Sykes, M.T., I.C. Prentice, and W. Cramer. 1996. A bioclimatic model for the potential distributions of north European tree species under present and future climates. *Journal of Biogeography 23(2):203-233.*

A bioclimatic model based on physiological constraints to plant growth and regeneration is used here in an empirical way to describe the present natural distributions of northern Europe's major trees. Bioclimatic variables were computed from monthly means of temperature, precipitation and sunshine (%) interpolated to a 10' grid taking into account elevation. Minimum values of mean coldest-month temperature (T-c) and 'effective' growing degree days (GDD*) were fitted to species' range limits. GDD* is total annual growing degree days (GDD) minus GDD to budburst (GDD(o)). Each species was assigned to one of the chilling-response categories identified by Murray, Cannell & Smith (1989) to calculate GDD(o). Maximum T-c values were fitted to continental species' mild-winter limits and other deciduous species' warm-winter limits. Minimum values of relative growing-season moisture availability (alpha*) were estimated from silvics. Growth indices were calculated based on potential net assimilation (a quadratic in daily temperature) and alpha*. Growth can be rapid near a range limit, e.g. Picea abies (L.) Karsten in southern Sweden. Climate changes expected for CO2 doubling were projected on to the grid. Simulated distribution changes reflected interspecific differences in response to changing seasonality. Chilling responses proved important, e.g. the predicted range limit of Fagus sylvatica L. contracts in the west while expanding northwards as winters warm more than summers. Transient responses to climate change can be modelled using the same information provided that fundamental and realized niche limitations are distinguished-a caveat that underlines the dearth of experimental information on the climatic requirements for growth, and especially regeneration, of many important trees.

KEYWORDS: AMERICA, BUDBURST, FORESTS, FROST DAMAGE, PICEA-SITCHENSIS, RESPONSES, VEGETATION

2306

Syvertsen, J., and J.H. Graham. 1997. Carbon budgets of two Citrus sp. in response to elevated CO2 VA mycorrhizae and phosphorus status. *Plant Physiology 114(3):111.*

2307

Syvertsen, J.P., and J.H. Graham. 1999. Phosphorus supply and arbuscular mycorrhizas increase growth and net gas exchange responses of two Citrus spp. grown at elevated [CO2]. *Plant and Soil 208(2):209-219.*

We hypothesized that greater photosynthate supply at elevated [CO2] could compensate for increased below-ground C demands of arbuscular mycorrhizas. Therefore, we investigated plant growth, mineral nutrition, starch, and net gas exchange responses of two Citrus spp. to phosphorus (P) nutrition and mycorrhizas at elevated atmospheric [CO2]. Half of the seedlings of sour orange (C. aurantium L.) and `Ridge Pineapple' sweet orange (C. sinensis L. Osbeck) were inoculated with the arbuscular mycorrhizal (AM) fungus, Glomus intraradices Schenck and Smith and half were non-mycorrhizal (NM). Plants were grown at ambient or 2X ambient [CO2] in unshaded greenhouses for 11 weeks and fertilized daily with nutrient solution either without added P or with 2 mM P in a low-P soil. High P supply reduced AM colonization whereas elevated [CO2] counteracted the depressive effect of P on intraradical colonization and vesicle development. Seedlings grown at either elevated [CO2], high P or with G. intraradices had greater growth, net assimilation of CO2 (A(CO2)) in leaves, leaf water-use efficiency, leaf dry wt/area, leaf starch and carbon/nitrogen (C/N) ratio. Root/whole plant dry wt ratio was decreased by elevated [CO2], P, and AM colonization. Mycorrhizal seedlings had higher leaf-P status but lower leaf N and K concentrations than nonmycorrhizal seedlings which was due to growth dilution effects. Starch in fibrous roots was increased by elevated [CO2] but reduced by G. intraradices, especially at low-P supply. In fibrous roots, elevated [CO2] had no effect on C/N, but AM colonization decreased C/N in both Citrus spp. grown at low-P supply. Overall, there were no species differences in growth or A(CO2). Mycorrhizas did not increase plant growth at ambient [CO2]. At elevated [CO2], however, mycorrhizas stimulated growth at both P levels in sour orange, the more mycorrhiza-dependent species, but only at low- P in sweet orange, the less dependent species. At low-P and elevated [CO2], colonization by the AM fungus increased A(CO2) in both species but more so in sour orange than in sweet orange. Leaf P and root N concentrations were increased more and root starch level was decreased less by AM in sour orange than in sweet orange. Thus, the additional [CO2] availability to mycorrhizal plants increased CO2 assimilation, growth and nutrient uptake over that of NM plants especially in sour orange under P limitation.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, COLONIZATION, DEPENDENCY, ENRICHMENT, NITROGEN, PLANTAGO-LANCEOLATA, ROOT, SOUR ORANGE, TREES

2308

Szente, K., Z. Nagy, and Z. Tuba. 1998. Enhanced water use efficiency in dry loess grassland species grown at elevated air CO2 concentration. *Photosynthetica 35(4):637-640.*

Net CO2 assimilation rate (P-N), Stomatal conductance (g(s)), transpiration rate (E), and water use efficiency (WUE) in four perennial C-3 species (grasses: Dactylis glomerata, Festuca rupicola, dicots: Filipendula vulgaris, Salvia nemorosa) grown for 231 d in open-top chambers at ambient (CA, 350 mu mol mol(- 1)) or elevated (CE, 700 mu mol mol(-1)) CO2 concentrations were compared. When measured at CE, PN was significantly higher in CE plants of all four species than in the CA ones. The increase in P-N was less prominent in the two grasses than in the two dicots. The E was significantly higher in the CE-grass F. rupicola and CE-dicot F. vulgaris than in the CA plants. There was no change in E owing to CE in the other grass and dicot. The g(s) in F. vulgaris and F. rupicola increased, while there was a decrease in D. glomerata and no change in S. nemorosa. WUE increased in all species grown in CE: four- to five-fold in the dicots and less than two-fold in the grasses. The increase in WUE was primarily due to an increase in P-N and not to a decrease in E.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, GAS-EXCHANGE, LONG-TERM, PHOTOSYNTHESIS, PLANTS, RESPONSES, STEPPE, STOMATAL CONDUCTANCE, TRANSPIRATION

2309

Tajiri, T. 1997. Studies on the cultivation and storage quality of bean sprouts .13. Growth and quality of thick bean sprouts cultivated with a CO2-enriched rotary method. *Journal of the Japanese Society for Food Science and Technology-Nippon Shokuhin Kagaku Kogaku Kaishi 44(4):332-339.*

Thick bean sprouts cultivated using a rotary box (rotary cultivation, RC) have a decreased yield and inferior quality, although the growth of sprouts from the beans is promoted and the nutrient content of the sprouts is improved(1)2)). Because exposure to high levels of carbon dioxide was useful for promoting the growth of the hypocotyl and increasing the quantity of harvested sprouts(3)), we combined the rotary box method with the CO2-enriched method(1)). Herein the usefulness of this combination method for improving the physical properties and the yield of bean sprouts by controlling hypocotyl growth were

examined.

2310

Takagi, M., K. Gyokusen, and A. Saito. 1998. Increase in the CO2 exchange rate of leaves of Ilex rotunda with elevated atmospheric CO2 concentration in an urban canyon. *International Journal of Biometeorology 42(1):16-21.*

It was found that the atmospheric carbon dioxide (CO2) concentration in an urban canyon in Fukuoka city, Japan during August 1997 was about 30 mu mol mol(-1) higher than that in the suburbs. When fully exposed to sunlight, in situ the rate of photosynthesis in single leaves of Ilex rotunda planted in the urban canyon was higher when the atmospheric CO2 concentration was elevated. A biochemically based model was able to predict the in situ rate of photosynthesis well. The model also predicted an increase in the daily CO2 exchange rate for leaves in the urban canyon with an increase in atmospheric CO2 concentration. However, in situ such an increase in the daily CO2 exchange rate may be offset by diminished sunlight, a higher air temperature and a lower relative humidity. Thus, the daily CO2 exchange rate predicted using the model based soleley on the environmental conditions prevailing in the urban canyon was lower than that predicted based only on environmental factors found in the suburbs.

KEYWORDS: BOUNDARY-LAYER, CANOPY PHOTOSYNTHESIS, CARBON DIOXIDE, CITY, CONDUCTANCE, LEAF PHOTOSYNTHESIS, MODEL, TEMPERATURE, TRANSPIRATION

2311

Takle, E.S., D.J. Bramer, W.E. Heilman, and M.R. Thompson. 1994. A synoptic climatology for forest-fires in the ne US and future implications from gcm simulations. *International Journal of Wildland Fire 4(4):217-224.*

We studied surface-pressure patterns corresponding to reduced precipitation, high evaporation potential, and enhanced forest- fire danger for West Virginia, which experienced extensive forest-fire damage in November 1987. From five years of daily weather maps we identified eight weather patterns that describe distinctive flow situations throughout the year. Map patterns labeled extended-high, back-of-high, and pre-high were the most frequently occurring patterns that accompany forest fires in West Virginia and the nearby four-stare region. Of these, back- of-high accounted for a disproportionately large amount of fire-related damage. Examination of evaporation acid precipitation data showed that these three patterns and high- to-the-south patterns ail led to drying conditions and all other patterns led to moistening conditions. Surface-pressure fields generated by the Canadian Climate Centre global circulation model for simulations of the present (1xCO(2)) climate and 2xCO(2) climate were studied to determine whether forest-fire potential would change under increased atmospheric CO2. The analysis showed a tendency for increased frequency of drying in the NE US, but the results were not statistically significant.

2312

Talbott, L.D., A. Srivastava, and E. Zeiger. 1996. Stomata from growth-chamber-grown Vicia faba have an enhanced sensitivity to CO2. *Plant, Cell and Environment 19(10):1188-1194.*

Abaxial stomata from Vicia faba leaves grown in a growth chamber under constant light, temperature and humidity showed an elaborate pattern of aperture changes over the course of a light cycle. These aperture changes, were tightly correlated with changes in chamber COL concentration (r(2)=0.83). Changes in chamber [CO2] resulted, in turn, from substantial daily fluctuations in ambient [CO2], typical of the Los Angeles environment, with a constant offset caused by photosynthesis and respiration of the plants within the chamber, The dominant role of the stomatal response to CO2 in the control of aperture tvas confirmed by manipulation of chamber [CO2]. Fast (15 min) increases and decreases in [CO2] caused rapid decreases and increases in aperture, while constant [CO2] resulted in constant aperture. In contrast, aperture changes in comparable plants grown under greenhouse conditions were tightly correlated with changes in incident solar radiation (r(2)=0.80), and poorly correlated with changes in [CO2] (r(2)=0.09). Greenhouse-grown plants transferred to growth chamber conditions showed no apparent response to CO2. These data indicate that growth-chamber-grown V. faba leaves provide an experimental system optimally suited for the study of the stomatal response to CO2, and suggest that acclimation to environmental conditions alters the sensitivity of stomata to CO2.

KEYWORDS: ABSCISIC- ACID, BEHAVIOR, BLUE-LIGHT, CARBON DIOXIDE, CONDUCTANCE, GUARD-CELLS, IRRADIANCE, PLANTS, RED, SUGAR

2313

Talkkari, A., S. Kellomaki, and H. Peltola. 1999. Bridging a gap between a gap model and a physiological model for calculating the effect of temperature on forest growth under boreal conditions. *Forest Ecology and Management 119(1-3):137-150.*

The applicability of the parabolic function of the Jabowa gap model for the relationship between tree growth and temperature sum for aggregating short-term temperatures responses was investigated by determining parameter values for the temperature function in a gap model from material generated by means of a physiological model (Kellomaki et al,, 1993; Kellomaki and Vaisanen, 1997), in which the growth and development of a tree stand is linked with the climate and soil through photosynthesis, respiration, transpiration and the uptake of water and nitrogen. Predictions of stand volume and total stand production were compared using the following functions for Scots pine (Pinus sylvestris L.): (i) the original parabolic function of the Jabowa model with parameter values based on the geographical distribution of trees (TO), (ii) the same parabolic function with parameter values obtained by fitting data generated using the physiological model (T1), and (iii) a fit of a truncated parabolic function to data generated using the physiological model (T2). The differences in volume and total production between the functions were greater at the site in northern Finland than at the sites in southern and central Finland, although absolute timber production was lowest at the northern site. The stand volume and timber production were highest at all three sites with the truncated parabola (T2) under conditions of climate change. Total production following climate change (average of TO, T1, and T2) was an average of 104% of that observed under current climatic conditions at the southern site, 105% at the central site and 121% at the northern site. The gap model was not found to be sensitive to the growing degree-days (gdd) response curve when the model was applied to Finnish conditions, and thus appeared to be satisfactory for aggregating the short-term physiological responses of Scots pine to temperature. The situation would be more problematic, however, if the model were applied under the conditions prevailing near the southern or northern edge of the geographical distribution of Scots pine. (C) 1999 Elsevier Science B.V. All rights reserved.

KEYWORDS: ATMOSPHERIC CO2 CONCENTRATION, CO2-INDUCED CLIMATE CHANGE, COMPUTATIONS, ELEVATED CO2, FINLAND, PHOTOSYNTHESIS, SCOTS PINE, SIMULATION-MODEL, SOIL MOISTURE, TRANSIENT RESPONSES

2314

Tanaka, M., T. Takamura, H. Watanabe, M. Endo, T. Yanagi, and K. Okamoto. 1998. In vitro growth of Cymbidium plantlets cultured under superbright red and blue light-emitting diodes (LEDs). *Journal of Horticultural Science & Biotechnology 73(1):39-44.*

The effects of light generated by superbright blue and red LEDs on the growth of Cymbidium plantlets cultured in vitro have been studied. Leaf growth, chlorophyll content and shoot and root weights were affected by different LED irradiations. Red light promoted leaf growth but decreased chlorophyll content. This was reversed by blue Light. The growth of Cymbidium plantlets in terms of increase in total shoot and root weights was comparable under red plus blue LEDs and the fluorescent systems. Generally, the response to different LED was similar for plantlets grown on sugar-free medium with or without CO2 enrichment and sugar-containing medium but without CO2 enrichment. The growth of Cymbidium plantlets was enhanced by CO2 enrichment. Our study demonstrates the effectiveness of a total irradiation system for Cymbidium plantlets growth in vitro. The significance of our findings in relation to the development of a suitable lighting system for plant tissue culture is discussed.

KEYWORDS: LETTUCE, PEPPER, PHOTOSYNTHESIS, QUALITY

2315

Tanaka, M., D.C.H. Yap, C.K.Y. Ng, and C.S. Hew. 1999. The physiology of Cymbidium plantlets cultured in vitro under conditions of high carbon dioxide and low photosynthetic photon flux density. *Journal of Horticultural Science & Biotechnology 74(5):632-638.*

Cymbidium plantlets were grown in vitro under conditions of high CO2 and low photosynthetic photon flux density using the Miracle Pack(R) culture system. Shoots and roots of plantlets showed differential growth characteristics. Shoot growth was not different in plantlets cultured under CO2-enriched (CDE) and non-enriched (NCDE) conditions. Root growth was promoted in plantlets cultured under CDE in the presence or absence of 2% sucrose (S) with rockwool (R) as the supporting material. Growth was poor in plantlets cultured in 1% agar, Root growth was best in plantlets cultured under CDE R;S. Sucrose is still an important component for root growth under CDE conditions even though CO2 can be used as an alternative carbon source. Photosynthetic measurements (CO2 uptake and total Rubisco activity) showed the presence of active and operational photosynthetic machinery in plantlets cultured under CDE and NCDE conditions. The apparent lack of photoautotrophy (as evident from the lack of starch grains in chloroplasts) in plantlets cultured under NCDE conditions is not the result of a lesser potential for photoautotrophy; rather it is a consequence of sub-optimal CO2 concentrations within the culture vessels.

KEYWORDS: ACCLIMATION, ACCUMULATION, CO2-ENRICHMENT, ETHYLENE, INVITRO

2316

Tang, K.L., X.H. Feng, and G. Funkhouser. 1999. The delta C-13 of tree rings in full-bark and strip-bark bristlecone pine trees in the White Mountains of California. *Global Change Biology 5(1):33-40.*

Dendrochronological work at Sheep Mountain in the White Mountains, CA has demonstrated that bristlecone pine trees in two forms, full-bark and strip-bark, have experienced different cambial growth rates over the past century or longer. The strip-bark trees showed a greater growth increase than the full-bark ones. A calculation of the plant water-use efficiency (W) in response to anthropogenic CO2 released into the atmosphere shows that W of trees in both forms has increased for the past 200 years. However, there is no significant difference between the two tree forms in the rate of increase in W. This implies at least two possibilities with respect to the CO2 fertilization effect. First, the biomass in both tree forms might have increased, but carbon distribution among different parts of a tree was different. Second, the biomass may increase without causing any corresponding change in the plant water-use efficiency.

KEYWORDS: ATMOSPHERIC CO2 ENRICHMENT, CARBON ISOTOPE DISCRIMINATION, DIOXIDE, ECOSYSTEMS, ELEVATED CO2, FERTILIZATION, NITROGEN, PHOTOSYNTHESIS, RESPONSES, WATER-USE

2317

Tanigawa, T., Y. Kobayashi, H. Matsui, and Y. Sakai. 1995. Effects of co2 enrichment on growth and vase life of cut flowers of dendranthema-grandiflorum (ramat) kitamura. *Journal of the Japanese Society for Horticultural Science 64(2):417-424.*

The effects of CO2 enrichment of chrysanthemum (Dendranthema grandiflorum) on the subsequent growth and mineral and carbohydrate contents of the plant and on CO2 and C2H4 production and vase life of cut flowers were investigated. By enriching the atmosphere with 1,000 and 2,000 ppm CO2 for 2-1/2 hours each morning, stem length, fresh weight, and leaf number of cut flowers were increased by 3 to 11%, and vase life was extended 3 days compared with flowers grown in ambient CO2 concentration of 350 ppm. N, K, Mg, and Na concentrations, especially in the lower leaves were lower, whereas P and Ca concentrations were either the same or higher in the CO2 treatment than they were in leaves of plants grown in the ambient CO2. Starch and sugar contents in the leaves and stem were increased under CO2 enriched condition. CO2 production in the leaves was significantly reduced by the CO2 treatments; C2H4 production was unaffected. From these data, we propose that the decline of [N+K]/Ca ratio (Funakoshi, 1984) and the increase in starch and sugar contents in the leaves and seem as a result of the CO2 enriched atmosphere effectively prolonged vase life of the cut flowers.

KEYWORDS: ACCLIMATION, ETHYLENE

2318

Tanigawa, T., M. Nagaoka, H. Ikeda, and A. Shimizu. 1993. Effects of co-2 enrichment on growth, photosynthesis and physiological-activity of roots of dendranthema X grandiflorum (ramat) kitamura. *Journal of the Japanese Society for Horticultural Science 61(4):873-878.*

To assess the effect of CO2 enrichment on growth of greenhouse chrysanthemum, the plants were cultivated in the phytotron with 300, 600 and 1,200 ppm CO2. i. CO2 enriched plants showed a significant increase in stem length, number of leaves, leaf area, and fresh and dry weights. The greatest rate of increase after 60 days of CO2 enrichment was observed in the dry weight of roots (39%). Flower bud formation was delayed 3 days under CO2 enriched condition. 2. No difference in photosynthetic rates of whole plants measured in 400 and 800 ppm CO2 was observed among those grown under high CO2 (600 or 1,200 ppm) and those grown in ambient air (300 ppm). After 60 days of exposure to ambient and high CO2, the photosynthetic rate measured in 800 PPM CO2 declined markedly compared to the rate at the beginning of the treatment. 3. TTC (2, 3, 5-triphenyl tetrazolium chloride) reductive activity of roots decreased under CO2 enriched atmosphere, but it increased on a per plant basis because fresh weight of the roots increased. There was a high positive correlation between TTC reduction per plant and the fresh weight of the top (aerial part).

KEYWORDS: CHRYSANTHEMUM-MORIFOLIUM RAMAT, CO2-ENRICHMENT, ENVIRONMENT, GREENHOUSE PLANTS, LIGHT, RESPONSES

2319

Tanimoto, H., T. Kagi, and S. Morita. 1993. Relationship between the utilization of sugars by cultured petiole segments of begoniaxhiemalis and the optimum time for co2 enrichment. *Journal of the Japanese Society for Horticultural Science 62(2):437-441.*

By monitoring the utilization of sugars by petiole segments of Begonia X hiemalis cultured in medium containing the plant grwoth regulators, kinetin (1 PPM), NAA (1 ppm), the optimum time for beginning the CO2 enrichment treatment was established. The total sugar concentration in the medium decreased rapidly after 40 days of culturing. The cessation of sugar depletion by the tissues after 60 days is attributed to the onset of photosynthesis by the plantlets. CO2 administration at this time promoted leaf development, whereas CO2 enrichment 10 to 20 days earlier halted the development of adventitious shoots. These observations suggest that the optimum period to begin CO2 enrichment to promote shoot growth and to enhance photosynthesis is about 60 days after the culturing the petiole segments.

2320

Tarnawski, M.G., T.G.A. Green, B. Buedel, A. Meyer, H. Zellner, and O.L. Lange. 1994. Diel changes of atmospheric co2 concentration within, and above, cryptogam stands in a new-zealand temperate rain-forest. *New Zealand Journal of Botany 32(3):329-336.*

Atmospheric CO2 levels were determined (at 2m height) in the rainforest and in a clearing outside the forest, during spring (November) 1991, Urewera National Park, New Zealand. CO2 levels within the forest were 30 ppm higher and showed a more variable diel pattern (range up to 70 ppm) than outside the forest. CO2 levels were generally higher at night than during the day. Detailed measurements were made at several sites at a depth of 25 mm in the phylloplane of three moss species and under, or between, the thalli of four lichen species. Mean levels were 50% (moss phylloplane) and 10% (lichen thalli) higher than the levels in the clearing and, in 80% of sites, also higher than air within the rainforest. The diel pattern of the CO2 concentration at each of the sites was not predictable from measurements of CO2 in the bulk air of the forest. High levels of CO2 may be important in elevating photosynthetic rates of mosses and, to a lesser extent, lichens in the field.

KEYWORDS: FIELD, FOREST, LICHENS, MICROCLIMATE, PHOTOSYNTHESIS, PSEUDOCYPHELLARIA, THALLUS WATER-CONTENT

2321

Tate, K.R. 1992. Assessment, based on a climosequence of soils in tussock grasslands, of soil carbon storage and release in response to global warming. *Journal of Soil Science 43(4):697-707.*

A soil climosequence in tussock grasslands in South Island, New Zealand, encompassing climates ranging from cold to warm temperate provided a spatial analogue of climate change for investigating the effects of global warming on soil C contents and turnover. Mean annual temperature (T) and annual precipitation (P) ranged from 2 to 10-degrees-C, and 350 to 5000 mm, respectively. Soil C contents were curvilinearly related to T/P across the sequence (r = -0.95, significant at P < 0.01), indicating that east of the Southern Alps, increased decomposition of organic matter with global warming would provide a positive feedback to further increase atmospheric CO2. This decrease in New Zealand's soil C, estimated to be up to 10% of the current content for a global temperature rise of 0.03 K a-1 to 2050, could contribute about 0.5 x 10(15) g C to the atmosphere over the next 60 years. These conclusions were generally supported by changes in soil C turnover estimated from 'bomb' C-14 enrichment. The unexpectedly slow turnover found for two soils was explained by a 'memory' effect from the former southern beech forest that grew on these soils in prehistoric times. Accumulation of Al-humus under the forest may be responsible for the slow C turnover observed.

KEYWORDS: ALUMINUM, ANDOSOLS, CO2, EMISSIONS, FRACTIONS, MICROBIAL BIOMASS, MINERALIZATION, NEW-ZEALAND, ORGANIC-MATTER, VEGETATION

2322

Tate, K.R., and D.J. Ross. 1997. Elevated CO2 and moisture effects on soil carbon storage and cycling in temperate grasslands. *Global Change Biology 3(3):225-235.*

In grassland ecosystems, most of the carbon (C) occurs below- ground. Understanding changes in soil fluxes induced by elevated atmospheric CO2 is critical for balancing the global C budget and for managing grassland ecosystems sustainably. In this review, we use the results of short-term (1-2 years) studies of below-ground processes in grassland communities under elevated CO2 to assess future prospects for longer-term increases in soil C storage. Results are broadly consistent with those from other plant communities and include: increases in below-ground net primary productivity and an increase in soil C cycling rate, changes in soil faunal community, and generally no increase in soil C storage. Based on other experimental data, future C storage could be favoured in soils of moderate nutrient status, moderate-to-high clay content, and low (or moderately high) soil moisture status. Some support for these suggestions is provided by preliminary results from direct measurements of soil C concentrations near a New Zealand natural CO2-venting spring, and by simulations of future changes in grassland soils under the combined effects of CO2 fertilization and regional climate change. Early detection of any increase in soil C storage appears unlikely in complex grassland communities because of (a) the difficulty of separating an elevated CO2 effect from the effects of soil factors including moisture status, (b) the high spatial variability of soil C and (c) the effects of global warming. Several research imperatives are identified for reducing the uncertainties in the effects of elevated atmospheric CO2 on soil C.

KEYWORDS: AGGREGATE STABILITY, ATMOSPHERIC CO2, CLIMATE CHANGE, DIOXIDE, ENRICHMENT, LONG-TERM RESPONSE, MICROBIAL BIOMASS, NITROGEN, PLANT-RESPONSES, TALLGRASS PRAIRIE

2323

Tateno, M., and F.S. Chapin. 1997. The logic of carbon and nitrogen interactions in terrestrial ecosystems. *The American Naturalist 149(4):723-744.*

Simple ecosystem models of carbon (C) and nitrogen (N) interactions between plants and soil show that differences in N-use efficiency cause convergence of plant growth in ecosystems with a closed N cycle because rapid growth associated with high N-use efficiency results in litter with a high C:N ratio and a low N mineralization rate, whereas slow growth associated with low N-use efficiency leads to a low C:N ratio and a high N mineralization rate. This plant-induced negative feedback on production contrasts with the positive feedback that had previously been hypothesized. Our model explains the causes and results of several important ecological patterns. First, all ecosystems with a fixed N pool will show a small increase in C storage (especially in soils) in response to elevated CO2 despite constraints by litter-quality feedbacks to N mineralization rate. Second, the decreased N-use efficiency and plateauing of primary production in forest ecosystems with a high N supply reflect saturation of photosynthetic rate with high plant N pools. Finally, the addition of inorganic N to ecosystems induces a quick increase in productivity and N supply. However, these increases disappear if N additions are not sustained. These findings suggest that

those global changes that alter N input to or output from ecosystems are likely to have larger long-term impact on biomass, productivity, and C storage of ecosystems with a tightly closed N cycle than would changes in plant N-use efficiency.

KEYWORDS: ELEVATED CO2, GLOBAL CHANGE, GRASSES, NUTRIENT, PATTERNS, PHOTOSYNTHESIS, PLANTS, POLYGONUM-CUSPIDATUM, RESPONSES, USE EFFICIENCY

2324

Taulavuori, E., K. Taulavuori, K. Laine, T. Pakonen, and E. Saari. 1997. Winter hardening and glutathione status in the bilberry (Vaccinium myrtillus) in response to trace gases (CO2, O-3) and nitrogen fertilization. *Physiologia Plantarum 101(1):192-198.*

Bilberry plants (Vaccinium myrtillus L.) at a field site in northern Finland (65 degrees N) were subjected to nitrogen fertilization [6.5 mmol m(-2) NH4NO3 x Ca(OH)(2)] at the beginning of 3 growing seasons in late May and to trace gas fumigation (CO2 and O-3) for 5 months (May-September) in 1993- 1995 in order to investigate frost resistance and glutathione concentrations during the winter hardening period, and to assess the correlation between these variables. Harvesting was performed twice in the autumn of both 1994 and 1995, and the two-year data for each harvest were pooled. The frost resistance of the bilberry stems increased by about 10 degrees C during the hardening period between the two harvests. Nitrogen fertilization increased the frost resistance towards late autumn. The fumigation treatments had no marked effect on it. The combination of elevated CO2 and nitrogen fertilization induced a decrease in frost resistance. Increases in total glutathione concentrations and the proportion of reduced glutathione (GSH) in the stems were evident during hardening. Nitrogen fertilization positively affected the total glutathione concentration and the proportion of GSH at the beginning of the hardening period but the effect disappeared during the hardening process. Trace gas fumigation as such had no marked effect on glutathione concentration. Increases in glutathione concentrations during hardening did not correlate with frost resistance, possibly due to different timing of the appearence of the response to fertilization treatment, i.e., glutathione responded in the beginning of hardening while frost resistance at the end. The lack of correlation with frost resistance, and especially the different responses to nitrogen fertilization, may reflect the indirect role of glutathione in the development of winter hardening, as a transport and storage form of reduced nitrogen and sulphur. In conclusion, winter hardening and glutathione status in the bilberry seems to be sensitive to nitrogen fertilization, and not affected by elevated CO2 and O-3.

KEYWORDS: AIR- POLLUTANTS, ATMOSPHERIC CO2, CARBON DIOXIDE, FREEZING-INJURY, FROST HARDINESS, PICEA-ABIES L, PINE NEEDLES, RED SPRUCE, RUBENS SARG, SEASONAL-VARIATION

2325

Tausz, M., L.J. DeKok, I. Stulen, and D. Grill. 1996. Physiological responses of Norway spruce trees to elevated CO2 and SO2. *Journal of Plant Physiology 148(3-4):362-367.*

Young Norway spruce (Picea abies (L.) Karst.) trees were exposed to elevated CO2 (0.8 mL L(-1)), SO2 (0.06 mu L L(-1)), and elevated CO2 and SO2 (0.8 mL L(-1) and 0.06 mu L L(-1), respectively) for three months. Exposure to elevated CO2 resulted in an increased biomass production of the needles, while the pigment content was decreased. Exposure to SO2 hardly affected growth and pigment contents. Chlorophyll/carotenoid- and chlorophyll a/chlorophyll b-ratios were not affected by either CO2 or SO2. The epoxidation state of the xanthophyll-cycle was changed upon SO2-exposure, due to a higher zeaxanthin and a lower violaxanthin content. Chlorophyll fluorescence measurements showed F-v/F-m-ratios of 0.7 or higher for all needles, which indicated a healthy photosynthetic apparatus. Exposure to SO2 resulted in increased foliar contents of sulfate, total glutathione (reduced and oxidized form), cyst(e)ine, and a slightly more reduced redox state of glutathione. Exposure to elevated CO2 resulted in a slight decrease in glutathione contents, but it did not affect sulfate or cyst(e)ine contents of the spruce needles. Neither ascorbic acid content nor its redox state were affected by CO2 or SO2. The effects of CO2 and SO2 were independent from each other, since significant interactions CO(2)xSO(2) were not observed.

KEYWORDS: AIR- POLLUTANTS, CARBON DIOXIDE, LEAVES, O-3, OZONE

2326

Taylor, G., S.D.L. Gardner, C. Bosac, T.J. Flowers, M. Crookshanks, and L. Dolan. 1995. Effects of elevated co2 on cellular mechanisms, growth and development of trees with particular reference to hybrid poplar. *Forestry 68(4):379-390.*

Growth is often stimulated when C-3 plants, including trees, are exposed to elevated CO2, although evidence from the literature suggests that the responsiveness of trees to CO2 varies, depending on species. This paper explores some of the cellular mechanisms which underlie increased growth, using both the authors' own data and information from the literature. Mechanisms include photosynthetic fixation of CO2 and the role of Rubisco, the link between carbon fixation and growth, in particular, how increased carbon is thought to influence the process of plant cell expansion and cell production and finally the consequences of cellular effects for the growth and development of whole planes. Data are presented for the growth and development of hybrid poplars in elevated CO2, following both field (open-top chambers) and laboratory experiments which suggest that this type of tree with indeterminate, rapid growth may be favoured by the CO2 concentrations of the next century.

KEYWORDS: ACCLIMATION, BETULA-PENDULA ROTH, CARBON DIOXIDE, EFFICIENCY, PHOTOSYNTHESIS, PLANTS, RESPONSES, ROOT

2327

Taylor, G., S. Ranasinghe, C. Bosac, S.D.L. Gardner, and R. Ferris. 1994. Elevated co2 and plant-growth - cellular mechanisms and responses of whole plants. *Journal of Experimental Botany 45(280):1761-1774.*

Much research has focused on the photosynthetic responses of plants to elevated CO2, with less attention given to the post- photosynthetic events which may lead to changes in the growth of tissues, organs and whole plants. The aim of this review is to identify how plant growth is altered in elevated CO2 and to determine which growth processes or cellular mechanisms are sensitive to carbon supply. For leaves, both the expansion of individual leaves and the initiation of leaf primordia are stimulated in elevated CO2. When lamina growth is promoted, this is usually associated with increased leaf cell expansion rather than increased leaf cell production. Using several clones of hybrid poplar (Populus euramericana, P. interamericana) two native herbs (Plantago media, Sanguisorba minor) and bean (Phaseolus vulgaris) we have identified the mechanism through which leaf cell expansion is promoted in elevated CO2. Changes in the water relations, turgor pressure (P) and yield turgor (Y) of growing leaves cannot explain increased cell expansion; this appears to occur because cell wall loosening is promoted, as suggested by three pieces of evidence. (i) The rate of decline of water potential (psi) with time is accelerated when growing leaves are placed in psychrometers and allowed to relax, (ii) Instron-measured cell wall extensibility (WEX), is greater for leaves exposed to elevated CO2 and

(iii) the activity of the putative wall loosening enzyme, XET is increased for leaves of P. vulgaris exposed to elevated CO2. Species differences do, however, exist; in the herb Lotus corniculatus small stimulations of leaf growth in elevated CO2 are due to increased leaf cell production and decreased cell size in elevated CO2. These results are discussed in relation to the concept of functional types. There is evidence to suggest that both cell production and cell expansion are promoted in roots of plants exposed to elevated CO2. For native herbs (Anthyllis vulneraria, Lotus corniculatus, P. media and S. minor), increased root growth in elevated CO2 is due to increased cell elongation. In contrast to leaves, this appears to occur because both root cell turgor pressure (P) and root cell wall extensibility (WEX) are promoted by exposure of shoots to elevated CO2. In longer-term studies on root growth, the effects of additional carbon on the production of root primordia and root branching are of overriding importance, suggesting that carbon supply may influence some aspect of the cell cycle, when effects on the extension of individual roots may not be apparent.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, ENRICHMENT, LEAF GROWTH, PHOTOSYNTHESIS, ROOT-GROWTH, SOURCE-SINK RELATIONS, WALL EXTENSIBILITY, WATER POTENTIALS, XYLOGLUCAN ENDOTRANSGLYCOSYLASE, YIELD THRESHOLD

2328

Taylor, J., and A.S. Ball. 1994. The effect of plant-material grown under elevated co2 on soil respiratory activity. *Plant and Soil 162(2):315-318.*

The biodegradability of aerial material from a C4 plant, sorghum grown under ambient (345 mu mol mol(-1)) and elevated (700 mu mol mol(-1)) atmospheric CO2 concentrations were compared by measuring soil respiratory activity. Initial daily respiratory activity (measured over 10 h per day) increased four fold from 110 to 440 cm(3) CO2 100g dry weight soil(-1) in soils amended with sorghum grown under either elevated or ambient CO2. Although soil respiratory activity decreased over the following 30 days, respiration remained significantly higher (t-test; p>0.05) in soils amended with sorghum grown under elevated CO2 concentrations. Analysis of the plant material revealed no significant differences in C:N ratios between sorghum grown under elevated or ambient CO2. The reason for the differences in soil respiratory activity have yet to be elucidated. However if this trend is repeated in natural ecosystems, this may have important implications for C and N cycling.

KEYWORDS: CARBON DIOXIDE, ESTUARINE MARSH, LITTER, NITROGEN

2329

Taylor, J.A., and J. Lloyd. 1992. Sources and sinks of atmospheric co2. *Australian Journal of Botany 40(4-5):407-418.*

The biosphere plays an important role in determining the sources, sinks, levels and rates of change of atmospheric CO2 concentrations. Significant uncertainties remain in estimates of the fluxes of CO2 from biomass burning and deforestation, and uptake and storage of CO2 by the biosphere arising from increased atmospheric CO2 concentrations. Calculation of probable rates of carbon sequestration for the major ecosystem complexes and global 3-D tracer transport model runs indicate the possibility that a significant net CO2 uptake (> 1 Pg C yr-1), a CO2 'fertilisation effect', may be occurring in tropical rainforests, effectively accounting for much of the 'missing sink'. This sink may currently balance much of the CO2 added to the atmosphere from deforestation and biomass burning. Interestingly, CO2 released from biomass burning may itself be playing an important role in enhanced carbon storage by tropical rainforests. This has important implications for predicting future CO2 concentrations. If tropical rainforest destruction continues then much of the CO2 stored as a result of the CO2 'fertilisation effect' will be rereleased to the atmosphere and much of the 'missing sink' will disappear. These effects have not been considered in the IPCC (Intergovernmental Panel on Climate Change) projections of future atmospheric CO2 concentrations. Predictions which take account of the combined effects of deforestation, the return of carbon previously stored through the CO2 'fertilisation effect' and the loss of a large proportion of the 'missing sink' as a result of deforestation, would result in much higher predicted concentrations and rates of increase of atmospheric CO2 and, as a consequence, accelerated rates of climate change.

KEYWORDS: BIOSPHERE, BUDGET, CARBON DIOXIDE, EMISSIONS

2330

Taylor, K., and C. Potvin. 1997. Understanding the long-term effect of CO2 enrichment on a pasture: the importance of disturbance. *Canadian Journal of Botany-Revue Canadienne De Botanique 75(10):1621-1627.*

This study is part of a research program examining the effects of elevated atmospheric carbon dioxide on a pasture. It was designed to examine (i) the interaction between disturbance and the atmospheric CO2 concentration at the community level, and (ii) the response of a major weed Chenopodium album to CO2 enrichment in a natural field situation. Although both the total number of species and Simpson's index increased upon disturbance, these traits did not respond to CO2 fertilization. Counter to our expectation, we found no significant interaction between disturbance and CO2. The composition of the community that established in the open, disturbed spaces was a function of seed availability and as such independent of the atmospheric CO2 concentration. Using height of the background vegetation to assess the impact of elevated CO2, we found some evidence for density dependence in the undisturbed quadrats but not in the disturbed ones. For C. album, the disturbance regimes outweigh the CO2 increase in importance. Neighboring plants have a strong influence on C. album growth, this even though the C. album photosynthetic mechanisms are potentially responsive to elevated CO2. The present study highlights the complex feed- back interactions occurring when a community is exposed to elevated CO2 concentration.

KEYWORDS: C-3, CHENOPODIUM-ALBUM L, COMMUNITY, COMPETITION, ELEVATED CO2, GROWTH, LIGHT, PHYTOCHROME, PLANTS, RESPONSES

2331

Teese, P. 1995. Intraspecific variation for co2 compensation point and differential growth among variants in a C-3-C-4 intermediate plant. *Oecologia 102(3):371-376.*

CO2 compensation point (Gamma), the concentration of CO2 at which photosynthesis and respiration are at equilibrium, is a commonly used diagnostic for the C-4 photosynthetic pathway, since it reflects the reduced photorespiration that is a property of C-4 photosynthesis. Geographic variation for Gamma was examined within Flaveria linearis, a C-3-C-4 intermediate species. Collections from four widely separated Floridian populations were propagated in a greenhouse and measured for Gamma. Little differentiation among populations was found, but significant within-population variation was present. Temperature is a hypothesized selective agent for the C-4 photosynthetic pathway. To test this hypothesis, plants exhibiting a range of Gamma were cloned and placed in growth chambers at 25 degrees C and 40 degrees C. After 7 weeks, Gamma valves were remeasured and plants were harvested and weighed. There was a poor correlation between initial and final measures of Gamma for a given genotype ($r = 0.38$, $P > 0.1$). Broad sense heritability for Gamma was computed to be 0.10. At 25 degrees C, there was no relationship between final size and Gamma. At 40 degrees C,

more C,like plants, as indicated by their low Gamma, had grown larger. Differences in relative growth rate were attributable more to differences in net assimilation rate than in leaf area ratio. Taken together, these results demonstrate that although significant plasticity exists in the amount of photorespiration in this C-3-C-4 species, high temperature appears to be an effective selective agent for the reduction of photorespiration and the enhancement of C-4-like traits.

KEYWORDS: ASSIMILATION, C-4 PHOTOSYNTHESIS, C3-C4, EVOLUTION, FLAVERIA, LEAF ANATOMY, PATHWAYS, QUANTITATIVE GENETICS, ULTRASTRUCTURE

2332

Telewski, F.W., R.T. Swanson, B.R. Strain, and J.M. Burns. 1999. Wood properties and ring width responses to long-term atmospheric CO2 enrichment in field-grown loblolly pine (Pinus taeda L.). *Plant, Cell and Environment 22(2):213-219.*

Loblolly pine (Pinus taeda L.) were grown in the field, under non-limiting nutrient conditions, in open-top chambers for 4 years at ambient CO2 partial pressures (pCO(2)) and with a CO2- enriched atmosphere (+ 30 Pa pCO(2) compared to ambient concentration). A third replicate of trees were grown without chambers at ambient pCO(2). Wood anatomy, wood density and tree ring width were analysed using stem wood samples. No significant differences were observed in the cell wall to cell lumen ratio within the latewood of the third growth ring formed in 1994. No significant differences were observed in the density of resin canals or in the ratio of resin canal cross- sectional area to xylem area within the same growth ring. Ring widths were significantly wider in the CO2-enrichment treatment for 3 of 4 years compared to the ambient chamber control treatment. Latewood in the 1995 growth ring was significantly wider than that in the ambient control and represented a larger percentage of the total growth-ring width. Carbon dioxide enrichment also significantly increased the total wood specific gravity (determined by displacement). However, when determined as total sample wood density by X-ray densitometry, the density of enriched samples was not significantly higher than that of the ambient chamber controls. Only the 1993 growth ring of enriched trees had a significantly higher maximum latewood density than that of trees grown on non-chambered plots or ambient chambered controls. No significant differences were observed in the minimum earlywood density of individual growth rings between chambered treatments. These results show that the most significant effect of CO2 enrichment on wood production in loblolly pine is its influence on radial growth, measured as annual tree ring widths. This influence is most pronounced in the first year of growth and decreases with age.

KEYWORDS: ALLOCATION, CARBON DIOXIDE, CLIMATE, ELEVATED CO2, FOREST, INCREASING CO2, MECHANICAL PERTURBATION, PHOTOSYNTHESIS, TREE GROWTH, TRENDS

2333

Teramura, A.H., and J.H. Sullivan. 1994. Effects of uv-b radiation on photosynthesis and growth of terrestrial plants. *Photosynthesis Research 39(3):463-473.*

The photosynthetic apparatus of some plant species appears to be well-protected from direct damage from UV-B radiation. Leaf optical properties of these species apparently minimizes exposure of sensitive targets to UV-B radiation. However, damage by UV-B radiation to Photosystem II and Rubisco has also been reported. Secondary effects of this damage may include reductions in photosynthetic capacity, RuBP regeneration and quantum yield. Furthermore, UV-B radiation may decrease the penetration of PAR, reduce photosynthetic and accessory pigments, impair stomatal function and alter canopy morphology, and thus indirectly retard photosynthetic carbon assimilation. Subsequently, UV-B radiation may limit productivity in many plant species. In addition to variability in sensitivity to UV- B radiation, the effects of UV-B radiation are further confounded by other environmental factors such as CO2, temperature, light and water or nutrient availability. Therefore, we need a better understanding of the mechanisms of tolerance to UV-B radiation and of the interaction between UV-B and other environmental factors in order to adequately assess the probable consequences of a change in solar radiation.

KEYWORDS: CUCUMBER SEEDLINGS, ELEVATIONAL GRADIENT, FIELD CONDITIONS, LOBLOLLY-PINE, OZONE DEPLETION, PHOTON FLUX- DENSITY, PISUM-SATIVUM, REACTION CENTER PROTEIN, ULTRAVIOLET-B, VISIBLE-LIGHT

2334

Teramura, A.H., J.H. Sullivan, and L.H. Ziska. 1990. Interaction of elevated ultraviolet-b radiation and CO2 on productivity and photosynthetic characteristics in wheat, rice, and soybean. *Plant Physiology 94(2):470-475.*

2335

Teskey, R.O. 1995. A field-study of the effects of elevated co2 on carbon assimilation, stomatal conductance and leaf and branch growth of pinus-taeda trees. *Plant, Cell and Environment 18(5):565-573.*

A study was conducted in 21-year-old loblolly pine (Pinus taeda L.) trees growing in plantation in north central Georgia, USA, The experiment used branch chambers to impose treatments of ambient, ambient+165 and ambient+ 330 mu mol mol(-1) CO2. After one growing season there was no indication of acclimation to elevated CO2. In August and September, carbon assimilation, measured by two different methods, was twice as high at ambient +330 mu mol mol(-1) CO2 than at ambient, Dark respiration was suppressed by 6% at ambient+l65 and by 14% at ambient+330 mu mol mol(-1) CO2. This suppression was immediate, and not an effect of exposure to elevated CO2 during growth, since respiration was reduced by the same amount in all treatments when measured at a high CO2 concentration, Elevated CO2 increased the growth of foliage and woody tissue, It also increased instantaneous transpiration efficiency, but it had no effect on stomatal conductance, Since the soil at the study site had low to moderate fertility, these results suggest that the growth potential of forests on many sites may be enhanced by global increases in atmospheric CO2 concentration.

KEYWORDS: COOCCURRING BIRCH, DIOXIDE ENRICHMENT, GAS-EXCHANGE, LIRIODENDRON-TULIPIFERA L, LONG-TERM EXPOSURE, PHOTOSYNTHESIS, RESPIRATION, RESPONSES, SCIRPUS- OLNEYI, SEEDLINGS

2336

Teskey, R.O. 1997. Combined effects of elevated CO2 and air temperature on carbon assimilation of Pinus taeda trees. *Plant, Cell and Environment 20(3):373-380.*

Branches of 22-year-old loblolly pine (Pinus taeda, L.) trees growing in a plantation were exposed to ambient CO2, ambient + 165 mu mol mol(-1) CO2 or ambient + 330 mu mol mol(-1) CO2 concentrations in combination with ambient or ambient + 2 degrees C air temperatures for 3 years. Field measurements in the third year indicated that net carbon assimilation was enhanced in the elevated CO2 treatments in all seasons. On the basis of A/C-i curves, there was no indication of photosynthetic down-regulation. Branch growth and leaf area also increased significantly in the elevated CO2 treatments. The imposed 2 degrees C increase in air temperature only had slight effects on net assimilation and growth. Compared with the ambient CO2 treatment, rates of net

assimilation were approximate to 1.6 times greater in the ambient + 165 mu mol mol(-1) CO2 treatment and 2.2 times greater in the ambient + 330 mu mol mol(-1) CO2 treatment. These ratios did not change appreciably in measurements made in all four seasons even though mean ambient air temperatures during the measurement periods ranged from 12.6 to 28.2 degrees C. This indicated that the effect of elevated CO2 concentrations on net assimilation under field conditions was primarily additive. The results also indicated that the effect of elevated CO2 (+ 165 or + 330 mu mol mol(-1)) was much greater than the effect of a 2 degrees C increase in air temperature on net assimilation and growth in this species.

KEYWORDS: ENRICHMENT, FIELD, GAS-EXCHANGE, GROWTH, LEAF, PHOTOSYNTHESIS, RESPONSES, SEEDLINGS, SENSITIVITY

2337

Teughels, H., I. Nijs, P. VanHecke, and I. Impens. 1995. Competition in a global change environment: The importance of different plant traits for competitive success. *Journal of Biogeography 22(2-3):297-305.*

Plant traits of both structural and physiological nature have been reported to play an important role in the outcome of a competitive interaction. In this experiment a survey of the importance of characteristics such as height, leaf area and vertical distribution, leaf inclination, light transmission through a leaf and through the canopy together with leaf photosynthesis rates, was made for two grasses: Lolium perenne L. and Festuca arundinacea Schreb. Both species were grown in a competitive set-up with minimal belowground interactions under four different global change conditions of CO2 concentration and air temperature (ambient, elevated CO2 concentration 700 mu mol mol(-1), increased air temperature+4 degrees C, combined) in naturally sunlit air-conditioned half-open plastic greenhouses. Plants were grown for a whole growing season with regular (every 4 weeks) clippings at 3.5 cm height. Results demonstrate that Lolium has a much greater competitive ability when compared to Festuca (aggressivity = 0.465). This may be a consequence of the slightly higher leaf photosynthesis rates (+15%) in combination with a larger amount of foliage area, which could result in a higher canopy photosynthesis. The greater leaf area remaining after mowing may lead to an additional advantage for Lolium. Height, leaf inclination, optical properties and the vertical distribution of leaf area seem to be of minor importance in this experiment. Global change treatments (elevated CO2 concentration and increased temperature) influence leaf photosynthesis rates predominantly and have little or no direct effect on structural traits such as height, leaf angles and vertical leaf distribution; nor do they exert an influence on light transmission through a leaf or through the canopy. However, treatment effects on leaf area can add to explain differences in canopy photosynthesis. In this competition experiment, focused on above-ground interactions, both a structural (leaf area) and a physiological feature (leaf photosynthesis) contribute to the competitive success of a species.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CANOPY, ELEVATED CO2, LIGHT, LOLIUM-PERENNE, MODEL, PHOTOSYNTHESIS, RESPONSES, SHOOT COMPETITION, TEMPERATURE

2338

Theobald, J.C., R.A.C. Mitchell, M.A.J. Parry, and D.W. Lawlor. 1998. Estimating the excess investment in ribulose-1,5-bisphosphate carboxylase/oxygenase in leaves of spring wheat crown under elevated CO2. *Plant Physiology 118(3):945-955.*

Wheat (Triticum aestivum L.) was grown under CO2 partial pressures of 36 and 70 Pa with two N-application regimes. Responses of photosynthesis to varying CO2 partial pressure were fitted to estimate the maximal carboxylation rate and the nonphotorespiratory respiration rate in flag and preceding leaves. The maximal carboxylation rate was proportional to ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) content, and the light-saturated photosynthetic rate at 70 Pa CO2 was proportional to the thylakoid ATP-synthase content. Potential photosynthetic rates at 70 Pa CO2 were calculated and compared with the observed values to estimate excess investment in Rubisco. The excess was greater in leaves grown with high N application than in those grown with low N application and declined as the leaves senesced. The fraction of Rubisco that was estimated to be in excess was strongly dependent on leaf N content, increasing from approximately 5 % in leaves with 1 g N m(-2) to approximately 40 % in leaves with 2 g N m(-2). Growth at elevated CO2 usually decreased the excess somewhat but only as a consequence of a general reduction in leaf N, since relationships between the amount of components and N content were unaffected by CO2. We conclude that there is scope for improving the N-use efficiency of C-3 crop species under elevated CO2 conditions.

KEYWORDS: CARBON-DIOXIDE CONCENTRATION, ELECTRON-TRANSPORT, GAS-EXCHANGE, LIGHT, MESOPHYLL CONDUCTANCE, PHASEOLUS-VULGARIS L, PHOTOSYNTHETIC ACCLIMATION, PLANTS, RISING ATMOSPHERIC CO2, WINTER-WHEAT

2339

Thibaud, M.C., N. Cortez, H. Riviere, and T. Betsche. 1995. Photorespiration and related enzymes in pea (pisum-sativum) grown in high co2. *Journal of Plant Physiology 146(5-6):596-603.*

The adaptation of pea (Pisum sativum L. cv. Douce Provence) to the low photorespiratory conditions imposed by high CO2 was investigated at the level of enzymes and gas exchange. Seedlings were CO2-enriched (1000 and 4800 mu L CO(2)L(-1)) during most of the vegetative period, yielding <<acclimated leaves>>. Alternatively, young plants were pre-grown in ambient CO2 and then CO2-enriched, yielding <<transferred leaves>>. The level of nutrient supply was high. High CO2 did not significantly alter the specific activities of the photorespiratory enzymes glycolate oxidase, NADH- and NADPH- hydroxypyruvate reductase and glutamine synthetase in either of the experiments. Moreover, no significant effect of high CO2 on specific carboxylase activity and relative abundance of ribulose bisphosphate carboxylase-oxygenase (Rubisco) was observed. In contrast, high CO2 markedly affected the photorespiratory enzymes catalase (Cat) and phosphoglycolate phosphatase, the activity of the latter being increased. Decline of Cat activity was detected 1 day after transfer to high CO2 and in the course of 7 days, the inhibition reached values of 33% (1000 mu L CO(2)L(-1)) and 50% (4800 mu L CO(2)L(-1)). The relative abundance of Cat protein also declined, but no change in the isoform pattern was observed. Photorespiratory O-2 uptake, determined with O-18(2), decreased by 54% in an atmosphere containing 1000 mu L CO(2)L(-1). This suggests that Rubisco-oxygenase activity occurred at a substantial rate at threefold that of the current atmospheric CO2 concentration. CO2 enrichment to 4000 mu L CO(2)L(-1) further inhibited photorespiratory O-2, uptake. The decline of Cat was thus positively correlated with the inhibition of light O-2 uptake. In <<acclimated leaves>>, Cat inhibition was slight or absent, depending on the level of CO2 enrichment. This suggests that Cat inhibition in <<transferred leaves>> is a transient response that can be overcome by yet unidentified adaptative mechanisms.

KEYWORDS: CARBON DIOXIDE, CATALASE, GENE-EXPRESSION, GLUTAMINE-SYNTHETASE, GLYCINE DECARBOXYLASE, HYDROXYPYRUVATE REDUCTASE, LEAVES, LIGHT, PHOTORESPIRATION, TRIFOLIUM-SUBTERRANEUM L

2340

Thom, R.M. 1996. CO2-enrichment effects on eelgrass (Zostera marina

L) and bull kelp (Nereocystis luetkeana (Mert) P & R). *Water, Air, and Soil Pollution 88(3-4):383-391.*

I investigated the effect of CO2-enrichment on productivity of two aquatic plant species [Zostera marina L., Nereocystis luetkeana (Mert.) P. & R.] that form significant components of coastal ecosystems in the Pacific Northwest. Short-term (i.e., 2-hr) experiments showed that doubling CO2 resulted in up to a 2.5-fold increase in Zostera net apparent productivity (NAP). Nereocystis NAP was increased 2.2 - 2.8 fold. In experiments involving seven enrichment treatments, NAP increased with increasing CO2 between ambient (1.0x) and 2.5x CO2 in both Zostera and Nereocystis. Nereocystis acid Zostera NAP was lowest at highest (i.e., 5x) CO2 concentrations. In growth experiments, mean growth rate of Zostera increased with increasing CO2 during one of the two trials. I conclude that increasing CO2 in the surface waters of the coastal ocean would predictably result in increased NAP of these two species. These results supplement limited published data showing that shallow estuarine and marine systems are vulnerable to increased carbon dioxide.

KEYWORDS: DYNAMICS, METABOLISM, NITROGEN, PATTERNS, PLANTS

2341

Thomas, R.B., and K.L. Griffin. 1994. Direct and indirect effects of atmospheric carbon-dioxide enrichment on leaf respiration of glycine-max (L) merr. *Plant Physiology 104(2):355-361.*

Long-term and short-term effects of CO2 enrichment on dark respiration were investigated using soybean (Glycine max [L.] Merr.) plants grown at either 35.5 or 71.0 Pa CO2. Indirect effects, or effects of growth in elevated CO2, were examined using a functional model that partitioned respiration into growth and maintenance components. Direct effects, or immediate effects of a short-term change in CO2, were examined by measuring dark respiration, first, at the CO2 partial pressure at which plants were grown, and second, after equilibration in the reciprocal CO2 partial pressure. The functional component model indicated that the maintenance coefficient of respiration increased 34% with elevated CO2, whereas the growth coefficient was not significantly affected. Changes in maintenance respiration were correlated with a 33% increase in leaf total nonstructural carbohydrate concentration, but leaf nitrogen content of soybean leaves was not affected by CO2 enrichment. Thus, increased maintenance respiration may be a consequence of increased nonstructural carbohydrate accumulation. When whole soybean plants were switched from low CO2 to high CO2 for a brief period, leaf respiration was always reduced. However, this direct effect of CO2 partial pressure was approximately 50% less in plants grown in elevated CO2. We conclude from this study that there are potentially important effects of CO2 enrichment on plant respiration but that the effects are different for plants given a short-term increase in CO2 partial pressure versus plants grown in elevated CO2.

KEYWORDS: ELEVATED CO2, FIELD, FRUIT, GROWTH, MAINTENANCE RESPIRATION, METABOLISM, PHOSPHOENOLPYRUVATE, PLANTS, SOYBEAN LEAVES, TERM

2342

Thomas, R.B., J.D. Lewis, and B.R. Strain. 1994. Effects of leaf nutrient status on photosynthetic capacity in loblolly-pine (pinus-taeda L) seedlings grown in elevated atmospheric co2. *Tree Physiology 14(7-9):947-960.*

We measured needle photosynthesis of loblolly pine seedlings grown in a factorial experiment with two CO2 partial pressures (35 and 65 Pa) and three nutrient treatments (7 mM NH4NO3 + 1 mM PO4; 7 mM NH4NO3 + 0.2 mM PO4; 1 mM NH4NO3 + 1 mM PO4). The data were used to parameterize a physiologically based photosynthetic model that included limitations imposed by ribulose-1,5-bisphosphate carboxylase/oxygenase activity, electron transport capacity and inorganic phosphate availability. With nonlimiting nutrients, seedlings grown at 65 Pa CO2 had significantly higher net photosynthesis and lower stomatal conductance than seedlings grown at 35 Pa CO2. Nutrient limitations by either N or P significantly reduced photosynthetic capacity. When either N or P was limiting, there was no effect of growth CO2 partial pressure on photosynthesis, but stomatal conductance was significantly lower for seedlings grown at 65 Pa CO2. Modeled biochemical parameters suggest that, in all cases, photosynthesis was co-limited by carboxylation, electron transport and phosphate regeneration. Acclimation to growth in elevated CO2 involved a reduction in leaf N content. In the low-N and low-P treatments, modeled parameters indicated that the biochemical processes of photosynthesis were down regulated to the point that there was no effect of increasing CO2 partial pressure. The capacity to regenerate phosphate was reduced in both low nutrient treatments, but was only reduced by elevated C02 when seedlings were grown under low soil P conditions. Increased photosynthetic water use efficiency and nutrient use efficiency in response to CO2 enrichment occurred in all three nutrient treatments and have important implications for whole-plant water and nutrient balance. These data support the contention that soil nutrient status in forest ecosystems will be a critical influence on tree seedling response to increasing atmospheric CO2 partial pressures.

2343

Thomas, R.B., C.D. Reid, R. Ybema, and B.R. Strain. 1993. Growth and maintenance components of leaf respiration of cotton grown in elevated carbon-dioxide partial-pressure. *Plant, Cell and Environment 16(5):539-546.*

Elevated atmospheric carbon dioxide partial pressures have been shown to have variable direct and indirect effects on plant respiration rates. In this study, growth, leaf respiration, and leaf nitrogen and carbohydrate partitioning were measured in Gossypium hirsutum L. grown in 35 and 65Pa CO2 for 30 d. Growth and maintenance coefficients of leaf respiration were estimated using gas exchange techniques both at night and during the day. Elevated CO2 stimulated biomass production (107%) and net photosynthetic rates (35-50%). Total day-time respiration (R(d)) was not significantly affected by growth CO2 partial pressure. However, night respiration (R(n)) of leaves grown in 65 Pa CO2 Was significantly greater than that of plants grown in 35 Pa CO2. Correlation of R(d) and R(n) with leaf expansion rates indicated that plants in both CO2 treatments had equivalent growth respiration coefficients but maintenance respiration was significantly greater in elevated CO2. Increased maintenance coefficients in elevated CO2 appeared to be related to increased starch accumulation rather than to changes in leaf nitrogen.

KEYWORDS: CARBOHYDRATE CONTENT, CO2- ENRICHMENT, DARK RESPIRATION, EFFLUX, GAS-EXCHANGE, LEAVES, PHOTOSYNTHESIS, PLANT GROWTH, RESPONSES, SHORT- TERM

2344

Thomas, R.B., D.D. Richter, H. Ye, P.R. Heine, and B.R. Strain. 1991. Nitrogen dynamics and growth of seedlings of an n-fixing tree (Gliricidia sepium (jacq) walp) exposed to elevated atmospheric carbon-dioxide. *Oecologia 88(3):415-421.*

Seeds of Gliricidia sepium (Jacq.) Walp., a tree native to seasonal tropical forests of Central America, were inoculated with N-fixing Rhizobium bacteria and grown in growth chambers for 71 days to investigate interactive effects of atmospheric CO2 and plant N status on early seedling growth, nodulation, and N accretion. Seedlings were

grown with CO2 partial pressures of 350 and 650-mu-bar (current ambient and a predicted partial pressure of the mid-21st century) and with plus N or minus N nutrient solutions to control soil N status. Of particular interest was seedling response to CO2 when grown without available soil N, a condition in which seedlings initially experienced severe N deficiency because bacterial N-fixation was the sole source of N. Biomass of leaves, stems, and roots increased significantly with CO2 enrichment (by 32%, 15% and 26%, respectively) provided seedlings were supplied with N fertilizer. Leaf biomass of N-deficient seedlings was increased 50% by CO2 enrichment but there was little indication that photosynthate translocation from leaves to roots or that plant N (fixed by Rhizobium) was altered by elevated CO2. In seedlings supplied with soil N, elevated CO2 increased average nodule weight, total nodule weight per plant, and the amount of leaf nitrogen provided by N-fixation (as indicated by leaf delta-N-15). While CO2 enrichment reduced the N concentration of some plant tissues, whole plant N accretion increased. Results support the contention that increasing atmospheric CO2 partial pressures will enhance productivity and N-fixing activity of N-fixing tree seedlings, but that the magnitude of early seedling response to CO2 will depend greatly on plant and soil nutrient status.

KEYWORDS: ALLOCATION, CO2- ENRICHMENT, FIXATION, NODULATION, PHYSIOLOGY, PINE, PISUM-SATIVUM, PLANTS, QUERCUS-ALBA, WATER

2345

Thomas, R.B., and B.R. Strain. 1991. Root restriction as a factor in photosynthetic acclimation of cotton seedlings grown in elevated carbon-dioxide. *Plant Physiology 96(2):627-634.*

Interactive effects of root restriction and atmospheric CO2 enrichment on plant growth, photosynthetic capacity, and carbohydrate partitioning were studied in cotton seedlings (Gossypium hirsutum L.) grown for 28 days in three atmospheric CO2 partial pressures (270, 350, and 650 microbars) and two pot sizes (0.38 and 1.75 liters). Some plants were transplanted from small pots into large pots after 20 days. Reduction of root biomass resulting from growth in small pots was accompanied by decreased shoot biomass and leaf area. When root growth was less restricted, plants exposed to higher CO2 partial pressures produced more shoot and root biomass than plants exposed to lower levels of CO2. In small pots, whole plant biomass and leaf area of plants grown in 270 and 350 microbars Of CO2 were not significantly different. Plants grown in small pots in 650 microbars Of CO2 produced greater total biomass than plants grown in 350 microbars, but the dry weight gain was found to be primarily an accumulation of leaf starch. Reduced photosynthetic capacity of plants grown at elevated levels Of CO2 was clearly associated with inadequate rooting volume. Reductions in net photosynthesis were not associated with decreased stomatal conductance. Reduced carboxylation efficiency in response to CO2 enrichment occurred only when root growth was restricted suggesting that ribulose-1,5- bisphosphate carboxylase/oxygenase activity may be responsive to plant source-sink balance rather than to CO2 concentration as a single factor. When root-restricted plants were transplanted into large pots, carboxylation efficiency and ribulose-1, 5-bisphosphate regeneration capacity increased indicating that acclimation of photosynthesis was reversible. Reductions in photosynthetic capacity as root growth was progressively restricted suggest sink-limited feedback inhibition as a possible mechanism for regulating net photosynthesis of plants grown in elevated CO2.

KEYWORDS: BEAN-PLANTS, CARBOXYLASE, ENRICHMENT, EXCHANGE, HIGH ATMOSPHERIC CO2, INHIBITION, LEAVES, LONG-TERM EXPOSURE, SOYBEANS, TEMPERATURE

2346

Thomas, S.C., and F.A. Bazzaz. 1996. Elevated CO2 and leaf shape: Are dandelions getting toothier? *American Journal of Botany 83(1):106-111.*

Heteroblastic leaf development in Taraxacum officinale is compared between plants grown under ambient (350 ppm) vs. elevated (700 ppm) CO2 levels. Leaves of elevated CO2 plants exhibited more deeply incised leaf margins and relatively more slender leaf laminae than leaves of ambient CO2 plants. These differences were found to be significant in allometric analyses that controlled for differences in leaf size, as well as analyses that controlled for leaf developmental order. The effects of elevated CO2 on leaf shape were most pronounced when plants were grown individually, but detectable differences were also found in plants grown at high density. Although less dramatic than in Taraxacum, significant effects of elevated CO2 on leaf shape were also found in two other weedy rosette species, Plantago major and Rumex crispus. These observations support the long-standing hypothesis that leaf carbohydrate level plays an important role in regulating heteroblastic leaf development, though elevated CO2 may also affect leaf development through direct hormonal interactions or increased leaf water potential. In Taraxacum, pronounced modifications of leaf shape were found at CO2 levels predicted to occur within the next century.

KEYWORDS: ALLOMETRY, AMBIENT, CARBON-DIOXIDE ENRICHMENT, COMPETITION, GROWTH, KUDZU PUERARIA-LOBATA, MORPHOLOGY, PLANTS, SYSTEM, TEMPERATURE

2347

Thomas, S.M., D. Whitehead, J.A. Adams, J.B. Reid, R.R. Sherlock, and A.C. Leckie. 1996. Seasonal root distribution and soil surface carbon fluxes for one-year-old Pinus radiata trees growing at ambient and elevated carbon dioxide concentration. *Tree Physiology 16(11-12):1015-1021.*

The increase in number of fine (< 0.5 mm diameter) roots of one-year-old clonal Pinus radiata D. Don trees grown in large open-top field chambers at ambient (362 mu mol mol(-1)) or elevated (654 mu mol mol(-1)) CO2 concentration was estimated using minirhizotron tubes placed horizontally at a depth of 0.3 m. The trees were well supplied with water and nutrients. Destructive harvesting of roots along an additional tube showed that there was a linear relationship between root number estimated from the minirhizotron and both root length density, L(v), and root carbon density, C-v, in the surrounding soil. Root distribution decreased with horizontal distance from the tree. At a depth of 0.3 m, 88% of the total C-v was concentrated within a 0.15-m radius from tree stems in the elevated CO2 treatment, compared with 35% for trees in the ambient CO2 treatment. Mean C-v along the tubes ranged up to 5 x 10(-2) mu g mm(-3) and tended to be greater for trees grown at elevated CO2 concentration, although the differences between CO2 treatments were not significant. Root growth started in spring and continued until late summer. There was no significant difference in seasonal rates of increase in C-v between treatments, but roots were observed four weeks earlier in the elevated CO2 treatment. No root turnover occurred at a depth of 0.3 m during the first year after planting. Mean values of carbon dioxide flux density at the soil surface, F, increased from 0.02 to 0.13 g m(-2) h(-1) during the year, and F was 30% greater for trees grown at elevated CO2 concentration than at ambient CO2. Diurnal changes in F were related to air temperature. The seasonal increase in F continued through the summer and early autumn, well after air temperature had begun to decline, suggesting that the increase was partly caused by increase in C-v as the roots colonized the soil profile.

KEYWORDS: ATMOSPHERIC CO2, BIOMASS, NITROGEN, PLANTATIONS, RESPIRATION, RESPONSES, TURNOVER

2348

Thomas, S.M., D. Whitehead, J.B. Reid, F.J. Cook, J.A. Adams, and A.C. Leckie. 1999. Growth, loss, and vertical distribution of Pinus radiata fine roots growing at ambient and elevated CO2 concentration. *Global Change Biology 5(1):107-121.*

Increased below-ground carbon allocation in forest ecosystems is a likely consequence of rising atmospheric CO2 concentration. If this results in changes to fine root growth, turnover and distribution long-term soil carbon cycling and storage could be altered. Bi-weekly measurements were made to determine the dynamics and distribution of fine roots (<1 mm diameter) for Pinus radiata trees growing at ambient (350 mu mol mol(-1)) and elevated (650 mu mol mol(-1)) CO2 concentration in large open-top chambers. Measurements were made using minirhizotrons installed horizontally at depths of 0.1, 0.3, 0.5 and 0.9 m. During the first year, at a depth of 0.3 m, the increase in relative growth rate of roots occurred 6 weeks earlier in the elevated CO2 treatment and the maximum rate was reached 10 weeks earlier than for trees in the ambient treatment. After 2 years, cumulative fine root growth (P-t) was 36% greater for trees growing at elevated CO2 than at ambient CO2 concentration, although this difference was not significant. A model of root growth driven by daily soil temperature accounted for between 43 and 99% of root growth variability. Total root loss (L-t) was 9% in the ambient and 14% in the elevated CO2 treatment, although this difference was not significant. Root loss was greatest at 0.3 m. In the first year, 62% of fine roots grown between mid-summer and late-autumn disappeared within a year in the elevated CO2 treatment, but only 18% in the ambient CO2 treatment (P < 0.01). An exponential model relating L-t to time accounted for between 74 and 99% of the variability. Root cohort half-lives were 951 d for the ambient and 333 d for the elevated treatment. Root length density decreased exponentially with depth in both treatments, but relatively more fine roots grown in the elevated CO2 treatment tended to occur deeper in the soil profile.

KEYWORDS: ATMOSPHERIC CO2, BELOWGROUND RESPONSES, BETULA- PAPYRIFERA, CARBON-DIOXIDE CONCENTRATION, COTTON ROOT, FORESTS, KIWIFRUIT ACTINIDIA-DELICIOSA, N-AVAILABILITY, NITROGEN, PONDEROSA PINE

2349

Thompson, G.B., J.K.M. Brown, and F.I. Woodward. 1993. The effects of host carbon-dioxide, nitrogen and water-supply on the infection of wheat by powdery mildew and aphids. *Plant, Cell and Environment 16(6):687-694.*

In two experiments, winter wheat (Triticum aestivum cv. Cerco) was grown in 350 (ambient) and 700 mumol mol-1 (elevated) atmospheric CO2 concentrations. In the first experiment, plants were grown at five levels of nitrogen fertilization, and in the second experiment, plants were grown at three levels of water supply. All plants were infected with powdery mildew, caused by the fungus Erysiphe graminis. Plants grown in elevated atmospheric CO2 concentrations had significantly reduced % shoot nitrogen contents and significantly increased % shoot water contents. At elevated atmospheric CO2 concentrations, where plant nitrogen content was significantly reduced, the severity of mildew infection was significantly reduced, and where host water content was significantly increased, the severity of mildew infection was significantly increased. In a moderate water supply treatment, the plants grown in elevated atmospheric CO2 concentrations had significantly reduced nitrogen contents (9.9%) and significantly increased water content (4%), the amount of mildew infection was unchanged. The severity of mildew infection appeared to be more sensitive to host water content than to host nitrogen content.

KEYWORDS: ATMOSPHERIC CO2, BARLEY, CO2- ENRICHMENT, FERTILIZATION, GRAIN-YIELD, INSECT HERBIVORE, PLANT GROWTH, SEEDLING GROWTH, WINTER-WHEAT

2350

Thompson, G.B., and B.G. Drake. 1994. Insects and fungi on a C-3 sedge and a C-4 grass exposed to elevated atmospheric co2 concentrations in open-top chambers in the field. *Plant, Cell and Environment 17(10):1161-1167.*

The effects of elevated atmospheric CO2 concentration on plant- fungi and plant-insect interactions were studied in an emergent marsh in the Chesapeake Bay. Stands of the C-3 sedge Scirpus olneyi Grey. and the C-4 grass Spartina patens (Ait.) Muhl. have been exposed to elevated atmospheric CO2 concentrations during each growing season since 1987. In August 1991 the severities of fungal infections and insect infestations were quantified. Shoot nitrogen concentration ([N]) and water content (WC) were determined. In elevated concentrations of atmospheric CO2, 32% fewer S. olneyi plants were infested by insects, and there was a 37% reduction in the severity of a pathogenic fungal infection, compared with plants grown in ambient CO2 concentrations. S. olneyi also had reduced [N], which correlated positively with the severities of fungal infections and insect infestations. Conversely, S. patens had increased WC but unchanged [N] in elevated concentrations of atmospheric CO2 and the severity of fungal infection increased. Elevated atmospheric CO2 concentration increased or decreased the severity of fungal infection depending on at least two interacting factors, [N] and WC; but it did not change the number of plants that were infected with fungi. In contrast, the major results for insects were that the number of plants infected with insects decreased, and that the amount of tissue that each insect ate also decreased.

KEYWORDS: BARLEY, CARBON DIOXIDE, GROWTH, NITROGEN-FERTILIZATION, PHOTOSYNTHESIS, POWDERY MILDEW, RESISTANCE, WATER-STRESS, WHEAT, YIELD

2351

Thompson, G.B., and F.I. Woodward. 1994. Some influences of co2 enrichment, nitrogen nutrition and competition on grain-yield and quality in spring wheat and barley. *Journal of Experimental Botany 45(276):937-942.*

Spring wheat and spring barley were grown in elevated atmospheric CO2 in controlled environments. Wheat was grown in monoculture and in competition with three weed species. In monoculture, wheat had 30% more grain yield and 28% less grain nitrogen in elevated compared to ambient atmospheric CO2. In competition, wheat had no significant increase in yield with elevated atmospheric CO2. In competition, grain nitrogen concentration was reduced in response to CO2 with the largest reduction occurring with the smallest competitor and the smallest reduction occurring with the largest competitor. Spring barley was grown in monoculture at three nitrogen fertilizer supplies. In elevated atmospheric CO2 there were significant increases in grain yield and reductions in grain nitrogen concentration at all levels of nitrogen supply. In both species the reductions in grain nitrogen concentration were large enough to affect current bread making processes.

KEYWORDS: ATMOSPHERES, CARBON DIOXIDE, ELEVATED CO2, GENOTYPES, GROWTH, PARTITIONING EFFICIENCY, PLANTS, TRITICUM-AESTIVUM L, WINTER-WHEAT

2352

Thornley, J.H.M. 1998. Dynamic model of leaf photosynthesis with acclimation to light and nitrogen. *Annals of Botany 81(3):421-430.*

A simple model of photosynthesis in a mature C-3 leaf is described, based on a non-rectangular hyperbola: the model allows the high-light asymptote of that equation (P-max) to respond dynamically to light and nitrogen. This causes the leaf light response equation to acclimate continuously to the current conditions of light and N nutrition, which

can vary greatly within a crop canopy, and through a growing season, with important consequences for gross production. Predictions are presented for the dynamics of acclimation, acclimated and non-acclimated photosynthetic rates are compared, and the dependence of leaf properties on light and N availability is explored. There is good correspondence of predictions with experimental results at the leaf level. The model also provides a mechanism for a down regulation of photosynthesis in response to increased carbon dioxide concentrations, whose magnitude will depend on conditions, particularly of nitrogen nutrition. (C) 1998 Annals of Botany Company.

KEYWORDS: ALLOCATION, DAILY CANOPY PHOTOSYNTHESIS, ELEVATED CO2, FERTILIZATION, GRASSLAND, GROWTH, LEAVES, NET PHOTOSYNTHESIS, PLANTS, WATER

2353

Thornley, J.H.M., and M.G.R. Cannell. 1996. Temperate forest responses to carbon dioxide, temperature and nitrogen: A model analysis. *Plant, Cell and Environment 19(12):1331-1348.*

The ITE Edinburgh Forest Model, which describes diurnal and seasonal changes in the pools and fluxes of C, N and water in a fully coupled forest-soil system, was parametrized to simulate a managed conifer plantation in upland Britain, The model was used to examine (i) the transient effects on forest growth of an IS92a scenario of increasing [CO2] and temperature over two future rotations, and (ii) the equilibrium (sustainable) effects of all combinations of increases in [CO2] from 350 to 550 and 750 mu mol mol(-1), mean annual temperature from 7.5 to 8.5 and 9.5 degrees C and annual inputs of 20 or 40 kg N ha(- 1), Changes in underlying processes represented in the model were then used to explain the responses, Eight conclusions were supported by the model for this forest type and climate. (1) Increasing temperatures above 3 degrees C alone may cause forest decline owing to water stress. (2) Elevated [CO2] can protect trees from water stress that they may otherwise suffer in response to increased temperature. (3) In N-limiting conditions, elevated [CO2] can increase allocation to roots with little increase in leaf area, whereas in N-rich conditions elevated [CO2] may not increase allocation to roots and generally increases leaf area. (4) Elevated [CO2] can decrease water use by forests in N-limited conditions and increase water use in N-rich conditions. (5) Elevated [CO2] can increase forest productivity even in N-limiting conditions owing to increased N acquisition and use efficiency. (6) Rising temperatures (along with rising [CO2]) may increase or decrease forest productivity depending on the supply of N and changes in water stress. (7) Gaseous losses of N from the soil can increase or decrease in response to elevated [CO2] and temperature. (8) Projected increases in [CO2] and temperature (IS92a) are likely to increase net ecosystem productivity and hence C sequestration in temperate forests.

KEYWORDS: ATMOSPHERIC CO2 CONCENTRATIONS, CLIMATE CHANGE, ELEVATED CO2, GROWTH-RESPONSE, INCREASING CO2, NORTHERN FINLAND, NUTRIENT-UPTAKE, SCOTS PINE, SHORT- TERM, SOUR ORANGE TREES

2354

Thornley, J.H.M., and M.G.R. Cannell. 1997. Temperate grassland responses to climate change: An analysis using the Hurley pasture model. *Annals of Botany 80(2):205-221.*

The Hurley Pasture Model is process-based and couples the carbon, nitrogen and water cycles in the soil-grass-animal system. It was used to examine the responses of grasslands in southern, lowland and northern, upland climates in Britain. Short-term response to step-wise increases in CO2 concentration (350 to 700 mu mol mol(-1)) and temperature (5 degrees C) were contrasted with long-term equilibrium (the term 'equilibrium' is equivalent to 'steady state' throughout this paper) responses and with responses to gradually increasing [CO2] and temperature. Equilibrium responses to a range of climate variables were also examined. Three conclusions were drawn regarding the interpretation of experiments: (1) initial ecosystem responses to stepwise changes can be different in both magnitude and sign to equilibrium responses, and this can continue for many years; (2) grazing can drastically alter the magnitude and sign of the response of grasslands to climate change, be highly site-specific. It was concluded that experiments should try to lessen uncertainty about processes within models rather than try to predict ecosystem responses directly. Three conclusions were also drawn about the operation of grasslands as carbon sinks: (1) increasing [CO2] alone will produce a carbon sink, as long as it continues to accelerate photosynthesis and increase net primary productivity; (2) by contrast, increasing temperatures alone are likely to produce a carbon source, because soil respiration is accelerated more than net primary productivity, even when assuming the same temperature function for most soil and plant biochemical processes; and (3) the net effect of projected increases in [CO2] and temperature is likely to be a carbon sink of 5-15 g C m(-2) yr(-1) in humid, temperate grasslands for several decades, which is consistent with the magnitude of the hypothesized current global terrestrial carbon sink. (C) 1997 Annals of Botany Company.

KEYWORDS: ATMOSPHERIC CO2, BIOMASS, CARBON-CYCLE, ELEVATED CO2, GROWTH, LOLIUM-PERENNE, NITROGEN-CONTENT, ORGANIC-MATTER DYNAMICS, SOIL, STORAGE

2355

Thron, C., K. Hahn, and C. Lutz. 1997. In situ effects of elevated CO2 on chlorophyll fluorescence and chloroplast pigments of alpine plants. *Acta Oecologica-International Journal of Ecology 18(3):193-200.*

Alpine vegetation responds to elevated CO2 with downward adjustment of photosynthesis. The experiments should show if doubling of ambient CO2 reduces the maximum quantum yield and the chlorophylls thus altering the pigment composition of the thylakoid membranes in typical species of an alpine grassland (Caricetum curvulae). The studies were part of a CO2 enrichment experiment with open-top chambers in the Swiss Central Alps in 2 470 m altitude over a period of four years. The leaves of Carer curvula and Trifolium alpinum were analysed ill situ under ambient (355 mu l/l) or elevated (680 mu l/l) CO2 and at two different nutrient levels. In each vegetation period both species showed a tendency to lower ratios of variable to maximum fluorescence (F-v/F-m) in plants with elevated CO2 treatment compared to the ambient variants. These reductions in F-v/F-m were statistically different only for Carer curvula in 1993 and 1995. CO2 enrichment caused reductions of leaf pigment concentrations of 10-30% especially far Trifolium alpinum whereas Carer curvula was less affected. The lower pigment contents per leaf were probably due to reductions of thylakoid membranes. In most cases, the influences of elevated CO2 or of nutrient treatments on pigment composition and primary photochemistry were very small. This indicates that the downward regulation begins at early stages in the photosynthetic process. Some changes of the photosynthetic apparatus are species-specific and possibly reflect different strategies of protective acclimation processes of alpine vegetation.

KEYWORDS: ALTITUDES, AVOIDANCE, CARBON DIOXIDE, EXPOSURE, FIELD, LEAVES, PHOTOINHIBITION, PHOTOSYNTHESIS, SEASON

2356

Tian, H., C.A.S. Hall, and Y. Qi. 1998. Modeling primary productivity of the terrestrial biosphere in changing environments: Toward a dynamic biosphere model. *Critical Reviews in Plant Sciences 17(5):541-557.*

There is a widespread perception that the atmosphere and the climate are

beginning to change, and that these changes could have profound impacts on the primary productivity of the terrestrial biosphere. The terrestrial biosphere is a dynamic system that interacts with the atmosphere and climate principally through the exchanges of energy, water, and elements. Due to the limitations of equilibrium terrestrial biosphere models, new generation models - dynamic biosphere models, are critically needed for assessing and predicting the primary production and biogeochemical cycles of the terrestrial biosphere in changing global environment. The goal of dynamic biosphere modeling is to model terrestrial ecosystem dynamics induced by natural and anthropogenic disturbances, as well as the interactions of energy, water, and carbon cycles within the terrestrial biosphere and between the terrestrial biosphere and the atmosphere. The critical gaps in developing such a terrestrial biosphere model are not our inability to construct model code but instead the poorly developed links between empiricism and the concepts we used to construct our models, especially a lack of data that would help to make our models mechanistic, an incomplete fundamental knowledge about how complex terrestrial ecosystems work, a poor understanding of how to scale up what we do know and of how to validate such a model. The interaction among data, model structure, parameter sets, and predictive uncertainty will Bead to important progress in the development of dynamic biosphere models.

KEYWORDS: ATMOSPHERIC CO2, CLIMATE CHANGE, EASTERN NORTH-AMERICA, ECOSYSTEM PROCESSES, GLOBAL CARBON-CYCLE, LAND-USE CHANGE, MISSING CO2 SINK, NET PRIMARY PRODUCTION, TRANSIENT-RESPONSE, TROPICAL DEFORESTATION

2357

Ticha, I. 1996. Optimization of photoautotrophic tobacco in vitro culture: Effect of suncaps closures on plantlet growth. *Photosynthetica 32(3):475-479.*

Maintenance of high carbon dioxide concentration during in vitro culture of tobacco plantlets by using suncaps closures (Sigma) and CO2 enrichment in the cultivation chamber increased dramatically the growth of plantlets measured as total dry matter accumulation and total leaf area production. The effect was enhanced with duration of culture. Photomixotrophically grown plantlets with 3 % saccharose in the Murashige-Skoog medium accumulated more dry matter and developed a larger total leaf area than plantlets grown strictly photoautotrophically without saccharose but the effect of better CO2 supply (suncaps) was seven (dry matter) to ten (leaf area) times higher in photoautotrophic plantlets as compared with photomixotrophic ones.

