachepsky, L.B., J.D. Haskett, and B. Acock. 1995. A two-dimensional model of leaf gas exchange with special reference to leaf anatomy. *Journal of Biogeography* 22(2-3):209-214.

This model of leaf gas exchange includes (1) two-dimensional CO₂, O₂ and water vapour diffusion in intercellular space schematized according to leaf anatomy, (2) CO₂ assimilation by mesophyll cells as described by Farquhar's model of photosynthesis and (3) stomatal movements as a regulating factor. Parameters describing the leaf cross-section and gas diffusion properties replace the empirical parameters of earlier models. The model was tested for soybean and performed well in representing light, CO₂ concentration ([CO₂]), and temperature response curves as well as the dependence of transpiration on temperature and water vapour deficit. The model allows the calculation of the steady state distribution of CO₂ and water vapour concentrations in the intercellular space and the boundary layer. The direct calculation of diffusion in leaves showed that stomatal aperture effectively regulates the transpiration rate but usually has a much smaller effect on the rate of assimilation.

KEYWORDS: LEAVES, MATHEMATICAL-MODEL, PHOTOSYNTHESIS, TRANSPIRATION, WATER-USE EFFICIENCY

1773

Paffen, B.G.P., and J.G.M. Roelofs. 1991. Impact of carbon-dioxide and ammonium on the growth of submerged *Sphagnum cuspidatum*. *Aquatic Botany* 40(1):61-71.

In a culture experiment, the influence of carbon dioxide and ammonium on the growth of *Sphagnum cuspidatum* Hoffm. was studied. During a 12-week period, *S. cuspidatum* was grown in a solution with various concentrations of carbon dioxide and ammonium. The culture experiment clearly demonstrated that the biomass and the length of *S. cuspidatum* only increased strongly when the carbon dioxide concentration of the water was high. Further it is shown that ammonium enrichment without CO₂ enrichment does not lead to an increase in biomass of *S. cuspidatum*.

KEYWORDS: ACIDIFICATION, EUTROPHICATION, MACROPHYTE COMMUNITIES, NITRATE REDUCTASE-ACTIVITY, SOFT WATERS

1774

Pajari, B. 1995. Soil respiration in a poor upland site of scots pine stand

subjected to elevated-temperatures and atmospheric carbon concentration. *Plant and Soil* 169:563-570.

Soil respiration rates under elevated temperature and atmospheric CO₂ concentrations were studied in eastern Finland (62 degrees 47'N, 30 degrees 58'E, 144 m.a.s.l.) around naturally regenerated 20 - 30 years old Scots pine trees, enclosed in open top chambers. The production of CO₂ varied spatially and temporally, but clearly followed the changes in temperature measured at the soil surface. However, soil respiration in the open control was higher than that in chambers; i.e. the chamber itself changed the conditions by increasing the temperature, altering the movement of water, and thereby soil moisture. Nevertheless, an elevation in the concentration of atmospheric CO₂ raised soil respiration and brought it nearer to the level in the open control. An increase in temperature seemed to inhibit this rise, possibly because of an imbalance between temperature and moisture.

KEYWORDS: CO₂, DIOXIDE, ECOSYSTEMS, MODEL

1775

Pal, R.K., and R.W. Buescher. 1993. Respiration and ethylene evolution of certain fruits and vegetables in response to carbon-dioxide in controlled- atmosphere storage. *Journal of Food Science and Technology-Mysore* 30(1):29-32.

Respiration was depressed by 10-30% CO₂ in ripening bananas, pink tomatoes and pickling cucumbers; increased by 20-30% in carrot roots and unaffected by CO₂ exposure in guava, orange and onion bulb. Changes in respiration seldom coincided with changes in C₂H₄ evolution. Evolution of C₂H₄ from guavas and tomatoes was substantially reduced by all levels of CO₂. However, 30% CO₂ accelerated C₂H₄ evolution in bananas, carrot roots, cucumbers, onions and potatoes which may have been due to an early injury response.

1776

Palet, A., M. Ribascarbo, J.M. Argiles, and J. Azconbieto. 1991. Short-term effects of carbon-dioxide on carnation callus cell respiration. *Plant Physiology* 96(2):467-472.

The addition of potassium bicarbonate to the electrode cuvette immediately stimulated the rate of dark O₂ uptake of photomixotrophic and heterotrophic carnation (*Dianthus caryophyllus* L.) callus, of *Elodea canadensis* (Michx) leaves, and of other plant tissues. This phenomenon occurred at pH values lower than 7.2 to 7.8, and the stimulation depended on the concentration of gaseous CO₂ in the solution. These stimulatory responses lasted several minutes and then decreased, but additional bicarbonate or gaseous CO₂ again stimulated respiration, suggesting a reversible effect. Carbonic anhydrase in the solution increased the stimulatory effect of potassium bicarbonate. The CO₂/bicarbonate dependent stimulation of respiration did not occur in animal tissues such as rat diaphragm and isolated hepatocytes, and was inhibited by salicylhydroxamic acid in carnation callus cells and *E. canadensis* leaves. This suggested that the alternative oxidase was engaged during the stimulation in plant tissues. The cytochrome pathway was severely inhibited by CO₂/bicarbonate either in the absence or in the presence of the uncoupler carbonyl-cyanide m-chlorophenyl hydrazone. The activity of cytochrome c oxidase of callus tissue homogenates was also inhibited by CO₂/bicarbonate. The results suggested that high carbon dioxide levels (mainly free CO₂) Partially inhibited the cytochrome pathway (apparently at the oxidase level), and this block in electron transport elicited a large transient engagement of the alternative oxidase when present uninhibited.

KEYWORDS: CYANIDE-INSENSITIVE RESPIRATION, ELEVATED CO₂ CONCENTRATIONS, LEAF, LEAVES, METABOLISM,

PATHWAY, PEAR FRUIT, PH, PHOTOSYNTHESIS, PLANT-MITOCHONDRIA

1777

Palutikof, J.P., C.M. Goodess, and X. Guo. 1994. Climate-change, potential evapotranspiration and moisture availability in the mediterranean basin. *International Journal of Climatology* 14(8):853-869.

Simple methods for estimating potential evapotranspiration, requiring only temperature and day length data, are compared by reference to the results from the Penman method. A modification of the Blaney and Criddle method, in which the c parameter is calculated from seasonal regression equations with the mean monthly temperature as the independent variable, is proposed and tested. It is found to work sufficiently well in the area of interest, the Mediterranean Basin. For a network of 248 Mediterranean temperature stations, present-day seasonal mean potential evapotranspiration is estimated by this method. Using the results from four equilibrium-mode general circulation models, seasonal mean scenarios of potential evapotranspiration per 1-degree-C rise in global mean temperature caused by the enhanced greenhouse effect are presented. Comparison of scenarios of the change in potential evapotranspiration and scenarios of the change in precipitation indicates an unfavourable shift in moisture availability due to the enhanced greenhouse effect, throughout the Mediterranean region.

KEYWORDS: CO₂, SENSITIVITY

1778

Pan, Q., Z. Wang, and B. Quebedeaux. 1998. Responses of the apple plant to CO₂ enrichment: changes in photosynthesis, sorbitol, other soluble sugars, and starch. *Australian Journal of Plant Physiology* 25(3):293-297.

There is no information on the effects of elevated [CO₂] on whole-plant photosynthesis and carbohydrate metabolism in apple (*Malus domestica* Borkh.) and other sorbitol-translocating plants. Experiments were conducted in controlled growth chambers to evaluate how increases in [CO₂] affect plant photosynthesis and carbon partitioning into soluble sugars and starch in apple leaves. Apple plants (cv, Gala), 1-year-old, were exposed to [CO₂] of 200, 360, 700, 1000, and 1600 μ mol L⁻¹ up to 8 d. Whole-plant net photosynthetic rates were analysed daily after [CO₂] treatments. Newly expanded mature leaves were sampled at 1, 2, 4, and 8 d after [CO₂] treatments for sorbitol, sucrose, glucose, fructose, and starch analysis. Midday whole-plant net photosynthetic rates increased linearly with increasing [CO₂], but the differences in whole-plant photosynthesis between CO₂-enrichment and ambient [CO₂] treatments were less significant as apple plants acclimated to high atmospheric [CO₂] for 8 d. Increases in [CO₂] significantly increased sorbitol and starch, but did not affect sucrose concentrations. As a result, the ratios of starch to sorbitol and starch to sucrose at 8 d after [CO₂] treatments were increased from 0.05 and 0.06 to 0.8 and 1.6 as [CO₂] increased from ambient [CO₂] (360 μ mol L⁻¹) to 1000 μ mol L⁻¹ [CO₂], respectively. The sorbitol to sucrose ratio also increased from 1.3 to 2.2 as [CO₂] increased from 360 to 1000 μ mol L⁻¹. Elevated [CO₂] enhanced the photosynthesis of apple plants and altered carbohydrate accumulation in mature leaves in favour of starch and sorbitol over sucrose.

KEYWORDS: CARBOHYDRATE ACCUMULATION, CARBON DIOXIDE, ELEVATED CO₂, EXCHANGE, GROWTH, RICE, WATER-STRESS

1779

Pan, Y.D., J.M. Melillo, A.D. McGuire, D.W. Kicklighter, L.F.

Pitelka, K. Hibbard, L.L. Pierce, S.W. Running, D.S. Ojima, W.J. Parton, and D.S. Schimel. 1998. Modeled responses of terrestrial ecosystems to elevated atmospheric CO₂: a comparison of simulations by the biogeochemistry models of the Vegetation/Ecosystem Modeling and Analysis Project (VEMAP). *Oecologia* 114(3):389-404.

Although there is a great deal of information concerning responses to increases in atmospheric CO₂ at the tissue and plant levels, there are substantially fewer studies that have investigated ecosystem-level responses in the context of integrated carbon, water, and nutrient cycles. Because our understanding of ecosystem responses to elevated CO₂ is incomplete, modeling is a tool that can be used to investigate the role of plant and soil interactions in the response of terrestrial ecosystems to elevated CO₂. In this study, we analyze the responses of net primary production (NPP) to doubled CO₂ from 355 to 710 ppmv among three biogeochemistry models in the Vegetation/Ecosystem Modeling and Analysis Project (VEMAP): BIOME-BGC (BioGeochemical Cycles), Century, and the Terrestrial Ecosystem Model (TEM). For the conterminous United States, doubled atmospheric CO₂ causes NPP to increase by 5% in Century, 8% in TEM, and 11% in BIOME-BGC. Multiple regression analyses between the NPP response to doubled CO₂ and the mean annual temperature and annual precipitation of biomes or grid cells indicate that there are negative relationships between precipitation and the response of NPP to doubled CO₂ for all three models. In contrast, there are different relationships between temperature and the response of NPP to doubled CO₂ for the three models: there is a negative relationship in the responses of BIOME-BGC, no relationship in the responses of Century, and a positive relationship in the responses of TEM. In BIOME-BGC, the NPP response to doubled CO₂ is controlled by the change in transpiration associated with reduced leaf conductance to water vapor. This change affects soil water, then leaf area development and, finally, NPP. In Century, the response of NPP to doubled CO₂ is controlled by changes in decomposition rates associated with increased soil moisture that results from reduced evapotranspiration. This change affects nitrogen availability for plants, which influences NPP. In TEM, the NPP response to doubled CO₂ is controlled by increased carboxylation which is modified by canopy conductance and the degree to which nitrogen constraints cause down-regulation of photosynthesis. The implementation of these different mechanisms has consequences for the spatial pattern of NPP responses, and represents, in part, conceptual uncertainty about controls over NPP responses. Progress in reducing these uncertainties requires research focused at the ecosystem level to understand how interactions between the carbon, nitrogen, and water cycles influence the response of NPP to elevated atmospheric CO₂.

KEYWORDS: CARBON DIOXIDE, CLIMATE CHANGE, FOREST-BGC, GAS-EXCHANGE, GENERAL-MODEL, NET PRIMARY PRODUCTION, REGIONAL APPLICATIONS, SOIL CARBON, TALLGRASS PRAIRIE, WATER-USE

1780

Panina, L.I., I.V. Motorina, M.N. Mamedov, and S.A. Makhmudov. 1997. Physicochemical conditions of the development of the tertiary trachybasalt-phonolite formation in the Talysh zone (Azerbaijan). *Geologiya I Geofizika* 38(4):730-739.

It has been established by mineral thermobarogeochemistry that the magmas initial of the trachybasalt-phonolite series in the Talysh zone were crystallized according to Bowen's scheme at the following temperatures and order of phenocryst formation: O1 (>1350 degrees C) --> Cpx (1280-1170 degrees C) --> Ap (1240-1030 degrees C) --> P1 (1190-1035 degrees C). The fluid phase at the time of olivine phenocryst crystallization was composed of 90 mol. % CO₂ and 10 mol. % N₂, while at the stage of pyroxene and plagioclase formation it was 100 mol. % N₂. A drastic change in fluid composition is related to a discontinuity in time and place of phenocryst formation: olivine

crystallization in deep-seated conditions, and formation of pyroxene and plagioclase in shallow depth of the Earth's crust. A microprobe study of silicate melt inclusions has shown that the evolution of the initial magma proceeded by means of differentiation and fractionation of minerals. In the process of crystallization the derivative melts were enriched in SiO₂ (up to 64%), Al₂O₃ (up to 21%), alkalis (up to 10-11 wt.%) and were depleted in feric components (totalled to few per cent). Residual rhyolite-dacite alkali-enriched melts (67- 73% SiO₂, 14-17% Al₂O₃, 4-8% alkalis) appeared in the final stages of magma evolution. The presence of alkalis brings us back to the problem of the mantle, <<basalt>>, origin of some siliceous rocks, as well as of the possibility to overcome an <<impassable>> barrier between quartz-normative acid melts and alkaline leucite-bearing rocks.

1781

Paoletti, E., G. Nourrisson, J.P. Garrec, and A. Raschi. 1998. Modifications of the leaf surface structures of *Quercus ilex* L in open, naturally CO₂-enriched environments. *Plant, Cell and Environment* 21(10):1071-1075.

Two Italian CO₂ springs allowed us to study the long-term effect of a 350-2600 $\mu\text{mol mol}^{-1}$ increase in CO₂ concentrations on the surface structures of leaves of *Quercus ilex* L. Carbon dioxide increased the quantity of cuticular waxes, above an apparent threshold of 750 $\mu\text{mol mol}^{-1}$ CO₂. Leaf wettability was not modified by CO₂ concentrations. Reduction in stomatal frequency was observable up to 750 $\mu\text{mol mol}^{-1}$ CO₂, the slope being almost the same as that estimated for the increase in CO₂ concentration from preindustrial times to the present. At higher concentrations, CO₂ seemed to exert no more impact on stomatal frequency.

KEYWORDS: ATMOSPHERIC CO₂ CONCENTRATIONS, CARBON DIOXIDE, CUTICLES, ELEVATED CO₂, EPICUTICULAR WAX, LEAVES, NEEDLES, NORWAY SPRUCE, RESPONSES, STOMATAL DENSITY

1782

Papadopoulos, A.P., and X.M. Hao. 1997. Effects of three greenhouse cover materials on tomato growth, productivity, and energy use. *Scientia Horticulturae* 70(2-3):165-178.

Effects of single-layered glass (glass), double inflated polyethylene film (D-poly), and rigid-twin wall acrylic panels (acrylic), as greenhouse covers on tomato (*Lycopersicon esculentum* Mill) growth, productivity and energy use were investigated over two spring seasons in 1993 and 1994. There was no significant difference in early marketable yield (harvested until April 30) between the D-poly and glass houses. Early marketable yield in the acrylic houses was similar to that in the glass houses, but higher than that in the D-poly houses in 1994. Mid-season yield in the D-poly houses was lower than in the glass houses. Final marketable yield in the D-poly and acrylic houses was similar to that in the glass houses. Fruit size during the early and mid-season in the D-poly houses was smaller than in the glass or acrylic houses. This reduction in fruit size shifted 6-12% of grade #1 fruit from extra large to large. Fruit size in the glass and acrylic houses was similar. In 1993, there was a higher BER (blossom-end rot) incidence in the glass houses than in D-poly or acrylic houses, but a higher percentage of grade #1 fruit in the D-poly houses than in the glass or acrylic houses. The D-poly and acrylic houses saved 30% in heating energy compared to the glass houses. (C) 1997 Elsevier Science B.V.

KEYWORDS: CO₂- ENRICHMENT, CUCUMBERS, GLASSHOUSE TOMATOES, HUMIDITY, QUALITY, TEMPERATURES, YIELD

1783

Parton, W.J., D.S. Ojima, and D.S. Schimel. 1994. Environmental change in grasslands - assessment using models. *Climatic Change* 28(1-2):111-141.

Modeling studies and observed data suggest that plant production, species distribution, disturbance regimes, grassland biome boundaries and secondary production (i.e., animal productivity) could be affected by potential changes in climate and by changes in land use practices. There are many studies in which computer models have been used to assess the impact of climate changes on grassland ecosystems. A global assessment of climate change impacts suggest that some grassland ecosystems will have higher plant production (humid temperate grasslands) while the production of extreme continental steppes (e.g., more arid regions of the temperate grasslands of North America and Eurasia) could be reduced substantially. All of the grassland systems studied are projected to lose soil carbon, with the greatest losses in the extreme continental grassland systems. There are large differences in the projected changes in plant production for some regions, while alterations in soil C are relatively similar over a range of climate change projections drawn from various General Circulation Models (GCM's). The potential impact of climatic change on cattle weight gains is unclear. The results of modeling studies also suggest that the direct impact of increased atmospheric CO₂ on photosynthesis and water use in grasslands must be considered since these direct impacts could be as large as those due to climatic changes. In addition to its direct effects on photosynthesis and water use, elevated CO₂ concentrations lower N content and reduce digestibility of the forage.

KEYWORDS: BIOGEOCHEMISTRY, CLIMATE CHANGE, ECOSYSTEMS, GLOBAL CHANGE, GREAT-PLAINS, NITROGEN, SENSITIVITY, SOIL, TALLGRASS PRAIRIE, UNITED-STATES

1784

Parton, W.J., J.M.O. Scurlock, D.S. Ojima, D.S. Schimel, and D.O. Hall. 1995. Impact of climate-change on grassland production and soil carbon worldwide. *Global Change Biology* 1(1):13-22.

The impact of climate change and increasing atmospheric CO₂ was modelled for 31 temperate and tropical grassland sites, using the CENTURY model. Climate change increased net primary production, except in cold desert steppe regions, and CO₂ increased production everywhere. Climate change caused soil carbon to decrease overall, with a loss of 4 Pg from global grasslands after 50 years. Combined climate change and elevated CO₂ increased production and reduced global grassland C losses to 2 Pg, with tropical savannas becoming small sinks for soil C. Detection of statistically significant change in plant production would require a 16% change in measured plant production because of high year to year variability in plant production. Most of the predicted changes in plant production are less than 10%.

KEYWORDS: DECOMPOSITION, GREAT-PLAINS, MODEL, NITROGEN, ORGANIC-MATTER DYNAMICS, STORAGE

1785

Pasquier-Cardin, A., P. Allard, T. Ferreira, C. Hatte, R. Coutinho, M. Fontugne, and M. Jaudon. 1999. Magma-derived CO₂ emissions recorded in C-14 and C-13 content of plants growing in Furnas caldera, Azores. *Journal of Volcanology and Geothermal Research* 92(1-2):195-207.

The environmental impact of fumarolic and soil emanations of magma-derived carbon dioxide across Furnas caldera has been investigated by measuring the C-14 and C-13 content of 40 specimens of different C3 plants (leaves) growing within and outside the degassing areas. The results demonstrate a significant to large C-14 depletion in many of the

plants due to assimilation of C-14-free endogenous CO₂ during photosynthesis and leading to artificial radiocarbon ageing of up to 4400 years. The extent of C-14 ageing broadly correlates with the intensity of gas manifestations at the sampling sites, as inferred from field observations and measurements of excess CO₂ concentrations in the volcanic ground. It also provides a time-integrated measure of the amount of volcanic CO₂ locally admixed to the ambient air; at several sites this accounts for 15 to 40% of total CO₂ (420 to 600 ppm) in enriched air. In some of the plant species (Azalea, Camellia and fern) C-14 depletion is correlated with an enrichment of C-13 due to assimilation of magma-derived CO₂ with a 4 parts per thousand higher $\delta^{13}C$ than normal atmosphere. The rate of C-13 enrichment averages ca. 0.18 parts per thousand by percent of volcanic carbon fixed in the plant and includes enhanced C-13 discrimination during photosynthesis as a consequence of increased ambient pCO₂ (inferred at - 0.0306 parts per thousand per added ppm of volcanic CO₂). Furnas is one of the few Volcanoes where clear C-13 enrichment in plants due to endogenous degassing has been evidenced. Our results can be used to estimate the local intensity of volcanic soil gas fluxes in the emanating areas of Furnas caldera. They also have implications for radiocarbon dating of past eruptive events in the caldera, since plants artificially aged by previous degassing could be trapped in volcanic deposits. (C) 1999 Elsevier Science B.V. All rights reserved.

KEYWORDS: ATMOSPHERIC CO₂, CARBON, CRATER, SAO-MIGUEL, VULCANO-ISLAND

1786

Pataki, D.E., R. Oren, and D.T. Tissue. 1998. Elevated carbon dioxide does not affect average canopy stomatal conductance of *Pinus taeda* L. *Oecologia* 117(1-2):47-52.

While photosynthetic responses of C-3 plants to elevated CO₂ are fairly well documented, whole-plant water use under such conditions has been less intensively studied. Woody species, in particular, have exhibited highly variable stomatal responses to high CO₂ as determined by leaf-level measurements. In this study, sap flux of *Pinus taeda* L. saplings was periodically monitored during the 4th year of an open-top chamber CO₂ fumigation experiment. Water use per unit sapwood area did not differ between treatments. Furthermore, the ratio of leaf area to sapwood area did not change under high CO₂, so that average canopy stomatal conductance (on a unit leaf area basis) remained unaffected by the CO₂ treatment. Thus, the only effect of high CO₂ was to increase whole-plant water use by increasing sapling leaf area and associated conducting sapwood area. Such an effect may not directly translate to forest-level responses as the feedback effects of higher leaf area at the canopy scale cannot be incorporated in a chamber study. These feedbacks include the potential effect of higher leaf area index on rainfall and light interception, both of which may reduce average stomatal conductance in intact forest canopies.

KEYWORDS: ATMOSPHERIC CO₂ CONCENTRATION, ENRICHMENT, FOREST, GROWTH, LEAF GAS- EXCHANGE, LIQUIDAMBAR- STYRACIFLUA, RESPONSES, SAP FLOW, SEEDLINGS, WATER-STRESS

1787

Paterson, E., J.M. Hall, E.A.S. Rattray, B.S. Griffiths, K. Ritz, and K. Killham. 1997. Effect of elevated CO₂ on rhizosphere carbon flow and soil microbial processes. *Global Change Biology* 3(4):363-377.

Direct effects of increased above-ground CO₂ concentration on soil microbial processes are unlikely, due to the high pCO₂ of the soil atmosphere in most terrestrial ecosystems. However, below-ground microbial processes are likely to be affected through altered plant inputs at elevated CO₂. A major component of plant input is derived from litter

fall and root turnover. Inputs also derive from rhizodeposition (loss of C-compounds from active root systems) which may account for up to 40% of photoassimilate. This input fuels the activity of complex microbial communities around roots. These communities are centrally important not only to plant-microbe interactions and consequent effects on plant growth, but also, through their high relative activity and abundance, to microbially mediated processes in soil generally. This review focuses on approaches to measure C-flow from roots, in particular, as affected by increased atmospheric CO₂ concentration. The available evidence for impacts on microbial communities inhabiting this niche, which constitutes an interface for possible perturbations on terrestrial ecosystems through the influence of environmental change, will also be discussed. While methodologies for measuring effects of increased CO₂ concentration on plant growth, physiology and C-partitioning are abundant and widely reported, there is relatively little information on plant-mediated effects on soil microbial communities and processes. Importantly, many studies have also neglected to recognize that any secondary effects on microbial communities may have profound effects on plant parameters measured in relation to environmental change. We critically review approaches which have been used to measure rhizodeposition under conditions of increased atmospheric CO₂ concentration, and then consider evidence for changes in microbial communities and processes, and the methodologies which have been recently developed, and are appropriate to study such changes.

KEYWORDS: ATMOSPHERIC CO₂, CLIMATE CHANGE, LOLIUM-PERENNE, ORGANIC-CARBON, PERENNIAL RYEGRASS, PSEUDOMONAS-FLUORESCENS, ROOT EXUDATION, TERRESTRIAL ECOSYSTEMS, WHITE CLOVER, ZEA MAYS L

1788

Paterson, E., A. Hodge, B. Thornton, P. Millard, and K. Killham. 1999. Carbon partitioning and rhizosphere C-flow in *Lolium perenne* as affected by CO₂ concentration, irradiance and below-ground conditions. *Global Change Biology* 5(6):669-678.

Plant responses to increasing atmospheric CO₂ concentrations have received considerable interest. However, major uncertainties in relation to interactive effects of CO₂ with above- and below-ground conditions remain. This microcosm study investigated the impacts of CO₂ concentration on plant growth, dry matter partitioning and rhizodeposition as affected by: (i) photon flux density (PFD), and (ii) growth matrix. Plants were grown in a sandy loam soil for 28 d under two photon flux densities: 350 (low PFD) and 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (high PFD) and two CO₂ concentrations: 450 (low CO₂) and 720 $\mu\text{mol mol}^{-1}$ (high CO₂). Partitioning of recent assimilate amongst plant and rhizosphere C-pools was determined by use of (CO₂)-C-14 pulse-labelling. In treatments with high PFD and/or high CO₂, significant ($P < 0.05$) increases in dry matter production were found in comparison with the low PFD/low CO₂ treatment. In addition, significant ($P < 0.05$) reductions in shoot %N and SLA were found in treatments imposing high PFD and/or high CO₂. Root weight ratio (RWR) was unaffected by CO₂ concentration, however, partitioning of C-14 to below ground pools was significantly ($P < 0.05$) increased. In a separate study, *L. perenne* was grown for 28 d in microcosms percolated with nutrient solution, in either a sterile sand matrix or nonsterile soil, under high or low CO₂. Dry matter production was significantly ($P < 0.01$) increased for both sand and soil grown seedlings. Dry matter partitioning was affected by matrix type. C-14-allocation below ground was increased for sand grown plants. Rhizodeposition was affected by CO₂ concentration for growth in each matrix, but was increased for plants grown in the soil matrix, and decreased for those in sand. The results illustrate that plant responses to CO₂ are potentially affected by (i) PFD, and (ii) by feedbacks from the growth matrix. Such feedbacks are discussed in relation to soil nutrient status and interactions with the rhizosphere microbial biomass.

KEYWORDS: DIOXIDE, DRY-MATTER, ELEVATED ATMOSPHERIC

CO₂, ENRICHMENT, GROWTH, NITROGEN, RESPONSES, ROOT EXUDATION, SOIL SYSTEM, WHOLE-PLANT LEVEL

1789

Paterson, E., E.A.S. Rattray, and K. Killham. 1996. Effect of elevated atmospheric CO₂ concentration on C-partitioning and rhizosphere C-flow for three plant species. *Soil Biology and Biochemistry* 28(2):195-201.

The effects of elevated atmospheric CO₂ concentration on the partitioning of dry matter and recent assimilate was investigated for three plant species (rye grass, wheat and Bermuda grass). This was evaluated in plant-soil microcosm systems maintained at specific growth conditions, under two CO₂ regimes (450 and 720 $\mu\text{mol mol}^{-1}$). The distribution of recent assimilate between plant, microbial and soil pools was determined by (CO₂)-C-14 pulse chase, for each plant species at both CO₂ concentrations. Growth of rye grass and wheat (both C-3) was Ca. doubled at the higher CO₂ concentration. Dry matter partitioning was also significantly affected, with an increased root-to-shoot ratio for wheat (0.72-1.03), and a decreased root-to-shoot ratio for rye grass (0.68-0.47) at elevated CO₂. For Bermuda grass (C-4), growth and partitioning of dry matter and C-14 were not affected by CO₂ concentration. C-14-allocation to the rhizospheres of rye-grass and wheat was found to be increased by 62 and 19%, respectively, at the higher CO₂ concentration. The partitioning of C-14 within the rhizospheres of the two C-3 species was also found to be affected by CO₂ concentration. At the higher CO₂ concentration, proportionately less C-14 was present in the microbial fraction, relative to that in the soil. This indicates altered microbial utilisation of root-released compounds at the higher CO₂ concentration, which may be a consequence of altered quantity or quality of rhizodeposits derived from recent assimilate.

KEYWORDS: CARBON, ENRICHMENT, GROWTH, MAINTENANCE, MAIZE, NITROGEN, PHOTOSYNTHESIS, RESPIRATION, SOIL MICROBIAL BIOMASS, VEGETATION

1790

Patterson, B.W., X.J. Zhang, Y.P. Chen, S. Klein, and R.R. Wolfe. 1997. Measurement of very low stable isotope enrichments by gas chromatography mass spectrometry: Application to measurement of muscle protein synthesis. *Metabolism-Clinical and Experimental* 46(8):943-948.

