

ENVIRONMENTAL SCIENCES

Khulna University Studies 2(1): 79-90

CONSEQUENCES OF ELEVATED ATMOSPHERIC CO₂
AND RELATED PHENOMENA ON PLANT LIFE

Khaled Misbahuzzaman*

Forestry and Wood Technology Discipline, Khulna University, Khulna 9208, Bangladesh

Manuscript received: May 07, 2000; Accepted: July 27, 2000

Abstract: In this study, effects of elevated CO₂ and associated phenomena such as increased atmospheric temperatures and nutrient deposition have been discussed in terms of plant growth and regeneration, population and biodiversity issues. Elevated CO₂ may result in enhanced carbon sequestration to soil, though it is not clear if an increased soil carbon pool will contribute to higher plant productivity. However, there is evidence that an increased anthropogenic nitrogen deposition co-occurring with elevated CO₂ may act as a missing sink for the excessive carbon in the ecosystem and thereby contribute to enhanced plant productivity. Although elevated CO₂ may improve plant water use efficiency and reduce light compensation point for effective photosynthesis, associated effects of extreme temperatures may damage plant tissues, and consequently limit the survival of certain plant species in some regions. Rapid changes in climate may result in substantial tree mortality; as a consequence large expanses of forested regions may become increasingly dominated by early successional vegetation of small size which may suppress saplings of dominant canopy tree species. High resource availability associated with elevated CO₂ may cause a smaller number of individuals to proportionately dominate biomass and reproductive output within a population that may act to reduce effective population size in genetic terms. Thus plant biodiversity will be affected due to rising CO₂. However, speciation rates would be little affected due to shortness of the time scale.

Key words: elevated CO₂; plant productivity; photosynthesis; succession; ecosystem; biodiversity

Introduction

The occurrence of increased concentrations of CO₂ on earth generated from anthropogenic sources has been presumed to be the most important cause of global warming. There have been decades of high quality research on the impact of elevated CO₂ on plant physiology (Lemon, 1983; Strain and Cure, 1985; Rey *et al.*, 1997; Tjoelker *et al.*, 1998). This area has received high research priority, since of all the elements of global change, CO₂ increase has been the best documented and is of greatest concern (Mooney, 1996). The early results of a new network of CO₂ investigators sponsored by the Global Change and Terrestrial Ecosystem Programme (Steffen *et al.*, 1992) are common to all experiments, such as the increase of carbon to nitrogen ratios of plant tissues, the accumulation of carbohydrates and the differential responses of species within a community because of rising CO₂. Although the results accumulating from those

* Corresponding address: Tel.: 880-41-721791, 720171-3 Ext. 228; Fax: 880-41-731244, 731521; E-mail: <ku@bdonline.com>
DOI: <https://doi.org/10.53808/KUS.2000.2.1.79-90-Ls>

experiments have given much deeper understanding of the complex responses that can be anticipated in natural systems on our earth, much more work needs to be done (Mooney, 1996).

The ecological interest arose when it became apparent that atmospheric CO₂ levels are increasing at unprecedented speed and possibly will influence plant life all over the world. While it has been predicted with confidence that doubling ambient CO₂ levels under horticultural or agro-industrial conditions will facilitate CO₂-stimulated enhancements of seasonal yields by about one-third compared with controls (Cure, 1985), very little is known about CO₂ responses of non-agroecosystems such as forests (Körner, 1993). Forest trees form approximately 90% of the global biomass compared with 1% crop biomass (Körner, 1996). All whole-plant CO₂ enrichment experiments that have been conducted with forest tree species were, for practical reasons, done with seedlings, mostly grown in isolation and in highly disturbed or even horticultural substrates (Eamus and Jarvis, 1989). Therefore, results of experiments, if conducted on trees in the forests, are expected to vary. Once interspecific interaction and resource limitation of growth come into play (which are not uncommon in forests), CO₂ responses would not fit the patterns observed in agrosystems, making sound predictions for the future development of the biosphere impossible.

The present work is a critical review of current literature relevant to the possible effects of elevated CO₂ on performance of plant life on earth. Attempt has been made to discuss the important issues such as relationships between plant growth and ecosystem carbon pool, effects of extreme temperatures and nutrient deposition on plant growth, changes in landscape, and effects on plant population and biodiversity.