KEYWORDS: ACCLIMATIZATION, AGROBACTERIUM, CO2 CONCENTRATION, DEPENDENCE, GAS-EXCHANGE, INVITRO, PHOTOSYNTHESIS, REGENERANTS, STRAWBERRY PLANTLETS

2358

Tingey, D.T., M.G. Johnson, D.L. Phillips, D.W. Johnson, and J.T. Ball. 1996. Effects of elevated CO2 and nitrogen on the synchrony of shoot and root growth in ponderosa pine. *Tree Physiology 16(11-12):905-914.*

We monitored effects of elevated CO2 and N fertilization on shoot and fine root growth of Pinus ponderosa Dougl. ex P. Laws. and C. Laws. grown in native soil in open-top field- exposure chambers at Placerville, CA, over a 2-year period. The experimental design was a replicated 3 x 3 factorial with the center treatment missing; plants were exposed to ambient (similar to 365 mu mol mol(-1)) air or ambient air plus either 175 or 350 mu mol mol(-1) CO2 in combination with one of three rates of N addition (0, 100 or 200 kg ha(-1) year(-1)). All CO2 by N interactions were nonsignificant. Both the CO2 and N treatments increased plant height, stem diameter and leaf area index (LAI). Elevated CO2 increased fine root area density and the occurrence of mycorrhizae, whereas N fertilization increased coarse root area density but had no effect on fine root area density. Spring flushes of shoot height and diameter growth were initiated concurrently with the increase in new root area density but height and diameter growth reached their maxima before that of fine roots. The temporal patterns of root and shoot growth were not altered by providing additional CO2 or N. Greatest root loss occurred in the summer, immediately following the period of greatest new fine root growth. Elevated N initially reduced the fine root area density/LAI ratio independently of CO2 treatment, indicating that the relationship between fine roots and needles was not changed by CO2 exposure.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, ECOSYSTEMS, ENRICHMENT, FINE ROOTS, MYCORRHIZAL, QUERCUS-ALBA, RESPONSES, SEEDLINGS, SITKA SPRUCE PLANTATION, SOIL N

2359

Tingey, D.T., M.G. Johnson, D.L. Phillips, and M.J. Storm. 1995. Effects of elevated CO2 and nitrogen on ponderosa pine fine roots and associated fungal components. *Journal of Biogeography 22(2-3):281-287.*

The effects of CO2 and nitrogen treatments on ponderosa pine (Pinus ponderosa Dougl. ex P. Laws. & C. Laws.) fine roots and associated fungal structures were monitored for a year (October 1992 to October 1993) using a minirhizotron camera system. The trees were grown in native soil in open-top field-exposure chambers at PlacerviUe, CA and exposed to ambient (similar to 350 mu mol mol(-1)) air or ambient air plus either 175 or 350 mu mol mol(-1) CO2 and three levels of nitrogen addition (0, 100 and 200 kg ha(-1)); however, the 100 kg ha(-1) N treatment at ambient plus 175 mu mol mol(-1) CO2 treatment was omitted from the experimental design. Roots were classified as new, white, brown, decaying or missing and their lengths and diameters measured. The occurrence of mycorrhizae and fungal hyphae was also recorded. The majority (>90%) of roots observed were smaller than 2 mm and the mean diameter decreased during the study. None of the root parameters measured showed a significant response to elevated CO2. The elevated CO2 treatments consistently showed an increase in root area density averaging 50% larger compared to ambient CO2, but this response was not statistically significant due to the high spatial variability of root distribution. Only new root area density showed a significant nitrogen response. The most new roots were initiated between April and June and the highest level of root loss occurred between June and August. The occurrence of mycorrhizae and fungal hyphae increased in response to CO2 treatment but not the nitrogen. Their highest levels of occurrence were during August and October 93.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, ECOSYSTEMS, FORESTS, MYCORRHIZAL, PHOTOSYNTHETIC ACCLIMATION, PRODUCTIVITY, QUERCUS-ALBA, SEEDLINGS, SOIL

2360

Tingey, D.T., B.D. McVeety, R. Waschmann, M.G. Johnson, D.L. Phillips, P.T. Rygiewicz, and D.M. Olszyk. 1996. A versatile sun-lit controlled-environment facility for studying plant and soil processes. *Journal of Environmental Quality 25(3):614-625.*

A new environmental-tracking, sun-lit controlled-environment facility (terracosm) that can control and manipulate climatic and edaphic factors while maintaining natural environmental variability was developed to study the effects of environmental stresses on a model ecosystem (i.e., plant and soil processes). An analysis of terracosm performance data indicates that the terracosms simulated natural seasonal and diurnal changes in atmospheric CO2, air and soil temperatures, vapor pressure

deficit (VPD), and soil moisture. The terracosm performance data indicate that between 92 and 100% of the hourly CO2 concentrations are within +/-50 mu mol mol(-1) of the target concentrations for both ambient and elevated treatments (1 Nov. 1993 through 30 Nov. 1994). Air temperatures are within 2 degrees C of the target temperature between 85 and 100% of the hours for both ambient and elevated temperature treatments. The VPD was approximately the same (0.09 kPa difference between treatments) in the ambient and elevated temperature treatments. Distributed process control was implemented to minimize down- time. Terracosm downtime, periods when terracosm environmental conditions could not be reliably controlled, varied between 2.4 and 2.8% of all hours, and was equally distributed between biological sampling and equipment problems.

KEYWORDS: CO2, ECOSYSTEMS, FIELD, PHOTOSYNTHESIS

2361

Tingey, D.T., D.L. Phillips, D.G. Johnson, D.W. Johnson, and J.A. Weber. 1997. Elevated CO2 increases fine root growth and fine root turnover in Pinus ponderosa. *Plant Physiology 114(3):1358.*

2362

Tingey, D.T., D.L. Phillips, M.G. Johnson, M.J. Storm, and J.T. Ball. 1997. Effects of elevated CO2 and N fertilization on fine root dynamics and fungal growth in seedling Pinus ponderosa. *Environmental and Experimental Botany 37(2-3):73-83.*

The effects of elevated CO2 and N fertilization on fine root growth of Pinus ponderosa Dougl. ex P. Laws. C. Laws., grown in native soil in open-top held-exposure chambers at Placerville, CA, were monitored for a 2-year period using minirhizotrons. The experimental design was a replicated 3 x 3 factorial with a treatment missing; plants were exposed to ambient (approximate to 365 mu mol mol(-1)) air or ambient air plus either 175 or 350 mu mol mol(-1) CO2 and three levels of N addition (0, 100 and 200 kg ha(-1) year(-1)). By the second year, elevated CO2 increased fine root occurrence and root length while N fertilization had no effect. The CO2 x N interactions were not significant. Neither elevated CO2 nor N fertilization altered fine root diameter. Fine root mortality was increased by increasing soil N but was reduced in elevated CO2. Highest fine root mortality occurred during summer and was lowest during winter. Elevated CO2 increased mycorrhizal and fungal occurrence earlier than N fertilization. (C) 1997 Elsevier Science B.V.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, ECOSYSTEMS, ENRICHMENT, LOBLOLLY-PINE, MYCORRHIZAL COLONIZATION, NITROGEN, QUERCUS-ALBA, SOIL RESPIRATION, TEMPERATURE, TURNOVER

2363

Tinker, B., and H. Mooney. 1996. Plant-soil carbon belowground: The effects of elevated CO2 selected papers from an International GCTE Workshop, 20-23 September 1995, Mansfield College, University of Oxford, UK - Introduction. *Plant and Soil 187(2):107.*

2364

Tischler, C.R., H.W. Polley, H.B. Johnson, and H.S. Mayeux. 1998. Environment and seedling age influence mesquite response to epicotyl removal. *Journal of Range Management 51(3):361-365.*

Herbivory by small mammals is a major factor controlling survival of honey mesquite (Prosopis glandulosa Torr. var, glandulosa) seedlings. Clipping below the cotyledons is lethal; removal of the epicotyl may not be lethal but can severely limit seedling growth. Seedlings of other woody species sometimes compensate for epicotyl removal by prolonging the life of cotyledons. Also, projected future increases in atmospheric CO2 concentration could influence survival and growth after epicotyl removal. Objectives of this study were to determine effects of epicotyl removal at various seedling ages, atmospheric CO2 concentrations, and soil fertility, on (1) seedling survival, (2) cotyledonary leaf longevity, and (3) shoot and root growth of young seedlings. Mesquite seedlings were grown at 350, 700, and 1,000 mu L liter(-1) atmospheric CO2 concentration in nutrient poor and nutrient rich soils. All ages of seedlings survived epicotyl removal. Cotyledonary leaf fresh mass and chlorophyll content were higher in plants where epicotyls were clipped. Root and shoot mass of both clipped and unclipped plants generally increased at higher CO2 concentrations when mineral nutrition was adequate, but responded less to CO2 when soil fertility was low. Responses to epicotyl clipping in mesquite seedlings are complex, being strongly influenced by soil fertility, atmospheric CO2 concentration, seedling age at clipping, and interactions between these factors.

KEYWORDS: ENRICHMENT, ESTABLISHMENT, GROWTH, INCREASING CO2, PLANT, PROSOPIS, RATES

2365

Tissue, D.T., K.L. Griffin, and J.T. Ball. 1999. Photosynthetic adjustment in field-grown ponderosa pine trees after six years of exposure to elevated CO2. *Tree Physiology 19(4-5):221-228.*

Photosynthesis of tree seedlings is generally enhanced during short-term exposure to elevated atmospheric CO2, but longer- term photosynthetic responses are often more variable because they are affected by morphological, biochemical and physiological feedback mechanisms that regulate carbon assimilation to meet sink demand. To examine biochemical and morphological factors that might regulate the long-term photosynthetic response of field-grown trees to elevated CO2, we grew ponderosa pine (Pinus ponderosa Dougl. ex Laws.) trees in open-top chambers for six years in native soil at ambient CO2 (35 Pa) and elevated CO2 (70 Pa) at a site near Placerville, CA. Trees were well watered and exposed to natural light and ambient temperature. At the end of the sixth growing season at elevated CO2, net photosynthesis was enhanced 53%, despite reductions in photosynthetic capacity. The positive net photosynthetic response to elevated CO2 reflected greater relative increases in Rubisco sensitivity compared with the decreases resulting from biochemical adjustments. Analyses of net photosynthetic rate versus internal CO2 partial pressure curves indicated that reductions in photosynthetic capacity in response to elevated CO2 were the result of significant reductions in maximum photosynthetic rate (20%), Rubisco carboxylation capacity (36%), and electron transport capacity (21%). Decreased photosynthetic capacity was accompanied by reductions in various photosynthetic components, including total chlorophyll (24%), Rubisco protein content (38%), and mass-based leaf nitrogen concentration (14%). Net photosynthesis was unaffected by morphological adjustments because there was no change in leaf mass per unit area at elevated CO2. An apparent positive response of photosynthetic adjustment in the elevated CO2 treatment was the redistribution of N within the photosynthetic system to balance Rubisco carboxylation and electron transport capacities. We conclude that trees, without apparent limitations to root growth, may exhibit photosynthetic adjustment responses in the field after long-term exposure to elevated CO2.

KEYWORDS: ACCLIMATION, CARBON DIOXIDE, ENRICHMENT, FOLIAR GAS-EXCHANGE, LEAF, LONG-TERM, PHASEOLUS-VULGARIS, PLANTS, RISING ATMOSPHERIC CO2, STOMATAL CONDUCTANCE

2366

Tissue, D.T., K.L. Griffin, R.B. Thomas, and B.R. Strain. 1995. Effects of low and elevated co2 on C-3 and C-4 annuals .2. Photosynthesis and leaf biochemistry. *Oecologia 101(1):21-28.*

Abutilon theophrasti (C-3) and Amaranthus retroflexus (C-4), were grown from seed at four partial pressures of CO2: 15 Pa (below Pleistocene minimum), 27 Pa (pre-industrial), 35 Pa (current), and 70 Pa (future) in the Duke Phytotron under high light, high nutrient, and well-watered conditions to evaluate their photosynthetic response to historic and future levels of CO2. Net photosynthesis at growth CO2 partial pressures increased with increasing CO2, for C-3 plants, but not C-4 plants. Net photosynthesis of Abutilon at 15 Pa CO2 was 70% less than that of plants grown at 35 Pa CO2, due to greater stomatal and biochemical limitations at 15 Pa CO2. Relative stomatal limitation (RSL) of Abutilon at 15 Pa CO2 was nearly 3 times greater than at 35 Pa CO2. A photosynthesis model was used to estimate ribulose-1,5-bisphosphate carboxylase (rubisco) activity (Vc(max)), electron transport mediated RuBP regeneration capacity (J(max)), and phosphate regeneration capacity (PiRC) in Abutilon from net photosynthesis versus intercellular CO2 (A-C-i) curves. All three component processes decreased by approximately 25% in Abutilon grown at 15 Pa compared with 35 Pa CO2. Abutilon grown at 15 Pa CO2 had significant reductions in total rubisco activity (25%), rubisco content (30%), activation state (29%), chlorophyll content (39%), N content (32%), and starch content (68%) compared with plants grown at 35 Pa CO2. Greater allocation to rubisco relative to light reaction components and concomitant decreases in J(max) and PiRC suggest co-regulation of biochemical processes occurred in Abutilon grown at 15 Pa CO2. There were no significant differences in photosynthesis or leaf properties in Abutilon grown at 27 Pa CO2 compared with 35 Pa CO2, suggesting that the rise in CO2 since the beginning of the industrial age has had little effect on the photosynthetic performance of Abutilon. For Amaranthus, limitations of photosynthesis were balanced between stomatal and biochemical factors such that net photosynthesis was similar in all CO2 treatments. Differences in photosynthetic response to growth over a wide range of CO2 partial pressures suggest chang es in the relative performance of C-3 and C-4 annuals as atmospheric CO2 has fluctuated over geologic time.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, ELECTRON-TRANSPORT, ENRICHMENT, GROWTH, LEAVES, LIGHT-INTENSITY, PHASEOLUS-VULGARIS L, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE, STOMATAL CONDUCTANCE

2367

Tissue, D.T., J.P. Megonigal, and R.B. Thomas. 1997. Nitrogenase activity and N-2 fixation are stimulated by elevated CO2 in a tropical N-2-fixing tree. *Oecologia 109(1):28-33.*

Seeds of Gliricidia sepium, a fast-growing woody legume native to seasonal tropical forests of Central America, were inoculated with N-2-fixing Rhizobium bacteria and grown in environmentally controlled glasshouses for 67-71 days under ambient CO2 (35 Pa) and elevated CO2 (70 Pa) conditions. Seedlings were watered with an N-free, but otherwise complete, nutrient solution such that bacterial N-2 fixation was the only source of N available to the plant. The primary objective of our study was to quantify the effect of CO2 enrichment on the kinetics of photosynthate transport to nodules and determine its subsequent effect on N-2 fixation. Photosynthetic rates and carbon storage in leaves were higher in elevated CO2 plants indicating that more carbon was available for transport to nodules. A (CO2)-C-14 pulse-chase experiment demonstrated that photosynthetically fixed carbon was supplied by leaves to nodules at a faster rate when plants were grown in elevated CO2. Greater rates of carbon supply to nodules did not affect nodule mass per plant, but did increase specific nitrogenase activity (SNA) and total nitrogenase activity (TNA) resulting in greater N-2 fixation. In fact, a 23% increase in the rate of carbon supplied to nodules coincided with a 23% increase in SNA for plants grown in elevated CO2, suggesting a direct correlation between carbon supply and nitrogenase activity. The improvement in plant N status produced much larger plants when grown in elevated CO2. These results suggest that Gliricidia, and possibly other N-2-fixing trees, may show an early and positive growth response to elevated CO2, even in severely N- deficient soils, due to increased nitrogenase activity.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, DEFOLIATION, ECOSYSTEMS, ENRICHMENT, GROWTH, NODULATION, PISUM-SATIVUM, SEEDLINGS, WHITE CLOVER, WOODY-PLANTS

2368

Tissue, D.T., R.B. Thomas, and B.R. Strain. 1993. Long-term effects of elevated co2 and nutrients on photosynthesis and rubisco in loblolly-pine seedlings. *Plant, Cell and Environment 16(7):859-865.*

The effects of long-term CO2 enhancement and varying nutrient availability on photosynthesis and ribulose-1,5-bisphosphate carboxylase/oxygenase (rubisco) were studied on loblolly pine (Pinus taeda L.) seedlings grown in two atmospheric CO2 partial pressures (35 and 65 Pa) and three nutrient treatments (low N, low P, and high N and P). Measurements taken in late autumn (November) after 2 years Of CO2 enrichment and nutrient addition showed that photosynthetic rates were higher for plants grown at elevated CO2 only when they received supplemental N. Total rubisco activity and rubisco content decreased at elevated CO2, but there was an increase in activation state. At elevated CO2, proportionately less N was found in rubisco and more N was found in the light reaction components. These results demonstrate acclimation of photosynthetic processes to elevated CO2 through reallocation of N. Loblolly pine grown in nutrient conditions similar to native soils (low N availability) had lower needle N and chlorophyll content, lower total rubisco activity and content, and lower photosynthetic rates than plants grown at high N and P. This suggests that the magnitude of the photosynthetic response to a future, high-CO2 environment will be dependent on soil fertility in the system.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CARBON-DIOXIDE, C-3, CHLOROPHYLL, ELECTRON-TRANSPORT, LEAVES, NITROGEN-USE EFFICIENCY, PHASEOLUS-VULGARIS L, PLANTS, RIBULOSE BISPHOSPHATE CARBOXYLASE

2369

Tissue, D.T., R.B. Thomas, and B.R. Strain. 1996. Growth and photosynthesis of loblolly pine (Pinus taeda) after exposure to elevated CO2 for 19 months in the field. *Tree Physiology 16(1-2):49-59.*

To detect seasonal and long-term differences in growth and photosynthesis of loblolly pine (Pinus taeda L.) exposed to elevated CO2 under ambient conditions of precipitation, light, temperature and nutrient availability, seedlings were planted in soil representative of an early, abandoned agricultural field and maintained for 19 months in the field either in open- top chambers providing one of three atmospheric CO2 partial pressures (ambient, ambient +15 Pa, and ambient +30 Pa) or in unchambered control plots. An early and positive response to elevated CO2 substantially increased total plant biomass. Peak differences in relative biomass enhancement occurred after 11 months of CO2 treatment when biomass of plants grown at +15 and +30 Pa CO2 was 111 and 233% greater, respectively, than that of plants grown at ambient CO2. After 19 months, there was no significant difference in biomass between +15 Pa CO2-treated plants and ambient CO2-treated plants, whereas biomass of +30 Pa CO2-treated plants was 111% greater than that of ambient CO2-treated plants. Enhanced rates of leaf-level photosynthesis were maintained in plants in the elevated CO2 treatments throughout the 19-month exposure period despite reductions in both

leafN concentration and ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) activity during the first 11 months of CO2 exposure. Reductions in Rubisco activity indicated photosynthetic adjustment to elevated CO2, but Rubisco-mediated control of photosynthesis was small. Seasonal shifts in sink strength affected photosynthetic rates, greatly magnifying the positive effects of elevated CO2 on photosynthesis during periods of rapid plant growth. Greater carbon assimilation by the whole plant accelerated plant development and thereby stimulated new sinks for carbon through increased plant biomass, secondary branching and new leaf production. We conclude that elevated CO2 will enhance photosynthesis and biomass accumulation in loblolly pine seedlings under high nutrient conditions; however, reductions over time in the relative biomass response of plants to elevated CO2 complicate predictions of the eventual magnitude of carbon storage in this species under future CO2 conditions.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, ENRICHMENT, FORESTS, GAS-EXCHANGE, LIQUIDAMBAR- STYRACIFLUA, NITROGEN, RESPONSES, SEEDLINGS, SOUR ORANGE TREES, UNITED-STATES

2370

Tissue, D.T., R.B. Thomas, and B.R. Strain. 1997. Atmospheric CO2 enrichment increases growth and photosynthesis of Pinus taeda: a 4 year experiment in the field. *Plant, Cell and Environment 20(9):1123-1134.*

Forest trees are major components of the terrestrial biome and their response to rising atmospheric CO2 plays a prominent role in the global carbon cycle. In this study, loblolly pine seedlings were planted in the field in recently disturbed soil of high fertility, and CO2 partial pressures were maintained at ambient CO2 (Amb) and elevated CO2 (Amb + 30 Pa) for 4 years. The objective of the study was to measure seasonal and long- term responses in growth and photosynthesis of loblolly pine exposed to elevated CO2 under ambient field conditions of precipitation, light, temperature and nutrient availability. Loblolly pine trees grown in elevated CO2 produced 90% more biomass after four growing seasons than did trees grown in ambient CO2. This large increase in final biomass was primarily due to a 217% increase in leaf area in the first growing season which resulted in much higher relative growth rates for trees grown in elevated CO2. Although there was not a sustained effect of elevated CO2 on relative growth rate after the first growing season, absolute production of biomass continued to increase each year in trees grown in elevated CO2 as a consequence of the compound interest effect of increased leaf area on the production of more new leaf area and more biomass. Allometric analyses of biomass allocation patterns demonstrated size-dependent shifts in allocation, but no direct effects of elevated CO2 on partitioning of biomass. Leaf photosynthetic rates were always higher in trees grown in elevated CO2, but these differences were greater in the summer (60-130% increase) than in the winter (14-44% increase), reflecting strong seasonal effects of temperature on photosynthesis. Our results suggest that seasonal variation in the relative photosynthetic response to elevated CO2 will occur in natural ecosystems, but total non-structural carbohydrate (TNC) levels in leaves indicate that this variation may not always be related to sink activity. Despite indications of canopy-level adjustments in carbon assimilation, enhanced levels of leaf photosynthesis coupled with increased total leaf area indicate that net carbon assimilation for the whole tree was greater for trees grown under elevated CO2 compared with ambient CO2. If the large growth enhancement observed in loblolly pine were maintained after canopy closure, then these trees could be a large sink for fossil carbon emitted to the atmosphere and produce a negative feedback on atmospheric CO2.

KEYWORDS: BIOMASS ALLOCATION, COMPENSATORY RESPONSES, ELEVATED CARBON-DIOXIDE, FOLIAR GAS-EXCHANGE, LOBLOLLY-PINE, PLANT-RESPONSES, PONDEROSA PINE, SOIL FERTILITY, SOUR ORANGE TREES, WATER-STRESS

2371

Titus, J.E. 1992. Submersed macrophyte growth at low ph .2. Co2 X sediment interactions. *Oecologia 92(3):391-398.*

The submersed macrophyte Vallisneria americana was grown for seven weeks in a greenhouse to test for differences in the ability of three different sediments to support growth stimulation in response to CO2 enrichment at low pH. Plants accumulated 21- to 24-fold greater biomass at 10 x ambient CO2 concentrations than at ambient CO2 on all sediments. At both CO2 levels, plants grown on sediment from an acidified lake accumulated ca. 81%, and those grown on oligotrophic lake sediment ca. 47% as much biomass as plants grown on alkaline lake sediment. Despite striking CO2 and sediment effects on biomass accumulation, there was no significant interaction (using log-transformed data) between CO2 and sediment effects, indicating that all sediments allowed similar proportionate growth responses to CO2 enrichment. Plants grown on the less fertile sediments showed greater relative allocation to horizontal versus vertical growth by producing more rosette- bearing stolons in relation to plant height (leaf length) than plants grown on relatively fertile, alkaline lake sediment. Tissue analysis suggested that sediment effects on Vallisneria growth could be attributed neither to mineral nutrient (nitrogen and phosphorus) limitation nor to aluminum toxicity in these low pH treatments. In any case, CO2 availability can be an important regulator of submersed macrophyte growth at low pH on a variety of sediment types, including those from oligotrophic and acidic lakes.

KEYWORDS: AQUATIC MACROPHYTES, ATMOSPHERIC CO2, ENRICHMENT, LAKE ACIDIFICATION, NATURAL SEDIMENTS, NITROGEN, RESPONSES, TISSUE CHEMISTRY, VALLISNERIA-AMERICANA, WATER

2372

Titus, J.E., and J.H. Andorfer. 1996. Effects of CO2 enrichment on mineral accumulation and nitrogen relations in a submersed macrophyte. *Freshwater Biology 36(3):661-671.*

1. Six- to eight-week greenhouse experiments with independent control of pH and dissolved CO2 evaluated the potential for CO2 enrichment to stimulate the accumulation of Al, Fe, P and N in shoots of Vallisneria americana, particularly at pH 5. These minerals were provided only as they occurred in natural lake sediments. 2. The effect of CO2 enrichment at pH 5 v pH 7.3 on growth and tissue N concentration was also determined. 3. CO2 enrichment at pH 5 effected 5.5- and 7-fold increases in total shoot accumulation of Al and Fe, respectively. In a two-way factorial experiment, CO2 enrichment yielded 6- to 11-fold greater total shoot P accumulation in plants grown on less and more fertile sediments, respectively. 4. In a three-way factorial experiment, CO2 enrichment stimulated Vallisneria growth, especially at pH 5, and resulted in a 31-58% reduction in tissue [N] for different pH x sediment combinations. These are greater reductions than previously reported. It also increased total shoot N accumulation up to 6-fold, and there were significant interactions with pH and sediment source: the CO2 enrichment effect on shoot N accumulation was greater at pH 5 than at pH 7.3, and it was greater with the more fertile sediment at pH 5. 5. Water chemistry (pH and/or [CO2]) and sediment fertility thus both indirectly influenced the accumulation of sediment-derived minerals in macrophyte shoots within the water column.

KEYWORDS: AQUATIC MACROPHYTES, DISSOLVED INORGANIC CARBON, FRESH-WATER MACROPHYTES, INSECT HERBIVORE, MYRIOPHYLLUM- SPICATUM, NATURAL SEDIMENTS, SEDIMENT INTERACTIONS, SOIL EXTRACTS, TISSUE CHEMISTRY, VALLISNERIA-AMERICANA

2373

Titus, J.E., R.S. Feldman, and D. Grise. 1990. Submersed macrophyte growth at low ph .1. CO2 enrichment effects with fertile sediment. *Oecologia 84(3):307-313.*

2374

Tjoelker, M.G., J. Oleksyn, and P.B. Reich. 1998. Seedlings of five boreal tree species differ in acclimation of net photosynthesis to elevated CO2 and temperature. *Tree Physiology 18(11):715-726.*

Biochemical models of photosynthesis suggest that rising temperatures will increase rates of net carbon dioxide assimilation and enhance plant responses to increasing atmospheric concentrations of CO2. We tested this hypothesis by evaluating acclimation and ontogenetic drift in net photosynthesis in seedlings of five boreal tree species grown at 370 and 580 mu mol mol(-1) CO2 in combination with day/night temperatures of 18/12, 21/15, 24/18, 27/21, and 30/24 degrees C. Leaf-area-based rates of net photosynthesis increased between 13 and 36% among species in plants grown and measured in elevated CO2 compared to ambient CO2. These CO2-induced increases in net photosynthesis were greater for slower-growing Picea mariana (Mill.) B.S.P., Pinus banksiana Lamb., and Larix laricina (Du Roi) K. Koch than for faster-growing Populus tremuloides Michx. and Betula papyrifera Marsh., paralleling longer-term growth differences between CO2 treatments. Measures at common CO2 concentrations revealed that net photosynthesis was down-regulated in plants grown at elevated CO2. In situ leaf gas exchange rates varied minimally across temperature treatments and, contrary to predictions, increasing growth temperatures did not enhance the response of net photosynthesis to elevated CO2 in four of the five species. Overall, the species exhibited declines in specific leaf area and leaf nitrogen concentration, and increases in total nonstructural carbohydrates in response to CO2 enrichment. Consequently, the elevated CO2 treatment enhanced rates of net photosynthesis much more when expressed on a leaf area basis (25 %) than when expressed on a leaf mass basis (10%). In all species, rates of leaf net CO2 exchange exhibited modest declines with increasing plant size through ontogeny. Among the conifers, enhancements of photosynthetic rates in elevated CO2 were sustained through time across a wide range of plant sizes. In contrast, for Populus tremuloides and B. papyrifera, mass-based photosynthetic rates did not differ between CO2 treatments. Overall, net photosynthetic rates were highly correlated with relative growth rate as it varied among species and treatment combinations through time. We conclude that interspecific variation may be a more important determinant of photosynthetic response to CO2 than temperature.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, ENRICHMENT, GROWTH-RESPONSE, LEAF, NITROGEN-USE, PLANT-TISSUE, PRODUCTIVITY, SOURCE-SINK RELATIONS, STARCH

2375

Tjoelker, M.G., J. Oleksyn, and P.B. Reich. 1998. Temperature and ontogeny mediate growth response to elevated CO2 in seedlings of five boreal tree species. *New Phytologist 140(2):197-210.*

We tested the extent to which growth responses to elevated carbon dioxide (CO2) are temperature-dependent and change through early seedling ontogeny among boreal tree species of contrasting relative growth rates (RGR). Populus tremuloides Michx, Betula papyrifera Marsh, Larix laricina (Du Roi) K. Koch, Pinus banksiana Lamb., and Picea mariana (Mill.) B.S.P. were grown from seeds for 3 months in controlled-environment chambers at two CO2 concentrations (370 and 580 mu mol mol-L) and five temperature regimes of 18/12, 21/15, 24/18, 27/21 and 30/24 degrees C (light/dark). Growth increases in response to CO2 enrichment were minimal at the lowest temperature and maximal at 21/15 OC for the three conifers and at 24/18 degrees C or higher for the two broadleaved species, corresponding with differences in optimal temperatures for growth. In both CO2 treatments, RGR among species and temperatures correlated positively with leaf area ratio (LAR) (r greater than or equal to 0.90, P < 0.0001). However, at a given LAR, RGR was higher in elevated CO2, owing to enhanced whole-plant net assimilation rate. On average in all species and temperatures at a common plant mass, CO2 enrichment increased RGR (9 %) through higher whole-plant net assimilation rate (22 %), despite declines in LAR in high CO2 (11 %). Reductions in LAR are thus an important feedback mechanism reducing positive plant growth responses to CO2. Proportional allocation of dry mass to roots did not vary between CO2 treatments. Early in the experiment, proportional increases in plant dry mass in elevated CO2 were larger in faster-growing Populus tremuloides and B. papyrifera than in the slower-growing conifers. However, growth increases in response to CO2 enrichment fell with time for broadleaved species and increased for the conifers. With increasing plant size over time, compensatory adjustments to CO2 enrichment in the factors that determine RGR, such as LAR, were much larger in broadleaves than in conifers. Thus, the hypothesis that faster-growing species are more responsive to elevated CO2 was not supported, given contrasting patterns of growth response to CO2 with increasing plant size and age.

KEYWORDS: ATMOSPHERIC CO2, BIOMASS ALLOCATION, CARBON DIOXIDE, COMPENSATORY RESPONSES, GAS-EXCHANGE, PHOTOSYNTHETIC ACCLIMATION, PLANTS, PONDEROSA PINE, RESPIRATION, SOURCE-SINK RELATIONS

2376

Tjoelker, M.G., J. Oleksyn, and P.B. Reich. 1999. Acclimation of respiration to temperature and CO2 in seedlings of boreal tree species in relation to plant size and relative growth rate. *Global Change Biology 5(6):679-691.*

The role of acclimation of dark respiration to temperature and CO2 concentration and its relationship to growth are critical in determining plant response to predicted global change. We explored temperature acclimation of respiration in seedlings of tree species of the North American boreal forest. Populus tremuloides, Betula papyrifera, Larix laricina, Pinus banksiana, and Picea mariana plants were grown from seed in controlled-environments at current and elevated concentrations of CO2 (370 and 580 mu mol mol(-1)) in combination with three temperature treatments of 18/12, 24/18, and 30/24 degrees C (light/dark period). Specific respiration rates of roots and shoots acclimated to temperature, damping increases in rates across growth-temperature environments compared to short-term temperature responses. Compared at a standard temperature, root and shoot respiration rates were, on average, 40% lower in plants grown at the highest compared to lowest growth temperature. Broad-leaved species had a lower degree of temperature acclimation of respiration than did the conifers. Among species and treatment combinations, rates of respiration were linearly related to size and relative growth rate, and relationships were comparable among growth environments. Specific respiration rates and whole-plant respiratory CO2 efflux as a proportion of daily net CO2 uptake increased at higher growth temperatures, but were minimally affected by CO2 concentration. Whole-plant specific respiration rates were two to three times higher in broad-leaved than coniferous species. However, compared to faster-growing broad-leaved species, slower-growing conifers lost a larger proportion of net daily CO2 uptake as respiratory CO2 efflux, especially in roots. Interspecific variation in acclimation responses of dark respiration to temperature is more important than acclimation of respiration to CO2 enrichment in modifying tree seedling growth responses to projected increases in CO2 concentration and temperature.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CONSTRUCTION, ELEVATED CO2, ENRICHMENT, LEAF DARK RESPIRATION,

LEAVES, MAINTENANCE RESPIRATION, NITROGEN, RESPONSES, ROOT RESPIRATION

2377

Tjoelker, M.G., P.B. Reich, and J. Oleksyn. 1999. Changes in leaf nitrogen and carbohydrates underlie temperature and CO2 acclimation of dark respiration in five boreal tree species. *Plant, Cell and Environment 22(7):767-778.*

We tested the hypothesis that acclimation of foliar dark respiration to CO2 concentration and temperature is associated with adjustments in leaf structure and chemistry. Populus tremuloides Michx, Betula papyrifera Marsh, Larix laricina (Du Roi) K, Koch, Pinus banksiana Lamb., and Picea mariana (Mill,) B.S.P. were grown from seed in combined CO2 (370 or 580 mu mol mol(-1)) and temperature treatments (18/12, 24/18, or 30/24 degrees C), Temperature and CO2 effects were predominately independent. Specific respiration rates partially acclimated to warmer thermal environments through downward adjustment in the intercept, but not Q(10) of the temperature-response functions. Temperature acclimation of respiration was larger for conifers than broad-leaved species and was associated with pronounced reductions in leaf nitrogen concentrations in conifers at higher growth temperatures. Shortterm increases in CO2 concentration did not inhibit respiration. Growth in the elevated CO2 concentration reduced leaf nitrogen and increased non-structural carbohydrate concentrations. However, for a given nitrogen concentration, respiration was higher in leaves grown in the elevated CO2 concentration, as rates increased with increasing carbohydrates, Across species and treatments, respiration rates were a function of both leaf nitrogen and carbohydrate concentrations (R-2 = 0.71, P < 0.0001). Longterm acclimation of foliar dark respiration to temperature and CO2 concentration is largely associated with changes in nitrogen and carbohydrate concentrations.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, ELEVATED CO2, ENRICHMENT, GAS-EXCHANGE, GROWTH TEMPERATURE, LEAVES, MAINTENANCE RESPIRATION, PHOTOSYNTHESIS, PLANT RESPIRATION, RESPONSES

2378

Tognetti, R., A. Giovannelli, A. Longobucco, F. Miglietta, and A. Raschi. 1996. Water relations of oak species growing in the natural CO2 spring of Rapolano (central Italy). *Annales Des Sciences Forestieres 53(2-3):475-485.*

The effect of elevated atmospheric carbon dioxide on water relations was examined on downy oak (Quercus pubescens) and helm oak (Q ilex) trees. The study was conducted on trees growing in a naturally enriched CO2 spring. Sap velocity and sap flow were measured by the heat pulse technique. On the same trees, daily courses of xylem water potential, leaf conductance and transpiration were monitored. Plant water relations were evaluated by pressure-volume analysis method on shoots; on the same branches, relative conductivity of xylem was measured. Both species exhibited increased osmotic potential and decreased symplasmic fraction of water in trees adapted to increased CO2. Downy oak showed lower stomatal conductance under elevated CO2, but helm oak did not. Both species displayed higher sap flow in control trees. In both species, increased carbon dioxide did not influence xylem embolism formation.

KEYWORDS: DROUGHT, EFFICIENCY, ELEVATED CO2, FORESTS, PRESSURE, RESPONSES, TEMPERATE

2379

Tognetti, R., and J.D. Johnson. 1999. The effect of elevated atmospheric CO2 concentration and nutrient supply on gas exchange, carbohydrates and foliar phenolic concentration in live oak (Quercus virginiana Mill.) seedlings. *Annals of Forest Science 56(5):379-389.*

We determined the direct effects of atmospheric CO2 concentration ([CO2]) on leaf gas exchange, phenolic and carbohydrate allocation in live oak seedlings (Quercus virginiana Mill.) grown at present (370 mu mol.mol(-1)) or elevated (520 mu mol.mol(-1)) [CO2] for 6 months in open-top chambers. Two soil nitrogen (N) treatments (20 and 90 mu mol.mol(-1) total N, low N and high N treatments, respectively) were imposed by watering the plants every 5 d with modified water soluble fertilizer. Enhanced rates of leaf-level photosynthesis were maintained in plants subjected to elevated [CO2] over the 6-month treatment period in both N treatments. A combination of increased rates of photosynthesis and decreased stomatal conductance was responsible for nearly doubling water use efficiency under elevated [CO2]. The sustained increase in photosynthetic rate was accompanied by decreased dark respiration in elevated [CO2]. Elevated [CO2] led to increased growth rates; while total non-structural carbohydrate (sugars and starch) concentrations were not significantly Affected by elevated [CO2] treatment. The concentration of phenolic compounds increased significantly under elevated [CO2]. ((C) Inra/Elsevier, Paris.).

KEYWORDS: BETULA-PENDULA ROTH, CARBON-DIOXIDE ENRICHMENT, CO2-ENRICHED ATMOSPHERES, GROWTH DYNAMICS, MINERAL NUTRITION, PHOTOSYNTHETIC ACCLIMATION, ROBUR PLANTS, STOMATAL CONDUCTANCE, TREE SEEDLINGS, WATER-USE EFFICIENCY

2380

Tognetti, R., and J.D. Johnson. 1999. Responses of growth, nitrogen and carbon partitioning to elevated atmospheric CO2 concentration in live oak (Quercus virginiana Mill.) seedlings in relation to nutrient supply. *Annals of Forest Science 56(2):91-105.*

Live oak (Quercus virginiana Mill.) seedlings were exposed at two concentrations of atmospheric carbon dioxide ([CO2], 370 or 520 mu mol.mol(-1)) in combination with two soil nitrogen (N) treatments (20 and 90 mu mol.mol(-1) total N) in open-top chambers for 6 months. Seedlings were harvested at 5-7 weeks interval. CO2 treatment had a positive effect on seedling growth. Differences in biomass between elevated and ambient CO2-treated plants increased over the experimental period. Soil N availability did not significantly affect growth. Nevertheless, growth in elevated [CO2] in combination with high N levels led to a consistently higher accumulation of total biomass by the end of the experiment (30-40 %). Biomass allocation between plant parts was similar for seedlings in all treatments, but was significantly different between harvests. The N regimes did not result in different relative growth rate (RGR) and net assimilation rate (NAR), while CO2 treatment had an overall significant effect. Across all [CO2] and N levels, there was a positive relationship between plant mass and subsequent RGR, and this relationship did not differ between treatments. Overall, specific leaf area (SLA) dl:creased in CO2-enriched air. Fine root-foliage mass ratio was increased by elevated [CO2] and decreased by high N. High CO2- and high N- treated plants had the greatest height and basal stem diameter. The allometric relationships between shoot and root dry weight and between height and basal stem diameter were not significantly affected by elevated [CO2]. Leaf N concentrations were reduced by low soil N. Plant N concentrations decreased with time. Elevated [CO2] increased the C/N ratio of all plant compartments, as a result of decreasing N concentrations. High CO2-grown plants reduced N concentrations relative to ambient CO2-grown plants when compared at a common time, but similar when compared at a common size. ((C) Inra/Elsevier, Paris.).

KEYWORDS: ALLOCATION, BETULA-PENDULA ROTH, DIOXIDE, ENRICHMENT, EXPOSURE, LOBLOLLY-PINE, MINERAL NUTRITION, PINUS-TAEDA, PLANT-RESPONSES, SOURCE-SINK RELATIONS

2381

Tognetti, R., and J.D. Johnson. 1999. Responses to elevated atmospheric CO2 concentration and nitrogen supply of Quercus ilex L-seedlings from a coppice stand growing at a natural CO2 spring. *Annals of Forest Science 56(7):549-561.*

Quercus ilex acorns were collected from a population of trees with a lifetime exposure to elevated atmospheric CO2 concentration (CO2), and after germination seedlings were exposed at two [CO2] (370 or 520 mu mol mol(-1)) in combination with two soil N treatments (20 and 90 mu mol mol(-1) total N) in open-tap chambers for 6 months. Increasing [CO2] stimulated photosynthesis and leaf dark respiration regardless of N treatment. The increase in photosynthesis and leaf dark respiration was associated with a moderate reduction in stomatal conductance, resulting in enhanced instantaneous transpiration efficiency in leaves of seedlings in CO2-enriched air. Elevated [CO2] increased biomass production only in the high-N treatment. Fine root/foliage mass ratio decreased with high-N treatment and increased with CO2 enrichment. There was evidence of a preferential shift of biomass to below-ground tissue at a low level of nutrient addition. Specific leaf area (SLA) and leaf area ratio (LAR) decreased significantly in leaves of seedlings grown in elevated [CO2] irrespective of N treatment. Leaf N concentration decreased significantly in elevated [CO2] irrespective of N treatment. As a result of patterns of N and carbon concentrations, C/N ratio generally increased with elevated [CO2] treatment and decreased with high nutrient supply. Afternoon starch concentrations in leaves did not increase significantly with increasing [CO2], as was the case for morning starch concentrations at low-N supply. Starch concentrations in leaves, stem and roots increased with elevated [CO2] and decreased with nutrient addition. The concentration of sugars was not significantly affected by either CO2 or N treatments. Total foliar phenolic concentrations decreased in seedlings grown in elevated [CO2] irrespective of N treatment, while nutrient supply had less of an effect. We conclude that available soil N will be a major controlling resource for the establishment and growth of Q. ilex in rising [CO2] conditions. (C) 1999 Editions scientifiques et medicales Elsevier SAS.

KEYWORDS: CARBON NUTRIENT BALANCE, DIOXIDE ENRICHMENT, FOLIAR GAS-EXCHANGE, GROWTH, LOBLOLLY-PINE, PLANT-RESPONSES, PONDEROSA PINE, RISING CO2, SOIL NUTRIENT, TREE SEEDLINGS

2382

Tognetti, R., J.D. Johnson, M. Michelozzi, and A. Raschi. 1998. Response of foliar metabolism in mature trees of Quercus pubescens and Quercus ilex to long-term elevated CO2. *Environmental and Experimental Botany 39(3):233-245.*

Long-term effects on and adaptations of the carbon physiology of long-lived trees exposed to increasing atmospheric levels of CO2 are unknown. We compared two indigenous Quercus species, Q. ilex and Q. pubescens, growing in a natural CO2 spring located in central Italy and at a nearby control site. In May, 1995 photosynthetic rate at least doubled when measured with supplemental CO2 in both species and sites. Dark respiration was much higher at the CO2 spring site in both species. Foliar sugar and starch concentrations in Q. ilex exhibited significant site and diurnal differences (May and September). In July, 1995 there was little difference in the water potential values of the measured trees at the different sites over the diurnal period. Photosynthetic rate was higher for both species in the CO2 spring, particularly in the early morning and late afternoon. Mid-day stomatal closure reduced photosynthesis to similar levels. In the morning leaf conductance and transpiration were generally lower in the CO2 spring trees, contributing to higher instantaneous water use efficiency for both species. Isoprene emission rates were higher in Q. pubescens trees growing in the CO2 spring. The maximum difference between control and CO2 spring trees occurred in late afternoon. In contrast, Q. ilex exhibited isoprene emission near background level. Foliage and branch carbon and nitrogen status showed increased concentrations of starch and tannins in Q. ilex and of soluble sugars in Q. pubescens in the elevated CO2 environment, while nitrogen concentration decreased in both species. Wood gravity increased 6 and 3% in Q. ilex and Q. pubescens, respectively, growing in the CO2 spring. Q. ilex exhibited afternoon recovery of water potential compared to Q. pubescens which had better night-time recovery. Q. ilex and e. pubescens exposed to elevated CO2 for prolonged periods exhibit different mechanisms for dealing with additional reduced carbon and do maintain an altered carbon physiology, even in midst of the region's characteristic summer drought. (C) 1998 Elsevier Science B.V. All rights reserved.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, ENRICHMENT, GAS-EXCHANGE, ISOPRENE EMISSION, LIQUIDAMBAR-STYRACIFLUA, LIVE OAK, LOBLOLLY-PINE SEEDLINGS, PHOTOSYNTHESIS, TAEDA SEEDLINGS, TEMPERATURE

2383

Tognetti, R., A. Longobucco, F. Miglietta, and A. Raschi. 1998. Transpiration and stomatal behaviour of Quercus ilex plants during the summer in a Mediterranean carbon dioxide spring. *Plant, Cell and Environment 21(6):613-622.*

Variations in the water relations and stomatal response of Quercus ilex were analysed under field conditions by comparing trees at two locations in a Mediterranean environment during two consecutive summers (1993 and 1994), We used the heat-pulse velocity technique to estimate transpirational water use of trees during a 5 month period from June to November 1994, At the end of sap flow measurements, the trees were harvested, and the foliage and sapwood area measured, A distinct environmental gradient exists between the two sites with higher atmospheric CO2 concentrations in the proximity of a natural CO, spring. Trees at the spring site have been growing for generations in elevated atmospheric CO2 concentrations. At both sites, maximum leaf conductance was related to predawn shoot water potential. The effects of water deficits on water relations and whole- plant transpiration during the summer drought were severe. Leaf conductance and water potential recovered after major rainfall in September to predrought values. Sap flow leaf conductance and predawn water potential decreased in parallel with increases in hydraulic resistance, reaching a minimum in mid-summer. These relationships are in agreement with the hypothesis of the stomatal control of transpiration to prevent desiccation damage but also to avoid 'runaway embolism'. Trees at the CO2 spring underwent less reduction in hydraulic resistance for a given value of predawn water potential. The decrease in leaf conductance caused by elevated CO2 was limited and tended to be less at high than at low atmospheric vapour pressure deficit. Mean land diurnal) sap flux were consistently higher in the control site trees than in the CO2 spring trees. The degree of reduction in water use between the two sites varied among the summer periods. The control site trees had consistently higher sap flow at corresponding values of either sapwood cross-sectional area or foliage area, Larger trees displayed smaller differences than smaller trees, between the control and the CO2 spring trees. A strong association between foliage area and sapwood cross-sectional area was found in both the control and the CO2 spring trees, the latter supporting a smaller foliage area at the corresponding sapwood stem cross- sectional area. The specific leaf area (SLA) of the foliage was not influenced by site. The results are discussed in terms of the effects of elevated CO2 on plant water use at the organ and whole-tree scale.

KEYWORDS: AIR CO-2 ENRICHMENT, ARBUTUS-UNEDO L, ATMOSPHERIC CO2, COMPUTER-TOMOGRAPHY, ELEVATED CO2, FOREST TREES, GAS-EXCHANGE, LONG-TERM EXPOSURE, SAP FLOW, WATER RELATIONS

2384

Tognetti, R., A. Longobucco, F. Miglietta, and A. Raschi. 1999. Water relations, stomatal response and transpiration of Quercus pubescens trees during summer in a Mediterranean carbon dioxide spring. *Tree Physiology 19(4-5):261-270.*

Variations in water relations and stomatal response of Quercus pubescens Willd. were analyzed under Mediterranean field conditions during two consecutive summers (1993 and 1994) at two locations characterized by different atmospheric CO2 concentrations because of the presence at one of them of a CO2 spring. Trees at the CO2 spring site have been growing for generations in elevated atmospheric CO2 concentrations. The heat-pulse velocity technique was used to estimate water use of trees during a 5-month period from June to November 1994. At the end of the sap flow measurements, the trees were harvested and foliage and sapwood area measured. At both sites, maximum leaf conductance was related to predawn shoot water potential. Effects of summer drought on plant water relations, including whole-plant transpiration, were severe, but leaf conductance and water potential recovered to predrought values after major rainfall in September. Leaf conductance, predawn water potential, and sometimes sap flow, decreased in parallel with increases in hydraulic resistance, reaching a minimum in midsummer. Hydraulic resistance was higher in trees at the control site than in trees at the CO2 spring site. The effect of elevated CO2 concentration on leaf conductance was less at high leaf-to-air water vapor pressure difference than at low leaf-to-air water vapor pressure difference. Mean and diurnal sap fluxes were consistently higher in trees at the control site than in trees at the CO2 spring site. During the summer period, plant water use varied between the two sites. Trees at the control site had consistently higher sap flow at corresponding values of sapwood cross-sectional area than trees at the CO2 spring site. Because trees at the CO2 spring site supported a smaller foliage area for a corresponding sapwood cross-sectional area than trees at the control site, the overall mean sap flux/foliage area ratio did not differ between sites. The results are discussed in terms of effects of elevated CO2 concentration on plant water use at the organ and whole-tree scale.

KEYWORDS: AIR CO-2 ENRICHMENT, ARBUTUS-UNEDO L, ATMOSPHERIC CO2, BIOMASS ALLOCATION, COMPUTER-TOMOGRAPHY, ELEVATED CO2, FOREST TREES, GAS-EXCHANGE, PINUS-CONTORTA, WOODY-PLANTS

2385

Tognetti, R., A. Longobucco, and A. Raschi. 1999. Seasonal embolism and xylem vulnerability in deciduous and evergreen Mediterranean trees influenced by proximity to a carbon dioxide spring. *Tree Physiology 19(4-5):271-277.*

We investigated how proximity to natural CO2 springs affected the seasonal patterns of xylem embolism in Quercus ilex L., Quercus pubescens Willd., Fraxinus ornus L., Populus tremula L. and Arbutus unedo L., which differ in leaf phenology and wood anatomy. Xylem embolism was evaluated in both artificially dehydrated branches and in hydrated apical branches collected at monthly intervals during a 20-month sampling period. Initial specific hydraulic conductivity was also evaluated. We found species-dependent differences in xylem hydraulic properties in response to elevated CO2 concentration. Populus tremula was the most embolized and A. unedo was the least embolized of the species examined. Effects of elevated CO2 were significant in Q. pubescens, P. tremula and A. unedo, whereas the overall response to elevated CO2 was less evident in F, ornus and Q. ilex. Specific hydraulic conductivity differed among species but not between sites, although. the interaction between species and site was significant. Differences in xylem vulnerability between trees growing near to the CO2 spring and those growing in control areas were small. Although differences in hydraulic properties in response to elevated CO2 concentration were small, they may be of great importance in determining future community composition in Mediterranean-type forest ecosystems. The possible causes and ecological significance of such differences are discussed in relation to elevated CO2 concentration and other environmental conditions.

KEYWORDS: ATMOSPHERIC CO2, CAVITATION, ELEVATED CO2, FAGUS-SYLVATICA, FOREST TREES, GROWTH, HYDRAULIC CONDUCTIVITY, QUERCUS, STOMATAL CONDUCTANCE, WATER-STRESS

2386

Tognetti, R., A. Longobucco, A. Raschi, F. Miglietta, and I. Fumagalli. 1999. Responses of two Populus clones to elevated atmospheric CO2 concentration in the field. *Annals of Forest Science 56(6):493-500.*

Two poplar clones, hybrid Populus deltoides Bartr. Ex Marsh x Populus nigra L. (Populus x euramericana), clone I-214, and Populus deltoides, clone Lux, were grown from clonal hardwood cuttings for one growing season in either ambient (360 mu mol mol(-1)) or elevated (560 mu mol mol(-1)) [CO2] in FACE-system rings at Rapolano Terme (Siena, Italy). Both clones I-214 and Lux exhibited a higher above-ground biomass, photosynthesis at light saturation and instantaneous transpiration efficiency (ITE) in CO2-enriched air. The elevated [CO2]-induced responses of clone I-214 included increased investment in branch and leaf biomass, and enhanced stem volume. The elevated [CO2]-induced responses of clone Lux included an increase in the number of branches and leaf area (which might result in a higher leaf area index, LAI). Photosynthetic acclimation under elevated [CO2] was found only during the early morning and only in clone I-214. Stomatal conductance and transpiration ton a leaf area basis) decreased under elevated [CO2] particularly in clone Lux and at the end of the experiment. The effects of elevated [CO2] on leaf osmotic potential were limited, at least in conditions of non-limiting water availability. Clonal differences in response to elevated [CO2] should be taken in account when planning future poplar plantations in the forecast warmer and drier Mediterranean sites. ((C) Inra/Elsevier, Paris.).

KEYWORDS: ALLOCATION, CARBON DIOXIDE, DROUGHT, ENRICHMENT, GROWTH, PHOTOSYNTHETIC ACCLIMATION, POPLAR CLONES, PRESSURE-VOLUME, SEEDLINGS, WATER RELATIONS

2387

Tomlinson, P.T., and P.D. Anderson. 1995. Elevated co2 compensates for water-stress in red oak. *Plant Physiology 108(2):36.*

2388

Tomlinson, P.T., and P.D. Anderson. 1998. Ontogeny affects response of northern red oak seedlings to elevated CO2 and water stress - II. Recent photosynthate distribution and growth. *New Phytologist 140(3):493-504.*

Northern red oak in the western Lake States area of the USA exists on the most xeric edge of its distribution range. Future climate-change scenarios for this area predict decreased water availability along with increased atmospheric CO2. We examined recent photosynthate distribution and growth in seedlings as a function of CO2 mole fraction (400, 530 and 700 mu mol mol(-1) CO2), water regime (well watered and water-stressed), and ontogenic stage. Water stress effects on growth were largely offset by elevated CO2. Water stress increased root mass ratio without concurrently increasing allocation of recent photosynthate to the roots. However, apparent sink strength of water-stressed seedlings at the completion of the third growth stage tended to be greater than that

of well watered seedlings, as shown by continued high export, which may contribute carbon reserves to support preferential root growth under water- stressed conditions. Elevated CO2 decreased apparent shoot sink strength associated with the rapid expansion of the third flush. Carbon resources for the observed enhanced growth under elevated CO2 could be provided by enhanced photosynthetic rate over an increased leaf area (Anderson & Tomlinson, 1998, this volume). Increased sink strength of LG seedlings under water- stressed conditions, together with decreased apparent shoot sink strength associated with growth in elevated CO2 provide mechanisms for offsetting water stress effects by growth in elevated CO2. Careful control of ontogeny was necessary to discern these changes and provides further evidence of the need for such careful control in mechanistic studies.

KEYWORDS: ALLOCATION, ATMOSPHERIC CO2, CACAO SEEDLINGS, CARBON DIOXIDE, CASTANEA-SATIVA, ENRICHMENT, GAS-EXCHANGE, LIQUIDAMBAR- STYRACIFLUA, PINUS-TAEDA SEEDLINGS, QUERCUS-ROBUR

2389

Topp, C.F.E., and C.J. Doyle. 1996. Simulating the impact of global warming on milk and forage production in Scotland .2. The effects on milk yields and grazing management of dairy herds. *Agricultural Systems 52(2-3):243-270.*

The potential impact of global warming and the enhanced atmospheric CO2 concentration on grassland management on dairy farms within the UK requires assessment. This has led to the development of a mathematical model of the grazing dairy cow. The model, that embraces grass and grass-white clover swards, has been used to assess the effects that the projected increases in temperature and rainfall under global warming and the increased levels of CO2 might have on milk production and on silage conservation for a typical dairy farm. The results suggest that the impact on milk production for grass-based systems will vary depending on the locality. On the other hand, for herds grazed on grass-white clover swards milk output might increase regardless of site, when the concentration of CO2 is enhanced. As regards silage production from grass-white clover swards, under global warming and at current levels of CO2 there is an apparent tendency to increase the percentage of total silage yield obtained from the first cut, although this does nor occur for grass swards. At the same time, there are also indications that global warming will increase the percentage of clover in the herbage cut for conservation. Copyright (C) 1996 Published by Elsevier Science Ltd

KEYWORDS: CLIMATE, GRASS-CLOVER LEYS, GROWTH, HERBAGE INTAKE, MODEL, NUTRITIONAL-VALUE, PARAMETERS, RYEGRASS, SCENARIOS, VALIDATION

2390

Torbert, H.A., S.A. Prior, and H.H. Rogers. 1995. Elevated atmospheric carbon-dioxide effects on cotton plant residue decomposition. *Soil Science Society of America Journal 59(5):1321-1328.*

Assessing the impact of elevated atmospheric CO2 concentration on the global environment is hampered due to a lack of understanding of global C cycling. Carbon fixed within plant biomass ultimately enters the soil via plant residues, but the effects of elevated-CO2-grown plant material on decomposition rates and long-term soil C storage are unknown. The objective of this study was to determine the decomposition rate of plant residues grown under an elevated CO2 environment as affected by soil type. Cotton (Gossypium hirsuturn L. 'Delta Pine 77') samples were collected from a free-air CO2 enrichment (550 mu L L(-1)) experiment. The plant residues were incubated under ambient CO2 conditions to determine decomposition rates of leaves, stems, and roots and potential N and P mineralization- immobilization in three soil series: a Blanton loamy sand (loamy siliceous, thermic Grossarenic Paleudult), a Decatur silt loam (clayey, kaolinitic, thermic Rhodic Paleudult), and a Houston clay loam (very fine, montmorillonitic Typic Chromudert). No significant difference was observed between plant residue grown under CO2 enrichment vs. ambient CO2 conditions for soil respiration or P mineralization- immobilization. Significantly greater net N immobilization was observed during the incubation in all soil types for plant residue grown at elevated CO2. These results indicate that while decomposition of plant residue may not be reduced by CO2 enrichment, N dynamics may be markedly changed.

KEYWORDS: CO2- ENRICHMENT, NITROGEN

2391

Torbert, H.A., S.A. Prior, H.H. Rogers, and G.B. Runion. 1998. Crop residue decomposition as affected by growth under elevated atmospheric CO2. *Soil Science 163(5):412-419.*

Increasing atmospheric CO2 level has led to concerns about process changes in the biosphere. Elevated atmospheric CO2 concentration has been Shown to increase plant biomass, resulting in greater amounts of residue returned to soil. However, the effects on long-term storage of C in soil are highly debated. Changes in both quantity and quality of plant residue, as well as residue management, may alter soil C and N dynamics that will, in turn, affect the ability of soil to store C. Plant residues were collected from an experiment using open top chambers to increase CO2 levels under field conditions. A soil incubation study was conducted with a Blanton loamy sand (loamy siliceous, thermic, Grossarenic Paleudults) to examine the effect of residue additions to two crop species (soybean, Glycine max (L.) Merr. and grain sorghum, Sorghum bicolor (L.) Moench), grown at two CO2 concentrations (ambient and twice ambient), and two incorporation treatments (incorporated or surface placement) on potential C and N mineralization. The difference in biomass inputs between plants grown in ambient and elevated atmospheric CO2 was also considered. Simulated residue incorporation reduced inorganic N concentration but had no effect on C mineralization. Both inorganic N content and C mineralization were higher with soybean than with grain sorghum. Although changes to both plant residue quality and quantity caused by elevated CO2 concentration affected C cycling in soil, residue quality may be more important for determining C storage. Nitrogen cycling in soil may be a controlling factor for C storage in terrestrial ecosystems.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, LITTER QUALITY, NITROGEN, SORGHUM

2392

Torbert, H.A., S.A. Prior, H.H. Rogers, W.H. Schlesinger, G.L. Mullins, and G.B. Runion. 1996. Elevated atmospheric carbon dioxide in agroecosystems affects groundwater quality. *Journal of Environmental Quality 25(4):720-726.*

Increasing atmospheric carbon dioxide (CO2) concentration has led to concerns about global changes to the environment, One area of global change that has not been addressed is the effect of elevated atmospheric CO2 on ground water quality below agroecosystems, Elevated CO2 concentration alterations of plant growth and C/N ratios may modify C and N cycling in soil and affect nitrate (NO3-) leaching to groundwater. This study was conducted to examine the effects of a legume soybean [Glycine max (L.) Merr.] and a nonlegume grain sorghum [Sorghum bicolor (L.) Moench] CO2-enriched agroecosystems on NO3- movement below the root zone in a Blanton loamy sand (loamy siliceous, thermic, Grossarenic Paleudults). The study was a split-plot design replicated three times with plant species (soybean and grain sorghum) as the main plots and CO2 concentration (approximate to 360 and similar to 720 mu L L(-1) CO2) as subplots using open-top held chambers. Fertilizer

application was made with N-15-depleted NH4NO3 to act as a fertilizer tracer, Soil solution samples were collected weekly at 90-cm depth for a 2-yr period arid monitored for NO3-N concentrations. Isotope analysis of soil solution indicated that the decomposition ol organic matter was the primary source of NO3--N in soil solution below the root zone through most of the monitoring period. Significant differences were observed for NO3--N concentrations between soybean and grain sorghum, with soybean having the higher NO3--N concentrations. Elevated CO2 increased total dry weight, total N content, and C/N ratio of residue returned to soil in both years. Elevated CO2 significantly decreased NO3--N concentrations below the root zone in both soybean and grain sorghum. The results of this study indicate that retention of N in organic pools because of elevated atmospheric CO2 could reduce the nitrate concentration in groundwater beneath agroecosystems as indicated by NO3- movement.

KEYWORDS: CO2, DECOMPOSITION, LITTER QUALITY, LOSSES, NITRATE, NITROGEN

2393

Torbert, H.A., H.H. Rogers, S.A. Prior, W.H. Schlesinger, and G.B. Runion. 1997. Effects of elevated atmospheric CO2 in agro-ecosystems on soil carbon storage. *Global Change Biology 3(6):513-521.*

Increasing global atmospheric CO2 concentration has led to concerns regarding its potential effects on the terrestrial environment. Attempts to balance the atmospheric carbon (C) budget have met with a large shortfall in C accounting (approximate to 1.4 x 10(15) g C y(-1)) and this has led to the hypothesis that C is being stored in the soil of terrestrial ecosystems. This study examined the effects of CO2 enrichment on soil C storage in C3 soybean (Glycine max L.) Merr. and C4 grain sorghum (Sorghum bicolor L.) Moench. agroecosystems established on a Blanton loamy sand (loamy siliceous, thermic, Grossarenic Paleudults). The study was a split-plot design replicated three times with two crop species (soybean and grain sorghum) as the main plots and two CO2 concentration (ambient and twice ambient) as subplots using open top field chambers. Carbon isotopic techniques using delta(13)C were used to track the input of new C into the soil system. At the end of two years, shifts in delta(13)C content of soil organic matter carbon were observed to a depth of 30 cm. Calculated new C in soil organic matter with grain sorghum was greater for elevated CO2 vs. ambient CO2 (162 and 29 g m(-2), respectively), but with soybean the new C in soil organic matter was less for elevated CO2 vs. ambient CO2 (120 and 291 g m(-2), respectively). A significant increase in mineral associated organic C was observed in 1993 which may result in increased soil C storage over the long-term, however, little change in total soil organic C was observed under either plant species. These data indicate that elevated atmospheric CO2 resulted in changes in soil C dynamics in agro-ecosystems that are crop species dependent.

KEYWORDS: CONSERVATION, COTTON, ENRICHMENT, FIELD, NITROGEN, ORGANIC-MATTER, PLANT-RESPONSES, RESIDUE DECOMPOSITION, RHIZOSPHERE, TURNOVER

2394

Torres, M.P., J.L.J. Houpis, and J.C. Pushnik. 1995. The effects of long-term co2 enrichment on photosynthesis, stomatal conductance and internal/external co2 concentrations in pinus-ponderosa. *Plant Physiology 108(2):113.*

2395

Townend, J. 1993. Effects of elevated carbon-dioxide and drought on the growth and physiology of clonal sitka spruce plants (picea-sitchensis (bong) carr). *Tree Physiology 13(4):389-399.*

Two-year-old Sitka spruce (Picea sitchensis (Bong.) Carr.) plants from four clones were grown in naturally lit growth chambers for 6 months at either ambient (350 ppm) or ambient + 250 ppm (600 ppm) CO2 concentration. Plants were grown in large boxes filled with peat, in a system that allowed the roots of individual plants to be harvested easily at the end of the growing season. Half of the boxes were kept well watered and half were allowed to dry out slowly over the summer. Plants growing in elevated CO2 showed a 6.9% increase in mean relative growth rate compared to controls in the drought treatment and a 9.8% increase compared to controls in the well-watered treatment, though there was considerable variation in response among the different clones and water treatments. Rates of net CO2 assimilation were higher and stomatal conductances were lower in plants grown in elevated CO2 than in ambient CO2 in both the well-watered and drought treatments. Both of these factors contributed to the doubling of instantaneous water use efficiency. The partitioning of biomass to roots was unaffected by elevated CO2, but the ratio of needle mass/stems + branches mass decreased. Together with reduced stomatal conductance, this probably caused the observed increases in xylem pressure potentials with elevated CO2.

2396

Townend, J. 1995. Effects of elevated co2, water and nutrients on picea- sitchensis (bong) carr seedlings. *New Phytologist 130(2):193-206.*

Sitka spruce (Picea sitchensis (Pong.) Carr.) seedlings were grown from seed for one year in naturally lit growth chambers with either ambient or ambient + 250 ppm concentrations of CO2. In the following year the plants were grown in the same CO2 treatments for the whole growing season at two concentrations of nutrients and were either well-watered or subjected to a long-term, gradually increasing drought. Elevated CO2 increased significantly growth in all treatments except the well-watered, unfertilized treatment. The relative increases in end-of-year biomass in the elevated CO2 treatment compared with the ambient treatment were: well-watered, fertilized + 52%, well-watered, unfertilized + 19%, droughted, fertilized + 44%, and droughted, unfertilized + 49%. Growth analysis revealed that treatment effects on both unit leaf rates and leaf area duration were important in determining the final masses of the plants. Plants growing in elevated CO2 had increased relative growth rates in the first half of the growing season but only slightly increased or even slightly decreased relative growth rates in the later part of the growing season in all water x nutrient treatments. Overall there was a significant CO2 x water x nutrient interaction on end-of-year biomass. A combination of small nutrient concentration and adequate water supply led to the smallest growth response to elevated CO2.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CASTANEA-SATIVA MILL, COOCCURRING BIRCH, GROWTH-RESPONSE, LIQUIDAMBAR- STYRACIFLUA, MINERAL NUTRITION, NITROGEN CONCENTRATION, PINUS-TAEDA SEEDLINGS, SHOOT GROWTH, SOURCE-SINK RELATIONS

2397

Townend, J., and A.L. Dickinson. 1995. A comparison of rooting environments in containers of different sizes. *Plant and Soil 175(1):139-146.*

Experiments on plants are often carried out in growth chambers or greenhouses which necessitate the use of an artificial rooting environment, though this is seldom characterized in detail. Measurements were made to compare the rooting environment in large boxes (0.25 m(3)) with that in small pots (0.19, 0.55 and 1.90 dm(3)) in naturally lit chambers. Diurnal temperature fluctuations of 14.6, 11.6 and 7.7 degrees C occurred in the pots compared with only 1.9 degrees

C in the boxes. Soil drying to a matric potential of -50 kPa was approximately 25 times faster in the pots. The mean heights of 2 year old Sitka spruce (Picea sitchensis (Bong.) Carr.) seedlings grown throughout their second growing season in the three sizes of pots were 38, 62 and 92% of the mean height of those grown in the boxes. Soil solution nutrient concentrations in the boxes were considerably increased by soil drying, an aspect which seems to have received little attention in experiments involving artificially imposed drought. An alternative system of constraining the roots of individual plants within nylon fabric bags, embedded in larger volumes of soil, to facilitate harvesting of complete root systems is described. The importance of the rooting environment in determining the outcome of physiological experiments is also briefly discussed.

KEYWORDS: CARBON DIOXIDE, ELEVATED CO2, GROWTH, PHOTOSYNTHETIC ACCLIMATION, SEEDLINGS, SHOOT, SOIL TEMPERATURES, SPRUCE, WATER-STRESS

2398

Traw, M.B., R.L. Lindroth, and F.A. Bazzaz. 1996. Decline in gypsy moth (Lymantria dispar) performance in an elevated CO2 atmosphere depends upon host plant species. *Oecologia 108(1):113-120.*

Plant species differ broadly in their responses to an elevated CO2 atmosphere, particularly in the extent of nitrogen dilution of leaf tissue. Insect herbivores are often limited by the availability of nutrients, such as nitrogen, in their host plant tissue and may therefore respond differentially on different plant species grown in CO2-enriched environments. We reared gypsy moth larvae (Lymantria dispar) in situ on seedlings of yellow birch (Betula allegheniensis) and gray birch (B. populifolia) grown in an ambient (350 ppm) or elevated (700 ppm) CO2 atmosphere to test whether larval responses in the elevated CO2 atmosphere were species- dependent. We report that female gypsy moths (Lymantria dispar) reared on gray birch (Betula populifolia) achieved similar pupal masses on plants grown at an ambient or an elevated CO2 concentration. However, on yellow birch (B. allegheniensis), female pupal mass was 38% smaller on plants in the elevated-CO2 atmosphere. Larval mortality was significantly higher on yellow birch than gray birch, but did not differ between the CO2 treatments. Relative growth rate declined more in the elevated CO2 atmosphere for larvae on yellow birch than for those on gray birch. In preference tests, larvae preferred ambient over elevated CO2-grown leaves of yellow birch, but showed no preference between gray birch leaves from the two CO2 atmospheres. This differential response of gypsy moths to their host species corresponded to a greater decline in leaf nutritional quality in the elevated CO2 atmosphere in yellow birch than in gray birch. Leaf nitrogen content of yellow birch dropped from 2.68% to 1.99% while that of gray birch leaves only declined from 3.23% to 2.63%. Meanwhile, leaf condensed tannin concentration increased from 8.92% to 11.45% in yellow birch leaves while gray birch leaves only increased from 10.72% to 12.34%. Thus the declines in larval performance in a future atmosphere may be substantial and host-species-specific.

KEYWORDS: CARBON-DIOXIDE ATMOSPHERES, ENRICHMENT, GROWTH, INSECT HERBIVORE INTERACTIONS, JUNONIA-COENIA, LEPIDOPTERA, NITROGEN-CONTENT, PAPER BIRCH, RESPONSES, SEEDLINGS

2399

Tremblin, G., P. Jolivet, and A. Coudret. 1993. Light quality effects on subsequent dark 14co2-fixation in fucus-serratus. *Hydrobiologia 261:471-475.*

The intensity and fate Of (CO2)-C-14-fixation in the dark are studied on Fucus serratus apices previously maintained under low illumination conditions using white, blue, red or yellow isoquantic lights. In the case of a 180 s pulse, light quality affected dark carbon-fixation, with a higher level of incorporation into ethanol-soluble organic matter in the case of yellow light cultivated apices. After a 30 s pulse C-14 was mainly fixed into glycerate and aspartate-malate pools whatever the pre-treatment light conditions, with a higher level into glycerate when apices were pre-illuminated with blue or yellow light. After a 180 s pulse, C-14 was mainly transferred into amino acids (glutamate and alanine) at the expense of aspartate and malate in red and yellow pre-illumination conditions, as found in the white light reference experiment, and only at the expense of glycerate in blue light pre-illumination conditions. The metabolic pathway of glycerate formation, principally enhanced by blue light preillumination, remains unexplained under these non-photosynthetic conditions. Results are discussed with reference to CO2-fixation via phosphoenolpyruvate carboxykinase and light quality effects on its in vitro activity.

KEYWORDS: CARBON FIXATION, CYSTOSEIRA-ELEGANS SAUVAGEAU, METABOLISM, PATHWAY

2400

Tremmel, D.C., and D.T. Patterson. 1993. Responses of soybean and 5 weeds to co2 enrichment under 2 temperature regimes. *Canadian Journal of Plant Science 73(4):1249-1260.*

Rising atmospheric CO2 levels could affect plant growth both directly, through effects on physiology, and indirectly, through the effects of possible CO2-induced temperature increases. In this study we examined the interacting effects of CO2 enrichment and temperature on the growth and allocation of soybean and five weeds. individual plants of soybean [Glycine max (L.) Merr. 'Braxton'], johnsongrass [Sorghum halepense (L.) Pers. quackgrass [Elytrigia repens (L.) Nevski], redroot pigweed (Amaranthus retroflexus L.), sicklepod (Cassia obtusifolia L.). and velvetleaf (Abutilon theophrasti Medic.) were grown in growth chambers in all combinations of two temperatures (avg. day/night of 26/19-degrees-C and 30/23- degrees-C) and two CO2 concentrations (350 and 700 ppm) for 35 d. Leaf area and plant biomass were greater at higher temperatures, regardless of CO2 level, in all species except quackgrass. Quackgrass (C3) produced its greatest leaf area and biomass at elevated CO2, whereas johnsongrass (C4) showed little response. Redroot pigweed (C4) and the C3 dicotyledenous species (soybean, sicklepod, velvetleaf) produced their greatest biomass at high CO2, though effects on leaf area were less consistent or absent. In general, when significant CO2 by temperature interactions were found, CO2 responses were smallest at higher temperatures. These differential responses to elevated CO2 concentrations may cause changes in the relative importance of competitive pressure from these weeds.

KEYWORDS: AIR- TEMPERATURE, ANNUALS, ATMOSPHERIC CO2, C-4 GRASS, CARBON-DIOXIDE CONCENTRATION, COMPETITION, ELEVATED CO2, GROWTH, NITROGEN, YIELD

2401

Tremmel, D.C., and D.T. Patterson. 1994. Effects of elevated co2 and temperature on development in soybean and 5 weeds. *Canadian Journal of Plant Science 74(1):43-50.*

Developmental rates of soybean [Glycine max (L.) Merr. 'Braxton'],johnsongrass [Sorghum halepense (L.) Pers.], quackgrass [Elytrigia repens (L.) Nevski], redroot pigweed (Amaranthus retroflexus L.), sicklepod (Cassia obtusifolia L.), and velvetleaf (Abutilon theophrasti Medic.) were compared among plants grown in all combinations of two temperature levels (avg. day/night of 26/19 degrees C and 30/23 degrees C) and two CO2 levels (350 and 700 ppm). Neither temperature nor CO2 affected johnsongrass tillering rate, but plants began tillering earlier at higher temperatures. Adverse effects of higher temperatures on quackgrass development were alleviated by elevated

CO2 conditions. Plastochron rate was higher at higher temperatures in all dicot species (soybean, redroot pigweed, sicklepod, and velvetleaf), and was higher at elevated CO2 in all dicots except velvetleaf. Calculating plastochron rates on a degree day basis removed differences between temperature treatments, but did not affect responses to CO2. Responses of dicot branch and branch leaf production to treatments varied among species. Branch production per day increased with higher temperatures in redroot pigweed, decreased with higher temperatures in sicklepod, and was unaffected by temperature in soybean. The relationship between main axis and branch developmental rates was altered by temperature in soybean, and by both temperature and CO2 in sicklepod, but was unaffected by either treatment in redroot pigweed. These results indicate that developmental responses to temperature and CO2 depend on both the species and the aspect of development being considered.

KEYWORDS: CARBON-DIOXIDE CONCENTRATION, ENRICHMENT, GLYCINE-MAX, GROWTH, PHOTOSYNTHESIS, WHEAT, YIELD

2402

Trenberth, K.E. 1999. Conceptual framework for changes of extremes of the hydrological cycle with climate change. *Climatic Change 42(1):327-339.*

A physically based conceptual framework is put forward that explains why an increase in heavy precipitation events should be a primary manifestation of the climate change that accompanies increases in greenhouse gases in the atmosphere. Increased concentrations of greenhouse gases in the atmosphere increase downwelling infrared radiation, and this global heating at the surface not only acts to increase temperatures but also increases evaporation which enhances the atmospheric moisture content. Consequently all weather systems, ranging from individual clouds and thunderstorms to extratropical cyclones, which feed on the available moisture through storm- scale moisture convergence, are likely to produce correspondingly enhanced precipitation rates. Increases in heavy rainfall at the expense of more moderate rainfall are the consequence along with increased runoff and risk of flooding. However, because of constraints in the surface energy budget, there are also implications for the frequency and/or efficiency of precipitation. It follows that increased attention should be given to trends in atmospheric moisture content, and datasets on hourly precipitation rates and frequency need to be developed and analyzed as well as total accumulation.

KEYWORDS: CO2, DAILY PRECIPITATION, FREQUENCY, MODEL, NORTH-AMERICA, SENSITIVITY, TRENDS, UNITED-STATES, VARIABILITY, WATER-VAPOR

2403

Treonis, A.M., and J.F. Lussenhop. 1997. Rapid response of soil protozoa to elevated CO2. *Biology and Fertility of Soils 25(1):60-62.*

Short-term changes in bacterial and protozoan populations from the soil of plants grown under elevated atmospheric CO2 were quantified. We grew Brassica nigra at either ambient or twice- ambient CO2 levels within open-top chambers in the field for 4 weeks. Plant biomass, above- and belowground, was unaffected by elevated CO2. Direct count bacterial density was unchanged under elevated CO2. Flagellate density tended to increase, whereas amoebal density significantly declined under elevated CO2. This change in protozoan community structure suggests trophic transfer of the elevated CO2 fertilization effect through the soil food chain.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, ENRICHMENT, FEEDBACK, POPULATIONS, RHIZOSPHERE

2404

Tripp, K.E., W.K. Kroen, M.M. Peet, and D.H. Willits. 1992. Fewer whiteflies found on co2-enriched greenhouse tomatoes with high C-n ratios. *Hortscience 27(10):1079-1080.*

Eight tomato (Lycopersicon esculentum) cultivars were grown for 16 weeks in greenhouses enriched for an average of 8.1 hours daily to 1000 mul CO2/liter of air or in greenhouses maintained at ambient CO2. Carbon dioxide enrichment significantly decreased the mean number of greenhouse whiteflies [Trialeurodes vaporariorum (Westward), Homoptera: Aleyrodidae] as measured by counts from commercial yellow sticky traps. The number of whiteflies present was negatively correlated with both seasonal foliar C:N ratio and percent C but positively correlated with percent N in the foliage. Thus, CO2 enrichment apparently alters plant composition in such a way as to reduce significantly the population growth of greenhouse whiteflies.

KEYWORDS: CARBON-DIOXIDE ATMOSPHERES, INSECT HERBIVORE, LEPIDOPTERA, NITROGEN-CONTENT, NOCTUIDAE, PLANTS

2405

Tripp, K.E., M.M. Peet, D.M. Pharr, D.H. Willits, and P.V. Nelson. 1991. CO2-enhanced yield and foliar deformation among tomato genotypes in elevated CO2 environments. *Plant Physiology 96(3):713-719.*

Yield increases observed among eight genotypes of tomato (Lycopersicon esculentum Mill.) grown at ambient CO2 (about 350) or 1000 microliters per liter CO2 were not due to carbon exchange rate increases. Yield varied among genotypes while carbon exchange rate did not. Yield increases were due to a change in partitioning from root to fruit. Tomatoes grown with CO2 enrichment exhibited nonepinastic foliar deformation similar to nutrient deficiency symptoms. Foliar deformation varied among genotypes, increased throughout the season, and became most severe at elevated CO2. Foliar deformation was positively related to fruit yield. Foliage from the lower canopy was sampled throughout the growing season and analysed for starch, K, P, Ca, Mg, Fe, and Mn concentrations. Foliar K and Mn concentrations were the only elements correlated with deformation severity. Foliar K decreased while deformation increased. In another study, foliage of half the plants of one genotype received foliar applications of 7 millimolar KH2PO4. Untreated foliage showed significantly greater deformation than treated foliage. Reduced foliar K concentration may cause CO2-enhanced foliar deformation. Reduced K may occur following decreased nutrient uptake resulting from reduced root mass due to the change in partitioning from root to fruit.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, FRUITS, GREENHOUSES, RESPONSES, STORAGE

2406

Tripp, K.E., M.M. Peet, D.H. Willits, and D.M. Pharr. 1991. CO2-enhanced foliar deformation of tomato-relationship to foliar starch concentration. *Journal of the American Society for Horticultural Science 116(5):876-880.*

Two cultivars of greenhouse tomato (Lycopersicon esculentum Mill.) were grown with ambient or 1000-mu-l CO2/liter during Jan.-June 1987 and 1988. In both years, CO2-enrichment increased foliar deformation and foliar starch, but during the season, foliar starch levels decreased while deformation increased. 'Laura' had more deformation, while 'Michigan-Ohio' had higher foliar starch concentration. During an entire season, there was no significant relationship between foliar starch concentration and deformation severity. Foliar C exchange rates in the

lower canopy were not affected by severity of deformation. Data from these experiments do not support the hypothesis that excess foliar starch is responsible for foliar deformation at elevated CO2.

KEYWORDS: CO2- ENRICHMENT, LONG-TERM EXPOSURE, PHOTOSYNTHETIC INHIBITION, RESPONSES

2407

Tschaplinski, T.J., R.J. Norby, and S.D. Wullschleger. 1993. Responses of loblolly-pine seedlings to elevated co2 and fluctuating water-supply. *Tree Physiology 13(3):283-296.*

Osmotic adjustment of loblolly pine (Pinus taeda L.) seedlings to fluctuating water supply in elevated CO2 was investigated. Seedlings were grown in controlled-environment chambers in either 350 or 700 mul l-1 CO2 with weekly watering for four months, after which they were either watered weekly (well- watered treatment) or every two weeks (water-stress treatment) for 59 days. Osmotic adjustment was assessed by pressure-volume analysis of shoots and by analysis of soluble carbohydrates and free amino acids in roots during the last drying cycle. In well-watered seedlings, elevated CO2 increased the concentration of soluble sugars in roots by 68%. Water stress reduced the soluble sugar concentration in roots of seedling growing in ambient CO2 to 26% of that in roots of well-watered seedlings. Elevated CO2 mitigated the water stress-induced decrease in the concentration of soluble sugars in roots. However, this was probably due, in part, to carbohydrate loading during the first four months when all seedlings were grown in the presence of a high water supply, rather than to osmotic adjustment to water stress. Water stress caused a doubling in the concentration of free primary amino acids in roots, whereas elevated CO2 reduced primary amino acid and nitrogen concentrations to 32 and 74%, respectively, of those in roots of seedlings grown in ambient CO2. There was no indication of large-scale osmotic adjustment to water stress or that elevated CO2 enhanced osmotic adjustment in loblolly pine.

2408

Tschaplinski, T.J., D.B. Stewart, P.J. Hanson, and R.J. Norby. 1995. Interactions between drought and elevated co2 on growth and gas-exchange of seedlings of 3 deciduous tree species. *New Phytologist 129(1):63-71.*

Interactions between elevated atmospheric CO2 and drought on growth and gas exchange of American sycamore (Platanus occidentalis L.), sweetgum (Liquidambar styraciflua L.) and sugar maple (Acer saccharum Marsh.) were investigated using 1- yr-old seedlings, planted in 81 pots and grown in four open-top chambers, containing either ambient air or ambient air enriched with 300 mu mol mol(-1) CO2. Two soil moisture regimes were included within each chamber: a 'well-watered' treatment with plants watered daily and a 'drought' treatment in which plants were subjected to a series of drought cycles. Duration and depth of the drought cycles were determined by soil matric potential. Mean soil water potential at rewatering for the water-stressed seedlings under ambient CO2 for sugar maple, sweetgum and sycamore was -0.5, -0.7 and -1.8 MPa, respectively, compared with > -0.1 MPa for all well-watered plants. Elevated CO2 increased relative growth rate of well-watered sugar maple by 181%, resulting in a 4.3-fold increase in total plant dry weight after 81 d, compared with 1.4 and 1.6-fold increases for sweetgum and sycamore, respectively, after 69 d. Although elevated CO2 increased net CO2 assimilation rate of sugar maple by 115 %, there was a 10-fold increase in leaf area which contributed to the growth response. Although drought did not eliminate a growth response of sugar maple to elevated CO2, it greatly reduced the elevated CO2- induced enhancement of relative growth rate. In contrast, relative growth rates of sweetgum and sycamore were not significantly increased by elevated CO2. Drought, under elevated CO2, reduced leaf area of all three species to a greater extent than it reduced net CO2 assimilation rate. The response ranged from no effect in sugar maple to a 40 % reduction in sycamore, with sweetgum exhibiting an intermediate response. Results indicate that drought may alter the growth response, gas exchange and water relations of tree species growing in an elevated CO2 atmosphere. Under high nutrient and water availability, sugar maple may benefit the most (of the three species studied) from a CO2-enriched atmosphere, but productivity gains will be limited if frequent drought is prevalent.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, DIFFERENT IRRADIANCE LEVELS, ENRICHMENT, LIQUIDAMBAR-STYRACIFLUA, PHOSPHORUS DEFICIENCY, PINUS-TAEDA SEEDLINGS, RESPONSES, STOMATAL CONDUCTANCE, WATER-STRESS

2409

Tschaplinski, T.J., D.B. Stewart, and R.J. Norby. 1995. Interactions between drought and elevated co2 on osmotic adjustment and solute concentrations of tree seedlings. *New Phytologist 131(2):169-177.*

Although drought tolerance of tree species is a critical determinant of forest composition, how elevated CO2 affects drought tolerance is uncertain. Interactions between elevated CO2 and drought on osmotic potential and osmotic adjustment of American sycamore (Platanus occidentalis L.), sweetgum (Liquidambar styraciflua L.), and sugar maple (Acer saccharum Marsh.) were investigated using l-yr-old seedlings, planted in 81 pots and grown in four open-top chambers, containing either ambient air or ambient air enriched with 300 mu mol mol(-1) CO2. A well-watered treatment with plants watered daily and a droughted treatment in which plants were subjected to a series of drought cycles were included within each chamber. Sugar maple and sweetgum seedlings completed a total of seven drying cycles, whereas sycamore seedlings, because of their greater leaf area and plant size, completed 11 cycles. The mean soil water potential at re-watering for droughted seedlings in ambient CO2 was -0.5, -0.7, and -1.8 MPa for sugar maple, sweetgum and sycamore, respectively, compared with -0.2, -0.7, and -1.2 MPa, respectively, under elevated CO2. By contrast, all well-watered plants were maintained at soil water potential >-0.1 MPa. Drought under ambient CO2 reduced osmotic potential at saturation for leaves of sycamore and sweetgum by 0.30 MPa and 0.61 MPa, respectively, but leaves of sugar maple did not display osmotic adjustment to drought. Elevated CO2 increased osmotic potential at turgor loss for leaves of sugar maple by 0.33 MPa under well-watered conditions, and 0.48 MPa under drought. This response was not evident in the other species and might be related to the rapid growth of sugar maple causing a depletion of solutes. Whereas drought reduced the total solute concentration in roots of sugar maple, primarily the result of a reduction in K, elevated CO2 did not alter the concentration of total solutes in roots of any of the three species. Elevated CO2 has differing effects on drought tolerance among tree species, and thus might alter the competitive relations between species.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, ENRICHMENT, FORESTS, NITROGEN RESPONSE, PHYSIOLOGICAL INDICATORS, ROTATION SYCAMORE PLANTATION, STRESS, WATER RELATIONS

2410

Tsygankov, A.A., L.T. Serebryakova, K.K. Rao, and D.O. Hall. 1998. Acetylene reduction and hydrogen photoproduction by wild-type and mutant strains of Anabaena at different CO2 and O-2 concentrations. *Fems Microbiology Letters 167(1):13-17.*

Hydrogen photoproduction by growing cultures of Anabaena variabilis and A. azollae did not occur under air+CO2 or argon+CO2 atmospheres at saturating light but did take place under argon alone. It was shown that CO2 inhibited photoproduction of H-2 as a result of the

photosynthetic production of O-2 whereas photoreduction of C2H2 by these cyanobacteria was not inhibited by O-2 concentrations up to 20% in the assay gas phase. In contrast to the wild type of A. variabilis and of A. azollae, H-2 photoproduction by the hydrogenase-impaired mutant A. variabilis PK84 showed only a slight dependence on O-2 concentration. Thus, in the wild-type Anabaena the decrease in the observed rate of H-2 evolution at elevated O-2 concentrations could be the result of an increase in hydrogenase-mediated uptake of H-2 via an oxyhydrogen reaction. (C) 1998 Federation of European Microbiological Societies. Published by Elsevier Science B.V. All rights reserved.

