availability in two different treatment implementations: (1) from seedlings exposed to 360, 550, and 700 mu mol mol(-1) CO2 in a glasshouse; and (2) from intact adults exposed to 360 and 550 mu mol mol(-1) CO2 at the Nevada Desert FACE (Free Air CO2 Enrichment) Facility. FACE and glasshouse wed-watered Larrea significantly down-regulated photosynthesis at elevated CO2, reducing maximum photosynthetic rate (A(max)), carboxylation efficiency (CE), and Rubisco catalytic sites, whereas droughted Larrea showed a differing response depending on treatment technique. A(max) and CE were lower in droughted Larrea compared with well-watered plants, and CO2 had no effect on these reduced photosynthetic parameters. However, Rubisco catalytic sites decreased in droughted Larrea at elevated CO2. Operating C-i increased at elevated CO2 in droughted plants, resulting in greater photosynthetic rates at elevated CO2 as compared with ambient CO2. In well-watered plants, the changes in operating C-i, CE andA(max) resulted in similar photosynthetic rates across CO2 treatments. Our results suggest that drought can diminish photosynthetic down-regulation to elevated CO2 in Larrea, resulting in seasonally transient patterns of enhanced carbon gain. These results suggest that water status may ultimately control the photosynthetic response of desert systems to rising CO2.

KEYWORDS: ACCLIMATION, CARBON DIOXIDE, DESERT, ECOSYSTEMS, GAS-EXCHANGE, GROWTH, INTACT LEAVES, RESPONSES, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE, TEMPERATURE

988

Hymus, G.J., D.S. Ellsworth, N.R. Baker, and S.P. Long. 1999. Does free-air carbon dioxide enrichment affect photochemical energy use by evergreen trees in different seasons? A chlorophyll fluorescence study of mature loblolly pine. *Plant Physiology 120(4):1183-1191.*

Previous studies of the effects of growth at elevated CO2 on energy partitioning in the photosynthetic apparatus have produced conflicting results. The hypothesis was developed and tested that elevated CO2 increases photochemical energy use when there is a high demand for assimilates and decreases usage when demand is low. Modulated chlorophyll a fluorescence and leaf gas exchange were measured on needles at the top of a mature, 12-m loblolly pine (Pinus taeda L.) forest. Trees were exposed to ambient CO2 or ambient plus 20 Pa CO2 using free-air CO2 enrichment. During April and August, periods of shoot growth, light-saturated photosynthesis and linear electron transport were increased by elevated CO2. In November, when growth had ceased but temperatures were still moderate, CO2 treatment had no significant effect on linear electron transport. In February, when low temperatures were likely to inhibit translocation, CO2 treatment caused a significant decrease in linear electron transport. This coincided with a slower recovery of the maximum photosystem II efficiency on transfer of needles to the shade, indicating that growth in elevated CO2 induced a more persistent photoinhibition. Both the summer increase and the winter decrease in linear electron transport in elevated CO2 resulted from a change in photochemical quenching, not in the efficiency of energy transfer within the photosystem II antenna. There was no evidence of any effect of CO2 on photochemical energy sinks other than carbon metabolism. Our results suggest that elevated CO2 may increase the effects of winter stress on evergreen foliage.

KEYWORDS: ANTIOXIDATIVE ENZYMES, ASSIMILATION, ELEVATED CO2, LEAVES, LONG-TERM EXPOSURE, NET PHOTOSYNTHESIS, PHOTOSYNTHETIC ELECTRON-TRANSPORT, PHOTOSYSTEM-II ACTIVITY, QUANTUM YIELD, RISING ATMOSPHERIC CO2

989

Hyodo, H., C. Hashimoto, S. Morozumi, W.Z. Hu, and K. Tanaka. 1993. Characterization and induction of the activity of 1-aminocyclopropane-1-carboxylate oxidase in the wounded mesocarp tissue of cucurbita-maxima. *Plant and Cell Physiology 34(5):667-671.*

1-Aminocyclopropane-1-carboxylate (ACC) oxidase (ethylene- forming enzyme) was isolated from wounded mesocarp tissue of Cucurbita maxima (winter squash) fruit, and its enzymatic properties were investigated. The enzyme required Fe2+ and ascorbate for its activity as well as ACC and O2 as substrates. The in vitro enzyme activity was enhanced by CO2. The apparent K(m) value for ACC was 175 muM under atmospheric conditions. The enzyme activity was inhibited by sulfhydryl inhibitors and divalent cations such as Co2+, Cu2+, and Zn2+. ACC oxidase activity was induced at a rapid rate by wounding in parallel with an increase in the rate of ethylene production. The exposure of excised discs of mesocarp to 2,5-norbornadiene (NBD), an inhibitor of ethylene action, strongly suppressed induction of the enzyme, and the application of ethylene significantly accelerated the induction of the activity of ACC oxidase in the wounded mesocarp tissue. These results suggests that endogenous ethylene produced in response to wounding may function in promoting the induction of ACC oxidase.

KEYWORDS: ACID SYNTHASE, APPLE FRUIT, BIOSYNTHESIS, CANTALOUPE, CONVERSION, ETHYLENE-FORMING ENZYME, WINTER SQUASH FRUIT

990

Idso, C.D., S.B. Idso, and R.C. Balling. 1998. The urban CO2 dome of Phoenix, Arizona. *Physical Geography 19(2):95-108.*

Air temperatures, relative humidities, and atmospheric carbon dioxide concentrations were measured at a height of 2 m at approximate 1.6-km intervals prior to sunrise and in the middle of the afternoon on five days in January along a number of different transects through the extended metropolitan area of Phoenix, Arizona. Spatially interpolated maps of the data indicate the presence of an "urban CO2 dome" that reaches concentrations as high as 555 ppmv in the city center and decreases to a value of approximately 370 ppmv on the outskirts of the city at this time of year. Pre-dawn CO2 values inside the dome are considerably higher than mid-afternoon values, suggesting that solar-induced convective mixing and the photosynthetic uptake of CO2 by urban vegetation may play significant roles in diurnally redistributing the anthropogenically produced CO2 that, together with that produced by plant respiration, accumulates near the ground during the night and early morning hours. Temperature and relative humidity appear to have little influence on either the concentration or location of the CO2 dome, but variations in wind speed and direction at times may disrupt the pattern that develops under normally fair conditions. The high CO2 concentrations within the dome may help to ameliorate the deleterious effects of urban air pollution on vegetation growing within the city. Together with the urban heat island phenomenon, they may also provide a natural laboratory for studying the effects of contemporaneous warming and atmospheric CO2 enrichment within the context of predicted future global change.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, ELEVATED CO2, HEAT-ISLAND, NET PHOTOSYNTHESIS, PLANT-RESPONSES, RURAL TRANSECT, SULFUR-DIOXIDE, TEMPORAL ANALYSIS, WATER-USE, YIELD

991

Idso, K.E., and S.B. Idso. 1994. Plant-responses to atmospheric co2 enrichment in the face of environmental constraints - a review of the past 10 years research. *Agricultural and Forest Meteorology 69(3-4):153-203.*

This paper presents a detailed analysis of several hundred plant carbon

exchange rate (CER) and dry weight (DW) responses to atmospheric CO2 enrichment determined over the past 10 years. It demonstrates that the percentage increase in plant growth produced by raising the air's CO2 content is generally not reduced by less than optimal levels of light, water or soil nutrients, nor by high temperatures, salinity or gaseous air pollution. More often than not, in fact, the data show the relative growth-enhancing effects of atmospheric CO2 enrichment to be greatest when resource limitations and environmental stresses are most severe.

KEYWORDS: CARBON-DIOXIDE ENRICHMENT, DRY-MATTER PRODUCTION, ELEVATED CO2, GAS-EXCHANGE, NET PHOTOSYNTHESIS, PINUS-TAEDA SEEDLINGS, RADIATA D-DON, SOUR ORANGE TREES, SOYBEAN CANOPY PHOTOSYNTHESIS, WATER-USE EFFICIENCY

992
Idso, S.B. 1991. A general relationship between CO2-induced increases in net photosynthesis and concomitant reductions in stomatal conductance. *Environmental and Experimental Botany 31(4):381-383.*

Simultaneous measurements of net photosynthesis and stomatal conductance of leaves of sour orange trees growing in normal and CO2-enriched air, together with similar data for cotton, cotton, soybeans and water hyacinth, suggest that a plant's photosynthetic response to atmospheric CO2 enrichment is inversely proportional to its degree of CO2-induced stomatal closure.

KEYWORDS: ATMOSPHERIC CO2 ENRICHMENT

993
Idso, S.B. 1992. Net photosynthesis - corrections required of leaf chamber measurements. *Agricultural and Forest Meteorology 58(1-2):35-42.*

Direct measurements of trunk and branch volumes and fine-root biomass confirm that the growth rate of sour orange trees supplied with an extra 300 cm3 of CO2 m-3 of air is approximately 2.8 times greater than that of similar trees growing in ambient air. Net CO2 exchange measurements made on individual leaves over three 24 h periods in May, June and July 1990, however, suggest a relative growth enhancement for the CO2-enriched trees of the order of five to seven, which is clearly impossible on the basis of the direct growth measurements. It is shown that this discrepancy is due to a problem inherent in the act of enclosing a leaf in a leaf chamber, but that its effects can be removed by means of a simple correction procedure.

KEYWORDS: BASE-LINE ANALYSIS, COMPATIBILITY, HUMIDITY, POROMETRY, TEMPERATURE, WATER-STRESS

994
Idso, S.B. 1992. Shrubland expansion in the american southwest. *Climatic Change 22(1):85-86.*

KEYWORDS: CARBON DIOXIDE, CO2, ENRICHMENT, SOUR ORANGE TREES

995
Idso, S.B. 1997. The poor man's biosphere, including simple techniques for conducting CO2 enrichment and depletion experiments on aquatic and terrestrial plants. *Environmental and Experimental Botany 38(1):15-38.*

This paper reports the results of a 3-year experimental program designed to develop an inexpensive, low-technology approach for conducting atmospheric CO2 enrichment and depletion studies of aquatic and terrestrial plants. It begins by demonstrating the effectiveness of a number of simple techniques for creating a wide range of sub-and supra-ambient atmospheric CO2 concentrations in a set of low-cost experimental enclosures. It then describes the utilization of this approach in a variety of experiments that lead to the derivation of CO2-growth response relationships for a common terrestrial plant and for both a submerged and a floating aquatic species. Finally, it provides a description of a simple procedure for obtaining accurate assessments of atmospheric CO, concentrations in such experiments. (C) 1997 Elsevier Science B.V.

KEYWORDS: ATMOSPHERIC CO2, GROWTH, TEMPERATURE

996
Idso, S.B. 1998. CO2-induced global warming: a skeptic's view of potential climate change. *Climate Research 10(1):69-82.*

Over the course of the past 2 decades, I have analyzed a number of natural phenomena that reveal how Earth's near-surface air temperature responds to surface radiative perturbations. These studies all suggest that a 300 to 600 ppm doubling of the atmosphere's CO2 concentration could raise the planet's mean surface air temperature by only about 0.4 degrees C. Even this modicum of warming may never be realized, however, for it could be negated by a number of planetary cooling forces that are intensified by warmer temperatures and by the strengthening of biological processes that are enhanced by the same rise in atmospheric CO2 concentration that drives the warming. Several of these cooling forces have individually been estimated to be of equivalent magnitude, but of opposite sign, to the typically predicted greenhouse effect of a doubling of the air's CO2 content, which suggests to me that little net temperature change will ultimately result from the ongoing buildup of CO2 in Earth's atmosphere. Consequently, I am skeptical of the predictions of significant CO2-induced global warming that are being made by state-of-the-art climate models and believe that much more work on a wide variety of research fronts will be required to properly resolve the issue.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CO2-ENRICHMENT, DIMETHYL SULFIDE, EQUATORIAL PACIFIC-OCEAN, ICE-FORMING NUCLEI, INORGANIC CARBON, RADIATION BUDGET EXPERIMENT, SOLAR IRRADIANCE, SUBMERSED MACROPHYTE GROWTH, SURFACE AIR-TEMPERATURE

997
Idso, S.B. 1999. The long-term response of trees to atmospheric CO2 enrichment. *Global Change Biology 5(4):493-495.*

KEYWORDS: GROWTH, PLANTS

998
Idso, S.B., S.G. Allen, and B.A. Kimball. 1990. Growth-response of water lily to atmospheric CO2 enrichment. *Aquatic Botany 37(1):87-92.*

999
Idso, S.B., and R.C. Balling. 1992. United-states drought trends of the past century. *Agricultural and Forest Meteorology 60(3-4):279-284.*

One of the primary concerns about potential global change is that the steadily rising CO2 content of earth's atmosphere may lead to significant increases in the severity and frequency of drought, especially in the agricultural heartland of the USA (Manabe et al., 1981; Gleick, 1987;

Manabe and Wetherald, 1986, 1987, McCabe et al., 1990). This consequence has been postulated to result from minor changes in the atmospheric supply of moisture (precipitation) and major changes in the atmospheric demand for moisture (potential evapotranspiration), as a result of increased surface temperatures. Waggoner (1989), for example, has shown how a 10% drop in precipitation can lead to a 46% increase in the frequency of drought; while Rind et al. (1990) have demonstrated that CO2-induced global warming, if it occurs as projected, could raise the frequency of severe drought in the USA from 5 to 50% by the year 2050. If drought is truly this responsive to changes in precipitation and potential evapotranspiration, and there is little reason to believe it is not, it could serve as a sensitive indicator of global warming and as a reliable test for identifying its onset. Hence, as the effective CO2 content of the atmosphere has already risen by nearly 50% above its pre-industrial level (Michaels, 1990; Houghton et al., 1990), studies of drought trends of the past century might even now provide evidence for the reality of global warming. However, there are three separate factors that could complicate this simple test.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, INCREASE, PRECIPITATION, RECORD

1000
Idso, S.B., K.E. Idso, R.L. Garcia, B.A. Kimball, and J.K. Hoober. 1995. Effects of atmospheric co2 enrichment and foliar methanol application on net photosynthesis of sour orange tree (citrus- aurantium, rutaceae) leaves. *American Journal of Botany 82(1):26-30.*

Foliar spray applications of 40% aqueous methanol were made to sunlit leaves of sour orange trees that had been grown continuously in clear-plastic-wall open-top enclosures maintained out-of-doors at Phoenix, Arizona, for over 5.5 years in ambient air of approximately 400 mu mol mol(-1) CO2 and in air enriched with CO2 to a concentration of approximately 700 mu mol mol(-1). No unambiguous effects of the methanol applications were detected in net photosynthesis measurements made on foliage in either of the two CO2 treatments. The 75% increase in CO2 however, raised the upper-limiting leaf temperature for positive net photosynthesis by approximately 7 C, which resulted in a 75% enhancement in net photosynthesis at a leaf temperature of 31 C, a 100% enhancement at a leaf temperature of 35 C, and a 200% enhancement at 42 C.

KEYWORDS: ELEVATED CO2, FIELD, GAS-EXCHANGE, GROWTH, TEMPERATURE

1001
Idso, S.B., and B.A. Kimball. 1991. Downward regulation of photosynthesis and growth at high CO2 levels - no evidence for either phenomenon in 3-year study of sour orange trees. *Plant Physiology 96(3):990-992.*

Numerous photosynthesis and growth measurements of sour orange (Citrus aurantium L.) trees maintained in ambient air and air enriched with an extra 300 microliters per liter of CO2 have revealed the CO2-enriched trees to have consistently sequestered approximately 2.8 times more carbon than the control trees over a period of three full years. Under field conditions in the natural environment, plants may not experience the downward regulation of photosynthetic capacity typically observed in long-term CO2 enrichment experiments with plants growing in pots.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, COTTON, ELEVATED LEVELS, EXPOSURE, INHIBITION, PLANTS

1002
Idso, S.B., and B.A. Kimball. 1991. Effects of 2 and a half years of atmospheric CO2 enrichment on the root density distribution of 3-year-old sour orange trees. *Agricultural and Forest Meteorology 55(3-4):345-349.*

Eight sour orange trees planted directly into the ground at Phoenix, Arizona, as small seedlings in July 1987 have been enclosed by four clear-plastic-wall, open-top chambers since November of that year, half of which have been continuously supplied with a CO2 enriched atmosphere consisting of an extra 300 cm3 CO2 m-3 of air. Extensive soil coring of the trees' root zones conducted in July 1990 indicated that two and a half years of growth under these conditions produced a fine root biomass enhancement of 175% in the CO2 enriched trees. This growth enhancement is of the same order of magnitude as our previously reported results for net photosynthesis and trunk and branch volumes for these trees.

1003
Idso, S.B., and B.A. Kimball. 1992. Aboveground inventory of sour orange trees exposed to different atmospheric co2 concentrations for 3 full years. *Agricultural and Forest Meteorology 60(1-2):145-151.*

Sour orange trees have been grown from the seedling stage out- of-doors at Pheonix, Arizona in clear-plastic-wall, open-top enclosures for 3.5 years. For the last 3 years of this period, half of the trees have been continuously exposed to air enriched with an extra 300 cm3 of CO2 m-3 of air. Inventories of all aboveground plant parts conducted at the conclusions of the second and third years of the study reveal that the total number of branches per tree, the total number of leaves per tree, and the total trunk plus branch volume per tree can all be adequately inferred from measurements of trunk cross- sectional area. They also reveal a sustained beneficial impact of atmospheric CO2 enrichment. After 3 full years of differential CO2 exposure, the CO2-enriched trees had nearly 100% more branches, 75% more leaves, approximately 160% more trunk and branch volume, and 190% more trunk, branch and fruit rind volume than the ambient-treatment trees.

KEYWORDS: ENRICHMENT

1004
Idso, S.B., and B.A. Kimball. 1992. Effects of atmospheric co2 enrichment on photosynthesis, respiration, and growth of sour orange trees. *Plant Physiology 99(1):341-343.*

Numerous net photosynthetic and dark respiratory measurements were made over a period of 4 years on leaves of 24 sour orange (Citrus aurantium) trees; 8 of them growing in ambient air at a mean CO2 concentration of 400 microliters per liter, and 16 growing in air enriched with CO2 to concentrations approaching 1000 microliters per liter. Over this CO2 concentration range, net photosynthesis increased linearly with CO2 by more than 200%, whereas dark respiration decreased linearly to only 20% of its initial value. These results, together with those of a comprehensive fine-root biomass determination and two independent above-ground trunk and branch volume inventories, suggest that a doubling of the air's current mean CO2 concentration of 360 microliters per liter would enhance the growth of the trees by a factor of 3.8.

KEYWORDS: CARBON DIOXIDE, YIELD

1005
Idso, S.B., and B.A. Kimball. 1992. Seasonal fine-root biomass development of sour orange trees grown in atmospheres of ambient and elevated co2 concentration. *Plant, Cell and Environment 15(3):337-341.*

Sour orange trees have been grown from the seedling stage out- of-doors at Phoenix, Arizona, USA, in open-top enclosures with clear plastic walls for 3.5 years. For the last 3 years of this period, half of the trees have been continuously exposed to air enriched with CO2 to 300-mu-mol mol-1 above the ambient concentration. At 2-month intervals over the last 12 months, we have determined the fine-root biomass in the top 0.4 m of the soil profile beneath the trees. Results from both treatments define a single relationship between fine-root biomass and trunk cross-sectional area. The data also show the CO2-enriched trees to have approximately 2.3 times more fine-root biomass in this soil layer than the trees grown in ambient air.

KEYWORDS: ENRICHMENT, GLOBAL CARBON-CYCLE, STORAGE

1006
Idso, S.B., and B.A. Kimball. 1993. Effects of atmospheric co2 enrichment on net photosynthesis and dark respiration rates of 3 australian tree species. *Journal of Plant Physiology 141(2):166-171.*

Net photosynthesis and dark respiration rates of leaves of three Australian tree species exposed to a range of atmospheric CO2 concentrations were measured throughout the summer of 1991. For all three species - the Australian bottle tree (Brachychiton populneum (Schott.) R. Br.) and two eucalyptus (Eucalyptus microtheca F. Muell. and E. polyanthemus Schauer) - dark respiration dropped by approximately 50 % for a 360 to 720 muL/L doubling of the air's CO2 concentration, while net photosynthesis rose by a factor of two. These results were not significantly different from results obtained previously for the common sour orange tree (Citrus aurantium L.).

KEYWORDS: CARBON DIOXIDE, CO2- ENRICHMENT, ELEVATED CO2, SOUR ORANGE TREES, TERM

1007
Idso, S.B., and B.A. Kimball. 1993. Tree growth in carbon-dioxide enriched air and its implications for global carbon cycling and maximum levels of atmospheric co2. *Global Biogeochemical Cycles 7(3):537-555.*

In the longest carbon dioxide enrichment experiment ever conducted, well-watered and adequately fertilized sour orange tree seedlings were planted directly into the ground at Phoenix, Arizona, in July 1987 and continuously exposed, from mid-November of that year, to either ambient air or air enriched, with an extra 300 ppmv of CO2 in clear-plastic-wall open-top enclosures. Only 18 months later, the CO2-enriched trees had grown 2.8 times larger than the ambient-treated trees; and they have maintained that productivity differential to the present day. This tremendous growth advantage is due to two major factors: a CO2-induced increase in daytime net photosynthesis and a CO2-induced reduction in nighttime dark respiration. Measurements of these physiological processes in another experiment have shown three Australlian tree species to respond similarly; while an independent study of the atmosphere's seasonal CO2 cycle suggests that all earth's trees, in the mean, probably share this same response. A brief review of the plant science literature outlines how such a large growth response to atmospheric CO2 enrichment might possibly be maintained in light of resource limitations existing in nature. Finally, it is noted that a CO2 "fertilization effect" of this magnitude should substantially slow the rate at which anthropogenic carbon dioxide would otherwise accumulate in the atmosphere, possibly putting an acceptable upper limit on the level to which the CO2 content of the air may ultimately rise.

KEYWORDS: BUSH PLANT- RESPONSE, ELEVATED CO2, LYCOPERSICON-ESCULENTUM MILL, PHOTOSYNTHETIC ACCLIMATION, PINUS-RADIATA, RADIATA D-DON, ROOT RESTRICTION, SOUR ORANGE TREES, STOMATAL CONDUCTANCE, WATER-USE

1008
Idso, S.B., and B.A. Kimball. 1994. Effects of atmospheric co2 enrichment on biomass accumulation and distribution in eldarica pine trees. *Journal of Experimental Botany 45(280):1669-1672.*

Eight Eldarica pine tree (Pinus eldarica L.) seedlings planted directly into the ground at Phoenix, Arizona within four clear- plastic-wall open-top enclosures were grown for a period of 2 years at mean atmospheric CO2 concentrations of 408, 554, 680, and 812 mu L L(-1). Biomass accumulations in needles, branches and boles were all linear functions of CO2 over this concentration range. For a 75% increase in ambient CO2, i.e. for an increase from 400-700 mu L L(-1), the trees experienced a 3.42-fold increase in total above-ground biomass; while for a CO2 concentration doubling from 400-800 mu L L(-1), they experienced a 4.23-fold increase. Bore biomass responded similarly. Needle biomass, however, increased by a smaller amount (2.84-fold and 3.45-fold, respectively, for 400-700 and 400-800 mu L L(-1) increases in CO2); while branch biomass was increased considerably more (by 4.73-fold and 5.97-fold for corresponding increases in CO2).

KEYWORDS: CARBON DIOXIDE, GROWTH, PHOTOSYNTHETIC ACCLIMATION, SEEDLINGS, SOUR ORANGE TREES

1009
Idso, S.B., and B.A. Kimball. 1994. Effects of atmospheric co2 enrichment on regrowth of sour orange trees (citrus-aurantium rutaceae) after coppicing. *American Journal of Botany 81(7):843-846.*

Sixteen sour orange tree (Citrus aurantium L.) seedlings were grown out-of-doors at Phoenix, Arizona, in eight clear-plastic- wall open-top enclosures maintained at four different atmospheric CO2 concentrations for a period of 2 years. Over the last year of this period, the trees were coppiced five times. The amount of dry matter harvested at each of these cuttings was a linear function of the atmospheric CO2 concentration to which the trees were exposed. For a 75% increase in atmospheric CO2 from 400 to 700 microliter per liter (mu L liter(-1)), total aboveground biomass rose, in the mean, by a factor of 3.19; while for a 400 to 800 mu L liter(- 1) doubling of the air's CO2 content, it rose by a factor of 3.92. The relative summer (mean air temperature of 32.8 C) response to CO2 was about 20% greater than the relative winter (mean air temperature of 16.4 C) response.

KEYWORDS: AIR, CARBON DIOXIDE, CROP RESPONSES, GROWTH, PAST 2 CENTURIES, PHOTOSYNTHETIC ACCLIMATION, SEEDLINGS

1010
Idso, S.B., and B.A. Kimball. 1995. Effects of atmospheric CO2 enrichment on the growth of a desert succulent: Agave vilmoriniana Berger. *Journal of Arid Environments 31(4):377-382.*

Small well-watered 'plantlets' of Agave vilmoriniana Berger collected from the flower stalk of a single parent plant were grown out-of-doors at Phoenix, Arizona in clear-plastic-wall open-top enclosures exposed to ambient air and air enriched with CO2 to 300 mu l. l(-1) above ambient. Analysis of 12 harvests of three plantings conducted over a period of 4 years revealed a temperature-dependent CO2-induced growth enhancement for this desert succulent. The linear function used to describe the relationship was indistinguishable from a similar relationship previously derived for 16 non-CAM plants. (C)1995 Academic Press Limited

KEYWORDS: CROP RESPONSES, ELEVATED CARBON-DIOXIDE, PHOTOSYNTHETIC ACCLIMATION, PLANTS, PRODUCTIVITY, SEEDLINGS

1011
Idso, S.B., and B.A. Kimball. 1997. Effects of long-term atmospheric CO2 enrichment on the growth and fruit production of sour orange trees. *Global Change Biology 3(2):89-96.*

In July of 1987, we planted eight 30-cm-tall sour orange tree seedlings in a field of Avondale loam at Phoenix, Arizona and enclosed them in pairs in clear-plastic-wall open-top chambers. Since 18 November of that year, we have continuously pumped ambient air of approximate to 400 ppmv [CO2] through two of these enclosures, while through the other two we have continuously pumped air of approximate to 700 ppmv [CO2]. By the end of the second year of the study, the trunk plus branch volume of the [CO2]-enriched trees was approximate to 2.75 times greater than that of the ambient-treatment trees. Three years later, this factor had dropped to approximate to 2.0; but the decline in the [CO2]-enriched/ambient-treatment ratio of trunk plus branch volume was nearly perfectly offset by the relative fruit production advantage enjoyed by the [CO2]- enriched trees over that period. In Years 6, 7 and 8, however, there was a moderate drop in total productivity enhancement. This decline may be a delayed acclimation response, or it could be due to enhanced self-shading in the [CO2]-enriched trees or to the fact that, starting early in Year 6, many branches of the [CO2]-enriched trees grew all the way to the walls of their enclosures, so that many blossoms and young fruit were destroyed by intermittent physical trauma produced by the action of wind against the taut plastic in that year and in all succeeding years. Hence, we will have to maintain our experiment for several more years for this lateral growth obstruction to occur to the same degree in the ambient-air chambers as it has in the [CO2]-enriched chambers, in order to determine the long-term equilibrium effects of atmospheric [CO2] enrichment in a spatially confined environment.

KEYWORDS: BRANCH BAG, CARBON DIOXIDE, ELEVATED CO2, EXPOSURE, FIELD, FOLIAR GAS-EXCHANGE, PHOTOSYNTHETIC ACCLIMATION, RESPONSES, SCIRPUS- OLNEYI, TUSSOCK TUNDRA

1012
Idso, S.B., B.A. Kimball, D.E. Akin, and J. Kridler. 1993. A general relationship between co2-induced reductions in stomatal conductance and concomitant increases in foliage temperature. *Environmental and Experimental Botany 33(3):443-446.*

Simultaneous measurements of the temperatures and stomatal conductances of leaves of sour orange trees growing in normal and CO2-enriched air, together with similar data for water hyacinths and cotton, suggest that a plant's foliage temperature response to atmospheric CO2-enrichment is directly proportional to its degree of stomatal closure, i.e. that plants that experience a greater stomatal closure in response to atmospheric CO2 enrichment experience a greater warming of their foliage. The data also suggest that this primary relationship may be modified by CO2-induced changes in leaf chlorophyll content that may have implications for global climate change.

KEYWORDS: ATMOSPHERIC CO2, CARBON-DIOXIDE ENRICHMENT, CROP YIELD, GROWTH, PHOTOSYNTHETIC ACCLIMATION, WATER-USE

1013
Idso, S.B., B.A. Kimball, and S.G. Allen. 1991. CO2 enrichment of sour orange trees - 2.5 years into a long- term experiment. *Plant, Cell and Environment 14(3):351-353.*

Eight sour orange trees have been grown from seedling stage in the field at Phoenix, Arizona, U.S.A., in four identically-vented, open-top, clear-plastic-wall chambers for close to 2.5 years. Half of the chambers have been maintained at ambient atmospheric CO2 concentrations over this period, while half of them have been maintained at 300 ppm (300-mu-mol CO2 per mol air) above ambient. Initially, the trees in each treatment were essentially identical; but in less than 2 years, the trunks of the CO2-enriched trees had become twice as large as their ambient-treatment counterparts. After 2 full years of growth, the enriched trees had 79% more leaves, 56% more primary branches with 172% more volume, 70% more secondary branches with 190% more volume, and 240% more tertiary branches with 855% more volume. In addition, the CO2-enriched trees also had fourth-, fifth- and sixth-order branches, while the ambient- treatment trees had no branches above third order. Total trunk plus branch volume of the CO2-enriched trees was 2.79 times that of the ambient-treatment trees after 2 full years of growth.

KEYWORDS: CARBON DIOXIDE

1014
Idso, S.B., B.A. Kimball, and S.G. Allen. 1991. Net photosynthesis of sour orange trees maintained in atmospheres of ambient and elevated CO2 concentration. *Agricultural and Forest Meteorology 54(1):95-101.*

Eight sour orange trees planted directly into the ground at Phoenix, Arizona, as small seedlings in July 1987 have been enclosed by four clear-plastic-wall, open-top chambers since November of that year. Half of the trees have been continuously supplied with a CO2-enriched atmosphere consisting of an extra 300 cm3 of CO2 per m3 of air. Data from a comprehensive inventory of all above-ground plant parts at the conclusion of two full years of growth under these conditions have revealed that the net effect of the CO2-enriched air was to more than double the normal production of biomass over that time interval. Here we report net photosynthesis measurements made throughout the last summer of the period, which suggest that the primary impetus for this large growth response was an equivalent enhancement of the net photosynthetic rates of the CO2-enriched trees.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT

1015
Idso, S.B., B.A. Kimball, and D.L. Hendrix. 1993. Air-temperature modifies the size-enhancing effects of atmospheric co2 enrichment on sour orange tree leaves. *Environmental and Experimental Botany 33(2):293-299.*

Every other month for a period of 2 years, leaf area and dry weight measurements were made on the foliage of sour orange trees growing in ambient air and in air enriched with an extra 300 mul/l CO2. Leaf starch content measurements were made at approximate 2-month intervals for a period of 1 year. The data demonstrated that all three plant parameters were significantly increased by atmospheric CO2 enrichment, except in the coldest portion of the year. A plot of the ratio of CO2-enriched leaf dry weight to ambient-treatment leaf dry weight against the mean air temperature of the preceding month revealed this relationship with temperature to be linear. The relationship shows atmospheric CO2 enrichment to have a negligible effect on leaf dry weight at a mean air temperature of approximately 5- degrees-C. At a mean air temperature of 35-degrees-C, however, it shows individual CO2-enriched leaves of our experiment to weigh 40% more than their ambient-treatment counterparts. This phenomenon helps to explain the vastly different effects of atmospheric CO2 enrichment that have been reported for a number of diverse ecosystems.

KEYWORDS: CARBON, COMMUNITIES, ELEVATED CO2, ENVIRONMENT, ESTUARINE MARSH, GROWTH-RESPONSE, PHOTOSYNTHETIC ACCLIMATION, PLANTS, PRODUCTIVITY, TUSSOCK TUNDRA

1016

Idso, S.B., B.A. Kimball, and D.L. Hendrix. 1996. Effects of atmospheric CO2 enrichment on chlorophyll and nitrogen concentrations of sour orange tree leaves. *Environmental and Experimental Botany 36(3):323-331.*

Since 18 November 1987, eight sour orange (Citrus aurantium L.) trees have been maintained under well watered and fertilized conditions within four clear-plastic-wall open-top enclosures, two of which have been continuously supplied with ambient air of approximately 400 mu l 1(-1) CO2 and two of which have been supplied with air enriched to approximately 700 mu l 1(-1) CO2. At weekly intervals throughout years 4-7 of this long-term experiment, we measured chlorophyll a contents of 60 leaves on each of the trees with a hand-held chlorophyl meter that was specifically calibrated for our study. At bi-monthly intervals, we also measured the areas, dry weights and nitrogen contents of 68 leaves from each tree. Expressed on a per-unit-leaf-area basis, leaves from the CO2-enriched trees contained 4.8% less chlorophyll and nitrogen than leaves from the trees exposed to ambient air. Because of their greater leaf numbers, however, the CO2-enriched trees contained 75% more total chlorophyll and nitrogen than thr ambient-treatment trees; the total productivity of the CO2-enriched trees was 175% greater. Consequently, although per-unit-leaf-area chlorophyll and nitrogen contents were slightly lowered by atmospheric CO2 enrichment in our experiment, their use efficiencies were greatly enhanced.

KEYWORDS: EXTRACTABLE CHLOROPHYLL, GROWTH, LEAF GREENNESS, METER, PHOTOSYNTHESIS, TEMPERATURE, WHEAT

1017

Idso, S.B., B.A. Kimball, G.W. Wall, R.L. Garcia, R. Lamorte, P.J. Pinter, J.R. Mauney, G.R. Hendrey, K. Lewin, and J. Nagy. 1994. Effects of free-air co2 enrichment on the light response curve of net photosynthesis in cotton leaves. *Agricultural and Forest Meteorology 70(1-4):183-188.*

Daytime measurements of leaf CO2 exchange rates in a free-air CO2 enrichment (FACE) experiment reveal that at photosynthetically active radiation (PAR) flux rates in excess of 1000 mumol m-2 s-1, cotton leaves exposed to an atmospheric CO2 concentration of approximately 500 mumol mol-1 exhibit net photosynthetic rates about 30% greater than those for leaves of similar plants growing in ambient air. As PAR flux rates drop below this value, the stimulatory effect of elevated CO2 rises, suggesting that the relative benefits of atmospheric CO2 enrichment will be greater for shaded cotton leaves that for those exposed to full sunlight.

KEYWORDS: CARBON DIOXIDE, GROWTH, QUANTUM YIELD, TRANSPIRATION

1018

Idso, S.B., G.W. Wall, and B.A. Kimball. 1993. Interactive effects of atmospheric co2 enrichment and light- intensity reductions on net photosynthesis of sour orange tree leaves. *Environmental and Experimental Botany 33(3):367-375.*

In a tong-term study of the effects of a 300 mul l-1 enrichment of the air's CO2 content on the growth of sour orange trees, a comprehensive set of net photosynthesis and light intensity data was obtained. From these measurements we derived single- leaf light response curves, which together with complementary leaf area index data allowed us to derive full-canopy light response curves. The results showed our 85% enhancement of the air's CO2 content to more than double canopy net photosynthesis at full sunlight. Our analysis demonstrated that the positive direct effect of atmospheric CO2 enrichment on net photosynthesis more than compensated for the negative self- shading effect produced by the CO2-induced proliferation of leaf area.

KEYWORDS: AMBIENT, CARBON DIOXIDE, GROWTH, PLANTS, QUANTUM YIELD, RESPIRATION, RESPONSES, TRANSPIRATION

1019

Igamberdiev, A.U., and I.V. Zabrovskaya. 1994. The effect of light, carbon nutrition, and salinity on the oxidative-metabolism of wolffia-arrhiza. *Russian Journal of Plant Physiology 41(2):208-214.*

The effects of varying conditions of carbon nutrition (sucrose and an inorganic source of carbon in the growth medium), light, and salinity on oxidative metabolism were studied in Wolffia arrhiza (L.) Hork. ex Wimmer. In cells grown on 1% sucrose, the level of the cyanide-resistant (CO2)-C-14 evolution from 1,4-C- 14-succinate as a respiratory substrate was considerably higher than in autotrophically grown plants. When the medium was enriched in inorganic carbon (CO2 or bicarbonate), the rate of metabolization of glucose and other respiratory substrates diminished, and total protein and chlorophyll content decreased. Light incubation enhanced glucose metabolization two- to threefold, whereas succinate transformation was increased by a factor of 1.5 to 2, with a concomitant rise in the electron flow via the cyanide-resistant pathway. Inhibition of the photorespiratory metabolism with alpha-hydroxypyridine- 2-methanesulfonate slowed down glucose and succinate metabolism. NaCl activated glycolate metabolism in autotrophically grown plants and did not influence the rates of glucose and succinate transformation. In contrast, under photoheterotrophic (mixothrophic) growth conditions on sucrose, NaCl added to the cultivation medium led to a considerably higher (three- to fourfold) (CO2)-C-14 evolution from 1,4-C-14- succinate and 1-C-14-glucose. The authors conclude that the adaptation of Wolffia plants to different environmental conditions is accompanied by changes in the metabolic fluxes via cyanide-resistant oxidase, along the glycolate pathway, and other oxidative pathways. These changes conform to the alterations in enzyme activities participating in the oxidative metabolism.

KEYWORDS: CYANIDE, DEHYDROGENASE, PLANTS

1020

Igamberdiev, A.U., G.Q. Zhou, G. Malmberg, and P. Gardestrom. 1997. Respiration of barley protoplasts before and after illumination. *Physiologia Plantarum 99(1):15-22.*

Respiratory O-2 consumption was investigated in dark-adapted barley (Hordeum vulgare L. cv. Gunilla) protoplasts and after illumination for 10 min at high and very low CO2 in the presence of respiratory and photorespiratory inhibitors. In dark-adapted protoplasts no difference was observed between inhibitor treatments in high and very low CO2. The respiratory rate increased somewhat after illumination and a difference in responce to inhibitors was in some cases observed between high and very low CO2. Thus, the operation of the mitochondrial electron transport chain is affected following a period of active photosynthesis. In all situations tested, oligomycin inhibited respiratiory O-2 uptake indicating that respiration of mitochondria in protoplasts is not strictly ADP limited. Antimycin A inhibited respiration more in dark-adapted protoplasts than after illumination whereas SHAM gave the opposite response. Rotenone inhibited respiration both in dark adapted protoplasts (about 30%) and after illumination where the inhibition was much greater in very low CO2 (50%) than in high CO2 (10%). After iilumination in very low CO2, SHAM + rotenone inhibited respiration almost completely (70%). Photorespiratory inhibitors had very small effect on O-2 consumption in darkness. After illumination the effect of aminoacetonitrile (AAN) was also very low whereas a-hydroxypyridine-2-methane sulphonate (HPMS) in photorespiratory conditions inhibited O-2 uptake much stronger (35%). The addition of glyoxylate enhanced respiration in the presence of HPMS up to the

control level suggesting that alternative pathways of glyoxylate conversion might be operating. The differences in inhibitor responses may reflect fine mechanisms for the regulation of energetic balance in the plant cell which consists of switching from electron transport coupled to ATP production to non-coupled transport. Photorespiratory flux is also very flexible, and the suppression of glycine decarboxylation can induce bypass reactions of glyoxylate metabolism.

KEYWORDS: ALTERNATIVE OXIDASE ACTIVITY, CARBOHYDRATE STATUS, CELLS, CHLOROPLASTS, LEAVES, MESOPHYLL PROTOPLASTS, PATHWAY, PEA, PHOTOSYNTHETIC METABOLISM, PLANT-MITOCHONDRIA

1021

Imai, K., and M. Okamotosato. 1991. Effects of temperature on CO2 dependence of gas exchanges in C3 and C4 crop plants. *Japanese Journal of Crop Science 60(1):139-145.*

The effects of elevated CO2 in the atmosphere and the accompanied temperature rise predicted for the future on gas exchanges of two summer C3 (rice, soybean) and two C4 (Japanese millet, finger millet) crop plants were examined. Plants were grown in artificially illuminated growth cabinets under 350 and 500-mu-mol mol-1 ambient CO2 (C(a)) and were measured for rates of CO2 exchange (CER) and transpiration (E) of leaves at 23, 28 and 33-degrees-C in terms of C(a) (0-500-mu-mol mol-1). The responses of CER to C(a) were slightly lower in plants grown in high C(a) than those in normal C(a) and were largely influenced by temperature. The promotive effect of elevating C(a) on CER was larger at higher temperatures, especially in C4 crop plants. With the rise of C(a), the E in C4 crop plants decreased more than in C3 crop plants and it was correlated with the decrease in stomatal conductance to CO2 transfer. The water use efficiency (WUE) of leaves increased with the rise in C(a) but the effect of temperature on WUE was unclear. It is concluded that, whthin limits, under high C(a), C4 crop plants expand their photosynthetic capacity in an environment of high temperature.

1022

Ineichen, K., V. Wiemken, and A. Wiemken. 1995. Shoots, roots and ectomycorrhiza formation of pine-seedlings at elevated atmospheric carbon-dioxide. *Plant, Cell and Environment 18(6):703-707.*

The effect of elevated atmospheric CO2 concentration on the growth of shoots, roots, mycorrhizas and extraradical mycorrhizal mycelia of pine (Pinus silvestris L.) was examined, Two and a half-month-old seedlings were inoculated axenically with the mycorrhizal fungus Pisolithus tinctorius (Pers,) by a method allowing rapid mycorrhiza formation in Petri dishes, The plants were then cultivated for 3 months in growth chambers with daily concentrations of 350 and 600 mu mol mol(-1) CO2 during the day, Whereas plants harvested after 1 and 2 months did not differ appreciably between ambient and increased CO2 concentrations, after 3 months they developed a considerably higher root biomass (+57%) at elevated CO2, but did not increase significantly in root length, The mycorrhizal fungus Pisolithus tinctorius, which depended entirely on the plant assimilates in the model system, grew much faster at increased CO2: 3 times more mycorrhizal root clusters were formed and the extraradical mycelium produced had twice the biomass at elevated as at ambient CO2. No difference in shoot biomass was found between the two treatments after 91d, However, since the total water consumption of seedlings was similar in the two treatments, the water use efficiency was appreciably higher for the seedlings at increased CO2 because of the higher below- ground biomass.

KEYWORDS: AMBIENT, CO2 CONCENTRATION, ENRICHMENT, GROWTH, PLANTS, TREES

1023

Ineson, P., M.F. Cotrufo, R. Bol, D.D. Harkness, and H. Blum. 1996. Quantification of soil carbon inputs under elevated CO2:C-3 plants in a C-4 soil. *Plant and Soil 187(2):345-350.*

The objective of this investigation was to quantify the differences in soil carbon stores after exposure of birch seedlings (Betula pendula Roth.) over one growing season to ambient and elevated carbon dioxide concentrations. One-year- old seedlings of birch were transplanted to pots containing 'C- 4 soil' derived from beneath a maize crop, and placed in ambient (350 mu L L-1) and elevated (600 mu L L-1) plots in a free-air carbon dioxide enrichment (FACE) experiment. After 186 days the plants and soils were destructively sampled, and analysed for differences in root and stem biomass, total plant tissue and soil C contents and delta(13)C values. The trees showed a significant increase (+50%) in root biomass, but stem and leaf biomasses were not significantly affected by treatment. C isotope analyses of leaves and fine roots showed that the isotopic signal from the ambient and elevated CO2 supply was sufficiently distinct from that of the 'C-4 soil' to enable quantification of net root C input to the soil under both ambient and elevated CO2. After 186 days, the pots under ambient conditions contained 3.5 g of C as intact root material, and had gained an additional 0.6 g C added to the soil through root exudation/turnover; comparable figures for the pots under elevated CO2 were 5.9 g C and 1.5 g C, respectively. These data confirm the importance of soils as an enhanced sink for C under elevated atmospheric CO2 concentrations. We propose the use of 'C-4 soils' in elevated CO2 experiments as an important technique for the quantification of root net C inputs under both ambient and elevated CO2 treatments.

KEYWORDS: ATMOSPHERIC CO2 CONCENTRATION, DIOXIDE, ENRICHMENT, RESPONSES, ROOTS, SYSTEM

1024

Ineson, P., P.A. Coward, and U.A. Hartwig. 1998. Soil gas fluxes of N2O, CH4 and CO2 beneath Lolium perenne under elevated CO2: The Swiss free air carbon dioxide enrichment experiment. *Plant and Soil 198(1):89-95.*

Fluxes of nitrous oxide, methane and carbon dioxide were measured from soils under ambient (350 mu L L-1) and enhanced (600 mu L L-1) carbon dioxide partial pressures (pCO(2)) at the 'Free Air Carbon Dioxide Enrichment' (FACE) experiment, Eidgenossische Technische Hochschule (ETH), Eschikon, Switzerland in July 1995, using a GC housed in a mobile laboratory. Measurements were made in plots of Lolium perenne maintained under high N input. During the data collection period N fertiliser was applied at a rate of 14 g m(-2) of N. Elevated pCO(2) appeared to result in an increased (27%) output of N2O, thought to be the consequence of enhanced root-derived available soil C, acting as an energy source for denitrification. The climate, agricultural practices and soils at the FACE experiment combined to give rise to some of the largest N2O emissions recorded for any terrestrial ecosystem. The amount of CO2-C being lost from the control plot was higher (10%) than for the enhanced CO2 plot, and is the reverse of that predicted. The control plot oxidised consistently more CH4 than the enhanced plot, oxidising 25.5 +/- 0.8 mu g m(-2) hr(- 1) of CH4 for the control plot, with an average of 8.5 +/- 0.4 mu g m(-2) hr(-1) of CH4 for the enhanced CO2 plot. This suggests that elevated pCO(2) may lead to a feedback whereby less CH4 is removed from the atmosphere. Despite the limited nature of the current study (in time and space), the observations made here on the interactions of elevated pCO(2) and soil trace gas release suggest that significant interactions are occurring. The feedbacks involved could have importance at the global scale.

KEYWORDS: ATMOSPHERIC CO2, DENITRIFICATION, STIMULATION

1025

Ingestad, T., O. Hellgren, H. Hesseldahl, and A.B.L. Ingestad. 1996. Methods and applications to control the uptake rate of carbon. *Physiologia Plantarum 98(3):667-676.*

Methods to control carbon and nutrient uptake at different availability of carbon were tested on plants of birch (Betula pendula Roth.) and tomato (Lycopersicon esculentum Mill. cv. Solentos). The present paper accounts for the methods and the possibility to maintain steady-state, i.e., a long-term and stable physiological state of acclimated plants. Steady-state comprises, by definition, equality between constant relative growth rates, and relative uptake rates of carbon and nutrients. Two methods were tested. The first, not previously applied, method (a), was based on a constant relative addition rate of carbon, R(AC). In the second method (b), a constant concentration of CO2 in the air, c(a), was used to attain non- limiting conditions. The methods are analogous to those used by us to control plant nutrition, and the generality of fluxes to quantify supply as well as uptake and growth was verified. Thus, different R(AC) resulted suited in clear-cut responses, from strong reduction to non-limitation of uptake and growth, whereas different c(a) levels in the range 100 to 700 ppm had comparatively small effects, with an unclear causality. Non- limiting conditions were achieved at c(a) greater than or equal to 200 ppm. Effects reported in the literature have been based upon the control of c(a), similarly to method (b), whereas results comparable to those obtained with method (a) are lacking. Transpiration rate increased rapidly at c(a) < 200 ppm CO2, and at low R(AC) levels, less than or equal to 0.1 day(- 1), wilting tendencies were observed. Elevated c(a) 500 or 700 ppm, did not increase the relative growth rate (R(G)) but reduced transpiration and increased both nitrogen productivity (growth rate per unit of nitrogen in the plant) and transpiration productivity (growth rate per unit of water transpired by the plant). Obviously, effects of c(a) may be due to changed transpiration rate rather than to changed quantitative availability of CO2. Relative uptake (R(OC)) and growth (R(G)) rates were closely equal to the R(AC) applied (R(AC) approximate to R(UC) approximate to R(G)); i.e., the purely mathematical conditions defining steady-state were fulfilled. This unambiguous and straightforward test of reliability confirms that experimental artefacts did not produce uncontrolled or unintended effects, so that the new technique allows an accurate control of CO2 uptake and plant growth. The results add to previous databases and reference systems, where limiting conditions grade and classify plant performance as deviations from maximum growth. Evidently, methodology in experimentation and in evaluation of plant responses, can be based upon unifying concepts and general theories.

KEYWORDS: BIRCH SEEDLINGS, GROWTH, NITROGEN STRESS, PLANT NUTRITION

1026

Ingvardsen, C., and B. Veierskov. 1994. Response of young barley plants to co2 enrichment. *Journal of Experimental Botany 45(279):1373-1378.*

Barley (Hordeum vulgare L. cv. Digger) was grown for 22 d in enclosed chambers with a CO2 enrichment of 35, 155, 400 or 675 mu mol CO2 mol(-1). CO2 enrichment increased photosynthetic capacity in the plants grown at either of the two highest levels of pCO(2). A CO2 enrichment of 675 mu mol CO2 caused a significant increment of shoot dry weight, whereas no changes were observed in fresh weight, chlorophyll or protein levels. At a light intensity of 860 mu mol m(-2) s(-1) CO2 enrichment caused photosynthetic capacity to increase by 250%, whereas no effect was observed at 80 mu mol m(-2) s(-1). Over time, photosynthesis decreased by 70% independent of CO2. A time-dependent increase in the level of extractable fructose was observed whereas total extractable carbohydrate only changed slightly.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, GROWTH, LEAVES, PHOTOSYNTHESIS, PHYSIOLOGY, RESPIRATION, WHEAT, YIELD

1027

Innes, J.L. 1994. Climatic sensitivity of temperature forests. *Environmental Pollution 83(1-2):237-243.*

Climatic change and associated global changes are of major interest to foresters, both in terms of forest ecology and of future forest production. Predicting the likely effects of global change on forests is extremely difficult due to the critical lack of information on regional changes in meteorological factors relevant to forests. However, existing models of forest production and forest distribution fail to take adequate account of what is already known. Climate and carbon dioxide concentrations have shown substantial changes over the last 100 years. Although the rate of change is likely to increase, recent proposed and implemented control strategies, together with better climatic models, are tending to suggest that the rate of change will be less than initially thought. This means that past changes may provide an increasingly useful source of information. In particular, information on the impact on forests of both long-term climate change and short-term climatic events is rapidly increasing. Such information should be built into future forest response models.

KEYWORDS: CO2, EMISSIONS, FERTILIZATION, GERMANY, GROWTH, INCREASE, MOUNTAINS, NITROGEN, PRODUCTIVITY, RESPONSES

1028

Inoue, Y., B.A. Kimball, J.R. Mauney, R.D. Jackson, P.J. Pinter, and R.J. Reginato. 1990. Stomatal behavior and relationship between photosynthesis and transpiration in field-grown cotton as affected by CO2 enrichment. *Japanese Journal of Crop Science 59(3):510-517.*

1029

Insam, H., E. Baath, M. Berreck, A. Frostegard, M.H. Gerzabek, A. Kraft, F. Schinner, P. Schweiger, and G. Tschuggnall. 1999. Responses of the soil microbiota to elevated CO2 in an artificial tropical ecosystem. *Journal of Microbiological Methods 36(1-2):45-54.*

Plants in artificial tropical ecosystems were grown under ambient (340 mu l l(-1)) and elevated (610 mu l l(-1)) atmospheric CO2 for 530 d under low-nutrient conditions on a substrate free of organic C. At the end of the experiment a number of soil chemical and microbiological variables were determined. Although we found no changes in total soil organic matter under elevated CO2, we did find that after physical fractionation the amount of organic C in the supernatant (< 0.2 mu m) and the amount of water extractable organic C (WEOC) was lower under elevated CO2. The extractable optical density (OD) indicated a higher degree of humification for the elevated than for the ambient CO2 samples (P = 0.032). Microbial biomass C was not significantly altered under high CO2, but total bacterial counts were significantly higher. The microbial biomass C-to-N ratio was also higher at elevated (15.0) than at ambient CO2 (10.0). The number of mycorrhizal spores was lower at high CO2, but ergosterol contents and fungal hyphal lengths were not significantly affected. Changes were found neither in community level physiological profiles (CLPPs) nor in the structural attributes (phospholipid fatty acids, PLFAs) of the microbial community. Overall, the effects on the soil microbiota were small, perhaps as a result of the low nutrient supply and low organic matter content of the soil used in our study. The few significant results showing changes in specific, though relatively minor, organic matter pools may point to possible long-term changes of the more major pools. Furthermore, the data suggest increased competition between plants and microbes for N at high CO2.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, BIOMASS, BOUTELOUA-GRACILIS, COMMUNITIES, COTTON, DECOMPOSITION, ENRICHMENT, NITROGEN, ORGANIC-MATTER, ROOT

1030

Inubushi, K., W.G. Cheng, and K. Chander. 1999. Carbon dynamics in submerged soil microcosms as influenced by elevated CO2 and temperature. *Soil Science and Plant Nutrition 45(4):863-872.*

A 45-d incubation experiment was conducted under controlled laboratory conditions to study the interactive effects of elevated CO2 and temperature on the dynamics of microbial biomass C and organic C in hooded paddy soil microcosms amended or unamended with rice straw. The microcosms with the two treatments were transferred separately to four growth chambers to incubate them under 16 h/8 h light and dark conditions. Two of the growth chambers set at 25 and 35 degrees C provided a continuous how of elevated CO2 (equivalent to 800 mu L L-1). Similarly the other two growth chambers were run under near ambient CO2 (400 mu L L-1) conditions at each of the two temperatures. The amounts of soluble carbon, microbial biomass C, chlorophyll-type compounds, and organic C in the surface (0- 1 cm) and sub-surface (below 1 cm) soil layers were measured at 15, 30, and 45 d after incubation. The amount of soluble carbon in the straw-amended soil gradually decreased throughout the incubation period, while no significant differences were detected among the four different conditions. The interactive effects of both elevated CO2 and temperature were found to be positive in terms of the size of the microbial biomass in surface soil, although no significant differences were detected in the subsurface. However, the amount of total soil organic C was larger in the soils incubated at a lower temperature. The amounts of chlorophyll-type compounds doubled in the surface soil when the soils were incubated under elevated CO2 conditions, indicating that the higher incubation concentration of CO2 promoted the growth of algae in surface soil.

KEYWORDS: ATMOSPHERIC CO2, MICROBIAL BIOMASS, NITROGEN, ORGANIC-MATTER

1031

Ioslovich, I., I. Seginer, P.O. Gutman, and M. Borshchevsky. 1995. Suboptimal co2 enrichment of greenhouses. *Journal of Agricultural Engineering Research 60(2):117-136.*

Greenhouse CO2 enrichment in warm climates is restricted by the need to ventilate, leading some growers to intermittent enrichment, where enrichment and ventilation alternate several times an hour. This strategy relies on the heat and CO2 capacity of the system, characterized by a heating time constant of the order of 10 min, during which period ventilation may be suspended. It is shown that, for slowly changing weather, the optimal CO2 enrichment is basically not intermittent (bang-bang control), but rather quasi steady state (smoothly varying singular control). As the disturbance (weather) frequency increases, the quasi steady-state (QSS) solution becomes less and less optimal. Nevertheless, due to the difficulties involved in implementing a truly optimal control (the need for accurate weather forecast and high control fluxes), the sub-optimal QSS control may be a better choice. We chose to try a controller which aims to follow the QSS temperature and CO2 setpoints at all disturbance frequencies. The performance of this controller for high disturbance frequencies is a few per cent lower than the truly optimal solution, but over the whole season this effect may not be significant. On the other hand, the controller is likely to be more robust. Implementation of the QSS solution requires simulaneous ventilation and enrichment, properly balanced.

KEYWORDS: GROWTH, INTERMITTENT

1032

Islam, K.R., C.L. Mulchi, and A.A. Ali. 1999. Tropospheric carbon dioxide or ozone enrichments and moisture effects on soil organic carbon quality. *Journal of Environmental Quality 28(5):1629-1636.*

Carbon, as an active component of organic matter, has considerable effects on soil quality and productivity. The objective of this study was to examine the effect of climate change variables on soil organic C (C-T) quality in an agroecosystem. Wheat (Triticum aestivum L.) and soybean [Glycine max (L.) Merr] plants were grown in 3 m in diam, open- top field chambers and exposed to charcoal-filtered (CF) air at 350 mu L CO2 L-1; CF air + 150 mu L CO2 L-1; nonfiltered (NF) air + 35 nL O-3 L-1; and NF air + 35 nL O-3 L-1 + 150 mu L CO2 L-1 at two soil moisture levels from 1994 to 1996. The 150 mu L CO2 L-1 addition was 18 h d(-1) and the 35 nL O-3 L-l was 7 h d(-1) from April until late October. In response to treatments, the CT contents did not change significantly; however, particulate, oxidizable, dissolved, humic (C-HA) and fulvic (C- FA) acid, and carbohydrate C pools increased in soils under CO2 enrichment and well-watered conditions but decreased under O-3 stress compared with soils under CF ambient air quality. Tropospheric CO2 enrichment and well-watered condition increased, and O-3, stress decreased the log optical density slope for both C-HA and C-FA fractions more than CF ambient air and restricted moisture treatment. Also, the E-465/E-665 ratios of both C-HA and C-FA fractions were higher for the CO2 enrichment and smaller for the O-3 stress compared With CF ambient air quality, Results suggest that tropospheric CO2 enrichment and well-watered conditions may favor an accumulation of low molecular weight and more aliphatic quality of C and O-3 stress favor high molecular weight and more aromatic quality of C.

KEYWORDS: ALLOCATION, DECOMPOSITION, FERTILIZATION, HUMIC SUBSTANCES, INCREASING ATMOSPHERIC CO2, LEAF LITTER, LITTER QUALITY, MATTER DYNAMICS, O-3, WATER

1033

Islam, M.S., T. Matsui, and Y. Yoshida. 1995. Effect of preharvest carbon dioxide enrichment on the postharvest quality of tomatoes. *Journal of the Japanese Society for Horticultural Science 64(3):649-655.*

The effect of preharvest application of elevated CO2 throughout the fruit growing period on organic acid, sugar content, acid invertase activity (beta-fructofuranoside fructohydrolase, EC 3.2.1.26), and color quality in tomato (Lycopersicon esculentum Mill. cv. Momotaro) fruit during storage at 20 degrees C was determined. The CO2-enriched tomato fruits contained significantly lower concentrations of citric, malic and oxalic acids, but had significantly higher reducing sugars and acid invertase activity at harvest and during storage. The concentration of these acids decreased with storage, whereas the activity of acid invertase and reducing sugar contents increased in the treated fruits; they were relatively constant in the control fruits. Furthermore, the elevated CO2 resulted in a deeper red color during storage.

KEYWORDS: ACCUMULATION, FLAVOR, FRUITS, INVERTASE, STARCH, SUGAR

1034

Islam, M.S., T. Matsui, and Y. Yoshida. 1996. Effect of carbon dioxide enrichment on physico-chemical and enzymatic changes in tomato fruits at various stages of maturity. *Scientia Horticulturae 65(2-3):137-149.*

The influence of CO2 enrichment on fruit growth, firmness and colour, together with its effect on the concentrations of ascorbic acid, organic acids and sugars, and the activities of sucrose synthase (SS) (UDP glucose: D-fructose 2- glucosyltransferase, E. C. 2, 4, 1, 13) and sucrose phosphate synthase (SPS) (UDP glucose: D-fructose-6-phosphate 2-glucosyltransferase, E. C. 2. 4. 1. 14) were determined at various stages of maturity in fruits of tomato (Lycopersicon esculentum Mill. cv. Momotaro), CO2 enriched tomatoes had lower amounts of citric, malic and oxalic acids, and higher amounts of ascorbic acid, fructose, glucose and sucrose synthase activity than the control. Elevated CO2 enhanced fruit growth and colouring during development. Citric acid was the primary organic acid followed by malic and oxalic acids. The concentration of organic acids (mg g(-1) fresh weight) and of ascorbic acid (mg 100g(-1) fresh weight) increased with the maturity of fruits; their maximum concentrations were found at the pink stage of ripening, but declined slightly at the red stage. The amount of reducing sugars (mg g(-1) fresh weight) increased with the advancement of maturity, with fructose being the predominant sugar. The decrease in SS activity was accompanied by an increase in the concentrations of reducing sugars. There were no significant differences in fruit firmness, sucrose concentration and SPS activity between the treatments. The SPS activity did not change, but remained relatively constant throughout fruit development. The results also suggest that SS levels correlated positively with sucrose concentration but negatively with the concentration of reducing sugars.

KEYWORDS: CO2, ENZYMES, GREENHOUSES, INVERTASE, MUSKMELON FRUIT, RESPONSES, SINK METABOLISM, SUCROSE PHOSPHATE SYNTHASE, SUGAR ACCUMULATION

1035

Israel, A.A., and P.S. Nobel. 1994. Activities of carboxylating enzymes in the cam species opuntia- ficus-indica grown under current and elevated co2 concentrations. *Photosynthesis Research 40(3):223-229.*

Responses of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) and phosphoenolpyruvate carboxylase (PEPCase) to an elevated atmospheric CO2 concentration were determined along with net CO2 uptake rates for the Crassulacean acid metabolism species Opuntia ficus-indica growing in open-top chambers. During the spring 13 months after planting, total daily net CO2 uptake of basal and first-order daughter cladodes was 28% higher at 720 than at 360 mu l CO2 1(-1). The enhancement, caused mainly by higher CO2 assimilation during the early part of the night, was also observed during late summer (5 months after planting) and the following winter. The activities of Rubisco and PEPCase measured in vitro were both lower at the elevated CO2 concentration, particularly under the more favorable growth conditions in the spring and late summer. Enzyme activity in second-order daughter cladodes increased with cladode age, becoming maximal at 6 to 10 days. The effect of elevated CO2 on Rubisco and PEPCase activity declined with decreasing irradiance, especially for Rubisco. Throughout the 13-month observation period, O. ficus-indica thus showed increased CO2 uptake when the atmospheric CO2 concentration was doubled despite lower activities of both carboxylating enzymes.

KEYWORDS: ACCLIMATION, AGAVE-VILMORINIANA, ATMOSPHERIC CO2, CARBON DIOXIDE, CRASSULACEAN ACID METABOLISM, PHOTOSYNTHESIS, PLANTS, PRODUCTIVITY, RESPONSES, SHORT- TERM

1036

Israel, D.W., T.W. Rufty, and J.D. Cure. 1990. Nitrogen and phosphorus nutritional interactions in a CO2 enriched environment. *Journal of Plant Nutrition 13(11):1419-1433.*

Nonnodulated soybean plants (Glycine max. [L.] Merr. 'Lee') were supplied with nutrient solutions containing growth limiting concentrations of N or P to examine effects on N- and P-uptake efficiencies (mg nutrient accumulated/gdw root) and utilization efficiencies in dry matter production (gdw2/mg nutrient). Nutritional treatments were imposed in aerial environments containing either 350 or 700-mu-L/L atmospheric CO2 to determine whether the nutrient interactions were modified when growth rates were altered. Nutrient-stress treatments decreased growth and N- and P-uptake and utilization efficiencies at 27 days after transplanting (DAT) and seed yield at maturity (98 DAT). Atmospheric CO2 enrichment increased growth and N- and P-utilization efficiencies at 27 DAT and seed yield in all nutritional treatments and did not affect N- and P-uptake efficiencies at 27 DAT. Parameter responses to nutrient stress at 27 DAT were not altered by atmospheric CO2 enrichment and vice versa. Nutrient-stress treatments lowered the relative seed yield response to atmospheric CO2 enrichment. Decreased total-N uptake by P- stressed plants was associated with both decreased root growth and N-uptake efficiency of the roots. Nitrogen-utilization efficiency was also decreased by P-stress. This response was associated with decreased plant growth as total-N uptake and plant growth were decreased to the same extent by P stress resulting in unaltered tissue N concentrations. In contrast, decreased total P-uptake by N-stressed plants was associated with a restriction in root growth as P-uptake efficiency of the roots was unaltered. This response was coupled with an increased root-to-shoot dry weight ratio; thus shoot and wholeplant growth were decreased to a much greater extent than total-P uptake which resulted in elevated P concentrations in the tissue. Therefore, P-utilization efficiency was markedly reduced by N stress.

KEYWORDS: AMMONIUM, ELEVATED CARBON-DIOXIDE, GROWTH, NITRATE, PLANTS, RESPONSES, SEED YIELD, TRANSPORT

1037

Isutsa, D.K., M.P. Pritts, and K.W. Mudge. 1994. Rapid propagation of blueberry plants using ex-vitro rooting and controlled acclimatization of micropropagules. *Hortscience 29(10):1124-1126.*

A protocol is presented that enables a propagator to produce field-sized blueberry transplants within 6 months of obtaining microshoots from tissue culture. The protocol involves subjecting microshoots to ex vitro rooting in a fog chamber under 100 mumol.m-2.s-1 photosynthetic photon flux for 7 weeks, transferring plants to a fog tunnel for 2 weeks, then to a greenhouse for 7 more weeks. Plant survival and rooting of cultivars Berkeley (Vaccinium corymbosum L.) and Northsky (Vaccinium angustifolium xcorymbosum) were near 100% under these conditions. Plantlets in fog chambers receiving 100 mumol.m-2.s-1 grew rapidly, while those at lower irradiance levels grew more slowly, and supplemental CO, enhanced growth only at 50 mumol.m-2.s-1. Growth rates slowed when plants were moved into the fog tunnel; but by the end of 16 weeks, plants that were under high irradiance in the fog chamber had root systems that were 15 to 30 times larger than plants under low irradiance. Within 6 months, these plants were 30 to 60 cm tall and suitable for field planting.

KEYWORDS: CO2, CULTURE, ENRICHMENT, GROWTH, HIGHBUSH BLUEBERRY, INVITRO, LIGHT, LOWBUSH BLUEBERRY

1038

Ito, J., S. Hasegawa, K. Fujita, S. Ogasawara, and T. Fujiwara. 1999. Effect of CO2 enrichment on fruit growth and quality in Japanese pear (Pyrus serotina reheder cv. Kosui). *Soil Science and Plant Nutrition 45(2):385-393.*

Six year-old Japanese pear (Pyrus serotina Reheder cv. Kosui) trees

grafted on P. serotina cv. Nihonyamanashi were grown in containers filled with Granite Regosol under glasshouse conditions. At different stages of fruit growth, pear trees were exposed to an elevated CO2 concentration (130 Pa CO2) along with a control (35 Pa CO2). For one group of plants, CO2 enrichment was applied for 79 d from 52 d after full bloom (DAB) to fruit maturity (long-term CO2 enrichment) and for another group the same treatment was applied for 35 d from 96 DAB to fruit maturity (short-term CO2 enrichment). The effects of the elevated CO2 concentration on vegetative growth, mineral contents, and fruit production and quality were examined. Long- term CO2 enrichment enhanced vegetative growth, without any significant effect on the mineral contents in either flower bud or fruit except for a remarkable increase in the K content. Long-term CO2 enrichment increased the fruit size and fresh weight, but had no significant effect on the fruit quality. On the other hand, the short-term CO2 enrichment did not induce any significant change in the fruit size but increased the fruit sugar concentration. Along with the reduction of the sorbitol concentration in fruit, the fructose and sucrose concentrations increased and these changes occurred earlier at elevated CO2 than at ambient CO2 concentrations. From these results, we concluded that the effect of CO2 enrichment on fruit growth varies depending upon the growth stages of fruit: during the initial and fruitlet stages when fruit expansion occurs, CO2 enrichment increases the fruit size, whereas, during maturation when fruit expansion has slowed down and sugar accumulation in fruit is active, it increases the fruit sugar concentration.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, CARBON DIOXIDE, INVERTASE, METABOLISM, PASTURE, PHOTOSYNTHESIS, PLANTS, SORBITOL-RELATED ENZYMES, SOUR ORANGE TREES

1039

Iverson, L.R., and A.M. Prasad. 1998. Predicting abundance of 80 tree species following climate change in the eastern United States. *Ecological Monographs 68(4):465-485.*

Projected climate warming will potentially have profound effects on the earth's biota, including a large redistribution of tree species. We developed models to evaluate potential shifts for 80 individual tree species in the eastern United States. First, environmental factors associated with current ranges of tree species were assessed using geographic information systems (GIS) in conjunction with regression tree analysis (RTA). The method was then extended to better understand the potential of species to survive and/or migrate under a changed climate. We collected, summarized, and analyzed data for climate, soils, land use, elevation, and species assemblages for >2100 counties east of the 100th meridian. Forest Inventory Analysis (FIA) data for >100000 forested plots in the East provided the tree species range and abundance information for the trees. RTA was used to devise prediction rules from current species-environment relationships, which were then used to replicate the current distribution as well as predict the future potential distributions under two scenarios of climate change with twofold increases in the level of atmospheric CO2. Validation measures prove the utility of the RTA modeling approach for mapping current tree importance values across large areas, leading to increased confidence in the predictions of potential future species distributions. With our analysis of potential effects, we show that roughly 30 species could expand their range and/or weighted importance at least 10%, while an additional 30 species could decrease by at least 10%, following equilibrium after a changed climate. Depending on the global change scenario used, 4-9 species would potentially move out of the United States to the north. Nearly half of the species assessed (36 out of 80) showed the potential for the ecological optima to shift at least 100 km to the north, including seven that could move >250 km. Given these potential future distributions, actual species redistributions will be controlled by migration rates possible through fragmented landscapes.

KEYWORDS: BALANCE, CLASSIFICATION, CONTINENTAL-SCALE, DECISION-TREE, FORESTS, MODEL, PINE, RESPONSES, TEMPERATURE, VEGETATION

1040

Iverson, L.R., A. Prasad, and M.W. Schwartz. 1999. Modeling potential future individual tree-species distributions in the eastern United States under a climate change scenario: a case study with Pinus virginiana. *Ecological Modelling 115(1):77-93.*

We are using a deterministic regression tree analysis model (DISTRIB) and a stochastic migration model (SHIFT) to examine potential distributions of similar to 66 individual species of eastern US trees under a 2 x CO2 climate change scenario. This process is demonstrated for Virginia pine (Pinus virginiana). USDA Forest Service Forest Inventory and Analysis data for more than 100 000 plots and nearly 3 million trees east of the 100th meridian were analyzed and aggregated to the county level to provide species importance values for each of more than 2100 counties. County-level data also were compiled on climate, soils, land use, elevation, and spatial pattern. Regression tree analysis (RTA) was used to devise prediction rules from current species-environment relationships, which were then used to replicate the current distribution and predict the potential future distributions under two scenarios of climate change (2 x CO2). RTA allows different variables to control importance value predictions at different regions, e.g. at the northern versus southern range limits of a species. RTA outputs represent the potential 'environmental envelope' shifts required by species, while the migration model predicts the more realistic shifts based on colonization probabilities from varying species abundances within a fragmented landscape. The model shows severely limited migration in regions of high forest fragmentation, particularly when the species is low in abundance near the range boundary. These tools are providing mechanisms for evaluating the relationships among various environmental and landscape factors associated with tree- species importance and potential migration in a changing global climate.

KEYWORDS: BALANCE, FORESTS, MIGRATION, RANGE, RESPONSES, VEGETATION

1041

Iwasaki, I., N. Kurano, and S. Miyachi. 1996. Effects of high-CO2 stress on photosystem II in a green alga, Chlorococcum littorale, which has a tolerance to high CO2. *Journal of Photochemistry and Photobiology B-Biology 36(3):327-332.*

A green alga, Chlorococcum littorale, is known to have a tolerance to high CO2 conditions. By a sudden change from stir to high CO2, PSII activity of C. littorale decreased temporarily and then recovered, while PSI activity showed the opposite change (Pesheva et al., Plant Cell Physiol, 35 (1994) 379-387). To investigate the efficiency of energy captured by open PSII reaction centers, the quenching of chlorophyll fluorescence of intact cells of C. littorale was analyzed. The data obtained are compared with those obtained with cells of Stichococcus bacillaris which has little tolerance to high CO2. Activities of photosynthetic oxygen evolution of the intact cells and DCIP photoreduction with the crude membrane fraction of C. littorale decreased within 1-2 days, and after about 4 days both activities recovered and/or were elevated to higher levels than those in the air conditions. During this temporal decrease in these activities, the effective quantum yield of PSII also lowered to about 50% of that in air. The values of F- v/F-m transiently decreased indicating photoinhibition in PSII. Such fluorescence quenching parameters recovered after about 4 days. On the other hand, the activities of PSII and other photosynthetic characteristics did not recover in S. bacillaris.

KEYWORDS: CHLOROPHYLL FLUORESCENCE, FLUOROMETER, LIGHT, PH, PHOTOSYNTHESIS

1042
Izrael, Y.A., S.M. Semenov, I.M. Kunina, and T.V. Zamaraeva. 1994. Modification of direct effect of carbon-dioxide on higher- plants due to tropospheric ozone impact. *Doklady Akademii Nauk 338(5):711-713.*

KEYWORDS: ATMOSPHERIC CO2 ENRICHMENT, GROWTH

1043
Jablonski, L.M. 1997. Responses of vegetative and reproductive traits to elevated CO2 and nitrogen in Raphanus varieties. *Canadian Journal of Botany-Revue Canadienne De Botanique 75(4):533-545.*

The relationships between the responses to elevated CO2 of the vegetative and reproductive phase were investigated in radish, used as a test system. The hypothesis that an increase in nonfoliar vegetative storage capacity promotes reproductive output was tested. Three cultivars of Raphanus sarivus and the wild, Raphanus raphanistrum, differing in root to shoot ratios, were grown under two levels of CO2 and two levels of nitrogen fertilization. Varieties possessed different strategies of carbon storage and showed distinct responses to CO2 at each vegetative harvest time. Vegetative sinks of hypocotyls, petioles, and young blades were enhanced by CO2. Nitrogen promoted vegetative shoot growth, but did not enhance the reproductive response to CO2. By the end of the reproductive phase, varieties did not differ in total biomass. Reproductive response to CO2 may have been limited by the lack of an effect on the timing of flowering. Correlations in CO2 enhancement ratios were examined in 12 traits of each phase. Only vegetative total leaf area correlated with reproductive mass. Foliar starch correlated with decreased abortion. Enhancements in vegetative biomass did not correlate with any reproductive response. Detailed studies of the reproductive phase are needed to understand the whole-plant response to elevated CO2.

KEYWORDS: C-3 PLANTS, CARBON-DIOXIDE ENRICHMENT, GROWTH, LEAVES, NITRATE, NUTRITION, PHOTOSYNTHESIS, PRODUCTIVITY, RAPHANISTRUM, WILD RADISH

1044
Jach, M.E., and R. Ceulemans. 1999. Effects of elevated atmospheric CO2 on phenology, growth and crown structure of Scots pine (Pinus sylvestris) seedlings after two years of exposure in the field. *Tree Physiology 19(4-5):289-300.*

Three-year-old Scots pine (Pinus sylvestris L.) seedlings were grown for two years in the ground in open-top chambers supplied with either an ambient or elevated (ambient + 400 mu mol mol(- 1)) CO2 concentration. Phenological observations and measurements of height and stem diameter growth, absolute and relative growth rates, starch and soluble carbohydrate concentrations of the needles, and crown structure and needle properties were made at frequent intervals throughout the two growing seasons. Elevated CO2 significantly advanced the date of bud burst in both years. The increase in total needle area in response to elevated CO2 was accounted for by longer shoots and an increase in individual needle area in the first year, and by an increase in the number and length of shoots in the second year. Stem diameter and tree height were enhanced more by the elevated CO2 treatment in the first year than in the second, indicating a decreased effect of CO2 on growth over time. This was confirmed by a study of absolute and relative growth rates of leader shoots. During the first growing season of CO2 enrichment, mean weekly relative growth rates over the growing season (RGR(m)) were significantly enhanced. During the second year, RGR(m) in ambient CO2 closely matched that in elevated CO2.

KEYWORDS: ABIES L KARST, BIOMASS ALLOCATION, CARBON-DIOXIDE ENRICHMENT, FROST DAMAGE, MINERAL NUTRITION, PHOTOSYNTHESIS, PLANT-RESPONSES, SEASONAL-CHANGES, SPRUCE PICEA-SITCHENSIS, WATER-STRESS

1045
Jackson, R.B., Y. Luo, Z.G. Cardon, O.E. Sala, C.B. Field, and H.A. Mooney. 1995. Photosynthesis, growth and density for the dominant species in a CO2-enriched grassland. *Journal of Biogeography 22(2-3):221-225.*

Although increased atmospheric CO2 frequently increases short- term photosynthetic rates, longer-term photosynthetic responses are more variable. Plant size, reproduction and ecosystem carbon gain are determined, in part, by such photosynthetic responses. Here we examine photosynthetic regulation for the dominant species in a grassland exposed to elevated CO2 and examine whether the observed photosynthetic responses contribute to changes in growth, reproduction and plant density in the same grassland. Avena barbata in the field showed little evidence of photosynthetic downregulation with elevated CO2 at the end of the growing season (differences between treatments <10%). Glasshouse studies also showed little evidence for downregulation of photosynthesis measured at various light and intercellular CO2. concentrations. Although specific leaf mass (leaf mass per unit leaf area) for Avena increased 20% in the field with elevated CO2, leaf nitrogen concentrations decreased 25%, resulting in an 11% reduction in leaf N on a leaf-area basis. For the relatively wet 1993 growing season, Avena barbata increased its size and reproduction approximately 30% in elevated CO2, with a 21% decrease in population density. For the relatively dry 1994 season Avena density was almost doubled in elevated CO2, but increases in individual size and reproduction with CO2 were small (6-18%). The primary effect of CO2 in the drier year appears to have been greater Avena survival, rather than increased individual size.

KEYWORDS: AMBIENT, ATMOSPHERIC CO2, CARBON DIOXIDE, ECOSYSTEM RESPONSES, ELEVATED CO2 CONCENTRATIONS, EXPOSURE, PLANT

1046
Jackson, R.B., and H.L. Reynolds. 1996. Nitrate and ammonium uptake for single- and mixed-species communities grown at elevated CO2. *Oecologia 105(1):74-80.*

Sustained increases in plant production in elevated CO2 depend on adequate belowground resources. Mechanisms for acquiring additional soil resources include increased root allocation and changes in root morphology or physiology. CO2 research to date has focused almost exclusively on changes in biomass and allocation. We examined physiological changes in nitrate and ammonium uptake in elevated CO2, hypothesizing that uptake rates would increase with the amount of available CO2. We combined our physiological estimates of nitrogen uptake with measurements of root biomass to assess whole root-system rates of nitrogen uptake. Surprisingly, physiological rates of ammonium uptake were unchanged with CO2, and rates of nitrate uptake actually decreased significantly ($P<0.005$). Root biomass increased 23% in elevated CO2 ($P<0.005$), but almost all of this increase came in fertilized replicates. Rates of root-system nitrogen uptake in elevated CO2 increased for ammonium in nutrient-rich soil ($P<0.05$) and were unchanged for nitrate ($P>0.80$). Root-system rates of nitrogen uptake were more strongly correlated with physiological uptake rates than with root biomass in unamended soil, but the reverse was true in fertilized replicates. We discuss nitrogen uptake and changes in root biomass in the context of root nutrient concentrations (which were generally

unchanged with CO2) and standing pools of belowground plant nitrogen. In research to date, there appears to be a fairly general increase in root biomass with elevated CO2, and little evidence of up-regulation in root physiology.

KEYWORDS: ANNUAL GRASSLAND, ATMOSPHERE, CARBON DIOXIDE, ECOSYSTEMS, ENRICHMENT, NITROGEN, PLANT, PRODUCTIVITY, RESPONSES, SOIL

1047

Jackson, R.B., O.E. Sala, C.B. Field, and H.A. Mooney. 1994. Co2 alters water-use, carbon gain, and yield for the dominant species in a natural grassland. *Oecologia 98(3-4):257-262.*

Global atmospheric CO2 is increasing at a rate of 1.5-2 ppm per year and is predicted to double by the end of the next century. Understanding how terrestrial ecosystems will respond in this changing environment is an important goal of current research. Here we present results from a field study of elevated CO2 in a California annual grassland. Elevated CO2 led to lower leaf- level stomatal conductance and transpiration (approximately 50%) and higher mid-day leaf water potentials (30-35%) in the most abundant species of the grassland, Avena barbata Brot. Higher CO2 concentrations also resulted in greater midday photosynthetic rates (70% on average). The effects of CO2 on stomatal conductance and leaf water potential decreased towards the end of the growing season, when Avena began to show signs of senescence. Water-use efficiency was approximately doubled in elevated CO2, as estimated by instantaneous gas-exchange measurements and seasonal carbon isotope discrimination. Increases in CO2 and photosynthesis resulted in more seeds per plant (30%) and taller and heavier plants (27% and 41%, respectively). Elevated CO2 also reduced seed N concentrations (9%).

KEYWORDS: ANNUALS, ELEVATED CO2, ENRICHMENT, GROWTH, PLANTS, RESPONSES, SEEDLINGS, TREES

1048

Jackson, R.B., O.E. Sala, J.M. Paruelo, and H.A. Mooney. 1998. Ecosystem water fluxes for two grasslands in elevated CO2: a modeling analysis. *Oecologia 113(4):537-546.*

The need to combine data from CO2 field experiments with climate data remains urgent, particularly because each CO2 experiment cannot run for decades to centuries. Furthermore, predictions for a given biome need to take into account differences in productivity and leaf area index (LAI) independent of CO2-derived changes. In this study, we use long-term weather records and field data from the Jasper Ridge CO2 experiment in Pale Alto, California, to model the effects of CO2 and climate variability on ecosystem water fluxes. The sandstone and serpentine grasslands at Jasper Ridge provide a range of primary productivity and LAI, with the sandstone as the more productive system. Modeled soil water availability agreed well with published observations of time-domain reflectometry in the CO2 experiment. Simulated water fluxes based on 10-year weather data (January 1985-December 1994) showed that the sandstone grassland had a much greater proportion of water movement through plants than did the serpentine; transpiration accounted for approximately 30% of annual fluxes in the sandstone and only 10% in the serpentine. Although simulated physiological and biomass changes were similar in both grasslands, the consequences of elevated CO2 were greater for the sandstone water budget. Elevated CO2 increased soil drainage by 20% in the sandstone, despite an approximately one-fifth increase in plant biomass; in the serpentine, drainage increased by <10% and soil evaporation was unchanged for the same simulated biomass change. Phenological changes, simulated by a 15-day lengthening of the growing season, had minimal impacts on the water budget. Annual variation in the timing and amount of rainfall was important for water fluxes in both grasslands. Elevated CO2 increased sandstone drainage > 50 mm in seven of ten years, but the relative increase in drainage varied from 10% to 300% depending on the year. Early-season transpiration in the sandstone decreased between 26% and 41%, with elevated CO2 resulting in a simulated water savings of 54-76 mm. Even in years when precipitation was similar (e.g., 505 and 479 mm in years 3 and 4), the effect of CO2 varied dramatically. The response of grassland water budgets to CO2 depends on the productivity and structure of the grassland, the amount and timing of rainfall, and CO2-induced changes in physiology. In systems with low LAT, large physiological changes may not necessarily alter total ecosystem water budgets dramatically.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CANOPY, EXCHANGE, GROWTH, LEAF, NITROGEN, PHOTOSYNTHESIS, PLANT, RESPONSES, TRANSPIRATION

1049

Jacob, J., and B.G. Drake. 1993. Long-term co2 enrichment effects on the rubisco content and activity in 2 field-grown C3 plants. *Plant Physiology 102(1):46.*

1050

Jacob, J., C. Greitner, and B.G. Drake. 1995. Acclimation of photosynthesis in relation to rubisco and nonstructural carbohydrate contents and in-situ carboxylase activity in scirpus-olneyi grown at elevated co2 in the field. *Plant, Cell and Environment 18(8):875-884.*

Stands of Scirpus olneyi, a native saltmarsh sedge with C-3 photosynthesis, had been exposed to normal ambient and elevated atmospheric CO2 concentrations (C-a) in their native habitat since 1987, The objective of this investigation was to characterize the acclimation of photosynthesis of Scirpus olneyi stems, the photosynthesizing organs of this species, to long-term elevated C-a treatment in relation to the concentrations of Rubisco and non-structural carbohydrates, Measurements were made on intact stems in the field under existing natural conditions and in the laboratory under controlled conditions on stems excised in the field early in the morning, Plants grown at elevated C-a had a significantly higher (30-59%) net CO2 assimilation rate (A) than those grown at ambient C-a when measurements were performed on excised stems at the respective growth C-a. However, when measurements were made at normal ambient C-a, A was smaller (45-53%) in plants grown at elevated C-a than in those grown at ambient C-a. The reductions in A at normal ambient C-a, carboxylation efficiency and in situ carboxylase activity were caused by a decreased Rubisco concentration (30-58%) in plants grown at elevated C-a; these plants also contained less soluble protein (39-52%). The Rubisco content was 43 to 58% of soluble protein, and this relationship was not significantly altered by the growth CO2 concentrations. The Rubisco activation state increased slightly, but the in situ carboxylase activity decreased substantially in plants grown at elevated C-a. When measurements were made on intact stems in the field, the elevated C-a treatment caused a greater stimulation of A (100%) and a smaller reduction in carboxylation efficiency (which was not statistically significant) than when measurements were made on excised stems in the laboratory. The possible reasons for this are discussed. Plants grown at elevated C-a contained more non-structural carbohydrates (25-53%) than those grown at ambient C-a. Plants grown at elevated C-a appear to have sufficient sink capacity to utilize the additional carbohydrates formed during photosynthesis. Overall, our results are in agreement with the hypothesis that elevated C-a leads to an increased carbohydrate concentration and the ensuing acclimation of the photosynthetic apparatus in C-3 plants results in a reduction in the protein complement, especially Rubisco, which reduces the photosynthetic capacity in plants grown at elevated C-a, relative to plants grown at normal ambient C-a. Nevertheless, when compared at their respective growth C-a, Scirpus olneyi plants grown at

elevated C-a in their native habitat maintained a substantially higher rate of photosynthesis than those grown at normal ambient C-a even after 8 years of growth at elevated C-a.

KEYWORDS: ACTIVATION, C-3, CARBON-DIOXIDE CONCENTRATION, ENRICHMENT, HIGH ATMOSPHERIC CO2, LEAVES, PLANTS, RESPONSES, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE, SUNFLOWER

1051
Jacoby, G.C., and R.D. DArrigo. 1997. Tree rings, carbon dioxide, and climatic change. *Proceedings of the National Academy of Sciences of the United States of America 94(16):8350-8353.*

Tree rings have been used in various applications to reconstruct past climates as well as to assess the effects of recent climatic and environmental change on tree growth, In this paper we briefly review two wags that tree rings provide information about climate change and CO2: (i) in determining whether recent: warming during the period of instrumental observations is unusual relative to prior centuries to millennia, and thus might be related to increasing greenhouse gases; and (ii) in evaluating whether enhanced radial growth has taken place in recent decades that appears to be unexplained by climate and might instead be due to increasing atmospheric CO2 or other nutrient fertilization, It is found that a number of tree-ring studies from temperature-sensitive settings indicate unusual recent warming, although there are also exceptions al. certain sires, The present tree-ring evidence for a possible CO2 fertilization effect under natural environmental conditions appears to be very limited.

KEYWORDS: AMERICA, ATMOSPHERIC CO2, ENHANCEMENT, GROWTH, TRENDS

1052
Jager, H.J., U. Hertstein, and A. Fangmeier. 1999. The European Stress Physiology and Climate Experiment - project 1. wheat (ESPACE-wheat): introduction, aims and methodology. *European Journal of Agronomy 10(3-4):155-162.*

The response of crops to CO2 enrichment represents an issue of major concern both for scientists and for policymakers. In a concerted programme funded by the Commission of the European Communities, a Europe-wide experimental and modeling study was carried out to investigate the effects of increasing atmospheric CO2 concentrations, and of environmental stresses such as ozone or water/nutrient shortage, under different climatic conditions on wheat (Triticum aestivum L.). This contribution describes the experimental network and the standard protocol set-up for the assessments which served to improve and to validate process-orientated wheat growth simulation models. (C) 1999 Elsevier Science B.V. All rights reserved.