CO₂ Assimilation and Plant Growth

Plant growth is generally considered as a consequence of CO₂ assimilation through photosynthesis. However, growth at the level of an individual cannot be predicted from photosynthesis alone, simply because most of the other growth determinants (such as seed quality and seed germination, carbon investment in root exudation and mycorrhiza formation, plant maturation and senescence, competition for resources, nutrient recycling etc.) are quantitatively or even qualitatively unknown (Strain, 1987). In particular, phenological controls (such as floral initiation, fruiting etc.) are poorly understood, but they are of key importance for all other growth determinants (e. g. Coleman *et al.*, 1994). Growth requires resources other than CO₂ and their availability, and in particular, their pool size also cannot be expected to increase proportionally along with enhanced CO₂ (Körner, 1996). Therefore, the most common initial response of plants to CO₂ fertilization is overshooting of assimilate levels in leaves (mostly starch) reflecting limitations to export of these photosynthetic products from chloroplasts to the plant parts (Ehret and Joliffe, 1985; Körner *et al.*, 1995; Rey *et al.*, 1997). Although growth enhancement in tree seedlings grown under elevated CO₂ have been reported (Rey *et al.*, 1997; Staddon and Fitter, 1998), CO₂-induced net photosynthesis has been found to be greater for slower-growing species than for faster-growing species (Tjoelker *et al.*, 1998). Species-specific and environmental characteristics may therefore determine the long-term response to elevated CO₂.

It is assumed that elevated CO₂ will induce an increase of Leaf Area Index (LAI) (Leith *et al.*, 1986; Long and Drake, 1992; Tjoelker *et al.*, 1998). The basis for this assumption is the reduction of the light compensation point of photosynthesis under elevated CO₂ (Valle *et al.*, 1985; Wong and Dunin, 1987; Long and Drake, 1991). Leaves living under limiting light conditions can be expected to profit relatively more from CO₂ enrichment, although the absolute carbon gain may still be small. However, when mineral nutrient availability is limiting growth which may be the case even in moderately fertile soils, it appears that plants in dense communities could respond in a different way (Körner, 1996). Despite improved carbon balance in their shaded leaves, the nitrogen trapped in these leaves could be invested much more efficiently in the fully sunlit crown, where the relative stimulation by CO₂ enrichment may be smaller but the absolute carbon gain due to elevated CO₂ is much greater. However, this does not apply to understory plants which are bound to the lowest canopy level (Körner, 1996).

Plants grown under elevated CO₂ have almost always been found to produce tissues that contain more carbon and less nitrogen, even when subtracting starch accumulation (e. g. DeLucia *et al.*, 1985; Curtis *et al.*, 1989; Wong, 1990; Körner and Miglietta, 1994). It has been assumed that this CO₂ induced increase in C/N ratio (and possibly increased lignin content) will lead to reduced rates of decomposition, and thereby facilitate increased carbon sequestration to soils (Van Veen *et al.*, 1991). There is another pathway by which CO₂ fertilization may influence the soil environment namely through priming effects of increased rates of turnover in fine roots and exudation of low molecular weight organic compounds (sugars, amino acids) to the rhizosphere (Zak *et al.*, 1993). This may enhance microbial activity that could result in increased rates of litter decomposition leading to decreasing soil carbon pool. These two avenues of carbon into the soil may have quite contrasting effects on the soil carbon pool, and currently it is still uncertain in which direction soil carbon pool actually will work (Körner, 1996).

Relationship of Plant Growth Rate and Ecosystem Carbon Pool

Plant growth stimulation is almost always seen as a self-evident indicator of enhanced carbon sequestering, which is not true (Prentice, 1993). The carbon pool of an ecosystem is not correlated with its growth rate, as can be seen when old growth and early successional forests are compared (Körner, 1996). Despite a limited carbon pool, the speed of carbon cycling in early successional forests is higher compared to old growth forests which is why they grow faster, mature earlier and also die earlier. However, the mean residence time of carbon in the ecosystem is of greater importance than the speed of carbon cycling through the system to contain excessive carbon in a CO₂-enriched environment (Körner, 1996). In forests, which form the only significant biomass carbon pool of the biosphere, the speed of closure and reopening of gaps, to large extent, determine the carbon pool per unit area (Körner, 1996). There is no evidence that the carbon residence in biomass is likely to increase in a CO₂-enriched world (Körner, 1996). Rather the reverse may be true, an idea which found recent support in the observation that tree turnover in tropical forests has been increased significantly in recent decades (Phillips and Gentry, 1994).

Animals and microbes may strongly interfere with CO₂ effects on plant growth, ecosystem dynamics and the ultimate carbon pool size per unit land area. Compensatory

feeding on CO₂ grown food (high C/N ratio) has been demonstrated (reviewed by Lincoln *et al.*, 1993), but in nature herbivores may exhibit alternative feeding and select the remaining best food rather than feed more on the protein depleted food. There is evidence that elevated CO₂ may increase the extent of colonisation by mycorrhizal fungi through allocation of more carbohydrates in roots (Lovelock *et al.*, 1996; Rey *et al.*, 1997; Staddon and Fitter, 1998). However, mycorrhizae in a CO₂-enriched environment may behave symbiotically or parasitically depending on species-specific effects (Sanders, 1996).