KEYWORDS: BLUE GREEN ALGA, FIXATION, NITROGEN, OXYGEN, VARIABILIS

2411

Tuba, Z., Z. Csintalan, K. Szente, Z. Nagy, and J. Grace. 1998. Carbon gains by desiccation-tolerant plants at elevated CO2. *Functional Ecology 12(1):39-44.*

1. There have been no reports of the long-term responses of the desiccation-tolerant (DT) plants to elevated CO2. Xerophyta scabrida is a DT woody shrub, which loses chlorophylls and thylakoids during desiccation: a so-called poikilochlorophyllous desiccation-tolerant species (PDT), When the leaves of X. scabria are allowed to desiccate, the species shows many of the normal features of (P)DT plants. 2. However, the duration of:photosynthesis in X. scabria is prolonged by 300% when the measurements are: made at 700 as opposed to 350 p.p.m. CO2. The implication is that the carboxylating enzymes must still have been active at this time to enable appreciable photosynthetic activity, This response could have far-reaching implications for the success of such species in a future climate. 3. Lichens and mosses, representing the homoiochlorophyllous DTs (HDT), retain their chlorophyll content and photosynthetic apparatus during desiccation, We show the desiccation responses of two common HDT species (Cladonia convoluta and Tortula ruralis) to elevated CO2 for comparison, Both HDT species showed increased net CO2 uptake in the material grown at high CO2 by more than 30% in moss and by more than 50% in lichen. It is concluded that desiccation- tolerant plants will be among the main beneficiaries of a high CO2 future.

KEYWORDS: ATMOSPHERIC CO2, BORYA-NITIDA LABILL, CHLOROPHYLLS, LEAVES, PHOTOSYNTHESIS, RECONSTITUTION, REHYDRATION, RESPIRATION, WATER-CONTENT, XEROPHYTA-SCABRIDA

2412

Tuba, Z., M.B. Jones, K. Szente, Z. Nagy, L. Garvey, and R. Baxter. UNKNOWN YEAR. Some ecophysiological and production responses of grasslands to long-term elevated CO2 under continental and atlantic climates. *Stress of Life :241-250.*

KEYWORDS: INCOMPLETE, ATMOSPHERIC CO2, C-3 PLANTS, CARBON DIOXIDE, COMMUNITIES, CROP RESPONSES, GROWTH, LEAVES, PHOTOSYNTHETIC CAPACITY, TRANSPIRATION, WATER-USE EFFICIENCY

2413

Tuba, Z., M.C.F. Proctor, and Z. Takacs. 1999. Desiccation-tolerant plants under elevated air CO2: A review. *Zeitschrift Fur Naturforschung C-A Journal of Biosciences 54(9-10):788-796.*

This article summarises present knowledge of the ecophysiological responses to elevated atmospheric CO2 of desiccation tolerant (DT) plants. It deals primarily with lichens and bryophytes, as the most prominent groups of DT photosynthetic organisms, but includes some comment on algae and vascular DT plants. Results of research on DT plants are compared with those on desiccation sensitive vascular Cg plants, the most widely investigated group in the field of global change. Both DT and non-DT plants show an immediate positive response of photosynthesis to elevated CO2, but in both groups the longer term effect is generally reduced (or even reversed) by down-regulation or feedback inhibition of photosynthesis, or other limitations on production and growth. In bryophytes and lichens, enhanced short-term photosynthesis may or may not be reflected in increased production; bryophytes have limited source-sink differentiation, and lichens invest excess photosynthate in secondary metabolites. DT plants may gain some advantage from elevated CO2 at both low and excessive water contents. Neither theoretical considerations nor experimental results suggest that elevated atmospheric CO2 will lead to any substantial shift in the balance of advantage between DT and non-DT plants.

KEYWORDS: ATMOSPHERIC CO2, CARBON-DIOXIDE CONCENTRATION, GREEN-ALGAL, GROWTH, LICHENS, PHOTOSYNTHESIS, RESPONSES, SOIL RESPIRATION, VEGETATION, WATER-CONTENT

2414

Tuba, Z., K. Szente, and J. Koch. 1994. Response of photosynthesis, stomatal conductance, water-use efficiency and production to long-term elevated co2 in winter- wheat. *Journal of Plant Physiology 144(6):661-668.*

Responses of photosynthesis, stomatal conductance, water use efficiency (at the beginning of flowering) and production allocation (at full ear/grain ripening) to long-term elevated CO2 were assessed in winter wheat (Triticum aestivum L. cv. MV16). Plants were grown in open top chambers under a temperate-continental climate from germination at ambient (350 mu molmol(-1)) and elevated (700 mu molmol(-1)) CO2 concentrations. High CO2 plants displayed a decreased initial slope of the A/C-i response curve, with the assimilation rate (A) continuing to increase above 400 mu molmol(-1) internal CO2 concentration (C-i). A in the ambient plants showed P regeneration limitation while RuBP regeneration appeared to be limiting A in the high CO2 treatment. Variable fluorescence ratios (Rfd 690) were lower in the high CO2 plants indicating a lower potential photochemical activity. The increase in the values for the chlorophyll fluorescence ratio F690/F735 in the high CO2 plants was in agreement with the lower chlorophyll a+b concentrations. The high CO2 plants had higher concentrations of starch in their leaves and roots that the ambient plants. Stomatal conductance (g(s)) was lower in the high CO2 plants at every CO2 concentration (C-a) and C-i and the C-i-dependent g(s) response had a large influence on the A/g(s), function. The higher water use efficiency (WUE) values (at C-a's > 350 mu molmol(-1)) in the high CO2 wheat plants were the result of a larger decrease in transpiration rate (E) in the high CO2 plants than in the ambient plants, and of a simultaneous larger increase in A in the range of C-a above 350 mu molmol(-1) COP. The integrated and combined effect of the photosynthetic and stomatal acclimation to elevated CO2 produced a higher C- assimilation in high CO2 plants at elevated CO2 than in the ambient plants, however, this was not followed by an acclimation in C-allocation. These were reflected in a slightly increased (6.7%) overall dry matter production and lower reproductive allocation (RA).

KEYWORDS: ACCLIMATION, ATMOSPHERIC CARBON-DIOXIDE, C-3 PLANTS, CHLOROPHYLL CONTENT, ENRICHMENT, EXPOSURE, INHIBITION, LEAVES, NITROGEN, PHYSIOLOGY

2415

Tuba, Z., K. Szente, Z. Nagy, Z. Csintalan, and J. Koch. 1996. Responses of CO2 assimilation, transpiration and water use efficiency to long-term elevated CO2 in perennial C-3 xeric loess steppe species.

Journal of Plant Physiology 148(3-4):356-361.

CO2 assimilation (A), transpiration (E), water use efficiency (WUE), leaf-nitrogen and carbohydrate responses to 11 months elevated (700 mu mol mol(-1)) CO2 exposure in four perennial C- 3 species (Festuca rupicola, Dactylis glomerata, Filipendula vulgaris, Salvia nemorosa) from a xeric temperate loess steppe are reported. The responses in the species varied greatly owing to their differing acclimation. The acclimation of photosynthesis was somewhat downward in F. rupicola, fully downward in D. glomerata, and upward in S. nemorosa and F. vulgaris. The reduction in the initial slope of the A/c(i) response curve in E rupicola and D. glomerata suggested a decrease in Rubisco capacity. Net CO2 assimilation at 700 mu mol mol(-1) CO2 c(a) in the high CO2 F. rupicola was higher than in those grown at present (350 mu mol mol(-1)) CO2; there was no difference in D. glomerata. The initial slope of the A/c(i) curve indicated an increased Rubisco capacity in high CO2 F. vulgaris and S. nemorosa. Their net CO2 assimilation was higher in the plants grown in the high CO2 treatment at c(i)'s over 200 mu mol mol(-1) than that in the plants grown at present CO2. The A/c(i) response curves, which were saturated in all species grown at present CO2, did not reach saturation in the plants grown at elevated CO2, reflecting that the Pi limitation of CO2 assimilation was alleviated in the plants grown at high CO2. Transpiration decreased with an increase in c(i) in both the present and elevated CO2 F. rupicola and D. glomerata. In F. vulgaris, an increase in ci caused a reduction in transpiration in the plants grown at high CO2 only. Transpiration rate in both the present and elevated CO2 S. nemorosa was not affected by any change in c(i). It is suggested then that long-term exposure to high CO2 causes a similar acclimation of stomatal regulation and transpiration to that of photosynthesis. High CO2 caused a significant decrease in protein-nitrogen content only in D. glomerata. Starch increased in F. rupicola and D. glomerata and soluble sugar content was higher in all species grown at high CO2 than at ambient. Instantaneous WUE significantly increased in ail species grown at elevated CO2.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CARBON-DIOXIDE, COMMUNITIES, EXCHANGE, EXPOSURE, GROWTH, INHIBITION, LEAVES, PHOTOSYNTHETIC CAPACITY, PLANTS

2416

Tubiello, F.N., G. Lin, J.W. Druitt, and B.D.V. Marino. 1999. Ecosystem-level evapotranspiration and water-use efficiency in the desert biome of Biosphere 2. *Ecological Engineering 13(1-4):263-271.*

We estimate whole-system water and carbon fluxes for the desert biome of Biosphere 2 under two different daily-mean CO2 concentrations: 450 ppmv and 850 ppmv. The desert mesocosm occupies an area of approximately 1500 m(2), has a total atmospheric Volume of about 25000 m(3) and contains a heterogeneous distribution of plants and soils. Atmospheric water content and CO2 concentrations were measured continuously using a variety of sensors, including a Li-cor 6262 for CO2 deployed within the experimental area. Daily carbon and water budgets were calculated in the desert biome, isolated from the rest of Biosphere 2 by deploying isolation curtains for 24-h periods. Data collected for six closure periods suggest that elevated CO2 concentration increased whole-system carbon uptake, while evapotranspiration remained constant. As a result, whole-system water-use efficiency (WUE, defined as net ecosystem carbon uptake per unit water transpired) in the Biosphere 2 desert increased by more than 40%. Our measurements investigate soil-plant processes at a medium scale, ideally bridging the gap between traditional controlled-environment growth chambers and open-held studies. (C) 1999 Elsevier Science B.V. All rights reserved.

KEYWORDS: CARBON, CO2, RESPONSES

2417

Tubiello, F.N., T. Mahato, T. Morton, J.W. Druitt, T. Volk, and B.D.V. Marino. 1999. Growing wheat in Biosphere 2 under elevated CO2: Observations and modeling. *Ecological Engineering 13(1-4):273-286.*

Spring wheat (Triticum aestivum L., cv. Yecora Rojo) was grown in the intensive agricultural biome (IAB) of Biosphere 2 during the 1995-1996 winter/spring season. Environmental conditions were characterized by a day/night temperature regime of 27/17 degrees C, relative humidity (RH) levels around 45%, mean atmospheric CO2 concentration of 450 ppmv, and natural light conditions with mean intensities about half of outside levels. Weekly samples of above-ground plant matter were collected throughout the growing season and phenological events recorded. A computer model, CERES-Wheat, previously tested under both field and controlled conditions, was used to simulate the observed crop growth and to help in data analysis. We found that CERES-Wheat simulated the data collected at Biosphere 2 to within 10% of observed, thus suggesting that wheat growth inside the IAB was comparable to that documented in other environments. The model predicts phenological stages and final dry matter (DM) production within 10% of the observed data. Measured DM production rates, normalized for light absorbed by the crop, suggested photosynthetic efficiencies intermediate between those observed under optimal field conditions and those recorded in NASA-Controlled Ecological Life-Support Systems (CELSS). We suggest that such a difference can be explained primarily in terms of low light levels inside the IAB, with additional effects due to elevated CO2 concentrations and diffuse light fractions. (C) 1999 Elsevier Science B.V. All rights reserved.

KEYWORDS: CARBON DIOXIDE, CLIMATE CHANGE, CROP PRODUCTIVITY, EFFICIENCY, ENRICHMENT, GROWTH, RADIATION, RESPONSES, TEMPERATURE, WINTER-WHEAT

2418

Tubiello, F.N., C. Rosenzweig, B.A. Kimball, P.J. Pinter, G.W. Wall, D.J. Hunsaker, R.L. LaMorte, and R.L. Garcia. 1999. Testing CERES-wheat with free-air carbon dioxide enrichment (FACE) experiment data: CO2 and water interactions. *Agronomy Journal 91(2):247-255.*

Dynamic crop-growth models are used to project the effects of rising atmospheric CO2 concentration and associated climate change on crop yields. Such model predictions are largely untested in the field, for lack of experimental data. We tested the CERES-Wheat model, modified to include leaf-level photosynthesis response to elevated CO2, using field data from 2 yr of Free-Air Carbon Dioxide Enrichment (FACE) experiments with spring wheat (Triticum aestivum L. cv. Yecora Rojo) in Mariclopa, AZ. Two irrigation treatments (well-watered, WW; water-deficit stressed, WS) and two atmospheric CO2 concentrations (ambient, 350 mu mol mol(-1); elevated, 550 mu mol mol(-1)) were simulated. The model was evaluated using measurements of crop phenology, aboveground dry matter (DM) production, grain yield, and evapotranspiration (ET). Model calculations of crop phenology were within 2 to 3 d of observed values under WW, ambient CO2 conditions in both years. The model did not simulate the accelerated crop phenology (5-8 d at physiological maturity) observed in the WW and elevated CO2 treatments, indicating the need to include effects of increased stomatal resistance on canopy temperature. Simulations of DM and grain yield were within 10% of measured values, except for a tendency to overcalculate DM response to CO2 by 10 to 15% in Year 1 for WS treatments. The model undercalculated cumulative ET under WW conditions by 15%; model sensitivity analyses suggest that simulation of potential evapotranspiration (PET) was too low for this arid site. The model reproduced measured dynamics of CO2-water interactions. Simulated reductions in water loss due to elevated CO2 were about 4%, in agreement with measurements. The model simulated

larger increases in DM production and yield due to elevated CO2 under WS than under WW conditions. In Year 1, simulated crop response to CO2 was 2% larger (measured: 3%) under WS than under WW conditions; in Year 2, it was 11% larger (measured: 9%). The ability to simulate CO2-water interactions, though it needs to be further evaluated with additional experimental datasets, is an important attribute of models used to project crop yields under elevated CO2 and climate change.

KEYWORDS: CLIMATE CHANGE, ECOSYS, GROWTH, RESPONSES, SIMULATIONS, TEMPERATURE, USE EFFICIENCY, WINTER-WHEAT, YIELD

2419

Tubiello, F.N., C. Rosenzweig, and T. Volk. 1995. Interactions of co2, temperature and management-practices - simulations with a modified version of ceres-wheat. *Agricultural Systems 49(2):135-152.*

A new growth subroutine was developed for CERES-Wheat, a computer model of wheat (Triticum aestivum) growth and development. The new subroutine simulates canopy photosynthetic response to CO2 concentrations and light levels, and includes the effects of temperature on canopy light-use effciency. Its performance was compared to the original CERES-Wheat V-2.10 in 30 different cases. Biomass and yield predictions of the two models were well correlated (correlation coefficient r > 0.95). As an application, summer growth of spring wheat was simulated at one site. Modeled crop responses to higher mean temperatures, different amounts of minimum and maximum warming, and doubled CO2 concentrations were compared to observations. The importance of irrigation and nitrogen fertilization in modulating the wheat crop climatic responses were also analyzed. Specifically, in agreement with observations, rainfed crops were found to be more sensitive to CO2 increases than irrigated ones. On the other hand, low nitrogen applications depressed the ability of the wheat crop to respond positively to CO2 increases. In general, the positive effects of high CO2 grain yield were found to be almost completely counterbalanced by the negative effects of high temperatures. Depending on how temperature minima and maxima were increased, yield changes averaged across management practices ranged from -4% to 8%.

KEYWORDS: CARBON DIOXIDE, CLIMATE, CROP, ENRICHMENT, LEAF-AREA, PHOTOSYNTHESIS, PLANT GROWTH, PRODUCTIVITY, YIELD

2420

Turnbull, M.H., D.T. Tissue, K.L. Griffin, G.N.D. Rogers, and D. Whitehead. 1998. Photosynthetic acclimation to long-term exposure to elevated CO2 concentration in Pinus radiata D. Don. is related to age of needles. *Plant, Cell and Environment 21(10):1019-1028.*

The effects of CO2 enrichment on photosynthesis and ribulose- 1,5-bisphosphate carboxylase/oxygenase (Rubisco) in current year and 1-year-old needles on the same branch were studied on Pinus radiata D. Don. trees growing for 4 years in large, open- top chambers at ambient (36 Pa) and elevated (65 Pa) CO2 partial pressures. At this age trees were 3.5-4 m tall. Measurements made late in the growing cycle (March) showed that photosynthetic rates at the growth CO2 concentration [(pCO(2))(a)] were lower in 1-year-old needles of trees grown at elevated CO2 concentrations than in those of trees grown at ambient (pCO(2))(a). At elevated CO2 concentrations V-cmax (maximum carboxylation rate) was reduced by 13% and J(max) (RuBP regeneration capacity mediated by maximum electron transport rate) by 17%. This corresponded with photosynthetic rates at the growth (pCO(2))(a) of 4.68 +/- 0.41 mu mol m(-2) s(-1) and 6.15 +/- 0.46 mu mol m(-2) s(-1) at 36 and 65 Pa, respectively (an enhancement of 31%). In current year needles photosynthetic rates at the growth (pCO(2))(a) were 6.2 +/- 0.72 mu mol m(-2) s(-1) at 36 Pa and 10.15 +/- 0.64 mu mol m(- 2) s(-1) at 65 Pa (an enhancement of 63%). The smaller enhancement of photosynthesis in 1-year-old needles at 65 Pa was accompanied by a reduction in Rubisco activity (39%) and content (40%) compared with that at 36 Pa. Starch and sugar concentrations in 1-year-old needles were not significantly different in the CO2 treatments. There was no evidence in biochemical parameters for down-regulation at elevated (pCO(2))(a) in fully fexpanded needles of the current year cohort. These data show that enhancement of photosynthesis continues to occur in needles after 4 years' exposure to elevated CO2 concentrations. Photosynthetic acclimation reduces the degree of this enhancement, but only in needles after 1 year of growth. Thus, responses to elevated CO2 concentration change during the lifetime of needles, and acclimation may not be apparent in current year needles. This transitory effect is most probably attributable to the effects of developmental stage and proximity to actively growing shoots on sink strength for carbohydrates. The implications of such age-dependent responses are that older trees, in which the contribution of older needles to the photosynthetic biomass is greater than in younger trees, may become progressively more acclimated to elevated CO2 concentration.

KEYWORDS: CARBON-DIOXIDE CONCENTRATION, CARBOXYLASE ACTIVITY, GAS-EXCHANGE, NOTHOFAGUS-FUSCA, NUTRIENT STATUS, PHASEOLUS-VULGARIS, RISING ATMOSPHERIC CO2, RUBISCO ACTIVITY, SOUR ORANGE TREES, STOMATAL CONDUCTANCE

2421

Tyree, M.T., and J.D. Alexander. 1993. Plant water relations and the effects of elevated co2 - a review and suggestions for future-research. *Vegetatio 104:47-62.*

Increased ambient carbon dioxide (CO2) has been found to ameliorate water stress in the majority of species studied. The results of many studies indicate that lower evaporative flux density is associated with high CO2-induced stomatal closure. As a result of decreases in evaporative flux density and increases in net photosynthesis, also found to occur in high CO2 environments, plants have often been shown to maintain higher water use efficiencies when grown at high CO2 than when grown in normal, ambient air. Plants grown at high CO2 have also been found to maintain higher total water potentials, to increase biomass production, have larger root-to-shoot ratios, and to be generally more drought resistant (through avoidance mechanisms) than those grown at ambient CO2 levels. High CO2- induced changes in plant structure (i.e., vessel or tracheid anatomy, leaf specific conductivity) may be associated with changes in vulnerability to xylem cavitation or in environmental conditions in which runaway embolism is likely to occur. Further study is needed to resolve these important issues. Methodology and other CO2 effects on plant water relations are discussed.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, DRY-MATTER PRODUCTION, HYDRAULIC ARCHITECTURE, INDUCED XYLEM EMBOLISM, LIQUIDAMBAR- STYRACIFLUA, OLD- FIELD PERENNIALS, PINUS-TAEDA SEEDLINGS, RADIATA D-DON, SUB-STOMATAL CAVITIES, WOODY-PLANTS

2422

Ueda, Y., and J.H. Bai. 1993. Effect of short-term exposure of elevated co2 on flesh firmness and ester production of strawberry. *Journal of the Japanese Society for Horticultural Science 62(2):457-464.*

Strawberry fruits (Fragaria X ananasa cv. Hokowase) were treated with 20% CO2 for 12 to 48 hr at 1-degrees-C and then stored at the same temperature for an additional 24 to 48 hr; subsequently they were transferred to 20-degrees-C and held for 8 hours. 1. Berries exposed to CO2, including those stored for 8 hr at 20-degrees-C were firmer than the control berries exposed to air. 2. The CO2 treatment had a little

effect on the evolution of methyl acetate and methyl butyrate, the predominant volatiles. However, the evolution of ethyl acetate and ethyl butyrate, the minor volatiles, was increased sharply by the CO2 treatment. These changes in the concentration of volatiles gave the berries an unnatural aroma. 3. In berries given the same CO2 treatment for 24 hr but stored longer period at 1-degrees-C, the abnormal aroma formation persisted for at least 5 days.

KEYWORDS: ATMOSPHERES, DECAY, METHYLESTERASE, QUALITY

2423
Uprety, D.C. 1998. Carbon dioxide enrichment technology: Open top chambers a new tool for global climate research. *Journal of Scientific & Industrial Research 57(5):266-270.*

There are many technical difficulties in conducting crop response studies for elevated carbon dioxide. Available facilities include green house, leaf cuvettes, phytotron, and air exclusion systems. The environmental control on these systems induces uncertainity in the extrapolation of results to the variable natural environments. However, open top chamber technology does not modify the micro-climate and induces realistic natural conditions. Open top chambers are cylindrical, aluminium frames with clear flexible covering and frustrum to reduce the incursion of external air. CO2 enriched air is introduced into the chamber through a perforated spurt with the help of a blower to distribute CO2 uniformly. A relatively simpler 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 exposures of crops and other ecosystems.

2424
Uprety, D.C., N. Dwivedi, and R. Mohan. 1998. Characterization of CO2 responsiveness in a Brassica oxycamp interspecific hybrid. *Journal of Agronomy and Crop Science-Zeitschrift Fur Acker Und Pflanzenbau 180(1):7-13.*

A study of the characterization of CO2 responsiveness in Brassica oxycamp and its parents Brassica oxyrrhina and Brassica campestris was done using open top chamber technology. The response of the X. B. oxycamp (hybrid) to elevated CO2 was significantly positive in respect of photosynthesis and growth and similar to that of its parent B. campestris is. X B. oxycamp and B. campestris with greater sink potential responded significantly, whereas B. oxyrrhina with a poor sink did not respond to CO2 enrichment. Photosynthetic changes at elevated CO2 levels in the hybrid and parents are partially attributed to the CO2 effects on stomatal conductance and chlorophyll fluorescence.

KEYWORDS: GROWTH, PHOTOSYNTHESIS, RESPONSES

2425
Uprety, D.C., R.S. Mishra, and Y.P. Abrol. 1995. Effect of elevated CO2 on the photosynthesis, growth and water relation of Brassica species under moisture stress. *Journal of Agronomy and Crop Science-Zeitschrift Fur Acker Und Pflanzenbau 175(4):231-237.*

An attempt has been made to study the interactive effect of elevated CO2 and moisture stress on photosynthesis, growth and water relations of Brassica species using open top chambers. It was observed that plants responded to elevated CO2 significantly under moisture stress condition mitigating the adverse effects on photosynthesis and growth of Brassica species. Relatively drought susceptible species, viz. B. campestris and B. nigra, responded to elevated CO2 markedly as compared to less sensitive B. carinata and B. juncea plants. The water status of plants significantly improved under elevated CO2 concentration possibly by increasing stomatal resistance and/or by increased root growth.

KEYWORDS: C-3, LEAVES, TERM, WHEAT

2426
Uprety, D.C., and B.K. Rabha. 1999. Effect of elevated CO2 and moisture stress on the carbon and nitrogen contents in Brassica juncea. *Biologia Plantarum 42(1):133-136.*

The responses of Brassica juncea cv, Pusa Bold to elevated CO2 was studied under water stress. Carbon accumulation in leaves, stem and roots was significantly higher at elevated CO2 concentration, The water stress decreased the carbon content in these plant parts and this adverse effect was reduced by CO2 enrichment. On the contrary nitrogen content of leaves, stem and roots was significantly reduced at elevated CO2. Water stress caused reduction in nitrogen content in these plant parts, similar at ambient as well as elevated CO2 concentration.

KEYWORDS: C-3, GROWTH, PHOTOSYNTHESIS, PLANTS, ROOT FRACTION

2427
Uselman, S.M., R.G. Qualls, and R.B. Thomas. 1999. A test of a potential short cut in the nitrogen cycle: The role of exudation of symbiotically fixed nitrogen from the roots of a N-fixing tree and the effects of increased atmospheric CO2 and temperature. *Plant and Soil 210(1):21-32.*

N-fixing trees facilitate the growth of neighboring trees of other species. These neighboring species benefit from the simple presence of the N fixation symbiosis in their surroundings. Because of this phenomenon, it has been hypothesized that a change in atmospheric CO2 concentration may alter the role of N-fixing trees in their environment. It is thought that the role of N-fixing trees in ecosystems of the future may be more important since they may help sustain growth increases due to increased CO2 concentration in nitrogen limited forests. We examined: (1) whether symbiotically fixed N was exuded from roots, (2) whether a doubled atmospheric CO2 concentration would result in increased organic N exudation from roots, and (3) whether increased temperature or N availability affected N exudation from roots. This study analyzed exudation of dissolved organic N from the roots of seedlings of the N-fixing tree Robinia pseudoacacia L. in a full factorial design with 2 CO2 (35.0 and 70.0 Pa) x 2 temperature (26 or 30 degrees C during the day) x 2 N fertilizer (0 and 10.0 mM N concentration) levels. Trees with no other source of N except N fixation exuded about 1% to 2% of the fixed N through their roots as dissolved organic N. Increased atmospheric CO2 concentrations did not, however, increase N exudation rates on a per gram belowground biomass basis. A 4 degrees C increase in temperature and N fertilization did, however, significantly increase N exudation rates. These results suggest that exudation of dissolved organic N from roots or nodules of N-fixing trees could be a significant, but minor, pathway of transferring N to neighboring plants in a much more rapid and direct way than cycling through death, decomposition and mineralization of plant residues. And, while exudation rates of dissolved organic N from roots were not significantly affected by atmospheric CO2 concentration, the previously observed 'CO2 fertilization effect' on N-fixing trees suggests that N exudation from roots could play a significant but minor role in sustaining increases in forest growth, and thus C storage, in a CO2 enriched atmosphere.

KEYWORDS: BLACK LOCUST, CARBON DIOXIDE, ELEVATED CO2, FOREST, GROWTH, N2 FIXATION, NODULATION, SOUTHERN APPALACHIANS, TRIFOLIUM-REPENS L, WOODY-PLANTS

2428

Usuda, H., and K. Shimogawara. 1998. The effects of increased atmospheric carbon dioxide on growth, carbohydrates, and photosynthesis in radish, Raphanus sativus. *Plant and Cell Physiology 39(1):1-7.*

The effects of sink capacity on the regulation of the acclimation of photosynthetic capacity to elevated levels of carbon dioxide are important from a global perspective. We investigated the effeocts of elevated (750 mu mol mol(-1)) and ambient (350 mu mol mol(-1)) atmospheric CO2 on growth, carbohydrate levels, and photosynthesis in radish seedlings from 15 to 46 d after planting. In radish, a major sink is the storage root, and its thickening is initiated early. Elevated CO2 increased the accumulation of dry matter by 111% but had no effect on the acclimation of the rate of photosynthesis or on the levels of carbohydrates in leaves at dawn, Elevated CO2 increased the dry weight in storage roots by 105% by 46 d after planting, apparently enhancing the sink capacity, This enhanced capacity seemed to be responsible for absorption of elevated levels of photosynthate and to result in the absence of any over-accumulation of carbohydrates in source leaves and the absence of negative acclimation of photosynthetic capacity at the elevated level of CO2.

KEYWORDS: CO2- ENRICHMENT, ELEVATED CO2, GAS-EXCHANGE, PLANT GROWTH, SINK STRENGTH, TEMPERATURE, WHEAT, YIELD

2429

Utriainen, J., and T. Holopainen. 1998. Ultrastructural and growth responses of young Scots pine seedlings (Pinus sylvestris) to increasing carbon dioxide and ozone concentrations. *Chemosphere 36(4-5):795-800.*

Three-year-old Scots pine seedlings were exposed to ambient or elevated (2 x ambient) O-3 and CO2 levels, singly and in combination, during one growth period in open-top field chambers. Growth measurements showed increased shoot length and needle width in response to CO2 enrichment, whereas O-3 exposure resulted in visible injury (chlorotic mottling and increased yellowing of previous year needles). At the ultrastructural level, O-3 caused increased electron density of chloroplast stroma and increased number of cytoplasmic ribosomes at both CO2 levels. CO2 enrichment also resulted in an increase in the size of starch grains in chloroplasts. In general, simultaneous exposure to elevated O-3 reduced the impact of elevated CO2. (C)1998 Elsevier Science Ltd.

KEYWORDS: ELEVATED CO2, EXPOSURE, L KARST, LEAF, NEEDLES, NORWAY SPRUCE, O-3, PICEA-ABIES L, TROPOSPHERIC OZONE

2430

Vadstrup, M., and T.V. Madsen. 1995. Growth limitation of submerged aquatic macrophytes by inorganic carbon. *Freshwater Biology 34(3):411-419.*

1. This study determined the effects of CO2 and HCO3- enrichment on in situ growth of two submerged macrophytes, Elodea canadensis and Callitriche cophocarpa, in two Danish lakes: Lake Hampen and Lake Vaeng. Lake Hampen is an oligotrophic low-alkaline lake (0.4 meg 1(-1)) and Lake Vaeng is mesotrophic with an alkalinity of 1.1 meg 1(-1). In Lake Hampen experiments were carried out throughout the growth season, whereas experiments in Lake Vaeng were restricted to late summer. The CO2 and HCO3- enrichment procedures used increased the concentration of free-CO2 by 500-1000 mu M and the concentration of HCO3- by about 80 CIM. 2. The concentration of free-CO2 in Lake Hampen was about five times atmospheric equilibrium concentration (55 mu M) in early summer declining to virtually zero at the end of summer. 3. Under ambient conditions Callitriche, which is restricted to CO2 use, was unable to grow and survive in both lakes. In contrast, Elodea, which has the potential to use HCO3- in photosynthesis, grew at rates varying from 0.046 to 0.080 day(-1) over the season. 4. Under CO2 enrichment the growth rate of Callitriche varied from 0.089 to 0.124 day-l and for Elodea from 0.076 to 0.117 day(-1) over the season. Enrichment with HCO3- affected Elodea only and only to a limited extent. This may be a result of insufficient increase in [HCO3-] upon enrichment or to a limited capacity of the plants to take up HCO3-. 5. The substantial stimulation of in situ growth of Elodea and Callitriche by enhanced concentrations of free-CO2 shows that inorganic carbon is an important determinant of growth of submerged macrophytes and that inorganic carbon limitation of in situ growth may be a common phenomenon in nature, even in lakes with an alkalinity as high a 1 meg 1(-1). Inorganic carbon, however, is only one of many parameters important for growth, and the growth rates of Elodea at both ambient and high free-CO2 were closely coupled to day length and photon irradiance, indicating that light had an ultimate control on growth.

KEYWORDS: BICARBONATE, COMMUNITIES, DIOXIDE, FRESH-WATER MACROPHYTES, LIGHT, PH, PHOTOSYNTHESIS, TEMPERATURE

2431

Vaisanen, H., H. Standman, and S. Kellomaki. 1994. A model for simulating the effects of changing climate on the functioning and structure of the boreal forest ecosystem - an approach based on object-oriented design. *Tree Physiology 14(7-9):1081-1095.*

We have developed a forest ecosystem model to assess the effects of climate change on the functioning and structure Of boreal coniferoUS forests assuming that temperature and precipitation are the major variables of the niche occupied by a tree species. We specified weather patterns to a level representing the time constant of different physiological and ecological processes relevant to the survival, growth and death of trees. We thereby coupled the long-term dynamics of the forest ecosystem with climate through physiological mechanisms such as photosynthesis and respiration in terms of energy flow through the ecosystem. The hydrological and nutrient cycles couple the dynamics of the forest ecosystem with climate change through soil processes, which represent the thermal and hydraulic properties of the soil, and the decomposition of litter and humus with mineralization of nutrients. Simulations for southern Finland (62-degrees-N) indicated that an increase in temperature of 5-degrees-C over one hundred years could reduce soil water in Scots pine-dominated forest ecosystems. At the same time, the temperature increase could enhance photosynthesis up to 6-8% under current CO2 concentrations (330 ppm) and up to 8-10% under elevated CO2 concentrations (660 ppm). Because the elevated temperature and CO2 concentration caused an increase in respiration (12-14% more than under the current climate), total stem production increased only up to 4% with a 5-degrees-C increase in temperature and up to 6% when temperature and atmospheric CO2 concentration were increased simultaneously. Because transpiration only increased up to 5% in response to elevated temperature and C02 Concentration, the water use efficiency of Scots-pine dominated forest ecosystems increased up to 3%, particularly during the late rotation.

2432

van Breemen, N., A. Jenkins, R.F. Wright, D.J. Beerling, W.J. Arp, F. Berendse, C. Beier, R. Collins, D. van Dam, L. Rasmussen, P.S.J. Verburg, and M.A. Wills. 1998. Impacts of elevated carbon dioxide and temperature on a boreal forest ecosystem (CLIMEX project). *Ecosystems 1(4):345-351.*

To evaluate the effects of climate change on boreal forest ecosystems,

both atmospheric CO2 (to 560 ppmv) and air temperature (by 3 degrees-5 degrees C above ambient) were increased at a forested headwater catchment in southern Norway. The entire catchment (860 m(2)) is enclosed within a transparent greenhouse, and the upper 20% of the catchment area is partitioned such that it receives no climate treatment and serves as an untreated control. Both the control and treatment areas inside the greenhouse receive deacidified rain. Within 3 years, soil nitrogen (N) mineralization has increased and the growing season has been prolonged relative to the control area. This has helped to sustain an increase in plant growth relative to the control and has also promoted increased N export in stream water. Photosynthetic capacity and carbon-nitrogen ratio of new leaves of most plant species did not change. While the ecosystem now loses N, the long-term fate of soil N is a key uncertainty in predicting the future response of boreal ecosystems to climate change.

KEYWORDS: ATMOSPHERIC CO2, LEAF LITTER, MODEL, NITROGEN

2433

Vandasselaar, A.V., and E.A. Lantinga. 1995. Modeling the carbon-cycle of grassland in the netherlands under various management strategies and environmental-conditions. *Netherlands Journal of Agricultural Science 43(2):183-194.*

A simulation model of the carbon cycle of grassland (CCGRASS) was developed to evaluate the long-term effects of different management strategies and various environmental conditions on carbon sequestration in the soil. The results presented here refer to permanent grassland on a young sedimentary loam soil in the Netherlands. The model predicted that the rate of increase in the amount of soil organic carbon will be highest at low to moderate application rates of nitrogen (100 - 250 kg N ha(-1) yr(-1)). This is due to the fact that the annual gross photosynthetic uptake of CO2 in permanent grassland is hardly influenced by the level of N supply. Since N shortage stimulates the growth of the unharvested plant parts (roots and stubble) the carbon supply to the soil is highest at low to moderate N application rates. The rate of increase in the amount of soil organic carbon will be higher under grazing than under mowing as a result of a greater amount of carbon added to the soil. Increase of atmospheric CO2 concentration may induce an increase in decomposition rate of soil organic matter due to simultaneously increased temperatures. At the same time: plant productivity and thus carbon supply to the soil will be stimulated due to the CO2-fertilization effect. Under the assumption of a temperature increase of 3 degrees C if the present atmospheric CO2 concentration doubles, the model predicted that the combined effect of elevated CO2 and temperature will slightly reduce the rate of increase in the amount of organic carbon in grassland soils compared to that under unchanged environmental conditions. There was 2% less carbon sequestration by grassland at the end of a period of 100 years as a result of these changes in environmental conditions. The separate effects of increased temperature or elevated CO2 were 10% less and 10% more carbon storage at the end of a period of 100 years, respectively.

KEYWORDS: BIOSPHERE, CROP RESIDUES, DYNAMICS, ECOSYSTEMS, MINERALIZATION, NITROGEN, ORGANIC-MATTER, SIMULATION, SOILS, TEMPERATURE

2434

Vandegeijn, S.C., J. Vos, J. Groenwold, J. Goudriaan, and P.A. Leffelaar. 1994. The wageningen rhizolab - a facility to study soil-root-shoot- atmosphere interactions in crops .1. Description of main functions. *Plant and Soil 161(2):275-287.*

A research facility is described for the integrated study of soil-root-shoot-atmosphere relationships in crops. The Wageningen Rhizolab has been in use since 1990, and consists of two rows, each with eight below-ground compartments aligned along a corridor. A rain shelter automatically covers the experimental area at the start of rainfall. Compartments are 125 cm x 125 cm and 200 cm deep. Each compartment has a separate drip irrigation system. Crop canopy photosynthesis, respiration, and transpiration can be measured simultaneously and continuously on four out of eight compartments at a time. Each compartment can be filled with a selected soil material (repacked soil) and is accessible from the corridor over its full depth. Multiple sensors for measuring soil moisture status, electrical conductivity, temperature, soil respiration, trace gases and oxygen are installed in spatial patterns in accordance with the requirements of the experiments. Sensors are connected to control and data-acquisition devices. Likewise, provisions have been made to sample manually the soil solution and soil atmosphere. Root observation tubes (minirhizotrons) are installed horizontally at depth intervals ranging from 5 cm (upper soil layers) to 25 cm (below 1 m). The facility is at present in use to study growth and development of vegetation (crops) in relation to drought, nutrient status, soil-borne diseases, and underground root competition. One important application is the study of elevated CO2 concentration and climate change and the way they affect crops and their carbon economy. Growth and development of field grown vegetables and winter cover crops are also evaluated. The common aspect of those studies is to gain a better understanding of crop growth under varying environmental conditions, and to collect datasets that may help to improve mechanistic crop growth simulation models that can address suboptimal growth conditions.

KEYWORDS: GROWTH, MINIRHIZOTRON, WATER

2435

VanderKooij, T.A.W., and L.J. DeKok. 1996. Impact of elevated CO2 on growth and development of Arabidopsis thaliana L. *Phyton-Annales Rei Botanicae 36(2):173-184.*

After germination, Arabidopsis thaliana L (cv. Landsberg) was grown at 350 mu l l(-1) (control) or 700 mu l l(-1) (elevated) CO2. Total shoot biomass at the end of the vegetative growth period was increased by 56% due to a short transient stimulation of the relative growth rate by elevated CO2 at the onset of the exposure. Thereafter the relative growth rate was comparable for both CO2 levels during the remaining vegetative part of the life cycle (0.42 g g(-1) day(-1)). Flowering architecture was not affected by elevated CO2, but seed production was 51% higher. Starch content of the shoot was substantially increased upon exposure to elevated CO2, while the soluble sugar content remained unaffected. Total nitrogen content, on a dry mass basis, was decreased at elevated CO2 mainly as a result of the increased starch content. Photosynthesis wag stimulated at elevated CO2 and no acclimation of the photosynthesis at elevated CO2 was observed. Even though the stimulation of relative growth rate was only temporary, elevated CO2 resulted in an increased fitness of Arabidopsis thaliana by an increased reproductive output.

KEYWORDS: ACCLIMATION, ALLOCATION, ATMOSPHERIC CO2, CARBON DIOXIDE, ENRICHMENT, PHOTOSYNTHESIS, PLANTAGO-MAJOR, RESPIRATION, RESPONSES, SHOOTS

2436

Van der Kooij, T.A.W., L.J. De Kok, and I. Stulen. 1999. Biomass production and carbohydrate content of Arabidopsis thaliana at atmospheric CO2 concentrations from 390 to 1680 mu l l(-1). *Plant Biology 1(4):482-486.*

The concentration dependency of the impact of elevated atmospheric CO2 concentrations on Arabidopsis thaliana L. was studied. Plants were exposed to nearly ambient (390), 560, 810, 1240 and 1680 mu l l(-1)

CO2 during the vegetative growth phase for 8 days. Shoot biomass production and dry matter content were increased upon exposure to elevated CO2. Maximal increase in shoot fresh and dry weight was obtained at 560 mu l l(-1) CO2, which was due to a transient stimulation of the relative growth rate for up to 3 days. The shoot starch content increased with increasing CO2 concentrations up to two-fold at 1680 mu l l(-1) CO2, whereas the contents of soluble sugars and phenolic compounds were hardly affected by elevated CO2. The chlorophyll and carotenoid contents were not substantially affected at elevated CO2 and the chlorophyll a/b ratio remained unaltered. There was no acclimation of photosynthesis at elevated CO2; the photosynthetic capacity of leaves, which had completely developed at elevated CO2 was similar to that of leaves developed in ambient air. The possible consequences of an elevated atmospheric CO2 concentration to Arabidopsis thaliana in its natural habitat is discussed.

KEYWORDS: ACCLIMATION, CARBON DIOXIDE, ELEVATED CO2, GROWTH, METABOLISM, PHOTOSYNTHESIS, PLANTAGO-MAJOR, RISING CO2, STARCH, TOMATO

2437

van der Westhuizen, M.M., and M.D. Cramer. 1998. The influence of elevated rhizosphere dissolved inorganic carbon concentrations on respiratory O-2 and CO2 flux in tomato roots. *Journal of Experimental Botany 49(329):1977-1985.*

Respiratory CO2 and O-2 flux were measured in hydroponically grown Lycopersicon esculentum (L.) Mill. cv. F144 plants at either low (0 mu mol mol(-1)) or elevated CO2 concentrations (>2000 mu mol mol-1) supplied to the roots. In NO3--fed plants the consumption of O-2 and the engagement of the alternative pathway were increased by elevated dissolved inorganic carbon (DIC=CO2+ HCO3-) concentrations. This was ascribed to the influence of organic acids on the ICA cycle and electron transport pathways. Inhibition of O-2 consumption by elevated DIC in NH4+-fed plants may be due to the reduction requirements of anaplerotic carbon entering the TCA cycle or the removal of carbon from the TCA cycle for amino acid synthesis. In both NO3- and NH4+-fed plants elevated DIC inhibited root CO2 release due to high rates of DIC incorporation by phosphoenolpyruvate carboxylase (PEPc) activity. Transient net CO2 consumption due to the inhibition of respiration by salicylhydroxamic acid and KCN, together with high respiratory quotients after the addition of inhibitors of carbonic anhydrase (CA) activity, were also ascribed to high rates of DIC incorporation at elevated DIC concentrations. Ethoxyzolamide, an inhibitor of CA activity, inhibited both D[C-14 incorporation into organic products and NO3- uptake by 81% and 40%, respectively. This, together with a 32% increase in (DIC)-C-14 accumulation and inhibition of NO3- uptake upon inhibition of anion transport by diisothiocyanato-stilbene- 2,2'-disulphonic acid (DIDS) may indicate the exchange of HCO3- for NO3- across the root plasmalemma. It was concluded that dark incorporation of HCO3- by PEPc increased at elevated rhizosphere DIC concentrations and that the products of DIC incorporation may stimulate respiratory electron transport. Additional reducing energy and carbon skeletons from the tricarboxylic acid (TCA) cycle would therefore be available for respiration and the reduction and incorporation of NO3- into amino acids.

KEYWORDS: ASSIMILATION, ATMOSPHERIC CO2, DIOXIDE, LEAF RESPIRATION, LONG-TERM EXPOSURE, METABOLISM, NUTRITION, PLANTS, RESPONSES, TRANSPORT

2438

vandeStaaij, J.W.M., E. Bolink, J. Rozema, and W.H.O. Ernst. 1997. The impact of elevated UV-B (280-320 nm) radiation levels on the reproduction biology of a highland and a lowland population of Silene vulgaris. *Plant Ecology 128(1-2):172-179.*

A highland (altitude 1600 m) and a lowland (altitude -2 m) population of the perennial herb Silene vulgaris were tested on the effects of elevated levels of UV-B radiation on their reproductivity. Highland populations receive higher natural UV- B doses than lowland populations. Therefore adaptation to high W-B levels of the highland population is to be expected. The lowland population showed a decrease in the number of seed producing flowers and the number of seeds produced per plant under elevated UV-B levels. The highland population increased the number of seeds per plant under elevated UV-B levels. In both populations individual seed mass as well as seed germination percentages were unaffected by the UV-B flux received by the parental plant. Possible effects of UV-B induced alterations in reproductivity on the geographical distribution of the different populations are discussed.

KEYWORDS: ALPINE LIFE ZONE, CARBON-DIOXIDE CO2, ELEVATIONAL GRADIENT, GREENHOUSE, GROWTH, INHIBITION, PHOTOSYNTHESIS, PLANTS, SENSITIVITY, ULTRAVIOLET-RADIATION

2439

Vandestaaij, J.W.M., R. Huijsmans, W.H.O. Ernst, and J. Rozema. 1995. The effect of elevated uv-b (280-320 nm) radiation-levels on silene vulgaris - a comparison between a highland and a lowland population. *Environmental Pollution 90(3):357-362.*

Highland (altitude 1600 m above sea level) and lowland (altitude -2 m below sea level) populations of the perennial herb Silene vulgaris (Moench) Garcke, were tested on their response to elevated levels of UV-B radiation. Highland populations typically receive high natural UV-B fluxes, whereas lowland populations receive a lower natural UV-B dose. Adaptation to high UV-B levels of the highland population is to be expected. Experimental comparison of growth rates, gas exchange rates, transpiration and biochemical parameters using adult plants as well as seedlings did not show a difference in the response to elevated UV-B levels between the two populations. Individuals of both populations were relatively insensitive to elevated UV-B radiation. The response of alpine and lowland populations of Silene vulgaris is discussed in relation to the dispersal of this species after the last ice age.

KEYWORDS: ACCLIMATION, ALPINE LIFE ZONE, CARBON-DIOXIDE CO2, GRADIENT, GROWTH, INHIBITION, MECHANISMS, PLANTS, RESPONSES, VEGETATION

2440

Vandestaaij, J.W.M., G.M. Lenssen, M. Stroetenga, and J. Rozema. 1993. The combined effects of elevated co2 levels and uv-b radiation on growth-characteristics of elymus-athericus (= e-pycnanathus). *Vegetatio 104:433-439.*

Elymus athericus (Link) Kerguelen, a C3 grass, was grown in a greenhouse experiment to determine the effect of enhanced atmospheric CO2 and elevated UV-B radiation levels on plant growth. Plants were subjected to the following treatments; a) ambient CO2-Control UV-B, b) ambient CO2-elevated UV-B, c) double CO2-control UV-B, d) double CO2-elevated UV-B. Elevated CO2 concentrations stimulated plant growth, biomass production was 67% higher than at ambient CO2. Elevated UV-B radiation had a negative effect on growth, biomass production was depressed by 31%. Enhanced CO2 combined with elevated UV-B levels caused a biomass depression of 8% when compared with the control plants. UV-B induced growth depression can be modified by a growth stimulus caused by high CO2 concentrations. Growth analysis has been performed and possible physiological mechanisms behind changing growth parameters are discussed.

KEYWORDS: CARBON DIOXIDE, INHIBITION, PLANTS

2441

Vangardingen, P.R., J. Grace, D.D. Harkness, F. Miglietta, and A. Raschi. 1995. Carbon-dioxide emissions at an italian mineral spring - measurements of average co2 concentration and air-temperature. *Agricultural and Forest Meteorology 73(1-2):17-27.*

Emissions of carbon dioxide from vents at the Bossoleto mineral spring in Central Italy have been calculated to exceed 12 t day(-1), This emission leads to enhanced atmospheric concentrations of CO2 over an area of more than 3000 m(2). The vent gas is over 99% pure CO2, with a characteristic isotopic signature that is totally depleted in C-14. At night, concentrations at the bottom of the bowl-like depression can increase to levels approaching 75%. In the morning, this high concentration of CO2 is associated with a rapid temperature increase of over 10 degrees C before the CO2 disperses. This site is being used in a number of studies of the response of plant communities to long-term enhanced CO2 concentrations. The problem of defining CO2 concentrations in these studies was approached by comparing estimates determined by gas analysis measurements and isotopic analysis of leaf material, The isotopic method used C-14 as a tracer, integrating effective concentration over the life of a leaf by calculating from the ratio of C-14 measurements of plant material growing near the spring and at a control site. The estimates obtained using isotopic analysis of leaf material were similar to gas analysis measurements obtained during the day. This suggests that plants at this site are responding to the concentrations during the day, rather than the much higher night-time concentrations, making the system useful for biological research.

KEYWORDS: ENVIRONMENT, FORESTS

2442

van Ginkel, J.H., and A. Gorissen. 1998. In situ decomposition of grass roots as affected by elevated atmospheric carbon dioxide. *Soil Science Society of America Journal 62(4):951-958.*

The effects of elevated CO2 on belowground C input, on decomposition of roots in situ vs. decomposition of disturbed roots, and on soil microbial biomass were investigated in a perennial grass species. Forty ryegrass (Lolium perenne L.) plants were homogeneously C-14-labeled in two controlled environments for 115 d in a continuous (CO2)-C-14 atmosphere at 350 and 700 mu L CO2 L-1 and two soil N levels (low, LN, and high, HN). Thereafter, some of the plants were destructively harvested, Undisturbed root systems of the remaining plants were incubated in situ (IRS) for comparison with a disturbed incubation of the dried and ground roots (DRS) in their original soils. At the start of the incubation, elevated CO2 had increased total C-14-labeled soil C input by 44 and 27% at LN and HN, respectively, compared with input at ambient CO2, After incubation for 230 d, 40% of C-14 soil content was mineralized to (CO2)-C-14 in the disturbed system and 52% in the intact system. Native soil organic matter (SOM) decomposition of the DRS was lower than the SOM decomposition of the IRS, The formation of C-14-labeled soil microbial biomass (C-14-SMB) in the soil with DRS was 130% higher than in the soil with the IRS. Elevated CO2 decreased the decomposition of roots and root-derived products by 10% and increased the size of the C-14-SMB by 28% for both IRS and DRS, whereas the decomposition of SOM was not affected by CO2 at either LN or HN, After plant growth and in situ incubation, the C-14-labeled C in the soil solution showed a highly positive correlation with the amount of C-14-SMB, The ratio between C-14-labeled microorganisms and total (CO2)-C-14 evolved was not affected by elevated CO2, It seems that micrroorganisms adapt to changing soil C input under elevated CO2 and there is no effect on their turnover and behavior.

KEYWORDS: BETULA-PENDULA ROTH, CO2 CONCENTRATIONS, FINE ROOTS, LITTER DECOMPOSITION, LOLIUM-PERENNE, MICROBIAL BIOMASS, NITROGEN, PLANT MATERIALS, SOIL, TURNOVER

2443

vanGinkel, J.H., A. Gorissen, and J.A. vanVeen. 1996. Long-term decomposition of grass roots as affected by elevated atmospheric carbon dioxide. *Journal of Environmental Quality 25(5):1122-1128.*

Carbon input into the soil and decomposition professes under elevated CO2 are highly relevant for C sequestering in the soil. Plant growth and decomposition of root material under ambient and elevated atmospheric CO2 concentrations were monitored in wind tunnels. Grass roots (Lolium perenne L.) were homogeneously C-14-labeled at 350 and 700 mu L L(-1) CO2 and at two N levels to obtain roots of different qualities. This root material was mixed with fresh loamy sand and transferred to four wind tunnels to observe its decomposition in bare soil and as affected by plant growth (L. perenne) at ambient CO2 and elevated CO2 for two growing seasons. After the second growing season, elevated CO2 had stimulated shoot and root growth by 13 and 92%, respectively. The CO2 and N concentrations at which the grass roots had been grown affected the decomposition rate. After the first growing season, the overall decomposition of 700 roots was 19% loner than that of 350 roots. The C-14- labeled microbial biomass in the soil with 700 roots was higher (44%) compared with 350 roots. After the second growing season, the decomposition of 700 low N roots was 14% lower than that of 350 low N roots, whereas the decomposition of the high N roots was unaffected. The C-14-labeled microbial biomass in the soil with 700 roots was still higher (30%) than with 350 roots. The combination of higher root yields at elevated Co-2 combined with a decrease in root decomposition will lead to a longer residence Lime of C in the soil and probably to a higher C storage.

KEYWORDS: CO2- ENRICHMENT, LEAF LITTER, LITTER DECOMPOSITION, MINERALIZATION, NITROGEN, PLANT, QUALITY, RESPONSES, RHIZOSPHERE, SOIL ORGANIC MATTER

2444

vanGinkel, J.H., A. Gorissen, and J.A. vanVeen. 1997. Carbon and nitrogen allocation in Lolium perenne in response to elevated atmospheric CO2 with emphasis on soil carbon dynamics. *Plant and Soil 188(2):299-308.*

The effect of elevated CO2 on the carbon and nitrogen distribution within perennial ryegrass (L. perenne L.) and its influence on belowground processes were investigated. Plants were homogeneously C-14-labelled in two ESPAS growth chambers in a continuous C-14-CO2 atmosphere of 350 and 700 mu L L-1 CO2 and at two soil nitrogen regimes, in order to follow the carbon flow through all plant and soil compartments. After 79 days, elevated CO2 increased the total carbon uptake by 41 and 21% at low (LN) and high nitrogen (HN) fertilisation, respectively. Shoot growth remained unaffected, whereas CO2 enrichment stimulated root growth by 46% and the root/soil respiration by 111%, irrespective of the nitrogen concentration. The total C- 14-soil content increased by 101 and 28% at LN and HN, respectively. The decomposition of the native soil organic matter was not affected either by CO2 or by the nitrogen treatment. Elevated CO2 did not change the total nitrogen uptake of the plant either at LN or at HN. Both at LN and HN elevated CO2 significantly increased the total amount of nitrogen taken up by the roots and decreased the absolute and relative amounts translocated to the shoots. The amount of soil nitrogen immobilised by micro-organisms and the size of the soil microbial biomass were not affected by elevated CO2, whereas both were significantly increased at the higher soil N content. Most striking was the 88% increase in net carbon input into the soil expressed as: C-14-roots plus total C-14-soil content minus the C-12-carbon released by decomposition of native soil organic matter. The net carbon input into the soil at ambient CO2 corresponded with 841 and 1662 kg ha(-1) at LN and HN, respectively. Elevated CO2 increased these amounts with an extra carbon input of 950 and 1056 kg ha(-1). Combined with a reduced decomposition rate of

plant material grown at elevated CO2 this will probably lead to carbon storage in grassland soils resulting in a negative feed back an the increasing CO2 concentration of the atmosphere.

KEYWORDS: DIOXIDE, ENRICHMENT, FEEDBACK, GROWTH, MICROBIAL BIOMASS, PLANT, RHIZOSPHERE, TEMPERATURE, TURNOVER, WHEAT

2445

van Ginkel, J.H., A.P. Whitmore, and A. Gorissen. 1999. Lolium perenne grasslands may function as a sink for atmospheric carbon dioxide. *Journal of Environmental Quality 28(5):1580-1584.*

Model calculations and scenario studies suggest the existence of a considerable positive feedback between temperature and CO2 levels in the atmosphere. Rising temperatures are supposed to increase decomposition of soil organic C leading to increased production of CO2 and this extra CO2 induces a positive feedback by raising the temperature still further. Evidence was found that negative feedback mechanisms also exist: more primary production is allocated to roots as atmospheric CO2 rises and these roots decompose more slowly than roots grown at ambient CO2 levels. Experimental data partly obtained with C- 14-techniques were applied in a grassland C model. The model results show that at an atmospheric CO2 concentration of 700 mu L L-1 increased belowground C storage will be more than sufficient to balance the increased decomposition of soil organic C in a ryegrass (Lolium perenne L.) grassland soil. Once a doubling of the present atmospheric CO2 concentration has been reached, C equivalent to 55% of the annual CO2 increase above 1 ha ryegrass can be withdrawn from the atmosphere. This indicates that grassland soils represent a significant sink for rising atmospheric CO2.

KEYWORDS: CLIMATE CHANGE, DECOMPOSITION, DYNAMICS, ELEVATED CO2, EMISSIONS, MICROBIAL BIOMASS, MODEL, NET PRIMARY PRODUCTION, PLANT, SOIL ORGANIC MATTER

2446

VanHenten, E.J., J. Bontsema, and G. VanStraten. 1997. Improving the efficiency of greenhouse climate control: an optimal control approach. *Netherlands Journal of Agricultural Science 45(1):109-125.*

In this paper a method to improve the efficiency of greenhouse climate control is described. This method is based on the framework of optimal control theory. By exploiting a dynamic model of the greenhouse crop production process, information of the auction price, the operating costs of the climate conditioning equipment and the outdoor climate conditions, the optimal greenhouse climate control scheme balances on a purely objective basis costs against revenues of operating the climate conditioning equipment. Though optimal control of greenhouse climate has received considerable attention in the literature, until now little evidence supported by experimental work has been reported as to the possible improvement in efficiency which can be realised using this approach during a whole growing period. This paper reports a first exploration of this matter for a lettuce crop. In a greenhouse experiment the behaviour of conventional greenhouse climate control supervised by the grower was measured. Then, in simulation experiments, optimal control strategies were calculated for the same conditions (outdoor climate, auction price, energy price). The results obtained support the conclusion that a considerable improvement in the efficiency of greenhouse climate management is possible. This improvement may well exceed 15%.

KEYWORDS: CO2- ENRICHMENT, CROP, FORECAST WIND-SPEED, GROWTH-MODEL, LETTUCE

2447

Vanhinsberg, N., and R.F. Horton. 1992. Ethylene metabolism in pulvini of phaseolus-vulgaris L. *Biochemie Und Physiologie Der Pflanzen 188(1):51-55.*

The ability of leaf blade, pulvinar and petiolar tissue from primary leaves of Phaseolus vulgaris to release ethylene when incubated in a 1 mM solution of the ethylene-biosynthesis precursor, 1-aminocyclopropane-1-carboxylic acid, was determined over a 6h period. Ethylene release was measured under CO2-enriched and CO2-depleted conditions in the light and dark. In contrast to blade and petiolar tissue, the pulvini released more ethylene in the light than in the dark when held in sealed flanks. The amount of the gas released is largely independent of external levels of carbon dioxide.

KEYWORDS: ABSCISSION, ACID, COCCINEUS-L, LEAVES, MOVEMENT, RELEASE

2448

Van Labeke, M.C., and P. Dambre. 1998. Effect of supplementary lighting and CO2 enrichment on yield and flower stem quality of Alstroemeria cultivars. *Scientia Horticulturae 74(4):269-278.*

The effects of CO2 enrichment and supplementary lighting on the production and Rower stem quality of five Alstroemeria cultivars ('Barbara', 'Fiona', 'Helios', 'Mona Lisa' and 'Tiara') were studied. CO2 enrichment up to 900 mu l l(-1) alone was beneficial for an increase in the number of flower stems and flower stem quality regardless of the use of supplementary lighting. Supplementary lighting alone enhanced flower stem production and quality to a lower extent than CO2 enrichment. The combination of both supplementary lighting and CO2 enrichment resulted in superior flower stem production for Alstroemeria 'Fiona', 'Helios' and 'Mona Lisa', and flower stem quality for Alstroemeria 'Barbara', 'Fiona' and 'Mona Lisa'. (C) 1998 Elsevier Science B.V.

KEYWORDS: AIR, CHRYSANTHEMUM-MORIFOLIUM RAMAT, ENVIRONMENT, GREENHOUSE PLANTS, GROWTH-RESPONSES, PHOTOPERIOD, REGINA, TEMPERATURES

2449

vanMinnen, J.G., K.K. Goldewijk, and R. Leemans. 1995. The importance of feedback processes and vegetation transition in the terrestrial carbon cycle. *Journal of Biogeography 22(4-5):805-814.*

The Integrated Model to Assess the Greenhouse Effect (IMAGE 2) is developed to simulate dynamically the global society- biosphere-climate system. The terrestrial C cycle model is an important component of this model. It is implemented on a grid, runs on a annual time step and simulates the major C fluxes between the atmosphere and the biosphere and controls the storage capacity of C in different compartments. The C fluxes are influenced by the direct and indirect response of ecosystems to changing atmospheric CO2 concentrations and climates. Each ecosystem is characterized by its NPP, which depends on environmental conditions. Incorporation of grid cell specific feedback processes is an innovation in this model. Implemented feedback processes are CO2 fertilization, effects of climate change on photosynthesis, plant respiration and decomposition and shifts in vegetation patterns due to climate change and changes in water use efficiency. This paper presents an evaluation of the importance of feedback processes on global and regional scales. Temperature feedback on plant growth is the most important feedback process at the global scale, while CO? fertilization is of lesser importance. However, CO2 fertilization is the most significant feedback in low latitudes, while temperature change most strongly influences the C cycle in the high latitudes. The C dynamics of land cover change, including feedbacks, depend on characteristics of the

former and actual land cover type. The shifts in land cover are parameterized so that they mimic succession. The course and duration of the transitional phase strongly affect the C fluxes. We applied both an equilibrium approach with instantaneous transitions and dynamic approaches with gradual type-dependent transitions. Transitions in natural vegetation between 1990 and 2050 involve about one-third of all grid cells, especially in the higher latitudes. The impact of vegetation transitions on C fluxes differs depending on the instantaneous or gradual transition strategy. The latter results in higher and delayed NEP fluxes, resulting in significantly different atmospheric CO2 concentrations. The dynamic approach is more realistic and should be included in integrated assessment models that project future atmospheric CO2 levels.

KEYWORDS: BIOSPHERE, CLIMATIC CHANGE, CO2-ENRICHMENT, ECOSYSTEMS, NITROGEN, PLANT GROWTH, STORAGE, TEMPERATURE, TRANSIENT-RESPONSE

2450

van Noordwijk, M., P. Martikainen, P. Bottner, E. Cuevas, C. Rouland, and S.S. Dhillion. 1998. Global change and root function. *Global Change Biology 4(7):759-772.*

Global change includes land-use change, elevated CO2 concentrations, increased temperature and increased rainfall variability. All four aspects by themselves and in combination will influence the role of roots in linking below- and above- ground ecosystem function via organic and inorganic resource flows. Root-mediated ecosystem functions which may be modified by global change include below-ground resource (water, nutrients) capture, creation and exploitation of spatial heterogeneity, buffering of temporal variations in above-ground factors, supply and storage of C and nutrients to the belowground ecosystem, mobilization of nutrients and C from stored soil reserves, and gas exchange between soil and atmosphere including the emission from soil of greenhouse gases. The theory of a functional equilibrium between root and shoot allocation is used to explore predicted responses to elevated CO2 in relation to water or nutrient supply as limiting root function. The theory predicts no change in root:shoot allocation where water uptake is the limiting root function, but substantial shifts where nutrient uptake is (or becomes) the limiting function. Root turnover will not likely be influenced by elevated CO2, but by changes in regularity of water supply. A number of possible mechanisms for root-mediated N mineralization is discussed in the light of climate change factors. Rhizovory (root consumption) may increase under global change as the balance between plant chemical defense and adapted root. consuming organisms may be modified during biome shifts in response to climate change. Root-mediated gas exchange allows oxygen to penetrate into soils and methane (CH4) to escape from wetland soils of tundra ecosystems as well as tropical rice production systems. The effect on net greenhouse gas emissions of biome shifts (fens replacing bogs) as well as of agricultural land management will depend partly on aerenchyma in roots.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, ELEVATED CO2, METHANE EMISSION, MYCORRHIZAL COLONIZATION, NITROUS-OXIDE, NORTHERN PEATLANDS, ORGANIC-MATTER, PLANTAGO-MAJOR, TEMPERATE GRASS SWARD, WETLAND PLANTS

2451

van Oene, H., F. Berendse, and C.G.F. de Kovel. 1999. Model analysis of the effects of historic CO2 levels and nitrogen inputs on vegetation succession. *Ecological Applications 9(3):920-935.*

(S)imulation models are useful to analyze and predict the effects of changes in atmospheric CO2 concentration and N deposition on terrestrial ecosystems. The effects of such abiotic changes on ecosystem variables such as nitrogen mineralization and carbon accumulation can affect plant species composition, which in turn may affect various ecosystem processes. However, these interacting effects of plant species composition on ecosystem processes and vice versa are often not included in simulation models. In this paper, a model is developed that includes both plant competition and the flows of nutrients, carbon, and water through the ecosystem. Direct effects of changing atmospheric CO2 on biomass, plant nitrogen concentrations, and litter quantity and quality are simulated together with indirect effects through changes in plant species composition. This model is validated against data from a primary succession chronosequence sere of Dutch inland dunes. For this validation, historical N deposition and atmospheric CO2 concentration records are used. Simulated plant species biomass, organic matter C and N, and total C and N accumulation were found to correspond to measured data. The model simulated plant species replacement well at the different sites of the chronosequence even though the historic conditions differed much between the sites. Additional analyses of the effect of N deposition (preindustrial to present-day) and elevated CO2 (preindustrial to present-day) in this ecosystem showed that N deposition had a strong effect both on vegetation development and on C and N accumulation. Compared to this, the stimulating effects of elevated CO2 on vegetation development were relatively small. Elevated CO2 affected early vegetation development, but the long-term response of vegetation development is dependent on N availability. In old mature forest, N deposition had only small effects while elevated CO2 delayed forest aging. Indirect effects of CO2 on C and N accumulation through changing plant competitive relations may ultimately be larger than direct CO2 effects.

KEYWORDS: CARBON DIOXIDE, CLIMATE, ECOSYSTEMS, ELEVATED CO2, FOREST, GROWTH, MINERALIZATION, NET PRIMARY PRODUCTION, ROOT DISTRIBUTIONS, SCENARIOS

2452

van Oijen, M., and F. Ewert. 1999. The effects of climatic variation in Europe on the yield response of spring wheat cv. Minaret to elevated CO2 and O-3: an analysis of open-top chamber experiments by means of two crop growth simulation models. *European Journal of Agronomy 10(3-4):249-264.*

In the ESPACE-Wheat programme, 25 open-top chamber experiments were carried out in 1994, 1995 and 1996, on nine locations, divided over eight European countries. In most experiments, spring wheat cv. Minaret was subjected to two levels of atmospheric CO2 and two levels of ozone. Grain yields in the control treatments (ambient levels of CO2 and O-3) varied strongly between sites. Also, yield response to elevated CO2 and O-3 showed great variation. The present study was conducted to determine whether climatic differences between sites could account for the observed variation. Two simulation models were used for the analysis: AFRCWHEAT2-O3 and LINTULCC. AFRCWHEAT2- O3 simulates phenology, canopy development and photosynthesis in greater detail than LINTULCC. Both models account for the effects of radiation and temperature on crop growth. New algorithms were developed to simulate the effects of CO2 and O- 3. Weather data that were measured in the experiments were used as input, and simulated growth responses to CO2 and O-3 were compared with measurements. No attempt was made to merge the two models. Thus two independent tools for analysis of data related to climate change were developed and applied. The average measured grain yield in the control treatment, across all 25 experiments, was 5.9 tons per hectare (t ha(-1)), with a standard deviation (SD) of 1.9 t ha(-1). The models predicted similar average yields (5.5 and 5.8 t ha(-1) for AFRCWHEAT2-O3 and LINTULCC, respectively), but smaller variation (SD for both models: 1.2 t ha(-1)). Average measured yield increase due to CO2-doubling was 30% (SD 22%). AFRCWHEAT2-O3 expected a slightly lower value (24%, SD 9%), whereas LINTULCC overestimated the response (42%, SD 11%). The average measured yield decrease due to nearly-doubled O-3 levels was 9% (SD 11%). Both models showed similar results, albeit at lower

variation (7% yield decrease at SDs of 6 and 4%). Simulations accounted well for the observation that, at elevated CO2, the percentage yield loss due to O-3 was lower than at ambient CO2. The models predicted lower variation among sites and years than was measured. Yield response to CO2 and O-3 was predicted to depend on the climate, with a predominant effect of temperature on the response to CO2. In the measurements, these climatic effects were indeed observed, but a greater part of the variation was not related to light intensity, temperature, CO2, or O-3. This unexplained variability in the measured dataset was probably caused by factors not accounted for in the models, possibly related to soil characteristics. We therefore conclude that even perfect information on the climate variables examined in ESPACE-Wheat, i.e. light intensity and temperature, by itself would be insufficient for accurate prediction of the response of spring wheat to future elevated levels of CO2 and O-3. (C) 1999 Elsevier Science B.V. All rights reserved.

KEYWORDS: CARBON DIOXIDE, PLANT-RESPONSES

2453

Van Oijen, M., A.H.C.M. Schapendonk, M.J.H. Jansen, C.S. Pot, and R. Maciorowski. 1999. Do open-top chambers overestimate the effects of rising CO2 on plants? An analysis using spring wheat. *Global Change Biology 5(4):411-421.*

The microclimate in facilities for studying effects of elevated CO2 on crops differs from ambient conditions. Open-top chambers (OTCs) increase temperature by 1-3 degrees C. If temperature and CO2 interact in their effect on crops, this would limit the value of OTC experiments. Furthermore, interaction of CO2 and temperature deserves study because increases in atmospheric CO2 concentration are expected to cause global warming. This paper describes two experiments in which a recently developed cooling system for OTCs was used to analyse the effects of temperature on photosynthesis, growth and yield of spring wheat (Triticum nestivum L., cv. Minaret). Two levels of CO2 were used (350 and 700 ppm), and two levels of temperature, with cooled OTCs being 1.6-2.4 degrees C colder than noncooled OTCs. Photosynthetic rates were increased by elevated CO2, but no effect of temperature was found. Cross-switching CO2 concentrations as well as determination of A-Ci curves showed that plant photosynthetic capacity after anthesis acclimated to elevated CO2. The acclimation may be related to the effects of CO2 on tissue composition: elevated CO2 decreased leaf nitrogen concentrations and increased sugar content. Calculations of the seasonal mean crop light-use efficiency (LUE) were consistent with the photosynthesis data in that CO2 increased LUE by 20% on average whereas temperature had no effect. Both elevating CO2 and cooling increased grain yield, by an average of 11% and 23%, respectively. CO2 and temperature stimulated yield via different mechanisms: CO2 increased photosynthetic rate, but decreased crop light interception capacity (LAI), whereas cooling increased grain yield by increasing LAI and extending the growing season with 10 days. The effects of CO2 and temperature were not additive: the CO2 effect was about doubled in the noncooled open-top chambers. In most cases, effects on yield were mediated through increased grain density rather than increased individual grain weights. The higher growth response to elevated CO2 in noncooled vs. cooled OTCs shows that a cooling system may remove a bias towards overestimating crop growth response to CO2 in open-top chambers.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, GROWTH, LEAVES, NITROGEN, PHOTOSYNTHESIS, RESPONSES, RUBISCO, TEMPERATURE, WINTER-WHEAT

2454

van Oijen, M., A.H.C.M. Schapendonk, M.J.H. Jansen, C.S. Pot, J. van Kleef, and J. Goudriaan. 1998. Effects of elevated CO2 on development and morphology of spring wheat grown in cooled and non-cooled open-top chambers. *Australian Journal of Plant Physiology 25(5):617-626.*

Facilities for studying effects of elevated CO2 on crops affect the microclimate in the crop. Open-top chambers may increase temperature by 1-3 degrees C compared to ambient conditions. This paper describes a newly developed cooling system for open- top chambers. In 1995 and 1996, experiments were carried out to test the system and analyse the effects of temperature on crop phenological and morphological response to elevated CO2. Spring wheat (Triticum aestivum L. cv. Minaret) was subjected to ambient and doubled CO2 concentration in both cooled and non- cooled chambers. The cooling system reduced temperature by 1.6-2.4 degrees C, and this delayed maturity by 10 days. In contrast, elevated CO2 did not affect phenological development. Elevated CO2 reduced tiller density, green leaf number per tiller and specific leaf area, thereby reducing the capacity for light interception of the crop. Crop height growth before anthesis mainly responded to temperature, but after anthesis it was only affected by CO2, indicating a shift from sink- to source-limited growth. For none of the parameters studied, a significant statistical interaction of CO2 and temperature was found. The cooling system proved effective. A temperature difference of about 2 degrees C affected crop development and morphology more strongly than CO2 doubling. However, the absence of CO2-temperature interaction suggests that CO2 effects may validly be investigated even without a cooling system.

KEYWORDS: CARBON-DIOXIDE CONCENTRATION, ENRICHMENT, ENVIRONMENT, FIELD, PLANT-RESPONSES, POLLUTANTS, SORGHUM, TEMPERATURE, TRITICUM-AESTIVUM L, YIELD

2455

Vanoosten, J.J., D. Afif, and P. Dizengremel. 1992. Long-term effects of a co-2 enriched atmosphere on enzymes of the primary carbon metabolism of spruce trees. *Plant Physiology and Biochemistry 30(5):541-547.*

The long-term effects of an enriched CO2 atmosphere on the primary carbon metabolism of 4-year-old spruce trees (Picea abies L. Karst) were examined. Eight key enzymes were studied in 1-year-old needles of trees submitted for two years in open- top chambers to three CO2 levels (350, 480 and 570 ppm V). The specific activity and quantity of ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO, EC 4.1.1.39), and the specific activities of photorespiratory enzymes, glycolate oxidase (EC 1.1.3.15) and hydroxypyruvate reductase (HPR, EC 1.1.1.29) showed a significant decrease in the CO2-enriched atmospheres. By contrast, a net increase was found for the specific activities of the mitochondrial enzymes, NAD-malic enzyme (NAD- ME, EC 1.1.1.39) and especially fumarase (EC 4.2.1.2). The specific activity of phosphofructophosphotransferase (PFP, EC 2.7.1.90), a glycolytic enzyme, did not change while a slight decrease of the activity of glucose 6-phosphate dehydrogenase (G6PDH, EC 1.1.1.49), a pentose phosphate pathway enzyme, was observed. The carboxylating enzyme, phosphoenolpyruvate carboxylase (PEPC, EC 4.1.1.31) showed a marked decrease in activity. These results clearly demonstrate both increases in enzyme activities linked to the respiratory process and decreases in activities of CO2-fixing enzymes as a result of long-term exposure to less than twice the ambient level of CO2.

KEYWORDS: ACCLIMATION, DIOXIDE, ELEVATED CO2, GROWTH, INCREASES, MITOCHONDRIA, PHOSPHOENOLPYRUVATE CARBOXYLASE, PHOTOSYNTHETIC INHIBITION, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, SPECTROPHOTOMETRIC ASSAY

2456

Vanoosten, J.J., and R.T. Besford. 1994. Sugar feeding mimics effect of acclimation to high co2-rapid down-regulation of rubisco small-subunit transcripts but not of the large subunit transcripts. *Journal of Plant Physiology 143(3):306-312.*

The abundance of rbcS transcripts, derived from the nuclear gene-family coding for the small subunit of RuBisCO, was dramatically reduced in tomato plants exposed to high CO2 for 4 days or more whereas the decline in the rbcL RNA transcripts, from the chloroplast gene coding for the large subunit of RuBisCO, was less pronounced. The rate of decline in the abundance of the rbcs transcripts was enhanced when leaves were detached and supplied with water so as to deprive them of any major sink and simultaneously exposed to high CO2. The reduction in the abundance of rbcS mRNA, but nor rbcL, was mimicked when sucrose or glucose was supplied to leaf tissue, whereas acetate or sorbitol had no effect. Based on these and other published data a molecular model involving the repression of transcription of nuclear-encoded genes for chloroplast proteins by photosynthetic end-products is proposed to account for photosynthetic acclimation to high CO2 in tomato and other species.

KEYWORDS: CALVIN CYCLE ENZYMES, EXPRESSION, GENES, HIGH ATMOSPHERIC CO2, LEAVES, PHOTOSYNTHESIS, PLANTS, PROTEIN, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, SUCROSE

2457

Vanoosten, J.J., and R.T. Besford. 1995. Some relationships between the gas-exchange, biochemistry and molecular-biology of photosynthesis during leaf development of tomato plants after transfer to different carbon-dioxide concentrations. *Plant, Cell and Environment 18(11):1253-1266.*

Tomato plants were exposed to four concentrations of CO2 (350, 700, 1050 or 1400 mu mol CO2 mol(-1)) for 31 d. The light- saturated rate of photosynthesis (A) of the unshaded fifth leaf was measured at either an ambient CO2 concentration of 350 mu mol CO2 mol(-1) [A (350)] or at the level of CO2 at which the plants were grown. The chloroplast protein composition and the level of transcripts of nuclear or plastid photosynthesis- associated genes (PAGs), as well as the main carbohydrate content of the fifth leaf maintained horizontal and unshaded, were also measured during leaf development. At 60 and 95 % leaf expansion, the A of high CO2-grown plants measured at growth CO2 was higher than the A (350) of the plants grown at ambient CO2. However, in the fully mature leaves, A (growth CO2) declined linearly as growth CO2 concentration increased. The A (350) of plants exposed to elevated CO2 up to 60% leaf expanion had not acclimated to high CO2. At 95% leaf expansion, A (350) was lower in plants grown at high CO2. A versus CO2 (C-i) for mature leaves showed that A of the plants grown at high CO2 was lower over the entire range than that for plants grown at present ambient CO2 concentration. Lines fitted to the linear part of the A/C-l curves were concurrent at a C-i of 49 mu mol CO2 mol(-1) and A=-1.21 mu mol CO2 m(-2)s(-1). This C-i value is close to Gamma* (46 mu mol CO2 mol(-1)), the compensation point at 27 degrees C calculated from the equation described in Brooks & Farquhar (1985, Planta 165, 397-406). This A is an estimate of respiration in the light (R(1)) and was not affected by acclimation to elevated CO2. Thylakoid proteins (photosystem I core protein, D-1 and D-2 of the photosystem II core complex, cytochrome f) were all reduced by elevated CO2 only in the fully mature leaves (310 exposure), whereas the large and small subunits of Rubisco and Rubisco activase proteins had already declined after 22 d exposure. Transcript levels of the plastid-encoded FAG (rbcL, psbA, psaA-B) were reduced in the mature leaves by elevated CO2 when expressed on a total RNA basis, but they were not sensitive to elevated CO2 when expressed on a chloroplast 16S rRNA basis. However, rbcS, rca and cab mRNA transcripts were lower in the plants grown at high CO2 than in control plants after 22 d exposure when expressed on a nuclear rRNA basis. The loss of these nuclear PAGs was correlated with an accumulation of soluble sugars and starch.

KEYWORDS: ACCLIMATION, ELEVATED CO2, EXPRESSION, GENES, HIGH ATMOSPHERIC CO2, LEAVES, RESPIRATION, RESPONSES, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, RUBISCO ACTIVASE

2458

VanOosten, J.J., and R.T. Besford. 1996. Acclimation of photosynthesis to elevated CO2 through feedback regulation of gene expression: Climate of opinion. *Photosynthesis Research 48(3):353-365.*

Although down-regulation of photosynthesis in higher C-3 plants exposed to long-term elevated CO2 has been recognized in plants with low sink activity or poor nutrient status, the underlying molecular mechanisms remain unclear. This review covers aspects of rising CO2 on plant productivity in general, and then focuses on photosynthesis, biochemistry (stroma and thylakoid proteins, Rubisco activities and metabolites), and gene expression in tomato plants grown under ambient or elevated CO2. Taking into account these data and the recent discovery that glucose triggers repression of photosynthetic gene transcription, a molecular mechanism is proposed for feedback regulation of photosynthesis under high CO2. Different living organisms such as bacteria, yeast, and mammals have been investigated for the sensing mechanisms of the carbohydrate status of their cells, and this information is used together with some recent data obtained for plants to propose how hexose levels might be sensed in higher plant cells.

KEYWORDS: CALVIN CYCLE ENZYMES, CARBON-DIOXIDE CONCENTRATIONS, GAS-EXCHANGE, GLUCOSE REPRESSION, LEAF DEVELOPMENT, PAST 2 CENTURIES, PROTEIN-KINASE, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, RISING ATMOSPHERIC CO2, TOMATO PLANTS

2459

Vanoosten, J.J., D. Wilkins, and R.T. Besford. 1994. Regulation of the expression of photosynthetic nuclear genes by co2 is mimicked by regulation by carbohydrates - a mechanism for the acclimation of photosynthesis to high co2. *Plant, Cell and Environment 17(8):913-923.*

The abundance of transcripts of cab-7 and cab-3C, which code for the chlorophyll a/b binding proteins of the light- harvesting complexes I and II, respectively, and the abundance of transcripts of Rca, which encodes Rubisco activase, were reduced in tomato plants exposed to high CO2 for up to 9d, whereas the abundance of mRNA from psa A-psa B and psb A, which encode the proteins of the core complex of PSI and the D1 protein of PSII, respectively, and the abundance of glycolate oxidase, which is involved in photorespiration, were not affected. However, the abundance of the transcript for the B subunit of ADP-glucose pyrophosphorylase was increased after 1 d at elevated CO2. The chlorophyll am ratio decreased significantly over 9 d of exposure to elevated CO2. The responses of the nuclear genes to high CO2 were enhanced when leaves were detached so as to deprive them of any major sink. The responses of these transcripts to high CO2 were mimicked when sucrose or glucose was supplied to the leaf tissue, whereas acetate or sorbitol had no effect. Carbohydrate analyses of leaves grown in high CO2 or supplied with sucrose revealed that major increases occurred in the amount of glucose and fructose. Based on these and other published data, a molecular model involving the repression or activation of the transcription of nuclear genes coding for chloroplast proteins by photosynthetic end-products is proposed to account for photosynthetic acclimation to high CO2 in tomato plants and other species.

KEYWORDS: ADP-GLUCOSE PYROPHOSPHORYLASE, CALVIN

CYCLE ENZYMES, CARBON-DIOXIDE CONCENTRATION, CDNA CLONE, ELEVATED LEVELS, HIGH ATMOSPHERIC CO2, MESSENGER-RNA LEVELS, PLANTS, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, TOMATO

2460

Vanoosten, J.J., D. Wilkins, and R.T. Besford. 1995. Acclimation of tomato to different carbon-dioxide concentrations - relationships between biochemistry and gas- exchange during leaf development. *New Phytologist 130(3):357-367.*

Tomato plants were transferred to different CO2 mole fractions (350, 700, 1050 and 1400 mu mol CO2 mol(-1)) 31 d after sowing (2% of full expansion) and the light saturated rate of photosynthesis (P-max) of the unshaded 5th leaf was measured at either an ambient CO2 mole fraction, C-a of 350 mu mol CO2 mol(-1) [P-max (350)] or at the mole fraction of CO2 at which the plants were grown. At 60% and 95% leaf expansion, P-max of high CO2 grown plants measured at growth CO2, was greater than the P-max (350) of the ambient CO2 grown plants. However, by leaf maturity, P-max (growth CO2) declined linearly as growth CO2 concentration increased. P-max (350) of plants exposed to elevated CO2 up to 60% leaf expansion had not acclimated to high CO2. At 95% leaf expansion, P-max (350) was smaller in the high CO2 grown plants. P-max (350) was predicted from Rubisco in vitro carboxylation capacity using tomato Rubisco kinetic constants. By 95% leaf expansion, high CO2 grown plants showed similarities to the response of plants to low nitrogen supply, in terms of Rubisco and chlorophyll content. The observed and theoretical relationships between the initial slopes of the P- max/C-i responses and Rubisco activity were statistically equivalent. Both short-term and long-term effects of elevated CO2 on dark respiration (R(n)) were also investigated at two stages of leaf development (50 and 100% expansion). R(a) (growth CO2) was smaller for the high CO2 grown plants compared with the control plants, whereas R(n) (350) was either equal or greater for the plants grown in high CO2.

KEYWORDS: ANTISENSE RBCS, CALVIN CYCLE ENZYMES, ELEVATED CO2, HIGH ATMOSPHERIC CO2, NITROGEN NUTRITION, PHASEOLUS-VULGARIS L, PHOTOSYNTHESIS, RIBULOSE BISPHOSPHATE CARBOXYLASE, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, SHORT- TERM

2461

Vantelgen, H.J., A. Vanmil, and B. Kunneman. 1992. Effect of propagation and rooting conditions on acclimatization of micropropagated plants. *Acta Botanica Neerlandica 41(4):453-459.*

Plantlets of Calathea ornata rooted at frequencies varying between 75 and 100% irrespective of the presence of 6- benzylaminopurine (BAP) or indolebutyric acid (IBA). After transfer to soil all plants grew rapidly with the exception of BAP-rooted plants, probably because these plants lacked lateral roots. Plantlets of Malus showed slightly improved rooting and considerably improved survival at increasing sucrose concentration from 20 to 30 g l(-1) during multiplication. Their survival and performance after planting in soil depended upon the number of roots formed in rooting medium. Elevated CO2-levels (800 ml m-3) during acclimatization increased survival rate and plant height of rooted and non-rooted plantlets.

KEYWORDS: STRAWBERRY PLANTLETS

2462

Vanveen, J.A., E. Liljeroth, L.J.A. Lekkerkerk, and S.C. Vandegeijn. 1991. Carbon fluxes in plant-soil systems at elevated atmospheric CO2 levels. *Ecological Applications 1(2):175-181.*

The flow of carbon from photosynthesizing tissues of higher plants, through the roots and into the soil is one of the key processes in terrestrial ecosystems. An increased level of CO2 in the atmosphere will likely result in an increased input of organic carbon into the soil due to the expected increase in primary production. Whether this will lead to accumulation of greater amounts of organic carbon in soil depends on the flow of carbon through the plant into the soil and its subsequent transformation in the soil by microorganisms. In this paper the major controls of carbon translocation via roots into the soil as well as the subsequent microbial turnover of root-derived carbon are reviewed. We discuss possible consequences of an increased CO2 level in the atmosphere on these processes.