Measurement of muscle protein synthesis using stable isotopically labeled tracers usually requires isotope ratio mass spectrometry (IRMS) because of the need to measure very low enrichments of stable isotopically labeled tracers (tracer to tracee ratio [TTR], 0.005% to 0.10%). This approach is laborious, requiring purification of the metabolite of interest and combustion to a gas for IRMS analysis, and is best suited for use with C-13 tracers. We have developed an approach whereby low enrichments can be conveniently measured by a conventional gas chromatography/mass spectrometry (GC/MS) instrument. The approach includes three critical elements: (1) use of a highly substituted tracer containing three or more labeled atoms, to measure enrichment above a very low natural abundance of highly substituted isotopomers; (2) use of a highly substituted natural abundance isotopomer as a base ion for comparison rather than the most abundant $m + 0$ isotopomer, to reduce the dynamic range of the isotopomer ratio measurement; and (3) a sensitive mass spectrometric analysis that measures the natural abundance of the isotopomer used as a tracer with a high signal to noise ratio ($> 100:1$). This approach was used to measure the rate of synthesis of muscle protein following a primed continuous infusion of L-[C-13(6)]-phenylalanine (PHE) in eight fasted dogs and L-[H-2(3)]-leucine in five fasted human subjects. Values for [C-13(6)]-PHE enrichment by GC/MS rates were virtually identical to those obtained by a conventional approach using high-

performance liquid chromatography (HPLC) to isolate PHE, combustion to CO₂, and measurement of (CO₂)-C-13 enrichment by IRMS (IRMS enrichment = 0.9988 x GC/MS enrichment, R-2 = .891), resulting in identical values for muscle fractional synthesis rates ([FSRs] mean +/- SEM: 2.7 +/- 0.2 and 2.5 +/- 0.2%/d for GC/MS and IRMS, respectively). Human muscle synthesis rates measured by GC/MS analysis of [H-2(3)]-leucine enrichment (1.90 +/- 0.17%/d) were similar to published values based on IRMS analysis using a 1-C-13-leucine tracer. We conclude that compared with the IRMS approach, the GC/MS approach offers faster throughput, has a lower sample requirement, and is suitable for a wider variety of tracers such as H-2. The principles outlined here should be applicable to the measurement of low enrichments by GC/MS in a wide variety of stable isotope tracer applications. Copyright (C) 1997 by W.B. Saunders Company.

KEYWORDS: AMINO-ACIDS, HUMAN SKELETAL-MUSCLE

1791

Patterson, D.T. 1995. Effects of environmental-stress on weed/crop interactions. *Weed Science* 43(3):483-490.

All environmental factors that influence plant growth potentially can affect the ability of weeds and crops to exploit the environmental resources for which plants compete. Stressful levels of environmental factors such as temperature, light, and water and nutrient availability influence weed/crop interactions directly and also may interfere with (or enhance) weed control. Weed and crop species differing in photosynthetic pathway (C-3 VS C-4) are likely to respond differently to many of these factors. Long-term changes in the atmospheric concentrations of CO₂ and other radiatively-active "greenhouse gases" may exert direct physiological and indirect climatic effects on weed/crop interactions and influence weed management strategies. This review focuses on the effects of temperature, light, soil nutrients, water stress, and CO₂ concentration on weed/crop interactions with consideration of the potential impact of climate change.

KEYWORDS: ANODA ANODA-CRISTATA, BROADLEAF WEEDS, CORN ZEA-MAYS, COTTON GOSSYPIMUM- HIRSUTUM, GROWTH-ANALYSIS, JIMSONWEED DATURA-STRAMONIUM, PIGWEED AMARANTHUS-RETROFLEXUS, SOYBEANS GLYCINE-MAX, VELVETLEAF ABUTILON-THEOPHRASTI, WATER RELATIONS

1792

Patterson, D.T. 1995. Weeds in a changing climate. *Weed Science* 43(4):685-700.

Current and projected increases in the concentrations of CO₂ and other radiatively-active gases in the Earth's atmosphere lead to concern over possible impacts on agricultural pests. All pests would be affected by the global warming and consequent changes in precipitation, wind patterns, and frequencies of extreme weather events which may accompany the "greenhouse effect." However, only weeds are likely to respond directly to the increasing CO₂ concentration. Higher CO₂ will stimulate photosynthesis and growth in C-3 weeds and reduce stomatal aperture and increase water use efficiency in both C-3 and C-4 weeds. Respiration, and photosynthate composition, concentration, and translocation may be affected. Perennial weeds may become more difficult to control, if increased photosynthesis stimulates greater production of rhizomes and other storage organs. Changes in leaf surface characteristics and excess starch accumulation in the leaves of C-3 weeds may interfere with herbicidal control. Global warming and other climatic changes will affect the growth, phenology, and geographical distribution of weeds. Aggressive species of tropical and subtropical origins, currently restricted to the southern U.S., may expand northward. Any direct or indirect consequences of the CO₂ increase that differentially affect the growth or fitness of weeds and crops will alter

weed-crop competitive interactions, sometimes to the detriment of the crop and sometimes to its benefit.

KEYWORDS: ANODA ANODA-CRISTATA, ATMOSPHERIC CO₂ ENRICHMENT, COTTON GOSSYPIMUM- HIRSUTUM, ELEVATED CARBON-DIOXIDE, LONG-TERM EXPOSURE, PANICUM PANICUM-TEXANUM, PLANT GROWTH, SOYBEAN GLYCINE-MAX, VELVETLEAF ABUTILON-THEOPHRASTI, WATER-USE EFFICIENCY

1793

Paul, M.J., and S.P. Driscoll. 1997. Sugar repression of photosynthesis: The role of carbohydrates in signalling nitrogen deficiency through source:sink imbalance. *Plant, Cell and Environment* 20(1):110-116.

The aim of this work was to examine whether carbohydrates are involved in signalling N deficiency through source:sink imbalance. Photosynthetic metabolism in tobacco was studied over 8 d during the withdrawal of N from previously N- sufficient plants in which the source:sink ratio was manipulated by shading leaves on some of the plants. In N- sufficient plants over this timescale, there was a small decline in photosynthetic rate, Rubisco protein and amino acid content, with a larger decrease in carbohydrate content. Withdrawal of N from the growing medium induced a large decrease in the rate of photosynthesis (35% reduction after 8 d under the growing conditions, with a reduction also apparent at high and low measuring CO₂), which was caused by a large decrease in the amount of Rubisco protein (62% after 8 d) and Rubisco activity. Higher amounts of hexoses preceded the loss of photosynthetic activity and sucrose and starch accumulation. Reduction of the source:sink ratio by shading prevented the loss of photosynthetic activity and the increase in hexoses and other carbohydrates. These data indicate that the reduction of photosynthesis that accompanies N deficiency in intact plants has the characteristics of sugar repression of photosynthesis observed in model systems, but that the accumulation of hexose prior to the decline in photosynthesis is small. The possibility that sugar repression of photosynthesis under physiological conditions depends more crucially on the C:N status of leaves than the carbohydrate status alone is discussed.

KEYWORDS: ACCLIMATION, CARBON METABOLISM, ELEVATED CO₂, GAS-EXCHANGE, HIGHER-PLANTS, LEAF DEVELOPMENT, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, SPINACH LEAVES, SUCROSE, TEMPERATURE

1794

Paustian, K., E.T. Elliott, H.P. Collins, C.V. Cole, and E.A. Paul. 1995. Use of a network of long-term experiments for analysis of soil carbon dynamics and global change: The North American model. *Australian Journal of Experimental Agriculture* 35(7):929-939.

Soils contain a large proportion of the carbon (C) in the terrestrial biosphere, yet the role of soils as a sink or a source of net atmospheric C flux is uncertain. In agricultural systems, soil C is highly influenced by management practices and there is considerable interest in adapting management systems to promote soil C sequestration, thereby helping to mitigate atmospheric CO₂ increases. Long-term field experimental sites represent a unique source of information on soil C dynamics, and networks of such sites provide a key ingredient for making large-scale assessments of soil C change across ranges in climate and soil conditions and management regimes. Currently, there are collaborative efforts to develop such site networks in Australia, Europe, and North America. A network of long-term experiments in North America was established to provide baseline information on the effects of management (i.e. tillage, crop rotations, fertilisation, organic amendments) on soil organic matter. Historical data on soils, primary productivity, climate, and management

were synthesised by scientists from the individual field sites, representing a total of 35 long-term field experiments. An additional cross-site soil sampling campaign was carried out to provide uniform comparisons of soil C and nitrogen (N), both within and across sites. Long-term field experiments are a principle component necessary for regional assessments of soil C dynamics. We describe a general methodology for combining long-term data with process-oriented simulation models and regional-level, spatially resolved databases. Such analyses are needed to assess past and present changes in soil C at regional to global scales and to make projections of the potential impacts of changes in climate, CO₂, and landuse patterns on soil C in agroecosystems.

KEYWORDS: NITROGEN, ORGANIC-MATTER

1795

Paustian, K., E.T. Elliott, G.A. Peterson, and K. Killian. 1996. Modelling climate, CO₂ and management impacts on soil carbon in semi-arid agroecosystems. *Plant and Soil* 187(2):351-365.

In agroecosystems, there is likely to be a strong interaction between global change and management that will determine whether soil will be a source or sink for atmospheric C. We conducted a simulation study of changes in soil C as a function of climate and CO₂ change, for a suite of different management systems, at four locations representing a climate sequence in the central Great Plains of the US. Climate, CO₂ and management interactions were analyzed for three agroecosystems: a conventional winter wheat-summer fallow rotation, a wheat-corn-fallow rotation and continuous cropping with wheat. Model analyses included soil C responses to changes in the amount and distribution of precipitation and responses to changes in temperature, precipitation and CO₂ as projected by a general circulation model for a 2xCO₂ scenario. Overall, differences between management systems at all the sites were greater than those induced by perturbations of climate and/or CO₂. Crop residue production was increased by CO₂ enrichment and by a changed climate. Where the frequency of summer fallowing was reduced (wheat-corn-fallow) or eliminated (continuous wheat), soil C increased under all conditions, particularly with increased (640 μmol L⁻¹) CO₂. For wheat-fallow management, the model predicted declines in soil C under both ambient conditions and with climate change alone. Increased CO₂ with wheat-fallow management yielded small gains in soil C at three of the sites and reduced losses at the fourth site. Our results illustrate the importance of considering the role of management in determining potential responses of agroecosystems to global change. Changes in climate will determine changes in management as farmers strive to maximize profitability. Therefore, changes in soil C may be a complex function of climate driving management and management driving soil C levels and not be a simple direct effect of either climate or management.

KEYWORDS: AGRICULTURE, ATMOSPHERIC CO₂, CROP RESPONSES, DYNAMICS, ENRICHMENT, FERTILIZATION, GREAT-PLAINS, ORGANIC-MATTER, ROTATIONS, SIMULATION

1796

Pearson, M., R.T. Besford, and D.W. Hand. 1994. The effects of oxides of nitrogen and carbon-dioxide enrichment on growth and content of ribulose-1, 5-bisphosphate carboxylase-oxygenase and nitrite reductase in glasshouse lettuce. *Journal of Horticultural Science* 69(2):257-266.

Different systems of CO₂ enrichment and heating were used to produce glasshouse atmospheres with varying concentrations of NO(x) and CO₂ (ambient NO(x) and CO₂, ambient NO(x) and 1000 vpm CO₂, and three concentrations of NO(x) varying between 0.5 and 2.5 vpm with concurrent CO₂ concentrations between 1000- 2500 vpm). The growth

response of winter lettuce in these environments was assessed for three contrasting cultivars (Ambassador, Berlo and Pascal). Contents of ribulose-1, 5-bisphosphate carboxylase-oxygenase (RuBPco) and nitrite reductase (NiR) in the leaf tissue were also determined using immunoblotting and enzyme-linked immunosorbent assay (ELISA). 'Ambassador' produced the heaviest 'head' weights, but on marketable criteria 'Berlo' performed better. CO₂ enrichment enhanced yields, but the High NO(x) treatments reduced growth relative to that in the Low NO(x) and unpolluted environments. Growth assessments suggested a greater tolerance of NO(x) in cvs Berlo and Pascal than in cv. Ambassador. Immunoblots showed that the antibodies used here were specific. Using these antibodies in ELISA, 'Pascal' was found to contain more RuBPco and NiR on a leaf area basis than 'Ambassador'. There were reductions in RuBPco and NiR contents in response to growth in elevated CO₂. Elevated CO₂ caused a reduction in RuBPco and NiR in 'Ambassador', but in 'Pascal' only RuBPco levels were reduced. This may account for the greater relative tolerance of 'Pascal' and the sensitivity of 'Ambassador' to NO(x) pollution.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO₂, C-3 PLANTS, CALVIN CYCLE ENZYMES, LEAVES, PHOTOSYNTHETIC CO₂ ASSIMILATION, RESPIRATION

1797

Pearson, M., and G.L. Brooks. 1995. The influence of elevated CO₂ on growth and age-related-changes in leaf gas-exchange. *Journal of Experimental Botany* 46(292):1651-1659.

Rumex obtusifolius plants were grown for several months in daylight environment chambers (Solardomes) force-ventilated with air containing 350 or 600 μmol mol⁻¹ CO₂. Elevated CO₂ was found to accelerate the natural ontogenic decline in photosynthesis, but did not reduce leaf duration. In both CO₂ treatments photosynthetic rates declined progressively with increasing leaf age, the decline being greater for plants grown in elevated CO₂ such that rates became lower than in ambient CO₂. The degree of CO₂-induced photosynthetic down-regulation as determined by A/C-I analysis was found to be dependent on leaf age. The major contribution to the decline in photosynthesis was likely to be a reduction in Rubisco activity as changes in stomatal and mesophyll limitations were small. Instantaneous water use efficiency (WUE(i)) was greater for plants in elevated CO₂, but these values declined rapidly with leaf age, whereas in ambient CO₂ values were always lower, but were maintained for longer. Growth analysis indicated an increased root: shoot ratio for plants grown in elevated CO₂, this occurring almost entirely as a result of increased root growth. Greater root proliferation and increased WUE(i) are characteristics which should give this persistent and troublesome weed an increased competitive under projected conditions of climate change.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO₂, CARBON DIOXIDE, CARBOXYLASE, PHOTOSYNTHESIS, PROTEIN, RESPONSES, RUMEX-OBTUSIFOLIUS L, TRANSPIRATION, WATER-USE EFFICIENCY

1798

Pearson, M., and G.L. Brooks. 1996. The effect of elevated CO₂ and grazing by *Gastrophysa viridula* on the physiology and regrowth of *Rumex obtusifolius*. *New Phytologist* 133(4):605-616.

Plants of *Rumex obtusifolius* L. were grown in Solardomes under ambient and elevated (+ 250 μmol mol⁻¹) mole fractions of CO₂ and were exposed to two levels of herbivory by *Gastrophysa viridula* Degeer larvae. The herbivory treatment lasted 1 month, thereafter half of the plants were harvested and over the following month during a period of regrowth physiological measurements were made on the remaining plants. At the termination of the herbivory treatment uninfested plants

showed no damage, whereas the low and high herbivore treatments caused 20-40% and 50-70% loss of leaf area as a proportion of total leaf area, respectively. The CO₂ treatment did not affect the degree of defoliation. Total leaf area was not significantly affected by either CO₂ or herbivory. Uninfested plants grown in elevated concentrations of CO₂ showed increased growth, root- to-shoot ratios (RS), rates of photosynthesis and reduced stomatal conductance compared with uninfested plants grown in ambient CO₂. A/C-i analysis revealed that plants grown in elevated CO₂ showed reductions in V_c(max). For plants grown in ambient CO₂ the high herbivory treatment led to increased rates of photosynthesis and decreased rates of dark respiration per unit leaf area, and caused increases in stomatal conductance and RS. For plants grown in elevated CO₂ the high herbivory treatment increased plant biomass and RS. The increases in RS in response to elevated CO₂ and herbivory appeared to be additive. Defoliation did not reduce the degree of photosynthetic down-regulation caused by growth in elevated concentrations of CO₂, but appeared to reduce the rate of ontogenic decline in photosynthesis in ambient CO₂.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CARBON-DIOXIDE, CHRYSOMELID BEETLE, GROWTH, HERBIVORY, PHOTOSYNTHETIC CAPACITY, PLANTS, RESPIRATION, SHORT-TERM, SOURCE-SINK RELATIONS

1799

Pearson, M., W.J. Davies, and T.A. Mansfield. 1995. Asymmetric responses of adaxial and abaxial stomata to elevated CO₂ - impacts on the control of gas-exchange by leaves. *Plant, Cell and Environment* 18(8):837-843.

The response of adaxial and abaxial stomatal conductance in *Ruiner obtusifolius* to growth at elevated atmospheric concentrations of CO₂ (250 $\mu\text{mol mol}^{-1}$ above ambient) was investigated over two growing seasons. The conductance of both the adaxial and abaxial leaf surfaces was found to be reduced by elevated concentrations of CO₂. Elevated CO₂ caused a much greater reduction in conductance for the adaxial surface than for the abaxial surface. The absence of effects upon stomatal density indicated that the reductions were probably the result of changes in stomatal aperture. Partitioning of gas exchange between the leaf surfaces revealed that increased concentrations of CO₂ caused increased rates of photosynthesis only via the abaxial surface. Additionally, leaf thickness was found to increase during growth at elevated concentrations of CO₂. The tendency for these amphistomatous leaves to develop a distribution of conductance approaching that of hypostomatous leaves clearly reduced their maximum photosynthetic potential. This conclusion was supported by measurements of stomatal limitation, which showed greater values for the adaxial surfaces, and greater values at elevated CO₂. This reduction in photosynthesis may in part be caused by higher diffusive limitations imposed because of increased leaf thickness, in an uncoupled canopy, asymmetrical stomatal responses of the kind identified here may appreciably reduce transpiration. Species which show symmetrical responses are less likely to show reduced transpirational rates, and a redistribution of water loss between species may occur. The implications of asymmetrical stomatal responses for photosynthesis and canopy transpiration are discussed.

KEYWORDS: ACCLIMATION, CONDUCTANCE, GROWTH, PHOTOSYNTHESIS, SCALE, TOMATO

1800

Pearson, S., T.R. Wheeler, P. Hadley, and A.E. Wheldon. 1997. A validated model to predict the effects of environment on the growth of lettuce (*Lactuca sativa* L): Implications for climate change. *Journal of Horticultural Science* 72(4):503-517.

A mechanistic model is described that predicts the effects of changes to

the environment on the growth, yield and maturity of lettuce. The model assumes that lettuce has structural and storage carbon pools. The storage pool is supplied by photosynthesis and depleted by respiratory losses and the conversion of assimilate to the structural pool. The model incorporated both instantaneous effects of temperature and CO₂, and long term effects of thermal time on photosynthetic rate. The rate of structural dry-matter production was related to a simple temperature dependent partitioning coefficient. The model was calibrated on eight separate crops of lettuce and validated with independent data from seven sources. The validated model was then used to simulate changes in head weight and time to maturity with systematic changes in temperature (-2 to +5 degrees C in 1K steps) and carbon dioxide (350 to 700 ppm in 50 ppm steps) superimposed on baseline meteorological data from Rothamsted (1984-1995). These predicted that changes to temperature of up to +3 degrees C would reduce the production time from about 96 to 79 d for April plantings, and from 63 to 52 d for August plantings. Head weight would increase by approximately 32% with an increase in CO₂ of from 350 to 700 ppm, whilst the magnitude of this response varied little with planting date. For any sowing date, increasing temperature was predicted to have little effect on final head weight, however, head weight was predicted to decrease with later transplanting. The potential effects of changes to climate on lettuce production are discussed.

KEYWORDS: CARBON DIOXIDE, CARROT, CO₂, CROPS, ENRICHMENT, GREENHOUSE, LIGHT INTERCEPTION, TEMPERATURE, YIELD

1801

Pedersen, O., and K. SandJensen. 1997. Transpiration does not control growth and nutrient supply in the amphibious plant *Mentha aquatica*. *Plant, Cell and Environment* 20(1):117-123.

Mentha aquatica L. was grown at different nutrient availabilities in water and in air at 60% RH. The plants were kept at 600 $\mu\text{mol m}^{-3}$ free CO₂ dissolved in water (40 times air equilibrium) and at 30 $\mu\text{mol m}^{-3}$ CO₂ in air to ensure CO₂ saturation of growth in both environments. We quantified the transpiration-independent water transport from root to shoot in submerged plants relative to the transpiration stream in emergent plants and tested the importance of transpiration in sustaining nutrient flux and shoot growth. The acropetal water flow was substantial in submerged *Mentha aquatica*, reaching 14% of the transpiration stream in emergent plants. The transpiration-independent mass flow of water from the roots, measured by means of tritiated water, was diverted to leaves and adventitious shoots in active growth. The plants grew well and at the same rates in water and air, but nutrient fluxes to the shoot were greater in plants grown in air than in those that were submerged when they were rooted in fertile sediments. Restricted O₂ supply to the roots of submerged plants may account for the smaller nutrient concentrations, though these exceeded the levels required to saturate growth. In hydroponics, the root medium was aerated and circulated between submerged and emergent plants to minimize differences in medium chemistry, and here the two growth forms behaved similarly and could fully exploit nutrient enrichment. It is concluded that the lack of transpiration from leaf surfaces in a vapour-saturated atmosphere, or under water, is not likely to constrain the transfer of nutrients from root to shoot in herbaceous plants. Nutrient deficiency under these environmental conditions is more likely to derive from restricted development and function of the roots in waterlogged anoxic soils or from low porewater concentrations of nutrients.

KEYWORDS: INORGANIC CARBON, ION-TRANSPORT, MACROPHYTES, PRESSURE, SAP, WATER TRANSPORT

1802

Peiris, D.R., J.W. Crawford, C. Grashoff, R.A. Jefferies, J.R.

Porter, and B. Marshall. 1996. A simulation study of crop growth and development under climate change. *Agricultural and Forest Meteorology* 79(4):271-287.

Climate changes of the order predicted by Global Circulation Models have important implications for arable crop production. We have studied the impact in Scotland using simulation models for three crops of contrasting developmental type: faba or field bean, potato, spring and winter wheat. The models used were the FABEAN, SCRI water-constrained potato model and AFRCWHEAT2 models respectively. Consideration has been made of the natural year-to-year variation in weather which causes yield variability by using 100 years of input weather data produced by a weather generator. The models were run for four Scottish sites and five Scottish soils. Based on GCM predictions, we used eight scenarios of future climate which combine both temperature and rainfall changes. Current temperature (T-0) and rainfall (R(0)) were used as a baseline, and each of T-0 + 1 degrees C, T-0 + 2 degrees C, T-0 + 3 degrees C were used with rainfall unchanged at R(0), and increased by seasonally adjusted amounts ranging from 0 to 1.5 mm per wet day. Possible enhancements due to CO₂ fertilisation were not included in the study. Increased temperatures increase crop development rate, which shortens the growing season for wheat and faba bean, but, given a fixed harvest date, lengthens the season for potatoes. Yields of potato increased by up to 33% over all our sites and scenarios, whereas wheat yields decreased by 5-15% and faba bean by 11-41%. Rainfall increases of the amount suggested here do not affect the yield of potatoes or spring wheat, but winter wheat yields are reduced, due to leaching, and faba bean yields increase through alleviation of water shortage. Faba beans also show a reduction in yield variability as a result of increased rainfall. Changes in variability in wheat and potato were less pronounced and tended to reflect the increase in variability which was assumed to accompany the increased rainfall. Predictions for the changes in the frequencies of high and low yields are also presented. The results give an indication of the level of changes in crop production which would be expected in these future climates.

KEYWORDS: MODEL, SENSITIVITY, VARIABILITY, WATER

1803

Peisker, M., I. Heinemann, and M. Pfeffer. 1998. A study on the relationship between leaf conductance, CO₂ concentration and carboxylation rate in various species. *Photosynthesis Research* 56(1):35-43.

Leaf conductance $g(L)$ is strongly influenced by environmental factors like CO₂, irradiance and air humidity. According to Ball et al. (1987), $g(L)$ is correlated with an index calculated as the product of net CO₂ exchange rate A and ambient water vapour concentration $W-a$, divided by ambient CO₂ concentration $c(a)$. However, this empirical model does not apply to high values of $g(L)$ observed at $c(a)$ below CO₂ compensation concentration Γ . Therefore, we applied modified indices in which A is replaced by estimates for the rate of carboxylation. Such estimates, $P-1$ and $P-2$, were determined by adding to A the quotient of Γ and the sum of gas phase resistance $r(g)$ and intracellular resistance for CO₂ exchange $r(i)$, $P-1 = A + \Gamma / (r(g) + r(i))$, or the quotient of Γ and $r(i)$, $P-2 = A + \Gamma / r(i)$. If $P-2$ is chosen, $c(a)$ in the Ball index has to be replaced by the intercellular CO₂ concentration $c(i)$. By using the modified indices $P-1.W-a/c(a)$ and $P-2.W-a/c(i)$, we analysed data from the C-3 species *Nicotiana tabacum* and *Nicotiana plumbaginifolia*, the C-3-C-4 intermediate species *Diplotaxis tenuifolia*, and the C-4 species *Zea mays*. The data were collected at widely varying levels of irradiance and CO₂ concentration. For all species uniform relationships between $g(L)$ and the new indices were found for the whole range of CO₂ concentrations below and above Γ . Correlations between $g(L)$ and $P-1.W-a/c(a)$ were closer than those between $g(L)$ and $P-2.W-a/c(i)$ because $P-1/c(a)$ implicitly contains $g(L)$. Highly significant correlations were also obtained for the

relationships between $g(L)$ and the ratios $P-1/c(a)$ and $P-2/c(i)$.

KEYWORDS: C-3 PLANTS, ELEVATED CO₂, EMPIRICAL-MODEL, GAS-EXCHANGE, GUARD-CELLS, HUMIDITY, LEAVES, PHOTOSYNTHESIS, RESPONSES, STOMATAL CONDUCTANCE

1804

Peker, H., M.P. Srinivasan, J.M. Smith, and B.J. McCoy. 1992. Caffeine extraction rates from coffee beans with supercritical carbon dioxide. *Aiche Journal* 38(5):761-770.

The extraction of caffeine from whole coffee beans with supercritical carbon dioxide was studied in a continuous-flow extraction apparatus. Decaffeination rates were determined as a function of CO₂ flow rate, temperature and pressure by continuously monitoring the caffeine in the effluent with a flame ionization detector. Soaking the raw beans in water prior to decaffeination enhanced the rate of extraction, which increased markedly with water content. Using CO₂ saturated with water also increased the rate of extraction. The rate of decaffeination increased with pressure and temperature and was influenced by both intraparticle diffusion in the water-soaked beans and external mass transfer. A mathematical model based on a linear-driving-force approximation of mass transfer and partitioning of caffeine between the water and the supercritical CO₂ describes the time-dependent process. The partition coefficient for caffeine distributed between water and supercritical CO₂, the only parameter determined from the dynamic extraction rate data, increases with temperature and pressure.

KEYWORDS: ACTIVATED CARBON, DESORPTION, MASS-TRANSFER

1805

Peng, C.H., and M.J. Apps. 1998. Simulating carbon dynamics along the Boreal Forest Transect Case Study (BFTCS) in central Canada - 2. Sensitivity to climate change. *Global Biogeochemical Cycles* 12(2):393-402.

The effects of climate change and doubling atmospheric CO₂ on carbon dynamics of the boreal forest in the area of the Boreal Forest Transect Case Study in central Canada were investigated using the process-based plant-soil model CENTURY 4.0. The results presented here suggest that (1) across the transect climate change would result in increased total carbon in vegetation biomass but decreased overall carbon in soil; (2) increased atmospheric CO₂ concentration under current climatic patterns would result in increased total carbon in vegetation and in soil organic matter; and (3) combined climate change and elevated CO₂ would increase both net primary productivity and decomposition rates relative to the current climate condition, but their combined action would be a reduction of soil carbon losses relative to those due to climate change alone. The interactive effects of climate change and elevated CO₂, however, are not a simple additive combination of the individual responses. The responses to climate change and elevated CO₂ vary across the climate gradient from southern to northern sites on the transect. The present simulations indicate that the northern sites are more sensitive to climate change than the southern sites are, but these simulations do not consider likely changes in the disturbance regime or changes in forest species distribution.

KEYWORDS: BIOSPHERE-MODEL, C STORAGE, ECOSYSTEM PROCESSES, ELEVATED CO₂, GENERAL-MODEL, LAND-USE, REGIONAL APPLICATIONS, RESPONSES, SOIL ORGANIC MATTER, TERRESTRIAL ECOSYSTEMS

1806

Peng, C.H., and M.J. Apps. 1999. Modelling the response of net

primary productivity (NPP) of boreal forest ecosystems to changes in climate and fire disturbance regimes. *Ecological Modelling* 122(3):175-193.

This study reports on the use of the process-based ecosystem model CENTURY 4.0 to investigate the patterns of net primary productivity (NPP) along a transect across the boreal forests of central Canada and the influence of climate change, CO₂ fertilization and changing fire disturbance regimes on changes in NPP over time. Simulated NPP was tested against observed NPP data from northern sites near Thompson (Manitoba) and southern sites near Prince Albert (Saskatchewan) and shown to be consistent with the data. The temporal dynamics of NPP were very different for the southern, central and northern sites, consistent with the hypothesis that different climate-driven processes regulate forest growth in the various regions of the boreal forest transect case study (BFTCS). The simulations suggest that climate change would result in increased NPP for most sites across the transect. According to the model results, increases in atmospheric CO₂ also show increased NPP. The combined influence of climate change and elevated CO₂ appear to interact in a positive, but non-linear manner. Statistical analysis of the simulation results indicate that changes in NPP are also positively correlated with changes in net N mineralization ($R^2 = 0.89$). This supports the conclusion that feedback via N cycling - a coupling of aboveground production with changes in belowground decomposition - is very important for understanding the NPP dynamics of the boreal forest under a changing climate. It was also found that NPP increases with greater fire frequency under current climate conditions, at least over the range of fire return intervals considered (50- 200 years). The influence of other changes in disturbance regimes (e.g. altered fire severity and concurrent changes in climate or CO₂ fertilization), however, were not considered. (C) 1999 Elsevier Science B.V. All rights reserved.