KEYWORDS: AIR CO-2 ENRICHMENT, ATMOSPHERIC CO2, CARBON DIOXIDE, ELEVATED CO2, GROWTH, O-3, OZONE, RESPONSES, TEMPERATURE, YIELD

1053
Jalil, A., and R.M. Carlson. 1993. Potassium uptake by marianna plum under limited oxygen and elevated carbon-dioxide levels in the root atmosphere. *Journal of Plant Nutrition 16(4):723-737.*

Potassium (K) uptake rates were determined for Marianna 2624 rootstocks with 'French' prune scions using th nutrient solution depletion technique. The nutrient solutions were bubbled with factorial combinations of nitrogen (N2), oxygen (O2), and carbon dioxide (CO2) to create treatment root atmospheres with O2 ranging from 0.01 to 0.10 m3/m3 and CO2 ranging from 0 to 0.05 m3/m3. The K+ uptake rate was more susceptible to 02 deprivation than to elevated CO2 in the root atmosphere. Decreasing 02 levels from 0.10 M3/M3 decreased K+ uptake in a hyperbolic fashion to no net uptake at 0.01 M3/M3 02. Increasing root atmosphere CO2 from 0 to 0.05 M3/M3 had a small depressing effect on net K+ influx from 60 muM K+ solutions at 0.10 and 0.05 M3/M3 02, but no effect when 02 was 0.025 or 0.01 M3/M3. Elevating CO2 decreased Km for the net K+ influx rate at 0.10 and 0.05 M3/M3 02. Increased pH buffering from higher HCO3 concentration at the plasma membrane surface was suggested to explain the CO2 effect on Km.

KEYWORDS: GROWTH, WHEAT SEEDLINGS

1054
Jansen, D.M. 1990. Potential rice yields in future weather conditions in different parts of asia. *Netherlands Journal of Agricultural Science 38(4):661-680.*

Future climate change is expected to vary between regions, with possible different effects on crop growth. Various sites in Asia were selected to represent major rice growing environments. Historic weather data of these sites were adapted to possible changes in temperature and in CO2 level, to mimic climate change. Potential rice yields at present, and for the years 2020 and 2100 were calculated with a crop growth simulation model. Simulated yields rose in low and middle temperature change scenarios, but decreased in the high temperature scenario. Effects were stronger in the year 2100, when also regional differences became clear: more than elsewhere, yields were affected by high temperatures between 10 and 35-degrees-N. Water use efficiency decreased in the high temperature scenario irrespective of CO2 scenario, and increased otherwise.

KEYWORDS: CO2- ENRICHMENT, GROWTH, NITROGEN, ORYZA SATIVA L, PHOTOSYNTHESIS, TEMPERATURE

1055
Janssens, I.A., M. Crookshanks, G. Taylor, and R. Ceulemans. 1998. Elevated atmospheric CO2 increases fine root production, respiration, rhizosphere respiration and soil CO2 efflux in Scots pine seedlings. *Global Change Biology 4(8):871-878.*

In this study, we investigated the impact of elevated atmospheric CO2 (ambient + 350 mu mol mol(-1)) on fine root production and respiration in Scots pine (Pinus sylvestris L.) seedlings. After six months exposure to elevated CO2, root production measured by root in-growth bags, showed significant increases in mean total root length and biomass, which were more than 100% greater compared to the ambient treatment. This increased root length may have lead to a more intensive soil exploration. Chemical analysis of the roofs showed that the roots in the elevated treatment accumulated more starch and had a lower C/N-ratio. Specific root respiration rates were significantly higher in the elevated treatment and this was probably attributed to increased nitrogen concentrations in the roots. Rhizospheric respiration and soil CO2 efflux were also enhanced in the elevated treatment. These results clearly indicate that under elevated atmospheric CO2 root production and development in Scots pine seedlings is altered and respiratory carbon losses through the root system are increased.

KEYWORDS: ALLOCATION, CARBON-DIOXIDE ENRICHMENT, COMPENSATORY RESPONSES, GROWTH, LOBLOLLY-PINE, NITROGEN, PLANTAGO-MAJOR, PONDEROSA PINE, TEMPERATURE, TREES

1056

Jarvis, A.J., T.A. Mansfield, and W.J. Davies. 1999. Stomatal behaviour, photosynthesis and transpiration under rising CO2. *Plant, Cell and Environment 22(6):639-648.*

The literature reports enormous variation between species in the extent of stomatal responses to rising CO2. This paper attempts to provide a framework within which some of this diversity can be explained. We describe the role of stomata in the short-term response of leaf gas exchange to increases in ambient CO2 concentration by developing the recently proposed stomatal model of Jarvis gr Davies (1998). In this model stomatal conductance is correlated with the functioning of the photosynthetic system so that the effects of increases in CO2 on stomata are experienced through changes in the rate of photosynthesis in a simple and mechanistically transparent way This model also allows us to consider the effects of evaporative demand and soil moisture availability on stomatal responses to photosynthesis and therefore provides a means of considering these additional sources of variation. We emphasize that the relationship between the rate of photosynthesis and the internal CO2 concentration and also drought will have important effects on the relative gains to be achieved under rising CO2.

KEYWORDS: ASSIMILATION, ATMOSPHERIC CO2, CARBON DIOXIDE, CONDUCTANCE, ELEVATED CO2, EMPIRICAL-MODEL, LEAF GAS- EXCHANGE, PARTIAL-PRESSURE, RESPONSES, WATER-VAPOR

1057
Jarvis, P.G. 1995. The role of temperate trees and forests in CO2 fixation. *Vegetatio 121(1-2):157-174.*

The global flask network data indicate that the temperate and boreal forests of the northern hemisphere are a significant sink for anthropogenic CO2. Bowen ratio and eddy covariance technology have been used to measure the net CO2 exchange of deciduous and coniferous forest. Some results from an earlier study on spruce with the Bowen ratio technique are presented. New technology that has been developed to measure fluxes continuously by forest stands is described and data are presented to show the net exchange flux of CO2 by temperate forests. These data support the hypothesis that temperate and boreal forests are significant sinks for carbon dioxide. An extensive programme of experimental impact studies is being carried out by a network of 12 laboratories in Europe funded by the European Commission. Parallel studies are in progress in North America and elsewhere. These studies indicate that doubling the atmospheric CO2 concentration results in increases in tree biomass of 30-40%. Interactions with nutrition are particularly significant. If nitrogen is added at a commensurate rate, the overall effect is that trees grow larger more quickly in elevated CO2 than in ambient air but they are essentially very similar in structure and physiology. However, if nutrients are in short supply, developmental and physiological changes occur. Then elevated CO2 causes changes in dry mass allocation to roots, in phenology of bud burst and set, in photosynthesis, in respiration, and in tree water relations. These changes are exaggerated in low nutrition situations. Process-based models have been developed to scale- up from leaf and tree to the stand scale. These models contain explicit description of processes affected by CO2, and are parameterised using the data collected in the impact studies. It is concluded that forests in the temperate and boreal region can effectively contribute to the removal of anthropogenic CO2 from the atmosphere and that tree growth and production of long-lived wood products should be encouraged as a major contribution towards off-setting the greenhouse effect caused by the burning of fossil fuels.

KEYWORDS: ATMOSPHERE-BIOSPHERE EXCHANGE, CARBON, ENRICHMENT, EVAPOTRANSPIRATION, MAESTRO, SINKS, SITKA SPRUCE, STANDS, STORAGE, WEATHER

1058
Jauhiainen, J., and J. Silvola. 1999. Photosynthesis of Sphagnum fuscum at long-term raised CO2 concentrations. *Annales Botanici Fennici 36(1):11-19.*

Rate of net photosynthesis in Sphagnum fuscum (Schimp.) Klinggr. was measured during long-term (50-122 days), and subsequently during short-term (1/2 h), exposure to 350, 700, 1000 or 2000 ppm CO2 concentrations. Raised CO2 concentrations caused a general increase in the rate of net photosynthesis, increasing the rate of photosynthesis at light saturation and causing a given rate of net CO2 exchange to be reached at lower light fluxes. The relative increase in the rate of net photosynthesis by increasing radiation fluxes was independent of the CO2 treatment. The rates of net photosynthesis at enhanced CO2 concentrations gradually decreased compared to rates found with the 350 ppm treatment and this acclimation was also noticed during short-term exposure to all four CO2 concentrations. At 2000 ppm of CO2, the depression of net photosynthesis at high water contents, found at lower CO2 concentrations, was removed. Observed rates of net photosynthesis indicated that water-use efficiency of Sphagna was not coupled with constant long-term CO2 concentrations.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, CARBON DIOXIDE, CARBOXYLASE, ELEVATED CO2, EXPOSURE, MOSS HYLOCOMIUM-SPLENDENS, NORTHERN PEATLANDS, PEAT MOSSES, WATER-CONTENT

1059
Jauhiainen, J., J. Silvola, K. Tolonen, and H. Vasander. 1997. Response of Sphagnum fuscum to water levels and CO2 concentration. *Journal of Bryology 19:391-400.*

Sphagnum fuscum samples collected from an ombrotrophic bog were grown in a greenhouse at six water levels (0,5. 10, 15, 25 and 30 cm) below the capitulam level and in four concentrations of CO2 (350, 700, 1000 and 2000 ppm). The cores of S, fuscum were treated for 87 days and length increment was measured by the plastic strip method and by innate time markers, Water content of the shoot, dry mass of the capitulum, dry mass per unit length of stem and production of dry mass were measured at the end of the experiment. The water content, capitulum dry mass, dry mass per unit length of stem, length increment and dry mass production differed markedly for S. fuscum grown in different water levels. With lower water levels, the water content of the shoot decreased and the dry mass of both the capitulum and unit length of stem increased. The total length increment was highest when the water level was at or near the capitulum level (0-10 cm). No clear trend in dry mass production on an areal basis could be found due to uncoupled responses in length increment and stem dry mass at the experimental water levels. Neither capitulum dry mass nor dry mass per unit length of stem showed distinct trends in S. fuscum grown at different ambient CO2 concentrations. Some increase in length increment and in dry mass production was detected at CO2 concentrations above 350 ppm, but this effect appeared only at high water levels. It is suggested that the low response in length increment and production to CO2 concentration resulted in part from insufficient moisture for photosynthesis at the lower water levels. Also, the possibility of increased nonstructural production is discussed.

KEYWORDS: DECAY, ELEVATED CO2, ENVIRONMENT, FOREST, GROWTH, HABITAT, PEAT MOSSES, PHOTOSYNTHESIS, SOUTHERN FINLAND, SWEDISH RAISED BOG

1060
Jauhiainen, J., H. Vasander, and J. Silvola. 1994. Response of sphagnum-fuscum to n deposition and increased co2. *Journal of Bryology 18:83-96.*

The length increment and production of Sphagnum fuscum with enhanced nitrogen deposition (0, 10, 30 and 100 kg N ha(-1) yr(-1)) and CO2 concentration (350, 700, 1000 and 2000 ppm) were measured. The experiment was carried out in the glasshouse, where S. fuscum was grown with the water table maintained at 10 cm below the moss surface for 120 d. For length growth, 10 kg N ha(-1) yr(-1): and for biomass production, 30 kg N ha(-1) yr(-1) were found to be the optimal loads. A load of 100 kg N ha(-1) yr(-1) inhibited elongation and biomass production almost completely. An increased CO2 concentration reduced length increment slightly, but it did not have a significant effect on biomass production. However, above ambient CO2 concentrations increased capitulum density and stem dry mass per unit length. In addition, increased CO2 concentration accelerated relative growth in Sphagnum carpets when these also received additional nitrogen. The study highlights the high degree of spatial variability that occurs within Sphagnum fuscum. Differences in growth and biomass production between samples, not found in natural conditions, emerged during the experiment. On the basis of our results, the present nitrogen deposition load in Southern Finland (ca 6-10 kg N ha(-1) yr(-1)) is quite suitable for the growth and production of S. fuscum. If N deposition increased substantially, differences in the vitality of the species might be expected.

KEYWORDS: ATMOSPHERIC NITROGEN, BALANCE, CARBON DIOXIDE, GROWTH, MOSSES, PHOTOSYNTHESIS, RAISED BOG, SOUTHERN FINLAND, TEMPERATURE, TUSSOCK TUNDRA

1061

Jauhiainen, J., H. Vasander, and J. Silvola. 1998. Nutrient concentration in Sphagna at increased N-deposition rates and raised atmospheric CO2 concentrations. *Plant Ecology 138(2):149-160.*

Sphagnum fuscum, S. magellanicum, S. angustifolium and S. warnstorfii were treated with N deposition rates (0, 10, 30 and 100 kg ha(-1) a(-1)) and with four atmospheric CO2 concentrations (350, 700, 1000 and 2000 ppm) in greenhouse for 71-120 days. Thereafter, concentrations of total N, P, K, Ca and Mg in the capitulae of the Sphagna were determined. The response of each species to N deposition was related to ecological differences. With increasing N deposition treatments, moss N concentrations increased and higher N:P- ratios were found, the increase being especially clear at the highest N load. Sphagnum fuscum, which occupies ombrotrophic habitats, was the most affected by the increased nitrogen load and as a consequence the other elements were decreased. Oligotrophic S. magellanicum, wide nutrient status tolerant S. angustifolium and meso-eutrophic S. warnstorfii tolerated better increased N deposition, though there were increased concentrations of Ca and Mg in S. warnstorfii and Mg in S. magellanicum. Nitrogen and P concentrations decreased with raised CO2 concentrations, except for S. magellanicum. This seems to be the first time this kind of response in nutrient concentrations to enhanced CO2 concentration has been shown to exist in bryophytes. The concentration of K clearly decreased in S. fuscum as did the concentration of Mg in the other Sphagna with increasing CO2. Sphagnum angustifolium and S. magellanicum, which are the less specialized species, were the least affected by the CO2 treatments.

KEYWORDS: ELEMENT CONCENTRATIONS, ELEVATED CARBON-DIOXIDE, GROWTH, MIRE WATER, NITRATE REDUCTASE, NITROGEN, PEAT BOGS, PHOTOSYNTHESIS, RESPONSES, WATER CHEMISTRY

1062

Jenkinson, D.S., D.E. Adams, and A. Wild. 1991. Model estimates of CO2 emissions from soil in response to global warming. *Nature 351(6324):304-306.*

ONE effect of global warming will be to accelerate the decomposition of soil organic matter, thereby releasing CO2 to the atmosphere, which will further enhance the warming trend 1- 7. Such a feedback mechanism could be quantitatively important, because CO2 is thought to be responsible for approximately 55% of the increase in radiative forcing arising from anthropogenic emissions of gases to the atmosphere 8, and there is about twice as much carbon in the top metre of soil as in the atmosphere 9. Here we use the Rothamsted model for the turnover of organic matter in soil 3 to calculate the amount of CO2 that would be released from the world stock of soil organic matter if temperatures increase as predicted, the annual return of plant debris to the soil being held constant. If world temperatures rise by 0.03-degrees-C yr-1 (the increase considered as most likely by the Intergovernmental Panel on Climate Change 8), we estimate that the additional release of CO2 from soil organic matter over the next 60 years will be 61 x 10(15) gC. This is approximately 19% of the CO2 that will be released by combustion of fossil fuel during the next 60 years if present use of fuel continues unabated.

KEYWORDS: C-14-LABELED RYEGRASS, DECOMPOSITION, FIELD, PLANT- MATERIAL, STRAW, TERRESTRIAL CARBON STORAGE

1063

Jiang, G.M., and G.H. Lin. 1997. Changes of photosynthetic capacity of some plant species under very high CO2 concentrations in Biosphere 2. *Chinese Science Bulletin 42(10):859-864.*

KEYWORDS: ATMOSPHERIC CO2, ENRICHMENT, RESPONSES

1064

Jiang, W.B., A. Lers, E. Lomaniec, and N. Aharoni. 1999. Senescence-related serine protease in parsley. *Phytochemistry 50(3):377-382.*

During leaf senescence protein degradation is enhanced. In order to obtain information on the enzymes involved in this process, a study was initiated to identify and characterize proteases whose activity is elevated in artificially senescing parsley leaves. A 70-kDa serine protease (EC 3.4.21) was identified by an activity gel assay. This protease activity, which is low in young leaves, was found to increase considerably in parallel to the advance of senescence and the reduction in the protein content of the leaves. A high correlation between the progress of senescence and the increase in the activity of the 70 kDa serine protease was demonstrated. Treatments with CO2 or gibberellic acid, which retard senescence, reduced the protease's activity, whereas acceleration of senescence with ethylene enhanced it.

KEYWORDS: CYSTEINE, INDUCTION, PLANTS

1065

Jiao, J., P. Goodwin, and B. Grodzinski. 1999. Inhibition of photosynthesis and export in geranium grown at two CO2 levels and infected with Xanthomonas campestris pv. Pelargonii. *Plant, Cell and Environment 22(1):15-25.*

The effects of CO2 enrichment on growth of Xanthomonas campestris pv. pelargonii and the impact of infection on the photosynthesis and export of attached, intact, 'source' leaves of geranium (Pelargonium x domesticum, 'Scarlet Orbit Improved') are reported. Two experiments were performed, one with plants without flower buds, and another with plants which were flowering. Measurements were made on healthy and diseased leaves at the CO2 levels (35 Pa or 90 Pa) at which the plants were grown. There were no losses of chlorophyll, or any signs of visible chlorosis or necrosis due to infection. Lower numbers of bacteria were

found in leaves at high CO2, suggesting growth at elevated CO2 created a less favourable condition in the leaf for bacterial growth. Although high CO2 lowered the bacterial number in infected leaves, reductions in photosynthesis and export were greater than at ambient CO2. The capacity of infected source leaves to export photoassimilates at rates observed in the controls was reduced in both light and darkness. In summary, the severity of infection on source leaf function by the bacteria was increased, rather than reduced by CO2 enrichment, underscoring the need for further assessment of plant diseases and bacterial virulence in plants growing under varying CO2 levels.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, C-3, CARBOXYLASE, ELEVATED CO2, LEAF, LEAVES, PLANTS, STEADY-STATE PHOTOSYNTHESIS, TRANSLOCATION

1066

Jiao, J.R., and B. Grodzinski. 1998. Environmental influences on photosynthesis and carbon export in greenhouse roses during development of the flowering shoot. *Journal of the American Society for Horticultural Science 123(6):1081-1088.*

Photosynthesis and concurrent export rates of expanded leaves on the flowering shoot of Rosa hybrida L. 'Samantha' were measured at three stages of shoot and flower bud development. At 35 and 90 Pa CO2 photosynthesis and concurrent export rates of the upper expanded leaves were greater at Stage 3 (i.e., when petal color of the flower bud was visible) than at the two earlier stages of shoot and flower development. The optimum for leaf photosynthesis and concurrent export at ambient CO2 and saturating irradiance were approximate to 25 degrees C. Export was more sensitive to increased temperature than was carbon fixation. For example, at 40 degrees C photosynthesis was 40% lower while the export rate during photosynthesis was reduced by 80 %. Increasing the photon fluence flux rate from 200 to 1000 mu mol.m(-2).s(-1) PAR increased the photosynthetic rate and the concurrent export rate at 35 and 90 Pa CO2, but the increase in export was proportionally greater than that of photosynthesis. At 35 Pa CO2, the rate of C export during photosynthesis increased from 31 to 59% of the concurrent C fixation rate. At 90 Pa CO2, export during photosynthesis increased from 38 to 62% of the photosynthesis rate. The importance of irradiance on translocation processes was further demonstrated by comparing the disappearance of label during the feed period and during an extended night period. Plants grown at each CO2 level exported about three times as much of the C- 14 fixed during a 2-hour feed period in the light as during a subsequent 15-hour dark chase period. The nighttime export and respiration rates of leaves which had been exposed to elevated CO2 levels during the feed were higher than those rates observed at ambient CO2. However, at the end of the chase period, the leaves of plants which had been exposed to CO2 enrichment during the feed also retained more C-14 than did the leaves of the plants which were at ambient CO2. Thus, although more C-14 was fixed and exported under high CO2, the same proportion of labelled assimilates were exported, respired, and retained in the dark as at ambient CO2.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, CO2-ENRICHMENT, LEAF AGE, LEAVES, NET CO-2 EXCHANGE, PLANTS, TEMPERATURE, TOMATO, TRANSLOCATION

1067

Jiao, J., M.J. Tsujita, and B. Grodzinski. 1991. Influence of radiation and CO2 enrichment on whole plant net CO2 exchange in roses. *Canadian Journal of Plant Science 71(1):245-252.*

At three stages of flowering shoot development, varying the irradiance and CO2 levels had a similar effect on the whole- plant net CO2 exchange rate (NCER) of Samantha rose plants. At 22-degrees-C, the NCER was saturated at 1000-mu-mol m-2 s-1 photosynthetically active radiation (PAR). The duration of the light period was also important in determining daily carbon (C) gain. When roses were exposed to a constant daily radiant energy dose of 17.6-mu-mol m-2 provided either as a 12-h irradiation interval at 410-mu-mol m-2 s-1 PAR or 24 h of irradiation at 204-mu-mol m-2 s-1 PAR, the plants exposed to 24 h of continuous irradiation at the lower photon flux density retained 80% more C. Under saturating irradiance, the net photosynthetic rate at an enriched (1000-mu-L L-1) CO2 level was almost double that at ambient (350-mu-L L-1) CO2. However, plants grown at ambient and enriched CO2 levels had similar whole-plant NCERs when compared at the same assay CO2 level. Under CO2 enrichment the flower stem was longer and thicker but the flower bud size at harvest was not significantly different to that of roses grown at the ambient CO2 level.

KEYWORDS: CARBON DIOXIDE, CO2, GROWTH, PHOTOSYNTHESIS

1068

Jiao, J., M.J. Tsujita, and B. Grodzinski. 1991. Influence of temperature on net CO2 exchange in roses. *Canadian Journal of Plant Science 71(1):235-243.*

The effect of temperature on net CO2 exchange of source and sink tissues of the flowering shoots and of whole plants was examined using single-stemmed Samantha roses. At all stages of shoot development, the optimal temperature range for whole-plant carbon (C) gain at saturating irradiance and ambient CO2 level was between 20-degrees and 25-degrees-C, narrower than the temperature range for optimal leaf net photosynthesis. Dark respiration increased more dramatically than photosynthesis with temperatures between 15 and 35-degrees-C. At 25-degrees-C, C loss due to respiration from the flower bud at colour bud stage accounted for 45% of the C loss of the flowering shoot. At low irradiance levels (e.g. 200-mu-mol m-2 s-1) whole-plant net photosynthesis was greater at 16-degrees than at 22-degrees-C because of a greater reduction in respiration. Lowering the night temperature from 27 to 17- degrees-C also increased daily C gain due to a reduction in the C lost at night. Whole-plant net photosynthesis of plants grown and measured at enriched (1000 +/- 100-mu-L L-1) CO2 was greater than that of plants grown and measured at ambient (350 +/- 50-mu-L L-1) level at temperatures between 15-degrees and 35-degrees-C. Furthermore, the optimal temperatures for whole- plant net photosynthesis in CO2 enrichment was higher than at ambient CO2 level.

KEYWORDS: AGE, CARBON, LEAF, PHOTOSYNTHESIS, PLANTS, TRANSPORT

1069

Jifon, J.L., A.L. Friend, and P.C. Berrang. 1995. Species mixture and soil-resource availability affect the root- growth response of tree seedlings to elevated atmospheric co21. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 25(5):824-832.*

The effects of CO2 enrichment on root proliferation of loblolly pine (Pinus taeda L.) and sweetgum (Liquidambar styraciflua L.) seedlings were studied under varied water and nitrogen (N) regimes and in competitive interaction. Seedlings of each species were grown from seed as monocultures or as 50:50 pine- sweetgum mixtures in 22-L pots filled with forest soil. Seedlings were exposed to either ambient (400 ppm) or CO2- enriched (ambient plus 400 ppm) air for 32 weeks in continuously stirred tank reactors. Detailed sampling of very fine roots (<0.5 mm diam.) showed a general increase (up to 2- fold) in root length density (RLD, cm . cm(-3)) with elevated CO2; however, the effects of CO2 on RLD differed according to species, culture type, water, and N availability. In monoculture, low water with low N conditions produced the largest RLD responses to elevated CO2: 75% increase for sweetgum

and 31% increase for pine. In mixed culture, by contrast, the largest RLD responses to CO2 were observed under high water, high N regimes: pine showed a 110% increase and sweetgum a 96% increase. The total RLD of the standing crop in mixture under elevated CO2, high water, and high N was 2.6 cm . cm(-3) compared with 1.6 cm . cm(-3) in ambient CO2, with sweetgum accounting for >75% of the total RLD in both cases. These findings suggest that resource-rich rather than resource- poor soil environments could be the circumstances under which belowground interference from sweetgum would intensify in pine-sweetgum mixtures with rising atmospheric CO2.

KEYWORDS: CARBON DIOXIDE, COMPETITION, ECOSYSTEMS, ENRICHMENT, LIQUIDAMBAR- STYRACIFLUA, LOBLOLLY-PINE SEEDLINGS, PATTERNS, PLANTS, QUANTIFICATION, TAEDA SEEDLINGS

1070

Jitla, D.S., G.S. Rogers, S.P. Seneweera, A.S. Basra, R.J. Oldfield, and J.P. Conroy. 1997. Accelerated early growth of rice at elevated CO2 - Is it related to developmental changes in the shoot apex? *Plant Physiology 115(1):15-22.*

The influence of elevated CO2 on the development of the shoot apex and on subsequent vegetative growth and grain yield was investigated using rice (Oryza sativa L. cv Jarrah) grown in flooded soil at either 350 or 700 mu L CO2 L-1. At 8 d after planting (DAP), elevated CO2 increased the height and diameter of the apical dome and lengths of leaf primordia and tiller buds but had no effect on their numbers. By 16 DAP, there were five tiller buds in the apex at 700 mu L CO2 L-1 compared with only three tiller buds at 350 mu L CO2 L-1. These changes in development of the shoot apex at high CO2 were forerunners to faster development of the vegetative shoot at elevated CO2 between 11 and 26 DAP as evidenced by increases in the relative growth rates of the shoot and tillers. Accelerated development at high CO2 was responsible for the 42% increase in tiller number at the maximum tillering stage and the 57% enhancement of grain yield at the final harvest. The link between high CO2 effects on development during the first 15 DAP and final tiller number and grain yield was demonstrated by delaying exposure of plants to high CO2 for 15 d. The delay totally inhibited the tillering response to high CO2, and the increase in grain yield of 20% arose from a greater number of grains per panicle. Consequently, it can be concluded that accelerated development in the shoot apex early in development is crucial for obtaining maximum increases in grain yield at elevated atmospheric CO2 concentrations.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, CELL, ELONGATION, LEAF, LEAVES, PLANTS, PROTEINS, YIELD

1071

John-McKay, M.E., and B. Colman. 1997. Variation in the occurrence of external carbonic anhydrase among strains of the marine diatom Phaeodactylum tricornutum (Bacillariophyceae). *Journal of Phycology 33(6):988-990.*

Eleven different strains of Phaeodactylum tricornutum Bohlin were obtained from three culture collections and were examined for the presence of external and internal carbonic anhydrase (CA). Cells of all strains, grown in standing culture at alkaline pH and low dissolved inorganic carbon had internal CA, but only eight were found to have external CA. External CA activity was reduced when cultures were bubbled with air and was completely repressed when they were grown on 5% CO2. Expression of external CA activity appears to be regulated by CO2 concentration in the growth medium, but within one species, there appears to be a variation in occurrence of external CA and consequently in the mode of inorganic carbon acquisition.

KEYWORDS: ACCUMULATION, CHLORELLA-SACCHAROPHILA, CO2, CYANOBACTERIA, DISSOLVED INORGANIC CARBON, HIGHER-PLANTS, MICROALGAE, PHYTOPLANKTON

1072

Johnsen, K.H. 1993. Growth and ecophysiological responses of black spruce seedlings to elevated co2 under varied water and nutrient additions. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 23(6):1033-1042.*

Two controlled-environment studies examined growth and ecophysiological responses of black spruce (Picea mariana (Mill.) B.S.P.) seedlings to elevated CO2 under varied water and nutrient additions. Growth analyses were conducted followed by measurements of gas exchange, xylem pressure potential and foliar N concentrations. Growth under elevated CO2 (700 ppm) increased final seedling dry weights by 20-48% compared with seedling growth under ambient CO2 (350 ppm). Percent increases in seedling dry weight were greater under drought versus well- watered conditions and higher versus lower nutrient additions. Seedlings grown under elevated CO2 displayed higher water use efficiency than seedlings grown under ambient CO2. This was apparent based upon instantaneous gas exchange as well as xylem potential pressure measurements. Elevated CO2-induced stimulation of relative growth rate was greatest shortly after seedling emergence and decreased with increased seedling size. Acclimation of net photosynthesis was observed and was reversible. Analyses using allometric principles indicate net photosynthetic acclimation resulted from: (i) growth-induced nutrient dilution; (ii) a decrease in foliar N levels not owing to dilution; and (iii) a decrease in net photosynthetic activity.

KEYWORDS: ANATOMY, ATMOSPHERIC CARBON-DIOXIDE, ENRICHMENT, FORESTS, LIQUIDAMBAR- STYRACIFLUA, LOBLOLLY-PINE, PHYSIOLOGY, PINUS-TAEDA SEEDLINGS, ROOT, SHOOT

1073

Johnsen, K.H. 1994. Growth and ecophysiological responses of black spruce seedlings to elevated co2 under varied water and nutrient additions (vol 23, pg 1033, 1993). *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 24(3):646.*

1074

Johnsen, K.H., and J.E. Major. 1998. Black spruce family growth performance under ambient and elevated atmospheric CO2. *New Forests 15(3):271-281.*

Seedlings from 20 families of black spruce (Picea mariana (Mill.) B.S.P.), representing a large range in field productivity, were subjected to a greenhouse retrospective test under ambient (409 ppm - year 1, 384 ppm - year 2) and high (686 ppm - year 1, 711 ppm - year 2) atmospheric CO2 environments. After one and two growth cycles, seedling height and diameter growth significantly increased under elevated CO2. At the end of the experiment, seedlings grown under high CO2 had a mean above-ground dry weight of 48.77 g as compared to 26.36 g for seedlings grown under ambient atmospheric CO2. Families were a significant source of variation for all growth parameters. Although the family x CO2 environment interaction was not a statistically significant source of variation in the analysis of variance, the correlation between greenhouse and IS-year field height growth was weaker ($r = 0.29$, $p = 0.2177$) under elevated CO2 compared to ambient CO2 ($r = 0.51$, $p = 0.0223$) following the first growth cycle. However, following the second growth cycle, greenhouse-field correlations were similar between the two CO2 environments (ambient CO2: $r = 0.55$, p

= 0.0115; elevated CO2: r = 0.56, p = 0.0101). Thus, with this set of families, growth performance ranking after two years appears relatively stable under ambient and elevated CO2.

KEYWORDS: EARLY SELECTION, FULL-SIB FAMILIES, GAS-EXCHANGE, PHENOLOGY, RESPONSES, SEEDLINGS, TREES, WATER-STRESS

1075

Johnsen, K.H., and J.R. Seiler. 1996. Growth, shoot phenology and physiology of diverse seed sources of black spruce .1. Seedling responses to varied atmospheric CO2 concentrations and photoperiods. *Tree Physiology 16(3):367-373.*

We conducted a greenhouse experiment to determine: (1) if diverse provenances of black spruce (Picea mariana (Mill.) B.S.P.) respond similarly in growth, phenology and physiology to an approximately 300 ppm increase in atmospheric CO2 concentration, and (2) the influence of photoperiod on both provenance and provenance x CO2 interaction effects. Seedlings from provenances that originated from the Yukon (63 degrees 34' N, 135 degrees 55' W), British Columbia (58 degrees 47' N, 123 degrees 38' W), Alberta (52 degrees 22' N, 115 degrees 15' W), Newfoundland (50 degrees 54' N, 56 degrees 06' W) and Ontario (48 degrees 59' N, 80 degrees 38' W and 45 degrees 10' N, 77 degrees 10' W) were subjected to growth analysis in greenhouse growth chambers supplied with 712 +/- 93 (SD) ppm CO2 (elevated) or 394 +/- 59 ppm CO2 (ambient). Seedlings from Provenances 7000 and 6901 were also subjected to an extended photoperiod treatment and periodically measured for shoot and root gas exchange. In response to a natural photoperiod, southern provenances grew more, broke and set bud later, and partitioned more biomass to shoot versus root than northern provenances. These differences among provenances were influenced by the extended photoperiod treatment but not by the elevated CO2 treatment. Averaged across all provenances, elevated CO2 increased seedling final weights by 55%; however, the elevated CO2 treatment had no effect on the provenance differences in any measured trait. We conclude that the large differences in physiology, phenology and growth among these diverse provenances of black spruce were expressed similarly in both ambient and elevated atmospheric CO2 concentrations.

KEYWORDS: ELEVATED CO2, FAMILIES, LOBLOLLY-PINE

1076

Johnson, B.G., B.A. Hale, and D.P. Ormrod. 1996. Carbon dioxide and ozone effects on growth of a legume-grass mixture. *Journal of Environmental Quality 25(4):908-916.*

Atmospheric carbon dioxide (CO2) and photochemical ozone (O-3) have been increasing in the biosphere and will continue to do so with further industrialization and burning of fossil fuels, The purpose of this study was to examine the interaction of CO2 and O-3 on plant growth and aboveground competition using a forage mixture of alfalfa (Medicago sativa L.) and timothy (Phleum pratense L.). Mixtures were grown at two CO2 levels (350 and 700 mu L/L) in controlled environment chambers and exposed to four weekly O-3 episodes of 8-h duration with peak daily concentrations of 0.03, 0.08, 0.13, or 0.18 mu L/L on Days (d) 21, 28, 35, and 42 after seeding. Roots of individual plants were in separate containers, The plants were harvested 2 d after the fmal O-3 exposure. Total dry biomass of alfalfa and timothy was 50 and 40%, respectively, greater at 700 than at 350 mu L CO2/L with low O-3. Increasing peak O-3 concentration decreased alfalfa shoot dry biomass at 700 mu L CO2/L but not at 350 mu L/L and decreased root dry biomass at both CO2 levels. In timothy, intermediate O-3 levels reduced shoot growth but the highest level of O-3 resulted in more shoot growth in the mixture at both CO2 levels. Partitioning of dry matter to alfalfa roots was strongly retarded by increasing O- 3, particularly in the CO2-enriched environment, while timothy root growth vias unaffected by O-3. The enhancement of timothy shoot biomass is, the mixture by exposure to the highest level of O-3 at either CO2 level could not be fully explained by changes in competition between timothy and alfalfa in relation to differential O-3 tolerance.

KEYWORDS: AIR- POLLUTANTS, CLOVER, FORAGE, PASTURE, PLANTS, QUALITY, YIELD

1077

Johnson, D.W. 1999. Simulated nitrogen cycling response to elevated CO2 in Pinus taeda and mixed deciduous forests. *Tree Physiology 19(4-5):321-327.*

Interactions between elevated CO2 and N cycling Introduction were explored with a nutrient cycling model (NuCM, Johnson et ai. 1993, 1995) for a Pinus taeda L, site at Duke University, North Carolina, and a mixed deciduous site at Walker Branch, Tennessee. The simulations tested whether N limitation would prevent growth increases in response to elevated CO2, and whether growth responses to CO2 in N-limited systems could be facilitated by increasing the biomass/N ratio (reducing N concentration) or increasing litter N mineralization, or both. Nitrogen limitation precluded additional growth when target growth rates and litterfall were increased (simulating potential response to elevated CO2) at the Duke University site. At the Walker Branch site, increasing target growth and litterfall caused a 7% increase in growth. Reducing foliar N concentrations reduced growth because of N limitation created by reduced litter quality (C:N ratio), reduced decomposition and increased N accumulation on the forest floor. These effects were most pronounced at the Duke University site, because the forest floor N turnover rate was lower than at the Walker Branch site. Reducing wood N concentration allowed prolonged increases in growth because of greater biomass/N; however, N uptake was reduced, allowing greater N immobilization on the forest floor and in soil. Increased N mineralization caused increased growth at the Duke University site, but not at the Walker Branch site. These simulations pose the counterintuitive hypothesis that increased biogeochemical cycling of N (as a result of increased litterfall N) causes reduced growth in an N-limited system because of increased accumulations of N on the forest floor and in soil. Translocation of N from senescing leaves before litterfall mitigates this response by allowing the trees to retain a greater proportion of N taken up rather than recycle it back to the forest floor and soil where it can be immobilized. Eliminating N translocation at Walker Branch changed the direction as well as the magnitude of the responses in three of the four scenarios simulated. Because the NuCM model does not currently allow translocation in coniferous species, the effects of translocation on N cycling in the Duke University simulations are not known.

KEYWORDS: CARBON DIOXIDE, CYCLES, DEPOSITION, ECOSYSTEMS, FEEDBACK, MODEL, STORAGE

1078

Johnson, D.W., and J.T. Ball. 1990. Environmental-pollution and impacts on soils and forests nutrition in north-america. *Water, Air, and Soil Pollution 54:3-20.*

The effects of acid deposition, excess N deposition, and elevated CO2 on forest soils and nutrition in North America are reviewed. While there remains the possibility that acid deposition and excess N deposition are contributing to declines in red spruce, sugar maple, and southern pines, clear-cut cause and effects are still not evident. Climate is clearly a major factor in red spruce decline in the northeastern U.S., but air pollution may contribute. There is some evidence that soil solution Al may be approaching deleterious levels in southeastern red spruce forests. Lack of proper management may be a major factor in the sugar maple and southern pine declines, but once again, air pollution as a potential

contributor cannot be ignored. Nutrient budget analyses and discoveries of soils base cation depletion in certain sites suggest that base cation status is declining in forests of the southeastern U.S., but thus far, base cation deficiences are uncommon. Recent research has revealed that there are more cases of N-saturated forests in North America than was previously suspected. These systems are characterized by high rates of soil N mineralization, high atmospheric N inputs, low uptakes, or some combination of these factors. Soil leaching and Al mobilization in such systems is often dominated by nitrate. However, the geographical extent of these types of systems is limited, and the traditional view that most forest ecosystems are N limited remains valid, especially where forest management is intensive. The limited information available on tree response to CO2 suggests N-deficient plants often grow faster with elevated CO2, whereas P-deficient plants often do not. Research is needed to 1) determine if the differences in response between N- and P-deficient plants is common, 2) the responses of plants deficient in other nutrients to elevated CO2, and 3) the interactions of CO2 increase, nutrient deficiencies, climate change.

KEYWORDS: CARBON-DIOXIDE ENRICHMENT, CO2-ENRICHMENT, DECIDUOUS FOREST, EASTERN UNITED STATES, ELEVATED CO2, LOBLOLLY-PINE, NITROGEN MINERALIZATION, PINUS-RADIATA SEEDLINGS, RED SPRUCE, SIMULATED ACID-RAIN

1079

Johnson, D.W., J.T. Ball, and R.F. Walker. 1997. Effects of CO2 and nitrogen fertilization on vegetation and soil nutrient content in juvenile ponderosa pine. *Plant and Soil 190(1):29-40.*

This paper summarizes the data on nutrient uptake and soil responses in opentop chambers planted with ponderosa pine (Pinus ponderosa Laws.) treated with both N and CO2. Based upon the literature, we hypothesized that 1) elevated CO2 would cause increased growth and yield of biomass per unit uptake of N even if N is limiting, and 2) elevated CO2 would cause increased biomass yield per unit uptake of other nutrients only by growth dilution and only if they are non-limiting. Hypothesis 1 was supported only in part: there were greater yields of biomass per unit N uptake in the first two years of growth but not in the third year. Hypothesis 2 was supported in many cases: elevated CO2 caused growth dilution (decreased concentrations but not decreased uptake) of P, S, and Mg. Effects of elevated CO2 on K, Ca, and B concentrations were smaller and mostly non-significant. There was no evidence that N responded in a unique manner to elevated CO2, despite its unique role in rubisco. Simple growth dilution seemed to explain nutrient responses in almost all cases. There were significant declines in soil exchangeable K+, Ca2+, Mg2+ and extractable P over time which were attributed to disturbance effects associated with plowing. The only statistically significant treatment effects on soils were negative effects of elevated CO2 on mineralizeable N and extractable P, and positive effects of both N fertilization and CO2 on exchangeable Al3+. Soil exchangeable K+, Ca2+, and Mg2+ pools remained much higher than vegetation pools, but extractable P pools were lower than vegetation pools in the third year of growth. There were also large losses of both native soil N and fertilizer N over time. These soil N losses could account for the observed losses in exchangeable K+, Ca2+, Mg2+ if N was nitrified and leached as NO3-.

KEYWORDS: CARBON DIOXIDE, DEFICIENCY, ELEVATED ATMOSPHERIC CO2, ENHANCEMENT, ENRICHMENT, FEEDBACK, FOREST, GROWTH-RESPONSES, PHOSPHORUS, SPRUCE SEEDLINGS

1080

Johnson, D.W., T. Ball, and R.F. Walker. 1995. Effects of elevated co2 and nitrogen on nutrient-uptake in ponderosa pine-seedlings. *Plant and Soil 169:535-545.*

This paper reports on the results of a controlled-environment study on the effects of CO2 (370, 525, and 700 mu mol mel(-1)) and N [0, 200, and 400 mu g N g soil(-1) as (NH4)SO4] on ponderosa pine (Pinus ponderosa) seedlings. Based upon a review of the literature, we hypothesized that N limitations would not prevent a growth response to elevated CO2. The hypothesis was not supported under conditions of extreme N deficiency (no fertilizer added to a very poor soil), but was supported when N limitations were less severe but still suboptimal (lower rate of fertilization), The growth increases in N-fertilized seedlings occurred mainly between 36 and 58 weeks without any additional N uptake. Thus, it appeared that elevated CO2 allowed more efficient use of internal N reserves in the previously-fertilized seedlings, whereas internal N reserves in the unfertilized seedlings were insufficient to allow this response, Uptake rates of other nutrients were generally proportional to growth. Nitrogen treatment caused reductions in soil exchangeable K+, Ca2+, and Mg2+ (presumably because of nitrification and NO3- leaching) but increases in extractable P (presumably due to stimulation of phosphatase activity). The results of this and other seedling studies show that elevated CO2 causes a reduction in tissue N concentration, even under N- rich conditions. The unique response of N is consistent with the hypothesis that the efficiency of Rubisco increases with elevated CO2. These results collectively have significant implications for the response of mature, N-deficient forests to elevated CO2.

KEYWORDS: ATMOSPHERIC CO2, DIOXIDE, ECOSYSTEMS, ENRICHMENT, FOREST, GLOBAL CARBON-CYCLE, GROWTH-RESPONSES, LIMITATIONS, SOIL, SPRUCE SEEDLINGS

1081

Johnson, D., D. Geisinger, R. Walker, J. Newman, J. Vose, K. Elliot, and T. Ball. 1994. Soil pco(2), soil respiration, and root activity in co2-fumigated and nitrogen-fertilized ponderosa pine. *Plant and Soil 165(1):129-138.*

The purpose of this paper is to describe the effects of CO2 and N treatments on soil pCO(2), calculated CO2 efflux, root biomass and soil carbon in open-top chambers planted with Pinus ponderosa seedlings. Based upon the literature, it was hypothesized that both elevated CO2 and N would cause increased foot biomass which would in turn cause increases in both total soil CO2 efflux and microbial respiration. This hypothesis was only supported in part: both CO2 and N treatments caused significant increases in root biomass, soil pCO(2), and calculated CO2 efflux, but there were no differences in soil microbial respiration measured in the laboratory. Both correlative and quantitative comparisons of CO2 efflux rates indicated that microbial respiration contributes little to total soil CO2 efflux in the field. Measurements of soil pCO(2) and calculated CO2 efflux provided inexpensive, non-invasive, and relatively sensitive indices of belowground response to CO2 and N treatments.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, CO2 EVOLUTION, ECOSYSTEMS, PLANTATIONS, RESPONSES

1082

Johnson, D.W., R.B. Thomas, K.L. Griffin, D.T. Tissue, J.T. Ball, B.R. Strain, and R.F. Walker. 1998. Effects of carbon dioxide and nitrogen on growth and nitrogen uptake in ponderosa and loblolly pine. *Journal of Environmental Quality 27(2):414-425.*

The purpose of this paper is to summarize the results of a series of greenhouse and open-top chamber studies on the effects of N and elevated atmospheric CO2 on ponderosa and loblolly pine (Pinus ponderosa Laws, and P. taeda L.) to evaluate common patterns of

response. Growth response to elevated CO2 ranged from zero to more than 1000%, depending largely upon N status, In both species, growth response to CO2 was greater under moderate N deficiency than under extreme N deficiency or N sufficiency/excess. Elevated CO2 generally caused lowered tissue N concentrations in many (but not all) cases, which in turn resulted in smaller increases in N uptake than in biomass. Growth response to N ranged from -50 (in ponderosa pine) to more than 1000%, depending upon the N status of the control medium. Growth response to N was enhanced by elevated CO2 when N was in the extreme deficiency range but not when N was in the moderate deficiency range. In two separate studies, ponderosa pine responded negatively to high N inputs, and in each case this response was mitigated by elevated CO2. Collectively, these results show that (i) N deficiency is a continuum rather than a step function, (ii) responses to elevated CO2 vary across this continuum of N deficiency, and (iii) elevated CO2 greatly enhances growth response to N additions when N is initially in the extremely deficient range.

KEYWORDS: ATMOSPHERIC CO2 ENRICHMENT, ECOSYSTEMS, ELEVATED CO2, FOREST, LEAF LITTER, LITTER QUALITY, NUTRIENT STATUS, RESPONSES, SOIL N, SPRUCE SEEDLINGS

1083

Johnson, D.W., R.F. Walker, and J.T. Ball. 1995. Combined effects of nitrogen and elevated CO2 on soils from controlled environment studies. *Water, Air, and Soil Pollution 85(3):1551-1556.*

This paper describes the effects of elevated CO2 and N fertilization on soils planted with ponderosa pine (Pinus Ponderosa) seedlings in short-term greenhouse studies. The high degree of homogeneity in the soils used allowed sensitive evaluation of soil changes in response to treatments. Elevated CO2 had no detectable effect upon soil N availability, but both CO2 and N fertilization caused significant changes in soil available (NH4F/HCl-extractable) P. Some of these changes could be accounted for by plant uptake, some were apparently due to differences in P immobilization (biotic or abiotic). N fertilization caused reductions in exchangeable K, Ca and Mg which could not be accounted for by plant uptake and were probably due to increased leaching. None of the reductions in soil available nutrients observed were of sufficient magnitude to cause nutrient deficiencies over the approximate 1-year duration of these studies.

KEYWORDS: CARBON DIOXIDE, ECOSYSTEMS, RESPONSES

1084

Johnson, D.W., R.F. Walker, and J.T. Ball. 1995. Lessons from lysimeters - soil n release from disturbance compromises controlled environment study. *Ecological Applications 5(2):395-400.*

A controlled environment study of the effects of carbon dioxide (CO2) and nitrogen (N) on growth of ponderosa pine seedlings produced results contradictory to those obtained in the field with the same species, soil, and treatments. In the controlled environment study, there was a significant negative growth response to N fertilization, whereas in the field there was a significant positive response to N. The difference was due to high rates of native N mineralization after soil disturbance during potting. This was evident from soil solution NO3- concentrations that peaked at approximate to 5000 mu mol/L in the unfertilized pots and 20 000 mu mol/L in the fertilized pots. These concentrations are orders of magnitude greater than those typically observed in the field. The effects of soil disturbance on N mineralization and nitrification need to be carefully considered before initiating controlled environment studies. The results of this study show that excessive N mineralization caused by soil disturbance can seriously compromise the results of controlled environment studies

KEYWORDS: ECOSYSTEMS, ELEVATED CARBON-DIOXIDE, FOREST

1085

Johnson, H.B., H.W. Polley, and H.S. Mayeux. 1993. Increasing co2 and plant-plant interactions - effects on natural vegetation. *Vegetatio 104:157-170.*

Plant species and functional groups of species show marked differences in photosynthesis and growth in relation to rising atmospheric CO2 concentrations through the range of the 30 % increase of the recent past and the 100 % increase since the last glaciation. A large shift was found in the compositional mix of 26 species of C3's and 17 species of C4's grown from a native soil seed bank in a competitive mode along a CO2 gradient that approximated the CO2 increase of the past 150 years and before. The biomass of C3's increased from near zero to 50 % of the total while that of the C4's was reduced 25 % as CO2 levels approached current ambient. The proposition that acclimation to rising CO2 will largely negate the fertilization effect of higher CO2 levels on C3's is not supported. No signs of photosynthetic acclimation were evident for Avena sativa, Prosopis glandulosa, and Schizachyrium scoparium plants grown in subambient CO2. The effects of changing CO2 levels on vegetation since the last glaciation are thought to have been at least as great, if not greater, than those which should be expected for a doubling of current CO2 levels. Atmospheric CO2 concentrations below 200 ppm are thought to have been instrumental in the rise of the C4 grasslands of North America and other extensive C4 grasslands and savannas of the world. Dramatic invasion of these areas by woody C3 species are accompanying the historical increase in atmospheric CO2 concentration now in progress.

KEYWORDS: C-3, CARBON-DIOXIDE CONCENTRATION, CLIMATE CHANGE, ELEVATED ATMOSPHERIC CO2, ENRICHMENT, ESTUARINE MARSH, GROWTH, OLD- FIELD PERENNIALS, PHOTOSYNTHESIS, TUSSOCK TUNDRA

1086

Johnson, L.C., G.R. Shaver, A.E. Giblin, K.J. Nadelhoffer, E.R. Rastetter, J.A. Laundre, and G.L. Murray. 1996. Effects of drainage and temperature on carbon balance of tussock tundra microcosms. *Oecologia 108(4):737-748.*

We examined the importance of temperature (7 degrees C or 15 degrees C) and soil moisture regime (saturated or field capacity) on the carbon (C) balance of arctic tussock tundra microcosms (intact blocks of soil and vege tation) in growth chambers over an 81-day simulated growing season. We measured gaseous CO2 exchanges, methane (CH4) emissions, and dissolved C losses on intact blocks of tussock (Eriophorum vaginatum) and in tertussock (moss-dominated). We hypothesized that under increased temperature and/or enhanced drainage, C losses from ecosystem respiration (CO2 respired by plants and heterotrophs) would exceed gains from gross photosynthesis causing tussock tundra to become a net source of C to the atmosphere. The field capacity moisture regime caused a decrease in net CO2 storage (NEP) in tussock tundra microcosms. This resulted from a stimulation of ecosystem respiration (probably mostly microbial) with enhanced drainage, rather than a decrease in gross photosynthesis. Elevated temperature alone had no effect on NEP because CO2 losses from increased ecosystem respiration at elevated temperature were compensated by increased CO2 uptake (gross photosynthesis). Although CO2 losses from ecosystem respiration were primarily limited by drainage, CH4 emissions, in contrast, were dependent on temperature. Furthermore, substantial dissolved C losses, especially organic C, and important microhabitat differences must be considered in estimating C balance for the tussock tundra system. As much as similar to 20% of total C fixed in photosynthesis was lost as dissolved organic C. Tussocks

stored similar to 2x more C and emitted 5x more methane than intertussocks. In spite of the limitations of this microcosm experiment, this study has further elucidated the critical role of soil moisture regime and dissolved C losses in regulating net C balance of arctic tussock tundra.

KEYWORDS: ALASKAN TUNDRA, ARCTIC TUNDRA, ATMOSPHERIC CO2, CLIMATIC CHANGE, DIOXIDE, GREENHOUSE, METHANE, RESPONSES, TERRESTRIAL ECOSYSTEMS, WATER-TABLE

1087

Johnson, R.H., and D.E. Lincoln. 1991. Sagebrush carbon allocation patterns and grasshopper nutrition - the influence of CO2 enrichment and soil mineral limitation. *Oecologia 87(1):127-134.*

Artemisia tridentata seedlings were grown under carbon dioxide concentrations of 350 and 650-mu-l l-1 and two levels of soil nutrition. In the high nutrient treatment, increasing CO2 led to a doubling of shoot mass, whereas nutrient limitation completely constrained the response to elevated CO2. Root biomass was unaffected by any treatment. Plant root/shoot ratios declined under carbon dioxide enrichment but increased under low nutrient availability, thus the ratio was apparently controlled by changes in carbon allocation to shoot mass alone. Growth under CO2 enrichment increased the starch concentrations of leaves grown under both nutrient regimes, while increased CO2 and low nutrient availability acted in concert to reduce leaf nitrogen concentration and water content. Carbon dioxide enrichment and soil nutrient limitation both acted to increase the balance of leaf storage carbohydrate versus nitrogen (C/N). The two treatment effects were significantly interactive in that nutrient limitation slightly reduced the C/N balance among the high-CO2 plants. Leaf volatile terpene concentration increased only in the nutrient limited plants and did not follow the overall increase in leaf C/N ratio. Grasshopper consumption was significantly greater on host leaves grown under CO2 enrichment but was reduced on leaves grown under low nutrient availability. An overall negative relationship of consumption versus leaf volatile concentration suggests that terpenes may have been one of several important leaf characteristics limiting consumption of the low nutrient hosts. Digestibility of host leaves grown under the high CO2 treatment was significantly increased and was related to high leaf starch content. Grasshopper growth efficiency (ECI) was significantly reduced by the nutrient limitation treatment but co-varied with leaf water content.

KEYWORDS: DIOXIDE ATMOSPHERES, ELEVATED CO2, GROWTH, INSECT HERBIVORE, LEPIDOPTERA, LIMITING CONDITIONS, NITROGEN, NOCTUIDAE, PLANT-TISSUE, VOLATILE LEAF TERPENES

1088

Johnston, K.M., and O.J. Schmitz. 1997. Wildlife and climate change: Assessing the sensitivity of selected species to simulated doubling of atmospheric CO2. *Global Change Biology 3(6):531-544.*

We explored, using computer simulations, the sensitivity of four mammal species (elk, Cervus canadensis; white-tailed deer, Odocoileus virginianus; Columbian ground squirrel, Spermophilus columbianus; and chipmunk, Tamias striatus) within the continental USA to the effect of anticipated levels of global climate change brought about by a doubling of atmospheric CO2. Sensitivity to the direct effects of climate change were evaluated using a climate-space approach to delineate the range of thermal conditions tolerable by each species. Sensitivity to indirect effects were evaluated by quantifying the association of each species to the current vegetation distribution within the continental USA and using this association to assess whether wildlife species distributions might shift in response to vegetation shifts under climate change. Results indicate that altered thermal conditions alone should have little or no effect on the wildlife species' distributions as physiological tolerance to heat load would allow them to survive. Analyses of the effects of vegetation change indicate that deer and chipmunks should retain their current distributions and possibly expand westward in the USA. For Elk and ground squirrels, there is a possibility that their current distributions would shrink and there is little possibility that each species would spread to new regions. This work emphasizes that the distributions of the four mammalian species are likely to be influenced more by vegetation changes than by thermal conditions. Future efforts to understand the effects of global change on wildlife species should focus on animal-habitat and climate-vegetation linkages.

KEYWORDS: CONSTRAINTS, ECOLOGY, MODELS, SCALE, VEGETATION, WHITE-TAILED DEER

1089

Joles, D.W., A.C. Cameron, A. Shirazi, P.D. Petracek, and R.M. Beaudry. 1994. Modified-atmosphere packaging of heritage red raspberry fruit - respiratory response to reduced oxygen, enhanced carbon- dioxide, and temperature. *Journal of the American Society for Horticultural Science 119(3):540-545.*

'Heritage' raspberries (Rubus idaeus L.) were sealed in low- density polyethylene packages and stored at 0, 10, and 20C during Fall 1990 and 1991 to study respiratory responses under modified atmospheres. A range of steady-state O2 and CO2 partial pressures were achieved by varying fruit weight in packages of a specific surface area and film thickness. Film permeability to O2 and CO2 was measured and combined with surface area and film thickness to estimate total package permeability. Rates of O2 uptake and CO2 production and respiratory quotient (RQ) were calculated using steady-state O2 and CO2 partial pressures, total package permeability, and fruit weight. The O2 uptake rate decreased with decreasing O2 partial pressure over the range of partial pressure studied. The Michaelis-Menten equation was used to model O2 uptake as a function of O2 partial pressure and temperature. The apparent K(m) (K1/2) remained constant (5.6 kPa O2) with temperature, while Q10 was estimated to be 1.9. RQ was modeled as a function of O2 partial pressure and temperature. Headspace ethanol increased at RQs >1.3 to 1.5. Based on RQ, ethanol production, and flavor, we recommend that raspberries be stored at O2 levels above 4 kPa at 0C, 6 kPa at 10C, and 8 kPa at 20C. Steady-state CO2 partial pressures of 3 to 17 kPa had little or no effect on O2 uptake or headspace ethanol partial pressures at 20C.

KEYWORDS: BLUEBERRY, CO2, FRESH PRODUCE, QUALITY, STORAGE

1090

Jones, C.G., and S.E. Hartley. 1999. A protein competition model of phenolic allocation. *Oikos 86(1):27-44.*

We present a Protein Competition Model (PCM) for predicting total phenolic allocation and concentration in leaves of terrestrial higher plants. In contrast to predictions based on the carbon composition of end products, the PCM is based on metabolic origins of pathway constituents, alternative fates of pathway precursors, and biochemical regulatory mechanisms. Protein and phenolic synthesis compete for the common, limiting resource phenylalanine, so protein and phenolic allocation are inversely correlated. Phenolic allocation can be predicted from the effects of development, inherent growth rate and environment on leaf functions that create competing demands for proteins or phenolics. We present the model general principles. We predict phenolic concentrations as leaves develop; in inherently fast versus slow growing species; and in response to the environment (nitrogen, light, phosphorus, heat shock, herbivore and pathogen injury, and carbon dioxide). Because

predictions generally fit observed patterns, we argue that, for phenylalanine-derived phenolics, the mechanistically distinctive PCM complements the Growth Differentiation and Resource Availability Hypotheses, and is a viable, testable alternative to the Carbon Nutrient Balance Hypothesis.

KEYWORDS: CARBON NUTRIENT BALANCE, CHEMICAL-COMPOSITION, DELAYED INDUCIBLE RESISTANCE, ELEVATED ATMOSPHERIC CO2, MINERAL NUTRITION, PHENYLALANINE AMMONIA-LYASE, PHENYLPROPANOID METABOLISM, PLANT-GROWTH RATE, RESOURCE AVAILABILITY HYPOTHESIS, SECONDARY METABOLISM

1091
Jones, M.B., J.C. Brown, A. Raschi, and F. Miglietta. 1995. The effects on arbutus-unedo L of long-term exposure to elevated co2. *Global Change Biology 1(4):295-302.*

Arbutus unedo is a sclerophyllous evergreen, characteristic of Mediterranean coastal scrub vegetation. In Italy, trees of A. unedo have been found close to natural CO2 vents where the mean atmospheric carbon dioxide concentration is about 2200 mu mol mol(-1). Comparisons were made between trees growing in elevated and ambient CO2 concentrations to test for evidence of adaptation to long-term exposure to elevated CO2. Leaves formed at elevated CO2 have a lower stomatal density and stomatal index and higher specific leaf area than those formed at ambient CO2, but there was no change in carbon to nitrogen ratios of the leaf tissue. Stomatal conductance was lower at elevated CO2 during rapid growth in the spring. In mid-summer, under drought stress, stomatal closure of all leaves occurred and in the autumn, when stress was relieved, the conductance of leaves at both elevated and ambient CO2 increased. In the spring, the stomatal conductance of the new flush of leaves at ambient CO2 was higher than the leaves at elevated CO2, increasing instantaneous water use efficiency at elevated CO2. Chlorophyll fluorescence measurements suggested that elevated CO2 provided some protection against photoinhibition in mid- summer. Analysis of A/C-i curves showed that there was no evidence of either upward or downward regulation of photosynthesis at elevated CO2. It is therefore anticipated that A. unedo will have higher growth rates as the ambient CO2 concentrations increase.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, ENRICHMENT, GAS-EXCHANGE, INCREASE, LEAVES, PHOTOSYNTHESIS, PLANTS, STOMATAL DENSITY, TREES

1092
Jones, M.B., and M. Jongen. 1996. Sensitivity of temperate grassland species to elevated atmospheric CO2 and the interaction with temperature and water stress. *Agricultural and Food Science in Finland 5(3):271-283.*

The annual cycle of growth of many temperate grasses is limited by low temperatures during the winter and spring and water stress during the summer. Climate change, induced by increase in the concentration of greenhouse gases in the atmosphere, can affect the growth and community structure of temperature grasslands in two ways. The first is directly through changes in atmospheric concentration of CO2 and the second is indirectly through changes in temperature and rainfall. At higher latitudes, where growth is largely temperature limited, it is probable that the direct effects of enhanced CO2 will be less than at low latitudes. However, interactions with increasing temperature and water stress are complex. Temperate grasslands range from intensively managed monocultures of sown species to species-rich natural and semi-natural communities whose local distributions are controlled by variations in soil type and drainage. The different species can show marked differences in their responses to increasing CO2 concentrations, rising temperatures and water stress. This will probably result in major alterations in the community structure of temperate grasslands in the future. In addition to impacts on primary productivity and community structure, a long-term effect of elevated CO2 on grasslands is likely to be a significant increase in soil carbon storage. However, this may be counteracted by increases in temperature.

KEYWORDS: CARBON DIOXIDE, CLIMATE CHANGE, ENRICHMENT, GAS-EXCHANGE, GROWTH, PHOTOSYNTHESIS, PLANT, RESPONSES, STOMATAL CONTROL, USE EFFICIENCY

1093
Jones, M.B., M. Jongen, and T. Doyle. 1996. Effects of elevated carbon dioxide concentrations on agricultural grassland production. *Agricultural and Forest Meteorology 79(4):243-252.*

Open-top chambers have been used on a field-grown perennial ryegrass (Lolium perenne) sward to investigate the long-term responses to elevated CO2 concentrations. A concentration of 2 x ambient CO2 increased annual harvestable yield by about 20%, but the proportional stimulation was not constant throughout the growing season nor from one season to the next. Other effects of elevated CO2 were an increase in carbon/nitrogen ratio of tissues and a decrease in specific leaf area and canopy conductance. There was no effect of CO2 on the digestibility of the harvested grass. It is likely that climate change during the next century will lead to significant increases in agricultural grassland production in northern Europe. Production will be stimulated by a direct fertiliser effect due to the increasing CO2 concentration of the atmosphere.

KEYWORDS: CANOPIES, CO2 CONCENTRATION, FIELD, LOLIUM-PERENNE, PERENNIAL RYEGRASS, PHOTOSYNTHESIS, RESPONSES

1094
Jones, M.H., J.T. Fahnestock, D.A. Walker, M.D. Walker, and J.M. Welker. 1998. Carbon dioxide fluxes in moist and dry arctic tundra during season: Responses to increases in summer temperature and winter snow accumulation. *Arctic and Alpine Research 30(4):373-380.*

Climate-induced environmental changes are likely to have pronounced impacts on CO2 flux patterns in arctic ecosystems. We initiated a long-term experiment in 1994 in moist tussock and dry heath tundra in arctic Alaska in which we increased summer air temperature (ca. 2 degrees C) and increased winter snow accumulation (shortening the growing season approximately 4 wk). During the 1996 snow-free season, we measured ecosystem CO2 flux weekly in order to quantify net carbon gain or loss from these systems. Over the duration of the snow-free season, both dry heath and moist tussock tundra exhibited a net loss of carbon to the atmosphere, ranging from 12 to 81 g C m(-2) depending upon experimental treatment. Elevated summer temperatures accelerated net CO2 loss rates over ambient temperatures in both deep and ambient snow treatments, and increased the total amount of carbon emitted during the snow- free season by 26 to 38% in ambient snow plots and by 112 to 326% in deep snow plots. Increased snow accumulation had less impact on CO2 flux than did warming, and snow effects on total carbon loss were not consistent between the two temperature regimes. Ecosystem respiration exceeded assimilation on most sampling dates throughout the season. These data, coupled with winter carbon losses recently demonstrated in the same ecosystems, indicate that the moist and dry arctic ecosystems we examined are currently net sources of atmospheric carbon on an annual basis, and that anticipated global warming may increase carbon losses from these systems.

KEYWORDS: ALASKA, BALANCE, CLIMATE CHANGE, CO2, ECOSYSTEMS, EFFLUX, SOILS, STORAGE, TUSSOCK TUNDRA,

USA

KEYWORDS: CARBON DIOXIDE, CO2, DESIGN, ENVIRONMENT, EXPOSURE, PLANTS

1095
Jones, M.H., S.E. Macdonald, and G.H.R. Henry. 1999. Sex- and habitat-specific responses of a high arctic willow, Salix arctica, to experimental climate change. *Oikos 87(1):129-138.*

Dioecious plant species and those occupying diverse habitats may present special analytical problems to researchers examining effects of climate change. Here we report the results from two complementary studies designed to determine the importance of sex and habitat on gas exchange and growth of male and female individuals of a dioecious, circumpolar willow, Salix arctica, in the Canadian High Arctic. In field studies, male and female willows from dry and wet habitats were subjected to passively enhanced summer temperature (similar to 1.3 degrees C) using small open-top chambers over three years. Peak season gas exchange varied significantly by willow sex and habitat. Overall net assimilation was higher in the dry habitat than in the wet, and higher in females than in males. In the dry habitat, net assimilation of females was enhanced by experimental warming, but decreased in males. In the wet habitat, net assimilation of females was substantially depressed by experimental warming, while males showed an inconsistent response. Development and growth of male and female catkins were enhanced by elevated temperature more than leaf fascicles, but leaf fascicle development and growth varied more between the two habitats, particularly in males. In a controlled environment study, male and female willows from these same wet and dry habitats were grown in a 2x2 factorial experiment including 1 x or 2 x ambient [CO2] and 5 or 12 degrees C. The sexes responded very differently to the experimental treatments, but we found no effect of original habitat. Net assimilation in males was affected by the interaction of temperature and CO2, but in females by CO2 only. Our results demonstrate (a) significant intraspecific and intersexual differences in arctic willow physiology and growth, (b) that these differences are affected by environmental conditions expected to accompany global climate change, and (c) that sex- and habitat-specific responses should be explicitly accounted for in studies of dioecious species.

KEYWORDS: DWARF WILLOW, ELEVATED CO2, GAS-EXCHANGE, GROWTH, PHYSIOLOGY, PLANT SILENE LATIFOLIA, WATER RELATIONS

1096
Jones, P., L.M. Collins, and K.T. Ingram. 1995. Open-top chambers for field studies of crop response to elevated co2 and temperature. *Transactions of the Asae 38(4):1195-1201.*

A new design for Open Top Chambers (OTCs) is described. In addition to providing CO2 controls as do several other existing OTCs, the system is designed to provide elevated temperature control. To provide a more natural vertical microclimate profile, the newly designed system pulls air down through the chamber and out the bottom rather than injecting air at the bottom and venting it out the top of the chamber. A prototype was constructed and performance tests were conducted. Over a 24-h test period with a CO2 concentration setpoint of 660 ppm, individual measurements of concentration taken every 5 min averaged 660.5 ppm with a standard deviation of 26.6 ppm. Temperature controls were rested over 24-h periods for two different setpoints-ambient +4 degrees C and ambient +6 degrees C. For the two test periods the average chamber temperature measurements were 3.98 degrees and 5.99 degrees C above ambient, respectively. Twenty chambers based on the prototype design were constructed and installed at the International Rice Research Institute, Los Banos, Philippines. As intended, the chambers are currently being used to conduct research on rice crop response to elevated CO2 and temperature.

1097
Jones, T.H., L.J. Thompson, J.H. Lawton, T.M. Bezemer, R.D. Bardgett, T.M. Blackburn, K.D. Bruce, P.F. Cannon, G.S. Hall, S.E. Hartley, G. Howson, C.G. Jones, C. Kampichler, E. Kandeler, and D.A. Ritchie. 1998. Impacts of rising atmospheric carbon dioxide on model terrestrial ecosystems. *Science 280(5362):441-443.*

In model terrestrial ecosystems maintained for three plant generations at elevated concentrations of atmospheric carbon dioxide, increases in photosynthetically fixed carbon were allocated below ground, raising concentrations of dissolved organic carbon in soil. These effects were then transmitted up the decomposer food chain. Soil microbial biomass was unaffected, but the composition of soil fungal species changed, with increases in rates of cellulose decomposition. There were also changes in the abundance and species composition of Collembola, fungal-feeding arthropods. These results have implications for long-term feedback processes in soil ecosystems that are subject to rising global atmospheric carbon dioxide concentrations.

KEYWORDS: COLLEMBOLA, COLONIZATION, COMMUNITIES, DECOMPOSITION, ELEVATED CO2, FUNGI, PLANT-RESPONSES, PREFERENCES, RHIZOSPHERE, SOIL

1098
Jongen, M., P. Fay, and M.B. Jones. 1996. Effects of elevated carbon dioxide and arbuscular mycorrhizal infection on Trifolium repens. *New Phytologist 132(3):413-423.*

Trifolium repens L. cv. aran was grown for 58 d at ambient (350 mu mol mol(-1)) and elevated (700 mu mol mol(-1)) atmospheric CO2, with and without the arbuscular mycorrhizal fungus Glomus mosseae (Nicol. & Gerd.) Gerd. St Trappe cv. YV. Plant biomass, mycorrhizal infection, non-structural carbohydrates, C, N and P content were examined. Elevated CO2 (a) significantly increased above- and below-ground biomass, (b) decreased specific leaf area and specific root length, (c) decreased tissue %N and increased the C:N ratio, and (d) significantly increased total non-structural carbohydrates. Inoculating T. repens with Glomus mosseae (a) significantly increased above- and below-ground biomass, (b) increased the total root length and total leaf area, and (c) significantly decreased tissue %P. Evidence of an increased influence of mycorhiza on the P nutrition of T. repens at elevated CO2 was found in the 22% increase in leaf total P (P less than or equal to 0.05) of mycorrhizal plants grown at elevated CO2 compared with nonmycorrhizal plants. No significant interactions were found between CO2 and mycorrhiza treatments. The proportion of T. repens root length colonized by Glomus mosseae was not affected by CO2 concentration. The percentage mycorrhizal infection was 29% at ambient CO2 and 35% at elevated CO2. However, exposure to elevated CO2 significantly increased the total mycorrhizal root length from 3.4 to 6.1 m per plant. The results show little evidence that the role of arbuscular mycorrhiza in the growth and nutrition of T. repens would increase if atmospheric CO2 were to increase as predicted.

KEYWORDS: ATMOSPHERIC CO2, DYNAMICS, GROWTH, INSECT HERBIVORE, NITROGEN, PHOSPHATE, PHOTOSYNTHESIS, PLANTS, SUBTERRANEUM L, WHITE CLOVER

1099
Jongen, M., and M.B. Jones. 1998. Effects of elevated carbon dioxide on plant biomass production and competition in a simulated neutral grassland community. *Annals of Botany 82(1):111-123.*

Using open-top chambers, four prominent species (Lolium perenne, Cynosurus cristatus, Holcus lanatus and Agrostis capillaris) of Irish neutral grasslands were grown at ambient and elevated (700 mu mol mol(-1)) atmospheric CO2 for a period of 8 months. The effects of interspecific competition on plant responses to CO2 enrichment were investigated by growing the species in a four-species mixture. The results indicate that the species differ in their ability to respond to elevated CO2. CO2-enrichment had the largest effect on the biomass production of H. lanatus, but substantial stimulations in biomass production were also found for the other three species. The CO2-stimulation of biomass production for H. lanatus was accompanied by increased tillering. In addition, reductions in specific leaf area were found for all species. Exposure to elevated CO2 increased the community biomass of the four- species mixture. This increase can be mainly attributed to a significant increase in the biomass of H. lanatus at elevated CO2. No statistically-significant changes in species composition of community biomass were found. However, H. lanatus did increase its share of community biomass at each of the harvests, with the other three species, mainly L. perenne, suffering losses in their shares at elevated CO2. The results show that: (1) the species varied in their response to elevated CO2; and (2) species composition in natural plant communities is likely to change at elevated CO2, but these changes may occur rather slowly. Much longer periods of exposure to elevated atmospheric CO2 may be required to permit detection of significant changes in species composition. (C) 1998 Annals of Botany Company.

KEYWORDS: ATMOSPHERIC CO2, CO2- ENRICHMENT, DRY-MATTER, GROWTH, HOLCUS- LANATUS, LOLIUM-PERENNE, PASTURE TURVES, SEASONAL-CHANGES, TRIFOLIUM- REPENS, WHITE CLOVER

1100

Jongen, M., M.B. Jones, T. Hebeisen, H. Blum, and G. Hendrey. 1995. The effects of elevated co2 concentrations on the root-growth of lolium-perenne and trifolium-repens grown in a face system. *Global Change Biology 1(5):361-371.*

Lolium perenne and Trifolium repens were grown in a Free Air CO2 Enrichment (FACE) system at elevated (600 mu mol mol(-1)) and ambient (340 mu mol mol(-1)) carbon dioxide concentrations during a whole growing season. Using a root ingrowth bag technique the extent to which CO2 enrichment influenced the growth of L. perenne and T. repens roots under two contrasting nutrient regimes was examined. Root ingrowth bags were inserted for a fixed time into the soil in order to trap roots. It was also possible to follow the mortality of roots in bags inserted for different time intervals. Root ingrowth of both L. perenne and T. repens increased under elevated CO2 conditions. In L. perenne, root ingrowth decreased with increasing nutrient fertilizer level, but for T. repens the root ingrowth was not affected by the nutrient application rate. Besides biomass measurements, root length estimates were made for T. repens. These showed an increase under elevated CO2 concentrations. Root decomposition appeared to decrease under elevated CO2 concentrations. A possible explanation for this effect is the observed changes in tissue composition, such as the increase in the carbon:nitrogen ratio in roots of L. perenne at elevated CO2 concentrations.

KEYWORDS: ALLOCATION, ATMOSPHERIC CO2, CARBON DIOXIDE, CO2- ENRICHMENT, DRY-MATTER, INSECT HERBIVORE, NITROGEN, PHOSPHORUS, PLANT, RESPONSES

1101

Jordan, D.N., S.F. Zitzer, G.R. Hendrey, K.F. Lewin, J. Nagy, R.S. Nowak, S.D. Smith, J.S. Coleman, and J.R. Seeman. 1999. Biotic, abiotic and performance aspects of the Nevada Desert Free-Air CO2 Enrichment (FACE) Facility. *Global Change Biology 5(6):659-668.*

Arid and semiarid climates comprise roughly 40% of the earth's terrestrial surface. Deserts are predicted to be extremely responsive to global change because they are stressful environments where small absolute changes in water availability or use represent large proportional changes. Water and carbon dioxide fluxes are inherently coupled in plant growth. No documented global change has been more substantial or more rapid than the increase in atmospheric CO2. Free Air CO2 Enrichment (FACE) technology permits manipulation of CO2 in intact communities without altering factors such as light intensity or quality, humidity or wind. The Nevada Desert FACE Facility (NDFF) consists of three 491 m(2) plots in the Mojave Desert receiving 550 mu L L-1 CO2, and six ambient plots to assess both CO2 and fan effects. The shrub community was characterized as a Larrea-Ambrosia-Lycium species complex. Data are reported through 12 months of operation.

KEYWORDS: DIOXIDE, FIELD, WINTER ANNUALS

1102

Julkunentiitto, R., J. Tahvanainen, and J. Silvola. 1993. Increased co2 and nutrient status changes affect phytomass and the production of plant defensive secondary chemicals in salix- myrsinifolia (salisb). *Oecologia 95(4):495-498.*

The effect of CO2 enrichment (700 and 1050 ppm) on phytomass, soluble sugars, leaf nitrogen and secondary chemicals of three Salix myrsinifolia clones was studied in plants cultivated at very poor (sand seedlings) and moderate (peat seedlings) nutrient availability and under low illumination. The total shoot phytomass production of sand seedlings was less than 10% of that of the peat seedlings. Carbon dioxide increased the total shoot phytomass of peat seedlings. When the ambient carbon supply was doubled (to 700 ppm) the growth of sand seedlings was slightly enhanced but 1050 ppm CO2 gave growth figures similar to those at the control CO2 level. Leaf nitrogen content and total soluble sugar contents were significantly higher in peat seedlings than in sand seedlings. Leaf nitrogen showed a decreasing trend in relation to CO2 increase. On the other hand, CO2 did not have any clear-cut effect on total sugars. At the control CO2 level the content of salicortin, which is a dynamic phenolic, was higher in the peat seedlings than in the sand seedlings, but salicin showed the opposite trend. CO2 enrichment considerably decreased these phenolics in the peat seedlings. At the control CO2 level, the content of more static phenolics, such as proanthocyanidins, was higher in sand seedlings. An increased carbon supply considerably increased static phenolics in the peat seedlings. Willow defence against generalist herbivores is moderately decreased by enhancement of atmospheric carbon dioxide.

KEYWORDS: ALLOCATION, BALANCE, PERFORMANCE, PHENOLIC CONSTITUENTS, WILLOWS

1103

Kainulainen, P., J.K. Holopainen, and T. Holopainen. 1998. The influence of elevated CO2 and O-3 concentrations on Scots pine needles: changes in starch and secondary metabolites over three exposure years. *Oecologia 114(4):455-460.*

Scots pine (Pinus sylvestris L.) trees, aged about 20 years old, growing on a natural pine heath were exposed to two concentrations of CO2 (ambient CO2 and double-ambient CO2) and two O-3 regimes (ambient O-3 and double-ambient O-3) and their combination in open-top chambers during growing seasons 1994, 1995 and 1996. Concentrations of foliar starch and secondary compounds are reported in this paper. Starch concentrations remained unaffected by elevated CO2 and/or O-3 concentrations during the first 2 study years. But in the autumn of the last study year, a significantly higher concentration of starch was found in current-year needles of trees exposed to elevated CO2 compared with ambient air. There were large differences in concentrations of starch and

secondary compounds between individual trees. Elevated concentrations of CO2 and/or O-3 did not have any significant effects on the concentrations of foliar total monoterpenes, total resin acids or total phenolics. Significantly higher concentrations of monoterpenes and resin acids and mostly lower concentrations of starch were found in trees growing without chambers than in those growing in open-top chambers, while there were no differences in concentrations of total phenolics between trees growing without or in chambers. The results suggest that elevated concentrations of CO2 might increase foliar starch concentrations in Scots pine, while secondary metabolites remain unaffected. Realistically elevated O-3 concentrations do not have clear effects on carbon allocation to starch and secondary compounds even after 3 exposure years.

KEYWORDS: ACID-RAIN, CARBON NUTRIENT BALANCE, DIOXIDE, GROWTH, L KARST, NORWAY SPRUCE, OZONE, SEEDLINGS, SPRUCE PICEA-ABIES, SYLVESTRIS L

1104

Kajfezbogataj, L., and A. Hocevar. 1994. Assessment of climate-change effects on productivity of beech stand in slovenia using simulation methods. *Agricultural and Forest Meteorology 72(1-2):47-56.*

On the basis of observed climatic trends in Slovenia obtained from 142 years of meteorological observation in Ljubljana (Slovenia) 15 climatic scenarios for the next 60 years are constructed regarding temperature rise and various levels of increasing CO2 concentration. Yearly gross primary production of 80 year old beech stand (Fagus sylvatica) is simulated in daily scale by the PERUN 3 model for healthy trees assuming no water stress. The influence of increased CO2 concentration on physiological processes is assessed over enhanced maximal photosynthesis, lower compensation point and increased stomatal resistance. Results of the simulation, giving decreased primary production of beech stand under the mentioned assumption, are discussed.

KEYWORDS: CARBON DIOXIDE

1105

Kaji, H., M. Ueno, T. Ikebe, and Y. Osajima. 1993. Effects of low o-2 and elevated co2 concentrations on the quality of matsutake [tricholoma-matsutake (s ito et imai) sing] during storage. *Bioscience Biotechnology and Biochemistry 57(3):363-366.*

Matsutake [Tricholoma matsutake (S. ITO et IMAI) SING.] was stored under conditions of low O2 and elevated CO2 concentrations. The storage conditions were as follows: with an O2 concentration of 2.5+/-0.5%, the CO2 concentrations were 5%, 10%, 15%, and 20%, and relative humidity (RH) was about 100%; with an O2 concentration of 2.0+/-0.5%, the CO2 concentrations were 0%, 5%, 10%, and 15%, and RH was about 100%; the storage temperature was 1.0+/-0.1-degrees-C. The fruit was also stored in air and under 100% N2 as controls. Quality factors such as 'neto' (slimy microbial flora which develop on the moist surface of the fruiting body), weight loss, whiteness, firmness, and off-odor were measured. The development of neto and browning (loss of whiteness) of the inner stipe were suppressed for more than 14 days, except with storage under 100% N2. Storage in air and under 0% or a high concentration (> 10%) of CO2 caused an early development of off-odor, compared to storage under 5% and 10% CO2. In air, the development of mold was observed after 14 days. Under a low O2 concentration and 5% to 10% CO2, the quality factors of matsutake were most retained, and the fruit was still acceptable after 14 days of storage. A weight decrease of the fruit was recognized as the CO2 concentration was increased.

KEYWORDS: MUSHROOMS

1106

Kalina, J., and R. Ceulemans. 1997. Clonal differences in the response of dark and light reactions of photosynthesis to elevated atmospheric CO2 in poplar. *Photosynthetica 33(1):51-61.*

Two hybrid poplar (Populus) clones (i.e., fast growing clone Beaupre and slow growing clone Robusta) were grown for two years from cuttings at close spacings in open top chambers (OTCs) under ambient (AC) and elevated [EC = AC + 350 mu mol(CO2) mol(-1)] CO2 treatments, For clone Beaupre no down- regulation of photosynthesis was observed. Two years of growing under EC resulted in an increase in quantum yield of photosystem 2 (PS2), steady state irradiance saturated rate of net photosynthesis (P-Nmax), chlorophyll (Chl) content, and ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBPC) activity for this clone. We suppose that under nonlimiting conditions of nitrogen and phosphorus content the response to EC was by building up light-harvesting complexes of PS2 and increasing photochemical efficiency of PS2, Due to a high rate of the primary reactions of photosynthesis and a high RuBPCO activity the end product of the response to EC was an increase in P-Nmax and a larger saccharides content, The Robusta clone showed a depression in the primary reactions of photosynthesis under EC, We found a decrease in quantum yield of PS2, Chl and phosphorus contents, and in RuBPCO activity. However, an increase in P-Nmax, saccharides content and Chi a/b ratio was observed. We speculate (1) that the phosphorus deficiency in combination with an increase in CO2 concentrations may lead to a potential damage of the assimilation apparatus of the primary reactions of photosynthesis and to a decrease in photochemical efficiency of PS2; (2) that the primary target of "down-regulation" takes place at PS2 for irradiances above 150 mu mol m(-2) s(-1).

KEYWORDS: ACCLIMATION, CARBON DIOXIDE, CHLOROPHYLL FLUORESCENCE, GROWTH, PHOTOSYSTEM, PLANTS, POPULUS, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, RUBISCO, TOBACCO

1107

Kampichler, C., E. Kandeler, R.D. Bardgett, T.H. Jones, and L.J. Thompson. 1998. Impact of elevated atmospheric CO2 concentration on soil microbial biomass and activity in a complex, weedy field model ecosystem. *Global Change Biology 4(3):335-346.*

Although soil organisms play an essential role in the cycling of elements in terrestrial ecosystems, little is known of the impact of increasing atmospheric CO2 concentrations on soil microbial processes. We determined microbial biomass and activity in the soil of multitrophic model ecosystems housed in the Ecotron (NERC Centre for Population Biology, Ascot, UK) under two atmospheric CO2 concentrations (ambient vs. ambient + 200 ppm). The model communities consist of four annual plant species which naturally co-occur in weedy fields and disturbed ground throughout southern England, together with their herbivores, parasitoids and soil biota. At the end of two experimental runs lasting 9 and 4.5 months, respectively, root dry weight and quality showed contradictory responses to elevated CO2 concentrations, probably as a consequence of the different time-periods (and hence number of plant generations) in the two experiments. Despite significant root responses no differences in microbial biomass could be detected. Effects of CO2 concentration on microbial activity were also negligible. Specific enzymes (protease and xylanase) showed a significant decrease in activity in one of the experimental runs. This could be related to the higher C:N ratio of root tissue. We compare the results with data from the literature and conclude that the response of complex communities cannot be predicted on the basis of oversimplified experimental set-ups.

KEYWORDS: CARBON DIOXIDE, DECOMPOSITION, ENRICHMENT, LEAF LITTERS, LITTER QUALITY, NITROGEN-CONTENT, NUTRIENT-UPTAKE, PLANT GROWTH, RESPONSES, TALLGRASS PRAIRIE

1108

Kandeler, E., D. Tscherko, R.D. Bardgett, P.J. Hobbs, C. Kampichler, and T.H. Jones. 1998. The response of soil microorganisms and roots to elevated CO2 and temperature in a terrestrial model ecosystem. *Plant and Soil 202(2):251-262.*

We investigate the response of soil microorganisms to atmospheric CO2 and temperature change within model terrestrial ecosystems in the Ecotron. The model communities consisted of four plant species (Cardamine hirsuta, Poa annua, Senecio vulgaris, Spergula arvensis), four herbivorous insect species (two aphids, a leaf-miner, and a whitefly) and their parasitoids, snails, earthworms, woodlice, soil-dwelling Collembola (springtails), nematodes and soil microorganisms (bacteria, fungi, mycorrhizae and Protista). In two successive experiments, the effects of elevated temperature (ambient plus 2 degrees C) at both ambient and elevated CO2 conditions (ambient plus 200 ppm) were investigated. A 40:60 sand:Surrey loam mixture with relatively low nutrient levels was used. Each experiment ran for 9 months and soil microbial biomass (C-mic and N-mic), soil microbial community (fungal and bacterial phospholipid fatty acids), basal respiration, and enzymes involved in the carbon cycling (xylanase, trehalase) were measured at depths of 0-2, 0-10 and 10-20 cm. In addition, root biomass and tissue C:N ratio were determined to provide information on the amount and quality of substrates for microbial growth. Elevated temperature under both ambient and elevated CO2 did not show consistent treatment effects. Elevation of air temperature at ambient CO2 induced an increase in C-mic of the 0-10 cm layer, while at elevated CO2 total phospholipid fatty acids (PLFA) increased after the third generation. The metabolic quotient qCO(2) decreased at elevated temperature in the ambient CO2 run. Xylanase and trehalase skewed no changes in both runs. Root biomass and C:N ratio were not influenced by elevated temperature in ambient CO2. In elevated CO2, however, elevated temperature reduced root biomass in the 0-10 cm and 30-40 cm layers and increased N content of roots in the deeper layers. The different response of root biomass and C:N ratio to elevated temperature may be caused by differences in the dynamics of root decomposition and/or in allocation patterns to coarse or fine roots (i.e. storage vs. resource capture functions). Overall, our data suggests that in soils of low nutrient availability, the effects of climate change on the soil microbial community and processes are likely to be minimal and largely unpredicatable.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, COMMUNITIES, ENRICHMENT, GRASSLAND, MANAGEMENT, MICROBIAL BIOMASS, NINHYDRIN-REACTIVE NITROGEN, RESPIRATION, SYSTEMS, TALLGRASS PRAIRIE

1109

Kanechi, M., M. Ochi, M. Abe, N. Inagaki, and S. Maekawa. 1998. The effects of carbon dioxide enrichment, natural ventilation, and light intensity on growth, photosynthesis, and transpiration of cauliflower plantlets cultured in vitro photoautotrophically and photomixotrophically. *Journal of the American Society for Horticultural Science 123(2):176-181.*

The effects of natural ventilation and CO2 enrichment during the rooting stage on the growth and the rates of photosynthesis and transpiration of in vitro cauliflower (Brassica oleracea L.) plantlets were investigated. In vitro plantlets were established in airtight or ventilated vessels with or without CO2 supplied (approximate to 1200.mu g L-1) through gas permeable films attached to the vessel's cap for 15 days before transplanting ex vitro. Leaves generated in vitro in ventilated vessels had a higher photosynthetic rate than those produced in airtight vessels, which lead to greater leaf expansion and shoot and root dry matter accumulation during in vitro culture and acclimatization. Enhanced photosynthesis in leaves of ventilated plantlets was positively correlated with chlorophyll content. Increasing photosynthetically active radiation from 70 to 200 mu mol.m(-1)-s(-1) enhanced the growth of in vitro plantlets under ventilated conditions but it depressed photosynthesis of the leaves grown photomixotrophically with sugar and CO2 enrichment which might be due to the feedback inhibition caused by marked accumulations of sucrose and starch. Higher CO2 levels during in vitro culture enhanced photosynthesis under photoautotrophic conditions, but inhibited it under photomixotrophic conditions. Fifteen days after transplanting ex vitro, high photosynthetic ability and stomatal resistance to transpiratory water loss of ventilated plantlets in vitro had important contributions to rooting and acclimatization. Our findings show that the ventilated culture is effective for accelerating photoautotrophic growth of plantlets by increasing photosynthesis, suggesting that, especially for plantlets growing in vitro without sugar, CO2 enrichment may be necessary to enhance photosynthetic ability.