KEYWORDS: AMMONIUM-ENRICHED RAINWATER, DRY-MATTER, MAIZE, MICROBIAL BIOMASS, NITROGEN, ORGANIC-MATTER, ROOT-DERIVED MATERIAL, TURNOVER, WHEAT ROOTS, YOUNG CONIFEROUS TREES

2463

VanVuuren, M.M.I., D. Robinson, A.H. Fitter, S.D. Chasalow, L. Williamson, and J.A. Raven. 1997. Effects of elevated atmospheric CO2 and soil water availability on root biomass, root length, and N, P and K uptake by wheat. *New Phytologist 135(3):455-465.*

We investigated interactions between the effects of elevated atmospheric carbon dioxide concentrations ([CO2]) and soil water availability on root biomass, root length and nutrient uptake by spring wheat (Triticum aestivum cv. Tonic). We grew plants at 350 and 700 mu mol mol(-1) CO2 and with frequent and infrequent watering ('wet' and 'dry' treatments, respectively). Water use per plant was 1.25 times greater at 350 than at 700 mu mol CO2 mol(-1), and 1.4 times greater in the 'wet' than in the 'dry' treatment. Root biomass increased with [CO2] and with watering frequency. Elevated [CO2] changed the vertical distribution of the roots, with a greater stimulation of root growth in the top layers of the soil. These data were confirmed by the video data of root lengths in the 'dry' treatment, which showed a delayed root development at depth under elevated [CO2]. The apparent amount of N mineralized appeared to be equal for all treatments. Nutrient uptake was affected by [CO2] and by watering frequency, and there were interactions between these treatments. These interactions were different for N, K and P, which appeared to be related to differences in nutrient availability and mobility in the soil. Moreover, these interactions changed with time as the root system became larger with [CO2] and with watering frequency, and as fluctuations in soil moisture contents increased. Elevated [CO2] affected nutrient uptake in contrasting ways. Potassium uptake appeared to be reduced by the smaller mass how of water reaching the root surface. However, this might be countered with time by the greater root biomass at elevated [CO2], by the greater soil moisture contents at elevated [CO2], enabling faster diffusion, or both. Phosphorus uptake appeared to be increased by the greater root biomass at elevated [CO2]. We conclude that plant nutrient uptake at elevated [CO2] is affected by interactions with water availability, though differences between nutrients preclude generalizations of the response.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, FIELD, GROWTH, NITROGEN, PHOTOSYNTHESIS, PLANT-RESPONSES, WINTER-WHEAT

2464

VargasSuarez, M., A. RinconGuzman, C. MujicaJimenez, R.A. MunozClares, and E.S. deJimenez. 1996. Influence of carbon source and CO2-enrichment on biochemical parameters associated with photomixotrophia in maize callus cultures. *Journal of Plant Physiology 149(5):585-591.*

To learn about the biochemical processes underlying the induction of

photomixotrophia in maize cell culture, maize calli were cultured in medium containing either glucose or starch as the carbon source. The effect of a CO2-enriched atmosphere on different parameters was tested. Levels of chlorophyll and CO2 fixing enzymes were measured to assess the greening process concomitant to histological observations of chloroplast development. Both starch and glucose promoted higher chlorophyll accumulation in callus cultured under light than sucrose. Histological analysis of green callus grown on glucose-containing medium revealed the formation of poorly developed chloroplasts containing starch grains, whereas in starch medium a large number of elongated chloroplasts containing thylakoids were observed. Exposure of these calli to a CO2-enriched atmosphere enhanced the plastid differentiation process up to mature chloroplasts with grana and intergranal thylakoids. Western-blot analysis demonstrated the presence of CO2-fixing enzymes, Rubisco (EC 4.1.1.39) and PEP carboxylase (EC 4.1.1.31), as well as Rubisco activase in greening callus. Rubisco and PEP carboxylase activities showed large values when starch was me carbon source in the medium. Results of histological analysis and a/b chlorophyll ratios indicated that the chloroplasts formed were of the C-3-type. PEP carboxylase kinetic properties were also consistent with a C-3-type enzyme involved in anaplerotic functions. It is concluded that under the experimental conditions tested, starch plus CO2-enriched atmosphere are the best carbon source for inducing and supporting photomixotrophia in maize cultures, as indicated by several biochemical parameters.

KEYWORDS: BINDING, C-3, CHLOROPLASTS, EXPRESSION, LEAVES, PHOSPHOENOLPYRUVATE CARBOXYLASE, PLANT, POPULATIONS, YIELD, ZEA-MAYS

2465

Varoquaux, P., J. Mazollier, and G. Albagnac. 1996. The influence of raw material characteristics on the storage life of fresh-cut butterhead lettuce. *Postharvest Biology and Technology 9(2):127-139.*

The physiological characteristics of 5 butterhead lettuce cultivars (Lactuca sativa L.) were investigated using etiolated leaves. Their storage life under modified and controlled atmospheres was assessed. When prepacked butterhead lettuce was maintained under a low oxygen atmosphere to prevent enzymatic browning, high CO2 content was the main factor increasing the rate of decay. Shelf life was negatively correlated with respiration rate and susceptibility to CO2. Potassium leakage was a good indicator of physiological disorders. High oxygen and low CO2 enhanced enzymatic browning, while low oxygen and, more significantly, high carbon dioxide enhanced CO2 injury (brown stain). Maintaining CO2 concentration within the packs below 5% resulted in an improved preservation of the lettuce leaves. Practical means for obtaining modified atmospheres which were in equilibrium yet were low in both O-2 and CO2 are discussed.

KEYWORDS: CO2, CRISPHEAD LETTUCE, GROWTH-CONDITIONS, NITROGEN, PLANT-AGE, QUALITY

2466

Vasseur, L., and C. Potvin. 1998. Natural pasture community response to enriched carbon dioxide atmosphere. *Plant Ecology 135(1):31-41.*

We examined the response of a pasture community in southern Quebec (Canada) to long-term exposure of enriched atmospheric CO2 conditions. The study was conducted using open-top growth chambers directly placed on top of the natural pasture community. To investigate the change in the overall species composition in time and space, we used canonical correspondence analysis, a direct ordination method. Over the three years, the overall community responded significantly to enriched CO2. The analyses show that, after three years, CO2 was the most important environmental variable affecting the species composition. Initially the presence of the wall of the chambers influenced the composition but CO2 became more important by the third year. Soil and air temperatures only slightly influenced the community composition. The first two axes of the canonical correspondence analysis explained a large proportion of the variation in the three years and these trends appeared to increase with time. Species such as Agropyron repens appeared to be positively influenced by the presence of the wall (slightly warmer conditions). However, the analyses suggest that Phleum pratense and Trifolium repens, for example, were favored by the increase in atmospheric CO2. The variation in species composition in enriched versus ambient CO2 chambers suggests that the effect of the environmental factors, particularly CO2, were important in affecting the rate and pattern of succession. Furthermore, the temporal increase in importance of the variable CO2 in the present analyses indicates that there might be a time-lag in response to atmospheric enrichment.

KEYWORDS: COMPETITION, ECOSYSTEMS, ELEVATED CO2, GROWTH, LOLIUM-PERENNE, NITROGEN, PHENOTYPIC PLASTICITY, PLANTS, TRIFOLIUM- REPENS

2467

Veisz, O., N. Harnos, L. Szunics, and T. Tischner. 1996. Overwintering of winter cereals in Hungary in the case of global warming. *Euphytica 92(1-2):249-253.*

Under phytotronic conditions investigations were made on the effect of important environmental factors, such as temperature, water and an increasing concentration of atmospheric CO2, on the hardening of young cereal plants. In all the varieties derived from the major wheat growing regions of the world the hardening process was favourably influenced by a doubling of atmospheric CO2 content, so that a significantly larger number of plants survived the frost test than for plants of the same variety raised under normal conditions. A reduction in freezing temperature and an increase in soil moisture content caused a slight reduction in survival % for varieties with excellent frost resistance and a great reduction for those with medium or poor frost resistance. Predictions suggest that in Central Europe, as the result of global climatic changes, there will be a reduction in the quantity of winter precipitation, a considerable rise in winter temperatures and an increase in atmospheric CO2 concentration. Judging by the experimental results, these changes could improve the overwintering of winter cereals; at the same time, however, a number of factors (mainly the reduction of precipitation) leading to yield losses must be expected during the vegetation period.

KEYWORDS: COLD HARDINESS, ELEVATED CO2, GROWTH, TEMPERATURE, WHEAT, YIELD

2468

Velikova, V., T. Tsonev, and I. Yordanov. 1999. Light. and CO2 responses of photosynthesis and chlorophyll fluorescence characteristics in bean giants after simulated acid rain. *Physiologia Plantarum 107(1):77-83.*

The effects of simulated acid rain on some chlorophyll fluorescence characteristics and photosynthetic gas exchange at different light intensities and CO2 concentrations of bean plants were investigated. Measurements were carried out 3, 5 and 24 h after spraying. The results showed that a single acid rain (pH 1.8) treatment of bean plants reduced gas exchange, the maximal carboxylating efficiency and photochemical quenching, This treatment led also to increased CO2 compensation point and non-photochemical quenching and changed the shape of CO2 and light curves of photosynthesis, Both stomatal and non-stomatal factors contributed to the decreased photosynthetic rate, but their proportion changed with time of recovery of the photosynthetic apparatus. Three hours after the treatment, the stomatal factors predominated in

photosynthesis reduction, while during the next experimental period (5-24 h), mainly non-stomatal factors determined the decreased photosynthetic rate, It is suggested that the effects observed in consequence of acid rain treatment could be due to an increased intracellular accumulation of H+ and harmful ions contained in the cocktail, This probably led to impaired membrane permeability, enhancement of stroma acidity, uncoupled electron transport and insufficient accumulation of ATP and NADPH, which affected carbon metabolism.

KEYWORDS: CHLOROPLASTS, DAMAGE, ELECTRON-TRANSPORT, GAS-EXCHANGE, GROWTH, LEAVES, OZONE, PHASEOLUS-VULGARIS, STRESS, TEMPERATURE

2469

Ver, L.M.B., F.T. Mackenzie, and A. Lerman. 1999. Biogeochemical responses of the carbon cycle to natural and human perturbations: Past, present, and future. *American Journal of Science 299(7-9):762-801.*

In the past three centuries, human perturbations of the environment have affected the biogeochemical behavior df the global carbon cycle and that of the other three nutrient elements closely coupled to carbon: nitrogen, phosphorus, and sulfur. The partitioning of anthropogenic CO2 among its various sinks in the past, for the present, and for projections into the near future is controlled by the interactions of these four elemental cycles within the major environmental domains of the land, atmosphere, coastal oceanic zone, and open ocean. We analyze the past, present, and future behavior of the global carbon cycle using the Terrestrial-Ocean-aTmosphere Ecosystem Model (TOTEM), a unique process-based model of the four global coupled biogeochemical cycles of carbon, nitrogen, phosphorus, and sulfur. We find that during the past 300 yrs, anthropogenic CO2 was mainly stored in the atmosphere and in the open ocean. Human activities on land caused an enhanced loss of mass from the terrestrial organic matter reservoirs (phytomass and humus) mainly through deforestation and consequently increased humus remineralization, erosion, and transport to the coastal margins by rivers and runoff. Photosynthetic uptake by the terrestrial phytomass was enhanced owing to fertilization by increasing atmospheric CO2 concentrations and supported by nutrients remineralized from organic matter. TOTEM results indicate that through most of the past 300 yrs, the loss of C from deforestation and other land-use activities was greater than the gain from the enhanced photosynthetic uptake. During the decade of the 1980s, the terrestrial organic reservoirs were in rough carbon balance. Organic and carbonate carbon accumulating in coastal marine sediments is a small but significant sink for anthropogenic CO2. Increasing inputs of terrestrial organic matter and its subsequent oxidation in the coastal margin (increasing heterotrophy) were significant sources of CO2 in coastal waters in the 20th century. However, the coastal ocean did not evolve into a greater net source of CO2 to the atmosphere during this period because of the opposing pressure from rising atmospheric CO2. Since pre-industrial time (since 1700), the net nux of CO2 from the coastal waters has decreased by 40 percent, from 0.20 Gt C/yr to 0.12 Gt C/yr. TOTEM analyses of atmospheric CO2 concentrations for the 21st century were based on the fossil-fuel emission projections of IPCC ("business as usual" scenario) and of the more restrictive UN 1997 Kyoto Protocol. By the mid-21st century, the projected atmospheric CO2 concentrations range from about 550 ppmv (TOTEM,based on IPCC projected emissions) to 510 ppmv (IPCC projection) and to 460 ppmv (TOTEM, based on the Kyoto Protocol reduced emissions). The difference of about 40 ppmv between the IPCC and TOTEM estimates by the year 2050 reflects the different mechanisms within the C-N-P-S cycles on land that are built into our model. The effects of the reduced emissions prescribed by the Kyoto Protocol begin to show in the atmospheric CO2 concentrations by the mid-21st century, when our model projects a rise to 460 (year 2050) and 490 ppmv (2075), relative to about 360 ppmv in 1995. However, these projected increases assume no major changes in the present biogeochemical feedback mechanisms within the system of the coupled C-N-P-S cycles, no global changes in the kind and distribution of ecosystems in response to the rising CO2 and possibly temperature, and no changes in the mechanisms of CO2 exchange between the atmosphere and the ocean, such as could be induced by changes in the intensity of oceanic thermohaline circulation.

KEYWORDS: ATMOSPHERIC CO2, C-13/C-12 RATIO, GLOBAL CLIMATE-CHANGE, ICE CORE, NET PRIMARY PRODUCTION, ORGANIC-CARBON, PRECIPITATION FLUCTUATIONS, SULFUR-OXIDES, TERRESTRIAL ECOSYSTEMS, TROPICAL DEFORESTATION

2470

Verburg, P.S.J., A. Gorissen, and W.J. Arp. 1998. Carbon allocation and decomposition of root-derived organic matter in a plant-soil system of Calluna vulgaris as affected by elevated CO2. *Soil Biology and Biochemistry 30(10-11):1251-1258.*

The effect of elevated CO2 on C allocation in plant and soil was assessed using soil cores planted with 1-y-old heather (Calluna vulgaris (L.) Hull). Plants were pulse-labeled with (CO2)-C-14 at ambient and elevated CO2 and two nitrogen regimes (low and high). After harvesting the plants, the soil was incubated to monitor total respiration and decomposition of C- 14-labeled rhizodeposits. Total and shoot biomass increased at high N but were not affected by CO2. Root biomass was not affected by either N or CO2 treatments. Total C-14 uptake and shoot-C-14 increased upon adding N and elevating CO2 but the N effect was strongest. Total C-14 uptake per unit shoot mass decreased with N, but increased with CO2. Root-C-14 content was not significantly affected by the N or CO2 treatment. Total soil-C-14 slightly increased at elevated CO2 whereas microbial C-14 increased due to high N. C allocation to shoots increased at the expense of roots, soil and respiration at high N but was not affected by the CO2 treatment. Variation in C-14 distribution within each treatment was small compared to variation in total C-14 amounts in each plant-soil compartment. Initially, C-14 respiration from rhizodeposits correlated well with root-C-14, total soil-C-14, soil solution-C-14 and microbial C-14, at harvest time and was increased by elevated CO2. By the end of the incubation, however, decomposition of labeled organic matter was not affected by the treatments whereas total (=C-12+C-14) respiration was lowest for the elevated-CO2 soils. We speculate that initially, respiration is dominated by decomposition of fresh root exudates whereas in the longer term, respiration originates from decomposition of more recalcitrant root material that had been formed during the entire experiment. The increased net C-14 uptake and unchanged distribution pattern, combined with an increased decomposition of easily-decomposable compounds and a decreased decomposition of more recalcitrant root-derived material indicated a small sink function of a Calluna plant-soil system under elevated CO2. (C) 1998 Elsevier Science Ltd. All rights reserved.

KEYWORDS: ATMOSPHERIC CO2, DIOXIDE, ECOSYSTEMS, ENRICHMENT, GROWTH, NITROGEN, RESPIRATION, RESPONSES, RHIZOSPHERE, TURNOVER

2471

Verburg, P.S.J., W.K.P. Van Loon, and A. Lukewille. 1999. The CLIMEX soil-heating experiment: soil response after 2 years of treatment. *Biology and Fertility of Soils 28(3):271-276.*

Most model predictions concerning the response of boreal forest ecosystems to climate change are inferred from small-scale experiments on artificial, simplified systems. Whole-ecosystem experiments designed to validate these models are scarce. We experimentally manipulated a small forested catchment in southern Norway by increasing soil temperature (+3 degrees C in summer to +5 degrees C in winter) using

heating cables installed at 1 cm depth in the litter layer. Especially nitrification in the 0 to 10-cm soil layer increased as a result of the climate manipulation. Betula litter, produced after exposing trees for 2 years to ambient and elevated CO2 in greenhouses, was incubated for 1 year in the manipulated catchment. Exposure to elevated CO2 did not affect the C/N ratio or decomposition of the Betula litter, but lignin content decreased by 10%. We found no effect of elevated temperature on litter decomposition, probably due to desiccation of the litter. The heating cables caused a permanent increase in soil temperature in this soil layer, but when soils were dry, the temperature difference between control and heated plots decreased with increasing distance from the cables. When soils were wet, no gradients in temperature increase occurred.

KEYWORDS: C STORAGE, DISTURBANCE, ELEVATED CO2, LEAF LITTER, LITTER DECOMPOSITION, NITROGEN MINERALIZATION, QUALITY, TEMPERATURE, TERRESTRIAL, WET HEATHLAND ECOSYSTEMS

2472

Vervuren, P.J.A., S.M.J.H. Beurskens, and C.W.P.M. Blom. 1999. Light acclimation, CO2 response and long-term capacity of underwater photosynthesis in three terrestrial plant species. *Plant, Cell and Environment 22(8):959-968.*

To characterize underwater photosynthetic performance in some terrestrial plants, we determined (i) underwater light acclimation (ii) underwater photosynthetic response to dissolved CO2, and (iii) underwater photosynthetic capacity during prolonged submergence in three species that differ in submergence tolerance: Phalaris arundinacea, Rumex crispus (both submergence-tolerant) and Arrhenatherum elatius (submergence-intolerant). None of the species had adjusted to low irradiance after 1 week of submergence. Under non-submerged (control) conditions, only R. crispus displayed shade acclimation, Submergence increased the apparent quantum yield in this species, presumably because of the enhanced CO2 affinity of the elongated leaves, In control plants of the grass species II arundinacea and A. elatius, CO2 affinities were higher than for R, crispus. The underwater photosynthetic capacity of R. crispus increased during 1 month of submergence. In P. arundinacea photosynthesis remained constant during 1 month of submergence at normal irradiance; at low irradiance a reduction in photosynthetic capacity was observed after 2 weeks, although there was no tissue degeneration, In contrast, underwater photosynthesis of the submergence-intolerant species A, elatius collapsed rapidly under both irradiances, and this was accompanied by leaf decay, To describe photosynthesis versus irradiance curves, four models were evaluated, The hyperbolic tangent produced the best goodness-of-fit, whereas the rectangular hyperbola (Michaelis-Menten model) gave relatively poor results.

KEYWORDS: AQUATIC MACROPHYTES, ASSIMILATION, GROWTH, HCO3, INORGANIC CARBON, PHYTOPLANKTON, RICE, SUBMERGENCE, TOLERANCE

2473

Vidal, R., A. Gerbaud, and D. Vidal. 1996. Short-term effects of high light intensities on soybean nodule activity and photosynthesis. *Environmental and Experimental Botany 36(3):349-357.*

There is little information available on the effects of highlight intensity (HLI) on nitrogenase activity in legume nodules. Inhibitory as well as stimulatory effects have been described. The hypothesis that an increase in carbohydrate production is involved in these effects was tested by comparing the effects of high light, high CO2, or low O-2 exposure of the shoot. The HLI treatment consisted of tripling the light intensity to 1200 mu E m(-2) s(-1), compared with the growth intensity of 400 mu E m(-2) s(-1). Acetylene reduction activity (ARA) measuring nitrogenase activity was studied in relation to shoot CO:! exchange. HLI stimulated ARA. The stimulation was progressive and reached 17% after 10 hr of treatment. Photosynthesis (P) was initially doubled, but photoinhibition appeared after about 8 hr of HLI. Under HLI, P became limited by N fixation. Other treatments increasing photosynthesis were compared with HLI: elevating the ambient CO2 concentration around the shoot to 900 ppm, or lowering the O-2 concentration to 2%, increased photosynthesis, respectively, by 55% and 70% without effect on ARA. It is concluded that ARA was not regulated by the availability of carbon assimilates and that specific factors promoting or inhibiting ARA are produced by leaves under HLI.

KEYWORDS: ACETYLENE, ACTIVITY C2H2 REDUCTION, CO2-ENRICHMENT, LEGUME NODULES, NITROGEN-FIXATION, OXYGEN, PHOTOINHIBITION, PHOTORESPIRATION, ROOT-NODULES

2474

Viil, J., and T. Parnik. 1992. Fast regulation of ribulose-1,5-bisphosphate carboxylase oxygenase activity during light dark light transitions. *Soviet Plant Physiology 39(4):483-487.*

On the basis of estimates of rubisco activity in leaves of barley (Hordeum vulgare L.), we established that it declined by 30-50% in 3-4 sec following disconnection of light in the presence of CO2. In a medium without CO2, rubisco activity did not change in this time. Keeping leaves at elevated CO2 concentration lowered rubisco activity. This effect had a lasting aftereffect. With a sharp change of CO2 concentration, the rate of assimilation in the first second was proportional to the increase of CO2 concentration up to at least 1000 mul- liter-1. It is recorded that CO2 binds directly with the enol form of ribulose-1,5-bisphosphate (RuBP) without preliminary binding with the enzyme molecule.

KEYWORDS: CO2, LEAVES, RIBULOSE BISPHOSPHATE CARBOXYLASE, RUBISCO ACTIVASE

2475

Visser, A.J., M. Tosserams, M.W. Groen, G. Kalis, R. Kwant, G.W.H. Magendans, and J. Rozema. 1997. The combined effects of CO2 concentration and enhanced UV-B radiation on faba bean .3. Leaf optical properties, pigments, stomatal index and epidermal cell density. *Plant Ecology 128(1-2):208-222.*

Seedlings of Vicia faba L. (cv. Minica) were grown in a factorial experiment in a greenhouse. The purpose of the study was to determine whether CO2 enrichment and supplemental UV-B radiation affect leaf optical properties and whether the combined effects differ from single factor effects. Seedlings were grown at either 380 mu mol mol(-1) 750 mu mol mol(-1) CO2 and at four levels of W-B radiation. After 20 and 40 days of treatment, absorptance, transmittance and reflectance of photosynthetically active radiation (PAR) were measured on the youngest fully developed leaf. On the same leaf, the specific leaf area on a fresh weight basis (SLA(fw)), chlorophyll content, UV-B absorbance, transmittance of UV light and stomatal index were measured. W-B radiation significantly increased PAR absorptance and decreased PAR transmittance. The increased PAR absorptance can be explained by an increased chlorophyll content in response to W-B radiation. Leaf transmittance of UV radiation decreased with increasing UV-B levels mainly caused by increased absorbance of UV absorbing compounds. UV-B radiation decreased both the stomatal density and epidermal cell density of the abaxial leaf surface, leaving the stomatal index unchanged. Effects of CO2 enrichment were less pronounced than those of W-B radiation. The most important CO2 effect was an increase in stomatal density and epidermal cell density of the adaxial leaf surface.

The stomatal index was not affected. No interaction between CO2 and UV-B radiation was found. The results are discussed in relation to the internal light environment of the leaf.

KEYWORDS: 280-320 NM, ATMOSPHERIC CARBON-DIOXIDE, CROP PLANTS, ELEVATED CO2, GROWTH, RICE ORYZA-SATIVA, STARCH CONTENT, STRATOSPHERIC OZONE, TERRESTRIAL PLANTS, ULTRAVIOLET-RADIATION

2476

Visser, A.J., M. Tosserams, M.W. Groen, G.W.H. Magendans, and J. Rozema. 1997. The combined effects of CO2 concentration and solar UV-B radiation on faba bean grown in open-top chambers. *Plant, Cell and Environment 20(2):189-199.*

The response of faba bean seedlings to the combined effects of increased atmospheric CO2 concentrations ([CO2]) and solar UV-B irradiance was studied using open-top chambers transparent to W-B radiation. The purpose of the study was to determine whether effects of increased [CO2] on growth and physiology are modified by the present solar UV-B fluence rate in the Netherlands. Seedlings were exposed to 350 or 700 mu mol mol(- 1) CO2. At both [CO2], solar UV-B irradiance was either present or reduced using polyester foil opaque to UV-B radiation. To obtain information on the time dependence of increased [CO2] and UV-B radiation effects, three harvests were performed during the experiment, CO2 enrichment resulted in increased biomass production at all harvests. At the final harvest, UV-B radiation did not affect biomass production but a significant decrease was observed after 14 d of treatment. A reduction of the UV-B fluence increased shoot length at both [CO2] throughout the experiment, UV-B radiation slightly altered biomass allocation. Plants grown at reduced levels of UV-B radiation invested less biomass in flowers and more in stem material compared to plants grown at ambient UV-B levels. CO2 enrichment resulted in a stimulation of net photosynthesis after 26 and 38 d of treatment. UV-B reduction did not alter this response. After 26 d of treatment, photosynthetic acclimation to CO2 enrichment was observed, which was probably the result of accumulation of carbohydrates in the leaves. After 38 d, photosynthetic acclimation was no longer present. The UV absorbance of methanolic leaf extracts was increased by CO2 enrichment only. Both CO2 enrichment and solar UV-B reduced the transmittance of radiation through intact attached leaves. Interaction between [CO2] and UV-B radiation was limited to UV- A transmittance of leaves. Under prevalent experimental conditions, UV-B radiation did not affect the measured physiological parameters. Most open-top chambers used for climate change research are constructed of materials which do not transmit UV-B radiation. Our results indicate that part of the 'chamber effects' on plant height often described in the literature might be explained by the absence of solar UV-B radiation in these chambers.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, CARBON DIOXIDE, CROP RESPONSES, ELEVATED CO2, ENHANCEMENT, IRRADIANCE, PHOTOSYNTHESIS, TERRESTRIAL PLANTS, ULTRAVIOLET-B

2477

Vitousek, P.M. 1994. Beyond global warming - ecology and global change. *Ecology 75(7):1861-1876.*

While ecologists involved in management or policy often are advised to learn to deal with uncertainty, there are a number of components of global environmental change of which we are certain-certain that they are going on, and certain that they are human-caused. Some of these are largely ecological changes, and all have important ecological consequences. Three of the well-documented global changes are: increasing concentrations of carbon dioxide in the atmosphere; alterations in the biogeochemistry of the global nitrogen cycle; and ongoing land use/land cover change. Human activity-now primarily fossil fuel combustion-has increased carbon dioxide concentrations from similar to 280 to 355 mu L/L since 1800; the increase is unique, at least in the past 160 000 yr, and several lines of evidence demonstrate unequivocally that it is human-caused. This increase is likely to have climatic consequences-and certainly it has direct effects on biota in all Earth's terrestrial ecosystems. The global nitrogen cycle has been altered by human activity to such an extent that more nitrogen is fixed annually by humanity (primarily for nitrogen fertilizer, also by legume crops and as a byproduct of fossil fuel combustion) than by all natural pathways combined. This added nitrogen alters the chemistry of the atmosphere and of aquatic ecosystems, contributes to eutrophication of the biosphere, and has effects on biological diversity in the most affected areas. Finally, human land use/land cover change has transformed one-third to one-half of Earth's ice-free surface. This in and of itself probably represents the most important component of global change now and will for some decades to come; it has profound effects on biological diversity on land and on ecosystems downwind and downstream of affected areas. Overall, any clear dichotomy between pristine ecosystems and human-altered areas that may have existed in the past has vanished, and ecological research should account for this reality. These three and other equally certain components of global environmental change are the primary causes of anticipated changes in climate, and of ongoing losses of biological diversity. They are caused in turn by the extraordinary growth in size and resource use of the human population. On a broad scale, there is little uncertainty about any of these components of change or their causes. However, much of the public believes the causes-even the existence-of global change to be uncertain and contentious topics. By speaking out effectively, we can help to shift the focus of public discussion towards what can and should be done about global environmental change.

KEYWORDS: AMAZON DEFORESTATION, ATMOSPHERIC CO2, CARBON ISOTOPE DISCRIMINATION, CHALK GRASSLAND, CLIMATE CHANGE, CO2 CONCENTRATION, FRESH-WATER ECOSYSTEMS, NITROUS-OXIDE, PINNATUM L BEAUV, POPULATION GROWTH

2478

Vitousek, P.M., and C.B. Field. 1999. Ecosystem constraints to symbiotic nitrogen fixers: a simple model and its implications. *Biogeochemistry 46(1):179-202.*

The widespread occurrence of N limitation to net primary production (NPP) and other ecosystem processes, despite the ubiquitous occurrence of N-fixing symbioses, remains a significant puzzle in terrestrial ecology. We describe a simple simulation model for an ecosystem containing a generic nonfixer and a symbiotic N fixer, based on: (1) a higher cost for N acquisition by N fixers than nonfixers; (2) growth of fixers and fixation of N only when low N availability limits the growth of nonfixers, and other resources are available; and (3) losses of fixed N from the system only when the quantity of available N exceeds plant and microbial demands. Despite the disadvantages faced by the N fixer under these conditions, N fixation and loss adjust N availability close to the availability of other resources, and biomass and NPP in this simple model can be substantially but only transiently N limited. We then modify the model by adding: (1) losses of N in forms other than excess available N (e.g., dissolved organic N, trace gases produced by nitrification); and (2) constraints to the growth and activity of N fixers imposed by differential effects of shading, P limitation, and grazing. The combination of these processes is sufficient to describe an open system, with input from both precipitation and N fixation, that is nevertheless strongly N-limited at equilibrium. This model is useful for exploring causes and consequences of constraints to N fixation, and hence of N limitation, and we believe it will also be useful for evaluating how N fixation and limitation interact with elevated CO2 and other components

of global enviromental change.

KEYWORDS: ATMOSPHERIC CO2 ENRICHMENT, CARBON DIOXIDE, ELEVATED CO2, FIXATION, FOREST ECOSYSTEMS, GROWTH, LIMITATION, PHOSPHORUS, RESPONSES, TALLGRASS PRAIRIE

2479

Vivin, P., P. Gross, G. Aussenac, and J.M. Guehl. 1995. Whole-plant co2 exchange, carbon partitioning and growth in quercus-robur seedlings exposed to elevated co2. *Plant Physiology and Biochemistry 33(2):201-211.*

Pedunculate oak acorns (Quercus robur L.) were germinated and grown under nonlimiting nutritional and water conditions in controlled-environment greenhouses with ambient (350 mu mol mol(-1)) or elevated (700 mu mol mol(-1)) CO2 concentrations. A semiclosed gas exchange measurements, and (CO2)-C-13 labelling, system (1.5% (CO2)-C-13) was used to simultaneously assess (a) the CO2 exchange of both aerial and below-ground (roots plus soil) compartments of the soil-plant system and (b) the partitioning of the recently photo-assimilated carbon. Measurements were made during the fast aerial growth phase (July 30) and at the end of the growing season (October 15). On July 30, whole-plant dry mass had been increased by 44% since the beginning of the growing season in the elevated CO2 treatment, whereas at the end of the growing season the enhancing effect was only 17%. Elevated CO2 stimulated net CO2 assimilation rate per unit leaf area (A) in July (+40%), whereas in October this stimulation had disappeared. The respiratory CO2 evolution of the root-soil compartment (individual plant basis) was stimulated by 35% under the elevated CO2 conditions on July 30, but not on October 15. In July, relative specific allocation (RSA), a parameter expressing the sink strength, was higher in all compartments under 700 mu mol mol(-1) compared to 350 mu mol mol(-1). Moreover in root tips, the RSA values determined 4 h after the labelling were particularly high (7.8%)with elevated CO2, whereas under ambient CO2 RSA values were close to zero.

KEYWORDS: ALLOCATION, C-13, ENRICHMENT, NITROGEN, PHOTOSYNTHESIS, RESPIRATION, SOURCE-SINK RELATIONS, SOYA BEAN- PLANTS, STEADY-STATE CONDITIONS, ZEA MAYS L

2480

Vivin, P., and J.M. Guehl. 1997. Changes in carbon uptake and allocation patterns in Quercus robur seedlings in response to elevated CO2 and water stress: an evaluation with C-13 labelling. *Annales Des Sciences Forestieres 54(7):597-610.*

A semi-closed (CO2)-C-13 labelling system (1.5% C-13) was used to assess both carbon uptake and allocation within pedunculate oak seedlings (Quercus robur L) grown under ambient (350 vpm) and elevated (700 vpm) atmospheric CO2 concentration ([CO2]) and in either well-watered or droughted conditions. Pulse-chase C-13 labelling data highlighted the direct positive effect of elevated CO2 on photosynthetic carbon acquisition. Consequently, in well-watered conditions, CO2-enriched plants produced 1.52 times more biomass (dry mass at harvest) and 1.33 times more dry root matter (coarse plus fine roots) over the 22-week growing period than plants grown under ambient [CO2]. The root/shoot biomass ratio was decreased both by drought and [CO2], despite lower N concentrations in CO2-enriched plants. However, both long-term and short-term C allocation to fine roots were not altered by CO2, and relative specific allocation (RSA), a parameter expressing sink strength, was hip her in all plant organs under 700 vpm compared to 350 vpm. Results showed that C availability for growth and metabolic processes was greater in fine roots of oaks grown under an elevated CO2 atmosphere irrespective of soil water availability.

KEYWORDS: ATMOSPHERIC CO2, CASTANEA-SATIVA MILL, DRY-WEIGHT, ENRICHMENT, GAS-EXCHANGE, GROWTH-RESPONSE, LOBLOLLY-PINE, MINERAL NUTRITION, RADIATA D-DON, SOIL SYSTEM

2481

Vivin, P., J.M. Guehl, A.M. Clement, and G. Aussenac. 1996. The effects of elevated CO2 and water stress on whole plant CO2 exchange, carbon allocation and osmoregulation in oak seedlings. *Annales Des Sciences Forestieres 53(2-3):447-459.*

Seedlings of Quercus robur L grown under present (350 mu mol mol(-1)) or twice the present (700 mu mol mol(-1)) atmospheric CO2 concentrations, were either maintained well-watered or subjected to a drought constraint late in the growing season (25 August 1993). Despite an initial stimulation of biomass growth (+44%) by elevated CO2, there was no significant difference in plant dry weight at the end of the growing season (15 October 1993) between the two CO2 treatments, irrespective of watering regime. Under drought conditions, although there was no growth increase in response to elevated CO2 concentration, there was a stimulation in net photosynthesis. In addition, the respiration rate of the root + soil system (root dry matter basis) was slightly lower in the elevated than in the ambient CO2 concentration. These results, together with the results from short-term C-13 labelling, suggest enhanced plant carbon losses through processes not assessed here (aerial respiration, root exudation, etc) under elevated CO2 concentration. In the droughted conditions, new carbon relative specific allocation values (RSA) were greater under elevated CO2 than under ambient CO2 concentration in both leaf and root compartments. Osmotic potentials at full turgor (pi(o)) were lowered in response to water stress in leaves by 0.4 MPa for the elevated CO2 treatment only. In roots, osmotic adjustment (0.3 MPa) occurred in both the CO2 treatments.

KEYWORDS: ALBA L, AMBIENT, ATMOSPHERIC CO2, ENRICHMENT, GROWTH, LIMITED CONDITIONS, OSMOTIC ADJUSTMENT, PHOTOSYNTHESIS, RESOURCE USE, RESPONSES

2482

Vivin, P., F. Martin, and J.M. Guehl. 1996. Acquisition and within-plant allocation of C-13 and N-15 in CO2-enriched Quercus robur plants. *Physiologia Plantarum 98(1):89-96.*

We assessed the effects of doubling atmospheric CO2 concentration, [CO2], on C and N allocation within pedunculate oak plants (Quercus robur L.) grown in containers under optimal water supply. A short-term dual (CO2)-C-13 and (NO3-)-N-15 labelling experiment was carried out when the plants had formed their third growing flush. The 22-week exposure to 700 mu l l(- 1) [CO2] stimulated plant growth and biomass accumulation (+53% as compared with the 350 mu l l(-1) [CO2] treatment) but decreased the root/shoot biomass ratio (-23%) and specific leaf area (-18%). Moreover, there was an increase in net CO2 assimilation rate (+37% on a leaf dry weight basis; +71% on a leaf area basis), and a decrease in both above- and below- ground CO2 respiration rates (-32 and -26%, respectively, on a dry mass basis) under elevated [CO2]. C-13 acquisition, expressed on a plant mass basis or on a plant leaf area basis, was also markedly stimulated under elevated [CO2] both after the 12-h (CO2)-C-13 pulse phase and after the 60-h chase phase. Plant N content was increased under elevated CO2 (+36%), but not enough to compensate for the increase in plant C content (+53%). Thus, the plant C/N ratio was increased (+13%) and plant N concentration was decreased (-11%). There was no effect of elevated [CO2] on fine root-specific N-15 uptake (amount of recently assimilated N-15 per unit fine root dry mass), suggesting that modifications of plant N pools were merely linked to root size and not to root function. N concentration was decreased in the leaves of the first and second growing flushes and in the coarse roots, whereas it was unaffected by [CO2] in the stem and in the

actively growing organs (fine roots and leaves of the third growth flush). Furthermore, leaf N content per unit area was unaffected by [CO2]. These results are consistent with the short-term optimization of N distribution within the plants with respect to growth and photosynthesis. Such an optimization might be achieved at the expense of the N pools in storage compartments (coarse roots, leaves of the first and second growth flushes). After the 60-h C-13 chase phase, leaves of the first and second growth flushes were almost completely depleted in recent C-13 under ambient [CO2], whereas these leaves retained important amounts of recently assimilated C-13 (carbohydrate reserves?) under elevated [CO2].

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CASTANEA-SATIVA MILL, DARK RESPIRATION, ELEVATED CO2, ENRICHMENT, GROWTH-RESPONSE, NITROGEN UPTAKE, SOIL SYSTEM, TREE SEEDLINGS, WOODY-PLANTS

2483

Vloedbeld, M., and R. Leemans. 1993. Quantifying feedback processes in the response of the terrestrial carbon-cycle to global change - the modeling approach of image-2. *Water, Air, and Soil Pollution 70(1-4):615-628.*

The terrestrial biosphere component of the Integrated Model to Assess the Greenhouse Effect (IMAGE 2) uses changes in land cover to compute dynamically the C fluxes between the terrestrial biosphere and the atmosphere. The model explores the potential impact of feedback processes incorporated in the model, which are the enhancement of plant growth (CO2 fertilization) and a more efficient use of water under increased CO2 concentrations in the atmosphere; the temperature response of photosynthesis and respiration of plants; the temperature and soil water response of decomposition processes; and the climate-induced changes in vegetation and agricultural patterns with the consequent changes in land cover. In this paper we discuss the implementation and operation of the different feedback processes in the IMAGE 2 model. Results are shown for each process separately as well as the combined processes. The aim of this paper is to quantify the importance of these feedback processes geographically. The main results are that vegetation shifts due to climatic change and increased water use efficiency, CO2 fertilization decreases net C emissions, while changed decomposition rates strongly increase C emissions to the atmosphere. Changes in the global balance between photosynthesis and respiration make little net difference. With the IPPC business-as-usual scenario the terrestrial biosphere continues to emit C into the atmosphere. This behavior is governed by changes in land-use, caused by a multitude of anthropogenic processes.

KEYWORDS: CLIMATE CHANGE, ELEVATED CO2, ENRICHMENT, MATTER, PHOTOSYNTHESIS, PLANT GROWTH, PRODUCTIVITY, SENSITIVITY, STORAGE, TEMPERATURE

2484

Voesenek, L.A.C.J., W.H. Vriezen, M.J.E. Smekens, F.H.M. Huitink, G.M. Bogemann, and C.W.P.M. Blom. 1997. Ethylene sensitivity and response sensor expression in petioles of Rumex species at low O-2 and high CO2 concentrations. *Plant Physiology 114(4):1501-1509.*

Rumex palustris, a flooding-tolerant plant, elongates its petioles in response to complete submergence. This response can be partly mimicked by enhanced ethylene levels and low O-2 concentrations. High levels of CO2 do not markedly affect petiole elongation in R. palustris. Experiments with ethylene synthesis and action inhibitors demonstrate that treatment with low O-2 concentrations enhances petiole extension by shifting sensitivity to ethylene without changing the rate of ethylene production. The expression level of the R. palustris gene coding for the putative ethylene receptor (RP-ERS1) is up- regulated by 3% O-2 and increases after 20 min of exposure to a low concentration of O-2, thus preceding the first significant increase in elongation observable after 40 to 50 min. In the flooding-sensitive species Rumex acetosa, submergence results in a different response pattern: petiole growth of the submerged plants is the same as for control plants. Exposure of R. acetosa to enhanced ethylene levels strongly inhibits petiole growth. This inhibitory effect of ethylene on R. acetosa can be reduced by both low levels of O-2 and/or high concentrations of CO2.

KEYWORDS: CARBON DIOXIDE, DEEP-WATER RICE, FLOODING RESISTANCE, GRASS ECHINOCHLOA-ORYZOIDES, GROWTH-RESPONSES, MARITIMUS L, ORYZA-SATIVA, OXYGEN, SHOOT ELONGATION, SUBMERGENCE

2485

Vogel, C.S., and P.S. Curtis. 1995. Leaf gas-exchange and nitrogen dynamics of n-2-fixing field- grown alnus-glutinosa under elevated atmospheric co2. *Global Change Biology 1(1):55-61.*

Few studies have investigated the effects of elevated CO2 on the physiology of symbiotic N-2-fixing trees. Tree species grown in low N soils at elevated CO2 generally show a decline in photosynthetic capacity over time relative to ambient CO2 controls. This negative adjustment may be due to a reallocation of leaf N away from the photosynthetic apparatus, allowing for more efficient use of limiting N. We investigated the effect of twice ambient CO2 on net CO2 assimilation (A), photosynthetic capacity, leaf dark respiration, and leaf N content of N-2- fixing Alnus glutinosa (black alder) grown in field open top chambers in a low N soil for 160 d. At growth CO2, A was always greater in elevated compared to ambient CO2 plants. Late season A vs. internal leaf p(CO2) response curves indicated no negative adjustment of photosynthesis in elevated CO2 plants. Rather, elevated CO2 plants had 16% greater maximum rate of CO2 fixation by Rubisco. Leaf dark respiration was greater at elevated CO2 on an area basis, but unaffected by CO2 on a mass or N basis. In elevated CO2 plants, leaf N content (mu g N cm(- 2)) increased 50% between Julian Date 208 and 264. Leaf N content showed little seasonal change in ambient CO2 plants. A single point acetylene reduction assay of detached, nodulated root segments indicated a 46% increase in specific nitrogenase activity in elevated compared to ambient CO2 plants. Our results suggest that N-2-fixing trees will be able to maintain high A with minimal negative adjustment of photosynthetic capacity following prolonged exposure to elevated CO2 on N-poor soils.

KEYWORDS: ACETYLENE-REDUCTION, CARBON DIOXIDE, CLIMATE CHANGE, ENRICHMENT, INHIBITION, NODULATION, PHOTOSYNTHESIS, PLANT RESPIRATION, TEMPERATURE, WHOLE PLANT

2486

Vogel, C.S., P.S. Curtis, and R.B. Thomas. 1997. Growth and nitrogen accretion of dinitrogen-fixing Alnus glutinosa (L) Gaertn under elevated carbon dioxide. *Plant Ecology 130(1):63-70.*

Short-term studies of tree growth at elevated CO2 suggest that forest productivity may increase as atmospheric CO2 concentrations rise, although low soil N availability may limit the magnitude of this response. There have been few studies of growth and N-2 fixation by symbiotic N-2-fixing woody species under elevated CO2 and the N inputs these plants could provide to forest ecosystems in the future. We investigated the effect of twice ambient CO2 on growth, tissue N accretion, and N-2 fixation of nodulated Alnus glutinosa (L.) Gaertn. grown under low soil N conditions for 160 d. Root, nodule, stem, and leaf dry weight (DW) and N accretion increased significantly in response to elevated CO2. Whole-plant biomass and N accretion increased 54% and 40%, respectively. Delta-N-15 analysis of leaf tissue indicated that

plants from both treatments derived similar proportions of their total N from symbiotic fixation suggesting that elevated CO2 grown plants fixed approximately 40% more N than did ambient CO2 grown plants. Leaves from both CO2 treatments showed similar relative declines in leaf N content prior to autumnal leaf abscission, but total N in leaf litter increased 24% in elevated compared to ambient CO2 grown plants, These results suggest that with rising atmospheric CO2 N-2-fixing woody species will accumulate greater amounts of biomass N through N-2 fixation and may enhance soil N levels by increased litter N inputs.

KEYWORDS: ATMOSPHERIC CO2 ENRICHMENT, AUTUMN OLIVE, BLACK ALDER, CLIMATE CHANGE, FIXATION, LEAF GAS-EXCHANGE, MINERAL NUTRITION, SOIL-NITROGEN, TISSUE NITROGEN, WOODY-PLANTS

2487

Volin, J.C., and P.B. Reich. 1996. Interaction of elevated CO2 and O-3 on growth, photosynthesis and respiration of three perennial species grown in low and high nitrogen. *Physiologia Plantarum 97(4):674-684.*

Seedlings of three species native to central North America, a C-3 tree, Populus tremuloides Michx., a C-3 grass, Agropyron smithii Rybd., and a C-4 grass, Bouteloua curtipendula Michx., were grown in all eight combinations of two levels each of CO2, O-3 and nitrogen (N) for 58 days in a controlled environment. Treatment levels consisted of 360 or 674 mu mol mol(-1) CO2, 3 or 92 nmol mol(-1) O-3, and 0.5 or 6.0 mM N. In situ photosynthesis and relative growth rate (RGR) and its determinants were obtained at each of three sequential harvests, and leaf dark respiration was measured at the second and third harvests. In all three species, plants grown in high N had significantly greater whole-plant mass, RGR and photosynthesis than plants grown in low N. Within a N treatment, elevated CO2 did not significantly enhance any of these parameters nor did it affect leaf respiration, However, plants of all three species grown in elevated CO2 had lower stomatal conductance compared to ambient CO2-exposed plants. Seedlings of P. tremuloides (in both N treatments) and B. curtipendula (in high N) had significant ozone-induced reductions in whole-plant mass and RGR in ambient but not under elevated CO2. This negative O-3 impact on RGR in ambient CO2 was related to increased leaf dark respiration, decreased photosynthesis and/or decreased leaf area ratio, none of which were noted in high O-3 treatments in the elevated CO2 environment. In contrast, A. smithii was marginally negatively affected by high O-3.

KEYWORDS: ACCLIMATION, CARBON DIOXIDE, ENRICHMENT, GAS-EXCHANGE, LEAF, LIGHT ENVIRONMENT, NET PHOTOSYNTHESIS, OZONE, PINE SEEDLINGS, TUNDRA

2488

Volin, J.C., P.B. Reich, and T.J. Givnish. 1998. Elevated carbon dioxide ameliorates the effects of ozone on photosynthesis and growth: species respond similarly regardless of photosynthetic pathway or plant functional group. *New Phytologist 138(2):315-325.*

Due to their different physiological effects, elevated carbon dioxide and elevated ozone might have interactive impacts on plants, and differentially so on plants differing in photosynthetic pathway and growth rate. To test several hypotheses related to these issues, we examined the physiological, morphological and growth responses of six perennial species grown at various atmospheric concentrations of carbon dioxide and ozone. The species involved (two C-3 trees: Populus tremuloides Michx., Quercus rubra L.; two C-3 grasses: Agropyron smithii Rybd., Koeleria cristata L.; two C-4 grasses: Bouteloua curtipendula Michx., Schizachyrium scoparium Michx.) differed in growth form, stomatal conductance and photosynthetic pathway. In situ photosynthesis, relative growth rate (RGR) and its determinants (leaf area ratio, specific leaf area, leaf weight ratio and root weight ratio) were determined via sequential harvests of seedlings that were grown in all combinations of 366 or 672 mu mol mol(-1) CO2 and 3 or 95 nmol mol(-1) O-3 over a 101-d period. Elevated CO2 had minimal effect on either photosynthesis or RGR. By contrast, RGR for all six species was lower in high O-3 concentrations at ambient CO2, significantly so in A. smithii and P. tremuloides. Five of the six species also exhibited reductions in in situ photosynthesis at ambient CO2 in high-O-3-grown compared with low-O-3-grown plants. For all species, these O-3-induced reductions in RGR and photosynthesis were absent in the elevated CO2 environment. Root weight ratio was significantly reduced by elevated O-3 in A. smithii and P. tremuloides in ambient but not elevated CO2. Species with high stomatal conductance were the most susceptible to oxidant injury, while those with low stomatal conductance, such as the C-4 species and Q. rubra, were not as detrimentally affected by O-3. Elevated levels of CO2 will reduce stomatal conductance and O-3 uptake, and might therefore reduce the potential for oxidant damage. However, there was a stronger relationship of the percent reduction in whole-plant mass due to O-3, related to the ratio of photosynthesis to stomatal conductance. In general, results of this study of six functionally diverse plant species suggest that O-3 pollution effects on carbon balance and growth are likely to be ameliorated by elevated concentrations of atmospheric CO2.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, DARK RESPIRATION, ENRICHMENT, NET PHOTOSYNTHESIS, NITROGEN-AVAILABILITY, O-3, PINE SEEDLINGS, SPRUCE PICEA-ABIES, WINTER HARDINESS

2489

Volin, J.C., M.G. Tjoelker, J. Oleksyn, and P.B. Reich. 1993. Light environment alters response to ozone stress in seedlings of acer-saccharum marsh and hybrid populus L .2. Diagnostic gas-exchange and leaf chemistry. *New Phytologist 124(4):637-646.*

Diagnostic gas exchange measurements and foliar chemical assays were conducted on hybrid poplar (Populus tristis Fisch. x P. balsamifera L. cv. Tristis) and sugar maple (Acer saccharum Marsh.) seedlings grown under contrasting light and ozone treatments. Seedlings were grown in low irradiance (c. 2.5 mol m-2 d-1) and six-fold greater irradiance (c. 16.6 mol m-2 d-1) in combination with low (< 10 nl l-1) and elevated (99-115 nl l-1) ozone. Analysis of light response curves showed ozone-induced reductions in photosynthetic capacity and quantum yield for unshaded poplar and shaded sugar maple, but not the contrasting light treatments. Photosynthesis at saturating CO2 concentrations was decreased in the elevated ozone treatment in both the unshaded and shaded poplar and in shaded sugar maple. Poplar had significant reductions in chlorophyll concentration due to ozone exposure in both unshaded and shaded treatments. Older leaves of unshaded poplar plants had significantly greater reductions in chlorophyll levels due to ozone than older leaves of shaded plants. In maple, only shade-grown leaves had significant decreases in chlorophyll concentration due to ozone exposure. The diagnostic gas exchange measurements in conjunction with chlorophyll measurements indicate that in hybrid poplar, unshaded leaves may be more sensitive to ozone than shade leaves, while in sugar maple, shade leaves are more sensitive to ozone. For hybrid poplar a decrease in photosynthetic capacity, quantum yield and chlorophyll concentration in the unshaded, moderately high light environment due to elevated ozone is consistent with prior studies. The results indicating that sugar maple seedlings may be more detrimentally affected by elevated ozone in the lower light environment may have serious implications for this and other shade-adapted species with respect to their performance in an understorey environment.

KEYWORDS: BIOSYNTHESIS, CARBOXYLASE, CHLOROPHYLL, CO2 EXCHANGE, CONDUCTANCE, GLUTATHIONE, LEAVES, NET PHOTOSYNTHESIS, PHOTON FLUX- DENSITY, POPLAR

2490

von Tiedemann, A., and K.H. Firsching. 1998. Combined whole-season effects of elevated ozone and carbon dioxide concentrations on a simulated wheat leaf rust (Puccinia recondita f. sp. tritici) epidemic. *Zeitschrift Fur Pflanzenkrankheiten Und Pflanzenschutz-Journal of Plant Diseases and Protection 105(6):555-566.*

A complete growth season with the physical climate and ozone pollution from 1 April to 31 July as recorded at a field site in Northern Germany, averaged over several years, was simulated in climate chambers and combined either with a current (370-400 mu l l(-1)) or enriched (620-650 mu l l(-1)) CO2 atmosphere. Wheat, grown from seedling emergence to maturity under the different physico-chemical climates, was inoculated with leaf rust (Puccinia recondita f. sp. tritici) at tillering stage and a rust epidemic was induced by repeated re-inoculations with the newly Formed inoculum. Ozone significantly reduced disease severity, uredospore production and increased the latent period of leaf rust on young planes, consequently inhibiting the epidemic spread on upper leaves of mature plants. Inhibiting effects of ozone on leaf rust development were not reflected by the early infection stages such as spore germination, germ tube growth, formation of infection hyphae, haustorial mother cells and haustoria, which remained largely unaffected by the ozone treatments. However, ozone induced a significantly higher extent of hypersensitive responses of the infected leaf tissue. Additionally, plants exposed to elevated ozone turned senescent much earlier than plants without this stress which prematurely degraded the growth conditions for the fungal pathogen. Enrichment with CO2 increased the rotal carbohydrate content in leaves but this had only minor effects on the disease. Thus, elevated CO2 only poorly compensated for the disease-inhibiting effects of ozone. The compensation of ozone effects on wheat leaf rust by elevated CO2 is much smaller than known compensatory effects of both gases on plans productivity.

KEYWORDS: CO2, GRAMINIS, GROWTH, INFECTION PROCESSES, O-3, OXIDATIVE BURST, RESISTANCE, RESPONSES

2491

Vose, J.M., K.J. Elliott, D.W. Johnson, D.T. Tingey, and M.G. Johnson. 1997. Soil respiration response to three years of elevated CO2 and N fertilization in ponderosa pine (Pinus ponderosa Dong Ex Laws). *Plant and Soil 190(1):19-28.*

We measured growing season soil CO2 evolution under elevated atmospheric [CO2] and soil nitrogen (N) additions. Our objectives were to determine treatment effects, quantify seasonal variation, and compare two measurement techniques. Elevated [CO2] treatments were applied in open-top chambers containing ponderosa pine (Pinus ponderosa L.) seedlings. N applications were made annually in early spring. The experimental design was a replicated factorial combination of CO2 (ambient, +175, and +350 mu L L-1 CO2) and N (0, 10, and 20 g m(-2) N as ammonium sulphate). Soils were irrigated to maintain soil moisture at > 25 percent. Soil CO2 evolution was measured over diurnal periods (20-22 hours) in October 1992, and April, June, and October 1993 and 1994 using a flow- through, infrared gas analyzer measurement system and corresponding pCO(2) measurements were made with gas wells. Significantly higher soil CO2 evolution was observed in the elevated CO2 treatments; N effects were not significant. Averaged across all measurement periods, fluxes, were 4.8, 8.0, and 6.5 for ambient + 175 CO2, and +350 CO2 respectively). Treatment variation was linearly related to fungal occurrence as observed in minirhizotron tubes. Seasonal variation in soil CO2 evolution was non-linearly related to soil temperature; i.e., fluxes increased up to approximately soil temperature (10cm soil depth) and decreased dramatically at temperatures > 18 degrees C. These patterns indicate exceeding optimal temperatures for biological activity. The dynamic, flow-through measurement system was weakly correlated (r = 0.57; p < 0.0001; n = 56) with the pCO(2) measurement method.

KEYWORDS: CARBON-DIOXIDE EVOLUTION, CHAMBERS, EFFLUX, FOREST FLOOR, INTERIOR ALASKA, MOISTURE, PATTERNS, TEMPERATURE, TRACE GAS FLUXES

2492

Vose, J.M., K.J. Elliott, D.W. Johnson, R.F. Walker, M.G. Johnson, and D.T. Tingey. 1995. Effects of elevated co2 and n fertilization on soil respiration from ponderosa pine (pinus-ponderosa) in open-top chambers. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 25(8):1243-1251.*

We measured growing season soil CO2 evolution under elevated atmospheric CO2 and soil nitrogen (N) additions. Our objectives were to determine treatment effects, quantify seasonal variation, and determine regulating mechanisms. Elevated CO2 treatments were applied in open-top chambers containing 3-year- old ponderosa pine (Pinus ponderosa Dougl. ex Laws.) seedlings. Nitrogen applications were made annually in early spring. The experimental design was a replicated factorial combination of CO2 (ambient, +175, and +350 mu L . L(-1) CO2) and N (0, 10, and 20 g . m(-2) N as ammonium sulfate). Soils were irrigated to maintain soil moisture at >25%. Soil CO2 evolution was measured over diurnal periods (20-22 h) in April, June, and October 1993 using a flow-through, infrared gas analyzer measurement system. To examine regulating mechanisms, we linked our results with other studies measuring root biomass with destructive sampling and root studies using minirhizotron techniques. Significantly higher soil CO2 evolution was observed in the elevated CO2 treatments in April and October; N effects were not significant. In October, integrated daily values for CO2 evolution ranged from 3.73 to 15.68 g CO2 . m(- 2)day(-1) for the ambient CO2 + 0 N and 525 mu L . L(-1) CO2 + 20 g . m(-2) N, respectively. Soil CO2 flux among treatments was correlated with coarse root biomass (r(2) = 0.40; p >F = 0.0380), indicating that at least some of the variation observed among treatments was related to variation in root respiration. Across ail sample periods and treatments, there was a significant correlation (r(2) = 0.63; p >F = 0.0001) between soil CO2 evolution acid percent fungal hyphae observed in minirhizotron tubes. Hence, some of the seasonal and treatment variation was also related to differences in heterotrophic activity.

KEYWORDS: CARBON-DIOXIDE EVOLUTION, DECIDUOUS FOREST FLOOR, ECOSYSTEMS, EFFLUX, HARDWOOD FOREST, INTERIOR ALASKA, MOISTURE, PATTERNS, ROOT RESPIRATION, TEMPERATURE

2493

Vourlitis, G.L., W.C. Oechel, S.J. Hastings, and M.A. Jenkins. 1993. A system for measuring insitu co2 and ch4 flux in unmanaged ecosystems - an arctic example. *Functional Ecology 7(3):369-379.*

1. A passive, rapid response, closed system was developed to measure in situ ecosystem CO2 and CH4 flux in 0.5-m2 plots over diurnal, seasonal, and annual time scales in arctic tundra ecosystems. The system consists of a chamber measuring 0.75 m on a side, 0.3 m in height, with acrylic sides, a mylar top, and 6-10 cm radial fans to ensure thorough mixing of the chamber environment. 2. CO2 concentration and flux rates were measured using a Li-Cor 6200 Portable Photosynthesis System, which is capable of measuring 0.1 p.p.m. s-1 changes in CO2 concentration. CH4 flux rates were measured by sequential sampling of the CH4 concentration in the chamber over the duration of a 15-20-min incubation period. 3. Performance analyses indicate that light attenuation was less-than-or- equal-to 10% of ambient light. The rate of temperature increase within the chamber over the duration of the measurement period was approximately 1-5-degrees-C and 0.2-degrees-

C for the majority of the sampling days at tussuck tundra and wet coastal tundra sites, respectively. The maximum increase in thaw depth due to the bases was approximately 10%, and was a function of the site water balance and the amount of time that the bases were in place. Generally, thaw depth in plots with bases was greater when the bases were in place for a longer period of time (greater-than-or-equal-to 1 year), while the bases that were installed during the current growing season had a small effect on plot thaw depths. 4. The system had a minimal effect on ecosystem CO2 flux, compared to plots that lacked bases in a wet coastal tundra and southern California turf ecosystem. 5. The system was successfully used to measure the effect of light intensity, soil temperature, and water balance on ecosystem CO2 flux. 6. Due to the rapid response of the system, high sensitivity to low flux rates, high portability, low cost, potential for use in field experiments, and non-invasive sampling design, the system allows for the reliable measurement of CO2, CH4, and other trace gas flux rates in a variety of ecosystem types.

2494

Vu, J.C.V., L.H. Allen, K.J. Boote, and G. Bowes. 1997. Effects of elevated CO2 and temperature on photosynthesis and Rubisco in rice and soybean. *Plant, Cell and Environment 20(1):68-76.*

Rice (Oryza sativa L. cv. IR-72) and soybean (Glycine max L. Merr. cv. Bragg), which have been reported to differ in acclimation to elevated CO2, were grown for a season in sunlight at ambient and twice-ambient [CO2], and under daytime temperature regimes ranging from 28 to 40 degrees C. The objectives of the study were to test whether CO2 enrichment could compensate for adverse effects of high growth temperatures on photosynthesis, and whether these two C-3 species differed in this regard. Leaf photosynthetic assimilation rates (A) of both species, when measured at the growth [CO2], were increased by CO2 enrichment, but decreased by supraoptimal temperatures. However, CO2 enrichment more than compensated for the temperature-induced decline in A. For soybean, this CO2 enhancement of A increased in a linear manner by 32-95% with increasing growth temperatures from 28 to 40 degrees C, whereas with rice the degree of enhancement was relatively constant at about 60%, from 32 to 38 degrees C. Both elevated CO2 and temperature exerted coarse control on the Rubisco protein content, but the two species differed in the degree of responsiveness. CO2 enrichment and high growth temperatures reduced the Rubisco content of rice by 22 and 23%, respectively, but only by 8 and 17% for soybean. The maximum degree of Rubisco down-regulation appeared to be limited, as in rice the substantial individual effects of these two variables, when combined, were less than additive. Fine control of Rubisco activation was also influenced by both elevated [CO2] and temperature. In rice, total activity and activation were reduced, but in soybean only activation was lowered. The apparent catalytic turnover rate (K-cat) of rice Rubisco was unaffected by these variables, but in soybean elevated [CO2] and temperature increased the apparent K-cat by 8 and 22%, respectively. Post-sunset declines in Rubisco activities were accelerated by elevated [CO2] in rice, but by high temperature in soybean, suggesting that [CO2] and growth temperature influenced the metabolism of 2-carboxyarabinitol-1-phosphate, and that the effects might be species-specific. The greater capacity of soybean for CO2 enhancement of A at supraoptimal temperatures was probably not due to changes in stomatal conductance, but may be partially attributed to less down- regulation of Rubisco by elevated [CO2] in soybean than in rice. However, unidentified species differences in the temperature optimum for photosynthesis also appeared to be important. The responses of photosynthesis and Rubisco in rice and soybean suggest that among C-3 plants species-specific differences will be encountered as a result of future increases in global [CO2] and air temperatures.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CARBON-DIOXIDE, GROWTH, LEAVES, LIGHT, METABOLISM, PLANTS, RESPIRATION, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, SPECIFICITY

2495

Vu, J.C.V., L.H. Allen, G. Bowes, and K.J. Boote. 1997. Kinetic properties of rubisco in rice and soybean grown under elevated CO2, supraoptimal temperature, and drought. *Plant Physiology 114(3):1092.*

2496

Vu, J.C.V., J.T. Baker, A.H. Pennanen, L.H. Allen, G. Bowes, and K.J. Boote. 1998. Elevated CO2 and water deficit effects on photosynthesis, ribulose bisphosphate carboxylase-oxygenase, and carbohydrate metabolism in rice. *Physiologia Plantarum 103(3):327-339.*

Rice (Oryza sativa [L.] cv. IR-72) was grown for a season in sunlit, controlled-environment chambers at 350 or 700 mu mol CO2 mol(-1) under continuously flooded (unstressed) or drought- imposed periods at panicle initiation (stressed). The midday canopy photosynthetic rates (P-n), measured at the CO2 concentration ([CO2]) used for growth, were enhanced by high [CO2] but reduced by drought. High [CO2] increased P-n by 18 to 34% for the unstressed plants, and 6 to 12% for the stressed plants. In the unstressed plants, CO2 enrichment increased water-use efficiency (WUE) by 26%, and reduced evapotranspiration (ET) by 8 to 14%. Both high [CO2] and severe drought decreased the activity and content of ribulose bisphosphate carboxylase-oxygenase (Rubisco). High-CO2- unstressed plants had 6 to 22% smaller content and 5 to 25% lower activity of Rubisco than ambient-CO2-unstressed plants. Under severe drought, reductions of Rubisco were 53 and 27% in activity and 40 and 12% in content, respectively, for ambient- and high-CO2 treatments. The apparent catalytic turnover rate (K-cat) of midday fully activated Rubisco was not altered by high [CO2], but severe drought reduced K-cat by 17 to 23%. Chloroplasts of the high-CO2 leaves contained more, and larger starch grains than those of the ambient-CO2 leaves. High [CO2] did not affect the leaf sucrose content of unstressed plants. In contrast, severe drought reduced the leaf starch and increased the sucrose content in both CO2 treatments. The activity of leaf sucrose phosphate synthase of unstressed plants was not affected by high [CO2], whereas that of ambient- CO2-grown plants was reduced 45% by severe drought. Reduction in ET and enhancements in both P-n and WUE for rice grown under high [CO2] helped to delay the adverse effects of severe drought and allowed the stressed plants to assimilate CO2 for an extra day. Thus, rice grown in the next century may utilize less water, use water more efficiently, and be able to tolerate drought better under some situations.

KEYWORDS: ATMOSPHERIC CO2, CARBON-DIOXIDE ENRICHMENT, CHAMBERS, CLIMATE, LEAVES, PHASEOLUS-VULGARIS, PLANTS, RESPONSES, STRESS, SUCROSE PHOSPHATE SYNTHASE

2497

Vu, J.C.V., R.W. Gesch, L.H. Allen, K.J. Boote, and G. Bowes. 1999. CO2 enrichment delays a rapid, drought-induced decrease in Rubisco small subunit transcript abundance. *Journal of Plant Physiology 155(1):139-142.*

Rice (Oryza sativa L. cv. IR-72) was grown in sunlit chambers at 350 and 700 mu mol CO2 mol(-1) under conditions of continuous flooding (control) or drought which was imposed at panicle initiation, to evaluate the effects of CO2 enrichment and soil water deficit on photosynthesis and Rubisco gene expression. Leaf and canopy photosynthetic rates were enhanced by high [CO2] but reduced by drought. High [CO2] and severe drought both reduced rbcS transcript abundance, along with the

activity, activation and protein content of Rubisco, but the K- m (CO2) was not affected. The transition from moderate to severe drought caused a rapid decline, within 24 h, in the rbcS transcript abundance. High [CO2], however, delayed the adverse effects of severe drought on rbcS transcript abundance and activities of Rubisco, and permitted photosynthesis to continue for an extra day during the drought-stress cycle.

KEYWORDS: ACCLIMATION, ARABIDOPSIS-THALIANA, ATMOSPHERIC CARBON-DIOXIDE, DOWN- REGULATION, ELEVATED CO2, EXPRESSION, PHOTOSYNTHESIS, RBCS, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE, RICE RESPONSES

2498

Vugts, H.F. 1993. The need for micrometeorological research of the response of the energy-balance of vegetated surfaces to co2 enrichment. *Vegetatio 104:321-328.*

A Penman-Monteith equation has been used to evaluate a change in canopy resistance on the evapotranspiration of a savannah and agricultural area in Botswana. After a short introduction, some problems concerning the K-theory or 'first order closure' are indicated when one uses it for transport modelling within and above a canopy. The Penman-Monteith equation was used to calculate the canopy resistance for a savannah vegetation and sorghum under the same environmental conditions. After that, by changing the stomatal resistance due to an increase of the CO2 content, the change in the evapotranspiration was estimated. Finally some recommendations for future research are given and an outline of a proposed FACE experiment is presented.

KEYWORDS: WATER

2499

Vuorinen, A.H., and W.M. Kaiser. 1997. Dark CO2 fixation by roots of willow and barley in media with a high level of inorganic carbon. *Journal of Plant Physiology 151(4):405-408.*

Willow (Salix cv. Aquatica gigantea) and barley (Hordeum vulgare L.) plants were grown in a nutrient solution (pH 7) enriched with HCO3- or gaseous CO2. The initial and potential in vivo rates of dark CO2 fixation in the roots were measured using 0.015 mmol/L and 0.74 mmol/L (HCO3-)-C-14 as substrates of phosphoenolpyruvate carboxylase (PEPC). Enrichment of the nutrient solution with HCO3- or CO2 increased the initial rate of dark CO2 fixation in roots of both willow and barley compared with the corresponding control roots. In plants grown with NO3- the initial activity of PEPC was 38 and 89% higher than in control willow and barley, respectively, after the addition of HCO3-. When the nutrient solutions were enriched with CO2 the initial activity of PEPC increased 52% in willows and 58% in barley, compared with the controls. The supply of HCO3- into NH4+ media increased the initial activity of PEPC in the roots of willows and barley by 50% and 17%, respectively. The amount of soluble protein in the roots was also higher in plants grown with inorganic carbon than in the control plants.

KEYWORDS: AMMONIUM NUTRITION, DIOXIDE FIXATION, NITRATE, NODULE DEVELOPMENT, PHOSPHOENOLPYRUVATE CARBOXYLASE ACTIVITY, PLANTS

2500

Waibel, A.E., T. Peter, K.S. Carslaw, H. Oelhaf, G. Wetzel, P.J. Crutzen, U. Poschl, A. Tsias, E. Reimer, and H. Fischer. 1999. Arctic ozone loss due to denitrification. *Science 283(5410):2064-2069.*

Measurements from the winter of 1994-95 indicating removal of total reactive nitrogen from the Arctic stratosphere by particle sedimentation were used to constrain a microphysical model. The model suggests that denitrification is caused predominantly by nitric acid trihydrate particles in small number densities. The denitrification is shown to increase Arctic ozone Loss substantially. Sensitivity studies indicate that the Arctic stratosphere is currently at a threshold of denitrification. This implies that future stratospheric cooling, induced by an increase in the anthropogenic carbon dioxide burden, is likely to enhance denitrification and to delay until late in the next century the return of Arctic stratospheric ozone to preindustrial values.

KEYWORDS: CLIMATE, CO2, DEHYDRATION, DEPLETION, POLAR STRATOSPHERIC CLOUDS, VERTICAL PROFILES, VORTEX, WINTER

2501

Wait, D.A., C.G. Jones, J. Wynn, and F.I. Woodward. 1999. The fraction of expanding to expanded leaves determines the biomass response of Populus to elevated CO2. *Oecologia 121(2):193-200.*

We examined whether the effects of elevated CO2 on growth of 1- year old Populus deltoides saplings was a function of the assimilation responses of particular leaf developmental stages. Saplings were grown for; 100 days at ambient (approximately 350 ppm) and elevated (ambient + 200 ppm) CO2 in forced-air greenhouses. Biomass, biomass distribution, growth rates, and leaf initiation and expansion rates were unaffected by elevated CO2. Leaf nitrogen (N), the leaf C:N ratio, and leaf lignin concentrations were also unaffected. Carbon gain was significantly greater in expanding leaves of saplings grown at elevated compared to ambient CO2. The Rubisco content in expanding leaves was not affected by CO2 concentration. Carbon gain and Rubisco content were significantly lower in fully expanded leaves of saplings grown at elevated compared to ambient CO2, indicating CO2-induced down-regulation in fully expanded leaves. Elevated CO2 likely had no overall effect on bio mass accumulation due to the more rapid decline in carbon gain as leaves matured in saplings grown at elevated compared to ambient CO2. This decline in carbon gain has been documented in other species and shown to be related to a balance between sink/source balance and acclimation. Our data suggest that variation in growth responses to elevated CO2 can result from differences in leaf assimilation responses in expanding versus expanded leaves as they develop under elevated CO2.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, CARBON-DIOXIDE ENRICHMENT, CARBOXYLASE, GROWTH, LEAF GAS-EXCHANGE, NITROGEN, PHOTOSYNTHESIS, SEEDLINGS, TOMATO PLANTS

2502

Walker, R.F., D.R. Geisinger, D.W. Johnson, and J.T. Ball. 1995. Enriched atmospheric co2 and soil p effects on growth and ectomycorrhizal colonization of juvenile ponderosa pine. *Forest Ecology and Management 78(1-3):207-215.*

Interactive effects of atmospheric CO2 enrichment and soil P fertility on above- and below-ground development of juvenile ponderosa pine (Pinus ponderosa Dougl. ex Laws.) were examined. Seedlings were reared from seed in atmospheres with 700 mu l l(-1), 525 mu l l(-1), or ambient CO2 concentrations, and in a potting mix with 68, 43, or 18 mu g g(-1) soil P, and all were inoculated with the mycobiont Pisolithus tinctorius (Pers.) Coker and Couch shortly after emergence. At 4-month intervals over the 1-year duration of the study, three whole seedlings of each combination of CO2 and P treatments were harvested to permit detailed assessment of shoot and root growth and ectomycorrhizal colonization. After 4 months, shoot volume, root dry weight, and total root length of seedlings grown in 700 mu l(-1) CO2 were greater than those of seedlings grown in the other atmospheres regardless of P

treatment, and shoot/root ratios decreased as the CO2 concentration increased within each P treatment as well. After 8 months, the smallest shoot volumes and root weights and lengths within each P treatment were those of seedlings grown in ambient CO2. Root weight and total length increased as the CO2 concentration increased in high soil P, but the greatest root weights and lengths within the medium and low P treatments were those of seedlings reared in the 525 mu l(-1) CO2 atmosphere. Nevertheless, shoot/root ratios decreased with increasing CO2 in both high and medium soil P at the second harvest, and the highest shoot/root ratio in low P was that of seedlings grown in ambient CO2. After 1 year, the largest shoot and root volumes within the high and medium P treatments were those of seedlings grown in intermediate CO2, while the reverse was true in low P. The effects of CO2 concentration on dry weights, total root length, and shoot/root ratio at the final harvest were nonsignificant. As proved true with seedling growth, CO2 effects on ectomycorrhizal colonization varied temporally, as mycorrhizal development was not affected by the atmospheric treatments after 4 months, while seedlings grown in ambient CO2 exhibited the highest percent infections within each P treatment at the second harvest but those grown in 700 mu l l(-1) CO2 had the highest percentages after 1 year. These results suggest that elevated CO2 exerts stimulatory effects on shoot and root development of juvenile ponderosa pine which may be dependent on P availability to some degree, but these effects are somewhat transient and vary in magnitude over time.

KEYWORDS: ANATOMY, CARBON-DIOXIDE ENRICHMENT, ELEVATED CO2, INCREASES, QUERCUS-ALBA, RESPONSES, SEEDLING GROWTH, WATER

2503

Walker, R.F., D.R. Geisinger, D.W. Johnson, and J.T. Ball. 1995. Interactive effects of atmospheric co2 enrichment and soil n on growth and ectomycorrhizal colonization of ponderosa pine- seedlings. *Forest Science 41(3):491-500.*

Interactive effects of elevated atmospheric CO2 and soil N fertility on above- and belowground development of juvenile ponderosa pine (Pinus ponderosa Dougl, ex Laws.) were examined. Seedlings were grown from seed in atmospheres containing 700 mu l l(-1), 525 mu l l(-1), or ambient CO2. Medium and high soil N treatments were created by adding sufficient (NH4)(2)SO4 to the potting mix to increase total N by 100 mu g g(-1) and 200 mu g g(-1), respectively, while unamended mix, which had a total N concentration of approximately 300 mu g g(-1), served as the low N treatment. Three whole-seedling harvests at 4-month intervals permitted assessment of shoot and root growth and ectomycorrhizal formation resulting from inoculation with Pisolithus tinctorius (Pers.) Coker and Couch. After 4 months, CO2 enrichment increased shoot volume and dry weight of seedlings grown in high soil N, but this result was not evident in the other N treatments and did not persist to the second harvest. Root weight, however, increased, and shoot/root ratio decreased as the CO2 concentration increased within all three N treatments at the first harvest. At the second harvest, root weights within the high and intermediate N treatments were lowest in seedlings grown in ambient CO2 and shoot/root ratios decreased as CO2 increased in these two N treatments as well. Although the ectomycorrhizal infection percentage of seedlings grown in 700 mu l l(-1) CO2 was highest among the seedlings grown in high N after 4 months, mycorrhizal colonization was variable overall at the first and second harvests. After 1 yr, the 525 mu l l(-1) CO2 concentration stimulated above- and belowground growth more than the high CO2 atmosphere in both high and medium soil N. These seedlings also had relatively extensive ectomycorrhizal formation, but colonization was again variable. Results presented here suggest the response of juvenile ponderosa pine to CO2 enrichment is ephemeral, with the effects on roots more pronounced and persistent overall than those on shoots, and that the response is dependent on N availability.

KEYWORDS: ANATOMY, CARBON-DIOXIDE ENRICHMENT, ELEVATED CO2, INCREASES, QUERCUS-ALBA, RESPONSES, WATER

2504

Walker, R.F., D.R. Geisinger, D.W. Johnson, and J.T. Ball. 1997. Elevated atmospheric CO2 and soil N fertility effects on growth, mycorrhizal colonization, and xylem water potential of juvenile ponderosa pine in a field soil. *Plant and Soil 195(1):25-36.*

Interactive effects of atmospheric CO2 enrichment and soil N fertility on above- and below-ground development and water relations of juvenile ponderosa pine (Pinus ponderosa Dougl. ex Laws.) were examined. Open-top field chambers permitted creation of atmospheres with 700 mu L L-1, 525 mu L L-1, or ambient CO2 concentrations. Seedlings were reared from seed in field soil with a total N concentration of approximately 900 mu g g(-1) or in soil amended with sufficient (NH4)(2)SO4 to increase total N by 100 mu g g(-1) or 200 mu g g(-1). The 525 mu L L-1 CO2 treatment within the intermediate N treatment was excluded from the study. Following each of three consecutive growing seasons, whole seedlings of each combination of CO2 and N treatment were harvested to permit assessment of shoot and root growth and ectomycorrhizal colonization. In the second and third growing seasons, drought cycles were imposed by withholding irrigation during which predawn and midday xylem water potential and soil water potential were measured. The first harvest revealed that shoot weight and coarse and fine root weights were increased by growth in elevated CO2. Shoot and root volume and weights were increased by CO2 enrichment at the second harvest, but growth stimulation by the 525 mu L L-1 CO2 concentration exceeded that in 700 mu L L-1 CO2 during the first two growing seasons. At the third harvest, above-and below-ground growth increases were largely confined to the 700 mu L L-1 CO2 treatment, an effect accentuated by high soil N but evident in all N treatments. Ectomycorrhizal formation was reduced by elevated CO2 after one growing season, but thereafter was not significantly affected by CO2 and was unaffected by soil N throughout the study. Results of the xylem water potential measurements were variable, as water potentials in seedlings grown in elevated CO2 were intermittently higher on some measurement days but lower on others than that of seedlings grown in the ambient atmosphere. These results suggest that elevated CO2 exerts stimulatory effects on shoot and root growth of juvenile ponderosa pine under held conditions which are somewhat dependent on N availability, but that temporal variation may periodically result in a greater response to a moderate rise in atmospheric CO2 than to a doubling of the current ambient concentration.

KEYWORDS: ANATOMY, CARBON-DIOXIDE ENRICHMENT, ECTOMYCORRHIZAL COLONIZATION, PHOSPHORUS, QUERCUS-ALBA, RESPONSES, RHIZOSPHERE, SEEDLING GROWTH, STRESS, TAEDA

2505

Walker, R.F., D.R. Geisinger, D.W. Johnson, and J.T. Ball. 1998. Atmospheric CO2 enrichment and soil N fertility effects on juvenile ponderosa pine: Growth, ectomycorrhizal development, and xylem water potential. *Forest Ecology and Management 102(1):33-44.*

Interactive effects of elevated atmospheric CO2 and soil N fertility on above-and below-ground growth, mycorrhizal colonization, and water relations of juvenile ponderosa pine (Pious ponderosa Dougl. ex Laws.) were investigated. One-year- old seedlings were planted in undisturbed field soil within open-top chambers which permitted creation of atmospheres with 700 mu l l(-1), 525 mu l l(-1), or ambient CO2 concentrations. High and medium soil N treatments were imposed by incorporating sufficient (NH4)(2)SO4 to increase total N by 200 mu g g(-1) and 100 mu g g(-1), respectively, while unamended soil, which had

a total N concentration of approximately 900 mu g g(-1), constituted the low N treatment. Following each of two consecutive field growing seasons, whole seedlings of every combination of CO2 and N treatment were harvest-ed to permit assessment of shoot and root growth and quantification of ectomycorrhizal development. Late in the second growing season, a simulated drought episode was imposed by withholding irrigation during which predawn and midday xylem water potential and soil water potential were measured. The initial harvest revealed that coarse and fine root weights were increased by CO2 enrichment during the first growing season. This result was most apparent in the 525 mu l l(-1) CO2 treatment and high soil N, which produced the greatest root volume as well. Shoot/root ratio decreased with increasing CO2 at the first harvest. After two growing seasons, elevated CO2 increased seedling diameter, shoot and root volume, and shoot and coarse root weight, again most prominently in high N. Unlike the initial results, however, stimulation of seedling growth by the 700 mu l l(-1) CO2 atmosphere exceeded that in 525 mu l l(-1) CO2 after two growing seasons, and shoot/root ratio was unaffected by either CO2 or N. At both harvests, seedlings grown in the enriched atmospheres generally had higher mycorrhizal counts and greater percentages of colonized root length, but differences among treatments in ectomycorrhizal development were nonsignificant regardless of quantification method. During the imposed drought episode, xylem water potential of seedlings grown in elevated CO2 descended below that of seedlings grown in the ambient atmosphere as soil water potential decreased, most notably in the predawn measurements. These results suggest that CO2 enrichment stimulates shoot and root growth of juvenile ponderosa pine under field conditions, a response somewhat dependent on soil N availability. However, below-ground growth is not increased proportionally more than that above ground, which may predispose this species to greater stress when soil water is limited. (C) 1998 Elsevier Science B.V.

KEYWORDS: CARBON-DIOXIDE ENRICHMENT, ELEVATED CO2, MYCORRHIZAL COLONIZATION, NUTRIENT STATUS, PHOSPHORUS, QUERCUS-ALBA, RESPONSES, RHIZOSPHERE, SEEDLING GROWTH, TAEDA

2506

Walker, R.F., D.W. Johnson, D.R. Geisinger, and J.T. Ball. 1998. Growth and ectomycorrhizal colonization of ponderosa pine seedlings supplied different levels of atmospheric CO2 and soil N and P. *Forest Ecology and Management 109(1-3):9-20.*

Individual and interactive effects of atmospheric CO2 enrichment and soil N and P fertility on above- and below- ground growth and mycorrhizal colonization of juvenile ponderosa pine (Pinus ponderosa Dougl. ex Laws.) were examined. Seedlings were grown from seed in atmospheres with 700 mu 11(- 1), 525 mu 11(-1), or ambient CO2 concentrations. High and low soil N treatments were created by adding sufficient (NH4)(2)SO4 to an infertile soil mixture to establish total N concentrations of 500 mu g g(-1) and 400 mu g g(-1) respectively, while high and low P treatments consisted of 68 mu g g(-1) and 43 mu g g(-1) concentrations, respectively, of extractable P created by additions of CaHPO4. All seedlings were inoculated with the mycobiont Pisolithus tinctorius (Pers.) Coker and Couch shortly after emergence. Three whole- seedling harvests at four month intervals permitted assessment of treatment effects on shoot and root growth and ectomycorrhizal development. Initially, 525 mu 11(-1) CO2 and high N and P were all influential factors in aboveground growth, with each of these treatments increasing shoot weight while the latter increased height, diameter and volume. Stimulation of root growth was evident in dry weight and length measurements at the first harvest, with N and P main treatment effects again evident, but the response to elevated CO2 was most pronounced in the 700 mu 11(-1) atmosphere. After eight months, soil P was of little consequence above- or below- ground, but high N increased shoot dimensions, volume, and weight and root weight and length. Furthermore, the 525 mu 11(- 1) CO2 treatment emerged as the dominant stimulatory atmosphere both above- and belowground, as seedlings grown in intermediate CO2 exhibited the largest shoot diameters, greatest shoot and root weights, and the longest root systems at the second harvest. At the final harvest, interactive effects of 525 mu 11(-1) CO2 and high N were prominent, as this treatment combination produced the largest shoot dimensions, volume and weight, and the greatest root volume and coarse and fine root weights. Intermediate CO2 also produced the longest root systems after 12 months. Shoot/root ratios were lowered by growth in 700 mu 11(-1) CO2 after four months and by both enriched atmospheres after eight months, but this effect was no longer evident at the final harvest. Greater numbers of mycorrhizae were formed by seedlings grown in 700 mu 11(-1) CO2 after four months and by those grown in 525 mu 11(-1) CO2 after eight months. Both enriched atmospheres increased mycorrhizal counts after 12 months, and seedlings grown in high CO2 and low N exhibited the highest percentage of total root system length colonized at the final harvest as well. Overall, these results indicate that CO2 enrichment stimulates shoot and root growth of juvenile ponderosa pine, a response dependent on soil N rather than P availability, and that the magnitude of the growth increase is greater in 1.5 x ambient than in 2 x ambient CO2. (C) 1998 Elsevier Science B.V.

KEYWORDS: ANATOMY, CARBON-DIOXIDE ENRICHMENT, ELEVATED CO2, MYCORRHIZAL COLONIZATION, NUTRIENT STATUS, PHOSPHORUS, QUERCUS-ALBA, RESPONSES, RHIZOSPHERE, WATER-USE

2507

Walklate, P.J., Z.G. Xu, and A.R. McLeod. 1996. A new gas injection method to enhance spatial utilization within a free-air CO2 enrichment (FACE) system. *Global Change Biology 2(1):75-78.*

Visual observations of smoke dispersion in a wind tunnel and a computational fluid dynamics (CFD) model were used to evaluate methods of improving the performance of Free-Air CO2 Enrichment (FACE) Systems for field studies of the effects of elevated CO2 on vegetation. A special baffle, named an Enhanced Local Mixing (ELM) system, was observed to increase the turbulence and consequent dilution of fumigant gas in the atmosphere. Modelling results suggest that the ELM design reduces the spatial variation of fumigant gas concentration in small experimental plots. The potential reduction in CO2 use and costs warrants further evaluation under field conditions.