KEYWORDS: ATMOSPHERIC CO₂, CASE-STUDY BFTCS, CENTRAL CANADA, ELEVATED CO₂, GLOBAL-MODEL, MISSING CO₂ SINK, SIMULATING CARBON DYNAMICS, SOIL ORGANIC MATTER, TALLGRASS PRAIRIE, TERRESTRIAL BIOSPHERE

1807

Peng, C.H., J. Guiot, and E. Van Campo. 1998. Past and future carbon balance of European ecosystems from pollen data and climatic models simulations. *Global and Planetary Change* 18(3-4):189-200.

As climate changes, there is considerable uncertainty whether northern hemisphere ecosystems will act as atmospheric CO₂ sinks or sources. Here, we used statistical models calibrated on field measurements, past terrestrial biomes and climates inferred from pollen and future climatic change scenarios simulated by General Circulation Models (GCMs), to investigate the processes controlling past, present and future CO₂ fluxes in the European ecosystems. Our results suggest that climatic change can significantly affect spatial and temporal variations of net primary production and soil respiration, and alter the net ecosystem exchange of CO₂. Most of the potential terrestrial biomes in Europe will likely change from a net CO₂ sink, which provided a negative feedback for atmospheric CO₂ during the last 13 000 yr BP, to a net CO₂ source, providing a positive feedback following global warming. The results further illustrate that there is no analogue in the recent past (Late Quaternary) for the probable future ecosystem dynamics. (C) 1998 Elsevier Science B.V. All rights reserved.

KEYWORDS: ARCTIC TUNDRA, ATMOSPHERIC CO₂, CYCLE, ELEVATED CO₂, MISSING CO₂ SINK, SOIL RESPIRATION, STORAGE, TERRESTRIAL BIOSPHERE, VEGETATION, YR BP

1808

Pennanen, A., V. Kempfi, D. Lawlor, and E. Pehu. 1992. The effect

of elevated CO₂ on photosynthesis and chloroplast thylakoid structure of crop plants. *Photosynthesis Research* 34(1):243.

1809

Pennanen, A.H., J.C.V. Vu, L.H. Allen, and G. Bowes. 1995. Elevated CO₂ and temperature effects on enzymes of sucrose and starch synthesis in soybean. *Plant Physiology* 108(2):90.

1810

Penuelas, J., C. Biel, and M. Estiarte. 1995. Growth, biomass allocation, and phenology responses of pepper to elevated CO₂ concentrations and different water and nitrogen supply. *Photosynthetica* 31(1):91-99.

Fifty-day old plants of *Capsicum annum* L. with two developed leaves were placed into controlled environment chambers at atmospheric (350 cm³ m⁻³, ACO(2)) and elevated (700 cm³ m⁻³, ECO(2)) CO₂ concentrations under different nitrogen and water supply. Plant response to ECO(2) and the modulating effect of the availability of nitrogen and water were evaluated. CO₂ effects were significant only after 40 d of treatment. An increase in plant growth and yield was found in ECO(2) plants only under a good supply of both water (HW) and nitrogen (HN). Chlorophyll concentration responded only to N supply. Root/shoot ratio was higher under ECO(2) only under low N (LN) and low water (LW) supply. Leaf area and specific leaf area decreased under ECO₂. Flowering and fructification took place earlier in ECO(2) under HN and HW. Thus, all CO₂ effects were modulated by the N and water supply and the duration of exposure.

KEYWORDS: ATMOSPHERIC CO₂, CARBON-DIOXIDE ENRICHMENT, COTTON, CROP RESPONSES, LAST 3 CENTURIES, LEAF-AREA, MINERAL NUTRITION, PLANTS, TEMPERATURE, YIELD

1811

Penuelas, J., C. Biel, R. Save, and M. Estiarte. 1995. Detrimental effects of fluctuating high CO₂ concentrations on peppers. *Photosynthetica* 31(3):361-370.

Plants of pepper (*Capsicum annum* L.) were grown in controlled environment chambers at ambient (360 μmol mol⁻¹) and fluctuating pulse-enriched CO₂ concentrations (700 μmol mol⁻¹) daily average, ranging from 500 to 3500 μmol mol⁻¹ = ECO(2)) under two water regimes. A decrease in plant growth and yield together with frequent visual injuries was found in plants growing under ECO(2). Root/shoot ratio was greater, chlorophyll concentration and respiration rates were lower, and stomatal conductance and relative importance of alternative pathway respiration were higher under ECO(2). The negative effects of ECO(2) were more intense under high water availability. The symptoms produced by ECO(2) were similar to those of resource limitation, and were alleviated with increased nutrient supply. Constant elevated CO₂ concentrations (700 μmol mol⁻¹) increased pepper production and did not produce any of the injuries described for this erratic ECO(2) treatment. Thus, it is probably the erratic nature of the CO₂ concentration and not the gas itself that was causing the injury.

KEYWORDS: CARBON DIOXIDE, CUCUMBERS, ENRICHMENT, FOLIAR DEFORMATION, LAST 3 CENTURIES, PLANTS, RESPONSES, STARCH, TOMATO, YIELD

1812

Penuelas, J., and M. Estiarte. 1997. Trends in plant carbon

concentration and plant demand for N throughout this century. *Oecologia* 109(1):69-73.

Atmospheric CO₂ concentration has increased by 25% over the preindustrial level. A parallel increase in C concentration and decreases in N concentration and delta(13)C of plants grown throughout this century have been observed in plant specimens stored in herbaria. We tested our previous results in a study of 12 more species collected in the western Mediterranean throughout this century (1920-1930, 1945-1955, and 1985-1990) and tree rings of *Quercus pubescens* from the same area. These changes were accompanied by apparent increases in condensed tannin concentration. A decreasing trend in delta(15)N both in herbarium material and tree rings was also found, indicating that ecosystems might cope with higher plant N demand by decreasing N losses and increasing N fixation and mineralization. These results may contribute to a better understanding of the effects of global change on carbon and nitrogen cycling.

KEYWORDS: ABUNDANCE, BALANCE, CO₂, DIOXIDE, ECOSYSTEMS, FRACTIONATION, INCREASE, N-15, NITROGEN, NUTRITION

1813

Penuelas, J., M. Estiarte, B.A. Kimball, S.B. Idso, P.J. Pinter, G.W. Wall, R.L. Garcia, D.J. Hansaker, R.L. LaMorte, and D.L. Hendrix. 1996. Variety of responses of plant phenolic concentration to CO₂ enrichment. *Journal of Experimental Botany* 47(302):1463-1467.

A wide range of responses to elevated CO₂ was found for leaf total phenolic concentration of one grass species (wheat) growing in a Free-Air CO₂ Enrichment (FACE) system and two woody species (orange and pine trees) growing in Open-Top Chambers (OTC). The total phenolic concentration of wheat flag leaves grown at elevated [CO₂] was increased for most of the grain-filling stages studied; there was no significant change in phenolic concentration of CO₂-enriched orange tree leaves and CO₂-enriched pine tree needles had reduced total phenolic concentration. There was an inverse relationship between the increase in leaf total phenolic concentration and increase in biomass of these pine trees. Different rates of increase in growth (carbon sink) produced by different environmental conditions or different resource availabilities apart from CO₂ itself must be considered in order to understand the response of carbon-based-secondary-compounds to elevated CO₂.

KEYWORDS: AIR, ALLELOCHEMICALS, ATMOSPHERIC CO₂, CARBON NUTRIENT BALANCE, DIOXIDE, ELEVATED CO₂, GROWTH, LAST 3 CENTURIES, SECONDARY METABOLITES, SUSCEPTIBILITY

1814

Penuelas, J., M. Estiarte, and J. Llusia. 1997. Carbon-based secondary compounds at elevated CO₂. *Photosynthetica* 33(2):313-316.

From literature sources we compiled the data on carbon-based-secondary compounds CBSC (phenolics and terpenoids) and biomass of 17 plant species grown at different CO₂ concentrations under low and high nutrient availabilities. With a low nutrient availability a possible inverse correlation was found between the biomass and CBSC changes. On the contrary, under a high nutrient availability, both the CBSC and biomass increased with elevated CO₂. The wide variation in the CBSC production among species and compounds (larger responses in phenolics than in terpenoids) indicates that the allocation to CBSC may not completely be governed by changes in CO₂ and nutrient availabilities per se. Yet the comparison shows that elevated CO₂ generally loads the carbon into CBSC [their leaf concentration increased an overall average of 14 % at 700 mu mol(CO₂) mol(-1)] which may improve our

understanding of the carbon storage and cycling in ecosystems under the "global change" of climate.

KEYWORDS: ALLELOCHEMICALS, BIRCH, DECOMPOSITION, DIOXIDE, ENRICHMENT, GROWTH, METABOLITES, NUTRIENT BALANCE, PLANTS, WATER-STRESS

1815

Penuelas, J., S.B. Idso, A. Ribas, and B.A. Kimball. 1997. Effects of long-term atmospheric CO₂ enrichment on the mineral concentration of *Citrus aurantium* leaves. *New Phytologist* 135(3):439-444.

Leaf mineral concentration of *Citrus aurantium* (sour orange tree) was measured at bi-monthly intervals from 30 to 85 months of exposure in a long-term study on the effects of a 300 mu mol mol(-1) enrichment of atmospheric CO₂, under conditions of high nutrient and water supply. There were clear seasonal trends in the concentrations of most of the elements studied. There were initial decreases in the leaf concentrations of N and the xylem-mobile, phloem-immobile elements Mn, Ca and Mg, as well as a significant and sustained increase in the leaf concentration of B, and no changes in the concentrations of K, Fe, Na, P, S, Zn and Cu. Interestingly, the initial reductions in the leaf concentrations of Mn, N, Ca and Mg gradually disappeared with time.

KEYWORDS: ALLOCATION, CARBON DIOXIDE, ELEVATED CO₂, GROWTH, INSECT HERBIVORE INTERACTIONS, LAST 3 CENTURIES, NUTRIENT-UP TAKE, SOUR ORANGE TREES, TEMPERATURE, TERRESTRIAL ECOSYSTEMS

1816

Penuelas, J., and J. Llusia. 1997. Effects of carbon dioxide, water supply, and seasonality on terpene content and emission by *Rosmarinus officinalis*. *Journal of Chemical Ecology* 23(4):979-993.

Rosmarinus officinalis L. plants were grown under carbon dioxide concentrations of 350 and 700 mu mol/mol (atmospheric CO₂ and elevated CO₂) and under two levels of irrigation (high water and low water) from October 1, 1994 to May 31, 1996. Elevated CO₂ led to increasingly larger monthly growth rates than the atmospheric CO₂ treatments. The increase was 9.5% in spring 1995, 23% in summer 1995, and 53% in spring 1996 in the high-water treatments, whereas in low-water treatments the growth response to elevated CO₂ was constrained until the second year spring, when there was a 47%, increase. The terpene concentration was slightly larger in the elevated CO₂ treatments than in atmospheric CO₂ treatments and reached a maximum 37% difference in spring 1996. There was no significant effect of water treatment, likely as a result of a mild low water treatment for a Mediterranean plant. Terpene concentration increased throughout the period of study, indicating possible age effects. The most abundant terpenes were alpha-pinene, cineole, camphor, borneol, and verbenone, which represented about 75% of the total. No significant differences were found in the terpene composition of the plants in the different treatments or seasons. The emission of volatile terpenes was much larger in spring (about 75 mu g/dry wt/hr) than in autumn (about 10 mu g/dry wt/hr), partly because of higher temperature and partly because of seasonal effect, but no significant difference was found because of CO₂ or water treatment. The main terpene emitted was alpha-pinene, which represented about 50% of the total. There was no clear correlation between content and emission, either quantitatively or qualitatively. More volatile terpenes were proportionally more important in the total emission than in total content and in autumn than in spring.

KEYWORDS: ALLOCATION, BIRCH, CO₂, FIR PSEUDOTSUGA-MENZIESII, MONOTERPENES, PLANTS, RESPONSES

1817

Penuelas, J., and R. Matamala. 1993. Variations in the mineral composition of herbarium plant- species collected during the last 3 centuries. *Journal of Experimental Botany* 44(266):1523-1525.

Mineral content (dry weight basis) was determined for herbarium specimens of 12 C3 plants (trees, shrubs and herbs) collected during the last 250 years in N.E. Spain. Present values of Al, Ca, Cu, Sr, Fe, P, Mg, Mn, K, Na, S, and Zn were always lower than in any other period of the last three centuries. Only one C4 plant was analysed. It presented a similar pattern to the C3 plants. These results are in accordance with experimental results that have shown that the mineral content of plants grown in elevated CO₂ is generally lowered. Increased atmospheric CO₂ and other anthropogenic environmental changes are suggested as possible causes of the changes in mineral content.

KEYWORDS: ATMOSPHERIC CO₂, INCREASE, PAST 2 CENTURIES

1818

Percival, D.C., J.T.A. Proctor, and M.J. Tsujita. 1996. Whole-plant net CO₂ exchange of raspberry as influenced by air and root-zone temperature, CO₂ concentration, irradiation, and humidity. *Journal of the American Society for Horticultural Science* 121(5):838-845.

The influence of irradiance, CO₂, and temperature on whole- plant net CO₂ exchange rate (NCER) of *Rubus idaeus* L. 'Heritage' micropropagated raspberries was examined. Within the set of environmental conditions examined, irradiation was the most important factor, accounting for 58% of the whole-plant irradiance/CO₂ concentration/temperature NCER model variation, followed by CO₂ concentration (28%) and temperature (2.5%). Net photosynthesis (Pn) required irradiance levels >600 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ PPF for saturation, greatly increased under CO₂ enrichment (up to 1500 $\mu\text{L} \cdot \text{L}^{-1}$), and was optimum at a whole-plant temperature of 20 degrees C. Temperature effects were partitioned in an experiment using varying air and root-zone temperatures (15, 20, 25, 30, and 35 degrees C) under saturated light and ambient CO₂ levels (350 $\mu\text{L} \cdot \text{L}^{-1}$). Air and root-zone temperature influenced Pn, with maximum rates occurring at an air x root-zone temperature of 17/25 degrees C. The contribution of air and root-zone temperature to the NCER model varied, with air and root-zone temperature contributing 75% and 24%, respectively, to the total model variation (R² = 0.96). Shoot dark respiration increased with air and root-zone temperature, and root respiration rates depended on air and root-zone temperature and shoot assimilation rate. Humidity also influenced Pn with a saturated vapor pressure deficit threshold >0.25 kPa resulting in a Pn decrease. Quantifying the physiological response of raspberries to these environmental parameters provides further support to recent findings that cool shoot/warm root conditions are optimum for raspberry plant growth.

KEYWORDS: ACQUISITION, CO₂ EXCHANGE, ENRICHMENT, GROWTH, LEAVES, NUTRITION, PHOTOSYNTHESIS, RED RASPBERRY, RESPIRATION, RESPONSES

1819

Perezsoba, M., T.A. Dueck, G. Puppi, and P.J.C. Kuiper. 1995. Interactions of elevated CO₂, NH₃ and O₃ on mycorrhizal infection, gas-exchange and N-metabolism in saplings of scots pine. *Plant and Soil* 176(1):107-116.

Four-year-old saplings of Scots pine (*Pinus sylvestris* L.) were exposed for 11 weeks in controlled-environment chambers to charcoal-filtered air, or to charcoal-filtered air supplemented with NH₃ (40 $\mu\text{g} \cdot \text{m}^{-3}$), O₃ (110 $\mu\text{g} \cdot \text{m}^{-3}$) during day/ 40 $\mu\text{g} \cdot \text{m}^{-3}$ during night) or NH₃ + O₃. All treatments were carried out at ambient (350 $\mu\text{L} \cdot \text{L}^{-1}$) and at elevated CO₂ concentration (700 $\mu\text{L} \cdot \text{L}^{-1}$). Total tree biomass,

mycorrhizal infection, net CO₂ assimilation (P-n), stomatal conductance (g(s)), transpiration of the shoots and NH₃ metabolism of the needles were measured. In ambient CO₂ (1) gaseous NH₃ decreased mycorrhizal infection, without significantly affecting tree biomass or N concentration and it enhanced the activity of glutamine synthetase (GS) and glutamate dehydrogenase (GDH) in one-year-old needles; (2) ozone decreased mycorrhizal infection and the activity of GS in the needles, while it increased the activity of GDH; (3) exposure to NH₃ + O₃ lessened the effects of single exposures to NH₃ and O₃ on reduction of mycorrhizal infection and on increase in GDH activity. Similar lessening effects on mycorrhizal infection as observed in trees exposed to NH₃ + O₃ at ambient CO₂, were measured in trees exposed to NH₃ + O₃ at elevated CO₂. Exposure to elevated CO₂ without pollutants did not significantly affect any of the parameters studied, except for a decrease in the concentration of soluble proteins in the needles. Elevated CO₂ + NH₃ strongly decreased root branching and mycorrhizal infection and temporarily stimulated P-n and g(s). The exposure to elevated CO₂ + NH₃ + O₃ also transiently stimulated P-n. The possible mechanisms underlying and integrating these effects are discussed. Elevated CO₂ clearly did not alleviate the negative effects of NH₃ and O₃ on mycorrhizal infection. The significant reduction of mycorrhizal infection after exposure to NH₃ or O₃, observed before significant changes in gas exchange or growth occurred, suggest the use of mycorrhizal infection as an early indicator for NH₃ and O₃ induced stress.

KEYWORDS: ACCLIMATION, AMMONIUM-SULFATE, ATMOSPHERIC CARBON-DIOXIDE, DOUGLAS-FIR, FIR PSEUDOTSUGA-MENZIESII, GROWTH, OZONE, RESPONSES, SEEDLINGS, STRESS

1820

Perezsoba, M., L.J.M. Vandereerden, I. Stulen, and P.J.C. Kuiper. 1994. Gaseous ammonia counteracts the response of scots pine needles to elevated atmospheric carbon-dioxide. *New Phytologist* 128(2):307-313.

Four-year-old saplings of Scots pine (*Pinus sylvestris* L.) were exposed for 8 wk in controlled-environment chambers to charcoal-filtered air (FB), FA supplemented with 754 $\mu\text{g} \cdot \text{m}^{-3}$ (650 $\mu\text{L} \cdot \text{L}^{-1}$) CO₂, FA supplemented with 100 $\mu\text{g} \cdot \text{m}^{-3}$ NH₃ and FA + CO₂ + NH₃. Elevated CO₂ induced a significant increase in the concentrations of NH₄⁺ and NO₃⁻ in the soil solution, while exposure to NH₃ enhanced the soil NH₄⁺ concentration. Elevated CO₂ significantly increased needle biomass and area, and decreased specific leaf area (SLA) and N concentration in the needles. The activity of peroxidase (POD) was decreased, while the activities of glutamine synthetase (GS) and glutamate dehydrogenase (GDH) were only slightly affected. Gaseous NH₃ enhanced the concentration of N, soluble proteins and the GS activity in the needles, while it decreased the POD and GDH activities. The effects of elevated CO₂ + NH₃ on needle biomass production, N metabolism and POD activity were smaller than the effects of single exposures to elevated CO₂ or NH₃, suggesting that elevated CO₂ and NH₃ counteract each other and disturb needle physiology. The possible mechanisms underlying the negative interactions of elevated CO₂ and NH₃ are discussed. The expected stimulation of biomass production by elevated CO₂ may be reduced in the presence of atmospheric NH₃.

KEYWORDS: ALLOCATION, CO₂- ENRICHMENT, FORESTS, LEAVES, NH₃, NITROGEN, PLANT GROWTH, SEEDLINGS, SOIL, SYLVESTRIS

1821

Perruchoud, D., F. Joos, A. Fischlin, I. Hajdas, and G. Bonani. 1999. Evaluating timescales of carbon turnover in temperate forest soils with radiocarbon data. *Global Biogeochemical Cycles* 13(2):555-573.

Timescales of soil organic carbon (SOC) turnover in forests were investigated with soil radiocarbon data. The C-12/C-14 ratios were measured by accelerated mass spectroscopy on soil sampled from a deciduous temperate forest in Switzerland during 1969-1995. The resulting Delta(14)C values (125-174 parts per thousand) were in line with previously published C-14 soil data. We applied FORCLIM-D, a model of nonliving organic matter decomposition including nine litter and two soil compartments to estimate SOC turnover times for this forest type. Carbon 14 aging in woody vegetation was explicitly accounted for. Parameters were calibrated to match radiocarbon ratios observed for forest soils at Meathop Wood, United Kingdom [Harkness et al., 1986]. We estimated that roughly 50-94% (best estimate, 49%) of foliar litter carbon and 11-74% (73%) of fine root litter carbon are eventually respired as CO₂ at Meathop Wood; the rest is transferred to soil humus, where it undergoes further decomposition. Turnover times for the 0-20 cm mineral soil layer ranged from 9-50 years (25 years) for a fast overturning soil compartment comprising 38-74% (68%) of bulk SOC and 155-10,018 years (3,570 years) for a slowly overturning compartment. For the Swiss site, SOC turnover times were in the same range. Parameter uncertainties were correlated and induced by uncertainties in C-14 observations from small-scale spatial inhomogeneities, sample preparation and by lack of reliable C-14 observations for the "prebomb" test period. Model-based estimates of soil organic C turnover derived from C-14 data must be used cautiously since they depend on the underlying model structure: bypassing litter in FORCLIM-D overestimated SOC turnover by a factor of 2.5. Such an error might remain undetected in studies lacking samples from the late 1960s and early 1970s. Thus litter C turnover should be included when estimating SOC turnover in temperate forests from C-14 data.

KEYWORDS: ATMOSPHERIC CO₂, CLIMATE CHANGE, ECOSYSTEMS, ELEVATED CO₂, LAND-USE, LITTER PRODUCTION, NITROGEN, ORGANIC-MATTER TURNOVER, STORAGE, TERRESTRIAL

1822

Permal, J.V., and M.A. Maun. 1999. The role of mycorrhizal fungi in growth enhancement of dune plants following burial in sand. *Functional Ecology* 13(4):560-566.

1, Burial in sand of *Agropyron psammophilum* and *Panicum virgatum* plants had a stimulating effect on carbon dioxide exchange rate, leaf area and biomass, irrespective of whether sand used for burial did or did not contain mycorrhizal fungi. 2, Plants of both *A. psammophilum* and *P. virgatum* species grown in mycorrhiza-containing sand and then buried with mycorrhiza-containing sand had the highest CO₂ exchange rate, leaf area and biomass. 3, The growth stimulation following a burial episode is probably a composite response of several factors. The major contribution of mycorrhizal fungi will possibly be the exploitation of resources in the burial deposit.

KEYWORDS: AMMOPHILA-BREVILIGULATA, CALAMOVILFA-LONGIFOLIA, COMMUNITY STRUCTURE, MORPHOLOGY, PHOTOSYNTHESIS, SOIL

1823

Pesheva, I., M. Kodama, M.L. Dionisiosese, and S. Miyachi. 1994. Changes in photosynthetic characteristics induced by transferring air-grown cells of *Chlorococcum-littorale* to high-co₂ conditions. *Plant and Cell Physiology* 35(3):379-387.

When air-grown cells of *Chlorococcum littorale* was enriched with CO₂, growth was enhanced after a lag period of one to two days at 20% CO₂, and 3 to 6 days at 40% CO₂. Changes in the rate of photosynthesis measured as oxygen evolution and CO₂ fixation, were similar to those observed for growth. During the initial inhibition of photosynthesis in

40% CO₂, the activity of PSII was suppressed. In contrast, PSI activity was greatly enhanced. Air-grown cells of *C. littorale* possessed comparatively high carbonic anhydrase (CA) activity which was localized inside the cells and on the cell surface. Under high CO₂ concentrations extracellular CA activity was greatly suppressed and intracellular activity almost completely abolished. Phosphoenol pyruvate carboxylase activity was also suppressed in high CO₂-grown cells. Ribulose-1,5-bisphosphate carboxylase activity was higher in high-CO₂ grown cells than in air-grown cells. The above results indicated that the lag phase induced by 40% CO₂ was due to suppression of PSII activity.

KEYWORDS: BISPSPHATE, CARBONIC-ANHYDRASE, CARBOXYLASE OXYGENASE CONTENT, CHLORELLA, CO₂ CONCENTRATION, DIOXIDE, FIXATION, INDUCTION, INORGANIC CARBON, PLANTS

1824

Peterson, A.G., J.T. Ball, Y. Luo, C.B. Field, P.S. Curtis, K.L. Griffin, C.A. Gunderson, R.J. Norby, D.T. Tissue, M. Forstreuter, A. Rey, and C.S. Vogel. 1999. Quantifying the response of photosynthesis to changes in leaf nitrogen content and leaf mass per area in plants grown under atmospheric CO₂ enrichment. *Plant, Cell and Environment* 22(9):1109-1119.

Previous modelling exercises and conceptual arguments have predicted that a reduction in biochemical capacity for photosynthesis (A(area)) at elevated CO₂ may be compensated by an increase in mesophyll tissue growth if the total amount of photosynthetic machinery per unit leaf area is maintained (i.e. morphological upregulation). The model prediction was based on modelling photosynthesis as a function of leaf N per unit leaf area (N-area), where N-area = N-mass x LMA. Here, N-mass is percentage leaf N and is used to estimate biochemical capacity and LMA is leaf mass per unit leaf area and is an index of leaf morphology. To assess the relative importance of changes in biochemical capacity versus leaf morphology we need to control for multiple correlations that are known, or that are likely to exist between CO₂ concentration, N-area, N-mass, LMA and A(area). Although this is impractical experimentally, we can control for these correlations statistically using systems of linear multiple-regression equations. We developed a linear model to partition the response of A(area), to elevated CO₂ into components representing the independent and interactive effects of changes in indexes of biochemical capacity, leaf morphology and CO₂ limitation of photosynthesis. The model was fitted to data from three pine and seven deciduous tree species grown in separate chamber-based field experiments. Photosynthetic enhancement at elevated CO₂ due to morphological upregulation was negligible for most species. The response of A(area), in these species was dominated by the reduction in CO₂ limitation occurring at higher CO₂ concentration. However, some species displayed a significant reduction in potential photosynthesis at elevated CO₂ due to an increase in LMA that was independent of any changes in N-area. This morphologically based inhibition of A(area) combined additively with a reduction in biochemical capacity to significantly offset the direct enhancement of A(area) caused by reduced CO₂ limitation in two species. This offset was 100% for *Acer rubrum*, resulting in no net effect of elevated CO₂ on A(area) for this species, and 44% for *Betula pendula*. This analysis shows that interactions between biochemical and morphological responses to elevated CO₂ can have important effects on photosynthesis.

KEYWORDS: ACCLIMATION, C-3 PLANTS, ELEVATED CARBON-DIOXIDE, FIELD, GAS-EXCHANGE, LEAVES, MODEL, OPEN-TOP CHAMBERS, TEMPERATURE, TREES

1825

Peterson, A.G., J.T. Ball, Y.Q. Luo, C.B. Field, P.B. Reich, P.S. Curtis, K.L. Griffin, C.A. Gunderson, R.J. Norby, D.T. Tissue, M.

Forstreuter, A. Rey, and C.S. Vogel. 1999. The photosynthesis leaf nitrogen relationship at ambient and elevated atmospheric carbon dioxide: a meta-analysis. *Global Change Biology* 5(3):331-346.

Estimation of leaf photosynthetic rate (A) from leaf nitrogen content (N) is both conceptually and numerically important in models of plant, ecosystem, and biosphere responses to global change. The relationship between A and N has been studied extensively at ambient CO₂ but much less at elevated CO₂. This study was designed to (i) assess whether the A-N relationship was more similar for species within than between community and vegetation types, and (ii) examine how growth at elevated CO₂ affects the A-N relationship. Data were obtained for 39 C₃ species grown at ambient CO₂ and 10 C₃ species grown at ambient and elevated CO₂. A regression model was applied to each species as well as to species pooled within different community and vegetation types. Cluster analysis of the regression coefficients indicated that species measured at ambient CO₂ did not separate into distinct groups matching community or vegetation type. Instead, most community and vegetation types shared the same general parameter space for regression coefficients. Growth at elevated CO₂ increased photosynthetic nitrogen use efficiency for pines and deciduous trees. When species were pooled by vegetation type, the A-N relationship for deciduous trees expressed on a leaf-mass basis was not altered by elevated CO₂, while the intercept increased for pines. When regression coefficients were averaged to give mean responses for different vegetation types, elevated CO₂ increased the intercept and the slope for deciduous trees but increased only the intercept for pines. There were no statistical differences between the pines and deciduous trees for the effect of CO₂. Generalizations about the effect of elevated CO₂ on the A-N relationship, and differences between pines and deciduous trees will be enhanced as more data become available.