KEYWORDS: ACCLIMATIZATION, GREENHOUSE, INVITRO, MERISTEM CULTURE, MICROPROPAGATION, SUCROSE, ULTRASTRUCTURE, WATER-LOSS

1110

Kano, A., Y. Fukazawa, M. Aono, and K. Ohkawa. 1992. Effect of age of cuttings, propagation media, and cutting methods on rooting of stephanotis-floribunda brongn. *Journal of the Japanese Society for Horticultural Science 61(3):619-624.*

The effects of cutting methods, cutting media, and age of cutting on rooting capacity of Stephanotis floribunda Brongn. were investigated to improve propagation efficiency. The effects of CO2 enrichment and a new acclimatization technique for cutting were also tested. 1. Cuttings made from older shoots showed a higher rooting percentage than those made from younger ones. 2. Rockwool mats were found to be useful as a cutting medium for S. floribunda. 3. Cuttings with differentiated leaf buds showed higher rooting percentage than those without buds. 4. Rooting was stimulated by placing cuttings in a closed frame, especially when CO2 concentration was high. 5. An acclimatization technique using a computer controlled fan was developed to decrease water stress during the acclimatization period.

1111

Karban, R., and J.S. Thaler. 1999. Plant phase change and resistance to herbivory. *Ecology 80(2):510-517.*

All plants pass through a series of predictable developmental stages during their lives, called phase changes. The phase change from juvenile to adult leaves is known to be associated with changes in resistance against plant pathogens and herbivores in several species. Virtually nothing is known about changes in resistance associated with the transition from embryonic tissue to autotrophic tissue in seedlings. We studied the consequences of transitions from cotyledons to juvenile true leaves to adult true leaves in cotton seedlings (Gossypium hirsutum) for their resistance to spider mites (Tetranychus urticae). Mite populations grew much more rapidly on cotyledons than on true leaves. However, there was no detectable difference in the population growth of mites on juvenile vs. adult true leaves. We suggest that population growth of mites is positively affected by the high rates of photosynthesis of cotyledons relative to true leaves, or by some process or attribute correlated with photosynthesis. Conditions that caused increased rates of photosynthesis (exposure to light and elevated concentrations of CO2) caused mite populations to increase. Greater mite population growth on

cotyledons was not associated with stored reserves in the cotyledons, as the mites did poorly on cotyledons kept in the dark. This study indicates that phase changes can have profound effects on plant resistance to herbivores. Because the seedling stage is so vulnerable to herbivory and so critical to understanding plant population dynamics, a broader consideration of phase changes associated with seedlings is warranted.

KEYWORDS: AGE, CARBON DIOXIDE, COTTON, LEAF ABSCISSION, MATURATION, MITES, PHOTOSYNTHESIS, TREE

1112

Karnosky, D.F., B. Mankovska, K. Percy, R.E. Dickson, G.K. Podila, J. Sober, A. Noormets, G. Hendrey, M.D. Coleman, M. Kubiske, K.S. Pregitzer, and J.G. Isebrands. 1999. Effects of tropospheric O-3 on trembling aspen and interaction with CO2: Results from an O-3-gradient and a face experiment. *Water, Air, and Soil Pollution 116(1-2):311-322.*

Over the years, a series of trembling aspen (Populus tremuloides Michx.) clones differing in O-3 sensitivity have been identified from OTC studies. Three clones (216 and 271[(O- 3 tolerant] and 259 [O-3 sensitive]) have been characterized for O-3 sensitivity by growth and biomass responses, foliar symptoms, gas exchange, chlorophyll content, epicuticular wax characteristics, and antioxidant production. In this study we compared the responses of these same clones exposed to O-3 under field conditions along a natural O-3 gradient and in a Free-Air CO2 and O-3 Enrichment (FACE) facility. In addition, we examined how elevated CO2 affected O-3 symptom development. Visible O-3 symptoms were consistently seen (5 out of 6 years) at two of the three sites along the O-3 gradient and where daily one-hour maximum concentrations were in the range of 96 to 125 ppb. Clonal differences in O-3 sensitivity were consistent with our OTC rankings. Elevated CO2 (200 ppm over ambient and applied during daylight hours during the growing season) reduced visible foliar symptoms for all three clones from 31 to 96% as determined by symptom development in elevated O-3 versus elevated O-3 + CO2 treatments. Degradation of the epicuticular wax surface of all three clones was found at the two elevated O-3 gradient sites. This degradation was quantified by a coefficient of occlusion which was a measure of stomatal occlusion by epicuticular waxes. Statistically significant increases in stomatal occlusion compared to controls were found for all three clones and for all treatments including elevated CO2, elevated O-3, and elevated CO2 + O-3. Our results provide additional evidence that current ambient O- 3 levels in the Great Lakes region are causing adverse effects on trembling aspen. Whether or not elevated CO2 in the future will alleviate some of these adverse effects, as occurred with visible symptoms but not with epicuticular wax degradation, is unknown.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, CLONES, GROWTH, NATURAL-SELECTION, OZONE TOLERANCE, PHOTOSYNTHESIS, PHYSIOLOGY, POPULUS-TREMULOIDES, SENSITIVITY

1113

Karnosky, D.F., G.K. Podila, Z. Gagnon, P. Pechter, A. Akkapeddi, Y. Sheng, D.E. Riemenschneider, M.D. Coleman, R.E. Dickson, and J.G. Isebrands. 1998. Genetic control of responses to interacting tropospheric ozone and CO2 in Populus tremuloides. *Chemosphere 36(4-5):807-812.*

We exposed trembling aspen (Populus tremuloides Michx.) clones differing in tropospheric ozone (O-3) tolerance in various open-top chamber studies for three growing seasons, and examined the effects of O-3, CO2, and O-3 + CO2 on growth and physiological processes. Ozone in the range of 80 ppm hr (Sum 00) per growing season decreased height, diameter, and stem and leaf biomass slightly in a tolerant clone but severely in a sensitive clone. Elevated CO2 (150 ppm over ambient) did not compensate for the O-3 effects. Antioxidant enzyme analysis showed elevated SOD levels in the tolerant clone but not in the sensitive clone following O-3 exposure. Northern blot analysis indicated that the chloroplastic and cytosolic Cu/Zn SOD's were significantly increased in response to O-3 in the tolerant but not the sensitive clone. Currently, we are conducting molecular analysis to determine the functional significance of SOD's in regulating O-3 tolerance in aspen. (C) 1997 Elsevier Science Ltd.

KEYWORDS: ALLOCATION, ASPEN CLONES, ATMOSPHERIC CO2, BIOMASS, EXPOSURES, FIELD, GROWTH, NATURAL-SELECTION, PRODUCTIVITY, SENSITIVITY

1114

Karowe, D.N., D.H. Seimens, and T. Mitchell-Olds. 1997. Species-specific response of glucosinolate content to elevated atmospheric CO2. *Journal of Chemical Ecology 23(11):2569-2582.*

The carbon/nutrient balance hypothesis has recently been interpreted to predict that plants grown under elevated CO2 environments will allocate excess carbon to defense, resulting in an increase in carbon-based secondary compounds. A related prediction is that, because plant growth will be increasingly nitrogen-limited under elevated CO2 environments, plants will allocate less nitrogen to defense, resulting in decreased levels of nitrogen-containing secondary compounds. We present the first evidence of decreased investment in nitrogen- containing secondary compounds for a plant grown under elevated CO2. We also present evidence that plant response is species specific and is not correlated with changes in leaf nitrogen content or leaf carbon-nitrogen ratio. When three crucifers were grown at 724 +/- 8 ppm CO2, total foliar glucosinolate content decreased significantly for mustard, but not for radish or turnip. Glucosinolate content of the second and fourth young est mustard leaves decreased by 45% and 31%, respectively. In contrast, no significant change in total glucosinolate content was observed in turnip or radish leaves, despite significant decreases in leaf nitrogen content. Total glucosinolate content differed significantly among leaves of different age; however, the trend differed among species. For both mustard and turnip, glucosinolate content was significantly higher in older leaves, while the opposite was true for radish. No significant CO2 x leaf age interaction was observed, suggesting that intraplant patterns of allocation to defense will not change for these species. Changes in nitrogen allocation strategy are likely to be species-specific as plants experience increasing atmospheric CO2 levels. The ecological consequences of CO2-induced changes in plant defensive investment remain to be investigated.

KEYWORDS: ALLELOCHEMICALS, CARBON-DIOXIDE ATMOSPHERES, CRUCIFERAE, DIAMONDBACK MOTH, GROWTH, HERBIVORY, IDENTIFICATION, MUSTARD, NUTRIENT BALANCE, PLUTELLA-XYLOSTELLA

1115

Kartschall, T., S. Grossman, P.J. Pinter, R.L. Garcia, B.A. Kimball, G.W. Wall, D.J. Hunsaker, and R.L. LaMorte. 1995. A simulation of phenology, growth, carbon dioxide exchange and yields under ambient atmosphere and free-air carbon dioxide enrichment (FACE) Maricopa, Arizona, for wheat. *Journal of Biogeography 22(4-5):611-622.*

The impact of increased atmospheric CO2 concentration on the growth and productivity of field grown wheat has been evaluated. Meteorological and soil information from this study were used to validate a model (DEMETER) for simulation of vegetation response to climate change scenarios. The model simulations of phenology, carbon exchange rate, growth and yield for the treatment conditions of the experiment show a reasonable accordance with the experimental data.

KEYWORDS: LEAVES, MODEL

1116

Karunaratne, C., G.A. Moore, R. Jones, and R. Ryan. 1997. Phosphine and its effect on some common insects in cut flowers. *Postharvest Biology and Technology 10(3):255-262.*

The most effective fumigant for insect disinfestation of cut flowers is currently methyl bromide, which will soon be unavailable in several countries. The toxicity of an alternative fumigant, phosphine (2% PH3 and 98% N-2), was tested at 24 degrees C on adult greenhouse thrips (Heliothrips haemorrhoidalis), adult aphids (Myzus persicae) and lightbrown apple moth larvae (LBAM; Epiphyas postvittana). These are commonly found as insect pests on many cut flower crops. Thrips were exposed to phosphine concentrations ranging from 20-600 mu l/l for 1 or 2 h. All thrips were killed within 18 h of exposure after a treatment of 300 mu l/l phosphine for 2 h. Adult aphids and fifth instar LBAM larvae were more resistant to phosphine, and trials were therefore conducted using higher phosphine concentrations (> 500 mu l/l) combined with atmospheric (0.035%) or elevated (33%) CO2. The most effective treatment for aphids was 1000 mu l/l phosphine +33% CO2 for 4 h, which killed all insects within 36 h of exposure. Under atmospheric CO2 levels, 92% of aphids were killed within 36 h after exposure to 1000 mu l/l phosphine for 6 h, with 100% kill attained after exposure to 5000-8000 mu l/l phosphine for 6 h. Elevated CO2 levels did not improve the efficacy of phosphine on LBAM larvae. The optimal treatment was 2000-2500 mu l/l phosphine for 4 or 6 h, which killed 96 or 100% of the larvae, respectively. Under atmospheric CO2 levels, 4000 mu l/l phosphine killed 74% of LBAM larvae after 4 h. and 94% after 6 h exposure. (C) 1997 Elsevier Science B.V.

KEYWORDS: ATMOSPHERES, CARBON DIOXIDE, TOXIC ACTION

1117

Kasurinen, A., H.S. Helmisaari, and T. Holopainen. 1999. The influence of elevated CO2 and O-3 on fine roots and mycorrhizas of naturally growing young Scots pine trees during three exposure years. *Global Change Biology 5(7):771-780.*

Young Scots pine trees naturally established at a pine heath were exposed to two concentrations of CO2 (ambient and doubled ambient) and two O-3 regimes (ambient and doubled ambient) and their combination in open-top field chambers during growing seasons 1994, 1995 and 1996 (late May to 15 September). Filtered ozone treatment and chamberless control trees were also included in the treatment comparisons. Root in-growth cores were inserted to the undisturbed soil below the branch projection of each tree at the beginning of the fumigation period in 1994 and were harvested at the end of the fumigation periods in 1995 and 1996. Root biomasses were determined from different soil layers in the ingrowth cores, and the infection levels of different mycorrhizal types were calculated. Elevated O-3 and CO2 did not have significant effects on the biomass production of Scots pine coarse (diameter >2 mm) or fine roots (diameter <2 mm) and roots of grasses and dwarf shrubs. Elevated O-3 caused a transient stimulation, observable in 1995, in the proportion of tuber-like mycorrhizas, total mycorrhizas and total short roots but this stimulation disappeared during the last study year. Elevated CO2 did not enhance carbon allocation to root,growth or mycorrhiza formation, although a diminishing trend in the mycorrhiza formation was observed. In the combination treatment increased CO2 inhibited the transient stimulating effect of ozone, and a significant increase of old mycorrhizas was observed. Our conclusion is that doubled CO2 is not able to increase carbon allocation to growth of fine roots or mycorrhizas in nutrient poor forest sites and realistically elevated ozone does not cause a measurable limitation to roots within a period of three exposure years.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, COLONIZATION, ENRICHMENT, FIELD, GROWTH, LOBLOLLY-PINE, PHOTOSYNTHESIS, RESPONSES, SOIL, TROPOSPHERIC OZONE

1118

Kaufman, Y.J., and M.D. Chou. 1993. Model simulations of the competing climatic effects of so2 and co2. *Journal of Climate 6(7):1241-1252.*

Sulfur dioxide-derived cloud condensation nuclei are expected to enhance the planetary albedo, thereby cooling the planet. This effect might counteract the global warming expected from enhanced greenhouse gases. A detailed treatment of the relationship between fossil fuel burning and the SO2 effect on cloud albedo is implemented in a two-dimensional model for assessing the climate impact. Although there are large gaps in our knowledge of the atmospheric sources and sinks of sulfate aerosol, it is possible to reach some general conclusions. Using a conservative approach, results show that the cooling induced by the SO2 emission can presently counteract 50% of the CO2 greenhouse warming. Since 1980, a strong warming trend has been predicted by the model, 0.15-degrees-C, during the 1980- 1990 period alone. The model predicts that by the year 2060 the SO2 cooling reduces climate warming by 0.5-degrees-C or 25% for the Intergovernmental Panel on Climate Change (IPCC) business as usual (BAU) scenario and 0.2-degrees-C or 20% for scenario D (for a slow pace of fossil fuel burning). The hypothesis is examined that the different responses between the Northern Hemisphere (NH) and the Southern Hemisphere (SH) can be used to validate the presence of the SO2-induced cooling. Despite the fact that most of the SO2-induced cooling takes place in the Northern Hemispheric continents, the model-predicted difference in the temperature response between the NH and the SH of -0.2- degrees-C in 1980 is expected to remain about the same at least until 2060. This result is a combined effect of the much faster response of the continents than the oceans and of the larger forcing due to CO2 than due to the SO2. The climatic response to a complete filtering of SO2 from the emission products in order to reduce acid rain is also examined. The result is a warming surge of 0.4-degrees-C in the first few years after the elimination of the SO2 emission.

KEYWORDS: AEROSOLS, ATMOSPHERIC SULFUR, EFFECTIVE PARTICLE RADIUS, FEEDBACK PROCESSES, GLOBAL CLOUD ALBEDO, OPTICAL- THICKNESS, PARAMETERIZATIONS, POLLUTION, SENSITIVITY, SOLAR-RADIATION MEASUREMENTS

1119

Ke, D.Y., E. Yahia, M. Mateos, and A.A. Kader. 1994. Ethanolic fermentation of bartlett pears as influenced by ripening stage and atmospheric composition. *Journal of the American Society for Horticultural Science 119(5):976-982.*

Changes in fermentation volatiles and enzymes were studied in preclimacteric and postclimacteric 'Bartlett' pears (Pyrus communis L.) kept in air, 0.25% O2, 20% O2 + 80% CO2, or 0.25% O2 + 80% CO2 at 20C for 1, 2, or 3 days. All three atmospheres resulted in accumulation of acetaldehyde, ethanol, and ethyl acetate. The postctimacteric pears had higher activity of pyruvate decarboxylase (PDC) and higher concentrations of fermentation volatiles than those of the preclimacteric fruit. For the preclimacteric pears, the 0.25% O2 treatment dramatically increased alcohol dehydrogenase (ADH) activity, which was largely due to the enhancement of one ADH isozyme. Exposure to 20% O2 + 80% CO2 slightly increased ADH activity, but the combination of 0.25% O2 + 80% Co2 resulted in lower ADH activity than 0.25% O2 alone. For the postclimacteric pears, the three atmospheres resulted in higher PDC and ADH activities than those of air control fruit. Ethanolic fermentation in 'Bartlett' pears could be induced by low O2 and/or high CO2 via 1) increased amounts of PDC and ADH;

2) PDC and ADH activation caused by decreased cytoplasmic pH; or 3) PDC and ADH activation or more rapid fermentation due to increased concentrations of their substrates (pyruvate, acetaldehyde, or NADH).

KEYWORDS: ALCOHOL-DEHYDROGENASE, ANAEROBIC NITROGEN, CARBON-DIOXIDE ATMOSPHERES, FRUIT TOLERANCE, INDUCTION, LOW-OXYGEN ATMOSPHERES, POST-HARVEST QUALITY, PYRUVATE DECARBOXYLASE, SHORT- TERM, STORAGE

1120

Ke, D.Y., L.L. Zhou, and A.A. Kader. 1994. Mode of oxygen and carbon-dioxide action on strawberry ester biosynthesis. *Journal of the American Society for Horticultural Science 119(5):971-975.*

'Chandler' strawberries (Fragaria ananassa Duck.) were kept in air, 0.25% O2, 21% O2 + 50% CO2, or 0.25 O2 + 50% CO2 (balance N2) at 5C for 1 to 7 days to study the effects of controlled atmospheres (CAs) on volatiles and fermentation enzymes. Concentrations of acetaldehyde, ethanol, ethyl acetate, and ethyl butyrate were greatly increased, while concentrations of isopropyl acetate, propyl acetate, and butyl acetate were reduced by the three CA treatments compared to those of air-control fruit. The CA treatments enhanced activities of pyruvate decarboxylase (PDC) and alcohol dehydrogenase (ADH) but slightly decreased activity of alcohol acetyltransferase (AAT). The results indicate that the enhanced PDC and ADH activities by CA treatments cause ethanol accumulation, which in turn drives the biosynthesis of ethyl esters. The increased ethanol concentration also competes with other alcohols for carboxyl groups for esterification reactions. The reduced AAT activity and limited availability of carboxyl groups due to ethanol competition decrease production of other acetate esters.

KEYWORDS: ATMOSPHERES, CO2, DECAY, FRUIT, QUALITY, SHORT-TERM EXPOSURE, STORAGE, VOLATILES

1121

Keeling, R.F. 1995. The atmospheric oxygen cycle - the oxygen isotopes of atmospheric co2 and o-2 and the o-2/n-2 ratio. *Reviews of Geophysics 33:1253-1262.*

KEYWORDS: DIOXIDE, ENRICHMENT, FRACTIONATION, GLOBAL CARBON-CYCLE, ICE, LEAF WATER, LEAVES, PLANTS, RESPIRATION, SEA

1122

Keith, H., R.J. Raison, and K.L. Jacobsen. 1997. Allocation of carbon in a mature eucalypt forest and some effects of soil phosphorus availability. *Plant and Soil 196(1):81-99.*

Pools and annual fluxes of carbon (C) were estimated for a mature Eucalyptus pauciflora (snowgum) forest with and without phosphorus (P) fertilizer addition to determine the effect of soil P availability on allocation of C in the stand. Aboveground biomass was estimated from allometric equations relating stem and branch diameters of individual trees to their biomass. Biomass production was calculated from annual increments in tree diameters and measurements of litterfall. Maintenance and construction respiration were calculated for each component using equations given by Ryan (1991a). Total belowground C flux was estimated from measurements of annual soil CO2 efflux less the C content of annual litterfall (assuming forest floor and soil C were at approximate steady state for the year that soil CO2 efflux was measured). The total C content of the standing biomass of the unfertilized stand was 138 t ha(-1), with approximately 80% aboveground and 20% belowground. Forest floor C was 8.5 t ha(-1). Soil C content (0-1 m) was 369 t ha(-1) representing 70% of the total C pool in the ecosystem. Total gross annual C flux aboveground (biomass increment plus litterfall plus respiration) was 11.9 t ha(-1) and gross flux belowground (coarse root increment plus fine root production plus root respiration) was 5.1 t ha(-1). Total annual soil efflux was 7.1 t ha(-1), of which 2.5 t ha(- 1) (35%) was contributed by litter decomposition. The short- term effect of changing the availability of P compared with C on allocation to aboveground versus belowground processes was estimated by comparing fertilized and unfertilized stands during the year after treatment. In the P-fertilized stand annual wood biomass increment increased by 30%, there was no evidence of change in canopy biomass, and belowground C allocation decreased by 19% relative to the unfertilized stand. Total annual C flux was 16.97 and 16.75 t ha(-1) yr(-1) and the ratio of below-to aboveground C allocation was 0.43 and 0.35 in the unfertilized and P-fertilized stands, respectively. Therefore, the major response of the forest stand to increased soil P availability appeared to be a shift in C allocation; with little change in total productivity. These results emphasise that both growth rate and allocation need to be estimated to predict changes in fluxes and storage of C in forests that may occur in response to disturbance or climate change.

KEYWORDS: BIOMASS, CLIMATE CHANGE, DIOXIDE EVOLUTION, ECOSYSTEMS, ELEVATED ATMOSPHERIC CO2, FINE ROOTS, LITTER, NET PRIMARY PRODUCTION, PINE PLANTATIONS, RESPIRATION

1123

Keller, T., J. Guiot, and L. Tessier. 1997. Climatic effect of atmospheric CO2 doubling on radial tree growth in south eastern France. *Journal of Biogeography 24(6):857-864.*

The climatic effect of a doubling of atmospheric CO2 on radial growth of trees was studied in ten populations of three species in south eastern France using an Atmospheric General Circulation Model (AGCM) predicting a 3 degrees C increase of mean temperature and a light rise of precipitation. Results are based on empirical growth climate models, involving an Artificial Neural Network (ANN) technique. Only two of the studied populations, on the boundaries of their ecological area, are sensitive to the climatic variations. One is the larch (Larix decidua Mill.) population located at 2300m on elevation (near the timberline) which shows a radial growth increase. The other is the most southern French Scots pine (Pinus sylvestris L.) population which reacts with a severe growth rate reduction.

1124

Kellogg, E.A., E.J. Farnsworth, E.T. Russo, and F. Bazzaz. 1999. Growth responses of C-4 grasses of contrasting origin to elevated CO2. *Annals of Botany 84(3):279-288.*

Nine grass species representing three independent origins of the C-4 photosynthetic pathway were grown at ambient (350 ppm) and elevated (700 ppm) CO2 and were harvested after flowering. Setaria and Arundinella are both members of the subfamily Panicoideae, and represent a single origin of the pathway. Aristida and Stipagrostis are sister genera in the subfamily Aristidoideae (formerly classified in subfamily Arundinoideae), and represent a second origin. Sporobolus, a member of the subfamily Chloridoideae, represents the third. By investigating two genera each within Panicoideae and Aristidoideae, we test the hypothesis that genera sharing the same origin of C-4 respond similarly. To explore variation among congeneric species, five species of Setaria were also examined to test the hypothesis that congeneric species have similar responses. Plant height and numbers of tillers, branches and inflorescences were measured, both over time and at final harvest. Biomass of roots, shoots, and inflorescences was also measured. Members of the Aristidoideae were generally significantly larger in

elevated CO2, as indicated by measurements of biomass and plant height, whereas representatives of the Panicoideae varied considerably in their response. The two subfamilies differed significantly in their responses to elevated CO2 and this effect outweighed any effect of CO2 alone. Sporobolus, though equally distantly related to Panicoideae and Aristidoideae, had a CO2 response similar to that of some panicoid species. Even within the genus Setaria, some species were significantly smaller at elevated than at ambient CO2, whereas others were larger. This may reflect diversity in internal regulation rather than acclimation or changes in source-sink allocation of carbon. The variation complicates any prediction of responses of C-4 plants to future atmospheric change. Comparison of closely related species, however, may well lead to intriguing new insights into how regulatory pathways of CO2 assimilation are modified during evolution. (C) 1999 Annals of Botany Company.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, ENRICHMENT, FAMILY POACEAE, GAS-EXCHANGE, GENE-EXPRESSION, PHOTOSYNTHETIC ACCLIMATION, PLANTS, SEQUENCE DATA, STRESS

1125

Kellomaki, S., T. Karjalainen, and H. Vaisanen. 1997. More timber from boreal forests under changing climate? *Forest Ecology and Management 94(1-3):195-208.*

The effects of increases in temperature, precipitation and atmospheric CO2 concentration on timber yields from stands of Scots pine (Pinus sylvestris L.) in southern Finland (61 degrees N) are addressed. The assessment is based on simulations using a process-based model in which temperature, precipitation, and atmospheric CO2 are among the main drivers linking the dynamics of the tree stands directly and indirectly with the changing climate. These factors control photosynthesis, respiration, transpiration and the uptake of nitrogen and water, with consequent effects on the growth and development of tree stands. The timing of thinnings and the length of the rotation were related to the dynamics of the tree stand in compliance with the thinning rules applied in practical forestry. The simulations indicated that an increase in precipitation of 9 mm per decade alone did not affect timber yields. However, a temperature increase of 0.4 degrees C per decade, and the combination of temperature and precipitation increases would increase timber yields by 10% during one rotation. An elevation in the concentration of atmospheric CO2 by 33 mu mol mol(-1) per decade alone would increase removals of timber by 20%, and a combination of increases in temperature, precipitation and CO2 concentration would increase removals by 30%. A rise in precipitation did not have any effect on the length of the rotation, but the other combinations shortened the rotation; by 9 years in the case of elevating temperature, by 17 years in the case of elevating atmospheric CO2 concentration, and by 23 years in the case of the combined elevation of temperature, precipitation, and CO2 concentration due to more rapid tree growth and development. These changes can be expected to affect the supply of timber and also the profitability of forestry. (C) 1997 Elsevier Science B.V.

KEYWORDS: ATMOSPHERIC CO2, CARBON, ELEVATED CO2, GAS-EXCHANGE, MATTER, PHOTOSYNTHESIS, SCOTS PINE, SIMULATION, SOIL MOISTURE, TEMPERATURE

1126

Kellomaki, S., and H. Vaisanen. 1997. Modelling the dynamics of the forest ecosystem for climate change studies in the boreal conditions. *Ecological Modelling 97(1-2):121-140.*

This paper summarizes a forest ecosystem model developed for assessing the effects of climate change on the functioning and structure of boreal coniferous forests under the assumption that temperature and precipitation are the basic dimensions of the niche occupied by any one tree species. Special attention is paid to specifying weather patterns to a level representing the time constant of different physiological and ecological processes relevant to the regeneration, growth and death of trees. The long-term dynamics of the forest ecosystem have been coupled with climatic factors at the level of mechanisms, e.g., photosynthesis and respiration, in terms of the energy flow through the ecosystem. Furthermore, hydrological and nutrient cycles couple the dynamics of the forest ecosystem with climate change through soil processes representing the thermal and hydraulic properties of the soil and the decomposition of litter and humus with the mineralization of nutrients. Simulations for southern Finland (62 degrees N) and northern Finland (66 degrees N) indicated that a transient increase in temperature by 4 degrees C over a period of 100 years could substantially increase soil temperature and reduce soil moisture in forest ecosystems dominated by Scots pine. At the same time, the temperature increase could enhance photosynthetic production and consequent stemwood growth in southern Finland by about 8% and in northern Finland by about 19%. Given the current temperature but elevating CO2 concentration, the increase in photosynthesis in southern Finland could be about 23% and in northern Finland about 21%, but the concurrent elevation in temperature and CO2 concentration increased photosynthesis by about 32% in southern Finland and by about 40% in northern Finland. Transpiration decreased by as much as 10-20% under the changing climate with the consequence that water-use efficiency increased by as much as 25-45%, the higher values representing southern Finland. (C) 1997 Elsevier Science B.V.

KEYWORDS: ELEVATED CO2, GAS-EXCHANGE, HABITAT, IRRADIANCE, NITROGEN, PHOTOSYNTHESIS, REGENERATION, RESPIRATION, SCOTS PINE, SIMULATION

1127

Kellomaki, S., H. Vaisanen, and T. Kolstrom. 1997. Model computations on the effects of elevating temperature and atmospheric CO2 on the regeneration of Scots pine at the timber line in Finland. *Climatic Change 37(4):683-708.*

Based on model computations, the regeneration of Scots pine (Pinus sylvestris L.) was studied at the northern timber line in Finland (70 degrees N) in relation to elevating temperature and atmospheric CO2. If a transient increase of 4 degrees C was assumed during the next 100 years, the length of growing season increased from the current 110-120 days to 150-160 days. This was associated with ca. 5 degrees C increase in the soil temperature over June-August with larger variability in temperature and deeper freezing of the soil due to the reduced depth and duration of the snow cover, At the same time, the moisture content of the surface soil decreased ca. 10% and was more variable, due to less infiltration of water into the soil as a consequence of the enhanced evapotranspiration and deeper freezing of the soil. The temperature elevation alone, or combined with elevating CO2, increased flowering and the subsequent seed crop of Scots pine with a decrease in the frequency of zero crops. In both cases, temperature elevation substantially increased the success of regeneration in terms of the number of seedlings produced after each seed crop. The increasing number of mature seeds was mainly responsible for the enhanced regeneration, but increasing soil temperature also increased the success of regeneration. The soil moisture was seldom limited for seed germination. In terms of the density of seedling stands, and the height and diameter growth of the seedlings, the establishment of a seedling stand was substantially improved under the combined elevation of temperature and CO2 in such a way that the temperature increased the number of mature seeds and enhanced germination of seeds and CO2 increased seedling growth. Even under the changing climatic conditions, however, the growth of the seedling stands was slow, which indicated that the northward advance of the timber line would probably be very slow, even though regeneration was no longer a limiting factor.

KEYWORDS: CHANGING CLIMATE, FORESTS, HABITAT, NITROGEN, PHOTOSYNTHESIS, SIMULATION, SOIL MOISTURE, TREES, WATER

1128

Kellomaki, S., and K.Y. Wang. 1996. Photosynthetic responses to needle water potentials in Scots pine after a four-year exposure to elevated CO2 and temperature. *Tree Physiology 16(9):765-772.*

Effects of needle water potential (psi(1)) on gas exchange of Scots pine (Pinus sylvestris L.) grown for 4 years in open-top chambers with elevated temperature (ET), elevated CO2 (EC) or a combination of elevated temperature and CO2 (EC + ET) were examined at a high photon flux density (PPFD), saturated leaf to air water vapor pressure deficit (VPD) and optimal temperature (T). We used the Farquhar model of photosynthesis to estimate the separate effects of psi 1 and the treatments on maximum carboxylation efficiency (V-c,V-max), ribulose-1,5- bisphosphate regeneration capacity (J), rate of respiration in the light (R(d)), intercellular partial pressure of CO2 (Ci) and stomatal conductance (G(s)). Depression of CO2 assimilation rate at low psi(1) was the result of both stomatal and non- stomatal limitations on photosynthetic processes; however, stomatal limitations dominated during short-term water stress (psi(1)<-1.2 MPa), whereas nonstomatal limitations dominated during severe water stress. Among the nonstomatal components, the decrease in J contributed more to the decline in photosynthesis than the decrease in Long-term elevation of CO2 and temperature led to differences in the maximum values of the parameters, the threshold values of psi(1) and the sensitivity of the parameters to decreasing psi(1). The CO2 treatment decreased the maximum values of V-c,V-max J and R(d) but significantly increased the sensitivity of V-c,V-max J and Rd to decreasing psi(1) ($P < 0.05$). The effects of the ET and EC + ET treatments on V-c,V-max J and R(d) were opposite to the effects of the EC treatment on these parameters. The values of G(s), which were measured simultaneously with maximum net rate of assimilation (A(max)), declined in a curvilinear fashion as psi(1) decreased. Both the EC + ET and ET treatments significantly decreased the sensitivity of G(s) to decreasing psi(1-). We conclude that, in the future, acclimation to increased atmospheric CO2 and temperature could increase the tolerance of Scots pine to water stress.

KEYWORDS: COTTON, DROUGHT, GAS-EXCHANGE, IRRADIANCE, LEAVES, STOMATAL CONDUCTANCE, STRESS

1129

Kellomaki, S., and K.Y. Wang. 1997. Effects of elevated O-3 and CO2 concentrations on photosynthesis and stomatal conductance in Scots pine. *Plant, Cell and Environment 20(8):995-1006.*

Naturally regenerated Scots pines (Pinus sylvestris L.), aged 28-30 years old, were grown in open-top chambers and subjected in situ to three ozone (O-3) regimes, two concentrations of CO2, and a combination of O-3 and CO2 treatments from 15 April to 15 September for two growing seasons (1994 and 1995), The gas exchanges of current-year and 1-year-old shoots were measured, along with the nitrogen content of needles, In order to investigate the factors underlying modifications in photosynthesis, five parameters linked to photosynthetic performance and three to stomatal conductance were determined, Elevated O-3 concentrations led to a significant decline in the CO2 compensation point (I*), maximum RuP2-saturated rate of carboxylation (V-emax), maximum rate of electron transport (J(max)) maximum stomatal conductance (g(smax)) and sensitivity of stomatal conductance to changes in leaf-to-air vapour pressure difference (partial derivative g(s)/partial derivative D-v) in both shoot-age classes, However, the effect of elevated O-3 concentrations on the respiration rate in light (R-d) was dependent on shoot age, Elevated CO2 (700 mu mol mol(-1)) significantly decreased J(max) and g(smax) but increased R-d in 1-year-old shoots and the partial derivative(s)/partial derivative D-v in both shoot-age classes, The interactive effects of O-3 and CO2 on some key parameters (e.g. V-emax and J(max)) were significant. This may be closely related to regulation of the maximum stomatal conductance and stomatal sensitivity induced by elevated CO2. As a consequence, the injury induced by O-3 was reduced through decreased ozone uptake in 1-year-old shoots, but not in the current-year shoots, Compared to ambient O-3 concentration, reduced O-3 concentrations (charcoal-filtered air) did not lead to significant changes in any of the measured parameters, Compared to the control treatment, calculations showed that elevated O-3 concentrations decreased the apparent quantum yield by 35% and by 18%, and the maximum rate of photosynthesis by 21% and by 29% in the current-year and 1-year-old shoots, respectively, Changes in the nitrogen content of needles resulting from the various treatments were associated with modifications in photosynthetic components.

KEYWORDS: CARBON DIOXIDE, DARK RESPIRATION, GAS-EXCHANGE, L KARST, LONG-TERM EXPOSURE, NET PHOTOSYNTHESIS, NORWAY SPRUCE, OPEN-TOP CHAMBERS, PICEA-ABIES L, SOURCE-SINK RELATIONS

1130

Kellomaki, S., and K.Y. Wang. 1997. Effects of elevated O-3 and CO2 on chlorophyll fluorescence and gas exchange in Scots pine during the third growing season. *Environmental Pollution 97(1-2):17-27.*

Naturally regenerated, 30-year-old Scots pines (Pinus Sylvestris L.) were grown in open-top chambers and exposed in situ to doubled ambient O-3, doubled ambient CO2 and a combination of elevated O-3 and CO2 from 15 April to 15 September for three growing seasons (1994-1996). To examine the effects of O-3 and/or CO2 on photosynthesis, chlorophyll a fluorescence and gas exchange were measured simultaneously. Doubled ambient O-3 significantly decreased the rates of photosynthesis at all levels of photon flux density. This was related mainly to a significant decrease in the photochemical efficiency of photosystem II (PS II) and the rate of whole electron transport, rather than to a decrease in stomatal conductance. When measurements were made at doubled ambient concentration of CO2 (700 mu mol mol(-1)), doubled ambient CO2 treatment did not lend to a significant change in the intrinsic capacity of photosynthesis, as manifested by no changes in PS II, the rate of electron transport, the maximal rate of photosynthesis and the apparent quantum yield of CO2 assimilation. However, elevated CO2 increased the sensitivity of stomatal conductance to light and decreased maximal stomatal conductance. When O-3 and CO2 were combined, the O-3-induced decrease in photosynthesis rate was reduced significantly by a high concentration of CO2. This may be partly related to the decrease in stomatal conductance induced by the high concentration of CO2. The complete mechanism behind this interaction is, however, still unclear. (C) 1997 Elsevier Science Ltd.

KEYWORDS: ABIES L KARST, CARBON DIOXIDE, ELECTRON-TRANSPORT, LIGHT-RESPONSE CURVES, LONG-TERM EXPOSURE, NET PHOTOSYNTHESIS, NORWAY SPRUCE, OPEN-TOP CHAMBERS, PHOTOSYSTEM-II ACTIVITY, SOURCE-SINK RELATIONS

1131

Kellomaki, S., and K.Y. Wang. 1997. Effects of long-term CO2 and temperature elevation on crown nitrogen distribution and daily photosynthetic performance of Scots pine. *Forest Ecology and Management 99(3):309-326.*

Single Scots pines (Pinus sylvestris L.), aged 20-25 years, were grown in open-top chambers and exposed to elevated temperature (Elev. T), elevated CO2 (Elev. C) and a combination of elevated CO2 and temperature (Elev. C + T) for 3 years. The vertical distribution of needle

nitrogen concentration was measured simultaneously with gas exchange of attached shoots. Based on the measurements, the dependencies on needle nitrogen concentrations of four photosynthetic parameters, i.e., RuP2 (ribulose 1,5-bisphosphate)-saturated rate of carboxylation (V-cmax), maximum potential electron transport (J(max)), the rate of respiration in the light (R-d) and light-use-efficiency factor (delta), were determined. Using a crown multilayer model, the performance of daily crown photosynthesis in Scots pine was predicted. Compared to the control treatment, the mean concentration of nitrogen in the foliage decreased by 20% and by 17% for trees grown under Elev. C and under Elev. C + T, respectively, but increased by 4% for trees grown under Elev. T. However, the total content of foliage nitrogen per unit ground area increased by 25% for trees grown under Elev. C, by 19% for trees grown under Elev. C + T and by 6% for trees grown under Elev. T; these were due to the increase in the total needle area index. Regressions showed that the foliage grown under Elev. C and Elev. C + T had steeper slopes representing the responses of V-cmax, and R-d and delta to leaf nitrogen concentrations, while Elev. C + T and Elev. T had steeper slopes representing the response of J(max) to needle nitrogen concentrations. Predictions showed that, on a typical sunny day, the daily total of crown photosynthesis increased 22% and 27%, separately for Elev. C and Elev. C + T, and by only 9% for Elev. T alone. Furthermore, the increased daily crown photosynthesis, resulting from treatments involving elevated CO2, can be attributed mainly to an increase in the ambient CO2 concentration and the needle area index, while modification of the intrinsic photosynthetic capacity had only a marginal effect. Based on the current pattern of crown nitrogen allocation, the prediction showed also that the relationship between daily crown photosynthesis and crown nitrogen content was strongly dependent on the daily incident PAR and air temperature. The CO2-elevated treatments led to an increase in the sensitivity of daily crown photosynthesis to changes in crown nitrogen content, daily incident PAR and temperature, while the temperature-elevated treatment had the opposite effect on the sensitivity. (C) 1997 Elsevier Science B.V.

KEYWORDS: ACCLIMATION, CANOPY PHOTOSYNTHESIS, CARBON GAIN, ENRICHMENT, EUCALYPTUS-GRANDIS, GAS-EXCHANGE, GROWTH, LEAF NITROGEN, MINERAL NUTRITION, SPATIAL DISTRIBUTIONS

1132

Kellomaki, S., and K.Y. Wang. 1997. Photosynthetic responses of Scots pine to elevated CO2 and nitrogen supply: Results of a branch-in-bag experiment. *Tree Physiology 17(4):231-240.*

Naturally seeded Scots pine (Pinus sylvestris L.) trees, age 25-30 years, were subjected to two soil-nitrogen-supply regimes and to elevated atmospheric CO2 concentrations by the branch- in-bag method from April 15 to September 15 for two or three years. Gas exchange in detached shoots was measured in a diffuse radiation field. Seven parameters associated with photosynthetic performance and two describing stomatal conductance were determined to assess the effects of treatments on photosynthetic components. An elevated concentration of CO2 did not lead to a significant downward regulation in maximum carboxylation rate (V-cmax) or maximum electron transport rate (J(max)), but it significantly decreased light-saturated stomatal conductance (g(sat)) and increased minimum stomatal conductance (g(min)). Light-saturated rates of CO2 assimilation were higher (24-31 %) in shoots grown and measured at elevated CO2 concentration than in shoots grown and measured ured at ambient CO2 concentration, regardless of treatment time or nitrogen-supply regime. High soil-nitrogen supply significantly increased photosynthetic capacity, corresponding to significant increases in V-cmax and J(max). However, the combined elevated CO2 + high nitrogen-supply treatment did not enhance the photosynthetic response above that observed in the elevated CO2 treatment alone.

KEYWORDS: ATMOSPHERIC CO2, C-3 PLANTS, CARBON DIOXIDE, DARK RESPIRATION, ELECTRON-TRANSPORT, GAS-EXCHANGE, GROWTH, QUANTUM YIELD, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE, TERM

1133

Kellomaki, S., and K.Y. Wang. 1998. Daily and seasonal CO2 exchange in Scots pine grown under elevated O-3 and CO2: experiment and simulation. *Plant Ecology 136(2):229-248.*

Starting in early spring of 1994, naturally regenerated, 30- year-old Scots pine (Pinus sylvestris L.) trees were grown in open-top chambers and exposed in situ to doubled ambient O-3, doubled ambient CO2 and a combination of O-3 and CO2 from 15 April to 15 September. To investigate daily and seasonal responses of CO2 exchange to elevated O-3 and CO2, the CO2 exchange of shoots was measured continuously by an automatic system for measuring gas exchange during the course of one year (from 1 Januray to 31 December 1996). A process-based model of shoot photosynthesis was constructed to quantify modifications in the intrinsic capacity of photosynthesis and stomatal conductance by simulating the daily CO2 exchange data from the field. Results showed that on most days of the year the model simulated well the daily course of shoot photosynthesis. Elevated O-3 significantly decreased photosynthetic capacity and stomatal conductance during the whole photosynthetic period. Elevated O-3 also led to a delay in onset of photosynthetic recovery in early spring and an increase in the sensitivity of photosynthesis to environmental stress conditions. The combination of elevated O-3 and CO2 had an effect on photosynthesis and stomatal conductance similar to that of elevated O-3 alone, but significantly reduced the O-3 induced depression of photosynthesis. Elevated CO2 significantly increased the photosynthetic capacity of Scots pine during the main growing season but slightly decreased it in early spring and late autumn. The model calculation showed that, compared to the control treatment, elevated O-3 alone and the combination of elevated O-3 and CO2 decreased the annual total of net photosynthesis per unit leaf area by 55% and 38%, respectively. Elevated CO2 increased the annual total of net photosynthesis by 13%.

KEYWORDS: 4-YEAR EXPOSURE, ABIES L KARST, AIR-POLLUTANTS, CARBON DIOXIDE, CHLOROPHYLL FLUORESCENCE, MIDDAY STOMATAL CLOSURE, NET PHOTOSYNTHESIS, OZONE POLLUTION, PHOTOSYNTHETIC RESPONSES, SOLAR RADIATION

1134

Kellomaki, S., and K.Y. Wang. 1998. Growth, respiration and nitrogen content in needles of Scots pine exposed to elevated ozone and carbon dioxide in the field. *Environmental Pollution 101(2):263-274.*

Single Scots pine (Pinus sylvestris L.) trees, aged 30 years, were grown in open-top chambers and exposed to two atmospheric concentrations of ozone (O-3; ambient and elevation) and carbon dioxide (CO2) as single variables or in combination for 3 years (1994-96). Needle growth, respiration and nitrogen content were measured simultaneously over the period of needle expansion. Compared to ambient treatment (33 nmol mol(-1) O-3 and 350 mu mol mol(-1) CO2) doubled ambient O-3 (69 nmol mol(-1)) significantly reduced the specific growth rates (SGRs) of the needles in the early stage of needle expansion and needle nitrogen concentration (N-1) in the late stage, but increased apparent respiration rates (ARRs) in the late stage. Doubled ambient CO2 (about 650 mu mol mol(-1)) significantly increased maximum SGR but reduced ARR and N-1 in the late stage of needle expansion. The changes in ARR induced by the different treatments may be associated with treatment-induced changes in needle growth, metabolic activities and turnover of nitrogenous compounds. When ARR was partitioned into its two functional components, growth and maintenance respiration, the results

showed that neither doubled ambient O-3 nor doubled ambient CO2 influenced the growth respiration coefficients (R-g). However, doubled ambient O-3 significantly increased the maintenance respiration coefficients (R-m) regardless of the needle development stage, while doubled ambient CO2 significantly reduced R-m only in the late stage of needle expansion. The increase in R-m under doubled ambient O-3 conditions appeared to be related to an increase in metabolic activities, whereas the decrease in R-m under doubled ambient CO2 conditions may be attributed to the reduced N-1 and turnover rate of nitrogenous compounds per unit. The combination of elevated O-3 and CO2 had very similar effects on growth, respiration and N-1 to doubled ambient O-3 alone, but the interactive mechanism of the two gases is still not clear.

KEYWORDS: CO2- ENRICHMENT, DARK RESPIRATION, GAS-EXCHANGE, L KARST, MAINTENANCE RESPIRATION, NONSTRUCTURAL CARBOHYDRATE CONTENT, NORWAY SPRUCE, OPEN-TOP CHAMBERS, PICEA-ABIES L, PLANT RESPIRATION

1135

Kellomaki, S., and K.Y. Wang. 1998. Sap flow in Scots pines growing under conditions of year-round carbon dioxide enrichment and temperature elevation. *Plant, Cell and Environment 21(10):969-981.*

Starting in 1996, individual trees of Scots pine (Pinus sylvestris L.) aged 30 years were grown in closed-top chambers and exposed to normal ambient conditions (CON), elevated CO2 (Elev. C), elevated temperature (Elev. T) and a combination of elevated CO2 and temperature (Elev. C + T). Using the constant- power heat balance method, sap flow was monitored simultaneously in a total of 16 trees, four for each treatment, over a 32 d period (after the completion of needle expansion and branch elongation in 1997). An overall variation in diurnal sap flow totals (F-t) was evident during the period of measurement (days 167-198, 1997) regardless of the treatments, with a range from 0.15 to 2.82 kg tree(-1) d(-1). Elev. C reduced F-t by 4.1-13.7% compared with CON on most days (P varies from 0.042 to 0.108), but slightly increased it on some days (P greater than or equal to 0.131), depending on the weather conditions. Although the decrease in F-t caused by Elev. C was statistically significant on only a few days (P < 0.042), the cumulative F-t, for the 32 d decreased by 14.4% (P = 0.047), indicating that Elev. C may have an important influence on seasonal water use of the Scots pine. Analysis of the diurnal courses of sap flow combined with corresponding weather factors indicated that the CO2-induced decrease in F-t could be largely attributed to an increase in stomatal sensitivity to vapour pressure deficit (VPD), whereas the CO2- induced increase in F-t related to an increase in stomatal sensitivity to low light levels. Elev. T increased F-t by 11.2- 35.6% throughout the measuring period and the cumulative F-t for the 32 d by 32.5% (P = 0.019), which could be largely attributed to the temperature-induced increase in current-year needle area and decrease in stomatal sensitivity to high levels of VPD. There were no significant interactive effects of CO2 and temperature on sap flow, so that Elev. C + T had approximately the same F-t as Elev. T and similar diurnal patterns of sap flow, suggesting that the temperature factor played a dominant role in the case of Elev. C + T.

KEYWORDS: 4-YEAR EXPOSURE, ATMOSPHERIC CO2, CLIMATE CHANGE, CO2- ENRICHMENT, GROWTH, PHOTOSYNTHETIC RESPONSES, SOIL MOISTURE, STOMATAL CONDUCTANCE, TRANSPIRATION RESPONSES, WATER-USE EFFICIENCY

1136

Kellomaki, S., and K.Y. Wang. 1999. Short-term environmental controls of heat and water vapour fluxes above a boreal coniferous forest: model computations compared with measurements by eddy correlation. *Ecological Modelling 124(2-3):145-173.*

Eddy correlation and stern how measurements were coupled with detailed microclimate and soil measurements made in a boreal Scots pine forest in the late growing season of 1998 to determine sensible and latent heat fluxes from the soil and the canopy separately. A 'resistance/energy' model is constructed and parametrized in order to reproduce the dynamics of water and heat exchange between the soil, the canopy and the atmosphere as a part of a larger forest ecosystem model (FinnFor; Kellomaki and Vaisanen, 1997). Unique features of the present model are that (1) energy flux equations are expressed in terms of conceptual resistances and their solutions are obtained by closing two surface energy budget equations defined separately for canopy and soil surface; (2) the forest canopy is divided into shaded and sunlit fractions in the radiation transfer submodel and the canopy resistance submodels; (3) a numerical integrating solutions are derived separately for net radiation absorption in the canopy, bulk canopy resistance and the bulk aerodynamic resistances of the forest; and (4) iterative determinations of canopy water potential based on a classical one-dimensional water how model enable the model to represent explicitly the interaction between the above-ground and the below-ground water dynamics. The model is validated against 19-day flux measurements. In general, the total system sensible heat flux (H), total system latent heat flux (lambda E), canopy latent heat flux (lambda E-c), and soil surface heat flux (G(s)) computed by the model matched well with the measured data. Based on 1/2 h flux measurements, daily lambda E varied from 0.50-7.38 MW m(-2), H from 0.64-8.3 MW m(-2): and lambda E-c from 0.30-6.93 MW m(-2). The Bowen ratio (H/lambda E) ranged from -4.5 to 9.8, but 82% of the values for the Bowen ratio were within 0.5-2.5. The model computations showed that daily lambda E-c and H-c accounted for 21-64% and 43-66% of the daily total system flux, respectively. Daily soil latent heat (lambda E,) and soil sensible heat (H-s) fluxes accounted for 0.02-4.5% and 0.05-7.6%, respectively, and the daily energy storage within the canopy (S-c) and G(s) accounted for 0.1-7.2% and 0.8-5.6%, respectively. Plotting of 1/2 h flux data against a single environmental factor indicated that a 68% change in lambda E-c and a 72% change in H-c can be explained by a change in canopy radiation absorption (R-nc) at the 5% probability level. The high correlation between the canopy fluxes and R-nc could be related to the moderate weather conditions and high soil water content during the selected days, whereas lambda E- s, H-s, S-c and G(s) give no significant correlation with R-n. As expected. lambda E-c was strongly dependent on canopy resistance (r(cs)), but less impact on aerodynamic resistances during most of the measuring time. The proportion of energy partitioning in H and lambda E exhibited a clear diurnal trend and was mainly controlled by the system total resistance and the vapour pressure deficit, but less related to changes in soil water content.

KEYWORDS: 4-YEAR EXPOSURE, DOUGLAS-FIR, ELEVATED CO2, ENERGY- TRANSPORT, PINUS-PINASTER AIT, SAP FLOW, SCOTS PINE, SPARSE CROPS, STOMATAL CONDUCTANCE, SURFACE-TEMPERATURE

1137

Kelly, D.W., P.R. Hicklenton, and E.G. Reekie. 1991. Photosynthetic response of geranium to elevated co2 as affected by leaf age and time of co2 exposure. *Canadian Journal of Botany-Revue Canadienne De Botanique 69(11):2482-2488.*

Geranium plants were grown from seed in chambers maintained at 350 or 1000-mu-L.L-1 CO2. Photopsynthesis as affected by leaf age and by leaf position was determined. Elevated CO2 enhanced photosynthesis to the greatest extent in middle-aged leaves; very young leaves exhibited little enhancement, and net photosynthesis in the oldest leaves was depressed by elevated CO2. Temporary increases in net photosynthesis (relative to leaves developed at high CO2) resulted when young leaves grown at 350-mu-L.L-1 CO2 were switched to 1000-mu-L.L-1 CO2.

Leaves switched later in development exhibited permanent enhancement. Middle-aged leaves exhibited a temporary depression followed by permanent enhancement. Leaves developed at high CO2 and switched to low CO2 did not exhibit any photosynthetic depression relative to plants grown continuously at low CO2. Similarly, leaves developed at low CO2 switched to high CO2 for various lengths of time, and returned to low CO2 showed no photosynthetic depression. Leaves developed at low CO2 and switched to high CO2 exhibited increases in specific leaf weight and leaf thickness. The increase in leaf thickness was proportional to length of time spent at high CO2. High CO2 depressed the rate at which stomata developed but did not affect final stomatal density. Results suggest that photosynthesis at low CO2 was limited by CO2 regardless of developmental environment, whereas photosynthesis at high CO2 was limited by the developmental characteristics of the leaf. Further, both biochemical and structural modifications appear to be involved in this response. Because of the very different responses of young versus old leaves, future studies should be careful to consider leaf age in assessing response to elevated CO2.

KEYWORDS: ACCLIMATION, CARBON DIOXIDE, ENRICHMENT, EXCHANGE, LEAVES, LONG-TERM EXPOSURE, PLANTS, RIBULOSE BISPHOSPHATE CARBOXYLASE, SOYBEAN PHYSIOLOGY, STARCH

1138

Kemp, P.R., D.G. Waldecker, C.E. Owensby, J.F. Reynolds, and R.A. Virginia. 1994. Effects of elevated co2 and nitrogen-fertilization pretreatments on decomposition on tallgrass prairie leaf-litter. *Plant and Soil 165(1):115-127.*

Standing dead and green foliage litter was collected in early November 1990 from Andropogon gerardii (C-4), Sorghastrum nutans (C-4), and Poa pratensis (C-3) plants that were grown in large open-top chambers under ambient or twice ambient CO2 and with or without nitrogen fertilization (45 kg N ha(-1)). The litter was placed in mesh bags on the soil surface of pristine prairie adjacent to the growth treatment plots and allowed to decay under natural conditions. Litter bags were retrieved at fixed intervals and litter was analyzed for mass loss, carbon chemistry, and total Kjeldahl nitrogen and phosphorus. The results indicate that growth treatments had a relatively minor effect on the initial chemical composition of the litter and its subsequent rate of decay or chemical composition. This suggests that a large indirect effect of CO2 on surface litter decomposition in the tallgrass prairie would not occur by way of changes in chemistry of leaf litter However, there was a large difference in characteristics of leaf Litter decomposition among the species. Paa leaf fitter had a different initial chemistry and decayed more rapidly than C-4 grasses. We conclude that an indirect effect of CO2 on decomposition and nutrient cycling could occur if CO2 induces changes in the relative aboveground biomass of the prairie species.

KEYWORDS: ACCUMULATION, ATMOSPHERIC CO2, CHIHUAHUAN DESERT, DETRITUS, ECOSYSTEMS, LIGNIN CONTENT, PHOSPHORUS DYNAMICS, PINE NEEDLE LITTER, PLANTS, RESPONSES

1139

Kennedy, A.D. 1995. Antarctic terrestrial ecosystem response to global environmental-change. *Annual Review of Ecology and Systematics 26:683-704.*

Geographical isolation and climatic constraints are responsible for the low biodiversity and structural simplicity of the antarctic terrestrial ecosystem Under projected scenarios of global change, both limiting factors may be released. Alien species immigration is likely to be facilitated as modified ocean and atmospheric circulation introduce exotic water- and air-borne propagules from neighboring continents. Elevated temperature, UV radiation, CO2, and precipitation will combine additively and synergistically to favor new trajectories of community development. It can be predicted that existing patterns of colonization, recruitment, succession, phenology and mortality will be perturbed with concomitant effects for ecosystem function through changes in biomass, trophodynamics, nutrient cycling, and resource partitioning. Soil propagule banks will play an important role through founder effects. Uniquely in Antarctica, many of the short-term consequences of global change will depend on the ecophysiological relationships of cryptogamic plants. However, in the long term, climatic warming will favor an increase in phanerogamic biomass since these species are currently excluded by the low cumulative degree-days > 0 degrees C. It has been suggested that antarctic communities may be particularly vulnerable to global change: Their slow rate of development and restricted gene flow limit response to new conditions. However, vulnerability must be defined with respect to both the direction and rate of change and it is likely that some perturbations will enhance the complexity and productivity of the biota, with negative feedback to the global carbon cycle. The chapter concludes with a discussion of institutional issues surrounding this topic.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, CLIMATIC CHANGE, COLD TOLERANCE, CONTINENTAL ANTARCTICA, CRYPTOPYGUS-ANTARCTICUS, ICE CORES, OZONE DEPLETION, PHOTOSYNTHETIC RESPONSE, TUSSOCK TUNDRA

1140

Kennedy, A.D. 1995. Simulated climate-change - are passive greenhouses a valid microcosm for testing the biological effects of environmental perturbations. *Global Change Biology 1(1):29-42.*

This paper considers the use of passive greenhouse apparatus in field experiments investigating the biological consequences of climate change. The litreature contains many accounts of such experiments claiming relevance of greenhouse treatment effects to global change scenarios. However, inadequacies in microclimate monitoring, together with incomplete understanding of greenhouse modes of action, cast doubt upon such claims. Here, treatment effects upon temperature (magnitude, range, variation, rates of change), moisture (humidity, precipitation, soil water content), light (intensity, spectral distribution), gas composition, snow cover, and wind speed are reviewed in the context of Intergovernmental Panel on Climate Change (IPCC) predictions. It is revealed that greenhouses modify each of these potentially limiting factors in a complex and interactive manner, but that the relationship between this modification and forecast conditions of climate change is poor. Interpretation of biological responses, and their extrapolation to predictive models, is thus unreliable. In order that future greenhouse experiments may overcome criticisms of artefact and lack of rigour, two amendments to methodology are proposed: (1) objective-orientated design of greenhouse apparatus (2) multiple controls addressing individual environmental factors. The importance of a priori testing of microclimate treatment effects is stressed.

KEYWORDS: ALASKAN TUSSOCK TUNDRA, CO2, ERIOPHORUM VAGINATUM, GROWTH, PLANTS, RESPONSES, SENSITIVITY, TEMPERATURE, ULTRAVIOLET-RADIATION, VEGETATION

1141

Kennedy, A.D. 1995. Temperature effects of passive greenhouse apparatus in high- latitude climate-change experiments. *Functional Ecology 9(2):340-350.*

1. Passive greenhouse apparatus is commonly used to investigate the in situ biological response of terrestrial communities to global warming. 2. Although close conformity of greenhouse treatment effects to general circulation model (GCM) scenarios is widely claimed, no proof of such

a relationship has yet been published. 3. Here, the relationship between passive greenhouse thermal environment and future climate conditions is considered using temperature data collected from within and without greenhouses deployed in the maritime Antarctic. It is revealed that in terms of thermal extremes, diel and annual variation, and overall distribution across the temperature spectrum, such apparatus achieves only poor simulation of GCM forecasts. 4. During summer, greenhouses induce an amplified daily range of temperatures, elevated maxima and accelerated rates of change. 5. During spring and autumn, diel temperature variation continues inside the greenhouses while snow cover protects the controls. 6. During winter, an inverse treatment effect occurs, in which the relative depth of snow cover causes lower temperatures in greenhouses than in controls. 7. These treatment effects differ significantly from GCM climate predictions. Changes recorded in the composition, structure and function of greenhouse biota may thus be artefacts of the methodology. 8. Thorough a priori testing of greenhouse treatment effects is recommended for future climate change studies that are to be conducted in environments subject to seasonal snowfall, solar elevation and day length.

KEYWORDS: ALASKAN TUSSOCK TUNDRA, COLD TOLERANCE, DESIGN, ECOSYSTEMS, ELEVATED CO2, ERIOPHORUM VAGINATUM, GROWTH, HABITATS, POLAR, RESPONSES

1142

Kerbel, E.L., A.A. Kader, and R.J. Romani. 1990. Respiratory and glycolytic response of suspension-cultured passe-crassane pear fruit cells to elevated CO2 concentrations. *Journal of the American Society for Horticultural Science 115(1):111-114.*

1143

Kerslake, J.E., S.J. Woodin, and S.E. Hartley. 1998. Effects of carbon dioxide and nitrogen enrichment on a plant- insect interaction: the quality of Calluna vulgaris as a host for Operophtera brumata. *New Phytologist 140(1):43-53.*

Calluna vulgaris L. (Hull) is not one of the usual hosts of the winter moth, Operophtera brumata L., but outbreaks have caused extensive damage to heather moorland in Scotland in recent years. This study investigated the potential role of environmental change in such outbreaks by rearing O. brumata larvae on C. vulgaris plants grown in open-top chambers for 20 months with enriched CO2 (600 ppm) and nitrogen supply (average 52.5 kg N ha(-1) yr(-1)) in factorial combination. This prolonged exposure to elevated CO2 caused no change in shoot growth, photosynthesis or foliar C:N ratio of C, vulgaris, even with increased N supply, indicating that the absence of response was not due to N limitation. Increased N supply itself resulted in increased shoot growth and a decrease in tissue C:N ratio. Phenolic content did not change in response to either CO2 or N enrichment, contrary to the predictions of the carbon/nutrient balance hypothesis. In line with the absence of plant response, there was no effect of CO2 on the development of Operophtera brumata on C, vulgaris, and so continued increase in atmospheric CO2 concentration is unlikely to affect directly O. brumata outbreaks on heather moorland. Operophtera brumata showed increased larval development, growth rate and pupal weight on N-treated plants, correlated both to the decrease in foliar C:N ratio, and to the increase in shoot extension which was predictive of survivorship. Thus, increased atmospheric N deposition, or increased rates of mineralization in a warmer environment, might increase the severity of O. brumata outbreaks on C. vulgaris. Since the combination of high N availability and disturbance of heather canopy by herbivory is known to result in increased dominance of grasses, it is suggested that this could lead to further degradation of moorland in upland Britain.

KEYWORDS: AVAILABILITY, DECIDUOUS TREES, ELEVATED ATMOSPHERIC CO2, GROWTH, HEATHER MOORLAND, HERBIVORE INTERACTIONS, L HULL, LARVAL EMERGENCE, NUTRIENT BALANCE HYPOTHESIS, SOIL NUTRIENT

1144

Kerstiens, G. 1995. Cuticular water permeance of european trees and shrubs grown in polluted and unpolluted atmospheres, and its relation to stomatal response to humidity in beech (fagus-sylvatica L). *New Phytologist 129(3):495-503.*

Cuticular water permeance (P) of astomatous adaxial surfaces of intact leaves was determined in Acer pseudoplatanus L., Betula pubescens Ehrh., Corylus avellana L., Fagus sylvatica L. and Prunus avium L. Water evaporating from the stomata-bearing abaxial leaf surface could not reach the moisture analyzer and the values of P presented here are therefore free from errors that often arise from unintentional inclusion of residual stomatal transpiration. Plants were exposed from before bud-break for several months to 20-50 ppb SO2 (Fagus), a combination of 50-60 ppb SO2 and 50-60 ppb NO2 (Betula), 300- 400 ppb NO (Acer, Corylus, Fagus), regular ozone episodes of up to 120 ppb (Fagus, Prunus), or an elevated level of CO2 (600 ppm for 2 yr; Acer, Fagus). Permeances were in the range 0.6- 2.9 x 10(-5) m s-1 and were unaffected by most treatments. In Prunus, P increased slightly but significantly in the NO treatment. In Corylus and Fagus, P was sometimes found to be reduced by fumigation with NO, but not always. Betula leaves grown under elevated SO2 and NO2 showed higher values of P only if they were visibly damaged. Minimum conductances (g(min) estimated from water loss rates of both sides of detached hypostomatous leaves were higher than P, and were more strongly affected by treatments. In these cases, the most probable explanation is some damage to stomatal function resulting in a reduced ability to close after leaf excision. Effects of growing conditions and time of year on P were found, which allowed a hypothetical interaction between P and stomatal sensitivity to air humidity to be tested in beech. No unambiguous indication of such a relationship was found.

KEYWORDS: AIR-POLLUTION, CARBON DIOXIDE, FUMIGATION, LEAVES, OZONE, PERMEABILITY, PLANT CUTICLES, STRESS, SYSTEM, TRANSPIRATION

1145

Kerstiens, G. 1997. Why is increasing shade-tolerance of trees correlated with increasing stimulation of growth by elevated CO2? *Plant Physiology 114(3):371.*

1146

Kerstiens, G. 1998. Shade-tolerance as a predictor of responses to elevated CO2 in trees. *Physiologia Plantarum 102(3):472-480.*

Evidence from 10 studies comparing angiosperm trees and 5 studies comparing conifers or differing shade-tolerance was analysed. The number of intraphyletic comparisons in which the more shade-tolerant species showed the greater relative increase of biomass in elevated CO2 was significantly higher than would be expected by chance alone. It is suggested that more shade-tolerant species are inherently better disposed. in terms of plant architecture and partitioning of biomass and nitrogen, to utilise resources (light, water, nutrients) that are potentially limiting in elevated CO2 and that these traitu are responsible for the interaction between shade-tolerance and CO2 concentration. Compared with less shade-tolerant angiosperm trees, more shade-tolerant angiosperm species generally have a lower lear area ratio in ambient CO2 and show a smaller relative reduction in elevated CO2. Furthermore, leaf nitrogen content is usually lower in more shads-tolerant angiosperm species and tends to be more strongly reduced by

elevated CO2 in those species. Within angiosperm trees, more shade-tolerant species showed a stronger stimulation of net leaf photosynthetic I ate in most experiments, but this trend was not significant.

KEYWORDS: ATMOSPHERIC CO2, C-3 PHOTOSYNTHETIC SYSTEM, CARBON-DIOXIDE ENRICHMENT, FAGUS-SYLVATICA L, GROWTH-RESPONSES, LEAF GAS- EXCHANGE, LOW-LIGHT, NITROGEN-AVAILABILITY, RAIN-FOREST TREES, SUCCESSIONAL STATUS

1147

Kerstiens, G., and C.V. Hawes. 1994. Response of growth and carbon allocation to elevated co2 in young cherry (prunus-avium L) saplings in relation to root environment. *New Phytologist 128(4):607-614.*

The hypothesis that inadequate rooting volume may reduce the growth stimulation by elevated CO2 in potted tree seedlings and saplings was tested experimentally and by surveying the literature. One-year-old cherry saplings were grown for one season in naturally lit growth chambers in eight combinations of CO2 concentration (ambient; ambient + 250 ppm) and root environment (four types). The latter included (1) moderately restrictive pot volume (4 l) in combination with two levels of fertilizer addition (1a, 1b); (2) 10 l pots with total fertilizer content per pot as in treatment 1a, and (3) 20 l pots with five plants sharing five times the space and nutrient resources of treatment 1a. Plants were harvested in April, May, June, August and September. The overall mean effect of high CO2 plant dry mass by the end of the season was +24%. Interactive effects of root environments and CO2 concentrations on dry mass were not significant at the 5% level, but repeated measurements of basal stem diameter of individual plants indicated a significant impact of root environment on the response to CO2. Overall growth enhancement by elevated CO2 did not differ significantly between harvests, but it tended to increase during the season in those root environments which restricted growth in ambient CO2 most strongly (1a and 3). The hypothesis was rejected for this experiment. Leaf area and stem height were not affected by any treatment. The variation of carbon allocation to roots and shoots with plant size was very similar in all treatments. Plants grew faster in elevated CO2 very early in the season, and this resulted in small but significant differences between seasonal patterns of biomass partitioning in ambient and elevated CO2. A survey of 33 studies on growth responses of 47 tree species to elevated CO2 (600-800 ppm) showed that the relative change in biomass was not related to the ratio of plant biomass and pot volume found in either ambient or elevated CO2. We conclude that there is no evidence that inadequate pot volume had a negative impact on the stimulation of growth of tree species in elevated CO2.

KEYWORDS: DIOXIDE, PHOTOSYNTHETIC ACCLIMATION, PLANTS, SEEDLINGS

1148

Kerstiens, G., J. Townend, J. Heath, and T.A. Mansfield. 1995. Effects of water and nutrient availability on physiological- responses of woody species to elevated co2. *Forestry 68(4):303-315.*

The growth responses to elevated CO2 found in experiments are highly variable and depend on other experimental parameters such as irrigation, fertilization, light regime, etc. As yet, the strength or even the sign of most interactions is all but impossible to predict from first principles. Experiments in ambient and CO2-enriched ambient air (+250 p.p.m.) have been conducted in specially adapted greenhouses (Solardomes) at Lancaster University for the past four seasons on Sitka spruce (Picea sitchensis (Bong.) Carr.), wild cherry (Prunus avium L.), beech (Fagus sylvatica L.) and pedunculate oak (Quercus robur L.). These experiments are reviewed together with other published studies on interactive effects of elevated CO2 and water and nutrient supply on physiological processes, in particular gas exchange, in tree species. It is often assumed that drought tolerance will increase in elevated CO2 because of a suppression of stomatal conductance and an increase in instantaneous water use efficiency. There is, however, some evidence that such effects could be more than offset in beech by CO2-induced increases in leaf area. It is tentatively suggested that in beech, drought tolerance could already have been reduced by the increase in atmospheric CO2 over the last century.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, ENRICHMENT, GAS-EXCHANGE, GROWTH, LIQUIDAMBAR-STYRACIFLUA, LOBLOLLY-PINE SEEDLINGS, PHOTOSYNTHETIC ACCLIMATION, PLANTS, TAEDA SEEDLINGS

1149

Keutgen, N., K. Chen, and F. Lenz. 1997. Responses of strawberry leaf photosynthesis, chlorophyll fluorescence and macronutrient contents to elevated CO2. *Journal of Plant Physiology 150(4):395-400.*

Gas exchange, chlorophyll fluorescence parameters, and macronutrient contents were investigated in young (< 3 weeks), medium (4 - 6 weeks) and old (7 - 9 weeks) strawberry leaves growing at 300, 450, 600, 750, and 300 ppm CO2. An increase of the CO2 level to 600 ppm promoted leaf net photosynthesis, but a further rise led to a decrease of net CO2 assimilation. The reduction of net photosynthetic rate was less distinct in young leaves exposed to CO2 levels above 600 ppm for less than 3 weeks, indicating that the reduction might depend on the period of exposition or leaf age. Transpiration and stomatal conductance were significantly affected by leaf age, but not by CO2 concentrations. Medium leaves were characterised by a higher transpiration rate and stomatal conductance than young and old ones. In leaves growing at high CO2 levels Chl a and b contents as well as the a/b ratio decreased. The contents of N, P, K, Ca and Mg were lower in leaves growing at high CO2 concentrations than in those at low ones. An elevated CO2 level above 750 ppm led to a general macronutrient deficiency and was accompanied by a distinct decrease of optimal quantum yield, due to a rise of basal fluorescence, and an increase of non- photochemical energy dissipation in old leaves.

KEYWORDS: BIOCHEMISTRY, GAS-EXCHANGE, GROWTH, LEAVES, STEADY-STATE PHOTOSYNTHESIS, TOMATO PLANTS

1150

KhavariNejad, R.A. 1996. Growth of tomato plants under carbon dioxide enrichment. *Photosynthetica 32(3):471-474.*

Under short-term CO2 enrichment (1200 cm(3) m(-3)) Of 4-weeks old tomato plants (Lycopersicon esculentum Mill., Eurocross BB, F-1-hybrid) net assimilation rate increased by about 58 %, leaf area increased slightly, fresh matters were not much influenced, but dry matters (except for roots) increased. Stomatal opening in tomato plants was enhanced under CO2 enrichment and the enhancement decreased with time.

KEYWORDS: CO2-ENRICHED ATMOSPHERES

1151

Kickert, R.N., G. Tonella, A. Simonov, and S.V. Krupa. 1999. Predictive modeling of effects under global change. *Environmental Pollution 100(1-3):87-132.*

The status of computer simulation models from around the world for evaluating the possible ecological, environmental, and societal consequences of global change is presented in this paper. In addition, a

brief synopsis of the state of the science of these impacts is included. Issues considered include future changes in climate and patterns of land use for societal needs, Models dis cussed relate to vegetation (e.g, crop), soil, bio-geochemistry, water, and wildlife responses to conventional, forecasted changes in temperature and precipitation. Also described are models of these responses, alone and interactively, to increased CO2, other air pollutants and UV-B radiation, as the state of the science allows. Further, models of land-use change are included. Additionally, global multiple sector models of environment, natural resources, human population dynamics, economics, energy, and political relations are reviewed for integrated impact assessment. To the extent available, information on computer software and hardware requirements is presented for the various models. The paper concludes with comments about using these technologies as they relate to ecological risk assessment for policy decision analysis. Such an effort is hampered by considerable uncertainties with the output of existing models, because of the uncertainties associated with input data and the definitions of their dose-response relationships. The concluding suggestions point the direction for new developments in modeling and analyses that are needed for the 21st century.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, BIOSPHERE-MODEL, CLIMATE-CHANGE SCENARIOS, ELEVATED CO2, FOREST ECOSYSTEM PROCESSES, GENERIC PLANT SIMULATOR, LAND-USE CHANGE, OF-THE- ART, ORGANIC-MATTER DYNAMICS, SOLLING SPRUCE SITE

1152

Kicklighter, D.W., M. Bruno, S. Donges, G. Esser, M. Heimann, J. Helfrich, F. Ift, F. Joos, J. Kaduk, G.H. Kohlmaier, A.D. McGuire, J.M. Melillo, R. Meyer, B. Moore, A. Nadler, I.C. Prentice, W. Sauf, A.L. Schloss, S. Sitch, U. Wittenberg, and G. Wurth. 1999. A first-order analysis of the potential role of CO2 fertilization to affect the global carbon budget: a comparison of four terrestrial biosphere models. *Tellus Series B-Chemical and Physical Meteorology 51(2):343-366.*

We compared the simulated responses of net primary production, heterotrophic respiration, net ecosystem production and carbon storage in natural terrestrial ecosystems to historical (1765 to 1990) and projected (1990 to 2300) changes of atmospheric CO2 concentration of four terrestrial biosphere models: the Bern model, the Frankfurt Biosphere Model (FBM), the High- Resolution Biosphere Model (HRBM) and the Terrestrial Ecosystem Model (TEM). The results of the model intercomparison suggest that CO2 fertilization of natural terrestrial vegetation has the potential to account for a large fraction of the so-called "missing carbon sink" of 2.0 Pg C in 1990. Estimates of this potential are reduced when the models incorporate the concept that CO2 fertilization can be limited by nutrient availability. Although the model estimates differ on the potential size (126 to 461 Pg C) of the future terrestrial sink caused by CO2 fertilization, the results of the four models suggest that natural terrestrial ecosystems will have a limited capacity to act as a sink of atmospheric CO2 in the future as a result of physiological constraints and nutrient constraints on NPP. All the spatially explicit models estimate a carbon sink in both tropical and northern temperate regions, but the strength of these sinks varies over time. Differences in the simulated response of terrestrial ecosystems to CO2 fertilization among the models in this intercomparison study reflect the fact that the models have highlighted different aspects of the effect of CO2 fertilization on carbon dynamics of natural terrestrial ecosystems including feedback mechanisms. As interactions with nitrogen fertilization, climate change and forest regrowth may play an important role in simulating the response of terrestrial ecosystems to CO2 fertilization, these factors should be included in future analyses. Improvements in spatially explicit data sets, whole-ecosystem experiments and the availability of net carbon exchange measurements across the globe will also help to improve future evaluations of the role of CO2 fertilization on terrestrial carbon storage.

KEYWORDS: ATMOSPHERIC CARBON, CLIMATE CHANGE, DIOXIDE ENRICHMENT, EDDY-COVARIANCE, LAND-USE CHANGE, NET PRIMARY PRODUCTION, NITROGEN DEPOSITION, RAIN-FOREST, TROPICAL DEFORESTATION, WATER-VAPOR

1153

Kim, H.Y., T. Horie, H. Nakagawa, and K. Wada. 1996. Effects of elevated CO2 concentration and high temperature on growth and yield of rice. *Japanese Journal of Crop Science 65(4):634-643.*

Phenological development, biomass production and the related growth characteristics of rice (cv Akihikari) in canopy were measured over the entire growth period under different CO2 concentrations and air temperature regimes in temperature gradient chambers (TGCs), in order to clarify the effects of anticipated global climate change on rice production. The TGC is a plastic tunnel with the dimensions of 26m in length, 2. 05m in width and 1.7m in height in which air was ventilated at varying rates to created a 4 degrees C temperature gradient along its longitudinal axis. Two TGCs were used for this experiment;one was kept at ambient CO2 (congruent to 350 mu LL(-1)) concentration and the other at 690 mu LL(-1) throughout the entire growth period. CO2 x temperature treatmets were applied to potted rice plants displaced in TGC at the density of 20 hills m(-2) in 1991, and on transplanted plants on soil bed in TGC at 25 hills m(-2) in 1992. In both years, a sufficient amount of nutrition was applied in split. The nearly doubled CO2 concentration (690 mu LL(-1)) accelerated phenological development of rice toward heading with more pronounced effects at higher temperatures. The number of days to heading of elevated CO2 plants at 30 degrees C was 11% less than that of ambient CO2 plants. The elevated CO2 concentration remarkably promoted both total and productive tiller numbers, whereas it gave a negligibly small effect on plant height. Also, the elevated CO2 concentration gave minor effects on leaf area index except at the initial growth stage, coinciding with the previous workers' results. The elevated CO2 concentration markedly promoted crop dry matter production, on which temperature appeared to give negligibly small effects. The relative enhancement rate by the doubled CO2 on crop dry weight at maturity was estimated to be 24% as average over the entire temperature range (26 similar to 30 degrees C) in both years. The insensitive temperature response in the enhancement rate was contrary to previous workers' results. This is considered to be due to previous workers' results being based on largely isolated plants where radiation might less limit the growth than in the present experiment in the canopy condition.

KEYWORDS: ACCLIMATION, CARBON DIOXIDE, ORYZA-SATIVA

1154

Kim, H.Y., T. Horie, H. Nakagawa, and K. Wada. 1996. Effects of elevated CO2 concentration and high temperature on growth and yield of rice .2. The effect on yield and its components of Ahihikari rice. *Japanese Journal of Crop Science 65(4):644-651.*

Yield and its component organs of rice (cv. Akihikari) were examined for populations grown under two different CO2 concentrations (350 and 690 mu LL(-1)) x four temperature regimes in temperature gradient chambers (TGCs) in two cropping seasons of 1991 and 1992. The temperature treatments ranged 27.2 similar to 31.1 degrees C in 1991 and 26.0 similar to 29.3 degrees C in 1992 on average over the entire growth period. The relative yield increases by nearly doubling the CO2 concentration under the lowest temperature conditions were 40% and 22% in 1991 and 1992, respectively. These yield increases were mainly attributable to the increased spikelet number per unit area by elevated CO2, whereas the CO2 effects on ripening percentage and weight of single grain mass were relatively small. The difference in the CO2

enhancement rate in the spikelet number and hence in the yield between the two years was considered to reflect the difference in the nitrogen (N) application rate, as total amounts of N applied were 24 g m(-2) in 1991 and 12 g m(-2) in 1992. With the increase in temperature, yields at ambient and elevated CO2 concentrations decreased drastically with a more pronounced reduction with elevated CO2, resulting in no CO2 enrichment effect on rice yield at higher temperatures. The yield decline at higher temperatures was primarily due to an increase in the number of sterile spikelets and slightly due to the increase in imperfectly ripened grains. The spikelet sterility was most closely related to the daily maximum temperature averaged over the flowering period.

KEYWORDS: CARBON DIOXIDE, ORYZA-SATIVA

1155
Kimball, B.A., R.L. LaMorte, P.J. Pinter, G.W. Wall, D.J. Hunsaker, F.J. Adamsen, S.W. Leavitt, T.L. Thompson, A.D. Matthias, and T.J. Brooks. 1999. Free-air CO2 enrichment and soil nitrogen effects on energy balance and evapotranspiration of wheat. *Water Resources Research 35(4):1179-1190.*

In order to determine the likely effects of the increasing atmospheric CO, concentration on future evapotranspiration, ET, plots of field-grown wheat were exposed to concentrations of 550 mu mol/mol CO2 (or 200 mu mol/mol above current ambient levels of about 360 mu mol/mol) using a free-air CO2 enrichment (FACE) facility. Data were collected for four growing seasons at ample water and fertilizer (high N) and for two seasons when soil nitrogen was limited (low N). Measurements were made of net radiation, R-n; soil heat flux; air and soil temperatures; canopy temperature, T-s; and wind speed. Sensible heat flux was calculated from the wind and temperature measurements. ET, that is, latent heat flux, was determined as a residual in the energy balance. The FACE treatment increased daytime T-s about 0.6 degrees and 1.1 degrees C at high and low N, respectively. Daily total R-n was reduced by 1.3% at both levels of N. Daily ET was consistently lower in the FACE plots, by about 6.7% and 19.5% for high and low N, respectively.

KEYWORDS: 1989 FACE EXPERIMENT, ATMOSPHERIC CO2, CARBON-DIOXIDE ENRICHMENT, COTTON, DOWNWIND EVOLUTION, LOCAL ADVECTION, RADIATIVE SURFACE-TEMPERATURE, SAP FLOW, SCALAR FLUXES, WATER-USE

1156
Kimball, B.A., R.L. Lamorte, R.S. Seay, P.J. Pinter, R.R. Rokey, D.J. Hunsaker, W.A. Dugas, M.L. Heuer, J.R. Mauney, G.R. Hendrey, K.F. Lewin, and J. Nagy. 1994. Effects of free-air co2 enrichment on energy-balance and evapotranspiration of cotton. *Agricultural and Forest Meteorology 70(1-4):259-278.*

The effects of free-air CO2 enrichment (FACE) at 550 mumol mol- 1 on the energy balance and evapotranspiration, ET, of cotton (Gossypium hirsutum L.) were investigated. Latent heat flux, lambdaET, was calculated as the residual in an energy balance approach from determinations of net radiation, R(n), minus surface soil heat flux, G0, minus sensible heat flux, H. R(n) was directly measured. G0 was determined from measurements with soil heat flux plates at 10 mm depth, corrected for temperature changes in the soil above. H was determined from measurements of air temperature with aspirated psychrometers, of foliage temperature with IR thermometers, and of wind speed with cup anemometers. Under ambient CO2 (control) conditions (about 370 mumol mol-1), the lambdaET from the energy balance approach agreed fairly well with values from several other methods, including the Bowen ratio method, lending credence to the technique. However, the results had an uncertainty of the order of 20% associated with the R(n) measurements. Therefore, an apparent increase in ET of about 13% in the FACE plots was judged insignificant. The conclusion that any effects of CO2 enrichment to 550 mumol mol-1 on the ET of cotton were too small to be detected was consistent with the results of other investigators who determined ET in the same experiment using stem flow gauges and the soil water balance.

KEYWORDS: CARBON DIOXIDE, CROP YIELD, EVAPORATION, INCREASING ATMOSPHERIC CO2, LATENT-HEAT, RADIATIVE SURFACE-TEMPERATURE, WATER-USE, WHEAT CANOPY

1157
Kimball, B.A., and J.R. Mauney. 1993. Response of cotton to varying co2, irrigation, and nitrogen - yield and growth. *Agronomy Journal 85(3):706-712.*

The CO2 concentration of the atmosphere is increasing and is expected to double sometime near the middle of the next century. To determine the effects of such a CO2 increase on cotton (Gossypium hirsutum L.) growth and productivity, a series of experiments from 1983 through 1987 were conducted with open-top CO2-enriched field chambers at ample as well as limiting levels of water and N at Phoenix, AZ. Comparisons with open-field plots showed that there was a significant chamber effect, amounting to a 30% average increase in growth inside, but under dry conditions in 1985, the situation was reversed. No significant effects of CO2 on harvest index, root-shoot ratio, or lint percentage were found, so the primary effect of elevated CO2 was to produce plants that were larger. Comparing the results of 500 and 650 mumol mol-1 CO2 treatments, the increments of growth from ambient (about 350 mumol mol-1) to 500 mumol mol-1 were not significantly different from increments from 500 to 650 mumol mol-1. No statistically significant interactions were detected between CO2 level and either irrigation or nitrogen level, even when these variables were sufficiently low enough to limit growth. However, under well-maintained water stress conditions, the growth response to CO2 tended to be somewhat larger than under normal irrigation levels. Averaging over all the data available from these experiments, seed cotton yield (lint plus seed) and above- ground biomass were increased by 60 and 63%, respectively, by CO2 enrichment to 650 mumol mol-1.

KEYWORDS: CARBON DIOXIDE, CHAMBERS, ELEVATED LEVELS, ENRICHMENT, FIELD, PLANT GROWTH, POPULATIONS, SOIL, STRESS, WATER-USE

1158
Kimball, B.A., J.R. Mauney, F.S. Nakayama, and S.B. Idso. 1993. Effects of elevated co2 and climate variables on plants. *Journal of Soil and Water Conservation 48(1):9-14.*

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, TEMPERATURE, YIELD

1159
Kimball, B.A., J.R. Mauney, F.S. Nakayama, and S.B. Idso. 1993. Effects of increasing atmospheric co2 on vegetation. *Vegetatio 104:65-75.*

The increasing atmospheric CO2 concentration probably will have significant direct effects on vegetation whether predicted changes in climate occur or not. Averaging over many prior greenhouse and growth chamber studies, plant growth and yield have typically increased more than 30%, with a doubling of CO2 concentration. Such a doubling also causes stomatal conductance to decrease about 37 which typically increases leaf temperatures more than 1-degrees-C, and which may decrease evapotranspiration, although increases in leaf area counteract the latter effect. Interactions between CO2 and climate variables also appear important. In one study the growth increase from near-doubled

CO2 ranged from minus 60% at 12- degrees-C to 0% at 19-degrees-C to plus 130% at 34-degrees-C, suggesting that if the climate warms, the average growth response to doubled CO2 could be consistently higher than the 30% mentioned above. Even when growing in nutrient-poor soil, the growth response to elevated CO2 has been large, in contrast to nutrient solution studies which showed little response. Several studies have suggested that under water-stress, the CO2 growth stimulation is as large or larger than under wellwatered conditions. Therefore, the direct CO2 effect will compensate somewhat, if not completely, for a hotter drier climate. And if any climate change is small, then plant growth and crop yields will probably be significantly higher in the future high-CO2 world.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, TEMPERATURE, YIELD

1160

Kimball, B.A., P.J. Pinter, R.L. Garcia, R.L. LaMorte, G.W. Wall, D.J. Hunsaker, G. Wechsung, F. Wechsung, and T. Kartschall. 1995. Productivity and water use of wheat under free-air CO2 enrichment. *Global Change Biology 1(6):429-442.*

A free-air CO2 enrichment (FACE) experiment was conducted at Maricopa, Arizona, on wheat from December 1992 through May 1993. The FACE apparatus maintained the CO2 concentration, [CO2], at 550 mu mol mol(-1) across four replicate 25-m- diameter circular plots under natural conditions in an open field. Four matching Control plots at ambient [CO2] (about 370 mu mol mol(-1)) were also installed in the field. In addition to the two levels of [CO2], there were ample (Wet) and limiting (Dry) levels of water supplied through a subsurface drip irrigation system in a strip, split-plot design. Measurements were made of net radiation, R(n); soil heat flux, G(o); soil temperature; foliage or surface temperature; air dry and wet bulb temperatures; and wind speed. Sensible heat flux, H, was calculated from the wind and temperature measurements. Latent heat nux, lambda ET, and evapotranspiration, ET, were determined as the residual in the energy balance. The FACE treatment reduced daily total R(n) by an average 4%. Daily FACE sensible heat flux, H, was higher in the FACE plots. Daily latent heat flux, lambda ET, and evapotranspiration, ET, were consistently lower in the FACE plots than in the Control plots for most of the growing season, about 8% on the average. Net canopy photosynthesis was stimulated by an average 19 and 44% in the Wet and Dry plots, respectively, by elevated [CO2] for most of the growing season. No significant acclimation or down regulation was observed. There was little above-ground growth response to elevated [CO2] early in the season when temperatures were cool. Then, as temperatures warmed into spring, the FACE plants grew about 20% more than the Control plants at ambient [CO2], as shown by above-ground biomass accumulation. Root biomass accumulation was also stimulated about 20%. In May the FACE plants matured and senesced about a week earlier than the Controls in the Wet plots. The FACE plants averaged 0.6 degrees C warmer than the Controls from February through April in the well-watered plots, and we speculate that this temperature rise contributed to the earlier maturity. Because of the acceleration of senescence, there was a shortening of the duration of grain filling, and consequently, there was a narrowing of the final biomass and yield differences. The 20% mid-season growth advantage of FACE shrunk to about an 8% yield advantage in the Wet plots, while the yield differences between FACE and Control remained at about 20% in the Dry plots.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, COTTON, CROP YIELD, GROWTH, TEMPERATURE

1161

King, A.W., W.R. Emanuel, S.D. Wullschleger, and W.M. Post. 1995. In search of the missing carbon sink - a model of terrestrial biospheric response to land-use change and atmospheric co2. *Tellus Series B-Chemical and Physical Meteorology 47(4):501-519.*

Estimates of the net exchange of carbon between the terrestrial biosphere and the atmosphere may be too large because the models of carbon release from changes in land use do not allow for enhanced carbon assimilation by the terrestrial biosphere in response to increasing atmospheric CO2. We address this deficiency with a model of terrestrial biosphere that includes both ecosystem response to land-use perturbation and vegetation response to atmospheric CO2. Model inputs specify the areas affected by land-use change since 1700. The carbon dynamics of the affected areas are described by an area distribution function for vegetation carbon density and a compartment model of carbon in vegetation, litter, and soil. Vegetation growth is modeled as the difference between net primary production (NPP) and mortality. NPP, the net flux of carbon from atmosphere to vegetation, is a logistic function of vegetation carbon density. The response of NPP to atmospheric CO2 is modeled with three response functions: a logarithmic, a rectangular- hyperbolic, and a response function derived from a biochemical model of C-3 photosynthesis. The response functions are parameterized by ecosystem type with data from CO2 exposure experiments. Elevated CO2 affects the NPP of both undisturbed and recovering ecosystems. We use the model to test the hypothesis that the CO2 enhancement of terrestrial NPP explains the historical missing carbon sink of the the global carbon cycle budget. Our estimates of the biosphere's CO2 enhanced carbon flux are much smaller than the reconstructed missing carbon sink. We conclude that our model results do not support the hypothesis.