2508

Wall, G.W., J.S. Amthor, and B.A. Kimball. 1994. Cotco2 - a cotton growth simulation-model for global change. *Agricultural and Forest Meteorology 70(1-4):289-342.*

In conjunction with the Free-Air-CO2-Enrichment (FACE) project, a new, physiologically based, mechanistic, modular simulation model of cotton (Gossypium hirsutum L.) physiology, growth, development, yield and water use has been constructed. It is named COTCO2 for cotton response to atmospheric CO2 concentration. The model is capable of predicting cotton crop responses to elevated atmospheric CO2 concentrations and potential concomitant changing climate variables. The major plant processes known to be influenced by CO2 are simulated explicitly, i.e. photosynthesis, photorespiration, and stomatal conductance, and its role in leaf energy balance. The model explicitly simulates the impact of atmospheric CO2 concentration on C3 photosynthesis and photorespiration at the level of carboxylation and oxygenation. Growth is simulated for individual organs, i.e. leaf blade, stem segment, taproot and lateral roots, and fruit which includes squares and bolls. Potential growth is calculated and the carbohydrate and nitrogen required to meet this potential are calculated. Actual growth is

based on substrate availability, the potential growth, and water stress. Our intent here is to describe the overall structure of the model, its present status, and future development plans. Further development, documentation, calibration, and validation of the model is in progress. The long range goal of the project is to provide quantitative estimates of global cotton production in a future higher-CO2 world.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, C-4 PLANTS, CLIMATE CHANGE, ELEVATED CO2, GOSSYPIUM HIRSUTUM L, INTACT LEAVES, LEAF GROWTH, QUANTUM YIELD, STOMATAL CONDUCTANCE, WATER-USE

2509

Wallick, K., and T.M. Zinnen. 1990. Basil chlorosis - a physiological disorder in CO2-enriched atmospheres. *Plant Disease 74(2):171-173.*

2510

Wand, S.J.E., G.F. Midgley, M.H. Jones, and P.S. Curtis. 1999. Responses of wild C4 and C3 grass (Poaceae) species to elevated atmospheric CO2 concentration: a meta-analytic test of current theories and perceptions. *Global Change Biology 5(6):723-741.*

C4 plants contribute approximate to 20% of global gross primary productivity, and uncertainties regarding their responses to rising atmospheric CO2 concentrations may limit predictions of future global change impacts on C4-dominated ecosystems. These uncertainties have not yet been considered rigorously due to expectations of C4 low responsiveness based on photosynthetic theory and early experiments. We carried out a literature review (1980-97) and meta-analysis in order to identify emerging patterns of C4 grass responses to elevated CO2, as compared with those of C3 grasses. The focus was on nondomesticated Poaceae alone, to the exclusion of C4 dicotyledonous and C4 crop species. This provides a clear test, controlled for genotypic variability at family level, of differences between the CO2-responsiveness of these functional types. Eleven responses were considered, ranging from physiological behaviour at the leaf level to carbon allocation patterns at the whole plant level. Results were also assessed in the context of environmental stress conditions (light, temperature, water and nutrient stress), and experimental growing conditions (pot size, experimental duration and fumigation method). Both C4 and C3 species increased total biomass significantly in elevated CO2, by 33% and 44%, respectively. Differing tendencies between types in shoot structural response were revealed: C3 species showed a greater increase in tillering, whereas C4 species showed a greater increase in leaf area in elevated CO2. At the leaf level, significant stomatal closure and increased leaf water use efficiency were confirmed in both types, and higher carbon assimilation rates were found in both C3 and C4 species (33% and 25%, respectively). Environmental stress did not alter the C4 CO2-response, except for the loss of a significant positive CO2-response for above-ground biomass and leaf area under water stress. In C3 species, stimulation of carbon assimilation rate was reduced by stress (overall), and nutrient stress tended to reduce the mean biomass response to elevated CO2. Leaf carbohydrate status increased and leaf nitrogen concentration decreased significantly in elevated CO2 only in C3 species. We conclude that the relative responses of the C4 and C3 photosynthetic types to elevated CO2 concur only to some extent with expectations based on photosynthetic theory. The significant positive responses of C4 grass species at both the leaf and the whole plant level demand a re-evaluation of the assumption of low responsiveness in C4 plants at both levels, and not only with regard to water relations. The combined shoot structural and water use efficiency responses of these functional types will have consequential implications for the water balance of important catchments and range lands throughout the world, especially in semiarid subtropical and temperate regions. It may be premature to predict that C4 grass species will lose their competitive advantage over C3 grass species in elevated CO2.

KEYWORDS: BOUTELOUA-GRACILIS C-4, BUNDLE SHEATH-CELLS, CARBON-DIOXIDE CONCENTRATIONS, LEAF GAS-EXCHANGE, OLD- FIELD PERENNIALS, OPEN-TOP CHAMBERS, PASCOPYRUM-SMITHII C-3, SOURCE-SINK RELATIONS, UV-B RADIATION, WATER-USE

2511

Wand, S.J.E., G.F. Midgley, and C.F. Musil. 1996. Growth, phenology and reproduction of an arid-environment winter ephemeral Dimorphotheca pluvialis in response to combined increases in CO2 and UV-B radiation. *Environmental Pollution 94(3):247-254.*

The winter ephemeral Dimorphotheca pluvialis was grown in open- top chambers in ambient or elevated CO2 (350 or 650 mu mol mol(-1)), combined with ambient (2.39 to 7.59 kJ m(-2) d(-1)) or increased (4.94 to 11.13 kJ m(-2) d(-1)) UV-B radiation. Net CO2 assimilation rate and leaf water use efficiency increased in elevated CO2, but increased UV-B did not affect gas exchange. Leaf biomass was greater under increased UV-B, but vegetative biomass was unaffected in elevated CO2. initiation of reproduction was delayed, and proportional investment in reproductive biomass at harvest was reduced in elevated CO2. increased UV-B stimulated reproduction, particularly in ambient CO2, but also in elevated CO2 at a later stage. Changes in reproductive phenology and prolonged development in elevated CO2 during the stressful late season could indirectly be detrimental to reproductive success of D. pluvialis, but stimulation of reproduction by enhanced UV-B may to some extent mitigate this. (C) 1997 Elsevier Science Ltd.

KEYWORDS: AMBIENT, ATMOSPHERIC CARBON-DIOXIDE, DENSITY, ELEVATED CO2, ENRICHMENT, NAMAQUALAND, PHARBITIS, PHOTOSYNTHESIS, PLANTS, VEGETATION

2512

Wand, S.J.E., G.F. Midgley, and C.F. Musil. 1996. Physiological and growth responses of two African species, Acacia karroo and Themeda triandra, to combined increases in CO2 and UV-B radiation. *Physiologia Plantarum 98(4):882-890.*

The interactive effects of increased carbon dioxide (CO2) concentration and ultraviolet-B (UV-B, 280-320 nm) radiation on Acacia karroo Hayne, a C-3 tree, and Themeda triandra Forsk., a C-4 grass, were investigated. We tested the hypothesis that A. karroo would show greater CO2-induced growth stimulation than T. triandra, which would partially explain current encroachment of A. karroo into C-4 grasslands, but that increased UV-B could mitigate this advantage. Seedlings were grown in open-top chambers in a greenhouse in ambient (360 mu mol mol(-1)) and elevated (650 mu mol mol(-1)) CO2, combined with ambient (1.56 to 8.66 kJ m(-2) day(-1)) or increased (2.22 to 11.93 kJ m(-2) day(-1)) biologically effective (weighted) UV-B irradiances. After 30 weeks, elevated CO2 had no effect on biomass of A. karroo, despite increased net CO2 assimilation rates. Interaction between UV-B and CO2 on stomatal conductance was found, with conductances decreasing only where elevated CO2 and UV-B were supplied separately. Increases in water use efficiencies, foliar starch concentrations, root nodule numbers and total nodule mass were measured in elevated CO2. Elevated UV-B caused only an increase in foliar carbon concentrations. In T. triandra, net CO2 assimilation rates were unaffected in elevated CO2, but stomatal conductances and foliar nitrogen concentrations decreased, and water use efficiencies increased. Biomass of all vegetative fractions, particularly leaf sheaths, was increased in elevated CO2, and was accompanied by increased leaf blade lengths and individual leaf and leaf sheath masses. However, tiller numbers were reduced in elevated CO2. Significantly moderating effects of elevated UV-B were apparent only in individual masses of leaf blades and sheaths, and in total sheath and

shoot biomass. The direct CO2-induced growth responses of the species therefore do not support the hypothesis of CO2-driven woody encroachment of C-4 grasslands. Rather, differential changes in resource use efficiency between grass and woody species, or morphological responses of grass species, could alter the competitive balance. Increased UV-B radiation is unlikely to substantially alter the CO2 response of these species.

KEYWORDS: ATMOSPHERIC CO2, C-4, CARBON DIOXIDE, ELEVATED CO2, ENHANCEMENT, ENRICHMENT, GRASSLAND, NODULATION, PHOTOSYNTHETIC ACCLIMATION, PLANT-PLANT INTERACTIONS

2513

Wang, B., and K. Adachi. 1999. Methane production in a flooded soil in response to elevated atmospheric carbon dioxide concentrations. *Biology and Fertility of Soils 29(2):218-220.*

CH4 production in a flooded soil as affected by elevated atmospheric CO2 was quantified in a laboratory incubation study. CH4 production in the flooded soil increased by 19.6%, 28.2%, and 33.4% after a 2-week incubation and by 38.2%, 62.4%, and 43.0% after a 3-week incubation under atmospheres of 498, 820, and 1050 mu l l(-1) CO2, respectively, over that in soil under the ambient CO2 concentration. CH4 production in slurry under 690, 920, and 1150 mu l l(-1) CO2 increased by 2.7%, 5.5%, and 5.0%, respectively, after a 3-day incubation, and by 6.7%, 12.8%, and 5.4%, respectively, after a 6-day incubation over that in slurry under the ambient CO2 concentration. The increase in CH4 production in the soil slurry under elevated CO2 concentrations in a N-2 atmosphere was more pronounced than that under elevated CO2 concentrations in air. These data suggested that elevated atmospheric CO2 concentrations could promote methanogenic activity in flooded soil.

KEYWORDS: CO2, EMISSION, RICE

2514

Wang, D.L. 1999. Effect of elevated CO2 on CH4 emission. *Chinese Science Bulletin 44(13):1153-1157.*

Global CH4 emission may increase under CO2 enrichment condition, which is projected for the future. CO2 enrichment could affect CH4 emission in two ways: (i) Photosynthesis of plants that also include plants in rice paddies and natural wetlands will be stimulated under CO2 enrichment condition. CH4 emission rate may be increased due to the accumulation of more plant biomass, root exudes and soil organic matters. (ii) Combined with other global warming forces, CO2 enrichment may bring a change of atmospheric temperature and precipitation around the world. CH4 emission will also be changed with the variation of the area and distribution of rice paddies and natural wetlands.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, METHANE EMISSION, RESPONSES, RICE PADDIES

2515

Wang, K.Y. 1996. Apparent quantum yield in Scots pine after four years of exposure to elevated temperature and CO2. *Photosynthetica 32(3):339-353.*

The carbon-dioxide and temperature responses of the apparent quantum yield, alpha(A), were measured in a uniform, diffuse radiation field for two shoot age classes of Scots pine (Pinus sylvestris L.) that had been exposed to elevated CO2 and temperature for four years (1991-4) in open-top chambers. The treatments were (I) ambient temperature and CO2 concentration (ACT), (2) elevated temperature (ET), (3) elevated CO2 concentration (EC), and (4) elevated CO2 concentration and temperature (ECT). ET and ECT increased alpha(A) in the one- year-old shoots, but did not affect alpha(A) in the current- year shoots. When measured at the same partial pressure of CO2 and a leaf temperature of 20 degrees C, EC had no significant effect on alpha(A) in two shoot age classes. However, when the comparison was made between shoots grown in and measured in 35 Pa CO2 and those grown in and measured in 70 Pa CO2, EC and ECT led to a significant increase in alpha(A), by 22.4 and 24.5 %, respectively, for the current-year shoots and by 21.6 and 27.5 %, respectively, for one-year-old shoots. Furthermore, in the one-year-old shoots, ET and ECT led to relatively higher alpha(A) values at higher temperatures, but EC alone led to relatively lower values of alpha(A). In contrast, this effect was not significant in the current-year shoots. The differences in alpha(A) between different treatments and between the shoot age classes could be attributed separately to changes in the efficiency of radiant energy capture. The Kok effect was observed at all partial pressures of CO2 during measurements. However, with an increase in the partial pressure of CO2, a parallel decrease was observed in both the measured rate of dark respiration, R(D), and the regressed rate of dark respiration, R(r). This decrease occurred regardless of growth treatment and age class. Consequently, the ratio of R(r)/R(D) was nearly identical in all treatments and age classes having a mean of 0.69.

KEYWORDS: ABIES L KARST, CARBON DIOXIDE, DARK RESPIRATION, DIFFERENT AGES, LIGHT-RESPONSE, LONG-TERM EXPOSURE, NET PHOTOSYNTHESIS, NORWAY SPRUCE, OPEN-TOP CHAMBERS, PHOTOSYNTHETIC RESPONSE

2516

Wang, K.Y. 1996. Canopy CO2 exchange of Scots pine and its seasonal variation after four-year exposure to elevated CO2 and temperature. *Agricultural and Forest Meteorology 82(1-4):1-27.*

Single Scots pines (Pinus sylvestris L.), aged 20-25 years, have been grown in open-topped chambers with elevated temperature (during winter and summer, the mean temperature was 5-20 degrees C and 2 degrees C above the outside ambient temperature, respectively), elevated CO2 (550-600 mu mol mol(- 1) from 15 April to 15 September) and a combination of elevated temperature and CO2 for four years. The vertical and seasonal variations of key physiological parameters concerning photosynthesis and stomatal conductance were measured. The annual canopy photosynthesis and respiration were predicted by using a multilayer model in which the profile of the canopy properties and the microclimate data through a whole year (1994) were used as inputs to the model. The results indicate that during the main growing season (day number 121 to 243), the elevated CO2 increased the maximum apparent quantum yield by 24% and the mean light-saturated rate of assimilation by 41%, and decreased the mean light-saturated stomatal conductance by 13%. However, elevated temperature had no significant effect on these parameters. During early spring and late autumn, elevated temperature increased significantly the apparent quantum yield, the light-saturated rate of assimilation and stomatal conductance. The predicted annual net photosynthesis increased by 40% for elevated CO2 alone, by 58% for elevated CO2 and temperature, and by 10% for elevated temperature alone. The annual sum of respiration increased by 39% for elevated temperature alone and by 29% for elevated CO2 and temperature. Elevated CO2 alone caused a depression of 7% in the annual respiration. Seasonal variations of the CO2-exchange rate between treatments were evident, and they can be largely attributed to changes in the apparent quantum yield, the light-saturated rate of assimilation, leaf area index, and the ability to adapt to environmental stress conditions.

KEYWORDS: C-3, DECIDUOUS FOREST, LEAF NITROGEN, LEAVES, MIDDAY STOMATAL CLOSURE, MODEL, PHOTOSYNTHETIC ACCLIMATION, QUANTUM YIELDS, SCALING

CARBON-DIOXIDE, WATER-VAPOR EXCHANGE

2517

Wang, K.Y., and S. Kellomaki. 1997. Effects of elevated CO2 and soil-nitrogen supply on chlorophyll fluorescence and gas exchange in Scots pine, based on a branch- in-bag experiment. *New Phytologist 136(2):277-286.*

Applying the branch-in-bag method, naturally seeded Scots pine (Pinus sylvestris L.) trees, 25-30 yr old, were subjected to two CO2 concentrations (350 and 700 mu mol mol(-1)) and two soil-nitrogen-supply regimes for three growing seasons (1994- 96). Gas exchange and chlorophyll a fluorescence in detached shoots were measured simultaneously in a diffuse radiation field. Elevated CO2 did not lead to a significant 'downward regulation' in the light-saturated rate of net photosynthesis (P-n.max), the maximum apparent quantum yield (alpha(A.max)) or the maximum photochemical efficiency (F-v/F-m) of photosystem II (PS II). However, the elevated CO2 significantly decreased the light-saturated stomatal conductance and increased the sensitivity of stomatal conductance to change in low photon- flux densities. The high soil-nitrogen supply significantly increased photosynthetic capacity, as manifested by increases in P-n.max, alpha(A.max), F-v/F-m, and the effective photochemical efficiency (Delta F/F'(m)) at low photon-flux densities, did not, on the other hand, enhance the magnitude of photosynthetic response to elevated CO2 concentration. In addition, the treatment-induced modifications in fluorescence parameters are discussed in detail.

KEYWORDS: BETULA-PENDULA ROTH, CARBON DIOXIDE, ENHANCEMENT, ENRICHMENT, GROWTH, PHOTOSYNTHESIS, PLANTS, RESPONSES, SEEDLINGS, TEMPERATURE

2518

Wang, K.Y., and S. Kellomaki. 1997. Stomatal conductance and transpiration in shoots of Scots pine after 4-year exposure to elevated CO2 and temperature. *Canadian Journal of Botany-Revue Canadienne De Botanique 75(4):552-561.*

Single Scots pines (Pinus sylvestris L.) trees were subjected to elevated temperature (year-round elevation), elevated CO2 (elevation from April 15 to September 15), and a combination of elevated temperature and CO2 for 4 years in open-topped chambers. Measurements and modelling were performed to determine if long-term growth at elevated CO2 concentration and temperature altered water use efficiency (W-e) and the responses of stomatal conductance (g(s)) to photon flux density (Q(p)), the leaf-to-air vapour pressure difference (D-v), leaf temperature (T-l), and intercellular concentration of CO2 (C- i). Long-term elevation of CO2 led to a significant decline in the absolute value of g(s) at almost all levels of Q(p), D-v, C-i and T-l. Elevated temperature treatment increased the absolute value of g(s) only at higher D-v and T-l. The effect of the combination of elevated CO2 and temperature did not appear as a mean of the effects of the two single factors, while there was an interaction between the two factors. The modifications in the sensitivity of stomata, resulting from different treatments, did not have the same pattern as the change in g(s), but depended on levels of Q(p), D-v, and T-l. Compared with the control treatment, elevated concentration of CO2 or a combination of elevated CO2 and temperature led, on average, to 50 and 30% increases in W-E, respectively, which can be attributed mainly to an increase in the rate of net assimilation. In contrast, elevated temperature alone did not significantly change W-E, although transpiration rate was increased.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, GAS-EXCHANGE, HUMIDITY, LIGHT, PHOTOSYNTHETIC RESPONSE, SITCHENSIS BONG CARR, SITKA SPRUCE, VAPOR-PRESSURE, WATER-USE EFFICIENCY

2519

Wang, K.Y., S. Kellomaki, and K. Laitinen. 1995. Effects of needle age, long-term temperature and co2 treatments on the photosynthesis of scots pine. *Tree Physiology 15(4):211-218.*

Naturally regenerated 20-25-year-old Scots pine (Pinus sylvestris L.) trees were grown in open-top chambers in the presence of an elevated temperature or CO2 concentration, or both. The elevated temperature treatment was administered year- round for 3 years. The CO2 treatment was applied between April 15 and September 15 for 2 years. The photosynthetic responses of 1- and 2-year-old needles to varying photon flux densities (0-1500 mu mol m(-2) s(-1)) and CO2 concentrations (350, 700 and 1400 mu mol mol(-1)) during measurement were determined. The CO2 treatment alone increased maximum photosynthetic rate and light-use efficiency, but decreased dark respiration rate, light compensation and light saturation regardless of needle age. In contrast, the temperature treatment decreased maximum photosynthetic rate and photosynthetic efficiency, but increased dark respiration rate, light compensation and light saturation. The aging of needles affected the photosynthetic performance of the shoots; values of all parameters except photosynthetic efficiency were less in 2- than in I-year-old needles. The CO2 treatment decreased and the temperature treatment enhanced the reduction in maximum photosynthesis due to needle aging.

KEYWORDS: ACCLIMATION, CARBON-DIOXIDE CONCENTRATION, DIRECT-RADIATION, ELEVATED CO2, GAS-EXCHANGE, GROWTH, LEAVES, RESPIRATION, RESPONSES, SHOOT

2520

Wang, K.Y., S. Kellomaki, and K. Laitinen. 1996. Acclimation of photosynthetic parameters in Scots pine after three years exposure to elevated temperature and CO2. *Agricultural and Forest Meteorology 82(1-4):195-217.*

Single Scots pine (Pinus sylvestris L.) was subjected to elevated temperature (year-round elevation), elevated CO2 (elevation from April 15 to September 15) and a combination of elevated temperature and CO2 for three years in open-topped chambers. Using the data obtained from field measurements of gas exchange, Farquhar and von Caemmerer's basic equations for photosynthesis of C-3 plants were parameterized. The values of the estimated parameters at five ranges of leaf-temperature for trees growing in four different environments are presented and discussed. The estimates of the parameters show that Scots pine grown at elevated CO2 or elevated temperature, compared to those grown in the ambient conditions, did not show significant decreases in the maximum RuP2 (ribulose-1,5-bisphosphate) saturated rate of carboxylation, V-cmax, the maximum rate of electron transport, J(max) and the 'day respiration rate', R(d), within a given range of measuring temperatures (5-25 degrees C). But at high measuring temperature (> 30 degrees C), the elevated CO2 treatment significantly decreased V(cmax) and J(max) whereas the elevated temperature or the combination of CO2 and temperature significantly increased V-cmax and J(max). Furthermore, elevated CO, led to a slight leftward drift of the whole temperature-response curves for V-cmax and J(max); while elevated temperature or the combination of CO2 and temperature led a slight rightward drift of the curves. The model computations show that given a constant intercellular CO2 concentration, C-i (230 or 540 mu mol mol(-1)), there are no significant differences in the maximum rates of assimilation among treatments; when C-i was doubled, the maximum rate of assimilation increased by 28%-34% with no significant differences among treatments.

KEYWORDS: CARBON DIOXIDE, EUCALYPTUS-PAUCIFLORA, GAS-EXCHANGE, HIGH ATMOSPHERIC CO2, NET

PHOTOSYNTHESIS, PLANT GROWTH, QUANTUM YIELD, RIBULOSE 1;5-BISPHOSPHATE, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, SCIRPUS- OLNEYI

2521

Wang, N., and P.S. Nobel. 1996. Doubling the CO2 concentration enhanced the activity of carbohydrate-metabolism enzymes, source carbohydrate production, photoassimilate transport, and sink strength for Opuntia ficus-indica. *Plant Physiology 110(3):893-902.*

After exposure to a doubled CO2 concentration of 750 mu mol mol(-1) air for about 3 months, glucose and starch in the chlorenchyma of basal cladodes of Opuntia ficus-indica increased 175 and 57%, respectively, compared with the current CO2 concentration of 370 mu mol mol(-1), but sucrose content was virtually unaffected. Doubling the CO2 concentration increased the nocturnal malate production in basal cladodes by 75%, inorganic phosphate (Pi) by 32%, soluble starch synthase activity by 30%, and sucrose-Pi synthase activity by 146%, but did not affect the activity of hexokinase. Doubling CO2 accelerated phloem transport of sucrose out of the basal cladodes, resulting in a 73% higher dry weight for the daughter cladodes. Doubling CO2 increased the glucose content in 14-d- old daughter cladodes by 167%, increased nocturnal malate production by 22%, decreased total amino acid content by 61%, and increased soluble starch synthase activity by 30% and sucrose synthase activity by 62%. No downward acclimation of photosynthesis during long-term exposure to elevated CO2 concentrations occurs for O. ficus-indica (M. Cui, P.M. Miller, P.S. Nobel [1993] Plant Physiol 103: 519-524; P.S. Nobel, A.A. Israel [1994] J Exp Bot 45: 295-303), consistent with its higher source capacity and sink strength than under current CO2. These changes apparently do not result in Pi limitation of photosynthesis or suppression of genes governing photosynthesis for this perennial Crassulacean acid metabolism species, as occur for some annual crops.

KEYWORDS: ACCLIMATION, ELEVATED CO2, HIGH ATMOSPHERIC CO2, LEAVES, PHOTOSYNTHESIS, PLANT, STARCH, SUCROSE PHOSPHATE SYNTHASE, SUGAR, WHEAT ENDOSPERM

2522

Wang, X.F., S.Y. Li, K.Z. Bai, and T.Y. Kuang. 1998. Influence of doubled CO2 on plant growth and soil microbial biomass C and N. *Acta Botanica Sinica 40(12):1169-1172.*

Salix babylonica L. Triticum aestivum L. Chenopodium album L. and Amaranthus cruentus L. were grown in the N-deficient soil in open-top chambers blown with ambient or doubled ambient CO2 air, and their growth was measured. Soil samples were collected to assess the influence of doubled CO2 on the soil microbial biomass C (C-mic) and N (N-mic). Results showed that the biomass of shoot and root was increased by doubled CO2 in the four species of plants. Doubled CO2 increased C-mic in S. babylonica and decreased C-mic in T. aestivum and C. album. On the other hand, N-mic in three species except T. aestivum was stimulated by doubled CO2. Doubled CO2 had no significant effect on C-mic in A. cruentus and N-mic in T. aestivum. However, the ratios of C-mic- to -N-mic of all four species were consistently declined under doubled CO2 treatment. It implies that CO2 enrichment may have positive influence on the quality of organic matter of N-low soil in global change.

KEYWORDS: CHLOROFORM FUMIGATION, EXTRACTION METHOD, NITROGEN, RELEASE, RESPONSES

2523

Wang, Y.P., A. Rey, and P.G. Jarvis. 1998. Carbon balance of young birch trees grown in ambient and elevated atmospheric CO2 concentrations. *Global Change Biology 4(8):797-807.*

We constructed a carbon budget for young birch trees grown in ambient and elevated CO2 concentrations over their fourth year of growth. The annual total of net leaf photosynthesis was 110% more in elevated CO2 than in ambient CO2. However, the trees in elevated COP grew only 59% more biomass than the trees in ambient COP over the year. Modelling studies showed that larger loss of carbon from fine-root production and growth of the root-associated mycorrhiza by the trees in elevated CO2 probably accounted for all the remaining difference in net photosynthesis between the two treatments. Our modelling also showed that the fraction of net photosynthate consumed by respiration of nonleaf tissue was similar in the two CO2 treatments, and was 26% and 24% for trees in ambient and elevated CO2, respectively. Trees in elevated CO2 had 43% more leaves, and produced 110% more net photosynthate than trees in ambient CO2, even though the maximum rate of carboxylation per unit leaf nitrogen decreased by 21%. Sensitivity studies showed that down-regulation reduced the annual net photosynthetic production of the trees in elevated CO2 by only 6%. Direct effects of higher CO2 on photosynthesis and greater leaf area of the trees in elevated CO2 increased the net photosynthesis of the trees by 68% and 60%, respectively; and together accounted for most of the difference in net photosynthesis between the two treatments.

KEYWORDS: CYCLE, DIOXIDE, ENRICHMENT, FORESTS, GAS-EXCHANGE, LEAVES, MAINTENANCE, MODEL, PHOTOSYNTHESIS, PLANTS

2524

Wang, Y.Q., H.J. Zhang, D. Yang, K.Z. Bai, and T.Y. Kuang. 1998. Fractal analysis for root growth of plant seedlings under doubled CO2 concentration. *Chinese Science Bulletin 43(22):1891-1893.*

Fractal geometry was applied and box dimension was used as an indicator to analyze the effects of doubled CO2 concentration on the root growth of plant seedlings. Results showed that doubled CO2 concentration displayed different effects on root branching characteristics of C-3 and C-4 plants. There was an obvious increase of root branches in spring wheat while there were no significant effects on roots of sweet sorghum, In different soil layers, root branching of spring wheat was stimulated and this promotion was most significant in the second layer (10-20 cm), which denoted that elevated CO2 altered the root branching pattern. That means higher CO2 concentration influences not only root growth but also its differentiation and development.

2525

Wang, Y.X., and G.M. Shpeyzer. 1997. Genesis of thermal groundwaters from Siping'an district, China. *Applied Geochemistry 12(4):437-445.*

Thermal groundwaters (40-52 degrees C, pH = 7.4-7.8, Eh = 210- 245 mV) from Siping' an district, Shanxi Province, northwestern China, are hydrogeochemically unique. Their occurrence is controlled by faulted structures in Precambrian host rocks. Their hydrochemical type (5 springs and 2 wells) is mainly Cl- SO4-Na, with TDS values around 1.0 g/l. Some minor elements such as Si, Pr, Sr, and Li, as well as neutral and acid bituminous substances are so enriched that the thermal waters can also be regarded as mineral waters. Their origin is meteoric, as indicated by 3 lines of geochemical evidence: (1) their delta D and delta(18)O compositions are very close to the Craig meteoric line; (2) their dissolved gas compositions are N-2-dominated, with less O-2 and CO2; and (3) the He-3/He-4 ratios are low (0.028). Geochemical processes responsible for the genesis of the hydrochemical features of the waters include dissolution, mixing, and oxidation. The most

important water- rock interaction is dissolution or hydrolysis of alumino-silicate minerals in the magmatic and metamorphic host rocks, since the waters are still undersaturated with respect to albite, anorthite, K-spar, and chlorite, as shown by saturation indices. The tritium contents of some thermal waters (46-53 TU), higher than the tritium concentration of local meteoric water, result from the mixing of thermal waters with cold, shallow-lying groundwaters that are from the 1960s. The predominant species of Fe in the thermal waters is Fe(OH)(3), as a result of oxidation processes under aerobic conditions of the aquifers. (C) 1997 Elsevier Science Ltd.

2526

Wang, Z.M., M.J. Lechowicz, and C. Potvin. 1994. Early selection of black spruce seedlings and global change - which genotypes should we favor. *Ecological Applications 4(3):604-616.*

We investigated the effects of both soil fertility and predicted changes in climate on the performance of different families of black spruce, Picea mariana (Mill.) B.S.P., during the first growing season. The results were used to examine whether reforestation programs should consider changing their preferred family lines in anticipation of altered performance given global climate change. We grew seedlings of 16 open- pollinated maternal families of black spruce under phytotron conditions simulating present and mid-21 st century climatic conditions during the growing season. The realistic, simulated future climate included both elevated CO2 levels and seasonally appropriate increases in mean daily temperature. To explore the dependence of climatic responses on site quality, seedlings were irrigated with solutions having either 5 or 100 mg/L of nitrogen. The lower nitrogen level represents a poor site for black spruce growth and survival, but the higher level provides ample nitrogen. We also recorded seed size for each seedling to evaluate the degree to which maternal investments might buffer responses to future climate and fertility during the first year on the seedbed. Seedling survival and growth increased both under the future climate regime and with nitrogen fertilization. The two factors interacted synergistically, with nitrogen enrichment significantly enhancing the positive effects of the future climate regime. Nitrogen-poor conditions, however, did not preclude a positive seedling response to the future climate. Our results indicate that seedling survival and height growth are highly dependent upon initial seed mass: larger seeds produced more vigorous 1 st-yr seedlings. The families differed in seed mass, seed germination, and seedling survival and growth, but their relative performances did not vary significantly among the treatments. These results suggest that black spruce families selected for rapid growth under present conditions will also do well in the future, at least in terms of early establishment and performance on sites regenerated by seeding.

KEYWORDS: ATMOSPHERIC CO2 CONCENTRATIONS, BOREAL FORESTS, CLIMATE CHANGE, COASTAL DOUGLAS-FIR, ELEVATED CO2, GROWTH, PRODUCTIVITY, SEED WEIGHT, TEMPERATURE, TUSSOCK TUNDRA

2527

Wang, Z.M., M.J. Lechowicz, and C. Potvin. 1995. Responses of black spruce seedlings to simulated present versus future seedbed environments. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 25(4):545-554.*

We investigated the effects of nitrogen availability and present versus future atmospheric environments (i.e., climate) on the seedling performance of 16 open-pollinated maternal families of Picea mariana (Mill.) B.S.P. over two simulated growing seasons. Diurnal and seasonal patterns of temperature, relative humidity, photoperiod, and light intensity were simulated. The simulated future climate included both elevated CO2 and seasonally appropriate increases in mean monthly temperatures. Compared with the present, the future climate increased seedling survival, total and root dry mass, rate of winter bud development, net photosynthetic rate, and water and nitrogen use efficiencies; decreased needle nitrogen content; and altered biomass allocation patterns. Greater nitrogen availability greatly improved seedling performance and changed biomass allocation patterns. Climate and nitrogen level interacted synergistically to promote seedling growth (branch number and root dry mass), survival, and bud development. The future climate increased seedling survival, rate of bud development, and nitrogen use efficiency much more in the low than in the high nitrogen regime. Seedling performance in the second season was dependent on initial seed mass, but less than in the 1st year. Some of the differences among the families and in their interactions with the climate and (or) nitrogen fertilization suggest that families selected for rapid growth under present conditions may not do well in the future, at least in terms of early establishment. Forest managers and tree breeders should take this possibility into consideration in their tree improvement and reforestation programs.

KEYWORDS: AMERICA, ATMOSPHERIC CARBON-DIOXIDE, ECOSYSTEMS, ELEVATED CO2, GLOBAL CLIMATE-CHANGE, GROWTH, NITROGEN, PHOTOSYNTHESIS, PRODUCTIVITY, STRATEGIES

2528

Wang, Z., Q. Pan, and B. Quebedeaux. 1999. Carbon partitioning into sorbitol, sucrose, and starch in source and sink apple leaves as affected by elevated CO2. *Environmental and Experimental Botany 41(1):39-46.*

Experiments were conducted in controlled growth chambers to evaluate how increases in CO2 concentration ([CO2]) affected carbon metabolism and partitioning into sorbitol, sucrose, and starch in;various ages of apple leaves. Apple plants (Mabs domestica), 1 year old, were exposed to [CO2] of 200, 360, 700, 1000, and 1600 mu l 1(-1) up to 8 days. Six groups of leaves (counted from the shoot apex): leaves 1-5 (sink), 6-7 (sink to source transition): 8-9 (sink to source transition), 10-11 (nearly-matured source), 21-22 (mid-age source), and 30-32 (aged source), were sampled at 1, 2, 4, and 8 days after [CO2] treatments for carbohydrate analysis. Increases in [CO2] from a sub-ambient (200 mu l 1(-1)) to an ambient level (360 mu l 1(- 1)) significantly increased the concentrations of sorbitol, sucrose, glucose, and fructose tested in all ages of leaves. Continuous increase in [CO2] from ambient to super-ambient levels up to 1600 mu l 1(-1) also increased sorbitol concentration by approximate to 50% in source leaves, but not in sink and sink to source transition leaves. Increases in [CO2] from 360 to 1600 mu l 1(-1), however, had little effect on sucrose content in all ages of leaves. Starch concentrations increased in all ages of leaves as [CO2] increased. Rapid starch increases (e.g. 5-, 6-, 20-, and 50-fold increases for leaf groups 1-5, 6-7, 10-11, and 21-22, respectively) occurred from 700 to 1600 mu l 1(-1) [CO2] during which increases in sorbitol concentration either ceased or slowed down. Our results indicate that changes in carbohydrates were much more responsive to CO2 enrichment in source leaves than in sink and sink to source transition leaves. Carbon partitioning was favored into starch and sorbitol over sucrose in all ages of leaves when [CO2] was increased from 200 to 700 mu l 1(-1), and was favored into starch over sorbitol from 700 to 1600 mu l 1(- 1) [CO2]. (C) 1999 Elsevier Science B.V. All rights reserved.

KEYWORDS: METABOLISM

2529

Wangwacharakul, V., and R. Bowonwiwat. 1995. Economic evaluation of CO2 response options in the forestry sector: The case of Thailand. *Biomass & Bioenergy 8(5):293-307.*

Using the benefit-cost analysis approach, this paper attempts to evaluate

the potential of the forestry sector in Thailand to reduce carbon emissions of the country. Protecting conserved forests can avoid a substantial amount of carbon emission from deforestation, although certain costs are attached. Reforestation also enhances carbon sequestration and, in most cases, incurs no cost to society. Under the present government's commitment to fully protect the conserved forests and reforest the deforested areas in the country, Thailand could reduce the growth of carbon emission by as much as 260 million tons over the next two decades. The costs to society, if any, would be small given other, non-quantifiable, benefits of the forests.

2530

Ward, J.K., and B.R. Strain. 1997. Effects of low and elevated CO2 partial pressure on growth and reproduction of Arabidopsis thaliana from different elevations. *Plant, Cell and Environment 20(2):254-260.*

Atmospheric CO2 partial pressure may have been as low as 18 Pa during the Pleistocene and is expected to increase from 35 to 70 Pa before the end of the next century. Low CO2 reduces the growth and reproduction of C-3 plants, whereas elevated CO2 often increases growth and reproduction. Plants at high elevation are exposed to reduced CO2 partial pressure and may be better adapted to the low CO2 of the Pleistocene, me examined genotypes of Arabidopsis thaliana from different elevations for variation in growth and reproduction at the CO2 levels of the Pleistocene, the present and the future. Genotypes exhibited limited genetic variation in the response of the production of biomass to changes in CO2, but showed significant variation in reproductive characters. We found evidence that plants from high elevations may be better adapted to low CO2 when considering seed number, which is an important component of fitness. Genotypes showed greater variation in the response of seed number between 35 and 20 Pa CO2 compared to 35 and 70 Pa CO2. We conclude that present-day C-3 annuals may have greater potential for evolution in response to the low CO2 of the Pleistocene relative to the elevated CO2 predicted for the future.

KEYWORDS: AMBIENT, ATMOSPHERIC CO2, C-4 ANNUALS, CARBON DIOXIDE, ENRICHMENT, HIGH- ALTITUDES, INTRASPECIFIC VARIATION, PHOTOSYNTHESIS, PLANTS, RESPONSES

2531

Ward, J.K., and B.R. Strain. 1999. Elevated CO2 studies: past, present and future. *Tree Physiology 19(4-5):211-220.*

Increasing concentrations of atmospheric CO2 are predicted to impact both current and future ecosystems. Elevated CO2 is also predicted to affect biological processes at many levels of organization. In this overview, we summarize the responses of plants to elevated CO2 including primary physiological and molecular responses, growth and reproductive responses, effects on plant-plant competition and interactions with other organisms, evolutionary responses, and effects at the ecosystem level. The objectives of this paper are to: (a) overview studies in this issue that were presented at a 1997 meeting entitled "Critical Assessment of the Response of Forest Ecosystems to Elevated Atmospheric Carbon Dioxide," which was sponsored by the Global Change and Terrestrial Ecosystems (GCTE) group of the International Geosphere Biosphere Program (IGBP), (b) review areas of recent progress in CO2 research, (c) generalize patterns arising from past research, and (d) list critical areas of research for the future.

KEYWORDS: ARABIDOPSIS-THALIANA, ATMOSPHERIC CO2, C-4 ANNUALS, CARBON-DIOXIDE ENRICHMENT, GAS-EXCHANGE, LONG-TERM ELEVATION, PINUS-TAEDA, QUANTUM YIELD, REPRODUCTIVE EFFORT, STOMATAL CONDUCTANCE

2532

Wardle, D.A., K.I. Bonner, G.M. Barker, G.W. Yeates, K.S. Nicholson, R.D. Bardgett, R.N. Watson, and A. Ghani. 1999. Plant removals in perennial grassland: Vegetation dynamics, decomposers, soil biodiversity, and ecosystem properties. *Ecological Monographs 69(4):535-568.*

The consequences of permanent loss of species or species groups from plant communities are poorly understood, although there is increasing evidence that individual species effects are important in modifying ecosystem properties. We conducted a field experiment in a New Zealand perennial grassland ecosystem, creating artificial vegetation gaps and imposing manipulation treatments on the reestablishing vegetation. Treatments consisted of continual removal of different subsets or "functional groups" of the flora. We monitored vegetation and soil biotic and chemical properties over a 3-yr period. Plant competitive effects were clear: removal of the C-3 grass Lolium perenne L. enhanced vegetative cover, biomass, and species richness of both the C-4 grass and dicotyledonous weed functional groups and had either positive or negative effects on the legume Trifolium repens L., depending on season. Treatments significantly affected total plant cover and biomass; in particular, C-4 grass removal reduced total plant biomass in summer, because no other species had appropriate phenology. Removal of C-4 grasses reduced total root biomass and drastically enhanced overall shoot-to-root biomass ratios. Aboveground net primary productivity (NPP) was not strongly affected by any treatment, indicating strong compensatory effects between different functional components of the flora. Removing all plants often negatively affected three further trophic levels of the decomposer functional food web: microflora, microbe-feeding nematodes, and predaceous nematodes. However, as long as plants were present, we did not find strong effects of removal treatments, NPP, or plant biomass on these trophic groupings, which instead were most closely related to spatial variation in soil chemical properties across all trophic levels, soil N in particular. Larger decomposer organisms, i.e., Collembola and earthworms, were unresponsive to any factor other than removal of all plants, which reduced their populations. We also considered five functional components of the soil biota at finer taxonomic levels: three decomposer components (microflora, microbe-feeding nematodes, predaceous nematodes) and two herbivore groups (nematodes and arthropods). Taxa within these five groups responded to removal treatments, indicating that plant community composition has multitrophic effects at higher levels of taxonomic resolution. The principal ordination axes summarizing community-level data for different trophic groups in the soil food web were related to each other in several instances, but the plant ordination axes were only significantly related to those of the soil microfloral community. There were time lag effects, with ordination axes of soil-associated herbivorous arthropods and microbial-feeding nematodes being related to ordination axes representing plant community structure at earlier measurement dates. Taxonomic diversity of some soil organism groups was linked to plant removals or to plant diversity. For herbivorous arthropods, removal of C-4 grasses enhanced diversity; there were negative correlations between plant and arthropod diversity, presumably because of negative influences of C-4 species in the most diverse treatments. There was evidence of lag relationships between diversity of plants and that of the three decomposer groups, indicating multitrophic effects of altering plant diversity. Relatively small effects of plant removal on the decomposer food web were also apparent in soil processes regulated by this food web. Decomposition rates of substrates added to soils showed no relationship with treatment, and rates of CO2 evolution from the soil were only adversely affected when all plants were removed. Few plant functional-group effects on soil nutrient dynamics were identified. Although some treatments affected temporal variability (and thus stability) of soil biotic properties (particularly CO2 release) throughout the experiment, there was no evidence of destabilizing effects of plant removals. Our data provide evidence that permanent exclusion of plant species from the species pool can have important consequences for overall vegetation composition in addition to the direct effects of

vegetation removal, and various potential effects on both the above- and belowground subsystems. The nature of many of these effects is driven by which plant species are lost from the system, which depends on the various attributes or traits of these species.

KEYWORDS: ASPARAGUS CROPPING SYSTEMS, EXPLOITATION ECOSYSTEMS, FOOD-WEB, INDUCED RESPIRATION METHOD, MICROBIAL BIOMASS, NEMATODE COMMUNITIES, OLD-FIELD COMMUNITY, SPECIES-DIVERSITY, TROPHIC RELATIONSHIPS, WEED-MANAGEMENT STRATEGIES

2533

Wardle, D.A., H.A. Verhoef, and M. Clarholm. 1998. Trophic relationships in the soil microfood-web: predicting the responses to a changing global environment. *Global Change Biology 4(7):713-727.*

In this article, we evaluate how global environmental change may affect microfood-webs and trophic interactions in the soil, and the implications of this at the ecosystem level. First we outline how bottom-up (resource control) and top-down (predation-control) forces regulate food-web components. Food- web components can respond either positively or negatively to shifts in NPP resulting from global change, thus creating difficulties in developing general principles about the response of soil biota to global change phenomena. We also demonstrate that top-down effects can be important in soil food-webs, creating negative feed-backs which may partially counter bottom-up effects. Secondly we determine how soil food- webs and the processes they regulate respond to various global change phenomena. Enhanced atmospheric CO2 levels can have two main effects on plants which are relevant for the sail food- web, i.e. enhanced NPP (often positive) and diminished organic matter quality (with negative effects, at least in the short term). Climate change effects resulting from elevated CO2 levels may be mainly secondary through alteration of vegetation, as shown by examples. Intensification of land management is usually associated with greater disturbance, which alters soil food-web composition and key processes; this is particularly apparent in comparisons of conventionally tilled and nontilled agroecosystems. Global change involves shifts in plant species composition and diversity, possibly affecting soil food-webs; we interpret this in terms of theories relating biodiversity to ecosystem function. We conclude that a more detailed understanding of interactions between NPP, soil organic matter and components of the soil food-web, as well as their regulation of biogeochemical processes and ultimately ecosystem-level properties, is essential in better understanding longterm aspects of global change phenomena.

KEYWORDS: CARBON DIOXIDE, CLIMATE CHANGE, DECOMPOSITION PROCESSES, ECOSYSTEM FUNCTION, ELEVATED ATMOSPHERIC CO2, FOOD-WEBS, LEAF LITTER, MICROBIAL BIOMASS, PLANT GROWTH, TALLGRASS PRAIRIE

2534

Warwick, K.R., G. Taylor, and H. Blum. 1998. Biomass and compositional changes occur in chalk grassland turves exposed to elevated CO2 for two seasons in FACE. *Global Change Biology 4(4):375-385.*

Artificial turves composed of 7 chalk grassland species (Festuca ovina L; Briza media L.; Bromopsis erecta (Hudson) Fourr.; Plantago media L; Sanguisorba minor Scop.; Anthyllis vulneraria L. and Lotus corniculatus L.) were grown from seed and exposed to two seasons of elevated (600 mu mol mol(-1)) and ambient (340 mu mol mol(-1)) CO2 concentrations in free air CO2 enrichment (ETH-FACE, Zurich). The turves were clipped regularly to a height of 5 cm and assessed for above ground biomass production and relative abundance based on accumulated clipped dry biomass as well as by point quadrat recording. Below ground biomass production was assessed with root in- growth bags during the second season of growth. Increases in total biomass (> 30%) were noted in elevated CO2, but the differences did not become significant until the second season of growth. Individual species' biomass varied in response to elevated CO2, with significant increases in biomass in elevated CO2 turves for both legume species, and no significant CO2 effect on S. minor or P. media. An initial positive CO2 effect on biomass of combined grass species was reversed by the end of the experiment with less biomass and a significantly smaller proportion of total biomass present in elevated CO2, which was attributed primarily to changes in proportion of F. ovina. Species relative abundance was significantly affected by elevated CO2 in the final 4 of the 6 clip events, with the legume species increasing in proportion at the expense of the other species, particularly the grasses. Root length and dry weight were both significantly increased in elevated CO2 (77% and 89%, respectively), and these increases were greater than increases in shoot biomass (36%) from the same period. Species responses to elevated CO2, within the model community, were not consistent with predictions made from data on individual species, leading to the conclusion that responses to elevated CO2, at the community level, and species within the community level, are the result of direct physiological effects and indirect competitive effects. These conclusions are discussed with respect to the ecological responses of natural communities, and the chalk grassland community in particular, to elevated CO2.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, COMMUNITY, ENRICHMENT, GAS-EXCHANGE, NATIVE HERBS, PLANT GROWTH, RESPONSES, ROOT-GROWTH, VEGETATION

2535

Watada, A.E., N.P. Ko, and D.A. Minott. 1996. Factors affecting quality of fresh-cut horticultural products. *Postharvest Biology and Technology 9(2):115-125.*

Fresh-cut products, also known as lightly or minimally processed products, are highly perishable because a large proportion of their surface area is without epidermis, the outer protective layer of tissue. Temperature, atmosphere, relative humidity and sanitation must be regulated to maintain quality of fresh-cuts. In the 0-10 degrees C range, Q(10) of respiration rates ranged from 2.0 to 8.6 among various fresh-cut fruits and vegetables. Low Oz and elevated CO2 atmosphere reduced the respiration rate; however, the respiratory quotient approached 3.0 with some fresh-cuts. Film bags or coatings are necessary to maintain high relative humidity. Microorganisms were present in chlorine-washed spinach, and populations increased during storage. Stress from the physical action of processing and low O-2 atmosphere affects physiology and biochemistry of the fresh-cuts, which can affect quality and shelf-life. Research in all of these areas is needed to ensure that wholesome, high-quality fresh-cut products are marketed to consumers.

KEYWORDS: ATMOSPHERE, CHLOROPHYLL, DEGRADATION, FILM, LIGHTLY PROCESSED FRUITS, PERMEABILITY, SHREDDED CARROTS, STORAGE, TEMPERATURE, VEGETABLES

2536

Watanabe, Y., N. Ohmura, and H. Saiki. 1992. Isolation and determination of cultural-characteristics of microalgae which functions under co2 enriched atmosphere. *Energy Conversion and Management 33(5-8):545-552.*

A fresh-water microalgae, which functions under CO2 enriched atmosphere conditions, was isolated and its cultural characteristics were investigated. The HA-1 strain, identified as genus Chlorella, was newly isolated from a paddy field by an enrichment culture using reproduced stack gases from a thermal power plant with a concentration of CO2 and O2 of 15 % and 2 % respectively. It showed maximum growth at 10 % CO2 enriched air flowing condition, and showed a good growth rate in

a broad range of physically controllable conditions, including CO2 enriched air flow rate, temperature and pH value. The results indicated the feasibility of the HA-1 strain for mass cultivation using stack gases.

2537

Watling, J.R., and M.C. Press. 1997. How does elevated CO2 affect the relationship between the C-3 root hemiparasite Striga hermonthica and the C-4 host Sorghum bicolor? *Plant Physiology 114(3):46.*

2538

Watling, J.R., and M.C. Press. 1997. How is the relationship between the C-4 cereal Sorghum bicolor and the C-3 root hemi-parasites Striga hermonthica and Striga asiatica affected by elevated CO2? *Plant, Cell and Environment 20(10):1292-1300.*

The C-4 cereal Sorghum bicolor was grown under either ambient (350 mu mol mol(-1)) or elevated (700 mu mol mol(-1)) [CO2] in either the presence or absence of the C-3 obligate root hemi- parasites Striga hermonthica or S. asiatica. Both uninfected and infected sorghum plants were taller and had greater biomass, photosynthetic rates, water-use efficiencies and leaf areas under elevated compared with ambient [CO2]. There was no evidence of any downregulation of photosynthesis in sorghum grown at elevated [CO2]. Biomass of infected sorghum was lower under both ambient and elevated [CO2], and although infected plants were larger under elevated [CO2] the relative impact of infection on host biomass was either the same (S. asiatica) or only slightly less (S. hermonthica) than under ambient [CO2]. In contrast, biomass of S. hermonthica and S. asiatica per host was lower under elevated than ambient [CO2], although rates of photosynthesis were higher at elevated [CO2] and parasite stomatal conductance was not responsive to [CO2]. Parasites emerged above-ground and flowered earlier under ambient compared with elevated [CO2]. It appears that the mechanism(s) by which the parasites affect host growth is (are) relatively insensitive to increased atmospheric [CO2] although the parasites themselves were adversely affected by growth at elevated [CO2].

KEYWORDS: ACQUISITION, ASSOCIATION, CARBON DIOXIDE, ENRICHMENT, FIELD, GAS-EXCHANGE, GROWTH, PHOTOSYNTHESIS, RESPONSES, WATER RELATIONS

2539

Watt, M., and J.R. Evans. 1999. Linking development and determinancy with organic acid efflux from proteoid roots of white lupin grown with low phosphorus and ambient or elevated atmospheric CO2 concentration (vol 120, pg 705, 1999). *Plant Physiology 121(3):1057.*

2540

Wayne, P.M., and F.A. Bazzaz. 1995. Seedling density modifies the growth-responses of yellow birch maternal families to elevated carbon-dioxide. *Global Change Biology 1(5):315-324.*

We studied seedling growth responses to ambient and elevated CO2 (350 and 700 mu L L(-1)) of three maternal families of yellow birch (Betula alleghaniensis), raised both individually and in high-density stands. Seedlings in competitive, dense stands exhibited markedly lower average CO2-induced growth enhancements than individually grown plants (16% vs. 49%). Maternal families differed in their growth responses to elevated CO2. However, differences among families were contingent upon density; families which exhibited the greatest CO2-induced growth at low density exhibited the least CO2- responsiveness at high density. These data are discussed in two separate contexts; the reliability of estimates of the CO2 fertilization potential of forest species based solely on individually grown plants, and the potential evolutionary consequences of rising CO2 on regenerating forest tree populations.

KEYWORDS: AMBIENT, ATMOSPHERIC CO2 ENRICHMENT, COMPETITION, ECOSYSTEMS, FOREST, GAS-EXCHANGE, INCREASE, NITROGEN, PLANTS, TREE

2541

Wayne, P.M., and F.A. Bazzaz. 1997. Light acquisition and growth by competing individuals in CO2- enriched atmospheres: Consequences for size structure in regenerating birch stands. *Journal of Ecology 85(1):29-42.*

1 To investigate how CO2-enriched atmospheres may influence plant competition and stand size structure in regenerating forests, experimental populations comprised of three maternal families of yellow birch (Betula alleghaniensis Britt.) were grown in both ambient (350 mu L L(-1)) and elevated (700 mu L L(-1)) CO2 concentrations in a controlled environment facility. Individual seedling growth, light acquisition, and stand size structure were monitored throughout the first year of growth. 2 Elevated CO2 increased average seedling biomass in stands by 14%, a value much lower than the average enhancement reported elsewhere for individually grown yellow birch seedlings. Maternal families within stands differed significantly in their growth responsiveness to elevated CO2, ranging from +51% to - 16%. As a result, CO2 altered the genetic identity of dominants in regenerating stands. 3 Seedling size inequalities were generally lower in CO2-enriched environments, a result that contrasts with other studies that have reported increased size inequality with increased productivity in resource-rich environments. Distribution modifying functions relating initial seedling size and subsequent growth suggest that there was a relatively smaller advantage to being larger in elevated vs. ambient CO2 environments. Together, these results suggest that competition in CO2-enriched environments was less size- asymmetric. 4 Differences in stand size structure between CO2 treatments were related to competition for light. Empirical measures of seedling light acquisition per unit biomass suggest competition for light was less size-asymmetric in CO2-enriched environments. Decreased size-asymmetric competition for light was attributable both to differences in the CO2-use efficiency of high-light canopy dominants vs. low-light canopy subordinates, and to CO2-induced differences in plant allometry. 5 This study highlights the importance of stand- level competition studies in global change research, and more generally, the value of studies that combine phenomenological descriptions of stand development with physiological mechanisms of competition.

KEYWORDS: CARBON DIOXIDE, ELEVATED CO2, EMERGENCE TIME, ENRICHMENT, ENVIRONMENTS, EXPERIMENTAL POPULATIONS, PLANT-POPULATIONS, RADISH RAPHANUS-RAPHANISTRUM, SEED SIZE, SOURCE-SINK RELATIONS

2542

Wayne, P.M., A.L. Carnelli, J. Connolly, and F.A. Bazzaz. 1999. The density dependence of plant responses to elevated CO2. *Journal of Ecology 87(2):183-192.*

1 Stands of the annual Brassica kaber were grown at a range of six densities in both ambient and elevated CO2 environments, and measurements of shoot growth were made from seedling emergence through to reproduction. 2 Early in stand development (21 days following emergence), CO2 enhancement (beta) for above-ground biomass was highly density-dependent, ranging from 1.41 at the lowest density (20 plants m(-2)) to 0.59 at the highest density (652 plants m(-2)). 3 As stands matured and total biomass exceeded a relatively low threshold level (< 10.0 g m(-2); c. 20% of final yield), the density-

dependence of beta disappeared. Above this shoot biomass threshold, beta-values remained remarkably stable (beta = 0.34) across a broad range of stand biomass, independent of a stand's initial density or age. 4 Average stand-level reproductive beta-values at a final harvest were very similar to biomass values (beta = 0.38) and, as with biomass values at later stages, showed no apparent density-dependence. 5 These results highlight the importance of considering density and the time-course of stand development simultaneously when assessing the potential for CO2-induced growth enhancements in plants.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, ENRICHMENT, ENVIRONMENTS, GROWTH-RESPONSE, POPULATIONS, REPRODUCTION

2543

Wayne, P.M., E.G. Reekie, and F.A. Bazzaz. 1998. Elevated CO2 ameliorates birch response to high temperature and frost stress: implications for modeling climate-induced geographic range shifts. *Oecologia 114(3):335-342.*

Despite predictions that both atmospheric CO2 concentrations and air temperature will rise together, very limited data are currently available to assess the possible interactive effects of these two global change factors on temperate forest tree species. Using yellow birch (Betula alleghaniensis) as a model species, we studied how elevated CO2 (800 vs. 400 mu l l(-1)) influences seedling growth and physiological responses to a 5 degrees C increase in summer air temperatures (31/26 vs. 26/21 degrees C day/night), and how both elevated CO2 and air temperature during the growing season influence seedling ability to survive freezing stress during the winter dormant season. Our results show that while increased temperature decreases seedling growth, temperature-induced growth reductions are significantly lower at elevated CO2 concentrations (43% vs. 73%). The amelioration of high-temperature stress was related to CO2-induced reductions in both whole-shoot dark respiration and transpiration. Our results also show that increased summer air temperature, and to a lesser degree CO2 concentration, make dormant winter buds less susceptible to freezing stress. We show the relevance of these results to models used to predict how climate change will influence future forest species distribution and productivity, without considering the direct or interactive effects of CO2.

KEYWORDS: AIR- TEMPERATURE, ATMOSPHERIC CO2, CARBON DIOXIDE, EFFICIENCY, FOREST, PICEA-SITCHENSIS, PLANT GROWTH, RESPIRATION, SCOTS PINE, SEEDLINGS

2544

Webb, A.A.R., M.R. McAinsh, T.A. Mansfield, and A.M. Hetherington. 1996. Carbon dioxide induces increases in guard cell cytosolic free calcium. *Plant Journal 9(3):297-304.*

The hypothesis that increases in cytosolic free calcium ([Ca2+](i)) are a component of the COP signal transduction pathway in stomatal guard cells of Commelina communis has been investigated. This hypothesis was tested using fura-2 fluorescence ratio photometry to measure changes in guard cell [Ca2+](i) in response to challenge with 700 mu l l(-1) CO2. Elevated CO2 induced increases in guard cell [Ca2+](i) which were similar to those previously reported in response to abscisic acid. [Ca2+](i) returned to resting values following removal of the CO2 and further application of CO2 resulted in a second increase in [Ca2+](i). This demonstrated that the CO2- induced increases in [Ca2+](i) were stimulus dependent. Removal of extracellular calcium both prevented the CO2-induced increase in [Ca2+](i) and inhibited the associated reduction in stomatal aperture. These data suggest that Ca2+ acts as a second messenger in the CO2 signal transduction pathway and that an increase in [Ca2+](i) may be a requirement for the stomatal response to CO2.

KEYWORDS: ABSCISIC- ACID, ANION CHANNELS, CA-2, CO2, ELEVATION, INDUCED STOMATAL CLOSURE, INOSITOL TRISPHOSPHATE, PLANT-CELLS, PLASMA-MEMBRANE, SIGNAL-TRANSDUCTION

2545

Webber, A.N., G.Y. Nie, and S.P. Long. 1994. Acclimation of photosynthetic proteins to rising atmospheric co2. *Photosynthesis Research 39(3):413-425.*

In this review we discuss how the photosynthetic apparatus, particularly Rubisco, acclimates to rising atmospheric CO2 concentrations (c(a)). Elevated c(a) alters the control exerted by different enzymes of the Calvin cycle on the overall rate of photosynthetic CO2 assimilation, so altering the requirement for different functional proteins. A decreased flux of carbon through the photorespiratory pathway will decrease requirements for these enzymes. From modeling of the response of CO2 uptake (A) to intracellular CO2 concentration (c(i)) it is shown that the requirement for Rubisco is decreased at elevated c(a), whilst that for proteins limiting ribulose 1,5 bisphosphate regeneration may be increased. This balance may be altered by other interactions, in particular plasticity of sinks for photoassimilate and nitrogen supply; hypotheses on these interactions are presented. It is speculated that increased accumulation of carbohydrate in leaves developed at elevated c(a) may signal the 'down regulation' of Rubisco. The molecular basis of this 'down regulation' is discussed in terms of the repression of photosynthetic gene expression by the elevated carbohydrate concentrations. This molecular model is then used to predict patterns of acclimation of perennials to long term growth in elevated c(a).

KEYWORDS: AIR- TEMPERATURE, CALVIN CYCLE ENZYMES, CARBONIC-ANHYDRASE, CARBOXYLASE-OXYGENASE, CHLAMYDOMONAS-REINHARDTII, ELEVATED CO2, GENE-EXPRESSION, SINK REGULATION, SPINACH LEAVES, TOBACCO PLANTS

2546

Wechsung, G., F. Wechsung, G.W. Wall, F.J. Adamsen, B.A. Kimball, R.L. Garcia, P.J. Pinter, and T. Kartschall. 1995. Biomass and growth rate of a spring wheat root system grown in free-air CO2 enrichment (FACE) and ample soil moisture. *Journal of Biogeography 22(4-5):623-634.*

The response of a wheat crop root system to full-season CO2-enrichment was investigated using a free-air CO2 enrichment (FACE) apparatus. A spring wheat (Triticum aestivum L. cv. Yecora Rojo) crop was growing at 0.25 m row spacing and 130 plants m(-2) on a Trix clay loam (hyperthermic Typic Torrifluvent) under two atmospheric CO2 concentrations (FACE: similar to 550 mu mol mol(-1); control: similar to 370 mu mol mol(-1)) and ample soil moisture (100% replacement of poten tial evapotranspiration). Irrigation was applied with a subsur face drip irrigation system. Root cores were collected at five growth stages (three-leaf, tillering, stem elongation, anthesis, dough development and final harvest, which corresponded with day of year (DOY) 16, 36, 63, 92, 113 and 159, respectively), using a soil core device (86 mm i). Two cores were taken in-row and one in the inter-row space position to examine the horizontal and vertical distribution of roots to a I-m depth. Root biomass was summed over the entire root profile across all positions to obtain a total. Total root mass was higher in FACE compared to control for all growth stages (i.e. 34% at three-leaf, 21% at tillering, 23% at stem elongation, 28% at dough development and 19% at harvest). Root growth rate was significantly higher in FACE compared to control for both in-row and inter-row positions. Root senescence rate were similar between FACE and control grown plants,

but the absolute difference in root mass during the senescence phase was greater in FACE compared to control grown plants. Roots from FACE grown plants explored a greater proportion of the soil profile earlier in the season than roots from control grown plants. However, there was no evidence that plants grown in FACE had a deeper root system than plants grown in control.

KEYWORDS: ELEVATED CARBON-DIOXIDE, FEEDBACK, NITROGEN, PARTIAL-PRESSURE

2547

Wechsung, G., F. Wechsung, G.W. Wall, F.J. Adamsen, B.A. Kimball, P.J. Pinter, R.L. Lamorte, R.L. Garcia, and T. Kartschall. 1999. The effects of free-air CO2 enrichment and soil water availability on spatial and seasonal patterns of wheat root growth. *Global Change Biology 5(5):519-529.*

Spring wheat [Triticum aestivum (L). cv. Yecora Rojo] was grown from December 1992 to May 1993 under two atmospheric CO2 concentrations, 550 mu mol mol(-1) for high-CO2 plots, and 370 mu mol mol(-1) for control plots, using a Free-Air CO2 Enrichment (FACE) apparatus. In addition to the two levels of atmospheric CO2, there were ample and limiting levels of water supply through a subsurface trip irrigation system in a strip, split-plot design. In order to examine the temporal and spatial root distribution, root cores were extracted at six growth stages during the season at in-row and inter-row positions using a soil core device (86 mm ID, 1.0 m length). Such information would help determine whether and to what extent root morphology is changed by alteration of two important factors, atmospheric CO2 and soil water, in this agricultural ecosystem. Wheat root growth increased under elevated CO2 conditions during all observed developmental stages. A maximum of 37% increase in total root dry mass in the FACE vs. Control plots was observed during the period of stem elongation. Greater root growth rates were calculated due to CO2 enhancement until anthesis. During the early vegetative growth, root dry mass of the inter-row space was significantly higher for FACE than for Control treatments suggesting that elevated CO2 promoted the production of first-order lateral roots per main axis. Then, during the reproductive period of growth, more branching of lateral roots in the FACE treatment occurred due to water stress. Significant higher root dry mass was measured in the inter-row space of the FACE plots where soil water supply was limiting. These sequential responses in root growth and morphology to elevated CO2 and reduced soil water supports the hypothesis that plants grown in a high-CO2 environment may better compensate soil-water-stress conditions.

KEYWORDS: BIOMASS, CARBON-DIOXIDE ENRICHMENT, COTTON, DECOMPOSITION, ELEVATED ATMOSPHERIC CO2, FACE, LOLIUM-PERENNE, NITROGEN, PRODUCTIVITY, RESPONSES

2548

Weerakoon, W.M., D.M. Olszyk, and D.N. Moss. 1999. Effects of nitrogen nutrition on responses of rice seedlings to carbon dioxide. *Agriculture Ecosystems & Environment 72(1):1-8.*

Global atmospheric CO2 concentration is increasing, likely increasing the productivity of crops as higher CO2 enhances plant photosynthesis. Responsiveness to nitrogen supply is an essential trait of modem rice cultivars, and may play a role in the response of rice cultivars to CO2. To determine the relationship between these two important production variables on young rice plants, seedlings of Oryza sativa L. 'IR72' and 'KDML 105' were exposed for 28 days after sowing to CO2 levels of 373, 545, 723 and 895 mu molmoI(-1), and 3 levels of nitrogen fertility. There were large increases in leaf CO2 assimilation and biomass production whereas leaf nitrogen concentration dropped sharply as CO2 increased from 373 to 545 mu mol mol(-l), with little additional effect from higher levels of CO2. Root and shoot biomass, and tiller number per plant increased with increasing nitrogen supply and with increasing atmospheric CO2 concentration. The biomass response to CO2 was slight at low N supply, but became dramatically greater as the N supply increased. Mean root/shoot ratio increased slightly as atmospheric CO2 concentration increased, but decreased sharply as nitrogen fertility rate increased. These results suggest that careful attention to nitrogen fertilization will be necessary for rice fanning to get the full benefit of any future increases in atmospheric CO2. (C) 1999 Published by Elsevier Science B.V. All rights reserved.

KEYWORDS: ATMOSPHERIC CO2, GROWTH, ORYZA-SATIVA, PHOTOSYNTHESIS, YIELD

2549

Weigel, H.J., and U. Dammgen. 1999. The Braunschweig carbon project - atmospheric flux monitoring and free air carbon dioxide enrichment. *Berichte Uber Landwirtschaft 77(1):49-58.*

With respect to the predicted climate change it has become evident that the role of terrestrial ecosystems in the global carbon turnover is not yet fully understood. This is also true for carbon fluxes in agricultural ecosystems. As increasing atmospheric CO2 concentrations will directly affect plant photosynthesis, plant biomass production and plant water relations, it is of particular importance to predict the dynamics of carbon fluxes between the atmosphere and agricultural canopies and the related consequences for agroecosystems under future atmospheric CO2 conditions. There are hardly any experimental approaches under real field conditions in crop rotation systems to simulate future CO2 scenarios. The Braunschweig carbon project is a combination of micrometeorological flux measurements of atmospheric trace gases and other air constituents and of a large scale free air carbon dioxide enrichment (FACE) experiment. The project is particularly designed to meet the data requirement of process and landscape models. The data will also contribute to the improvement and validation of models to predict the consequences of climate changes for agricultural ecosystems. The present contribution is a description of the structure of the experiments and the involvement of modelling approaches.

KEYWORDS: CYCLE, ELEVATED CO2, PLANTS, RESPONSES, SOIL

2550

Weigel, H.J., R. Manderscheid, H.J. Jager, and G.J. Mejer. 1994. Effects of season-long co2 enrichment on cereals .1. Growth-performance and yield. *Agriculture Ecosystems & Environment 48(3):231-240.*

Two cultivars each of spring wheat (Triticum aestivum L., cultivars 'Star' and 'Turbo') and spring barley (Hordeum vulgare L., cultivars 'Alexis' and 'Arena') were exposed throughout the growing season to ambient (384 p.p.m.) and above ambient CO2 concentrations (471, 551, 624,718 p.p.m.) in open- top chambers. Plant samples were taken four times during plant development and biomass partitioning into stem, leaves and ear was measured. Total above-ground biomass increased mainly in the C02 concentration range between 400-550 p.p.m. for wheat, and between 400-700 p.p.m. for barley. Stimulation of biomass was largely due to an increase in tillering rate. At the tiller level CO2 enrichment revealed a decrease in leaf dry weight at anthesis stage, which was due to a reduction in leaf size (barley) and in leaf number (wheat). Specific leaf weight of the mature flag leaf was unaffected by CO2. Stem biomass per tiller was temporarily ('Star', 'Alexis') or during the whole growth period ('Turbo', 'Arena') increased by CO2 exposure, while ear dry weight was increased (barley) or even decreased ('Star'). Except for the barley cultivar 'Arena', which showed a 84% increase in the number of grains per ear, the number of ears was almost entirely responsible for the

increased grain yield among the CO2 treatments. At the highest CO2 concentration yield increase amounted to 19% and 27% for the two wheat cultivars, and 5 2% and 8 9% for the two barley cultivars in comparison with the ambient CO2 level. Among all cultivars there was an inverse relationship between the total shoot biomass produced at ambient CO2 conditions and the plant's response to the CO2 enrichment. This indicates that the genetic potential of wheat unlike barley is highly adapted to present atmospheric CO2 conditions and thus responsible for the small CO2 effect on wheat.

KEYWORDS: ATMOSPHERIC CO2, DRY-MATTER, ELEVATED CARBON-DIOXIDE, ENVIRONMENTS, NITROGEN, PHOTOSYNTHETIC ACCLIMATION, PHYSIOLOGY, RESPONSES, SPRING WHEAT, WINTER-WHEAT

2551

Weishampel, J.F., R.G. Knox, and E.R. Levine. 1999. Soil saturation effects on forest dynamics: scaling across a southern boreal/northern hardwood landscape. *Landscape Ecology 14(2):121-135.*

Patch modeling can be used to scale-up processes to portray landscape-level dynamics. Via direct extrapolation, a heterogeneous landscape is divided into its constituent patches; dynamics are simulated on each representative patch and are weighted and aggregated to formulate the higher level response. Further extrapolation may be attained by coarsening the resolution of or lumping environmental data (e.g., climatic, edaphic, hydrologic, topographic) used to delimit a patch. Forest patterns at the southern boreal/northern hardwood transition zone are often defined by soil heterogeneity, determined primarily by the extent and duration of soil saturation. To determine how landscape-level dynamics predicted from direct extrapolation compare when coarsening soil parameters, we simulated forest dynamics for soil series representing a range of drainage classes from east-central Maine. Responses were aggregated according to the distribution of soil associations comprising a 600 ha area based on local- (1.12,000), county- (1:120,000) and state- (1:250,000) scale soil maps. At the patch level, simulated aboveground biomass accumulated more slowly in poorer draining soils. Different soil series yielded different communities comprised of species with various tolerances for soil saturation. When aggregated, removal of waterlogging caused a 20-60% increase in biomass accumulation during the first 50 years of simulation. However, this early successional increase and the maximum level of biomass accumulation over a 200 year period varied by as much as 40% depending on the geospatial data. This marked discrepancy suggests caution when extrapolating with forest patch models by coarsening parameters and demonstrates how rules used to rescale environmental data need to be evaluated for consistency.

KEYWORDS: BOREAL FORESTS, CO2-INDUCED CLIMATE CHANGE, ECOSYSTEMS, GAP MODELS, GLOBAL CHANGE, MOISTURE, MULTIFREQUENCY, NORTHERN FORESTS, SIMULATION, TEMPERATURE

2552

Welker, J.M., and D.D. Briske. 1992. Clonal biology of the temperate, caespitose, graminoid schizachyrium-scoparium - a synthesis with reference to climate change. *Oikos 63(3):357-365.*

Caespitose graminoids are characterized by the compact spatial arrangement of ramets within clones and the absence of rhizomes or stolons. Resource allocation is principally acropetal with established ramets supporting juvenile ramets during early development. However, after juvenile ramet maturation a responsive resource transfer system is maintained by a low level of continuous resource allocation between parental and juvenile ramets. Isotopic and severing experiments demonstrated that physiological integration in the caespitose graminoid Schizachyrium scoparium is restricted to individual ramet sequences consisting of three connected ramet generations as opposed to all ramets within the clone. This number of ramet generations comprising the physiological individual is determined by demographic variables influencing the recruitment and longevity of individual ramets. Restricted resource allocation among ramet sequences within clones is primarily caused by the disintegration of vascular connections among ramet sequences following death of the seminal ramet. The survival value conferred by a clonal architecture composed of an assemblage of autonomous physiological individuals growing within close proximity requires further evaluation but may center on intra-plant competitive interactions. The response of this large sub-group of clonal plants to climate change will significantly impact community structure and function because of their diversity and dominance in numerous biomes. The impact of climate change on the caespitose graminoid growth form is difficult to anticipate because: 1) caespitose graminoids consist of both C3 and C4 species which will complicate the response of the growth form, 2) our understanding about the clonal biology and population ecology of this growth form is still evolving and 3) the modular construction of this growth form may result in variable responses at the ramet, clone and population levels of organization.

KEYWORDS: DEFOLIATION, ELEVATED CO2, GLECHOMA-HEDERACEA, GROWTH, PHOTOSYNTHESIS, PLANT, POPULATIONS, RESPONSES, STRESS, WATER RELATIONS

2553

Wellburn, A.R. 1998. Atmospheric nitrogenous compounds and ozone - is NOx fixation by plants a possible solution? *New Phytologist 139(1):5-9.*

Air quality thresholds for O-3 for the protection of human health and vegetation set by the European Union (EU) have been exceeded in Europe regularly in the 1990s. Because target reductions for oxides of nitrogen (NOx) set for the year 2000 are unlikely to be achieved, these O-3 exceedances are likely to continue into the next millenium. Improvements of plant tolerance towards O-3 are being investigated but very little work has been done to explore NOx tolerance and plant acclimation to NO2 and NO. However, it is clear that within the populations of some plant species there is wide variation, and some individuals can fix NOx, and use the nitrogen directly from the atmosphere, rather than rely upon, for example, root uptake of nitrate. It is possible that individuals capable of fixing NOx could be selected for a range of species, and genotypes with high rates of uptake could be of value as crops or for forestation in polluted areas (e.g. landscaping in the vicinity of motorways) to reduce tropospheric concentrations of NOx significantly and also to decrease the potential for O-3 production.

KEYWORDS: CO2- ENRICHMENT, GROWTH, NITRATE, RESPONSES

2554

Welsh, D.T., S. Bourgues, R. deWit, and I. Auby. 1997. Effect of plant photosynthesis, carbon sources and ammonium availability on nitrogen fixation rates in the rhizosphere of Zostera noltii. *Aquatic Microbial Ecology 12(3):285-290.*

Rates of nitrogen fixation (measured as acetylene reduction) in the rhizosphere of the seagrass Zostera noltii were highly dependent upon plant photosynthetic activity being significantly stimulated at elevated CO2 concentrations and by light, both in the short-term and over diurnal cycles. Stimulation by light became insignificant when 5 mM sucrose was added to the sediment porewater, indicating that in the absence of added carbon sources, light stimulation was due to direct inputs of plant photosynthate to the rhizosphere. Addition of a range of carbon sources to the rhizosphere sediment stimulated rates of acetylene reduction, with this stimulation being significant for sucrose and lactate. Surprisingly,

whilst low additions of ammonium to the sediment porewater (10 to 50 mu M) inhibited 50% of acetylene reduction activity, approximately 30% of this activity persisted in the presence of 1 mM ammonium chloride; this indicating that in at least a proportion of the N-fixing community, nitrogenase activity was not regulated in the short term by the availability of alternative nitrogen sources.

KEYWORDS: AUSTRALIA, BACTERIAL PRODUCTIVITY, CARPENTARIA, GRASS SPARTINA-ALTERNIFLORA, GROWTH, GULF, ORGANIC-CARBON, SEDIMENTS

2555

Weltzin, J.F., S. Archer, and R.K. Heitschmidt. 1997. Small-mammal regulation of vegetation structure in a temperate Savanna. *Ecology 78(3):751-763.*

Explanations for documented increases in woody plant dominance in grasslands and savannas of North America include atmospheric CO2 enrichment and changes in climate, livestock grazing, and fire regimes. However, tree/shrub encroachment has also coincided with the eradication of a once widespread native herbivore, the black-tailed prairie dog (Cynomys ludovicianus). We used field experiments and repeat aerial photography to demonstrate that prairie dogs, and the herbivores and granivores associated with their colonies, probably maintained grassland and savanna by preventing woody species such as Prosopis glandulosa (honey mesquite) from establishing or attaining dominance. Prosopis seed and pod disappearance was 3- 99 times greater within prairie dog colonies. Ants were the primary agent of seed removal, whereas prairie dogs and associated vertebrates were the primary agents of pod removal. Survival of Prosopis seedlings protected from vertebrate herbivory was similar on and off prairie dog colonies (approximate to 60%), whereas survival of unprotected seedlings was 3 times greater off- than on-colony. On-colony, prairie dogs and associated herbivores girdled and destroyed all Prosopis saplings within 2 d of planting; survival of 1-yr-old seedlings was reduced by 50% after 3 mo of exposure to on- colony herbivores. Despite high levels of woody plant seed disappearance and seedling herbivory, on-colony "seedling" reserves were substantial (950 plants/ha). Thus, prairie dogs and the fauna that occur on their colonies suppressed rather than eliminated Prosopis from the colony site. Removal of prairie dogs led to rapid development of Prosopis stands. Repeat aerial photography showed that Prosopis canopy cover on a colony eradicated in 1950 (27%) increased to a level (61%) comparable to that of off-colony Prosopis stands (65%) within 23 yr. These data illustrate how transitions from grassland to woodland vegetation can be mediated by a rodent herbivore. They further demonstrate how purposeful or inadvertent removal of native herbivores can have unforeseen effects on plant species composition and landscape physiognomy. Investigations of environmental constraints on vegetation distribution and abundance should take into account the historical role of herbivores in shaping the present system. Inconsistencies among historic accounts of woody plant distribution and abundance in semiarid western North America may be resolved by considering population dynamics of prairie dogs. Widespread eradication of this formerly abundant rodent has eliminated a significant constraint to woody plant establishment on many semiarid grassland and savanna landscapes and has thereby facilitated transitions to shrubland and woodland states. Past land management designed to remove one perceived impediment to livestock production appears to have contributed significantly to development of another management problem that is now a major detriment to sustainable livestock production.

KEYWORDS: AMERICAN SOUTHWEST, C-4 GRASS, DYNAMICS, INCREASING CO2, MIXED-GRASS PRAIRIE, PLANT-HERBIVORE INTERACTIONS, PROSOPIS- GLANDULOSA, SERENGETI-NATIONAL-PARK, SOUTHERN NEW-MEXICO, WOODY PLANT

2556

West, D.C., T.W. Doyle, M.L. Tharp, J.J. Beauchamp, W.J. Platt, and D.J. Downing. 1993. Recent growth increases in old-growth longleaf pine. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 23(5):846-853.*

Longleaf pine (Pinus palustris Mill.) tree-ring data were obtained from an old-growth stand located in Thomas County, Georgia. The tree-ring chronology from the pine stand is composed of a collection of cores extracted from 26 trees ranging in age from approximately 100 to 400 years. These cores were prepared, dated, and measured, and the resulting data were examined with dendrochronological and statistical techniques. Beginning in approximately 1950 and continuing to the present, annual increments of all age classes examined in this study have increased. resulting in an average annual ring increment approximately 40% greater in 1987 than in 1950. When compared with expected annual increment, the increase for 100- to 150- year-old trees is approximately 45%, while the increase for 200- to 400-year-old trees is approximately 35%. In terms of stand-level aboveground biomass accumulation, the increased growth has resulted in approximately 5% more biomass than expected. The increased growth cannot be explained by disturbance; stand history; or trends in precipitation, temperature, or Palmer drought severity index over the last 57 years. Increased atmospheric CO2 is a possible explanation for initiation of the observed trend, while SO(x) and NO(x) may be augmenting continuation of this phenomenon.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CLIMATE, CO2-ENRICHMENT, COMPETITION, LIQUIDAMBAR- STYRACIFLUA, TAEDA SEEDLINGS, UNITED-STATES

2557

Wheeler, R.M., K.A. Corey, J.C. Sager, and W.M. Knott. 1993. Gas-exchange characteristics of wheat stands grown in a closed, controlled environment. *Crop Science 33(1):161-168.*

Information on gas exchange of crop stands grown in controlled environments is limited, but is vital for assessing the use of crops for human life-support in closed habitats envisioned for space. Two studies were conducted to measure gas exchange of wheat stands (Triticum aestivum L. cv. Yecora Rojo) grown from planting to maturity in a large (20 m2 canopy area), closed growth chamber. Daily rates of dark-period respiration and net photosynthesis of the stand were calculated from rates of CO2 build-up during dark cycles and subsequent CO2 drawdown in the light (i.e., a closed-system approach). Lighting was provided as a 20-h photoperiod by high-pressure sodium lamps, with canopy-level photosynthetic photon flux density (PPFD) ranging from 500 to 800 mumol m-2 s-1 as canopy height increased. Net photosynthesis rates peaked near 27 mumol CO2 m-2 s-1 at 25 d after planting, which corresponded closely with stand closure, and then declined slowly with age. Similarly, dark-period respiration rates peaked near 14 mumol CO2 m-2 s-1 at 25 d and then gradually declined with age. Responses to short-term changes in irradiance after canopy closure indicated the stand light compensation point for photosynthesis to be near 200 mumol m-2 s-1 PPFD. Tests in which CO2 concentration was raised to almost-equal-to 2000 mumol mol-1 and then allowed to draw down to a compensation point showed that net photosynthesis was nearly saturated at > 1000 mumol mol-1; below almost-equal-to 500 mumol mol-1, net photosynthesis rates dropped sharply with decreasing CO2. The CO2 compensation point for photosynthesis occurred near 50 mumol mol-1. Short-term (24 h) temperature tests showed net photosynthesis at 20-degrees-C greater-than- or-equal-to 16-degrees-C > 24-degrees-C, while dark-period respiration at 24-degrees-C > 20-degrees-C > 16-degrees-C. Rates of stand evapotranspiration peaked near Day 25 and remained relatively constant until about Day 75, after which rates declined slowly. Results from these tests will be used to model the use of plants for CO2 removal, O2 production, and water evaporation for controlled ecological life support systems proposed for

extraterrestrial environments.

KEYWORDS: CARBON-DIOXIDE EXCHANGE, CO2, CROP, ENRICHMENT, INHIBITION, LEAF-AREA INDEX, PHOTOSYNTHESIS, SHORT- TERM, SOYBEAN CANOPIES

2558

Wheeler, R.M., C.L. Mackowiak, J.C. Sager, and W.M. Knott. 1994. Growth of soybean and potato at high co2 partial pressures. *Life Sciences and Space Research XXV (3) 14(11):251-255.*

Soybean and potato plants were grown in controlled environments at carbon dioxide (CO2) partial pressures ranging from 0.05 to 1.00 kPa. The highest yields of edible biomass occurred at 0.10 kPa for both species, with higher CO2 levels being supraoptimal, but not injurious to the plants. Stomatal conductance rates of upper canopy leaves were lowest at 0.10 kPa CO2, while conductance rates at 0.50 and 1.00 kPa were significantly greater than 0.10 kPa. Total water use by the plants was greatest at the highest CO2 pressures (i.e. 0.50 and 1.00 kPa); consequently, water use efficiencies (biomass produced / water used) were low at the highest CO2 pressures. Based on previous CO2 studies in the literature, the increased conductance and water use at the highest CO2 pressures were surprising and pose interesting challenges for managing plants in a CELSS, where CO2 pressures may exceed optimal levels.

KEYWORDS: ENRICHMENT, GAS-EXCHANGE

2559

Wheeler, R.M., C.L. Mackowiak, L.M. Siegriest, and J.C. Sager. 1993. Supraoptimal carbon-dioxide effects on growth of soybean [glycine-max (L) merr]. *Journal of Plant Physiology 142(2):173-178.*

In tightly closed environments used for human life support in space, carbon dioxide (CO2) partial pressures can reach 500 to 1000 Pa, which may be supraoptimal or toxic to plants used for life support. To study this, soybeans [Glycine max (L.) Merr. cvs. McCall and Pixie] were grown for 90 days at 50, 100, 200, and 500 Pa partial pressure CO2 (500, 1000, 2000, and 5000 ppm). Plants were grown using recirculating nutrient film technique with a 12-h photoperiod, a 26-degrees-C/20-degrees-C thermoperiod, and approximately 300 mumol m-2 s-1 photosynthetic photon flux (PPF). Seed yield and total biomass were greatest at 100 Pa for cv. McCall, suggesting that higher CO2 levels were supraoptimal. Seed yield and total biomass for cv. Pixie showed little difference between CO2 treatments. Average stomatal conductance of upper canopy leaves at 50 Pa CO2 almost-equal-to 500 Pa > 200 Pa > 100 Pa. Total water use over 90 d for both cultivars (combined on one recirculating system) equalled 822 kg water for 100 Pa CO2, 845 kg for 50 Pa, 879 kg for 200 Pa, and 1194kg for 500 Pa. Water use efficiences for both cultivars combined equaled 3.03 (g biomass kg-1 water) for 100 Pa CO2, 2.54 g kg-1 for 200 Pa, 2.42 g kg-1 for 50 Pa, and 1.91 g kg-1 for 500 Pa. The increased stomatal conductance and stand water use at the highest CO2 level (500 Pa) were unexpected and pose interesting considerations,for managing plants in a tightly closed system where CO2 concentrations may reach high levels.

KEYWORDS: CO2, ENRICHMENT, EXPOSURE, PHOTOSYNTHESIS, PHYSIOLOGY, PLANTS, TEMPERATURE, YIELD

2560

Wheeler, R.M., C.L. Mackowiak, G.W. Stutte, N.C. Yorio, and W.L. Berry. UNKNOWN YEAR. Effect of elevated carbon dioxide on nutritional quality of tomato. *Life Sciences: Life Support Systems Studies-I :1975-1978.*

Tomato (Lycopersicon esculentum Mill.) cvs. Red Robin (RR) and Reimann Philipp (RP) were grown hydroponically for 105 d with a 12 h photoperiod, 26 degrees C /22 degrees C thermoperiod, and 500 mu mol.m(-2).s(-1) PPF at either 400, 1200, 5000, or 10,000 mu mol.mol(-1) (0.04, 0.12, 0.50, 1.00 kPa) CO2. Harvested fruits were analyzed for proximate composition, total dietary fiber, nitrate, and elemental composition. No trends were apparent with regard to CO2 effects on proximate composition, with fruit from all treatments and both cultivars averaging 18.9% protein, 3.6% fat, 10.2% ash, and 67.2% carbohydrate. In comparison, average values for field-grown fruit are 16.6% protein, 3.8% fat, 8.1% ash, and 71.5% carbohydrate (Duke and Atchely, 1986). Total dietary fiber was highest at 10,000 mu mol.mol(-1) (28.4% and 22.6% for RR and RP) and lowest at 1000 mu mol.mol(-1) (18.2% and 15.9% for RR and RP), but showed no overall trend in response to CO2. Nitrate values ranged from 0.19% to 0.35% and showed no trend with regard to CO2. K, Mg, and P concentrations showed no trend in response to CO2 but Ca levels increased from 198 and 956 ppm in RR and RP at 400 mu mol.mol(-1), to 2537 and 2825 ppm at 10,000 mu mol.mol(-1). This increase in Ca caused an increase in fruit Ca/P ratios from 0.07 and 0.37 for RR and RP at 400 mu mol.mol(-1). to 0.99 and 1.23 for RR and RP at 10,000 mu mol.mol(-1), suggesting that more dietary Ca should be available from high CO2-grown fruit. Published by Elsevier Science Ltd on behalf of COSPAR.