KEYWORDS: CO₂, FIELD, GAS-EXCHANGE, GROWTH, LEAVES, LIFE-SPAN, MODEL, NET PRIMARY PRODUCTION, OPEN-TOP CHAMBERS, USE EFFICIENCY

1826

Peterson, R.B. 1991. Effects of O₂ and CO₂ concentrations on quantum yields of photosystem-I and photosystem-II in tobacco leaf tissue. *Plant Physiology* 97(4):1388-1394.

The interactive effects of irradiance and O₂ and CO₂ levels on the quantum yields of photosystems I and II have been studied under steady-state conditions at 25-degrees-C in leaf tissue of tobacco (*Nicotiana tabacum*). Assessment of radiant energy utilization in photosystem II was based on changes in chlorophyll fluorescence yield excited by a weak measuring beam of modulated red light. Independent estimates of photosystem I quantum yield were based on the light-dark in vivo absorbance change at 830 nanometers, the absorption band of P700+. Normal (i.e. 20.5%, v/v) levels of O₂ generally enhanced photosystem II quantum yield relative to that measured under 1.6% O₂ as the irradiance approached saturation. Photorespiration is suspected to mediate such positive effects of O₂ through increases in the availability of CO₂ and recycling of orthophosphate. Conversely, at low intercellular CO₂ concentrations, 41.2% O₂ was associated with lower photosystem II quantum yield compared with that observed at 20.5% O₂. Inhibitory effects of 41.2% O₂ may occur in response to negative feedback on photosystem II arising from a build-up in the thylakoid proton gradient during electron transport to O₂. Covariation between quantum yields of photosystems I and II was not affected by concentrations of either O₂ or CO₂. The dependence of quantum yield of electron transport to CO₂ measured by gas exchange upon photosystem II quantum yield as determined by fluorescence was unaffected by CO₂ concentration.

KEYWORDS: ABSORBANCE CHANGES, ASSIMILATION, CHLOROPHYLL FLUORESCENCE, CHLOROPLASTS, ELECTRON-TRANSPORT, EXCHANGE, LEAVES, PHOSPHATE,

PHOTOREDUCTION, PHOTOSYNTHESIS

1827

Petschel- Held, G., H.J. Schellnhuber, T. Bruckner, F.L. Toth, and K. Hasselmann. 1999. The tolerable windows approach: Theoretical and methodological foundations. *Climatic Change* 41(3-4):303-331.

The tolerable windows (TW) approach is presented as a novel scheme for integrated assessment of climate change. The TW approach is based on the specification of a set of guardrails for climate evolution which refer to various climate-related attributes. These constraints, which define what we call tolerable windows, can be purely systemic in nature - like critical thresholds for the North Atlantic Deep Water formation - or of a normative type - like minimum standards for per-capita food production worldwide. Starting from this catalogue of knock-out criteria and using appropriate modeling techniques, those policy strategies which are compatible with all the constraints specified are sought to be identified. In addition to the discussion of the basic elements and the general theory of the TW approach, a modeling exercise is carried out, based on simple models and assumptions adopted from the German Advisory Council on Global Change (WBGU). The analysis shows that if the global mean temperature is restricted to 2 degrees C beyond the preindustrial level, the cumulative emissions of CO₂ are asymptotically limited to about 1550 Gt C. Yet the temporal distribution of these emissions is also determined by the climate and socio-economic constraints: using, for example, a maximal tolerable rate of temperature change of 0.2 degrees C/dec and a smoothly varying emissions profile, we obtain the maximal cumulative emissions, amounting to 370 Gt C in 2050 and 585 Gt C in 2100.

KEYWORDS: CLIMATE CHANGE, ECONOMICS, MODEL, THERMOHALINE CIRCULATION

1828

Pettersson, R., and A.J.S. McDonald. 1992. Effects of elevated carbon-dioxide concentration on photosynthesis and growth of small birch plants (*Betula pendula* Roth) at optimal nutrition. *Plant, Cell and Environment* 15(8):911-919.

Small birch plants (*Betula Pendula* Roth.) were grown from seed for periods of up to 70 d in a climate chamber at optimal nutrition and at present (350 $\mu\text{mol mol}^{-1}$) or elevated (700 $\mu\text{mol mol}^{-1}$) concentrations of atmospheric CO₂. Nutrients were sprayed over the roots in Ingstad-type units. Relative growth rate and net assimilation rate were slightly higher at elevated CO₂, whereas leaf area ratio was slightly lower. Smaller leaf area ratio was associated with lower values of specific leaf area. Leaves grown at elevated CO₂ had higher starch concentrations (dry weight basis) than leaves grown at present levels of CO₂. Biomass allocation showed no change with CO₂, and no large effects on stem height, number of side shoots and number of leaves were found. However, the specific root length of fine roots was higher at elevated CO₂. No large difference in the response of carbon assimilation to intercellular CO₂ concentration (A/C(i) curves) were found between CO₂ treatments. When measured at the growth environments, the rates of photosynthesis were higher in plants grown at elevated CO₂ than in plants grown at present CO₂. Water use efficiency of single leaves was higher in the elevated treatment. This was mainly attributable to higher carbon assimilation rate at elevated CO₂. The difference in water use efficiency diminished with leaf age. The small treatment difference in relative growth rate was maintained throughout the experiment, which meant that the difference in plant size became progressively greater. Thus, where plant nutrition is sufficient to maintain maximum growth, small birch plants may potentially increase in size more rapidly at elevated CO₂.

KEYWORDS: CO₂ CONCENTRATION, ENRICHMENT, FORESTS,

1829

Pettersson, R., and A.J.S. McDonald. 1994. Effects of nitrogen supply on the acclimation of photosynthesis to elevated CO₂. *Photosynthesis Research* 39(3):389-400.

A common observation in plants grown in elevated CO₂ concentration is that the rate of photosynthesis is lower than expected from the dependence of photosynthesis upon CO₂ concentration in single leaves of plants grown at present CO₂ concentration. Furthermore, it has been suggested that this apparent down regulation of photosynthesis may be larger in leaves of plants at low nitrogen supply than at higher nitrogen supply. However, the available data are rather limited and contradictory. In this paper, particular attention is drawn to the way in which whole plant growth response to N supply constitutes a variable sink strength for carbohydrate usage and how this may affect photosynthesis. The need for further studies of the acclimation of photosynthesis at elevated CO₂ in leaves of plants whose N supply has resulted in well-defined growth rate and sink activity is emphasised, and brief consideration is made of how this might be achieved.

KEYWORDS: ATMOSPHERIC PARTIAL-PRESSURE, BETULA-PENDULA ROTH, CARBON-DIOXIDE CONCENTRATION, CHENOPODIUM-ALBUM L, DRY-MATTER, LONG-TERM EXPOSURE, MINERAL NUTRITION, PHASEOLUS-VULGARIS L, PHOTON FLUX- DENSITY, PLANT GROWTH

1830

Pettersson, R., A.J.S. McDonald, and I. Stadenberg. 1993. Response of small birch plants (betula-pendula roth) to elevated CO₂ and nitrogen supply. *Plant, Cell and Environment* 16(9):1115-1121.

Small birch plants were grown for up to 80 d in a climate chamber at varied relative addition rates of nitrogen in culture solution, and at ambient (350 $\mu\text{mol mol}^{-1}$) or elevated (700 $\mu\text{mol mol}^{-1}$) concentrations of CO₂. The relative addition rate of nitrogen controlled relative growth rate accurately and independently of CO₂ concentration at sub- optimum levels. During free access to nutrients, relative growth rate was higher at elevated CO₂. Higher values of relative growth rate and net assimilation rate were associated with higher values of plant N-concentration. At all N-supply rates, elevated CO₂ resulted in higher values of net assimilation rate, whereas leaf weight ratio was independent of CO₂. Specific leaf area (and leaf area ratio) was less at higher CO₂ and at lower rates of N-supply. Lower values of specific leaf area weight partly because of starch accumulation. Nitrogen productivity (growth rate per unit plant nitrogen) was higher at elevated CO₂. At sub-optimal N-supply, the higher net assimilation rate at elevated CO₂ was offset by a lower leaf area ratio. Carbon dioxide did not affect root/shoot ratio, but a higher fraction of plant dry weight was found in roots at lower N-supply. In the treatment with lower N-supply, five times as much root length was produced per amount of plant nitrogen in comparison with optimum plants. The specific fine root length at all N-supplies was greater at elevated CO₂. These responses of the root system to lower N- supply and elevated CO₂ may have a considerable bearing on the acquisition of nutrients in depleted soils at elevated CO₂. The advantage of maintaining steady-state nutrition in small plants while investigating the effects of elevated CO₂ on growth is emphasized.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, ENRICHMENT, GROWTH, INCREASE, NUTRITION, PHOTON FLUX- DENSITY, PRODUCTIVITY, SEEDLINGS, SOURCE-SINK RELATIONS, TEMPERATURE

1831

Pfirrmann, T., J.D. Barnes, K. Steiner, P. Schramel, U. Busch, H. Kuchenhoff, and H.D. Payer. 1996. Effects of elevated CO₂, O₃ and K deficiency on Norway spruce (*Picea abies*): Nutrient supply, content and leaching. *New Phytologist* 134(2):267-278.

Two clones of 5-yr-old Norway spruce (*Picea abies* [L.] Karst.) were exposed to two atmospheric concentrations of CO₂ (350 and 750 $\mu\text{mol mol}^{-1}$) and of O₃ (20 and 75 nmol mol^{-1}) in a phytotron at the GSF-Forschungszentrum (Munich) over the course of a single season (April-October). The phytotron was programmed to recreate an artificial climate similar to that at a high elevation site in the Inner Bavarian forest, and trees were grown in 401 containers of soil (pH 3.5) fertilized to achieve two levels of potassium nutrition; well fertilized and K-deficient. Foliar nutrient analyses performed at the beginning of the exposure indicated that the fertilization programmes achieved their goal without significantly altering the levels of other nutrients or the soil pH. At the beginning of the fumigation, foliar K concentrations were 7-9 mg g⁻¹ d. wt for well fertilized trees and 4-5 mg g⁻¹ d. wt for trees receiving no supplemental K. Over the course of the season, differences between K treatments intensified so that by the end of the experiment there was a five to sixfold difference between foliar K concentrations. This was associated with slight, but significant (P < 0.05), decreases in S and Zn (and of Cu in the 1989 needle year age class) and higher levels of C, N and Mg in K-deficient trees. Foliar N concentrations were low for all trees (9-15 mg g⁻¹ needle d. wt) but were similar to levels found in the field. Elevated O₃ was found to decrease significantly the C (P < 0.05) and N (P < 0.001) content of both current-year (1989) and previous-year (1988) needles independent of CO₂ concentration, but apart from some minor changes in the concentrations of Cu and Mn in the current-year needles no other effects of the pollutant on plant nutrient status were found. In contrast, CO₂ enrichment resulted in significantly (P < 0.01) lower concentrations of K and P (effects on Mg were also on the borderlines of statistical significance) in current-year needles, but there was no influence on the nutrient composition of the previous-year needles (although effects on N were on the borderlines of statistical significance). CO₂ enrichment also increased (P < 0.05) the C:N ratio of both current-year and previous-year needles. One factor contributing to the decline in foliar K at elevated CO₂ appeared to be a marked increase (25-30%) in the rate at which cations were leached from the canopy by repeated simulated acid mist (pH 4.0) events, and this effect occurred independently of the O₃ concentration. The information presented will aid the interpretation of parallel studies examining the effects of elevated CO₂ and/or O₃ on seasonal changes in photosynthesis, non-structural carbohydrate content, antioxidants, tree growth and water use efficiency, and sheds further light on the growing scepticism concerning the role of O₃ in the development of Mg and K-deficiency symptoms characteristic of certain types of forest decline in central Europe.

KEYWORDS: ACID MIST, ATMOSPHERIC CO₂, BIOMASS PRODUCTION, CARBON DIOXIDE, GROWTH, L KARST, MINERAL NUTRITION, OZONE, TREES, TRITICUM-AESTIVUM L

1832

Phillips, D.L., J.J. Lee, and R.F. Dodson. 1996. Sensitivity of the US corn belt to climate change and elevated CO₂. 1. Corn and soybean yields. *Agricultural Systems* 52(4):481-502.

Climate models indicate that increasing atmospheric concentrations of CO₂ and other greenhouse gases could alter climate globally. The EPIC (Erosion Productivity Impact Calculator) model was used to examine the sensitivity of corn and soybean yields over the US corn belt to changes in temperature, precipitation, wind and atmospheric CO₂ concentration. A statistically representative sample of 100 corn and soybean production sites was selected from the 1987 National Resources Inventory (NRI). One-hundred-year simulations were run for each site under 36 different

climate/CO₂ scenarios. The results were area weighted according to the NRI area expansion factor's to produce a regionally aggregated estimate of yields. EPIC did an excellent job of reproducing current regional mean expected yields under the baseline scenario. There were 3% decreases in both corn and soybean yields in response to a 2 degrees C temperature increase at baseline precipitation levels, with larger and smaller temperature effects under drier and wetter conditions, respectively. Crop yields increased and decreased in response to increases and decreases of 10% or 20% precipitation. A 10% precipitation increase roughly balanced the negative effect of the 2 degrees C temperature increase. Whether the precipitation changes resulted from altered precipitation event frequency or amount per event had little effect on mean crop yields; however interannual yield variability was higher when precipitation decreases were due to frequency rather than intensity. The opposite was true, though to a lesser extent, for precipitation increases. Potential evapotranspiration responded linearly to changes in mean wind speed, leading to modest changes of 1-3 days of water stress per growing season, yield increases of up to 2% for decreased wind, and yield decreases of up to 6% for increased wind. Elevated CO₂ concentrations of 625 ppmv gave the greatest yield increases, +17% for corn and +27% for soybean at baseline temperature and precipitation levels. The relative CO₂ effect was larger under drier conditions. Copyright (C) 1996 Published by Elsevier Science Ltd

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CROP RESPONSES, ENRICHMENT, GROWTH, MODEL, PLAINS, TEMPERATURE

1833

Phillips, O.L., and A.H. Gentry. 1994. Increasing turnover through time in tropical forests. *Science* 263(5149):954-958.

Tree turnover rates were assessed at 40 tropical forest sites. Averaged across inventoried forests, turnover, as measured by tree mortality and recruitment, has increased since the 1950s, with an apparent pantropical acceleration since 1980. Among 22 mature forest sites with two or more inventory periods, forest turnover also increased. The trend in forest dynamics may have profound effects on biological diversity.

KEYWORDS: ATMOSPHERIC CO₂, CARBON DIOXIDE, CLIMATIC CHANGE, DEFORESTATION, ECOSYSTEMS, ENRICHMENT, GROWTH, MOUNTAINS, PRODUCTIVITY, TREES

1834

Piastuch, W.C., and E.C. Stryjewski. 1995. Arabidopsis-thaliana growth, morphology and ultrastructure at elevated and super-elevated CO₂ concentrations. *Plant Physiology* 108(2):62.

1835

Picon, C., A. Ferhi, and J.M. Guehl. 1997. Concentration and delta C-13 of leaf carbohydrates in relation to gas exchange in Quercus robur under elevated CO₂ and drought. *Journal of Experimental Botany* 48(313):1547-1556.

The variations of leaf carbohydrate concentration, carbon isotope discrimination (Delta) of leaf soluble carbohydrate, gas-exchange and growth during a soil drying cycle under 350 and 700 mu mol mol(-1) CO₂ concentrations ([CO₂]) in Quercus robur seedlings were analysed. In well-watered conditions, a doubling of [CO₂] caused an increase of CO₂ assimilation rate (A) (+47%) and a decrease of stomatal conductance for water vapour (g) (-25%), and doubled the intrinsic water-use efficiency (A/g). The values of Delta were not affected by elevated [CO₂] which was consistent with the 2-fold increase of A/g.

Elevated [CO₂] also significantly increased sucrose and starch leaf concentrations as well as aerial growth and plant dry weight. The stimulating effect of CO₂ enrichment on A and A/g was maintained in moderate drought conditions, but disappeared in the most severe drought conditions. Drought induced an increase of hexose concentrations in both [CO₂], but this effect was more pronounced under elevated [CO₂], which may contribute to increase osmoregulation. From the onset of drought, starch was depleted in both [CO₂]. Carbon isotope discrimination decreased in response to drought, which corresponded to an increase in A/g according to the two-step model of isotopic discrimination. In contrast, the A/g values derived from instantaneous leaf gas-exchange measurements decreased along the drying cycle. The discrepancy observed between the two independent estimates of water-use efficiency is discussed in terms of time-scale integration. The results obtained with the isotopic approach using soluble carbohydrate suggest a predominant stomatal limitation of CO₂ assimilation in response to drought.

KEYWORDS: ATMOSPHERIC CO₂, C-3 PLANTS, CARBON ISOTOPE DISCRIMINATION, FIELD CONDITIONS, LEAVES, OAK SEEDLINGS, OSMOTIC ADJUSTMENT, RISING CO₂, STRESS, WATER-USE EFFICIENCY

1836

Picon, C., J.M. Guehl, and G. Aussenac. 1996. Growth dynamics, transpiration and water-use efficiency in Quercus robur plants submitted to elevated CO₂ and drought. *Annales Des Sciences Forestieres* 53(2-3):431-446.

Seedlings of pedunculate oak (Quercus robur L) were grown for one growing season under ambient (350 mu mol mol(-1)) and elevated (700 mu mol mol(-1)) atmospheric CO₂ concentration ([CO₂]) either in well-watered or in droughted (the water supply was 40% of the well-watered plants transpiration in both [CO₂] conditions. In the droughted conditions, gravimetric soil water content (SWC) was on average 4.10(-2) g g(-1) lower under elevated [CO₂]. In well-watered conditions, biomass growth was 39% higher in the elevated [CO₂] treatment than under ambient [CO₂]. However relative growth rate (RGR) was stimulated by the elevated [CO₂] only for 17 days, in July, at the end of the stem elongation phase (third growing flush), which corresponded also to the phase of maximum leaf expansion rate. Both the number of leaves per plant and the plant leaf area were 30% higher in the elevated [CO₂] treatment than under ambient [CO₂]. In the droughted conditions, no significant enhancement in biomass growth and in plant leaf area was brought about by the elevated [CO₂]. Transpiration rate was lower in the elevated [CO₂] conditions, but whole plant water use was similar in the two [CO₂] treatments, reflecting a compensation between leaf area and stomatal control of transpiration. Transpiration efficiency (W = biomass accumulation/plant water use) was improved by 47% by the elevated [CO₂] in well-watered conditions but only by 18% in the droughted conditions. Carbon isotope discrimination (Delta) was decreased by drought and was increased by the elevated [CO₂]. A negative linear relationship was found between transpiration efficiency divided by the atmospheric [CO₂] and Delta, as predicted by theory.

KEYWORDS: ALBA L, ATMOSPHERIC CO₂, CARBON-DIOXIDE ENRICHMENT, GAS-EXCHANGE, ISOTOPIC COMPOSITION, LIQUIDAMBAR- STYRACIFLUA, OLD- FIELD PERENNIALS, PHOSPHORUS, PINUS-TAEDA SEEDLINGS, STRESS

1837

Picon, C., J.M. Guehl, and A. Ferhi. 1996. Leaf gas exchange and carbon isotope composition responses to drought in a drought-avoiding (Pinus pinaster) and a drought-tolerant (Quercus petraea) species under present and elevated atmospheric CO₂ concentrations. *Plant, Cell and Environment* 19(2):182-190.

The responses of predawn leaf water potential ($\Psi(wp)$), leaf conductance to water vapour diffusion (g), CO_2 assimilation rate (A) and carbon isotope competition ($\delta(13)C$) to a soil drying cycle were assessed in *Pinus pinaster*, a drought-avoiding species with high stomatal sensitivity to drought, and *Quercus petraea*, a drought-tolerant species with lower stomatal sensitivity to drought, under present (350 $\mu\text{mol mol}^{-1}$) and elevated (700 $\mu\text{mol mol}^{-1}$) atmospheric CO_2 concentrations ($[CO_2]$). In *P. pinaster*, decreasing A in response to drought was associated with increasing plant intrinsic water use efficiency (A/g) and with decreasing calculated intercellular $[CO_2]$ (C_i), suggesting a stomatal limitation of A . In contrast, in *Q. petraea*, A/g declined and C_i increased during the drying cycle, which suggests a non-stomatal origin for the decrease in A . In *P. pinaster*, a negative relationship was observed between the gas exchange-derived values of C_i/C_a and $\delta(13)C$, which conforms to the classical two-step carbon isotope discrimination model. In *Q. petraea*, the relationship between C_i/C_a and $\delta(13)C$ was positive. Possible causes of this discrepancy are discussed. Lower g values were observed under elevated $[CO_2]$ than under present $[CO_2]$ in *Q. petraea*, whereas g was unaffected in *P. pinaster*. A stimulation of A by elevated $[CO_2]$ was found in *P. pinaster* but not in *Q. petraea*. In both species, A/g was markedly higher under elevated than under present $[CO_2]$. Whether the differences in the g response to elevated $[CO_2]$ found here can be generalized to other drought-avoiding and non-avoiding species remains to be assessed.

KEYWORDS: DIOXIDE, DISCRIMINATION, LEAVES, PHOTOSYNTHESIS, PLANTS, RISING CO_2 , SEEDLINGS, SOIL, STRESS, WATER-USE EFFICIENCY

1838

Picon-Cochard, C., and J.M. Guehl. 1999. Leaf gas exchange and carbohydrate concentrations in *Pinus pinaster* plants subjected to elevated CO_2 and a soil drying cycle. *Annals of Forest Science* 56(1):71-76.

Plants of maritime pine (*Pinus pinaster* Ait.) were acclimated for 2 years under ambient (350 $\mu\text{mol mol}^{-1}$) and elevated (700 $\mu\text{mol mol}^{-1}$) CO_2 concentrations ($[CO_2]$). In the summer of the second growing season, the plants were subjected to a soil drying cycle for 6 days. Drought reduced plant transpiration rate and net CO_2 assimilation rate (A) by about 80%. Elevated $[CO_2]$ induced a substantial increase of A (+105% and +229% in well-watered and in droughted plants, respectively) and of the needle starch (+145%) and sucrose (+20%) concentrations, whatever the watering regime. Drought did not significantly affect starch acid sucrose concentrations, while hexose concentrations were slightly increased in the most severe drought condition (predawn water potential value equal to -1.5 MPa). The stimulating effect of elevated $[CO_2]$ on A was maintained along the drying cycle, whereas no significant CO_2 effect was observed on the soluble carbohydrate concentration. These compounds did not contribute to an enhancement of osmotic adjustment under elevated $[CO_2]$ in *P. pinaster*. ((C) Inra/Elsevier, Paris.)

KEYWORDS: ATMOSPHERIC CO_2 , DROUGHT, LEAVES, OSMOREGULATION, OSMOTIC ADJUSTMENT, RESPONSES, SEEDLINGS, WATER-STRESS

1839

Pinter, P.J., S.B. Idso, D.L. Hendrix, R.R. Rokey, R.S. Rauschkolb, J.R. Mauney, B.A. Kimball, G.R. Hendrey, K.F. Lewin, and J. Nagy. 1994. Effect of free-air CO_2 enrichment on the chlorophyll content of cotton leaves. *Agricultural and Forest Meteorology* 70(1-4):163-169.

In vivo chlorophyll concentrations were estimated using a Minolta SPAD 502 meter on upper-canopy leaves of cotton plants exposed to air enriched to an atmospheric CO_2 concentration of approximately 550

$\mu\text{mol mol}^{-1}$ in a free-air CO_2 enrichment (FACE) study. Measurements were made on 27 days during the final 90 days of the 1991 growing season. In both well-watered and moderately water-stressed plants, leaves in the FACE plots had greater chlorophyll concentrations than leaves in the ambient air control plots (about 370 $\mu\text{mol } CO_2 \text{ mol}^{-1}$): season-long chlorophyll averages were 7.1% greater in the 'wet' treatment and 8.2% greater in the 'dry' treatment. This finding differs from what has been observed in a number of studies where experimental plants were grown in small pots. It is, however, typical of what has been observed in studies employing larger pots and open fields, and is a compelling rationale for conducting additional studies of this nature in FACE projects.

KEYWORDS: CARBON DIOXIDE, DENSITY, DRY-MATTER, EXTRACTABLE CHLOROPHYLL, GROWTH, LEAF GREENNESS, NITROGEN, PHOTOSYNTHETIC ACCLIMATION, PLANTS, ROOT

1840

Pinter, P.J., B.A. Kimball, J.R. Mauney, G.R. Hendrey, K.F. Lewin, and J. Nagy. 1994. Effects of free-air carbon-dioxide enrichment on par absorption and conversion efficiency by cotton. *Agricultural and Forest Meteorology* 70(1-4):209-230.

Anticipated changes in global climate and atmospheric CO_2 concentrations have very important, albeit poorly understood consequences for production agriculture. Effects of these changes on plants have usually been examined in controlled-environment enclosures, glass-houses, or open-top field chambers. Beginning in 1989, an innovative experimental free-air CO_2 enrichment (FACE) facility was operated in central Arizona to evaluate crop response to increased CO_2 levels within a large, open-field production environment. Cotton (*Gossypium hirsutum* L.) was grown for three consecutive seasons under exposed to either ambient (control, about 370 $\mu\text{mol mol}^{-1}$) or elevated (FACE, 550 $\mu\text{mol mol}^{-1}$) CO_2 concentrations. Deficit irrigation regimes supplying 75% (beginning in July 1990) or 67% (beginning in mid-May 1991) of the crop's evapotranspiration requirement were included as additional treatment variables. Plant growth was monitored by periodic sampling. Canopy reflectances in visible (blue, 0.45-0.52 μm ; green, 0.05-0.59 μm ; red, 0.61-0.68 μm) and near-infrared (NIR; 0.79-0.89 μm) wavebands were measured frequently with an Exotech radiometer and related to absorbed photosynthetically active radiation (PAR; 0.4-0.7 μm) measured with a line quantum sensor. Dry biomass of plants in the FACE treatment was significantly ($P < 0.05$) greater than control values during each year of the study. The FACE plant canopy also absorbed significantly more PAR than controls during the early and middle portion of the 1990 and 1991 seasons. Light use efficiency (LUE, biomass produced per unit absorbed PAR) was significantly higher in FACE plots during each year. In the well-watered irrigation treatment, the 3 year mean LUE was 1.97 g MJ⁻¹ for FACE and 1.56 g MJ⁻¹ for controls. The deficit irrigation treatment in 1991 produced significantly smaller plants, which absorbed less PAR and had lower LUE than plants in the well-watered treatment ($P < 0.05$). No interaction was observed between CO_2 and irrigation treatments. FACE research under realistic field conditions revealed positive consequences of increased CO_2 on cotton plant biomass, PAR absorption, and LUE. It also demonstrated the effectiveness of this new technology for examining community-level plant responses to possible changes in global environment.

KEYWORDS: CANOPY REFLECTANCE, CO_2 , CORN CANOPIES, FIELD, GROWTH, PHOTOSYNTHETICALLY ACTIVE RADIATION, SOLAR RADIATION, VEGETATION INDEXES, WINTER-WHEAT, YIELD

1841

Pirjola, L. 1999. Effects of the increased UV radiation and biogenic

VOC emissions on ultrafine sulphate aerosol formation. *Journal of Aerosol Science* 30(3):355-367.

A sectional model (AEROFOR) for the formation of sulphuric acid-water particles has been developed. The model includes gas-phase chemistry and aerosol dynamics. An increased UV-B irradiation penetrating into the troposphere due to stratospheric ozone depletion causes via the SO₂ oxidation route an enhanced nucleation potential for new H₂SO₄-H₂O particles as well as the growth of particles to CCN size. Using AEROFOR we show that after a nucleation event the nucleated particle concentration is linearly dependent on increased UV-B irradiation with a positive slope. On the other hand, due to increased CO₂ concentration photosynthetic rates of plants will increase, and it is likely that enhanced photosynthesis in forests will increase emissions of biogenic volatile organic compounds (BVOC) such as isoprene and monoterpenes. We show that the nucleated particle concentration decreases with increasing BVOC emission, but this dependence is not linear. We investigate the strength of these opposite effects and fit a straight line for such UV-B and BVOC conditions which yield a certain particle number density. The coupling between O₃, OH and particle concentrations as a function of UV-B and BVOC emission is also demonstrated. (C) 1999 Elsevier Science Ltd. All rights reserved.

KEYWORDS: ATMOSPHERIC CO₂, CLOUD CONDENSATION NUCLEI, GREENHOUSE GASES, ISOPRENE EMISSION, MARINE BOUNDARY-LAYER, OZONE DEPLETION, SOUTHEASTERN UNITED-STATES, STRATOSPHERIC OZONE, SULFATE AEROSOLS, SULFURIC-ACID

1842

Pitelka, L.F. 1994. Ecosystem response to elevated CO₂. *Trends in Ecology and Evolution* 9(6):204-207.

KEYWORDS: ATMOSPHERIC CO₂

1843

Plaut, Z., and E. Federman. 1991. Acclimation of CO₂ assimilation in cotton leaves to water- stress and salinity. *Plant Physiology* 97(2):515-522.