KEYWORDS: CLIMATIC CHANGE, CYCLE, DEPOSITION, ECOSYSTEMS, GLOBAL CLIMATE, PLANTS, STORAGE, TROPICAL DEFORESTATION

1162

King, A.W., W.M. Post, and S.D. Wullschleger. 1997. The potential response of terrestrial carbon storage to changes in climate and atmospheric CO2. *Climatic Change 35(2):199-227.*

We use a georeferenced model of ecosystem carbon dynamics to explore the sensitivity of global terrestrial carbon storage to changes in atmospheric CO2 and climate. We model changes in ecosystem carbon density, but we do not model shifts in vegetation type. A model of annual NPP is coupled with a model of carbon allocation in vegetation and a model of decomposition and soil carbon dynamics. NPP is a function of climate and atmospheric CO2 concentration. The CO2 response is derived from a biochemical model of photosynthesis. With no change in climate, a doubling of atmospheric CO2 from 280 ppm to 560 ppm enhances equilibrium global NPP by 16.9%; equilibrium global terrestrial ecosystem carbon (TEC) increases by 14.9%. Simulations with no change in atmospheric CO2 concentration but changes in climate from five atmospheric general circulation models yield increases in global NPP of 10.0-14.8%. The changes in NPP are very nearly balanced by changes in decomposition, and the resulting changes in TEC range from an increase of 1.1% to a decrease of 1.1%. These results are similar to those from analyses using bioclimatic biome models that simulate shifts in ecosystem distribution but do not model changes in carbon density within vegetation types. With changes in both climate and a doubling of atmospheric CO2, our model generates increases in NPP of 30.2-36.5%. The increases in NPP and litter inputs to the soil more than compensate for any climate stimulation of decomposition and lead to increases in global TEC of 15.4-18.2%.

KEYWORDS: BIOSPHERE, CYCLE, MODEL, PHYSIOLOGY, SENSITIVITY, SIMULATION, SOIL, TEMPERATURE, TURNOVER, VEGETATION

1163
King, D.A. 1995. Equilibrium-analysis of a decomposition and yield model applied to pinus-radiata plantations on sites of contrasting fertility. *Ecological Modelling 83(3):349-358.*

Recent models of growth and nutrient cycling relate forest productivity to canopy photosynthesis, as influenced by the effect of nutrient cycling on foliar nitrogen concentration. A useful approach for analysing the impact of elevated CO2 or altered nitrogen inputs on production is to consider model solutions where recycling leaves, fine roots, litter and soil organic pools of intermediate turnover time are in equilibrium, while tree stems and recalcitrant humus are accumulating or releasing carbon and nitrogen. This equilibrium analysis, employed by the Generic Decomposition and Yield (G'DAY) model, was applied to Pinus radiata plantations growing on an infertile site in Australia and a fertile site in New Zealand. Predicted productivities and foliar nitrogen concentrations were substantially lower than observed for the young (12-year- old) stands, particularly for the fertile site. The model predictions were closer to values expected for older stands late in the commercial rotation cycle when reduced wood production rates reduce the net nitrogen requirements for growth. These results underscore the importance of the net release of nitrogen from soil organic matter early in the life of a stand and suggest that care should be taken in using equilibrium analyses to estimate the impacts of elevated [CO2] on forest production.

KEYWORDS: BIOMASS, FERTILIZATION, FOREST, GROWTH, NEW-ZEALAND, NITROGEN, NUTRIENT, PRODUCTIVITY, STAND DEVELOPMENT, WATER

1164
King, J.S., R.B. Thomas, and B.R. Strain. 1996. Growth and carbon accumulation in root systems of Pinus taeda and Pinus ponderosa seedlings as affected by varying CO2, temperature and nitrogen. *Tree Physiology 16(7):635-642.*

It has been hypothesized that increasing atmospheric CO2 concentration enhances accumulation of carbon in fine roots, thereby altering soil carbon dynamics and nutrient cycling. To evaluate possible changes to belowground pools of carbon and nitrogen in response to elevated CO2, an early and a late successional species of pine (Pinus taeda L. and Pinus ponderosa Dougl. ex Laws, respectively) were grown from seed for 160 days in a 35 or 70 Pa CO2 partial pressure at low or high temperature (30-year weekly mean and 30 year weekly mean + 5 degrees C) and a soil solution nitrogen concentration of 1 or 5 mM NH4NO3 at the Duke University Phytotron. Seedlings were harvested at monthly intervals and growth parameters of the primary root, secondary root and tap root fractions evaluated. Total root biomass of P. ponderosa showed a positive CO2 response (105% increase) (P = 0.0001) as a result of significant increases in all root fractions in the elevated CO2 treatment, but all other main effects and interactions were insignificant. In I? taeda, there were significant interactions between CO2 and temperature (P = 0.04) and CO2 and nitrogen (P = 0.04) for total root biomass. An allometric analysis indicated that modulation of the secondary root fraction was the main response of the trees to altered environmental conditions. In P. ponderosa, there was an increase in the secondary root fraction relative to the primary and tap root fractions under conditions of low temperature. In P. taeda, there was a shift in carbon accumulation to the secondary roots relative to the primary roots under low temperature and low nitrogen. Neither species exhibited shifts in carbon accumulation in response to elevated CO2. We conclude that both species have the potential to increase be lowground biomass substantially in response to rising atmospheric CO2 concentration, and this response is sensitive to temperature and nitrogen in P. taeda. Both species displayed small shifts in belowground carbon accumulation in response to altered temperature and nitrogen that may have substantial ecosystem consequences over time.

KEYWORDS: ECOSYSTEMS

1165
King, J.S., R.B. Thomas, and B.R. Strain. 1997. Morphology and tissue quality of seedling root systems of Pinus taeda and Pinus ponderosa as affected by varying CO2, temperature, and nitrogen. *Plant and Soil 195(1):107-119.*

Rising atmospheric carbon dioxide, nitrogen deposition and warmer temperatures may alter the quantity and quality of plant-derived organic matter available to soil biota, potentially altering rates of belowground herbivory and decomposition. Our objective was to simulate future growth conditions for an early successional (loblolly) and late successional (ponderosa) species of pine to determine if the physical and chemical properties of the root systems would change. Seedlings were grown for 160 days in greenhouses at the Duke University Phytotron at 35 or 70 Pa CO2 partial pressure, ambient or ambient +5 degrees C temperature, and 1 or 5 mMNH(4)O(3). Roots from harvested seedlings were analyzed for changes in surface area, specific root length, mass, total nonstructural carbohydrates (TNC), and concentrations of macro-nutrients. Surface area increased in both species under elevated CO2, due primarily to increases in root length, and this response was greatest (+138%) in loblolly pine at high temperature. Specific root length decreased in loblolly pine at elevated CO2 but increases in mass more than compensated for this, resulting in net increases in total length. TNC was unaffected and nutrient concentrations decreased only slightly at elevated CO2, possibly from anatomical changes to the root tissues. We conclude that future growth conditions will enhance soil exploration by some species of pine, but root carbohydrate levels and nutrient concentrations will not be greatly affected, leaving rates of root herbivory and decomposition unaltered.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, AVAILABILITY, ELEVATED CO2, ENRICHMENT, GROWTH, LOBLOLLY-PINE, PLANTS, RESPONSES, SOIL BIOTA, WATER

1166
King, S.P., M.R. Badger, and R.T. Furbank. 1998. CO2 refixation characteristics of developing canola seeds and silique wall. *Australian Journal of Plant Physiology 25(3):377-386.*

The potential for developing canola (Brassica napus L.) seeds and the interior silique (pod) wall to refix respired CO2 has been investigated. From ribulose-1,5-bisphosphate carboxylase- oxygenase (Rubisco) and phosphoenolpyruvate carboxylase (PEPC) activities, seeds were estimated to have a greater CO2, fixation capacity than silique wall endocarp during oil filling. The major component of seed fixation capacity was embryo Rubisco, which had a total activity of 6.3 nmol min(-1) embryo(-1) (3.7 mu mol min(-1) mg chlorophyll(-1)) at 28 days after anthesis (DAA) with smaller contributions from seed coat and embryo PEPC. Rubisco activities were probably maximal in vivo because of high silique cavity CO2 concentrations (0.8 to 2.5%). Seed chlorophyll content rapidly increased over 10-fold from 20 to 30 DAA and, with 20% of incident light transmitted through the silique wall, embryos demonstrated appreciable photosynthetic electron transport rates and most energy produced appeared to be used for Rubisco-catalysed CO2 fixation. Endocarp refixation capacity was less than seeds because chlorophyll content was not enriched and PEPC activities were relatively small. These data indicate that developing seeds and also endocarp refix respired CO2 and that embryo chlorophyll plays a critical role in this refixation.

KEYWORDS: ACCUMULATION, BRASSICA-CAMPESTRIS L, CHLOROPHYLL FLUORESCENCE, EMBRYOS, FIXATION, INVIVO, NAPUS, OILSEED RAPE, PISUM SATIVUM L, POD WALL

1167

Kinney, K.K., and R.L. Lindroth. 1997. Responses of three deciduous tree species to atmospheric CO2 and soil NO3- availability. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 27(1):1-10.*

This research evaluated the direct and interactive effects of atmospheric CO2 and soil NO3- availability on growth and biomass partitioning of quaking aspen (Populus tremuloides Michx.), red oak (Quercus rubra L.), and sugar maple (Acer saccharum Marsh.). In the split split plot experimental design, NO3- availability (low and high) and tree species were nested in two levels of atmospheric CO2 (ambient, 355 mu L/L; elevated, 650 mu L/L). Seedlings were grown for 57 days in environmental control rooms. Increased CO2 and NO3- availability positively and (mostly) independently influenced total growth and relative growth rates. Moderate to weak interactions between CO2 and NO3- for several growth parameters (e.g., leaf production, shoot length, root collar diameter) in some species indicated an enhanced response to CO2 enrichment under conditions of high NO3- availability. Interactive effects were most pronounced in aspen. Seedling growth and allocation responses to CO2 and NO3- were frequently species specific and associated with successional status. For example, proportional increases in growth in response to elevated CO2 were greatest for sugar maple and least for quaking aspen, whereas the converse was hue with respect to response to high NO3- availability. This research indicates that the impact of enriched CO2 atmospheres on forest communities will be influenced by both nutrient availability and unique species characteristics.

KEYWORDS: CARBON DIOXIDE, ECOSYSTEMS, ELEVATED CO2, FORESTS, NITROGEN, NUTRIENTS, PLANTS, SEEDLINGS

1168

Kinney, K.K., R.L. Lindroth, S.M. Jung, and E.V. Nordheim. 1997. Effects of CO2 and NO3- availability on deciduous trees: Phytochemistry and insect performance. *Ecology 78(1):215-230.*

Increasing concentrations of atmospheric CO2 will interact with other environmental factors to influence the physiology and ecology of trees. This research evaluated how plant phytochemical responses to enriched atmospheric CO2 are affected by the availability of soil nitrate (NO3-) and how these chemical changes, in turn, alter the performance of a tree-feeding folivore. Seedlings of three deciduous tree species-quaking aspen (Populus tremuloides), red oak (Quercus rubra), and sugar maple (Acer saccharum)-were grown in ambient (355 mu L/L) or elevated (650 mu L/L) CO2 in combination with low (1.25 mmol/L) or high (7.5 mmol/L) soil NO3- availability. After 60 d, foliage was analysed for changes in nutrients and allelochemicals likely to be influenced by the availability of CO2 and NO3-. Penultimate gypsy moth larvae (Lymantria dispar) were reared on foliage (aspen and maple) to determine how performance would be affected by host chemical changes. Using the framework of carbon-nutrient balance (CNB) theory, we tested three hypotheses regarding the impact of CO2 and NO3- availability on plant chemistry and insect performance: (1) nitrogen-based compounds will decrease, and carbon-based compounds will increase in response to elevated CO2 and/or low NO3-; (2) aspen will exhibit the greatest change in C:N ratios, and maple the least; and (3) phytochemical changes will influence gypsy moth performance, with larvae fed aspen being affected more than those fed maple. Concentrations of nitrogen and soluble protein decreased, whereas concentrations of starch, condensed tannins, and ellagitannins increased, in response to elevated CO2 and/or low NO3-. Responses of simple carbohydrates and phenolic glycosides were variable, however, suggesting that foliar accumulations of "dynamic metabolites" do not follow the predictions of CNB theory as well as do those of stable end products. With respect to Hypothesis 2, we found that absolute (net) changes in foliar C:N ratios were greatest for aspen and least for oak, whereas relative (proportional) changes were greatest for maple and least for aspen. Thus, Hypothesis 2 was only partially supported by the data. Considering Hypothesis 3, we found that elevated CO2 treatments had little effect on gypsy moth development time, growth rate, or larval mass. Larvae reared on aspen foliage grown under elevated CO2 exhibited increased consumption but decreased conversion efficiencies. Gypsy moth responses to NO3- were strongly host specific: the highest consumption and food digestibility occurred in larvae on high-NO3- aspen, whereas the fastest growth rates occurred in larvae on high-NO3- maple. In short, our results again only partially supported the predicted pattern, They indicate, however, that the magnitude of insect response elicited by resource-mediated shifts in host chemistry will depend on how levels of compounds with specific importance to insect fitness (e.g., phenolic glycosides in aspen) are affected. Overall, we observed relatively few true interactions (i.e,, nonadditive) between carbon and nitrogen availability vis a vis foliar chemistry and insect performance. Tree species, however, frequently interacted with CO2 and/or NO3- availability to affect both sets of parameters. These results suggest that the effects of elevated atmospheric CO2 on terrestrial plant communities will not be homogeneous, but will depend on species composition and soil nutrient availability.

KEYWORDS: ATMOSPHERIC CO2, CARBON NUTRIENT BALANCE, CHEMISTRY, ELEVATED CO2, GROWTH, MINERAL NUTRITION, NITROGEN, PAPER BIRCH, PLANTS, RESPONSES

1169

Kinsman, E.A., C. Lewis, M.S. Davies, J.E. Young, D. Francis, I.D. Thomas, K.H. Chorlton, and H.J. Ougham. 1996. Effects of temperature and elevated CO2 on cell division in shoot meristems: Differential responses of two natural populations of Dactylis glomerata L. *Plant, Cell and Environment 19(6):775-780.*

The aim was to establish whether temperature and/or elevated [CO2] (similar to 700 mu mol mol(-1)) affects the cell doubling time (cdt) in the different zones of the shoot apex of two natural populations of Dactylis glomerata originating in Portugal (38 degrees 53' N) and in Sweden (63 degrees 09' N). In the Portuguese population at ambient [CO2], only the pith rib meristem (PRM) exhibited a significant shortening of cdts from 10 to 30 degrees C, Elevated [CO2] resulted in a significant shortening of cdt, particularly in the PRM where cdt was reduced 4 . 8- and 6 . 1-fold at 10 and 20 degrees C, respectively, but only 2-fold at 30 degrees C, In the Swedish population at ambient [CO2], there were no consistent temperature-dependent alterations to cdt and this population was less responsive to elevated [CO2] than the Portuguese population, Nevertheless, elevated [CO2] resulted in a significant shortening of the cdt for some of the zones; the maximum reduction occurred in the PRM at 30 degrees C. We concluded that in the shoot apex of the Portuguese population, and most notably in the PRM, 10 and 20 degrees C were non- optimal temperatures for cell division, whilst the Swedish population was relatively buffered against temperature change, Elevated [CO2] resulted in substantially greater reductions in cdts in the shoot meristem of the Portuguese population than in that of the Swedish population.

KEYWORDS: PLANTS

1170

Kinsman, E.A., C. Lewis, M.S. Davies, J.E. Young, D. Francis, B. Vilhar, and H.J. Ougham. 1997. Elevated CO2 stimulates cells to divide in grass meristems: a differential effect in two natural populations of Dactylis glomerata. *Plant, Cell and Environment 20(10):1309-1316.*

In this study, we tested the hypothesis that elevated [CO2] shortens the cell cycle in meristems of Dactylis glomerata, more in a Portuguese population (38 degrees 53'N) than in a Swedish population (63 degrees

09'N). In the shoot meristem, the cell cycle shortened to about the same extent (approximate to 26%) in both populations exposed to the elevated [CO2] treatment, In the root meristem, the cell cycle shortened by 17% in the Portuguese and by 8% in the Swedish population, However, the proportion of rapidly cycling cells increased in the Portuguese much more than in the Swedish population in both meristems, In the root meristem, there was a 1.86-fold increase in the Portuguese compared with a 1.31-fold increase in the Swedish, In the shoot meristem, the increases were 1.5-3-fold for the Portuguese and 1.2-fold for the Swedish, The data are consistent in showing that a major response to the elevated [CO2] treatment was an increase in the proportion of cells that were cycling and that this was more marked for the Portuguese population, A more general response to the elevated [CO2] treatment was a shortening of the cell cycle regardless of population.

KEYWORDS: ALTITUDES, CYCLE, DIVISION, GROWTH, PLANTS, RATES, SHOOT APEX, SINAPIS, TEMPERATURE, TRANSITION

1171

Kirdmanee, C., Y. Kitaya, and T. Kozai. 1995. Effects of co2 enrichment and supporting material in-vitro on photoautotrophic growth of eucalyptus plantlets in-vitro and ex-vitro. *In Vitro Cellular & Developmental Biology-Plant 31(3):144-149.*

Eucalyptus camaldulensis shoots were cultured photoautotrophically in vitro for 6 wk with four different types of supporting materials (agar matrix, Gelrite matrix, plastic net, or vermiculite) under CO2-nonenriched or CO2- enriched conditions. Plantlets from each treatment in vitro were then grown ex vitro in a greenhouse for 4 wk. The growth and net photosynthetic rate of plantlets in, vitro, as well as subsequent growth, survival percentage, transpiration rate, and net photosynthetic rate of plantlets ex vitro were evaluated. CO2 enrichment significantly increased growth (total dry weight and number of primary roots) and net photosynthetic rate of plantlets in vitro, as well as the growth and survival percentage of plantlets ex vitro regardless of the type of supporting materials. The growth in vitro was greatest in the vermiculite, followed by the plastic net, Gelrite matrix, and agar matrix (in descending order) under either the CO2- nonenriched or CO2-enriched conditions. The growth and survival percentage of plantlets ex vitro were highest in the vermiculite under the CO2-enriched condition. The extensive root system produced in vitro was necessary for growth and survival of plantlets ex vitro.

KEYWORDS: ACCLIMATIZATION, ASPARAGUS, CULTURE, INVITRO, LIGHT, RASPBERRY

1172

Kirkham, M.B., H. He, T.P. Bolger, D.J. Lawlor, and E.T. Kanemasu. 1991. Leaf photosynthesis and water-use of big bluestem under elevated carbon-dioxide. *Crop Science 31(6):1589-1594.*

With the atmospheric concentration of CO2 increasing, it is important to know how this will affect crop growth. The objective of the study was to determine the effect of elevated CO2 on big bluestem (Andropogon gerardii Vitman) growing in a tallgrass prairie on a Tully silty clay loam (fine, mixed, mesic Pachic Argiustoll) kept at a high water level (field capacity) or a low water level (half field capacity). Sixteen cylindrical plastic chambers were placed on the prairie to maintain the two levels of CO2 (mean +/- SD: 337 +/- 32 Ind 658 +/- 81-mu-mol mol-1) over a full growing season. Soil-water content was measured weekly with a neutron probe. Photosynthesis, transpiration, stomatal resistance, and intercellular CO2 concentration were determined with a portable leaf Photosynthetic system. Canopy temperature was monitored with an infrared thermometer. Elevated (doubled) CO2 reduced transpiration rate of big bluestem by 25 and 35% under the high- and low-water treatments, respectively. Under both watering regimes, stomatal resistance was greater by almost- equal-to 1.6 s cm-1 with doubled CO2 than with ambient CO2. Plants grown with doubled CO2 at high- and low-water levels had warmer canopy temperatures (average 1.15 and 0.70-degrees-C warmer, respectively) than plants grown at ambient CO2. Carbon- dioxide concentration did not affect the rate of photosynthesis, even though intercellular CO2 concentration was increased under high CO2. Elevated CO2 did not increase the height of plants grown at the high water level, but it did increase the height at the low water level by an average of 9 cm.

KEYWORDS: ATMOSPHERIC CO2, CROP YIELD, ENRICHMENT, RESPONSES

1173

Kirschbaum, M.U.F. 1994. The sensitivity of C-3 photosynthesis to increasing co2 concentration - a theoretical-analysis of its dependence on temperature and background co2 concentration. *Plant, Cell and Environment 17(6):747-754.*

The atmospheric CO2 concentration has increased from the pre-industrial concentration of about 280 mu mol mol(-1) to its present concentration of over 350 mu mol mol(-1), and continues to increase. As the rate of photosynthesis in C-3 plants is strongly dependent on CO2 concentration, this should have a marked effect on photosynthesis, and hence on plant growth and productivity. The magnitude of photosynthetic responses can be calculated based on the well-developed theory of photosynthetic response to intercellular CO2 concentration. A simple biochemically based model of photosynthesis was coupled to a model of stomatal conductance to calculate photosynthetic responses to ambient CO2 concentration. In the combined model, photosynthesis was much more responsive to CO2 at high than at low temperatures. At 350 mu mol mol(-1), photosynthesis at 35 degrees C reached 51% of the rate that would have been possible with non-limiting CO2, whereas at 5 degrees C, 77% of the CO2 non-limited rate was attained. Relative CO2 sensitivity also became smaller at elevated CO2, as CO2 concentration increased towards saturation. As photosynthesis was far from being saturated at the current ambient CO2 concentration, considerable further gains in photosynthesis were predicted through continuing increases in CO2 concentration. The strong interaction with temperature also leads to photosynthesis in different global regions experiencing very different sensitivities to increasing CO2 concentrations.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, CARBON DIOXIDE, CONDUCTANCE, ELEVATED CO2, ENVIRONMENTS, GROWTH, HUMIDITY, MODELS, RESPONSES

1174

Kirschbaum, M.U.F. 1999. Modelling forest growth and carbon storage in response to increasing CO2 and temperature. *Tellus Series B-Chemical and Physical Meteorology 51(5):871-888.*

The response of plant growth to increasing climate change remains one of the unresolved issues in understanding the future of the terrestrial biosphere. It was investigated here by using the comprehensive forest growth model CenW 1.0.5 which integrates routines for the fluxes of carbon and water, interception of radiation and the cycling of nutrients. It was run with water and/or nutrient limitations on a background of naturally observed climate at Canberra, Australia. It was parameterised for Pinus radiata, the commercially most important plantation species in Australia. The simulations showed that under water-limited conditions, forest growth was highly sensitive to doubling CO2, with growth increases of over 50% on average and even greater increases in dry years. In contrast, when water supply was adequate, but nutrients were limiting, growth increases were smaller, with an initial increase of about 15% during the first year after CO2 was doubled. This growth increase diminished further over subsequent years so that after 20 years, there

was virtually no remaining effect. This diminishing response was due to developing nutrient limitations caused by extra carbon input which immobilised nutrients in the soil. When both water and nutrients were adequate, growth was increased by about 15-20% with no decrease over time. Increasing ambient temperature had a positive effect on growth under nutrient limited conditions by stimulating nitrogen mineralisation rates, but had very little effect when nutrients were non-limiting. Responses were qualitatively similar when conditions were changed gradually. In response to increasing CO2 by 2 mu mol mol(-1) yr(-1) over 50 years, growth was increased by only 1% under nutrient- limited condition but by 16% under water-limited conditions. When temperature and CO2 were both changed to emulate conditions between 1950 and 2030, growth was enhanced between 5-15% over the 80-year period due to the effect of CO2 on photosynthesis and water economy especially under water-limited conditions, and due to the effect of increasing temperature in mineralising greater amounts of nutrients. These results show that there is not one universally applicable biological growth response to increasing temperature and CO2, but that they interact in complex ways with a number of other growth limiting factors. Any response factor of plants to CO2 can only be quantified if the important interacting factors can be independently characterised for different situations.

KEYWORDS: ATMOSPHERIC CO2, C STORAGE, CLIMATE CHANGE, DIOXIDE, ELEVATED CO2, LIMITED CONDITIONS, LONG-TERM, NET PRIMARY, RESPIRATION, TERRESTRIAL ECOSYSTEMS

1175

Kirschbaum, M.U.F. 2000. Will changes in soil organic carbon act as a positive or negative feedback on global warming? *Biogeochemistry 48(1):21-51.*

The world's soils contain about 1500 Gt of organic carbon to a depth of 1m and a further 900 Gt from 1-2m. A change of total soil organic carbon by just 10% would thus be equivalent to all the anthropogenic CO2 emitted over 30 years. Warming is likely to increase both the rate of decomposition and net primary production (NPP), with a fraction of NPP forming new organic carbon. Evidence from various sources can be used to assess whether NPP or the rate of decomposition has the greater temperature sensitivity, and, hence, whether warming is likely to lead to an increase or decrease in soil organic carbon. Evidence is reviewed from laboratory-based incubations, field measurements of organic carbon storage, carbon isotope ratios and soil respiration with either naturally varying temperatures or after experimentally increasing soil temperatures. Estimates of terrestrial carbon stored at the Last Glacial Maximum are also reviewed. The review concludes that the temperature dependence of organic matter decomposition can be best described as: d(T) = exp[3.36 (T - 40)/(T + 31.79)] where d(T) is the normalised decomposition rate at temperature T (in degrees C). In this equation, decomposition rate is normalised to '1' at 40 degrees C. The review concludes by simulating the likely changes in soil organic carbon with warming. In summary, it appears likely that warming will have the effect of reducing soil organic carbon by stimulating decomposition rates more than NPP. However, increasing CO2 is likely to simultaneously have the effect of increasing soil organic carbon through increases in NPP. Any changes are also likely to be very slow. The net effect of changes in soil organic carbon on atmospheric CO2 loading over the next decades to centuries is, therefore, likely to be small.

KEYWORDS: ATMOSPHERIC CO2, BOREAL FOREST, CLIMATE CHANGE, LAND-USE, LAST GLACIAL MAXIMUM, MATTER DYNAMICS, NITROGEN MINERALIZATION, SPRUCE-FIR FOREST, TEMPERATURE-DEPENDENCE, TRACE GAS FLUXES

1176

Kirschbaum, M.U.F., D.A. King, H.N. Comins, R.E. McMurtrie, B.E. Medlyn, S. Pongracic, D. Murty, H. Keith, R.J. Raison, P.K. Khanna, and D.W. Sheriff. 1994. Modeling forest response to increasing co2 concentration under nutrient-limited conditions. *Plant, Cell and Environment 17(10):1081-1099.*

The growth rates of woody plants depend on both the rate of photosynthetic carbon gain and the availability of essential nutrients. Instantaneous carbon gain is known to increase in response to increasing atmospheric CO2 concentration, but it is uncertain whether this will translate into increased growth in the longer term under nutrient-limited conditions. An analytical model to address this question was developed by Comins and McMurtrie (1993, Ecological Applications 3, 666- 681). Their model was further tested and analysed. Manipulation of various assumptions in the model revealed its key assumptions and allowed a more confident prediction of expected growth responses to CO2 enrichment under nutrient-limited conditions. The analysis indicated that conclusions about the CO2 sensitivity of production were strongly influenced by assumptions about the relationship between foliar and heartwood nitrogen concentrations. With heartwood nitrogen concentration proportional to foliar nitrogen concentration, the model predicted a strong response of plant productivity to increasing CO2 concentration, whereas with heartwood nitrogen concentration set constant, the model predicted only a very slight growth response to changing CO2 concentration. On the other hand, predictions were only slightly affected by: (1) assumptions about the extent of nitrogen retranslocation out of senescing roots and foliage or wood during heartwood formation; (2) the effects of nitrogen status on specific Leaf area or (3) leaf longevity; (4) carbon allocation between different plant parts; or (5) changes in the N:C ratio of organic matter sequestered in the passive pool of soil organic matter. Modification of the effect of foliar nitrogen concentration on the light utilization coefficient had only a small effect on the CO2 sensitivity for pines. However, this conclusion was strongly dependent on the chosen relationship between single- leaf photosynthesis and leaf nitrogen concentration. Overall, the analysis suggested that trees growing under nitrogen- limited conditions can respond to increasing atmospheric CO2 concentration with considerable increases in growth.

KEYWORDS: CARBON DIOXIDE, DARK RESPIRATION, ELEVATED CO2, INTERNAL NITROGEN CONCENTRATION, LEAF LIFE-SPAN, ORGANIC-MATTER, PHOTOSYNTHETIC ACCLIMATION, PINUS-RADIATA FOLIAGE, PLANT- COMMUNITIES, SHOOT RATIOS

1177

Kirschbaum, M.U.F., B.E. Medlyn, D.A. King, S. Pongracic, D. Murty, H. Keith, P.K. Khanna, P. Snowdon, and R.J. Raison. 1998. Modelling forest-growth response to increasing CO2 concentration in relation to various factors affecting nutrient supply. *Global Change Biology 4(1):23-41.*

It is well recognized that photosynthesis of C3 plants is highly responsive to CO2 concentration. However, in natural ecosystems, plants are subject to a range of feedback effects that can interact with increased photosynthetic carbon gain in different ways so that it is not clear to what extent increased photosynthesis will translate into increased growth. To assess the probable growth response of nutrient-limited forests to increasing CO2 concentration, we use a previously developed modelling framework and apply it under conditions where the supply of nutrients is affected by a range of different factors. Our analysis indicates that forest growth is likely to be highly stimulated by increasing CO2 concentration in forests with high fertility, in forests with nitrogen fixing plants, in those subject to fire or where nitrogen in wood is effectively removed from the biologically active cycle either through physical removal of stems in harvesting or through continued stem growth over long time periods. Forest growth is likely to be stimulated by CO2 concentration in both phosphorus-and sulphur-

limited forests provided nutrients in heartwood of trees are removed from the active nutrient cycle. Without this removal from the cycling system, however, sulphur-limited forests should show little response to increasing CO2. In phosphorus-limited forests without phosphorus removal, the response to increasing CO2 depends further on the equilibration state of the large pool of unavailable secondary phosphorus. Considered over periods of centuries during which the secondary pool has equilibrated, growth of phosphorus-limited forests is likely to be only weakly stimulated by increasing CO2 concentration. However, over shorter periods, increasing CO2 concentration should lead to a substantial increase in productivity. In general, it can be concluded that systems that are more open with respect to nutrient gains and losses are likely to be more responsive to increasing CO2 concentration than systems where the amount of available nutrients is less variable. In more open systems, operation at a lower internal nutrient concentration as a result of increasing atmospheric CO2 concentration can lead to reduced nutrient losses per unit carbon gain. Our analysis shows that the effect of increasing CO2 on forest growth can differ substantially between forests due to interactions with a range of factors that affect nutrient supply. The response of a particular forest to increasing CO2 concentration can only be predicted if the main factors controlling nutrient supply and growth in that forest are understood and incorporated into an assessment.

KEYWORDS: ATMOSPHERE, CARBON DIOXIDE, DYNAMICS, ECOSYSTEM PROCESSES, ELEVATED CO2, ENRICHMENT, LONG-TERM RESPONSE, SEEDLINGS, SPRUCE, TEMPERATURE

1178

Kitao, M., T.T. Lei, and T. Koike. 1997. Comparison of photosynthetic responses to manganese toxicity of deciduous bread-leaved trees in northern Japan. *Environmental Pollution 97(1-2):113-118.*

The effects of manganese (Mn) toxicity on photosynthesis of four tree species in northern Japan representing different successional traits were examined. The four species are: Betula ermanii (Be) and Alnus hirsuta (Ah) representing two early successional species, Ulmus davidiana var. japonica (Ud) as the mid-successional species, and Acer mono (Am) as the late successional species. Seedlings were grown hydroponically in a solution containing nutrients and Mn of four concentrations (1, 10, 50, 100 mg litre(-1)) for 50 days. Gas exchange measurements indicate that in all species, Mn accumulation in leaves resulted in the decline of light-saturated net photosynthetic rate at ambient CO2 pressure (35 Pa, Pn(amb)) and at saturating (5%) CO2 pressure (Pn(sat)), and of carboxylation efficiency but has little effect on the maximum efficiency of photochemistry. Sensitivity to elevated levels of Mn differed among species where the decline of Pn(amb) was much more modest in the two early successional species of Be and Ah than the mid-and late successional species of Ud and Am. The same trends were observed in both Pn(sat) and carboxylation efficiency. Based on these results, we suggest that early successional species (Betula ermanii and Alnus hirsuta) have greater tolerance for excess Mn in leaves than mid-and late successional species. (C) 1997 Elsevier Science Ltd.

KEYWORDS: C-3 PLANTS, CARBOXYLASE, CHLOROPHYLL, COWPEA VIGNA-UNGUICULATA, GROWTH, LIGHT, PHYSIOLOGY, TEMPERATURE, TOBACCO, TOLERANCE

1179

Kitaya, Y., G.H. Niu, T. Kozai, and M. Ohashi. 1998. Photosynthetic photon flux, photoperiod, and CO2 concentration affect growth and morphology of lettuce plug transplants. *Hortscience 33(6):988-991.*

Lettuce (Lactuca sativa L. cv. Summer-green) plug transplants were grown for 3 weeks under 16 combinations of four levels (100, 150, 200, and 300 mu mol.m(-2).s(-1)) of photosynthetic photon flux (PPF), two photoperiods (16 and 24 h), and two levels of CO2 (400 and 800 mu mol.mol(-1)) in growth chambers maintained at an air temperature of 20 +/- 2 OC. As PPF increased, dry mass (DM), percent DM, and leaf number increased, while ratio of shoot to root dry mass (S/R), ratio of leaf length to leaf width (LL/LW), specific leaf area, and hypocotyl length decreased. At the same PPF, DM was increased by 25% to 100% and 10% to 100% with extended photoperiod and elevated CO2 concentration, respectively. Dry mass, percent DM, and leaf number increased linearly with daily light integral (DLI, the product of PPF and photoperiod), while S/R, specific leaf area, LL/LW and hypocotyl length decreased as DLI increased under each CO2 concentration. Hypocotyl length was influenced by PPF and photoperiod, but not by CO2 concentration. Leaf morphology, which can be reflected by LL/LW, was substantially influenced by PPF at 100 to 200 mu mol.m(-2).s(-1), but not at 200 to 300 mu mol.m(-2).s(-1). At the same DLI, the longer photoperiod promoted growth under the low CO2 concentration, but not under the high CO2 concentrat ion. Longer photoperiod and/or higher CO2 conce ntration compensated for a low PPF.

KEYWORDS: GREENHOUSE, LIGHT, PLANTS, QUALITY, TOMATO

1180

Kleemola, J., J. Peltonen, and P. Peltonensainio. 1994. Apical development and growth of barley under different co2 and nitrogen regimes. *Journal of Agronomy and Crop Science-Zeitschrift Fur Acker Und Pflanzenbau 173(2):79-92.*

Increases in atmospheric carbon dioxide (CO2) concentration have stimulated interest in the response of agricultural crops to elevated levels of CO2. Several studies have addressed the response of C3 cereals to CO2, but the interactive effect of nutrient supply and CO2 on apical development and spikelet set and survival has not been investigated thoroughly. Hence, an experiment was conducted in the greenhouse to evaluate the effect of high (700 mumol CO2mol-1 air) and low (400 mumol mol- 1) levels of atmospheric CO2 on apical development, spikelet set and abortion, and pre- and post-anthesis growth in spring barley (Hordeum vulgare L.) grown under high N (0.3 g N pot-1 before sowing +0.11 g N pot-1 week-1) and low N (0.3 g N pot-1) regimes. The plants were grown in 5 L pots. Development of spike was hastened due to CO2 enrichment, and the C+ plants pollinated few days earlier than the C- plants. Carbon dioxide enrichment had no effect on date of ripening. Development of spike slowed following application of extra N, and plants pollinated 10 days later and matured 2 weeks later when compared with plants under low N. Carbon dioxide enrichment did not affect the number of spikelets at anthesis. Excess N decreased spikelet abortion and the increased maximum number of spikelets under both [CO2]. Barley plants did not tiller when grown in low [CO2] and low N. Increased endogenous IAA concentration in those plants, recorded three days before tillers appeared in other treatments, may have contributed to this. Carbon dioxide enrichment increased the C concentration of plants, but decreased the N concentration under high N regime. Both the C and N concentration of plants were increased under high N regime. Carbon dioxide enrichment increased the total dry matter of mature plants by 9% under high N regime and by 21% under low N regime. Under high [CO2] increased kernel number on tiller spikes, and increased kernel weight both on main stem and on tiller spikes resulted in a 23% increase in kernel yield under low N regime and 76% increase in kernel yield under high N regime. The rate of N application influenced growth and yield components to a greater extent than CO2 enrichment. At maturity, plant dry matter, kernel weight, the number of kernels per spike, and the number of spikes per plant were higher under high N regime than under low N regime. Long days (16 h), low light intensity (280 mumol m-2s-1), and at constant temperature of 20-degrees-C high [CO2] increased kernel weight and the number of kernels on tiller spikes under high and low N application rate, but did not increase the number of kernels on main stem spike, or the number of tillers or tiller spikes per plant.

KEYWORDS: CARBON DIOXIDE, CO2- ENRICHMENT, GRAIN-YIELD, PHYSIOLOGY, SPRING WHEAT, TEMPERATURE, YIELD COMPONENTS

1181
Klieber, A., B. Ratanachinakorn, and D.H. Simons. 1996. Effects of low oxygen and high carbon dioxide on tomato cultivar 'Bermuda' fruit physiology and composition. *Scientia Horticulturae 65(4):251-261.*

Breaker stage tomatoes (Lycopersicon esculentum Mill., cultivar 'Bermuda') were treated in air, 0.5% or 1.0% oxygen (O-2) in nitrogen (N-2) or 80% carbon dioxide (CO2) in air for 1, 3, 5 or 7 days at 22 degrees C, A 1 day low O-2 treatment delayed ripening after treatment by 1-2 days compared to a ripening period of 4 days for the control; elevated CO2 for 1 day had no effect on ripening after treatment, Low O-2 increased production of ethanol and acetaldehyde compared to the control and high CO2. Fruit treated for 3 or more days in low O-2 or high CO2 showed skin injury and blotchy ripening. Disease incidence increased with treatment time, but could be controlled in 1 day treatments by reducing relative humidity to about 70%, Firmness, total soluble solids, titratable acidity and pH of pericarp and gel of 1 day treated fruit were not different from the control.

KEYWORDS: ACETALDEHYDE, ATMOSPHERE, ETHANOL, EXPOSURES, NITROGEN, QUALITY, STORAGE

1182
Klironomos, J.N., M.C. Rillig, and M.F. Allen. 1996. Below-ground microbial and microfaunal responses to Artemisia tridentata grown under elevated atmospheric CO2. *Functional Ecology 10(4):527-534.*

1. Soil microbes are fed primarily by root-derived substrates, fulfil functions such as mineralization, immobilization, decomposition, pathogeneity and improvement of plant nutrition, and form the basis of the below-ground food web. Hitherto, belowground processes have generally been monitored using a 'black-box' approach, thereby ignoring effects of global change at a finer level of resolution. We describe shifts in the activity between microbial functional groups associated with roots of Artemisia tridentata, and the influence of this change on higher trophic levels, 2. We tested the hypothesis that elevated atmospheric CO2 causes the soil community to change qualitatively. We measured the responses of several soil microbe and soil microfaunal parameters to a double-ambient CO2 concentration and nutrient additions. The soil community, as measured by those parameters, showed great changes in response to the treatments. There was a very strong interaction between elevated CO2 and the nutrient addition. 3. Under low nutrient conditions, total microbial biomass did not change under elevated atmospheric CO2, but doubled under conditions of elevated CO2 and added nutrients. As we increased the resolution of our analysis, however, results shifted. Under low nutrient conditions, mycorrhizal fungi responded positively to elevated CO2, whereas with added soil nutrients they responded negatively to the same elevated CO2 concentration. Bacteria and non-mycorrhizal fungi did not respond under the former conditions but more than doubled in biomass under conditions of elevated CO2 and added nutrients. Soil fauna was also affected by the treatments. Overall, elevated CO2 shifted carbon flow in the plant-soil system to a more mutualistic-closed, mycorrhizal-dominated system, whereas the combination of elevated CO2 and nutrient addition shifted carbon flow to a more opportunistic-open, saprobe/pathogen-dominated one. 4. This indicates that elevated atmospheric CO2 may lead to far less predictable feedback patterns than previously thought and that qualitative shifts in the soil community may be far more important than mere changes in total C sink strength.

KEYWORDS: ARBUSCULAR MYCORRHIZAL FUNGI, CARBON DIOXIDE, COLLEMBOLA, COLONIZATION, ENRICHMENT, FEEDBACK, NATURAL ECOSYSTEMS, RHIZOSPHERE, ROOTS, SOIL

1183
Klironomos, J.N., M.C. Rillig, M.F. Allen, D.R. Zak, M. Kubiske, and K.S. Pregitzer. 1997. Soil fungal-arthropod responses to Populus tremuloides grown under enriched atmospheric CO2 under field conditions. *Global Change Biology 3(6):473-478.*

We investigated the influence of elevated CO2 and soil N availability on the growth of arbuscular mycorrhizal and non- mycorrhizal fungi, and on the number of mycophagous soil microarthropods associated with the roots of Populus tremuloides. CO2 concentration did not significantly affect percentage infection of Populus roots by mycorrhizal or non-mycorrhizal fungi. However, the extra-radical hyphal network was altered both qualitatively and quantitatively, and there was a strong interaction between CO2 and soil N availability. Under N-poor soil. conditions, elevated CO2 stimulated hyphal length by arbuscular mycorrhizal fungi, but depressed growth by non-mycorrhizal fungi. There was no CO2 effect at high N availability. High N availability stimulated growth by opportunistic saprobic/pathogenic fungi. Soil mites were not affected by any treatment, but collembolan numbers were positively correlated with the increase in non-mycorrhizal fungi. Results indicate a strong interaction between CO2 concentration and soil N availability on mycorrhizal functioning and on fungal-based soil food webs.

KEYWORDS: ARBUSCULAR MYCORRHIZAL FUNGI, CARBON DIOXIDE, CLIMATE CHANGE, COLONIZATION, ECOSYSTEMS, ELEVATED CO2, NITROGEN, PLANT, RHIZOSPHERE, ROOTS

1184
Klironomos, J.N., M.C. Rillig, M.F. Allen, D.R. Zak, K.S. Pregitzer, and M.E. Kubiske. 1997. Increased levels of airborne fungal spores in response to Populus tremuloides grown under elevated atmospheric CO2. *Canadian Journal of Botany-Revue Canadienne De Botanique 75(10):1670-1673.*

Soil fungi are important components of terrestrial ecosystems. They function as decomposers, pathogens, parasites, and mutualistic symbionts. Their main mode of dispersal is to liberate spores into the atmosphere. In this study we tested the hypothesis that a higher atmospheric CO2 concentration will induce greater sporulation in common soil fungi, leading to higher concentrations of fungal propagules in the atmosphere. In our field experiment, the concentration of airborne fungal propagules, mostly spores, increased fourfold under twice- ambient CO2 concentrations. Analysis of decomposing leaf litter (likely the main source of airborne fungal propagules) indicated that the fungi produced fivefold more spores under elevated CO2. Our results provide evidence that elevations in atmospheric CO2 concentration can directly affect microbial function, which may have important implications for litter decay, fungal dispersal, and human respiratory health.

KEYWORDS: CARBON DIOXIDE, DIAGNOSIS, NITROGEN

1185
Klironomos, J.N., M. Ursic, M. Rillig, and M.F. Allen. 1998. Interspecific differences in the response of arbuscular mycorrhizal fungi to Artemisia tridentata grown under elevated atmospheric CO2. *New Phytologist 138(4):599-605.*

Arbuscular mycorrhizal (AM) fungi form mutualistic symbioses with the root systems of most plant species. These mutualisms regulate nutrient exchange in the plant-soil interface and might influence the way in

which plants respond to increasing atmospheric CO2. In other experiments, mycorrhizal responses to elevated CO2 have been variable, so in this study we test the hypothesis that different genera of AM fungi differ in their response, and in turn alter the plant's response, to elevated CO2. Four species from three genera of AM fungi were tested. Artemisia tridentata Nutt. seedlings were inoculated with either Glomus intraradices Schenck & Smith, Glomus etunicatum Becker & Gerdemann, Acaulospora sp. or Scutellospora calospora (Nicol. & Gerd.) Walker & Sanders and grown at either ambient CO2 (350 ppm) or elevated CO2 (700 ppm). Several significant inter-specific responses were detected. Elevated CO2 caused percent arbuscular and hyphal colonization to increase for the two Glomus species, but not for Acaulospora sp. or S. calospora. Vesicular colonization was not affected by elevated CO2 for any fungal species. In the extra-radical phase, the two Glomus species produced a significantly higher number of spores in response to elevated CO2, whereas Acaulospora sp. and S. calospora developed significantly higher hyphal lengths. These data show that AM fungal taxa differ in their growth allocation strategies and in their responses to elevated CO2, and that mycorrhizal diversity should not be overlooked in global change research.

KEYWORDS: BOUTELOUA-GRACILIS, CARBON DIOXIDE, COLONIZATION, DIVERSITY, ECOLOGY, ENRICHMENT, GRASSLAND, MORPHOLOGY, PATTERNS, PLANT

1186

Kloppenburg, W.D., B.G. Wolthers, F. Stellaard, H. Elzinga, T. Tepper, P.E. deJong, and R.M. Huisman. 1997. Determination of urea kinetics by isotope dilution with [C- 13]urea and gas chromatography isotope ratio mass spectrometry (GC-IRMS) analysis. *Clinical Science 93(1):73-80.*

1. Stable urea isotopes can be used to study urea kinetics in humans, The use of stable urea isotopes far studying urea kinetic parameters in humans on a large scale is hampered by the high costs of the labelled material, We devised a urea dilution for measurement of the distribution volume, production rate and clearance of urea in healthy subjects and renal failure patients using the inexpensive single labelled [C- 13]urea isotope with subsequent analysis by headspace chromatography-isotope ratio MS (GC-IRMS) of the [C-13]urea enrichment, 2. The method involves measurement of the molar percentage excess of [C-13]urea in plasma samples taken over a 4 h period after an intravenous bolus injection of [C-13]urea, During the sample processing procedure, the plasma samples together with calibration samples containing a known molar percentage excess of [C-13]urea are acidified with phosphoric acid to remove endogenous CO2, and are subsequently incubated with urease to convert the urea present in the plasma samples into CO2. The C-13 enrichment of the generated CO2 is analysed by means of GC-IRMS, This method allows measurement of the molar percentage excess of [C-13]urea to an accuracy of 0.02%. 3. Reproducibility studies showed that the sample processing procedure [within-run coefficient of variation (CV) <2.8% and between-run CV <8.8%] and the GC-IRMS analysis (within-day CV <1.3% and between-day CV <1.3%) could be repeated with good reproducibility, 4. In clinical urea kinetic studies in a healthy subject and in a renal failure patient without residual renal function, reproducible values of the distribution volume, production rate and clearance of urea were determined using minimal amounts of [C-13]urea (25-50 mg). 5. because only low [C-13]urea enrichments are needed in this urea dilution method using GC-IRMS analysis, the costs of urea kinetic studies are reduced considerably, especially in patients with renal failure.

KEYWORDS: HEMODIALYSIS, MODEL

1187

Knapp, A.K., M. Cocke, E.P. Hamerlynck, and C.E. Owensby. 1994. Effect of elevated co2 on stomatal density and distribution in a C-4 grass and a C-3 forb under field conditions. *Annals of Botany 74(6):595-599.*

Two common tallgrass prairie species, Andropogon gerardii, the dominant C-4 grass in this North American grassland, and Salvia pitcheri, a C-3 forb, were exposed to ambient and elevated (twice ambient) CO2 within open-top chambers throughout the 1993 growing season. After full canopy development, stomatal density on abaxial and adaxial surfaces, guard cell length and specific leaf mass (SLM; mg cm(-2) were determined for plants in the chambers as well as in adjacent unchambered plots. Record high rainfall amounts during the 1993 growing season minimized water stress in these plants (leaf xylem pressure potential was usually > -1.5 MPa in A. gerardii) and also minimized differences in water status among treatments. In A. gerardii, stomatal density was significantly higher (190 +/- 7 mm(-2); mean +/- s.e.) in plants grown outside of the chambers compared to plants that developed inside the ambient CO2 chambers (161 +/- 5 mm(-2)). Thus, there was a significant 'chamber effect' on stomatal density. At elevated levels of CO2, stomatal density was even lower ($P < 0.05$; 121 +/- 5 mm(- 2)). Most stomata were on abaxial leaf surfaces in this grass, but the ratio of adaxial to abaxial stomatal density was greater at elevated levels of CO2. In S. pitcheri, stomatal density was also significantly lower when plants were grown in the open-top chambers (235 +/- 10 mm(-2) outside vs. 140 +/- 6 mm(-2) in the ambient CO2 chamber). However, stomatal density was greater at elevated CO2 (218 +/- 12 mm(-2)) compared to plants from the ambient CO2 chamber. The ratio of stomata on adaxial vs. abaxial surfaces did not vary significantly in this herb. Guard cell lengths were not significantly affected by growth in the chambers or by elevated CO2 for either species. Growth within the chambers resulted in lower SLM in S. pitcheri, but CO2 concentration had no effect. In A. gerardii, SLM was lower at elevated CO2. These results indicate that stomatal and leaf responses to elevated CO2 are species specific, and reinforce the need to assess chamber effects along with treatment effects (CO2) when using open-top chambers.

KEYWORDS: ATMOSPHERIC CO2, DROUGHT, INCREASE, NUMBERS, PATTERNS, PHOTOSYNTHESIS, PLANT WATER RELATIONS, RESPONSES, TALLGRASS PRAIRIE

1188

Knapp, A.K., S.L. Conard, and J.M. Blair. 1998. Determinants of soil CO2 flux from a sub-humid grassland: Effect of fire and fire history. *Ecological Applications 8(3):760-770.*

Soil CO2 flux (J(CO2)) was measured at midday over a 2-yr period in undisturbed tallgrass prairie (Konza Prairie, Kansas, USA) to quantify seasonal and annual budgets, to evaluate temperature and moisture as determinants of soil CO2 flux, and to assess the effect of a common land management tool, spring fire, and fire history on soil respiration. We hypothesized that: (1) maximum rates and annual estimates of soil J(CO2) would be greater in more productive burned sites than in unburned sites, (2) soil J(CO2) would be greater in newly burned sites with a history of fire exclusion than in annually burned sites (consistent with differences in aboveground production), and (3) soil temperature and water availability would be primary abiotic determinants of soil J(CO2) in tallgrass prairie. A preliminary assessment of the effects of large herbivores on soil J(CO2) was included to evaluate the hypothesis that removal of aboveground biomass would reduce soil J(CO2). Results indicated that spring fire increased maximum monthly soil J(CO2) by 20-55% relative to unburned tallgrass prairie, with greatest monthly differences measured in April (fourfold higher in burned sites). In burned sites that differed in fire history, maximum monthly J(CO2) in annually burned prairie was 33% greater than in burned sites with a history of fire exclusion. Soil J(CO2) in these latter sites was still significantly higher than in unburned sites. Soil J(CO2) in sites grazed by bison was reduced by as much as 30% relative to adjacent ungrazed areas. Reduced root biomass and activity in grazed areas, unburned sites,

and sites with a history of fire exclusion suggest that plants play a major role in determining soil J(CO2) in this grassland. Soil temperature at 5 cm was related strongly to midday J(CO2) in both annually burned sites (r(2) = 0.58) and unburned sites (r(2) = 0.71). In contrast, differences in soil moisture among sites, enhanced by comparing irrigated grassland to control areas, increased maximum monthly J(CO2) by only 8%. Thus, soil temperature was the primary abiotic determinant of soil J(CO2) during this study. Maximum monthly estimates of soil J(CO2) in tallgrass prairie ranged from 10.3 mu mol CO2 . m(-2) . s(-1) in unburned sites to 15.1 mu mol . m(-2) . s(-1) in annually burned irrigated sites, whereas annual estimates varied from 4.7 to 7.8 kg CO2/m(2). Over the 2-yr period, spring fire increased estimated annual soil J(CO2) by 38-51% relative to unburned sites, while irrigation increased annual soil J(CO2) by 13%. These estimates for tallgrass prairie are much higher than those reported for most temperate ecosystems but are similar to estimates for tropical forests. Characteristics of undisturbed tallgrass prairie that may lead to high levels of soil J(CO2) include: high above- and belowground productivity; a relatively high proportion of C stored belowground; levels of soil microbial biomass and activity that are among the highest in native ecosystems in the United States; and the lack of a single dominant factor such as temperature, moisture, or nutrient availability, that consistently limits biotic processes during the growing season. The sensitivity of soil J(CO2) in tallgrass prairie to different land use practices (fire and grazing) suggests that it is critical to include these factors in the development of grassland C budgets, as well as in regional models that estimate biogeochemical responses to land use change.

KEYWORDS: ANDROPOGON-GERARDII, CARBON, EARTHWORM POPULATIONS, ELEVATED CO2, NORTH-AMERICA, PANICUM-VIRGATUM, RESPIRATION, TEMPERATE GRASSLAND, UNBURNED TALLGRASS PRAIRIE, WATER RELATIONS

1189

Knapp, A.K., J.T. Fahnestock, and C.E. Owensby. 1994. Elevated atmospheric co2 alters stomatal responses to variable sunlight in a C-4 grass. *Plant, Cell and Environment 17(2):189-195.*

Native tallgrass prairie in NE Kansas was exposed to elevated (twice ambient) or ambient atmospheric CO2 levels in open-top chambers. Within chambers or in adjacent unchambered plots, the dominant C-4 grass, Andropogon gerardii, was subjected to fluctuations in sunlight similar to that produced by clouds or within canopy shading (full sun > 1500 mu mol m(-2) s(-1) versus 350 mu mol m(-2) s(-1) shade) and responses in gas exchange were measured. These field experiments demonstrated that stomatal conductance in A. gerardii achieved new steady state levels more rapidly after abrupt changes in sunlight at elevated CO2 when compared to plants at ambient CO2. This was due primarily to the 50% reduction in stomatal conductance at elevated CO2, but was also a result of more rapid stomatal responses. Time constants describing stomatal responses were significantly reduced (29-33%) at elevated CO2. As a result, water loss was decreased by as much as 57% (6.5% due to more rapid stomatal responses). Concurrent increases in leaf xylem pressure potential during periods of sunlight variability provided additional evidence that more rapid stomatal responses at elevated CO2 enhanced plant water status. CO2-induced alterations in the kinetics of stomatal responses to variable sunlight will likely enhance direct effects of elevated CO2 on plant water relations in all ecosystems.

KEYWORDS: ANDROPOGON-GERARDII, CARBON DIOXIDE, GAS-EXCHANGE, GROWTH FORM, LEAVES, PHOTOSYNTHETIC INDUCTION STATE, SUBALPINE PLANTS, TALLGRASS PRAIRIE, TERM, WATER-USE EFFICIENCY

1190

Knapp, A.K., E.P. Hamerlynck, J.M. Ham, and C.E. Owensby. 1996. Responses in stomatal conductance to elevated CO2 in 12 grassland species that differ in growth form. *Vegetatio 125(1):31-41.*

Responses in stomatal conductance (g(st)) and leaf xylem pressure potential (psi(leaf)) to elevated CO2 (2x ambient) were compared among 12 tallgrass prairie species that differed in growth form and growth rate. Open-top chambers (OTCs, 4.5 m diameter, 4.0 m in height) were used to expose plants to ambient and elevated CO2 concentrations from April through November in undisturbed tallgrass prairie in NE Kansas (USA). In June and August, psi(leaf) was usually higher in all species at elevated CO2 and was lowest in adjacent field plots (without OTCs). During June, when water availability was high, elevated CO2 resulted in decreased g(st) in 10 of the 12 species measured. Greatest decreases in g(st) (ca. 50%) occurred in growth forms with the highest potential growth rates (C-3 and C-4 grasses, and C-3 ruderals). In contrast, no significant decrease in g(st) was measured in the two C-3 shrubs. During a dry period in September, reductions in g(st) at elevated CO2 were measured in only two species (a C-3 ruderal and a C-4 grass) whereas increased g(st) at elevated CO2 was measured in the shrubs and a C-3 forb. These increases in g(st) were attributed to enhanced psi(leaf) in the elevated CO2 plants resulting from increased soil water availability and/or greater root biomass. During a wet period in September, only reductions in g(st) were measured in response to elevated CO2. Thus, there was significant interspecific variability in stomatal responses to CO2 that may be related to growth form or growth rate and plant water relations. The effect of growth in the OTCs, relative to field plants, was usually positive for g(st) and was greatest (> 30%) when water availability was low, but only 6-12% when psi(leaf) was high. The results of this study confirm the importance of considering interactions between indirect effects of high CO2 of plant water relations and direct effects of elevated CO2 on g(st), particularly in ecosystems such as grasslands where water availability often limits productivity. A product of this interaction is that the potential exists for either positive or negative responses in g(st) to be measured at elevated levels of CO2.

KEYWORDS: ANDROPOGON-GERARDII, ATMOSPHERIC CO2, C-4 GRASS, CARBON DIOXIDE, GAS-EXCHANGE, PHOTOSYNTHETIC ACCLIMATION, PLANT-RESPONSES, TALLGRASS PRAIRIE, VARIABLE SUNLIGHT, WATER RELATIONS

1191

Knapp, A.K., E.P. Hamerlynck, and C.E. Owensby. 1993. Photosynthetic and water relations responses to elevated co-2 in the C-4 grass andropogon-gerardii. *International Journal of Plant Science 154(4):459-466.*

Undisturbed tallgrass prairie, dominated by the C-4 grass Andropogon gerardii, was exposed to ambient and elevated (double ambient) levels of atmospheric CO2 in large open-top chambers throughout the 1991 and 1992 growing seasons. Responses in leaf xylem pressure potential (psi), net photosynthesis (A), and stomatal conductance (g) were measured in both years for A. gerardii grown within chambers and from adjacent field plots. In 1992, maximum photosynthetic capacity (A(max)), apparent quantum requirement (Q(r)), the photosynthetic light compensation point (LCP), and dark respiration (R(d)) were also measured. Midday psi was significantly higher in plants grown at elevated CO2 in both years, and seasonally averaged psi was 0.48-0.70 MPa lower in 1991 (a dry year) than 1992 (a wet year). In 1991, A and g were significantly higher (regardless of measurement CO2 level) in plants grown at elevated vs. ambient CO2. These increases were measured in well-watered plants insuring that these plants differed only in CO2 growth conditions and previous exposure to low psi. Increased A at elevated CO2 occurred (as much as 7.1 mu mol m(-2) s(-1)) over a broad range of temperatures (17-35 C), but the temperature optimum for A was similar at both 350 and 700 mu L L(-1) CO2. In 1992, no differences in A, A(max), Q(r), LCP, or R(d) were detected when ambient and elevated CO2 plants were compared. In plants collected

from field plots, R(d), LCP, and leaf N were significantly higher than in plants within the chambers indicating that a chamber effect exists for these parameters. In both years, g was significantly reduced (21%-51%) when measured at 700 vs. 350 mu L L(-1) CO2. Peak aboveground biomass was increased at elevated CO2 in 1991 but not in 1992. These data indicate that for C-4 grasses, effects of elevated CO2 may only be detectable in years with significant water stress, a common occurrence in the central North American tallgrass prairies.

KEYWORDS: CARBON-DIOXIDE EFFLUX, CO2, GROWTH, LEAVES, PLANTS, SOIL MOISTURE, STRESS, TALLGRASS PRAIRIE, TERM

1192
Knapp, P.A., and P.T. Soule. 1998. Recent Juniperus occidentalis (western juniper) expansion on a protected site in central Oregon. *Global Change Biology 4(3):347-357.*

The expansion of Juniperus occidentalis (western juniper) has been extensive in the last century, and increases in density and cover have been linked with the indirect effects of domestic livestock grazing (i.e. cessation of periodic fires, increases of nurse-plant sites), and more favourable climatic conditions. In this study, we document changes in vegetation (including J. occidentalis) in central Oregon over a 23-year period and relate these changes to their probable causes. In June 1995 we returned to the Horse Ridge Research Natural Area (HRRNA), a site that has a history of minimal anthropogenic impacts, to replicate a 1972 vegetation survey. Using the canopy-intercept method, line intercept method, and aerial photography analysis to measure herbaceous cover, shrub cover and tree cover, respectively, we found significant changes had occurred in the 23-year period between studies. Relative changes of tree, shrub, and perennial herbaceous cover were 59%, 7%, and -38%, respectively. Relative increases in J. occidentalis density, as measured by the number of clumps and the number of stems, were 37% and 53%, respectively. Mean maximum height of J. occidentalis had increased by 10%. We examined the role of potentially confounding influences (e.g. fire, grazing, pathogens, climatic variability) and found that none of the traditional mechanisms implicated in J. occidentalis expansion adequately explained the observed changes. We suggest that the role of biological inertia of both anthropogenic and natural means may have had a profound effect on the J. occidentalis ecology of HRRNA.

KEYWORDS: ATMOSPHERIC CO2 ENRICHMENT, CARBON DIOXIDE, CLIMATE, DESERT, GROWTH, RESPONSES, VEGETATION CHANGE, WATER-USE EFFICIENCY, YIELD

1193
Knapp, T., and R. Mookerjee. 1996. Population growth and global CO2 emissions - A secular perspective. *Energy Policy 24(1):31-37.*

Considerable scientific effort has been applied to the question of whether worldwide fossil fuel combustion and the resultant emission of CO2 (as well as emissions of other greenhouse gases) will cause a discernible enhancement of the greenhouse effect in the next century, A more precise understanding of the contribution of human activity to potential global warming (vis-ri-vis natural climatic variability) is of critical policy interest, Surprisingly little research has been devoted to establishing the underlying statistical relationship between human activities and CO2 emissions, In this paper, we explore the nature of the relationship between global population growth and CO2 emissions by employing the test of causality developed by Granger on annual data for 1880-1989, as well as more comprehensive error correction and cointegration models, The results suggest a lack of a long-term equilibrium relationship, but imply a short-term dynamic relationship from CO2 to population growth.

KEYWORDS: CARBON DIOXIDE, CLIMATE, MODELS, TEMPERATURES, VARIABLES

1194
Kobayashi, K. 1994. Mapping results of crop growth simulation in a vector-space. *Agricultural and Forest Meteorology 68(1-2):43-61.*

Crop growth models can be used to address the mode-of-action of the global change impacts on crop yield as well as to predict the extent of the yield change. Presented in this paper are the framework to analyze the simulated yield change caused by the variations of many influencing factors and some methods to visualize the yield change. In the framework, the simulated yield change is mapped into an n-dimensional vector space, where n is the number of the simulated cases, e.g. years or locations. Yield changes owing to the individual impacts as well as the impact of simultaneous changes in all the factors are represented by vectors in the n-dimensional space. Contributions of the individual impacts to the simulated yield change and the interrelations between the impacts can be represented by the magnitude and orientation of the vectors. To visualize the vectors, however, the dimension n must be three or less. This is not the case, in general, and hence some methods are needed to reduce the dimension. By combining the influencing factors into three or less groups, the vectors for each group can be visualized in a subspace of dimension three or less. Impacts within each group may be further visualized in the same way. Taking an average is another way to reduce the dimension of the vector space. With it, the n-dimensional space is partitioned into a one-dimensional space for the mean and an (n - 1)-dimensional space for the deviation of the yield change. These methods were applied to an example of the simulated yield changes in soybean and maize owing to climate change (precipitation increase and temperature rise) and elevated CO2 (increases in the radiation use efficiency and the water use efficiency). The analyses revealed the differences between soybean and maize with respect to their responses to the simulated impacts of the climate change and the elevated CO2. These inter-specific differences were related to the differential changes in growth processes. The difference between the two impacts, i.e. the climate change and the CO2 increase, was also addressed. Utilities of the above approach were discussed and compared with the sensitivity analysis. Limitation of this approach was also discussed.

KEYWORDS: ADJUSTMENTS, CARBON, CLIMATE CHANGE, FARMER SCENARIO, MODEL, NITROGEN LIMITATIONS, PRESENT TECHNOLOGY, RADIATION, SOYBEAN YIELD, TEMPERATURE

1195
Kohlmaier, G.H., C. Hager, G. Wurth, M.K.B. Ludeke, P. Ramage, F.W. Badeck, J. Kindermann, and T. Lang. 1995. Effects of the age class distributions of the temperate and boreal forests on the global co2 source-sink function. *Tellus Series B-Chemical and Physical Meteorology 47(1-2):212-231.*

The role of the temperate and boreal forests as a global CO2 source or sink is examined, both for the present time and for the next hundred years. The results of the Forest Resource Assessment for 1990 of the Economic Comission for Europe and the Food and Agricultural Organisation of the United Nations (1992) serve as the main database in this study. Out of the estimated total area of approximately 20 . 10(6) km(2) of forests and wooded lands in tile temperate and boreal zone only approximately fifty percent is documented within the category of exploitable Forests, which are examined in detail here. In this study, a general formalism of the time evolution of an ensemble of forests within an ecological province is developed using the formalism of the Leslie matrix. This matrix can be formulated if the age class dependent mortalities which arise from the disturbances are known. A distinction is made between the natural disturbances by fire, wind throw and insect

infestations and disturbances introduced through harvesting of timber. Through the use of Richards growth function each age class of a given biome is related to the corresponding biomass and annual increment. The data reported on the mean net annual increment and on the mean biomass serve to calibrate the model. The difference of the reported nut annual increment and annual fellings of approximately 550 . 10(6) m(3) roundwood correspond to a sink of 210-330 Mt of carbon per year excluding any changes in the soil balance. it could be shown that the present distribution of forest age classes for the United States, Canada, Europe, or the former Soviet Union does not correspond to a quasi-stationary state, in which biomass is accumulated only due to a stimulated growth under enhanced atmospheric CO2 levels. The present CO, sink function will not persist in the next century, if harvesting rates increase with 0.5% annually or even less. The future state will also be influenced by the effect of the greenhouse climate, the impact of which may range from a stimulating effect on growth. which is calculated by the Frankfurt biosphere model, up to a transitional negative effect through a shift in vegetation zones.

KEYWORDS: BIOMES, BUDGET, CARBON STORAGE, DIOXIDE, FORMER SOVIET-UNION, UNITED-STATES

1196

Koike, T. 1995. Effects of co2 in interaction with temperature and soil fertility on the foliar phenology of alder, birch, and maple seedlings. *Canadian Journal of Botany-Revue Canadienne De Botanique 73(2):149-157.*

The foliar phenology of potted 1-year-old seedlings of alder (Alnus hirsuta Turcz.), maple (Acer mono Maxim.), and birch (Betula platyphylla Sukatch, var. japonica Hara) was observed from May to September in eight growth environments: factorial combinations of temperatures (light:dark, 30:20 degrees C and 26:16 degrees C), CO2 level (70 and 36 Pa), and nutrient regime (high versus low levels of fertilization). Seedlings grown at high fertility always had more leaves, and under high CO2, shed leaves slightly later than seedlings grown at low fertility. Except for maple, production of newly formed shoots and leaves was accelerated by high CO2. In maple, high CO2 only increased the number of flushes of the leader shoot. Alder and birch accelerated sylleptic shoot and leaf production at high CO2 in fertile conditions. The production of new leaves by alder grown at high CO2 and low fertility was almost the same as that grown under normal CO2 at high fertility. At high CO2, the timing of winter bud formation of monopodial alder and maple was delayed, while that of sympodial birch was almost the same as at ambient CO2.

KEYWORDS: BETULA-PENDULA ROTH, DECIDUOUS TREES, ELEVATED CO2, ENRICHMENT, GROWTH, LEAF, LIQUIDAMBAR-STYRACIFLUA, NORTHEASTERN UNITED-STATES, PINUS-TAEDA SEEDLINGS, WOODY-PLANTS

1197

Koike, T., T.T. Lei, T.C. Maximov, R. Tabuchi, K. Takahashi, and B.I. Ivanov. 1996. Comparison of the photosynthetic capacity of Siberian and Japanese birch seedlings grown in elevated CO2 and temperature. *Tree Physiology 16(3):381-385.*

The effects of increased CO2 and temperature on the photosynthetic capacity of Siberian white birch and Japanese white birch (Betula platyphylla Sukatch. and B. platyphylla Sukatch. var. japonica Hara) were measured. Birch seedlings were raised with a CO2 partial pressure of 36 +/- 0.3 Pa (i.e., ambient) or 70 +/- 0.6 Pa at day/night temperatures of either 30/16 degrees C or 26/12 degrees C. Siberian birch leaves were smaller and thicker than Japanese birch leaves. Water use efficiency and nitrogen use efficiency of Siberian birch grown in the CO2-enriched air were higher than those of Japanese birch. Both species showed a physiological adjustment to the growth CO2 partial pressure. Carboxylation efficiency and quantum yield of both species grown in CO2-enriched air were lower than those of seedlings grown in ambient CO2. The adaptation of Siberian and Japanese birch to elevated CO2 and temperature are discussed in relation to predicted climate change.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, CARBON DIOXIDE, LIMITATIONS, NITROGEN-USE, PLANTS, RESPONSES, TUSSOCK TUNDRA

1198

Kojima, S. 1994. Effects of global climatic warming on the boreal forest. *Journal of Plant Research 107(1085):91-97.*

On the basis of the predictions of the global climatic warming induced by anthropogenic activities, as provided by climatologists, current state of knowledge regarding possible ecological consequences of the warming on the boreal biome was discussed. A 600 to 700 km northward advance of the biome along with the warming was predicted. Such a shift could take place for half a century or so, which would be an unprecedentedly fast rate of progression. This might cause a serious disorder in species composition of the biome, particularly in the boundary regions. As to the carbon sink or source issues, considerable uncertainties and knowledge gaps existed. Elevated temperature and CO2 levels would stimulate photosynthesis to result in an increase of CO2 uptake, while the temperature increase would promote decomposition of organic matter especially that stored in the soils to release CO2 to the atmosphere. Behaviors of northern peat bogs, where ca. 700 Gt of organic matter was thought to be accumulated, would seriously affect the balance. However, overall ecosystematic carbon balance was yet to be fully studied. It was realized that multifunctional approaches needed to be developed so as to integrate pieces of various information into a holistic picture. Need for international collaboration research efforts was also addressed.

KEYWORDS: ALASKAN TUNDRA, ARCTIC TUNDRA, ATMOSPHERIC CARBON-DIOXIDE, CANADA, ELEVATED CO2, GENERAL-CIRCULATION MODEL, INCREASE, SENSITIVITY, TEMPERATURE, TUSSOCK TUNDRA

1199

Kontak, D.J., and R. Kerrich. 1997. An isotopic (C, O, Sr) study of vein gold deposits in the Meguma terrane, Nova Scotia: Implication for source reservoirs. *Economic Geology and the Bulletin of the Society of Economic Geologists 92(2):161-180.*

Vein quartz, carbonate, and tourmaline from 19 Meguma gold deposits in the Meguma terrane of Nova Scotia have been analyzed for stable (delta(18)O, delta(13)C) and radiogenic (Sr-87/Sr-86) isotopes in order to assess the nature and origin of the vein-forming fluids. hs with other mesothermal gold provinces, the Meguma gold deposits are well suited to such a study because carbonate is the next most abundant phase after quartz in these mesothermal lode gold deposits. All vein types have been sampled for quartz and carbonate and, in addition, all compositional and textural varieties of carbonate have been sampled. Vein quartz is of uniform isotopic composition with most delta(18)O values between 10.2 to 17.6 per mil (avg ca. 14 parts per thousand), except for one deposit (West Gore Sb-Au) where values go to 19.4 per mil. There is no systematic variation for quartz within a deposit or position within the Meguma Group stratigraphy. Vein carbonate delta(18)O values range from 11.8 to 27.5 per mil, with most in the 13 to 16 per mil range. The relatively O-18-enriched carbonates reflect exchange with low-temperature fluids based on analyses of quartz-carbo;late pairs that indicate disequilibrium fractionation (Delta(quartz-carbonate) less than or equal to 0); this is best illustrated by the strong negative correlation between delta(18)O(carbonate) and Delta(quartz-carbonate). The

delta(18)O(water) is estimated at 10 +/- 3 per mil for a temperature of vein formation of 350 degrees to 400 degrees C and using the appropriate mineral-water fractionation equations. Whereas delta(water)(18) values partly overlap the field for magmatic fluids, the values are wholly consistent with a metamorphic fluid, and it is considered unlikely that a primary magmatic fluid signature has been substantially modified due to wall-rock influences given that mesothermal gold systems are sites of high fluid/rock ratios. Vein carbonate has delta(13)C values of -13.1 to -25.9 per mil, but a slight negative correlation between delta(13)C(carbonate) and Delta(quartz-carbonate) suggests that the primary values lie in the range -20 to -25 per mil. Thus, the delta(13)C values indicate a reduced, biogenic source for the carbon. Oxidation of the reduced carbon, as indicated by CO2 in fluid inclusions, may have occurred via hydrolysis of graphite or dissolution of carbonate minerals, both of which occur in the wall-rock lithologies of the Meguma Group, the latter of which has the appropriate isotopic composition. The initial Sr-87/Sr-66 of the vein fluid, estimated from the analyses of 52 vein carbonates (17 deposits) and four tourmalines (three deposits), ranges from 0.70118 to 0.72284 and within deposits considerable variation is observed. There is insufficient data to quantify the extent of the low-temperature overprint which has modified the C and O isotope data, although it is likely that some influence is present. Nevertheless, the data cannot be reconciled by a source confined exclusively to the Meguma Group, which suggests, therefore, involvement of another reservoir(s). The isotopic heterogeneity can be explained by variable amounts of contamination of a primary fluid with radiogenic Sr derived from Meguma Group lithologies by interaction along the fluid path or at the site of vein formation concomitant with wall-rock alteration; as discussed above, a dominantly magmatic source is not considered feasible. This fluid source is suggested to be within the structural basement to the Meguma Group, and the Liscomb gneisses are the favored source based on the combined results of the Sr isotope data presented herein and previously published Pb isotope data. Collectively, the data indicate that a primary fluid of metamorphic origin has had its isotopic signature variably modified due to interaction with different reservoirs. The most affected isotopic systems are C and S (based on earlier work on delta(35)S values) which are abundant as graphite carbonate and sulfides in the Meguma wall rock, respectively. The range in Sr-87/Sr-86 values of the fluid also reflects contamination, but this was quite variable. The uniform delta(18)O(water) value for the fluid indicates that this was the least affected isotopic system, except for the later exchange of carbonate at low temperatures.

KEYWORDS: ABITIBI GREENSTONE-BELT, BEAVER-DAM DEPOSIT, CANADIAN CORDILLERA, LISCOMB COMPLEX, NEW-ZEALAND, PLASMA-MASS SPECTROMETRY, SOUTH MOUNTAIN BATHOLITH, SOUTHEASTERN ALASKA, STABLE ISOTOPE, WESTERN-AUSTRALIA

1200

Koricheva, J., S. Larsson, E. Haukioja, and M. Keinanen. 1998. Regulation of woody plant secondary metabolism by resource availability: hypothesis testing by means of meta-analysis. *Oikos 83(2):212-226.*

Our aim in this study was to determine how well phenotypic variation iri foliar concentrations of carbon-based secondary compounds (CBSCs) in woody plants can be predicted on the basis of two resource-based hypotheses, i.e. the carbon-nutrient balance (CNB) and growth-differentiation balance (GDB) hypotheses. We conducted a meta-analysis of literature data with respect to responses of CBSCs, carbohydrates and nitrogen to six types of environmental manipulations (fertilization with nitrogen or phosphorus, shading, CO2 enrichment, drought stress, ozone exposure): Plant responses to nitrogen fertilization, shading and CO2 enrichment in terms of pooled CBSCs and carbohydrates were consistent with predictions made with the two hypotheses. However, among biosynthetically distinct groups of CBSCs only concentrations of phenylpropanoid-derived compounds changed as predicted; hydrolyzable tannins and terpenoids, in particular, were less responsive. Phosphorus fertilization did not affect concentrations of CBSC or primary metabolites. Plant responses to drought and ozone exposure presumably were driven by plant demands for particular types of compounds (osmolites in the case of drought and antioxidants in the case of ozone exposure) rather than by changes in resource availability. Based on the relative importance of the treatment effects, we propose a hierarchical model of carbon allocation to CBSCs. The model implies that CBSC production is determined by both resource availability and specific demand-side responses. However, these two mechanisms work at different hierarchical levels. The domain of the CNB and GDB hypotheses is at the high hierarchical levels, predicting the total amount of carbon that can be allocated to CBSCs. Predicting altered concentrations of individual CBSCs, i.e. low hierarchy levels, probably demands biosynthetically detailed models which also take into account the history of plant interactions with biotic and abiotic factors.

KEYWORDS: BETULA-PENDULA ROTH, CARBON-DIOXIDE ENRICHMENT, CITRUS RED MITE, DEER CERVUS-ELAPHUS, DELAYED INDUCIBLE RESISTANCE, ELEVATED ATMOSPHERIC CO2, GROWTH-DIFFERENTIATION BALANCE, LIRIODENDRON-TULIPIFERA L, PINUS TAEDA L, ULMUS-AMERICANA SEEDLINGS

1201

Korner, C. 1995. Towards a better experimental basis for upscaling plant- responses to elevated co2 and climate warming. *Plant, Cell and Environment 18(10):1101-1110.*

Few of the most common assumptions used in models of responses of plants and ecosystems to elevated CO2 and climate warming have been tested under realistic life conditions, It is shown that some unexpected discrepancies between predictions and experimental findings exist, suggesting that a better empirical basis is required for predictions, The following ten suggestions may improve our potential to scale up from experimental scales to the real world, (1) Experiments should be timed to account for non-linearity in system responsiveness, asynchrony of responses and developmental differences, (2) By altering mineral nutrient supply, a wide range of CO2 responses can be 'produced', thus requiring realistic soil conditions, (3) Distinctions should be made between 'doubling CO2 supply' and biologically effective degrees of CO2 enrichment. (4) Because of the non-linearity of plant responses to CO2, studies of at least three instead of two CO2 concentrations are necessary to describe future trends adequately, (5) Edge effects, in particular unscreened side light, may lead to allometric anomalies, strongly constraining up-scaling to stand-scale CO2 responses, (6) Variables such as growth, yield, net primary production and C turnover are often confused with carbon pools, carbon sequestration or net ecosystem production, (7) Mono- and interspecific interactions between individuals may lead to completely unpredictable CO2 responses, (8) Experiments with seedlings benefit from the absence of prehistory effects but are likely to be irrelevant for the responses of larger trees which, on the other hand, may be constrained by carryover effects, Tree ring research indicates immediate sensitivity of large trees to environmental changes, supporting their usefulness in short-term CO2-enrichment experiments, (9) In predicting temperature responses, acclimation deserves more attention, (10) The significance of developmental responses is largely under-represented in experimental research, although these responses may overrule many of the other effects of atmospheric change, Results of more realistic experiments which account for these problems will provide a better basis for modelling the future of the biosphere.

KEYWORDS: AMBIENT, ATMOSPHERIC CO2, CARBON DIOXIDE, COMPETITION, ECOSYSTEMS, GROWTH, LOLIUM-PERENNE, PHOTOSYNTHETIC ACCLIMATION, SEEDLINGS, TREES

1202
Korner, C. 1997. From alpine grassland to tropical forests: Biological consequences of elevated atmospheric CO2 (a synthesis of Swiss research) - Introduction. *Acta Oecologica-International Journal of Ecology 18(3):163-164.*

KEYWORDS: RESPONSES

1203
Korner, C. 1998. Tropical forests in a Co-2-rich world. *Climatic Change 39(2-3):297-315.*

Tropical forests resemble, besides their enormous genetic diversity, the single largest biomass carbon pool in the world. Only a 'small' annual increase of this pool could trap the current surplus of atmospheric CO2. The fact that this is not happening already today (after the world has seen a 27% increase in atmospheric CO2 in only 150 years) sets the boundaries of the likely trends to be expected in the future. In contrast to the possibly small overall responses of the tropical forest carbon pool, individual plant responses to CO2 enrichment will be significant. Since species and their genotypes will not respond in identical ways, selective processes will be induced which will lead to new community structures and alterations of numerous plant-plant, plant- animal and plant-microbe interactions. Examples are provided for such subtile CO2 effects, measured both in the greenhouse and in the field. From what is known currently it is concluded that in closed humid tropical forests leaf area index is unlikely to increase, mineral nutrient and water demand may (at least temporarily) become reduced, and leaf tissue quality plus associated consumer behavior will be altered. The big unknown is the behavior of tropical soils and their microflora and fauna. There is a realistic possibility that carbon turnover will be increased in tropical forests in a CO2-enriched world, which would have substantial implications for nutrient cycling.

KEYWORDS: CLIMATE CHANGE, ELEVATED CARBON-DIOXIDE, GROWTH-RESPONSES, INCREASING ATMOSPHERIC CO2, LONG-TERM EXPOSURE, MODEL-ECOSYSTEMS, NUTRIENT LIMITATION, PLANT- COMMUNITIES, TREES, WATER-USE

1204
Korner, C., and J.A. Arnone. 1992. Responses to elevated carbon-dioxide in artificial tropical ecosystems. *Science 257(5077):1672-1675.*

Carbon, nutrient, and water balance as well as key plant and soil processes were simultaneously monitored for humid tropical plant communities treated with CO2-enriched atmospheres. Despite vigorous growth, no significant differences in stand biomass (of both the understory and overstory), leaf area index, nitrogen or water consumption, or leaf stomatal behavior were detected between ambient and elevated CO2 treatments. Major responses under elevated CO2 included massive starch accumulation in the tops of canopies, increased fine-root production, and a doubling of CO2 evolution from the soil. Stimulated rhizosphere activity was accompanied by increased loss of soil carbon and increased mineral nutrient leaching. This study points at the inadequacy of scaling-up from physiological baselines to ecosystems without accounting for interactions among components, and it emphasizes the urgent need for whole-system experimental approaches in global-change research.

KEYWORDS: ATMOSPHERIC CO2 CONCENTRATION, COMMUNITIES, COTTON, ENRICHMENT, GROWTH, LONG-TERM EXPOSURE, PHOTOSYNTHETIC ACCLIMATION, SEEDLINGS, TEMPERATURE, TUSSOCK TUNDRA

1205
Korner, C., and M. Diemer. 1994. Evidence that plants from high-altitudes retain their greater photosynthetic efficiency under elevated co2. *Functional Ecology 8(1):58-68.*

1. Herbaceous plant species native to low and high altitudes in the Alps evolved under CO2 partial pressures (P-a) that differ as much as pre-industrial P-a differs from present day P-a at low altitude (e.g. 21% for a 2000-m difference in altitude). 2. In a previous study we showed that the efficiency of CO2 uptake (ECU) in typical high-altitude species is generally greater than in low-altitude species. Here we investigate whether this difference prevails under longer-term exposure to altered P-a. 3. Alpine and lowland species (mainly Ranunculus glacialis/R. acris and Geum reptans/G. rivale) were grown under various CO2 regimes in full daylight growth chambers at their respective natural growth temperature and photoperiod. When they were grown at twice the present CO2 level only moderate downward adjustment of photosynthesis was observed in both groups of species. The adjustments were not enough to compensate for the effect of increased CO2 supply. These trends prevailed under reciprocally exchanged alpine/lowland partial pressure of CO2 at the same total atmospheric pressure. 4. Irrespective of altitudinal origin, greatest downward adjustment of photosynthesis was found in species with the most pronounced accumulation of non-structural carbohydrate and dilution of leaf nitrogen when grown under elevated CO2 (e.g. in G. rivale). 5. These results suggest that, at least initially, the alpine plant species studied may attain relatively greater carbon gains in a CO2-enriched atmosphere than comparable lowland plant species.

1206
Korner, C., M. Diemer, B. Schappi, P. Niklaus, and J. Arnone. 1997. The responses of alpine grassland to four seasons of CO2 enrichment: a synthesis. *Acta Oecologica-International Journal of Ecology 18(3):165-175.*

Alpine grassland at 2 470 m altitude in the Swiss Central Alps was exposed to elevated CO2 by using open top chambers (16 ambient, 16 elevated CO2). Some plots received mineral fertilizer at a rate of N-deposition commonly measured in low altitude parts of Europe. Here we present a summary of results and data from the final harvest. Above-ground biomass measured after the completion of growth in the fourth season of treatment was not affected by CO2 enrichment as was found by previous biometric estimates, but mean below-ground biomass was slightly stimulated (+ 12%, n.s.). In con trast, net CO2 uptake per unit land area was strongly stimulated by CO2 enrichment al the beginning of the experiment, and during the early part of each season. However, the CO2 stimulation decreased during the later part of each growing season. By year four, also mid- season differences in CO2 uptake per unit land area had disappeared. Neither microbial biomass, soil respiration in the laboratory, nor in situ land-area-based CO2 evolution during the 10 week growing season increased under elevated CO2. The total biomass N-pool and free soil nitrate and ammonium (capture by ion exchange resin bags) remained unaffected, whereas leaf nitrogen concentration was reduced and nonstructural carbohydrate concentration increased under elevated CO2 in forbs. These differences in tissue composition largely disappeared during senescence and litter formation. Despite low CO2 responsiveness at ecosystem level, species responses differed in terms of nitrogen, carbohydrates, tillering and flowering, suggesting the possibility for long- term changes in community structure. Addition of NPK equivalent to 40 kg N ha(-1) a(-1) had massive effects on all plant traits studied, but did not enable stimulated growth under CO2 enrichment. However, when fertilizer and CO2 enrichment were provided jointly, soil microbes were stimulated indicating a co-limitation by carbon and nutrients (most likely nitrogen). Since responses to elevated CO2 were absent in both warm and cold growing seasons, we conclude that this late successional plant community is carbon saturated at current atmospheric CO2 concentrations for reasons not directly

related to nutrient supply and climate. Perhaps, contrary to our expectation, evolutionary adjustments of this "old" ecosystem to the life conditions at high altitudes caused carbon to become a surplus resource today.