KEYWORDS: INCOMPLETE, CO2

2561

Wheeler, R.M., C.L. Mackowiak, N.C. Yorio, and J.C. Sager. 1999. Effects of CO2 on stomatal conductance: Do stomata open at very high CO2 concentrations? *Annals of Botany 83(3):243-251.*

Potato and wheat plants were grown for 50 d at 400, 1000 and 10 000 mu mol mol(-1) carbon dioxide (CO2), and sweetpotato and soybean were grown at 1000 mu mol mol(-1) CO2 in controlled environment chambers to study stomatal conductance and plant water use. Lighting was provided with fluorescent lamps as a 12 h photoperiod with 300 mu mol m(-2) s(-1) PAR. Mid-day stomatal conductances for potato were greatest at 400 and 10 000 mu mol mol(-1) and least at 1000 mu mol mol(-1) CO2. Mid-day conductances for wheat were greatest at 400 pmol mol(-1) and least at 1000 and 10 000 mu mol mol(-1) CO2. Mid-dark period conductances for potato were significantly greater at 10 000 mu mol mol(-1) than at 400 or 1000 mu mol mol(-1), whereas dark conductance for wheat was similar in all CO2 treatments. Temporarily changing the CO2 concentration from the native 1000 mu mol mol(-1) to 400 mu mol mol(-1) increased mid-day conductance for all species, while temporarily changing from 1000 to 10 000 mu mol mol(-1) also increased conductance for potato and sweetpotato. Temporarily changing the dark period CO2 from 1000 to 10 000 mu mol mol(-1) increased conductance for potato, soybean and sweetpotato. In all cases, the stomatal responses were reversible, i.e. conductances returned to original rates following temporary changes in CO2 concentration. Canopy water use for potato was greatest at 10 000, intermediate at 400, and least at 1000 mu mol mol(-1) CO2, whereas canopy water use for wheat was greatest at 400 and similar at 1000 and 10 000 mu mol mol(-1) CO2. Elevated CO2 treatments (i.e. 1000 and 10 000 mu mol mol(-1)) resulted in increased plant biomass for both wheat and potato relative to 400 mu mol mol(-1), and no injurious effects were apparent from the 10 000 mu mol mol(-1) treatment. Results indicate that super-elevated CO2 (i.e. 10 000 mu mol mol(-1)) can increase stomatal conductance in some species, particularly during the dark period, resulting in increased water use and decreased water use efficiency. (C) 1999 Annals of Botany Company.

KEYWORDS: ATMOSPHERES, CARBON DIOXIDE, ELEVATED CO2, ENRICHMENT, ENVIRONMENT, PLANT GROWTH, POTATO GROWTH, SOLANUM TUBEROSUM L, WHEAT, YIELD

2562

Wheeler, R.M., and T.W. Tibbitts. 1997. Influence of changes in daylength and carbon dioxide on the growth of potato. *Annals of Botany 79(5):529-533.*

Potatoes (Solanum tuberosum L.) are highly productive in mid- to high-latitude areas where photoperiods change significantly throughout the growing season. To study the effects of changes in photoperiod on growth and tuber development of potato cv. Denali, plants were grown for 112 d with 400 mu mol m(-2) s(-1) photosynthetic photon flux (PPF) under a 12-h photoperiod (short days, SD), a 24-h photoperiod (long days, LD), and combinations where plants were moved between the two photoperiods 28, 56, or 84 d after planting. Plants given LD throughout growth received the greatest total daily PPF and produced the greatest tuber yields. At similar levels of total PPF, plants given SD followed by LD yielded greater tuber dry mass (DM) than plants given IID followed by SD. Stem DM per plant, leaf DM, and total plant DM all increased with an increasing proportion of LD and increasing daily PPF, regardless of the daylength sequence. When studies were repeated, but at an enriched (1000 mu mol mol(-1)) CO2 concentration, overall growth trends were similar, with high CO2 resulting in greater stem length, stem DM, leaf DM, and total plant DM; but high CO2 did not increase tuber DM. (C) 1997 Annals of Botany Company.

KEYWORDS: CUTTINGS, LIGHT, PHOTOPERIODS, SOLANUM TUBEROSUM L, SYSTEMS, TEMPERATURE, TUBERIZATION, YIELDS

2563

Wheeler, R.M., T.W. Tibbitts, and A.H. Fitzpatrick. 1991. Carbon-dioxide effects on potato growth under different photoperiods and irradiance. *Crop Science 31(5):1209-1213.*

Carbon dioxide concentration can exert a strong influence on plant growth, but this influence can vary depending on irradiance. To study this, potato plants (Solanum tuberosum L.) cultivars 'Norland'. 'Russet Burbank', and 'Denali' were grown in controlled-environment rooms at different levels of CO2 and irradiance. Carbon dioxide levels were maintained either at 350 or 100-mu-mol mol-1 and applied in combination with 12- or 24-h photoperiods at 400 or 800-mu-mol m-2 s-1 photosynthetic photon flux. Air temperatures and relative humidity were held constant at 16-degrees-C and 70%, respectively, and plants were harvested 90 d after planting. When averaged across all cultivars, CO2 enrichment increased tuber yield and total plant dry weight by 39 and 34%, respectively, under a 12-h photoperiod at 400-mu-mol m-2 s-1; 27 and 19% under 12 h at 800-mu-mol m-2 s-1; 9 and 9% under 24 h at 400-mu-mol m-2 s-1. It decreased dry weights by 9 and 9% under 24 h at 800-mu-mol m-2 s-1. Tuber yield of Denali showed the greatest increase (21%) in response to increased CO2 across all irradiance treatments, while tuber yields of Russet Burbank and Norland were increased 18 and 9%, respectively. The results show a pattern of greater plant growth from CO2 enrichment under lower PPF and a short photoperiod.

KEYWORDS: ATMOSPHERIC CO2, CO2- ENRICHMENT, CONTROLLED ENVIRONMENTS, DRY-MATTER PRODUCTION, LIFE SUPPORT SYSTEMS, LIGHT, PHOTOSYNTHESIS, PLANT GROWTH, SPACE, TEMPERATURE

2564

Wheeler, T.R., G.R. Batts, R.H. Ellis, P. Hadley, and J.I.L. Morison. 1996. Growth and yield of winter wheat (Triticum aestivum) crops in response to CO2 and temperature. *Journal of Agricultural Science 127:37-48.*

Crops of winter wheat (Triticum aestivum L. cv. Hereward) were grown within temperature gradient tunnels at a range of temperatures at either c. 350 or 700 mu mol mol(-1) CO2 in 1991/92 and 1992/93 at Reading, UK. At terminal spikelet stage, leaf area was 45% greater at elevated CO2 in the first year due to more tillers, and was 30% greater in the second year due to larger leaf areas on the primary tillers. At harvest maturity, total crop biomass was negatively related to mean seasonal temperature within each year and CO2 treatment, due principally to shorter crop durations at the warmer temperatures. Biomass was 6-31% greater at elevated compared with normal CO2 and was also affected by a positive interaction between temperature and CO2 in the first year only. Seed yield per unit area was greater at cooler temperatures and at elevated CO2 concentrations. A 7-44% greater seed dry weight at elevated CO2 in the first year was due to more ears per unit area and heavier grains. In the following year, mean seed dry weight was increased by > 72% at elevated CO2, because grain numbers per ear did not decline with an increase in temperature at elevated CO2. Grain numbers were reduced by temperatures > 31 degrees C immediately before anthesis at normal atmospheric CO2 in 1992/93, and at both CO2 concentrations in 1991/92. To quantify the impact of future climates of elevated CO2 concentrations and warmer temperatures on wheat yields, consideration of both interactions between CO2 and mean seasonal temperature, and possible effects of instantaneous temperatures on yield components at different CO2 concentrations are required. Nevertheless, the results obtained suggest that the benefits to winter wheat grain yield from CO2 doubling are offset by an increase in mean seasonal temperature of only 1.0 degrees C to 1.8 degrees C in the UK.

KEYWORDS: CARBON DIOXIDE, DRY-MATTER, ELEVATED CO2, ENRICHMENT, FIELD, GRAIN DEVELOPMENT, NITROGEN, PLANT GROWTH, PRODUCTIVITY, REPRODUCTIVE GROWTH

2565

Wheeler, T.R., R.H. Ellis, P. Hadley, and J.I.L. Morison. 1995. Effects of co2, temperature and their interaction on the growth, development and yield of cauliflower (brassica-oleracea L botrytis). *Scientia Horticulturae 60(3-4):181-197.*

Stands of summer cauliflower were grown within polyethylene- covered tunnels along which a temperature gradient was imposed. Two tunnels were maintained at either normal or elevated CO2 concentrations. At the last harvest (88 days from transplanting) no interaction between CO2 and temperature on total biomass was detected. The total dry weight of plants grown at 531 mu mol mol-L CO2 was 34% greater than those grown at 328 mu mol mol(-1) CO2, whereas a 1 degrees C rise reduced dry weight by 6%. From serial harvests the radiation conversion coefficient was 2.01 g MJ(-1) and 1.42 g MJ(-1) at 531 mu mol mol(-1) CO2 and 328 mu mol mol(-1) CO2, respectively, but was not greatly affected by differences in temperature. No effect of either CO2 or temperature on the canopy light extinction coefficient was detected. The rate of progress towards curd initiation increased to a maximum at 15.5 degrees C, and declined thereafter. Provided the effect of temperature was accounted for, CO2 enrichment did not affect the time of curd initiation. From serial harvests after curd initiation, the logarithm of curd weight or diameter were negative linear functions of mean temperature from initiation. Increases in curd weight and diameter at 531 compared with 328 mu mol mol(- 1) CO2 were greater at warmer temperatures (27% at 13 degrees C compared with 47% at 15 degrees C, 57 days after initiation). Effects of CO2 on curd diameter were less than those on curd dry weight because the curd dry matter content was greater at 531 compared with 328 mu mol mol(-1) CO2. Thus, the effects of elevated CO2 concentrations on fresh weight based yield parameters of cauliflower were less than the increase in total dry matter production.

KEYWORDS: AIR- TEMPERATURE, CARBON DIOXIDE, CROP, CURD INITIATION, EFFICIENCY, ENRICHMENT, IRRADIANCE, MATURITY, PLANT GROWTH, PRODUCTIVITY

2566

Wheeler, T.R., T.D. Hong, R.H. Ellis, G.R. Batts, J.I.L. Morison, and P. Hadley. 1996. The duration and rate of grain growth, and harvest index, of wheat (Triticum aestivum L) in response to temperature and CO2. *Journal of Experimental Botany 47(298):623-630.*

Winter wheat (Triticum aestivum L. cv. Hereward) was grown in the field inside polyethylene-covered tunnels at a range of temperatures at either 380 or 684 mu mol mol(-1) CO2. Serial harvests were taken from anthesis until harvest maturity. Grain yield was reduced by warmer temperatures, but increased by CO2 enrichment at all temperatures, During grain-filling, individual grain dry weight was a linear function of time from anthesis until mass maturity (attainment of maximum grain dry weight) within each plot, The rate of progress to mass maturity (the reciprocal of time to mass maturity) was a positive linear function of mean temperature, but was not affected by CO2 concentration, The rate of increase in grain dry weight per ear was 2.0 mg d(-1) greater per 1 degrees C rise, and was 8.0 mg d(-1) greater at 684 compared with 380 mu mol mol(-1) CO2 at a given temperature, The rate of increase in harvest index was 1.0% d(-1) in most plots at 380 mu mol mol(-1) CO2 and in open field plots, compared with 1.18% d(-1) in all plots at 684 mu mol mol(-1) CO2. Thus, the increased rate of grain growth observed at an elevated CO2 concentration could be attributed partly to a change in the partitioning of assimilates to the grain, In contrast, the primary effect of warmer temperatures was to shorten the duration of grain-filling, The rate of grain growth at a given temperature and the rate of increase in harvest index were only independent of the number of grains per ear above a critical grain number of 23-24 grains per ear (similar to 20 000 grains m(-2)).

KEYWORDS: CROPS, DRY-MATTER ACCUMULATION, FIELD, PRODUCTIVITY, WINTER-WHEAT, YIELD

2567

Wheeler, T.R., J.I.L. Morison, R.H. Ellis, and P. Hadley. 1994. The effects of co2, temperature and their interaction on the growth and yield of carrot (daucus-carota L). *Plant, Cell and Environment 17(12):1275-1284.*

Stands of carrot (Daucus carota L.) were grown in the field within polyethylene-covered tunnels at a range of soil temperatures (from a mean of 7.5 degrees C to 10.9 degrees C) at either 348 (SE = 4.7) or 551 (SE = 7.7) mu mol mol(-1) CO2. The effect of increased atmospheric CO2 concentration on root yield was greater than that on total biomass, At the last harvest (137 d from sowing), total biomass was 16% (95% CI=6%, 27%) greater at 551 than at 348 mu mol mol(-1) CO2, and 37% (95% CI=30%, 44%) greater as a result of a 1 degrees C rise In soil temperature, Enrichment with CO2, or a 1 degrees C rise in soil temperature increased root yield by 31% (95% CI=19%, 45%) and 34% (95% CI=27%, 42%), respectively, at this harvest, No effect on total biomass or root yield of an interaction between temperature and atmospheric CO2 concentration at 137 DAS was detected, When compared at a given leaf number (seven leaves), CO2 enrichment increased total biomass by 25% and root yields by 80%, but no effect of differences in temperature on plant weights was found, Thus, increases in total biomass and root yield observed in the warmer crops were a result of the effects of temperature on the timing of crop growth and development, Partitioning to the storage roots during early root expansion was greater at 551 than at 348 mu mol mol(-1) CO2. The root to total weight ratio was unaffected by differences in temperature at 551 mu mol mol(-1) CO2, but was reduced by cooler temperatures at 348 mu mol mol(-1) CO2. At a given thermal time from sowing, CO2 enrichment increased the leaf area per plant, particularly during early root growth, primarily as a result of an increase in the rate of leaf area expansion, and not an increase in leaf number.

KEYWORDS: AIR- TEMPERATURE, ATMOSPHERIC CO2, CARBON DIOXIDE, CULTIVAR, DRY-MATTER, ENRICHMENT, NITROGEN, PHOTOSYNTHESIS, PLANT GROWTH, PRODUCTIVITY

2568

Whetton, P.H., A.M. Fowler, M.R. Haylock, and A.B. Pittock. 1993. Implications of climate-change due to the enhanced greenhouse- effect on floods and droughts in australia. *Climatic Change 25(3-4):289-317.*

Potential impacts of climate change on heavy rainfall events and flooding in the Australian region are explored using the results of a general circulation model (GCM) run in an equilibrium enhanced greenhouse experiment. In the doubled CO, simulation, the model simulates an increase in the frequency of high-rainfall events and a decrease in the frequency of low- rainfall events. This result applies over most of Australia, is statistically more significant than simulated changes in total rainfall, and is supported by theoretical considerations. We show that this result implies decreased return periods for heavy rainfall events. The further implication is that flooding could increase, although we discuss here the many difficulties associated with assessing in quantitative terms the significance of the modelling results for the real world. The second part of the paper assesses the implications of climate change for drought occurrence in Australia. This is undertaken using an off-line soil water balance model driven by observed time series of rainfall and potential evaporation to determine the sensitivity of the soil water regime to changes in rainfall and temperature, and hence potential evaporation. Potential impacts are assessed at nine sites, representing a range of climate regimes and possible climate futures, by linking this sensitivity analysis with scenarios of regional climate change, derived from analysis of enhanced greenhouse experiment results from five GCMs. Results indicate that significant drying may be limited to the south of Australia. However, because the direction of change in terms of the soil water regime is uncertain at all sites and for all seasons, there is no basis for statements about how drought potential may change.

KEYWORDS: CO2, GENERAL-CIRCULATION MODEL, RAINFALL, SOIL MOISTURE, VARIABILITY

2569

Whiley, A.W., C. Searle, B. Schaffer, and B.N. Wolstenholme. 1999. Cool orchard temperatures or growing trees in containers can inhibit leaf gas exchange of avocado and mango. *Journal of the American Society for Horticultural Science 124(1):46-51.*

Leaf gas exchange of avocado (Persea americana Mill.) and mango (Mangifera indica L.) trees in containers and in an orchard (field-grown trees) was measured over a range of photosynthetic photon fluxes (PPF) and ambient CO2 concentrations (C-a). Net CO2 assimilation (A) and intercellular partial pressure of CO2 (Ci) were determined for all trees in early autumn (noncold- stressed leaves) when minimum daily temperatures were greater than or equal to 14 degrees C, and for field-grown trees in winter (cold-stressed leaves) when minimum daily temperatures were less than or equal to 10 degrees C. Cold-stressed trees of both species had lower maximum CO2 assimilation rates (A(max)), light saturation points (Q(A)), CO2 saturation points (C-aSAT) and quantum yields than leaves of noncold-stressed, field-grown trees. The ratio of variable to maximum fluorescence (F-v/F-m) was approximate to 50% lower for leaves of cold-stressed, field-grown trees than for leaves of nonstressed, field-grown trees, indicating chill-induced photoinhibition of leaves had occurred in winter. The data indicate that chill-induced photoinhibition of A and/or sink limitations caused by root restriction in container-grown trees can limit carbon assimilation in avocado and mango trees.

KEYWORDS: ATMOSPHERIC CO2, CHLOROPHYLL, ELEVATED CARBON-DIOXIDE, ENRICHMENT, LEAVES, LIGHT, PHOTOINHIBITION, PHOTOSYNTHETIC ACCLIMATION, PLANTS,

ROOT RESTRICTION

2570

White, A., M.G.R. Cannell, and A.D. Friend. 1999. Climate change impacts on ecosystems and the terrestrial carbon sink: a new assessment. *Global Environmental Change-Human and Policy Dimensions 9:S21-S30.*

Climate output from the UK Hadley Centre's HadCM2 and HadCM3 experiments for the period 1860 to 2100, with IS92a greenhouse gas forcing, together with predicted patterns of N deposition and increasing CO2, were input (offline) to the dynamic vegetation model, Hybrid v4.1 (Friend et al., 1997; Friend and White, 1999). This model represents biogeochemical, biophysical and biogeographical processes, coupling the carbon, nitrogen and water cycles on a sub-daily timestep, simulating potential vegetation and transient changes in annual growth and competition between eight generalized plant types in response to climate. Global vegetation carbon was predicted to rise from about 600 to 800 PgC (or to 650 PgC for HadCM3) while the soil carbon pool of about 1100 PgC decreased by about 8%. By the 2080s, climate change caused a partial loss of Amazonian rainforest, C-4 grasslands and temperate forest in areas of southern Europe and eastern USA, but an expansion in the boreal forest area. These changes were accompanied by a decrease in net primary productivity (NPP) of vegetation in many tropical areas, southern Europe and eastern USA tin response to warming and a decrease in rainfall), but an increase in NPP of boreal forests. Global NPP increased from 45 to 50 PgC y(-1) in the 1990s to about 65 PgC y(-1) in the 2080s (about 58 PgC y(-1) for HadCM3). Global net ecosystem productivity (NEP) increased from about 1.3 PgC y(-1) in the 1990s to about 3.6 PgC y(-1) in the 2030s and then declined to zero by 2100 owing to a loss of carbon from declining forests in the tropics and at warm temperate latitudes - despite strengthening of the carbon sink at northern high latitudes. HadCM3 gave a mon erratic temporal evolution of NEP than HadCM2, with a dramatic collapse in NEP in the 2050s. (C) 1999 Elsevier Science Ltd. All rights reserved.

KEYWORDS: BALANCE, BIOSPHERE, CYCLE, DYNAMICS, FOREST, MODELS, NITROGEN, PHOTOSYNTHESIS, STOMATAL CONDUCTANCE, TRANSPIRATION

2571

White, N.D.G., D.S. Jayas, and W.E. Muir. 1995. Toxicity of carbon-dioxide at biologically producible levels to stored-product beetles. *Environmental Entomology 24(3):640-647.*

The effect of concentrations of carbon dioxide (CO2) that can be produced by biological respiration (7.5-19.2%) on oviposition of adult Tribolium castaneum (Herbst), Cryptolestes pusillus (Schonherr), or C. ferrugineus (Stephens) was determined. Relative to controls, T. castaneum, C. pusillus, and C. ferrugineus, exposed to 7.5% CO2 for 1 wk, had numbers of offspring reduced by 43, 94, and 50%, respectively, and the total population at 6 wk was reduced 53, 84, and 19%, respectively. With levels of greater than or equal to 17.1% CO2 for 1 wk, no offspring were produced and exposed adults had high mortality. Eggs and subsequent immatures of Tribolium confusum J. du Val, T. castaneum, or C. ferrugineus were exposed for 3 wk to elevated levels of CO2 at 22 degrees C. Insect development was similar at 7.5 and 8.6% CO2 with mean mortality 43, 62, and 30% greater than controls for T. confusum, T. castancum, and C. ferrugineus, respectively. Also, mean levels of 5.8-8.3% CO2 for 7 wk reduced, on all sampling dates, populations of T. confusum by 85%, T. castaneum by 99%, C. pusillus by 68%, and C. ferrugineus by 54%. Although T. castaneum had a greater oviposition rate than C. pusillus at 7.5% CO2, immature mortality was greater for T. castaneum. Based on long-term exposure to levels of CO2 which can be produced by biological activity that affects oviposition and immature development, species in increasing order of sensitivity to CO2 are C. ferrugineus, C. pusillus, T. confusum, and T. castaneum.

KEYWORDS: COLEOPTERA, CRYPTOLESTES-FERRUGINEUS, CUCUJIDAE, MODEL, RUSTY GRAIN BEETLE, WHEAT

2572

Whitehead, D., K.P. Hogan, G.N.D. Rogers, J.N. Byers, J.E. Hunt, T.M. McSeveny, D.Y. Hollinger, R.J. Dungan, W.B. Earl, and M.P. Bourke. 1995. Performance of large open-top chambers for long-term field investigations of tree response to elevated carbon dioxide concentration. *Journal of Biogeography 22(2-3):307-313.*

In preparation for an investigation of the effects of elevated carbon dioxide (CO2) concentration on the two tree species Pinus radiata D. Don and Nothofagus fusca (Hook. f.) Oerst, the environmental conditions inside sixteen open-top chambers, of the design described by Heagle et al. (1989), were measured and compared with those outside. During a period in late summer, both air temperature and air saturation deficit were greater inside the chambers, with mean increases of 0.3 degrees C and 0.1 kPa, respectively. The increases were closely related to solar irradiance, reaching maximum differences for temperature and air saturation deficit of 4.3 degrees C and 0.8 kPa, respectively, when solar irradiance was greater than 1600 mu mol m(-2)s(-1). The mean (+/- standard deviation) CO2 concentrations for the ambient and elevated treatments were 362+/-37 and 654+/-69 mu mol mol(-1), respectively. However, the CO2 concentration in the elevated treatment decreased as windspeed increased, owing to incursions of ambient air into the chambers. Transmittance of visible solar irradiance (400- 700 nm) through the plastic wall material decreased by 7% after 1 year of exposure at the site. In cloudy conditions the mean transmittance of solar irradiance into the chambers was 81% and on clear days this decreased from 80% to 74% with increasing solar zenith angle. The ratio of diffuse to total solar irradiance in the chambers was 13% and 21% greater than that outside for cloudy and clear conditions, respectively. The implications of these differences on water use efficiency for the trees growing inside and outside the chamber are discussed. A cost effective system, built to separate the CO2 required for the experiment from waste biogas, is described. This project is contributing to the Global Change and Terrestrial Ecosystems (GCTE) Core Research Programme by providing data on the long- term effects of elevated CO2 concentration on the above and below-ground carbon balance for the two tree species.

KEYWORDS: CO2, DESIGN, VENTILATED CHAMBER

2573

Whitehead, S.J., S.J.M. Caporn, and M.C. Press. 1997. Effects of elevated CO2, nitrogen and phosphorus on the growth and photosynthesis of two upland perennials: Calluna vulgaris and Pteridium aquilinum. *New Phytologist 135(2):201-211.*

Bracken (Pteridium aquilinum (L.) Kuhn) and heather (Calluna vulgaris (L.) Hull) are important upland species which often grow in close proximity in the UK. The effects of factorial treatments of elevated atmospheric CO2 (539 mu mol mol(-1) as opposed to ambient atmospheric CO2 concentrations of 355 mu mol mol(-1)), added N (50 kg N hs(-1) as NH4NO3) and added P (20 kg P ha(-1) as NaH2PO4) on the performance of these two species were studied under controlled environmental conditions using container-grown plants. Plants grown and measured at high CO2 had higher rates of net photosynthesis than those grown and measured in ambient CO2. This increase was greater in heather than in bracken and resulted in a large stimulation of growth in the former. In bracken there was no significant change in plant size or phenology. The increase in biomass of heather in high CO2 was greatest in the absence of added nutrients and lowest when both N and P were supplied. The growth and photosynthesis of both plants responded

positively to the supply of P alone or P with N (in both CO2 atmospheres), but there was little response to N alone. The implications of these findings for bracken and heather growing in the held under conditions of an elevated CO2 atmosphere and greater nutrient availability are discussed.

KEYWORDS: BRACKEN, CONSERVATION, ENGLAND, ENRICHMENT, L HULL, L KUHN, MANAGEMENT, NUTRIENTS, TEMPERATURE, VEGETATION

2574

Whiting, D.C., J. Vandenheuvel, and S.P. Foster. 1992. Potential of low oxygen moderate carbon-dioxide atmospheres for postharvest disinfestation of new-zealand apples. *New Zealand Journal of Crop and Horticultural Science 20(2):217-222.*

Work on the mortality responses of four lepidopteran pests of apples in New Zealand-Epiphyas postvittana (Walker), Cydia pomonella (L.), Planotortrix octo Dugdale, and Ctenopseustis obliquana (Walker)-to low O2/moderate CO2 atmospheres is reviewed and additional data are presented. For both E. postvittana and C pomonella, reducing the O2 concentration and elevating the treatment temperature enhanced controlled atmosphere (CA) efficacy more than did increasing the CO2 concentration. Thus at 20-degrees-C, a 0.4% O2/5.0% CO2 CA gave the most rapid kill of the mixtures tested. The order of lifestage tolerance to this CA was similar for E. postvittana, C. pomonella, P. octo, and C. obliquana i.e., fifth instar > third instar > 3-day eggs > first instar. The four species exhibited a trend of tolerance of C pomonella > E. postvittana = P. octo = C obliquana. An increase in the temperature to 30- degrees-C decreased the time for high mortality for all four species. However, this decrease was much greater for P. octo and C obliquana than for C pomonella and E. postvittana. The potential of these CA treatments for disinfestation of New Zealand apples for the Japanese and United States markets is discussed.

2575

Whiting, G.J., and J.P. Chanton. 1993. Primary production control of methane emission from wetlands. *Nature 364(6440):794-795.*

WETLANDS, both natural and agricultural, contribute an estimated 40 to 50% of the total methane emitted to the atmosphere each year. Recent efforts in atmospheric modelling1 and attempts to constrain CH4 source strengths2 have indicated the need to delineate the processes responsible for the large variations in emission rates found within and across wetland types. Numerous biogeochemical factors are known to affect the activity of methanogenic bacteria3,4 and although there has been some success in relating water level5-7 and temperature8,9 to CH4 emissions within particular systems, these variables are insufficient for predicting emissions across a variety of wetlands2,10. From simultaneous measurements of CO2 and CH4 exchange in wetlands extending from subarctic peatlands to subtropical marshes, we report here a positive correlation between CH4 emission and net ecosystem production and suggest that net ecosystem production is a master variable, integrating many factors which control CH4 emission in vegetated wetlands. We find that about 3 per cent of the daily net ecosystem production is emitted back to the atmosphere as CH4. With projected stimulation of primary production and soil microbial activity in wetlands associated with elevated atmospheric CO2 concentrations11, we envisage the potential for increasing CH4 emissions from inundated wetlands, further enhancing the greenhouse effect.

KEYWORDS: ARCTIC TUNDRA, ATMOSPHERE, BELOWGROUND BIOMASS, CO2 EXCHANGE, METHANOGENESIS, RICE PADDIES, SOIL, SPARTINA-ALTERNIFLORA, TRANSPORT, VEGETATION

2576

Whitney, S.M., S. von Caemmerer, G.S. Hudson, and T.J. Andrews. 1999. Directed mutation of the Rubisco large subunit of tobacco influences photorespiration and growth. *Plant Physiology 121(2):579-588.*

The gene for the large subunit of Rubisco was specifically mutated by transforming the chloroplast genome of tobacco (Nicotiana tabacum). Codon 335 was altered to encode valine instead of leucine. The resulting mutant plants could not grow without atmospheric CO2 enrichment. In 0.3% (v/v) CO2, the mutant and wildtype plants produced similar amounts of Rubisco but the extent of carbamylation was nearly twice as great in the mutants. The mutant enzyme's substrate-saturated CO2-fixing rate and its ability to distinguish between CO2 and O-2 as substrates were both reduced to 25% of the wild type's values. Estimates of these parameters obtained from kinetic assays with the purified mutant enzyme were the same as those inferred from measurements of photosynthetic gas exchange with leaves of mutant plants. The Michaelis constants for CO2, O-2, and ribulose-1,5-bisphosphate were reduced and the mutation enhanced oxygenase activity at limiting O-2 concentrations. Consistent with the reduced CO2 fixation rate at saturating CO2, the mutant plants grew slower than the wild type but they eventually flowered and reproduced apparently normally. The mutation and its associated phenotype were inherited maternally. The chloroplast-transformation strategy surmounts previous obstacles to mutagenesis of higher-plant Rubisco and allows the consequences for leaf photosynthesis to be assessed.

KEYWORDS: BISPHOSPHATE, CARBAMYLATION, CHLOROPLAST GENOME, GENE, NICOTIANA-TABACUM, PHOTOSYNTHESIS, PLASTID TRANSFORMATION, RIBULOSE 1;5-BISPHOSPHATE, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, TRANSGENIC TOBACCO

2577

Whittaker, J.B. 1999. Impacts and responses at population level of herbivorous insects to elevated CO2. *European Journal of Entomology 96(2):149-156.*

Most studies of responses of insects to elevated carbon dioxide have been made using short-term exposures to treated food plants and have involved measurements of responses in growth, reproduction, food consumption and efficiencies of conversion at specific stages in the life cycle. These will be reviewed in the light of longer-term studies recently published where whole generations have been reared in chambers with simultaneous treatment of plants and where insects have been free to select their food and microenvironment. Factors such as seasonal change in plants, choice of food plant, mode of feeding, timing of exposure, temperature, the role of natural enemies are considered and the whole placed in the context of other aspects of climate change. It is concluded that in studies to date, the only feeding guild in which some species have shown increases in population density in elevated carbon dioxide are the phloem feeders. Chewing insects (both free-living,and mining) generally have shown no change or reduction in abundance, though relative abundance may be greatly affected. Compensatory feeding is common in these groups.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, AUCHENORRHYNCHA, CHAMBERS, CLIMATE CHANGE, COTTON, GROWTH, HOMOPTERA, LEPIDOPTERA, NOCTUIDAE, PERFORMANCE

2578

Wiemken, V., L. Kossatz, and K. Ineichen. 1996. Frost hardiness of Norway spruce grown under elevated atmospheric CO2 and increased nitrogen fertilizing. *Journal of Plant Physiology 149(3-4):433-438.*

Frost hardiness was tested on needles from 6-years-old Norway spruces that had been cultivated for 2 years in artificial ecosystems at an atmospheric CO2 concentration of 280, 420 or 560 ppm and a nitrogen fertilization corresponding to 0, 30, and 90 kg N ha(-1) yr(-1) (NH4NO3) as well as combinations of these treatments. Samples of previous year's needles were taken after completion of frost hardening in autumn, and at three dares during the dehardening process in spring when potentially harmful late frost events naturally occur. The needles were exposed to freezing temperatures down to -35 degrees C. Samples were taken at 5 degrees C intervals and frost injury was estimated by the electrolyte leakage technique. After autumnal hardening, needles were injured only below -25 degrees C (LT50 < -30 degrees C), while after dehardening in spring the critical frost temperature (LT50) was around -10 degrees C. Frost hardiness was not influenced by the different CO2 and nitrogen treatments of the trees neither in autumn nor during the dehardening phase in spring.

KEYWORDS: CARBOHYDRATE, CONTAINERIZED BLACK SPRUCE, METABOLISM, PHOTOPERIOD, RED SPRUCE, RESISTANCE, SEASONAL-CHANGES, SEEDLINGS, SITKA SPRUCE, TEMPERATURE

2579

Wiemken, V., L. Kossatz, K. Ineichen, and A. Wiemken. 1996. Frost hardiness of Norway spruce grown under elevated atmospheric CO2 and increased nitrogen fertilization. *Plant Physiology 111(2):612.*

2580

Wilkins, D., J.J. Vanoosten, and R.T. Besford. 1994. Effects of elevated co2 on growth and chloroplast proteins in prunus-avium. *Tree Physiology 14(7-9):769-779.*

To predict the future carbon sequestering capacity of trees, we need information about the possible acclimatory mechanisms of plant growth and photosynthesis in rising atmospheric CO2 under a variety of environmental conditions. We have, therefore, studied the growth response of a tree species (Prunus avium L. Stella (wild cherry)) to elevated CO2 and characterized the associated changes in photosynthetic machinery of the leaf tissue. Self-pollinated seedlings and mature cuttings (clones) from the same parent plant of P. avium were grown for two consecutive growing seasons (about 60 days each) in ambient CO2 (350 mumol mol-1 CO2) or elevated CO2 (700 mumol Mol-1 CO2) with a high or low nutrient supply. The degree of acclimation of leaf biochemistry and growth response to elevated CO2 was dependent on the plant material (seedling or mature cutting) and nutrient supply. There was little or no growth response to elevated CO2 in seedlings or cuttings in the low nutrient supply treatments, whereas, in both seasons, there was a strongly positive growth response to elevated CO2 in seedlings and cuttings in the high nutrient supply regimes, resulting in increases in the root/shoot ratio and in carbon allocation to the roots. In contrast, the protein content and activity of ribulose-1,5-bisphosphate carboxylase-oxygenase (Rubisco, EC 4.1.1.39) were down regulated in elevated CO2. The loss of Rubisco on an area basis in plants in the elevated CO2 treatments was compensated for at the canopy level by increased leaf area. The loss of Rubisco protein was accompanied by decreases in the contents of chlorophyll and the thylakoid membrane proteins D1, D2 and cytochrome f, which are involved in light harvesting and photo-electron transport. We conclude that, in the medium- to long-term, the initial stimulation of biomass production by elevated CO2 may be increasingly offset by a lower photosynthetic capacity per unit leaf area in perennial plants.

2581

Wilks, D.S., D.W. Wolfe, and S.J. Riha. 1995. Simple carbon assimilation response functions from atmospheric co2, and daily temperature and shortwave radiation. *Global Change Biology 1(5):337-346.*

A global 'CO2 fertilizer effect' multiplier is often used in crop or ecosystem models because of its simplicity. However, this approach does not take into account the interaction between CO2, temperature and light on assimilation. This omission can lead to significant under- or overestimation of the magnitude of beneficial effects from elevated CO2, depending on environmental conditions. We use a mechanistic model of the biochemistry of photosynthesis to represent the response of net assimilation to different levels of CO2, temperature and radiation, on the daily time scale. Instantaneous assimilation rates for an idealized canopy model are integrated through diurnal cycles of environmental variables derived from historical climate data at three locations in North America. The calculated CO2 fertilizer effect is greatest at high light and warm temperatures. The results are summarized by assimilation response surfaces specified by the CO2 concentration, the canopy leaf area index, and by daily values of temperature and radiation available from climatic records. These summary functions are suitable for incorporation into crop or ecosystem models for predicting carbon assimilation or biomass production on a daily time step. An example application of the function reveals that for a relatively cool, high latitude location, the beneficial effects from a CO2 doubling would be negligible during the early spring, even assuming a + 4 degrees C global warming scenario. In contrast, the beneficial effects from increasing CO2 at a relatively warm, lower latitude location are greatest in the spring, but decline in late summer because of excessively warm temperatures with a + 4 degrees C global warming.

KEYWORDS: C-3 PLANTS, CARBOXYLASE, DIOXIDE, ELECTRON-TRANSPORT, ELEVATED CO2, GROWTH, MODEL, PHOTOSYNTHESIS

2582

Will, R.E., and R. Ceulemans. 1997. Effects of elevated CO2 concentration on photosynthesis, respiration and carbohydrate status of coppice Populus hybrids. *Physiologia Plantarum 100(4):933-939.*

To determine how increased atmospheric CO2 will affect the physiology of coppiced plants, sprouts originating from two hybrid poplar clones (Populus trichocarpa x P. deltoides - Beaupre and P. deltoides x P. nigra - Robusta) were grown in open-top chambers containing ambient or elevated (ambient + 360 mu mol mol(-1)) CO2 concentration. The effects of elevated CO2 concentration on leaf photosynthesis, stomatal conductance, dark respiration, carbohydrate concentration and nitrogen concentration were measured. Furthermore, dark respiration of leaves was partitioned into growth and maintenance components by regressing specific respiration rate vs specific growth rate. Sprouts of both clones exposed to CO2 enrichment showed no indication of photosynthetic down-regulation. During reciprocal gas exchange measurements, CO2 enrichment significantly increased photosynthesis of all sprouts by approximately 60% ($P < 0.01$) on both an early and late season sampling date, decreased stomatal conductance of all sprouts by 10% ($P < 0.04$) on the early sampling date and nonsignificantly decreased dark respiration by an average of 11%. Growth under elevated CO2 had no consistent effect on foliar sugar concentration but significantly increased foliar starch by 80%. Respiration rate was highly correlated with both specific growth rate and percent nitrogen. Long-term CO2 enrichment did not significantly affect the maintenance respiration coefficient or the growth respiration coefficient. Carbon dioxide enrichment affected the physiology of the sprouts the same way it affected these plants before they were coppiced.

KEYWORDS: ATMOSPHERIC CO2, CARBON-DIOXIDE ENRICHMENT, ECOPHYSIOLOGY, EURAMERICANA, GAS-

EXCHANGE, GROWTH, MAINTENANCE RESPIRATION, POPLAR, REINVIGORATION, SHOOT DECAPITATION

2583

Will, R.E., and R.O. Teskey. 1997. Effect of elevated carbon dioxide concentration and root restriction on net photosynthesis, water relations and foliar carbohydrate status of loblolly pine seedlings. *Tree Physiology 17(10):655-661.*

To determine the effects of CO2-enriched air and root restriction on photosynthetic capacity, we measured net photosynthetic rates of 1-year-old loblolly pine seedlings grown in 0.6-, 3.8- or 18.9-liter pots in ambient (360 mu mol mol(-1)) or 2x ambient CO2 (720 mu mol mol(-1)) concentration for 23 weeks. We also measured needle carbohydrate concentration and water relations to determine whether feedback inhibition or water stress was responsible for any decreases in net photosynthesis. Across all treatments, carbon dioxide enrichment increased net photosynthesis by approximately 60 to 70%. Net photosynthetic rates of seedlings in the smallest pots decreased over time with the reduction occurring first in the ambient CO2 treatment and then in the 2x ambient CO2 treatment. Needle starch concentrations of seedlings grown in the smallest pots were two to three times greater in the 2x ambient CO2 treatment than in the ambient CO2 treatment, but decreased net photosynthesis was not associated with increased starch or sugar concentrations. The reduction in net photosynthesis of seedlings in small pots was correlated with decreased needle water potentials, indicating that seedlings in the small pots had restricted root systems and were unable to supply sufficient water to the shoots. We conclude that the decrease in net photosynthesis of seedlings in small pots was not the result of CO2 enrichment or an accumulation of carbohydrates causing feedback inhibition, but was caused by water stress.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, COTTON, GAS-EXCHANGE, GROWTH, LEAF, PERSPECTIVE, RESPONSES, STRESS, TREES

2584

Will, R.E., and R.O. Teskey. 1997. Effect of irradiance and vapour pressure deficit on stomatal response to CO2 enrichment of four tree species. *Journal of Experimental Botany 48(317):2095-2102.*

The stomatal response of seedlings grown in 360 or 720 mu mol mol(-1) to irradiance and leaf-to-air vapour pressure deficit (VPD) at both 360 and 720 mu mol mol(-1) CO2, was measured to determine how environmental factors interact with CO2 enrichment to affect stomatal conductance, Seedlings of four species with different conductances and life histories, Cercis canadensis (L.), Quercus rubra (L.), Populus deltoides (Bartr. ex Marsh.) x P. nigra (L.), and Pinus taeda (L.), were measured in hopes of identifying general responses, Conductance of seedlings grown at 360 and 720 mu mol mol-l CO2 were similar and responded in the same manner to measurement CO2 concentration, irradiance and VPD, Conductance was lower for all species where measured at 720 than when measured at 360 mu mol mol(-1) CO2 at both VPDs (similar to 1.5 and similar to 2.5 kPa) and all measured irradiances greater than zero (100, 300, 600, > 1600 mu mol m(-2) s(-1)). The average decrease in conductance due to measurement in elevated CO2 concentration was 32% for Cercis, 29% for Quercus, 26% for Populus, and 11% for Pinus, For all species, the absolute decrease in conductance due to measurement in CO2 enrichment decreased as irradiance decreased or VPD increased, The proportional decrease due to measurement in CO2 enrichment decreased in three of eight cases: from 0.46 to 0.10 in Populus and from 0.18 to 0.07 in Pinus as irradiance decreased from > 1600 to 100 mu mol m(-2) s(-1) and from 0.35 to 0.24 in Cercis as VPD increased from 1.3 to 2.6 kPa.

KEYWORDS: ASSIMILATION, CONDUCTANCE, EFFICIENCY, ELEVATED CARBON-DIOXIDE, HUMIDITY, LEAF GAS-EXCHANGE, LIGHT, PINUS TAEDA L, SENSITIVITY, WATER-STRESS

2585

Willekens, H., S. Chamnongpol, M. Davey, M. Schraudner, C. Langebartels, M. VanMontagu, D. Inze, and W. VanCamp. 1997. Catalase is a sink for H2O2 and is indispensable for stress defence in C-3 plants. *Embo Journal 16(16):4806-4816.*

Hydrogen peroxide (H2O2) has been implicated in many stress conditions, Control of H2O2 levels is complex and dissection of mechanisms generating and relieving H2O2 stress is difficult, particularly in intact plants, We have used transgenic tobacco with similar to 10% wild-type catalase activity to study the role of catalase and effects of H2O2 stress in plants, Catalase-deficient plants showed no visible disorders at low Light, but in elevated light rapidly developed white necrotic lesions on the leaves, Lesion formation required photorespiratory activity since damage was prevented under elevated CO2, Accumulation of H2O2 was not detected during leaf necrosis, Alternative H2O2-scavenging mechanisms may have compensated for reduced catalase activity, as shown by increased ascorbate peroxidase and glutathione peroxidase levels, Leaf necrosis correlated with accumulation of oxidized glutathione and a 4-fold decrease in ascorbate, indicating that catalase is critical for maintaining the redox balance during oxidative stress, Such control may not be limited to peroxisomal H2O2 production, Catalase functions as a cellular sink for H2O2, as evidenced by complementation of catalase deficiency by exogenous catalase, and comparison of catalase- deficient and control leaf discs in removing external H2O2. Stress analysis revealed increased susceptibility-of catalase- deficient plants to paraquat, salt and ozone, but not to chilling.

KEYWORDS: ASCORBATE PEROXIDASE, DEFICIENT MUTANT, DISEASE RESISTANCE RESPONSE, GLUTATHIONE-REDUCTASE, HORDEUM VULGARE L, HYDROGEN- PEROXIDE, OXIDATIVE STRESS, SIGNAL-TRANSDUCTION, SUPEROXIDE-DISMUTASE, TRANSGENIC TOBACCO

2586

Williams, D.W., and A.M. Liebhold. 1995. Herbivorous insects and global change: Potential changes in the spatial distribution of forest defoliator outbreaks. *Journal of Biogeography 22(4-5):665-671.*

The geographical ranges and the spatial extent of outbreaks of herbivorous species are likely to shift with climatic change. We investigated potential changes in spatial distribution of outbreaks of the western spruce budworm, Choristoneura occidentalis Freeman, in Oregon, U.S.A. and the gypsy moth, Lymantria dispnr (L.), in Pennsylvania, U.S.A. using maps of historical defoliation, climate and forest composition in a geographic information system. Maps of defoliation frequency were assembled using historical aerial reconnaissance data. Maps of monthly means of daily temperature maxima and minima and of monthly precipitation averaged over 30 years were developed using an interpolation technique. All maps were at a spatial resolution of 2 x 2 km. Relationships between defoliation status and the environmental variables were modelled using a linear discriminant function. Five climatic change scenarios were investigated: an increase of 2 degrees C, a 2 degrees increase with an increase of 0.5 mm per day in precipitation, a 2 degrees C increase with an equivalent decrease in precipitation, and equilibrium projections of temperature and precipitation by two general circulation models (GCMs) at doubled CO2. With an increase in temperature alone, the projected defoliated area decreased relative to ambient conditions for the budworm and increased slightly for the gypsy moth. With an increase in temperature and precipitation the defoliated area increased for both species.

Conversely, the defoliated area decreased for both when temperature increased and precipitation decreased. Results for the GCM scenarios contrasted sharply. For the Geophysical Fluids Dynamics Laboratory model, defoliation by budworm was projected to cover Oregon completely, whereas no defoliation was projected by gypsy moth in Pennsylvania. For the Goddard Institute for Space Studies model, defoliation disappeared completely for the budworm and slightly exceeded that under ambient conditions for the gypsy moth. The results are discussed :in terms of potential changes in forest species composition.

KEYWORDS: CLIMATIC CHANGE, PESTS

2587

Williams, M., and J.L. Harwood. 1997. Effects of carbon dioxide concentration and temperature on lipid synthesis by young wheat leaves. *Phytochemistry 45(2):243-250.*

The effects of incubation temperature and CO2 concentration on lipid synthesis in leaves from 7-day-old wheat plants were studied. Plants were cultivated at 350 mu mol mol(-1) (approximately ambient CO2) and 20 degrees so that, irrespective of the subsequent incubation conditions, the samples were all derived from plants at the same phenological stage of development. Leaf tissue was incubated with [1-C-14]acetate at 350 mu mol mol(-1) or 700 mu mol mol(-1) CO2 concentration and at 20 degrees or 24 degrees. Doubling the CO2 concentration had little or no effect on lipid metabolism. In contrast, a 4 degrees rise in incubation temperature not only increased the rate of radiolabelling but also altered lipid synthesis qualitatively. Most noticeable of these changes was a marked increase in phosphatidylcholine labelling evidently at the expense of that of diacylglycerol. The increase in carbon flux to this extrachloroplastic lipid appeared to be restricted to the distal portions of the leaf tissue, thus indicating that the stage of tissue development was critical. Surprisingly, an increase of polyunsaturated fatty acid labelling was found at the higher incubation temperature. This increase was accompanied by a decrease in labelling of oleate in the main radiolabelled membrane lipids. In phosphatidylcholine the decrease in oleate labelling was compensated by a rise in that of linoleate while in monogalactosyldiacylglycerol, both linoleate and a-linolenate were better labelled at 24 degrees. A molecular basis for these alterations in lipid synthesis and acyl desaturation is suggested. (C) 1997 Elsevier Science Ltd.

KEYWORDS: CO2 CONCENTRATION, ELEVATED CO2, FATTY-ACID SYNTHESIS, GRAIN LIPIDS, GREEN LEAVES, METABOLISM, NITROGEN APPLICATION, PHOTOSYNTHETIC ACCLIMATION, PLANTS, WINTER-WHEAT

2588

Williams, M., E.B. Rastetter, D.N. Fernandes, M.L. Goulden, S.C. Wofsy, G.R. Shaver, J.M. Melillo, J.W. Munger, S.M. Fan, and K.J. Nadelhoffer. 1996. Modelling the soil-plant-atmosphere continuum in a Quercus-Acer stand at Harvard forest: The regulation of stomatal conductance by light, nitrogen and soil/plant hydraulic properties. *Plant, Cell and Environment 19(8):911-927.*

Our objective is to describe a multi-layer model of C-3-canopy processes that effectively simulates hourly CO2 and latent energy (LE) fluxes in a mixed deciduous Quercus-Acer (oak- maple) stand in central Massachusetts, USA, The key hypothesis governing the biological component of the model is that stomatal conductance (g(s)) is varied so that daily carbon uptake per unit of foliar nitrogen is maximized within the limitations of canopy water availability, The hydraulic system is modelled as an analogue to simple electrical circuits in parallel, including a separate soil hydraulic resistance, plant resistance and plant capacitance for each canopy layer, Stomatal opening is initially controlled to conserve plant water stores and delay the onset of water stress, Stomatal closure at a threshold minimum leaf water potential prevents xylem cavitation and controls the maximum rate of water flux through the hydraulic system, We show a strong correlation between predicted hourly CO2 exchange rate (r(2) = 0 . 86) and LE (r(2) = 0 . 87) with independent whole-forest measurements made by the eddy correlation method during the summer of 1992, Our theoretical derivation shows that observed relationships between CO2 assimilation and LE flux can be explained on the basis of stomatal behaviour optimizing carbon gain, and provides an explicit link between canopy structure, soil properties, atmospheric conditions and stomatal conductance.

KEYWORDS: BOUNDARY-LAYER, CANOPY STRUCTURE, CARBON GAIN, CO2 ASSIMILATION, ELEVATED CO2, GAS-EXCHANGE, TERRESTRIAL ECOSYSTEMS, WATER-STRESS, WOODY-PLANTS, XYLEM DYSFUNCTION

2589

Williams, M., E.J. Robertson, R.M. Leech, and J.L. Harwood. 1998. The effects of elevated atmospheric CO2 on lipid metabolism in leaves from mature wheat (Triticum aestivum cv Hereward) plants. *Plant, Cell and Environment 21(9):927-936.*

Winter wheat (Triticum aestivum L. cv, Hereward) plants were grown for 35 d either at 350 mu mol mol(-1) CO2 or at 650 mu mol mol(-1) CO2. Lipid synthesis was studied in these plants by incubating the 5th leaf on the main stem with [1-C-14]acetate. Increased CO2 concentrations did not significantly affect the total incorporation of radiolabel into lipids of whole leaf tissue, but altered the distribution for individual lipid classes. Most noticeable amongst acyl lipids was the reduction in labelling of diacylglycerol and a corresponding increase in the proportion of phosphatidylcholine labelling. In the basal regions, there were similar changes and, in addition, phosphatidylglycerol labelling was particularly increased following growth in an enriched CO2 atmosphere. The stimulation of labelling of the mitochondrial-specific lipid, diphosphatidylglycerol, prompted an examination of the mitochondrial population in wheat plants. Mitochondria were localized in intact wheat sections by immunolabelling for the mitochondrial-specific chaperonin probe. Growth in elevated CO2 doubled the number of mitochondria compared to growth in ambient CO2. Fatty acid labelling was also significantly influenced following growth at elevated CO2 concentrations. Most noticeable were the changes in 16C:18C ratios for the membrane lipids, phosphatidylcholine, phosphatidylglycerol and monogalactosyldiacylglycerol. These data imply a change in the apportioning of newly synthesized fatty acids between the 'eukaryotic' and 'prokaryotic' pathways of metabolism under elevated CO2.

KEYWORDS: ACID, BIOSYNTHESIS, CARBON DIOXIDE, GRAIN LIPIDS, GREEN LEAVES, GROWTH, NITROGEN APPLICATION, PHOTOSYNTHETIC ACCLIMATION, TEMPERATURE, YIELD

2590

Williams, M., E.J. Robertson, R.M. Leech, and J.L. Harwood. 1998. Lipid metabolism in leaves from young wheat (Triticum aestivum cv. Hereward) plants grown at two carbon dioxide levels. *Journal of Experimental Botany 49(320):511-520.*

Lipid synthesis was studied in primary leaves from 7-d-old wheat plants which had been grown at either ambient CO2 concentration (350 mu mol mol(-1)) or elevated CO2 (650 mu mol mol(-1)) by incubating tissue samples with [1-C-14]acetate, Growth at different CO2 concentrations did not affect the total incorporation of radiolabel into lipids but it did influence the relative labelling of individual lipid classes, such as

diacylglycerol. The leaf basal segment was also studied separately and growth in an enriched CO2 atmosphere was associated with a dramatic increase (over 6-fold) in diphosphatidylglycerol (cardiolipin) labelling, indicating an increased rate of mitochondrial membrane biogenesis, Immunocytological observations correlated with this metabolic result. Both leaf samples showed significant decreases in pigment and surface wax labelling caused by growth at elevated CO2. Growth at different CO2 concentrations also influenced fatty acid labelling patterns, particularly those of the major labelled membrane lipids of the primary leaf whereby there were changes in their ratios of radiolabelled 16 carbon to 18 carbon fatty acids. Phosphatidylglycerol was characterized, for instance, by increased palmitate labelling after wheat was grown in elevated CO2 concentrations, In contrast, phosphatidylcholine was marked by a dramatic decrease in palmitate labelling but a corresponding increase in labelling of its 18 carbon unsaturated fatty acids, The diacylglycerol fraction showed increased unsaturation of its C18 fatty acids. In addition, changes to the fatty acid moieties from the basal segment lipids were also associated with changes in the amount of labelling of the polyenoic fatty acids of monogalactosyldiacylglycerol. Possible reasons for these changes in lipid labelling are discussed. The data show that growth in elevated atmospheric CO2 concentrations causes significant changes in the metabolism of leaf lipids as well as increasing mitochondrial biogenesis.

KEYWORDS: ATMOSPHERIC CO2, CO2 CONCENTRATION, ELEVATED CO2, GRAIN LIPIDS, GREEN LEAVES, INCREASING CO2, NITROGEN APPLICATION, TEMPERATURE, WINTER-WHEAT, YIELD

2591

Williams, M., P.R. Shewry, and J.L. Harwood. 1994. The influence of the greenhouse-effect on wheat (triticum- aestivum L) grain lipids. *Journal of Experimental Botany 45(279):1379-1385.*

There have been few studies conducted with the objective of investigating comprehensively the 'greenhouse effect' on wheat growth using field-grown crops and even less on the effects on the lipid composition of harvested grains. Therefore, the aim of this study was to define any changes in wheat grain acyl lipids which could result from alterations in environmental growth conditions predicted to mimic the 'greenhouse effect'. Quantitative changes were recorded for both the non-starch and starch lipids. When supplied with low concentrations of nitrogen fertilizer, plants showed increased amounts of total grain lipids when grown under an elevated (700 mu l l(-1)) carbon dioxide atmosphere. Increasing the ambient temperature by 4 degrees C, however, reduced the total lipid content of grains. Wheat plants treated with high concentrations of nitrogen fertilizer accumulated less lipid compared to low nitrogen controls. Qualitative changes were also observed in the proportions of non-starch and starch lipid classes. However, changes in total acyl composition were limited to starch grain acyl lipids, as a result of changes in atmospheric carbon dioxide, growth temperature and nitrogen fertilizer application. The alterations in wheat lipids observed are likely to affect the properties of the flour produced from the grains.

KEYWORDS: CARBON DIOXIDE, CO2 CONCENTRATION, ELEVATED CO2, NITROGEN, PHOTOSYNTHESIS, PHYSIOLOGY, TEMPERATURE, YIELD

2592

Williams, M., P.R. Shewry, D.W. Lawlor, and J.L. Harwood. 1995. The effects of elevated-temperature and atmospheric carbon- dioxide concentration on the quality of grain lipids in wheat (triticum-aestivum L) grown at 2 levels of nitrogen application. *Plant, Cell and Environment 18(9):999-1009.*

Wheat plants were cultivated under growth regimes combining two temperatures (ambient and 4 degrees C above ambient temperature) with two concentrations of carbon dioxide (350 and 700 mu mol mol(-1)) and two nitrogen fertilizer applications (high and low), The aim of this study was to define any changes in the acyl lipid composition of wheat grains which could result from alterations in the growth conditions, Qualitative and quantitative changes were observed in both non-starch and starch lipid fractions, Temperature was by far the most influential growth factor, although interactions between all three growth conditions occurred, as confirmed by analysis of variance, Growth at elevated temperatures had the general effect of reducing the amounts of accumulated lipids, particularly non-polar lipids (1322mg fatty acids per 100g fresh weight at ambient temperatures as opposed to 777mg fatty acids per 100 g fresh weight at 4 degrees C above ambient temperatures), There were changes in the proportions of the major non-starch as well as the starch lipids, In the former category, non-polar lipids (principally triacylglycerols), the membrane glycosylglycerides and phosphatidylcholine were the main constituents, whereas in the starch lipids, lysophosphatidylcholine and lysophosphatidylethanolamine represented over 70% of the total, Depending on the growth conditions, the percentages of lipids such as monogalactosyldiacylglycerol, digalactosyldiacylglycerol and phosphatidylcholine (non-starch) or the starch lysophosphatidylethanolamine varied 2-fold or more, Significant changes in the acyl composition of individual lipids were also observed, most often in the proportions of palmitate, oleate and linoleate, The observed alterations in wheat lipids are likely to affect the properties of any flours derived from grain grown under climate change conditions.

KEYWORDS: ACCLIMATION, AGRICULTURE, CLIMATE CHANGE, CO2 CONCENTRATION, PHOTOSYNTHESIS, PLANT GROWTH, WINTER-WHEAT, YIELD

2593

Williams, M.W., P.D. Brooks, and T. Seastedt. 1998. Nitrogen and carbon soil dynamics in response to climate change in a high-elevation ecosystem in the Rocky Mountains, USA. *Arctic and Alpine Research 30(1):26-30.*

We have implemented a long-term snow-fence experiment at the Niwot Ridge Long-Term Ecological Research (NWT) site in the Colorado Front Range of the Rocky Mountains, U.S.A., to assess the effects of climate change on alpine ecology and biogeochemical cycles, The responses of carbon (C) and nitrogen (N) dynamics in high-elevation mountains to changes in climate ate investigated by manipulating the length and duration of snow cover with the 2.6 X 60 m snow fence, providing a proxy for climate change. Results from the first year of operation in 1994 showed that the period of continuous snow cover was increased by 90 d. The deeper and earlier snowpack behind the fence insulated soils from winter air temperatures, resulting in a 9 degrees C increase in annual minimum temperature at the soil surface. The extended period of snow cover resulted in subnivial microbial activity playing a major role in annual C and N cycling. The amount of C mineralized under the snow as measured by CO2 production was 22 g m(-2) in 1993 and 35 g m(-2) in 1994, accounting for 20% of annual net primary aboveground production before construction of the snow fence in 1993 and 31% after the snow fence was constructed in 1994. In a similar fashion, maximum subnivial N2O flux increased 3-fold behind the snow fence, from 75 mu g N m(-2) d(-1) in 1993 to 250 mu g N m(-2) d(-1) in 1994. The amount of N lost from denitrification was greater than the annual atmospheric input of N in snowfall. Surface litter decomposition studies show that there was a significant increase in the litter mass loss under deep and early snow, with no significant change under medium and little snow conditions. Changes in climate that result in differences in snow duration, depth, and extent may therefore produce large changes in the C and N soil dynamics of alpine ecosystems.

KEYWORDS: ALPINE TUNDRA, CATCHMENT, COLORADO, FOREST, LITTER, METHANE, NIWOT RIDGE, OXIDE FLUX

2594

Williams, R.S., D.E. Lincoln, and R.J. Norby. 1998. Leaf age effects of elevated CO2-grown white oak leaves on spring-feeding lepidopterans. *Global Change Biology 4(3):235-246.*

Folivorous insect responses to elevated CO2-grown tree species may be complicated by phytochemical changes as leaves age. For example, young expanding leaves in tree species may be less affected by enriched CO2-alterations in leaf phytochemistry than older mature leaves due to shorter exposure times to elevated CO2 atmospheres. This, in turn, could result in different effects on early vs. late instar larvae of herbivorous insects. To address this, seedlings of white oak (Quercus alba L.), grown in open-top chambers under ambient and elevated CO2, were fed to two important early spring feeding herbivores; gypsy moth (Lymantria dispar L.), and forest tent caterpillar (Malacosoma disstria Hubner). Young, expanding leaves were presented to early instar larvae, and older fully expanded or mature leaves to late instar larvae. Young leaves had significantly lower leaf nitrogen content and significantly higher total nonstructural carbohydrate:nitrogen ratio as plant CO2 concentration rose, while nonstructural carbohydrates and total carbon-based phenolics were unaffected by plant CO2 treatment. These phytochemical changes contributed to a significant reduction in the growth rate of early instar gypsy moth larvae, while growth rates of forest tent caterpillar were unaffected. The differences in insect responses were attributed to an increase in the nitrogen utilization efficiency (NUE) of early instar forest tent caterpillar larvae feeding on elevated CO2-grown leaves, while early instar gypsy moth larval NUE remained unchanged among the treatments. Later instar larvae of both insect species experienced larger reductions in foliage quality on elevated CO2-grown leaves than earlier instars, as the carbohydrate:nitrogen ratio of leaves substantially increased. Despite this, neither insect species exhibited changes in growth or consumption rates between CO2 treatments in the later instar. An increase in NUE was apparently responsible for offsetting reduced foliar nitrogen for the late instar larvae of both species.

KEYWORDS: CARBON-DIOXIDE ENRICHMENT, CO2 ENVIRONMENTS, FOREST TENT CATERPILLAR, GROWTH, GYPSY-MOTH, INSECT HERBIVORE INTERACTIONS, JUNONIA-COENIA, LOBLOLLY-PINE, NUTRIENT BALANCE, NUTRITIONAL ECOLOGY

2595

Williams, R.S., D.E. Lincoln, and R.B. Thomas. 1994. Loblolly-pine grown under elevated co2 affects early instar pine sawfly performance. *Oecologia 98(1):64-71.*

Seedlings of loblolly pine Pinus taeda (L.), were grown in open-topped field chambers under three CO2 regimes: ambient, 150 mul l-1 CO2 above ambient, and 300 mul l-1 CO2 above ambient. A fourth, non-chambered ambient treatment was included to assess chamber effects. Needles were used in 96 h feeding trials to determine the performance of young, second instar larvae of loblolly pine's principal leaf herbivore, red-headed pine sawfly, Neodiprion lecontei (Fitch). The relative consumption rate of larvae significantly increased on plants grown under elevated CO2, and needles grown in the highest CO2 regime were consumed 21% more rapidly than needles grown in ambient CO2. Both the significant decline in leaf nitrogen content and the substantial increase in leaf starch content contributed to a significant increase in the starch:nitrogen ratio in plants grown in elevated CO2. Insect consumption rate was negatively related to leaf nitrogen content and positively related to the starch:nitrogen ratio. Of the four volatile leaf monoterpenes measured, only beta-pinene exhibited a significant CO2 effect and declined in plants grown in elevated CO2. Although consumption changed, the relative growth rates of larvae were not different among CO2 treatments. Despite lower nitrogen consumption rates by larvae feeding on the plants grown in elevated CO2, nitrogen accumulation rates were the same for all treatments due to a significant increase in nitrogen utilization efficiency. The ability of this insect to respond at an early, potentially susceptible larval stage to poorer food quality and declining levels of a leaf monoterpene suggest that changes in needle quality within pines in future elevated-CO2 atmospheres may not especially affect young insects and that tree-feeding sawflies may respond in a manner similar to herb-feeding lepidopterans.

KEYWORDS: CARBON-DIOXIDE ATMOSPHERES, DILUTED DIETS, FOOD-CONSUMPTION, INSECT HERBIVORE INTERACTIONS, JUNONIA-COENIA, NUTRIENT BALANCE, PLANT-TISSUE, PSEUDOPLUSIA-INCLUDENS, SPRUCE BUDWORM, VELVETBEAN CATERPILLARS

2596

Williams, R.S., D.E. Lincoln, and R.B. Thomas. 1997. Effects of elevated CO2-grown loblolly pine needles on the growth, consumption, development, and pupal weight of red- headed pine sawfly larvae reared within open-topped chambers. *Global Change Biology 3(6):501-511.*

Seedlings of loblolly pine, Pinus taeda, were grown in open- topped chambers under four levels of CO2: two ambient and two elevated. Larvae of the red-headed pine sawfly, Neoniprion lecontei, were reared from early instar to pupation, primarily on branches within chambers. Larval growth and mortality were assessed and leaf phytochemistry samples of immature and mature leaves collected weekly. Mature leaves grown under elevated CO2 had significant reductions in leaf nitrogen and increases in non-structural carbohydrate contents, resulting in foliage being a poorer food source for larvae, i.e. higher carbohydrate:nitrogen ratio. Nutritional constituents of immature needles were unaffected by seedling CO2 treatment. Volatile mono-and sesquiterpenes were unrelated to plant CO2 treatments for either leaf age class. Larval consumption of immature needles significantly increased on seedlings grown under CO2 enrichment, while mature needle consumption was not different between the treatments. The average weight gain per larva significantly declined in late instar larvae consuming elevated CO2-grown needles. In spite of this reduced growth, neither the days to pupation nor pupal weights were different among the CO2 treatments. This study suggests that enriched CO2-induced alterations in pine needle phytochemistry can affect red-headed pine sawfly performance, However, compensatory measures by larvae, such as choosing to consume more nutritious immature needles, apparently helps offset enriched CO2-induced reductions in the leaf quality of mature needles.

KEYWORDS: CARBON-DIOXIDE ATMOSPHERES, ENRICHED CO2 ATMOSPHERES, INSECT HERBIVORE INTERACTIONS, JUNONIA-COENIA, LEPIDOPTERA, NUTRIENT BALANCE, NUTRITIONAL ECOLOGY, TAEDA L SEEDLINGS, WATER-STRESS, WESTERN SPRUCE BUDWORM

2597

Williams, R.S., R.B. Thomas, B.R. Strain, and D.E. Lincoln. 1997. Effects of elevated CO2, soil nutrient levels, and foliage age on the performance of two generations of Neodiprion lecontei (Hymenoptera : Diprionidae) feeding on loblolly pine. *Environmental Entomology 26(6):1312-1322.*

We investigated how changes in loblolly Dine needle phytochemistry caused by elevated CO2, leaf age, and soil nutrient levels affected the performance of 2 individual generations of the multivoltine folivorous insect pest Neodiprion lecontei (Fitch). In 2 feeding trials, mature needles produced in the previous (spring) and current (fall) year from seedlings grown in open-topped chambers under 4 CO2 and 2 soil

nutrient levels were fed to 2 separate generations of redheaded pine sawfly larvae. Strong seasonal differences (i.e., spring versus fall) in leaf nutritional and defensive constituents resulted in significant between-generation differences in the growth, consumption, and growth efficiency of sawfly larvae, Enriched CO2-grown needles had higher levels of starch and starch/nitrogen ratios in older, overwintering spring needles, which were lower in leaf nitrogen and monoterpenes than younger, current year needles (fall). Overall, larval growth was higher and consumption lower on the fall needles, presumably because of higher levels of leaf nitrogen compared with the spring needles. The plant CO2 concentration significantly contributed to the larval consumption responses between seasons (significant CO2 X season interaction), demonstrating that the 2 sawfly generations were affected differently by CO2-induced phytochemical alterations in spring versus fall needles. The data presented here suggests that when investigating multivoltine folivorous insect responses to elevated CO2-grown tree seedlings in which multiple leaf flushes within a growing season expose insects to an array of leaf phytochemical changes, >1 insect generation should be investigated.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, GROWTH, INSECT HERBIVORE INTERACTIONS, MINERAL NUTRITION, NITROGEN, PLANT-TISSUE, SAWFLY PERFORMANCE, SEASONAL-CHANGES, TAEDA L SEEDLINGS

2598

Williams, T.G., and B. Colman. 1993. Identification of distinct internal and external isozymes of carbonic-anhydrase in chlorella-saccharophila. *Plant Physiology 103(3):943-948.*

External carbonic anhydrase (CA) was detected in whole cells of alkaline-grown Chlorella saccharophila but was suppressed by growth at acid pH or growth on elevated levels of CO2. Internal CA activity was measured potentiometrically as an increase in activity in cell extracts over that of intact cells. Cells grown under all conditions had equal levels of internal CA activity. Two isozymes were identified after electrophoretic separation of soluble proteins on cellulose acetate plates. The fast isozyme was found in cells grown under all conditions, whereas the slow isozyme was found only in cells grown at alkaline pH. Western blot analysis following sodium dodecyl sulfate-polyacrylamide gel electrophoresis using antibodies produced against the periplasmic form of CA from Chlamydomonas reinhardtii revealed a single band at 39 kD, which did not change in intensity between growth conditions and was associated only with proteins eluted from the fast band. The slow isozyme was inactivated by incubation of cell extract at 30 degrees C and by incubation in 10 mM dithiothreitol, whereas the internal form was unaffected. These results indicate that external and internal forms of CA differ in structure and their activities respond differently to environmental conditions.

KEYWORDS: CHLAMYDOMONAS-REINHARDTII, CO2 CONCENTRATION, ENZYME, EXPRESSION, PLANTS, SEQUENCE, SYNECHOCOCCUS PCC7942

2599

Williams, T.G., and B. Colman. 1995. Quantification of the contribution of co2, hco3-, and external carbonic-anhydrase to photosynthesis at low dissolved inorganic carbon in chlorella-saccharophila. *Plant Physiology 107(1):245-251.*

An equation has been developed incorporating whole-cell rate constants for CO2 and HCO3- that describes accurately photosynthesis (Phs) in suspensions of unicellular algae at low dissolved inorganic carbon. At pH 8.0 the concentration of CO2 available to the algal cells depends on the rate of supply from, and the loss to, HCO3- and the rate of use by the cells. At elevated cell densities (>30 mg chlorophyll [Chl] L(-1)), at which CO2 use by the cells is high, the slope of a graph of absolute Phs versus Chl concentration approaches the rate of Phs on a milligram of Chl basis because of HCO3- use alone. The slope of a graph of Phs versus HCO3- will be the rate constant for HCO3- and for Chlorella saccharophila it was 0.16 L mg(-1) Chl h(-1). The difference between the constants for dissolved inorganic carbon (measured in cells with external carbonic anhydrase) and HCO3-1 is the constant for CO2, which was 26 L mg(-1) Chl h(-1). This difference causes the half-saturation constant for Phs to increase 5- to 6-fold at high cell densities. The increase in CO2 use as a result of external carbonic anhydrase is described mathematically as a function of cell density.

KEYWORDS: ALGAE, CHLAMYDOMONAS-REINHARDTII, CO2-DEPENDENT PHOTOSYNTHESIS, CYANOBACTERIA, DIOXIDE, ELLIPSOIDEA, INHIBITION, TRANSPORT

2600

Wilsey, B.J. 1996. Plant responses to elevated atmospheric CO2 among terrestrial biomes. *Oikos 76(1):201-206.*

Although many researchers have stressed the importance of among-species variation in plant response to elevated CO2, none have quantitatively tested whether variation exists among biomes. I compiled data from the literature and found that, although C-3 plants did respond more than C-4 plants (as predicted), biome origin was a better predictor (accounted for more of the variation) of plant response to elevated CO2 than mode of photosynthesis, Variation in plant response among biomes was found both between and within latitudinal zones, with plant species from tropical and temperate biomes responding more than plant species from a polar biome. Within the temperate zone, species from forested biomes responded more than species from a grassland biome, and this provides further evidence that forests are acting as major sinks for increasing levels of atmospheric CO2. A more than 4-fold difference was found among ecosystems in coefficients of variation (calculated across mean species response within each ecosystem). Based on this difference, I suggest that ecosystems may vary in the amount of change in species composition in response to elevated CO2.

KEYWORDS: C-4 GRASS, CARBON-DIOXIDE ENRICHMENT, COMPETITION, GROWTH-RESPONSE, LIQUIDAMBAR-STYRACIFLUA, MINERAL NUTRITION, OPUNTIA FICUS INDICA, PINUS-TAEDA SEEDLINGS, QUERCUS-ALBA, SHORT- TERM

2601

Wilsey, B.J. 1996. Urea additions and defoliation affect plant responses to elevated CO2 in a C-3 grass from Yellowstone National Park. *Oecologia 108(2):321-327.*

A common grass from Yellowstone National Park, Stipa occidentalis, was grown in a factorial experiment to determine if its response to the direct effects of elevated CO2 would be affected by defoliation, and urea additions simulating the N in a urine hit. Plants were grown in tall pots (to mimic rooting depth in the field) in growth chambers under elevated (700 ppm) and ambient (370 ppm) CO2, were defoliated or left undefoliated, and given N-supply rates based on field mineralization rates (untreated) or with an additional 40 g N/m(2). Growth increases in response to elevated CO2 were largest when plants remained unclipped and received urea additions, and were found primarily in crowns and roots (storage organs). Aboveground biomass, which is the part of the plant consumed by grazing mammals, was not affected by elevated CO2. The elevated CO2 treatment caused a reduction in leaf percent N. However, there was a significant interaction between the CO2 and urea treatments, resulting in a larger difference in leaf percent N between urea-treated and control plants under elevated than under ambient CO2. Hence, elevations in atmospheric CO2 may cause an increase in the amount of urine- hit-induced spatial variability in temperate grasslands.

Since food quantity remained largely unchanged in response to elevated CO2, and forage N content went down, grazing mammals may be negatively affected by increases in atmospheric CO2.

KEYWORDS: ATMOSPHERES, CARBON DIOXIDE, DYNAMICS, ECOSYSTEM, ENVIRONMENTS, ESTUARINE MARSH, INSECT HERBIVORE INTERACTIONS, MINERAL NUTRITION, NITROGEN, URINE DEPOSITION

2602

Wilsey, B.J., J.S. Coleman, and S.J. McNaughton. 1997. Effects of elevated CO2 and defoliation on grasses: A comparative ecosystem approach. *Ecological Applications 7(3):844-853.*

Three plant species from each of three grassland ecosystems were grown under elevated (700 mL/m(3)) and ambient (350 mL/m(3)) CO2 and were defoliated or left undefoliated to test whether species response to elevated CO2 and grazing is related to evolutionary grazing history or to mode of photosynthesis. The three ecosystems represented a tropical grassland dominated by C-4 species (the Serengeti of Africa), a temperate grassland dominated by a mixture of C-3 and C-4 species (Flooding Pampa of South America), and a northern temperate grassland dominated by C-3 species (Yellowstone National Park of North America). Plants were grown in growth chambers under common conditions to compare relative responses to grazing and elevated CO2. Elevated CO2 caused an increase in total biomass and total productivity (biomass + clippings) only in Yellowstone species, and increases in growth occurred primarily in crowns and roots (storage organs). There were no significant CO2 effects on biomass or productivity in Serengeti or Flooding Pampa species, and no CO2 effects on aboveground biomass or productivity (aboveground biomass + clippings) in species from any of the three ecosystems. Since aboveground plant parts are the portions that are available to grazing mammals, this suggests that increased atmospheric CO2 may not affect food quantity in these three grasslands. There was no interaction between CO2 and defoliation for any species; thus, it appears that herbivores will not affect how grasses respond to elevated CO2 (at least under average nutrient conditions). Elevated CO2 caused a reduction in leaf percentage of N in species from Yellowstone and Flooding Pampa (especially the C-3 species, Briza subaristata), but not in Serengeti species. Because the quantity of food was unaffected by the CO2 treatments and forage N was reduced, grazing mammals in Yellowstone (elk, Cervus elaphus, and bison, Bison bison) and the Flooding Pampa (cattle) may be negatively affected. Responses to defoliation were fairly consistent among ecosystems in aboveground productivity, which did not differ between defoliated and undefoliated plants, and in leaf water potentials and percentage of N, both of which increased in response to defoliation. However, differences among ecosystems were found for crown and root biomass in response to defoliation: Serengeti species, on average, had higher crown and similar root biomasses after defoliation, whereas defoliated species from the other two ecosystems had reduced crown and root biomass. We suggest that the lower intensity and increased temporal variance in grazing pressure in Yellowstone vs. the Serengeti, selected for plants that shift allocation away from roots and crowns in order to compensate for aboveground herbivory.

KEYWORDS: C-4 GRASSES, DYNAMICS, ESTUARINE MARSH, GROWTH, NITROGEN ACCUMULATION, PLANTS, SERENGETI, SIMULATED HERBIVORY, TEMPERATE GRASSLAND, YELLOWSTONE NATIONAL PARK

2603

Wilsey, B.J., S.J. McNaughton, and J.S. Coleman. 1994. Will increases in atmospheric co2 affect regrowth following grazing in C-4 grasses from tropical grasslands - a test with sporobolus-kentrophyllus. *Oecologia 99(1-2):141-144.*

We grew a C-4 grass from the Serengeti ecosystem under ambient (370 ppm) and elevated (700 ppm) CO2, and under clipped and unclipped conditions to test whether regrowth following grazing would be affected by elevated CO2. Above-ground productivity was slightly decreased under elevated CO2, and was similar between clipped and unclipped plants. Regrowth (clipping offtake) following clipping was similar in the two CO2 treatments, and there was no CO2 by clipping interaction on biomass, productivity, or leaf nutrient concentrations. Based on this evidence, we suggest that C-4 grasses from the Serengeti will show little direct response to future increases in atmospheric CO2.

KEYWORDS: DEFOLIATION, ECOSYSTEM, GROWTH, PLANTS, SERENGETI

2604

Wilson, J.W., D.W. Hand, and M.A. Hannah. 1992. Light interception and photosynthetic efficiency in some glasshouse crops. *Journal of Experimental Botany 43(248):363-373.*

Productivity of glasshouse crops is strongly limited by light receipt, and efficient interception and use of light in photosynthesis is correspondingly important. Mature row crop canopies of cucumber and tomato intercepted about 76% of the light incident on their upper surfaces; about 18% was lost through gaps between the rows. Light transmitted through the entire depth of the canopy was reflected back by white plastic on the ground, so that the lower surface of the canopy received approximately 13% of the light incident on the upper surface. The light flux incident on the sides of these canopies (c. 2 m tall and 6 m x 16 m in area) amounted to some 20-30% of that incident on the upper surface. About 32% of daylight falling on the glasshouse (c. 9 m x 18 m in area) was intercepted by the glasshouse structure and glazing; of the 68% entering the house, some fell on headlands occupying 35% of the glasshouse area. The loss of light to headlands, and the gain from canopy side-lighting, would be relatively smaller for larger glasshouses. At near-ambient CO2 concentrations, net photosynthetic rates of the cucumber canopy were comparable to those of closed canopies of other glasshouse and field crops which have maximum light conversion efficiencies of 5-8-mu-g CO2 J-1 at 50-200 W m-2 incident light flux density. Efficiency decreases only slightly with stronger light. Glasshouse crops with CO2 enrichment to 1200 vpm achieve conversion efficiencies of 7-10-mu-g CO2 J-1. Efficiencies of utilization of intercepted light, on an energy basis, reach 6-10% in various field and glasshouse crops with near-ambient CO2, and reached an exceptional 11% for the cucumber canopy. Glasshouse crops with CO2 enrichment achieve maximum efficiency of light energy utilization between 12% and 13%.

KEYWORDS: CARBON BUDGET, ENRICHMENT, ENVIRONMENT, GROWTH, PENETRATION, RESPONSES, SOLAR RADIATION, STAND

2605

Wilson, K.B., and J.A. Bunce. 1997. Effects of carbon dioxide concentration on the interactive effects of temperature and water vapour on stomatal conductance in soybean. *Plant, Cell and Environment 20(2):230-238.*

Soybeans were grown at three CO2 concentrations in outdoor growth chambers and at two concentrations in controlled- environment growth chambers to investigate the interactive effects of CO2, temperature and leaf-to-air vapour pressure difference (LAVPD) on stomatal conductance, The decline in stomatal conductance with CO2 was a function of both leaf temperature and LAVPD. In the field measurements, stomatal conductance was more sensitive to LAVPD at low CO2 at 30 degrees C but not at 35 degrees C, There was also a direct increase in conductance with temperature, which was greater at the two

elevated carbon dioxide concentrations, Environmental growth chamber results showed that the relative stomatal sensitivity to LAVPD decreased with both leaf temperature and CO2. Measurements in the environmental growth chamber mere also performed at the opposing CO2, and these experiments indicate that the stomatal sensitivity to LAVPD was determined more by growth CO2 than by measurement CO2. Two models that describe stomatal responses to LAVPD were compared with the outdoor data to evaluate whether these models described adequately the interactive effects of CO2, LAVPD and temperature.

KEYWORDS: ASSIMILATION, BOUNDARY-LAYER, CO2 CONCENTRATIONS, ELEVATED CO2, HUMIDITY, MODEL, PHOTOSYNTHESIS, RESPONSES, TRANSPIRATION RATE, USE EFFICIENCY

2606

Winder, T.L., J.C. Anderson, and M.H. Spalding. 1992. Translational regulation of the large and small subunits of ribulose bisphosphate carboxylase oxygenase during induction of the co2-concentrating mechanism in chlamydomonas-reinhardtii. *Plant Physiology 98(4):1409-1414.*

In conditions of limiting external inorganic carbon, the unicellular alga Chlamydomonas reinhardtii induces a mechanism to actively transport and accumulate inorganic carbon within the cell. A high internal inorganic carbon concentration enables the cell to photosynthesize efficiently with little oxygen inhibition, even in conditions of limiting external inorganic carbon. A correlation between limiting inorganic carbon-induced induction of the CO2-concentrating mechanism and decreased synthesis of the large and small subunits of ribulose 1,5-bisphosphate carboxylase/oxygenase has been observed. Cells that had been transferred from elevated CO2 to limiting CO2 exhibit transient declines of label incorporation into both subunit polypeptides. We have found that this decrease in synthesis of large and small subunits results from specific and coordinated down-regulation of translation of both subunits possibly resulting, at least in part, from modification of large and small subunit transcripts.

KEYWORDS: AMARANTH, CARBONIC-ANHYDRASE, CHLOROPLAST GENE, COORDINATE, GENE-EXPRESSION, MESSENGER-RNAS, MUTANT, TRANSPORT

2607

Winder, T.L., J.D. Sun, T.W. Okita, and G.E. Edwards. 1998. Evidence for the occurrence of feedback inhibition of photosynthesis in rice. *Plant and Cell Physiology 39(8):813-820.*

The response of photosynthesis in the flag leaf of rice (Oryza sativa) to elevated CO2 or reduced O-2 was investigated relative to other environmental factors using steady-state gas exchange techniques. We found under moderate conditions of temperature and photosynthetic flux density (PFD) (26 degrees C and 700 mu mol quanta m(-2)s(-1), similar to growth conditions) photosynthesis in the flag leaf of rice during heading and grain filling saturated at near ambient levels of CO2, with a concomitant loss of O-2 sensitivity, when a high stomatal conductance was maintained by high humidity (low vapor pressure deficit). Under 18 degrees C there was near complete loss of O- 2 sensitivity of photosynthesis at normal ambient levels of CO2, This is in contrast to the large enhancement of photosynthesis by supra-atmospheric levels of CO2 and sub- atmospheric levels of O-2 by suppression of photorespiration when there is no limitation on utilizing the initial product of CO2 assimilation (triose-beta) as predicted from Ribulose-1,5- bisphosphate carboxylase/oxygenase (Rubisco) kinetic properties. Thus, loss of sensitivity to CO2 and O-2 has been previously explained as a limitation on utilization of triose- beta to synthesize carbohydrates. Under high PFD at 25 degrees C, the rate of photosynthesis in rice declined over a period of hours around midday, while the intercellular levels of CO2 remained constant suggesting a limitation on utilization of photosynthate, Short-term fluctuations in climatic factors including temperature, light and humidity could result in a feedback limitation on photosynthesis in rice which may be exacerbated by rising CO2.

KEYWORDS: C-3 PLANTS, CARBON METABOLISM, CHILLING INJURY, CHLOROPHYLL FLUORESCENCE, ELECTRON-TRANSPORT, ELEVATED CO2, MATURE LEAVES, ORYZA-SATIVA, STOMATAL CONDUCTANCE, VARIETAL DIFFERENCES

2608

Winjum, J.K., R.K. Dixon, and P.E. Schroeder. 1992. Estimating the global potential of forest and agroforest management-practices to sequester carbon. *Water, Air, and Soil Pollution 64(1-2):213-227.*

Forests play a prominent role in the global C cycle. Occupying one-third of the earth's land area, forest vegetation and soils contain about 60% of the total terrestrial C. Forest biomass productivity can be enhanced by management practices, which suggests that, by this means, forests could store more C globally and thereby slow the increase in atmospheric CO2. The question is how much C can be sequestered by forest and agroforest management practices. To address the question, a global database of information was compiled to assess quantitatively the potential of forestry practices to sequester C. The database presently has information for 94 forested nations that represent the boreal, temperate and tropical latitudes. Results indicate that the most promising management practices are reforestation in the temperate and tropical latitudes, afforestation in the temperate regions, and agroforestry and natural reforestation in the tropics. Across all practices, the median of the mean C storage values for the boreal latitudes is 16 tCha-1 (n=46) while in the temperate and tropical latitudes the median values are 71 tCha-1 (n=401) and 66 tCha-1 (n=170), respectively. Preliminary projections are that if these practices were implemented on 0.6 to 1.2 x 10(9) ha of available land over a 50-yr period, approximately 50 to 100 GtC could be sequestered.