Cotton (*Gossypium hirsutum* L. cv Acala SJ2) plants were exposed to three levels of osmotic or matric potentials. The first was obtained by salt and the latter by withholding irrigation water. Plants were acclimated to the two stress types by reducing the rate of stress development by a factor of 4 to 7. CO₂ assimilation was then determined on acclimated and nonacclimated plants. The decrease of CO₂ assimilation in salinity-exposed plants was significantly less in acclimated as compared with nonacclimated plants. Such a difference was not found under water stress at ambient CO₂ partial pressure. The slopes of net CO₂ assimilation versus intercellular CO₂ partial pressure, for the initial linear portion of this relationship, were increased in plants acclimated to salinity of -0.3 and -0.6 megapascal but not in nonacclimated plants. In plants acclimated to water stress, this change in slopes was not significant. Leaf osmotic potential was reduced much more in acclimated than in nonacclimated plants, resulting in turgor maintenance even at -0.9 megapascal. In nonacclimated plants, turgor pressure reached zero at approximately -0.5 megapascal. The accumulation of Cl⁻ and Na⁺ in the salinity-acclimated plants fully accounted for the decrease in leaf osmotic potential. The rise in concentration of organic solutes comprised only 5% of the total increase in solutes in salinity- acclimated and 10 to 20% in water-stress-acclimated plants. This acclimation was interpreted in light of the higher protein content per unit leaf area and the enhanced ribulose biphosphate carboxylase activity. At saturating CO₂ Partial pressure, the declined inhibition in CO₂ assimilation of stress-acclimated plants was found for both salinity and water stress.

KEYWORDS: CHLOROPLASTS, COWPEA LEAVES, GROWTH, INTACT LEAVES, ION CONTENT, LEAF CONDUCTANCE, OSMOTIC ADJUSTMENT, PHOTOSYNTHETIC CAPACITY, PLANTS, SALT STRESS

1844

Pleijel, H., J. Sild, H. Danielsson, and L. Klemetsson. 1998. Nitrous oxide emissions from a wheat field in response to elevated carbon dioxide concentration and open-top chamber enclosure. *Environmental Pollution* 102:167-171.

Soil emissions of nitrous oxide (N₂O) were measured using static field chambers, which were installed in a wheat field. The treatments were: open-top chambers with ambient CO₂ concentrations (OTC350), open-top chambers with 700 ppm CO₂ (OTC700) and ambient air plots without open-top chambers (AA). Measurements of N₂O emissions were made weekly starting at anthesis. The measurements continued for ten weeks, until two weeks after the harvest of the mature crop. During the first eight weeks the N₂O emissions were higher in the OTC350 treatment compared to OTC700. At the last two measurements, after the plants were harvested, the N₂O emissions of the chamber treatments were similar to each other and higher than during the preceding period. The accumulation of grain protein per unit area was higher in OTC700 compared with OTC350. These results suggest that a competition for soil nitrogen exists between plants and the microbial community. The AA plots emitted less N₂O during the green canopy period compared with the chamber treatments. After harvest, the emissions from AA increased up to the same magnitude as the chamber treatments. The lower emissions of the ambient air plots during the pre- harvest period can be explained partly by lower ambient temperatures and drier soil.

KEYWORDS: FLUXES, SOILS, YIELD

1845

Polderdijk, J.J., and G.J.P.M. van den Boogaard. 1998. Effect of reduced levels of O₂ and elevated levels of CO₂ on the quality of bunched radishes. *Gartenbauwissenschaft* 63(6):250-253.

In two trials bunched radishes were stored at 12 degrees C and different levels of O₂ (21%, 10%, 5%, 1%, 0.5%) combined with different levels of CO₂ (0%, 1%, 5%, 10%, 15%, 20%). Decreased levels of O₂ and increased levels of CO₂ proved to inhibit the yellowing of the leaves and the growth of new roots. The incidence of decay was inhibited by increased CO₂ concentrations. Levels of 1% and 0.5% O₂ caused abnormal discolouration of the radishes and increased the incidence of decay. Off-odours and/or off-taste were found at O₂ levels of 0.5% and/or CO₂ levels of 20%.

1846

Polglase, P.J., and Y.P. Wang. 1992. Potential CO₂-enhanced carbon storage by the terrestrial biosphere. *Australian Journal of Botany* 40(4-5):641-656.

Geochemical models that deduce latitudinal source/sink relationships of atmospheric CO₂ suggest that, in tropical regions, there is almost zero net exchange of CO₂ between the atmosphere and the terrestrial biosphere. The implication is that CO₂-enhanced carbon storage (CO₂-ECS) by tropical biomes is negating the output of CO₂ from deforestation. We describe here a 10-biome model for CO₂-ECS, in which carbon accumulation in living vegetation is coupled to the Rothamsted soil carbon model. A biotic growth factor (beta) was used to describe the relationship between literature estimates of net primary production (NPP) and atmospheric CO₂ concentration. Using beta = 0.3 as a reference state, CO₂-ECS by the global biosphere in 1990 was 1.1

Gt. When more appropriate values of beta were used (derived from a theoretical response of vegetation to increasing temperature and CO₂), CO₂-ECS was 1.3 Gt, of which tropical biomes accounted for 0.7 Gt. There are many uncertainties in this (and other) models; total CO₂-ECS is particularly sensitive to changes in NPP. Unless published surveys have underestimated tropical NPP by a factor of about 2, then it is unlikely that CO₂-ECS could have negated the 1.5- 3.0 Gt of carbon that are estimated to have been emitted by tropical deforestation in 1990.

KEYWORDS: ATMOSPHERIC CO₂ CONCENTRATIONS, DIOXIDE, ECOSYSTEMS, GROWTH, INSECT HERBIVORE, LATITUDINAL DISTRIBUTION, PRODUCTIVITY, SOIL, TROPICAL FORESTS, WATER-USE EFFICIENCY

1847

Polle, A., M. Eiblmeier, L. Sheppard, and M. Murray. 1997. Responses of antioxidative enzymes to elevated CO₂ in leaves of beech (*Fagus sylvatica* L.) seedlings grown under a range of nutrient regimes. *Plant, Cell and Environment* 20(10):1317-1321.

To study whether responses of antioxidative enzymes to enhanced atmospheric CO₂ concentrations are affected by plant nutrition, the activities of superoxide dismutase, catalase and peroxidase were investigated in leaves of 3-year-old beech trees grown with low (0.1 x optimum), intermediate (0.5 x optimum) and high (2 x optimum) nutrient supply rates in open-top chambers at either ambient (approximate to 355 $\mu\text{mol mol}^{-1}$) or elevated (700 $\mu\text{mol mol}^{-1}$) CO₂ concentrations. These treatments resulted in foliar C/N ratios of about 20 in the presence of high and > 30 in the presence of low nutrient supply rates. Pigment and malondialdehyde contents were determined to assess plant stress levels. Low nutrient supply rates caused pigment loss, whereas elevated CO₂ had no effect on pigmentation. Guaiacol peroxidase activities did not respond to either CO₂ or nutrient treatment. Catalase activity decreased with decreasing nutrient supply rate and also in response to elevated CO₂. Superoxidase dismutase activity was affected by both nutrient supply and CO₂ concentration. In leaves from trees grown with the high-nutrient treatment, superoxide dismutase activity was low irrespective of CO₂ concentration. In chlorotic leaves, superoxide dismutase activity was increased, suggesting an enhanced need for detoxification of reactive oxygen species. Leaves from plants grown under elevated CO₂ with medium nutrient supply rates showed decreased malondialdehyde contents and superoxide dismutase activities. This suggests that the intrinsic oxidative stress of leaves was decreased under these conditions. These results imply that intrinsic oxidative stress is modulated; by the balance between N and C assimilation.

KEYWORDS: ATMOSPHERIC CO₂, CHLOROSIS, DROUGHT STRESS, MAGNESIUM-DEFICIENCY, NEEDLES, PHOTORESPIRATION, PICEA-ABIES L, PLANTS, POTASSIUM, SYSTEMS

1848

Polle, A., T. Pfirrmann, S. Chakrabarti, and H. Rennenberg. 1993. The effects of enhanced ozone and enhanced carbon-dioxide concentrations on biomass, pigments and antioxidative enzymes in spruce needles (*picea-abies* L). *Plant, Cell and Environment* 16(3):311-316.

During one growing period, 5-year-old spruce trees (*Picea abies* L., Karst.) were exposed in environmental chambers to elevated concentrations of carbon dioxide (750 $\text{cm}^3 \text{m}^{-3}$) and ozone (0.08 $\text{cm}^3 \text{m}^{-3}$) as single variables or in combination. Control concentrations of the gases were 350 $\text{cm}^3 \text{m}^{-3}$ CO₂ and 0.02 $\text{cm}^3 \text{m}^{-3}$ ozone. To investigate whether an elevated CO₂ concentration can prevent adverse ozone effects by reducing oxidative stress, the activities of the protective

enzymes superoxide dismutase, catalase and peroxidase were determined. Furthermore, shoot biomass, pigment and protein contents of two needle age classes were investigated. Ozone caused pigment reduction and visible injury in the previous year's needles and growth reduction in the current year's shoots. In the presence of elevated concentrations of ozone and CO₂, growth reduction in the current year's shoots was prevented, but emergence of visible damage in the previous year's needles was only delayed and pigment reduction was still found. Elevated concentrations of ozone or CO₂ as single variables caused a significant reduction in the activities of superoxide dismutase and catalase in the current year's needles. Minimum activities of superoxide dismutase and catalase and decreased peroxidase activities were found in both needle age classes from spruce trees grown at enhanced concentrations of both CO₂ and ozone. These results suggest a reduced tolerance to oxidative stress in spruce trees under conditions of elevated concentrations of both CO₂ and ozone.

KEYWORDS: ATMOSPHERIC CO₂, CO₂- ENRICHMENT, ELEVATED CO₂, EXPOSURE, FIELD, GROWTH, NORWAYSPRUCE, RED SPRUCE, SEASONAL-CHANGES, SUPEROXIDE-DISMUTASE ACTIVITY

1849

Polley, H.W. 1997. Implications of rising atmospheric carbon dioxide concentration for rangelands. *Journal of Range Management* 50(6):562-577.

Extensive rangelands and other vegetation types that we know today formed while atmospheric carbon dioxide (CO₂) concentration was low (50 to 75% of today's concentration). Fossil fuel burning and deforestation and other land use changes during the last 200 years have increased CO₂ concentration by about 30%, to the present 360 parts per million (ppm). Atmospheric CO₂ will continue to rise during the next century, possibly to concentrations that are unprecedented for the last several million years. Much of the potential importance of CO₂ concentration to vegetation derives from its influence on plant carbon balance and water relations. Plants grow by assimilating CO₂ that diffuses into leaves through stomatal pores. Inevitably associated with CO₂ uptake is transpirational loss of water vapor through stomata. Transpiration rates usually decline as CO₂ increases, while, in many plants, photosynthesis and growth increase. These "primary" responses to CO₂ can lead to a multitude of changes at the plant and ecosystem levels, ranging from alteration of the chemical composition of plant tissues to changes in ecosystem function and the species composition of plant communities. The direct physiological responses of plants to CO₂ and expression of these responses at higher scales differ among species and growing conditions. Growth response to CO₂ is usually highest in rapidly-growing plants that quickly export the carbohydrates formed in leaves and use them for storage or new growth and allocate a high proportion of fixed carbon to produce leaves. Growth is also more responsive to CO₂ in plants with the C-3 (most woody plants and 'cool-season' grasses) than C-4 photosynthetic pathway (most 'warm-season' grasses). These and other differences among species could lead to changes in the composition of rangeland vegetation, but generalizations are difficult. On many rangelands, species abundances are determined more by morphological and phenological attributes that influence plant access to essential resources like nitrogen and light and reaction to fire, grazing, and other disturbances than by physiological traits that are sensitive to CO₂ concentration. Species composition probably will be most responsive to CO₂ on moderately water-limited and disturbed rangelands where multiple positive effects of CO₂ on plant water relations can be expressed and competition for light is minimized. Greatest initial changes in species composition likely will occur on C-3/C-4 grasslands and at the transition between grasslands and woodlands. Plant production should also increase on water-limited rangelands, but CO₂ may have little influence on production when nutrient elements like nitrogen are severely limiting.

KEYWORDS: C-4 GRASS, CLIMATE CHANGE, ELEVATED CO₂ CONCENTRATIONS, ICE-CORE RECORD, LONG-TERM EXPOSURE, PLANT GROWTH, SEASON GAS- EXCHANGE, STOMATAL DENSITY, TALLGRASS PRAIRIE, WATER-USE EFFICIENCY

1850

Polley, H.W., H.B. Johnson, B.D. Marino, and H.S. Mayeux. 1993. Increase in C3 plant water-use efficiency and biomass over glacial to present CO₂ concentrations. *Nature* 361(6407):61-64.

ATMOSPHERIC CO₂ concentration was 160 to 200 μmol mol⁻¹ during the Last Glacial Maximum (LGM; about 18,000 years ago)¹, rose to about 275 μmol mol⁻¹ 10,000 years ago^{2,3}, and has increased to about 350 μmol mol⁻¹ since 1800 (ref. 4). Here we present data indicating that this increase in CO₂ has enhanced biospheric carbon fixation and altered species abundances by increasing the water-use efficiency of biomass production of C3 plants, the bulk of the Earth's vegetation. We grew oats (*Avena sativa*), wild mustard (*Brassica kaber*) and wheat (*Triticum aestivum* cv. Seri M82 and Yaqui 54), all C3 annuals, and selected C4 grasses along daytime gradients of Glacial to present atmospheric CO₂ concentrations in a 38-m-long chamber. We calculated parameters related to leaf photosynthesis and water-use efficiency from stable carbon isotope ratios (C-13/C-12) of whole leaves. Leaf water-use efficiency and above-ground biomass/plant of C3 species increased linearly and nearly proportionally with increasing CO₂ concentrations. Direct effects of increasing CO₂ on plants must be considered when modelling the global carbon cycle and effects of climate change on vegetation.

KEYWORDS: AMBIENT, ATMOSPHERIC CO₂, BALANCE, CARBON-DIOXIDE CONCENTRATION, GROWTH, ISOTOPIC COMPOSITION, VEGETATION

1851

Polley, H.W., H.B. Johnson, and H.S. Mayeux. 1992. Growth and gas-exchange of oats (*avena-sativa*) and wild mustard (*brassica-kaber*) at subambient CO₂ concentrations. *International Journal of Plant Science* 153(3):453-461.

A repeated sequence of monocultures and mixtures of oats (*Avena sativa* L.) and wild mustard (*Brassica kaber* (DC.) Wheeler) was grown along a daytime gradient of CO₂ concentrations ([CO₂]) from near 330 to a minimum of 150 μmol mol⁻¹. The objectives were to determine effects of subambient [CO₂] on leaf gas exchange, biomass production, and competitive interactions of these C3 species. A decrease in stomatal conductance did not prevent a nearly linear increase in leaf internal [CO₂] and net assimilation of oat leaves as [CO₂] increased. Net assimilation of oats and wild mustard increased from 5.0 and 2.5 μmol m⁻² s⁻¹ at 150 μmol mol⁻¹, respectively, to 16.1 and 15.9 μmol m⁻² s⁻¹ at 330 μmol mol⁻¹ CO₂, respectively, when measured at 1,200-1,500 μmol m⁻² s⁻¹ incident light. Aboveground biomass per plant of wild mustard and oats increased 106% and 198%, respectively, and leaf area rose more than two- and threefold, respectively, from 154 to 331 μmol mol⁻¹ CO₂. The CO₂-induced increase in aboveground biomass of plants of each species did not vary among monocultures and mixtures. Responses of oats and wild mustard to higher subambient [CO₂] were large relative to reported responses of C3 species to comparable increases above the current atmospheric [CO₂]. This suggests that past changes in atmospheric [CO₂], including the 27% rise since the beginning of the nineteenth century, may have profoundly altered the productivity of C3 plants.

KEYWORDS: ATMOSPHERIC CO₂, CARBON-DIOXIDE CONCENTRATION, COTTON, ELEVATED CO₂, LEAVES, PHOTOSYNTHETIC ACCLIMATION, PLANT DRY- WEIGHT,

RESPONSES, STOMATAL DENSITY, WATER-USE EFFICIENCY

1852

Polley, H.W., H.B. Johnson, and H.S. Mayeux. 1994. Increasing CO₂ - comparative responses of the C-4 grass *Schizachyrium* and grassland invader *Prosopis*. *Ecology* 75(4):976-988.

The woody C-3 *Prosopis glandulosa* (honey mesquite) and C-4 perennial grass *Schizachyrium scoparium* (little bluestem) were grown along a gradient of daytime carbon dioxide concentrations from near 340 to 200 μmol/mol air in a 38 m long controlled environment chamber. We sought to determine effects of historical and prehistorical increases in atmospheric CO₂ concentration on growth, resource use, and competitive interactions of a species representative of C-4-dominated grasslands in the southwestern United States and the invasive legume *P. glandulosa*. Increasing CO₂ concentration stimulated N-2 fixation by individually grown *P. glandulosa* and elicited in C-3 seedlings a similar relative increase in leaf intercellular CO₂ concentration, net assimilation rate, and intrinsic water use efficiency (leaf net assimilation rate/stomatal conductance). Aboveground biomass of *P. glandulosa* was not altered by CO₂ concentration, but belowground biomass and whole-plant water and nitrogen use efficiencies increased linearly with CO₂ concentration in seedlings that were grown alone. Biomass produced by *P. glandulosa* that was grown with *S. scoparium* was not affected by CO₂ concentration. Stomatal conductance declined and leaf assimilation rates of *S. scoparium* at near maximum incident light increased at higher CO₂ concentration, but there was no effect of CO₂ concentration on biomass production or whole-plant water use efficiency of the C-4 grass. Rising CO₂ concentration, especially the 27% increase since the beginning of the 19th century, may have contributed to more abundant *P. glandulosa* on C-4 grasslands by stimulating the shrub's growth or reducing the amount of resources that the C-3 required. Much of the potential response of *P. glandulosa* to CO₂ concentration, however, appears to be contingent on the shrub's escaping competition with neighboring grasses.

KEYWORDS: ATMOSPHERIC CO₂, CARBON-DIOXIDE CONCENTRATION, DESERT, ELEVATED CO₂, GAS-EXCHANGE, GLANDULOSA, GREAT-BASIN, GROWTH, PLANTS, WATER-USE EFFICIENCY

1853

Polley, H.W., H.B. Johnson, and H.S. Mayeux. 1995. Nitrogen and water requirements of C3 plants grown at glacial to present carbon-dioxide concentrations. *Functional Ecology* 9(1):86-96.

1. Nitrogen- and water-use efficiencies in biomass production were determined for three C3 plant species at carbon dioxide concentrations ([CO₂]) that spanned glacial to present atmospheric levels [200-350 μmol CO₂ (mol air)⁻¹]. The species were annual grasses *Bromus tectorum* and *Triticum aestivum* (two cultivars) and a woody perennial *Prosopis glandulosa* (alone and in mixtures with the C4 grass, *Schizachyrium scoparium*). 2. Changes in nitrogen- and water- use efficiencies were used to investigate effects of increasing [CO₂] on the relative requirements of C3 plants for these frequently limiting resources. 3. Water-use efficiency (biomass produced/evapotranspiration; WUE) increased at higher [CO₂] in all species but relative responses to [CO₂] varied among species, cultivars and watering regimes. 4. Intrinsic WUE (net assimilation/stomatal conductance to water), calculated from stable carbon isotopes in plants, increased by about the same relative amount as did [CO₂] in all species. 5. Nitrogen-use efficiency (biomass produced/plant N; NUE) rose at higher [CO₂] only in well-watered *B. tectorum* and in *P. glandulosa* grown alone. 6. The more consistent increase in WUE than NUE in these species at higher [CO₂] implies that rising [CO₂] may have reduced the amount of water relative to nitrogen that some C3 plants require and

thereby altered the composition and function of terrestrial ecosystems.

KEYWORDS: ATMOSPHERIC CO₂, AVAILABILITY, ECOSYSTEMS, ELEVATED CO₂, GAS-EXCHANGE, ISOTOPE DISCRIMINATION, MARSH PLANTS, NUTRIENT USE EFFICIENCY, RESPONSES, SUBAMBIENT

1854

Polley, H.W., H.B. Johnson, and H.S. Mayeux. 1997. Leaf physiology, production, water use, and nitrogen dynamics of the grassland invader *Acacia smallii* at elevated CO₂ concentrations. *Tree Physiology* 17(2):89-96.

Invasion by woody legumes can alter hydrology, nutrient accumulation and cycling, and carbon sequestration on grasslands. The rate and magnitude of these changes are likely to be sensitive to the effects of atmospheric CO₂ enrichment on growth and water and nitrogen dynamics of leguminous shrubs. To assess potential effects of increased atmospheric CO₂ concentrations on plant growth and acquisition and utilization of water and nitrogen, seedlings of *Acacia smallii* Isely (huisache) were grown for 13 months at CO₂ concentrations of 385 (ambient), 690, and 980 $\mu\text{mol mol}^{-1}$. Seedlings grown at elevated CO₂ concentrations exhibited parallel declines in leaf N concentration and photosynthetic capacity; however, at the highest CO₂ concentration, biomass production increased more than 2.5-fold as a result of increased leaf photosynthetic rates, leaf area, and N₂ fixation. Measurements of leaf gas exchange and aboveground biomass production and soil water balance indicated that water use efficiency increased in proportion to the increase in atmospheric CO₂ concentration. The effects on transpiration of an accompanying decline in leaf conductance were offset by an increase in leaf area, and total water loss was similar across CO₂ treatments. Plants grown at elevated CO₂ fixed three to four times as much N as plants grown at ambient CO₂ concentration. The increase in N₂ fixation resulted from an increase in fixation per unit of nodule mass in the 690 $\mu\text{mol mol}^{-1}$ CO₂ treatment and from a large increase in the number and mass of nodules in plants in the 980 $\mu\text{mol mol}^{-1}$ CO₂ treatment. Increased symbiotic N₂ fixation by woody invaders in response to CO₂ enrichment may result in increased N deposition in litterfall, and thus increased productivity on many grasslands.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CARBON-DIOXIDE, ENRICHMENT, GAS-EXCHANGE, GROWTH, HONEY MESQUITE, NATURAL ABUNDANCE, PHOTOSYNTHESIS, STOMATAL RESPONSES, TALLGRASS PRAIRIE

1855

Polley, H.W., H.B. Johnson, H.S. Mayeux, D.A. Brown, and J.W.C. White. 1996. Leaf end plant water use efficiency of C-4 species grown at glacial to elevated CO₂ concentrations. *International Journal of Plant Science* 157(2):164-170.

Leaf gas exchange was measured on C-4 plants grown from near glacial to current CO₂ concentrations (200-350 $\mu\text{mol mol}^{-1}$) and from the current concentration to possible future levels (near 700 and 1000 $\mu\text{mol mol}^{-1}$) to test the prediction that intrinsic water use efficiency (CO₂ assimilation [A]/stomatal conductance to water [g]) would rise by a similar relative amount as CO₂ concentration. Studied were species differing in growth form or life history, the perennial grass *Schizachyrium scoparium* (little bluestem), perennial shrub *Atriplex canescens* (four-wing saltbush), and annual grass *Zea mays* (maize). Contrary to our prediction, leaf A/g of the C-4 species examined was stimulated proportionally more by a given relative increase in CO₂ over subambient than by elevated concentrations. The ratio of the relative increase in A/g to that in CO₂ exceeded unity in *S. scoparium* and, in 1 of 2 yr, in *Z. mays* as CO₂ rose from 200 to 350 $\mu\text{mol mol}^{-1}$, but

declined to near zero in *S. scoparium* and *A. canescens* as CO₂ rose from 700 to 1000 $\mu\text{mol mol}^{-1}$. At higher CO₂ concentrations, A/g of the C-4 perennials was similar to that expected for C-3 plants. Since much of the potential response of C-4 plants to CO₂ often derives from higher water use efficiency (WUE), these results indicated that potential productivity of some C-4 plants increased relatively more since glaciation than it will in the future. There also were large (>100%) differences in A/g and plant WUE (production/transpiration) at a given CO₂ level among the plants examined that could influence the relative productivities of C-4 species or growth forms and their interactions with C-3 plants.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, BIOMASS, CONDUCTANCE, GRADIENT, HUMIDITY, IRRADIANCE, PHOTOSYNTHESIS, RESPONSES, SENSITIVITY, STOMATA

1856

Polley, H.W., H.B. Johnson, H.S. Mayeux, and S.R. Malone. 1993. Physiology and growth of wheat across a subambient carbon-dioxide gradient. *Annals of Botany* 71(4):347-356.

KEYWORDS: AMBIENT, ATMOSPHERIC CO₂, ELEVATED CO₂, ENRICHMENT, PLANTS, RESPIRATION, RESPONSES, SOYBEAN CANOPY PHOTOSYNTHESIS, TEMPERATURE, TRANSPIRATION

1857

Polley, H.W., H.B. Johnson, H.S. Mayeux, C.R. Tischler, and D.A. Brown. 1996. Carbon dioxide enrichment improves growth, water relations and survival of droughted honey mesquite (*Prosopis glandulosa*) seedlings. *Tree Physiology* 16(10):817-823.

Low water availability reduces the establishment of the invasive shrub *Prosopis* on some grasslands. Water deficit survival and traits that may contribute to the postponement or tolerance of plant dehydration were measured on seedlings of *P. glandulosa* Torr. var. *glandulosa* (honey mesquite) grown at CO₂ concentrations of 370 (ambient), 710, and 1050 $\mu\text{mol mol}^{-1}$. Because elevated CO₂ decreases stomatal conductance, the number of seedlings per container in the elevated CO₂ treatments was increased to ensure that soil water content was depleted at similar rates in all treatments. Seedlings grown at elevated CO₂ had a greater root biomass and a higher ratio of lateral root to total root biomass than those grown at ambient CO₂ concentration; however, these seedlings also shed more leaves and retained smaller leaves. These changes, together with a reduced transpiration/leaf area ratio at elevated CO₂, may have contributed to a slight increase in xylem pressure potentials of seedlings in the 1050 $\mu\text{mol mol}^{-1}$ CO₂ treatment during the first 37 days of growth (0.26 to 0.40 MPa). Osmotic potential was not affected by CO₂ treatment. Increasing the CO₂ concentration to 710 and 1050 $\mu\text{mol mol}^{-1}$ more than doubled the percentage survival of seedlings from which water was withheld for 65 days. Carbon dioxide enrichment significantly increased survival from 0% to about 40% among seedlings that experienced the lowest soil water content. By increasing seedling survival of drought, rising atmospheric CO₂ concentration may increase abundance of *P. glandulosa* on grasslands where low water availability limits its establishment.

KEYWORDS: ATMOSPHERIC CO₂, CO₂- ENRICHMENT, ELEVATED CO₂, ESTABLISHMENT, GRASSLAND, OLD- FIELD PERENNIALS, PLANTS, RESPONSES, SONORAN DESERT, STRESS

1858

Polley, H.W., H.B. Johnson, C.R. Tischler, and H.A. Torbert. 1999. Links between transpiration and plant nitrogen: Variation with atmospheric CO₂ concentration and nitrogen availability. *International Journal of Plant Science* 160(3):535-542.

Transpiration is closely linked to plant nitrogen (N) content, indicating that global or other changes that alter plant N accumulation or the relative requirements of plants for water and N will affect transpiration. We studied effects of N availability and atmospheric CO₂ concentration, two components of global biogeochemistry that are changing, on relationships between whole-plant transpiration and N in two perennial C-3 species, *Pseudoroegneria spicata* (a tussock grass) and *Gutierrezia microcephala* (a half-shrub). Two indices of plant N requirement were used: N accretion (N in live and dead tissues) and N loss in litter (N in dead tissues). Transpiration was analyzed as the product of N accretion or loss by plants and the ratio of transpiration to N accretion or loss. The two indices of plant N requirement led to different conclusions as to the effects of N availability on plant use of water relative to N. Transpiration scaled proportionally with N accretion, but transpiration per unit of N loss declined at high N. Carbon dioxide enrichment had little effect on the ratio of transpiration to N accretion and no effect on transpiration per unit of N loss. The two species accumulated similar amounts of N, but the half-shrub used more than twice as much water as the grass. Nitrogen availability and CO₂ concentration influenced whole-plant transpiration more by changing plant N accumulation than by altering the stoichiometry between transpiration and plant N. Species differences in total water use, by contrast, reflected differences in the scaling of transpiration to plant N. A better understanding of species differences in water and N dynamics may thus be required to predict transpiration reliably.

KEYWORDS: DESERT EVERGREEN SHRUB, ECOLOGY, ELEVATED CO₂, LARREA-TRIDENTATA, PHOTOSYNTHESIS, USE EFFICIENCY, VARYING NITROGEN, WATER

1859

Polley, H.W., H.S. Mayeux, H.B. Johnson, and C.R. Tischler. 1997. Viewpoint: Atmospheric CO₂, soil water, and shrub/grass ratios on rangelands. *Journal of Range Management* 50(3):278-284.

The abundance of woody plants on grasslands and savannas often is controlled by the availability of water and its location in soil. Water availability to plants is limited by precipitation, but the distribution of soil water and period over which it is available in these ecosystems are influenced by the transpiration rates of grasses. We discuss implications of recent and projected increases in atmospheric CO₂ concentration for transpiration, soil water availability, and the balance of grasses and shrubs. An increase in CO₂ concentration often reduces potential transpiration/leaf area by reducing stomatal conductance. On grasslands where effects of stomatal closure on transpiration are not negated by an increase in leaf temperature and leaf area, rising CO₂ concentration should slow the depletion of soil water by grasses and potentially favor shrubs and other species that might otherwise succumb to water stress. Predicted effects of CO₂ are supported by results from CO₂-enrichment studies in the field and are compatible with recent models of interactions between resource levels and vegetation pattern and structure.