KEYWORDS: CARBON DIOXIDE, ELEVATED ATMOSPHERIC CO2, FEEDBACK, PLANTS

1207

Korner, C., and F. Miglietta. 1994. Long-term effects of naturally elevated co2 on mediterranean grassland and forest trees. *Oecologia 99(3-4):343-351.*

We investigated the carbon supply status in species-rich mediterranean plant communities growing in a bowl-shaped 1-ha "CO2 spring" area near Sienna, Italy. A geothermic "lime- kiln" has provided these communities, for as long as historical records are available, with pure CO2 that mixes with ambient air at canopy level to daytime means of 500-1000 ppm CO2. Immediately outside the spring area similar plant communities are growing on similar substrate, and in the same climate, but under ca. 355 ppm CO2. We found no evidence that plants in the CO2 spring area grow faster, flower earlier or become larger. However, we found very large differences in tissue quality among the 40 species studied inside and outside the spring area. Depending on weather conditions, the mean concentration of total non-structural carbohydrates (TNC, sugars and starch) in leaves of herbaceous plants was 38-47% higher in the spring area. Fast growing ruderals growing on garden soil inside and outside the spring area show the same response. Among trees, leaves of the deciduous Quercus pubscens contain twice as much TNC inside as outside the vent area, whereas evergreen Q. ilex leaves show no significant difference. TNC levels in branch wood paralleled leaf values. TNC in shade leaves was also higher. Elevated CO2 had no effect on the sugar fraction, therefore differences in TNC are due to starch accumulation. Leaf nitrogen concentration decreases under elevated CO2. These observations suggest that the commonly reported TNC accumulation and N depletion in leaves growing under elevated CO2 are not restricted to the artificial conditions of short-term CO2 enrichment experiments but persist over very long periods. Such an alteration of tissue composition can be expected to occur in other plant communities also if atmospheric CO2 levels continue to rise. Effects on food webs and nutrient cycling are likely.

KEYWORDS: ATMOSPHERIC CO2, CARBOHYDRATE CONTENT, CARBON DIOXIDE, ENRICHMENT, GROWTH, PHOTOSYNTHESIS, RESPIRATION, RESPONSES, SOUR ORANGE TREES, VEGETATION

1208

Korner, C., S. Pelaezriedl, and A.J.E. Vanbel. 1995. Co2 responsiveness of plants - a possible link to phloem loading. *Plant, Cell and Environment 18(5):595-600.*

Of the many responses of plants to elevated CO2, accumulation of total non-structural carbohydrates (TNC in % dry weight) in leaves is one of the most consistent, Insufficient sink activity or transport capacity may explain this obvious disparity between CO2 assimilation and carbohydrate dissipation and structural investment, If transport capacity contributes to the problem, phloem loading may be the crucial step, It has been hypothesized that symplastic phloem loading is less efficient than apoplastic: phloem loading, and hence plant species using the symplastic pathway and growing under high light and good water supply should accumulate more TNC at any given CO2 level, but particularly under elevated CO2. We tested this hypothesis by carrying out CO2 enrichment experiments with 28 plant species known to belong to groups of contrasting phloem loading type. Under current ambient CO2 symplastic loaders were found to accumulate 36% TNC compared with only 19% in apoplastic loaders (P = 0.0016), CO2 enrichment to 600 mu mol mol(-1) increased TNC in both groups by the same absolute amount, bringing the mean TNC level to 41% in symplastic loaders (compared to 25% in apoplastic loaders), which may be close to TNC saturation (coupled with chloroplast malfunction), Eight tree species, ranked as symplastic loaders by their minor vein companion cell configuration, showed TNC responses more similar to those of apoplastic herbaceous loaders, Similar results are obtained when TNC is expressed on a unit leaf area basis, since mean specific leaf areas of groups were not significantly different, We conclude that phloem loading has a surprisingly strong effect on leaf tissue composition, and thus may translate into alterations of food webs and ecosystem functioning, particularly under high CO2.

KEYWORDS: COTTON, ELEVATED CARBON-DIOXIDE, ENRICHMENT, GROWTH, LEAVES, RESPONSES, TEMPERATURE

1209

Korner, C., and M. Wurth. 1996. A simple method for testing leaf responses of tall tropical forest trees to elevated CO2. *Oecologia 107(4):421-425.*

The effects of atmospheric CO2 enrichment on mature trees in their natural environment are largely unknown. Here we present a new, and inexpensive technique which can be used in situ to address some key physiological questions related to the CO2 problem. Small, light-weight cups mounted on the lower side of rigid leaves at the top of tall tropical forest trees were supplied with CO2-enriched air derived from a low-technology air mixing device utilizing forest floor CO2 evolution. We present the scientific rationale for such field experiments, technical details, an assessment of potential cup artifacts and first results illustrating effects of elevated CO2 on stomata and carbohydrate accumulation in the canopies of mature trees.

KEYWORDS: ASSIMILATION, ATMOSPHERIC CARBON-DIOXIDE, BRANCH BAG, ENRICHMENT, GROWTH, PLANT, STOMATAL CONDUCTANCE

1210

Korthals, R.L., S.L. Knight, R.R. Crawford, and L.L. Christianson. 1995. Development and testing of a simple carbon-dioxide enrichment controller for growth chambers. *Transactions of the Asae 38(1):207-211.*

Proportional and proportional plus integral (PI) computer algorithms were implemented with a low cost pulse width modulated injection system to control CO2 in a 7.8 m(3) growth chamber. Experimental studies with plants in the growth chamber showed that average CO2 concentrations over 12 h were within 3 and 1 mu mol mol(-1) of set point for the proportional and PI controllers, respectively. The positive offset in CO2 concentration found for the proportional control was attributed to sampled measurements and pulse width modulated CO2 injection, and discussion was presented on how true errors differ from measured error estimates for pulse width modulated injection with long sampling periods relative to injection periods.

1211

Kostkarick, R., and W.J. Manning. 1993. Radish (raphanus-sativus L) - a model for studying plant- responses to air-pollutants and other environmental stresses. *Environmental Pollution 82(2):107-138.*

The use of Raphanus sativus L. as a model crop for studies on plant response to environmental stresses is reviewed with emphasis on the effects of different atmospheric pollutants (O3, SO2, NO2, acidic precipitation) and their combinations. Responses to temperature, light

supply, water stress, and atmospheric CO2 are also studied and discussed. In addition, the references reviewed are evaluated in terms of their experimental protocols on growth conditions and recommendations for optimal ranges of environmental and cultural variables, i.e. light, temperature, nutrient supply are given. Its distinct pattern of biomass partitioning, the small dimensions along with short and easy culture make radish an excellent experimental plant. The fleshy below-ground storage organ, formed by the hypocotyl and upper radicle, acts as the major sink during vegetative development. Abundant assimilate supply due to elevated levels of CO2 along with high irradiation frequently promote hypocotyl growth more than shoot growth, whereas under conditions of stress shoot growth is maintained at the expense of the hypocotyl. This makes the hypocotyl:shoot ratio of radish a very sensitive and suitable indicator for various environmental stresses. Potential weaknesses and short- comings of radish in its role as a model crop, particularly the high variability of injury and growth responses, are discussed along with possible solutions. Future research needs are derived from the summarized results presented and from some disparities among findings within the literature reviewed.

KEYWORDS: ATMOSPHERIC CO2 ENRICHMENT, CARBON DIOXIDE, FOLIAR INJURY, GROWTH-RESPONSE, NITROGEN-DIOXIDE, SIMULATED ACIDIC RAIN, SULFUR- DIOXIDE MIXTURES, VAR RADICULA-PERS, VEGETABLE PLANTS, WINTER CONDITIONS

1212
Kothavala, Z. 1999. The duration and severity of drought over eastern Australia simulated by a coupled ocean-atmosphere GCM with a transient increase in CO2. *Environmental Modelling & Software 14(4):243-252.*

The combined effects of precipitation and temperature simulated by a coupled ocean-atmosphere General Circulation Model that showed an El Nino-like pattern with a transient increase in CO2, was examined for its effects on drought over eastern Australia. The Palmer Drought Severity Index (PDSI) was applied to determine the duration and severity of drought over a 30- year period due to decreased precipitation over the region. Application of the PDSI, using monthly mean temperature and total monthly precipitation to the final 30 years of the transient CO2 simulation revealed more prolonged and more intense periods of drought under enhanced greenhouse conditions when compared to a similar time span of the present-day simulation.

KEYWORDS: CIRCULATION, CLIMATE CHANGE, EUROPE, FLOODS, INDEX, MODEL, PRECIPITATION, SPATIAL VARIABILITY

1213
Kottke, I. 1997. Fungal adhesion pad formation and penetration of root cuticle in early stage mycorrhizas of Picea abies and Laccaria amethystea. *Protoplasma 196(1-2):55-64.*

Primary events during the establishment of the fungus-root symbiosis in ectomycorrhizas are still little understood. No attention has been paid so far to the adhesion of hyphae to the root cuticle and penetration of this barrier, although the importance of the cuticle has been shown for pathogen-plant interactions. Early developmental stages of in vitro mycorrhization of Laccaria amethystea on Picea abies after short periods of incubation in growth chambers under elevated CO2 concentrations were studied by light and transmission electron microscopy. No structural changes in mycorrhization related to elevated CO2 were found, but fine roots and mycorrhizas developed faster. Adhesion pad formation was observed at hyphal tips in contact with the root cuticle. The adhesion pad was connected to the outer cell wall layer of the hypha and reacted positively to the Swift reaction for cysteine rich proteins. Although the reaction cannot be considered as totally specific, findings are discussed in respect to hydrophobins, which have recently been found to be expressed during early steps in ectomycorrhizal development. The root cuticle was dissolved and penetrated by fungal tips of the fingerlike branching mycelium attached to the root surface. The findings are compared with well documented pathogenic fungus-plant interactions at the cuticle. The possibility of restriction of hyphal attack to that part of the cuticle covering cell junctions is discussed.

KEYWORDS: A-BINDING SITES, ATTACHMENT, CUTINASE, ECTOMYCORRHIZAS, HARTIG NET, NECTRIA-HAEMATOCOCCA, PHENOLICS, PISOLITHUS-TINCTORIUS, SPORES, SURFACE

1214
Kozai, T., K. Iwabuchi, K. Watanabe, and I. Watanabe. 1991. Photoautotrophic and photomixotrophic growth of strawberry plantlets invitro and changes in nutrient composition of the medium. *Plant Cell Tissue and Organ Culture 25(2):107-115.*

Explants excised from strawberry (Fragaria x ananassa Duch.) plantlets were cultured in vitro for 21 days on half-strength MS (Murashige & Skoog 1962) basal liquid medium with 20 g l-1 sucrose and without sugar in the vessels capped with gas permeable microporous polypropylene film. The experiments were conducted under CO2 nonenriched (350-450-mu-mol mol-1 in the culture room) and CO2 enriched (2,000-mu-mol mol-1 during the photoperiod in the culture room) conditions with a PPF (photosynthetic photon flux) of 200-mu-mol m-2 s-1. The CO2 concentration in the vessels decreased to approximately 200-mu- mol mol-1 during the photoperiod on day 21 under CO2 nonenriched conditions. The fresh and dry weight, net photosynthetic rate (NPR) per plantlet, NPR per g leaf fresh weight, NPR per g leaf dry weight, the number of unfolded leaves, and ion uptake of PO4(3-), NO3-, Ca2+, Mg2+ and K+ on day 21 were the greatest under photoautotrophic (no sugar in the medium) and CO2 enriched conditions. The residual percent of PO4(3-) was 3% on day 21 under photoautotrophic and CO2 enriched conditions.

KEYWORDS: CULTURES, ENRICHMENT

1215
Kozai, T., C. Kubota, and B.R. Jeong. 1997. Environmental control for the large-scale production of plants through in vitro techniques. *Plant Cell Tissue and Organ Culture 51(1):49-56.*

Leafy or chlorophyllous explants of a number of plant species currently micropropagated have been found to have high photosynthetic ability. Their growth and development have been promoted on sugar-free medium rather than on sugar-containing medium, provided that the environmental factors, such as CO2 concentration, light intensity and relative humidity, are controlled for promoting photosynthesis and transpiration of explants/shoots/plantlets in. vitro. Thus, environmental control is essential for promoting photosynthetic growth and development of in vitro plantlets. Several types of sugar-free (photoautotrophic) culture systems for large-scale micropropagation of plants have been developed. Advantages of sugar-free over conventional (heterotrophic or photomixotrophic) micropropagation systems are as follows: growth and development of plantlets in vitro are faster and more uniform, plantlets in vitro have less physiological and morphological disorders, biological contamination in vitro is less, plantlets have a higher percentage of survival during acclimatization ex vitro, and larger culture vessels could be used because of less biological contamination. Hence, production costs could be reduced and plant quality could be improved significantly with photoautotrophic micropropagation. Methods for the measurement and control of in vitro environments and the beneficial effects of environmental control on photosynthetic growth, development, and morphogenesis in large-scale production of

micropropagated plantlets are presented.

KEYWORDS: CO2- ENRICHMENT, CULTURE VESSEL, ELONGATION, INVITRO, LIGHT, PHOTOAUTOTROPHIC GROWTH, PHOTOSYNTHETIC CHARACTERISTICS, REGENERANTS, TRANSPLANTS

1216

Kozai, T., S. Kushihashi, C. Kubota, and K. Fujiwara. 1992. Effect of the difference between photoperiod and dark period temperatures, and photosynthetic photon flux-density on the shoot length and growth of potato plantlets invitro. *Journal of the Japanese Society for Horticultural Science 61(1):93-98.*

Potato plantlets (Solanum tuberosum L. cv. Benimaru) under CO2 enriched and photoautotrophic culture conditions were subjected to three different photo-/dark period temperature combinations (25-degrees/15-degrees-C, 200/20-degrees-C and 15-degrees/25- degrees-C) and two levels of photosynthetic photon flux densities (74 and 147-mu-mol.m-2.sec-1). The shoot length of the plantlets under the same photosytnthetic photon flux density (PPF) was reduced with decreasing the difference between photoperiod and dark period temperatures (it is named DIF, photoperiod temperature minus dark period temperature). No marked differences in the fresh and dry weights per plantlet were observed among the three DIF treatments in each PPF treatment. The higher PPF led to a decrease in the shoot length, an increase in the fresh weight, dry weight and leaf area per plantlet in each DIF treatment. It is suggested that shoot length of plantlets in vitro under CO2 enriched and photoautotrophic culture conditions can be controlled without reducing the weight increments and leaf area per plantlet by regulating the difference between photoperiod and dark period temperatures.

1217

Kozai, T., K. Watanabe, and B.R. Jeong. 1995. Stem elongation and growth of solanum-tuberosum L in-vitro in response to photosynthetic photon flux, photoperiod and difference in photoperiod and dark period temperatures. *Scientia Horticulturae 64(1-2):1-9.*

Stem elongation and growth of potato plantlets under three DIF (difference in photoperiod and dark period temperatures) levels, -9, 0 and +9, combined with two PPF (photosynthetic photon flux) levels, 70 (low) and 140 (high) mu mol m(-2) s(-1) provided by white cool fluorescent lamps, under 16 h day(-1) (long) or 8 h day(-1) (short) photoperiods, were studied. Four nodal cuttings were cultured for 21 days on 0.6 X 10(-4) m(3) MS (Murashige and Skoog, 1962, Physiol. Plant., 15: 473-497) agar (8 kg m(-3)) medium with no added sugar in 3.7 X 10(-3) m(3) polycarbonate boxes. Each box had two 10 mm holes covered with microporous filter to facilitate air exchange (3.6 air exchanges per hour). The average daily temperature in the culture room was set the same at 23 degrees C for all treatments, and CO2 concentration and relative humidity were maintained at 400-500 mu mol mol(-1) and 50-70%, respectively. Stem length was significantly suppressed under 0 or -9 DIF, high PPF and long photoperiod. Stem diameter, leaf area and number of leaves were significantly enhanced by long photoperiod and high PPF, but affected little by DIF level. Specific leaf area was little affected by photoperiod, but decreased under high PPF and under low DIF. Long photoperiod and high PPF led to an increase in the fresh and dry weights maintaining similar percentage dry matter and to enhanced root growth. Under the same amount of integrated PPF, fresh and dry weights of leaf, stem, root and whole plantlet were significantly higher under the long photoperiod and low PPF conditions than under the short photoperiod and high PPF conditions. Because of suppressed root growth under short photoperiod, shoot to root dry weight ratio increased under short photoperiod, but was not affected by DIF. It is suggested that under photoautotrophic conditions a combination of high PPF level, long photoperiod, and zero or negative DIF produces potato plantlets in vitro of short and thick stem with similar number and increased area of leaves, which are desirable for transfer to ex vitro conditions.

KEYWORDS: ALTERNATIONS, CAMPANULA-ISOPHYLLA MORETTI, INITIAL GROWTH, INVITRO, LIGHT-QUALITY, MORPHOLOGY, NIGHT TEMPERATURE, SEEDLINGS

1218

Kramer, G.F., E.H. Lee, R.A. Rowland, and C.L. Mulchi. 1991. Effects of elevated CO2 concentration on the polyamine levels of field-grown soybean at 3 O3 regimes. *Environmental Pollution 73(2):137-152.*

Effects of increased ozone (O3) and carbon dioxide (CO2) on polyamine levels were determined in soybean (Glycine max L. Merr. cv. Clark) grown in open-top field chambers. The chamber treatments consisted of three O3 regimes equal to charcoal filtered (CF), non-filtered (NF), and non-filtered plus 40 nl litre-1 O3 and CO2 treatments equal to 350, 400 and 500-mu-l litre-1 for a total of nine treatments. Leaf samples were taken at three different times during the growing season. Examination of growth and physiological characteristics, such as photosynthesis, stomatal resistance, and shoot weight, revealed that increasing CO2 ameliorated the deleterious effects of increased O3. Results from the initial harvest, at the pre-flowering growth stage (23 days of treatment), showed that increasing O3 at ambient CO2 caused increases in putrescine (Put) and spermidine (Spd) of up to six-fold. These effects were lessened with increased CO2. Elevated CO2 increased polyamines in plants treated with CF air, but had no effect in the presence of ambient or enhanced O3 levels. Leaves harvested during peak flowering (37 days of treatment) showed O3-induced increases in Put and Spd at ambient CO2 concentrations. However, increased CO2 levels inhibited this response by blocking the O3-induced polyamine increase. Leaves harvested during the pod fill stage (57 days of treatment) showed no significant O3 or CO2 effects on polyamine levels. Our results demonstrate that current ambient O3 levels induce the accumulation of Put and Spd early in the growing season and that further increases in O3 could result in even greater polyamine increases. These results are consistent with a possible antiozonant function for polyamines. The ability of increased CO2 to protect soybeans from O3 damage, however, does not appear to involve polyamine accumulation.

KEYWORDS: AIR- POLLUTANTS, ASCORBIC-ACID, INHIBITION, LEAF, LEAVES, NET PHOTOSYNTHESIS, OZONE, PLANTS, STRESS, ZUCCHINI SQUASH

1219

Kramer, K., A. Friend, and I. Leinonen. 1996. Modelling comparison to evaluate the importance of phenology and spring frost damage for the effects of climate change on growth of mixed temperate-zone deciduous forests. *Climate Research 7(1):31-41.*

The importance of 3 phenological types of deciduous tree, and the effects of the occurrence of frost damage on growth of mixed-species forests, were evaluated using the models FORGRO and HYBRID, The climate change scenarios used were a doubling of the CO2 concentration (700 mu mol mol(-1)) and an increase in temperature ranging from 0 to 7 degrees C. Both FORGRO and HYBRID are mechanistic models treating eco-physiological processes in detail. FORGRO highlights potential growth in managed forests where all individuals of one species are of the same age and size, whereas HYBRID highlights growth in natural forests, including regeneration and mortality of individual trees that differ in age and size. Furthermore, the importance of inaccurate prediction of phenological events and frost hardiness for growth in mixed-species stands was evaluated by comparing dynamic models to

regression models. The dynamic models predict the timing of phenological events annually and the progression of frost hardiness during dormancy, whereas the regression models represent empirical relationships between the change in the average date of phenological events with a rise in mean winter temperature and the level of frost hardiness at the moment of leaf unfolding. The results of the climate change scenarios indicate for both FORGRO and HYBRID that: (1) the differences in net primary production (NPP) of the 3 phenological types considered are enhanced when grown in a mixed-species stand compared to a monospecies stand; and (2) the effects of frost damage on growth are more prominent in mixed-species stands than in monospecies stands. Regarding the accuracy of the dynamic approach compared to the regression approach for predicting the timing of leaf unfolding and spring frost damage, the dynamic approach for leaf unfolding results in a similar response of NPP to the regression approach, both for the monospecies and the mixed-species situation. The dynamic approach, however, yields larger differences in the NPP between the phenological types because the model predicts a greater advancement of leaf unfolding than does the regression approach. Comparing the regression approach to the dynamic approach with regard to frost hardiness, the regression approach shows a greater frequency of frost damage; because, according to the dynamic approach the minimum level of frost hardiness is attained after the date of leaf unfolding, thus reducing this frequency.

KEYWORDS: PHOTOSYNTHESIS, TRANSPIRATION, TREES

1220

Kramer, K., and G.M.J. Mohren. 1996. Sensitivity of FORGRO to climatic change scenarios: A case study on Betula pubescens, Fagus sylvatica and Quercus robur in the Netherlands. *Climatic Change 34(2):231-237.*

The impacts of the climate change predictions of four general circulation models (GFDL, GISS, OSU and UKMO) on net primary production (NPP) of Betula pubescens, Fagus sylvatica and Quercus robur in The Netherlands were analysed using the process-based model FORGRO. FORGRO is a model suitable to simulate growth of managed mono-species stands. For the GCMs mentioned, both transient and equilibrium 2 x CO2 scenarios of temperature and precipitation change were evaluated and compared with responses under current climate. It was found that the NPP increases in the transient scenarios, but remains the same or declines in the 2 x CO2 scenarios. This is because respiration increases more with rising temperature than photosynthesis. During the transient scenarios this effect gradually increases, while in the 2 x CO2 scenario this effect is operating over the entire simulation period. If water limitation is taken into account, then the NPP of the reference scenario is reduced. In both the transient and 2 x CO2 scenarios this water limitation is annulated, resulting in a stronger response of NPP compared to the situation without water limitation. This enhancement of the response is most pronounced in the transient scenario due to the gradual effect of temperature on respiration. Similar results were obtained with a version of FORGRO in which the photosynthesis module of HYBRID (PGEN) is incorporated, although the response in FORGRO- PGEN is usually higher than that of FORGRO. This is because the response of photosynthesis to CO2 rises with increasing temperature as defined in the PGEN-model, but not according to FORGRO.

KEYWORDS: CONDUCTANCE, GROWTH, MODEL, PHOTOSYNTHESIS, PREDICT

1221

Krapfenbauer, A., and K. Wriessnig. 1995. Anthropogenic environmental-pollution - the share of agriculture. *Bodenkultur 46(3):269-283.*

The increase of environmental pollution is in direct relation to the consumption of fossil coal, gas and oil and the progressive growth of the world population. Since 1950 these issues increased considerably and they will continue to increase in the future. At the moment the population increases by 1.9 %, the consumption of energy between 2 and 3 % and the environmental pollution up to 3.5 % annually. With the progressive growth of the world population and the increase in prosperity in the developed countries the demand for food increased also progressively and therewith the productivity index of the units of arable land, by growing consumption of fertilizers and the installation of irrigation systems. At the same time the pollution of air, water and soil caused by agriculture also grew progressively. But up to date there is still a shortcoming of reliable statistical facts and figures. A higher productivity index of the units of arable land in the different ecoclimatic zones of the earth leads to higher production and consumption by an inevitably higher turnover of plant nutrients and diverse gaseous substances, for example carbon mono- and dioxide, diverse compounds of nitrogen etc. At the same time an excess of the "critical loads" for soil, air and water must be expected. The main items of the emissions produced by an intensified agriculture are, besides carbon mono- and dioxide, methane, nitric and nitrous oxide, ammonia and diverse hydrocarbons. A higher productivity index is consequently related to a higher consumption. This also leads to an intensified turnover of carbon dioxide. There is consequently a progressive input of carbon dioxide resulting from the emissions of burning fossil fuel in the recently produced and consumed biomass. This inevitably leads to a higher level of carbon dioxide in the air. A main source of emissions of methane and ammonia is animal breeding. In Austria at this time from each of the 3,508.000 hectars of land used by agriculture annual emissions of 63 kg methane and 11 kg ammonia are resulting theoretically. The use of organic and inorganic fertilizers, the growing cultivation of legumes and the emissions of nitrogen compounds resulting from burning processes elevate likewise the pool and the annual turnover of nitrogen compounds by production and consumption of biomass. Inevitably related to it is a growing amount of the annual input of nitrogen compounds to the air, the soil and the water. A rough approximation says that at present agriculture contributes to the global anthropogenic pollution of the environment (air, soil and water) 85 % of the ammonia, 81 % of the nitrous oxide, 35 % of nitric mono- and dioxide, 70 % of the methane, 52 % of the carbon monoxide and 21 % of the carbon dioxide. Not considered in the figure for carbon dioxide is the inevitable increase of the level of CO2 in the air by the elevated turnover of biomass. The world population growth in the future leads to an increasing contribution of agriculture to the anthropogenic environmental pollution. For the developed countries this is an obligatory challenge to avoid surplus production. On a global scale there must be a sensible reduction of animal breeding to reduce the high emissions of methane and ammonia from this sector of agriculture. It must also be considered, that by feeding animals with vegetable food stuff, which also could be used for direct nutrition of man, the efficiency of it is lowered by a factor of 1:10. In spite of a growing crisis to maintain the alimentation of the growing world population in many countries the nutrition of man must rapidly be centered on vegetable food stuff rich in protein. At the same time an essential reduction of the environmental pollution resulting from animal breeding could be realized. Beside of it and other reducing issues a continuous growth of the world population, the energy consumption and environmental pollution will make it necessary to observe the development and reactions in the environment by monitoring and phenological observations. The results must be used to counteract finally by looking for adaptation strategies. Considering the realities it must be realized that by all means to mobilize for counteracting the environmental pollution directly, a certain climate change will be inevitable. The consequences will also be an outstanding challenge for the agriculture.

Krapp, A., B. Hofmann, C. Schafer, and M. Stitt. 1993. Regulation of the expression of rbcs and other photosynthetic genes by carbohydrates - a mechanism for the sink regulation of photosynthesis. *Plant Journal 3(6):817-828.*

These experiments were carried out to investigate whether accumulation of carbohydrate leads to decreased expression of genes involved in photosynthesis. Addition of glucose to autotrophic cell suspension cultures of Chenopodium led to a large and reversible decrease of the steady state transcript levels of rbcS, cab and atp-delta within 5 h, but did not decrease 18S rRNA or transcript for two glycolytic enzymes. Run-on transcription in isolated nuclei showed that transcription rate had been decreased. [S-35]Methionine feeding showed that de novo synthesis of Rubisco was inhibited. Decreased rbcS transcript was also found after feeding glucose to detached leaves, and in transgenic plants expressing invertase in the apoplast to inhibit phloem transport, and in leaves on intact tobacco and potato plants which were cold- girdled to decrease export. The decrease of rbcS transcript level occurred within 12 h of cold-girdling. Comparison of carbohydrate content and rbcS transcript level indicated that carbohydrate content per se is not the direct signal for regulation of gene expression. Feeding of transported analogues indicates that metabolism rather than transport of the sugars is required. Over-expression of rbcS was found in low CO2, again indicating metabolic control of expression. ft is proposed that photosynthetic gene expression is inhibited by metabolic factors related to high carbohydrate content, and that this represents a basic mechanism for the 'sink regulation' of photosynthesis.

KEYWORDS: ACCLIMATION, CALVIN CYCLE ENZYMES, CELL-WALL, ELEVATED CO2, INHIBITION, LEAVES, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, STARCH, SUCROSE SYNTHESIS, TRANSGENIC TOBACCO PLANTS

1223

Krapp, A., and M. Stitt. 1995. An evaluation of direct and indirect mechanisms for the sink- regulation of photosynthesis in spinach - changes in gas- exchange, carbohydrates, metabolites, enzyme-activities and steady-state transcript levels after cold-girdling source leaves. *Planta 195(3):313-323.*

Mature source leaves of spinach (Spinacia oleracea L.) plants growing hydroponically in a 9 h light (350 mu mol photons.m(- 2).s(-1))/15 h dark cycle at 20 degrees C in a climate chamber were fitted with a cold girdle around the petiole, 2 h into the light period. Samples were taken 1, 3 and 7 h later, and at the end of the photoperiod for the following 4 d. Control samples were taken from ungirdled leaves. in the first 7 h after fitting the cold girdle there was (compared to the control leaves) a two to fivefold accumulation of sucrose, glucose, fructose and starch, a 40-50% increase of hexose-phosphates and ribulose-1,5-bisphosphate, a decrease of glycerate-3-phosphate, a small decrease in sucrose-phosphate synthase activation, an increase of fructose-2,6-bisphosphate, increased activation of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco), but no significant change in photosynthetic rate or stomatal conductance. Steady-state transcript levels for rbcS (small subunit of Rubisco) and atp-D (D-subunit of the thylakoid ATP synthase) decreased 30%, cab (chlorophyll-a-binding protein) decreased by 15% and agp-S (S-isoenzyme of ADP-glucose pyrophosphorylase) and nra (nitrate reductase) rose twofold. On the following days, levels of carbohydrates continued to rise and the changes of metabolites were maintained. Transcripts for rbcS, cab and atpD declined to 20, 70 and 25% of the control values. From day 3 onward the maximum activity of Rubisco declined. This was accompanied by a further increase of Rubisco activation to over 90% and, from day 4 onwards, an inhibition of photosynthesis which was associated with high internal CO2 concentration (c(i)), high ribulose-1,5-bisphosphate, and low glycerate-3-phosphate. When the cold-girdle was removed on day 5 there was a gradual recovery of photosynthesis and decline of c(i) over the next 2 d. Hexose-phosphates levels and transcripts for rbcS, cab and atp-D completely recovered within 2 d, even though the levels of carbohydrates had not fully recovered. Activity of Rubisco only reverted partly after 2 d, and Rubisco activation state and the ribulose-1,5-bisphosphate/glycerate-3-phosphate ratio were still higher than in control leaves. Transcripts for nra and agp-S were also still higher than in control leaves. It is concluded (i) that a reversible modulation of gene expression in response to the export rate plays a central role in the mid-term feedback "sink" regulation of photosynthesis, and (ii) that feedback regulation of CO2 fixation by changes of P-i are of little importance in spinach under these conditions. Further (iii) the rapid and reciprocal changes in nra and agpS transcripts, compared to rbcS, provide evidence that gene expression could also contribute to the modulation of nitrate assimilation and carbohydrate storage in conditions of decreased sink demand.

KEYWORDS: ADP-GLUCOSE PYROPHOSPHORYLASE, CALVIN CYCLE ENZYMES, CHLOROPHYLL CONTENT, ELEVATED CO2, LIGHT ACTIVATION, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, SUCROSE PHOSPHATE SYNTHASE, TRANSGENIC TOBACCO PLANTS, YEAST- DERIVED INVERTASE

1224

Krauchi, N. 1993. Potential impacts of a climate change on forest ecosystems. *European Journal of Forest Pathology 23(1):28-50.*

Review of literature indicates that many uncertainties and assumptions exist in predicting the impacts of a climate change on forest ecosystems. However, current knowledge is sufficient to encourage any measures that are combating climate change, that is to reduce first and foremost the release of harmful substances to the atmosphere, lithosphere and biosphere.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, ELEVATED CO2, ENRICHMENT, GREENHOUSE, INCREASE, RADIATION BUDGET, RESPONSES, SENSITIVITY, TREES, VEGETATION

1225

Kriebitzsch, W.U., M. Liesebach, and F. Scholz. 1999. The influence of elevated CO2 on growth parameters of various provenances of European beech (Fagus sylvatica L.) at different irradiance. *Forstwissenschaftliches Centralblatt 118(1):51-65.*

In a greenhouse experiment one year old seedlings of seven provenances of beech (Fagus sylvatica L.) were grown under controlled conditions at two CO2 levels (350 ppm and 650 ppm) and different light intensities (2%, 17% and 100% relative irradiance). The response of the plants eo the various treatments was investigated by means of the leaf development during the growing season. At the end of the vegetation period leaf area and leaf dry weight per single leaf and per plant were measured. At the beginning of the growing period the provenances differed significantly in height and at the end of the vegetation period also in the mean leaf number, leaf area and leaf dry weight per plant. The area per single leaf is - in contrast to leaf dry weight and the specific leaf area - similar among all seven provenances. The light has an effect on all measured leaf parameters. In full light the leaf development started very early. Leaf number, leaf area, and leaf dry weight per single leaf and per plant decrease and specific leaf area increases under low light conditions. In the treatment "elevated CO2 environment and full irradiance" leaf number, leaf area and leaf dry weight per single leaf and per plant increased too. At reduced irradiance a higher CO2 content does not influence the measured leaf parameters. The results show already at this early stage that the climatic factors influencing plant growth and elevated CO2 interact strongly. For an overall view of the plants' reaction to growth conditions, investigations of the gas exchange of the leaves

and anatomical and morphological studies will be added.

KEYWORDS: ATMOSPHERIC CO2, AVAILABILITY, CARBON DIOXIDE, ENRICHMENT, GAS-EXCHANGE, LEAF ANATOMY, LIGHT, RESPONSES, SEEDLINGS, TREES

1226

Kriebitzsch, W.U., M. Liesebach, and F. Scholz. 1999. Interactions between CO2 content and light on growth parameters of various provenances of beech (Fagus sylvatica L.). *Berichte Uber Landwirtschaft 77(1):65-76.*

In a greenhouse experiment one year old seedlings of seven provenances of beech (Fagus sylvatica L.) were grown under controlled conditions at two CO2 levels (350 ppm and 650 ppm) and different light intensities (2%, 17% and 100% relative irradiance). The response of the plants to the various treatments was investigated by means of the leaf development during the growing season. At the end of the vegetation period leaf area and leaf dry weight per single leaf and per plant were measured. At the beginning of the growing period the provenances differed significantly in the mean leaf number, leaf area and leaf dry weight per plant. The area per single leaf is - in Contrast to leaf dry weight and the specific leaf area - similar among all seven provenances. The light has an effect on all measured leaf parameters. In full light the leaf development started very early. Leaf number, leaf area, and leaf dry weight per single leaf and per plant decrease and specific leaf area increases under low light conditions. In the treatment "elevated CO2 environment and full irradiance" leaf number, leaf area and leaf dry weight per single leaf and per plant increased too. At reduced irradiance a higher CO2 content does not influence the measured leaf parameters. The results show already at this early stage that genetic variation is important and the climatic factors influencing plant growth and elevated CO2 interact strongly. For an overall view of the plants' reaction to growth conditions, investigations of the gas exchange of the leaves and anatomical and morphological studies will be added.

KEYWORDS: AMBIENT, AVAILABILITY, ELEVATED CARBON-DIOXIDE, ENRICHMENT, FOREST, NUTRIENTS, RESPONSES, SEEDLINGS, TREES

1227

Krishnan, P., and G. Ramakrishnayya. 1999. Survival of rice during complete submergence: effect of potassium bicarbonate application. *Australian Journal of Plant Physiology 26(8):793-800.*

The effect of potassium bicarbonate application to floodwater on the survival and growth of submergence-tolerant (FR13A) and -intolerant (IR42) rice cultivars during complete submergence was investigated. Potassium bicarbonate, applied at different rates to enhance floodwater carbon dioxide concentrations, increased the floodwater oxygen concentration. The treatment that had CuSO4, added alone to reduce algal growth showed the lowest O-2 concentration at the time of submergence and after 10 d of submergence. Potassium bicarbonate at higher rates tended to maintain the floodwater pH near neutrality while copper sulfate affected pH increase during a 10-day period of complete submergence. Potassium bicarbonate addition led to 100% survival of tolerant FR13A. Potassium bicarbonate, even at 0.01 mol m(-3) enhanced the survival of intolerant IR42 to 69% and at 0.1, 0.5 and 1.0 mol m(-3), the survival was above 85%. Dry weights of submerged plants showed increases in both rice cultivars in floodwater treated with potassium bicarbonate. The dry weight and leaf chlorophyll concentration of both cultivars increased with increasing rates of potassium bicarbonate. Algal chlorophyll concentration of floodwater treated with potassium bicarbonate was comparable to that of the control without copper sulfate. The findings suggest a possibility of environmental manipulation of floodwater by potassium bicarbonate application to enhance the survival and growth of rice cultivars during complete submergence.

KEYWORDS: CO2, FLOODWATER, GROWTH, TOLERANCE

1228

Kronfuss, G., A. Polle, M. Tausz, W.M. Havranek, and G. Wieser. 1998. Effects of ozone and mild drought stress on gas exchange, antioxidants and chloroplast pigments in current-year needles of young Norway spruce [Picea abies (L.) Karst.]. *Trees-Structure and Function 12(8):482-489.*

To investigate the effects of ozone exposure and soil drought, singly and in combination, on gas-exchange, antioxidant contents and pigments in current-year needles of Norway spruce [Picea abies (L.) Karst.] 4-year-old seedlings were fumigated in growth chambers with either charcoal-filtered air or with 100 nl l(-1) ozone for 106 days. After 3 weeks a 20% reduction in gas exchange was observed In ozone-treated seedlings. However, no further decrease occurred in spite of continued ozone exposure. Whole needle ascorbate and apoplastic ascorbate increased until the end of the experiment and contents were 62% and 82%, respectively, higher than in ozone-free controls. This increase in ascorbate might have protected net photosynthesis from Further decline. Ozone pre-treated plants and ozone-free controls were subjected to soil drought for 38 days which caused stomatal narrowing. Thereby ozone uptake was reduced when compared to well watered seedlings. At the end of the experiment drought alone, and even more in combination with ozone, had also caused an increase in ascorbate. Glutathione increased only in drought-stressed seedlings. The redox states of the ascorbate and the glutathione pools were not affected by any treatment. Superoxide dismutase activity declined under both stresses but was most reduced by ozone alone. While chlorophyll and neoxanthin contents remained unchanged, carotenes were significantly decreased upon drought. The combination of O-3 and drought induced increased lutein contents, an increased pool size of the xanthophyll cycle as well as an increased epoxidation status of the xanthophyll cycle. These results suggest that spruce needles seem To be able to acclimate to ozone stress but also to drought stress by increasing their ascorbate pools and protecting pigments.

KEYWORDS: ELEVATED CO2, ENHANCED OZONE, EXPOSURE, FAGUS-SYLVATICA L, GROWTH-RESPONSES, LARIX-DECIDUA MILL, PHOTOSYNTHESIS, RED SPRUCE, SEEDLINGS, WATER DEFICIT

1229

Krug, H., and H.P. Liebig. 1995. Models for planning and control of transplant production in climate controlled greenhouses .2. Production control. *Gartenbauwissenschaft 60(1):22-28.*

A model has been developed to control transplant growth. It is based on growth curves, derived under varied greenhouse climates (global irradiances, artificial light, air and soil heating, CO2-concentration), and corresponding growth rates, which were related to the intensities of the climatic factors by a regression function. The best fit for the growth rates was obtained by splitting the raising period in an exponential phase, described by a constant Relative Growth Rate, and a linear phase, described by the Mean Growth Rate. As the frequency distribution shows, 81% of the 186 sets from October to March hit the 4 +/- 0.2 g data of the growth function in +/- 2 days. Simulations for the most extremes out of 36 years weather conditions for 5 dates from October to February show the deviations from the estimated curves based on long term normals, the potentials of climate control by decreasing or increasing set points of air temperature, CO2 concentration, and artificial light as well as the effects of the starting point for control. Aspects of application and completion as well as the necessity of timing

by CO2 enrichment and artificial lighting are discussed.

1230
Kruger, E.L., J.C. Volin, and R.L. Lindroth. 1998. Influences of atmospheric CO2 enrichment on the responses of sugar maple and trembling aspen to defoliation. *New Phytologist 140(1):85-94.*

Impacts of defoliation on the growth and physiology of sugar maple (Acev saccharum Marsh.) and trembling aspen (Populus tremuloides Michx.) were examined in ambient and CO2-enriched atmospheres. Saplings were grown for 70 d in controlled environments, wherein CO2 mole fractions averaged either 356 mu mol mol(-1) or 645 mu mol mol(-1), under a PPF of 500 mu mol m(-2) s(-1). On day 49 of the study, 50 % of the leaf area was removed from a subset of each species in both CO2 environments. Relative growth rate (RGR) and its physiological and morphological determinants were monitored before and after defoliation. For non-defoliated saplings of both species, a slight stimulation of RGR (c. 5 %) in elevated CO2 led to a modest increase (9-11 %) in final sapling weight. In the case of maple, the minimal growth response corresponded with minor CO2 effects on specific leaf area (SLA) and leaf weight ratio (LWR), and an apparent CO2-induced down-regulation of photosynthetic metabolism. For aspen, the CO2 stimulation of photosynthesis was largely offset by a decrease in SLA. Responses to defoliation differed markedly between species and CO2 environments. Defoliation decreased maple RGR in ambient CO2, whereas the opposite occurred in elevated CO2. The latter led to complete recovery of plant weight (compensation), and was attributed to a defoliation-induced increase in carbon allocation to new leaves, along with a reversal of photosynthetic CO2 acclimation in that foliage. In both environments, aspen RGR increased after defoliation, facilitating almost full compensation. Defoliation increased light penetration into the aspen canopy, and it was estimated that the resultant stimulation of photosynthesis in lower leaves would have more than offset the concomitant decrease in LWR. CO2 enrichment might substantially enhance the ability of certain tree species to recover from herbivory. Moreover, responses to elevated CO2 might be largest in the presence of stresses, such as herbivory, that decrease plant source:sink ratios.

KEYWORDS: CARBON DIOXIDE, DECIDUOUS TREES, ELEVATED CO2, GAS-EXCHANGE, INSECT PERFORMANCE, NO3 AVAILABILITY, PHOTOSYNTHETIC ACCLIMATION, PLANTS, RELATIVE GROWTH-RATE, SEEDLINGS

1231
Kruijt, B., C. Barton, A. Rey, and P.G. Jarvis. 1999. The sensitivity of stand-scale photosynthesis and transpiration to changes in atmospheric CO2 concentration and climate. *Hydrology and Earth System Sciences 3(1):55-69.*

The 3-dimensional forest model MAESTRO was used to simulate daily and annual photosynthesis and transpiration fluxes of forest stands and the sensitivity of these flutes to potential changes in atmospheric CO2 concentration ([CO2]), temperature, water stress and phenology. The effects of possible feed-backs from increased leaf area and limitations to leaf nutrition were simulated by imposing changes in leaf area and nitrogen content. Two different tree species were considered: Picea sitchensis (Bong.) Carr., a conifer with long needle longevity and large leaf area, and Betula pendula Roth., a broad-leaved deciduous species with an open canopy and small leaf area. Canopy photosynthetic production in trees was predicted to increase with atmospheric [CO2] and length of the growing season and to decrease with increased water stress. Associated increases in leaf area increased production further only in the B. pendula canopy, where the original leaf area was relatively small. Assumed limitations in N uptake affected B. pendula more than P. sitchensis. The effect of increased temperature was shown to depend on leaf area and nitrogen content. The different sensitivities of the two species were related to their very different canopy structure. increased [CO2] reduced transpiration, but larger leaf area, early leaf growth, and higher temperature all led to increased water use. These effects were limited by feedbacks from soil water stress. The simulations suggest that, with the projected climate change, there is some increase in stand annual 'water use efficiency', but that actual water losses to the atmosphere may not always decrease.

KEYWORDS: ELEVATED CO2, ENRICHMENT, FOREST ECOSYSTEMS, GAS-EXCHANGE, GROWTH-RESPONSE, LEAF, MODEL, PLANT GROWTH, SPRUCE PICEA-SITCHENSIS, TEMPERATURE

1232
Krupa, S.V. 1997. Global climate change: Processes and products - An overview. *Environmental Monitoring and Assessment 46(1-2):73-88.*

Our knowledge of global climate change has many uncertainties. Whether global air temperature will increase, by how much, and when, are subject to debate, but there is little doubt that tropospheric concentrations of several trace gases are increasing. While possible increases in the average air temperature is a product of these changes, the increases in the trace gases alone will have an effect on agriculture. Increases in the ambient concentrations of carbon dioxide are expected to have a positive net effect on crop production. In contrast, any increases in the penetration of surface-level ultraviolet-B (280-320 nm) radiation, and known increases in surface ozone concentrations, are considered to have adverse effects on certain crops. Our present knowledge of the joint effects on crops of elevated levels of carbon dioxide, ultraviolet-B radiation and ozone, and possible alterations in air temperature and precipitation patterns, is virtually zero. Therefore, any predictions of the effects of global climate change on agriculture are subject to significant uncertainties. In contrast, coupling of climate change (only temperature and precipitation) models to crop production has led to a number of future scenarios. In spite of their present limitations, results from these efforts can be useful in planning for future agriculture.

KEYWORDS: CO2, DEPLETION, EXPOSURES, RESPONSES, SOLAR ULTRAVIOLET-RADIATION, STRATOSPHERIC OZONE, SURFACE, TROPOSPHERIC OZONE, UV-B RADIATION, VEGETATION

1233
Krupa, S.V., and R.N. Kickert. 1993. The greenhouse-effect - the impacts of carbon-dioxide (co2), ultraviolet-b (uv-b) radiation and ozone (o3) on vegetation (crops). *Vegetatio 104:223-238.*

Man's influence on the 'greenhouse effect,' the heating of the atmosphere due to increasing concentrations of tropospheric trace gases, is of much international concern. Among the climatic variables, elevated levels of carbon dioxide (CO2), ultraviolet-B (UV-B) radiation and ozone (O3) are known to have a direct effect on vegetation. Our current knowledge of these effects is mainly based on studies involving single stress mode. Thus, the joint effects of CO2, UV-B and O3 on vegetation are poorly understood. Nevertheless, based on the literature analysis of plant response to individual stress factors, it can be concluded that sorghum, pea, bean, potato, oat, lettuce, cucumber, rice and tomato are among the crop species potentially sensitive to the joint effects of the aforementioned three variables. Similar information for tree species is essentially lacking. At least with some climatic variables such as O3, present modeling efforts of cause-effect relationships have proven to be controversial. While at a regional geographic scale ambient CO2 concentrations appear to be relatively homogeneous, ambient concentrations of O3 exhibit significant temporal and spatial variability. Because of the protective action of O3 against UV-B, similar but inverse

temporal and spatial variability is expected in the surface levels of UV-B. Thus, future experimental designs should consider these exposure dynamics and modeling cause-effect relationships should be directed to stochastic processes.

KEYWORDS: ATMOSPHERIC CO2, EXPOSURE, FIELD, PROTECT VEGETATION, RESPONSES, STRATOSPHERIC OZONE, SURFACE, TROPOSPHERIC OZONE, UNITED-STATES, YIELD

1234

Krupa, S.V., and A.H. Legge. 1995. Air-quality and its possible impacts on the terrestrial ecosystems of the north-american great-plains - an overview. *Environmental Pollution 88(1):1-11.*

Over the past several decades, numerous studies have been conducted on the impacts of air pollutants (air quality) on terrestrial ecosystems (crops and forests). Although ambient air is always composed of pollutant mixtures, in determining the relative air quality and its ecosystem impacts at a given geographic location and time, a predominant number of studies have shown that at the present time surface level O-3 is the most important phytotoxic air pollutant. Within the North American Great Plains, the precursors; for surface-level O-3 are mainly anthropogenic NOx and VOCs (volatile organic compounds). Texas and Alberta ta are the top regions of such emissions in the United States and Canada, respectively. This appears to be due mainly to the prevalence of natural gas and/or oil industry in the two regions and the consequent urbanization. Nevertheless, the total emissions of NOx and VOCs within the North American Great Plains represent only about 25- 36% of the corresponding total emissions within the contiguous United States and the whole of Canada. Within the Great Plains many major crop and tree species are known to be sensitive to O-3. This sensitivity assessment, however, is based mainly on our knowledge from univariate (O-3 only) exposure-plant response studies. In the context of global climate change, in almost all similar univariate studies, elevated CO2, concentrations have produced increases in plant biomass (both crop and tree species). The question remains as to whether this stimulation will offset any adverse effects of elevated surface O-3 concentrations. Future research must address this important issue both for the Great Plains and for all other geographic locations, taking into consideration spatial and temporal variabilities in the ambient concentrations of the two trace gases.

KEYWORDS: B RADIATION, OZONE

1235

Kubiske, M.E., and K.S. Pregitzer. 1996. Effects of elevated CO2 and light availability on the photosynthetic light response of trees of contrasting shade tolerance. *Tree Physiology 16(3):351-358.*

Photosynthetic light response curves (A/PPFD), leaf N concentration and content, and relative leaf absorbance (alpha(r)) were measured in 1-year-old seedlings of shade- intolerant Betula papyrifera Marsh., moderately shade-tolerant Quercus rubra L. and shade-tolerant Acer rubrum L. Seedlings were grown in full sun or 26% of full sun (shade) and in ambient (350 ppm) or elevated (714 ppm) CO2 for 80 days. In the shade treatments, 80% of the daily PPFD on cloud-free days was provided by two 30-min sun patches at midday. In e. rubra and A. rubrum, leaf N concentration and a, were significantly higher in seedlings in the shade treatments than in the sun treatments, and leaf N concentration was lower in seedlings in the ambient CO2 treatments than in the elevated CO2 treatments. Changes in a, and leaf N content suggest that reapportionment of leaf N into light harvesting machinery in response to shade and elevated CO2 tended to increase with increasing shade tolerance of the plant. Shifts induced by elevated CO2 in the A/PPFD relationship in sun plants were largest in B. papyrifera and least in A. rubrum: the reverse was true for shade plants. Elevated CO2 resulted in increased light-saturated A in every species x light treatment combination, except in shaded B. papyrifera. The light compensation point (T) decreased in response to shade in all species, and in response to elevated CO2 in A. rubrum and e. rubra. Acer rubrum had the greatest increases in apparent quantum yield (phi) in response to shade and elevated CO2. To illustrate the effects of shifts in A, r and phi on daily C gain, daily integrated C balance was calculated for individual sun and shade leaves. Ignoring possible stomatal effects, estimated daily (24 h) leaf C balance was 218 to 442% higher in the elevated CO2 treatments than in the ambient CO2 treatments in both sun and shade seedlings of e. rubra and A. rubrum. These results suggest that the ability of species to acclimate photosynthetically to elevated CO:! may, in part, be related to their ability to adapt to low irradiance. Such a relationship has implications for altered C balance and nitrogen use efficiency of understory seedlings.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, GAS-EXCHANGE, GROWTH, PHASEOLUS-VULGARIS L, PLANT-PLANT INTERACTIONS, SEEDLINGS, SUCCESSIONAL STATUS, TROPICAL TREES, WATER-STRESS

1236

Kubiske, M.E., and K.S. Pregitzer. 1997. Ecophysiological responses to simulated canopy gaps of two tree species of contrasting shade tolerance in elevated CO2. *Functional Ecology 11(1):24-32.*

1. One-year-old seedlings of shade tolerant Acer rubrum and intolerant Betula papyrifera were grown in ambient and twice ambient (elevated) CO2, and in full sun and 80% shade for 90 days. The shaded seedlings received 30-min sun patches twice during the course of the day, Gas exchange and tissue-wafer relations were measured at midday in the sun plants and following 20 min of exposure to full sun in the shade plants to determine the effect of elevated CO2 on constraints to sun- patch utilization in these species. 2. Elevated CO2 had the largest stimulation of photosynthesis in B. papyrifera sun plants and A. rubrum shade plants, 3. Higher photosynthesis per unit leaf area in sun plants than in shade plants of B. papyrifera was largely owing to differences in leaf morphology, Acer rubrum exhibited sun/shade differences in photosynthesis per unit leaf mass consistent with biochemical acclimation to shade. 4. Betula papyrifera exhibited CO2 responses that would facilitate tolerance to leaf water deficits in large sun patches, including osmotic adjustment and higher transpiration and stomatal conductance at a given leaf-water potential, whereas A. rubrum exhibited large increases in photosynthetic nitrogen-use efficiency. 5. Results suggest that species of contrasting successional ranks respond differently to elevated CO2, in ways that are consistent with the habitats in which they typically occur.

KEYWORDS: ATMOSPHERIC CO2, C-3 PLANTS, CARBON DIOXIDE, COOCCURRING BIRCH, GROWTH-RESPONSE, LEAF GAS- EXCHANGE, LIGHT CONDITIONS, LIQUIDAMBAR-STYRACIFLUA, PINUS-TAEDA SEEDLINGS, WATER RELATIONS

1237

Kubiske, M.E., K.S. Pregitzer, C.J. Mikan, D.R. Zak, J.L. Maziasz, and J.A. Teeri. 1997. Populus tremuloides photosynthesis and crown architecture in response to elevated CO2 and soil N availability. *Oecologia 110(3):328-336.*

We tested the hypothesis that elevated CO2 would stimulate proportionally higher photosynthesis in the lower crown of Populus trees due to less N retranslocation, compared to tree crowns in ambient CO2. Such a response could increase belowground C allocation, particularly in trees with an indeterminate growth pattern such as Populus tremuloides. Rooted cuttings of P. tremuloides were grown in ambient and twice ambient (elevated) CO2 and in low and high soil N

availability (89 +/- 7 and 333 +/- 16 ng N g(-1) day(-1) net mineralization, respectively) for 95 days using open-top chambers and open-bottom root boxes. Elevated CO2 resulted in significantly higher maximum leaf photosynthesis (A(max)) at both soil N levels. A(max) was higher at high N than at low N soil in elevated, but not ambient CO2. Photosynthetic N use efficiency was higher at elevated than ambient CO2 in both soil types. Elevated CO2 resulted in proportionally higher whole leaf A in the lower three-quarters to one-half of the crown for both soil types. At elevated CO2 and high N availability, lower crown leaves had significantly lower ratios of carboxylation capacity to electron transport capacity (V-cmax/J(max)) than at ambient CO2 and/or low N availability. From the top to the bottom of the tree crowns, V-cmax/J(max) increased in ambient CO2, but it decreased in elevated CO2 indicating a greater relative investment of N into light harvesting for the lower crown. Only the mid-crown leaves at both N levels exhibited photosynthetic down regulation to elevated CO2. Stem biomass segments (consisting of three nodes and internodes) were compared to the total A(leaf) for each segment. This analysis indicated that increased A(leaf) at elevated CO2 did not result in a proportional increase in local stem segment mass, suggest ing that C allocation to sinks other than the local stem segment increased disproportionally. Since C allocated to roots in young Populus trees is primarily assimilated by leaves in the lower crown, the results of this study suggest a mechanism by which C allocation to roots in young trees may increase in elevated CO2.

KEYWORDS: ATMOSPHERIC CO2, CARBON GAIN, ECOSYSTEMS, GAS-EXCHANGE, LEAF AGE, NITROGEN, NODAL REGION, PLANTS, POPLAR POPULUS, SHOOT GROWTH

1238

Kubiske, M.E., K.S. Pregitzer, D.R. Zak, and C.J. Mikan. 1998. Growth and C allocation of Populus tremuloides genotypes in response to atmospheric CO2 and soil N availability. *New Phytologist 140(2):251-260.*

We grew cuttings of two early (mid Oct.) and two late (early Nov.) leaf-fall Populus tremuloides Michx. genotypes (referred to as genotype pairs) for c. 150 d in open-top chambers to understand how twice-ambient (elevated) CO2 and soil N availability would affect growth and C allocation. For the study, we selected genotypes differing in leaf area duration to find out if late-season photosynthesis influenced C allocation to roots. Both elevated CO2 and high soil N availability significantly increased estimated whole-tree photosynthesis, but they did so in different ways. Elevated CO2 stimulated leaf-level photosynthesis rates, whereas high soil N availability resulted in greater total plant leaf area. The early leaf-fall genotype pair had significantly higher photosynthesis rates per unit leaf area than the late leaf-fall genotype pair and elevated CO2 enhanced this difference. The early leaf-fall genotype pair had less leaf area than the late leaf-fall genotype pair, and their rate of leaf area development decreased earlier in the season. Across both genotype pairs, high soil N availability significantly increased fine root length production and mortality by increasing both the amount of root length present, and by decreasing the life span of individual roots. Elevated CO2 resulted in significantly increased fine root production and mortality in high N but not low N soil and did not affect fine root life span. The early leaf-fall genotype pair had significantly greater fine root length production than the late leaf-fall genotype pair across all CO2 and N treatments. These differences in belowground C allocations are consistent with the hypothesis that belowground C and N cycling is strongly influenced by soil N availability and will increase under elevated atmospheric CO2. In addition, this study reinforces the need for better understanding of the variation in tree responses to elevated CO2, within and among species.

KEYWORDS: CARBON DIOXIDE, ELEVATED CO2, ENRICHMENT, FINE ROOTS, GAS-EXCHANGE, LEAF, NITROGEN STRESS, PHYSIOLOGY, PLANT, ROOT-GROWTH

1239

Kubo, Y., O. Hirata, A. Inaba, and R. Nakamura. 1996. Respiration and ethylene production in fruits and vegetables held in carbon dioxide-enriched atmospheres - Effects of temperature and carbon dioxide concentration. *Journal of the Japanese Society for Horticultural Science 65(2):403-408.*

The rates of respiration and ethylene production in various fruits and vegetables held in 0.60% CO2 at 25 degrees C or 60% CO2 at 5-25 degrees C were determined by an automated microcomputer system. In peaches, apples, tomatoes, and broccoli, dose-dependent decreases of O-2 uptake and C2H4 production were observed during treatment with various concentrations of CO2 at 25 degrees C. Oxygen uptake in bananas was inhibited at 10% CO2 and higher, whereas C2H4 production increased as the ambient CO2 concentration was elevated. CO2 concentration had little or no effect on O-2 uptake in satsuma mandarin. Oxygen uptake in lettuce at 20% CO2 and below was similar to that under air, whereas induction of C2H4 production and an enhanced O-2 uptake were observed in lettuce held in 40% CO2 and higher. Inhibition of O-2 uptake and C2H4 production in peaches by 60% CO2 declined as the temperature was lowered to the range of 5-25 degrees C. In broccoli held in 60% CO2, the inhibition of O-2 uptake was temperature-dependent, but C2H4 production was suppressed to trace level at all temperatures. The induction of C2H4 production and enhancement of O-2 uptake in lettuce by 60% CO2 occurred distinctly at 25 degrees C, slightly at 15 degrees C, but not at 10 degrees C and 5 degrees C.

KEYWORDS: CO2, CROPS, STORAGE

1240

Kubo, Y., A. Inaba, and R. Nakamura. 1990. Respiration and C2H4 production in various harvested crops held in CO2-enriched atmospheres. *Journal of the American Society for Horticultural Science 115(6):975-978.*

1241

Kubo, Y., K. Sakota, A. Inaba, and R. Nakamura. 1996. Effects of high carbon dioxide exposure on ethylene biosynthesis in peach and tomato fruits. *Journal of the Japanese Society for Horticultural Science 65(2):409-415.*

Ethylene production, oxygen uptake, the activities of 1-aminocyclopropane-1-carboxylic acid (ACC) synthase and ACC oxidase in vivo and the contents of ACC and 1- (malonylamino)cyclopropane-1-carboxylic acid (MACC) were determined in peach and tomato fruits held in carbon dioxide- enriched atmosphere. Ethylene production in peaches decreased to a trace level with 60% carbon dioxide and in tomatoes to 50% of the initial level. The ethylene production rates in both fruits reverted to the initial level when the fruits were transferred back to air. Oxygen uptake in both fruits was markedly inhibited during carbon dioxide exposure. In vivo activities of ACC oxidase and ACC synthase in both fruits were also inhibited during carbon dioxide exposure. ACC content in peaches held in carbon dioxide-enriched atmosphere decreased but it increased in tomatoes. The level of MACC in peaches was constant during carbon dioxide treatment, whereas that in tomatoes slightly increased. These results indicate that inhibition in ethylene production by carbon dioxide may be mediated mainly by reduced conversion of ACC to ethylene in tomatoes, whereas in peaches, the inhibition is attributed to both reduced conversion of S-adenosylmethionine to ACC and ACC to ethylene.

KEYWORDS: 1-AMINOCYCLOPROPANE-1-CARBOXYLIC ACID, ASSAY, ATMOSPHERES, CO2, CONVERSION, CROPS, IDENTIFICATION, RESPIRATION, VEGETABLES

1242

Kubo, Y., H. Tsuji, A. Inaba, and R. Nakamura. 1993. Effects of elevated co2 concentrations on the ripening in banana fruit by exogenous C2h4. *Journal of the Japanese Society for Horticultural Science 62(2):451-455.*

Green bananas were treated with 0 to 60% CO2 and 1 to 100 PPM C2H4 to study their interaction on the ripening process. 1. The CO2 treatment did not block completely the initiation of ripening of banana by exogenous C2H4. When the concentration of applied C2H4 was kept constant and the CO2 concentration high, the appearance of the yellow pigment in the peel was delayed. 2. The combination of various concentrations of CO2 and C2H4 on the respiratory climacterics in green banana, monitored with an automated microcomputer system, revealed that the onset of the climacteric rise of bananas under any CO2 concentration combined with 1 PPM C2H4 commenced simultaneously with fruits which were kept under air and 1 PPM C2H4. However, the progress of the climacteric rise was slower and the peaks were lower at high CO2 concentration than they were at low CO2 concentrations. With 60% CO2 and 100 PPM C2H4, the fruit color remained green until the end of the gas treatment, in spite of the slow respiratory rise and ripening of the flesh. Our results suggest that the elevated CO2 concentration has no effect on the initiation-time of banana ripening induced.by exogenous C2H4 but lowers the progress rate of ripening.

KEYWORDS: ATMOSPHERES, CROPS, ETHYLENE, RESPIRATION, VEGETABLES

1243

Kuehny, J.S., M.M. Peet, P.V. Nelson, and D.H. Willits. 1991. Nutrient dilution by starch in CO2-enriched chrysanthemum. *Journal of Experimental Botany 42(239):711-716.*

Increasing growth irradiance and CO2 generally decreases foliar nutrient concentration on a dry weight basis and increases foliar starch concentration. However, the extent to which starch concentrations 'dilute' foliar nutrient concentrations when the latter are expressed on a dry weight basis is not known. To determine the importance of differential starch accumulation in calculating nutrient concentrations on a dry weight basis, leaf nutrient and starch concentrations were measured in Chrysanthemum x morifolium 'Fiesta' (Ramat.) cuttings grown at three irradiance levels and two CO2 levels for eight weeks in both winter and spring. On a dry weight basis, foliar concentrations of most nutrients were lower in both seasons as a result of the elevated CO2 and irradiance levels, and total dry weights were higher. Per cent starch was greater at the high CO, level in both seasons but was only greater at higher irradiances in the winter experiment. When starch was subtracted from the leaf dry weights, the differences between CO2 and irradiance treatments disappeared with respect to N, P, K, Ca, Mg, S, and B but not for Fe, Mn, Zn, and Cu.

KEYWORDS: ACCLIMATION, CARBOHYDRATE, CARBON-DIOXIDE CONCENTRATION, GREENHOUSES, GROWTH, HIGH CO2, LIGHT-INTENSITY, MORIFOLIUM RAMAT, PHYSIOLOGY

1244

Kuhn, M., C. Niewohner, M. Isenbeck-Schroter, and H.D. Schulz. 1998. Determination of major and minor constituents in anoxic thermal brines of deep sandstone aquifers in Northern Germany. *Water Research 32(2):265-274.*

The common process of low energy geothermal exploitation is the doublet of production- and reinjection borehole. The quality of water reinjected into a elastic reservoir is essential for the reliability of an injection well. In order to estimate precipitation reactions it is necessary to obtain extensive reliable analysis data of the water for the use of thermodynamic modelling. For thermal anoxic brines, the analysis of major and especially minor ion content is difficult because of matrix effects and possible iron precipitation. A selection of analysing methods were applied to two anoxic thermal brines of deep sandstone aquifers of Northern Germany. Detection limits and measured data of the major constituents are presented of Na+, K+, NH4+, Ca2+, Mg2+, Ba2+, Sr2+, Fe- total, Mn2+, SiO44-, B(OH)(3), Zn2+, Pb2+, Cd2+, F-, Cl-, Br-, I-, SO42-, SO32-, S2-, PO43-, NO3-, NO2- and DOC. The measurements were done with ICP-OES, ionselective electrodes, photometry, polarography, titration methods, ion chromatography and TOC-analyzer. Except for SO(4)(2-)and Cl-, the anion analysis was done on-site, since the high iron content in the anoxic water requires acidification in order to prevent iron hydroxide precipitation. The minor constituents Zn2+, Pb2+, Cu2+, Cd2+, Cr3+, Sc3+, Co2+, Y3+, La3+, Ce3+, Al3+, were enriched by trace matrix separation using the cation exchange resin Chelex((R))100. The element concentrations in the acidic eluates of the Chelex((R))100 columns were measured using ICP- MS. The pH dependency of the exchange equilibrium at pH values of 4, 5 and 6 (buffered and unbuffered) as well as the relation to the salt content between 35 and 250 gl(-1) total dissolved solids of Na-K-Ca-Mg-Cl-SO4 were evaluated by sensitivity analysis.

KEYWORDS: CHELEX-100 RESIN, ELEMENTS, HEAVY-METALS, PRE-CONCENTRATION EFFICIENCY, SEAWATER, SPECTROMETRY

1245

Kull, O., A. Sober, M.D. Coleman, R.E. Dickson, J.G. Isebrands, Z. Gagnon, and D.F. Karnosky. 1996. Photosynthetic responses of aspen clones to simultaneous exposures of ozone and CO2. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 26(4):639-648.*

Current projections indicate steady increases in both trophospheric ozone and carbon dioxide well into the next century with concurrent increases in plant stress. Because information about effects of these interacting stresses on forest trees is limited, we have conducted ozone and carbon dioxide experiments using ozone-tolerant and ozone-sensitive trembling aspen (Populus tremuloides Michx.) clones (clones 216 and 259, respectively). Aspen plants were grown either in pots (square-wave study) or in the ground (episodic study) in open- top chambers. Plants in the square-wave study were exposed for a single growing season to charcoal-filtered air (CF) or to CF plus elevated carbon dioxide (CO2), ozone (O-3), or O-3 plus CO2 (O-3 + CO2). Plants in the episodic study were exposed for three growing seasons to CF, twice simulated ambient (2x) O-3 (2x O-3), or 2x O-3 plus CO2 (2x O-3 + CO2). Photosynthetic measurements were made either in the open-top chambers at treatment CO2 concentrations or in controlled-environment cuvettes with various CO2 concentrations, producing assimilation versus intercellular CO2 concentration (A/C-i) curves. Ozone decreased photosynthetic rate and stomatal conductance and accelerated leaf senescence. Elevated CO2 increased photosynthetic rate and decreased stomatal conductance when measured at treatment CO2 concentrations, and exacerbated the negative effect of O-3 on photosynthesis. For example, for clone 259, photosynthesis decreased 9% for the O-3 treatment compared with the CF treatment, but decreased 24% for the O-3 + CO2 treatment compared with the CO2 treatment. Similar decreases for clone 216 of 2% and 6% for O-3 and O-3 + CO2, respectively, were not significant. A/C-i curves showed that O-3 decreased carboxylation efficiency and maximum photosynthetic rate and that photosynthetic inhibition in response to O-3 was greater with

elevated CO2. The simultaneous declines in all factors of photosynthetic gas exchange measurements suggest that the equilibrium between stomatal conductance, carboxylation, and light harvesting systems was not disrupted by O-3 and O-3 x CO2 interactions. Carbon dioxide did not ameliorate the detrimental effects of O-3 on the leaf photosynthetic apparatus. In fact, the O-3-tolerant clone appeared more sensitive to O-3 with elevated CO2.

KEYWORDS: ATMOSPHERIC CO2, BISPHOSPHATE CARBOXYLASE OXYGENASE, CARBON DIOXIDE, DIFFERENTIAL RESPONSE, GAS-EXCHANGE, LOBLOLLY-PINE, NET PHOTOSYNTHESIS, PHASEOLUS-VULGARIS, POPULUS-TREMULOIDES MICHX, STOMATAL CONDUCTANCE

1246

Kunz, R.P., R.E. Schulze, and R.J. Scholes. 1995. An approach to modelling spatial changes of plant carbon:nitrogen ratios in southern Africa in relation to anticipated global climate change. *Journal of Biogeography 22(2-3):401-408.*

The carbon to nitrogen (C:N) ratio is the main factor determining the forage quality of a plant, with a low C:N ratio indicating relatively good plant digestibility and a high C:N ratio inferring relatively poor forage quality. Global atmospheric composition and climate change effects on plant carbon to nitrogen ratios are thus likely to be important when predicting possible second-order impacts of the enhanced greenhouse effect on rangeland forage quality and the resultant feeding habits of foraging animals and herbivorous insects. Equations relating the assimilation of total carbon and nitrogen rates to monthly air temperature, the ambient CO2 level and soil fertility were used together with detailed spatial climatic and soil databases to simulate regional patterns of C:N ratios over southern Africa. Carbon to nitrogen ratios were estimated for both the present climate and for a possible future climate scenario defined by a general 2 degrees C mean daily temperature increase over southern Africa (but with latitudinal, seasonal and diurnal adjustments made), an increase in atmospheric CO2 concentration from 360 to 560 ppmv, but with no changes in precipitation patterns. When C:N differences between future and present climates are examined, results indicate both relative increases and decreases over southern Africa in a regional context, ranging from - 8 to + 8%. Areas where the C:N ratios decreased indicate that for the future climate scenario which was assumed the relative increase in assimilated nitrogen would be greater than that for carbon. Similarly, areas where the C:N ratios increased indicate that the relative increase in assimilated carbon would be greater than that for nitrogen. In this study, regions sensitive to climate change effects on C:N ratios in southern Africa have therefore been identified and with that, those areas where the consumption of plant matter may be expected to increase or decrease as a result of anticipated global climate change.

1247

Kurets, V.K., S.N. Drozdov, and E.G. Popov. 1999. Intraspecies diversity in the response of net photosynthesis in cucumber plants to elevated concentrations of atmospheric carbon dioxide. *Russian Journal of Plant Physiology 46(2):159-162.*

Relationships between net photosynthesis of intact cucumber plants (Cucumis sativus L., cvs. Alma-Atinskii 1, Teplichnyi rannii 65, and Syurpriz 66) and irradiance, air and soil temperatures, and ambient CO2 concentration were simulated by the multiway factorial method. Analysis of the models demonstrated marked cultivar-specific differences in plant responses to environmental conditions, in terms of both the potential highest values and conditions for their expression. This allowed us to conclude that the models of relationships between CO2 exchange in intact plants and environmental conditions can be used for the assessment of biological diversity at the intraspecies level.

1248

Kurooka, H., S. Fukunaga, E. Yuda, S. Nakagawa, and S. Horiuchi. 1990. Effect of carbon-dioxide enrichment on vine growth and berry quality of kyoho grapes. *Journal of the Japanese Society for Horticultural Science 59(3):463-470.*

Although ambient temperature is kept adequate, grape cultivation under covered facilities during winter months in Japan gives rise to low yields of poor quality berries because of low light intensities. This investigation was conducted in leaf chamber, using Vitis labruscana Bailey cv. Kyoho, to determine the influence of leaf age, light intensity, and CO2 concentrations on photosynthesis. The effects of CO2 enrichment on vine growth and fruit quality were also investigated in growth chambers. 1. The rate of photosynthesis per unit leaf area (Pn) between May 28 and September 19 rapidly increased with leaf growth, reaching a maximum of 18.9 mg CO2/dm2/hr, 37 days after the unfolding of a leaf. Pn then gradually decreased with leaf age. In young leaves, higher CO2 concentrations and stronger light intensities resulted in a significant increase in Pn. Older leaves exhibited a similar enhancement of Pn upon exposure to high light intensity. Pn was saturated at 828 ppm CO2. 2. Administration of 1,000 to 1,100 ppm CO2 to vines for an 8 hr/day at a late stage of berry development until harvest had no effect on berry size but resulted in an increase in sugar and anthocyanin contents but a decrease in organic acid content. Dry weight of newly developed roots doubled as a result of CO2 enrichment. 3. Application of CO2 under a long-day photoperiod at an early stage of berry development to a week before veraison markedly promoted shoot elongation. Furthermore, CO2 enrichment gave a 36% increase in both berry and cluster weights and also a higher sugar-acid ratio at harvest.

KEYWORDS: CO2- ENRICHMENT, COTTON, PHOTOSYNTHETIC RATE, RESPONSES, TOMATOES, YIELD

1249

Kurschner, W.M., I. Stulen, and P.J.C. Kuiper. 1997. PREDICTIONS for plant and vegetation responses to global change (elevated CO2) within a palaeo-ecophysiological perspective. *Plant Physiology 114(3):21002.*

1250

Kurschner, W.M., I. Stulen, F. Wagner, and P.J.C. Kuiper. 1998. Comparison of palaeobotanical observations with experimental data on the leaf anatomy of durmast oak [Quercus petraea (Fagaceae)] in response to environmental change. *Annals of Botany 81(5):657-664.*

To test whether stomatal density measurements on oak leaf remains are reliable tools for assessing palaeoatmospheric carbon dioxide concentration [CO2], under changing Late Miocene palaeoenvironmental conditions, young seedings of oak (Quercus petraea, Liebl.) were grown at elevated vs. ambient atmospheric [CO2] and at high humidity combined with an increased air temperature. The leaf anatomy of the young oaks was compared with that of fossil leaves of the same species. In the experiments, stomatal density and stomatal index were significantly decreased at elevated [CO2] in comparison to ambient [CO2]. Elevated [CO2] induced leaf cell expansion and reduced the intercellular air space by 35%. Leaf cell size or length were also stimulated at high air humidity and temperature. Regardless of a temperate or subtropical palaeoclimate, leaf cell size in fossil oak was not enhanced, since neither epidermal cell density nor length of the stomatal apparatus changed. The absence of these effects may be attributed to the phenological response of trees to climatic changes that

balanced temporal changes in environmental variables to maintain leaf growth under optimal and stable conditions. Quercus petraea, which evolved under recurring depletions in the palaeoatmospheric [CO2], may possess sufficient phenotypic plasticity to alter stomatal frequency in hypostomatous leaves allowing high maximum stomatal conductance and high assimilation rates during these phases of low [CO2]. (C) 1998 Annals of Botany Company.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, ELEVATED CO2, ENRICHMENT, FOSSIL LEAVES, GROWTH, POPLAR CLONES, STOMATAL DENSITY, TREE, WOODY-PLANTS

1251

Kurschner, W.M., F. Wagner, E.H. Visscher, and H. Visscher. 1997. Predicting the response of leaf stomatal frequency to a future CO2-enriched atmosphere: constraints from historical observations. *Geologische Rundschau 86(2):512-517.*

The majority of the water flux from the earth's land surface to the atmosphere passes through the tiny pores (stomata) in the leaves of land plants. The maximum conductance to diffusion of the leaves, determined by the number and geometry of stomata, has a profound effect on the terrestrial water and energy balance. Among tree species, there is ever increasing evidence that anthropogenic increase in atmospheric CO2 concentrations results in a decrease in stomatal frequency. The rate of historical CO2 responsiveness of individual tree species can be used to calibrate empirical models of non-linear (sigmoid) stomatal frequency response to CO2 increase. Modelled response curves for European tree birches (Betula pendula, Betula pubescens) and Durmast oak (Quercus petraea) predict different response limits to CO2 increase (similar to 350 and similar to 400 ppmv, respectively), indicating that non-linear stomatal frequency responses may vary from one tree species to another. Information on a wider selection of species is needed, but the models suggest that the maximum effect of anthropogenic CO2 increase on stomatal frequency has already been reached. Further research is required to establish the effect of rapidly declining response rates on future stomatal conductance of the ecologically contrasting trees of boreal, temperate, subtropical and tropical forests.

KEYWORDS: CARBON DIOXIDE, CLIMATE, DENSITY RECORD, ELEVATED CO2, ENRICHMENT, FOSSIL LEAVES, INCREASE, OAK LEAVES, PAST 2 CENTURIES, PLANT-RESPONSES

1252

Kurz, C., U. Schmieden, P. Strobel, and A. Wild. 1998. The combined effect of CO2, ozone, and drought on the radical scavenging system of young oak trees (Quercus petraea) - A phytothron study. *Chemosphere 36(4-5):783-788.*

In order to study the combined effects of CO2, ozone, and drought, we simulated in a controlled environment the climatic conditions of a German oak stand with high ozone (daytime: 80 ppb, control: 20 ppb) during one vegetative period under a regime of low and high CO2 concentration (370 vs 720 ppm) and drought (4 weeks < -800 hPa). To investigate the effects of CO2, ozone and drought on the radical scavenging system, we monitored the level of glutathione, ascorbate, and a- tocopherol. However, it is important that, under the regime of elevated CO2, the antioxidative behaviour of glutathione and ascorbate appears to be masked by their function as storage molecules for sulfur or carbon. (C)1998 Elsevier Science Ltd.

KEYWORDS: AIR- POLLUTANTS, ANTIOXIDATIVE SYSTEMS, ASCORBIC-ACID, HEALTHY, MOUNTAIN SITES, NORWAY SPRUCE, PINE, PLANT-RESPONSES, SEEDLINGS, SPRUCE NEEDLES

1253

Kutik, J., L. Natr, H.H. DemmersDerks, and D.W. Lawlor. 1995. Chloroplast ultrastructure of sugar beet (Beta vulgaris L) cultivated in normal and elevated CO2 concentrations with two contrasted nitrogen supplies. *Journal of Experimental Botany 46(293):1797-1802.*

Sugar beet (Beta vulgaris L., cultivar Celt) plants were grown under simulated field conditions in pots and supplied with adequate or deficient nitrogen (HN and LN, respectively) combined with two CO2 concentrations, ambient (c. 350 mu mol mol(-1) CO2-AC), or elevated CO2 (c. 600 mu mol mol(-1) CO2- HC). Chloroplast structure in mesophyll palisade cells of mature leaves (leaf number 19 in HN and 9 in LN), sampled at midday on 16 August 1993 was studied by transmission elec- tron microscopy and quantified stereologically. The ultrastructure of palisade parenchyma chloroplasts was affected by the elevated CO2 concentration and strikingly affected by nitrogen supply. Chloroplast diameter (cross-sectional length) was slightly, but not significantly, greater in HC than AC treatments within an N treatment, but was smaller in LN than HN; chloroplast cross-sectional area also increased with HC in both N treatments, but only significantly so in LN. Elevated CO2 reduced the proportion of total thylakoids (significant at 5% and 0.1% in HN and LN, respectively) due to decreased granal thylakoids, but the proportion of inter-granal (stromal) thylakoid membranes was not affected compared to chloroplasts from plants grown with ambient CO2. Chloroplast stroma increased as a proportion of chloroplast volume with elevated compared to ambient CO2 with HN but not LN. Starch inclusions were not significantly different with elevated compared to ambient CO2 at HN, but the proportion of starch increased considerably at elevated compared to ambient CO2 at LN, indicating an over-production of assimilates. Plastoglobuli in chloroplasts increased with deficient N, but decreased with elevated CO2. Larger chloroplasts with a greater proportion of stroma, but a smaller proportion of granal thylakoids, suggest increased CO, assimilating capacity and decreased light harvesting/PSII capacity with elevated CO2.

KEYWORDS: LEAF, LEAVES, PHOTOSYNTHESIS, PLANTS, TEMPERATURE, WHEAT

1254

Kwa, S.H., Y.C. Wee, and P.P. Kumar. 1995. Ammonium and nitrate uptake and nitrate reductase activity of photoautotrophic callus cultures of the fern Platycerium coronarium (Koenig) DESV. *In Vitro Cellular & Developmental Biology-Plant 31(4):211-214.*

The uptake of nitrate and ammonium by callus of Platycerium coronarium from the culture medium was examined. Nitrate reductase activity of photoautotrophic callus cultures under CO2 enrichment was significantly lower compared to the cultures without CO2 enrichment, but higher than that of heterotrophic callus cultured on medium with 2% (wt/vol) sucrose. When sucrose concentration of the heterotrophic culture was lowered to 0.2%, nitrate reductase activity increased. The level of nitrate reductase activity increased by about 25% in the heterotrophic callus with an increase in 2,4-D from 2 mu M to 10 mu M, despite a decline in fresh weight gain. However, photoautotrophic cultures with 1% CO2 enrichment showed 20% decline in nitrate reductase activity and 45% decline in fresh weight gain with a similar increase in 2,4-D level. The rate of uptake of nitrate from the culture medium was unrelated to the level of nitrate reductase activity in the callus. For photoautotrophic callus under CO2 enrichment, the presence of 1% (vol/vol) CO2 generally resulted in the highest rate of nitrate uptake. The rate of uptake of ammonium was higher for callus cultured on 2 mu M 2,4-D compared to that on 10 mu M 2,4-D.

KEYWORDS: CO2, GROWTH, ROOTS

1255

Kwa, S.H., Y.C. Wee, and P.P. Kumar. 1997. Ribulose-1,5-bisphosphate carboxylase and phosphoenolpyruvate carboxylase activities of photoautotrophic callus of Platycerium coronarium (Koenig ex OF Muell.) Desv. under CO2 enrichment. *Plant Cell Tissue and Organ Culture 50(2):75-82.*

The in vitro activities of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) and phosphoenolpyruvate carboxylase (PEPC) were measured in cell-free extracts of Platycerium coronarium callus cultured for up to 42 days under photoautotrophic conditions with CO2 enrichment. With an increase in CO2 in the culture environment to 10% (v/v) at low light, the apparent photoautotrophic fixation of CO2 by Rubisco declined, whereas the non-photoautotrophic CO2 fixation by PEPC activity was enhanced. Hence, photosynthesis appears to play a lesser role in providing carbon skeletons and energy with prolonged culture in a CO2-enriched environment. Instead, the anaplerotic supply of C-skeletons by PEPC may be important under such a situation. Short-term (HCO3-)-C-14 fixation experiments indicated that photoautotrophic callus cultured for 3 weeks with 10% CO2 enrichment assimilated less (CO2)-C-14 than the control (0.03% CO2). Analyses of C-14-metabolites indicated that about 50% of the total soluble (CO2)-C-14 fixed was in the organic acid fraction and 35% in the amino acid fraction. Despite the changes in the in vitro Rubisco/PEPC activity-ratio, no significant change in the C-14 distribution pattern was apparent in response to increasing sucrose or CO2 concentrations. The suppression of Rubisco activity and total chlorophyll content in high sucrose or elevated CO2 concentrations suggests an inhibition of the capacity for photoautotrophic callus growth under these conditions.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, CELLS, CHLOROPHYLL SYNTHESIS, ELEVATED CO2, ESTABLISHMENT, EXPRESSION, PHOTOSYNTHESIS, SUCROSE SUPPRESSION, SUSPENSION-CULTURE

1256

Kwa, S.H., Y.C. Wee, T.M. Lim, and P.P. Kumar. 1995. Establishment and physiological analyses of photoautotrophic callus-cultures of the fern platycerium-coronarium (koenig) desv under co2 enrichment. *Journal of Experimental Botany 46(291):1535-1542.*

Gametophyte-derived callus cultures of Platycerium coronarium could be maintained under photoautotrophic conditions on Murashige and Skoog medium supplemented with 2 mu M 2,4- dichlorophenoxyacetic acid (2,4-D) and with CO2 enrichment. Progressive reduction of sucrose from the medium resulted in a reduction in growth, but an increase in total chlorophyll content. When subculturing was delayed beyond 2 weeks, callus cells differentiated into gametophytes on the medium with less than or equal to 0.2% sucrose and no CO2 enrichment. Enriching the photoautotrophic cultures on 2 mu M 2,4-D with 1% CO2 resulted in about 1.7-fold increase in fresh weight within 42 d. Total chlorophyll content was generally higher with 1% CO2 enrichment than with 10%. F-v/F-m ratio was higher for callus on low levels of sucrose (less than or equal to 0.5%) than that on sucrose greater than or equal to 1.0%. An increase in autofluorescence of chloroplasts, but not the size, was observed with decreasing sucrose levels in the medium. Autofluorescence decreased with increase in CO2 from 0.03%. Our data are in agreement with the view that long-term exposure to high levels of CO2 can cause a decrease in photosynthetic capacity.

KEYWORDS: CELLS, CHLOROPHYLL SYNTHESIS, ELEVATED CO2, GROWTH, PHOTOSYNTHESIS, SUCROSE SUPPRESSION

1257

Kytoviita, M.M., J. Pelloux, V. Fontaine, B. Botton, and P. Dizengremel. 1999. Elevated CO2 does not ameliorate effects of ozone on carbon allocation in Pinus halepensis and Betula pendula in symbiosis with Paxillus involutus. *Physiologia Plantarum 106(4):370-377.*

The effect of 700 mu mol CO2 mol(-1), 200 mmol ozone mol(-1) and a combination of the two on carbon allocation was examined in Pinus halepensis co-cultured with Betula pendula in symbiosis with the ectomycorrhizal fungus Paxillus involutus, The results show that under low nutrient and ozone levels, elevated CO2 has no effect on the growth of B. pendula or P. halepensis seedlings nor on net carbon partitioning between plant parts. Elevated CO2 did not enhance the growth of the fungus in symbiosis with the birch, On the other hand, ozone had a strong negative effect on the growth of the birch, which corresponded with the significantly reduced growth rates of the fungus. Exposure to elevated CO2 did not ameliorate the negative effects of ozone on birch; in contrast, it acted as an additional stress factor. Neither ozone nor CO2 had significant effects on biomass accumulation in the pine seedlings, Ozone stimulated the spread of mycorrhizal infection from the birch seedlings to neighbouring pines and had no statistically significant effects on phosphoenolpyruvate carboxylase (PEPC) or ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) activity in the pine needles or on PEPC activity in pine roots.

KEYWORDS: ATMOSPHERIC CO2, ECTOMYCORRHIZAL COLONIZATION, GAS-EXCHANGE, JUVENILE PONDEROSA PINE, MYCORRHIZAL COLONIZATION, NORWAY SPRUCE, PHOSPHOENOLPYRUVATE CARBOXYLASE ACTIVITY, PICEA-ABIES L, SPRUCE NEEDLES, TAEDA L SEEDLINGS

1258

Laforge, F., C. Lussier, Y. Desjardins, and A. Gosselin. 1991. Effect of light-intensity and CO2 enrichment during invitro rooting on subsequent growth of plantlets of strawberry, raspberry and asparagus in acclimatization. *Scientia Horticulturae 47(3-4):259-269.*

Growth of plantlets of asparagus (Asparagus officinalis L.), raspberry (Rubus idaeus L.) and strawberry (Fragaria X ananassa Duch.), treated during the in vitro rooting stage under three photosynthetic photon flux densities (PPFD) (80, 125 and 250- mu-mol s-1 m-2) (17.5, 26.9 and 53.8 W m-2 (PAR), respectively) and three CO2 enrichment levels (CDE) (330, 1650 and 3000-mu- mol mol-1), was monitored during the acclimatization stage. For the three species, generic differences were observed in the plant response to treatments. A significant residual growth enhancement was caused by CDE. High PPFD in vitro increased the dry weight of strawberry and fresh weight of asparagus in acclimatization. Raspberry leaf dry weight was increased by 262% in acclimatization after in vitro treatment with high CDE. This enhanced the performance of micropropagated plantlets in acclimatization and reduced by 2 weeks the acclimatization period with raspberry. Our results suggest that in vitro leaves may be a source of nutritional reserves for leaves initiated ex vitro, but do not exclude a morphogenetic effect of CO2 during the in vitro rooting stage.

KEYWORDS: ANATOMY, EXVITRO, SEEDLINGS, SOIL

1259

Laisk, A., and G.E. Edwards. 1997. CO2 and temperature-dependent induction in C-4 photosynthesis: an approach to the hierarchy of rate-limiting processes. *Australian Journal of Plant Physiology 24(4):505-516.*

Rate-limiting processes for C-4 photosynthesis were examined in Sorghum bicolor, an NADP-ME type species, and Amaranthus cruentus, an NAD-ME type C-4 species, by studying the kinetics of transient changes in photosynthetic rates following rapid changes in CO2 or temperature. Primary responses (faster than 15 s) to increasing CO2 or

temperature are considered direct effects on the turnover rate of the C-4 cycle, whereas medium transient changes (2-3 min) are considered due to build-up of C-4 cycle intermediates, and the slowest transient changes (20- 30 min) are thought to be related to end product synthesis. Reciprocal plot of carboxylation rates versus cell wall (dissolved) CO2 concentration (C-w) gives an apparent K-m (CO2) of 8 mu M and a V-m of 200 mu mol m(-2) s(-1) for PEP carboxylase, which is about 4 times higher than the maximum rate of photosynthesis. Under strictly limiting CO2, the rate of PEP carboxylation in C-4 photosynthesis is independent of temperature (20-35 degrees C), suggesting a physical rather than a biochemical limitation. It is suggested that the rates of C-3 and C-4 cycles are coordinated through the pool sizes of the C-4 cycle, which are in equilibrium with the pool of 3- phosphoglyceric acid. At low CO2, the C-4 pools decrease and are slowly regenerated at elevated CO2, restricting the CO2 response of C-4 photosynthesis.