2609

Winnett, S.M. 1998. Potential effects of climate change on US forests: a review. *Climate Research 11(1):39-49.*

Human-induced changes in climate are likely to affect U.S, domestic forests and the economic systems which rely on them. This paper reviews current knowledge of how changes in temperature and precipitation could affect tree species, forest ecosystems, and the forest products sector of the economy. The various types of models used to predict change and the results they calculate are examined. Models currently project both increases and decreases in the range of various species and ecosystems, and similar results for changes in the productivity, biomass and growth of forests in response to changes in climate. Results vary with the models used, the species or ecosystem studied, and the specific condition of the forest in question. The science of forests and global change is reviewed with regard to plant responses to enhanced CO2 environments and forests' response to other bioclimatic and indirect factors, such as insect predation, fire, climatic variation and ozone. Three studies of the economic effects of climate change on forests, which project a range of losses and benefits to the economy, are compared. Economic results vary directly with the results of the forest growth and productivity models which were employed as inputs. No one model can provide a complete answer, and current knowledge and models are limited in various ways which point to areas where further research could provide benefits.

KEYWORDS: AMBIENT OZONE, CARBON DIOXIDE, ELEVATED CO2, LOBLOLLY-PINE, NITROGEN LEVEL, NORTHEASTERN UNITED-STATES, NORTHERN HARDWOODS, OCEAN-

ATMOSPHERE MODEL, TRANSIENT-RESPONSE, WATER-STRESS

2610

Winter, K., and B. Engelbrecht. 1994. Short-term co2 responses of light and dark co2 fixation in the crassulacean acid metabolism plant kalanchoe-pinnata. *Journal of Plant Physiology 144(4-5):462-467.*

Short-term responses of net CO2 assimilation rate (A), in the light and dark, to ambient CO2 partial pressure (between about 30 and 1000 mu bar) were studied in leaves of the crassulacean acid metabolism (CAM) plant, Kalanchoe pinnata. The results show that it is possible to extrapolate from instantaneous measurements of net CO2 exchange to diurnal and nocturnal CO2 balances at different CO2 partial pressures. Instantaneous CO2 response curves were obtained by altering CO2 levels at 10-min intervals during the middle of the 12-h dark period (phase I of CAM) and during the last third of the 12-h light period (phase IV of CAM). CO2 partial pressures were also altered at longer, 12- to 24-h intervals and maximum rates of net CO2 uptake (A(max)) during light and dark periods were analysed in response to intercellular CO2 partial pressures (p(i)) occurring at the time of A(max). A(max)-p(i) relationships were identical to A-p(i)-curves from rapidly performed determinations during phases I and IV. Corresponding to previous findings with non-CAM species, A(max) and integrated net carbon gain during light and dark periods, respectively, showed a linear relationship. Nocturnal CO2 uptake in normal air was barely affected when light-period carbon gain was manipulated by alterations in CO2 partial pressure. Carbon gain during light periods, measured in normal air, was also independent of CO2-related changes in nocturnal carbon gain. Only after 12 h of darkness at the lowest CO2 concentration used (about 30 mu bar), was carbon gain increased under lighted conditions.

KEYWORDS: CARBON DIOXIDE, ELEVATED CO2, EXCHANGE, PHOTOSYNTHESIS

2611

Winter, K., and C.E. Lovelock. 1999. Growth responses of seedlings of early and late successional tropical forest trees to elevated atmospheric CO2. *Flora 194(2):221-227.*

Seedlings of nine tropical forest tree species were grown outdoors in open-top chambers at ambient and elevated (two times ambient) CO2 concentrations at the Smithsonian Tropical Research Institute, Republic of Panama. Plants were kept individually in large pots and received non-limiting supplies of water and mineral nutrients. The enhancement of biomass accumulation at elevated CO2 increased with increasing relative growth rates (RGR) of species at ambient CO2. Early successional pioneer trees (Cecropia longipes, Ficus insipida, Castilla elastica, Antirrhoea trichantha, Luehea seemannii, Pseudobombax septenatum) grew rapidly, and, at the end of 25 to 39 day treatments, dry matter accumulation was 74 +/- 26% higher at elevated than at ambient CO2 (mean increase +/- SD, n = 6). By contrast, seedlings of three late successional tree species (Calophyllum longifolium, Tetragastris panamensis, Virola surinamensis) grew slowly and, over an 84 day period, elevated CO2 led to either no (C. longifolium, T. panamensis) or only small enhancement in dry matter accumulation (V. surinamensis). These different responses to CO2 enrichment are a result of differences in growth kinetics between early and late successional species at ambient CO2 rather than a result of intrinsic physiological differences in CO2 responsiveness between plants from these two functional groups.

KEYWORDS: CARBON, ECOSYSTEMS, PLANTS

2612

Winter, K., A. Richter, B. Engelbrecht, J. Posada, A. Virgo, and M. Popp. 1997. Effect of elevated CO2 on growth and crassulacean-acid-metabolism activity of Kalanchoe pinnata under tropical conditions. *Planta 201(4):389-396.*

Kalanchoe pinnata (Lam.) Pers. (Crassulaceae), a succulent- leaved crassulacean-acid-metabolism plant, was grown in open- top chambers at ambient and elevated (two times ambient) CO2 concentrations under natural conditions at the Smithsonian Tropical Research Institute, Republic of Panama. Nocturnal increase in titratable acidity and nocturnal carbon gain were linearly related, increased with leaf age, and were unaffected by CO2 treatments. However, under elevated CO2, dry matter accumulation increased by 42-51%. Thus, the increased growth at elevated CO2 was attributable entirely to increased net CO2 uptake during daytime in the light. Malic acid was the major organic acid accumulated overnight. Nocturnal malate accumulation exceeded nocturnal citrate accumulation by six- to eightfold at both CO2 concentrations. Basal (predawn) starch levels were higher in leaves of plants grown at elevated CO2 but diurnal fluctuations of starch were of similar magnitude under both ambient and elevated CO2. In both treatments, nocturnal starch degradation accounted for between 78 and 89% of the nocturnal accumulation of malate and citrate. Glucose, fructose, and sucrose were not found to exhibit marked day- night fluctuations.

KEYWORDS: CAM, CARBON DIOXIDE, CLADODE DEVELOPMENT, EXCHANGE, LIGHT, OPUNTIA FICUS INDICA, PARTIAL-PRESSURE, PLANT, RESPONSES, SHORT- TERM

2613

Winter, K., and A. Virgo. 1998. Elevated CO2 enhances growth in the rain forest understory plant, Piper cordulatum, at extremely low light intensities. *Flora 193(3):323-326.*

Seedlings of the rain forest understory shrub Piper cordulatum were grown for several months at ambient and elevated concentrations of atmospheric CO2. Photon flux density (PFD) during 12-h photoperiods was maintained at extremely low levels (< 10 mu mol m(-2) s(-1)). Despite these low PFDs, dry matter accumulation and leaf area production were increased in air containing elevated (approximately twice-ambient) CO2 concentrations compared to ambient air. In leaves that had developed in deep shade and at ambient CO2, rates of net CO2 uptake, measured at 6 mu mol photons m(-2)s(-1), were 30% higher at elevated than at ambient CO2. Rates of net CO2 loss in the dark were 10% lower at elevated than at ambient CO2.

KEYWORDS: ATMOSPHERIC CO2, C-4 PLANTS, CARBON DIOXIDE, DARK RESPIRATION, ENRICHMENT, FUTURE, QUANTUM YIELD, RESPONSES

2614

Wise, R.R., A. Ortizlopez, and D.R. Ort. 1992. Spatial-distribution of photosynthesis during drought in field- grown and acclimated and nonacclimated growth chamber-grown cotton. *Plant Physiology 100(1):26-32.*

Inhomogeneous photosynthetic activity has been reported to occur in drought-stressed leaves. In addition, it has been suggested that these water stress-induced nonuniformities in photosynthesis are caused by "patchy" stomatal closure and that the phenomenon may have created the illusion of a nonstomatal component to the inhibition of photosynthesis. Because these earlier studies were performed with nonacclimated growth chamber-grown plants, we sought to determine whether such "patches" existed in drought-treated, field-grown plants or in chamber-grown plants that had been acclimated to low leaf water potentials (psi(leaf)). Cotton (Gossypium hirsutum L.) was grown in the field and subjected to drought by withholding irrigation and rain from 24 d after planting. The distribution of photosynthesis, which may

reflect the stomatal aperture distribution in a heterobaric species such as cotton, was assayed by autoradiography after briefly exposing attached leaves of field-grown plants to (CO2)-C-14. A homogeneous distribution of radioactive photosynthate was evident even at the lowest psi(leaf) of -1.34 MPa. "Patchiness" could, however, be induced by uprooting the plant and allowing the shoot to air dry for 6 to 8 min. In parallel studies, growth chamber-grown plants were acclimated to drought by withholding irrigation for three 5-d drought cycles interspersed with irrigation. This drought acclimation lowered the psi(leaf) value at which control rates of photosynthesis could be sustained by approximately 0.7 MPa and was accompanied by a similar decline in the psi(leaf) at which patchiness first appeared. Photosynthetic inhomogeneities in chamber-grown plants that were visible during moderate water stress and ambient levels of CO2 could be largely removed with elevated CO2 levels (3000 muL L-1), suggesting that they were stomatal in nature. However, advanced dehydration (less than approximately 2.0 MPa) resulted in "patches" that could not be so removed and were probably caused by nonstomatal factors. The demonstration that patches do not exist in drought-treated, field-grown cotton and that the presence of patches in chamber-grown plants can be altered by treatments that cause an acclimation of photosynthesis leads us to conclude that spatial heterogeneities in photosynthesis probably do not occur frequently under natural drought conditions.

KEYWORDS: ABSCISIC-ACID, CO2 EXCHANGE, FLUORESCENCE, GAS-EXCHANGE, INHIBITION, LOW WATER POTENTIALS, STATISTICAL DISTRIBUTION, STOMATAL APERTURES, STRESS, SUNFLOWER LEAVES

2615

Witjaksono Schaffer, B.A., A.M. Colls, R.E. Litz, and P.A. Moon. 1999. Avocado shoot culture, plantlet development and net CO2 assimilation in an ambient and CO2 enhanced environment. *In Vitro Cellular & Developmental Biology-Plant 35(3):238-244.*

The proliferation and survival of avocado nodal cultures of juvenile origin were affected by the form anti concentration of nitrogen. Optimum growth was achieved on modified Murashige and Skoog medium containing 67% KNO3 and 33% NH4NO3 with total N of 40 mM supplemented with 100 mg 1 (1) myo-inositol, 1 mg 1 (-1) thiamine HCl, 30 g l (1) sucrose, and 4.44 mu M BA with a 16-h photoperiod (120-150 mu mol m(-2) s(-1)). Proliferating shoots and plantlets, were photosyntheticallS active. Better shoot growth and accumulation of higher biomass occurred in a CO2- enrichcd environment than under ambient CO2 conditions. CO2 assimilation efficiency, however, was higher under the latter conditions than in a CO2-enhanced ;environment, e.g., 31 +/- 7 and 17+/- 2 mu mol CO2 m(-2) s(-1), respectively. The net CO2 assimilation rates of in vitro grown plantlets were comparable to those of seedlings ex vitro.

KEYWORDS: ACCLIMATIZATION, CARBON DIOXIDE, ENRICHMENT, INVITRO, INVITRO-PROPAGATION, LIGHT-INTENSITY, MUSA, PHOTOSYNTHESIS, SUBSEQUENT GROWTH

2616

Wittwer, S.H. 1990. Implications of the greenhouse-effect on crop productivity. *Hortscience 25(12):1560-1567.*

KEYWORDS: ATMOSPHERIC CO2 ENRICHMENT, CARBON DIOXIDE, CLIMATIC CHANGE, GROWTH, INCREASE, POTATO, SENSITIVITY, WATER, WHEAT, YIELD

2617

Wolf, J. 1996. Effects of nutrient (NPK) supply on faba bean response to elevated atmospheric CO2. *Netherlands Journal of Agricultural Science 44(3):163-178.*

The effects of increased atmospheric CO2 on crop growth and dry matter allocation may change if nutrient supply becomes insufficient for maximal growth. Increased atmospheric CO2 may also cause changes in maximum dilution of nutrients in plant tissue and hence, in the minimum nutrient concentration levels and the maximum yield-nutrient uptake ratios of crops. To study these effects for faba bean, pot experiments have been carried out in two glass houses at ambient and doubled CO2 concentration. Bean plants were grown at different supplies of N, P or K. Doubling of atmospheric CO2 resulted in a strong increase (+100%) in total yield. This CO2 effect disappeared rapidly with increasing nitrogen, phosphorus or potassium shortage. Doubling of atmospheric CO2 resulted in no change in minimum nitrogen concentration and a nil to slight decrease in minimum phosphorus concentration in crop residues. Nutrient requirements to attain a certain yield level might change with a future increase in atmospheric CO2. However, such conclusions cannot yet be drawn because nutrient concentrations in seeds were not available.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, GROWTH, NITROGEN, SEED YIELD, SOILS

2618

Wolf, J. 1996. Effects of nutrient supply (NPK) on spring wheat response to elevated atmospheric CO2. *Plant and Soil 185(1):113-123.*

The effects of increased atmospheric CO2 on crop growth and dry matter allocation may change if nutrient supply becomes insufficient for maximal growth. Increased atmospheric CO2 may also cause changes in minimum nutrient concentration in plant tissue and hence in the nutrient use efficiency or yield- nutrient uptake ratios of crops. To study these effects for spring wheat, pot experiments have been carried out in two glass houses at ambient and doubled CO2 concentration. Wheat plants were grown at different supplies of N, P or K. Doubling of ambient CO2 resulted in a large increase in total biomass (+70%) and grain yield when the nutrient supply was optimum. With strong N and K limitation this CO2 effect was about halved and with strong P limitation it became almost nil. Doubling of ambient CO2 resulted in a 10% lower minimum N concentration in plant tissue and in no change in the minimum P concentration.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, NITROGEN, PLANT GROWTH, SEED YIELD

2619

Wolf, J. 1998. Effects of nutrient (NPK) supply on sugar beet response to elevated atmospheric CO2. *Netherlands Journal of Agricultural Science 46(2):157-170.*

The effects of increased atmospheric CO2 on crop growth and dry matter allocation may change if nutrient supply becomes insufficient. Increased atmospheric CO2 may also cause changes in maximum dilution of nutrients in plant tissue and hence, in the minimum nutrient concentration levels and the maximum yield-nutrient uptake ratios of crops. To study these effects of increased CO2 for sugar beet (Beta vulgaris L.), pot experiments have been carried out at ambient and doubled CO2 concentration. Beet plants were grown for four monthes at different supplies of N, P or K. Doubling of ambient CO2 resulted in a moderate increase in total yield (+24%) and beet yield (+34%), however this CO2 effect disappeared with increasing nutrient shortage (in particular nitrogen). CO2 doubling did not result in significant changes in the minimum nutrient concentrations in leaves and beets.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, NITROGEN, PLANT GROWTH, SEED YIELD, SOILS, WHEAT

2620

Wolfe, D.W., R.M. Gifford, D. Hilbert, and Y.Q. Luo. 1998. Integration of photosynthetic acclimation to CO2 at the whole- plant level. *Global Change Biology 4(8):879-893.*

Primary events in photosynthetic (PS) acclimation to elevated CO2 concentration ([CO2]) occur at the molecular level in leaf mesophyll cells, but final growth response to [CO2] involves acclimation responses associated with photosynthate partitioning among plant organs in relation to resources limiting growth. Source-sink interactions, particularly with regard to carbon (C) and nitrogen (N), are key determinants of PS acclimation to elevated [CO2] at the whole-plant level. In the long term, PS and growth response to [CO2] are dependent on genotypic and environmental factors affecting the plant's ability to develop new sinks for C, and acquire adequate N and other resources to support an enhanced growth potential. Growth at elevated [CO2] usually increases N use efficiency because PS rates can be maintained at levels comparable to those observed at ambient [CO2] with less N investment in PS enzymes. A frequent acclimation response, particularly under N-limited conditions, is for the accumulation of leaf carbohydrates at elevated [CO2] to lead to repression of genes associated with the production of PS enzymes. The hypothesis that this is an adaptive response, leading to a diversion of N to plant organs where it is of greatest benefit in terms of competitive ability and reproductive fitness, needs to be more rigorously tested. The biological control mechanisms which plants have evolved to acclimate to shifts in source-sink balance caused by elevated [CO2] are complex, and will only be fully elucidated by probing at all scales along the hierarchy from molecular to ecosystem. Use of environmental manipulations and genotypic comparisons will facilitate the testing of specific hypotheses. Improving our ability to predict PS acclimation to [CO2] will require the integration of results from laboratory studies using simple model systems with results from whole-plant studies that include measurements of processes operating at several scales.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, BIOMASS ALLOCATION, ELEVATED CO2, GAS-EXCHANGE, LEAF-AREA, PHASEOLUS-VULGARIS L, POPLAR CLONES, SOURCE-SINK RELATIONS, SUCROSE PHOSPHATE SYNTHASE, WATER-USE

2621

Wolfe, D.W., J.J. Melkonian, and S.R. Boese. 1997. Elevated CO2 ameliorates chilling-induced water stress, photosynthetic depression, and leaf damage. *Plant Physiology 114(3):483.*

2622

Wolfenden, J., and P.J. Diggle. 1995. Canopy gas-exchange and growth of upland pasture swards in elevated co2. *New Phytologist 130(3):369-380.*

Vegetation monoliths (450 x 450 mm) from two contrasting upland grassland communities were grown in Solardomes in either ambient air or ambient air enriched with 250 ppm CO2. During the first two growing seasons measurements of canopy gas exchange showed that rates of photosynthesis of limestone swards were enhanced by growth in elevated CO2, by approx. 50% during spring and early summer. Although canopy respiration was also greater in elevated CO2, the overall effect was an average increase of 33% in net CO2 assimilation. Enhanced respiration rates persisted into the autumn, whereas the effect on photosynthesis diminished through the growing season, so that in September swards growing in high CO2 had net photosynthesis rates similar to, or even lower than those in ambient air. This response varied between swards of differing species composition. In acidic grassland no significant effects of CO2 on respiration or net CO2 uptake rates were detected at any time. The above ground productivity of limestone grassland was measured in several harvests throughout both seasons, and was not affected by CO2 concentration at any time. Similarly, the acidic grassland, harvested at the end of the second season, showed no significant effect of CO2 on above-ground biomass. The results suggest that increasing atmospheric CO2 concentration is unlikely to cause large changes in net primary productivity in these grasslands.

KEYWORDS: AMBIENT, ATMOSPHERIC CARBON-DIOXIDE, CLIMATE CHANGE, ENRICHMENT, NITROGEN, PERENNIAL RYEGRASS, PHOTOSYNTHESIS, PLANT RESPIRATION, TEMPERATURE, TUSSOCK TUNDRA

2623

Wong, S.C. 1990. Elevated atmospheric partial-pressure of CO2 and plant-growth .2. Nonstructural carbohydrate content in cotton plants and its effect on growth-parameters. *Photosynthesis Research 23(2):171-180.*

2624

Wong, S.C. 1993. Interaction between elevated atmospheric concentration of co2 and humidity on plant-growth - comparison between cotton and radish. *Vegetatio 104:211-221.*

Cotton plants (Gossypium hirsutum L. var Deltapine 90) and radish plants (Raphanus sativus L var Round Red) were grown under full sunlight using a factorial combination of atmospheric CO2 concentrations (350 mumol mol-1 and 700 mumol mol-1) and humidities (35% and 90% RH at 32-degrees-C during the day). Cotton plants showed large responses to increased humidity and to doubled CO2. In cotton plants, the enhanced dry matter yield due to doubled CO2 concentration was 1.6-fold greater at low humidity than at high humidity. Apart from the direct effect of elevated CO2 level on photosynthesis, the greater effect of doubled CO2 concentration on dry matter yield at low humidity was probably due to: (1) increased leaf water potential caused by reduction of transpiration resulting from the negative CO2 response of stomata to increased CO2 concentration the consequence being greater leaf area expansion. (2) reduction of CO2 assimilation rate at low humidity and normal CO2 concentration as a result of humidity response of stomata causing reduction of intercellular CO2 concentration. In contrast, apart from the very early stage of development, radish plants do not respond to increased humidity but had a relatively large response to doubled CO2 concentration. Furthermore, due to the determinate growth pattern as well as having a prominent storage root, the extra photoassimilate derived at doubled CO2 level is allocated to the storage root.

KEYWORDS: PARTIAL-PRESSURE

2625

Wong, S.C., P.E. Kriedemann, and G.D. Farquhar. 1992. CO2 X nitrogen interaction on seedling growth of 4 species of eucalypt. *Australian Journal of Botany 40(4-5):457-472.*

Four eucalypt species were selected to represent two ecologically disparate groups which would be expected to contrast in seedling vigour and in the nature of growth responses to CO2 X nitrogen supply. Eucalyptus camaldulensis and E. cypellocarpa were taken as examples of fast-growing species with a wide distribution, that develop into large trees. By contrast, E. pauciflora and E. pulverulenta become smaller trees, and show a more limited distribution. Seedlings were established in pots (5 L) of a loamy soil and supplied with nutrient solution containing either 1.2 or 6.0 mM NO3- in both ambient (33 Pa) and CO2-enriched (66 Pa) greenhouses. Analysis of growth response to treatments

(2 X 2 factorial) was based on destructive harvest of plants sampled on four occasions over 84 days for E. camaldulensis and E. cypellocarpa, and 100 days for E. pulverulenta and E. pauciflora. A positive CO2 X N interaction on plant dry mass and leaf area was expressed in all species throughout the study period. In E. camaldulensis and E. cypellocarpa, plant mass was doubled by high N at 33 Pa CO2, compared with a three to four- fold increase at 66 Pa to reach 34 g by final harvest. In E. pulverulenta and E. pauciflora, slower growth resulted in about 50% less mass at a given age, but relative increases due to CO2 and N were of a similar order. A distinction can be made between N and CO2 effects on growth processes as follows. When trees were grown on low N, elevated CO2 increased nitrogen-use efficiency (NUE) at both leaf and whole plant levels. On high N, leaf NUE was increased in E. camaldulensis and E. cypellocarpa, but decreased in E. pulverulenta and E. pauciflora. Whole plant NUE showed no consistent response to elevated CO2 when plants were supplied high N. Net assimilation rate (NAR) was increased by elevated CO2 in all species on either N treatment. Moreover, high N increased NAR under either CO2 treatment in all species. There was a positive N X CO2 interaction on NAR in E. camaldulensis and E. cypellocarpa, but not in E. pulverulenta and E. pauciflora. Growth indices for E. camaldulensis and E. cypellocarpa species, and especially E. camaldulensis, generally exceeded those for E. pulverulenta and E. pauciflora in terms of NAR, leaf NUE, N-enhancement of CO2 effects on leaf area and biomass, and non-structural carbohydrate content of foliage.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, GRANDIS SEEDLINGS, MODELS, PARTIAL-PRESSURE, PHOTOSYNTHESIS, PLANTS

2626

Wong, S.C., and C.B. Osmond. 1991. Elevated atmospheric partial-pressure of CO2 and plant-growth .3. Interactions between Triticum aestivum (C3) and Echinochloa frumentacea (C4) during growth in mixed culture under different CO2, N-nutrition and irradiance treatments, with emphasis on belowground responses estimated using the delta-C-13 value of root biomass. *Australian Journal of Plant Physiology 18(2):137-152.*

Wheat (Triticum aestivum L.), a C3 species, and Japanese millet (Echinochloa frumentacea Link), a C4 species, were grown in pots in monoculture and mixed culture (2 C3:1 C4 and 1 C3:2 C4) at two ambient partial pressures of CO2 (320 and 640-mu-bar), two photosynthetic photon flux densities (PPFDs) (daily maximum 2000 and 500-mu-mol m-2 s-1) and two levels of nitrogen nutrition (12 mM and 2 mM NO3BAR). Growth of shoots of both components in mixed culture was measured by physical separation, and the proportions of root biomass due to each component were calculated from delta-C-13 value of total root biomass. In air (320-mu-bar CO2) at high PPFD and with high root zone-N, the shoot biomass of C3 and C4 components at the first harvest (28 days) was in proportion to the sowing ratio. However, by the second harvest (36 days) the C4 component predominated in both mixtures. Under the same conditions, but with low PPFD, C3 plants predominated at the first harvest but C4 plants had overtaken them by the time of the second harvest. Elevated atmospheric CO2 (640-mu-bar) stimulated shoot growth of Triticum in 15 of 16 treatment combinations and the stimulation was greatest in plants provided with low NO3BAR. Root growth of the C3 plants was generally stimulated by elevated CO2, but was only occasionally sensitive to the presence of C4 plants in mixed culture. However, growth of the C4 plants was often sensitive to the presence of C3 plants in mixed culture. In mixed cultures, elevated CO2 plants stimulated growth of C4 plants at high PPFD, high-N and in all low-N treatments but this was insufficient to offset a marked decline in shoot growth with increasing proportion of C3 plants in mixed cultures. The unexpected stimulation of growth of C4 plants by elevated CO2 was correlated with more negative delta- C-13 values of C4 root biomass, suggesting a partial failure of the CO2 concentrating mechanism of C4 photosynthesis in Echinochloa under low-N. These experiments show that for these species nitrogen was more important than light or elevated pCO2 in determining the extent of competitive interactions in mixed culture.

KEYWORDS: C-3, CARBON ISOTOPE DISCRIMINATION, COMPETITION, GRASSES, NITROGEN, PHOTOSYNTHESIS, SOIL ORGANIC MATTER, USE EFFICIENCY

2627

Wood, C.W., H.A. Torbert, H.H. Rogers, G.B. Runion, and S.A. Prior. 1994. Free-air co2 enrichment effects on soil carbon and nitrogen. *Agricultural and Forest Meteorology 70(1-4):103-116.*

Since the onset of the industrial revolution, atmospheric CO2 concentration has increased exponentially to the current 370 mumol mol-1 level, and continued increases are expected. Previous research has demonstrated that elevated atmospheric CO2 results in larger plants returning greater amounts of C to the soil. However, the effects of elevated CO2 on C and N cycling and long-term storage of C in soil have not been examined. Soil samples (in 0-50, 50-100, and 100-200 mm depth increments) were collected after 3 years of cotton (Gossypium hirsutum L.) production under free-air CO2 enrichment (FACE, at 550 mumol CO2 mol-1), in combination with 2 years of different soil moisture regimes (wet, 100% of evapotranspiration replaced, or dry, 75% and 67% of evapotranspiration replaced in 1990 and 1991, respectively) on a Trix clay loam (fine, loamy, mixed (calcareous), hyperthermic Typic Torrifluvent) at Maricopa, Arizona. Ambient plots (370 mumol CO2 mol-1 (control)), in combination with the wet and dry soil moisture regimes, were also included in the study. Soil organic C and N concentrations, potential C and N mineralization, and C turnover were measured. Increased input of cotton plant residues under FACE resulted in treatment differences and trends toward increased organic C in all three soil depths. During the first 30 days of laboratory incubation, available N apparently limited potential C mineralization and C turnover in all treatments. Between 30 and 60 days of incubation, soils from FACE plots had greater potential C mineralization with both water regimes, but C turnover increased in soils from the dry treatment and decreased in soils where cotton was not water stressed. These data indicate that in high-CO2 environments without water stress, increased C storage in soil is likely, but it is less likely where water stress is a factor. More research is needed before the ability of soil to store additional C in a high-CO2 world can be determined.

KEYWORDS: ATMOSPHERIC CO2, COTTON, DIOXIDE, GROWTH, MINERALIZATION, RESPONSES, RHIZOSPHERE, ROOT

2628

Woodbury, P.B., J.E. Smith, D.A. Weinstein, and J.A. Laurence. 1998. Assessing potential climate change effects on loblolly pine growth: A probabilistic regional modeling approach. *Forest Ecology and Management 107(1-3):99-116.*

Most models of the potential effects of climate change on forest growth have produced deterministic predictions. However, there are large uncertainties in data on regional forest condition, estimates of future climate, and quantitative relationships between environmental conditions and forest growth rate. We constructed a new model to analyze these uncertainties along with available experimental results to make probabilistic estimates of climate change effects on the growth of loblolly pine (Pinus taeda L.) throughout its range in the USA. Complete regional data sets were created by means of spatial interpolation, and uncertainties in these data were estimated. A geographic information system (GIS) was created to integrate current and predicted climate data with regional data including forest distribution, growth rate, and stand characteristics derived from USDA Forest Service data. A probabilistic

climate change scenario was derived from the results of four different general circulation models (GCM). Probabilistic estimates of forest growth were produced by linking the GIS to a Latin Hypercube carbon (C) budget model of forest growth. The model estimated a greater than 50% chance of a decrease in loblolly pine growth throughout most of its range. The model also estimated a 10% chance that the total regional basal area growth will decrease by more than 24 X 10(6) m(2) yr(-1) (a 92% decrease), and a 10% chance that basal area growth will increase by more than 62 X 10(6) m(2) yr(-1) (a 142% increase above current rates). The most influential factor at all locations was the relative change in C assimilation. Of climatic factors, CO2 concentration was found to be the most influential factor at all locations. Substantial regional variation in estimated growth was observed, and probably was due primarily to variation in historical growth rates and to the importance of historical growth in the model structure. (C) 1998 Elsevier Science B.V.

KEYWORDS: CARBON DIOXIDE, CO2, GLOBAL CHANGE, NAPAP, OZONE, SCALE, SENSITIVITY, TREES, UNCERTAINTY

2629

Woodin, S., B. Graham, A. Killick, U. Skiba, and M. Cresser. 1992. Nutrient limitation of the long-term response of heather [calluna-vulgaris (L) hull] to co2 enrichment. *New Phytologist 122(4):635-642.*

In a 27-month C2-enrichment experiment, Calluna vulgaris plants were grown on peat obtained from an upland heath in NE Scotland and given a nutrient supply which mimicked that in precipitation in the area. Three CO2 concentrations were used; ambient, + 100 ppm and + 200 ppm. Calluna showed a negative growth response to increased CO2 over the first year of treatment and a positive response by the end of the experiment. Final above-ground biomass was greatest in the enriched CO2 treatments, showing an increase of 30 % in + 100 ppm CO2. Determination of tissue nutrient concentration, and calculation of total nutrient uptake, demonstrated that nutrient uptake did not increase with increased growth, resulting in significant dilution of elements in leaf tissue. This suggests that, in its typical, nutrient poor habitats, the growth response of Calluna to CO2 will be limited by nutrient deficiency, and will reach a maximum with a relatively small increase in CO2 concentration. Flowering was advanced and extremely prolific in + 100 ppm CO2 grown plants, but the ecological significance of this is uncertain. The results highlight the need for long term studies of native species on their natural soils, using lower CO2 concentrations than the usual 'double CO2'.

KEYWORDS: CARBON DIOXIDE, ELEVATED CO2, GROWTH, NITROGEN, NUTRITION, SEEDLINGS, TEMPERATURE, TUNDRA

2630

Woodrow, I.E. 1994. Control of steady-state photosynthesis in sunflowers growing in enhanced co2. *Plant, Cell and Environment 17(3):277-286.*

Control coefficients were used to describe the degree to which ribulose bisphosphate carboxylase/oxygenase (Rubisco) limits the steady-state rate of CO2 assimilation in sunflower leaves from plants grown at high (800 mu mol mol(-1)) and low (350 mu mol mol(-1)) CO2. The magnitude of a control coefficient is approximately the percentage change in the flux that would result from a 1% rise in enzyme active site concentration. In plants grown at low CO2, leaves of different ages varied considerably in their photosynthetic capacities. In a saturating light flux and an ambient CO2 concentration of 350 mu mol mol(-1), the Rubisco control coefficient was about 0.7 in all leaves, indicating that Rubisco activity largely limited the assimilation flux. The Rubisco control coefficient for leaves grown at 350 mu mol mol(-1) CO2 dropped to about zero when the ambient CO2 concentration was raised to 800 mu mol mol(-1). In relatively young, fully expanded leaves of plants grown at high CO2, the Rubisco control coefficient was also about 0.7 at a saturating light flux and at the CO2 concentration at which the plants were grown (800 mu mol mol(- 1)). This apparently resulted from a decrease in the concentration of Rubisco active sites. In older leaves, however, the control coefficient was about 0.2. Because, on the whole, Rubisco activity still largely limits the assimilation flux in plants grown at high CO2, the kinetics of this enzyme can still be used to model photosynthesis under these conditions. The relatively high Rubisco control coefficient under enhanced CO2 indicates that the young sunflower leaves have the capacity to acclimate their photosynthetic biochemistry in a way consistent with an optimal use of protein resources.

KEYWORDS: ANTISENSE RBCS, CARBON-DIOXIDE FIXATION, ELEVATED CO2, GROWTH, LEAVES, PLANTS, RESPONSES, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, RUBISCO

2631

Woodrow, I.E. 1994. Optimal acclimation of the C-3 photosynthetic system under enhanced co2. *Photosynthesis Research 39(3):401-412.*

A range of studies of C-3 plants have shown that there is a change in both the carbon flux and the pattern of nitrogen allocation when plants are grown under enhanced CO2. This paper examines evidence that allocation of nitrogen both to and within the photosynthetic system is optimised with respect to the carbon flux. A model is developed which predicts the optimal relative allocation of nitrogen to key enzymes of the photosynthetic system as a function of CO2 concentration. It is shown that evidence from flux control analysis is broadly consistent with this model, although at high nitrogen and under certain conditions at low nitrogen experimental data are not consistent with the model. Acclimation to enhanced CO2 is also assessed in terms of resource allocation between photosynthate sources and sinks. A means of assessing the optimisation of this source-sink allocation is proposed, and several studies are examined within this framework. It is concluded that C-3 plants probably possess the genetic feedback mechanisms required to efficiently 'smooth out' any imbalance within the photosynthetic system caused by a rise in atmospheric CO2.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, ELEVATED CO2, GROWTH, LEAVES, PHASEOLUS-VULGARIS L, PLANTS, RESPONSES, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, SOURCE-SINK RELATIONS

2632

Woodrow, L., and B. Grodzinski. 1993. Ethylene exchange in lycopersicon-esculentum mill - leaves during short-term and long-term exposures to co2. *Journal of Experimental Botany 44(259):471-480.*

The effects of long-term and transient exposure to elevated CO2 concentrations on photosynthetic gas exchange and ethylene release by tomato leaves were investigated. The net CO2 assimilation rate was enhanced when leaf tissue grown at ambient (35 Pa CO2) levels was assayed at 100 Pa CO2. Leaf tissue grown at high (130 Pa) CO2 exhibited a lower net CO2 assimilation rate at high CO2 levels than leaf tissue grown at ambient (35 Pa) CO2. This decrease in CO2 exchange rate in response to growth at high CO2 is typical Of C3 species. Rates of endogenous and 1-aminocyclopropane-1-carboxylic acid (ACC)-Stimulated ethylene release from leaf tissue were enhanced by exposure to elevated CO2 levels whether the leaf tissue had been grown at ambient or enriched CO2 levels, The data demonstrate that CO2 enhanced C2H4 release from leaf tissue in response to both short-term perturbations in CO2 concentration and long-term growth and development under high CO2. Prolonged growth at elevated CO2 concentrations induced a higher endogenous rate of C2H4 release

relative to that of leaf tissue grown at lower CO2 levels. Leaf tissue from all leaf positions of plants grown at high CO2 consistently evolved more C2H4 than corresponding tissue from ambient-grown plants when assayed under standardized conditions. Endogenous (ACC) tissue contents and rates of ACC-stimulated ethylene release were also higher at all leaf positions in CO2-enriched tissue. Thus the higher rates appeared to be due to both higher endogenous precursor (ACC) levels in the tissue and greater ACC to C2H4 conversion capacity. Growth at elevated CO2 levels resulted in a persistent increase in the rate of endogenous C2H4 release in leaf tissue. The capacity for increased ethylene release in response to CO2 did not decline after prolonged growth at high CO2.

KEYWORDS: 1-AMINOCYCLOPROPANE-1-CARBOXYLIC ACID, ACCLIMATION, CARBON DIOXIDE, GAS-EXCHANGE, HIGH ATMOSPHERIC CO2, PHOTOSYNTHESIS, RELEASE, WHOLE PLANT, XANTHIUM-STRUMARIUM L, ZEA-MAYS

2633

Woods, J., and W. Barkmann. 1993. The plankton multiplier - positive feedback in the greenhouse. *Journal of Plankton Research 15(9):1053-1074.*

The plankton multiplier is a positive feedback mechanism linking the greenhouse effect and biological pump (Woods,J.D., Royal Commission on Environmental Pollution, 1990). As pollution increases the atmospheric concentration of carbon dioxide, the enhanced greenhouse effect induces radiative forcing of the ocean, which diminishes the depth of winter convection, reducing the annual resupply of nutrients to the euphotic zone and therefore the annual primary production. That weakens the biological pump, which contributes to oceanic uptake of CO2. As the ocean takes up less CO2, more remains in the atmosphere, accelerating the rise in radiative forcing. We have used a mathematical model of the upper ocean ecosystem, based on the Lagrangian Ensemble method, to estimate the sensitivity of the biological pump to radiative forcing, which lies at the heart of the plankton multiplier. We conclude that increasing radiative forcing by 5 W m-2 (equivalent to doubling atmospheric CO2) reduces the deep flux of particulate carbon by 10%. That sensitivity is sufficient to produce significant positive feedback in the greenhouse. It means that the plankton multiplier will increase the rate of climate change in the 21st century. It also suggests that the plankton multiplier is the mechanism linking the Milankovich effect to the enhanced greenhouse effect that produces global warming at the end of ice ages.

KEYWORDS: BLOOM, CARBON DIOXIDE, DYNAMICS, MIXED LAYER, MODEL, NORTH-ATLANTIC, OCEAN, OXYGEN, SURFACE, WATERS

2634

Woodward, A. 1998. Relationships among environmental variables and distribution of tree species at high elevation in the Olympic mountains. *Northwest Science 72(1):10-22.*

Relationships among environmental variables and occurrence of tree species were investigated at Hurricane Ridge in Olympic National Park, Washington, USA. A transect consisting of three plots was established down one north-and one south-facing slope in stands representing the typical elevational sequence of tree species. Tree species included subalpine fir (Abies lasiocarpa), Douglas-fir (Pseudotsuga menziesii), mountain hemlock (Tsuga mertensiana), and Pacific silver fir (Abies amabilis). Air and soil temperature, precipitation, and soil moisture were measured during three growing seasons. Snowmelt patterns, soil carbon and moisture release curves were also determined. The plots represented a wide range in soil water potential, a major determinant of tree species distribution (range of minimum values = -1.1 to -8.0 MPa for Pacific silver fir and Douglas-fir plots, respectively). Precipitation intercepted at plots depended on topographic location, storm direction and storm type. Differences in soil moisture among plots was related to soil properties, while annual differences at each plot were most often related to early season precipitation. Changes in climate due to a doubling of atmospheric CO2 will likely shift tree species distributions within, but not among aspects. Change will be buffered by innate tolerance of adult trees and the inertia of soil properties.

KEYWORDS: CLIMATE, FIRE, PRECIPITATION, TOPOGRAPHY, WASHINGTON

2635

Woodward, F.I. 1992. Predicting plant-responses to global environmental-change. *New Phytologist 122(2):239-251.*

Predicting the future responses of plants and ecosystems to further changes in the CO2 concentration of the atmosphere and to the possibility of global warming are important current concerns. Predictions have been most frequently attempted using short-term, single-factor experiments in controlled environments. However, these experiments have failed to indicate the outcome of field experiments at larger spatial and temporal scales. Some of this failure is due to ignorance of environmental conditions and interactions while some is due to the use of inappropriate short-cuts, such as the addition of fertilizers for simulating enhanced mineralization, and some is due to ignorance of the processes involved in scaling-up from individual plants to populations. Long-term observations on plants in ecosystems nevertheless indicate that community-scale experiments may provide a useful but imperfect capacity to predict ecosystem responses. Although difficult to implement in practice, it is concluded that catchment-scale experiments offer the best opportunity to predict plant, community and ecosystem responses to environmental change.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CHENOPODIUM-ALBUM L, ELEVATED CO2, ESTUARINE MARSH, FAR-RED, GROWTH-RESPONSES, INSECT HERBIVORE INTERACTIONS, NITROGEN-FIXATION, PHOTOSYNTHESIS, SAXIFRAGA-CERNUA

2636

Woodward, F.I. 1993. The lowland-to-upland transition modeling plant-responses to environmental-change. *Ecological Applications 3(3):404-408.*

A published correlative model has predicted that the distributional limits of plants and vegetation zones on mountains will increase in altitude with global warming. I test this hypothesis using results from published experimental studies. Investigations and models of the responses of leaf growth to temperature are in accord with the prediction. However, the individualistic responses of species to CO2 enrichment indicate that the prediction is unlikely to be true for all species: growth is stimulated by CO2 enrichment for some species but not for others. Wind speed generally increases with altitude on mountains, and plants from high altitude tend to be more wind resistant than species from the lowland. Therefore it is expected that, particularly on wind-swept mountains, global warming will not necessarily be followed by the spread of lowland species into the uplands.

KEYWORDS: AREA, CLIMATE, DIVERSE ALTITUDINAL RANGES, DYNAMICS, ECOSYSTEMS, FIELD, GROWTH, LEAF EXTENSION, VEGETATION

2637

Woodward, F.I., and C.K. Kelly. 1995. The influence of co2 concentration on stomatal density. *New Phytologist 131(3):311-327.*

A survey of 100 species and 122 observations has shown an average reduction in stomatal density of 14.3% (SE+/-2.2%) with CO2 enrichment, with 74% of the cases exhibiting a reduction in stomatal density. A sign test demonstrated that stomatal density decreases, in response to CO2, significantly more often than expected by chance. Repeated observations on the same species indicated a significant repeatability in the direction of the stomatal response. Analyses which removed the potential effect of taxonomy on this data set showed no significant patterns in the dependency of the degree of stomatal change on growth form (woodiness vs. non-woodiness; trees vs. shrubs), habitat (cool vs. warm) or stomatal distribution on the leaf (amphi- vs. hypostomatous). Forty-three of the observations had been made in controlled environments and under a typical range in CO2 enrichment of 350-700 mu mol mol(-1). For these cases the average stomatal density declined by 9% (SE+/-3.3%) and 60% of the cases showed reductions in stomatal density. When analyses were restricted to these 43 observations, amphistomatous samples more frequently had greater changes in stomatal density than did hypostomatous samples. The degree of reduction in stomatal density with increasing CO2 increases with initial stomatal density, after the influence of taxonomy is removed using analyses of independent contrasts. When the data were examined for patterns that might be due explicitly to the effects of relatedness, the subclasses of the Hamamelidae and the Rosidae showed highly significant reductions in stomatal density with CO2 (87% of the species studied in the Hamamelidae and 80% of the species in the Rosidae showed reduction with CO2 enrichment) and correlations between initial stomatal density and degree of reduction in stomatal density. The species sampled in the Hamamelidae were dominantly trees, whereas herbs dominated the species in the Rosidae. There were insufficient species studied at lower taxonomic levels to warrant further statistical analyses. This problem results from experimental and observational data being most often restricted to one species per taxonomic level, typically up to the level of order, a feature which can severely limit the extraction of taxonomically-related and ecologically-related plant responses.

KEYWORDS: ATMOSPHERIC CO2, ELEVATED CO2, ENRICHMENT, GROWTH, INCREASE, LAST 3 CENTURIES, LEAF-AREA, LEAVES, RESPONSES, WATER-USE EFFICIENCY

2638

Woodward, F.I., T.M. Smith, and W.R. Emanuel. 1995. A global land primary productivity and phytogeography model. *Global Biogeochemical Cycles 9(4):471-490.*

A global primary productivity and phytogeography model is described. The model represents the biochemical processes of photosynthesis and the dependence of gas exchange on stomatal conductance, which in turn depends on temperature and soil moisture. Canopy conductance controls soil water loss by evapotranspiration. The assignment of nitrogen uptake to leaf layers is proportional to irradiance, and respiration and maximum assimilation rates depend on nitrogen uptake and temperature. Total nitrogen uptake is derived from soil carbon and nitrogen and depends on temperature. The long-term average annual carbon and hydrological budgets dictate canopy leaf area. Although observations constrain soil carbon and nitrogen, the distribution of vegetation types is not specified by an underlying map. Variables simulated by the model are compared to experimental results. These comparisons extend from biochemical processes to the whole canopy, and the comparisons are favorable for both current and elevated CO2 atmospheres. The model is used to simulate the global distributions of leaf area index and annual net primary productivity. These distributions are sufficiently realistic to demonstrate that the model is useful for analyzing vegetation responses to global environmental change.

KEYWORDS: C-3 PLANTS, CARBON ALLOCATION, CLIMATE CHANGE, FOREST ECOSYSTEM PROCESSES, GENERAL-CIRCULATION MODEL, HIGH-RESOLUTION RADIOMETER, LEAF NITROGEN, NET PRIMARY PRODUCTION, REGIONAL APPLICATIONS, STOMATAL CONDUCTANCE

2639

Woodward, F.I., G.B. Thompson, and I.F. McKee. 1991. The effects of elevated concentrations of carbon-dioxide on individual plants, populations, communities and ecosystems. *Annals of Botany 67:23-38.*

KEYWORDS: ATMOSPHERIC CO2 ENRICHMENT, BIOSPHERE EXCHANGE, CLOVER TRIFOLIUM-REPENS, CO2-ENRICHED ATMOSPHERE, DRY-MATTER, INSECT HERBIVORE, LONG-TERM EXPOSURE, PAST 2 CENTURIES, PHOTOSYNTHETIC INHIBITION, PISUM-SATIVUM

2640

Woolgrove, C.E., and S.J. Woodin. 1996. Ecophysiology of a snow-bed bryophyte Kiaeria starkei during snowmelt and uptake of nitrate from meltwater. *Canadian Journal of Botany-Revue Canadienne De Botanique 74(7):1095-1103.*

Snow is a very efficient scavenger of atmospheric pollutants and because of the dynamics of snowmelt, much of the pollutant load of a snowpack is released at very high concentrations in episodes known as the acid flush. The ecological effects of this are largely unknown, but any effects on the bryophyte- dominated vegetation of snow beds will depend in part on the physical environment and physiological state of plants under and just out of snow cover. These factors were investigated at a snow bed in the Cairngorm Mountains, Scotland. The subnivean environment is characterized by slightly elevated CO2 concentrations (up to 70 mu L/L above ambient), temperatures at and just above 0 degrees C, and very low light intensity, with no light penetrating through more than 50 cm depth of snow. Despite overwinter storage in these conditions, the bryophyte Kiaeria starkei is shown to be capable of photosynthetic activity immediately after removal of snow cover, and tissue chlorophyll and carbohydrate concentrations increase by 250 and 60%, respectively, during the 2 weeks thereafter. Comparison of photosynthetic light responses at 5 and 18 degrees C in plants collected from under and out of snow cover demonstrates acclimatization to seasonal environmental change that must enable maximization of growth during the short growing season available. Kiaeria starkei is also shown to be capable of nitrate reductase activity even at 2 degrees C and to assimilate more than 90% of the pollutant nitrate coming into contact with it in snowmelt. As nitrate is known to be damaging to bryophytes in excess, this demonstrates a real threat of pollutant deposition to rare snow-bed communities in Scotland today and is an important warning for other regions where snow- bed vegetation is important.

KEYWORDS: ATMOSPHERIC NITROGEN, CHEMICAL-COMPOSITION, CO2, COMMUNITY, DEPOSITION, ELEMENT, GROWTH, TEMPERATURE, TOLERANCE, WINTER

2641

Wright, R.F. 1998. Effect of increased carbon dioxide and temperature on runoff chemistry at a forested catchment in southern Norway (CLIMEX project). *Ecosystems 1(2):216-225.*

CLIMEX (Climate Change Experiment) is an integrated, whole-ecosystem research project that focuses on the response of forest ecosystems at the catchment scale to increased CO2 and temperature. I(IM catchment (860 m(2)) is completely enclosed by a transparent greenhouse, receives deacidifed "clean" rain, and has elevated CO2 (560 ppmv) and elevated air temperature (3 degrees-5 degrees C above ambient). The uppermost 20% of the catchment is partitioned off, is not subject to changed CO2 or temperature, and serves as an untreated control. Fluxes of nitrate and ammonium in runoff from I(IM catchment

increased from 2 mmol m(-2) y(-1) each in the 3 years before treatment to 6 and 3 mmol m(-2) y(-1), respectively, in the 3 years after treatment (May 1994-April 1997), despite a 15 mmol m(-2) y(-1) decrease in N dry deposition due to the sealing of the walls to the enclosure. N flux in runoff from three reference catchments and the control section did not change. The net loss of inorganic N was thus about 20 mmol m(-2) treated soil y(-1). There were no changes in organic N or total organic carbon in runoff. The ecosystem switched from a net sink to a net source of inorganic nitrogen (N). The increased loss of N may be due to accelerated decomposition of soil organic matter induced by higher temperature. Due to many decades of N deposition from long-range transported pollutants, the ecosystem prior to treatment was N saturated. If global change induces persistent losses of inorganic N on a regional scale, the result may be a significant increase in nitrate concentrations in fresh waters and N loading to coastal marine ecosystems. In regions with acid sensitive waters, such as southern Norway, the increased nitrate release caused by global change may offset improvements achieved by reduced sulfur and hi deposition.

KEYWORDS: NITROGEN

2642

Wu, W.H., J.Y. Lu, A.R. Jones, D.G. Mortley, P.A. Loretan, C.K. Bonsi, and W.A. Hill. 1997. Proximate composition, amino acid profile, fatty acid composition, and mineral content of peanut seeds hydroponically grown at elevated CO2 levels. *Journal of Agricultural and Food Chemistry 45(10):3863-3866.*

Peanut plants (Arachis hypogaea L. cv. Georgia Red) were grown hydroponically using a recirculating nutrient film technique. The effect of CO2 enrichment on nutritive composition of hydroponic peanut seeds was examined at two elevated CO2 levels (700 and 1400 ppm) that simulate potential conditions in National Aeronautics and Space Administration (NASA) Controlled Ecological Life-Support Systems (CELSS) and compared to ambient CO2 condition in hydroponics (the control). Plants were harvested at 97 days after planting, and the seeds were air- dried and analyzed for composition. Percentages of crude protein, crude fat, ash, and carbohydrate of hydroponic peanut seeds were around 30%, 30%, 3%, and 30%, respectively. The major amino acids were aspartic acid, glutamic acid, and arginine. The limiting amino acid of peanut, methionine, was 1.2%. Linoleic acid was the major fatty acid, followed by oleic and palmitic acids. The major mineral elements were K, P, Mg, and Ca. The results showed that certain peanut varieties can be grown hydroponically. The composition of the hydroponically grown peanuts is generally similar to reported peanut composition The nutrient composition was not affected at the elevated CO2 concentrations investigated.

KEYWORDS: STORAGE

2643

Wullschleger, S.D., J.P. Lynch, and G.M. Berntson. 1994. Modeling the belowground response of plants and soil biota to edaphic and climatic-change - what can we expect to gain. *Plant and Soil 165(1):149-160.*

As atmospheric CO2 concentrations continue to increase, so too will the emphasis placed on understanding the belowground response of plants to edaphic and climatic change. Controlled- exposure studies that address the significance of an increased supply of carbon to roots and soil biota, and the consequences of this to nutrient cycling will play a prominent role in this process. Models will also contribute to understanding the response of plants and ecosystems to changes in the earth's climate by incorporating experimental results into conceptual or quantitative frameworks from which potential feedbacks within the plant-soil system can be identified. Here we present five examples of how models can be used in this analysis and how they can contribute to the development of new hypotheses in the areas of root biology, soil biota, and ecosystem processes. Two examples illustrate the role of coarse and fine roots in nitrogen and phosphorus uptake from soils, the respiratory costs associated with this acquisition of nutrients, and the significance of root architecture in these relationships. Another example focuses on a conceptual model that has helped raise new ideas about the effects of elevated CO2 on root and microbial biomass, and on nutrient dynamics in the rhizosphere. Difficulties associated with modeling the contribution of mycorrhizal fungi to whole-plant growth are also discussed. Finally several broad-scale models are used to illustrate the importance of root turnover, litter decomposition, and nitrogen mineralization in determining an ecosystem's response to atmospheric CO2 enrichment. We conclude that models are appropriate tools for use both in guiding existing studies and in identifying new hypotheses for future research. Development of models that address the complexities of belowground processes and their role in determining plant and ecosystem function within the context of rising CO2 concentrations and associated climate change should be encouraged.

KEYWORDS: ALLOCATION, ATMOSPHERIC CO2 ENRICHMENT, CARBON, ELEVATED CO2, GLOBAL CHANGE, NITROGEN, QUERCUS-ALBA, ROOT, SEEDLING GROWTH, TERRESTRIAL ECOSYSTEMS

2644

Wullschleger, S.D., and R.J. Norby. 1992. Respiratory cost of leaf growth and maintenance in white oak saplings exposed to atmospheric co2 enrichment. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 22(11):1717-1721.*

Atmospheric CO2 enrichment reportedly reduces respiration of mature leaves in a number of woody and herbaceous perennials. It has vet to be determined, however, whether these reductions reflect changes in maintenance respiration alone or whether CO2 might affect growth respiration as well. This possibility was examined in white oak (Quercus alba L.) seedlings that had been planted directly into the ground within open-top chambers and exposed to ambient, ambient + 150 muL.L-1, and ambient + 300 muL.L-1 CO2 concentrations over a 3-year period. In the spring of 1992, respiration rates were measured repeatedly during leaf expansion, and the growth and maintenance coefficients were determined using a two-component model. Specific respiration rates (mg CO2.g-1.h-1) were consistently lower for leaves of CO2 enriched saplings than for leaves of ambient-grown saplings. Partitioning these reductions in leaf respiration to either the growth or maintenance coefficients indicated a strong effect of CO2 on both components. The growth coefficient for leaves exposed to the ambient CO2 treatment was 964 Mg CO2.g-1 compared with 849 and 664 mg CO2.g-1 for leaves from the two elevated CO2 concentrations, respectively. The maintenance coefficient was similarly reduced from a control rate of 114 mg CO2.g-1 d-1 to below 65 mg CO2.g-1.d-1 for leaves exposed to CO2 enrichment. Our results quantitatively describe the magnitude by which growth and maintenance respiration are affected by CO2 enrichment and as such should provide useful information for the future modeling of this phenomenon.

KEYWORDS: TREES

2645

Wullschleger, S.D., R.J. Norby, and C.A. Gunderson. 1992. Growth and maintenance respiration in leaves of liriodendron- tulipifera L exposed to long-term carbon-dioxide enrichment in the field. *New Phytologist 121(4):515-523.*

Specific respiration rate (SRR) was mathematically partitioned into its growth and maintenance components for leaves of yellow-poplar

(Liriodendron tulipifera L.) after 3 vr of CO2 enrichment in open-top field chambers. Despite the absence of a CO2 effect on individual leaf expansion or specific growth rate (SGR), increasing the CO2 concentration to ambient + 150 or + 300 cm3 m-3 decreased SRR by 28 to 45 % compared with ambient- grown controls. These lower leaf respiration rates were correlated with reduced leaf nitrogen concentrations. As described by the two-component model of growth and maintenance respiration, SRR was a linear function of SGR. Ambient-grown leaves had a growth respiration coefficient of 704 mg CO2 g-1 dry mass compared with 572 and 570 mg CO2 g-1 for leaves grown at the two higher CO2 concentrations. Leaves from the elevated CO2 treatments had an average maintenance respiration coefficient of 88 mg CO2 g-1 dry mass d-1 compared with 135 mg CO2 g-1 d-1 for leaves from the ambient treatment. Incorporating these growth and maintenance coefficients into a leaf growth simulation model indicated that total respiration would be reduced by 21 to 26 % for a leaf exposed to + 150 or + 300 cm3 m-3 CO2 throughout its 50-d lifespan compared with one grown at ambient CO2 conditions. Reductions in total respiration were dominated by a lower rate of maintenance respiration, while the contribution of a lower specific rate of growth respiration was largely offset by a greater dry mass for leaves grown at elevated CO2 concentrations. Although reductions in the respiratory loss of carbon could be beneficial, respiration is unlikely to decrease without a concomitant decrease in other metabolic processes. Whether these reductions are beneficial or detrimental to the long-term growth of plants exposed to elevated CO2 remains unresolved.

KEYWORDS: ATMOSPHERIC CO2, C-3, EFFLUX, ELEVATED CO2, INCREASE, MODEL, NITROGEN, PLANTS, RESPONSES

2646

Wullschleger, S.D., R.J. Norby, and P.J. Hanson. 1995. Growth and maintenance respiration in stems of quercus-alba after 4 years of co2 enrichment. *Physiologia Plantarum 93(1):47-54.*

Atmospheric CO2 enrichment is increasingly being reported to inhibit leaf and whole-plant respiration. It is not known, however, whether this response is unique to foliage or whether woody-tissue respiration might be affected as well. This was examined for mid-canopy stem segments of white oak (Quercus alba L.) trees that had been grown in open-top field chambers and exposed to either ambient or ambient + 300 mu mol mol(-1) CO2 over a 4-year period. Stem respiration measurements were made throughout 1992 by using an infrared nas analyzer and a specially designed in situ cuvette. Rates of woody-tissue respiration were similar between CO2 treatments prior to leaf initiation and after leaf senescence, but were several fold greater for saplings grown at elevated concentrations of CO2 during much of the growing season. These effects were most evident on 7 July when stem respiration rates for trees exposed to elevated CO2 concentrations were 7.25 compared to 3.44 mu mol CO2 m(-2) s(-1) for ambient-grown saplings. While other explanations must be explored, greater rates of stem respiration for saplings grown at elevated CO2 concentrations were consistent with greater rates of stem growth and more stem-wood volume present at the time of measurement. When rates of stem growth were at their maximum (7 July to 3 August), growth respiration accounted for about 80 to 85% of the total respiratory costs of stems at both CO2 treatments, while 15 to 20% supported the costs of stem-wood maintenance. Integrating growth and maintenance respiration throughout the season, taking into account treatment differences in stem growth and volume, indicated that there were no significant effects of elevated CO2 concentration on either respiratory process. Quantitative estimates that could be used in modeling the costs of woody-tissue growth and maintenance respiration are provided.

KEYWORDS: DARK RESPIRATION, EFFLUX, ELEVATED CARBON-DIOXIDE, FOREST, INHIBITION, LEAVES, PHOTOSYNTHESIS, PLANT RESPIRATION, TERM, TREE

2647

Wullschleger, S.D., R.J. Norby, and D.L. Hendrix. 1992. Carbon exchange-rates, chlorophyll content, and carbohydrate status of 2 forest tree species exposed to carbon-dioxide enrichment. *Tree Physiology 10(1):21-31.*

Seedlings of yellow-poplar (Liriodendron tulipifera L.) and white oak (Quercus alba L.) were exposed continuously to one of three CO2 concentrations in open-top chambers under field conditions and evaluated after 24 weeks with respect to carbon exchange rates (CER), chlorophyll (Chl) content, and diurnal carbohydrate status. Increasing the CO2 concentration from ambient to +150 or +300-mu-l l-1 stimulated CER of yellow- poplar and white oak seedlings by 60 and over 35%, respectively, compared to ambient-grown seedlings. The increases in CER were not associated with a significant change in stomatal conductance and occurred despite a reduction in the amounts of Chl and accessory pigments in the leaves of plants grown in CO2-enriched air. Total Chl contents of yellow-poplar and white oak seedlings grown at +300-mu-l l-1 were reduced by 27 and over 55%, respectively, compared with ambient-grown seedlings. Yellow-poplar and white oak seedlings grown at +300-mu-l l-1 contained 72 and 67% more morning starch, respectively, than did ambient-grown plants. In contrast, yellow-poplar and white oak seedlings grown at +300-mu-l l-1 contained 17 and 27% less evening sucrose, respectively, than did plants grown at ambient CO2 concentration. Diurnal starch accumulation and the subsequent depletion of sucrose contributed to a pronounced increase in the starch/sucrose ratio of plants grown in CO2-enriched air. All seedlings exhibited a substantial reduction in dark respiration as CO2 concentration increased, but the significance of this increase to the carbohydrate status and carbon economy of plants grown in CO2-enriched air remains unclear.

2648

Wullschleger, S.D., R.J. Norby, J.C. Love, and C. Runck. 1997. Energetic costs of tissue construction in yellow-poplar and white oak trees exposed to long-term CO2 enrichment. *Annals of Botany 80(3):289-297.*

Two methods were used to estimate construction costs for leaves, stems, branches and woody roots of yellow-poplar (Liriodendron tulipifera L.) trees grown at ambient (35 Pa) and elevated (65 Pa) CO2 for 2.7 years and trees of white oak (Quercus alba L.) grown at these same CO2 partial pressures for 4 years. Sample combustion in a bomb calorimeter combined with measurements of ash and nitrogen content provided the primary method of estimating tissue construction costs (W-G; g glucose g(-1) dry mass). These values were compared with a second, simpler method in which cost estimates were derived from tissue ash, carbon and nitrogen content (V-G). Estimates of W-G were lower for leaves, branches and roots of yellow-poplar and for leaves of white oak grown at elevated compared with ambient CO2 partial pressures. These CO2-induced differences in W-G ranged from 3.7% in yellow-poplar roots to 2.1% in white oak leaves. Only in the case of yellow-poplar leaves, however were differences in V-G observed between CO2 treatments. Leaf V-G was 1.46 g glucose g(-1) dry mass in ambient-grown trees compared with 1.41 g glucose g(-1) dry mass for CO2-enriched trees. Although paired-estimates of W-G and V-G clustered about a 1:1 line for leaves and branches, estimates of V-G were consistently lower than W-G for stems and roots. Construction costs per unit leaf area were 95 g glucose m(-2) for yellow- poplar trees grown at ambient CO2 and 106 g glucose m(-2) for trees grown at elevated CO2 partial pressures. No differences in area-based construction costs were observed for white oak. Whole-plant energy content was 1220 g glucose per tree in ambient-grown white oak compared with 2840 g glucose per tree for those grown at elevated CO2 partial pressures. These differences were driven largely by CO2-induced changes in total biomass. We conclude that while

construction costs were lower at elevated CO2 partial pressures, the magnitude of this response argues against an increased efficiency of carbon use in the growth processes of trees exposed to CO2 enrichment. (C) 1997 Annals of Botany Company.

KEYWORDS: CARBON-DIOXIDE ENRICHMENT, ELEVATED ATMOSPHERIC CO2, GROWTH EFFICIENCY, LEAF RESPIRATION, LEAVES, LIRIODENDRON-TULIPIFERA L, MAINTENANCE RESPIRATION, MAX L MERR, QUERCUS-ALBA, RESPONSES

2649

Wullschleger, S.D., L.H. Ziska, and J.A. Bunce. 1994. Respiratory responses of higher-plants to atmospheric co2 enrichment. *Physiologia Plantarum 90(1):221-229.*

Although the respiratory response of native and agricultural plants to atmospheric CO2 enrichment has been reported over the past 75 years, only recently have these effects emerged as prominent measures of plant and ecosystem response to the earth's changing climate. In this review we discuss this rapidly expanding field of study and propose that both increasing and decreasing rates of leaf and whole-plant respiration are likely to occur in response to rising CO2 concentrations. While the stimulatory effects of CO2 on respiration are consistent with our knowledge of leaf carbohydrate status and plant metabolism, we wish to emphasize the rather surprising short-term inhibition of leaf respiration by elevated CO2 and the reported effects of long-term CO2 exposure on growth and maintenance respiration. As is being found in many studies, it is easier to document the respiratory response of higher plants to elevated CO2 than it is to assign a mechanistic basis for the observed effects. Despite this gap in our understanding of how respiration is affected by CO2 enrichment, data are sufficient to suggest that changes in leaf and whole-plant respiration may be important considerations in the carbon dynamics of terrestrial ecosystems as global CO2 continues to rise. Suggestions for future research that would enable these and other effects of CO2 on respiration to be unravelled are presented.

KEYWORDS: CARBOHYDRATE STATUS, CARBON-DIOXIDE ENRICHMENT, CYANIDE- RESISTANT, DARK RESPIRATION, ELEVATED CO2, ENERGY OVERFLOW, EXCHANGE, GROWTH, PHOTOSYNTHESIS, SHORT- TERM

2650

Wurr, D.C.E., D.W. Hand, R.N. Edmondson, J.R. Fellows, M.A. Hannah, and D.M. Cribb. 1998. Climate change: a response surface study of the effects of CO2 and temperature on the growth of beetroot, carrots and onions. *Journal of Agricultural Science 131:125-133.*

Ten daylit, controlled-environment cabinets were used to investigate the possible impacts of global rises in atmospheric CO2 concentration and temperature on beetroot (Beta vulgaris L.), carrot (Daucus carota L.) and bulb onion (Allium cepa L.) plants. Their responses to CO2 concentrations of 350, 450, 550, 650 and 750 vpm and temperatures of 12, 13.5, 15, 16.5 and 18 degrees C were examined by using a fractional factorial design for the two treatment factors. Use of the daylit cabinets allowed the plants to be grown in natural light, common atmospheric humidities (vpd 0.7 kPa) and nonlimiting supplies of water and mineral nutrients. Polynomial models were used to summarize the whole plant dry weight and fresh weight yield responses and to indicate the potential impact of climate change. Additionally, the models were used to generate predictions of the percentage change in whole plant dry weight and plant fresh weight yield for the years 2025 and 2050 relative to 1992. Baseline values of 350 vpm for CO2 and a mean temperature of 13.5 degrees C for 1992 together with forecast CO2 values of 407 and 442 vpm and temperature increases of 0.7 and 1.1 C for 2025 and 2050 respectively were used. For 2025, fresh weight yield changes of + 19%, +9% and +13% were obtained for beetroot, carrot and onion crops respectively, while for 2050 the respective changes were + 32 %, + 13 % and +21 %. Measurements of the ratio of the maximum diameter of the bulb to the minimum diameter of the neck for onions showed that there was little or no influence of CO2, whereas the effect of temperature was substantial. Bulbing was accelerated by high temperature and was greatly delayed at low temperature. At temperatures < 15 degrees C, the delays to bulbing resulted in the development of undesirable, thick-necked onions which tended to remain green with erect leaves. These results suggest, therefore, that a warmer climate will be advantageous for the commercial production of bulb onions in Britain.

KEYWORDS: ATMOSPHERIC CO2, CROP, ENRICHMENT, YIELD

2651

Wurth, M.K.R., K. Winter, and C. Korner. 1998. In situ responses to elevated CO2 in tropical forest understorey plants. *Functional Ecology 12(6):886-895.*

1. Plants growing in deep shade and high temperature, such as in the understorey of humid tropical forests, have been predicted to be particularly sensitive to rising atmospheric CO2. We tested this hypothesis in five species whose microhabitat quantum flux density (QFD) was documented as a covariable. After 7 (tree seedlings of Tachigalia versicolor and Beilschmiedia pendula) and 18 months (shrubs Piper cordulatum and Psychotria limonensis, and grass Pharus latifolius) of elevated CO2 treatment (c. 700 mu l litre(-1)) under mean QFD of less than 11 mu mol m(-2) s(-1), ail species produced more biomass (25-76%) under elevated CO2. 2. Total plant biomass tended to increase with microhabitat QFD (daytime means varying from 5 to II mu mol m(-2) s(-1)) but the relative stimulation by elevated CO2 was higher at low QFD except in Pharus. 3. Non-structural carbohydrate concentrations in leaves increased significantly in Pharus (+ 27%) and Tachigalia (+ 40%). 4. The data support the hypothesis that tropical plants growing near the photosynthetic light compensation point are responsive to elevated CO2. An improved plant carbon balance in deep shade is likely to influence understorey plant recruitment and competition as atmospheric CO2 continues to rise.

KEYWORDS: CARBON DIOXIDE, COMMUNITIES, ECOSYSTEMS, ENVIRONMENTS, GROWTH-RESPONSES, MODEL, PHOTOSYNTHESIS, RAIN-FOREST, SEEDLINGS, TREE

2652

Wurth, M.K.R., K. Winter, and C. Korner. 1998. Leaf carbohydrate responses to CO2 enrichment at the top of a tropical forest. *Oecologia 116(1-2):18-25.*

The accumulation of non-structural leaf carbohydrates is one of the most consistent plant responses to elevated CO2. It has been found in both fast-and slow-growing plants and is largely independent of the duration of exposure. Changes in leaf quality are thus to be expected, irrespective of other plant responses to atmospheric CO2 enrichment. However, there is no experimental evidence from tropical forests, the biome with the largest biomass carbon pool. Here we report in situ mesophyll responses of mature tropical trees to a doubling of CO2, Individually CO2-enriched leaves on 25 to 35-m-tall forest trees living at 26-35 degrees C can be assumed to experience little sink limitation, and so, may be expected to exhibit no or very little carbohydrate accumulation. We tested this hypothesis using the leaf cup method on leaves accessible via the canopy crane of the Smithsonian Tropical Research Institute in a semi-deciduous tropical forest in Panama. We also investigated the influence of the leaf-specific light regime, another possible environmental determinant of leaf carbon gain and mobile leaf carbohydrates. Total non-structural carbohydrates (TNC) reached a new steady state concentration after less than 4 days of exposure to twice ambient CO2 concentration. Against expectation, all four tree species

investigated (Anacardium excelsum, Cecropia longipes, C. peltata, Ficus insipida) accumulated significant amounts of TNC (+41 to +61%) under elevated CO2. The effect was stronger at the end of the daylight period (except for Ficus), but was still significant in all four species at the end of the dark period. In contrast, neither artificial nor natural shading affected leaf TNC. Taken together, these observations suggest that TNC accumulation reflects a mesophyll-bound tissue response specific to elevated CO2, presumably unrelated to sink limitations. Thus, leaves of tropical forests seem not to be an exception, and will most likely contain more non-structural carbohydrates in a CO2-rich world.

KEYWORDS: CARBON, ELEVATED ATMOSPHERIC CO2, GROWTH, MODEL, PLANT-RESPONSES, TREES

2653

Xiao, X., D.S. Ojima, W.J. Parton, Z. Chen, and D. Chen. 1995. Sensitivity of Inner Mongolia grasslands to climate change. *Journal of Biogeography 22(4-5):643-648.*

We investigated the effects of global climate change and doubled atmospheric CO2 concentration to plant primary production and soil organic matter of typical steppe (Leymus chinense steppe and Stipa grandis steppe) and meadow steppe (Filifolium sibiricum steppe, S. baicalensis steppe and L. chinense steppe) at individual sites in Inner Mongolia, using the CENTURY ecosystem model. In the simulation of climate change, loss of soil organic C ranges from 783 gC.m(-2) in meadow steppe to 1485 gC.m(-2) in typical steppe, and annual above-ground net primary production (ANPP) decreases by 17.6 gC.m(-2) in meadow steppe to 29.5 gC.m(-2) in typical steppe under CCC (Canadian Climate Center). While under GFDL (Geophysical Fluid Dynamics Laboratory), loss of soil organic C varies from 584 gC.m(-2) in typical steppe to 1164 gC.m(-2) in meadow steppe, and ANPP decreases in the range of 18.3 gC.m(-2) in typical steppe to 32.1 gC.m(-2) in meadow steppe. In the simulations of climate change plus elevated CO2 (from 350 p.p.m. to 700 p.p.m.), ANPP decreases by 5.4 gC.m(-2) in meadow steppe to 11.3 gC.m(-2) in typical steppe under CCC + CO2, while ANPP varies from an increase of 1.8 gC.m(-2) in S. grrmdis steppe to a decrease of 20.6 gC.m(-2) in meadow steppe under GFDL + CO2. Losses of soil organic C are slightly lower (in the range of 42 gC.m(-2) to 248 gC.m(-2)) than losses of soil organic C under climate change only. These five steppe ecosystems are very sensitive to climate change, dependent upon projected change in temperature and precipitation by GCMs of CCC and GFDL.

KEYWORDS: BIOMASS, CO2, CONIFEROUS FORESTS, DYNAMICS

2654

Xu, D.Q., R.M. Gifford, and W.S. Chow. 1994. Photosynthetic acclimation in pea and soybean to high atmospheric co2 partial-pressure. *Plant Physiology 106(2):661-671.*

Nonnodulated pea (Pisum sativum L. cv Frosty) and soybean (Glycine max [L.] Merr. cv Wye) plants were grown under artificial lights from germination with ample nutrients, 600 mu mol photons m(-2) s(-1), and either 34 to 36 (control) or 64 to 68 Pa (enriched) CO2. For soybean, pod removal and whole-plant shading treatments were used to alter the source-sink balance and carbohydrate status of the plants. Growth of both species was substantially increased by CO2 enrichment despite some down-regulation of photosynthesis rate per unit leaf area ("acclimation"). Acclimation was observed in young pea leaves but not old and in old soybean leaves but not young. Acclimation was neither evident in quantum yield nor was it related to triose phosphate limitation of net photosynthesis. A correlation between levels of starch and sugars in the leaf and the amount of acclimation was apparent but was loose and only weakly related to the source-sink balance of the plant. A consistent feature of acclimation was reduced ribulose bisphosphate carboxylase (RuBPCase) content, although in vivo RuBPCase activity was not necessarily diminished by elevated growth CO2 owing to increased percentage of activation of the enzyme. A proposal is discussed that the complexity of photosynthetic acclimation responses to elevated CO2 is as an expression of re-optimization of deployment of within-plant resources at three levels of competition.

KEYWORDS: CARBON DIOXIDE, ELEVATED CO2, ENRICHMENT, EXCHANGE, GROWTH, LEAVES, PLANTS, RESPONSES, RUBISCO ACTIVITY, WATER HYACINTH

2655

Xue, X.P., D.A. Gauthier, D.H. Turpin, and H.G. Weger. 1996. Interactions between photosynthesis and respiration in the green alga Chlamydomonas reinhardtii - Characterization of light-enhanced dark respiration. *Plant Physiology 112(3):1005-1014.*

The rate of respiratory O-2 consumption by Chlamydomonas reinhardtii cell suspensions was greater after a period of photosynthesis than in the preceding dark period. This "light- enhanced dark respiration" (LEDR) was a function of both the duration of illumination and the photon fluence rate. Mass spectrometric measurements of gas exchange indicated that the rate of gross respiratory O-2 consumption increased during photosynthesis, whereas gross respiratory CO2 production decreased in a photon fluence rate-dependent manner. The rate of postillumination O-2 consumption provided a good measure of the O-2 consumption rate in the light. LEDR was substantially decreased by the presence of 3-(3,4-dichlorophenyl)-1,1- dimethylurea or glycolaldehyde, suggesting that LEDR was photosynthesis-dependent. The onset of photosynthesis resulted in an increase in the cellular levels of phosphoglycerate, malate, and phosphoenolpyruvate and a decrease in whole-cell ATP and citrate levels; all of these changes were rapidly reversed upon darkening. These results are consistent with a decrease in the rate of respiratory carbon flow during photosynthesis, whereas the increase in respiratory O-2 consumption during photosynthesis may be mediated by the export of photogenerated reductant from the chloroplast. We suggest that photosynthesis interacts with respiration at more than one level, simultaneously decreasing the rate of respiratory carbon flow while increasing the rate of respiratory O-2 consumption.

KEYWORDS: ALTERNATIVE PATHWAY, AMMONIUM ASSIMILATION, CO2- ENRICHED AIR, INORGANIC CARBON, MESOPHYLL PROTOPLASTS, MITOCHONDRIAL RESPIRATION, OXYGEN EVOLUTION, PLANT-CELLS, REGULATORY PROPERTIES, SELENASTRUM-MINUTUM

2656

Yakimchuk, R., and J. Hoddinott. 1994. The influence of ultraviolet-b light and carbon-dioxide enrichment on the growth and physiology of seedlings of 3 conifer species. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 24(1):1-8.*

Anthropogenic production of CO2 and stratospheric ozone depleting chemicals is altering the plant growth environment. Numerous studies have examined the influence of increasing CO2 and UV-B levels on plant physiology, but few studies examine their interaction. Jack pine (Pinus banksiana Lamb.), black spruce (Picea mariana (Mill.) B.S.P.), and white spruce (Picea glauca (Moench) Voss) were raised in growth rooms from seed for 16 weeks in air with either 350 or 700 mumol.mol-1 of CO2 in the presence or absence of supplemental UV-B irradiation. Classical and functional growth analyses were performed to identify treatment effects. Biomass production in all three species was increased by high CO2 levels while UV-B light reduced it. Shade-intolerant jack pine showed a greater production of UV-B absorbing pigments in UV-B light than did shade-tolerant spruce species. Overall, white spruce was the most sensitive species to both treatment factors. The relative

magnitude of the effects in the three species caused by enhanced CO2 and UV-B levels indicate that future conifer seedling growth and competitive ability will be altered by the changing environment.

KEYWORDS: CHLOROPHYLL, CO2, FIELD, LOBLOLLY-PINE, PHOTOSYNTHETIC ACCLIMATION, RADIATION, RICE

2657

Yamashita, I., K. Dan, and M. Shimomura. 1999. Active modified atmosphere packaging storage of cabbage plug seedlings. *Journal of the Japanese Society for Horticultural Science 68(5):1015-1021.*

When cabbage plug seedlings were stored under a modified atmosphere packaging (MAP) at 15 degrees C in the dark for 2 weeks, a passive MAP did not create an environment to inhibit stem elongation of seedling in the 0.1mm thick polyethylene (PE) film pouch. An active MAP by adjusting N-2 rich air with 2% O-2 did not successfully retard elongation either. In the active MAP where the internal atmosphere was replaced with N-2 enriched air (2.5% O-2) with elevated CO2, the elongation was delayed as CO2 concentration increased. When 16% CO2 was introduced to the 0.08mm thick nylon/PE film pouch, the inhibit of stem elongation was most successful. Analysis of plant weight, total number of leaves, green color intensity, ascorbic acid content in the leaf blade and head weight of harvested cabbage revealed that the elevated CO2 active MAP is a favorable storage condition for cabbage plug seedlings. The elevated CO2 active MAP, however, caused CO2 injury when CO2 concentration exceeded 24%.

2658

Yamauchi, N., and A.E. Watada. 1998. Chlorophyll and xanthophyll changes in broccoli florets stored under elevated CO2 or ethylene-containing atmosphere. *Hortscience 33(1):114-117.*

Chlorophylls and xanthophylls were monitored in broccoli (Brassica oleracea L. var. italica Plen.) florets stored in air, air + 10 ppm ethylene, or 10% CO2 + 1% O-2 controlled atmosphere (CA) at 15 degrees C. Chlorophylls a and b, as measured with high-performance liquid chromatography, decreased in florets held in air. The decrease was accelerated by ethylene treatment and suppressed in CA. Chlorophyllide a and pheophorbide a were present in fresh broccoli florets, but the levels decreased significantly in all treatments during storage. The oxidized product of chlorophyll a, 13(2)- hydroxychlorophyll a, did not accumulate, Xanthophylls decreased, but new pigments, suggested to be esterified xanthophylls, formed with yellowing in stored florets. The chlorophyll degradative pathway in broccoli florets was not altered by ethylene or CA and differed from that reported for parsley (Petroselium crisum Nym.) and spinach (Spinacia oleracea L.) leaves.

KEYWORDS: BREAKDOWN, DEGRADATION, OXIDASE, PARSLEY LEAVES, STORAGE

2659

Yavitt, J.B., R.K. Wieder, and G.E. Lang. 1993. Co2 and ch4 dynamics of a sphagnum-dominated peatland in west- virginia. *Global Biogeochemical Cycles 7(2):259-274.*

Climatic change could bring about net release of carbon dioxide (CO2) and/or methane (CH4) from the deep peat deposits in northern peatlands into the atmosphere. To provide insight into this hypothesis, we studied net flux of CO2 and CH4 in Big Run Bog, West Virginia, which has a temperate climate, making it an analog to evaluate climatic change imposed on more northern counterparts. Net CO2 flux ranged from -564 to 300 mg C m-2 hr- 1. Measurements made during the nighttime showed that net CO2 flux increased exponentially with increasing air temperature, whereas CO2 sequestration increased with increasing air temperature for daytime measurements. Net CH4 flux ranged from -2.3 to 70 mg C m-2 hr-1, showing no consistent relationship to temperature or water table level. Net efflux for both CO2 and CH4 was tenfold higher from peat cores incubated in a greenhouse compared to field measurements. Even cores drained and allowed to dry for 8 days showed moderately high flux for both CO2 and CH4. The enhanced efflux seemed to be due to altered hydrology rather than increased rates of bacterial production (measured in anoxic, in vitro incubations) which could account for only 50% of the whole-core flux. Presumably the remainder was CO2 and CH4 stored in the peat cores at the time of collection. Overall, the results suggest that a temperate climate imposed on northern peatlands could mobilize stored carbon and increase CO2 and CH4 efflux into the troposphere. Studies involving peat cores must insure that CO2 and CH4 dynamics measured in vitro mimic those in situ.

KEYWORDS: BALANCE, CARBON DIOXIDE, ECOSYSTEM, METHANE, MOUNTAINS, RAISED BOG, REDUCTION, SOILS, TUSSOCK TUNDRA, WATER

2660

Yearsley, C.W., N.H. Banks, and S. Ganesh. 1997. Effect of carbon dioxide on the internal lower oxygen limits of apple fruit. *Postharvest Biology and Technology 12(1):1-13.*

The effect of elevated CO2 between 0 and 8 kPa on steady-state lower O-2 limits based on internal atmospheres (LOLi) was estimated for postclimacteric 'Cox's Orange Pippin' and 'Braeburn' apples at 0 and 20 degrees C. Two types of LOLi were estimated: the anaerobic compensation point (ACP(i)), and the internal fermentation threshold based either on the respiratory quotient (FTRQi) or ethanol (EtOH) accumulation (FTEtOHi). ACP(i), for both cultivars and temperatures, remained constant at 0.5 kPa O-2 for 'Cox's Orange Pippin' and 0.8-1.0 O-2 for 'Braeburn' apples for levels of CO2 external to the fruit between 0 and 8 kPa. However, for FTRQi and FTEtOHi no consistent trend with level of CO2 was evident at 20 degrees C for either cultivar. In contrast, at 0 degrees C FTRQi and FTEtOHi were 0.2-0.8 kPa O-2 higher at 8 kPa CO2 than at 0 kPa CO2 (with the exception of FTRQi for 'Cox's Orange Pippin'). A small decrease in O-2 uptake (estimated from the difference in external and internal O-2 atmospheres) was observed between 2 and 8 kPa CO2 at 20 degrees C. Elevated CO2 slightly lowered the respiratory quotient (RQ(i), estimated from the ratio of differences between external and internal atmosphere partial pressures of CO2 and O-2) of 'Cox's Orange Pippin' in 8 kPa CO2 and 'Braeburn' in 2 to 8 kPa CO2 at 20 degrees C, and more markedly in 8 kPa CO2 at 0 degrees C. The RQ(i) of 'Cox's Orange Pippin' and 'Braeburn' apples was slightly and markedly higher respectively at 0 degrees C compared to 20 degrees C, The lower RQ(i) of 'Braeburn' at 20 degrees C compared to 'Cox's Orange Pippin' apples indicated 'Braeburn had a higher permeance to CO2 relative to O-2 compared to 'Cox's Orange Pippin'. This study indicates the tolerance of 'Cox's Orange Pippin' and 'Braeburn' apples to low O-2 levels may be affected by levels of CO2. (C) 1997 Elsevier Science B.V.

KEYWORDS: ATMOSPHERES, BLUEBERRY FRUIT, CO2, RESPIRATION, TEMPERATURE, VEGETABLES

2661

Yeates, G.W., P.C.D. Newton, and D.J. Ross. 1999. Response of soil nematode fauna to naturally elevated CO2 levels influenced by soil pattern. *Nematology 1:285-293.*

As experimental elevation of CO2 in short-term experiments may produce organic matter with decomposition characteristics different from those produced under long-term equilibrated conditions, we

sampled the soil nematode fauna near a natural CO2 vent in Northland, New Zealand. Various indices of the nematode fauna showed significant effects, with all being significantly correlated with soil pH, microbial carbon and atmospheric CO2 across the 33 sampling points. There was a general decrease in nematode abundance and diversity, but an increase in dominance and proportion of bacterial-feeding nematodes with increasing atmospheric CO2 concentration. However, when the nematode data from gley and organic soils present at the site were differentiated most of the significant correlations were with soil microbial carbon; they were positive in the organic soil but negative in the gley soil. That these responses can be related to soil carbon and to microbial carbon demonstrates that any general response to long-term CO2 enrichment represents an integration of specific responses by the soil biota in the various soils present.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, DECOMPOSITION, MICROBIAL BIOMASS

2662

Yeates, G.W., K.R. Tate, and P.C.D. Newton. 1997. Response of the fauna of a grassland soil to doubling of atmospheric carbon dioxide concentration. *Biology and Fertility of Soils 25(3):307-315.*

The effects of elevated CO2 on rhizosphere processes, including the response of soil faunal populations and community structure, have so far received little attention. We report on significant responses in the soil fauna of ryegrass/white clover swards to both increasing CO2 from 350 to 750 mu l . l(- 1) and, to a period of 60 days when some of the turves were subject to drought, in a controlled climate growth room experiment. The nematodes which increased were predominantly Enoplia, including dorylaimids, alaimids and trichodorids. This accords with both the doubling of Alaimus under elevated CO2 conditions reported in a similar experiment and with the common association of Enoplia with less disturbed habitats. The most marked decrease was in the bacterial-feeding Rhabditis (Secernentea). The increase in omnivorous and predacious nematodes may have been responsible for the decrease in populations of bacterial-feeding nematodes. However, in contrast to their standing crops, the turnover rate of bacterial-feeding nematodes and soil microbial biomass probably increased as a result of increased grazing by these omnivorous and predacious nematodes. Increases in earthworm and enchytraeid populations were related to increased below-ground productivity reported for the same trial.