KEYWORDS: ANDROPOGON-GERARDII, BIOMASS PRODUCTION, C-4 GRASS, CANOPY PHOTOSYNTHESIS, CLIMATIC CONTROL, ELEVATED CARBON-DIOXIDE, PHOTOSYNTHETIC RESPONSE, PLANT- COMMUNITIES, STOMATAL RESPONSES, TALLGRASS PRAIRIE

1860

Polley, H.W., C.R. Tischler, H.B. Johnson, and R.E. Pennington. 1999. Growth, water relations, and survival of drought-exposed seedlings from six maternal families of honey mesquite (*Prosopis glandulosa*): responses to CO₂ enrichment. *Tree Physiology* 19(6):359-366.

Low water availability is a leading contributor to mortality of woody

seedlings on grasslands, including those of the invasive shrub *Prosopis*. Increasing atmospheric CO₂ concentration could favor some genotypes of this species over others if there exists intraspecific variation in the responsiveness of survivorship to CO₂. To investigate such variation, we studied effects of CO₂ enrichment on seedling survival in response to uniform rates of soil water depletion in six maternal families of honey mesquite (*P. glandulosa* Torr. var. *glandulosa*). Three families each from the arid and mesic extremes of the species' distribution in the southwestern United States were studied in environmentally controlled glasshouses. Relative water content at turgor loss and osmotic potential were not affected by CO₂ treatment. Increased atmospheric CO₂ concentration, however, increased growth, leaf production and area, and midday xylem pressure potential, and apparently reduced transpiration per unit leaf area of seedlings as soil dried. Consequently, CO₂ enrichment about doubled the fraction of seedlings that survived soil water depletion. Maternal families of honey mesquite differed in percentage survival of drought and in several other characteristics, but differences were of similar or of smaller magnitude compared with differences between CO₂ treatments. There was no evidence for genetic variation in the responsiveness of survivorship to CO₂. By increasing seedling survival of drought, increasing atmospheric CO₂ concentration could increase the abundance of honey mesquite where establishment is limited by water availability. Genetic types with superior ability to survive drought today, however, apparently will maintain that advantage in the future.

KEYWORDS: AVAILABILITY, BALANCE, BIRCH, ELEVATED CARBON-DIOXIDE, EMERGENCE, GAS-EXCHANGE, GRASSLAND, POPULATIONS, STRESS, TEXAS

1861

Pons, T.L., and R.W. Pearcy. 1994. Nitrogen reallocation and photosynthetic acclimation in response to partial shading in soybean plants. *Physiologia Plantarum* 92(4):636-644.

The first trifoliolate of soybean was shaded when fully expanded, while the plant remained in high light; a situation representative for plants growing in a closed crop. Leaf mass and respiration rate per unit area declined sharply in the first few days upon shading and remained rather constant during the further 12 days of the shading treatment. Leaf nitrogen per unit area decreased gradually until the leaves were shed. Leaf senescence was enhanced by the shading treatment in contrast to control plants growing in low light. Shaded leaves on plants grown at low nutrient availability senesced earlier than shaded leaves on plants grown at high nutrient availability. The light saturated rate of photosynthesis decreased also gradually during the shading treatment, but somewhat faster than leaf N, whereas chlorophyll contents declined somewhat slower than leaf N. Partitioning of N in the leaf over main photosynthetic functions was estimated from parameters derived from the response of photosynthesis to CO₂. It appeared that the N exported from the leaf was more at the expense of compounds that make up photosynthetic capacity than of those involved in photon absorption, resulting in a change in partitioning of N within the photosynthetic apparatus. Photosynthetic nitrogen use efficiency increased during the shading treatment, which was for the largest part due to the decrease in leaf N content, to some extent to the decrease in respiration rate and only for a small part to change in partitioning of N within the photosynthetic apparatus.

KEYWORDS: ALOCASIA-MACRORRHIZA, CANOPY PHOTOSYNTHESIS, DIFFERENT IRRADIANCES, INDUCTION STATE, LEAF NITROGEN, LEAVES, LIGHT, LUCERNE CANOPY, USE EFFICIENCY, VULGARIS L

1862

Porter, H. 1993. Interspecific variation in the growth-response of

plants to an elevated ambient CO₂ concentration. *Vegetatio* 104:77-97.

The effect of a doubling in the atmospheric CO₂ concentration on the growth of vegetative whole plants was investigated. In a compilation of literature sources, the growth stimulation of 156 plant species was found to be on average 37%. This enhancement is small compared to what could be expected on the basis of CO₂-response curves of photosynthesis. The causes for this stimulation being so modest were investigated, partly on the basis of an experiment with 10 wild plant species. Both the source-sink relationship and size constraints on growth can cause the growth-stimulating effect to be transient. Data on the 156 plant species were used to explore interspecific variation in the response of plants to high CO₂. The growth stimulation was larger for C3 species than for C4 plants. However the difference in growth stimulation is not as large as expected as C4 plants also significantly increased in weight (41% for C3 vs. 22 % for C4). The few investigated CAM species were stimulated less in growth (15%) than the average C4 species. Within the group of C3 species, herbaceous crop plants responded more strongly than herbaceous wild species (58% vs. 35%) and potentially fast-growing wild species increased more in weight than slow-growing species (54% vs. 23%). C3 species capable of symbiosis with N₂-fixing organisms had higher growth stimulations compared to other C3 species. A common denominator in these 3 groups of more responsive C3 plants might be their large sink strength. Finally, there was some tendency for herbaceous dicots to show a larger response than monocots. Thus, on the basis of this literature compilation, it is concluded that also within the group of C3 species differences exist in the growth response to high CO₂.

KEYWORDS: ATMOSPHERIC CO₂, CARBON-DIOXIDE ENRICHMENT, CO₂-ENRICHED ATMOSPHERE, DRY-MATTER, LIQUIDAMBAR- STYRACIFLUA, LONG-TERM EXPOSURE, MINERAL NUTRITION, PHOTOSYNTHETIC INHIBITION, PINUS-TAEDA SEEDLINGS, RADIATA D-DON

1863

Poorter, H. 1998. Do slow-growing species and nutrient-stressed plants respond relatively strongly to elevated CO₂? *Global Change Biology* 4(6):693-697.

Mainly based on a simulation model, Lloyd & Farquhar (1996; *Functional Ecology*, 10, 4-32) predict that inherently slow-growing species and nutrient-stressed plants show a relatively strong growth response to an increased atmospheric CO₂ concentration. Compiling published experiments, I conclude that these predictions are not supported by the available data. On average, inherently fast-growing species are stimulated proportionately more in biomass than slow-growing species and plants grown at a high nutrient supply respond more strongly than nutrient-stressed plants.

KEYWORDS: ATMOSPHERIC CO₂, AVAILABILITY, CARBON-DIOXIDE ENRICHMENT, GROWTH-RESPONSE, MINERAL NUTRITION, NITROGEN, PHOSPHORUS, PHOTOSYNTHESIS, RADIATA D-DON, SEEDLINGS

1864

Poorter, H., and R. De Jong. 1999. A comparison of specific leaf area, chemical composition and leaf construction costs of field plants from 15 habitats differing in productivity. *New Phytologist* 143(1):163-176.

Laboratory experiments have shown a large difference in specific leaf area (SLA, leaf area:leaf mass) between species from nutrient-poor and nutrient-rich habitats, but no systematic difference in the construction costs (the amount of glucose required to construct 1 g biomass). We examined how far these patterns are congruent with those from field-grown plants. An analysis was made of the vegetation in a range of

grasslands and heathlands differing in productivity. The SLA of the dominant species in 15 different habitats was determined, as well as chemical composition and construction costs of bulk samples of leaves. SLA in the field was generally lower than in the laboratory, but showed consistency in that the ranking across species remained the same. Species from highly productive habitats had higher SLA than those from sites of low productivity, although individual species sometimes deviated substantially from the general trend. Construction costs were similar for plants from different habitats. This was mainly due to the positive correlation between an expensive class of compounds (proteins) and a cheap one (minerals).

KEYWORDS: CARBON, EFFICIENCY, ELEVATED CO₂, FLUX-DENSITY, LEAVES, LIGHT, NET ASSIMILATION RATE, NITROGEN-AVAILABILITY, NUTRITION, RELATIVE GROWTH-RATE

1865

Poorter, H., R.M. Gifford, P.E. Kriedemann, and S.C. Wong. 1992. A quantitative-analysis of dark respiration and carbon content as factors in the growth-response of plants to elevated CO₂. *Australian Journal of Botany* 40(4-5):501-513.

An analysis of elevated CO₂ effects (2-4 times ambient) on dark respiration rate and carbon content was undertaken for a wide range of plant species, using both published reports and new data. On average, leaf respiration per unit leaf area was slightly higher for plants grown at high CO₂ (16%), whereas a small decrease was found when respiration was expressed on a leaf weight basis (14%). For the few data on root respiration, no significant change due to high CO₂ could be detected. Carbon content of leaves and stem showed a small increase (1.2 and 1.7% respectively), whereas C-content of roots was not significantly affected. In both data sets direction of responses was variable. A sensitivity analysis of carbon budgets under elevated CO₂ identified changes in respiration rate, and to a lesser extent carbon content, as important factors affecting the growth response to elevated CO₂ in quite a number of cases. Any comprehensive analysis of growth responses to increased CO₂ should therefore include measurements of these two variables.

KEYWORDS: CARBOHYDRATE CONTENT, DIOXIDE EFFLUX, ENRICHMENT, EXCHANGE, NITROGEN, PHOTOSYNTHESIS, TEMPERATURE, TERM, WHITE CLOVER, YIELD

1866

Poorter, H., Y. VanBerkel, R. Baxter, J. DenHertog, P. Dijkstra, R.M. Gifford, K.L. Griffin, C. Roumet, J. Roy, and S.C. Wong. 1997. The effect of elevated CO₂ on the chemical composition and construction costs of leaves of 27 C-3 species. *Plant, Cell and Environment* 20(4):472-482.

We determined the proximate chemical composition as well as the construction costs of leaves of 27 species, grown at ambient and at a twice-ambient partial pressure of atmospheric CO₂. These species comprised wild and agricultural herbaceous plants as well as tree seedlings. Both average responses across species and the range in response were considered. Expressed on a total dry weight basis, the main change in chemical composition due to CO₂ was the accumulation of total non- structural carbohydrates (TNC). To a lesser extent, decreases were found for organic N compounds and minerals. Hardly any change was observed for total structural carbohydrates (cellulose plus hemicellulose), lignin and lipids. When expressed on a TNC-free basis, decreases in organic N compounds and minerals were still present. On this basis, there was also an increase in the concentration of soluble phenolics. In terms of glucose required for biosynthesis, the increase in costs for one chemical compound - TNC - was balanced by a decrease in the costs for organic N compounds. Therefore, the construction costs,

the total amount of glucose required to produce 1 g of leaf, were rather similar for the two CO₂ treatments; on average a small decrease of 3% was found. This decrease was attributable to a decrease of up to 30% in the growth respiration coefficient, the total CO₂ respired [mainly for NAD(P)H and ATP] in the process of constructing 1 g of biomass. The main reasons for this reduction were the decrease in organic N compounds and the increase in TNC.

KEYWORDS: ATMOSPHERIC CO₂, CARBON-DIOXIDE ENRICHMENT, GROWTH-RESPONSE, LEAF RESPIRATION, LITTER DECOMPOSITION, MAINTENANCE, MAX L MERR, NITROGEN, PARTIAL-PRESSURE, PLANTS

1867

Popova, L.P., T.D. Tsonev, G.N. Lazova, and Z.G. Stoinova. 1996. Drought- and ABA-induced changes in photosynthesis of barley plants. *Physiologia Plantarum* 96(4):623-629.

The changes caused by drought stress and abscisic acid (ABA) on photosynthesis of barley plants (*Hordeum vulgare* L. cv. Alfa) have been studied. Drought stress was induced by allowing the leaves to lose 12% of their fresh weight. Cycloheximide (CHI), an inhibitor of stress-induced ABA accumulation, was used to distinguish alterations in photosynthetic reactions that are induced after drought stress in response to elevated ABA levels from those that are caused directly by altered water relations. Four hours after imposition of drought stress or 2 h after application of ABA, the bulk of the leaf's ABA content measured by enzyme-amplified ELISA, increased 14- and 16-fold, respectively. CHI fully blocked the stress-induced ABA accumulation. Gas exchange measurements and analysis of enzyme activities were used to study the reactions of photosynthesis to drought stress and ABA. Leaf dehydration or ABA treatment led to a noticeable decrease in both the initial slope of the curves representing net photosynthetic rate versus intercellular CO₂ concentration and the maximal rate of photosynthesis; dehydration of CHI treated plants showed much slower inhibition of the latter. The calculated values of the intercellular CO₂ concentration, CO₂ compensation point and maximal carboxylating efficiency of ribulose 1,5-bisphosphate (RuBP) carboxylase support the suggestion that biochemical factors are involved in the response of photosynthesis to ABA and drought stress. RuBP carboxylase activity was almost unaffected in ABA- and CHI-treated, non-stressed plants. A drop in enzyme activity was observed after leaf dehydration of the control and ABA-treated plants. When barley plants were supplied with ABA, the activity of carbonic anhydrase (CA, EC 4.2.2.1) increased more than 2-fold. Subsequent dehydration caused an over 1.5-fold increase in CA activity of the control plants and a more than 2.5-fold increase in ABA-treated plants. Dehydration of CHI-treated plants caused no change in enzyme activity. It is suggested that increased activity of CA is a photosynthetic response to elevated ABA concentration.

KEYWORDS: ABSCISIC-ACID, INDUCTION, INHIBITORS, LEAVES, METABOLISM, STOMATA

1868

Porte, A., and D. Loustau. 1998. Variability of the photosynthetic characteristics of mature needles within the crown of a 25-year-old *Pinus pinaster*. *Tree Physiology* 18(4):223-232.

Photosynthetic characteristics of 1- and 2-year-old needles were determined in excised shoots of maritime pine (*Pinus pinaster* Ait.) with an open gas exchange system. We used the nonlinear least mean squares method to derive values for quantum yield of electron transport (alpha), maximum carboxylation velocity (V-cmax), and maximum electron transport rate (J(max)), from photosynthetic response curves to light and CO₂. Crown height had no significant effect on any of the parameters; however, V-cmax and J(max), as well as alpha were 43, 26 and 35% higher,

respectively, in 1-year-old needles than in 2-year-old needles. The main effect of irradiance on needles was a small decline in leaf concentrations of nitrogen and phosphorus from the top to the bottom of the canopy. Only J(max) demonstrated a linear relationship with both nitrogen content (R² = 0.42) and irradiance at the shoot level. Because needle age accounted for most of the variability in photosynthesis, we incorporated needle age into the photosynthesis model of Farquhar et al. (1980). The modified model underestimated the daily assimilation rate of 1-year-old needles in the field, especially when assimilation rates were high.

KEYWORDS: C-3 PLANTS, CANOPY PHOTOSYNTHESIS, CARBON DIOXIDE, CO₂/O₂ SPECIFICITY, ELEVATED CO₂, EUCALYPTUS-GRANDIS, LEAF NITROGEN, QUANTUM YIELD, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE, STOMATAL CONDUCTANCE

1869

Portielje, R., and L. Lijklema. 1995. Carbon-dioxide fluxes across the air-water-interface and its impact on carbon availability in aquatic systems. *Limnology and Oceanography* 40(4):690-699.

Diffusion of CO₂ across the air-water interface was analyzed with a model that simulates both transport and reaction of CO₂ in a stagnant boundary layer. The atmospheric C influx was determined in relation to several environmental variables: pH, total dissolved inorganic C, temperature, and the thickness of the stagnant boundary layer in relation to ambient windspeed. We used the model to calculate the atmospheric CO₂ influx into six experimental ditches for a period of 6 or 8 months, starting in early spring. Three of the six ditches were dominated by aquatic macrophytes and three by benthic algae. Each series received three levels of external N and P input. A comparison with net C assimilation during the same period, as estimated from continuous oxygen measurements, showed that, especially in the ditches dominated by submersed macrophytes, a sizable fraction of the C requirements during this period could have been obtained from atmospheric CO₂. In the ditches dominated by benthic algae, this fraction was considerably less, but nonetheless substantial, and was related to the level of N and P loading. Increased primary production due to enhanced external N and P loading increased the atmospheric C input due to the resultant higher pH values. The trophic state with respect to N and P and the availability of C are therefore interrelated.

KEYWORDS: ELODEA, INORGANIC CARBON, PHOTOSYNTHESIS, PLANTS, STRATEGIES

1870

Pospisilova, J., and J. Catsky. 1999. Development of water stress under increased atmospheric CO₂ concentration. *Biologia Plantarum* 42(1):1-24.

The increase in water use efficiency (the ratio of photosynthetic to transpiration rates) is likely to be the commonest positive effect of long-term elevation in CO₂ concentration (CE). This may not necessarily lead to decrease in long-term water use owing to increased leaf area. However, some plant species seem to cope better with drought stress under CE, because increased production of photosynthates might enhance osmotic adjustment and decreased stomatal conductance and transpiration rate under CE enable plants to maintain a higher leaf water potential during drought. In addition, at the same stomatal conductance, internal CO₂ concentration might be higher under CE which results in higher photosynthetic rate. Therefore plants under CE of the future atmosphere will probably survive eventual higher drought stress and some species may even be able to extend their biotope into less favourable sites.

KEYWORDS: ABIES L KARST, CARBON-DIOXIDE ENRICHMENT,

DRY-MATTER PRODUCTION, FAGUS-SYLVATICA L, LEAF GAS-EXCHANGE, OPEN-TOP CHAMBERS, SITCHENSIS BONG CARR, TERM ELEVATED CO₂, USE EFFICIENCY, VAPOR-PRESSURE DEFICIT

1871

Pospisilova, J., J. Solarova, and J. Catsky. 1992. Photosynthetic responses to stresses during invitro cultivation. *Photosynthetica* 26(1):3-18.

Present knowledge of photosynthesis, biomass production and water relations of plantlets cultivated in vitro and their responses to environmental conditions is reviewed. Acclimation of plantlets, firstly to very special in vitro conditions and secondly after transplantating to ex vitro conditions, is considered. Low irradiance and CO₂ concentration inside cultivation vessels restrict photosynthetic rate and accumulation of biomass by plantlets in situ. Nevertheless the photosynthetic apparatus is often fully developed. Therefore net photosynthetic rate and hence biomass accumulation can increase immediately after artificial increase in CO₂ concentration inside the vessels (this enables autotrophic cultivation of plantlets as one of important future technologies) or after transplanting to glasshouse or field. On the other hand, under very high humidity and low irradiance in vitro, efficient regulation of gas exchange does not operate. The development of functional stomata and cuticle requires some weeks of acclimation to natural conditions.

KEYWORDS: CARBON DIOXIDE, CO₂- ENRICHMENT, LEAF ANATOMY, LIQUIDAMBAR-STYRACIFLUA HAMAMELIDACEAE, MERISTEM CULTURE, PLANTS CULTURED INVITRO, PROLINE ACCUMULATION, STRAWBERRY PLANTLETS, TAEDA L CALLUS, WATER-STRESS

1872

Pospisilova, J., H. Synkova, D. Haisel, J. Catsky, N. Wilhelmova, and F. Sramek. 1999. Effect of elevated CO₂ concentration on acclimation of tobacco plantlets to ex vitro conditions. *Journal of Experimental Botany* 50(330):119-126.

Nicotiana tabacum L, plants grown in vitro were transferred to ex vitro conditions and grown for 28 d in a greenhouse under normal CO₂ concentration (C, 330 pmol mol⁻¹) or elevated CO₂ concentration (E, 1000 μmol mol⁻¹). Stomatal conductances of abaxial and adaxial epidermes measured under optimal conditions were not significantly affected by growth under E, but the stomatal regulation of gas exchange was better. Leaf photosynthetic rate (A) of elevated CO₂ plants was similar to that of control plants when both were measured under normal CO₂, but higher when both were measured under elevated CO₂. The A of elevated CO₂ plants was much higher than the A of control plants when measured under their respective growth CO₂ concentration, which resulted in their higher growth rate. Chlorophyll a and b contents, and activities of whole electron transport chain and of photosystem (PS) II were not markedly affected by growth under E, and the maximum efficiency of PSII measured as the ratio of variable to maximum fluorescence was even slightly increased. Hence no down-regulation of photosynthesis occurred in transplanted plants grown for 4 weeks under E. The contents of p-carotene and of xanthophyll cycle pigments (violaxanthin + antheraxanthin+zeaxanthin) were lower in E plants. The degree of de-epoxidation of xanthophyll cycle pigments was not changed or was even lower after transfer to ex vitro conditions, which indicated that no photoinhibition occurred, Therefore, CO₂ enrichment can improve acclimation of in vitro-grown plantlets to ex vitro conditions.

KEYWORDS: CARBON-DIOXIDE ENRICHMENT, CHLOROPHYLL FLUORESCENCE, GAS-EXCHANGE, GROWN IN-VITRO, INVITRO, LIGHT-INTENSITY, PHOTOSYNTHESIS, SUBSEQUENT GROWTH,

SUGAR-FREE MEDIUM, TEMPERATURE

1873

Pospisilova, J., N. Wilhelmova, H. Synkova, J. Catsky, D. Krebs, I. Ticha, B. Hanackova, and J. Snopek. 1998. Acclimation of tobacco plantlets to ex vitro conditions as affected by application of abscisic acid. *Journal of Experimental Botany* 49(322):863-869.

Plantlets of Nicotiana tabacum L. cv, Petit Havana SR1 were grown in vitro on Murashige and Skoog medium containing 2% saccharose, and then transplanted ex vitro into pots with coarse sand and Hewitt nutrient solution. In the first day after transplantation, the antitranspirant abscisic acid (ABA; 0.01, 0.05 or 0.10 mM) was added to the substrate. Leaf stomatal conductance (g(s)), which was high in plants during the first days after transplantation similarly as in plantlets grown in vitro, was considerably decreased by ABA-treatment. However, in the further days g(s) decreased more quickly in control than in ABA-treated plants, and after 2 or 3 weeks g(s) was significantly lower than that of plantlets grown in vitro but similar in control and ABA-treated plants. Two weeks after transplantation, net photosynthetic rate, chlorophyll a + b content, maximal photochemical efficiency, and actual quantum yield of photosystem II in plant leaves were higher in comparison with those in plantlets grown in vitro. ABA- treatment had slight positive or insignificant effect on photosynthetic parameters and enhanced plant growth. Thus ABA application can alleviate 'transplant shock' and speed up acclimation of plantlets to ex vitro conditions.

KEYWORDS: CO₂- ENRICHMENT, CULTURED APPLE SHOOTS, GAS-EXCHANGE, GROWN IN-VITRO, INVITRO, MICROPROPAGATED PLANTS, PHOTOSYNTHESIS, ROSE PLANTS, STOMATAL CONDUCTANCE, WATER RELATIONS

1874

Possingham, H.P. 1993. Impact of elevated atmospheric CO₂ on biodiversity - mechanistic population-dynamic perspective. *Australian Journal of Botany* 41(1):11-21.

Biodiversity is characteristically defined on three levels: genetic diversity, species diversity and ecosystem diversity. In this paper I consider the impact of elevated CO₂ and associated climate change on the biodiversity of terrestrial systems at the species level. I attempt to understand the impact of a rapidly changing physical environment mechanistically. The direct impact of elevated CO₂ is emphasised. A changing physical environment will cause behavioural and physiological responses in organisms that will affect population dynamics and interspecific relationships. In the short term, extinctions will occur via the direct interaction of species with their changing environment. Species exposed to new diseases, and species dependent on mutualists or keystone species that become extinct or change geographical range, may become extinct rapidly through interactions with other species. I hypothesise that the effect of environmental change on competitive interactions will play a minor role in causing declines in biodiversity. Existing literature on the impact of climate change on terrestrial ecosystems emphasises the way in which ecosystems and species should track suitable climates across the landscape. Here I argue that each species will be affected in one, or a combination, of the following ways: range change to track shifting climate zones, tolerating the environmental change, microevolutionary change, and extinction.

KEYWORDS: CLIMATE CHANGE, CONSEQUENCES, ECOSYSTEMS, FORESTS, GLOBAL CHANGE, GROWTH, INCREASING CO₂, PLANTS, RESPONSES, VEGETATION

1875

Post, W.M., J. Pastor, A.W. King, and W.R. Emanuel. 1992. Aspects

of the interaction between vegetation and soil under global change. *Water, Air, and Soil Pollution* 64(1-2):345-363.

Responses of terrestrial ecosystems to a world undergoing a change in atmospheric CO₂ concentration presents a formidable challenge to terrestrial ecosystem scientists. Strong relationships among climate, atmosphere, soils and biota at many different temporal and spatial scales make the understanding and prediction of changes in net ecosystem production (NEP) at a global scale difficult. Global C cycle models have implicitly attempted to account for some of this complexity by adapting lower pool sizes and smaller flux rates representing large regions and long temporal averages than values appropriate for a small area. However, it is becoming increasingly evident that terrestrial ecosystems may be experiencing a strong transient forcing as a result of increasing levels of atmospheric CO₂ that will require a finer temporal and spatial representation of terrestrial systems than the parameters for current global C cycle models allow. To adequately represent terrestrial systems, in the global C cycle it is necessary to explicitly model the response of terrestrial systems to primary environmental factors. While considerable progress has been made experimentally and conceptually in aspects of photosynthetic responses, and gross and net primary production, the application of this understanding to NEP at individual sites is not well developed. This is an essential step in determining effects of plant physiological responses on the global C cycle. We use a forest stand succession model to explore the effects of several possible plant responses to elevated atmospheric CO₂ concentration. These simulations show that ecosystem C storage can be increased by increases in individual tree growth rate, reduced transpiration, of increases in fine root production commensurate with experimental observations.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CO₂, CO₂-INDUCED CLIMATE CHANGE, FORESTS, LITTER DECOMPOSITION, MOUNTAIN HEMLOCK, NITROGEN MINERALIZATION, NORTH-AMERICA, NUTRIENT, TERRESTRIAL ECOSYSTEMS

1876

Potosnak, M.J., S.C. Wofsy, A.S. Denning, T.J. Conway, J.W. Munger, and D.H. Barnes. 1999. Influence of biotic exchange and combustion sources on atmospheric CO₂ concentrations in New England from observations at a forest flux tower. *Journal of Geophysical Research-Atmospheres* 104(D8):9561-9569.

Hourly data for concentrations and fluxes of CO₂ at 30 m in Harvard Forest (Petersham, Massachusetts) are analyzed using linear modeling to obtain regionally representative CO₂ concentrations at a continental site. The time series is decomposed into contributions due to regional combustion, local canopy exchange, monthly average regional biotic exchange (as modulated by the daily cycle of growth and decay of the planetary boundary layer (PBL)), and the regional monthly background concentration. Attributions are derived using time series analysis, data for a tracer for combustion (CO or acetylene (C₂H₂)), and measurements of indicators of proximate canopy exchange (CO₂ flux and momentum flux). Results are compared to observations at Cold Bay, Alaska. Combustion contributes on average 4-5 ppm to ambient CO₂ at Harvard Forest in winter and 2-3 ppm in summer. Regional biotic emissions elevate daily mean CO₂ by 4-6 ppm in winter, and the covariance of the biotic cycle of uptake and emission with PBL height enhances daily mean CO₂ by 1-2 ppm in summer; minimum values in late afternoon average 10 ppm lower than at Cold Bay in summer. The study shows that regionally representative concentrations of CO₂ can be determined at continental sites if suitable correlates (tracers, fluxes of CO₂, and momentum) are measured simultaneously with CO₂ itself.

KEYWORDS: CARBON DIOXIDE

1877

Potter, C.S., and S.A. Klooster. 1999. Detecting a terrestrial biosphere sink for carbon dioxide: Interannual ecosystem modeling for the mid-1980s. *Climatic Change* 42(3):489-503.

There is considerable uncertainty as to whether interannual variability in climate and terrestrial ecosystem production is sufficient to explain observed variation in atmospheric carbon content over the past 20-30 years. In this paper, we investigated the response of net CO₂ exchange in terrestrial ecosystems to interannual climate variability (1983 to 1988) using global satellite observations as drivers for the NASA-CASA (Carnegie-Ames-Stanford Approach) simulation model. This computer model of net ecosystem production (NEP) is calibrated for interannual simulations driven by monthly satellite vegetation index data (NDVI) from the NOAA Advanced Very High Resolution Radiometer (AVHRR) at 1 degree spatial resolution. Major results from NASA-CASA simulations suggest that from 1985 to 1988, the northern middle-latitude zone (between 30 and 60 degrees N) was the principal region driving progressive annual increases in global net primary production (NPP; i.e., the terrestrial biosphere sink for carbon). The average annual increase in NPP over this predominantly northern forest zone was on the order of +0.4 Pg (10¹⁵ g) C per year. This increase resulted mainly from notable expansion of the growing season for plant carbon fixation toward the zonal latitude extremes, a pattern uniquely demonstrated in our regional visualization results. A net biosphere source flux of CO₂ in 1983-1984, coinciding with an El Niño event, was followed by a major recovery of global NEP in 1985 which lasted through 1987 as a net carbon sink of between 0.4 and 2.6 Pg C per year. Analysis of model controls on NPP and soil heterotrophic CO₂ fluxes (R-h) suggests that regional warming in northern forests can enhance ecosystem production significantly. In seasonally dry tropical zones, periodic drought and temperature drying effects may carry over with at least a two-year lag time to adversely impact ecosystem production. These yearly patterns in our model-predicted NEP are consistent in magnitude with the estimated exchange of CO₂ by the terrestrial biosphere with the atmosphere, as determined by previous isotopic (delta(13)C) deconvolution analysis. Ecosystem simulation results can help further target locations where net carbon sink fluxes have occurred in the past or may be verified in subsequent field studies.