KEYWORDS: CARBON ASSIMILATION, ELECTRON-TRANSPORT, GAS-EXCHANGE, LEAVES, MATHEMATICAL-MODEL, NADP+-MALATE DEHYDROGENASE, PHOSPHOENOLPYRUVATE CARBOXYLASE, PYRUVATE, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, ZEA MAYS L

1260

Laitat, E., and H. Boussard. 1995. Comparative response on gas exchange of Picea spp exposed to increased atmospheric CO2 in open top chambers at two test sites. *Journal of Biogeography 22(2-3):241-248.*

We took comparative measurements of gas exchange response curves of two species of spruce (Picea abies (L.) Karst and Picea sitchensis (Bong.) Carr.) exposed to high levels of atmospheric carbon dioxide (CO2) in two test stations: Vielsalm (Belgium) and Glendevon (United Kingdom). The photosynthetic response of these two species to variations in concentrations of intercellular CO2 and to variations in light intensity were measured in situ using an integrated transportable differential CO2 and water vapour exchange measuring system. The response curves were adjusted by the Mitscherlich function. The statistical analysis of our measurements and adjustments reveal similarities in the reaction of Picea abies and Picea sitchensis to a doubling of the present level of atmospheric CO2. Regarding the photosynthesis response curves to intercellular CO2 variation, we noted a decrease in the maximum photosynthesis rate and the carboxylation rate accompanied by an increased compensation point. Regarding the photosynthesis response curves to the light variation, we found that dark respiration and photochemical efficiency remained unchanged, and the maximum photosynthesis rate was slightly higher in an atmosphere enriched in CO2. These experimental contexts would seem to indicate that the current and forecast levels of CO2 are not ecological factors limiting primary productivity, and that the increase in atmospheric CO2 interacts with other environmental factors.

KEYWORDS: CARBON DIOXIDE, PHOTOSYNTHESIS

1261

Lake, J.C., and L. Hughes. 1999. Nectar production and floral characteristics of Tropaeolum majus L. grown in ambient and elevated carbon dioxide. *Annals of Botany 84(4):535-541.*

Tropaeolum majus (nasturtiums) were grown from seed in growth cabinets, under 380 and 750 ppmv CO2. Elevated CO2 significantly increased nectar secretion rate, both in flowers milked of nectar daily and in once sampled, 3-d-old flowers. Elevated CO2 did not affect time to flowering, total number of flowers produced, pollen to ovule ratio, or the total or individual concentrations of nectar amino acids. The dry weight and longevity of individual flowers was also unchanged. Nectar sugar content was unchanged by elevated CO2 in a subset of flowers used to assess the 3-d-old nectar volume. This subset did not show the same increase in nectar volume under elevated CO2 as the full set, resulting in the concentration of sugars remaining unchanged. Overall, the quantity rather than the quality of the nectar changed under elevated CO2 while flower characteristics remained constant, implying that the identity of pollinators may remain the same while foraging behaviour (e.g. number of visits per plant, distance travelled) may change in the future. (C) 1999 Annals of Botany Company.

KEYWORDS: AMINO-ACIDS, BUTTERFLIES, CO2 LEVELS, FLOWER CONSTANCY, LONG, NITROGEN, PHENOLOGY, PLANT, REPRODUCTION, RESPONSES

1262

Lal, M., K.K. Singh, L.S. Rathore, G. Srinivasan, and S.A. Saseendran. 1998. Vulnerability of rice and wheat yields in NW India to future changes in climate. *Agricultural and Forest Meteorology 89(2):101-114.*

Agricultural sector is one of the sensitive areas which would be influenced by the projected global warming and associated climate change. In spite of the uncertainties about the precise magnitude of climate change on regional scales, an assessment of the possible impacts of changes in key climatic elements on our agricultural resources is important for formulating response strategies. In this study, vulnerability of wheat and rice crops in northwest India to the projected climate change is examined. CERES wheat and rice models adopted for the study were validated for their ability to reproduce yields at the selected NW Indian stations. The sensitivity experiments with these models showed higher yields for both wheat and rice (28% and 15% respectively for a doubling of CO2) under elevated CO2 levels. A 3 degrees C (2 degrees C) rise in air temperature nearly cancels out the positive effect of elevated CO2 on the wheat (rice) yields. While the wheat crops are found to be sensitive to increase in maximum temperature, the rice crops are vulnerable to increase in minimum temperature. The combined effect of enhanced CO2 and imposed thermal stress on the wheat (rice) crop is 21% (4%) increase in yield for the irrigation schedule presently practised in the region. While the adverse impacts of likely water shortage on wheat crops would be minimised to a certain extent under elevated CO2 levels, they would largely be maintained for the rice crops resulting in about 20% net decline in rice yields. In general, acute water shortage conditions combined with the thermal stress should adversely affect both the wheat and more severely the rice productivity in NW India even under the positive effects of elevated CO2 in the future. (C) 1998 Elsevier Science B.V.

KEYWORDS: AEROSOLS, GREENHOUSE GASES, SIMULATION, TEMPERATURE

1263

Lal, M., K.K. Singh, G. Srinivasan, L.S. Rathore, D. Naidu, and C.N. Tripathi. 1999. Growth and yield responses of soybean in Madhya Pradesh, India to climate variability and change. *Agricultural and Forest Meteorology 93(1):53-70.*

This study is aimed at assessing the impact of thermal and moisture stresses associated with observed intraseasonal and interannual variability in key climatic elements on the nature and extent of losses in growth and yield of soybean crop in central India through the use of CROPGRO model. The crops are found to be more sensitive to higher cumulative heat units during cropping season. The yields respond substantially to temporal variations in rainfall (associated with observed swings in the continuity of monsoon). Prolonged dry spells at critical life stages of the soybean crop are found to adversely affect crop development and growth and hence the yields at selected sites. We have also examined the plausible effects of future climate change on soybean

yields in the selected region based on simulations carried out for doubled atmospheric CO2 level and with modified weather variables using the available seasonal projections for the future. Our findings on the response of elevated CO2 concentrations in the atmosphere suggest higher yields (50% increase) for soybean crop for a doubling of CO2. However, a 3 degrees C rise in surface air temperature almost cancels out the positive effects of elevated CO2 on the yield. Soybean crops at selected site are more vulnerable to increases in maximum temperature than in minimum temperature. The combined effect of doubled CO2 and anticipated thermal stress (likely by middle of the next century) on soybean crop is about 36% increase in yield at the selected sites. A decline in daily rainfall amount by 10% restricts this yield gain to about 32%. Deficient rainfall with uneven distribution during the monsoon season could be a critical factor for the soybean productivity even under the positive effects of elevated CO2 in the future.

KEYWORDS: CARBON DIOXIDE, CO2, GRAIN LEGUMES, GREENHOUSE GASES, INCREASE, SENSITIVITY, SIMULATION, SULFATE AEROSOLS, TEMPERATURE, TRANSPIRATION

1264

Lal, M., P.H. Whetton, A.B. Pittock, and B. Chakraborty. 1998. Simulation of present-day climate over the Indian subcontinent by general circulation models. *Terrestrial Atmospheric and Oceanic Sciences 9(1):69-96.*

There continues to be some improvement in the ability of general circulation models to simulate the present-day climate on large scales although further improvements in the model resolution and parameterization of physical processes are still needed for the realistic simulation of regional climates. Quantitative assessment of the magnitude of climate change on a regional scale and its implications are essential for understanding, planning and management of resources at national/regional levels. In developing countries like India, where the economy is largely regulated by variability in summer monsoon rainfall, the consideration of measures for reducing the impacts of global change should begin as soon as possible, particularly with regard to floods and droughts, cyclone disaster preparedness, hydrological planning in semi-arid regions and coastal zone management issues. With this in view, we examine here the skill of a range of global climate models in simulating the regional climatology of the Indian subcontinent. This is a necessary first step in preparing climate change scenarios for the region. The simulation of the current broad scale patterns of mean sea level pressure, temperature and precipitation over the northern hemisphere and over the Indian subcontinent in particular are assessed for a broad range of global climate modelling experiments. The experiments included both slab ocean and coupled ocean experiments. Five experiments are identified as having a fairly realistic simulation and may be considered acceptable for use in regional climate change assessments. All of these are of relatively high resolution and use a Q-flux correction (in the slab ocean experiments) or a flux correction (in the coupled ocean experiments). A further four experiments, with somewhat poorer regional climate simulations, are acceptable but only to a moderate degree of confidence. However, some six experiments have such marked deficiencies in their simulation of present- day regional climatology that we consider them unacceptable for regional climate change assessment.

KEYWORDS: CARBON DIOXIDE, CO2, GCM, IMPACT, OCEAN-ATMOSPHERE MODEL, SENSITIVITY, SPATIAL VARIABILITY, TEMPERATURE

1265

Lal, R. 1997. Residue management, conservation tillage and soil restoration for mitigating greenhouse effect by CO2-enrichment. *Soil & Tillage Research 43(1-2):81-107.*

This manuscript reviews the potential impact of residue management, conservation tillage and soil restoration on carbon sequestration in world soils. The greenhouse effect is among four principal ecological issues of global concern that include: (i) adequacy of land resources to meet needs of present and future generations; (ii) role of world soils and agricultural practices in the 'greenhouse' effect; (iii) potential of crop residue management, restoration of degraded soils, and conservation tillage in carbon sequestration in soil; and (iv) minimizing risks of soil degradation by enhancing soil resilience and soil quality. Annual increase in CO, concentration in the atmosphere is 3.2 x 10(15) g, and there exists a potential to mitigate this effect through C sequestration in soils. Just as world soils are an important active pool of organic carbon and play a major role in the global carbon cycle, crop residue is a major renewable resource which also has an important impact on the global carbon cycle. I have estimated the annual production of crop residue to be about 3.4 billion Mg in the world. If 15% of C contained in the residue can be converted to passive soil organic carbon (SOC) fraction, it may lead to C sequestration at the rate of 0.2 x 10(15) g/yr. Similarly restoring presently degraded soils, estimated at about 2.0 billion ha, and increasing SOC content by 0.01%/yr may lead C sequestration at the rate of 3.0 Pg C/yr. Conservation tillage is an important tool for crop residue management, restoration of degraded soil, and for enhancing C sequestration in soil. Conservation tillage, any tillage system that maintains at least 30% of the soil surface covered by residue, was practised in 1995 on about 40 x 10(6) ha or 35.5% of planted area in USA. It is projected that by the year 2020, conservation tillage may be adopted on 75% of cropland in USA (140 x 10(6) ha), 50% in other developed countries (225 x 10(6) ha), and 25% in developing countries (172 x 10(6) ha). The projected conversion of conventional to conservation tillage may lead to a global C sequestration by 2020 at a low estimate of 1.5 x 10(15) g, and at a high estimate of 4.9 x 10(15) g of C. These potentials of C sequestration can be realized through adoption of regional, national and global soil policy that stipulate appropriate use of world soil resources.

KEYWORDS: C-13 NATURAL ABUNDANCE, CONTINUOUS CULTIVATION, LONG-TERM TRENDS, NO-TILLAGE, ORGANIC-MATTER TURNOVER, PARTICLE-SIZE FRACTIONS, PHYSICAL-PROPERTIES, REDUCED TILLAGE, SOUTHERN QUEENSLAND, WATER-STABLE AGGREGATION

1266

Lambers, H. 1993. Rising co2, secondary plant-metabolism, plant-herbivore interactions and litter decomposition - theoretical considerations. *Vegetatio 104:263-271.*

A brief account is given of the ecological significance of quantitatively important secondary plant compounds, mainly those of a phenolic nature, in herbivory and decomposition. Phenolic compounds accumulate to a greater extent in slow- growing species than in fast-growing ones, particularly when soil conditions (nutrients, water) restrict growth. Two hypotheses to explain the increased concentration of phenolics when soil conditions are unfavorable are presented. The first hypothesis (the 'carbon supply model of secondary plant metabolism') considers the increased levels of non-structural carbohydrates as the major trigger. The second hypothesis (the 'amino acid diversion model of secondary plant metabolism') states that increased accumulation of phenolics stems from a decreased use of a common precursor (phenylalanine or tyrosine) for protein synthesis. Current experimental evidence, though still fairly limited, supports the second hypothesis, but further testing is required before the first model can be rejected. So far, there is very little evidence for a direct effect of atmospheric CO2 on the concentration of secondary compounds in higher plants. However, there are likely to be indirect effects, due to a stronger limitation by the nitrogen supply in plants whose growth has been promoted by atmospheric CO2. It is concluded that it is very likely that phenolic compounds accumulate to a greater extent in plants exposed to elevated

CO2, due to a greater limitation of nutrients, rather than as a direct effect of elevated CO2.

KEYWORDS: CARBON-DIOXIDE ATMOSPHERES, CHEMICAL DEFENSE, ELEVATED CO2, ESTUARINE MARSH, GROWTH, INSECT HERBIVORE, LEAF LITTER, NITROGEN, NUTRIENT BALANCE, PHENOLICS

1267

Lambers, H., I. Stulen, and A. vanderWerf. 1996. Carbon use in root respiration as affected by elevated atmospheric CO-2. *Plant and Soil 187(2):251-263.*

The use of fossil fuel is predicted to cause an increase of the atmospheric CO2 concentration, which will affect the global pattern of temperature and precipitation. It is therefore essential to incorporate effects of temperature and water supply on the carbon requirement for root respiration of plants to predict effects of elevated [CO2] on the carbon budget of natural and managed systems. There is insufficient information to support the contentention that an increase in the concentration of CO2 in the atmosphere will enhance the CO2 concentration in the soil to an extent that is likely to affect root respiration. Moreover, there is no convincing evidence for a direct effect of elevated atmospheric [CO2] on the rate of root respiration per unit root mass or the fraction of carbon required for root respiration. However, there are likely to be indirect effects of elevated [CO2] on the carbon requirement of plants in natural systems. Firstly, it is very likely that the carbon requirement of root respiration relative to that fixed in photosynthesis will increase when elevated [CO2] induces a decrease in nutrient status of the plants. Although earlier papers have emphasized that elevated [CO2] favours investment of biomass in roots relative to that in leaves, these are in fact indirect effects. The increase in root weight ratio is due to the more rapid depletion of nutrients in the root environment as a consequence of enhanced growth. This will decrease the specific rate of root respiration, but increase the carbon requirement as a fraction of the carbon fixed in photosynthesis. It is likely that these effects will be minor in systems where the nutrient supply is very high, e.g, in many managed arable systems, and increase with decreasing soil fertility, i.e. in many natural systems. Secondly, a decrease in rainfall in some parts of the world may cause a shortage in water supply which favours the carbon partitioning to roots. Water stress is likely to reduce rates of root respiration per unit root mass, but enhance the fraction of total assimilates required for root respiration, due to greater allocation of biomass to roots. Increased temperatures are unlikely to affect the specific rate of root respiration in all species. Broadly generalized, the effect of temperature on biomass allocation is that the relative investment of biomass in roots is lowest at a certain optimum temperature and increases at both higher and lower temperatures. The root respiration of some species acclimates to growth temperature, so that the effect of global temperature rise is entirely accounted for by the effect of temperature on biomass allocation. The specific rate of root respiration of other species will increase with global warming. In response to global warming the carbon requirement of roots is likely to decrease in temperate regions, when temperatures are suboptimal for the roots' capacity to acquire water. Here global warming will induce a smaller biomass allocation to the roots. Conversely, the carbon requirements are more likely to increase in mediterranean environments, where temperatures are often supraoptimal and a rise in temperature will induce greater allocation of biomass to the roots.

KEYWORDS: CO2- ENRICHMENT, DARK RESPIRATION, DRYING SOIL, FERTILIZER APPLICATION, GROWTH, MOWN GRASSLAND, NITROGEN, PLANTAGO-MAJOR, SHOOT, TEMPERATURE

1268

Lambers, H., R. VandenBoogaard, E.J. Veneklaas, and R. Villar. 1995. Effects of global environmental change on carbon partitioning in vegetative plants of Triticum aestivum and closely related Aegilops species. *Global Change Biology 1(6):397-406.*

The use of fossil fuel is predicted to cause an increase of the atmospheric CO2 concentration, which will affect the global pattern of temperature and precipitation. It is therefore essential to incorporate effects of temperature and water supply on carbon partitioning of plants to predict effects of elevated [CO2] on growth and yield of Triticum aestivum. Although earlier papers have emphasized that elevated [CO2] favours investment of biomass in roots relative to that in leaves, it has now become clear that these are indirect effects, due to the more rapid depletion of nutrients in the root environment as a consequence of enhanced growth. Broadly generalized, the effect of temperature on biomass allocation in the vegetative stage is that the relative investment of biomass in roots is lowest at a certain optimum temperature and increases at both higher and lower temperatures. This is found not only when the temperature of the entire plant is varied, but also when only root temperature is changed whilst shoot temperature is kept constant. Effects of temperature on the allocation pattern can be explained largely by the effect of root temperature on the roots' capacity to transport water. Effects of a shortage in water supply on carbon partitioning are unambiguous: roots receive relatively more carbon. The pattern of biomass allocation in the vegetative stage and variation in water-use efficiency are prime factors determining a plant's potential for early growth and yield in different environments. In a comparison of a range of T. aestivum cultivars, a high water-use efficiency at the plant level correlates positively with a large investment in both leaf and root biomass, a low stomatal conductance and a large investment in photosynthetic capacity. We also present evidence that a lower investment of biomass in roots is not only associated with lower respiratory costs for root growth, but also with lower specific costs for ion uptake. We suggest the combination of a number of traits in future wheat cultivars, i.e. a high investment of biomass in leaves, which have a low stomatal conductance and a high photosynthetic capacity, and a low investment of biomass in roots, which have low respiratory costs. Such cultivars are considered highly appropriate in a future world, especially in the dryer regions. Although variation for the desired traits already exists among wheat cultivars, it is much larger among wild Aegilops species, which can readily be crossed with T. aestivum. Such wild relatives may be exploited to develop new wheat cultivars well-adapted to changed climatic conditions.

KEYWORDS: ABSCISIC-ACID, ALLOCATION, ATMOSPHERIC CO2 ENRICHMENT, GROWTH, MAIZE PLANTS, NITROGEN, ROOT TEMPERATURE, SHOOT, WATER DEFICIT, WHEAT

1269

Lamhamedi, M.S., and P.Y. Bernier. 1994. Ecophysiology and field performance of black spruce (picea- mariana) - a review. *Annales Des Sciences Forestieres 51(6):529-551.*

This paper presents a literature review of black spruce (Picea mariana [Mill] BSP) ecophysiology concerning the response of net photosynthesis and stomata to changes in environmental factors. Current knowledge on root growth, mineral nutrition and response to high temperature, CO2 enrichment and climate change, frosts, water stress and flooding are also covered. The review ends with an overview of stand establishment and field performance of planted seedlings. The authors highlight the need for research on the long-term effects of multiple stresses, such as climate change and air pollution on the black spruce ecosystem.

KEYWORDS: ATMOSPHERIC CO2 ENRICHMENT, CONTAINER SEEDLINGS, FROST HARDINESS, JACK PINE-SEEDLINGS, NORTHERN CONIFERS, PLANTED WHITE-PINE, ROOT-GROWTH CAPACITY, SOIL TEMPERATURE, WATER RELATIONS

1270
Landolt, W., and I. Pfenninger. 1997. The effect of elevated CO2 and soil type on non-structural carbohydrates in beech leaves and Norway spruce needles growing in model ecosystems. *Acta Oecologica-International Journal of Ecology 18(3):351-359.*

Young beech and Norway spruce trees from two Swiss provenances were both planted in an acidic and calcareous soil in 16 open- top chambers. Half of the plants were exposed to elevated CO2 (ambient, ambient + 200 mu l l(-1), 24 hrs/day, 365 days/year) and enhanced nitrogen deposition (2.5, 25 kg ha(-1) yr(-1)) throughout a single growing season. Leaf and needle samples from all 64 trees were collected (2 provenances x 2 soil types x 4 treatments x 4 replications) at the end of July and September. These were analysed for starch, soluble carbohydrates and total non-structural carbohydrates (TNC). Increased starch and TNC levels were found in plants under elevated CO2 and those growing on the acidic soil. These effects were not consistent in both species or on both sampling dates. Soluble carbohydrates were only effected significantly by sail type. So far no interactions have been found between CO2, N or soil type on any date and in any fraction. It is concluded that soil type should be considered when discussing the effects of elevated CO2 on starch, soluble carbohydrate or TNC contents in beech and spruce trees.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, DECLINE, GROWTH, NITROGEN, NUTRITION, PLANTS, SOURCE-SINK RELATIONS

1271
Landsberg, J., and M.S. Smith. 1992. A functional scheme for predicting the outbreak potential of herbivorous insects under global atmospheric change. *Australian Journal of Botany 40(4-5):565-577.*

There are many possible ways in which changes in the global atmosphere could influence the outbreak potential of herbivorous insects; we clarify these by developing a scheme for analysing insect populations in terms of functional attributes that are both important in population regulation and responsive to global change. This analysis shows that elevated CO2 is not likely to have a major influence on probability of insect outbreak, except possibly in systems in which nitrogen-based defensive compounds are produced by plants in response to herbivory. Systems that will have high potential to outbreak, if climatic conditions become more favourable for plant growth and responses are not constrained by other resources, include those in which both herbivorous insects and host plants have highly flexible growth patterns and activity cues. Global changes that increase environmental stress on host plants are most likely to favour sap-feeding insects. Critical enemy (predator or parasitoid) control of the dormant phase of herbivorous insects may be very important in preventing or allowing outbreaks, but is often poorly understood.

KEYWORDS: CARBON DIOXIDE, DEFOLIATION, FOLIAGE, GROWTH, MOTH, POPULATION-DYNAMICS, TREES

1272
Lange, D.L., and A.A. Kader. 1997. Changes in alternative pathway and mitochondrial respiration in avocado in response to elevated carbon dioxide levels. *Journal of the American Society for Horticultural Science 122(2):245-252.*

Partially ripened avocado [Persea americana (Mill.) cv, Hass] fruit harvested in either June or Aug, 1994 were kept at 10 degrees C in air (21% O-2), 20% CO2 (17% O-2, balance N-2), or 40% CO2 (13% O-2, balance N-2) for 7 to 12 days and then were transferred to air at 10 degrees C for 2 to 3 days, Mitochondrial respiration was stimulated in response to elevated CO, treatments at 10 degrees C. A shift to alternative pathway (Alt) respiration occurred on day 4 in experiments using avocados from both harvest dates, with a return to initial levels in only the 20% CO2-treated fruit (June- harvested fruit after return to air), Elevated CO2 at 20 degrees C decreased the in vitro O-2 consumption of isolated mitochondria compared to mitochondria kept in air, The Alt pathway contributed less to the total O-2 uptake of CO2-treated mitochondria compared to mitochondria kept in air, The respiratory control ratios of the CO2-treated fruit and mitochondria were higher and lower, respectively, than the air controls. Induction of 33 to 37 kD proteins (corresponding to the size of the alternative oxidase proteins) occurred in avocados after 4 days in 40% CO2. These results indicate that elevated CO2 has various effects depending on concentration, duration and temperature of exposure, and mitochondrial function of avocado fruit, such as increased and altered respiratory oxidation and up-regulation of alternative oxidase proteins.

KEYWORDS: CYANIDE-RESISTANT RESPIRATION, ETHYLENE, HIGHER-PLANT MITOCHONDRIA, METABOLISM, OXIDASE, SELF-RESTORATION, SENSITIVE METHOD, TOBACCO

1273
Lange, D.L., and A.A. Kader. 1997. Effects of elevated carbon dioxide on key mitochondrial respiratory enzymes in 'Hass' avocado fruit and fruit disks. *Journal of the American Society for Horticultural Science 122(2):238-244.*

Preclimacteric avocado [Persea americana (Mill.) cv, Hass] fruit or fruit disks as well as fruit harvested in either June (midseason) or August (late season) and partially ripened were kept in air (21% O-2 + 78% N-2), 20% CO2 + 17% O-2 (63% N-2), or 40% CO2 + 13% O-2 (47% N-2) at either 10 or 20 degrees C. Ethylene production by preclimacteric fruit completely inhibited during CO2 exposure, whereas there was only partial inhibition of ethylene production when partially ripened fruit were exposed, Compared to the fruit stored in air, O-2 uptake of fruit stored in 20% CO2 was decreased by 20%, whereas the fruit stored in 40% CO2 showed 25% more O-2 uptake than air- stored fruit, Fruit subjected to a storage regime of 40% CO2 at 10 degrees C followed by 2 d in air had the best visual quality, In general, climacteric fruit treated with 20% CO2 at 10 degrees C showed increased pyruvate dehydrogenase (PDH) activity and decreased cytochrome oxidase (CytOx) activity, Fruit stored in 40% CO2 had reduced CytOx activity compared to air-stored fruit, and PDH activity was variable depending on the harvest season of the fruit, Our results show that the effect of elevated CO2 on a given enzyme depends on concentration of CO2, duration of exposure, physiological state of the fruit, and type of tissue exposed.

KEYWORDS: ATMOSPHERES, ETHYLENE, METABOLISM, OXYGEN, PEAR FRUIT, QUALITY

1274
Lange, D.L., and A.A. Kader. 1997. Elevated carbon dioxide exposure alters intracellular pH and energy charge in avocado fruit tissue. *Journal of the American Society for Horticultural Science 122(2):253-257.*

Changes in cytosolic and vacuolar pH, ATP, ADP, and the ATP : ADP ratio were measured in whole fruit or mesocarp disks of avocado [Persea americana (Mill.) cv, Hass] during brief exposures to elevated CO2. Intact climacteric fruit exposed to air (21% O-2), 20% CO2(17% O-2, balance N-2), or 40% CO2 (13% O-2, balance N-2) had cytosolic pH values of 7.0, 6.6, and 6.4, respectively, while mesocarp disks had cytosolic pH values of 6.9, 6.7, and 6.4, respectively. The beta-ATP levels of intact climacteric fruit exposed to 20% CO2 or 40% CO2 for 2 h were reduced by 25% or 43%, respectively, relative to air-exposed fruit. HPLC analysis of nucleotide phosphates from preclimacteric

avocados revealed that ATP levels and the ATP : ADP ratio increased in 40% compared to the air-stored fruit. However, 1 day after transfer to air, the effects of elevated CO2 had dissipated. These modifications in cellular state could alter the activity of respiratory enzymes in fruit exposed to elevated CO2 atmospheres.

KEYWORDS: CELLS, CO2, RESPIRATION, VACUOLAR PH

1275

Lange, O.L., T.G.A. Green, H. Reichenberger, and A. Meyer. 1996. Photosynthetic depression at high thallus water contents in lichens: Concurrent use of gas exchange and fluorescence techniques with a cyanobacterial and a green algal Peltigera species. *Botanica Acta 109(1):43-50.*

Lichens, being poikilohydric, have varying thallus water contents (WC) and show a complex interaction between net photosynthesis (NP) and WC. NP can be depressed at low WC (desiccation effects) and, in some species, also at high WC. In the latter case the depression is normally ascribed to increased CO2 diffusion resistances through water blockage. Recently, an earlier explanation, that the depression at high WC is due to recycling of CO2 from increased dark respiration processes (DR), has been given renewed prominence. The two explanations were distinguished by the concurrent use of gas exchange and chlorophyll fluorescence techniques to investigate NP:WC relationships in the lichens Peltigero leucophlebia (green algal) and P. neckeri (cyanobacterial). Both species had a distinct optimal WC for NP with depressed values at low and high WC. The maximal quantum yield for both CO2 fixation (initial slope of light response curves of NP) and photosystem II (fluorescence signals of dark-adapted thalli) was depressed only at low WC and remained high at optimal and greater WC. In contrast, the relative electron transport rate (ETR, derived from fluorescence signals of thalli in the light) tracked NP and was depressed at low and high WC. The depression of both NP and ETR at high WC (not that at low WC) could be prevented by using elevated external CO2 concentrations. A single, linear relationship was found between all values of gross photosynthesis (NP + DR) and ETR regardless of external CO2 concentration or WC. Our results show that, for these lichens, the depression in NP at high WC is a real fall in photosynthetic rate of the photobionts and is not due to recycling of CO2. The removal of the depression in NP and ETR at high WC by using elevated external CO2 levels allows us to conclude that an additional CO2 diffusion resistance is present.

KEYWORDS: CARBON-DIOXIDE EXCHANGE, CHLOROPHYLL FLUORESCENCE, CO2 EXCHANGE, ELECTRON-TRANSPORT, RESISTANCES

1276

Lange, O.L., S.C. Hahn, G. Muller, A. Meyer, and J.D. Tenhunen. 1996. Upland tundra in the foothills of the Brooks Range, Alaska: Influence of light, water content and temperature on CO2 exchange of characteristic lichen species. *Flora 191(1):67-83.*

In a previous publication we described diel courses of CO2 exchange and microclimate conditions for characteristic Lichens in their natural habitat within upland tundra communities of northern Alaska. The influence of individual environmental factors on net photosynthesis (NP) of Cetraria cucullata, Dactylina arctica, Masonhalea richardsonii, Peltigera aphthosa, Peltigera malacea, Stereocaulon alpinum, and Thamnolia vermicularis was analyzed in the present study. CO2 exchange measurements were conducted in the laboratory, and clear response characteristics with respect to light, water content (WC), temperature, and external CO2 concentration were established under controlled conditions. In addition, dependencies of NP on these factors were extracted from field data. These measurements show a high scatter in data points, however, they represent the range of actual performance of the lichens under natural conditions. In general both, field and laboratory data sets, agree well with respect to absolute rates of photosynthetic capacity as well as response characteristics. The combined information from both sources enable us to identify and describe those physiological features which are relevant for photosynthetic production of the lichens at this tundra site. There were large differences in maximal rates of NP attained under natural ambient CO2 which were expressed more strongly under conditions of CO2 saturation. Photosynthetic capacity of the cyanobacterial P. malacea is ten times higher than that of the green algal M. richardsonii. In the field, actual photosynthesis often seemed to be depressed due to photoinhibition. Photosynthetic carbon gain occurred even with thallus temperatures of -10 degrees C, while the temperature optimum of NP was between 11 and 22 degrees C. Most of the species responded to supra-optimal degrees of WC with a pronounced depression in NP. Elevated ambient CO2 concentration prevented this decrease in NP, indicating that it was caused by increased resistance of the thallus to CO2 diffusion. Depression of NP at high thallus WC regularly occurred under natural conditions, impairing primary production. Response characteristic of the lichens to experimental increase in ambient CO2 is highly dependent on thallus hydration. At optimal WC some species are already saturated by natural ambient CO2 at least at lower light intensities. Possible future increase in natural ambient CO2 concentration will impact lichen NP in particular when the thalli are highly water saturated.

KEYWORDS: CARBON-DIOXIDE EXCHANGE, CAROTENOID COMPOSITION, CONTINENTAL ANTARCTIC CRYPTOGAMS, GREEN-ALGAL LICHENS, MOISTURE, PATTERNS, PHOTOINHIBITION, PHOTOSYNTHESIS, PHYSIOLOGICAL INVESTIGATIONS, USNEA-SPHACELATA

1277

Laporte, M.M., J.A. Galagan, J.A. Shapiro, M.R. Boersig, C.K. Shewmaker, and T.D. Sharkey. 1997. Sucrose-phosphate synthase activity and yield analysis of tomato plants transformed with maize sucrose-phosphate synthase. *Planta 203(2):253-259.*

Sucrose synthesis is a major element of the interactions between photosynthesis and plant growth and development. Tomato (Lycopersicon esculentum Mill. cv. UC82B) plants transformed with maize sucrose-phosphate synthase (SPS; EC 2.3.1.14) expressed from either a ribulose-1,5-bisphosphate carboxylase- oxygenase (Rubisco) small subunit promoter (SSU) or the cauliflower mosaic virus 35S promoter (35S) were used to study effects of increased sucrose synthesis rates on plant growth. The plants were grown in growth chambers, field plots, and open-top chambers. The 35S plants had a 2 to 3-fold increase in young-leaf SPS activity, a 10 to 20-fold increase in young-root SPS activity and no increase in young-fruit SPS activity. The leaf SPS activity in;one of the 35S lines fell to control levels by two months of age. The SSU plants had a 4 to 5-fold increase in leaf SPS activity and no significant increase in root or young-fruit SPS activity. One 35S line, which maintained high leaf SPS activity throughout development, yielded 70-80% more than controls at both normal and elevated CO2 in open-top chambers in the field and 20-30% more than controls in two additional field trials. The other 35S line and the two SSU lines either yielded less or did not differ from controls under several growth conditions. Since only one of four transformed lines showed an increase in yield, we can not yet conclude that increased leaf SPS activity leads to increased yield. However, increased leaf SPS activity appears to result in increased fruit sugar content since all three lines with increased leaf SPS usually also had increased fruit sugars.

KEYWORDS: CARBON DIOXIDE, CO2, EXPRESSION, GENES, LEAVES, MECHANISM, PHOTOSYNTHESIS, TEMPERATURE, TRANSGENIC PLANTS

1278
Larigauderie, A., J.F. Reynolds, and B.R. Strain. 1994. Root response to co2 enrichment and nitrogen supply in loblolly-pine. *Plant and Soil 165(1):21-32.*

This paper examines how elevated CO2 and nitrogen (N) supply affect plant characteristics of loblolly pine (Pinus taeda L.) with an emphasis on root morphology. Seedlings were grown in greenhouses from seeds during one growing season at two atmospheric CO2 concentrations (375 and 710 mu L L(-1)) and two N levels (High and Low). Root morphological characteristics were determined using a scanner and an image analysis program on a Macintosh computer. In the high N treatment, elevated CO2 increased total plant dry weight by 80% and did not modify root to shoot (R/S) dry weight ratio, and leaf and plant N concentration at the end of the growing season. In the low N treatment, elevated CO2 increased total dry weight by 60%. Plant and leaf N concentration declined and R/S ratio tended to increase. Nitrogen uptake rate on both a root length and a root dry weight basis was greater at elevated CO2 in the high N treatment and lower in the low N treatment. We argue that N stress resulting from short exposures to nutrients might help explain the lower N concentrations observed at high CO2 in other experiments; Nitrogen and CO2 levels modified root morphology. High N increased the number of secondary lateral roots per length of first order lateral root and high CO2 increased the length of secondary lateral roots per length of first order lateral root. Number and length of first order lateral roots were not modified by either treatment. Specific root length of main axis, and to a lower degree, of first order laterals, declined at high CO2, especially at high N. Basal stem diameter and first order root diameters increased at high CO2, especially at high N. Elevated CO2 increased the proportion of upper lateral roots within the root system.

KEYWORDS: CARBOHYDRATE, CARBON-DIOXIDE ENRICHMENT, GROWTH, NUTRITION, PLANTS, SEEDLINGS

1279
Larsen, M., and C.B. Watkins. 1995. Firmness and concentrations of acetaldehyde, ethyl-acetate and ethanol in strawberries stored in controlled and modified atmospheres. *Postharvest Biology and Technology 5(1-2):39-50.*

'Pajaro' strawberries (Fragaria x ananassa Duch.) were stored at 0 degrees C in a range of controlled atmosphere (CA) conditions with CO2 concentrations up to 24%, O-2 concentrations down to 1%, or a combination of 10% CO2 and 2% O-2 Elevated CO2 concentrations resulted in firmer fruit, while low O-2 did not affect texture. Off-flavours developed after 3 days of storage at 20% CO2, but decreased when fruit was subsequently held for 24 h at 20 degrees C. However, off- flavours were persistent after CA storage for 7 days or more. Off-flavours were related to increases in ethyl acetate and ethanol concentrations but not to acetaldehyde. Beneficial atmospheres of close to 10% CO2 and 2% O-2 resulted in a firmer texture and delayed ripening with no off-flavour development. However, fruit quality was poor when similar atmospheres were developed in modified atmosphere (MA)-producing polythene bags. Rapid imposition of CA resulted in better quality fruit than when MAs around the fruit were developed gradually.

KEYWORDS: DECAY, FRUIT, LIFE, QUALITY, STORAGE

1280
Larson, D.L. 1994. Potential effects of anthropogenic greenhouse gases on avian habitats and populations in the northern great-plains. *American Midland Naturalist 131(2):330-346.*

Biotic response to the buildup of greenhouse gases in Earth's atmosphere is considerably more complex than an adjustment to changing temperature and precipitation. The fertilization effect CO2 has on some plants, the impact UVB radiation has on health and productivity of organisms, and the resulting changes in competitive balance and trophic structure must also be considered. The intent of this paper is to review direct and indirect effects of anthropogenic greenhouse gases on wildlife, and to explore possible effects on populations of birds and their habitats in the northern Great Plains. Many of the potential effects of increasing greenhouse gases, such as declining plant nutritional value, changes in timing of insect emergence, and fewer and saltier wetlands, foreshadow a decline in avian populations on the Great Plains. However, other possible effects such as increased drought resistance and water use efficiency of vegetation, longer growing seasons, and greater overall plant biomass promise at least some mitigation. Effects of multiple simultaneous perturbations such as can be expected under doubled CO2 scenarios will require substantial basic research to clarify.

KEYWORDS: ACTIVE ULTRAVIOLET-RADIATION, ALPINE LIFE ZONE, ATMOSPHERIC CO2, CARBON DIOXIDE, CLIMATE CHANGE, ECOSYSTEM RESPONSES, ELEVATED CO2, LATITUDINAL GRADIENT, LESSER SNOW GEESE, PRAIRIE WETLANDS

1281
Lasceve, G., H. Gautier, J. Jappe, and A. Vavasseur. 1993. Modulation of the blue-light response of stomata of commelina-communis by co2. *Physiologia Plantarum 88(3):453-459.*

Effects of CO2 on stomatal movements of Commelina communis L. were studied with plants, epidermal strips and guard cell protoplasts. With plants, the stomatal response induced by a blue light pulse was studied for different ambient CO2 concentration ranging from CO2-deprived air to 100 Pa in darkness or under red light. It was observed that the blue light response could be obtained not only under a red light background but also in darkness and CO2-free air, the two responses being quite similar. With epidermal strips, the effect of CO2 on ferricyanide reductase activity at the guard cell plasmalemma was studied by transmission electron microscopy. In the presence of ferric ions, reduced ferricyanide gives an electron dense precipitate of Prussian Blue. In darkness and air, no precipitate was observed. In darkness and CO2-free air as well as under light and normal air, a precipitate was found along the plasmalemma of the guard cells, indicating a ferricyanide reductase activity. With guard cell protoplasts suspended in a medium either in equilibrium with air or in a CO2-free medium the H+ extrusion induced by a blue light pulse added to a red light background was measured. A low CO2 content was obtained by adding photosynthetic algae to the suspension of guard cell protoplasts. In a CO2-free medium the rate of H+ extrusion was enhanced. The results are discussed on the basis of a possible competition for reducing power between CO2 fixation and a putative blue light dependent redox chain located on the plasma membrane.

KEYWORDS: EXTRUSION, FERRICYANIDE, GUARD-CELL PROTOPLASTS, MESOPHYLL, METABOLISM, PLASMA-MEMBRANE, REDOX SYSTEM, REDUCTION, TRANSPORT, VICIA-FABA

1282
Lashof, D.A., B.J. DeAngelo, S.R. Saleska, and J. Harte. 1997. Terrestrial ecosystem feedbacks to global climate change. *Annual Review of Energy and the Environment 22:75-118.*

Anthropogenic greenhouse gases are expected to induce changes in global climate that can alter ecosystems in ways that, in turn, may further affect climate. Such climate-ecosystem interactions can generate either positive or negative feedbacks to the climate system, thereby

either enhancing or diminishing the magnitude of global climate change. Important terrestrial feedback mechanisms include CO2 fertilization (negative feedbacks), carbon storage in vegetation and soils (positive and negative feedbacks), vegetation albedo (positive feedbacks), and peatland methane emissions (positive and negative feedbacks). While the processes involved are complex, not readily quantifiable, and demonstrate both positive and negative feedback potential, we conclude that the combined effect of the feedback mechanisms reviewed here will likely amplify climate change relative to current projections that have not yet adequately incorporated these mechanisms.

KEYWORDS: ARCTIC TUNDRA, ATMOSPHERIC CARBON-DIOXIDE, ELEVATED CO2, ICE-CORE RECORD, LAST GLACIAL MAXIMUM, METHANE EMISSIONS, PLANT-RESPONSES, STOMATAL-RESISTANCE, TRACE GAS FLUXES, TROPICAL DEFORESTATION

1283
Lau, O.L. 1998. Effect of growing season, harvest maturity, waxing, low O-2 and elevated CO2 on flesh browning disorders in 'Braeburn' apples. *Postharvest Biology and Technology 14(2):131-141.*

British Columbia-grown 'Braeburn' apples (Malus x domestica Borkh.) stored for 6 months in air at 0 degrees C were, on average, 70 N in flesh firmness and had 0.48% titratable acidity. Fruit held in 1.2 or 1.5% O-2 + 1.0 or 1.2% CO2 controlled atmosphere (CA) storage were 8 N firmer, 20% higher in titratable acidity, and had significantly less core browning and superficial scald than fruit held in air for the same period. However, CA-stored fruit were highly susceptible to Braeburn browning disorder (BBD) and internal cavities (IC) after cool growing seasons [1993, 1995, and 1996; < 1300 degree-days > 10 degrees C (DD10) accumulated between May 1 and harvest]. Susceptibility of fruit to BED and IC was greatest in late-harvested fruit (starch index > 2.5 on a 0-9 scale) stored in 3.0% CO2 and 1.5% O-2. Storage at 1.7, 2.0, 3.0 and 4.0 degrees C did not decrease BED or IC incidence and tended to increase core browning (1996) and flesh softening (1994 and 1996) compared with fruit kept at 0 degrees C. Coating fruit with Shellac wax, but not Carnauba wax, increased BBD in air- stored fruit. Following a cool growing season it is recommended that 'Braeburn' apples be harvested at starch index values between 2.5 and 3.0 and stored in air storage at 0 degrees C to avoid the risks of scald, BED and IC. The fruit may be stored in <1.0% CO2 (preferably close to 0.1%) and > 1.5% O-2 after warm seasons (>1300 DD10). (C) 1998 Elsevier Science B.V. All rights reserved.

KEYWORDS: CARBON-DIOXIDE ATMOSPHERES, GOLDEN DELICIOUS APPLES, LOW OXYGEN, QUALITY, STORAGE PROCEDURES

1284
Lauber, W., and C. Korner. 1997. In situ stomatal responses to long-term CO2 enrichment in calcareous grassland plants. *Acta Oecologica-International Journal of Ecology 18(3):221-229.*

A calcareous grassland community growing under full season CO? enrichment at low altitude in the Swiss Jura mountains was investigated for diurnal and seasonal variations of leaf diffusive conductance. A new CO2 enrichment method (Screen aided CO2 control, SACC) permitted irt situ leaf porometry under natural climatic conditions without disturbance of plants. At 600 ppm CO2, leaf conductance in the dominant species, Bromus erectus (a species so far not showing a growth response to elevated CO2) was reduced to half the values measured in controls. Tn contrast, leaf conductance in Carex flacca, a species of low cover (the only species so far exhibiting a dramatic growth stimulation by CO2 fertilization) remained almost unaffected by elevated CO2. Sanguisorba minor; Plantago media, and Cirsium acaule showed intermediate responses. Trifolium montanum, studied only on a single day, showed a reduction like Bromus. Differences between treatments were largest under humid conditions and disappeared during dry periods. In none of the species studied did stomatal density or stomatal index differ between treatments. A parallel investigation of whole ecosystem evapotranspiration indicated only small (< 10%) and non significant CO2 responses, suggesting that both aerodynamic effects at the canopy level and a great interspecific variation of leaf level responses overshadow the clear CO2 response of Bromus stomata. The different stomatal responses to CO2 enrichment are likely to alter species specific water consumption, and may thus affect community structure in the long run.

KEYWORDS: ACCLIMATION, C-4 GRASS, CARBON DIOXIDE, CONDUCTANCE, DENSITY, ELEVATED ATMOSPHERIC CO2, EXPOSURE, GAS-EXCHANGE, LEAVES, PHOTOSYNTHETIC CAPACITY

1285
Laurila, H.A. 1995. Modelling the effects of elevated CO2 and temperature on Swedish and German spring wheat varieties with CERES-wheat and AFRC-wheat crop models. *Journal of Biogeography 22(4-5):591-595.*

A study validating the CERES-wheat and the AFRC-wheat crop models was performed on Swedish (cv. Polkka) and German (cv. Nandu) spring wheat (Triticum aestivum L.) varieties under northern long day conditions. Validation consisted of the calibration of the phenological submodels in both crop models for Finnish conditions. Calibration results were used in simulating the effects of elevated CO2 and temperature on the yields and biomass production and the phenological development of the Swedish and the German varieties. The Swedish variety is currently commonly-cultivated in Finland. Based on the validation work, the CERES-wheat and the AFRC-wheat models will be used in the climate change Geographical Information System (GIS) for Finnish national scale crop potential estimations: different climate change scenarios for cereals will simulate the future Finnish growing conditions currently prevailing in Denmark and northern Germany.

KEYWORDS: CARBON DIOXIDE, WINTER-WHEAT

1286
Lavelle, P., D. Bignell, M. Lepage, V. Wolters, P. Roger, P. Ineson, O.W. Heal, and S. Dhillion. 1997. Soil function in a changing world: the role of invertebrate ecosystem engineers. *European Journal of Soil Biology 33(4):159-193.*

In this review the interactions between plant, animal and microbial components of the soil biota are represented by a model which allocates a pivotal functional role to the large, abundant invertebrates which ingest or manipulate both organic and mineral material, forming long-lasting microstructures. These invertebrates are designated soil ecosystem engineers and it is argued using data on numerical and biomass densities, geographical distribution and known functional roles, that earthworms and termites are the most important engineers in terrestrial ecosystems. Evidence is presented that they may exert influence on the diversity and activity of biota in subordinate trophic levels, for example litter transformers, micropredators and microfloras mediating fundamental nutrient transformations. Links between the activity and diversity of engineers and the physical properties of soils, including structural heterogeneity, stability, distribution of organic matter and infiltration and retention of water are also described. In considering the probable effects of global change on engineers, it is hypothesized that living plants affect both the abundance and diversity of engineers, through the quantity and quality of litter and other effects. Changes in their communities will therefore affect engineers. Expected changes in

temperature will expand the latitudinal distribution of termites and favour humivorous termites and endogeic earthworm species that feed in the soil. In some regions, however, these changes will not occur since local fauna may not include representatives of these groups. Although elevated CO2 may impact engineers through effects on plant growth (notably an increase in C/N ratio), land use intensification, particularly physical disturbance of forests, is of more immediate concern as changes in the functional group balance within engineers communities can be demonstrated. In addition, exotic species of earthworms may colonize disturbed land, with adverse effects on soil structure. Disturbance affects termites by reducing diversity (especially of soil-feeding forms) and some species may reach crop pest status, owing to changes in the availability of organic matter.

KEYWORDS: ELEVATED ATMOSPHERIC CO2, FUNGUS-GROWING TERMITES, MBALMAYO FOREST RESERVE, MILLSONIA-ANOMALA, MOUND-BUILDING TERMITES, NO-TILLAGE AGROECOSYSTEMS, ORGANIC-MATTER, PONTOSCOLEX-CORETHRURUS GLOSSOSCOLECIDAE, SOUTHERN GUINEA SAVANNA, TROPICAL GEOPHAGOUS EARTHWORM

1287

Lavigne, C., A. Mignot, and J. Stocklin. 1999. Genetic variation in the response of pollen germination to nutrient availability and elevated atmospheric CO2 concentrations in Epilobium angustifolium. *International Journal of Plant Science 160(1):109-115.*

It is expected that global climatic changes could lead to shifts in the genotypic composition of species that exhibit genetic variation in the response of fitness-related traits to an increase of atmospheric CO2. In plants that reproduce sexually, fitness can be described both by a female and a male component. Whereas the existence of genetic variation in the response to elevated CO2 of traits related to female fitness has been the focus of recent studies, studies on the response of the male component of fitness are still missing. Here, we report on the effects of elevated atmospheric CO2 and nutrient availability on che pollen quality of five full-sib families of Epilobium angustifolium. We did not detect an effect of the treatments on the in vitro pollen tube growth. However, we observed significant variation among families for pollen germination probabilities and a significant family x CO2 x nutrient interaction on this trait. This indicates that, in combination with nutrients increased CO2 could exert a selection pressure resulting in changes in the genetic structure of populations and in their mean response to CO2. It seems important that this evolution is included in models simulating the consequences of climate change on plant communities.

KEYWORDS: ARABIDOPSIS-THALIANA, CARBON DIOXIDE, COMPETITIVE ABILITY, CUCURBITA-PEPO CUCURBITACEAE, ERYTHRONIUM-GRANDIFLORUM, GAMETOPHYTIC SELECTION, GROWTH-RESPONSE, MIMULUS-GUTTATUS, RAPHANUS-RAPHANISTRUM, WILD RADISH

1288

Lavigne, M.B. 1996. Comparing stem respiration and growth of jack pine provenances from northern and southern locations. *Tree Physiology 16(10):847-852.*

Stem respiration rates of 31-year-old jack pine (Pinus banksiana Lamb.) trees from northern and southern provenances growing in a common garden were compared. At 15 degrees C, the seasonal course of stem respiration rate of northern provenances was not statistically different from that of southern provenances. A relationship existed between maintenance respiration rate and stem growth rate. Because relationships between sapwood relative growth rate and annual growth and maintenance respiration rates were similar for northern and southern provenances, no clinal differences in stem respiration rates were observed.

KEYWORDS: CO2- ENRICHMENT, DARK RESPIRATION, LOLIUM-PERENNE, MAINTENANCE RESPIRATION, MATURE LEAVES, PERENNE CV S23, REQUIREMENTS, RESPONSES, SELECTION, SIMULATED SWARDS

1289

Lavola, A., and R. Julkunentiitto. 1994. The effect of elevated carbon-dioxide and fertilization on primary and secondary metabolites in birch, betula-pendula (roth). *Oecologia 99(3-4):315-321.*

Seedlings of European white birch (Betula pendula Roth) were grown in growth chambers for one growth season under four carbon dioxide regimes (350, 700, 1050 and 1400 pm) and at three fertilization levels (0, 100 and 500 kg ha(-1) monthly). The soluble carbohydrates and secondary phenolics in the leaves and stems were analysed. It was found that fertilizer addition reduced the amounts of glucose and fructose while sucrose remained almost unaffected. The sugar content of leaves increased at 700 ppm and 1050 ppm of CO2 and decreased at the highest CO2 concentration (1400 ppm). The amounts of proanthocyanidins and flavonoids in leaves decreased with fertilization addition and increased with CO2 enrichment. The production of simple phenolic glucosides varied according to the fertilization and CO2 treatments. The triterpenoid content of stems seemed to increase with fertilization and CO2 addition. Our results indicate that the production of phytochemicals in the birch seedlings is very sensitive to both fertilization and CO2 addition, which is in agreement with earlier studies, and thus provide some support for the hypothesis of carbon allocation to plant defence when there is an excess of carbon and nutrient. The considerable variation in the production of secondary components may indicate that the synthesis of these defensive metabolites can be regulated by a plant to certain extent, depending on the ability of the plant to acclimate to changes in the physical environment.

KEYWORDS: ALASKA PAPER BIRCH, ALLOCATION, ATMOSPHERIC CO2, CHLOROPHYLL CONTENT, CO2-ENRICHMENT, GROWTH, NITROGEN- FERTILIZATION, NUTRIENT BALANCE, PLANTS, SALIX-MYRSINIFOLIA

1290

Lawler, I.R., W.J. Foley, I.E. Woodrow, and S.J. Cork. 1997. The effects of elevated CO2 atmospheres on the nutritional quality of Eucalyptus foliage and its interaction with soil nutrient and light availability. *Oecologia 109(1):59-68.*

Seedlings of Eucalyptus tereticornis (Smith) were grown under two levels of availability each of CO2 (352 and 793 mu mol mol(-1)), soil nutrients (1/24 and 1/4 Hoagland's solution) and light (full and 30% sunlight). Low soil nutrient availability or high light increased the C:N ratio of leaves, leading to lower leaf nitrogen concentrations, higher leaf specific weights and higher levels of both total phenolics and condensed tannins. These results were consistent with other studies of the effect of environmental resource availability on foliage composition. Similar results were observed when the C:N ratio of leaves was increased under elevated CO2. The changes in leaf chemistry induced by the treatments affected the performance of 4th-instar larvae of Chrysophtharta flaveola (Chapuis) fed on the leaves. Increased C:N ratios of leaves reduced digestive efficiencies and pupal body sizes and increased mortality. Below a threshold nitrogen concentration of approximately 1% dry mass, severe reductions in the performance of larvae were recorded. Such changes may have significant consequences for herbivores of Eucalyptus, particularly in view of projected increases in atmospheric CO2.

KEYWORDS: ALLELOCHEMICALS, CARBON ALLOCATION, CHRYSOMELIDAE, COLEOPTERA, DIETARY FIBER, NITROGEN, PAROPSIS-ATOMARIA OLIVIER, PLANTS, POLYSACCHARIDES, RESPONSES

1291

Lawlor, D.W., and R.A.C. Mitchell. 1991. The effects of increasing CO2 on crop photosynthesis and productivity - a review of field studies. *Plant, Cell and Environment 14(8):807-818.*

Only a small proportion of elevated CO2 studies on crops have taken place in the field. They generally confirm results obtained in controlled environments: CO2 increases photosynthesis, dry matter production and yield, substantially in C3 species, but less in C4, it decreases stomatal conductance and transpiration in C3 and C4 species and greatly improves water-use efficiency in all plants. The increased productivity of crops with CO2 enrichment is also related to the greater leaf area produced. Stimulation of yield is due more to an increase in the number of yield-forming structures than in their size. There is little evidence of a consistent effect of CO2 on partitioning of dry matter between organs or on their chemical composition, except for tubers. Work has concentrated on a few crops (largely soybean) and more is needed on crops for which there are few data (e.g. rice). Field studies on the effects of elevated CO2 in combination with temperature, water and nutrition are essential; they should be related to the development and improvement of mechanistic crop models, and designed to test their predictions.

KEYWORDS: AGAVE-VILMORINIANA, AIR- TEMPERATURE, ATMOSPHERIC CO2, CO2-ENRICHED ATMOSPHERE, ELEVATED CARBON-DIOXIDE, LEAF-AREA, PLANT GROWTH, SOYBEAN PHYSIOLOGY, STOMATAL CONDUCTANCE, WATER-USE EFFICIENCY

1292

Lawlor, D.W., R.A.C. Mitchell, J. Franklin, V.J. Mitchell, S.P. Driscoll, and E. Delgado. 1993. Facility for studying the effects of elevated carbon-dioxide concentration and increased temperature on crops. *Plant, Cell and Environment 16(5):603-608.*

The requirements for the experimental study of the effects of global climate change conditions on plants are outlined. A semi-controlled plant growth facility is described which allows the study of elevated CO2 and temperature, and their interaction on the growth of plants under radiation and temperature conditions similar to the field. During an experiment on winter wheat (cv. Mercia), which ran from December 1990 through to August 1991, the facility maintained mean daytime CO2 concentrations of 363 and 692 cm3 m-3 for targets of 350 and 700 cm3 m-3 respectively. Temperatures were set to follow outside ambient or outside ambient +4-degrees-C, and hourly means were within 0.5-degrees-C of the target for 92% of the time for target temperatures greater than 6-degrees- C. Total photosynthetically active radiation incident on the crop (solar radiation supplemented by artifical light with natural photoperiod) was 2% greater than the total measured outside over the same period.

KEYWORDS: CO2, FIELD, PRODUCTIVITY, SOURCE-SINK RELATIONS, WHEAT, YIELD

1293

Lawton, J.H., S. Naeem, R.M. Woodfin, V.K. Brown, A. Gange, H.J.C. Godfray, P.A. Heads, S. Lawler, D. Magda, C.D. Thomas, L.J. Thompson, and S. Young. 1993. The ecotron - a controlled environmental facility for the investigation of population and ecosystem processes. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences 341(1296):181-194.*

This paper reports on aspects of the design and philosophy of the Ecotron, an integrated series of 16 controlled environmental chambers at the NERC Centre for Population Biology. The Ecotron serves as an experimental means for analysing population and community dynamics and ecosystem processes under controlled physical conditions. Within the chambers, terrestrial experimental communities are assembled into foodwebs of desired complexity from a pool of species selected for their preadaptations to the physical conditions of the Ecotron. These species include decomposers (earthworms, snails, microarthropods and microbes), primary producers (16 species of plants), primary consumers (four species of herbivorous arthropods), and secondary consumers (four species of parasitoids). The design of the Ecotron is unique in several aspects with respect to its blend of biology and technology. It supports small, dynamic communities of up to 30 plant and metazoan species, thereby making it among the more biologically complex controlled environmental systems currently in use. Its architecture permits replication and variation of spatial scale in experimental design. Its artificial climate simulates natural environmental conditions within chambers allowing experimental control over light, water, temperature, humidity, and in the near future CO2 and uv-B radiation. Sensors monitor both macro- and micro-environmental conditions of a number of physical factors within the chambers. Preliminary experiments show the Ecotron to be an excellent facility for long-term population and community-level experiments. We discuss the results of one of these early experiments and briefly consider ongoing and future experiments.

KEYWORDS: CLIMATE CHANGE, COMPETITION, DECIDUOUS WOODLAND, ELEVATED CO2, FIELD, HERBACEOUS VEGETATION, HOST-PARASITOID ASSOCIATIONS, PATCHY ENVIRONMENTS, PERSISTENCE, TREE LEAF LITTER

1294

Leadley, P.W., and B.G. Drake. 1993. Open top chambers for exposing plant canopies to elevated co2 concentration and for measuring net gas-exchange. *Vegetatio 104:3-15.*

Open top chamber design and function are reviewed. All of the chambers described maintain CO2 concentrations measured at a central location within +/- 30 ppm of a desired target when averaged over the growing season, but the spatial and temporal range within any chamber may be closer to 100 ppm. Compared with unchambered companion plots, open top chambers modify the microenvironment in the following ways: temperatures are increased up to 3-degrees-C depending on the chamber design and location of the measurement; light intensity is typically diminished by as much as 20%; wind velocity is lower and constant; and relative humidity is higher. The chamber environment may significantly alter plant growth when compared with unchambered controls, but the chamber effect on growth has not been clearly attributed to a single or even a few environmental factors. A method for modifying an open top chamber for tracking gas exchange between natural vegetation and the ambient air is described. This modification consists of the addition of a top with exit chimney to reduce dilution of chamber CO2 by external ambient air, is quickly made and permits estimation of the effects of elevated CO2 and water vapor exchange. The relatively simple design and construction of open top chambers make them the most likely method to be used in the near future for long-term elevated CO2 exposure of small trees, crops and grassland ecosystems. Improvements in the basic geometry to improve control of temperature, reduce the variation of CO2 concentrations, and increase the turbulence and wind speed in the canopy boundary layer are desirable objectives. Similarly, modifications for measuring water vapor and carbon dioxide gas exchange will extend the usefulness of open top chambers to include non-destructive monitoring of the responses of ecosystems to rising atmospheric CO2.

KEYWORDS: AIR-POLLUTION, ATMOSPHERIC CO2, CARBON DIOXIDE, COMMUNITIES, ESTUARINE MARSH, FIELD CHAMBERS, GROWTH, PHOTOSYNTHESIS, RESPONSES, TRANSPIRATION

1295

Leadley, P.W., P. Niklaus, R. Stocker, and C. Korner. 1997. Screen-aided CO2 control (SACC): a middle ground between FACE and open-top chambers. *Acta Oecologica-International Journal of Ecology 18(3):207-219.*

We have developed a novel CO2 exposure system for natural vegetation that is a middle ground between Free Air CO2 Enrichment (FACE) and traditional open-top chambers (OTC). Screen-Aided CO2 Control (SACC) technology uses much less CO2 per experiment and per replicate than FACE and is superior to OTCs in terms of its effects on microclimate. A SACC unit consists of a thin metal frame, a clear plastic "screen", and a pipe at the base of the screen through which CO2 enriched jets of air are directed into the unit. There is a gap between the ground and the bottom of the pipe and the screen is relatively short in comparison to the maximum height of the vegetation. Our SACC units are hexagonal and enclose a ground area of 1.27 m(2). SACC works in the following way: 1) the screen breaks the wind and creates turbulent mixing within the unit, 2) the mixing of the outside air with the CO2 enriched jets of air,generates relatively uniform CO2 concentrations within the screened-in vegetation, and 3) a fully automated system monitors CO2 concentrations and adjusts CO2 injection rates for each unit every ca. IO minutes to maintain preset CO2 concentrations. Twenty-four hour means of CO2 concentrations in the middle of a unit are typically maintained within 1 mu l l(- 1) of their set points. Spatial variation and short-term fluctuations in CO2 concentration are similar to those in OTCs and FACE. CO2 consumption at our site is 5 kg CO2 day(-1) replicate(-1) for a total of ca. 30 tons per year for 20 elevated CO2 SACC units. Compared to OTCs, SACC units have reduced temperature peaks at full sunlight, minimal effects on solar radiation, reduced rainfall interception by chamber walls, and freer access of small animals to experimental plots. We believe that SACC is the best method for exposing short stature vegetation to elevated CO2 when financial constraints do not allow for a properly replicated FACE experiment.

KEYWORDS: ENRICHMENT, ENVIRONMENT, FIELD

1296

Leadley, P.W., P.A. Niklaus, R. Stocker, and C. Korner. 1999. A field study of the effects of elevated CO2 on plant biomass and community structure in a calcareous grassland. *Oecologia 118(1):39-49.*

The effects of elevated CO2 on plant biomass and community structure have been studied for four seasons in a calcareous grassland in northwest Switzerland. This highly diverse, semi- natural plant community is dominated by the perennial grass Bromus erectus and is mown twice a year to maintain species composition. Plots of 1.3 m(2) were exposed to ambient or elevated CO2 concentrations (n = 8) using a novel CO2 exposure technique, screen-aided CO2 control (SACC) starting in March 1994. In the 1st year of treatment, the annual harvested biomass (sum of aboveground biomass from mowings in June and October) was not significantly affected by elevated CO2. However, biomass increased significantly at elevated CO2 in the 2nd (+20%, P = 0.05), 3rd (+21%, P = 0.02) and 4th years (+29%, P = 0.02). There were no detectable differences in root biomass in the top 8 cm of soil between CO2 treatments on eight out of nine sampling dates. There were significant differences in CO2 responsiveness between functional groups (legumes, non- leguminous forbs, graminoids) in the 2nd (P = 0.07) and 3rd (P < 0.001) years of the study. The order of CO2 responsiveness among functional groups changed substantially from the 2nd to the 3rd year; for example, non-leguminous forbs had the smallest relative response in the 2nd year and the largest in the 3rd year. By the 3rd year of CO2 exposure, large species- specific differences in CO2 response had developed. For five important species or genera the order of responsiveness was Lotus corniculatus (+271%), Carex flacca (+249%), Bromus erectus (+ 33%), Sanguisorba minor (no significant CO2 effect), and six Trifolium species (a negative response that was not significant). The positive CO2 responses in Bromus and Carex were most closely related to increases in tiller number. Species richness was not affected by CO2 treatment, but species evenness increased under elevated CO2 (modified Hill ratio; P = 0.03) in June of the 3rd year, resulting in a marginally significant increase in species diversity (Simpson's index; P = 0.09). This and other experiments with calcareous grassland plants show that elevated atmospheric CO2 concentrations can substantially alter the structure of calcareous grassland communities and may increase plant community biomass.

KEYWORDS: AMBIENT, ATMOSPHERIC CO2, CARBON, CHALK GRASSLAND, ECOSYSTEMS, ENRICHMENT, GROWTH, LEAF, LEVEL RESPONSES, ROOT

1297

Leadley, P.W., and J.F. Reynolds. 1992. Long-term response of an arctic sedge to climate change - a simulation study. *Ecological Applications 2(4):323-340.*

It appears that polar regions of the Ear-th will bear the brunt of global temperature increases. Because of the ecological importance of the sedge Eriophorum vaginatum in the arctic and the large amount ot data available on its growth and physiology, we chose this species as a test case to model the potential long-term response of arctic plants to global climate change. Our simulation model utilizes a mechanistic framework and includes the effects of light, temperature, season length, nitrogen availability, and CO2 concentration on E. vaginatum growth dynamics. The model was parameterized based on a series of published studies of the growth responses of E. vaginatum to nutrients and validated using (1) field studies on the growth responses of E. vaginatum to temperature and shading, and (2) the effects of elevated CO2 and temperature on E. vaginatum photosynthesis. The effect of a 50-yr period of climate change on peak biomass (overwintering biomass plus seasonal production) in E. vaginatum was explored. We use climate change here to refer to linear increases over a 50-yr period in temperature (from 8-degrees to 13-degrees-C), season length (from 100 to 120 d), and atmospheric CO2 (from 340 to 680 muL/L). Similarly, a wide range of nitrogen availabilities (from 9 to 18 g.m 2.vr-1) was also examined because of its importance in productivity. The model predicts that a simultaneous increase in the direct effects of temperature, season length, and CO2, with no change in nitrogen availability, will result in a slight decrease in peak biomass. A simulated long-term doubling of nitrogen availability results in an almost-equal-to 70% increase in peak biomass, whereas with concurrent changes in climate and nitrogen availability, the model predicts a slight decline in peak biomass compared to increases in nitrogen alone. In essence, the model predicts that climate change will have substantial effects on E. vaginatum only indirectly through changes in nitrogen availability. Simulated peak biomass responds linearly up to a doubling of current nitrogen availabilities. Therefore, at low- to-moderate increases in nitrogen availability, the predicted response of E. vaginatum to climate change is linearly (and almost exclusively) dependent on our ability to predict the effects of climate change on nitrogen cycling. At nitrogen availabilities > 2 x current availabilities, the relationship flattens out very rapidly because the plant becomes limited by carbon uptake. Thus, if nitrogen availabilities more than double in the future, E. vaginatum may shift from being a nutrient-limited to a carbon-limited system and, consequently, increased season length and elevated CO2 concentrations may play an important role in controlling E. vaginatum productivity.

KEYWORDS: ACCUMULATION, ALASKAN TUSSOCK TUNDRA,

BIOMASS, CARBON DIOXIDE, ERIOPHORUM VAGINATUM, GROWTH, PHOTOSYNTHESIS, PLANTS, TEMPERATURE, VEGETATION TYPES

1298

Leadley, P.W., and J. Stocklin. 1996. Effects of elevated CO2 on model calcareous grasslands: Community, species, and genotype level responses. *Global Change Biology 2(4):389-397.*

We investigated the responses of model calcareous grassland communities to three CO2 concentrations: 330, 500, and 660 mu L L(-1). The communities were composed of six species, Bromus erectus Hudson, Festuca ovina L., Prunella vulgaris L., Prunella grandiflora (L.) Scholler, Hieracium pilosella L., and Trifolium repens L., that are native to the calcareous grasslands of Europe. Genotypic variation in CO2 response was studied in Bromus erectus and Festuca ovina. Plants were harvested after c. 126 days of growth. We found that: 1 At the community level, there were marginally significant (0.1 greater than or equal to P > 0.05) increases in leaf and litter dry weight with increasing CO2 concentration. 2 There were significant differences between species in CO2 response, including both negative and positive responses. Prunella vulgaris had a significant negative response; Hieracium pilosella and Festuca ovina had significant positive responses; Prunella grandiflora had a marginally significant positive response; and Bromus erectus and Trifolium repens did not have significant responses. 3 There was significant variation among genotypes in the response to elevated CO2 in Bromus erectus, but not in Festuca ovina. Based on the observed species- and genotype-level variation in CO2 response of calcareous grassland plants in this and other studies, we speculate that increasing atmospheric CO2 concentrations will alter community structure in calcareous grasslands.

KEYWORDS: AMBIENT, ENRICHMENT, GROWTH, NITROGEN, NUTRIENTS, PLANTAGO, TEMPERATURE

1299

Leavitt, S.W., E.A. Paul, A. Galadima, F.S. Nakayama, S.R. Danzer, H. Johnson, and B.A. Kimball. 1996. Carbon isotopes and carbon turnover in cotton and wheat FACE experiments. *Plant and Soil 187(2):147-155.*

The Maricopa cotton and wheat FACE (free-air CO2 enrichment) experiments offer propitious opportunity to quantify carbon turnover. The commercial CO2 (delta(13)C approximate to-37 parts per thousand) used to elevate CO2 concentration in field plots provided a strongly C-12-depleted tracer. Soil CO2 and delta(13)C of soil organic carbon (SOC) in CO2-enriched and Control plots were measured between the final cotton FACE project (October 1991) and the end of the second wheat experiment (June 1994). The initial C-13-depletion in SOC of cotton FACE plots (measured by the difference in delta(13)C between FACE and Control plots) persisted at the same level (1.9 parts per thousand) 1.5 years after the experiment ended. A similar depletion was observed in soil CO2 evolved in the same plots, indicating ongoing decomposition of the new SOC. The SOC delta(13)C of wheat plots before and after two growing seasons showed increasing C-13-depletion in FACE relative to Control. Isotopic mass balance was consistent with 5-6% new carbon input from the two wheat crops. This is lower than the 12-13% calculated for FACE cotton and perhaps a consequence of the larger root system of cotton or the 3-year duration of the cotton experiments versus 2 years for the wheat.

KEYWORDS: DIOXIDE, DYNAMICS, NATURAL C-13 ABUNDANCE, SOIL ORGANIC MATTER

1300

Leavitt, S.W., E.A. Paul, B.A. Kimball, G.R. Hendrey, J.R. Mauney, R. Rauschkolb, H. Rogers, K.F. Lewin, J. Nagy, P.J. Pinter, and H.B. Johnson. 1994. Carbon-isotope dynamics of free-air co2-enriched cotton and soils. *Agricultural and Forest Meteorology 70(1-4):87-101.*

A role for soils as global carbon sink or source under increasing atmospheric CO2 concentrations has been speculative. Free-air carbon dioxide enrichment (FACE) experiments with cotton, conducted from 1989 to 1991 at the Maricopa Agricultural Center in Arizona, maintained circular plots at 550 mumol mol-1 CO2 with tank CO2 while adjacent ambient control plots averaged about 370 mumol mol-1 CO2. This provided an exceptional test for entry of carbon into soils because the petrochemically derived tank CO2 used to enrich the air above the FACE plots was depleted in both radiocarbon (C-14 content was 0% modern carbon (pmC)) and C-13 (delta13 C almost- equal-to -36 parts per thousand) relative to background air, thus serving as a potent isotopic tracer. Flask air samples, and plant and soil samples were collected in conjunction with the 1991 experiment. Most of the isotopic analyses on the plants were performed on the holecellulose component. Soil organic carbon was obtained by first removing carbonate with HCl, floating off plant fragments with a NaCl solution, and picking out remaining plant fragments under magnification. The delta C-13 of the air above the FACE plots was approximately - 15 to - 19 parts per thousand, i.e. much more C-13 depleted than the background air of approximately -7.5parts per thousand. The delta C-13 values of plants and soils in the FACE plots were 10-12 parts per thousand and 2 parts per thousand C-13-depleted, respectively, compared with their control counterparts. The C-14 content of the FACE cotton plants was approximately 40 pmC lower than that of the control cotton, but the C-14 results from soils were conflicting and therefore not as revealing as the delta C-13 of soils. Soil stable-carbon isotope patterns were consistent, and mass balance calculations indicate that about 10% of the present organic carbon content in the FACE soil derived from the 3 year FACE experiment. At a minimum, this is an important quantitative measure of carbon turnover, but the presence of C- 13-depleted carbon, even in the recalcitrant 6 N HCl resistant soil organic fraction (average age 2200 years before present (BP)), suggests that at least some portion of this 10% is an actual increase in carbon accumulation. Similar isotopic studies on FACE experiments in different ecosystems could permit more definitive assessment of carbon turnover rates and perhaps provide insight into the extent to which soil organic matter can accommodate the 'missing' carbon in the global carbon cycle.

KEYWORDS: ABUNDANCE, FLUXES, ROOT

1301

LeCain, D.R., and J.A. Morgan. 1998. Growth, gas exchange, leaf nitrogen and carbohydrate concentrations in NAD-ME and NADP-ME C-4 grasses grown in elevated CO2. *Physiologia Plantarum 102(2):297-306.*

Plants with the C-4 photosynthetic pathway have predominantly one of three decarboxylation enzymes in their bundle sheath cells. Within the grass family (Poaceae) bundle sheath leakiness to CO2 is purported to be lowest in the nicotinamide adenine dinucleotide phosphate-malic enzyme (NADP-ME, EC 1.1.1.40) group, highest in the NAD-ME (EC 1.1.1.39) group and intermediate in the phosphoenolpyruvate carboxykinase (PCK, EC 4.1.1.32) group. We investigated the hypothesis that growth and photosynthesis of NAD-ME C-4 grasses would respond more to elevated CO2 treatment than NADP-ME grasses. Plants were frown in 8-1 pots in growth chambers with ample water and fertilizer for 39 days at a continuous CO2 concentration of either 350 or 700 mu l 1(-1). NAD-ME species included Bouteloua gracilis Lag. ex Steud (Blue grama), Buchloe dactyloides (Nutt.) Engelm. (Buffalo grass) and Panicum virgatum L. (Switchgrass) and the NADP-ME species were Andropogon gerardii Vittman (Big bluestem), Schizachyrium scoparium (Michx.) Nash (Little bluestem), and Sorghastrum mutans (L.) Nash

(Indian grass). Contrary to our hypothesis, growth of the NADP-ME grasses was generally greater under elevated CO2 (significant for A. gerardii and S. mutans), while none of the NAD-ME grasses had a significant growth response. Increased leaf total non- structural carbohydrate (TNC) was associated with greater growth responses of NADP-ME grasses. Decreased leaf nitrogen in NADP-ME species grown at elevated CO2 was found to be an artifact of TNC dilution. Assimilation (A) vs intercellular CO2 (C-i) curves revealed that leaf photosynthesis was not saturated at 350 mu l 1(-1) CO2, in any of these C-4 grasses. Assimilation of elevated CO2-grown A. gerardii was higher than in plants grown in ambient CO2. In contrast, B. gracilis grown in elevated CO2 displayed lower A, a trait more commonly reported in C-3 plants. Photosynthetic acclimation is B. gracilis was not related to leaf TNC or nitrogen concentrations, but A:C-i curves suggest a reduction in activity of both phosphoenolpyruvate (PEP) carboxylase (EC 4.1.1.31) and ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco, EC 4.1.1.39). Some adaptation of stomatal functioning was also seen in B. gracilis and A. gerardii leaves grown in elevated CO2. Our study shows that C-4 grasses have the capacity for increased growth and photosynthesis under elevated CO2 even when water and nutrients are non-limiting. While it was the NADP-ME species which had significant responses in the present study, we have previously reported significant growth increases in elevated CO2 for B. gracilis.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, BOUTELOUA-GRACILIS C-4, CARBON DIOXIDE, ENRICHMENT, PASCOPYRUM-SMITHII C-3, PHOTOSYNTHESIS, PLANTS, RESPONSES, TEMPERATURE

1302

Lechowicz, M.J., and T. Koike. 1995. Phenology and seasonality of woody-plants - an unappreciated element in global change research. *Canadian Journal of Botany-Revue Canadienne De Botanique 73(2):147-148.*

KEYWORDS: BUDBURST, CO2, FROST DAMAGE, INCREASE, TEMPERATE TREES

1303

Ledergerber, S., P.W. Leadley, J. Stocklin, and B. Baur. 1998. Feeding behaviour of juvenile snails (Helix pomatia) to four plant species grown at elevated atmospheric CO2. *Acta Oecologica-International Journal of Ecology 19(1):89-95.*

The feeding behaviour of juveniles of the land snail Helix pomatia was examined in model plant communities consisting of Trifolium repens, Hieracium pilosella, Bromus erectus and Prunella vulgaris that are common species in extensively managed calcareous grasslands in the Swiss Jura mountains. The plant communities were grown either at ambient (350 ppm) or elevated (600 ppm) CO2 concentrations. Leaves of T. repens and P. vulgaris grown in elevated atmospheric CO2 had a lower specific leaf area, and leaves of T. repens had lower percentage N on a dry weight basis than leaves grown under ambient CO2 concentration. Snails fed on all four plant species, but showed a overwhelming preference for T. repens (percentages of total biomass consumed were 91.9 % at 350 ppm and 97.6 % at 600 ppm). The species-specific feeding intensity of juvenile H. pomatia did not differ between the two treatments. The total dry weight of T. repens consumed by the snails was marginally greater (P = 0.06) at elevated CO2, but there were no significant differences in leaf N or leaf area eaten. These findings are similar to numerous other studies showing that invertebrates increase their consumption of plant material to balance reductions in plant N concentrations at elevated CO2 treatments. Helix pomatia that fed on plants grown at elevated CO2 atmosphere showed a larger increase in relative wet weight than those that fed on plants from ambient CO2 conditions. However, the weight gain of H. pomatia was poorly correlated with amount of plant tissue consumed, so we suggest that the effect of CO2 on weight gain in H. pomatia was due to a change in the quality of T. repens leaves. (C) Elsevier, Paris.

KEYWORDS: HERBIVORY, PAPER BIRCH, PERFORMANCE, QUALITY, RESPONSES

1304

Ledergerber, S., G.H. Thommen, and B. Baur. 1997. Grazing damage to plants and gastropod and grasshopper densities in a CO2-enrichment experiment on calcareous grassland. *Acta Oecologica-International Journal of Ecology 18(3):255-261.*

Plant-herbivore interactions may change as atmospheric CO2 concentrations continue to rise. We examined the effects of elevated atmospheric CO2 and CO2-exposure chambers on the grazing damage to plants, and on the abundances of potential herbivores (terrestrial gastropods and grasshoppers) in a calcareous grassland in the Jura mountains of Switzerland (village of Nenzlingen). Individuals of most plant species examined showed slight grazing damage. However, plots with CO2 enrichment and plots with ambient atmosphere did not differ in the extent of grazing damage. Similarly, plots with CO2 enrichment and plots with ambient atmosphere did not differ in either gastropod or grasshopper density. Experimental plots with and without chambers did not differ in the number of gastropods. However, the densities of gastropods and grasshoppers and extent of grazing damage to plants were generally lower in the experimental area than in the grassland outside the experimental field.

KEYWORDS: ATMOSPHERES, CO2, INSECT HERBIVORE INTERACTIONS

1305

Lee, E.H., R.C. Pausch, R.A. Rowland, C.L. Mulchi, and B.F.T. Rudorff. 1997. Responses of field-grown soybean (cv. Essex) to elevated SO2 under two atmospheric CO2 concentrations. *Environmental and Experimental Botany 37(2-3):85-93.*

The objective of this research was to determine the effects of elevated concentrations of carbon dioxide (CO2) and sulfur dioxide (SO2) on field-grown soybean. Soybeans (Glycine max L. Merr. cv. 'Essex') were grown a full-season in open-top field chambers exposed to either ambient (350 mu l L-1) or elevated CO2 (500 mu l L-1) levels under two levels of SO2 (0.00 and 0.12 mu l L-1). Enriched CO2, with or without SO2 treatments, significantly increased net photosynthesis rates, leaf area index (LAI; in R4 growth stage) and leaf dry weight, but did not significantly affect stomatal resistance, transpiration rates, leaf area, plant height, total biomass or grain yield. Elevated SO2 treatments significantly decreased photosynthesis and LAI during pod fill stages, but did not significantly affect stomatal resistance, transpiration, total biomass, plant height or grain yield. Sulfur dioxide inhibited growth and development (i.e., LAI) during canopy coverage before any effects on photosynthesis were detected. The interactive effects of CO2 and SO2 treatments on the gas exchange parameters were significant during pod fill, where high SO2 reduced photosynthesis at ambient CO2 but not under elevated CO2. Leaf area index values were likewise reduced by SO2 exposure under ambient CO2 during late flowering and pod fill stages. Thus, enriched CO2 under high SO2 exposure partially compensated for the negative impact of SO2 stress on PS and LAI during the pod fill stages. (C) 1997 Elsevier Science B.V.

KEYWORDS: AIR- POLLUTANTS, CARBON DIOXIDE, CROP RESPONSES, ENRICHMENT, FUMIGATION, GLYCINE-MAX, PHOTOSYNTHESIS, PLANTS, SPRUCE TREES, SULFUR-DIOXIDE

1306
Lee, H.S.J., and P.G. Jarvis. 1995. Trees differ from crops and from each other in their responses to increases in CO2 concentration. *Journal of Biogeography 22(2-3):323-330.*

Length of exposure, degree of maturity and type of tissue all affect the results obtained in response to elevated CO2 treatment of trees. Seedlings are most responsive and, in many cases, the first few weeks or months of exposure may set the pattern for future growth. Measurements of leaf photosynthesis and respiration are not good predictors for incorporation of carbon into tissue. Seasonal changes in non-structural carbohydrates, emissions of isoprenes from leaves and exudation from roots can 'waste' photosynthate. However, these are difficult or impossible to quantify. Currently, the only generalization that can be made is that growth will be accelerated but the magnitude of this depends on tissue type, nutrition and environmental conditions. The implications of this for a future elevated atmospheric CO2 world are complex. Interactions and competition between species should be incorporated into long-term studies. These studies must, themselves, be incorporated into appropriate models which take into account regional soils and climates for use in prediction of the effects of global climate change on trees and forests.

KEYWORDS: ALLOCATION, ELEVATED CARBON-DIOXIDE, ENHANCEMENT, ENRICHMENT, GROWTH, NUTRIENTS, NUTRITION, PHOTOSYNTHETIC ACCLIMATION, PLANTS, SEEDLINGS

1307
Lee, H.Y., W.S. Chow, and Y.N. Hong. 1999. Photoinactivation of photosystem II in leaves of Capsicum annuum. *Physiologia Plantarum 105(2):377-384.*

Leaf discs of Capsicum annuum L. were illuminated in air enriched with 1% CO2 in the absence or presence of lincomycin, an inhibitor of chloroplast-encoded protein synthesis. The loss of functional photosystem (PS) II complexes with increase in cumulative light dose (photon exposure), assessed by the O-2 yield per single-turnover flash, was greater in leaves of plants grown in low light than those in high light; it was also exacerbated in the presence of lincomycin. A single exponential decay can describe the relationship between the loss of functional PSII and increase in cumulative photon exposure. From this relationship we obtained both the maximum quantum yield of photoinactivation of PSII at limiting photon exposures and the coefficient k, interpreted as the probability of photoinactivation of PSII per unit photon exposure. Parallel measurements of chlorophyll fluorescence after light treatment showed that 1/F-o--1/F-m was linearly correlated with the functionality of PSII, where F-o and F-m are the chlorophyll fluorescence yields corresponding to open and closed PSII reaction centers, respectively. Using 1/F-o--I/F-m as a convenient indicator of PSII functionality, it was found that PSII is present in excess; only after tbe loss of about 40% functional PSII complexes did PSII begin to limit photosynthetic capacity in capsicum leaves.

KEYWORDS: ANTENNA SIZE, COEFFICIENTS, FLUORESCENCE, GROWTH IRRADIANCE, LEAF-DISKS, LIGHT, PHOTOINHIBITION, PHOTOSYNTHETIC APPARATUS, RATE-CONSTANT, YIELD

1308
Lee, J.J., D.L. Phillips, and R.F. Dodson. 1996. Sensitivity of the US corn belt to climate change and elevated CO2 .2. Soil erosion and organic carbon. *Agricultural Systems 52(4):503-521.*

Climate models indicate that increasing atmospheric concentrations of carbon dioxide and other greenhouse gases could alter climate globally. The EPIC (Erosion/Productivity Impact Calculator) model was used to examine the sensitivity of soil erosion (wind, water) and soil organic carbon (SOC) (15 cm and 1 m depth) across the US corn belt to changes in temperature (+2 degrees C), precipitation (+/-10%, +/-20%), wind speed (+/-10%, +/-20%), and atmospheric CO2 concentration (350, 625 ppmv). One-hundred-year simulations were run for each of 100 sites under 36 climate/CO2 regimes. The 100-year regionally aggregated mean water erosion rates increased linearly with precipitation, whereas the wind erosion rates decreased and total erosion rates increased by 15-18%. Total erosion increased with increased temperature. Increasing CO2 from 350 to 625 ppmv (with temperature increased by 2 degrees C and mean wind speed held constant) had no effect on water erosion, despite increases in annual total and peak runoff; this was attributed to increased vegetation cover. Wind erosion decreased by 4-11% under increased CO2. Wind erosion was very sensitive to mean wind speed, increasing four-fold and decreasing 10-fold for a 20% increase or decrease in mean wind speed, respectively. This was attributed to a threshold effect. SOC to 1 m decreased 4.8 Mg-C ha(-1) from an initial value of 18.1 Mg-C ha(-1) during the 100-year baseline simulation. About 50% of this loss (2.3 Mg-C ha(-1)) was due to transport off- site by soil erosion. SOC in the top 15 cm decreased 0.8 Mg-C ha(-1) from an initial value of 4.9 Mg-C ha(-1). Increased temperature and precipitation accelerated these losses of SOC, whereas increased CO2 slowed the losses.

KEYWORDS: MODEL, YIELD

1309
Lee, X.H., J.D. Fuentes, R.M. Staebler, and H.H. Neumann. 1999. Long-term observation of the atmospheric exchange of CO2 with a temperate deciduous forest in southern Ontario, Canada. *Journal of Geophysical Research-Atmospheres 104(D13):15975-15984.*

This paper reports the results of the analysis of eddy covariance CO2 data obtained at a successional forest of maple and aspen at Camp Borden in southern Ontario, Canada, between July 1995 and December 1997. Main findings are (1) The Michaelis-Menton model explains >50-65% of the observed variance of the daytime net ecosystem carbon exchange (NEE) during the growing season; leaf wetness appears to be an important variable contributing to the remaining variance. (2) The whole-ecosystem respiration rate as a function of the 5-cm soil temperature shows a seasonal "hysteresis" (higher rate in the later part of the year), suggesting a nonnegligible contribution by deep soil/roots and the influence of litter age. (3) There is evidence of photosynthetic activities immediately after the spring snowmelt/soil warming, but the. daily NEE did not switch sign till about 40 days later; our best estimates of the annual net carbon uptake by the ecosystem net ecosystem production (NEP) are -1,0, -1.2, and -2.8 t C ha(-1) yr(-1) for the periods July 19, 1995, to July 18, 1996, January 1 to December 31, 1996, and January 1 to December 31, 1997, respectively, with an uncertainty of +/-0.4 t C ha(-1) yr(-1). (4) The higher NEP value in 1997 than in 1996 was caused by lower growing season soil temperature, cooler spring and fall transitional periods, and higher photon flux in 1997; possible enhancement in canopy photosynthetic capacity may also have played a role. In addition, three main sources of uncertainties, data gap, fetch, and mass flow, are discussed, it is suggested that collective use of the methods available for assessing the whole-ecosystem respiration (friction velocity threshold, mass flow theory, and dark respiration from the forest light response) may increase the confidence level of NEP estimates.

KEYWORDS: CARBON-DIOXIDE EXCHANGE, CLIMATE, EDDY-CORRELATION, FLUXES, RAIN-FOREST, SENSITIVITY, SOIL RESPIRATION, USE EFFICIENCY, VEGETATION, WATER-VAPOR EXCHANGE

1310
Leech, R.M., and J.L. Marrison. 1996. Immunofluorescent

quantitation of chloroplast proteins. *Plant Journal 10(6):1169-1175.*

Using scanning light microscopy software to detect and measure immunofluorescence in leaf sections Rubisco concentration in situ in chloroplasts has been accurately determined throughout development. The fluorescence measurements were calibrated by comparison with values for Rubisco accumulation obtained from rocket immunoelectrophoresis profiles of soluble protein from isolated cells and from chloroplasts using a purified sample of Rubisco as the standard. It has been shown that in situ immunofluorescence can be used for cytoquantitation of proteins within individual chloroplasts to a sensitivity of 1fg and also for the comparison of the protein levels in adjacent chloroplasts and cells. Several important applications of this new technique are discussed.