KEYWORDS: ELEVATED CO2, ENRICHMENT, PASTURE, PLANT GROWTH, POPULATIONS, RHIZOSPHERE, TURVES

2663

Yelle, S., R.C. Beeson, M.J. Trudel, and A. Gosselin. 1990. Duration of CO2 enrichment influences growth, yield, and gas- exchange of 2 tomato species. *Journal of the American Society for Horticultural Science 115(1):52-57.*

2664

Yeo, A. 1999. Predicting the interaction between the effects of salinity and climate change on crop plants. *Scientia Horticulturae 78(1-4):159-174.*

The human population is expected to double so there will be at least a doubled demand for food production. This will increase the demand for irrigation because irrigation gives a higher potential yield per unit area than non-irrigated agriculture, together with more yield stability. The demand for irrigation will be especially focused in semi-arid regions supporting a large population, such as the Mediterranean basin and the Indo- Gangetic plain of northern India and Pakistan. The 'hot/warm semi-arid' agro-climatic zone is the one projected most to expand in relative proportion as a consequence of climate change brought about by the increase in atmospheric carbon dioxide concentration. Irrigation in semi-arid climates is a major cause of secondary salinisation (that due to human activity) which already affects 1 ha in five of the irrigated lands. Increased demand for irrigation in semi-arid climates, as a result of both population increase and climate change, will tend to increase the extent of secondary salinisation. Any increase in the extent of secondary salinisation could be offset by positive effects of elevated atmospheric CO2 on crop yield per unit area and per unit input of water. In protected environments, or where CO2 is the only experimental variable, elevated CO2 usually enhances plant growth and water-use- efficiency in the short-term and can also do so in the longer term. However, far crop production in the field world-wide, elevated CO2 per se is not a factor that can be viewed separately from the climate change that it will bring about. Neither the anticipated 'CO2-fertilisation' nor the 'water-use-efficiency' benefits to the plant of elevated CO2 is certain to outweigh the climatic effects of elevated CO2 on temperature, water availability and evaporative demand. Climate change is expected to cause a net increase in the proportion of land classed as semi-arid. Raised temperatures may benefit some crops in some places but disadvantage others through increased evapotranspiration and thermal damage. Increased water-use- efficiency may not reduce leaf salt concentration in a saline environment. Buffering and feedback effects in both agricultural and ecological systems conspire to moderate or even to confound the anticipated gains in net assimilation and water-use-efficiency found in experimental systems. Elevated CO2 may not, therefore, provide the anticipated decrease in water-use, decrease in leaf salt concentration, and increase in fixed carbon available for re-allocation: factors that might enhance crop performance under salinity stress. If these benefits are not realised then elevated atmospheric CO2 will exacerbate rather than moderate the problems of secondary salinity in agriculture. (C) 1999 Elsevier Science B.V. All rights reserved.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CARBON-DIOXIDE, CO2, GAS-EXCHANGE, GROWTH, MODEL, RESPONSES, RICE, SODIUM UPTAKE, WHEAT

2665

Yokota, T., and A. Hagihara. 1998. Changes in the relationship between tree size and aboveground respiration in field-grown hinoki cypress (Chamaecyparis obtusa) trees over three years. *Tree Physiology 18(1):37-43.*

Respiration measurements of aerial parts of 18-year-old hinoki cypress (Chamaecyparis obtusa (Sieb. et Zucc.) Endl.) trees were made under field conditions over three years to study changing relationships with tree age between respiration and phytomass, phytomass increment, and leaf mass. The relationship between annual respiration (r(a)) and phytomass (w(T)) was approximated by a proportional function (r(a) = aw(T)), where the proportional constant (a) decreased year by year. The effect of time on the relationship between annual respiration and phytomass of each sample tree was fitted by a power function. Respiration of the tree suppressed by the canopy decreased year by year, but respiration of the other trees increased slightly with age. The relationship between annual respiration and leaf mass was also approximated by a generalized power function. Excluding the suppressed tree, the relationship between annual respiration (r(a)) and the annual increment of aboveground phytomass (Delta w(T)) was described by a proportional function (r(a) = 2.27 Delta w(T)), where the proportional constant, 2.27, was independent of sample tree and year, indicating that about 2.3 times of the annual aboveground phytomass increment equivalent was respired annually. For any tree. the time constant relationships between annual respiration and leaf mass and phytomass increment for different-sized trees were similar to the corresponding time continuum relationships. In contrast, the time continuum relationship between annual respiration and phytomass

differed from the time constant relationship, indicating that respiration of less active woody tissue contributed significantly to aboveground respiration. Based on the relationship between tree size and annual respiration, annual aboveground stand respiration was estimated to be 25.0, 26.9, and 25.8 Mg-dm ha(-1) year(-1) for the three consecutive years, respectively, and the corresponding above-ground stand biomass was 60.0, 69.0, and 76.8 Mg-dm ha(-1).

KEYWORDS: CO2- ENRICHMENT, FOREST TREE, MAINTENANCE RESPIRATION, PARTS, STAND DEVELOPMENT, STEMS

2666

Yoo, K.S., C.R. Andersen, and L.M. Pike. 1997. Internal CO2 concentrations in onion bulbs at different storage temperatures and in response to sealing of the neck and base. *Postharvest Biology and Technology 12(2):157-163.*

Internal CO2 concentrations were measured in onion (Allium cepa L. cv. TG 1015Y) bulbs stored at 1, 7, 13, 20, 27, or 34 degrees C for 12 weeks and their relationships with shoot growth and respiration rates were investigated. Maximum shoot growth was observed at 13 and 20 degrees C. Respiration rates were greatest at 13 and 20 degrees C for 8 weeks, then linearly increased with storage temperatures after 12 weeks. Internal CO2 concentrations ranging from 2 to 5% increased with increasing storage temperatures, while internal gas volume decreased. Bicarbonate concentrations in outer scales ranged from 130 to 190 mu M and increased with increasing storage temperatures. The centre scale tissues contained 11-17% CO2, which paralleled respiration rates. Searing the neck area of onion bulbs stored at 1 or 27 degrees C significantly increased internal CO2 concentrations, but had no effect on inhibiting shoot growth. Internal CO2 concentrations appeared to be regulated by gas exchange rates through the neck area and/or elevated HCO3- concentrations in outer scales. Elevated internal CO2 concentrations or high levels in centre scale tissues did not appear to be a primary reason for inhibited shoot growth at high storage temperatures. There seems to be thermo-dormancy controlling shoot growth and respiration in onion bulbs. (C) 1997 Elsevier Science B.V.

2667

Yoshioka, T., S. Satoh, and Y. Yamasue. 1998. Effect of increased concentration of soil CO2 on intermittent flushes of seed germination in Echinochloa crus-galli var. crus-galli. *Plant, Cell and Environment 21(12):1301-1306.*

Soil-buried seeds of barnyardgrass (Echinochloa crusgalli var. crus-galli) germinated from April to June in three intermittent flushes. The later two flushes of germination occurred after heavy rainfall. Carbon dioxide concentration in soil air transiently increased to 30 dm(3) m(-3) after the rainfall, probably due to the increase in soil temperature and water potential. Germination of exhumed seeds was stimulated by exposure to CO2 at 30 dm(3) m(-3). Fluctuating temperature, light, water, ethylene, and nitrate are known to promote seed germination in many species. However, of these environmental factors, within ranges found in the field, only CO2 was effective in enhancing the germination of barnyardgrass seeds. We conclude that soil CO2 is responsible for causing intermittent flushes of germination. Detection of vegetation gaps may be explained by the responsiveness of buried seeds to CO2.

KEYWORDS: TEMPERATURE

2668

Young, I.M., E. Blanchart, C. Chenu, M. Dangerfield, C. Fragoso, M. Grimaldi, J. Ingram, and L.J. Monrozier. 1998. The interaction of soil biota and soil structure under global change. *Global Change Biology 4(7):703-712.*

The structural framework of soil mediates all soil processes, at all relevant scales. The spatio-temporal heterogeneity prevalent in most soils underpins the majority of biological diversity in soil, providing refuge sites for prey against predator, flow paths for biota to move, or be moved, and localized pools of substrate for biota to multiply. Just as importantly, soil biota play a crucial role in mediating soil structure: bacteria and fungi aggregate and stabilize structure at small scales (mu m-cm) and earthworms and termites stabilize and create larger-scale structures (mm-m). The stability of this two-way interaction of structure and biota relations is crucial to the sustainability of the ecosystem. Soil is constantly reacting to changes in microclimates, and many of the soil-plant-microbe processes rely on the functioning of subtle chemical and physical gradients. The effect of global change on soil structure-biota interactions may be significant, through alterations in precipitation, temperature events, or land-use. Nonetheless, because of the complexity and the ubiquitous heterogeneity of these interactions, it is difficult to extrapolate from general qualitative predictions of the effects of perturbations to specific reactions. This paper reviews some of the main soil structure-biota interactions, particularly focusing on soil stability, and the role of biota mediating soil structures. The effect of alterations in climate and land-use on these interactions is investigated. Several case studies of the effect of land-use change are presented.

KEYWORDS: COTE- DIVOIRE, ECOSYSTEM, ELEVATED CO2, MACROTERMITINAE, MEGASCOLECIDAE, MICROBIAL PROCESSES, OLIGOCHAETA, ORGANIC-MATTER, POLYSACCHARIDE, TERMITES

2669

Yu, M., Q. Gao, and J.P. Guo. 1998. Sensitivity analysis of individual responses of plants to global change. *Acta Botanica Sinica 40(12):1143-1151.*

Today research on global change is becoming one of the three vital topics in ecology. Within this field, simulating an individual plant's physiological responses to global change, especially the combined effects of CO2 enrichment and the climatic change it caused, is a useful model in predicting the changes of either natural vegetation or agricultural crops, in that the physiological basis of the responses are mostly understood and the results of simulation can be checked with experiments at any level or step when needed. Since the scenarios of the global changes often differ with different GCM's, and will change as the GCM's are being improved, even though, the simulation programs can still be used to for new predictions. In this study, based on the physiological mechanisms, a systematic dynamic model of plant individual growth was established, which included a weather generator and a growth module. The combined effects of enriched CO2 and climatic change on the main physiological processes, such as photosynthesis, respiration, etc., and seasonal dynamics of biomass were considered in the model. The data sets of the long-term weather records of Beijing Meteorological Station and the observed values of many ecophysiological quantities, obtained in a CO2 enrichment experiment of soybean, were used to parameterize and to validate the model. The results showed that data obtained from the simulation were quite compatible with those from the observation. When the CO2 concentration was doubled, the peak values of the total biomass and green biomass were increased approximately by 70% and 56% respectively. Furthermore, the responses of the total net assimilation and the average specific dark respiration rate within the growth season explained the internal mechanism of the biomass responses. The result indicated that the total net assimilation increased, while the average specific dark respiration rate decreased. Thus, it can be deduced that the increase of biomass nas brought about not only by the increase of the net assimilation, but also by the decrease of the specific dark respiration rate. Sensitivity analysis was used to the soybean individual responses

to global change. The seasonal dynamics of the total biomass to the combined effects of different levels of CO2, temperature and precipitation were simulated. CO2 concentration and precipitation have positive, while temperature has negative effect on total biomass. The positive effect of precipitation became weaker with increasing temperatures, while the negative effect of temperature was strengthened by the increased precipitation. The positive effect of CO2 concentration became stronger with the increasing temperatures, but weaker under enhancing precipitations. The positive effect of precipitation and the negative effect of temperature were weakened by doubling the CO2 concentration. These are partly due to the enhanced water use efficiency caused by CO2 enrichment, which in turn renders the plant individual more resistant and adaptable to the environmental change.

KEYWORDS: CARBON-DIOXIDE CONCENTRATION, ELEVATED CO2, RESPIRATION

2670

Zadrazil, F., and A.K. Puniya. 1994. Influence of carbon-dioxide on lignin degradation and digestibility of lignocellulosics treated with pleurotus-sajor- caju. *International Biodeterioration & Biodegradation 33(3):237-244.*

This study investigates the effect of different CO2 concentrations on lignin degradation and in vitro digestibility of wheat straw used as growth substrate for Pleurotus sajor- caju. The degradation of wheat straw lignin by P. sajor-caju increased under the influence of CO2 (0-20%) in the atmosphere and then started declining at higher levels. The maximum loss of lignin (39.7%) was found in cultures grown with passive air exchange through cotton plugs while digestibility was higher in cultures actively aerated with 0-30% CO2. Aside from gases, the period of incubation, i.e. 40 days rather than 20 days, seems to be the most important variable for improving the digestibility of the product. Generally, the process efficiency for change in digestibility per gram loss of organic matter enhanced from 0 to 30% CO2 at a fixed level of O2 (20%) in the gaseous phase.

KEYWORDS: INVITRO DIGESTIBILITY, OXYGEN, SOLID-STATE FERMENTATION, WHEAT STRAW, WHITE-ROT FUNGI, WOOD

2671

Zak, D.R., K.S. Pregitzer, P.S. Curtis, J.A. Teeri, R. Fogel, and D.L. Randlett. 1993. Elevated atmospheric co2 and feedback between carbon and nitrogen cycles. *Plant and Soil 151(1):105-117.*

We tested a conceptual model describing the influence of elevated atmospheric CO2 on plant production, soil microorganisms, and the cycling of C and N in the plant-soil system. Our model is based on the observation that in nutrient- poor soils. plants (C3) grown in an elevated CO2 atmosphere often increase production and allocation to belowground structures. We predicted that greater belowground C inputs at elevated CO, should elicit an increase in soil microbial biomass and increased rates of organic matter turnover and nitrogen availability. We measured photosynthesis, biomass production, and C allocation of Populus grandidentata Michx. grown in nutrient-poor soil for one field season at ambient and twice-ambient (i.e., elevated) atmospheric CO2 concentrations. Plants were grown in a sandy subsurface soil i) at ambient CO2 with no open top chamber, ii) at ambient CO2 in an open top chamber, and iii) at twice-ambient CO2 in an open top chamber. Plants were fertilized with 4.5 g N m 2 over a 47 d period midway through the growing season. Following 152 d of growth, we quantified microbial biomass and the availabilities of C and N in rhizosphere and bulk soil. We tested for a significant CO2 effect on plant growth and soil C and N dynamics by comparing the means of the chambered ambient and chambered elevated CO2 treatments. Rates of photosynthesis in plants grown at elevated CO2 were significantly greater than those measured under ambient conditions. The number of roots, root length, and root length increment were also substantially greater at elevated CO2. Total and belowground biomass were significantly greater at elevated CO2. Under N-limited conditions, plants allocated 50-70% of their biomass to roots. Labile C in the rhizosphere of elevated-grown plants was significantly greater than that measured in the ambient treatments; there were no significant differences between labile C pools in the bulk soil of ambient and elevated-grown plants. Microbial biomass C was significantly greater in the rhizosphere and bulk soil of plants grown at elevated CO2 compared to that in the ambient treatment. Moreover, a short-term laboratory assay of N mineralization indicated that N availability was significantly greater in the bulk soil of the elevated-grown plants. Our results suggest that elevated atmospheric CO2 concentrations can have a positive feedback effect on soil C and N dynamics producing greater N availability. Experiments conducted for longer periods of time will be necessary to test the potential for negative feedback due to altered leaf litter chemistry.

KEYWORDS: BIOCIDAL TREATMENTS, DIOXIDE, MICROBIAL BIOMASS, MINERALIZATION, PLANTS, QUERCUS-ALBA, RESPONSES, SEEDLING GROWTH, SOIL ORGANIC-CARBON, TREES

2672

Zak, D.R., D.B. Ringelberg, K.S. Pregitzer, D.L. Randlett, D.C. White, and P.S. Curtis. 1996. Soil microbial communities beneath Populus grandidentata crown under elevated atmospheric CO2. *Ecological Applications 6(1):257-262.*

In most terrestrial ecosystems, the amount of substrate entering the soil from plant litter production is only sufficient to meet the maintenance requirements of soil microorganisms, allowing for no net annual growth. However, the rising atmospheric CO2 concentration has the potential to alter such a balance by increasing plant litter production, and hence the amount of substrate available for heterotrophic metabolism in soil. In a recent experiment, we observed that greater belowground plant litter production at elevated atmospheric CO2 significantly increased the biomass of soil microorganisms in both rhizosphere and non-rhizosphere soil. Because soil microorganisms differ in their ability to convert substrate into biomass, we hypothesized that greater plant litter production at elevated CO2 should shift community composition as fungal populations increase in response to greater substrate availability. We used a molecular technique, phospholipid fatty acid (PLFA) analysis, to gain insight into the composition of soil microbial communities beneath Populus grandidentata growing at ambient and twice-ambient atmospheric CO2. PLFAs extracted from rhizosphere and non-rhizosphere soil were derivatized and identified using gas chromatography and mass spectrometry. After one growing season the proportions of bacterial, actinomycetal, and fungal PLFAs were not significantly influenced by elevated atmospheric CO2 in either rhizosphere or non-rhizosphere soil. However, clear differences were present between microbial communities in rhizosphere and non-rhizosphere soil. Although enhanced belowground plant litter production under elevated atmospheric CO2 increased the biomass of soil microorganisms, we have no evidence to suggest that such an increase occurred through a shift in community composition, at least in the short term.

KEYWORDS: AMENDED SOIL, BIOMASS, CALIBRATION, CARBON DIOXIDE, CLIMATE CHANGE, FEEDBACK, FORESTS, GROWTH, NUTRIENT-UPTAKE, RHIZOSPHERE

2673

Zaller, J.G., and J.A. Arnone. 1997. Activity of surface-casting earthworms in a calcareous grassland under elevated atmospheric CO2. *Oecologia 111(2):249-254.*

Earthworms make up the dominant fraction of the biomass of soil animals in most temperate grasslands and have important effects on the structure and function of these ecosystems. We hypothesized that the effects of elevated atmospheric CO2 on soil moisture and plant biomass production would increase earthworm activity, expressed as surface cast production. Using a screen-aided CO2, control facility (open top and open bottom rings), eight 1.2-m(2) grassland plots in Switzerland have been maintained since March 1994 at ambient CO2 concentrations (350 mu l CO2 l(-1)) and eight at elevated CO2 (610 mu l CO2 l(-1)). Cumulative earthworm surface cast production measured 40 times over 1 year (April 1995-April 1996) in plots treated with elevated CO2 (2206 g dry mass m(-2) year(-1)) was 35% greater (P<0.05) than that measured in plant communities maintained at ambient CO2 (1633 g dry mass m(-2) year(-1)). At these rates of surface cast production, worms would require about 100 years to egest the equivalent of the amount of soil now found in the Ah horizon (top 15 cm) under current ambient CO2 concentrations, and 75 years under elevated CO2. Elevated atmospheric CO2 had no influence on the seasonality of earthworm activity. Cumulative surface cast production measured over the 7-week period immediately following the 6-week summer dry period in 1995 (no surface casting) was positively correlated (P<0.05) with the mean soil water content calculated over this dry and subsequent wetter period, when viewed across all treatments. However, no correlations were observed with soil temperature or with annual aboveground plant biomass productivity. No CO2- related differences were observed in total nitrogen (N-tot) and organic carbon (C-org) concentration of surface casts, although concentrations of both elements varied seasonally. The CO2- induced increase in earthworm surface casting activity corresponded to a 30% increase of the amount of N-tot (8.9 mg N m(-2) vs. 6.9 mg N m(-2)) and C-org (126 mg C m(-2) vs. 94 mg C m(-2)) egested by the worms in one year. m Thus, our results demonstrate an important indirect stimulatory effect of elevated atmospheric CO2 on earthworm activity which may have profound effects on ecosystem function and plant community structure in the long term.

KEYWORDS: BIOMASS PRODUCTION, CARBON DIOXIDE, COMMUNITY, ECOSYSTEM, LUMBRICIDAE, NITROGEN, PHOSPHORUS, RESPONSES, SOIL, TALLGRASS PRAIRIE

2674

Zaller, J.G., and J.A. Arnone. 1999. Earthworm responses to plant species' loss and elevated CO2 in calcareous grassland. *Plant and Soil 208(1):1-8.*

The objectives of this study were: (1) to quantify the effects of plant species' loss from designed calcareous grassland communities at a field site in northwestern Switzerland on the size and composition of earthworm communities, and (2) to evaluate how exposure of plant communities to elevated atmospheric CO2 might alter the effects of plant species' loss on earthworm communities. We non-destructively censused earthworm communities in each of 24 1.2 m(2) experimental plots in autumn 1996 when soils were wet and earthworms were active. Each plot contained an experimental plant community with 31, 12 or 5 native plant species (eight plots each). Half of the plots in each species treatment were exposed to ambient CO2 concentrations (350 mu L CO2 L-1) and half to elevated CO2 (600 mu L CO2 L-1) using screen-aided CO2 control. The study was conducted in the fourth year after community establishment and the third year of CO2 treatment as part of a long-term study on the interactive effects of plant species' loss and elevated CO2 on grassland communities. The size (density and biomass) of earthworm communities declined linearly when the number of plant species in the community was reduced from 31 to 5 species (e.g. 32 +/- 1 g m(-2) to 23 +/- 2 g m(-2)) due mainly to a decline in the endogeic worm species Allolobophora rosea which was the most abundant of nine earthworm species observed (nearly half of all worms in each plot). However, no changes in the relative contribution of individual species or the three main earthworm ecological groups (anecics, endogeics, epigeics) to the entire earthworm community were observed with declining number of plant species. The responses of earthworm communities to plant species' loss appear to reflect changes in community fine root biomass in the topsoil (e.g. declining worm biomass with declining fine root biomass) observed in parallel studies conducted at this site. Further the results of this study demonstrate that a loss of plant species' from these calcareous grassland communities may also alter the age structure of earthworm communities, but not significantly influence their diversity or composition. Our data also indicate that rising atmospheric CO2 may not greatly impact the size and composition of worm communities or alter the effects of plant species' loss on earthworm communities. Therefore, the disappearance of plant species from these native grasslands, as a result of ever increasing human activities, may be expected to lead to reductions in the size of earthworm communities and the ecosystem services they provide.

KEYWORDS: BIODIVERSITY, CARBON, DIVERSITY, ECOSYSTEMS, LUMBRICIDAE, SOIL, STABILITY

2675

Zaller, J.G., and J.A. Arnone. 1999. Interactions between plant species and earthworm casts in a calcareous grassland under elevated CO2. *Ecology 80(3):873-881.*

We tested the hypothesis that the spatial proximity of a plant species to nutrient-rich earthworm casts (e.g., 100% more ammonium and 30% more phosphate than in adjacent soil) is an important determinant of a plant's responsiveness to elevated atmospheric CO2. In 1995 we mapped the location of both earthworm surface casts and plants in each of 16 1.2-m(2) plots in a species-rich calcareous grassland in northwestern Switzerland. Eight plots have been maintained under current ambient CO2 concentrations (350 mu L CO2/ L), and eight have been maintained at elevated CO2 (600 mu L CO2/L) since March 1994. in addition, total ramet production of each species, as a measure of performance, and cumulative cast production at each location (cell) were recorded at peak community biomass in 1995. Plant species within functional groups (graminoids, non- legume forbs, and legumes) differed markedly in their degree of association with casts; however, after two growing seasons elevated CO2 had no effect on plant species or functional group associations with casts. No statistically significant relationship could be demonstrated between plant-species response (i.e., ramet production) to elevated CO2 and the degree of association with casts within any of the functional groups. However, a positive relationship was observed between the mean response of graminoid species to elevated CO2 (measured as the percentage change in mean total ramet production of graminoid species, relative to mean total ramet production at ambient CO2) and their mean degree of association (%) with surface casts at ambient CO2. Thus, graminoid species more frequently associated with casts (e.g., Anthoxanthum odoratum and Carer caryophyllea) produced more ramets per square meter at elevated CO2 than those less frequently associated with casts (e.g., Agrostis tenuis and Danthonia decumbens). These results, along with the strong and significant positive correlations observed between ramet production and associated cumulative cast mass across CO2 treatments for most plant species in all functional groups demonstrate: (1) that plant species differ significantly in their degree of association with nutrient-rich earthworm surface casts, regardless of the relative abundance of plant species in the community; (2) that graminoid species that are more highly associated with casts may respond more strongly to rising CO2 than those less highly associated with casts; and (3) that nutrient-rich earthworm casts stimulate the growth (ramet production) of most plant species in these grassland communities, even at current levels of atmospheric CO2. The data further suggest that these species-specific relationships between plants and casts have helped define the current structure of these highly diverse grassland communities and will likely influence their future structure as global CO2 levels continue to rise.

KEYWORDS: CAPTURE, CARBON, ECOSYSTEMS, EXPLOITATION, LOCALIZED SOIL ENRICHMENT, MICROSITES, PERENNIALS, RESPONSES, ROOT-GROWTH

2676

Zamolodchikov, D.G., D.V. Karelin, and A.I. Ivaschenko. 1997. Carbon balance of tundra landscape in Central Siberia: Observations, simulation and GIS-modelling. *Zhurnal Obshchei Biologii 58(2):15-34.*

Comprehensive statistical analysis of field measurements of CO2 fluxes in ecosystems of typical subarctic tundra in Taymir Peninsula (Central Siberia, Russia) was performed. Simulation models allowing to compute integrate seasonal values of basic components of carbon balance in the most characteristic plant communities of typical tundra were built. To access the landscape pattern of tundra carbon balance we applied GIS-approach based on the original computer map of ecosystem borders. In 1994 the seasonal (from the beginning of snow melting till the end of total soil freezing) carbon balance of typical tundra landscape was estimated as -4 g C . m-(2) . year(-1) (carbon sink), the ecosystem total respiration as +145 g C . m(-2) . year(-1), and gross primary production as -149 g C . m(-2) year(-1). Such a poorly expressed carbon sink conceptually should be considered as landscape equilibrium. Nevertheless the subsequent computer simulation of climate changes confirmed the hypothesis of positive feedback between global warming and change of carbon balance pattern in tundra ecosystems from sink to source. From the other side we found that regional peculiarities of ecological and climatic conditions can strongly effect the climate global change appearance.

KEYWORDS: CLIMATE CHANGE, CO2, DIOXIDE, ECOSYSTEMS, SOILS

2677

Zamorano, J.P., R. Alique, and W. Canet. 1999. Mechanical parameters to assess quality changes in cherimoya fruit. *Zeitschrift Fur Lebensmittel-Untersuchung Und-Forschung A-Food Research and Technology 208(2):125-129.*

Several mechanical parameters obtained by means of compression and penetration tests, and changes in cherimoya (Annona cherimola Mill.) fruit quality during storage in air and two controlled atmospheres (CA), (3% O-2 + 0% CO2 and 3% O-2 + 3% CO?) were analysed. A gradient of softening was found among the equatorial and the apical areas of the flesh during CA storage, as assessed by localized penetration tests. The combination of low O-2/elevated CO2 (3% O-2 + 3% CO2) increased this gradient and had a greater inhibiting effect on skin softening than low O-2. It appeared that the prevention of softening by CA was stronger in the less mature tissues (equatorial and outer areas) than in the more mature tissues (apical and inner areas around the longitudinal axis). CA delayed or inhibited changes in fruit quality observed during air storage: increases in total soluble solids (TSS), titratable acidity (TA), and yellowness of the flesh (b), and diminution in flesh lightness of colour (L). A good relationship between an objective quality index (QI, where QI = TSS + TA + L/b) and the compression slope (CS) was found during storage under all the conditions tested. It is suggested that the relationship, QI = 29.25 + 0.04 x CS- 0.0023 x CS2 could be useful when assessing stages of cherimoya fruit quality during storage under different conditions by performing a nondestructive, compression test.

KEYWORDS: ANNONA-CHERIMOLA, MILL FRUIT, STORAGE, VEGETABLES

2678

Zanetti, S., and U.A. Hartwig. 1997. Symbiotic N-2 fixation increases under elevated atmospheric pCO(2) in the field. *Acta Oecologica-International Journal of Ecology 18(3):285-290.*

Plant growth is stimulated by elevated atmospheric pCO(2), and hence demand for nutrients increases. In this context, nitrogen is a very prominent element; it can either be supplied from the limited available soil N or through biological (e.g. symbiotic) nitrogen fixation. In this study, the effect of elevated pCO(2) (60 Pa) on symbiotic N-2 fixation (N-15-isotope dilution method) was investigated using Free-Air-CO2-Enrichment (FACE) technology over a period of two growing seasons. Trifolium repens L, was cultivated either alone or in mixed swards together with Lolium perenne L. (non-fixing reference crop). In T. repens, percentage of plant N derived from symbiotic N-2 fixation (%Nsym) increased from 59 to 66% under elevated pCO(2). The major part of the additionally assimilated N was derived from symbiotic N-2 fixation. In the mixed swards, increased N yield was entirely due to increased symbiotic N-2 fixation. It is suggested that increased N-2 fixation is an important factor in the satisfaction of increased N demand in both clover and the associated grass under elevated pCO(2).

KEYWORDS: CLOVER, CO2, GROWTH, NITROGEN-FIXATION, RATES, WHITE

2679

Zanetti, S., U.A. Hartwig, A. Luscher, T. Hebeisen, M. Frehner, B.U. Fischer, G.R. Hendrey, H. Blum, and J. Nosberger. 1996. Stimulation of symbiotic N-2 fixation in Trifolium repens L under elevated atmospheric pCO(2) in a grassland ecosystem. *Plant Physiology 112(2):575-583.*

Symbiotic N-2 fixation is one of the main processes that introduces N into terrestrial ecosystems. As such, it may be crucial for the sequestration of the extra C available in a world of continuously increasing atmospheric CO2 partial pressure (pCO(2)). The effect of elevated pCO(2) (60 Pa) on symbiotic N-2 fixation (N-15-isotope dilution method) was investigated using Free-Air-CO2-Enrichment technology over a period of 3 years. Trifolium repens was cultivated either alone or together with Lolium perenne (a nonfixing reference crop) in mixed swards. Two different N fertilization levels and defoliation frequencies were applied. The total N yield increased consistently and the percentage of plant N derived from symbiotic N-2 fixation increased significantly in T. repens under elevated pCO(2). All additionally assimilated N was derived from symbiotic N-2 fixation, not from the soil. In the mixtures exposed to elevated pCO(2), an increased amount of symbiotically fixed N (+7.8, 8.2, and 6.2 g m(-2) a(-1) in 1993, 1994, and 1995, respectively) was introduced into the system. Increased N-2 fixation is a competitive advantage for T. repens in mixed swards with pasture grasses and may be a crucial factor in maintaining the C:N ratio in the ecosystem as a whole.

KEYWORDS: ACETYLENE-REDUCTION, CARBON DIOXIDE, CO2-ENRICHMENT, CV FJORD, GROWTH, NITROGEN-FIXATION, PISUM-SATIVUM, PLANTS, ROOT NODULE ACTIVITY, WHITE CLOVER

2680

Zanetti, S., U.A. Hartwig, and J. Nosberger. 1998. Elevated atmospheric CO2 does not affect per se the preference for symbiotic nitrogen as opposed to mineral nitrogen of Trifolium repens L. *Plant, Cell and Environment 21(6):623-630.*

The objective of this investigation was to examine the effect of an elevated atmospheric CO2 partial pressure (pCO(2)) on the N-sink strength and performance of symbiotic N-2 fixation in Trifolium repens L. cv. Milkanova, After initial growth under ambient pCO(2) in a nitrogen-free nutrient solution, T. repens in the exponential growth stage was exposed to ambient and elevated pCO(2) (35 and 60 Pa) and two

levels of mineral N (N- free and 7.5 mol m(-3) N) for 36 d in single pots filled with silica sand in growth chambers. Elevated pCO(2) evoked a significant increase in biomass production from day 12 after the start of CO2 enrichment. For plants supplied with 7.5 mol m(-3) N, the relative contribution of symbiotically fixed N (%N-sym) as opposed to N assimilated from mineral sources (N- 15-isotope-dilution method), dropped to 40%, However, in the presence of this high level of mineral N, %N-sym was unaffected by atmospheric pCO(2) over the entire experimental period. In plants fully dependent on N-2 fixation, the increase in N yield reflects a stimulation of symbiotic N-2 fixation that was the result of the formation of more nodules rather than of higher specific N-2 fixation. These results are discussed with regard to physiological processes governing symbiotic N-2 fixation and to the response of symbiotic N-2 fixation to elevated pCO(2) in field-grown T. repens.

KEYWORDS: CARBOHYDRATE CONTENT, CARBON, DEFOLIATION, ENRICHMENT, GROWTH, N2 FIXATION, NODULATED WHITE CLOVER, NODULES, PERMEABILITY, PLANTS

2681

Zanetti, S., U.A. Hartwig, C. vanKessel, A. Luscher, T. Hebeisen, M. Frehner, B.U. Fischer, G.R. Hendrey, H. Blum, and J. Nosberger. 1997. Does nitrogen nutrition restrict the CO2 response of fertile grassland lacking legumes? *Oecologia 112(1):17-25.*

The extent of the response of plant growth to atmospheric CO2 enrichment depends on the availability of resources other than CO2. An important growth-limiting resource under field conditions is nitrogen (N). N may, therefore, influence the CO2 response of plants. The effect of elevated CO2 (60 Pa) partial pressure (pCO(2)) on the N nutrition of field-grown Lolium perenne swards, cultivated alone or in association with Trifolium repens, was investigated using free air carbon dioxide enrichment (FACE) technology over 3 years. The established grassland ecosystems were treated with two N fertilization levels and were defoliated at two frequencies. Under elevated pCO(2), the above-ground plant material of the L. perenne monoculture showed a consistent and significant decline in N concentration which, in general, led to a lower total annual N yield. Despite the decline in the critical N concentration (minimum N concentration required for non-N- limited biomass production) under elevated pCO(2), the index of N nutrition (ratio of actual N concentration and critical N concentration) was lower under elevated pCO(2) than under ambient pCO(2) in frequently defoliated L. perenne monocultures. Thus, we suggest that reduced N yield under elevated pCO(2) was evoked indirectly by a reduction of plant- available N. For L. perenne grown in association with T. repens and exposed to elevated pCO(2) there was an increase in the contribution of symbiotically fixed N to the total N yield of the grass. This can be explained by an increased apparent transfer of N from the associated N-2-fixing legume species to the non-fixing grass. The total annual N yield of the mixed grass/legume swards increased under elevated pCO(2). All the additional N yielded was due to symbiotically fixed N. Through the presence of an N-2-fixing plant species more symbiotically fixed N was introduced into the system and consequently helped to overcome N limitation under elevated pCO(2).

KEYWORDS: ATMOSPHERIC CO2, CARBON, DECOMPOSITION, ECOSYSTEMS, ELEVATED CO2, ENRICHMENT, GROWTH, SWARD, TEMPERATURE, WHITE CLOVER

2682

Zebian, K.J., and E.G. Reekie. 1998. The interactive effects of atmospheric carbon dioxide and light on stem elongation in seedlings of four species. *Annals of Botany 81(2):185-193.*

Four species, Sinapis alba L., Medicago saliva L., Gypsophila paniculata L, and Picea abies (L.) Karsten, were grown in three light regimes: darkness, low light (25 mu mol m(-2) s(-1) for 10 min d(-1)) and high light (120 mu mol m(-2) s(-1) for 12 h d(-1)) and four levels of carbon dioxide: 0, 350, 700 and 1400 +/- 50 mu l l(-1). Germination was not affected by any of the treatments. The effects of carbon dioxide on stem elongation were identical in low and high light: stem length increased at a decreasing rate with level of carbon dioxide in all species. Level of carbon dioxide also affected stem elongation in complete darkness, but the pattern was more complex and varied among species. Total weight did not vary with level of carbon dioxide to any significant extent in either darkness or low light, but increased with level of carbon dioxide at high light in all four species. Due to the absence of any effect of carbon dioxide on growth in darkness and low light, we suggest the effects of carbon dioxide on stem elongation are independent of effects on growth and may be due to a direct interaction with developmental processes. In contrast, level of carbon dioxide had little effect on allocation patterns in the dark and low light experiments, but had marked effects in high light. Therefore, the effect of carbon dioxide on allocation was probably due to the effects of carbon dioxide on growth rather than to any direct interaction between carbon dioxide and development. An understanding of the mechanisms by which carbon dioxide affects development may help us understand the often variable effects of carbon dioxide upon plants. (C) 1998 Annals of Botany Company.

KEYWORDS: AMBIENT, ELEVATED CO2, ENRICHMENT, FOREST, GROWTH, PHARBITIS, PLANTS, RESPIRATION, RESPONSES, TREES

2683

Zeng, W., and J.L. Heilman. 1997. Sensitivity of evapotranspiration of cotton and sorghum in west Texas to changes in climate and CO2. *Theoretical and Applied Climatology 57(3-4):245-254.*

In regions such as west Texas where water is scarce, changes in the water balance may have a significant impact on agricultural production and management of water resources. We used the mechanistic soil-plant-atmosphere simulation model ENWATBAL to evaluate changes in soil water evaporation (E) and transpiration (T) in cotton and grain sorghum that may occur due to climate change and elevated CO2 in west Texas. Climatic and plant factors were varied individually, and in combination, to determine their impact on E and T. Of the climatic factors, E was most sensitive to changes in vapor pressure, and T to changes in irradiance. Simulations suggest that if warming is accompanied by higher humidity, the impact of climate change may be minimal. However, if the climate becomes warmer and less humid, ET may increase substantially. Simulations also suggest that enhanced growth due to elevated CO2 may have a greater impact on ET than climatic change.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, ENERGY, ENRICHMENT, ENVIRONMENT, EVAPORATION, FIELD, SIMULATION, SOIL, WHEAT

2684

Zhang, H.H., and P.S. Nobel. 1996. Photosynthesis and carbohydrate partitioning for the C-3 desert shrub Encelia farinosa under current and doubled CO2 concentrations. *Plant Physiology 110(4):1361-1366.*

Changes in photosynthesis (A) and carbohydrate partitioning were studied for Encelia farinosa, a common C-3 desert shrub in the southwestern United States, after a 3-month exposure to the current or a doubled CO2 concentration (750 mu L L(-1)). A remained unchanged under the current CO2 concentration but decreased during the day under the doubled CO2 concentration, resulting in a 46% enhancement in the

early morning, 26% at midday, and 15% in the late afternoon by the elevated CO2. The decrease during the day under the doubled CO2 concentration may represent end-product inhibition, because the sucrose and the starch contents increased during the day proportionally more than under the current CO2 concentration. The (CO2)-C-14 activity in sink leaves was maximal 3 h after labeling under the doubled and at 5 h under the current CO2 concentration, indicating faster movement of photosynthate out of source leaves and into sink tissues under the doubled CO2 concentration, which may have been responsible for the sustained enhancement in A under the doubled CO2 concentration.

KEYWORDS: ACCLIMATION, CARBOXYLASE, ELEVATED CO2, EXCHANGE, HIGH ATMOSPHERIC CO2, LEAVES, PHASEOLUS-VULGARIS, PLANT, STARCH, SUCROSE

2685

Zhang, J., and M.J. Lechowicz. 1995. Responses to co2 enrichment by 2 genotypes of arabidopsis- thaliana differing in their sensitivity to nutrient availability. *Annals of Botany 75(5):491-499.*

The responses of two genotypes of Arabidopsis thaliana, which differ in their sensitivities to nutrients to present and predicted future CO2 concentration were determined under rich vs. poor nutrient regimes on the basis of both single traits and the whole plant. Based on individual traits, the two genotypes responded similarly to CO2 enrichment for all the traits measured except for rate of increase in crown diameter, for which a decrease was observed in the less nutrient- sensitive genotype grown at increased CO2. Based on the overall response of the whole plant, by analysing groups of plant traits using multivariate analysis, the two genotypes differed substantially from one another and both responded more strongly to nutrient availability than to CO2 concentration, especially for traits measured at harvest that related to reproductive fitness. The less nutrient-sensitive genotype also showed a weaker overall response to CO2, and the pattern of the overall response was strikingly similar at different nutrient Supply. In contrast, the more nutrient-sensitive genotype responded more strongly to CO2 than the less nutrient-sensitive genotype, and responded differently to CO2 at low vs. high nutrient availability.

KEYWORDS: ACQUISITION, ALLOCATION, CARBON-DIOXIDE ENRICHMENT, ELEVATED CO2, GROWTH, NITROGEN, PHENOTYPIC PLASTICITY, PLANTS, RADISH, STRESS

2686

Zhang, Y.Q., and J.M. Welker. 1996. Tibetan alpine tundra responses to simulated changes in climate: Aboveground biomass and community responses. *Arctic and Alpine Research 28(2):203-209.*

High-elevation ecosystems are predicted to be some of the terrestrial habitats most sensitive to changing climates. The ecological consequences of changes in alpine tundra environmental conditions are still unclear especially for habitats in Asia. In this study we report findings from a field experiment where an alpine tundra grassland on the Tibetan plateau (37 degrees N, 101 degrees E) was exposed to experimental warming, irradiance was lowered, and wind speed reduced to simulate a suite of potential changes in environmental conditions. Our warming treatment increased air temperatures by 5 degrees C on average and soil temperatures were elevated by 3 degrees C at 5 cm depth. Aboveground biomass of grasses responded rapidly to the warmer conditions whereby biomass was 25% greater than that of controls after only 5 wk of experimental warming. This increase was accompanied by a simultaneous decrease in forb biomass, resulting in almost no net change in community biomass after 5 wk. Lower irradiance reduced grass biomass during the same period. Under ambient conditions total aboveground community biomass increased seasonally from 161 g m(-2) in July to a maximum of 351 g m(-2) in September, declining to 285 g m(-2) in October. However, under warmed conditions, peak community biomass was extended into October due in part to continued growth of grasses and the postponement of senescence. Our findings indicate that while alpine grasses respond favorably to altered conditions, others may not. And, while peak community biomass may actually change very little under warmer summers, the duration of peak biomass may be extended having feedback effects on net ecosystem CO2 balances, nutrient cycling, and forage availability.

KEYWORDS: ANNUAL GRASSLAND, ARCTIC SOILS, BUNCHGRASS SCHIZACHYRIUM-SCOPARIUM, DWARF-SHRUB, ECOSYSTEMS, MANIPULATIONS, MINERALIZATION, PERTURBATIONS, TEMPERATURE, WATER

2687

Zhu, J., D.P. Bartholomew, and G. Goldstein. 1997. Effect of elevated carbon dioxide on the growth and physiological responses of pineapple, a species with Crassulacean acid metabolism. *Journal of the American Society for Horticultural Science 122(2):233-237.*

Despite the potential impact of rising global CO2 levels, only a limited number of studies have been conducted on the effects of ambient and elevated CO2 on plants having Crassulacean acid metabolism (CAM), To our knowledge, there are no studies for pineapple [Ananas comosus (L.) Merr.], the most commercially important CAM plant, Pineapple plants were grown at CO2 levels of approximate to 330 (ambient) and approximate to 730 (elevated) mu mol . mol(-1) in open-top chambers for 4 months, The mean air temperature in the chambers was approximate to 39 degrees C day/24 degrees C night, Average plant dry mass at harvest was 180 g per plant at elevated CO2 and 146 g per plant at ambient CO2. More biomass was partitioned to stem and root but less to leaf for plants grown at elevated CO2; leaf thickness was 11% greater at elevated than at ambient CO2. The diurnal difference in leaf titratable acidity (H+) at elevated CO2 reached 347 mmol . m(-2), which was up to 42% greater than levels in plants grown in ambient CO2. Carbon isotopic discrimination (Delta) of plants was 3.75% at ambient CO2 and 3.17% at elevated CO2, indicating that CO2 uptake via the CAM pathway was enhanced more by elevated CO2 than uptake via the C-3 pathway, The nonphotochemical quenching coefficient (q(N)) of leaves was approximate to 45% lower in the early morning for plants grown at elevated than at ambient CO2, while afternoon values were comparable, The q(N) data suggested that the fixation of external CO2 was enhanced by elevated CO2 in the morning but not in the afternoon when leaf temperature was greater than or equal to 40 degrees C. We found no effect of CO2 levels on leaf N or chlorophyll content, Pineapple dry matter gain was enhanced by elevated CO2, mainly due to increased CO2 dark fixation in environments with day temperatures high enough to suppress C-3 photosynthesis.

KEYWORDS: ACCUMULATION, CAM, CO2 UPTAKE, FLUORESCENCE, GAS-EXCHANGE, OPUNTIA FICUS INDICA, PHOTOSYNTHESIS, PLANTS, RUBISCO, SOLUBLE SUGARS

2688

Zhu, J., G. Goldstein, and D.P. Bartholomew. 1999. Gas exchange and carbon isotope composition of Ananas comosus in response to elevated CO2 and temperature. *Plant, Cell and Environment 22(8):999-1007.*

Ananas comosus L. (Merr.) (pineapple) was grown at three day/night temperatures and 350 (ambient) and 700 (elevated) mu mol mol(-1) CO2 to examine the interactive effects of these factors on leaf gas exchange and stable carbon isotope discrimination (Delta,parts per thousand). All data were collected on the youngest mature leaf for 24 h every 6 weeks. CO2 uptake (mmol m(-2) d(-1)) at ambient and elevated CO2, respectively, were 306 and 352 at 30/20 degrees C, 175 and 346 at 30/25

degrees C and 187 and 343 at 35/25 degrees C, CO2 enrichment enhanced CO2 uptake substantially in the day in all environments. Uptake at night at elevated CO2, relative to that at ambient CO2, was unchanged at 30/20 degrees C, but was 80% higher at 30/25 degrees C and 44% higher at 35/25 degrees C suggesting that phosphoenolpyruvate carboxylase was not CO2- saturated at ambient CO2 levels and a 25 degrees C night temperature. Photosynthetic water use efficiency (WUE) was higher at elevated than at ambient CO2. Leaf Delta-values were higher at elevated than at ambient CO2 due to relatively higher assimilation in the light, Leaf Delta was significantly and linearly related to the fraction of total CO2 assimilated at night. The data suggest that a simultaneous increase in CO2 level and temperature associated with global warming would enhance carbon assimilation, increase WUE, and reduce the temperature dependence of CO2 uptake by A. comosus.

KEYWORDS: CRASSULACEAN ACID METABOLISM, DIOXIDE, DISCRIMINATION, GROWTH, LIGHT, OPUNTIA FICUS INDICA, PHOTOSYNTHESIS, PRODUCTIVITY, RESPIRATION, SHORT- TERM

2689

Zimmerman, R.C., D.G. Kohrs, D.L. Steller, and R.S. Alberte. 1997. Impacts of CO2 enrichment on productivity and light requirements of eelgrass. *Plant Physiology 115(2):599-607.*

Seagrasses, although well adapted for submerged existence, are CO2-limited and photosynthetically inefficient in seawater. This leads to high light requirements for growth and survival and makes seagrasses vulnerable to light limitation. We explored the long-term impact of increased CO2 availability on light requirements, productivity, and C allocation in eelgrass (Zostera marina L.). Enrichment of seawater CO2 increased photosynthesis 3-fold, but had no longterm impact on respiration. By tripling the rate of light-saturated photosynthesis, CO2 enrichment reduced the daily period of irradiance-saturated photosynthesis (H-sat) that is required for the maintenance of positive whole-plant C balance from 7 to 2.7 h, allowing plants maintained under 4 h of H-sat to perform like plants growing in unenriched seawater with 12 h of H-sat. Eelgrass grown under 4 h of H-sat without added CO2 consumed internal C reserves as photosynthesis rates and chlorophyll levels dropped. Growth ceased after 30 d. Leaf photosynthesis, respiration, chlorophyll, and sucrose-phosphate synthase activity of CO2-enriched plants showed no acclimation to prolonged enrichment. Thus, the CO2-stimulated improvement in photosynthesis reduced light requirements in the long term, suggesting that globally increasing CO2 may enhance seagrass survival in eutrophic coastal waters, where populations have been devastated by algal proliferation and reduced water-column light transparency.

KEYWORDS: ACCLIMATION, CARBON DIOXIDE, ELEVATED CO2, GROWTH, HIGH ATMOSPHERIC CO2, HIGHER-PLANTS, MARINA L EELGRASS, PHOTOSYNTHESIS, SAN-FRANCISCO BAY, TOMATO

2690

Ziska, L.H. 1998. The influence of root zone temperature on photosynthetic acclimation to elevated carbon dioxide concentrations. *Annals of Botany 81(6):717-721.*

Soybean (Glycine max 'Clark') was grown from germination to 21 d after sowing (DAS) at ambient (similar to 360 mu mol mol(-1)) or elevated (similar to 720 mu mol mol(-1)) carbon dioxide (CO2) at either one of two soil temperatures, 25 or 30 degrees C to determine the influence of root zone temperature on root growth and photosynthetic stimulation at ambient and elevated concentrations of carbon dioxide. Although the photosynthetic rate became less stimulate over time, a significant stimulation of whole plant photosynthesis and plant dry weight was observed at the elevated CO2 concentration during the experimental period irrespective of soil temperature. At neither carbon dioxide concentration did the warmer soil temperature (30 degrees C) stimulate whole plant growth compared to a soil temperature of 25 degrees C, but it did increase root growth relative to shoot (top) growth with a subsequent increase in root/shoot ratio. Increasing soil temperature at either carbon dioxide concentration also significantly stimulated whole plant photosynthetic rate. However, the degree of stimulation was reduced with time irrespective of carbon dioxide concentration so that at 21 DAS no difference in photosynthesis between ambient and elevated soil temperatures was observed. Data from this experiment indicate that for soybean, a higher soil temperature stimulates root/shoot ratio and enhances photosynthetic response to elevated carbon dioxide in the short-term (i.e. days), but increasing root/shoot ratios does not provide a satisfactory explanation of long-term stimulation of photosynthesis at elevated levels of carbon dioxide. (C) 1988 Annals of Botany Company.

KEYWORDS: ATMOSPHERIC CO2, ENRICHMENT, GROWTH, LEAVES, PLANTS, RESPONSES

2691

Ziska, L.H., and J.A. Bunce. 1993. The influence of elevated co2 and temperature on seed- germination and emergence from soil. *Field Crops Research 34(2):147-157.*

Seed of six crop species, alfalfa, Medicago sativa L. cv. 'Arc', soybean, Glycine max L. (Merrill) cv. 'Williams', maize, Zea mays L. cv. SS 885, pea, Pisum sativum L. cv. 'Maestro', sunflower, Helianthus annuus L. cv. 'Mammoth', and pumpkin Cucurbita pepo L. cv. 'Big Max' and four weedy species, Amaranthus hypochondriacus L., Amaranthus hybridus L., Chenopodium album L. and Abutilon theophrasti, were grown at two different CO2 concentrations of 350 mul l-1 (ambient) and 700 mul l-1 (elevated) in controlled-environment chambers to determine the effect of elevated CO2 on germination and emergence. Doubling the CO2 concentration resulted in an increase in the rate and final percentage of germination, for M. sativa, A. hybridus and C album. In a separate field experiment (silt-loam soil), elevated CO2 resulted in a significant increase in the total number of weed seedlings present 3 weeks after tilling. In a second set of experiments using controlled-environment chambers, the interaction between increased temperature and CO2 was examined in seven of the species used previously. No significant interaction was observed between CO2 and temperature on the germination response. Overall, this investigation suggests that as CO2 increases, differential changes in germination and/or emergence between crops and weeds could occur.

KEYWORDS: CARBON DIOXIDE, ETHYLENE, GROWTH

2692

Ziska, L.H., and J.A. Bunce. 1993. Inhibition of whole-plant respiration by elevated co2 as modified by growth temperature. *Physiologia Plantarum 87(4):459-466.*

Plants of alfalfa (Medicago sativa) and orchard grass (Dactylus glomerata) were grown in controlled environment chambers at two CO2 concentrations (350 and 700 mumol mol-1) and 4 constant day/night growth temperatures of 15, 20, 25 and 30-degrees-C for 50-90 days to determine changes in growth and whole plant CO2 efflux (dark respiration). To facilitate comparisons with other studies, respiration data were expressed on the basis of leaf area, dry weight and protein. Growth at elevated CO2 increased total plant biomass at all temperatures relative to ambient CO2, but the relative enhancement declined (P less-than-or-equal-to 0.05) as temperature increased. Whole plant respiration (R(d)) at elevated CO2 declined at 15 and 20- degrees-C in D. glomerata on an area, weight or protein basis and in M. sativa on a weight or protein basis when compared to ambient CO2. Separation of R(d) into respiration required for growth (R(g)) and maintenance (R(m)) showed

a significant effect of elevated CO2 on both components. R(m) was reduced in both species but only at lower temperatures (15-degrees-C in M. sativa and 15 and 20-degrees-C in D. glomerata). The effect on R(m) could not be accounted for by protein content in either species. R(g) was also reduced with elevated CO2; however no particular effect of temperature was observed, i.e. R(g) was reduced at 20, 25 and 30-degrees-C in M. sativa and at 15 and 25-degrees-C in D. glomerata. For the two perennial species used in the present study, the data suggest that both R(g) and R(m) can be reduced by anticipated increases in atmospheric CO2; however, CO2 inhibition of total plant respiration may decline as a function of increasing temperature.

KEYWORDS: CARBON DIOXIDE, CROP, DARK RESPIRATION, ENRICHMENT, FIELD, MAINTENANCE, SORGHUM, TREES

2693

Ziska, L.H., and J.A. Bunce. 1994. Direct and indirect inhibition of single leaf respiration by elevated co2 concentrations - interaction with temperature. *Physiologia Plantarum 90(1):130-138.*

Two herbaceous perennials, alfalfa (Medicago sativa L. cv. Arc) and orchard grass (Dactylus glomerata L. cv. Potomac), were grown at ambient (367 mumol mol-1) and elevated (729 mumol mol- 1) CO2 concentrations at constant temperatures of 15, 20, 25 and 30-degrees-C in order to examine direct and indirect changes in nighttime CO2 efflux rate (respiration) of single leaves. Direct (biochemical) effects of CO2 on nighttime respiration were determined for each growth condition by brief (<30 min) exposure to each CO2 concentration. If no direct inhibition of respiration was observed, then long-term reductions in CO2 efflux between CO2 treatments were presumed to be due to indirect inhibition, probably related to long-term changes in leaf composition. By this criterion, indirect effects of CO2 on leaf respiration were observed at 15 and 20- degrees-C for M. sativa on a weight basis, but not on a leaf area or protein basis. Direct effects however, were observed at 15, 20 and 25-degrees-C in D. glomerata; therefore the observed reductions in respiration for leaves grown and measured at elevated relative to ambient CO2 concentrations could not be distinguished as indirect inhibition. No inhibition of respiration at elevated CO2 was observed at the highest growth temperature (30-degrees-C) in either species. CO2 efflux increased with measurement and growth temperature for M. sativa at both CO2 concentrations; however, CO2 efflux in D. glomerata showed complete acclimation to growth temperature. Stimulation of leaf area and weight by elevated CO2 levels declined with growth temperature in both species. Data from the present study suggest that both direct and indirect inhibition of respiration are possible with future increases in atmospheric CO2, and that the degree of each type of respiratory inhibition is a function of growth temperature.

KEYWORDS: ATMOSPHERIC CO2, CARBON-DIOXIDE EFFLUX, DARK RESPIRATION, ENRICHMENT, GROWTH, LEAVES, SATIVA, TREES

2694

Ziska, L.H., and J.A. Bunce. 1994. Increasing growth temperature reduces the stimulatory effect of elevated co2 on photosynthesis or biomass in 2 perennial species. *Physiologia Plantarum 91(2):183-190.*

We examined how anticipated changes in CO2 concentration and temperature interacted to alter plant growth, harvest characteristics and photosynthesis in two cold-adapted herbaceous perennials, alfalfa (Medicago sativa L. cv. Are) and orchard grass (Dactylis glomerata L. cv. Potomac). Plants were grown at two CO2 concentrations (362 [ambient] and 717 [elevated] mu mol mol(-1) CO2) and four constant day/night temperatures of 15, 20, 25 and 30 degrees C in controlled environmental chambers. Elevated CO2 significantly increased total plant biomass and protein over a wide range of temperatures in both species. Stimulation of photosynthetic rare, however, was eliminated at the highest growth temperature in M. sativa and relative stimulation of plant biomass and protein at high CO2 declined as temperature increased in both species. Lack of a synergistic effect between temperature and CO2 was unexpected since elevated CO2 reduces the amount of carbon lost via photorespiration and photorespiration increases with temperature. Differences between anticipated stimulatory effects of CO2 and temperature and whole plant single and leaf measurements are discussed. Data from this study suggest that stimulatory effects of atmospheric CO2 on growth and photosynthesis may decline with anticipated increases in global temperature, limiting the degree of carbon storage in these two perennial species.

KEYWORDS: ACCLIMATION, CARBON-DIOXIDE EFFLUX, CARBOXYLASE, ENRICHMENT, INHIBITION, LEAVES, LIGHT, RESPIRATION, SEEDLINGS, SOYBEAN CANOPY PHOTOSYNTHESIS

2695

Ziska, L.H., and J.A. Bunce. 1995. Growth and photosynthetic response of 3 soybean cultivars to simultaneous increases in growth temperature and co2. *Physiologia Plantarum 94(4):575-584.*

Three soybean (Glycine max L. Merr.) cultivars (Maple Glen, Clark and CNS) were exposed to three CO2 concentrations (370, 555 and 740 mu mol mol(-1)) and three growth temperatures (20/15 degrees, 25/20 degrees and 31/26 degrees C, day/night) to determine intraspecific differences in single leaf/whole plant photosynthesis, growth and partitioning, phenology and final biomass. Based on known carboxylation kinetics, a synergistic effect between temperature and CO2 on growth and photosynthesis was predicted since elevated CO2 increases photosynthesis by reducing photorespiration and photorespiration increases with temperature. Increasing CO2 concentrations resulted in a stimulation of single leaf photosynthesis for 40-60 days after emergence (DAE) at 20/15 degrees C in all cultivars and for Maple Glen and CNS at all temperatures. For Clark, however, the onset of flowering at warmer temperatures coincided with the loss of stimulation in single leaf photosynthesis at elevated CO2 concentrations. Despite the season-long stimulation of single leaf photosynthesis, elevated CO2 concentrations did not increase whole plant photosynthesis except at the highest growth temperature in Maple Glen and CNS, and there was no synergistic effect on final biomass. Instead, the stimulatory effect of CO2 on growth was delayed by higher temperatures. Data from this experiment suggest that: (1) intraspecific variation could be used to select for optimum soybean cultivars with future climate change; and (2) the relationship between temperature and CO2 concentration may be expressed differently at the leaf and whole plant levels and may not solely reflect known changes in carboxylation kinetics.

KEYWORDS: ATMOSPHERIC CO2, C-3, CANOPY PHOTOSYNTHESIS, CARBOXYLASE-OXYGENASE, ENRICHMENT, LEAVES

2696

Ziska, L.H., and J.A. Bunce. 1997. Influence of increasing carbon dioxide concentration on the photosynthetic and growth stimulation of selected C-4 crops and weeds. *Photosynthesis Research 54(3):199-208.*

Plants of six weedy species (Amaranthus retroflexus, Echinochloa crus-galli, Panicum dichotomiflorum, Setaria faberi, Setaria viridis, Sorghum halapense) and 4 crop species (Amaranthus hypochondriacus, Saccharum officinarum, Sorghum bicolor and Zea mays) possessing the C-4 type of photosynthesis were,at-own at ambient (38 Pa) and elevated (69 Pa) carbon dioxide during early development (i.e. up to 60 days after sowing) to determine: (a) if plants possessing the C-4 photosynthetic pathway could respond photosynthetically or in biomass production to future increases in global carbon dioxide and (b) whether differences

exist between weeds and crops in the degree of response. Based on observations in the response of photosynthesis (measured as A, CO2 assimilation rate) to the growth CO2 condition as well as to a range of internal CO2 (C- i) concentrations, eight of ten C-4 species showed a significant increase in photosynthesis. The largest and smallest increases observed were for A. retroflexus (+30%) and Z. mays (+5%), respectively. Weed species (+19%) showed approximately twice the degree of photosynthetic stimulation as that of crop species (+10%) at the higher CO2 concentration. Elevated carbon dioxide also resulted in significant increases in whole plant biomass for four C-4 weeds (A. retroflexus, E. crus-galli, P. dichotomiflorum, S viridis) relative to the ambient CO2 condition. Leaf water potentials for three selected species (A. retroflexus, A. hypochondriacus, Z. mays) indicated that differences in photosynthetic stimulation were not due solely to improved leaf water status. Data from this study indicate that C-4 plants may respond directly to increasing CO2 concentration, and in the case of some C-4 weeds (e.g. A. retroflexus) may show photosynthetic increases similar to those published for C-3 species.

KEYWORDS: ACCLIMATION, CO2- ENRICHMENT, ELEVATED CO2, GRASS, PLANTS, RESPONSES, TEMPERATURE, YIELD

2697

Ziska, L.H., and J.A. Bunce. 1997. The role of temperature in determining the stimulation of CO2 assimilation at elevated carbon dioxide concentration in soybean seedlings. *Physiologia Plantarum 100(1):126-132.*

Soybean (Glycine max cv. Clark) was gown at both ambient (ca 350 mu mol mol(-1)) and elevated (ca 700 mu mol mol(-1)) CO2 concentration at 5 growth temperatures (constant day/night temperatures of 20, 25, 30, 35 and 40 degrees C) for 17-22 days after sowing to determine the interaction between temperature and CO2 concentration on photosynthesis (measured as A, the rate of CO2 assimilation per unit leaf area) at both the single leaf and whole plant level. Single leaves of soybean demonstrated increasingly greater stimulation of A at elevated CO2 as temperature increased from 25 to 35 degrees C (i.e. optimal growth rates). At 40 degrees C, primary leaves failed to develop and plants eventually died. in contrast, for both whole plant A and total biomass production, increasing temperature resulted in less stimulation by elevated CO2 concentration. For whole plants, increased CO2 stimulated leaf area more as growth temperature increased. Differences between the response of A to elevated CO2 for single leaves and whole plants may be related to increased self-shading experienced by whole plants at elevated CO2 as temperature increased. Results from the present study suggest that self-shading could limit the response of CO2 assimilation rate and the growth response of soybean plants if temperature and CO2 increase concurrently, and illustrate that light may be an important consideration in predicting the relative stimulation of photosynthesis by elevated CO2 at the whole plant level.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, CANOPY PHOTOSYNTHESIS, ENRICHMENT, GROWTH, LEAVES, PHOTOSYNTHETIC RESPONSE, PLANTS

2698

Ziska, L.H., and J.A. Bunce. 1998. The influence of increasing growth temperature and CO2 concentration on the ratio of respiration to photosynthesis in soybean seedlings. *Global Change Biology 4(6):637-643.*

Using controlled environmental growth chambers, whole plants of soybean, cv. 'Clark', were examined during early development (7-20 days after sowing) at both ambient (approximate to 350 mu L L-1) and elevated (approximate to 700 mu L L-1) carbon dioxide and a range of air temperatures (20, 25, 30, and 35 degrees C) to determine if future climatic change (temperature or CO2 concentration) could alter the ratio of carbon lost by dark respiration to that gained via photosynthesis. Although whole-plant respiration increased with short-term increases in the measurement temperature, respiration acclimated to increasing growth temperature. Respiration, on a dry weight basis, was either unchanged or lower for the elevated CO2 grown plants, relative to ambient CO2 concentration, over the range of growth temperatures. Levels of both starch and sucrose increased with elevated CO2 concentration, but no interaction between CO2 and growth temperature was observed. Relative growth rate increased with elevated CO2 concentration up to a growth temperature of 35 degrees C. The ratio of respiration to photosynthesis rate over a 24-h period during early development was not altered over the growth temperatures (20-35 degrees C) and was consistently less at the elevated relative to the ambient CO2 concentration. The current experiment does not support the proposition that global increases in carbon dioxide and temperature will increase the ratio of respiration to photosynthesis; rather, the data suggest that some plant species may continue to act as a sink for carbon even if carbon dioxide and temperature increase simultaneously.

KEYWORDS: CANOPY PHOTOSYNTHESIS, CARBON-DIOXIDE CONCENTRATION, DARK RESPIRATION, ELEVATED CO2, ENRICHMENT, INHIBITION, LONG-TERM, RESPONSES, SHORT-TERM, WHOLE-PLANT RESPIRATION

2699

Ziska, L.H., and J.A. Bunce. 1999. Effect of elevated carbon dioxide concentration at night on the growth and gas exchange of selected C-4 species. *Australian Journal of Plant Physiology 26(1):71-77.*

Biomass of certain C-4 species is increased when plants are grown at elevated CO2 concentrations. Experiments using four C- 4 species (Amaranthus retroflexus L., Amaranthus hypochondriacus L., Sorghum bicolor (L.) Moench and Zea mays L.) exposed both day and night from sowing to carbon dioxide concentrations of 370 (ambient) or 700 mu mol mol(-1) (elevated) or to 370 mu mol mol(-1) during the day and 700 mu mol mol(-1) at night, determined whether any biomass increase at elevated CO2 concentrations was related to a reduction in the night-time rate of CO2 efflux at high night-time CO2 concentrations. Of the four species tested, only A. retroflexus significantly increased both CO2 assimilation (+13%) and plant biomass (+21%) at continuous elevated relative to continuous ambient concentrations of CO2. This increase was not associated with improvement in leaf water potential during dark or light periods. In contrast, high CO2 only during the night significantly reduced plant biomass compared to the 24 h ambient CO2 treatment for both A. retroflexus and Z. mays. This indicates that the observed increase in biomass at elevated CO2 for A. retroflexus was not caused by a reduction of carbon loss at night (i.e. increased carbon conservation), but rather a direct stimulation of daytime CO2 assimilation, independent of any improvement in leaf water potential.

KEYWORDS: ACCLIMATION, CO2- ENRICHMENT, DARK RESPIRATION, GRACILIS C-4, IRRADIANCE, LEAVES, PASCOPYRUM-SMITHII C-3, PLANTS, RESPONSES, TEMPERATURE

2700

Ziska, L.H., J.A. Bunce, and F. Caulfield. 1998. Intraspecific variation in seed yield of soybean (Glycine max) in response to increased atmospheric carbon dioxide. *Australian Journal of Plant Physiology 25(7):801-807.*

The growth characteristics of six and the reproductive development of five soybean [Glycine max (L.) Merr.] cultivars were examined at 39 Pa (ambient) and 70 Pa (elevated) CO2 partial pressures in temperature-controlled glasshouses. Significant intraspecific variation for both

growth and seed yield in response to elevated CO2 was observed among the cultivars. At elevated CO2, total biomass increased an average of 42% at the end of the vegetative stage, while average seed yield increased by only 28%. No changes in % protein or % oil were observed for any cultivar at elevated CO2, relative to ambient CO2. The relative enhancement of either vegetative or reproductive growth at elevated CO2 was not correlated with changes in the absolute or relative increase in single leaf photosynthetic rate among cultivars at elevated CO2. For soybean, the greatest response of seed yield to elevated CO2 was associated with increased production of lateral branches, increased pod production or increased seed weight, suggesting different strategies of carbon partitioning in a high CO2 environment. Data from this experiment indicates that differences in carbon partitioning among soybean cultivars may influence reproductive capacity and fecundity as atmospheric CO2 increases, with subsequent consequences for future agricultural breeding strategies.

KEYWORDS: CO2- ENRICHMENT, CULTIVARS, GROWTH, RICE ORYZA-SATIVA, TEMPERATURE

2701

Ziska, L.H., B.G. Drake, and S. Chamberlain. 1990. Long-term photosynthetic response in single leaves of a C3 and C4 salt-marsh species grown at elevated atmospheric CO2 in Situ. *Oecologia 83(4):469-472.*

2702

Ziska, L.H., K.P. Hogan, A.P. Smith, and B.G. Drake. 1991. Growth and photosynthetic response of 9 tropical species with long-term exposure to elevated carbon-dioxide. *Oecologia 86(3):383-389.*

Seedlings of nine tropical species varying in growth and carbon metabolism were exposed to twice the current atmospheric level of CO2 for a 3 month period on Barro Colorado Island, Panama. A doubling of the CO2 concentration resulted in increases in photosynthesis and greater water use efficiency (WUE) for all species possessing C3 metabolism, when compared to the ambient condition. No desensitization of photosynthesis to increased CO2 was observed during the 3 month period. Significant increases in total plant dry weight were also noted for 4 out of the 5 C3 species tested and in one CAM species, Aechmea magdalenae at high CO2. In contrast, no significant increases in either photosynthesis or total plant dry weight were noted for the C4 grass, Paspallum conjugatum. Increases in the apparent quantum efficiency (AQE) for all C3 species suggest that elevated CO2 may increase photosynthetic rate relative to ambient CO2 over a wide range of light conditions. The response of CO2 assimilation to internal C(i) suggested a reduction in either the RuBP and/or Pi regeneration limitation with long term exposure to elevated CO2. This experiment suggests that: (1) a global rise in CO2 may have significant effects on photosynthesis and productivity in a wide variety of tropical species, and (2) increases in productivity and photosynthesis may be related to physiological adaptation(s) to increased CO2.

KEYWORDS: C-3, CO2, LEAVES, PHYSIOLOGY, PLANTS

2703

Ziska, L.H., P.A. Manalo, and R.A. Ordonez. 1996. Intraspecific variation in the response of rice (Oryza sativa L) to increased CO2 and temperature: Growth and yield response of 17 cultivars. *Journal of Experimental Botany 47(302):1353-1359.*

Seventeen rice (Oryza sativa L.) cultivars of contrasting ecosystems and origins were exposed to two CO2 concentrations (373 [ambient] and 664 mu l l(-1) CO2 [elevated]) at two different day/night temperatures (29/21 degrees C and 37/29 degrees C) in glasshouses at the International Rice Research Institute phytotron during the dry seasons of 1994 and 1995, Growth at elevated CO2 (as determined by total plant biomass at maturity) increased by an average of 70% and 22%, respectively, for all cultivars for growth temperatures of 29/21 degrees C and 37/29 degrees C relative to the ambient CO2 treatment. At the 29/21 degrees C optimal growth temperature, grain yield increased on average c. 50% with enriched CO2. In contrast, at the higher growth temperature (37/29 degrees C), grain yield was almost zero, presumably due, in part, to temperature- induced infertility (i.e. the percentage of filled spikelets was < 1%), Among cultivars, IAC 165, a tropical japonica from Brazil, showed the largest relative increase in both biomass and grain yield, While the range of responses to increased CO2 and/or temperature were quite large (e.g. 10-250%) and may not be applicable to field conditions, data indicate that lines are available which could maximize productivity as CO2 concentration increases. Additional work, however, would be needed to identify cultivars which would maintain maximum yields in a high CO2, high temperature environment.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, ELEVATED CARBON-DIOXIDE, SEEDLINGS

2704

Ziska, L.H., T.B. Moya, R. Wassmann, O.S. Namuco, R.S. Lantin, J.B. Aduna, E. Abao, K.F. Bronson, H.U. Neue, and D. Olszyk. 1998. Long-term growth at elevated carbon dioxide stimulates methane emission in tropical paddy rice. *Global Change Biology 4(6):657-665.*

Recent anthropogenic emissions of key atmospheric trace gases (e.g. CO2 and CH4) which absorb infra-red radiation may lead to an increase in mean surface temperatures and potential changes in climate. Although sources of each gas have been evaluated independently, little attention has focused on potential interactions between gases which could influence emission rates. In the current experiment, the effect of enhanced CO2 (300 mu L L-1 above ambient) and/or air temperature (4 degrees C above ambient) on methane generation and emission were determined for the irrigated tropical paddy rice system over 3 consecutive field seasons (1995 wet and dry seasons 1996 dry season). For all three seasons, elevated CO2 concentration resulted in a significant increase in dissolved soil methane relative to the ambient control. Consistent with the observed increases in soil methane, measurements of methane flux per unit surface area during the 1995 wet and 1996 dry seasons also showed a significant increase at elevated carbon dioxide concentration relative to the ambient CO2 condition (+49 and 60% for each season, respectively). Growth of rice at both increasing CO2 concentration and air temperature did not result in additional stimulation of either dissolved or emitted methane compared to growth at elevated CO2 alone. The observed increase in methane emissions were associated with a large, consistent, CO2-induced stimulation of root growth. Results from this experiment suggest that as atmospheric CO2 concentration increases, methane emissions from tropical paddy rice could increase above current projections.

KEYWORDS: CO2- ENRICHMENT, PHOTOSYNTHETIC ACCLIMATION, RESPONSES, RHIZOSPHERE, VEGETATION, YIELD

2705

Ziska, L.H., O. Namuco, T. Moya, and J. Quilang. 1997. Growth and yield response of field-grown tropical rice to increasing carbon dioxide and air temperature. *Agronomy Journal 89(1):45-53.*

Although the response of rice (Oryza sativa L.) to increasing atmospheric CO2 concentration and air temperature has been examined at the greenhouse or growth chamber level, no field studies have been conducted under the tropical, irrigated conditions where the bulk of the world's rice is grown. At the International Rice Research Institute, rice

(cv. IR 72) was grown from germination until maturity for the 1994 wet and 1995 dry seasons at three different CO2 concentrations (ambient, ambient + 200, and ambient + 300 mu L L(-1) CO2) and two different air temperatures (ambient and ambient + 4 degrees C) using open-top field chambers. Averaged for both seasons, increases in CO2 concentration alone (+ 200, + 300 mu L L(-1)) resulted in a significant increase in total plant biomass (+ 31%, + 40%) and crop yield (+ 15%, + 27%) compared with the ambient control. The increase in crop yield was associated with an increase in the number of panicles per square meter and a greater percentage of filled spikelets. Simultaneous increases in CO2 and air temperature did not alter the biomass at maturity (relative to elevated CO2 alone), but plant development was accelerated at the higher growth temperature regardless of CO2 concentration. Grain yield, however, became insensitive to CO2 concentration at the higher growth temperature. Increasing both CO2 and air temperature also reduced grain quality (e.g., protein content). The combination of CO2 and temperature effects suggests that, in warmer regions (i.e., > 34 degrees C) where rice is grown, quantitative and qualitative changes in rice supply are possible if both CO2 and air temperature continue to increase.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, BIOMASS, ELEVATED CO2, ENRICHMENT, ORYZA-SATIVA, PHOTOSYNTHESIS

2706

Ziska, L.H., R.C. Sicher, and J.A. Bunce. 1999. The impact of elevated carbon dioxide on the growth and gas exchange of three C-4 species differing in CO2 leak rates. *Physiologia Plantarum 105(1):74-80.*

Recent work has suggested that the photosynthetic rate of certain C-4 species can be stimulated by increasing CO2 concentration, [CO2], even under optimal water and nutrients.To determine the basis for the observed photosynthetic stimulation, we tested the hypothesis that the CO2 leak rate from the bundle sheath would be directly related to any observed stimulation in single leaf photosynthesis at double the current [CO2]. Three C-4 species that differed in the reported degree of bundle sheath leakiness to CO2, Flaveria trinervia. Panicum miliaceum, and Panicum maximum, were grown for 31-38 days after sowing at a [CO2] of 350 mu l l(-1) (ambient) or 700 mu l l(-1) (elevated). Assimilation as a function of increasing [CO2] at high photosynthetic photon flux density (PPFD, 1 600 mu mol m(-2) s(-1)) indicated that leaf photosynthesis was not saturated under current ambient [CO2] for any of the three C-4 species. Assimilation as a function of increasing PPFD also indicated that the response of leaf photosynthesis to elevated [CO2] was light dependent for all three C-4 species, The stimulation of leaf photosynthesis at elevated [CO2] was not associated with previously published values of CO2 leak rates from the bundle sheath, changes in the ratio of activities of PEP-carboxylase to RuBP carboxylase/oxgenase, or any improvement in day time leaf water potential for the species tested in this experiment. In spite of the simulation of leaf photosynthesis, a significant increase in growth at elevated [CO2] was only observed for one species, F. trinervia. Results from this study indicate that leaf photosynthetic rates of certain C-4 species can respond directly to increased [CO2] under optimal growth conditions, but that the stimulation of whole plant growth at elevated carbon dioxide cannot be predicted solely on the response of individual leaves.

KEYWORDS: ATMOSPHERIC CO2, BUNDLE SHEATH-CELLS, CARBOXYLASE, ENRICHMENT, IRRADIANCE, LEAVES, NITROGEN, PHOTOSYNTHESIS, PLANTS, RESPONSES

2707

Ziska, L.H., R.C. Sicher, and D.F. Kremer. 1995. Reversibility of photosynthetic acclimation of Swiss chard and sugarbeet grown at elevated concentrations of CO2. *Physiologia Plantarum 95(3):355-364.*

Although leaf photosynthesis and plant growth are initially stimulated by elevated CO2 concentrations, increasing insensitivity to CO2 (acclimation) is a frequent occurrence. In order to examine the acclimation process, we studied photosynthesis and whole plant development in swiss chard (Beta vulgaris L. Koch ssp. ciela) and sugarbeet (Beta vulgaris L. ssp. vulgaris) grown at either ambient or twice ambient concentrations of CO2. In an initial controlled environment study, photosynthetic acclimation to elevated CO2 levels was observed in both subspecies 24 days after sowing (DAS) but was not observed at 42 and 49 DAS for sugarbeet or at 49 DAS for swiss chard. Although sugarbeet and swiss chard differed in root size and morphology, this was not a factor in the onset of photosynthetic acclimation. The reversal of photosynthetic acclimation that was observed in older plants grown at elevated CO2 concentrations was associated with a rapid increase in root development (i.e. increased root: shoot [R/S] ratio), increased sucrose levels in sinks (roots) and no differences in total soluble leaf protein of either subspecies relative to the ambient CO2 condition. In a second set of experiments, swiss chard and sugarbeet were grown in outdoor Plexiglass chambers at different times of the year (i.e. summer and early fall). Average 24-h temperature was 30.7 and 19.4 degrees C for the summer and fall plantings, respectively. In agreement with the controlled environment study, lack of photosynthetic acclimation, determined from the response of photosynthesic rate to internal CO2 concentration, was correlated with increased root biomass and sucrose concentration relative to the ambient condition. However, photosynthetic acclimation was observed depending on the season, i.e. summer (swiss chard) or fall (sugarbeet), suggesting that acclimation was affected by environmental factors, such as temperature. Data from both experiments suggest that continued long-term photosynthetic stimulation may be dependent upon the ability of increased CO2 to stimulate new sink development which would allow full utilization of the additional carbon made available in a high CO2 environment.

KEYWORDS: CARBON DIOXIDE, EXCHANGE, LEAVES, LIGHT, PLANTS, TEMPERATURE

2708

Ziska, L.H., J.R. Teasdale, and J.A. Bunce. 1999. Future atmospheric carbon dioxide may increase tolerance to glyphosate. *Weed Science 47(5):608-615.*

We tested whether the efficacy of chemical weed control might change as atmospheric CO2 concentration [CO2] increases by determining if tolerance to a widely used, phloem mobile, postemergence herbicide, glyphosate, was altered by a doubling of [CO2]. Tolerance was determined by following the growth of Amaranthus retroflexus L. (redroot. pigweed), a C-4 species, and Chenopodium album L. (common lambsquarters), a C-3 species, grown at near ambient (360 mu mol mol(-1)) and twice ambient (720 mu mol mol(-1)) [CO2] for 14 d following glyphosate application at rates of 0.00 (control), 0.112 kg ai ha(-1) (0.1 x the commercial rate), and 1.12 kg ai ha(-1) (1.0 x the commercial rare) in four separate trials. Irrespective of [CO2], growth of the C-4 species, A. retroflexus, was significantly reduced and was eliminated altogether at glyphosate application rates of 0.112 and 1.12 kg ai ha(-1), respectively. However, in contrast to the ambient [CO2] treatment, an application rate of 0.112 kg ai ha(-1) had no effect on growth, and a 1.12 kg ai ha(-1) rate reduced but did not eliminate growth in elevated [CO2]-grown C. album. Although glyphosate tolerance does increase with plant size at the time of application, differences in glyphosate tolerance between CO2 treatments in C. album cannot be explained by size alone. These data indicate that rising atmospheric [CO2] could increase glyphosate tolerance in a C-3 weedy species. Changes in herbicide tolerance at elevated [CO2] could limit chemical weed control efficacy and increase weed-crop competition.

KEYWORDS: C-3, CO2- ENRICHMENT, CROP, GROWTH-

STIMULATION, PLANTS, WEEDS

2709

Ziska, L.H., and A.H. Teramura. 1992. Co2 enhancement of growth and photosynthesis in rice (oryza- sativa) - modification by increased ultraviolet-b radiation. *Plant Physiology 99(2):473-481.*

Two cultivars of rice (Oryza sativa L.) IR-36 and Fujiyama-5 were grown at ambient (360 microbars) and elevated CO2 (660 microbars) from germination through reproduction in unshaded greenhouses at the Duke University Phytotron. Growth at elevated CO2 resulted in significant decreases in nighttime respiration and increases in photosynthesis, total biomass, and yield for both curtivars. However, in plants exposed to simultaneous increases in CO2 and ultraviolet-B (UV-B) radiation, CO2 enhancement effects on respiration, photosynthesis, and biomass were eliminated in IR-36 and significantly reduced in Fujiyama-5. UV-B radiation simulated a 25% depletion in stratospheric ozone at Durham, North Carolina. Analysis of the response of CO2 uptake to internal CO2 concentration at light saturation suggested that, for IR-36, the predominant limitation to photosynthesis with increased UV- B radiation was the capacity for regeneration of ribulose bisphosphate (RuBP), whereas for Fujiyama-5 the primary photosynthetic decrease appeared to be related to a decline in apparent carboxylation efficiency. Changes in the RuBP regeneration limitation in IR-36 were consistent with damage to the photochemical efficiency of photosystem II as estimated from the ratio of variable to maximum chlorophyll fluorescence. Little change in RuBP regeneration and photochemistry was evident in cultivar Fujiyama-5, however. The degree of sensitivity of photochemical reactions with increased UV-B radiation appeared to be related to leaf production of UV-B- absorbing compounds. Fujiyama-5 had a higher concentration of these compounds than IR-36 in all environments, and the production of these compounds in Fujiyama-5 was stimulated by UV-B fluence. Results from this study suggest that in rice alterations in growth or photosynthesis as a result of enhanced CO2 may be eliminated or reduced if UV-B radiation continues to increase.

KEYWORDS: C-3, CARBON DIOXIDE, ELEVATED CO2, INHIBITION, LEAVES, LONG-TERM EXPOSURE, PLANTS, RESPIRATION

2710

Ziska, L.H., and A.H. Teramura. 1992. Intraspecific variation in the response of rice (oryza-sativa) to increased co2 - photosynthetic, biomass and reproductive characteristics. *Physiologia Plantarum 84(2):269-276.*

Two rice (Oryza sativa L.) cultivars of contrasting morphologies, IR-36 and Fujiyama-5, were exposed to ambient (360-mu-l l-1) and ambient plus 300-mu-l l-1 CO2 from time of emergence until ca 50% grain fill at the Duke University Phytotron, Durham, North Carolina. Exposure to increased CO2 resulted in about a 50% increase in the photosynthetic rate for both cultivars and photosynthetic enhancement was still evident after 3 months of exposure to a high CO2 environment. The photosynthetic response at 5% CO2 and the response of CO2 assimilation (A) to internal CO2 (C(i)) suggest a reallocation of biochemical resources from RuBP carboxylation to RuBP regeneration. Increases in total plant biomass at elevated CO2 were approximately the same in both cultivars, although differences in allocation patterns were noted in root/shoot ratio. Differences in reproductive characteristics were also observed between cultivars at an elevated CO2 environment with a significant increase in harvest index for IR-36 but not for Fujiyama-5. Changes in carbon allocation in reproduction between these two cultivars suggest that lines of rice could be identified that would maximize reproductive output in a future high CO2 environment.

KEYWORDS: ACCLIMATION, ASSIMILATION, C-3 PLANTS, CARBON DIOXIDE, CARBOXYLASE, ELEVATED CO2, HIGH ATMOSPHERIC CO2, INHIBITION, LEAVES, WHEAT

2711

Ziska, L.H., W. Weerakoon, and L.W. Hong. 1995. Photosynthetic acclimation of field-grown rice to elevated co2. *Plant Physiology 108(2):92.*

2712

Ziska, L.H., W. Weerakoon, O.S. Namuco, and R. Pamplona. 1996. Influence of nitrogen on the elevated CO2 response in field- grown rice. *Australian Journal of Plant Physiology 23(1):45-52.*

Rice (Oryza sativa L. cv. IR72) was grown in the tropics at ambient (345 mu L L(-1)) or twice ambient (elevated, 700 mu L L(-1)) CO2 concentration at three levels of supplemental nitrogen (N) (no additional N (N-0), 90 kg ha(-1) (N-1) and 200 kg ha(-1) (N-2)) in open-top chambers under irrigated field conditions from seeding until flowering. The primary objective of the study was to determine if N supply alters the sensitivity of growth and photosynthesis of field-grown rice to enriched CO2. A second objective was to determine the influence of elevated CO2 on N uptake and tissue concentrations. Although photosynthesis was initially stimulated at the leaf and canopy level with elevated CO2 regardless of supplemental N supply, with time the photosynthetic response became highly dependent on the level of supplemental N, increasing proportionally as N availability increased. Similarly, a synergistic effect was noted between CO2 and N with respect to above-ground biomass with no effect of elevated CO2 observed for the N-0 treatment. Most of the increase in above-ground biomass with increasing CO2 and N was associated with increased tiller and, to a lesser extent, root production. The concentration of above-ground N decreased at elevated CO2 regardless of N treatment; however, total aboveground N did not change for the N-1 and N-2 treatments because of the greater amount of biomass associated with elevated CO2. For rice, the photosynthetic and growth response to elevated CO2 may be highly dependent on the supply of N. If additional CO2 is given and N is not available, lack of sinks for excess carbon (e.g. tillers) may limit the photosynthetic and growth response.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, CARBON DIOXIDE, ENRICHMENT, NUTRITION, PLANTS, SEEDLINGS, STRESS, WHEAT, YIELD

2713

Zobayed, S.M.A., F. Afreen-Zobayed, C. Kubota, and T. Kozai. 1999. Stomatal characteristics and leaf anatomy of potato plantlets cultured in vitro under photoautotrophic and photomixotrophic conditions. *In Vitro Cellular & Developmental Biology-Plant 35(3):183-188.*

Potato plantlets (Solanum tuberosum L. cv. Benimaru) were cultured under photoautotrophic (without an) sucrose in the nutrient medium and with enriched CO2 and high photosynthetic photon flux and photomixotrophic conditions (20 g l(-1) sucrose in the medium). Leaf anatomy and stomatal characteristics of the leaves were studied in relation to stomatal size and density. Leaf diffusive resistance, transpiration rater and was content of the leaves were also investigated. In the photoautotrophic treatment, stomata behaved normally LI closing in the dark and opening in the light. The stomatal density increased twofold compared to that of the photomixotrophic treatment. Relatively thick leaves and an organized palisade layer were observed and the epicuticular wax content was remarkably higher in this treatment. i.e., seven times greater than that of photomixotrophic treatment. In general,

higher diffusive resistance of the leaves was observed than under photomixotrophic conditions; also the resistance increased in darkness and decreased in the light. All these characteristics led the plantlets to have a normal and controlled transpiration rater which was exceptionally; high in the photomixotrophic treatment throughout the light and the dark period.