KEYWORDS: CLIMATE VARIABILITY, EXCHANGE, GLOBAL-SCALE, NDVI DATA SET, SATELLITE, VEGETATION

1878

Potvin, C., and D. Tousignant. 1996. Evolutionary consequences of simulated global change: Genetic adaptation or adaptive phenotypic plasticity. *Oecologia* 108(4):683-693.

During the next century, natural and agricultural systems might need to adjust to a rapid increase in atmospheric CO₂ concentration and global temperature. Evolution of genotypes adapted to this global change could play a central role in plants' response. The main purpose of this study was to determine the relative importance of phenotypic and genotypic responses of plants to global change. To do so, we selected two populations of the short-lived *Brassica juncea*, one under ambient conditions and another one under conditions simulating global change. After seven generations of selection, differences between the two populations were examined using a reciprocal transplant garden. We monitored 14 different traits and found evidence for genetic adaptation only once, for vegetative biomass early in the growth cycle. Of the 14 traits, 11 responded plastically to the environment, but only one of these plastic changes had a possible adaptive value. Overall, the long-term evolutionary consequences of global change will depend on the response of fitness-related traits. None of the five reproductive traits measured showed any evolutionary responses. The main conclusion of our study is that *Brassica juncea* was apparently unable to respond evolutionarily to simulated global change either by genetic adaptation or by adaptive

phenotypic plasticity. The limit to selection was apparently due to inbreeding depression induced by the harsh conditions of the "predicted" environment.

KEYWORDS: BRASSICA, CLIMATE CHANGE, CO₂, HIGH-TEMPERATURE, IMPATIENS-CAPENSIS, INBREEDING DEPRESSION, OUTCROSSED PROGENY, PLANTS, POPULATIONS, STRESS

1879

Potvin, C., and L. Vasseur. 1997. Long-term CO₂ enrichment of a pasture community: Species richness, dominance, and succession. *Ecology* 78(3):666-677.

The present study addresses responses of a pasture community to CO₂ enrichment in situ. It focused on two levels of organization. We examined changes in both community properties and species-specific responses during long-term exposure to high CO₂ concentration. The underlying hypothesis is that CO₂ enrichment could change community composition. At the community level, we observed higher species richness and lesser dominance under enriched than ambient CO₂. Two species were apparently central in explaining our results, *Agropyron repens* and *Plantago major*. The cover of this first species increased only under ambient CO₂. Conversely, the cover of the latter species decreased under ambient CO₂ but remained stable under enriched CO₂. Species were pooled into dicots and monocots to examine space acquisition. Changes in monocot cover through time were more tightly coupled with that of dicots under ambient than high CO₂. Enrichment with CO₂ appeared to have a positive effect on the early-successional species, preventing the complete dominance by late-successional species. In fact, under elevated CO₂ early- and late-successional species were coexisting. Therefore, our results suggest the possibility that succession patterns might be altered by CO₂ enrichment apparently because enriched CO₂ stimulates the growth of dicots.

KEYWORDS: AVAILABILITY, COMPETITION, DISTURBANCE, ECOSYSTEM, ELEVATED CO₂, FERTILIZATION, FIELD PLANT COMMUNITY, GLOBAL CHANGE, GRASSLAND, RESPONSES

1880

Poulin, M.J., R. Belrhid, Y. Piche, and R. Chenevert. 1993. Flavonoids released by carrot (*Daucus-carota*) seedlings stimulate hyphal development of vesicular-arbuscular mycorrhizal fungi in the presence of optimal CO₂ enrichment. *Journal of Chemical Ecology* 19(10):2317-2327.

Carbon dioxide has been previously identified as a critical volatile factor that stimulates hyphal growth of *Gigaspora margarita*, a vesicular-arbuscular mycorrhizal fungus, and we determined the optimal concentration at 2.0%. The beneficial effect of CO₂ on fungal development is also visible in the presence of stimulatory (quercetin, myricetin) or inhibitory (naringenin) flavonoids. Sterile root exudates from carrot seedlings stimulate the hyphal development of *G. margarita* in the presence of optimal CO₂ enrichment. Three flavonols (quercetin, kaempferol, rutin or quercetin 3-rutinoside) and two flavones (apigenin, luteolin) were identified in carrot root exudates by means of HPLC retention time. Flavonols like quercetin and kaempferol are known to have stimulatory effects on hyphal growth of *G. margarita*.

KEYWORDS: ACTIVATION, DNA TRANSFORMED ROOTS, GIGASPOA-MARGARITA, GROWTH, HOST, INFECTION, INVITRO, NODULATION GENES, PLANTS, SPORE GERMINATION

1881

Prade, K., and V. Hagelgans. 1993. Enrichment of N₂ and Ar in the

atmosphere of CO₂-consuming soils. *Zeitschrift Fur Pflanzenernahrung Und Bodenkunde* 156(5):421-426.

The phenomenon of unexplained N₂/Ar-enrichment in soil air is quite frequently to be encountered in soil air studies on anthropogenically influenced sites. In the present study two anthropogenic deposits and a calcareous fluvisol were investigated for their soil air composition. While in the alkaline deposits extreme enrichments of N₂ and Ar (N₂ + Ar: up to 99%, v/v) were found as persistent site characteristics, the fluvisol showed only slight (about 1%, v/v) transient N₂/Ar-enrichments in summer. All sites, which did not show substantial vertical seepage percolation, exhibited enhanced CO₂-solubility either due to strong calcite precipitation or dissolution. So, it was concluded that intensive continuous depletion of CO₂ was responsible for the subsequent convective influx of atmospheric air. From the results obtained it was concluded that an encasement of the concerned soil volume rather impermeable to gas transport as well as intense dissolution of CO₂ in the pore water are prerequisites for substantial N₂/Ar-enrichments in soil air.

1882

Prakash, O., A. Sood, M. Sharma, and P.S. Ahuja. 1999. Grafting micropropagated tea [*Camellia sinensis* (L.) O. Kuntze] shoots on tea seedlings - a new approach to tea propagation. *Plant Cell Reports* 18(10):883-888.

Tea microshoots excised from well-established multiple shoot cultures grown in vitro and 8-week-old, three- to five-leaved seedlings from a local chinery stock (Banuri-96) and UPASI-9 (from southern India) were selected as scions and root stocks, respectively, for grafting. In addition, 4-month- and 12-month-old seedlings of Banuri-96 were also used as root stocks. Cut ends of root stocks and scions were pretreated with varying concentrations of BAP and NAA for 10 min. A treatment of BAP (5 mg/l) and NAA (5 mg/l) to both scion and stocks in water renewed foliar development at a relatively early stage (40-60 days). The grafted plants were kept in hardening chambers with CO₂-enriched air. No significant difference was observed between autograft (scion and root stock of Banuri clone) and heterograft (scion of the Banuri clone and root stock of UPASI-9). Of the three types (in terms of age) of seedling-raised root stocks employed, grafts on young tea (4-month-old) performed the best (88.33%). Grafts made in early summer established relatively faster and at a high rate of success. The percentage survival of plants transferred to the field was 88.33%.

KEYWORDS: INVITRO

1883

Pregitzer, K.S., D.R. Zak, P.S. Curtis, M.E. Kubiske, J.A. Teeri, and C.S. Vogel. 1995. Atmospheric CO₂, soil-nitrogen and turnover of fine roots. *New Phytologist* 129(4):579-585.

In most natural ecosystems a significant portion of carbon fixed through photosynthesis is allocated to the production and maintenance of fine roots, the ephemeral portion of the root system that absorbs growth-limiting moisture and nutrients. In turn, senescence of fine roots can be the greatest source of C input to forest soils. Consequently, important questions in ecology entail the extent to which increasing atmospheric CO₂ may alter the allocation of carbon to, and demography of, fine roots. Using microvideo and image analysis technology, we demonstrate that elevated atmospheric CO₂ increases the rates of both fine root production and mortality. Rates of root mortality also increased substantially as soil nitrogen availability increased, regardless of CO₂ concentration. Nitrogen greatly influenced the proportional allocation of carbon to leaves vs. fine roots. The amount of available nitrogen in the soil appears to be the most important factor regulating fine root

demography in *Populus* trees.

KEYWORDS: CARBON DIOXIDE, FORESTS, PLANTS, RESPONSES

1884

Prentice, I.C., M.T. Sykes, M. Lautenschlager, S.P. Harrison, O. Denissenko, and P.J. Bartlein. 1993. Modeling global vegetation patterns and terrestrial carbon storage at the last glacial maximum. *Global Ecology and Biogeography Letters* 3(3):67-76.

Global patterns of potential natural vegetation were simulated for present and last glacial maximum (LGM) climates. The LGM simulation showed good agreement with available evidence, most importantly in the humid tropics. Simple calculations based on these simulations indicate that terrestrial carbon storage increased by 300-700 Pg C after the LGM. The range is due to uncertainties in the mean carbon storage values for different biomes, and in the amount of carbon in boreal peats. These results are consistent with the global change in ocean delta-C-13, inferred from measurements on benthic foraminifera, reflecting the increased storage of isotopically light carbon on land.

KEYWORDS: AMAZON, ATMOSPHERIC CO₂, CLIMATE, CORE, ICE-AGE, LATE QUATERNARY, RECORD, SIMULATIONS, SURFACE

1885

Price, D.T., and M.J. Apps. 1995. The boreal forest transect case-study - global change effects on ecosystem processes and carbon dynamics in boreal Canada. *Water, Air, and Soil Pollution* 82(1-2):203-214.

The Boreal Forest Transect Case Study (BFTCS) is a multi-disciplinary ecological study organised around a 1000 km transect located in central Canada. The transect is oriented along an ecoclimatic gradient in a region likely to undergo significant environmental change within the next few decades, and crosses the climate-sensitive boreal forest biome, including the transitions north and south into tundra and grassland respectively. Originally conceived as an extension to the Boreal Ecosystem Atmosphere Study (BOREAS), the 10-year BFTCS project projects the intensive canopy-scale measurements and modelling advances obtained from BOREAS to a wider range of sites with a longer-term perspective. In addition to considering ecophysiological processes with time-frames of the order of one year or shorter, BFTCS addresses the effects of larger scale, longer term processes including vegetation succession and ecosystem disturbances. The BFTCS currently provides practical linkages among ecosystem monitoring, field experiments and regional scale modelling. It will ultimately provide a knowledge-base of key processes and their environmental sensitivities, and assessments of possible climate feedbacks, which can be used to assess the possible consequences of global change both regionally and globally.

KEYWORDS: BIOSPHERE, CLIMATE CHANGE, CO₂, CYCLE, DECOMPOSITION, MODEL, NORTHWESTERN MINNESOTA, PEATLANDS, SENSITIVITY, VEGETATION

1886

Prince, T.A., and M.S. Cunningham. 1991. Forcing characteristics of easter lily bulbs exposed to elevated-ethylene and elevated-carbon dioxide and low-oxygen atmospheres. *Journal of the American Society for Horticultural Science* 116(1):63-67.

Exposure of bulbs of Easter Lily (*Lilium longiflorum* Thunb.) to a maximum of 2- μ l ethylene/liter during vernalization delayed flowering by 5 to 7 days and decreased the number of flower buds. Ethylene exposure for 5 days at 21C after vernalization accelerated shoot

emergence and flowering by up to 3 days. No floral or plant abnormalities were observed after bulb exposure to ethylene. Exposure to atmospheres with 0%, 0.5%, or 1% O₂ at 21C for up to 2 weeks before or 10 days after vernalization did not significantly impair subsequent bulb forcing. Storage in 1% O₂ at 21C for 1 week before vernalization resulted in nearly one additional secondary bud initiated per plant. Exposure to up to 15% CO₂ at 21C for up to 2 weeks before or 10 days after vernalization did not significantly impair subsequent forcing.

1887

Prior, L.D., D. Eamus, and G.A. Duff. 1997. Seasonal and diurnal patterns of carbon assimilation, stomatal conductance and leaf water potential in *Eucalyptus tetrodonta* saplings in a wet-dry savanna in northern Australia. *Australian Journal of Botany* 45:241-258.

Seasonal and diurnal trends in carbon assimilation, stomatal conductance and leaf water potential were studied using 1-3 m tall saplings of *Eucalyptus tetrodonta* (F.Muell.). The study site was in an unburnt savanna near Darwin, where rainfall is strongly seasonal. Mean daily maximum assimilation rates ranged from 14.5 μ mol m⁻² s⁻¹ in May to 4.8 μ mol m⁻² s⁻¹ in October. There was a linear relationship between daily maximum assimilation rates and pre-dawn leaf water potential ($r = 0.62$, $n = 508$) and a log-log linear relationship between daily maximum stomatal conductance and pre-dawn leaf water potential ($r = 0.68$, $n = 508$). Assimilation rates and stomatal conductance were always higher in the morning than in the afternoon, irrespective of season. Stomatal conductance responded more strongly to leaf-to-air vapour pressure difference when pre-dawn leaf water potentials were moderately low (-0.5 to -1.5 MPa) than when they were very low (< -1.5 MPa) or high (> -0.5 MPa). Assimilation decreased sharply when temperature exceeded 35 degrees C. Seasonal trends in assimilation rate could be attributed primarily to stomatal closure, but diurnal trends could not. High leaf temperatures were a major cause of lower assimilation rates in the afternoon. Approximately 90% of leaves were lost by the end of the dry season, and above-ground growth was very slow. It is hypothesised that *E. tetrodonta* saplings allocate most photosynthate to root and lignotuber growth in order to tolerate seasonal drought and the high frequency of fire in northern Australian savannas.

KEYWORDS: CO₂, DEFICITS, ENRICHMENT, HUMIDITY, LEAVES, PHOTOSYNTHESIS, RESPONSES, TEMPERATURE, TRANSPIRATION, TREE

1888

Prior, S.A., S.G. Pritchard, G.B. Runion, H.H. Rogers, and R.J. Mitchell. 1997. Influence of atmospheric CO₂ enrichment, soil N, and water stress on needle surface wax formation in *Pinus palustris* (Pinaceae). *American Journal of Botany* 84(8):1070-1077.

Interactive effects of increasing atmospheric CO₂ with resource limitations on production of surface wax in plants have not been studied. *Pinus palustris* seedlings were grown for 1 yr at two levels of soil N (40 or 400 kg N/ha(-1).yr(-1)) and water stress (-0.5 or -1.5 MPa xylem pressure potential) in open-top field chambers under two levels of CO₂ (365 or 720 μ mol/mol). Needle surface wax content was determined at 8 mo (fall) and 12 mo (spring) and epicuticular wax morphology was examined using scanning electron microscopy (SEM) at 12 mo. Wax content expressed on both a leaf area and dry mass basis was increased due to main effects of low N and water stress. No main effects of CO₂ were observed; however, a CO₂ x N interaction at 12 mo indicated that under low soil N the elevated CO₂ treatment had less wax (surface area or dry mass basis) compared to its ambient counterpart. Morphologically, low N needle surfaces appeared rougher compared to those of high N needles due to more extensive wax ridges. Although the

main effect of water treatment on wax density was not reflected by changes in wax morphology, the CO₂ x N interaction was paralleled by alterations in wax appearance. Decreases in density and less prominent epicuticular wax ridges resulting from growth under elevated CO₂ and limiting N suggest that dynamics of plant/atmosphere and plant/pathogen interactions may be altered.

KEYWORDS: ELEVATED CARBON-DIOXIDE, EPICUTICULAR WAX, GROWTH, LEAF, LEAVES, NITROGEN, PHOTOSYNTHESIS, PLANT-RESPONSES, SEEDLINGS, ULTRASTRUCTURE

1889

Prior, S.A., and H.H. Rogers. 1995. Soybean growth-response to water-supply and atmospheric carbon- dioxide enrichment. *Journal of Plant Nutrition* 18(4):617-636.

Growth response of soybean [*Glycine max* (L.) Merr. 'Bragg'] grown in open top field chambers at five carbon dioxide (CO₂) concentrations ranging from 349 to 946 $\mu\text{mol mol}^{-1}$ and under two water regimes was examined. During reproductive growth, plants grown under CO₂ enrichment exhibited increases in total leaf area and dry weight. Water stress inhibited growth at all CO₂ levels, but the relative enhancement of growth due to CO₂ enrichment under water-stressed (WS) conditions was greater than under well-watered (WW) conditions. Water-stressed plants grown under 946 $\mu\text{mol mol}^{-1}$ CO₂ were larger than WW plants grown under 349 $\mu\text{mol mol}^{-1}$ CO₂. Reproductive yield increases were represented by increases in seed number rather than larger seeds. Although water stress reduced yield, the relative increase in seed number in response to elevated CO₂ was greater for WS plants. Leaf tissue analysis suggested that a phosphorus deficiency may have restricted the seed dry weight response to elevated CO₂. The mean relative growth rate (RGR) and mean net assimilation rate (NAR) increased with CO₂ concentration in the first interval (5 to 14 days after planting) and diminished with time thereafter for each CO₂ level. At the second interval (14 to 63 days), the direct effect of NAR was offset by lower leaf area ratio (LAR). However, the LAR was greater for WS plants but the response of RGR to CO₂ was similar under both water treatments. At the third interval (63 to 98 days), the RGR for WS plants remained constant across CO₂ treatments, whereas under WW conditions a level response of NAR coupled with a negative response of LAR resulted in a decrease in RGR under CO₂-enriched conditions. The decrease in LAR was attributed to a decrease in specific leaf area. Leaf weight ratio was unaffected by Co-2.

KEYWORDS: CO₂- ENRICHMENT, ELEVATED CO₂, FIELD, PHOSPHORUS, PHOTOSYNTHETIC ACCLIMATION, PLANTS, SEEDLINGS, STRESS, WHEAT, YIELD

1890

Prior, S.A., H.H. Rogers, and G.B. Runion. 1993. Effects of free-air co₂ enrichment on cotton root morphology. *Plant Physiology* 102(1):173.

1891

Prior, S.A., H.H. Rogers, G.B. Runion, and G.R. Hendrey. 1994. Free-air co₂ enrichment of cotton - vertical and lateral root distribution patterns. *Plant and Soil* 165(1):33-44.

The objective of this investigation was to determine how free- air carbon dioxide enrichment (FACE) of cotton (*Gossypium hirsutum* L.) affects root distribution in a natural soil environment. For two years cotton was grown on a Trix clay loam under two atmospheric CO₂ concentrations (370 and 550 $\mu\text{mol mol}^{-1}$) and two water treatments [wet, 100% of evapotranspiration (ET) replaced and dry, 75% (1990) and 67% (1991)

of ET replaced] at Maricopa, AZ. At early vegetative and mid-reproductive growth, 90 cm soil cores were taken at 0, 0.25, and 0.5 m perpendicular to row center; root variables were ascertained at three 30 cm depth increments. The effect of water stress alone or its interaction with CO₂ on measured variables during both samplings were rare and showed no consistent pattern. There was a significant CO₂ x position interaction for root length density at the vegetative stage (both years) and reproductive stage (1990 only); the positive effects of extra CO₂ were more evident at interrow positions (0.25 and 0.5 m). A CO₂ x depth x position interaction at the vegetative phase (1990) indicated that FACE increased root dry weight densities for the top soil depth increment at all positions and at the middle increment at the 0.5 m position. Similar trends were seen at the reproductive sampling for this measure as well as for root length density at both sample dates in 1990. In 1991, a CO₂ x depth interaction was noted at both periods; CO₂ enhancement of root densities (i.e., both length and dry weight) were observed within the upper and middle depths. Although variable in response, increases for root lineal density under high CO₂ were also seen. In general, results also revealed that the ambient CO₂ treatment had a higher proportion of its root system growing closer to the row center, both on a root length and dry wight basis. On the other hand, the FACE treatment had proportionately more of its roots allocated away from row center (root length basis only). Results from this field experiment clearly suggest that increased atmospheric CO₂ concentration will alter root distribution patterns in cotton.

KEYWORDS: AGRICULTURE, ATMOSPHERIC CARBON-DIOXIDE, GROWTH, PHOTOSYNTHETIC ACCLIMATION, RESPONSES, SOIL, SYSTEM, VEGETATION, WATER-USE, YIELD

1892

Prior, S.A., H.H. Rogers, G.B. Runion, B.A. Kimball, J.R. Mauney, K.F. Lewin, J. Nagy, and G.R. Hendrey. 1995. Free-air carbon-dioxide enrichment of cotton - root morphological-characteristics. *Journal of Environmental Quality* 24(4):678-683.

The response of plants to rising global CO₂ concentration is of critical research interest but one neglected aspect is its effect on roots. Root morphological changes in cotton [*Gossypium hirsutum* (L.) 'Delta Pine 77'] were examined in a 2- yr held study. The test crop was grown under two water regimes (wet, 100% of evapotranspiration [ET] replaced and dry, 75% [1990] and 67% [1991] of ET replaced) and two atmospheric CO₂ concentrations (ambient = 370 $\mu\text{mol mol}^{-1}$) and free-air CO₂ enrichment [FACE] = 550 $\mu\text{mol mol}^{-1}$). A FACE technique that allows for CO₂ exposure under held conditions with minimal alteration of plant microclimate was used. Excavated root systems were partitioned into taproot and lateral roots at two growth phases (vegetative and reproductive). Vertical root- pulling resistance was determined at the second sampling; this measure was higher because of CO₂ enrichment but was unaffected by water stress. Water stress affected root variables only at the second sampling; water stress reduced taproot variables more than lateral variables. The larger diameter taproots seen at all sample dates under FACE exhibited large increases in dry weight and volume. FACE often increased lateral root number and lateral dry weights were higher at all sample dates. The development of more robust taproot systems in CO₂-enriched environments may allow for greater carbohydrate storage for utilization during periods such as hop filling and to ensure root growth for continued exploration of the soil profile to meet nutrient and water demands during peak demand periods.

KEYWORDS: ATMOSPHERIC CO₂, GROWTH, PHOTOSYNTHETIC ACCLIMATION, RESISTANCE, RESPONSES, VEGETATION, WATER-USE, YIELD

1893

Prior, S.A., H.H. Rogers, G.B. Runion, and J.R. Mauney. 1994.

Effects of free-air CO₂ enrichment on cotton root-growth. *Agricultural and Forest Meteorology* 70(1-4):69-86.

The rise in atmospheric CO₂ concentration is predicted to have a positive effect on agro-ecosystem productivity. However, an area which requires further investigation centers on responses of crop root systems to elevated atmospheric CO₂ under field conditions. The advent of free-air CO₂ enrichment (FACE) technology provides a new method of CO₂ exposure with minimal alteration of plant microclimate. In 1990 and 1991, cotton (*Gossypium hirsutum* (L.) 'Deltapine 77') was grown under two atmospheric CO₂ levels (370 and 550 $\mu\text{mol mol}^{-1}$) and two water regimes (wet (100% of ET replaced) and dry (75% of ET replaced in 1990 and 67% in 1991)). Plant root samples were collected at early vegetative and mid-reproductive growth. Taproots of CO₂-enriched plants displayed greater volume, dry weight, length, and tissue density. Water treatment effects were noted for length, volume and dry weight of roots at the second sampling in 1991. In general, whole soil profile root densities (both length and dry weight densities) and root weight per unit length at the initial sampling were increased under CO₂ enrichment at each of three positions (0.00, 0.25, and 0.50 m) from row center to the middle of the inter-row space. At the second sampling, root length density and root dry weight density were generally unaffected by water stress, whereas root weight per unit length was somewhat higher. In addition, extra CO₂ increased whole profile root length density only at the 0.50 m inter-row position, whereas whole profile root dry weight density and root weight per unit length were generally higher under elevated CO₂ at all three positions. The results from this field experiment strongly indicated that increased atmospheric CO₂ level would enhance plant root growth.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, PHOTOSYNTHETIC ACCLIMATION, RESISTANCE, RESPONSES, SEEDLINGS, STRESS, VEGETATION, WATER RELATIONS, WHEAT, YIELD

1894

Prior, S.A., H.H. Rogers, G.B. Runion, H.A. Torbert, and D.C. Reicosky. 1997. Carbon dioxide-enriched agroecosystems: Influence of tillage on short-term soil carbon dioxide efflux. *Journal of Environmental Quality* 26(1):244-252.

Increasing atmospheric carbon dioxide (CO₂) concentration can increase biomass production that may influence carbon (C) dynamics in terrestrial ecosystems. Soil CO₂ efflux as affected by crop residues from high CO₂ environments managed under different tillage systems has not been explored. This study examined the effects of tillage systems in a legume soybean [*Glycine max* (L.) Merr.] and nonlegume grain sorghum [*Sorghum bicolor*] (L.) Moench. CO₂-enriched agroecosystem on the rates of short-term CO₂ evolution from a Blanton loamy sand (loamy siliceous, thermic Grossarenic Paleudults). In the spring of 1993, CO₂ efflux observations initiated within 5 s after a tillage event were compared to no-tillage conditions for 8 d in plots where both crop species had been grown in open top field chambers under two CO₂ conditions (ambient and twice ambient) for two seasons (1992 and 1993). Added CO₂ increased yields, residue, and root biomass; higher percent ground cover was also observed in CO₂-enriched plots prior to the tillage treatment. Differences in C/N ratio of the residue may have influenced CO₂ efflux rates; C/N ratio was highest for sorghum and was increased by elevated CO₂. Efflux patterns were characterized by flushes of CO₂ following initial tillage and rainfall events. Species x tillage and CO₂ x species interactions were noted on several days and for total CO₂ efflux values. Our results suggest that short-term CO₂ fluxes may be greater for tilled soybean and for soybean grown under elevated CO₂; however, short-term flux rates in the sorghum crop were affected by tillage, but not by CO₂ level. These short-term results should be viewed with caution when predicting long-term C turnover in agroecosystems.

KEYWORDS: AIR, ATMOSPHERIC CO₂ ENRICHMENT, CROP ROTATIONS, ELEVATED CO₂, GLOBAL CLIMATE-CHANGE, NITROGEN, ORGANIC-MATTER, PLANT-RESPONSES, TALLGRASS PRAIRIE, TERRESTRIAL BIOSPHERE

1895

Prior, S.A., H.H. Rogers, N. Sionit, and R.P. Patterson. 1991. Effects of elevated atmospheric CO₂ on water relations of soya bean. *Agriculture Ecosystems & Environment* 35(1):13-25.

Soya bean (*Glycine max* (L.) Merr. 'Bragg') plants were grown in large containers in open-top field chambers under five atmospheric CO₂ concentrations (349-946- $\mu\text{mol mol}^{-1}$) and two water regimes. Rate of soil water depletion for the high CO₂ treatments started to decrease under well-watered conditions during anthesis and by early pod formation under water-stressed conditions. During reproductive growth, normal and stressed plants at 349- $\mu\text{mol mol}^{-1}$ (ambient level) received irrigation water 29 and 12 times, respectively, compared with 21 and 9 times, respectively, at 946- $\mu\text{mol mol}^{-1}$ CO₂. At both anthesis and pod fill, plants grown under CO₂ enrichment exhibited greater leaf area. Nevertheless, water use per plant either remained constant (stressed plants at anthesis) or else declined (well-watered plants at pod fill; both moisture levels during pod fill) in response to CO₂ enrichment. At pod fill, leaves of CO₂-enriched plants generally displayed a higher stomatal resistance, except near the end of the sampling period when a sudden increase in resistance was observed under low CO₂ owing to low soil water availability. Midday xylem potential for well-watered plants was greater than values for stressed plants and was unaffected by CO₂ treatment. Under low moisture conditions, elevated CO₂ had no effect on xylem potential at anthesis; however, during pod fill potential increased significantly with increasing CO₂ concentration, as elevated CO₂ decreased water use rates, lowering soil water stress. Alleviation of water stress during critical reproductive phases was strongly suggested.

KEYWORDS: CARBON DIOXIDE, FIELD, GROWTH, PHOTOSYNTHESIS, RESPONSES, SOYBEANS, STRESS, WHEAT, YIELD

1896

Prior, S.A., G.B. Runion, R.J. Mitchell, H.H. Rogers, and J.S. Amthor. 1997. Effects of atmospheric CO₂ on longleaf pine: Productivity and allocation as influenced by nitrogen and water. *Tree Physiology* 17(6):397-405.

Longleaf pine (*Pinus palustris* Mill.) seedlings were exposed to two concentrations of atmospheric CO₂ (365 or 720 $\mu\text{mol mol}^{-1}$) in combination with two N treatments (40 or 400 kg N ha⁻¹ year⁻¹) and two irrigation treatments (target values of -0.5 or -1.5 MPa xylem pressure potential) in open-top chambers from March 1993 through November 1994. Irrigation treatments were imposed after seedling establishment (i.e., 19 weeks after planting). Seedlings were harvested at 4, 8, 12, and 20 months. Elevated CO₂ increased biomass production only in the high-N treatment, and the relative growth enhancement was greater for the root system than for the shoot system. In water-stressed trees, elevated CO₂ increased root biomass only at the final harvest. Root:shoot ratios were usually increased by both the elevated CO₂ and low-N treatments. In the elevated CO₂ treatment, water-stressed trees had a higher root:shoot ratio than well-watered trees as a result of a drought-induced increase in the proportion of plant biomass in roots. Well-watered seedlings consistently grew larger than water-stressed seedlings only in the high-N treatment. We conclude that available soil N was the controlling resource for the growth response to elevated CO₂ in this study. Although some growth enhancement was observed in water-stressed trees in the elevated CO₂ treatment, this response was contingent on available soil N.