KEYWORDS: CELLS, DIVISION, DNA, ELEVATED CO2, GROWN WHEAT LEAVES, TEMPERATURE

1311
Leemans, R. 1992. Modeling ecological and agricultural impacts of global change on a global scale. *Journal of Scientific & Industrial Research 51(8-9):709-724.*

The changing composition of the atmosphere could lead to significant changes in regional and continental climate. The methodology to develop consistent climate-change scenarios and to link them to different impact-models is discussed. Results of both static and dynamic models are presented and the advantages and disadvantages of the different approaches are addressed. Examples are drawn from different impact studies on large-scale vegetation patterns, forest dynamics and agricultural systems. General conclusions of these studies are that vegetation and agricultural zones will shift on global, continental and regional scales, but that large uncertainties still exist in the timing, actual response and rate of change of the current zones. Despite these uncertainties, the direction of these models indicates future developments and could be used for policy purposes.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CLIMATIC CHANGE, CO2, CONSEQUENCES, DYNAMICS, FORESTS, GROWTH, PHOTOSYNTHESIS, SENSITIVITY, VEGETATION

1312
Leemans, R., A. vanAmstel, C. Battjes, E. Kreileman, and S. Toet. 1996. The land cover and carbon cycle consequences of large-scale utilizations of biomass as an energy source. *Global Environmental Change-Human and Policy Dimensions 6(4):335-357.*

The use of modern biomass for energy generation has been considered in many studies as a possible measure for reducing or stabilizing global carbon dioxide (CO2) emissions. In this paper we assess the impacts of large-scale global utilization of biomass on regional and grid scale land cover, greenhouse gas emissions, and carbon cycle. We have implemented in the global environmental change model IMAGE the LESS biomass intensive scenario, which was developed for the Second Assessment Report of IPCC. This scenario illustrates the potential for reducing energy related emission by different sets of fuel mixes and a higher energy efficiency. Our analysis especially covers different consequences involved with such modern biomass scenarios. We emphasize influences of CO2 concentrations and climate change on biomass crop yield, land use, competition between food and biomass crops, and the different interregional trade patterns for modern biomass based energy. Our simulations show that the original LESS scenario is rather optimistic on the land requirements for large-scale biomass plantations. Our simulations show that 797 Mha is required while the original LESS scenario is based on 550 Mha. Such expansion of agricultural land will influence deforestation patterns and have significant consequences for environmental issues, such as biodiversity. Altering modern biomass requirements and the locations where they are grown in the scenario shows that the outcome is sensitive for regional emissions and feedbacks in the C cycle and that competition between food and modern biomass can be significant, We conclude that the cultivation of targe quantities of modern biomass is feasible, but that its effectiveness to reduce emissions of greenhouse gases has to he evaluated in combination with many other environmental land use and soclo-economic factors. Copyright (C) 1996 Elsevier Science Ltd

KEYWORDS: CROPS, EMISSIONS, GLOBAL CHANGE, MODEL, SCENARIOS, SEQUESTRATION

1313
Leishman, M.R., L. Hughes, K. French, D. Armstrong, and M. Westoby. 1992. Seed and seedling biology in relation to modeling vegetation dynamics under global climate change. *Australian Journal of Botany 40(4-5):599-613.*

The distribution of many plant species will change with global climate change, depending on their ability to disperse into, and establish in, new communities. Past migrations of species under climate change have been an order of magnitude slower than the rate of predicted climate change for the next century. The limited evidence available suggests that chance long distance dispersal events will be critically important in determining migration rates. We examine the JABOWA-derived gap replacement models and vital attributes/FATE models and ask: what do we need to know about dispersal and establishment to make improved projections of vegetation dynamics under climate change using these models? The minimal modifications of these models required to incorporate directional migration of species are described. To predict establishment success of species, we suggest that a more fundamental understanding is needed of how establishment ability under different conditions relates to seed and seedling attributes and how this may be affected by elevated CO2. Finally, we examine whether plant functional types based on vegetative attributes (used to model the response of adult plants) are correlated with functional types based on seed and seedling attributes. Available evidence suggests that the two sets of attributes are not strongly correlated; consequently, models of vegetation dynamics will need to incorporate seed biology explicitly.

KEYWORDS: CO2, COMPUTER-MODEL, DISPERSAL, ESTABLISHMENT, GROWTH, PATTERNS, RAIN-FOREST, SUCCESSION MODEL, TEMPERATURES, WOODY-PLANTS

1314
Lenssen, G.M., J. Lamers, M. Stroetenga, and J. Rozema. 1993. Interactive effects of atmospheric co2 enrichment, salinity and flooding on growth of C-3 (elymus-athericus) and C-4 (spartina- anglica) salt-marsh species. *Vegetatio 104:379-388.*

The growth response of Dutch salt marsh species (C3 and C4) to atmospheric CO2 enrichment was investigated. Tillers of the C3 species Elymus athericus were grown in combinations of 380 and 720 mul l-1 CO2 and low (0) and high (300 mM NaCl) soil salinity. CO2 enrichment increased dry matter production and leaf area development while both parameters were reduced at high salinity. The relative growth response to CO2 enrichment was higher under saline conditions. Growth increase at elevated CO2 was higher after 34 than 71 days. A lower response to CO2 enrichment after 71 days was associated with a decreased specific leaf area (SLA). In two other experiments the effect of CO2 (380 and 720 mul l-1) on growth of the C4 species Spartina anglica was studied. In the first experiment total plant dry weight was reduced by 20% at elevated CO2. SLA also decreased at high CO2. The effect of elevated CO2 was also studied in combination with soil salinity (50 and 400 mM NaCl) and flooding. Again plant weight was reduced (10%) at elevated

CO2, except under the combined treatment high salinity/non- flooded. But these effects were not significant. High salinity reduced total plant weight while flooding had no effect. Causes of the salinity-dependent effect of CO2 enrichment on growth and consequences of elevated CO2 for competition between C3 and C4 species are discussed.

KEYWORDS: CARBON-DIOXIDE ENRICHMENT, CHLOROPLASTS, GAS-EXCHANGE, IRRADIANCE, LEAVES, LONG-TERM EXPOSURE, PHOTOSYNTHETIC INHIBITION, RESPONSES, SEEDLINGS, WATER-STRESS

1315

Lenssen, G.M., W.E. Vanduin, P. Jak, and J. Rozema. 1995. The response of aster-tripolium and puccinellia-maritima to atmospheric carbon-dioxide enrichment and their interactions with flooding and salinity. *Aquatic Botany 50(2):181-192.*

The effects of 380 and 720 mumol mol-1 atmospheric CO2 on growth, dry matter allocation, net leaf photosynthesis and stomatal conductance of the C3 salt marsh species Aster tripolium L. and Puccinellia maritima (Hudson) Parl. were studied. Plants were grown in pots under combinations of low (50-250 mM NaCl) or high (450-550 mM NaCl) salinity and non- flooded or flooded salt marsh soil. High salinity reduced growth of both species, while flooding increased biomass production of A. tripolium. Root weight of A. tripolium and total plant weight of P. maritima was increased by atmospheric CO2 enrichment when the soil was flooded. Under non-flooded conditions, the effect of elevated CO2 on growth was small (P. maritima) or absent (A. tripolium). The relative increase in total plant weight of both species by elevated CO2 was higher under saline conditions. Dry matter allocation between root, stem and leaf, as reflected in leaf weight ratio and shoot to root ratio, was not changed by elevated CO2, while specific leaf area was slightly decreased by CO2 enrichment. Elevated CO2 stimulated net leaf photosynthesis of both species, while stomatal conductance decreased. These effects were not changed by salinity or flooding treatment.

KEYWORDS: C-3, COMMUNITIES, ELEVATED CO2, ELYMUS-ATHERICUS, ENVIRONMENT, ESTUARINE MARSH, GROWTH, HALOPHYTES, NITROGEN, PHOSPHORUS

1316

Leonardos, E.D., and B. Grodzinski. 1997. Photosynthesis, export and carbon partitioning in source leaves of C-3, C-3-C-4 intermediate and C-4 Panicum species at ambient and elevated CO2 levels. *Plant Physiology 114(3):221.*

1317

Leonardos, E.D., M.J. Tsujita, and B. Grodzinski. 1994. Net carbon-dioxide exchange-rates and predicted growth-patterns in alstroemeria-jacqueline at varying irradiances, carbon- dioxide concentrations, and air temperatures. *Journal of the American Society for Horticultural Science 119(6):1265-1275.*

The influence of irradiance, CO2 concentration, and air temperature on leaf and whole-plant net C exchange rate (NCER) of Alstroemeria 'Jacqueline' was studied. At ambient CO2, leaf net photosynthesis was maximum at irradiances above 600 mu mol.m(-2).s(-1) photosynthetically active radiation (PAR), while whole-plant NCER required 1200 mu mol.m(-2).s(-1) PAR to be saturated. Leaf and whole-plant NCERs were doubled under CO2 enrichment of 1500 to 2000 mu l CO2/liter. Leaf and whole-plant NCERs declined as temperature increased from 20 to 35C. Whereas the optimum temperature range for leaf net photosynthesis was 17 to 23C, whole-plant NCER, even at high light and high CO2, declined above 12C. Dark respiration of leaves and whole plants increased with a Q(10) of approximate to 2 at 15 to 35C. In an analysis of day effects, irradiance, CO2 concentration, and temperature contributed 58%, 23%, and 14%, respectively, to the total variation in NCER explained by a second-order polynomial model (R(2)=0.85). Interactions among the factors accounted for 4% of the variation in day C assimilation. The potential whole- plant growth rates during varying greenhouse day and night temperature regimes were predicted for short- and long-day scenarios. The data are discussed with the view of designing experiments to test the importance of C gain in supporting flowering and high yield during routine harvest of Alstroemeria plants under commercial greenhouse conditions.

KEYWORDS: CO2 EXCHANGE, PHOTOPERIOD, PLANT, REGINA

1318

LeThiec, D., and M. Dixon. 1996. Acclimation of photosynthesis in Norway spruce and red oak grown in open-top chambers and subjected to natural drought and to elevated CO2. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 26(1):87-94.*

Eight-year-old Norway spruce (Picea abies (L.) Karst.) and 6- year-old red oak (Quercus rubra L.) trees planted directly into the soil were enclosed in open-top chambers and exposed to either 350 or 700 mu mol . mol(-1) of CO2 for three growing seasons. During the third year a natural drought was allowed to develop, reducing the predawn leaf water potential to between - 0.80 and -1.15 MPa. Intensive gas-exchange measurements were performed before, during, and after the drought. CO2 response curves revealed mesophyll limitation to photosynthesis in drought-stressed trees grown in elevated levels of CO2. The water-use efficiency was greater for trees grown at elevated CO2, but less so during drought in red oak and the same between treatments for drought-stressed spruce. Diurnal measurements showed that enhancement of assimilation rates of trees grown at 700 mu mol . mol(-1) depended upon the time of day that measurements were made. There was an acclimation to increased CO2 in both species that could not be explained by leaf area differences, available soil for roots, nutrient limitation, or starch accumulation.

KEYWORDS: ASSIMILATION, EFFICIENCY, ENHANCEMENT, ENRICHMENT, GAS-EXCHANGE, IRRADIANCE, LEAVES, SEEDLINGS, WATER-STRESS

1319

Lethiec, D., M. Dixon, P. Loosveldt, and J.P. Garrec. 1995. Seasonal and annual variations of phosphorus, calcium, potassium and manganese contents in different cross-sections of picea-abies (L) karst needles and quercus-rubra L leaves exposed to elevated co2. *Trees-Structure and Function 10(2):55-62.*

Norway spruce and red oak trees were planted directly into the soil and enclosed in open-top chambers. For 2 years the trees were exposed to both ambient and elevated CO2 concentrations (700 mu mol mol(-1)) and during this time variations in nutrient concentrations were studied. CO2-treated plants had decreases in global leaf concentrations of nitrogen, potassium, calcium and manganese for both species. When different areas of the foliage were analysed however, the response showed much variability between the respective sites and between species. Furthermore the nutrient concentrations changed differently as the plant material aged and this change showed inter-treatment differences. These results show how it may be important to analyse plant material of different ages and at different cell sites when studying nutrient levels.

1320

Leung, L.R., and S.J. Ghan. 1999. Pacific northwest climate sensitivity simulated by a regional climate model driven by a GCM. Part II: 2xCO(2) simulations. *Journal of Climate 12(7):2031-2053.*

Global climate change due to increasing concentrations of greenhouse gases has stimulated numerous studies and discussions about its possible impacts on water resources. Climate scenarios generated by climate models at spatial resolutions ranging from about 50 km to 400 km may not provide enough spatial specificity for use in impact assessment. In Parts I and II of this paper. the spatial specificity issue is addressed by examining what information on mesoscale and small- scale spatial features can be gained by using a regional climate model with a subgrid parameterization of orographic precipitation and land surface cover, driven by a general circulation model. Numerical experiments have been performed to simulate the present-day climatology and the climate conditions corresponding to a doubling of atmospheric CO2 concentration. This paper describes and contrasts the large-scale and mesoscale features of the greenhouse warming climate signals simulated by the general circulation modal and regional climate model over the Pacific Northwest. Results indicate that changes in the large-scale circulation exhibit strong seasonal variability. There is an average warming of about 2 degrees C, and precipitation generally increases over the Pacific Northwest and decreases over California. The precipitation signal over the Pacific Northwest is only statistically significant during spring, when both the change in the large- scale circulation and increase in water vapor enhance the moisture convergence toward the north Pacific coast. The combined effects of surface temperature and precipitation changes are such that snow cover is reduced by up to 50% on average, causing large changes in the seasonal runoff. This paper also describes the high spatial resolution (1.5 km) climate signals simulated by the regional climate model. Reductions in snow cover of 50%-90% are found in areas near the snow line of the control simulation. Analyses of the variations of the climate signals with surface elevation ranging from sea level to 4000 m over two mountain ranges in the Pacific Northwest show that because of changes in the alitude of the freezing level, strong elevation dependency is found in the surface temperature, rainfall. snowfall, snow cover, and runoff signals.

KEYWORDS: ATMOSPHERIC CO2, WATER-RESOURCES

1321

Leverenz, J.W. 1995. Shade shoot structure of conifers and the photosynthetic response to light at 2 co2 partial pressures. *Functional Ecology 9(3):413-421.*

1. The response of net photosynthesis to irradiance was measured for shade-adapted shoots of different conifer species. Shoots were illuminated unidirectionally or in a light integrating sphere to study the effects of shoot structure. 2. Shoot structure was quantified as R(max) the ratio of the shoot-silhouette area to the leaf-silhouette area. 3. The initial slopes and the convexities (rate of bending) of the light response curves were strongly affected by R(max) during unilateral illumination. There was also a strong positive effect of R(max) on the maximum efficiency of net photosynthesis and a strong negative effect of R(max) on the light compensation point. 4. Increasing atmospheric CO2 partial pressure (C-a) from 35 to 70 Pa did not affect the convexity of the light response curves nor rates of dark respiration. 5. Increasing C-a affected the initial slope, the light compensation point, the maximum rate of photosynthesis and the efficiency of net photosynthesis. 6. Except for the maximum rate of net photosynthesis, the responses to C-a were controlled by shoot structure. 7. Studies of the effect of atmospheric CO2 on photosynthesis and growth in conifers need to consider variations in shoot structure.

KEYWORDS: AREA, CURVE, ELEVATED CO2, GROWTH, MODELS, SCOTS PINE, SEEDLINGS, STANDS, TEMPERATURES

1322

Levis, S., J.A. Foley, and D. Pollard. 1999. Potential high-latitude vegetation feedbacks on CO2-induced climate change. *Geophysical Research Letters 26(6):747-750.*

We use a fully coupled climate-vegetation model to examine the potential effects of changes in vegetation cover on simulations of CO2-induced climate change. We find that vegetation feedbacks, acting mainly through changes in surface albedo, enhance greenhouse warming in the northern high latitudes during spring and summer months. In spring and summer, land surfaces north of 45 degrees N are warmed by 3.3 and 1.7 degrees C by a doubling of CO2 alone; vegetation feedbacks produce an additional warming of between 1.1-1.6 and 0.4-0.5 degrees C, respectively. In winter, however, vegetation feedbacks appear to oppose the 5.6 degrees C radiative warming, particularly over Eurasia. These results demonstrate that vegetation feedbacks are potentially significant and must be included in assessments of anthropogenic climate change.

KEYWORDS: BALANCE, BOREAL FOREST, DOUBLED ATMOSPHERIC CO2, GLOBAL CLIMATE, MODEL, SURFACE ALBEDO

1323

Lewin, K.F., G.R. Hendrey, J. Nagy, and R.L. Lamorte. 1994. Design and application of a free-air carbon-dioxide enrichment facility. *Agricultural and Forest Meteorology 70(1-4):15-29.*

Growth chambers and other enclosures used in plant physiology and growth studies tend to introduce chamber effects that alter the microclimate around the plants compared with the natural environment. A free-air (chamberless) carbon dioxide enrichment (FACE) system has been developed by Brookhaven National Laboratory (BNL) to provide controlled fumigation conditions while minimizing the potential to impose a discernible chamber effect. This system is capable of exposing large numbers of field-grown plants to elevated levels of atmospheric carbon dioxide (CO2) from seedling emergence until physiologic maturity. A FACE User Facility was established at the Maricopa Agricultural Center, University of Arizona, for continuous enrichment of CO2 at a set point of 550 mumol mol-1 during daylight hours throughout the cotton crop growing seasons of 1989-1991. The facility consisted of four circular BNL FACE arrays and associated equipment placed in a commercial cotton plantation. FACE array diameters of 23, 25, and 27 m were tested. The FACE facility included the ability to operate the experimental plots under two watering regimes using an automated, sub-surface irrigation system. CO2 was stored in a 48 000 kg receiver and vaporized with a heat exchanger that used water at ambient temperature as the energy source. The 1 min average CO2 concentration was held to within +/- 20% of the set point more than 98% of the time that the arrays were operating during all three seasons. In 1991, the long term average CO2 concentration measured at 63 points throughout the volume of a 20 m diameter experimental plot (ground to canopy top) centered within a 25 m diameter FACE array was 568 mumol mol-1. All of the FACE arrays operated for more than 99% of the planned experimental period in 1991. These 3 years of operation have demonstrated that the BNL FACE technology can be used as a basis for a large scale facility devoted to studying the fate of carbon in the terrestrial environment.

1324

Lewis, C.E., G. Peratoner, A.J. Cairns, D.R. Causton, and C.H. Foyer. 1999. Acclimation of the summer annual species, Lolium temulentum, to CO2 enrichment. *Planta 210(1):104-114.*

Lolium temulentum L. Ba 3081 was grown hydroponically in air (350 mu mol mol(-1) CO2) and elevated CO2 (700 mu mol mol(-1) CO2) at two irradiances (150 and 500 mu mol m(-2) s(-1)) for 35 days at which point the plants were harvested. Elevated CO2 did not modify relative growth rate or biomass at either irradiance. Foliar carbon-to-nitrogen ratios were decreased at elevated CO2 and plants had a greater number of shorter tillers, particularly at the lower growth irradiance. Both light-limited and light-saturated rates of photosynthesis were stimulated. The amount of ribulose-1,5-bisphosphate carboxylase-oxygenase (Rubisco) protein was increased at elevated CO2, but maximum extractable Rubisco activities were not significantly increased. A pronounced decrease in the Rubisco activation stale was found with CO2 enrichment, particularly at the higher growth irradiance. Elevated-CO2-induced changes in leaf carbohydrate composition were small in comparison to those caused by changes in irradiance. No CO2-dependent effects on fructan biosynthesis were observed. Leaf respiration rates were increased by 68% in plants grown with CO2 enrichment and low light. We conclude that high CO2 will only result in increased biomass if total light input favourably increases the photosynthesis-to-respiration ratio. At low irradiances, biomass is more limited by increased rates of respiration than by CO2-induced enhancement of photosynthesis.

KEYWORDS: AMBIENT CO2, ATMOSPHERIC CO2, CARBON-DIOXIDE CONCENTRATION, ELEVATED CO2, EXCISED LEAVES, FRUCTAN BIOSYNTHESIS, NITRATE REDUCTASE, PHASEOLUS-VULGARIS, PHOTOSYNTHESIS, PLANT-GROWTH ANALYSIS

1325

Lewis, J.D., K.L. Griffin, R.B. Thomas, and B.R. Strain. 1994. Phosphorus supply affects the photosynthetic capacity of loblolly-pine grown in elevated carbon-dioxide. *Tree Physiology 14(11):1229-1244.*

Effects of phosphorus supply and mycorrhizal status on the response of photosynthetic capacity to elevated CO2 were investigated in loblolly pine (Pinus taeda L.) seedlings. Seedlings were grown in greenhouses maintained at either 35.5 or 71.0 Pa CO2 in a full factorial experiment with or without mycorrhizal inoculum (Pisolithus tinctorius (Pers.) Coker & Couch) and with an adequate or a limiting supply of phosphorus. Assimilation versus internal CO2 partial pressure (C(i)) curves were used to estimate maximum Rubisco activity (V(c,max)), electron transport mediated ribulose 1,5-bisphosphate regeneration capacity (J(max)), phosphate regeneration capacity (PiRC) and daytime respiration rates (R(d)). Nonmycorrhizal seedlings grown with limiting phosphorus had significantly reduced V(c,max) and PiRC compared to seedlings in other treatments. Elevated CO2 increased photosynthetic capacity in nonmycorrhizal seedlings in the low phosphorus treatment by increasing PiRC, whereas it induced phosphorus limitation in mycorrhizal seedlings in the low phosphorus treatment and did not affect the photosynthetic capacity of seedlings in the high phosphorus treatment. Despite the variety of effects on photosynthetic capacity, seedlings in the elevated CO2 treatments had higher net assimilation rates than seedlings in the ambient CO2 treatments. We conclude that phosphorus supply affects photosynthetic capacity during long-term exposure to elevated CO2 through effects on Rubisco activity and ribulose 1,5-bisphosphate regeneration rates.

1326

Lewis, J.D., D. Olszyk, and D.T. Tingey. 1999. Seasonal patterns of photosynthetic light response in Douglas- fir seedlings subjected to elevated atmospheric CO2 and temperature. *Tree Physiology 19(4-5):243-252.*

Increases in atmospheric CO2 concentration and temperature are predicted to increase the light response of photosynthesis by increasing light-saturated photosynthetic rates and apparent quantum yields. We examined the interactive effects of elevated atmospheric CO2 concentration and temperature on the light response of photosynthesis in Douglas-fir (Pseudotsuga menziesii (Mirb.) France) seedlings. Seedlings were grown in sunlit chambers controlled to track either ambient (similar to 400 ppm) CO2 or ambient + 200 ppm CO2, at ambient temperature or ambient +4 degrees C. Photosynthetic light response curves were measured over an 18-month period beginning 32 months after treatments were initiated. Light-response curves were measured at the growth CO2 concentration, and were used to calculate the light-saturated rate of photosynthesis, light compensation point, quantum yield and respiration rate. Elevated CO2 increased apparent quantum yields during two of five measurement periods, but did not significantly affect light- saturated net photosynthetic rates, light compensation points or respiration rates. Elevated temperature increased all parameters. There were no significant interactions between CO2 concentration and temperature. We conclude that down-regulation of photosynthesis occurred in the elevated CO2 treatments such that carbon uptake at a given irradiance was similar across CO2 treatments. In contrast, increasing temperature may substantially increase carbon uptake rates in Douglas-fir, assuming other environmental factors do not limit photosynthesis; however, it is not clear whether the increased carbon uptake will increase growth rates or be offset by increased carbon efflux through respiration.

KEYWORDS: CARBON-DIOXIDE CONCENTRATION, COMPENSATORY RESPONSES, DECIDUOUS FOREST, DIFFERENT IRRADIANCE LEVELS, GAS-EXCHANGE, GROWTH-RESPONSES, LIQUIDAMBAR- STYRACIFLUA, LOBLOLLY-PINE, PINUS-TAEDA SEEDLINGS, WATER-STRESS

1327

Lewis, J.D., and B.R. Strain. 1996. The role of mycorrhizas in the response of Pinus taeda seedlings to elevated CO2. *New Phytologist 133(3):431-443.*

The effects of mycorrhizal status, phosphorus supply and CO2 partial pressure on production and allocation of biomass in seedlings from two populations of Pinus taeda L. were examined. Seedlings from a North Carolina and a Florida population were grown in sterile soil in a full-factorial experiment with one of two phosphorus treatments (low P, high P) and at one of two CO2 partial pressures (35.5, 71.0 Pa). One half of the seedlings were inoculated with Pisolithus tinctorius (Pers.) Coker & Couch hyphae and spores. Seedlings were harvested 60, 90 and 120 d after emergence. Elevated CO2 significantly increased total seedling dry mass in all treatments at all three harvests. Phosphorus limitation reduced seedling growth, and mycorrhizas increased seedling growth in seedlings limited by phosphorus supply. Generally, however, there were no interactions between CO2, phosphorus supply and mycorrhizal status on dry mass of seedlings. Mycorrhizas probably did not affect the response of dry mass to elevated CO2 because phosphorus limitation did not reduce response of dry mass to elevated CO2. Phosphorus-limited seedlings responded to elevated CO2 as a result of increased phosphorus uptake, resulting from increased total root dry mass, and increased phosphorus use efficiency. Although mycorrhizal colonization did not affect the response of biomass to elevated CO2, it significantly reduced the response of needle area. As a result, specific leaf area (leaf area per unit plant biomass) was lower in mycorrhizal seedlings grown in elevated CO2 than in mycorrhizal seedlings grown in ambient CO2. Because there were no effects on relative growth rate or seedling dry mass, reductions in specific leaf area suggest that elevated CO2 reduced the relative cost of the symbiosis.

KEYWORDS: ATMOSPHERIC CO2, CARBON-DIOXIDE ENRICHMENT, FUNGUS PISOLITHUS-TINCTORIUS, LIQUIDAMBAR- STYRACIFLUA, LONG-TERM EXPOSURE, PHOSPHORUS DEFICIENCY, PHOTOSYNTHETIC ACCLIMATION,

RADIATA D-DON, TRIFOLIUM-SUBTERRANEUM L, UNITED-STATES

1328
Lewis, J.D., R.B. Thomas, and B.R. Strain. 1994. Effect of elevated co2 on mycorrhizal colonization of loblolly- pine (pinus-taeda L) seedlings. *Plant and Soil 165(1):81-88.*

Interactive effects of elevated atmospheric CO2 and phosphorus supply on mycorrhizal colonization rates were investigated using loblolly pine (Pinus taeda L.) seedlings from Florida and coastal North Carolina. Seedlings from both populations were grown in greenhouses maintained at either 35.5 Pa or 71.0 Pa CO2. In both CO2 treatments, seedlings were grown in a full factorial experiment with or without mycorrhizal inoculum and with an adequate or a limiting supply of phosphorus. Seedlings were harvested 60, 90 and 120 days after emergence and at each harvest root subsamples were examined to determine the percent of fine roots that were mycorrhizal. Additionally, root carbohydrate and nutrient levels were measured at each harvest. Root starch, sugar and total non-structural carbohydrate (TNC) concentrations were increased by growth in elevated CO2 and decreased by mycorrhizal colonization. Phosphorus stress decreased root starch concentrations, increased root sugar concentrations and did not significantly affect TNC concentrations. However, despite significant effects on root carbohydrate levels, there were generally no significant treatment effects on mycorrhizal colonization. Additionally, at all harvests, root starch and sugar concentrations were not correlated with percent of fine roots that were mycorrhizal. These results suggest that although elevated CO2 may significantly increase root carbohydrate levels, the increases may not affect the percent of fine roots that are mycorrhizal.

KEYWORDS: GROWTH, INCREASES, INFECTION, NUTRIENT, PHOSPHORUS, PLANTS, QUERCUS-ALBA, SOIL

1329
Lewis, J.D., D.T. Tissue, and B.R. Strain. 1996. Seasonal response of photosynthesis to elevated CO2 in loblolly pine (Pinus taeda L) over two growing seasons. *Global Change Biology 2(2):103-114.*

Trees growing in natural systems undergo seasonal changes in environmental factors that generate seasonal differences in net photosynthetic rates. To examine how seasonal changes in the environment affect the response of net photosynthetic rates to elevated CO2, we grew Pinus taeda L. seedlings for three growing seasons in open-top chambers continuously maintained at either ambient or ambient + 30 Pa CO2. Seedlings were grown in the ground, under natural conditions of light, temperature and nutrient and water availability. Photosynthetic capacity was measured bimonthly using net photosynthetic rate vs. intercellular CO2 partial pressure (A-C-i) curves. Maximum Rubisco activity (Vc(max) and ribulose 1,5-bisphosphate regeneration capacity mediated by electron transport (J(max)) and phosphate regeneration (PiRC) were calculated from A-C-i curves using a biochemically based model. Rubisco activity, activation state and content, and leaf carbohydrate, chlorophyll and nitrogen concentrations were measured concurrently with photosynthesis measurements. This paper presents results from the second and third years of treatment. Mean leaf nitrogen concentrations ranged from 13.7 to 23.8 mg g(-1), indicating that seedlings were not nitrogen deficient. Relative to ambient CO2 seedlings, elevated CO2 increased light-saturated net photosynthetic rates 60-110% during the summer, but < 30% during the winter. A relatively strong correlation between leaf temperature and the relative response of net photosynthetic rates to elevated CO2 suggests a strong effect of leaf temperature. During the third growing season, elevated CO2 reduced Rubisco activity 30% relative to ambient CO2 seedlings, nearly completely balancing Rubisco and RuBP- regeneration regulation of photosynthesis. However, reductions in Rubisco activity did not eliminate the seasonal pattern in the relative response of net photosynthetic rates to elevated CO2. These results indicate that seasonal differences in the relative response of net photosynthetic rates to elevated CO2 are likely to occur in natural systems.

KEYWORDS: ATMOSPHERIC CO2, C-3 PLANTS, CARBON DIOXIDE, GAS-EXCHANGE, LIQUIDAMBAR- STYRACIFLUA, PHASEOLUS-VULGARIS L, RIBULOSE 1;5-BISPHOSPHATE, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, SCIRPUS- OLNEYI, TUSSOCK TUNDRA

1330
Leymarie, J., G. Lasceve, and A. Vavasseur. 1998. Interaction of stomatal responses to ABA and CO2 in Arabidopsis thaliana. *Australian Journal of Plant Physiology 25(7):785-791.*

Stomatal responses to ABA and CO2 were investigated in Arabidopsis thaliana (L.) Heynh. wild-type and ABA insensitive mutants (abi1-1, abi2-1, abi1-1 abi2-1) at the whole plant and at the isolated epidermis levels. In wild-type plants, feeding roots with ABA (1-50 mu M) triggered a rapid drop in leaf conductance which levelled off during the following photoperiods, and strongly inhibited the increase in conductance induced by light. The rapid response was strongly inhibited in abi1-1, abi2-1 and abi1-1 abi2-1 double mutants, but a residual long-term decrease in leaf conductance was still observed. In wild-type plants, exogenous ABA strongly enhanced the response to CO2 removal. Conversely, in the absence of CO2 the effect of ABA was drastically reduced in epidermal strip experiments. These results reveal a strong interaction between sensing of ABA and CO2 in stomata of A. thaliana. Despite an initially wide stomatal aperture in abi-1, abi-2 and double mutant plants, their stomatal responses to light and CO2 removal were half those of wild-type plants. Moreover these responses were totally independent of the presence of ABA, suggesting that ABI1 and ABI2 are either directly involved in the interaction between the two signalling pathways or, alternatively located upstream of this point of interaction.

KEYWORDS: ABSCISIC- ACID, CALCIUM, CARBON DIOXIDE, GUARD-CELLS, MUTANTS, MUTATIONS, PROTEIN PHOSPHATASE, SIGNAL-TRANSDUCTION, SLOW ANION CHANNELS, WATER-STRESS

1331
Leymarie, J., G. Lasceve, and A. Vavasseur. 1999. Elevated CO2 enhances stomatal responses to osmotic stress and abscisic acid in Arabidopsis thaliana. *Plant, Cell and Environment 22(3):301-308.*

Carbon dioxide and abscisic acid (ABA) are two major signals triggering stomatal closure. Their putative interaction in stomatal regulation was investigated in well-watered air-grown or double CO2-grown Arabidopsis thaliana plants, using gas exchange and epidermal strip experiments. With plants grown in normal air, a doubling of the CO2 concentration resulted in a rapid and transient drop in leaf conductance followed by recovery to the pre-treatment level after about two photoperiods. Despite the fact that plants placed in air or in double CO2 for 2 d exhibited similar levels of leaf conductance, their stomatal responses to an osmotic stress (0.16-0.24 MPa) were different. The decrease in leaf conductance in response to the osmotic stress was strongly enhanced at elevated CO2, Similarly, the drop in leaf conductance triggered by 1 mu M ABA applied at the root level was stronger at double CO2. Identical experiments were performed with plants fully grown at double CO2, Levels of leaf conductance and carbon assimilation rate measured at double CO2 were similar for air-grown and elevated CO2-grown plants. An enhanced response to ABA was still observed at high CO2 in pre- conditioned plants. It is concluded that: (i) in the absence of stress, elevated CO2 slightly affects leaf conductance in A. thaliana; (ii) there is a strong interaction in stomatal responses to

CO2 and ABA which is not modified by growth at elevated CO2.

KEYWORDS: ANION CHANNELS, ATMOSPHERIC CO2, CARBOHYDRATE ACCUMULATION, CARBON DIOXIDE, CYTOSOLIC CA-2, GUARD-CELLS, SHORT- TERM, VICIA-FABA, WATER-USE EFFICIENCY

1332

Li, A., G.M. Berntson, D.L. Godbold, and F.A. Bazzaz. 1998. The dynamics of root production and loss in Betula papyrifera seedlings in response to elevated CO2 and an aluminium pulse. *Zeitschrift Fur Pflanzenernahrung Und Bodenkunde 161(1):17-21.*

Seedlings of Betula papyrifera were grown in sand/nutrient solution cultures in rhizotrone growth containers under elevated (700 ppm) or ambient (375 ppm) atmospheric CO2 concentrations for approximately 10 weeks. Thirty seven days after the begin of the experiment the plants were exposed to a 10 day pulse of 400 or 1200 mu M Al. Elevated atmospheric CO2 increased both root production and loss. Exposure to Al reduced root production and slightly reduced root loss. The reduced root production due to Al was amplified after the pulse had receded, resulting in a significantly lower net and gross root production at the end of the experiment. There were no clear CO2 x Al interactions.

KEYWORDS: CARBON, GROWTH, MALATE, PLANTS, RESISTANCE, RHIZOSPHERE

1333

Li, A.G., A. Trent, G.W. Wall, B.A. Kimball, Y.S. Hou, P.J. Pinter, R.L. Garcia, D.V. Hunsaker, and R.L. Lamorte. 1997. Free-air CO2 enrichment effects on rate and duration of apical development of spring wheat. *Crop Science 37(3):789-796.*

Rates and durations of individual phases of wheat (Triticum aestivum L.) apical development are among the most important factors that determine yield components. Because atmospheric CO2 has been increasing steadily, it is important to evaluate the effects of elevated CO2 on wheat development. This study was conducted to determine rates and durations of leaf, spikelet, and floret primordium initiation in a Free-Air Carbon Dioxide Enrichment (FACE) system. Spring wheat (cv. Yecora Roja) was planted at the University of Arizona Maricopa Agricultural Center. The two CO2 concentrations were 550 (elevated) and 370 (ambient) mu mol mol(-1) CO2. Individual plant samples were collected every 3 to 4 d. We dissected the main stem (MS), coleoptile tiller (T0), primary tillers (T1, T2, and T3) and secondary tillers (T00, T01, T02, T10, T11, and T12) and counted primordia. Apex primordium data were fitted to a four-piece linear-spline segmented regression model with the SAS proc NLIN. No influence of elevated CO2 (550 mu mol mol(- 1)) on leaf primordium initiation of MS was detected. Nevertheless, CO2 enrichment significantly increased rates of spikelet primordium initiation of MS, T1, T2, T10, and T11, and diminished the durations of spikelet development phase of MS, T1, T2, T3, T10, and T11. Within the floret phase, CO2 enrichment significantly increased rates of floret primordium initiation of MS, T0, T1, T2, and T3, and diminished the time to the completion of floret primordium initiation of MS, T0, T1, T3, and T11. The information from this study will be utilized to predict wheat apical development and grain production in the elevated atmospheric CO2 environments of the future.

KEYWORDS: EAR DEVELOPMENT, FIELD, GROWTH, INFLORESCENCE DEVELOPMENT, PHOTOPERIOD, PRIMORDIUM INITIATION, SPIKELET NUMBER, TEMPERATURE, WINTER-WHEAT, YIELD

1334

Li, A.G., G.W. Wall, A. Trent, and Y.S. Hou. 1999. Free-air CO2 enrichment effects on apex dimensional growth of spring wheat. *Crop Science 39(4):1083-1088.*

Although primordium initiation in wheat (Triticum aestivum L,) has been extensively researched, a complete description of the growth dynamics of the apex at elevated CO2 concentrations is lacking. This study determined the rates of main stem and tiller apical elongation and widening in plants grown under two levels of CO2 concentration. Spring wheat was grown at the University of Arizona's Maricopa Agricultural Center at elevated (550 mu mol mol(-1)) or ambient (370 mu mol mol(-1)) CO2 concentrations. Individual plant samples were collected at different developmental stages and dissected. After dissection, the Lengths and widths of the spires of the main stem (MS), coleoptile tiller (T0), primary tillers (T1, T2, and T3), and secondary tillers (T00, T01, T02, T10, T11, and T12) were measured with a stage micrometer. Apex dimensions were fitted to an exponential model, Elevated CO2 increased the apex lengths of T2 at the double ridge stage, and of T3 and T10 at the double ridge and the terminal spikelet stages, and the apex widths of T2 at double ridge stage, and of T2, T3, T10, and T11 at the flag leaf appearance stage. Combining these results with a parallel study, the longer apices did not have more spikelet primordia, but wider apices had more floret primordia, Elevated CO2 changed apex elongation or widening patterns within a plant by enhancing elongation or widening rates of the MS, and later formed tillers. Earlier-formed tillers were less responsive to elevated CO2 levels. This information will be used in modeling wheat apical development and grain production in the elevated atmospheric CO2 environments of the future.

KEYWORDS: APICAL DEVELOPMENT, NITROGEN, SHOOT APEX, TEMPERATURE

1335

Li, C.S., S. Frolking, and R. Harriss. 1994. Modeling carbon biogeochemistry in agricultural soils. *Global Biogeochemical Cycles 8(3):237-254.*

An existing model of C and N dynamics in soils was supplemented with a plant growth submodel and cropping practice routines (fertilization, irrigation, tillage, crop rotation, and manure amendments) to study the biogeochemistry of soil carbon in arable lands. The new model was validated against field results for short-term (1-9 years) decomposition experiments, the seasonal pattern of soil CO2 respiration, and long-term (100 years) soil carbon storage dynamics. A series of sensitivity runs investigated the impact of varying agricultural practices on soil organic carbon (SOC) sequestration. The tests were simulated for corn (maize) plots over a range of soil and climate conditions typical of the United States, The largest carbon sequestration occurred with manure additions; the results were very sensitive to soil texture (more clay led to greater sequestration). Increased N fertilization generally enhanced carbon sequestration, but the results were sensitive to soil texture, initial soil carbon content, and annual precipitation. Reduced tillage also generally (but not always) increased SOC content, though the results were very sensitive to soil texture, initial SOC content, and annual precipitation. A series of long-term simulations investigated the SOC equilibrium for various agricultural practices, soil and climate conditions, and crop rotations. Equilibrium SOC content increased with decreasing temperatures, increasing clay content, enhanced N fertilization, manure amendments, and crops with higher residue yield. Time to equilibrium appears to be one hundred to several hundred years. In all cases, equilibration time was longer for increasing SOC content than for decreasing SOC content. Efforts to enhance carbon sequestration in agricultural soils would do well to focus on those specific areas and agricultural practices with the greatest potential for increasing soil carbon content.

KEYWORDS: CORN, CROPLAND, DRIVEN, NITROUS-OXIDE

EVOLUTION, ORGANIC-CARBON, PLANTS, RAINFALL EVENTS, ROOT RESPIRATION, TILLAGE

1336

Li, J.H., P. Dijkstra, C.R. Hinkle, R.M. Wheeler, and B.G. Drake. 1999. Photosynthetic acclimation to elevated atmospheric CO2 concentration in the Florida scrub-oak species Quercus geminata and Quercus myrtifolia growing in their native environment. *Tree Physiology 19(4-5):229-234.*

Long-term effects of elevated CO2 concentration (ambient plus 350 mu mol mol(-1)) on leaf photosynthetic acclimation of two species of a scrub-oak community, Quercus myrtifolia Willd. and Quercus geminata Small, were studied. Plants of both species were grown in open-top chambers in their natural habitat at Kennedy Space Center, Florida, USA. Compared to ambient CO2, elevated CO2 stimulated photosynthetic rates by 73 and 51% for Q. geminata and Q. myrtifolia, respectively. Maximum rate of carboxylation (V-cmax) was significantly reduced by elevated CO2 in Q. myrtifolia (28%) but not in Q. geminata. Maximum rate of potential electron transport (J(max)) was not significantly reduced by elevated CO2 in either species. In response to elevated CO2, specific leaf area decreased in Q, myrtifolia (22%), but not in Q. geminata. Elevated CO:! caused a significant accumulation of sugars (54%) and starch (264%) in Q, myrtifolia leaves, but not in Q. geminata leaves. Total Rubisco activity in Q. myrtifolia leaves was reduced 40% by elevated CO2, whereas no significant reduction occurred in Q, geminata leaves. Although both species share a common habitat, they exhibited marked differences in photosynthetic acclimation to elevated CO2 concentration.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, GAS-EXCHANGE, GROWTH, LEAVES, LIQUIDAMBAR- STYRACIFLUA, PINUS-TAEDA SEEDLINGS, WATER-STRESS

1337

Li, J.H., J. Gale, A. Novoplansky, S. Barak, and M. Volokita. 1999. Response of tomato plants to saline water as affected by carbon dioxide supplementation. II. Physiological responses. *Journal of Horticultural Science & Biotechnology 74(2):238-242.*

Photosynthesis of tomato plants (Lycopersicon esculentum (L.) Mill. cv. F144) was studied under conditions of CO2 supplementation and salinity. The purpose of the study was to elucidate the mechanisms underlying the effects of salinity on the acclimation of tomato plants to CO2 supplementation. Plants were grown under either low (355 mu mol mol(-1)) or elevated (1200 +/- 50 mu mol mol(-1)) CO2 and were irrigated with low concentrations of mixed salts. The highest salinity level (E.C. 7 dS m(-1)) was that used to produce quality tomatoes in the Negev highlands, in Israel. During early development (three weeks after planting), the net photosynthetic rate of the leaves was much higher under elevated CO2, and other than a slight decrease in quantum yield efficiency as measured by fluorescence (Delta F/F-m'), no signs of acclimation to high levels of CO2 were apparent. Clear acclimation to high CO2 concentration was evident ten weeks after planting when the net photosynthetic rate, photosynthetic capacity, and carboxylation efficiency of leaves of non-salinized plants were strongly suppressed under elevated CO2. This was accompanied by reductions in carboxylation efficiency, Rubisco activity and PSII quantum yield, and an increased accumulation of leaf soluble sugars. The reduction in photosynthetic capacity in the high CO2 plants was less in plants grown at the highest salinity level. This was correlated with an increase in the PSII quantum yield parameters (F-v/F-m) and Delta F/F-m') but not with Rubisco activity which was affected by the Cat treatments only. These results explain the effects of high CO2 on yields in tomatoes grown at high levels of salt (Li ct al., 1999).

KEYWORDS: ATMOSPHERIC CO2, ELEVATED CO2, EXPRESSION, GAS-EXCHANGE, GENES, GROWTH, MECHANISM, PHOTOSYNTHETIC ACCLIMATION, STRESS

1338

Li, J.H., M. Sagi, J. Gale, M. Volokita, and A. Novoplansky. 1999. Response of tomato plants to saline water as affected by carbon dioxide supplementation. I. Growth, yield and fruit quality. *Journal of Horticultural Science & Biotechnology 74(2):232-237.*

Tomato plants (Lycopersicon esculentum (L.) Mill. cv. F144) were irrigated with low concentrations of mixed salts; the highest level (E.C. 7 dS m(-1)) simulated conditions used to produce quality tomatoes in the Negev highlands. CO2 enrichment (to 1200 mu mol mol(-1), given during the daytime) increased plant growth at the early stage of development. However, later growth enhancement was maintained only when combined with salt stress. In the absence of CO2 supplementation, overall growth decreased with salt (7 dS m(-1)) to 58% and fresh biomass yields to 53% of the controls. However, under elevated CO2 concentrations total plant dry biomass was not reduced by salt stress. CO2 enrichment of plants grown with 7 dS m(-1) salt increased total fresh fruit yields by 48% and maintained fruit quality in terms of total soluble salts, glucose and acidity. Fruit ripening was about 10 d earlier under CO2 enrichment, regardless of salinity treatment. It is suggested that a combined utilization of brackish water and CO2 supplementation may enable the production of high-quality fruits without incurring all the inevitable loss in yields associated with salt treatment.

KEYWORDS: CO2- ENRICHMENT, WHEAT

1339

Li, Q.L., and D.T. Canvin. 1997. Oxygen photoreduction and its effect on CO2 accumulation and assimilation in air-grown cells of Synechococcus UTEX 625. *Canadian Journal of Botany-Revue Canadienne De Botanique 75(2):274-283.*

Mass spectrometric measurements of O-16(2), O-18(2), and (CO2)- C-13 were used to measure the rates of gross O-2 evolution, O-2 uptake, and CO2 assimilation in relation to light intensity, temperature, pH, and O-2 concentration by air-grown cells of the cyanobacterium Synechococcus UTEX 625. CO2 fixation and O-2 photoreduction increased with increased light intensity and, although CO2 fixation was saturated at 250 mu mol . m(-2). s(- 1), O-2 photoreduction was not saturated until about 550 mu mol . m(-2). s(-1). At high light intensity addition of inorganic carbon to the cells stimulated O-2 photoreduction 2-fold when CO2 fixation was allowed and 5-fold when CO2 fixation was inhibited with iodoacetamide. The ability of O-2 to act as an acceptor of photosynthetically generated reducing power was dependent upon the O-2 concentration, and the substrate concentration required for half maximum rate (K-1/2(O-2)) was 53.2 +/- 4.2 mu M (mean +/- SD, n = 3). The Q(10) for oxygen photoreduction was about 2. A certain amount (10%) of O-2 appeared to be required for maximum photosynthesis, as photosynthesis was inhibited under anaerobic conditions, especially at high light intensity. The point of inhibition is unknown but it seemed unlikely to be on CO2 transport or the concentration of intracellular dissolved inorganic carbon (C- i), as the rate of initial CO2 transport was enhanced and the intracellular C-i pool increased in size under anaerobic conditions.

KEYWORDS: ACTIVE-TRANSPORT, CHLAMYDOMONAS-REINHARDTII, CHLOROPHYLL-A FLUORESCENCE, CYANOBACTERIUM, ELECTRON FLOW, INORGANIC CARBON, LEOPOLIENSIS, O-2 PHOTOREDUCTION, PHOTOSYNTHESIS, REDUCTION

1340
Li, W., and W.J. Campbell. 1996. Response of rubisco activase protein levels in two species following grown at elevated CO2. *Plant Physiology 111(2):347.*

1341
Liakatas, A., D. Roussopoulos, and W.J. Whittington. 1998. Controlled-temperature effects on cotton yield and fibre properties. *Journal of Agricultural Science 130:463-471.*

Temperature effects on cotton yield and fibre properties of three cotton cultivars were determined. Plants were grown in pots maintained in growth rooms at varying day and night temperatures representing seasonally constant or varying (C) or daily varying (V) regimes. Yield and fibre characters responded to variation of daily mean and amplitude of temperature. Mean temperature reduction improved yield components, but fibre length, uniformity, strength and micronaire were increased by high, particularly high day, temperatures. A large daily temperature amplitude produced an intermediate number of flowers and the lowest retention percentage. Fruiting and yield were increased by reduction in temperature down to the threshold mean temperature of 22 degrees C. However, V-regimes with a low minimum temperature acted as a further drop (below 22 degrees C) of temperature and adversely affected these characters, An adverse effect of low minimum temperature combined with a moderate day temperature was observed also on lint percentage and fibre properties. Varietal differences were more pronounced for highly heritable characters such as fibre properties, for which significant interactions between varieties and temperature also occurred. Differences in reproductive development were not sufficient to be of much practical importance.

KEYWORDS: ELEVATED CO2, LEAVES, PHOTOSYNTHETIC ACCLIMATION, SEEDLINGS

1342
Liang, N.S., and K. Maruyama. 1995. Interactive effects of CO2 enrichment and drought stress on gas exchange and water-use efficiency in Alnus firma. *Environmental and Experimental Botany 35(3):353-361.*

Independent and interactive effects of atmospheric CO2 enrichment and drought stress on leaf conductance, photosynthetic performance, transpiration and water-use efficiency in 2-year-old Alnus firma, a common pioneer tree species, were assessed. Measurements were conducted in a controlled environment laboratory at three CO2 concentrations [350 (ambient), 600 and 900 (enrichment) mu mol mol(-1)] and combined with five water regimes [leaf water potential of higher than -0.3 (well-watered), -0.5 and -0.8 (moderate drought), -1.0 and lower than -1.2 (serious drought stress) MPa]. Under well-watered conditions, rates of net photosynthesis significantly ($P<0.01$) increased with increasing CO2 concentrations; leaf conductance significantly decreased. With drought stress established, leaf conductance, photosynthesis and transpiration decreased. However, leaf water-use efficiency increased with drought stress, with potential transpiration affected sooner than potential photosynthesis. The combined effects of COP enrichment and drought stress on water-use efficiency were significant in that the result of net photosynthesis was stimulated while transpiration in CO2 enriched plants resembled that of unenriched plants under conditions of drought stress. The results presented here suggest that if a doubling of atmospheric COP concentration occurs by the mid-21st Century, then the photosynthetic rate of A. firma in drought-affected regions may be expected to increase. A reduction in total water use, however, is not indicated.

KEYWORDS: CARBON DIOXIDE, ELEVATED ATMOSPHERIC CO2, GROWTH, LIQUIDAMBAR-STYRACIFLUA, MODEL, PHOSPHORUS DEFICIENCY, PHOTOSYNTHESIS, PINUS-TAEDA SEEDLINGS, RESPONSES, WHEAT

1343
Liang, N., K. Maruyama, and Y. Huang. 1995. Interactions of elevated co2 and drought stress in gas-exchange and water-use efficiency in 3 temperate deciduous tree species. *Photosynthetica 31(4):529-539.*

The effect of CO2 increase on gas exchange and water-use efficiency (WUE) in three temperate deciduous species (Fagus crenata, Ginkgo biloba and Alnus firma) under gradually- developing drought-stress was assessed. Seedlings were grown within transparent open-top cabinets and maintained for 4 months at mean CO2 concentrations of either 350 (ambient; C- 350) Or 700 mu mol mol(-1) (elevated; C-700) and combined with five water regimes [leaf water potential, Psi(w), higher than - 0.3 (well-watered), -0.5 and -0.8 (moderate drought), -1.0 and fewer than -1.2 MPa (serious drought-stress)]. Increase in CO2 concentration induced a 60 % average increase in net photosynthetic rate (P-N) under well-watered conditions. The effect of C-700 became more pronounced with drought stress established, with an 80 % average increase in P-N at Psi(w), as low as -0.8 MPa; leaf conductance to water vapour transfer (g(s)) and transpiration rate (E), however, were significantly decreased. Consequently, WUE increased under drought, through drought stress affected potential E sooner than potential P-N. The interaction of CO2 x drought stress on WUE was significant in that P-N was stimulated while E in C-700 enriched plants resembled that of C-350 plants under drought. Hence if a doubling of atmospheric CO2 concentration occurs by the mid 21(st) century, then greater P-N in F. crenata, G. biloba and A. firma may be expected and the drought susceptibility of these species will be substantially enhanced.

KEYWORDS: ATMOSPHERE, CARBON DIOXIDE, ENRICHMENT, GROWTH, LIMITED CONDITIONS, PHOTOSYNTHESIS, PLANTS, RESPONSES, WHEAT, YIELD

1344
Liang, N., K. Maruyama, and Y. Huang. 1996. Effects of CO2 concentration on the photosynthetic and carboxylation efficiencies of Fagus crenata and Quercus crispula. *Photosynthetica 32(3):355-365.*

To determine the effects of limited and elevated CO2 concentrations on leaf photosynthesis which may suggest the effects of global CO2 level increase and global warming on forest structure, the photosynthetic and carboxylation efficiencies were investigated in two representative co-occurring tree species in the cool-temperate natural forests in central Japan, Fagus crenata and Quercus crispula. Measurements were performed for four-year-old seedlings in CO2-air mixtures of 175, 350, 700 and 900 mu mol mol(-1), respectively, with photosynthetic irradiance (I) decreasing gradually from 1200 mu mol m(-2) s(-1) to darkness, and at 25 +/- 0.2 degrees C leaf temperature and 1.8 +/- 0.2 kPa leaf to air vapour pressure deficit. The CO2 concentrations strongly stimulated net photosynthetic rate, P-N ($p<0.001$), and the photosynthetic efficiency, alpha, for both F. crenata and Q. crispula. Carboxylation efficiency of Q. crispula was dependent on I, with a significantly higher efficiency of CO2 utilization at an I of 1200 than of 500 mu mol m(-2) s(-1). A decrease in I from 1200 to 500 mu mol m(-2) s(-1), however, did not prevent a curvilinear increase in P-N at increased CO2 concentrations. In contrast, F. crenata seedlings showed less difference in PN between low-I and high-I environments. Nonetheless, F. crenata showed a greater CO2 response, with alpha increased by 25 % from 350 to 700 mu mol(CO2) mol(-1). alpha of Q. crispula, however, increased by less than 20 % as CO2 concentration increased from 350 to 700 mu mol mol(-1). The higher P-N at high CO2 concentration under low I was attributed to the CO2 concentration

accompanied by a significant decrease in compensation irradiance. These results suggest that the continuous increase in global CO2 concentrations will directly result in an increase in photosynthetic efficiencies of both F. crenata and Q. crispula. The competitive relationship between the two species will change if a doubling of atmospheric CO2 concentration occurs;by the mid of the 21(st) century, with F. crenata benefiting more from CO2 fertilization than Q. crispula.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, GAS-EXCHANGE, GROWTH, IRRADIANCE, LIGHT-INTENSITY, LIQUIDAMBAR-STYRACIFLUA, LONG-TERM ELEVATION, PINUS-TAEDA SEEDLINGS, WATER-STRESS

1345

Lim, L.Y., Y.C. Hew, S.C. Wong, and C.S. Hew. 1992. Effects of light-intensity, sugar and co-2 concentrations on growth and mineral uptake of dendrobium plantlets. *Journal of Horticultural Science 67(5):601-611.*

The effects of light intensity, sugar and CO2 concentrations on nitrate and ammonium uptake, growth and photosynthetic activity of dendrobium plantlets grown on agar medium were studied. There was a preferential uptake of ammonium over nitrate. Uptake of nitrate was relatively low and increased with increase in light intensity or when the culture medium was supplemented with sugar. Ammonium uptake was also affected by light. However, the rates of ammonium and nitrate uptake were sluggish. The fresh weight of plantlets increased with the presence of sugar in the media but the relative growth rate decreased. CO2 enrichment did not increase ion uptake or growth. The nutrition of plantlets in culture was mainly heterotrophic, as indicated by the changes in titratable acidity, delta-C-13 values and (CO2)-C-14 fixation.

KEYWORDS: CARBON DIOXIDE, CRASSULACEAN ACID METABOLISM, ELEVATED CO2, INVITRO, NITRATE UPTAKE, PHOTOSYNTHESIS, SHORT- TERM

1346

Lin, E.D., Y.F. Liu, and Y. Li. 1997. Agricultural C cycle and greenhouse gas emission in China. *Nutrient Cycling in Agroecosystems 49(1-3):295-299.*

This paper assesses the production, consumption and store of organic carbon in the agricultural system, including all products from agriculture, of China. An estimation showed that about 90% of carbon uptake by agricultural systems would be emitted or returned to the atmosphere by several types from 1990 to 2000, others remain in durable agricultural products and soil. Even though the fixation rate is getting lower, generally speaking Chinese agriculture is a "sink" but not a "source" in respect to the atmospheric CO2 and CH4 concentrations in both the current period and that after few decades. China's Soil stores 12% of the whole soil carbon in the World. Considering the different global warming potentials (GWP), an approach to the country budgets of CO2 and CH4 has been presented based on the measurements in rice paddies and in the Tibet and Inner Mongolia grasslands.

KEYWORDS: CLIMATE

1347

Lin, G.H., J. Adams, B. Farnsworth, Y.D. Wei, B.D.V. Marino, and J.A. Berry. 1999. Ecosystem carbon exchange in two terrestrial ecosystem mesocosms under changing atmospheric CO2 concentrations. *Oecologia 119(1):97-108.*

The ecosystem-level carbon uptake and respiration were measured under different CO2 concentrations in the tropical rainforest and the coastal desert of Biosphere 2, a large enclosed facility. When the mesocosms were sealed and subjected to step- wise changes in atmospheric CO2 between daily means of 450 and 900 mu mol mol(-1), net ecosystem exchange (NEE) of CO2 was derived using the diurnal changes in atmospheric CO2 concentrations. The step-wise CO2 treatment was effectively replicated as indicated by the high repeatability of NEE measurements under similar CO2 concentrations over a 12-week period. In the rainforest mesocosm, daily NEE was increased significantly by the high CO2 treatments because of much higher enhancement of canopy CO2 assimilation relative to the increase in the nighttime ecosystem respiration under high CO2. Furthermore, the response of daytime NEE to increasing atmospheric CO2, in this mesocosm was not linear, with a saturation concentration of 750 mu mol mol(-1). In the desert mesocosm, a combination of a reduction in ecosystem respiration and a small increase in canopy CO2 assimilation in the high CO2 treatments also enhanced daily NEE. Although soil respiration was not affected by the short-term change in atmospheric CO2 in either mesocosm, plant dark respiration was increased significantly by the high CO2 treatments in the rainforest mesocosm while the opposite was found in the desert mesocosm. The high CO2 treatments increased the ecosystem light compensation points in both mesocosms. High CO2 significantly increased ecosystem radiation use efficiency in the rainforest mesocosm, but had a much smaller effect in the desert mesocosm. The desert mesocosm showed much lower absolute response in NEE to atmospheric CO2 than the rainforest mesocosm, probably because of the presence of C-4 plants. This study illustrates the importance of large-scale experimental research in the study of complex global change issues.

KEYWORDS: AMAZONIA, DIOXIDE, ELEVATED CO2, FLUXES, GROWTH, RESPONSES, SYSTEM, TROPICAL RAIN-FOREST, WATER

1348

Lin, G.H., J.R. Ehleringer, P.T. Rygiewicz, M.G. Johnson, and D.T. Tingey. 1999. Elevated CO2 and temperature impacts on different components of soil CO2 efflux in Douglas-fir terracosms. *Global Change Biology 5(2):157-168.*

Although numerous studies indicate that increasing atmospheric CO2 or temperature data are available on the responses of three major components of soil respiration [i.e. rhizosphere respiration (root and root exudates), litter decomposition, and oxidation of soil organic matter] to different CO2 and temperature conditions. In this study, we applied a dual stable isotope approach to investigate the impact of elevated CO2 and elevated temperature on these components of soil CO2 efflux in Douglas-fir terracosms. We measured both soil CO2 efflux rates and the C-13 and O-18 isotopic compositions of soil CO2 efflux in 12 sun-lit and environmentally controlled terracosms with 4- year-old Douglas fir seedlings and reconstructed forest soils under two CO2 concentrations (ambient and 200 ppmv above ambient) and two air temperature regimes (ambient and 4 degrees C above ambient). The stable isotope data were used to estimate the relative contributions of different components to the overall soil CO2 efflux. In most cases, litter decomposition was the dominant component of soil CO2 efflux in this system, followed by rhizosphere respiration and soil organic matter oxidation. Both elevated atmospheric CO2 concentration and elevated temperature stimulated rhizosphere respiration and litter decomposition. The oxidation of soil organic matter was stimulated only by increasing temperature. Release of newly fixed carbon as root respiration was the most responsive to elevated CO2, while soil organic matter decomposition was most responsive to increasing temperature. Although some assumptions associated with this new method need to be further validated, application of this dual-isotope approach can provide new insights into the responses of soil carbon dynamics in forest ecosystems to future climate changes.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE,

DECOMPOSITION, PONDEROSA PINE, RESPIRATION, RESPONSES, RHIZOSPHERE, TRACE GAS FLUXES, TURNOVER, VEGETATION

1349
Lin, G.H., B.D.V. Marino, Y.D. Wei, J. Adams, F. Tubiello, and J.A. Berry. 1998. An experimental and modeling study of responses in ecosystems carbon exchanges to increasing CO2 concentrations using a tropical rainforest mesocosm. *Australian Journal of Plant Physiology 25(5):547-556.*

The ecosystem carbon exchanges in the enclosed rainforest of Biosphere 2, an enclosed apparatus comprised of large synthetic ecosystems, were measured and modeled during the winter of 1995-1996 under different atmospheric CO2 concentrations. On eight separate days, this mesocosm was exposed to various levels of CO2 ranging from about 380 to 820 mu mol mol(-1) daily mean and then sealed 24 hours for continuous measurements of ecosystem CO2 fluxes. Our results indicated that net ecosystem carbon exchange in the mesocosm was enhanced by increasing CO2 over the short periods studied (2-7 weeks), but, as expected from physiological studies, the response is not linear. The main effect of shortterm CO2 change was the enhancement of canopy CO2 assimilation, while soil respiration was not affected by the atmospheric CO2 concentration. The whole ecosystem radiation use efficiency was significantly higher under higher CO2. The results of direct measurements were predicted well by a simple canopy model (the 'big-leaf' model) that incorporates current physiological understanding of the biochemistry of leaf photosynthesis. Validation of this model with a range of CO2 and light levels indicates that it can be used with confidence to predict the responses of natural ecosystems to global climate change. Response of ecosystem processes to elevated CO2 with relaxation time longer than a few weeks could not be resolved in this study, but longer-term closure experiments are planned to examine these processes.

KEYWORDS: ACCLIMATION, AMAZONIA, ASSIMILATION, BIOSPHERE, DIOXIDE, ELEVATED CO2, PHOTOSYNTHESIS, PHYSIOLOGY, PLANTS, RAIN-FOREST

1350
Lin, W.H., K.Z. Bai, and T.Y. Kuang. 1999. Effects of elevated CO2 and high temperature on single leaf and canopy photosynthesis of rice. *Acta Botanica Sinica 41(6):624-628.*

The increase of atmospheric CO2 concentration is indisputable. In such condition, photosynthetic response of leaf is relatively well studied, while the comparison of that between single leaf and whole canopy is less emphasized. The stimulation of elevated CO2 on canopy photosynthesis may be different from that on single leaf level. In this study, leaf and canopy photosynthesis of rice (Oryza sativa L.) were studied throughout the growing season. High CO2 and temperature had. a synergetic stimulation on single leaf photosynthetic rate until grain filling. Photosynthesis of leaf was stimulated by high CO2, although the stimulation was decreased by higher temperature at grain filling stage. On the other hand, the simulation of elevated CO2 on canopy photosynthesis leveled off with time. Stimulation at canopy level disappeared by grain filling stage in both temperature treatments. Green leaf area index was not significantly affected by CO2 at maturity, but greater in plants grown at higher temperature. Leaf nitrogen content decreased with the increase of CO2 concentration although it was not statistically significant at maturity. Canopy respiration rate increased at flowering stage indicating higher carbon loss: Shading effect caused bu leaf development reached maximum at flowering stage. The CO2 stimulation on photosynthesis was greater in single leaf than in canopy, Since enhanced CO2 significantly increased biomass of rice stems and panicles, increase in canopy respiration caused diminishment of CO2 stimulation in canopy net photosynthesis. Leaf nitrogen in the canopy level decreased with CO2 concentration and may eventually hasten CO2 stimulation on canopy photosynthesis. Early senescence of canopy leaves in high CO2 is also a possible cause.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, TRANSPIRATION

1351
Lin, W.H., and D.L. Wang. 1998. Effects of elevated CO2 on growth and carbon partitioning in rice. *Chinese Science Bulletin 43(23):1982-1986.*

Rice (Oryza sativa cv. Jindao 1187) was grown in open-top chambers which contained ambient and enriched CO2. CO2 elevation stimulated rice tillering during early vegetative stage. However, panicle dry weight per plant did not change at maturity stage. Root biomass was enhanced by high CO2. Root/shoot ratio was increased under high CO2 at maturity, indicating more carbon allocation to the below-bround part in rice under high CO2.

KEYWORDS: ACCLIMATION, DIOXIDE, INSITU, YIELD

1352
Lin, W.H., L.H. Ziska, O.S. Namuco, and K. Bai. 1997. The interaction of high temperature and elevated CO2 on photosynthetic acclimation of single leaves of rice in situ. *Physiologia Plantarum 99(1):178-184.*

Rice (Oryza sativa L. cv. IR72) was grown at three different CO2 concentrations (ambient, ambient + 200 mu mol mol(-1), ambient + 300 mu mol mol(-1)) at two different growth temperatures (ambient, ambient + 4 degrees C) from sowing to maturity to determine longterm photosynthetic acclimation to elevated CO2 with and without increasing temperature. Single leaves of rice showed a cooperative enhancement of photosynthetic rate with elevated CO2 and temperature during tillering, relative to the elevated CO2 condition alone. However, after flowering, the degree of photosynthetic stimulation by elevated CO2 was reduced for the ambient + 4 degrees C treatment, This increasing insensitivity to CO2 appeared to be accompanied by a reduction in ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) activity and/or concentration as evidenced by the reduction in the assimilation (A) to internal CO2, C-1) response curve. The reproductive response (e.g. percent filled grains, panicle weight) was reduced at the higher growth temperature and presumably reflects a greater increase in floral sterility. Results indicate that while CO2 and temperature could act synergistically at the biochemical level, the direct effect of temperature on floral development with a subsequent reduction in carbon utilization may change sink strength so as to limit photosynthetic stimulation by elevated CO2, concentration.

KEYWORDS: ASSIMILATION, ATMOSPHERIC CO2, CARBON DIOXIDE, ENRICHMENT, LEAF-AREA, RESPONSES

1353
Lincoln, D.E. 1993. The influence of plant carbon-dioxide and nutrient supply on susceptibility to insect herbivores. *Vegetatio 104:273-280.*

The carbon/nutrient ratio of plants has been hypothesized to be a significant regulator of plant susceptibility of leaf-eating insects. As rising atmospheric carbon dioxide stimulates photosynthesis, host plant carbon supply is increased and the accompanying higher levels of carbohydrates, especially starch, apparently 'dilute' the protein content of the leaf. When host plant nitrogen supply is limited, plant responses include increased carbohydrate accumulation, reduced leaf protein content, but also increased carbon-based defensive chemicals. No

change, however, has been observed in the concentration of leaf defensive allelochemicals with elevated carbon dioxide during host plant growth. Insect responses to carbon-fertilized leaves include increased consumption with little change in growth, or alternatively, little change in consumption with decreased growth, as well as enhanced leaf digestibility, reduced nitrogen use efficiency, and reduced fecundity. The effects of plant carbon and nutrient supply on herbivores appear to result, at least in part, from independent processes affecting secondary metabolism.

KEYWORDS: ALLOCATION, CHEMICAL DEFENSE, ELEVATED CO2, ENRICHED CO2 ATMOSPHERES, GROWTH, JUNONIA-COENIA, LEPIDOPTERA, LIMITATION, NITROGEN-CONTENT, NOCTUIDAE

1354

Lincoln, D.E., E.D. Fajer, and R.H. Johnson. 1993. Plant insect herbivore interactions in elevated co2 environments. *Trends in Ecology and Evolution 8(2):64-68.*

The increasing concentration of CO2 in the atmosphere is expected to lead to global changes in the physical environment of terrestrial organisms. We are beginning to understand how these changes are transmitted into pervasive effects on the interactions between plants and their leaf-feeding insect herbivores. An elevated CO2 atmosphere often stimulates plant carbon assimilation and growth and alters carbon allocation patterns. This, in turn, determines the quality of plants as resources for herbivorous insects. These 'quality' factors include: the concentrations of water, nitrogen and allelochemicals in host-plant leaves, and the toughness and starch and fiber content of leaf tissue. Because these parameters change in plants grown in enriched CO2 environments, the doubled CO2 levels anticipated for the next century will alter the dynamics of plant-insect herbivore interactions because herbivore consumption, growth and fitness are affected by the typically lower quality of plants grown under these conditions.

KEYWORDS: ALLOCATION, CARBON-DIOXIDE ATMOSPHERES, COTTON, ENRICHMENT, GROWTH, JUNONIA-COENIA, LEPIDOPTERA, NITROGEN, NOCTUIDAE, QUERCUS-ALBA

1355

Lindhout, P., and G. Pet. 1990. Effects of CO2 enrichment on young plant-growth of 96 genotypes of tomato (Lycopersicon esculentum). *Euphytica 51(2):191-196.*

The early growth of 96 genotypes of tomato was studied at 320 ppm CO2 and at 750 ppm CO2 in separate climate rooms. Plants were harvested at 40 and 55 days after sowing. Fresh and dry weights were determined. Large differences between genotypes were found for average plant fresh and dry weights and for relative growth rates. The average overall growth enhancement by CO2 enrichment was 2.3. Two genotypes showed significant genotype x CO2 interaction. The consequences of these results for tomato breeding are discussed.

1356

Lindner, M., H. Bugmann, P. Lasch, M. Flechsig, and W. Cramer. 1997. Regional impacts of climatic change on forests in the state of Brandenburg, Germany. *Agricultural and Forest Meteorology 84(1-2):123-135.*

The changes of climate projected for the next century will most likely alter both the environment and the growth of forests, In a regional case study, the two forest gap models FORSKA and FORCLIM were applied to simulate vegetation composition using spatially differentiated site data on a 10 x 10-km grid across the state of Brandenburg, Northeast Germany, Three climate scenarios were used to investigate the possible consequences of a changing climate on the environmental constraints of forest,growth in the state. To test the: plausibility of the forest composition simulated by the two models, their results were compared with a map of potential natural vegetation as well as with each other. The simulation results show that both models respond realistically to the spatial variability of the environment and thus are suitable for regional applications. However, there are a number of quantitative differences between the simulation results of the models. FORSKA's strength is in simulating the ecological effects of the spatial variability of soil water holding capacity and nitrogen availability, whereas FORCLIM realistically portrays the climate-induced distribution limits of trees, e.g. beech (Fagus sylvatica L.). The study suggests that climatic change could have considerable consequences for future competitive relationships between species. According to the two models, the main driving force of vegetation change would be the increased occurrence of drought, which already today determines some distribution limits of tree species in Brandenburg, Under the strongest change of climate investigated in the present study, none of the species currently present on the landscape could grow any more in certain areas of Brandenburg. Conclusions are drawn concerning the importance of regional model applications for testing model performance under a wide variety of environmental conditions as well as for forest planning, Regional analyses of the impacts of climate change on forests may help to develop forest management strategies to cope with the risk of changing environmental conditions.

KEYWORDS: COMMUNITIES, DYNAMICS, ECOSYSTEMS, ELEVATED CO2, MODEL, NORTHERN FORESTS, SIMULATION

1357

Lindner, M., R. Sievanen, and H. Pretzsch. 1997. Improving the simulation of stand structure in a forest gap model. *Forest Ecology and Management 95(2):183-195.*

There is currently great interest in improving the applicability of forest gap models to changing environmental conditions, in order to facilitate the assessment of possible impacts of climatic change on forest ecosystems. Moreover, for the development of mitigation strategies, it is necessary to include forest management options in the models. Both the simulation of transient effects of climatic change and of forest management regimes require a realistic representation of stand structure in gap models, since tree species respond to variations in stand density in characteristic ways, depending on their ecological strategies. In this study, we compared the effect of five different height growth functions that are sensitive to stand density on simulated stand structure of the FORSKA forest gap model. We used long term observation data from a beech thinning trial at Fabrikschleichach, Bavaria, to test the alternative functions. First, we compared simulation results of the original FORSKA model with measured stand development from 1870 to 1990. Whereas simulated stand level variables (e.g. biomass, mean diameter and height) showed good correspondence with observations, individual tree dimensions and simulated stand structure were quite unrealistic. After calibrating parameters of the height growth functions with data from a lightly thinned plot at Fabrikschleichach, we ran the model with data from a heavily thinned plot for validation. All five functions considerably improved the simulation of height/diameter relationships and stand structure. However, there were distinct differences between functions. The best correspondence with measurements was shown by a function which uses the relative radiation intensity in the centre of a tree crown as an indicator of the competition status of the tree. This function is rather simple and needs only two growth parameters, which can be derived for different functional types of species, according to their shade tolerance. With the new, flexible height growth function it should be possible to extend the applicability of gap models to more realistic simulation experiments including forest management and

natural disturbances. To our knowledge, this was the first attempt to employ long term forest observation data for the calibration and validation of a forest gap model. The results suggest that such data could be very useful in model testing and improvement. (C) 1997 Elsevier Science B.V.

KEYWORDS: CO2, CO2-INDUCED CLIMATE CHANGE, DISTURBANCE, DYNAMICS, ECOSYSTEMS, GLOBAL CHANGE, GROWTH, LANDSCAPES, TRANSIENT-RESPONSE, VEGETATION

1358
Lindqvist, K., and R. Lignell. 1997. Intracellular partitioning of (CO2)-C-14 in phytoplankton during a growth season in the northern Baltic. *Marine Ecology-Progress Series 152(1-3):41-50.*

During the phytoplankton succession in the northern Baltic in 1988, the distribution of (CO2)-C-14 assimilated by algae into the main molecular groups [proteins, polysaccharides, lipids and low molar mass compounds (LMC)] after in situ Light (6 h) and Light to dark (20 h from ca 11:00 to 07:00 h) incubations at 2 m depth (just below maximum (CO2)-C-14 fixation) was studied. By early May, the high winter levels of mineral nutrients were depleted from the water column, and in middle May the spring bloom predominated by large dinoflagellates (diatoms subdominant) peaked. The proportion of C-14 lipids was usually ca 15% of total (CO2)-C-14 fixation, but it showed a distinct peak of 40% in middle May. The C-14-Lipid peak probably reflected nutrient stress of the algae, since nutrient (N+P) enrichment decreased this peak by 15 percentage points in 100 l enclosures. During the decline of the spring bloom, the proportion of C-14 proteins increased despite low ambient mineral N concentrations. In summer, the phytoplankton community (mainly small flagellates) consistently exhibited remarkable channelling of (CO2)-C-14 into proteins (50 to 60%), which conformed to the low particulate organic C:N ratios of ca 7 (mol/mol). Summer upwellings, which introduced nutrients into the mixed layer, seemed to be accompanied by the highest proportions of C-14 proteins. The proportion of C-14 polysaccharides was usually ca 20%. After 6 h incubations, this proportion was significantly (on average 10 percentage points) higher than after 20 h, while the inverse was true with C-14 proteins, which reflected continuous nocturnal synthesis of proteins (enzymes) at the expense of polysaccharide storage products. In con elusion, the high proportions of algal C-14 proteins in summer suggest that phytoplankton is usually not physiologically N limited in our study area and provides N- sufficient food for herbivores, hence enabling high efficiency of algal C transfer to higher trophic levels.

KEYWORDS: CARBON INCORPORATION, COMMUNITY, COPEPODS, MARINE-PHYTOPLANKTON, NITROGEN, NUTRIENT LIMITATION, PARTICULATE, PATTERNS, PHOTOSYNTHESIS, SPRING BLOOM

1359
Lindroth, R.L., G.E. Arteel, and K.K. Kinney. 1995. Responses of 3 saturniid species to paper birch grown under enriched co2 atmospheres. *Functional Ecology 9(2):306-311.*

1. Interactions between trees and tree-feeding insects are likely to shift under conditions of enriched atmospheric CO2 owing to changes in foliar chemical composition. This study addressed the effects of CO2-mediated changes in leaf chemistry on performance of three silkmoth (Saturniidae) species: cecropia (Hyalophora cecropia), luna (Actias luna) and polyphemus (Antheraea polyphemus polyphemus). 2. Growth under elevated CO2 atmospheres decreased nitrogen concentrations (23%) but tripled starch and doubled condensed tannin concentrations, resulting in a marked increase in foliar carbon:nitrogen ratio. 3. Survival of first stadium larvae was marginally reduced when reared on high CO2 leaves. 4. Development rates were prolonged, growth rates tended to decline, consumption increased and food processing efficiencies decreased for fourth stadium larvae reared on high CO2 leaves. The magnitude of responses varied among species. 5. Overall performance of these saturniid species, at least when feeding on birch, is predicted to decline under atmospheric CO2 conditions anticipated for the next century.

KEYWORDS: NITROGEN

1360
Lindroth, R.L., S.M. Jung, and A.M. Feuker. 1993. Detoxication activity in the gypsy-moth - effects of host co2 and no3-availability. *Journal of Chemical Ecology 19(2):357-367.*

We investigated the effects of host species and resource (carbon dioxide, nitrate) availability on activity of detoxication enzymes in the gypsy moth, Lymantria dispar. Larvae were fed foliage from quaking aspen or sugar maple grown under ambient or elevated atmospheric CO2, with low or high soil NO3- availability. Enzyme solutions were prepared from larval midguts and assayed for activity of cytochrome P-450 monooxygenase, esterase, glutathione transferase, and carbonyl reductase enzymes. Activity of each enzyme system was influenced by larval host species, CO2 or NO3- availability, or an interaction of factors. Activity of all but glutathione transferases was highest in larvae reared on aspen. Elevated atmospheric CO2 promoted all but transferase activity in larvae reared on aspen, but had little if any impact on enzyme activities of larvae reared on maple. High NO3- availability enhanced activity of most enzyme systems in gypsy moths fed high CO2 foliage, but the effect was less consistent for insects fed ambient CO2 foliage. This research shows that gypsy moths respond biochemically not only to interspecific differences in host chemistry, but also to resource-mediated, intraspecific changes in host chemistry. Such responses are likely to be important for the dynamics of plant-insect interactions as they occur now and as they will be altered by global atmospheric changes in the future.

KEYWORDS: ALLELOCHEMICALS, CHEMISTRY, DETOXIFICATION ENZYME-ACTIVITY, INDUCTION, LEPIDOPTERA, MICROSOMAL OXIDASES, NOCTUIDAE, PLANT, RESPONSES, SPODOPTERA-ERIDANIA

1361
Lindroth, R.L., and K.K. Kinney. 1998. Consequences of enriched atmospheric CO2 and defoliation for foliar chemistry and gypsy moth performance. *Journal of Chemical Ecology 24(10):1677-1695.*

Elevated concentrations of atmospheric CO2 are likely to interact with other factors affecting plant physiology to alter plant chemical profiles and plant-herbivore interactions. We evaluated the independent and interactive effects of enriched CO2 and artificial defoliation on foliar chemistry of quaking aspen (Populus tremuloides) and sugar maple (Acer saccharum), and the consequences of such changes for short-term performance of the gypsy moth (Lymantria dispar). We grew aspen and maple seedlings in ambient (similar to 360 ppm) and enriched (650 ppm) CO2 environments at the University of Wisconsin Biotron. Seven weeks after budbreak, trees in half of the rooms were subjected to 50% defoliation. Afterwards, foliage was collected for chemical analyses, and feeding trials were conducted with fourth-stadium gypsy moths. Enriched CO2 altered foliar levels of water, nitrogen, carbohydrates, and phenolics, and responses generally differed between the two tree species. Defoliation induced chemical changes only in aspen. We found no significant interactions between CO2 and defoliation for levels of carbon- based defenses (phenolic glycosides and tannins). CO2 treatment altered the performance of larvae fed aspen, but not maple, whereas defoliation had little effect on performance of insects. In general, results from this experimental system do not support the hypothesis that induction of carbon-based chemical defenses, and

attendant effects on insects, will be stronger in a CO2-enriched world.

KEYWORDS: ALLOCATION PATTERNS, CARBON NUTRIENT BALANCE, DECIDUOUS TREES, DIETARY NITROGEN, ELEVATED CO2, FOREST TENT CATERPILLARS, INSECT PERFORMANCE, NO3 AVAILABILITY, PHYTOCHEMISTRY, PLANTS

1362

Lindroth, R.L., K.K. Kinney, and C.L. Platz. 1993. Responses of deciduous trees to elevated atmospheric co2 - productivity, phytochemistry, and insect performance. *Ecology 74(3):763-777.*

Although rising levels of atmospheric carbon dioxide are expected to directly affect forest ecosystems, little is known of how specific ecological interactions will be modified. This research evaluated the effects of enriched CO2 on the productivity and phytochemistry of forest trees and performance of associated insects. Our experimental system consisted of three tree species (quaking aspen [Populus tremuloides], red oak [Quercus rubra], sugar maple [Acer saccharum]) that span a range from fast to slow growing, and two species of leaf- feeding insects (gypsy moth [Lymantria dispar] and forest tent caterpillar [Malacosoma disstria]). Carbon-nutrient balance theory provided a framework for tests of three hypotheses; in response to enriched CO2: (1) relative increases in tree growth rates will be greatest for aspen and least for maple, (2) relative decreases in protein and increases in carbon-based compounds will be greatest for aspen and least for maple, and (3) relative reductions in performance will be greatest for insects fed aspen and least for insects fed maple. We grew 1- yr-old seedlings for 60 d under ambient (385 +/- 5 muL/L) or elevated (642 +/- 2 muL/L) CO2 regimes at the University of Wisconsin Biotron. After 50 d, we conducted feeding trials with penultimate-instar gypsy moth and forest tent caterpillars. After 60 d, a second set of trees was harvested and partitioned into root, stem, and leaf tissues. We subsequently analyzed leaf material for a variety of compounds known to affect performance of insect herbivores. In terms of actual dry-matter production, aspen responded the most to enriched CO2 atmospheres whereas maple responded the least. Proportional growth increases (relative to ambient plants), however, were highest for oak and least for maple. Effects of elevated CO2 on biomass allocation patterns differed among the three species; root-to-shoot ratios increased in aspen, decreased in oak, and did not change in maple. Enriched CO2 altered concentrations of primary and secondary metabolites in leaves, but the magnitude and direction of effects were species-specific. Aspen showed the largest change in storage carbon compounds (starch), whereas maple experienced the largest change in defensive carbon compounds (condensed and hydrolyzable tannins). Consumption rates of insects fed high-CO2 aspen increased dramatically, but growth rates declined. The two species of insects differed in response to oak and maple grown under enriched CO2. Gypsy moths grew better on high-CO2 Oak, whereas forest tent caterpillars were unaffected; tent caterpillars tended to grow less on high-CO2 maple, whereas gypsy moths were unaffected. Changes in insect performance parameters were related to changes in foliar chemistry. Responses of plants and insects agreed with some, but not all, of the predictions of carbon-nutrient balance theory. This study illustrates that tree productivity and chemistry, and the performance of associated insects, will change under CO2 atmospheres predicted for the next century. Changes in higher level ecological processes, such as community structure and nutrient cycling, are also implicated.

KEYWORDS: BIRCH BETULA, CARBON-DIOXIDE CONCENTRATION, CHEMICAL DEFENSE, GROWTH-RESPONSES, MINERAL NUTRITION, NUTRIENT BALANCE, PHENOLIC GLYCOSIDES, PHOTOSYNTHETIC ACCLIMATION, QUAKING ASPEN, SECONDARY METABOLITES

1363

Lindroth, R.L., S. Roth, E.L. Kruger, J.C. Volin, and P.A. Koss. 1997. CO2-mediated changes in aspen chemistry: Effects on gypsy moth performance and susceptibility to virus. *Global Change Biology 3(3):279-289.*

We investigated the effects of long-term CO2 enrichment on foliar chemistry of quaking aspen (Populus tremuloides) and the consequences of chemical changes for performance of the gypsy moth (Lymantria dispar) and susceptibility of the gypsy moth to a nucleopolyhedrosis virus (NPV). Foliage was collected from outdoor open-top chambers and fed to insects in a quarantine rearing facility. Under enriched CO2, levels of leaf nitrogen declined marginally, levels of starch and phenolic glycosides did not change, and levels of condensed tannins increased. Long-term bioassays revealed reduced growth (especially females), prolonged development and increased consumption in larvae fed high-CO2 foliage but no significant differences in final pupal weights or female fecundity. Short-term bioassays showed weaker, and sex-specific, effects of CO2 treatment on larval performance. Correlation analyses revealed strong, negative associations between insect performance and phenolic glycoside concentrations, independent of CO2 treatment. Larval susceptibility to NPV did not differ between CO2 treatments, suggesting that effects of this natural enemy on gypsy moths are buffered from CO2-induced changes in foliar chemistry. Our results emphasize that the impact of enriched CO2 on plant- insect interactions will be determined Rot only by how concentrations of plant compounds are altered, but also by the relevance of particular compounds for insect fitness. This work also underscores the need for studies of genetic variation in plant responses to enriched CO2 and long-term population-level responses of insects to CO2-induced changes in host quality.

KEYWORDS: CARBON NUTRIENT BALANCE, CATERPILLARS, DEFENSE, ELEVATED ATMOSPHERIC CO2, FOOD-CONSUMPTION, HERBIVORE, INSECT PERFORMANCE, PAPER BIRCH, PHYTOCHEMISTRY, PLANTS

1364

Linker, R., I. Seginer, and P.O. Gutman. 1998. Optimal CO2 control in a greenhouse modeled with neural networks. *Computers and Electronics in Agriculture 19(3):289-310.*

CO, enrichment in warm climates requires a delicate balance between the need to ventilate and the desire to enrich. Model- based optimization can achieve this balance, but requires reliable models of the greenhouse environment and of the crop response. This study assumes that the crop response is known, and focuses on the greenhouse model. Neural network greenhouse models were trained using data collected over two summer months in a small greenhouse. The models were reduced to minimum size, by predicting separately the temperature and CO2 concentration, and by eliminating any unessential input. The resulting models not only fit the data well, they also seem qualitatively correct, and produce reasonable optimization results. Using these models, the effect of evaporative cooling on extending the enrichment duration is demonstrated. (C) 1998 Elsevier Science B.V. All rights reserved.

KEYWORDS: ENRICHMENT

1365

Lippert, M., K.H. Haberle, K. Steiner, H.D. Payer, and K.E. Rehfuess. 1996. Interactive effects of elevated CO2 and O-3 on photosynthesis and biomass production of clonal 5-year-old Norway spruce [Picea abies (L) Karst] under different nitrogen nutrition and irrigation treatments. *Trees-Structure and Function 10(6):382-392.*

To study the: single and combined effects of elevated carbon dioxide (CO2), ozone (O-3), nitrogen nutrition, and water supply on photosynthetic gas exchange and biomass accumulation of Norway

spruce, a four-factorial experiment was conducted in closed environmental chambers. Each factor was applied at two levels: (i) ambient and elevated (ambient + 200 mu l l(-1)) CO2, (ii) 20 and 80 nl l(-1) O-3. (iii) low and high nitrogen fertilization, and (iv) a well watered and a drought treatment. Neither elevated O-3 nor CO2 significantly changed stomatal conductances of spruce needles. Adverse effects of elevated O-3 on photosynthetic parameters such as net assimilation rate and carboxylation efficiency occurred only when tile plants were well watered and in a good nutritional status, After 6 weeks enhanced atmospheric CO2 resulted in increased net assimilation rates provided that nutrition was well balanced and plants were well watered, Acclimation processes became apparent and are interpreted as a consequence of sink regulation. While O-3 effects were apparent only in biomass of 1-year-old plant material. elevated CO2-resulted in higher biomass of the buds expanding during the exposure and increased root biomass significantly. Above- and below-ground biomass were strongly influenced by the water and nutrition treatments.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, CARBON DIOXIDE, CARBOXYLASE-OXYGENASE, GAS-EXCHANGE, GROWTH, LOW OZONE CONCENTRATIONS, PLANTS, SEEDLINGS, WATER-STRESS

1366

Lippert, M., K. Steiner, T. Pfirrmann, and H.D. Payer. 1997. Assessing the impact of elevated O-3 and CO2 on gas exchange characteristics of differently K supplied clonal Norway spruce trees during exposure and the following season. *Trees-Structure and Function 11(5):306-315.*

Well-supplied and K-deficient 4-year-old clonal Norway spruce trees were exposed to combinations of two levels of ozone (20 and 80 nl 1(-1) O-3) and carbon dioxide (350 and 750 mu 1 1(-1) CO2) to study the effects of possible future climate factors on gas exchange characteristics. The fumigation was performed in environmental chambers for a complete growing season. After the exposure, plants were cultivated outdoors to investigate possible recovery and delayed effects. During the exposure 1- year-old needles responded to the 80 nl 1(-1) O-3 treatment by a sharp but transient decrease of both apparent carboxylation efficiency (CE) and maximum photosynthetic capacity (A(2500)). Elevated CO2 also reduced CE and A(2500). The effect became stronger in the course of the exposure and was accompanied by decreases of N and P as well as chlorophyll contents. In case of K deficiency, the acclimation response of current-year needles was even more pronounced reflecting lower sink capacities for carbon metabolites. The joint application of elevated O-3 and CO2 resulted in the lowest values of gas exchange parameters and chlorophyll contents. At the beginning of the growing season after the exposure and under outdoor conditions, all these treatment effects disappeared in the needles which had developed during the fumigation. In the course of the development of the new flush, however, the well- supplied 1-year-old needles which had been treated with 80 nl 1(-1) O-3 and 350 mu 1 1(-1) CO2 in the year before, exhibited a sharp decline of CE and A(2500). Simultaneously, chlorotic mottle and bands developed. These delayed symptoms are discussed in the context of the previously published "memory" effect for O-3 (Sandermann et al. 1989). Additionally, evidence is presented that shoot development is altered in plants which had been exposed to elevated O-3.