Approximately 6.0 Pg of carbon per year are emitted into the atmosphere due to fossil fuel combustion, cement manufacturing and deforestation (Houghton *et al.*, 1990; Watson *et al.*, 1990). As a result, the concentration of CO₂ in the atmosphere has increased from preindustrial levels of 280 ppm to the current level approaching 360 ppm. Elevated CO₂ has a dual role in affecting global vegetation pattern, CO₂ and other green house gases may alter climate sufficiently such that climate zones may shift northward as well as higher in elevation, altering vegetation distributions considerably (e. g., Davis, 1989; Eamus and Jarvis, 1989; Peters, 1991; Davis and Zabinski, 1992). CO₂ also has direct, species-specific effects on the growth and physiology of plants, and these direct effects have the potential to alter plant community structure and ecosystem function (Arp *et al.*, 1993). At a biochemical level, CO₂ is the principal substrate of the most abundant enzyme on the planet (Rubisco, e. g., Bowes, 1991). At an ecological level, CO₂ is a widely used plant resource (Bazzaz and McConnaughay, 1992). At a global geophysical level, CO₂ is a primary link between vegetation and climate (Tans *et al.*, 1990; Houghton, 1991).

Elevated CO₂ and Effects of Extreme Temperatures

Limited data from studies with herbaceous species suggest that the combined effect of CO₂ and temperature are not necessarily additive and are, therefore, difficult to predict from knowledge of their individual effects (Idso *et al.*, 1987; Idso and Kimball, 1989; Long, 1991; Eamus, 1991; Farrar and Williams, 1991; Hogan *et al.*, 1991). Increased atmospheric temperatures are assumed to induce increased respiratory rates by organisms (Ryan, 1991; Bonan and Sirois, 1992) and thereby could mitigate CO₂ effects on photosynthesis. To make any anticipatory statement regarding the vegetation response to climate warming, one must consider the species-specific effects of temperature in combination with elevated CO₂ (Bazzaz *et al.*, 1996).

Both CO₂ and temperature are known to affect plant carbon gain independently by altering processes at many levels of plant organization. Such processes include photosynthesis and respiration (Bowes, 1991; Long, 1991), leaf energy budgets and water use deficiencies (Eamus, 1991), carbon and nutrient allocation (Hogan *et al.*, 1991; Farrar and Williams, 1991; Coleman and Bazzaz, 1992) and leaf area production, phenology and architecture (Ford, 1982; Ackerly *et al.*, 1992). Elevated CO₂ leads to higher leaf level water use efficiency via decreases in stomatal conductance (Lemon, 1983) and transpiration rate, and also via an increase in net photosynthesis (Norby and O'Neill, 1989; Eamus, 1991). In contrast, high temperatures may decrease water use efficiency due to greater vapour pressure deficits, and the increased need for transpirational cooling

of warmer leaves (Jones, 1992). Therefore, it is possible that the magnitudes of CO₂ enhancements of water use efficiency may decrease with increasing temperature.

On the other hand, extreme temperatures may damage plant tissues, and consequently limit the survival of certain plant species in some regions. The implication of extreme temperature events are highly species-specific (Coleman *et al.*, 1991; Pastor, 1993). Elevated concentrations of CO₂ in the atmosphere alter plant allocation, physiology, and growth, which may accentuate or ameliorate the damage from extreme temperatures. Growth in high CO₂ atmosphere tends to lower foliar conductance rates which may cause higher leaf temperatures (Idso *et al.*, 1987), leading to more damage during an extremely hot period. However, elevated CO₂ concentration may reduce the leaf area ratio (Bazzaz, 1990), thereby reducing the ratio of transpiring leaf area to water-acquiring roots, which may improve the plant's ability to cool under some conditions. The response of vegetation to rising CO₂ levels and temperature may not be simply predicted from the response of the plants to one or the other factor (Bazzaz, 1990). Rather, complex interactions make it necessary to consider these combinations of factors simultaneously in order to make coherent statements about the effects of climate change on vegetation.

Nitrogen Deposition and Feedbacks on the Carbon Cycle

Increases in the supply of nutrients (especially nitrogen) can lead to increased growth enhancements of trees with elevated CO₂ (Brown and Higginbotham, 1986; Johnson *et al.*, 1992; Wong *et al.*, 1992). Thus it is possible that increasing atmospheric CO₂ concentrations may feedback positively with regionally enhanced nitrogen supply rates from high levels of nitrogen deposition (through industrial combustion of fossil fuels, acid rain in temperate climates, atmospheric aerosol and particle deposition) so that both the carbon and nitrogen sink strengths of forest is enhanced. It has been suggested that this anthropogenic nitrogen fertilization may actually constitute a large portion of the missing sink for carbon (Hudson *et al.*, 1994). Preliminary evidence demonstrates that temperate deciduous forest tree seedlings of different species show differential pattern of growth enhancements under elevated CO₂ with different nutrient supply rates (Bazzaz and Miao, 1993). This differential growth behaviour under elevated CO₂ may therefore alter species' competitive abilities during regeneration and thus affect future forest composition (Bazzaz *et al.*, 1996).