KEYWORDS: AVAILABILITY, CARBON DIOXIDE, ELEVATED CO₂, ENRICHMENT, GROWTH, LIQUIDAMBAR- STYRACIFLUA, PHOSPHORUS, PLANT-RESPONSES, STRESS, TAEDA SEEDLINGS

1897

Prior, S.A., H.A. Torbert, G.B. Runion, G.L. Mullins, H.H. Rogers, and J.R. Mauney. 1998. Effects of carbon dioxide enrichment on cotton nutrient dynamics. *Journal of Plant Nutrition* 21(7):1407-1426.

The rise in atmospheric carbon dioxide (CO₂) concentration is predicted to have positive effects on agro-ecosystem productivity. However, an area which requires further study centers on nutrient dynamics of crops grown under elevated CO₂ in the field. In 1989 and 1990, cotton [*Gossypium hirsutum* (L.) Deltapine 77] was grown under two CO₂ levels [370 $\mu\text{mol mol}^{-1}$ =ambient and 550 $\mu\text{mol mol}^{-1}$ =free-air CO₂ enrichment(FACE)]. At physiological maturity, nutrient concentration and content of nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), copper (Cu), iron (Fe), manganese (Mn), and zinc (Zn) were determined for whole plant and individual plant organs. While the effects of added CO₂ on whole plant nutrient concentrations and contents were consistent, some differences among plant organs were observed between years. FACE often decreased tissue nutrient concentration, but increased total nutrient accumulation. Results indicate that under elevated CO₂, field grown cotton was more nutrient efficient in terms of nutrient retrieval from the soil and nutrient utilization in the plant. This implies more efficient fertilizer utilization, better economic return for fertilizer expenditures, and reduced environmental impact from agricultural fertilization practices in the future.

KEYWORDS: ATMOSPHERIC CO₂ ENRICHMENT, ENVIRONMENT, PHOTOSYNTHETIC ACCLIMATION, RESPONSES, RHIZOSPHERE, ROOT-GROWTH, SEEDLINGS, YIELD

1898

Prior, S.A., H.A. Torbert, G.B. Runion, H.H. Rogers, C.W. Wood, B.A. Kimball, R.L. LaMorte, P.J. Pinter, and G.W. Wall. 1997. Free-air carbon dioxide enrichment of wheat: Soil carbon and nitrogen dynamics. *Journal of Environmental Quality* 26(4):1161-1166.

The predicted positive impact of elevated atmospheric carbon dioxide (CO₂) concentration on crop biomass production suggests that more C will reach the soil. An aspect of soil C sequestration that requires further study is the effect of elevated CO₂ on C and N dynamics; this relationship is the key to understanding potential longterm C storage in soil. Soil samples (0-5, 5-10, and 10-20 cm increments) were collected after 2 yr of wheat (*Triticum aestivum* L.) production under two CO₂ levels [370 (ambient) and 550 $\mu\text{mol mol}^{-1}$ (free-air CO₂ enrichment) (FACE)] and two water treatments [100% of ET replaced (wet) and 50% of ET replaced (dry)] on a Trix clay loam [fine, loamy, mixed (calcareous), hyperthermic Typic Torrfluvents] at Maricopa, AZ. Organic C, total N, potential C and N mineralization, and C turnover were determined during a 60-d incubation study. Organic C content increased at all three soil depths under FACE and the total N content increased at the 5 to 10 and 10 to 20 cm depths. In general, increased N mineralization under dry conditions corresponded well with patterns of higher C mineralization and turnover. Nitrogen mineralization was unaffected by CO₂ treatment, indicating that factors other than N may limit C mineralization and turnover. Soil respiration and C turnover patterns were not affected by CO₂ treatment level at the 0 to 5 cm depth; however, these measures were lower under FACE at the lower depths. Soil respiration and C turnover at the 10 to 20 cm depth were increased by water stress under ambient CO₂; these measures under both water levels for FACE were similar to the ambient CO₂/wet treatment, suggesting that more C storage in wheat cropping systems is likely under elevated CO₂ regardless of water treatment.

KEYWORDS: DECOMPOSITION, ELEVATED ATMOSPHERIC CO₂, PLANT, RESPONSES

1899

Pritchard, S.G., C. Mosjidis, C.M. Peterson, G.B. Runion, and H.H. Rogers. 1998. Anatomical and morphological alterations in longleaf pine needles resulting from growth in elevated CO₂: Interactions with soil resource availability. *International Journal of Plant Science* 159(6):1002-1009.

Studies of anatomical changes in longleaf pine (*Pinus palustris* Mill.) needles for plants exposed to elevated atmospheric CO₂ may provide insight into the potential influences of global CO₂ increases on plant productivity. Longleaf pine seedlings were grown in open-top field chambers supplied with either ambient (similar to 365 $\mu\text{mol mol}^{-1}$) or elevated (similar to 720 $\mu\text{mol mol}^{-1}$) atmospheric CO₂ for 20 mo. Two levels of soil nitrogen (40 and 400 g ha⁻¹ yr⁻¹) and two soil moisture regimes (-0.5 or -1.5 MPa predawn xylem pressure potential) were used in combination with CO₂ treatments. Needle tissue was collected 12 and 20 mo after treatment initiation and subjected to light and scanning electron microscopy. There was no effect of elevated CO₂ on stomatal distribution or the proportion of internal leaf area allocated to a given tissue type at either sampling date. Although the relationships between vascular, transfusion, mesophyll, and epidermal tissue cross-sectional areas to total leaf cross-sectional areas appear nonplastic, leaves grown in elevated CO₂ with low N availability exhibit anatomical characteristics suggestive of reduced capacity to assimilate carbon, including decreased mesophyll cell surface area per unit needle volume (in low-N soil). Significantly greater (8%) needle fascicle volume as a result of growth in elevated CO₂ was observed after 12 mo because of thicker needles. After 20 mo of exposure, there was a trend indicating smaller fascicle volume (8%) in plants grown with elevated CO₂ compared with those grown in ambient conditions, resulting from shorter needles and smaller mesophyll, vascular tissue, and epidermal cell cross-sectional areas. These results indicate short-term stimulation and longterm inhibition of needle growth in longleaf pine as a result of exposure to elevated CO₂ and suggest at the leaf level that pine species are less responsive to elevated CO₂ than are dicotyledons, including other tree species.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO₂, CARBON-DIOXIDE ENRICHMENT, LEAF ANATOMY, PALUSTRIS, PLANT GROWTH, POPLAR CLONES, RESPONSES, SEEDLINGS, STOMATAL DENSITY

1900

Pritchard, S.G., C.M. Peterson, S.A. Prior, and H.H. Rogers. 1997. Elevated atmospheric CO₂ differentially affects needle chloroplast ultrastructure and phloem anatomy in *Pinus palustris*: Interactions with soil resource availability. *Plant, Cell and Environment* 20(4):461-471.

The response of forest species to increasing atmospheric CO₂, particularly under resource limitations, will require study in order to predict probable changes which may occur at the plant, community and ecosystem levels. Longleaf pine (*Pinus palustris* Mill.) seedlings were grown for 20 months at two levels of CO₂ (365 and 720 $\mu\text{mol mol}^{-1}$) in two levels of soil nitrogen (4 and 40 g m⁻²), and with two levels of soil moisture (-0.5 and -1.5 MPa xylem pressure potential). Leaf tissue was collected in the spring (12 months exposure) and autumn (20 months exposure) and examined using transmission electron microscopy (TEM) and light microscopy. During early spring, elevated CO₂ magnified effects of N and water treatment on starch accumulation and in some cases contributed to altered organization of mesophyll chloroplasts. Disruption of chloroplast integrity was pronounced under elevated CO₂, low N and water stress. In autumn, needles contained little starch; however, chloroplasts grown under high CO₂ exhibited

stress symptoms including increased plastoglobuli and shorter grana, A trend for reduced needle phloem cross-sectional area resulting from fewer sieve cells was also observed under elevated CO₂. These results suggest that, in nature, longleaf pine seedlings may not benefit from a doubling of CO₂, especially when soil resources are limiting.

KEYWORDS: ACCLIMATION, CARBON-DIOXIDE ENRICHMENT, GROWTH, LEAVES, PHOSPHORUS, PHOTOSYNTHESIS, PLANT-RESPONSES, SEEDLINGS, SPRUCE NEEDLES, TRANSLOCATION

1901

Pritchard, S., C. Peterson, G.B. Runion, S. Prior, and H. Rogers. 1997. Atmospheric CO₂ concentration, N availability, and water status affect patterns of ergastic substance deposition in longleaf pine (*Pinus palustris* Mill.) foliage. *Trees-Structure and Function* 11(8):494-503.

Leaf chemistry alterations due to increasing atmospheric CO₂ will reflect plant physiological changes and impact ecosystem function. Longleaf pine was grown for 20 months at two levels of atmospheric CO₂ (720 and 365 $\mu\text{mol mol}^{-1}$), two levels of soil N (4 g m^{-2} year⁻¹ and 40 g m^{-2} year⁻¹), and two soil moisture levels (-0.5 and -1.5 MPa) in open top chambers. After 20 months of exposure, needles were collected and ergastic substances including starch grains and polyphenols were assessed using light microscopy, and calcium oxalate crystals were assessed using light microscopy, scanning electron microscopy, and transmission electron microscopy. Polyphenol content was also determined using the Folin-Denis assay and condensed tannins were estimated by precipitation with protein. Evaluation of phenolic content histochemically was compared to results obtained using the Folin-Denis assay. Total leaf polyphenol and condensed tannin content were increased by main effects of elevated CO₂, low soil N and well-watered conditions. Elevated CO₂ and low soil N decreased crystal deposition within needle phloem. Elevated CO₂ had no effect on the percentage of cells within the mesophyll, endodermis, or transfusion tissue which contained visible starch inclusions. With respect to starch accumulation in response to N stress, mesophyll > endodermis > transfusion tissue. The opposite was true in the case of starch accumulation in response to main effects of water stress: mesophyll < endodermis < transfusion tissue. These results indicate that N and water conditions significantly affect deposition of leaf ergastic substances in longleaf pine, and that normal variability in leaf tissue quality resulting from gradients in soil resources will be magnified under conditions of elevated CO₂.

KEYWORDS: ALLELOCHEMICALS, CALCIUM-OXALATE CRYSTALS, CARBON NUTRIENT BALANCE, DIOXIDE, LEAVES, NEEDLES, NITROGEN, PLANTS, RESPONSES, TANNIN

1902

Pritchard, S.G., H.H. Rogers, S.A. Prior, and C.M. Peterson. 1999. Elevated CO₂ and plant structure: a review. *Global Change Biology* 5(7):807-837.

Consequences of increasing atmospheric CO₂ concentration on plant structure, an important determinant of physiological and competitive success, have not received sufficient attention in the literature. Understanding how increasing carbon input will influence plant developmental processes, and resultant form, will help bridge the gap between physiological response and ecosystem level phenomena. Growth in elevated CO₂ alters plant structure through its effects on both primary and secondary meristems of shoots and roots. Although not well established, a review of the literature suggests that cell division, cell expansion, and cell patterning may be affected, driven mainly by increased substrate (sucrose) availability and perhaps also by differential expression of genes involved in cell cycling (e.g. cyclins) or cell expansion (e.g. xyloglucan endotransglycosylase). Few studies, however,

have attempted to elucidate the mechanistic basis for increased growth at the cellular level. Regardless of specific mechanisms involved, plant leaf size and anatomy are often altered by growth in elevated CO₂, but the magnitude of these changes, which often decreases as leaves mature, hinges upon plant genetic plasticity, nutrient availability, temperature, and phenology. Increased leaf growth results more often from increased cell expansion rather than increased division. Leaves of crop species exhibit greater increases in leaf thickness than do leaves of wild species. Increased mesophyll and vascular tissue cross-sectional areas, important determinates of photosynthetic rates and assimilate transport capacity, are often reported. Few studies, however, have quantified characteristics more reflective of leaf function such as spatial relationships among chlorenchyma cells (size, orientation, and surface area), intercellular spaces, and conductive tissue. Greater leaf size and/or more leaves per plant are often noted; plants grown in elevated CO₂ exhibited increased leaf area per plant in 66% of studies, compared to 28% of observations reporting no change, and 6% reported a decrease in whole plant leaf area. This resulted in an average net increase in leaf area per plant of 24%. Crop species showed the greatest average increase in whole plant leaf area (+37%) compared to tree species (+14%) and wild, nonwoody species (+15%). Conversely, tree species and wild, nontrees showed the greatest reduction in specific leaf area (-14% and -20%) compared to crop plants (-6%). Alterations in developmental processes at the shoot apex and within the vascular cambium contributed to increased plant height, altered branching characteristics, and increased stem diameters. The ratio of internode length to node number often increased, but the length and sometimes the number of branches per node was greater, suggesting reduced apical dominance. Data concerning effects of elevated CO₂ on stem/branch anatomy, vital for understanding potential shifts in functional relationships of leaves with stems, roots with stems, and leaves with roots, are too few to make generalizations. Growth in elevated CO₂ typically leads to increased root length, diameter, and altered branching patterns. Altered branching characteristics in both shoots and roots may impart competitive relationships above and below the ground. Understanding how increased carbon assimilation affects growth processes (cell division, cell expansion, and cell patterning) will facilitate a better understanding of how plant form will change as atmospheric CO₂ increases. Knowing how basic growth processes respond to increased carbon inputs may also provide a mechanistic basis for the differential phenotypic plasticity exhibited by different plant species/functional types to elevated CO₂.

KEYWORDS: ATMOSPHERIC CO₂, CARBON-DIOXIDE ENRICHMENT, LEAF-AREA, NATURAL-POPULATIONS, PERENNIAL RYEGRASS, PINUS-TAEDA SEEDLINGS, POPLAR CLONES, SEEDLINGS CASTANEA-SATIVA, SOIL RESOURCE AVAILABILITY, SOURCE-SINK RELATIONS

1903

Prusky, D., H. Hamdan, R. Ardi, and N.T. Keen. 1996. Induction of biosynthesis of epicatechin in avocado suspension cells treated with an enriched CO₂ atmosphere. *Physiological and Molecular Plant Pathology* 48(3):171-178.

Exposure to an atmosphere of 30% carbon dioxide caused increased levels of phenylalanine ammonia-lyase (PAL) activity in avocado cell suspension cultures. The carbon dioxide treatment also enhanced chalcone synthase activity by 30% and resulted in a 1.5-2 fold greater accumulation of epicatechin than in untreated cells. It was concluded that the level of epicatechin in avocado suspension cells can be increased by carbon dioxide, and this increase appears to be regulated by PAL and CHS activation. (C) 1996 Academic Press Limited.

KEYWORDS: ANTIFUNGAL DIENE, COLLETOTRICHUM-GLOEOSPORIOIDES, FRUITS, INVOLVEMENT, LATENCY, LIPOXYGENASE

1904

Prusky, D., R.A. Plumbly, I. Kobiler, G. Zauberan, and Y. Fuchs. 1993. The effect of elevated CO₂ levels on the symptom expression of *Colletotrichum-gloeosporioides* on avocado fruits. *Plant Pathology* 42(6):900-904.

Exposure of freshly harvested avocado fruits to different concentrations of CO₂ (11, 16 and 30%) for different lengths of time (4, 17 and 26 h) affected the decay development caused by *Colletotrichum-gloeosporioides*. The delay in symptom development depended on the treatment given, the temperature regime of the fruit and time after harvest for treatment application. The most appropriate treatment was the application of 30% CO₂ for 24 h at a temperature of 20-25 degrees C on the day of harvest. Treatment for shorter time periods, at lower temperatures or 50 h after harvest, resulted in a reduced response and, in some cases, enhanced symptom expression. Concentrations of 11 or 16% CO₂ were less effective than 30% CO₂ as the fruits became more mature. It is concluded that treatment of avocado fruits with high levels of CO₂ for a short period has the potential to provide an alternative means of controlling anthracnose.

KEYWORDS: ANTHRACNOSE, ATMOSPHERE, CARBON DIOXIDE, INVOLVEMENT, LATENCY, RESISTANCE, STORAGE

1905

Pukhalskaya, N.V. 1997. Generative development of barley at an elevated atmospheric concentration of CO₂ and varying temperature conditions. *Russian Journal of Plant Physiology* 44(2):152-157.

Ear development in barley (*Hordeum vulgare* L.) was studied at normal (350 µl/l) and elevated (700 µl/l) atmospheric CO₂ concentrations and two temperature regimes. Plant productivity was found to increase by 63 and 47% at temperatures of 20/14 and 23/17 degrees C (day/night), respectively. Analysis of production showed that elevated CO₂ may induce an increase in the number of spikelets in the inflorescence primordium and in the size of the primordium beginning from the early stages of development. At 20/14 degrees C, a high level of CO₂ significantly elevated the yield of the main ear, increasing the number of caryopses by 18-28% and the grain weight in the main ear by 42-49%. At 23/17 degrees C, a double concentration of CO₂ increased plant production due to increased tiller formation (by 75-106%). It was found that the CO₂ concentration did not affect pollen fertility in barley at low temperature, but at elevated temperature, the number of sterile pollen grains increased. Thus, the experiments showed that an elevated CO₂ concentration affected the development of the barley ear during its whole ontogeny, including the early stages.

KEYWORDS: ENRICHMENT, GROWTH, MODEL, SENSITIVITY, SPRING WHEAT, YIELD

1906

Pukhal'skaya, N.V., and L.V. Osipova. 1999. Drought resistance of wheat plants in an atmosphere enriched with CO₂. *Russian Journal of Plant Physiology* 46(2):219-226.

Wheat (*Triticum aestivum* L.) plants were grown under natural (350 µl/l) and elevated (700 µl/l) CO₂ concentrations. Watering was discontinued for a portion of the plants during floret development in the primordial ear (the sixth stage of morphogenesis after Kuperman). The evapo-transpiration of the stand, leaf water deficit, membrane permeability for electrolytes, and final grain yield were evaluated. At the beginning of the growth period of the normally watered plants, the elevated CO₂ concentration reduced the evapo-transpiration of the stand, providing for slower tissue dehydration during drought. Under equal stress "doses," the drought-induced decrease in the grain yield was deeper in the CO₂-enriched atmosphere (37%) than in normal air (27%),

although the elevated CO₂ level alleviated some metabolic damages (increased membrane permeability in particular). However, the total grain yield was higher in the CO₂-enriched atmosphere under both normal watering (by 49%) and drought conditions (by 25%). It was concluded that, under a high CO₂ concentration in the air, plant sensitivity to tissue dehydration declined. However, this change was not always correlated with plant drought resistance.

KEYWORDS: CARBON DIOXIDE, GROWTH, PHOTOSYNTHESIS, WATER-USE, WINTER-WHEAT, YIELD

1907

Pukhalskaya, N.V., N. Romin, and E.N. Akanov. 1997. Growth and CO₂ exchange in wheat seedlings grown at an elevated concentration of CO₂. *Russian Journal of Plant Physiology* 44(2):147-151.

The effect of an elevated concentration of CO₂ (700 µl/l) on the growth and gas exchange of wheat (*Triticum aestivum* L.) seedlings was studied on the 4th day (germination), the 8th day (etiolated seedlings), and the 13th day (2-leaf stage) after sowing. The elevated concentration of CO₂ activated respiration of seeds germinating in the air but did not significantly affect their growth, gas exchange, and the time of shoot formation when the seeds were in soil. The increase in CO₂ concentration lowered the rate of respiration in etiolated seedlings by 25-40% and in the 13-day-old seedlings by 30-35%. In the 13-day-old seedlings, the elevated concentration of CO₂ in the air increased the rate of photosynthesis and, as a result, augmented twofold the net (per day) assimilation of CO₂ and activated growth processes. Thus, it was found that the CO₂ concentration in the air significantly affected the growth and gas exchange of the seedlings before the formation of assimilating machinery.

KEYWORDS: ENRICHMENT, YIELD

1908

Pulleman, M., and A. Tietema. 1999. Microbial C and N transformations during drying and rewetting of coniferous forest floor material. *Soil Biology and Biochemistry* 31(2):275-285.

Microbial C and N transformation rates in air-dried and subsequently rewetted coniferous forest floor material were examined in a laboratory incubation study. Gross N transformation rates were determined through parallel (NH₄⁺)-N-15 and (NO₃⁻)-N-15 enrichment experiments. After drying of the litter for 12 d to a water content of 10% of dry weight, CO₂ respiration, net N mineralization and nitrification rates were strongly restricted. Microbial biomass C was reduced to 67% of the amount in the continuously moist material. Remoistening of the dry litter to a water content of 340% resulted in a flush in C and net N mineralization within a few hours after rewetting. The increase in net N mineralization could be attributed to a larger increase in gross N mineralization relative to the increase in gross N immobilization. Gross N immobilization had increased to the same rate as gross N mineralization after 26 h, and a small secondary peak in respiration and microbial C was observed 48 h after rewetting. It was concluded that both biomass-derived substrate with a low C-to-N ratio and 'nonbiomass'-derived substrate with a high C-to-N ratio have been released, and metabolized, as a result of the drying-rewetting treatment. Despite the very extreme drying treatment, the mineralization flush after rewetting could not compensate for the large reduction in CO₂ and mineral N production during dry conditions due to its short duration. Since there was no increase in nitrification rate after drying and rewetting, the NO₃⁻ concentration at the end of the incubation was strongly reduced due to the extremely slow net nitrification rates during desiccation. (C) 1998 Elsevier Science Ltd. All rights reserved.

KEYWORDS: BIOMASS-C, CARBON, EXTRACTION METHOD,

1909

Pushnik, J.C., R.S. Demaree, J.L.J. Houpis, W.B. Flory, S.M. Bauer, and P.D. Anderson. 1995. The effect of elevated carbon dioxide on a Sierra-Nevadan dominant species: *Pinus ponderosa*. *Journal of Biogeography* 22(2-3):249-254.

The impact of increasing atmospheric CO₂ has not been fully evaluated on western coniferous forest species. Two year old seedlings of *Pinus ponderosa* were grown in environmentally controlled chambers under increased CO₂ conditions (525 $\mu\text{L L}^{-1}$ and 700 $\mu\text{L L}^{-1}$) for 6 months. These trees exhibited morphological, physiological and biochemical alterations when compared to our controls (350 $\mu\text{L L}^{-1}$). Analysis of whole plant biomass distribution has shown no significant treatment effect to the root to shoot ratios. However, while stem diameter and height growth generally increased with elevated CO₂, needles exhibited an increased overall specific needle mass and a decreased total needle area. Morphological changes at the needle level included decreased mesophyll to vascular tissue ratio and variations in starch storage in chloroplasts. The elevated CO₂ increased internal CO₂ concentrations and assimilation of carbon. Biochemical assays revealed that ribulose-bis-phosphate carboxylase (RuBPCase) specific activities increased on per unit area basis with CO₂ treatment levels. Sucrose phosphate synthase (SPS) activities exhibited an increase of 55% in the 700 $\mu\text{L L}^{-1}$ treatment. These results indicate that the sink-source relationships of these trees have shifted carbon allocation toward above ground growth, possibly due to transport limitations.

KEYWORDS: ATMOSPHERIC CO₂, CO₂- ENRICHMENT, FORMS, GROWTH, LEAF ANATOMY, PHOTOSYNTHETIC ACCLIMATION, RADIATA, SEEDLINGS, SUCROSE PHOSPHATE SYNTHASE, TREES

1910

Pushnik, J.C., D. Garcia-Ibilcieta, S. Bauer, P.D. Anderson, J. Bell, and J.L.J. Houpis. 1999. Biochemical responses and altered genetic expression patterns in ponderosa pine (*Pinus ponderosa* Doug ex P. Laws) grown under elevated CO₂. *Water, Air, and Soil Pollution* 116(1-2):413-422.

Biochemical and gene expression changes in response to elevated atmospheric CO₂ were investigated in five maternal half-sibling breeding families of Ponderosa pine. Seedlings were grown in a common garden located at Lawrence Livermore National Laboratory, in open-topped chambers (OTC) for two years. Chamber atmospheres were maintained at ambient, ambient + 175 $\mu\text{L L}^{-1}$ CO₂, or ambient + 350 $\mu\text{L L}^{-1}$ CO₂. Growth measurements showed significant increases in stem volumes and volume enhancement ratios in three of the five families studied when grown under elevated CO₂. Biochemical and gene expression studies were undertaken to gain a mechanistic understanding of these phenotypic responses. Biochemical studies focused on sucrose phosphate synthase (SPS) specific activities at increase CO₂ levels. Kinetic evaluations of SPS showed an increase in V-Max. Specific SPS probes revealed increases in the transcriptional levels of one SPS gene with exposure to increasing CO₂. RT-PCR differential gene displays showed that overall only a small fraction of visualized gene transcripts responded to elevated CO₂ (8-10%). There were also significant differences between the gene expression patterns of the different families, some of which correlated with alterations in growth at elevated CO₂ levels.

KEYWORDS: ALLOCATION, ANATOMY, CARBON-DIOXIDE ENRICHMENT, ENZYMES, LEAVES, METABOLISM, PROTEIN-PHOSPHORYLATION, SEEDLINGS, SUCROSE PHOSPHATE SYNTHASE, TREES

1911

Qi, J.E., J.D. Marshall, and K.G. Mattson. 1994. High soil carbon-dioxide concentrations inhibit root respiration of douglas-fir. *New Phytologist* 128(3):435-442.

Total and basal respiration (R(t) and R(b), respectively) of intact and undisturbed roots of one-year-old Douglas fir seedlings, *Pseudotsuga menziesii* var. *glauca* [Beissn] France, were measured at experimentally varied soil carbon dioxide concentrations ([CO₂]). Use of specially designed root boxes and a CO₂ gas-flow compensating system designed around an infrared gas analyzer (IRGA) allowed controlled delivery of CO₂ to roots and simultaneous measurements of CO₂ released by roots. Root respiration rate responded to each inlet [CO₂], independent of whether the previous concentration had been higher or lower, within two to three hours (paired t test = 0.041, P = 0.622, and n = 13). Total and basal respiration rates decreased exponentially as soil [CO₂] rose from 130 ppm, well below atmospheric [CO₂], to 7015 ppm, a concentration not uncommon in field soils. Analyses of variance (ANOVA) showed that the effects of soil [CO₂] on rates of total and basal root respiration were statistically significant. Root respiration rates decreased by 4 to 5 nmol CO₂ g⁻¹ dry weight of roots s⁻¹ for every doubling of [CO₂] according to the following equations: $\ln(R(t))$ (nmol CO₂ g⁻¹ s⁻¹) = $5.24 - 0.30 \cdot \ln[CO_2]$ with r = 0.78, P < 0.0001, and n = 70; and $\ln(R(b))$ (nmol CO₂ g⁻¹ s⁻¹) = $6.29 - 0.52 \cdot \ln[CO_2]$ with r = 0.82, P < 0.0001, and n = 35. The sensitivity of root respiration to [CO₂] suggests that some previous laboratory measurements of root respiration at atmospheric [CO₂], which is 3 to 10-fold lower than [CO₂] in field soils, overestimated root respiration in the field. Further, the potential importance of soil [CO₂] indicates that it should be accounted for in models of below-ground carbon budgets.

KEYWORDS: CO₂- ENRICHMENT, DARK RESPIRATION, EFFLUX, FIELD, GROWTH, LEAVES, LOLIUM-PERENNE, MAINTENANCE RESPIRATION, PERENNIAL RYEGRASS, SEEDLINGS

1912

Rabbinge, R., H.C. Vanlatesteijn, and J. Goudriaan. 1993. Assessing the greenhouse-effect in agriculture. *Ciba Foundation Symposia* 175:62-79.

Evidence that concentrations of CO₂ and trace gases in the atmosphere have increased is irrefutable. Whether or not these increased concentrations will lead to climate changes is still open to debate. Direct effects of increased CO₂ concentrations on physiological processes and individual plants have been demonstrated and the consequences for crop growth and production under various circumstances are evaluated with simulation models. The consequences of CO₂ enrichment are considerable under optimal growing conditions. However, the majority of crops are grown under sub-optimal conditions where the effects of changes in CO₂ are often less. The same holds for the possible indirect effects of environmental changes such as temperature rise. Studies on individual plants under optimal conditions are therefore not sufficient for evaluating the effects at a farm, regional, national or supra-national level. Simulation studies help to bridge the gap between the various aggregation levels and provide a basis for various studies of policy options at various aggregation levels.

KEYWORDS: CARBON DIOXIDE, CO₂- ENRICHMENT, GROWTH, PHOTOSYNTHESIS, RESPONSES, SOYBEAN LEAVES, YIELD

1913

Rabha, B.K., and D.C. Uprety. 1998. Effects of elevated CO₂ and moisture stress on *Brassica juncea*. *Photosynthetica* 35(4):597-602.

The interactive effect of elevated CO₂ (EC) and moisture stress (MS) on