KEYWORDS: AIR-POLLUTION, ATMOSPHERIC CO2, CARBON DIOXIDE, GROWTH, L KARST, OZONE, PHOTOSYNTHETIC ACCLIMATION, PICEA-ABIES L, RED SPRUCE, WATER-STRESS

1367

Liu, S.Y., and R.O. Teskey. 1995. Responses of foliar gas-exchange to long-term elevated co2 concentrations in mature loblolly-pine trees. *Tree Physiology 15(6):351-359.*

Branches of field-grown mature loblolly pine (Pinus taeda L.) trees were exposed for 2 years (1992 and 1993) to ambient or elevated CO2 concentrations (ambient + 165 mu mol mol(-1) or ambient + 330 mu mol mol(-1) CO2). Exposure to elevated CO2 concentrations enhanced rates of net photosynthesis (P-n) by 53-111% compared to P-n of foliage exposed to ambient CO2. At the same CO2 measurement concentration, the ratio of intercellular to atmospheric CO2 concentration (C-i/C-a) and stomatal conductance to water vapor did not differ among foliage grown in an ambient or enriched CO2 concentration. Analysis of the relationship between P-n and C-i indicated no significant change in carboxylation efficiency of ribulose-1,5- bisphosphate carboxylase/oxygenase during growth in elevated CO2 concentrations. Based on estimates derived from P-n/C-i curves, there were no apparent treatment differences in dark respiration, CO2 compensation point or P-n at the mean C-i. In 1992, foliage in the three CO2 treatments yielded similar estimates of CO2-saturated P-n (P-max), whereas in 1993, estimates of P-max were higher far branches grown in elevated CO2 than in ambient CO2. We conclude that field-grown loblolly pine trees do not exhibit downward acclimation of leaf-level photosynthesis in their long-term response to elevated CO2 concentrations.

KEYWORDS: ATMOSPHERIC CO2, BRANCH BAG, CARBON DIOXIDE, GROWTH, LEAF-AREA, PHOSPHORUS DEFICIENCY, PHOTOSYNTHETIC ACCLIMATION, SEEDLINGS, STOMATAL CONDUCTANCE, WATER-STRESS

1368

Liu, Y.T., T.M. Karnauchow, K.F. Jarrell, D.L. Balkwill, G.R. Drake, D. Ringelberg, R. Clarno, and D.R. Boone. 1997. Description of two new thermophilic Desulfotomaculum spp., Desulfotomaculum putei sp. nov, from a deep terrestrial subsurface, and Desulfotomaculum luciae sp. nov, from a hot spring. *International Journal of Systematic Bacteriology 47(3):615-621.*

Six strains of thermophilic, endospore-forming, sulfate- reducing bacteria were enriched and isolated from 2.7 km below the earth's surface in the Taylorsville Triassic Basin in Virginia, The cells of these strains were motile rods that were 1 to 1.1 mu m in diameter and 2 to 5 mu m long. The cells grew by oxidizing H-2, formate, methanol (weakly), lactate (incompletely, to acetate and CO2), or pyruvate (incompletely) while reducing sulfate to sulfide; acetate did not serve as a catabolic substrate, Thiosulfate or sulfite could replace sulfate as an electron acceptor, The results of a phylogenetic analysis of the 16S rRNA gene indicated that these strains belong to the genus Desulfotomaculum, but are distinct from previously described Desulfotomaculum species, Thus, we propose a new species, Desulfotomaculum putei, for them, with strain TH-11 (= SMCC W459) as the type strain, The results of our phylogenetic analysis also indicated that strain SLTT, which was isolated from a hot spring and has been described previously (T. M. Karnauchow, S. F. Koval, and K. F. Jarrell, Syst. Appl. Microbiol, 15:296-310, 1992), is also a member of the genus Desulfotomaculum and is distinct from other species in this genus, We therefore propose the new species Desulfotomaculum luciae for this organism; strain SLT (= SMCC W644) is the type strain of D. luciae.

KEYWORDS: 2,4-DICHLOROPHENOL, GEN-NOV, GROWTH, SEDIMENTS, SEQUENCE, SULFATE-REDUCING BACTERIUM, TEMPERATURE, WATER

1369

Livingston, N.J., D. Whitehead, F.M. Kelliher, Y.P. Wang, J.C. Grace, A.S. Walcroft, J.N. Byers, T.M. McSeveny, and P. Millard. 1998. Nitrogen allocation and carbon isotope fractionation in relation to intercepted radiation and position in a young Pinus radiata D. Don tree.

Plant, Cell and Environment 21(8):795-803.

The three dimensional distribution of intercepted radiation, intercellular CO2 concentration (C-i) and late summer needle nitrogen (N) concentration were determined at the tips of all 54 branches in a 6.2-m-tall Pinus radiata D, Don tree growing in a New Zealand plantation. Measurements included above- and below-canopy irradiance, leaf stable carbon isotopic composition (delta(13)C) and tree canopy architecture. The radiation absorption component of the model, MAESTRO, was tested on site and then used to determine the branch tip distribution of intercepted radiation. We hypothesized that in branch tip needles: (i) the allocation of nitrogen and other nutrients would be closely associated with the distribution of intercepted radiation, reflecting carbon gain optimization theory, and (ii) C-i would predominantly reflect changes in photosynthetic rate (A) rather than stomatal conductance (g(s)), indicating that the increase in A for a given increase in N concentration was larger than the corresponding increase in g(s). Needle nitrogen concentration was poorly related to intercepted radiation, regardless of the period over which the latter was calculated. At a given height, there was a large azimuthal variation in intercepted radiation but N concentration was remarkably uniform around the tree canopy, There was, however, a linear and positive correspondence between N concentration and delta(13)C and needle height above ground (r(2) = 0.73 and 0.68, respectively). The very strong linear correspondence between N concentration and C-i (r(2) = 0.71) was interpreted, using gas exchange measurements, as supporting our second hypothesis. Recognizing the strong apical control in P. radiata and possible effects of leaf nitrogen storage in an evergreen species, we propose that the tree leader must have constituted a very strong carbon sink throughout the growing season, and that the proximity of branch tip needles to the leader affected their photosynthetic capacity and nutrient concentration, independent of intercepted radiation. This implies an integrated internal determination of resource allocation within the tree and challenges the current convention that resources are optimally distributed according to the profile of intercepted radiation.

KEYWORDS: C-3 PLANTS, CANOPY, DIOXIDE, DISCRIMINATION, ELEVATED CO2, FOLIAR NITROGEN, LEAF NITROGEN, LEAVES, PHOTOSYNTHESIS, USE EFFICIENCY

1370
Lloyd, J. 1999. The CO2 dependence of photosynthesis, plant growth responses to elevated CO2 concentrations and their interaction with soil nutrient status, II. Temperate and boreal forest productivity and the combined effects of increasing CO2 concentrations and increased nitrogen deposition at a global scale. *Functional Ecology 13(4):439-459.*

1. Appropriate rates of carbon acquisition by temperate and boreal forests are re-evaluatted, Based on continental-scale forestry data it is suggested that the productivity of temperate and boreal forests has been overestimated previously. 2, Using these values, a model of the integrated response of ecosystems to carbon dioxide concentration and soil nitrogen availability is presented. The model does not assume constant C/N ratios in plant or soil and considers effects of increases in atmospheric CO2 concentrations and nitrogen deposition separately or together. 3, For temperate-zone forests a co- occurrence of a CO2 increase and nitrogen deposition doubles the increase in net primary productivity and carbon sequestration that would be the case for nitrogen deposition occurring on its own. Considered separately, the effect of the atmospheric CO2 increase is less than even moderate rates of anthropogenic N deposition for temperate or boreal forests. By contrast, for tropical forests, the atmospheric CO2 increase is sufficient to induce large rates of carbon accumulation in plants and soil. 4, Application of the model at the global scale suggests large localized sinks for CO2 in either tropical rain forests or in forested or grassland areas of Europe and North America where appreciable N deposition occurs. Overall, the model suggests a terrestrial sink owing to CO2 fertilization and N deposition of about 0.2 Pmol C per year. About half of this is in the mid-latitudes of the northern hemisphere and about half in the tropics.

KEYWORDS: ATMOSPHERIC CO2, BIOMASS, CARBON DIOXIDE, CYCLE, DIFFERENT CLIMATES, ECOSYSTEMS, MODEL, ORGANIC-MATTER, TERRESTRIAL BIOSPHERE, TROPICAL FORESTS

1371
Lloyd, J. 1999. Current perspectives on the terrestrial carbon cycle. *Tellus Series B-Chemical and Physical Meteorology 51(2):336-342.*

Over the last 5 or so years, there have been significant advances in the understanding of the current role of the terrestrial biosphere in the global carbon cycle, especially in terms of how pools and fluxes are affected by variations in climate (including interannual variability as well as longer-term climate change), increases in atmospheric CO, concentrations and changed rates of atmospheric nitrogen deposition. At the same time, significant advances have been made in terms of both direct. measurement of ecosystem productivity and in an understanding of the key underlying mechanisms modulating carbon fluxes from terrestrial systems. A brief synopsis of these advances is the subject of this paper.

KEYWORDS: ATMOSPHERIC CO2 CONCENTRATIONS, ECOSYSTEMS, ELEVATED CO2, EUROPEAN FORESTS, MYCORRHIZAL COLONIZATION, NET PRIMARY PRODUCTION, NITROGEN, PHOSPHORUS, PLANT GROWTH, TROPICAL RAIN-FOREST

1372
Lloyd, J., and G.D. Farquhar. 1996. The CO2 dependence of photosynthesis, plant growth responses to elevated atmospheric CO2 concentrations and their interaction with soil nutrient status .1. General principles and forest ecosystems. *Functional Ecology 10(1):4-32.*

KEYWORDS: AMBIENT PARTIAL-PRESSURE, CARBON-DIOXIDE ENRICHMENT, MAINTENANCE RESPIRATION, NET PRIMARY PRODUCTION, NITRATE ASSIMILATION, NITROGEN NUTRITION, PHOSPHORUS-NUTRITION, ROOT RESPIRATION, SIEB EX SPRENG, TREE GROWTH

1373
Loaiza, J., and M. Cantwell. 1997. Postharvest physiology and quality of cilantro (Coriandrum sativum L). *Hortscience 32(1):104-107.*

Respiration rates of freshly harvested cilantro were moderately high (CO2 at 15 to 20 mu L . g(-1). h(-1)) and ethylene production rates were low (<0.2 nL . g(-1). h(-1)) at 5 degrees C and were typical of green leafy tissues. Cilantro stored in darkness at a range of temperatures in air or controlled atmospheres was evaluated periodically for visual quality, decay, aroma, off-odor, color, and chlorophyll content. Cilantro stored in air at 0 degrees C had good visual quality for 18 to 22 days, while at 5 and 7.5 degrees C good quality was maintained for about 14 and 7 days, respectively. An atmosphere of air plus 5% or 9% CO2 extended the shelf-life of cilantro stored at 7.5 degrees C to about 14 days. Quality of cilantro stored in 3% O(2)plus CO2 was similar to that stored in air plus CO2. Atmospheres enriched with 9% to 10% CO2 caused dark lesions after 18 days; 20% CO2 caused severe injury after 7 days. Although visual quality could be maintained for up to 22 days, typical cilantro aroma decreased notably after 14 days, regardless of storage conditions.

KEYWORDS: ETHYLENE, LEAVES, STORAGE, VEGETABLES

1374
Loats, K.V., and J. Rebbeck. 1999. Interactive effects of ozone and elevated carbon dioxide on the growth and physiology of black cherry, green ash, and yellow- poplar seedlings. *Environmental Pollution 106(2):237-248.*

Potted seedlings of black cherry (Prunus serotina Ehrh.) (BC), green ash (Fraxinus pennsylvanica Marsh.) (GA), and yellow- poplar (Liriodendron tulipifera L.) (YP) were exposed to one of the four treatments: (1) charcoal-filtered air (CF) at ambient CO2 (control); (2) twice ambient O-3 (2XO(3)); (3) twice ambient CO2 (650 mu l l(-1)) plus CF air (2xCO(2)); or (4) twice ambient CO2 (650 yl l(-1)) plus twice ambient O-3 (2XCO(2)+2XO(3)) The treatments were duplicated in eight continuously stirred tank reactors for 10 weeks. Gas exchange was measured during the last 3 weeks of treatment and all seedlings were destructively harvested after 10 weeks. Significant interactive effects of O-3 and CO2 on the gas exchange of all three species were limited. The effects of elevated CO2 and O-3, singly and combined, on light-saturated net photosynthesis (A(max)) and stomatal conductance (g(s)) were inconsistent across species. In all three species, elevated O-3 had no effect on g(s). Elevated CO2 significantly increased A(max) in GA and YP foliage, and decreased g(s) in YP foliage. Maximum carbon exchange rates and quantum efficiencies derived from light-response curves increased, while compensation irradiance and dark respiration decreased in all three species when exposed to 2xCO(2). Elevated O-3 affected few of these parameters but any change that was observed was opposite to that fi-om exposure to 2xCO(2)-air. Interactive effects of CO2 and O-3 On light-response parameters were limited. Carboxylation efficiencies, derived from CO2-response curves (A/C-i curves) decreased only in YP foliage exposed to 2xCO(2)-air. In general, growth was significantly stimulated by 2xCO(2) in all three species; though there were few significant growth responses following exposure to 2xO(3) or the combination of 2xCO(2) plus 2xO(3). Results indicate that responses to interacting stressors such as O-3 and CO2 are species specific. (C) 1999 Published by Elsevier Science Ltd. All rights reserved.

KEYWORDS: ABIES L KARST, ACER- SACCHARUM MARSH, ATMOSPHERIC CO2, ENVIRONMENT ALTERS RESPONSE, GAS-EXCHANGE, HYBRID POPULUS L, LIRIODENDRON-TULIPIFERA L, NET PHOTOSYNTHESIS, STOMATAL CONDUCTANCE, TROPOSPHERIC OZONE

1375
Lockwood, J.G. 1999. Is potential evapotranspiration and its relationship with actual evapotranspiration sensitive to elevated atmospheric CO2 levels? *Climatic Change 41(2):193-212.*

The possibility is examined that potential evapotranspiration values may be sensitive to changes in atmospheric carbon dioxide content. Enhanced levels of atmospheric CO2 increase water use efficiency of vegetation by improving growth rates and suppressing transpiration per unit leaf area. Highly cultivated crops without water or nutrient constraints are able to show the greatest growth improvements. In many natural or semi-natural ecosystems, under enhanced atmospheric CO2 concentrations, limits on the availability of soil nutrients severely constrains the possibility of improvements in growth and significant increases in leaf area index that could compensate for a decrease in transpiration per unit leaf area. Thus, in many natural or semi-natural ecosystems, which often form water gathering grounds in river basins, enhanced levels of CO2 will suppress transpiration and perhaps increase the proporation of precipitation that forms runoff or ground water. In low vegetation covers, such as grassland, the rates of transpiration and also evaporation from canopies that are wet after rainfall (interception loss) are very similar. In these canopies, evapotranspiration is unlikely to be significantly increased by small increases in leaf area index. It is suggested that the suppression of potential evapotranspiration by enhanced CO2 levels will be small, but that actual transpiration from tall, slow growing vegetation covers may be significantly suppressed. Thus for some vegetation covers the relationship between actual and potential evapotranspiration may be sensitive to CO2 levels. If this is so, it could be of importance to many water balance calculations. The suppression of evapotranspiration by enhanced CO2 levels will be most noticeable in dry climates where interception loss is insignificant and largely masked in very wet climates where a large proportion of evapotranspiration consists of interception loss.

KEYWORDS: CARBON DIOXIDE, EVAPORATION, GLOBAL CLIMATE MODEL, INCREASES, PINE CANOPY, RESPONSES, STOMATAL-RESISTANCE, TEMPERATURE, TRANSPIRATION, VEGETATION

1376
Loehle, C. 1995. Anomalous responses of plants to co2 enrichment. *Oikos 73(2):181-187.*

A number of unexplained responses of plants to CO2 enrichment have been observed. These anomalies can be explained on the basis of growth analysis of whole plants. Some plants may fail to respond to enrichment because they are long-lived and have conservative growth responses or come from impoverished habitats. Apparent (but not real) acclimation to CO2 enrichment might be observed if only part of the growth curve over the life of a perennial is studied. The apparent increased efficiency of nitrogen use may merely be an increase in storage of nonstructural carbohydrate. A model analysis of these effects is presented. Discrepancies among species in relative responses of different plant parts are argued to be largely a function of where the plant typically stores nonstructural carbohydrates, which itself is a function of plant growth stage. Thus, a closer consideration of plant growth strategies and growth partitioning is needed to properly interpret results of CO2 enrichment studies.

KEYWORDS: ATMOSPHERIC CO2, CARBON-DIOXIDE ENRICHMENT, ELEVATED CO2, GROWTH, HABITAT TEMPLET, LIFE-HISTORY STRATEGIES, MINERAL NUTRITION, NITROGEN CONCENTRATION, ROOT, SHOOT RATIOS

1377
Loiseau, P., and J.F. Soussana. 1999. Elevated [CO2], temperature increase and N supply effects on the accumulation of below-ground carbon in a temperate grassland ecosystem. *Plant and Soil 212(2):123-134.*

The effects of elevated [CO2] (700 mu l l(-1) [CO2]) and temperature increase (+3 degrees C) on carbon accumulation in a grassland soil were studied at two N-fertiliser supplies (160 and 530 kgN ha(-1) year(-1)) in a long-term experiment (2.5 years) on well established ryegrass swards (Lolium perenne L.,) supplied with the same amounts of irrigation water. For all experimental treatments, the C:N ratio of the top soil organic matter fractions increased with their particle size. Elevated CO2 concentration increased the C:N ratios of the below-ground phytomass and of the macro-organic matter. A supplemental fertiliser N or a 3 degrees C increase in elevated [CO2] reduced it. At the last sampling date, elevated [CO2] did not affect the C:N ratio of the soil organic matter fractions, but increased significantly the accumulation of roots and of macro- organic matter above 200 mu m (MOM). An increased N-fertiliser supply stimulated the accumulation of the non harvested plant phytomass and of the OM between 2 and 50 mu m, without positive effect on the macro-organic matter > 200 mu m. Elevated [CO2] increased C accumulation in the OM fractions above 50 mu m by +2.1 tC ha(-1), on average, whereas increasing the fertiliser N supply led to an average supplemental accumulation of +0.8 tC ha(-1). There was no significant effect of a 3 degrees C temperature increase under elevated [CO2] on C accumulation in the OM fractions above 50 mu m.

KEYWORDS: ATMOSPHERIC CO2, BALANCE, COTTON, DECOMPOSITION, DIOXIDE, ENRICHMENT, MICROBIAL BIOMASS, NITROGEN, SOIL CARBON, SWARD

1378

Loiseau, P., and J.F. Soussana. 1999. Elevated [CO2], temperature increase and N supply effects on the turnover of below-ground carbon in a temperate grassland ecosystem. *Plant and Soil 210(2):233-247.*

The effects of elevated [CO2] (700 mu l l(-1) CO2) and temperature increase (+3 degrees C) on carbon turnover in grassland soils were studied during 2.5 years at two N fertiliser supplies (160 and 530 kg N ha(-1) y(-1)) in an experiment with well-established ryegrass swards (Lolium perenne) supplied with the same amounts of irrigation water. During the growing season, swards from the control climate (350 mu l l(-1) [CO2] at outdoor air temperature) were pulse labelled by the addition of (CO2)-C-13. The elevated [CO2] treatments were continuously labelled by the addition of fossil-fuel derived CO2 (C-13 of -40 to -50 parts per thousand). Prior to the start of the experimental treatments, the carbon accumulated in the plant parts and in the soil macro-organic matter ('old' C) was at -32 parts per thousand. During the experiment, the carbon fixed in the plant material ('new' C) was at -14 and -54 parts per thousand in the ambient and elevated [CO2] treatments, respectively. During the experiment, the C-13 isotopic mass balance method was used to calculate, for the top soil (0-15 cm), the carbon turnover in the stubble and roots and in the soil macro-organic matter above 200 mu (MOM). Elevated [CO2] stimulated the turnover of organic carbon in the roots and stubble and in the MOM at N+, but not at N-. At the high N supply, the mean replacement time of 'old' C by 'new' C declined in elevated, compared to ambient [CO2], from 18 to 7 months for the roots and stubble and from 25 to 17 months for the MOM. This resulted from increased rates of 'new' C accumulation and of 'old' C decay. By contrast, at the low N supply, despite an increase in the rate of accumulation of 'new' C, the soil C pools did not turnover faster in elevated [CO2], as the rate of 'old' C decomposition was reduced. A 3 degrees C temperature increase in elevated [CO2] decreased the input of fresh C to the roots and stubble and enhanced significantly the exponential rate for the 'old' C decomposition in the roots and stubble. An increased fertiliser N supply reduced the carbon turnover in the roots and stubble and in the MOM, in ambient but not in elevated [CO2]. The respective roles for carbon turnover in the coarse soil OM fractions, of the C:N ratio of the litter, of the inorganic N availability and of a possible priming effect between C- substrates are discussed.

KEYWORDS: ATMOSPHERIC CO2, DIOXIDE ENRICHMENT, GLOBAL CHANGE, LITTER QUALITY, NATURAL C-13 ABUNDANCE, ROOT-GROWTH, SOIL ORGANIC MATTER, TALLGRASS PRAIRIE, TERM DECOMPOSITION, WATER-USE

1379

Long, S.P., N.R. Baker, and C.A. Raines. 1993. Analyzing the responses of photosynthetic co2 assimilation to long-term elevation of atmospheric co2 concentration. *Vegetatio 104:33-45.*

Understanding how photosynthetic capacity acclimatises when plants are grown in an atmosphere of rising CO2 concentrations will be vital to the development of mechanistic models of the response of plant productivity to global environmental change. A limitation to the study of acclimatisation is the small amount of material that may be destructively harvested from long-term studies of the effects of elevation of CO2 concentration. Technological developments in the measurement of gas exchange, fluorescence and absorption spectroscopy, coupled with theoretical developments in the interpretation of measured values now allow detailed analyses of limitations to photosynthesis in vivo. The use of leaf chambers with Ulbricht integrating spheres allows separation of change in the maximum efficiency of energy transduction in the assimilation of CO2 from changes in tissue absorptance. Analysis of the response of CO2 assimilation to intercellular CO2 concentration allows quantitative determination of the limitation imposed by stomata, carboxylation efficiency, and the rate of regeneration of ribulose 1:5 bisphosphate. Chlorophyll fluorescence provides a rapid method for detecting photoinhibition in heterogeneously illuminated leaves within canopies in the field. Modulated fluorescence and absorption spectroscopy allow parallel measurements of the efficiency of light utilisation in electron transport through photosystems I and II in situ.

KEYWORDS: ABSORBANCE CHANGES, ACCLIMATION, APPARATUS, CHLOROPHYLL FLUORESCENCE, LEAVES, LIGHT, PHOTOINHIBITION, QUANTUM YIELD, RISING CO2, STOMATAL CONDUCTANCE

1380

Long, S.P., and B.G. Drake. 1991. Effect of the long-term elevation of CO2 concentration in the field on the quantum yield of photosynthesis of the C3 sedge, Scirpus olneyi. *Plant Physiology 96(1):221-226.*

CO2 concentration was elevated throughout 3 years around stands of the C3 sedge Scirpus olneyi on a tidal marsh of the Chesapeake Bay. The hypothesis that tissues developed in an elevated CO2 atmosphere will show an acclimatory decrease in photosynthetic capacity under light-limiting conditions was examined. The absorbed light quantum yield of CO2 uptake (phi- abs and the efficiency of photosystem II photochemistry were determined for plants which had developed in open top chambers with CO2 concentrations in air of 680 micromoles per mole, and of 351 micromoles per mole as controls. An Ulbricht sphere cuvette incorporated into an open gas exchange system was used to determine phi-abs and a portable chlorophyll fluorimeter was used to estimate the photochemical efficiency of photosystem II. When measured in an atmosphere with 10 millimoles per mole O2 to suppress photorespiration, shoots showed a phi-abs of 0.093 +/- 0.003, with no statistically significant difference between shoots grown in elevated or control CO2 concentrations. Efficiency of photosystem II photochemistry was also unchanged by development in an elevated CO2 atmosphere. Shoots grown and measured in 680 micromoles per mole of CO2 in air showed a phi- abs of 0.078 +/- 0.004 compared with O.065 +/- 0.003 for leaves grown and measured in 351 micromoles per mole CO2 in air; a highly significant increase. In accordance with the change in phi-abs, the light compensation point of photosynthesis decreased from 51 +/- 3 to 31 +/- 3 micromoles per square meter per second for stems grown and measured in 351 and 680 micromoles per mole of CO2 in air, respectively. The results suggest that even after 3 years of growth in elevated CO2, there is no evidence of acclimation in capacity for photosynthesis under light-limited conditions which would counteract the stimulation of photosynthetic CO2 uptake otherwise expected through decreased photorespiration.

KEYWORDS: C-4 PLANTS, CHAMBER, CHLOROPHYLL FLUORESCENCE, LEAVES, MARSH

1381

Long, S.P., and P.R. Hutchin. 1991. Primary production in grasslands and coniferous forests with climate change - an overview. *Ecological Applications 1(2):139-156.*

In energy terms primary production is the driving step of the global carbon cycle. To predict the interaction of ecosystems with the "greenhouse" effect, it is necessary to understand how primary production, consumption, and decomposition will respond to climate change. Most estimates of primary production have been made by extrapolation from measured standing crops. For grasslands we show this approach to be seriously in error. Even where detailed studies of

turnover and belowground production have been undertaken, errors are invariably high, severely limiting the value of models based on correlation of climate with measured production. Detailed information is available on the responses of individual plant processes to individual climatic variables at the leaf, plant, and stand level, giving potential for a more mechanistic approach in modelling. This approach is limited by lack of information on multivariate interactions and on some key physiological processes, and by uncertainties in scaling up to populations and communities. Despite this, some important insights to possible community responses, particularly those of C3 and C4 types, may be gained from knowledge of responses at the plant level and below. This review outlines the expected character of climate change in grasslands and coniferous forests. Knowledge of the responses of different physiological processes underlying production to individual aspects of climate change is considered, and its implications for higher levels of organization are discussed. Although feasible, mechanistic models of production compound the errors associated with individual process responses with uncertainties surrounding interaction and scaling up, and result in very large errors in any prediction of response to climate change. We conclude that there is insufficient information to predict accurately the response of primary production to climate change. The key processes for which information is inadequate and the parameters that have meaning at different scales need to be identified. Of particular promise is the approach of predicting production from light interception and conversion efficiency.

KEYWORDS: C-4 PHOTOSYNTHESIS, CARBONIC-ANHYDRASE, CHLOROPHYLL FLUORESCENCE, COLD-ACCLIMATED SEEDLINGS, DARK RESPIRATION, ELEVATED CO2 CONCENTRATIONS, FREEZING TEMPERATURES, HIGH LIGHT LEVELS, NITROGEN-USE EFFICIENCY, PINE PINUS-SYLVESTRIS

1382

Lootens, P., and J. Heursel. 1998. Irradiance, temperature, and carbon dioxide enrichment affect photosynthesis in Phalaenopsis hybrids. *Hortscience 33(7):1183-1185.*

The short-term effects of photosynthetic photon flux (PPF), day/night temperatures and CO2 concentration on CO2 exchange were determined for two Phalaenopsis hybrids. At 20 degrees C, the saturating PPF for photosynthesis was 180 mu mol.m(-2).s(- 1). At this PPF and ambient CO2 level (380 mu L.L-1), a day/night temperature of 20/15 degrees C resulted in the largest daily CO2 uptake. Higher night temperatures probably increased the respiration rate and lowered daily CO2 uptake in comparison with 20/15 degrees C. An increase in the CO2 concentration from 380 to 950 mu L.L-1 increased daily CO2 uptake by 82%.

KEYWORDS: CO2, CRASSULACEAN ACID METABOLISM, ENERGY-DISSIPATION, FLUORESCENCE, LEAVES, LIGHT, PHOTOCHEMICAL EFFICIENCY, REDUCTION STATE, RESPONSES, SHORT- TERM

1383

Lord, D., S. Morissette, and J. Allaire. 1993. Influence of light-intensity, nocturnal air-temperature and carbon-dioxide levels on greenhouse black spruce seedlings (picea-marianna). *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 23(1):101-110.*

Growth of containerized black spruce seedlings grown in greenhouses was studied in relation to factors known to influence plant growth. Artificial light intensity (3.80 and 72.04 mumol.m-2.s-1) and night air temperature (5, 10, 12.5, 15, and 20-degrees-C) were considered in a first experiment and artificial light intensity (4.24 and 59.57 mumol.m-2.s-1) and CO2 air concentration (ambient and 1000 muL.L-1) in a second one. Higher light intensity and CO2 enrichment increased dry biomass of seedlings as well as growth in height and stem diameter. Both factors similarly enhanced the last two parameters since height/diameter ratios showed little variation among treatments. Reducing night air temperature down to 10- degrees-C did not significantly influence height growth nor biomass increase when high intensity light was provided. Lower light intensity raised the threshold to 12.5-degrees-C. Shoot height, diameter, and dry biomass as well as the number of branches and buds per millimeter were strongly reduced by a 5- degrees-C night air temperature. High intensity light enhanced growth of containerized black spruce seedlings more than CO2 enrichment or a 5-degrees-C night air temperature. When used simultaneously, these growth enhancing factors had a synergistic effect during most of the treatment period; thereafter, the effect became partially additive. The relative growth rate peaked at the onset of exponential shoot growth and decreased after this point. However, the enhancing factors were still efficient since absolute growth differences between seedlings grown under the most-favorable conditions and controls kept increasing, The faster growing pace imposed by these growth enhancing conditions during the treatment period was maintained over the entire first growing season.

KEYWORDS: CO2- ENRICHMENT, DRY-MATTER PRODUCTION, GROWTH, PHOTOPERIOD

1384

Loretan, P.A., C.K. Bonsi, D.G. Mortley, R.M. Wheeler, C.L. Mackowiak, W.A. Hill, C.E. Morris, A.A. Trotman, and P.P. David. 1994. Effects of several environmental-factors on sweet-potato growth. *Life Sciences and Space Research XXV (3) 14(11):277-280.*

Effects of relative humidity, light intensity and photoperiod on growth of 'Ga Jet' and 'TI-155' sweetpotato cultivars, using the nutrient film technique (NFT), have been reported. In this study, the effect of ambient temperature regimes (constant 28 degrees C and diurnal 28:22 degrees C day:night) and different CO2 levels (ambient, 400,1 000, and 10 000 mu L/L - 400, 1 000 and 10 000 ppm) on growth of one or both of these cultivars in NFT are reported. For a 24-h photoperiod, no storage roots were produced for either cultivar in NFT when sweetpotato plants were grown at a constant temperature of 28 degrees C. For the same photoperiod, when a 28:22 degrees C diurnal temperature variation was used, there were still no storage roots for 'TI- 155' but the cv. 'Ga Jet' produced 537 g/plant of storage roots. For both a 12-h and 24-h photoperiod,'Ga Jet' storage root fresh and dry weight tended to be higher with a 28:22 degrees C diurnal temperature variation than with a constant 28 degrees C temperature regime. Preliminary results with both 'Ga Jet' and 'TI-155' cultivars indicate a distinctive diurnal stomatal response for sweetpotato grown in NFT under an ambient CO2 level. The stomatal conductance values observed for 'Ga Jet' at elevated CO2 levels indicated that the difference between the light- and dark-period conductance rates persisted at 400, 1 000, and 10 000 mu L/L.

KEYWORDS: POTATO

1385

Louche-Tessandier, D., G. Samson, C. Hernandez-Sebastia, P. Chagvardieff, and Y. Desjardins. 1999. Importance of light and CO2 on the effects of endomycorrhizal colonization on growth and photosynthesis of potato plantlets (Solanum tuberosum) in an in vitro tripartite system. *New Phytologist 142(3):539-550.*

A factorial analysis was conducted to investigate the effects of different levels of photosynthetic photon flux (PPF) and CO2 concentration on the interactions between the vesicular- arbuscular endomycorrhizal fungus Glomus intraradices and potato plantlets (Solanum tuberosum) cultured in an in vitro tripartite system. We observed that CO2 enrichment from 350 to 10000 ppm stimulated root colonization by the fungus, and that

this stimulation was more pronounced under high PPF (300 mu mol m(-2) s(-1)) than low PPF (60 mu mol m(-2) s(-1)). Consistent with these observations, the effects of G. intraradices on dry matter production in potato plantlets were strongly dependent on the CO2 and PPF levels during cultivation. There was no significant effect of the mycorrhizal fungus on dry matter production at 350 ppm of CO2 However, under the high CO, concentration, mycorrhiza had opposite effects on dry matter production depending on the PPF: a decrease (-21%) and a stimulation (+25%) of dry matter production after 2 wk of growth under low and high PPF, respectively, were observed in presence of G. intraradices relative to plantlets grown in its absence. Furthermore, in mycorrhizal plantlets grown under high levels of both PPF and CO2 the chlorophyll and carotenoid contents as well as the quantum yields of photosynthetic electron transport and the photochemical quenching qP of the chlorophyll-a fluorescence measured near the PPF during growth were all higher than in non-infected plantlets. Our results therefore indicate that mycorrhizal G. intraradices can alleviate the down regulation of photosynthesis related to sink limitation, and its effect on dry matter production is strongly dependent on the levels of CO2 and PPF during growth which determine the balance between the photosynthetic carbon uptake by the plantlets and the carbon cost by the fungus.

KEYWORDS: ARBUSCULAR MYCORRHIZAE, CHLOROPHYLL FLUORESCENCE, CULTURE, ELEVATED CO2, INFECTION, MYCORRHIZAL FUNGAL INOCULUM, PHOTOSYSTEM, PRENUCLEAR MINITUBERS, QUANTUM YIELD, RESPIRATION

1386

Lovelock, C.E., D. Kyllo, M. Popp, H. Isopp, A. Virgo, and K. Winter. 1997. Symbiotic vesicular-arbuscular mycorrhizae influence maximum rates of photosynthesis in tropical tree seedlings grown under elevated CO2. *Australian Journal of Plant Physiology 24(2):185-194.*

To investigate the importance of phosphorus and carbohydrate concentrations in influencing photosynthetic capacity of tropical forest tree seedlings under elevated CO2, we grew seedlings of Beilschmiedia pendula (Sw.) Hemsl. (Lauraceae) under elevated CO2 concentrations either with or without vesicular-arbuscular (VA) mycorrhizae. VA-mycorrhizae increased phosphorus concentrations in all plant organs (leaves, stems and roots). Maximum rates of photosynthesis (A(max)) measured under saturating levels of CO2 and light were correlated with leaf phosphorus concentrations. VA-mycorrhizae also increased leaf carbohydrate concentrations, particularly under elevated CO2, but levels were low and within the range observed in naturally occurring forest species. Root carbohydrate concentrations were reduced in VA-mycorrhizal plants relative to non-mycorrhizal plants. These results indicate an important role for VA-mycorrhizae in controlling photosynthetic rates and sink strength in tropical trees, and thus in determining their response to future increases in atmospheric CO2 concentrations.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, ENRICHMENT, INFECTION, MINERAL NUTRITION, PHOSPHORUS, PLANTS, RAIN-FOREST TREES, RESPONSES, SOIL, TRANSLOCATION

1387

Lovelock, C.E., D. Kyllo, and K. Winter. 1996. Growth responses to vesicular-arbuscular mycorrhizae and elevated CO2 in seedlings of a tropical tree, Beilschmiedia pendula (vol 10, pg 662, 1996). *Functional Ecology 10(6):784.*

1388

Lovelock, C.E., D. Kyllo, and K. Winter. 1996. Growth responses to vesicular-arbuscular mycorrhizae and elevated CO2 in seedlings of a tropical tree, Beilschmiedia pendula. *Functional Ecology 10(5):662-667.*

1. Vesicular-arbuscular (VA) mycorrhizae increased relative growth rates (RGR) of the shade-tolerant tropical tree species Beilschmiedia pendula at both ambient and doubled CO2 concentrations. 2. RGR was correlated with the net assimilation rate (NAR) of plants. Within this general correlation, in plants with similar RGR, NAR was decreased in VA-mycorrhizal plants compared with non-mycorrhizal plants. As RGR is the product of NAR and the leaf area ratio (LAR, the ratio of leaf area to plant mass), increases in RGR in VA-mycorrhizal plants were the results of increased LAR. Thus, VA-mycorrhizae increased growth rates of B. pendula by altering the morphology of the seedlings. 3. Under elevated CO2 the amount of fungus within roots increased in VA-mycorrhizal plants compared with those grown under ambient CO2 and this was associated with a greater post-inoculation depression in leaf growth. Post- inoculation depressions in leaf growth and the lower NAR (in plants with similar RGR) of VA-mycorrhizal plants indicate there is increased carbon transfer to soils under elevated CO2.

KEYWORDS: ASSOCIATIONS, ATMOSPHERIC CO2, CARBON, DEMAND, ECOSYSTEMS, FOREST, INFECTION, PLANTAGO-MAJOR, RESPIRATION

1389

Lovelock, C.E., J. Posada, and K. Winter. 1999. Effects of elevated CO2 and defoliation on compensatory growth and photosynthesis of seedlings in a tropical tree, Copaifera aromatica. *Biotropica 31(2):279-287.*

After defoliation by herbivores, some plants exhibit enhanced rates of photosynthesis and growth that enable them to compensate for lost tissue, thus maintaining their fitness relative to competing, undefoliated plants. Our aim was to determine whether compensatory photosynthesis and growth would be altered by increasing concentrations of atmospheric CO2. Defoliation of developing leaflets on seedlings of a tropical tree, Copaifera aromatica, caused increases in photosynthesis under ambient CO2, but not under elevated CO2. An enhancement in the development of buds in the leaf axils followed defoliation at ambient levels of CO2. In contrast, under elevated CO2, enhanced development of buds occurred in undefoliated plants with no further enhancement in bud development due to exposure to elevated CO2. Growth of leaf area after defoliation was increased, particularly under elevated CO2. Despite this increase, defoliated plants grown under elevated CO2 were further from compensating for tissue lost during defoliation after 5-1/2 weeks than those grown under ambient CO2 concentrations.

KEYWORDS: ACCLIMATION, CAPACITY, CARBON DIOXIDE, FITNESS, FOREST, PATTERNS, PLANT, RESPONSES, SIMULATED HERBIVORY, STRESS

1390

Lovelock, C.E., A. Virgo, M. Popp, and K. Winter. 1999. Effects of elevated CO2 concentrations on photosynthesis, growth and reproduction of branches of the tropical canopy tree species, Luehea seemannii Tr. & Planch. *Plant, Cell and Environment 22(1):49-59.*

Mature trees have already experienced substantial increases in CO2 concentrations during their lifetimes, and will experience continuing increases in the future. Small open-top chambers were used to enclose branchlets that were at a height of between 20 and 25 m in the canopy of the tree species Luehea seemannii Tr. & Planch. in a tropical forest in Panama. Elevated concentrations of CO2 increased the rate of photosynthetic carbon fixation and decreased stomatal conductance of leaves, but did not influence the growth of leaf area per chamber, the production of flower buds and fruit nor the concentration of

nonstructural carbohydrates within leaves. The production of flower buds was highly correlated with the leaf area produced in the second flush of leaves, indicating that the branchlets of mature trees of Luehea seemannii are autonomous to a considerable extent. Elevated levels of CO2 did increase the concentration of nonstructural carbohydrates in woody stem tissue. Elevated CO2 concentration also they increased the ratio of leaf area to total biomass of branchlets, and tended to reduce individual fruit weight. These data suggest that the biomass allocation patterns of mature trees may change under future elevated levels of CO2. Although there were no effects on growth during the experiment, the possibility of increased growth in the season following CO2 enrichment due to increased carbohydrate concentrations in woody tissue cannot be excluded.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, ENRICHMENT, FOREST, GAS-EXCHANGE, LEAF, PINUS-TAEDA TREES, RESPONSES, SOIL, WATER-USE

1391

Lovelock, C.E., K. Winter, R. Mersits, and M. Popp. 1998. Responses of communities of tropical tree species to elevated CO2 in a forest clearing. *Oecologia 116(1-2):207-218.*

Communities of ten species of tropical forest tree seedlings from three successional classes were grown at ambient and elevated CO2 in large open-top chambers on the edge of a forest in Panama. Communities grew from 20 cm to approximately 2 m in height in 6 months. No enhancements in plant biomass accumulation occurred under elevated CO2 either in the whole communities or in growth of individual species. Reductions in leaf area index under elevated CO2 were observed, as were decreases in leaf nitrogen concentrations and increases in the C:N ratio of leaf tissue. Species tended to respond individualistically to elevated CO2, but some generalizations of how successional groupings responded could be made. Early and mid-successional species generally showed greater responses to elevated CO2 than late-successional species, particularly with respect to increases in photosynthetic rates and leaf starch concentrations, and reductions in leaf area ratio. Late-successional species showed greater increases in C:N ratios in response to elevated CO2 than did other species. Our results indicate that there may not be an increase in the growth of regenerating tropical forest under elevated CO2, but that there could be changes in soil nutrient availability because of reductions in leaf tissue quality, particularly in late- successional species.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, DECOMPOSITION RATES, ECOSYSTEMS, ENRICHMENT, GROWTH ENHANCEMENT, LEAF LITTER, ORGANIC-MATTER, PLANT FUNCTIONAL TYPES, RAIN-FOREST, SOIL NUTRIENT

1392

Luan, J.S., Y.Q. Luo, and J.F. Reynolds. 1999. Responses of a loblolly pine ecosystem to CO2 enrichment: a modeling analysis. *Tree Physiology 19(4-5):279-287.*

The development of the Free-Air CO2 Enrichment (FACE) facilities represents a substantial advance in experimental technology for studying ecosystem responses to elevated CO2. A challenge arising from the application of this technology is the utilization of short-term FACE results for predicting long- term ecosystem responses. This modeling study was designed to explore interactions of various processes on ecosystem productivity at elevated CO2 on the decadal scale. We used a forest model (FORDYN) to analyze CO2 responses-particularly soil nitrogen dynamics, carbon production and storage-of a loblolly pine ecosystem in the Duke University Forest. When a 14-year-old stand was exposed to elevated CO2, simulated increases in annual net primary productivity (NPP) were 13, 10 and 7.5% in Years 1, 2 and 10, respectively, compared with values at ambient CO2. Carbon storage increased by 4% in trees and 9.2% in soil in Year 10 in response to elevated CO2. When the ecosystem was exposed to elevated CO2 from the beginning of forest regrowth, annual NPP and carbon storage in trees and soil were increased by 32, 18 and 20%, respectively, compared with values at ambient CO2. In addition, simulation of a 20% increase in mineralization rate led to a slight increase in biomass growth and carbon storage, but the simulated 20% increase in fine root turnover rate considerably increased annual NPP and carbon storage in soil. The modeling results indicated that (1) stimulation of NPP and carbon storage by elevated CO2, is transient and (2) effects of elevated CO2 on ecosystem processes-canopy development, soil nitrogen mineralization and root turnover-have great impacts on ecosystem C dynamics. A detailed understanding of these processes will improve our ability to predict long-term ecosystem responses to CO2 enrichment.

KEYWORDS: CARBON DIOXIDE, ELEVATED ATMOSPHERIC CO2, FOREST, GROWTH, NITROGEN, PHOTOSYNTHESIS, SEEDLINGS, TAEDA L, TERRESTRIAL ECOSYSTEMS, TREES

1393

Lucas, W.J., A. Olesinski, R.J. Hull, J.S. Haudenshield, C.M. Deom, R.N. Beachy, and S. Wolf. 1993. Influence of the tobacco mosaic-virus 30-kda movement protein on carbon metabolism and photosynthate partitioning in transgenic tobacco plants. *Planta 190(1):88-96.*

Transgenic tobacco (Nicotiana tabacum L.) plants expressing the 30-kDa movement protein of tobacco mosaic virus (TMV-MP) were employed to investigate the influence of a localized change in mesophyll-bundle sheath plasmodesmal size exclusion limit on photosynthetic performance and on carbon metabolism and allocation. Under conditions of saturating irradiance, tobacco plants expressing the TMV-MP were found to have higher photosynthetic CO2-response curves compared with vector control plants. However, this difference was significant only in the presence of elevated CO2 levels. Photosynthetic measurements made in the greenhouse, under endogenous growth conditions, revealed that there was little difference between TMV-MP- expressing and control tobacco plants. However, analysis of carbon metabolites within source leaves where a TMV-MP-induced increase in plasmodesmal size exclusion limit had recently taken place established that the levels of sucrose, glucose, fructose and starch were considerably elevated above those present in equivalent control leaves. Although expression of the TMV-MP did not alter total plant biomass, it reduced carbon allocation to the lower region of the stem and roots. This difference in biomass distribution was clearly evident in the lower root-to-shoot ratios for the TMV-MP transgenic plants. Microinjection (dye-coupling) studies established that the TMV- MP-associated reduction in photosynthate delivery (allocation) to the roots was not due to a direct effect on root cortical plasmodesmata. Rather, this change appeared to result from an alteration in phloem transport from young source leaves in which the TMV-MP had yet to exert its influence over plasmodesmal size exclusion limits. These results are discussed in terms of the rate-limiting steps involved in sucrose movement into the phloem.

KEYWORDS: BUNDLE SHEATH-CELLS, C-4 PLANTS, COMMELINA-BENGHALENSIS, EXCLUSION LIMIT, LEAVES, MINOR VEINS, PLASMODESMATAL FREQUENCY, ROOT, SHOOT, SYMPLASTIC CONNECTIONS

1394

Ludeke, M.K.B., S. Donges, R.D. Otto, J. Kindermann, F.W. Badeck, P. Ramge, U. Jakel, and G.H. Kohlmaier. 1995. Responses in npp and carbon stores of the northern biomes to a co2-induced climatic-change, as evaluated by the frankfurt biosphere model (fbm). *Tellus Series B-Chemical and Physical Meteorology 47(1-2):191-205.*

To assess the role of the boreal and temperate forests and the tundra ecosystems in a future CO2-induced climate change, the Frankfurt biosphere model(FBM) was applied to the 3xCO(2) climate as calculated by the GCM of the MPI fur Meteorologie in Hamburg. The FBM predicts on a 1 degrees x1 degrees spatial grid the seasonal and perannual course of leaf biomass and feeder roots, woody biomass, soil carbon and soil water in response to the seasonal course of light, precipitation and temperature. The phenology is controlled by the flux balance of carbon gains and losses, thus being dependent on the driving climate and the state of vegetation. Two equilibrium runs based on the 3xCO(2) climate were performed: (1) Considering the pure climate effect (with no direct CO2 fertilization) we obtained a 22% decrease of the net primary production (NPP) due to enhanced autotrophic respiration and increased water limitation. Together with the effect on the soils this results in a 170 Gt carbon source. (2) Considering a CO2-induced enhancement of the maximum photosynthesis the pure climate effect is more than compensated and we predict a NPP increase of 9% and a total carbon sink of 50 Ct C. This effect may even be an underestimate if one takes into consideration a shift in the optimum temperature for photosynthesis under enhanced levels of atmospheric CO2 as proposed by Long and Drake.

KEYWORDS: CO2, ECOSYSTEMS, EXCHANGE, FORESTS, GRASSLANDS, NET PRIMARY PRODUCTION, STORAGE, TEMPERATURE, VEGETATION

1395

Ludewig, F., U. Sonnewald, F. Kauder, D. Heineke, M. Geiger, M. Stitt, B.T. Muller-Rober, B. Gillissen, C. Kuhn, and W.B. Frommer. 1998. The role of transient starch in acclimation to elevated atmospheric CO2. *Febs Letters 429(2):147-151.*

Although increased concentrations of CO2 stimulate photosynthesis, this stimulation is often lost during prolonged exposure to elevated carbon dioxide, leading to an attenuation of the potential gain in yield. Under these conditions, a wide variety of species accumulates non-structural carbohydrates in leaves, It has been proposed that starch accumulation directly inhibits photosynthesis, that the rate of sucrose and starch synthesis limits photosynthesis, or that accumulation of sugars triggers changes in gene expression resulting in loser activities of Rubisco and inhibition of photosynthesis. To distinguish these explanations, transgenic plants unable to accumulate transient starch due to leaf mesophyll-specific antisense expression of AGP B were grown at ambient and elevated carbon dioxide. There was a positive correlation between the capacity for starch synthesis and the rate of photosynthesis at elevated CO2 concentrations, showing that the capability to synthesize leaf starch is essential for photosynthesis in elevated carbon dioxide, The results show that in elevated carbon dioxide, photosynthesis is restricted by the rate of end product synthesis, Accumulation of starch is not responsible for inhibition of photosynthesis, Although transgenic plants contained increased levels of hexoses, transcripts of photosynthetic genes were not downregulated and Rubisco activity was not decreased arguing against a role of sugar sensing in acclimation to high CO2, (C) 1998 Federation of European Biochemical Societies.

KEYWORDS: ADP-GLUCOSE PYROPHOSPHORYLASE, CARBON DIOXIDE, CLONING, EXPRESSION, GENES, INHIBITION, LEADS, PHOTOSYNTHESIS, SUCROSE, TOMATO PLANTS

1396

Lukewille, A., and R.F. Wright. 1997. Experimentally increased soil temperature causes release of nitrogen at a boreal forest catchment in southern Norway. *Global Change Biology 3(1):13-21.*

Boreal forest ecosystems are sensitive to global warming, caused by increasing emissions of CO2 and other greenhouse gases. Assessment of the biological response to future climate change is based mainly on large-scale models. Whole-ecosystem experiments provide one of the few available tools by which ecosystem response can be measured and with which global models can be evaluated. Boreal ecosystem response to global change may be manifest by alterations in nitrogen (N) dynamics, as N is often the growth limiting nutrient. The CLIMEX (Climate Change Experiment) project entails catchment-scale manipulations of CO2 (to 560 ppmv) and temperature (by + 3 to + 5 degrees C) to whole forest ecosystems in southern Norway. Soil temperature is increased at 400-m(2) EGIL catchment by means of electric cables placed on the soil surface. Soil warming at EGIL catchment caused an increase in nitrate and ammonium concentrations in runoff in the first year of treatment. We hypothesize that higher temperature increased N release by mineralization. Whether these responses are only transient will be shown by additional years' treatment.

KEYWORDS: ARCTIC TUNDRA, CARBON DIOXIDE, CO2, ECOSYSTEMS, MINERALIZATION, RESPONSES, SINK, WHOLE-CATCHMENT

1397

Lund, C.P., W.J. Riley, L.L. Pierce, and C.B. Field. 1999. The effects of chamber pressurization on soil-surface CO2 flux and the implications for NEE measurements under elevated CO2. *Global Change Biology 5(3):269-281.*

Soil and ecosystem trace gas fluxes are commonly measured using the dynamic chamber technique. Although the chamber pressure anomalies associated with this method are known to be a source of error, their effects have not been fully characterized. In this study, we use results from soil gas-exchange experiments and a soil CO2 transport model to characterize the effects of chamber pressure on soil CO2 efflux in an annual California grassland. For greater than ambient chamber pressures, experimental data show that soil-surface CO2 flux decreases as a nonlinear function of increasing chamber pressure; this decrease is larger for drier soils. In dry soil, a gauge pressure of 0.5 Pa reduced the measured soil CO2 efflux by roughly 70% relative to the control measurement at ambient pressure. Results from the soil CO2 transport model show that pressurizing the flux chamber above ambient pressure effectively flushes CO2 from the soil by generating a downward now of air through the soil air-filled pore space. This advective flow of air reduces the CO2 concentration gradient across the soil-atmosphere interface, resulting in a smaller diffusive flux into the chamber head space. Simulations also show that the reduction in diffusive flux is a function of chamber pressure, soil moisture, soil texture, the depth distribution of soil CO2 generation, and chamber diameter. These results highlight the need for caution in the interpretation of dynamic chamber trace gas flux measurements. A portion of the frequently observed increase in net ecosystem carbon uptake under elevated CO2 may be an artifact resulting from the impact of chamber pressurization on soil CO2 efflux.

KEYWORDS: ATMOSPHERIC CO2, CARBON, CLEAR-CUT, EFFLUX, EVOLUTION, FOREST SOILS, GAS-EXCHANGE, PRAIRIE, ROOT RESPIRATION, WATER-VAPOR

1398

Luo, Y., J.L. Chen, J.F. Reynolds, C.B. Field, and H.A. Mooney. 1997. Disproportional increases in photosynthesis and plant biomass in a Californian grassland exposed to elevated CO2: a simulation analysis. *Functional Ecology 11(6):696-704.*

1. Elevated CO2 concentrations often lead to increased photosynthetic carbon uptake in plants, but this does nor necessarily result in a proportional increase in plant biomass. We examined this paradox for grasslands in northern California that have been exposed to elevated

CO2 since 1992. We evaluated the effects of physiological adjustments on plant growth and carbon balance of the dominant species, Avena barbata, using a plant growth model. 2. Without physiological adjustments, an observed 70% increase in leaf photosynthesis in elevated CO2 was predicted to increase plant biomass by 97% whereas experimental measurements suggested 5 and 13% decreases in 1992 and 1993, respectively, and a 40% increase in 1994. 3. Simulations with an increase in carbon allocation to roots by 29%, or leaf death rate by 80%, or non-structural carbohydrate storage by 60%, or leaf mass per unit area by 25% each predicted an approximately 40% increase in plant biomass in 1994 under elevated CO2. It follows that greater suppression of the biomass responses to elevated CO2, in 1992 and 1993 resulted from variable combinations of these physiological adjustments. 4. This modelling study concludes that (a) an increase in carbon loss or (b) a decrease in carbon-use efficiency or (c) an increase in carbon allocation to root growth will result in an increase in biomass growth that is less than that in leaf photosynthesis under elevated CO2. Alternatively, if carbon loss is reduced (e.g, depressed respiration) and/or carbon allocation to leaf growth is increased, biomass growth may be stimulated more than leaf photosynthesis by atmospheric CO2 concentration. Moreover, this modelling exercise suggests that physiological adjustments may have substantial effects on ecosystem carbon processes by varying ecosystem carbon influx, litterfall and Litter quality.

KEYWORDS: CANOPY, CARBON BALANCE, ECOSYSTEMS, ENRICHMENT, GROWTH, NUTRIENT, RESPIRATION, RESPONSES

1399

Luo, Y., C.B. Field, and H.A. Mooney. 1994. Predicting responses of photosynthesis and root fraction to elevated [co2](a) - interactions among carbon, nitrogen, and growth. *Plant, Cell and Environment 17(11):1195-1204.*

At elevated atmospheric CO2 concentrations ([CO2](a)), photosynthetic capacity (A(max)) and root fraction (eta(R), the ratio of root to plant dry mass) increased in some studies and decreased in others. Here, we have explored possible causes of this, focusing on the relative magnitudes of the effects of elevated [CO2](a) on specific leaf (n(m)) and plant (n(p)) nitrogen concentrations, leaf mass per unit area (h), and plant nitrogen productivity (alpha). In our survey of 39 studies with 35 species, we found that elevated [CO2](a) led to decreased n(m) and n(p) in all the studies and to increased h and alpha in most of the studies. The magnitudes of these changes varied with species and with experimental conditions. Based on a model that integrated [CO2](a)-induced changes in leaf nitrogen into a biochemically based model of leaf photosynthesis, we predicted that, to a first approximation, photosynthesis will be upregulated (A(max) will increase) when growth at increased [CO2](a) leads to increases in h that are larger than decreases in n(m). Photosynthesis will be downregulated (A(max) will decrease) when increases in h are smaller than decreases in n(m). The model suggests that photosynthetic capacity increases at elevated [CO2](a) only when additional leaf mesophyll more than compensates the effects of nitrogen dilution. We considered two kinds of regulatory paradigms that could lead to varying responses of eta(R) to elevated [CO2](a), and compared the predictions of each with the data. A simple static model based on the functional balance concept predicts that eta(R) should increase when neither n(p) nor h is very responsive to elevated [CO2](a). The quantitative and qualitative agreement of the predictions with data from the literature, however, is poor. A model that predicts eta(R) from the relative sensitivities of photosynthesis and relative growth rate to elevated [CO2](a) corresponds much more closely to the observations. In general, root fraction increases if the response of photosynthesis to [CO2](a) is greater than that of relative growth rate.

KEYWORDS: ATMOSPHERIC CO2 ENRICHMENT, C-3 PLANTS, COOCCURRING BIRCH, DIOXIDE CONCENTRATION, LEAF NITROGEN, MINERAL NUTRITION, N2 FIXATION, SHOOT RATIO, VULGARIS L, WHITE CLOVER

1400

Luo, Y., C.B. Field, and H.A. Mooney. 1997. Adapting GePSi (generic plant simulator) for modeling studies in the Jasper Ridge CO2 project. *Ecological Modelling 94(1):81-88.*

In order to conduct modeling studies on the effects of elevated atmospheric carbon dioxide concentration ([CO2]) on plant and ecosystem processes at the Jasper Ridge grassland in northern California, the generic plant simulator (GePSi) (Chen: J.-L. and Reynolds, J.F., 1997. Ecol. Model., 94: 53-66), is modified to simulate grass dynamics. This modification was attempted by the authors of this paper, who had no prior experience with the model. Prior to this project, GePSi, which is implemented in the object-oriented programming (OOP) language, C++, had only been used to model trees and woody shrubs. This exercise addressed several of the concepts presented in this volume concerning the purported benefits of genericness, modularity, and OOP in plant modeling. The objective of this paper is to briefly summarize the extent to which these benefits were realized and some of the problems encountered. Our evaluation is presented in terms of: (1) design considerations, including the importance of how the modules in GePSi were defined; and (2) the implementation phase, which critiques the use of OOP for facilitating the transfer of the model. This study suggests that generic, modular models such as GePSi will facilitate the interactions of model developers and users and reduce duplication of effort in model development. (C) 1997 Elsevier Science B.V.

KEYWORDS: CARBON, ELEVATED CO2, ENRICHMENT, GROWTH, LOBLOLLY-PINE, NITROGEN, PHOTOSYNTHETIC CAPACITY, PREDICTING RESPONSES, SEEDLINGS

1401

Luo, Y.H., and B.R. Strain. 1992. Leaf water status in velvetleaf under long-term interactions of water-stress, atmospheric humidity, and carbon-dioxide. *Journal of Plant Physiology 139(5):600-604.*

Well watered and water-stressed Abutilon theophrastic, were grown with relative humidity of 45% or 85% at 30-degrees-C and CO2 concentrations of 350 or 650-mu-mol mol-1. Elevated leaf water potentials of the water-stressed plants grown in both high and low humidities were caused by CO2 enrichment. Elevated water content (kg m-2 leaf area) caused by CO2 enrichment, higher water content at a given water potential, and notably lower rate in desiccation from detached leaves all occurred only in the plants grown in low humidity. These results may be related to enhanced dehydration resistance of the plants that experienced long-term low humidity.

KEYWORDS: CO2- ENRICHMENT, DROUGHT, EXCHANGE, PLANTS, RESPONSES, SOIL

1402

Luo, Y.Q., R.B. Jackson, C.B. Field, and H.A. Mooney. 1996. Elevated CO2 increases belowground respiration in California grasslands. *Oecologia 108(1):130-137.*

This study was designed to identify potential effects of elevated CO2 on belowground respiration (the sum of root and heterotrophic respiration) in field and microcosm ecosystems and on the annual carbon budget. We made three sets of respiration measurements in two CO2 treatments, i.e., (1) monthly in the sandstone grassland and in microcosms from November 1993 to June 1994; (2) at the annual peak of live biomass (March and April) in the serpentine and sandstone grasslands in 1993 and 1994; and (3) at peak biomass in the microcosms with monocultures of seven species in 1993. To help understand ecosystem carbon cycling,

we also made supplementary measurements of belowground respiration monthly in sandstone and serpentine grasslands located within 500 m of the CO2 experiment site. The seasonal average respiration rate in the sandstone grassland was 2.12 mu mol m(-2) s(-1) in elevated CO2, which was 32% higher than the 1.49 mu mol m(-2) s(-1) measured in ambient CO2 (P = 0.007). Studies of seven individual species in the microcosms indicated that respiration was positively correlated with plant biomass and increased, on average, by 70% with CO2. Monthly measurements revealed a strong seasonality in belowground respiration, being low (0-0.5 mu mol CO2 m(-2) s(-1) in the two grasslands adjacent to the CO2 site) in the summer dry season and high (2-4 mu mol CO2 m(- 1) s(-1) in the sandstone grassland and 2-7 mu mol CO2 m(-1) s(-1) in the microcosms) during the growing season from the onset of fall rains in November to early spring in April and May. Estimated annual carbon effluxes from the soil were 323 and 440 g C m(-2) year(-1) for the sandstone grasslands in ambient and elevated CO2. That CO2-stimulated increase in annual soil carbon efflux is more than twice as big as the increase in aboveground net primary productivity (NPPa) and approximately 60% of NPPa in this grassland in the current CO2 environment. The results of this study suggest that below- ground respiration can dissipate most of the increase in photosynthesis stimulated by elevated CO2.

KEYWORDS: ATMOSPHERIC CO2, CARBON, ENRICHMENT, FLUX, FOREST, NITROGEN, PONDEROSA PINE, SOIL RESPIRATION, TEMPERATURE, TUSSOCK TUNDRA

1403

Luo, Y.Q., and H.A. Mooney. 1995. Long-term CO2 stimulation of carbon influx into global terrestrial ecosystems: Issues and approaches. *Journal of Biogeography 22(4-5):797-803.*

Estimating the additional amount of global photosynthetic carbon influx into terrestrial ecosystems (P-G) becomes possible with a leaf-level factor (L) developed by Luo & Mooney only when an increase in atmospheric CO2 concentration (C-a) is small. Applying the L factor to study long-term stimulation of P-G with a large increase in C-a needs understanding of adjustments in leaf properties, canopy structure and ecosystem nitrogen availability, which could, potentially, feedback to photosynthetic carbon influx. Leaf photosynthetic properties vary greatly with elevated CO2 among species. Aggregation over a group of species, however, shows a small change, suggesting that globally averaged changes in leaf properties may be trivial. Canopy adjustment in elevated CO2 is largely unknown whereas indirect measurements suggest faster development of foliar canopy in elevated than ambient CO2. Biogeochemical feedback of nitrogen on global carbon influx is involved with two general issues: CO2 effects on ecosystem nitrogen availability and interactive effects of nitrogen and CO2 on photosynthesis. Although nitrogen itself strongly influences photosynthesis, regulation of CO2 effects on photosynthesis by nitrogen is still inconclusive. Ecosystem nitrogen availability is determined by a balance of several nitrogen fluxes, including plant uptake. mineralization, deposition, fixation, denitrification, volatilization and leaching. Elevated CO2 stimulates more plant biomass growth, demanding more nitrogen uptake. Mineralization increased in two studies, decreased in one and was unchanged in one. CO2 stimulation of nitrogen fixation increases nitrogen availability in ecosystems, potentially to match increased photosynthetic potential in the long term. Effects of volatilization, denitrification and leaching are yet to be assessed. Overall, intact ecosystem studies of canopy structure and nitrogen dynamics in elevated CO2 are particularly needed for our quantifying long-term stimulation of global photosynthetic carbon influx.

KEYWORDS: ATMOSPHERIC CARBON, CLIMATE CHANGE, DIOXIDE, ELEVATED CO2, ENRICHMENT, GROWTH, NITROGEN STRESS, PHOTOSYNTHESIS, PLANTS, SEEDLINGS

1404

Luo, Y.Q., and P.S. Nobel. 1993. Growth-characteristics of newly initiated cladodes of opuntia- ficus-indica as affected by shading, drought and elevated co2. *Physiologia Plantarum 87(4):467-474.*

Biomass accumulation and area expansion of newly initiated cladodes of Opuntia ficus-indica were studied to help understand the high productivity of this Crassulacena acid metabolism species. In a glasshouse, both dry weight and area increased more and more rapidly for about 30 days and then increased linearly with time up to 63 days. The relative growth rate averaged 0.12 day-1, comparable to values for productive C3 and C, plants. New cladodes initiated on basal cladodes with 2-fold higher initial dry weight grew twice as fast. Drought reduced biomass accumulation and area expansion of new cladodes by 62 and 52%, respectively. A 70% reduction in irradiation decreased biomass accumulation of new cladodes by 17% and their thickness by 11%. In a growth chamber containing 720 mumol CO2 (mol air)-1, biomass of newly initiated cladodes was 7% higher, area was 8% less, specific mass was 16% higher and less carbohydrate was translocated from basal cladodes than for 360 mumol CO2 mol-1. The large capacity for storage of carbohydrate and water in basal cladodes of O. ficus-indica apparently buffered environmental stresses, thereby reducing their effects on growth of daughter cladodes.

KEYWORDS: ACID METABOLISM PLANT, WATER RELATIONS

1405

Luo, Y.Q., J. Reynolds, Y.P. Wang, and D. Wolfe. 1999. A search for predictive understanding of plant responses to elevated [CO2]. *Global Change Biology 5(2):143-156.*

This paper reviews two decades of effort by the scientific community in a search for predictive understanding of plant responses to elevated [CO2]. To evaluate the progress of research in leaf photosynthesis, plant respiration, root nutrient uptake, and carbon partitioning, we divided scientific activities into four phases: (I) initial assessments derived from our existing knowledge base to provide frameworks for experimental studies; (II) experimental tests of the initial assessments; (III) in cases where assessments were invalidated, synthesis of experimental results to stimulate alternative hypotheses and further experimentation; and (IV) formation of new knowledge. This paper suggests that photosynthetic research may have gone through all four phases, considering that (a) variable responses of photosynthesis to [CO2] are generally explainable, (b) extrapolation of leaf-level studies to the global scale has been examined, and (c) molecular studies are under way. Investigation of plant respiratory responses to [CO2] has reached the third phase: experimental results have been accumulated, and mechanistic approaches are being developed to examine alternative hypotheses in search for new concepts and/or new quantitative frameworks to understand respiratory responses to elevated [CO2]. The study of nutrient uptake kinetics is still in the second phase: experimental evidence has contradicted some of the initial assessments, and more experimental studies need to be designed before generalizations can be made. It is quite unfortunate that we have not made much progress in understanding mechanisms of carbon partitioning during the past two decades. This is due in part to the fact that some of the holistic theories, such as functional balance and optimality, have not evolved into testable hypotheses to guide experimental studies. This paper urges modelers to play an increasing role in plant-CO2 research by disassembling these existing theories into hypotheses and urges experimentalists to design experiments to examine these holistic concepts.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, GROWTH-RESPONSE, LEAF RESPIRATION, LONG-TERM EXPOSURE, NET PRIMARY PRODUCTION, NITROGEN CONCENTRATION, PHOTOSYNTHETIC ACCLIMATION, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE, SOURCE-SINK RELATIONS,

1406

Luo, Y.Q., D.A. Sims, and K.L. Griffin. 1998. Nonlinearity of photosynthetic responses to growth in rising atmospheric CO2: an experimental and modelling study. *Global Change Biology 4(2):173-183.*

Nonlinear responses of photosynthesis to the CO2 concentration at which plants were grown (C-g) have been often reported in the literature. This study was designed to develop mechanistic understanding of the nonlinear responses with both experimental and modelling approaches. Soybean (Glycine max) was grown in five levels of C-g (280, 350, 525, 700, 1000 ppm) with either a high or low rate of nitrogen fertilization. When the rate of nitrogen fertilization was high, the photosynthetic rate measured at C-g was highest in plants from the 700 ppm CO2 treatment. When the rate of nitrogen fertilization was low, little variation was observed in the photosynthetic rates of plants from the different treatments measured at their respective C-g. Measurements of CO2-induced changes in mass- based leaf nitrogen concentration (n(m) an index of changes in biochemical processes) and leaf mass per unit area (h, an index of morphological properties) were used in a model and indicate that the nonlinearity of photosynthetic responses to C-g is largely determined by relative changes in photosynthetic sensitivity, biochemical downregulation, and morphological upregulation. In order to further understand the nonlinear responses, we compiled data from the literature on CO2-induced changes in n(m) and h. These compiled data indicate that h generally increases and n(m) usually decreases with increasing C-g, but that the trajectories and magnitudes of the changes in h and n(m) vary with species and growth environments. Integration of these variables (n(m) and h) into a biochemically based model of photosynthesis enabled us to predict diverse responses of photosynthesis to C-g. Thus a general mechanism is suggested for the highly variable, nonlinear responses of photosynthesis to C-g reported in the literature.

KEYWORDS: ACCLIMATION, C-3 PLANTS, CARBON DIOXIDE, ELEVATED CO2, ENRICHMENT, FIELD, LEAF PHOTOSYNTHESIS, LEAVES, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, TEMPERATURE

1407

Luo, Y.Q., D.A. Sims, R.B. Thomas, D.T. Tissue, and J.T. Ball. 1996. Sensitivity of leaf photosynthesis to CO2 concentration is an invariant function for C-3 plants: A test with experimental data and global applications. *Global Biogeochemical Cycles 10(2):209-222.*

Rising atmospheric CO2 concentration (C-a) may alter two components (sensitivity and acclimation) of global photosynthetic carbon influx into terrestrial ecosystems (P-G). Most existing global models focus on long-term acclimation We have developed a leaf-level function (L) to quantify short-term increment of P-G associated with sensitivity. The L function is the normalized response of leaf photosynthesis to a small change in C-a and has been suggested to be an invariant function for C-3 plants grown in diverse environments. This paper tests the hypothesis that L is an invariant function. We calculated values of L from 9 sets of experimental data which incorporated photosynthetic responses of 12 plant species to measurement conditions of light and temperature and to growth in different light, temperature, nitrogen, phosphorus, water stress, and CO2 concentration. Absolute rates of leaf photosynthesis differed by more than tenfold due to species differences and environmental variation. However, L values derived from these data sets converged into a narrow range defined by two equations of the L function, confirming that L was insensitive to differences in photosynthetic capacity among species and between plants acclimated to different growth environments. Using the L function, we predict that a yearly increase of 1.5 parts per million (ppm) in C-a will induce an increase in P-G by 0.18 to 0.34 Gt (1 Gt = 10(15) g) C yr(-1) in 1993, provided that (1) P-G = 120 Gt C yr(-1), (2) 85% of P- g is generated by C-3 plant assimilation, and (3) the 1.5-ppm increase in C-a will not induce significant photosynthetic acclimation.

KEYWORDS: ASSIMILATION, CLIMATE CHANGE, CONDUCTANCE, ELEVATED CO2, LEAVES, LIMITATIONS, PARTIAL-PRESSURE, RESPIRATION, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE, TEMPERATURE

1408

Lurie, S. 1993. Modified atmosphere storage of peaches and nectarines to reduce storage disorders. *Journal of Food Quality 16(1):57-65.*

Low density polyethylene or polyolefin films were used to seal pack various varieties of peaches and nectarines. Low density polyethylene film of 40 micron thickness was beneficial in extending storage life of these fruits and decreasing internal flesh breakdown and reddening, while polyolefin film was ineffective. Six fruits per pack generated a higher CO2 and lower O2 modified atmosphere than two or four fruits per pack and gave better quality fruit after storage. The improvement of fruit quality was correlated with elevated CO2 levels rather than with decreased O2 levels.

1409

Luscher, A., G.R. Hendrey, and J. Nosberger. 1998. Long-term responsiveness to free air CO2 enrichment of functional types, species and genotypes of plants from fertile permanent grassland. *Oecologia 113(1):37-45.*

To test inter- and intraspecific variability in the responsiveness to elevated CO2, 9-14 different genotypes of each of 12 perennial species from fertile permanent grassland were grown in Lolium perenne swards under ambient (35 Pa) and elevated (60 Pa) atmospheric partial pressure of CO2 (pCO(2)) for 3 years in a free air carbon dioxide enrichment (FACE) experiment. The plant species were grouped according to their functional types: grasses (L. perenne, L. multiflorum, Arrhenatherum elatius, Dactylis glomerata, Festuca pratensis, Holcus lanatus, Trisetum flavescens), non-legume dicots (Rumex obtusifolius, R. acetosa, Ranunculus friesianus), and legumes (Trifolium repens, T. pratense). Yield (above a cutting height of 4.5 cm) was measured three times per year. The results were as follow. (1) There were highly significant differences in the responsiveness to elevated pCO(2) between the three functional types; legumes showed the strongest and grasses the weakest yield increase at elevated pCO(2). (2) There were differences in the temporal development of responsiveness to elevated pCO(2) among the functional types. The responsiveness of the legumes declined from the first to the second year, while the responsiveness of the non-legume dicots increased over the 3 years. During the growing season, the grasses and the non- legume dicots showed the strongest response to elevated pCO(2) during reproductive growth in the spring. (3) There were no significant genotypic differences in responsiveness to elevated pCO(2). Our results suggest that, due to interspecific differences in the responsiveness to elevated pCO(2), the species proportion within fertile temperate grassland may change if the increase in pCO(2) continues. Due to the temporal differences in the responsiveness to elevated pCO(2) among species, complex effects of elevated pCO(2) on competitive interactions in mixed swards must be expected. The existence of genotypic variability in the responsiveness to elevated pCO(2), on which selection could act, was not found under our experimental conditions.

KEYWORDS: ECOSYSTEM, ELEVATED CARBON-DIOXIDE, ENVIRONMENTS, GROWTH, LOLIUM-PERENNE, N2 FIXATION, NITROGEN, RESPONSES, SWARDS, TEMPERATURE

1410
Luscher, A., and J. Nosberger. 1997. Interspecific and intraspecific variability in the response of grasses and legumes to free air CO2 enrichment. *Acta Oecologica-International Journal of Ecology 18(3):269-275.*

Nine to fourteen genotypes of seven grass and two legume species from permanent grassland were grown at two levels of atmospheric CO2 concentration in gaps of established Lolium perenne swards in a Free Air Carbon dioxide Enrichment (FACE) experiment. Cumulative biomass of individual plants was determined for two growing seasons. In the first year, elevated CO2 increased biomass production in all species. The CO2- induced increase in the biomass of Trifolium repens and I: pratense (159%) was much greater than the increase in the grass species (27%). In the second year the response to elevated CO2 was weaker in gasses (2%, ns) and legumes (73%). However, interspecific differences in the response to CO2 remained significant. Interspecific differences in the response to elevated CO2 occurred between the two functional groups of grasses and legumes, while within these groups no significant interspecific differences were found. In contrast to the interspecific variability in the response to CO2, no significant intraspecific variability in the response to CO2 was detected. Our results suggest that significant interspecific differences in the response to CO2, occur. Intraspecific differences in the response to elevated CO2 were, however, not detected. Thus, it seems unlikely that evolutionary adaptation of the species' response to elevated CO2 will level out the inter specific differences in the response to CO2.

KEYWORDS: CARBON DIOXIDE, ELEVATED CO2, GROWTH-RESPONSE, N2 FIXATION, NITROGEN, PHOSPHORUS, PLANTS

1411
Lussenhop, J., A. Treonis, P.S. Curtis, J.A. Teeri, and C.S. Vogel. 1998. Response of soil biota to elevated atmospheric CO2 in poplar model systems. *Oecologia 113(2):247-251.*

We tested the hypotheses that increased belowground allocation of carbon by hybrid poplar saplings grown under elevated atmospheric CO2 would increase mass or turnover of soil biota in bulk but not in rhizosphere soil. Hybrid poplar saplings (Populus x euramericana cv. Eugenei) were grown for 5 months in open-bottom root boxes at the University of Michigan Biological Station in northern, lower Michigan. The experimental design was a randomized-block design with factorial combinations of high or low soil N and ambient (34 Pa) or elevated (69 Pa) CO2 in five blocks. Rhizosphere microbial biomass carbon was 1.7 times greater in high-than in low-N soil, and did not respond to elevated CO2. The density of protozoa did not respond to soil N but increased marginally ($P < 0.06$) under elevated CO2. Only in high-N soil did arbuscular mycorrhizal fungi and microarthropods respond to CO2. In high-N soil, arbuscular mycorrhizal root mass was twice as great, and extramatrical hyphae were 11% longer in elevated than in ambient CO2 treatments. Microarthropod density and activity were determined in situ using minirhizotrons. Microarthropod density did not change in response to elevated CO2, but in high-N soil, microarthropods were more strongly associated with fine roots under elevated than ambient treatments. Overall, in contrast to the hypotheses, the strongest response to elevated atmospheric CO2 was in the rhizosphere where (1) unchanged microbial biomass and greater numbers of protozoa ($P < 0.06$) suggested faster bacterial turnover, (2) arbuscular mycorrhizal root length increased, and (3) the number of microarthropods observed on fine roots rose.

KEYWORDS: ARBUSCULAR MYCORRHIZAL INFECTION, CARBON DIOXIDE, ENRICHMENT, GROWTH, MATTER CONTENTS, MICROBIAL BIOMASS, NITROGEN, POPULATIONS, RHIZOSPHERE, ROOTS

1412
Lutze, J.L., and R.M. Gifford. 1995. Carbon storage and productivity of a carbon dioxide enriched nitrogen limited grass sward after one year's growth. *Journal of Biogeography 22(2-3):227-233.*

Determining the response of nitrogen restricted ecosystems to carbon dioxide enrichment is important in evaluating the role of the terrestrial biosphere in the unidentified sink in global carbon cycle models. Swards of the C3 grass Danthonia richardsonii (Cashmere) were established in large pots filled with a soil of low C and N content. The swards were continuously supplied with N at rates of 2, 6 and 18 g m(-2) yr(-1), and exposed to atmospheric CO2 concentrations of either 357 or 712 mu L L(-1). After 1 year's growth the high CO2 treatments gained 19, 53 and 43% more C than at low CO2 concentrations for the low, medium and high N treatments, respectively. This extra C gain was found in all plant and soil pools at the medium N level. At the low N level no extra C was found in the roots. At the high N level no extra carbon was found in the soil. Leaf area index was not affected by growth at high CO2. The extra C was gained with the same total N investment in green leaf in the two lowest N treatments, and with 30% less N in green leaf at the highest N level. Growth at the high CO2 concentration resulted in all C pools having a higher C:N ratio. Total water use was decreased and water use efficiency increased by growth at the high CO2 concentration. It was noted that if these results were transferable to the held, and if the higher C:N ratios do not reduce longer term productivity by reducing N-mineralization rates, grasslands could form a substantial part of the unidentified C sink. The potential feedback of decreased N availability in the longer term is being investigated in the final 3 years of the experiment.

KEYWORDS: DECOMPOSITION, ELEVATED ATMOSPHERIC CO2, FEEDBACK, LEAF LITTER, PLANTS, ROOT, WEIGHT

1413
Lutze, J.L., and R.M. Gifford. 1998. Acquisition and allocation of carbon and nitrogen by Danthonia richardsonii in response to restricted nitrogen supply and CO2 enrichment. *Plant, Cell and Environment 21(11):1133-1141.*

Dry weight (DW) and nitrogen (N) accumulation and allocation were measured in isolated plants of Danthonia richardsonii (Wallaby Grass) for 37 d following seed imbibition, Plants were grown at approximate to 365 or 735 mu L L-1 CO2 with N supply of 0.05, 0.2 or 0.5 mg N plant(-1) d(-1). Elevated CO2 increased DW accumulation by 28% (low-N) to 103% (high-N), following an initial stimulation of relative growth rate. Net assimilation rate and leaf nitrogen productivity mere increased by elevated CO2, while N concentration was reduced. N uptake per unit root surface area was unaffected by CO2 enrichment, The ratio of leaf area to root surface area was decreased by CO2 enrichment. Allometric analysis revealed a decrease in the shoot-N to root-N ratio at elevated CO2, while the shoot-DW to root-DW ratio was unchanged. Allometric analysis showed leaf area was reduced, while root surface area was unchanged by elevated CO2, indicating a down-regulation of total plant capacity for carbon gain rather than a stimulation of mineral nutrient acquisition capacity Overall, growth in elevated CO2 resulted in changes in plant morphology and nitrogen use, other than those associated simply with changing plant size and non- structural carbohydrate content.

KEYWORDS: AVAILABILITY, DIOXIDE, ELEVATED CO2, GRASS, GROWTH-RESPONSES, NUTRIENT-UPTAKE, PHOTOSYNTHETIC ACCLIMATION, PINE, PLANTS, ROOT-GROWTH

1414
Lutze, J.L., and R.M. Gifford. 1998. Carbon accumulation, distribution and water use of Danthonia richardsonii swards in response to CO2 and nitrogen supply over four years of growth. *Global Change*

Biology 4(8):851-861.

Microcosms of Danthonia richardsonii (Cashmore) accumulated more carbon when grown under CO2 enrichment (719 mu L L-1 cf. 359 mu L L-1) over a four-year period, even when nitrogen availability severely restricted productivity (enhancement ratios for total microcosm C accumulation of 1.21, 1.14 and 1.29 for mineral N supplies of 2.2, 6.7 and 19.8 g N m-2 y-1, respectively). The effect of CO2 enrichment on total system carbon content did not diminish with time. Increased carbon accumulation occurred despite the development over time of a lower leaf area index and less carbon in the green leaf fraction at high CO2. The extra carbon accumulated at high CO2 in the soil, senesced leaf and leaf litter fractions at all N levels, and in root at high-N, while at low-and mid-N less carbon accumulated in the root fraction at high CO2. The rate of leaf turnover was increased under CO2 enrichment, as indicated by increases in the carbon mass ratio of senesced to green leaf lamina. Microcosm evapotranspiration rates were lower at high CO2 when water was in abundant supply, resulting in higher average soil water contents. The higher soil water contents at high CO2 have important implications for microcosm function, and may have contributed significantly to the increased carbon accumulation at high CO2. These results indicate that CO2 enrichment can increase carbon accumulation by a simple soil-plant system, and that any increase in whole system carbon accumulation may not be evident from snapshot measurements of live plant carbon.

KEYWORDS: ATMOSPHERIC CO2, BIOMASS, CONIFEROUS FORESTS, DIOXIDE, ELEVATED CO2, ENRICHMENT, PLANT, ROOTS, SOIL CARBON, TALLGRASS PRAIRIE

1415

Lutze, J.L., J.S. Roden, C.J. Holly, J. Wolfe, J.J.G. Egerton, and M.C. Ball. 1998. Elevated atmospheric [CO2] promotes frost damage in evergreen tree seedlings. *Plant, Cell and Environment 21(6):631-635.*

Growth under elevated [CO2] promoted spring frost damage in field grown seedlings of snow gum (Eucalyptus pauciflora Sieb, ex Spreng,), one of the most frost tolerant of eucalypts, Freezing began in the leaf midvein, consistent with it being a major site of frost damage under field conditions. The average ice nucleation temperature was higher in leaves grown under elevated [CO2] (- 5.7 degrees C versus - 4.3 degrees C), consistent with the greater incidence of frost damage in these leaves (34% versus 68% of leaves damaged). These results have major implications for agriculture, forestry and vegetation dynamics, as an increase in frost susceptibility may reduce potential gains in productivity from CO2 fertilization and may affect predictions of vegetation change based on increasing temperature.

KEYWORDS: TEMPERATURE

1416

Luxmoore, R.J., P.J. Hanson, J.J. Beauchamp, and J.D. Joslin. 1998. Passive nighttime warming facility for forest ecosystem research. *Tree Physiology 18(8-9):615-623.*

A nighttime warming experiment is proposed. Over the last four decades a significant rise in nighttime mini mum temperature has been determined from analysis of meteorological records from a global distribution of locations. The experiment involves nighttime deployment of infrared (IR) reflecting curtains around four sides of a forest canopy and across the top of the forest to mimic the top-down warming effect of cloud cover. The curtains are deployed with cable and pulley systems mounted on a tower and scaffolding structure built around the selected forest site. The trunk space is not enclosed except as an optional manipulation. The curtains reflect long-wave radiation emitted from the forest and ground back into the forest warming the trees, litter, and soil. Excellent infrared reflection can be obtained with commercially available fabrics that have aluminum foil bonded to one side. A canopy warming of 3 to 5 degrees C is expected on cloudless nights, and on cloudy nights, a warming of 1 to 3 degrees C is anticipated relative to a control plot. The curtains are withdrawn by computer control during the day and also at night during periods with precipitation or excessive wind. Examples of hypothesized ecosystem responses to nighttime warming include: (1) increase in tree maintenance respiration (decreasing carbon reserves and ultimately tree growth), (2) increase in the length of the growing season (increasing growth), (3) increase in soil respiration, (4) increase in litter decomposition, (5) increase in mineralization of N and other nutrients from soil organic matter, (6) increase in nutrient uptake (increasing growth), and (7) increase in N immobilization in litter. Hypothesis 1 has the opposite consequence for tree growth to Hypotheses 2 and 6, and thus opposite consequences for the feedback regulation that vegetation has on net greenhouse gas releases to the atmosphere. If Hypothesis 1 is dominant, warming could lead to more warming from the additional CO2 emissions. Site- specific meteorological, ecophysiological. and phenological measurements are obtained in the warming treatment and in a carefully selected control plot to investigate site-specific hypotheses, Measurements made on both plots for a baseline period and during the period of curtain deployment provide data to test the hypotheses statistically by the "before-after-control-impact" method applicable to unreplicated experiments. The enclosure has a modular design that can be adapted and combined with other forest-scale manipulation experiments such as free air CO2 enrichment and throughfall displacement.

KEYWORDS: CARBON DIOXIDE, CLIMATE CHANGE, CO2-ENRICHMENT, GROWTH, IMPACT ASSESSMENT, RESPIRATION, SOIL-NITROGEN MINERALIZATION, SPRUCE, TEMPERATURE-RANGE, UPLAND OAK FOREST

1417

Luxmoore, R.J., S.D. Wullschleger, and P.J. Hanson. 1993. Forest responses to co2 enrichment and climate warming. *Water, Air, and Soil Pollution 70(1-4):309-323.*

Two of the major uncertainties in forecasting future terrestrial sources and SinkS Of CO2 are the CO2-enhanced growth response of forests and soil warming effects on net CO2 efflux from forests. Carbon dioxide enrichment of tree seedlings over time periods less than 1 yr has generally resulted in enhanced rates of photosynthesis, decreased respiration, and increased growth, with minor increases in leaf area and small changes in C allocation. Exposure of woody species to elevated CO2 over several years has shown that high rates of photosynthesis may be sustained, but net C accumulation may not necessarily increase if CO2 release from soil respiration increases. The impact of the 25% rise in atmospheric CO2 with industrialization has been examined in tree ring chronologies from a range of species and locations. In contrast to the seedling tree results, there is no convincing evidence for CO2-enhanced stem growth of mature trees during the last several decades. However, if mature trees show a preferential root growth response to CO2 enrichment, the gain in root mass for an oak-hickory forest in eastern Tennessee is estimated to be only 9% over the last 40 years. Root data bases are inadequate for detecting such an effect. A very small shift in ecosystem nutrients from soil to vegetation could support CO2-enhanced growth. Climate warming and the accompanying increase in mean soil temperature could have a greater effect than CO2 enrichment on terrestrial sources and sinks Of CO2. Soil respiration and N mineralization have been shown to increase with soil temperature. If plant growth increases with increased N availability, and more C is fixed in growth than is released by soil respiration, then a negative feedback on climate warming will occur. If warming results in a net increase in CO2 efflux from forests, then a positive feedback will follow. A 2 to 4-degrees-C increase in soil temperature could increase CO2 efflux from soil by 15 to 32% in eastern deciduous forests. Quantifying C budget

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-aquatilis 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 mu M) and also at 0.55 mM DIC with elevated CO2 (350 mu M). For plants grown at air-equilibrium CO2, growth was limited by inorganic carbon below 1.6 mM DIC and