The single largest pool of terrestrial carbon is in the soils. There is evidence that elevated CO₂ does not result in higher rates of root exudation per unit mass of root (Norby *et al.*, 1987). Rather, total root mass increases under elevated CO₂ and thus substantially more carbon is transported into the soil (Norby *et al.*, 1992; Zak *et al.*, 1993). Increases in the total amount of carbon input into the soil may in turn increase the amount of carbon retained in the soil due to preferential metabolism of readily decomposable (N-rich) material by microbes (Lekkerkerk *et al.*, 1990). Decreases in the decomposability of tissue due to increased C/N ratios in plants exposed to elevated CO₂ (Lovelock *et al.*, 1998; Gahrooe, 1998) may also play a role in increasing soil carbon retention (Strain and Bazzaz, 1983). Therefore, N sink strength in carbon rich soil increases which may be favorable for plant growth through anthropogenic N deposition. For example, it has been observed that the elevated CO₂ may ameliorate nitrogen saturation in forests of the

dominant deciduous tree species in the Harvard Forest when exposed to high chronic nitrogen deposition (Bazzaz and Miao, 1993).

Changing Landscape: Importance of Forest Regeneration

Changes in the global temperature and precipitation patterns due to elevated CO₂ may result in significant alterations in species distributions and community composition (Solomon, 1986; Davis and Zabinski, 1992). If the climate changes very rapidly there may be land areas with substantial tree mortality (Bazzaz *et al.*, 1996). In such a situation, regeneration will become increasingly important and large expanses of forested regions may become increasingly dominated by early successional vegetation. The CO₂ responsiveness of early growth has been found to be very large in a number of early successional species in Eastern deciduous forest communities including striped maple (*Acer pensylvanicum*) and grey birch (*Betula populifolia*) (Rochefort and Bazzaz, 1992; Bazzaz and Miao, 1993). These species do not attain large sizes, but often are important in suppressing the growth of seedlings and saplings of dominant canopy tree species (Burns and Honkala, 1990). In the evergreen forests of western North America, a similar differential enhancement in growth has been observed in the earlier successional red alder (*Alnus rubra*) (Arnone and Gordon, 1990) relative to the later successional Douglas fir (*Pseudotsuga menziesii*) (Hollinger, 1987). Enhanced regeneration of early successional species under elevated CO₂ could thus constitute the important negative feedback on the regeneration of these forests to a mature phase system (El Kohen *et al.*, 1993).

Effects of Elevated CO₂ on Plant Populations

For forest trees, the maximal life spans are commonly 100+ years; however, generation times are often of the order of 10-60 years (Harper and White, 1974). One implication of multi-generational time scales is that CO₂ must be considered in the context of all phases of a plant's life cycle, including seed germination, seedling establishment, plant growth, reproductive onset, flowering, ovule fertilization, seed and fruit development, and seed dispersal. A second implication is that long-term responses to elevated CO₂ may be determined not only by individual or canopy-level physiology, but by population level phenomena such as altered density-dependent reproduction (Bazzaz *et al.*, 1992) or accelerated plant senescence (St Omer and Horvath, 1983).

It has been clear for some time that elevated CO₂ atmospheres may alter reproduction in a fashion that is distinct from effects on vegetative growth and development. In some species, elevated CO₂ accelerates floral initiation (Hovland and Dybing, 1973; Enoch *et al.*, 1976), while in many other species a significant delay has been documented (Hesketh and Hellmers, 1973; Marc and Gifford, 1984). In some cases, either response may occur, depending on growth conditions (Reekie and Bazzaz, 1991). Other reported effects of CO₂ on reproduction development include altered sex expression (Imazu *et al.*, 1967) and diminished self-incompatibility (Palloix *et al.*, 1985).

The effects of increasing CO₂ on plant populations may be predictable in terms of general theory regarding population level responses to increasing resources (Bazzaz and McConnaughay, 1992). High resource levels have generally been found to accelerate the process of size hierarchy formation in plant populations such that a smaller number of

individuals come to proportionately dominate biomass and reproductive output within the population (Weiner and Thomas, 1986). Elevated CO₂ may also act to reduce effective population size in genetic terms (Heywood, 1986). Also population fluctuations may be exaggerated by elevated CO₂, increasing the likelihood of local population extinction.

There is a growing body of evidence for genetic variation in CO₂ responses within natural plant populations (Curtis *et al.*, 1994). In addition to genotype-specific effects, CO₂ might also affect selection rates by altering fecundity distributions within plant populations (Thomas and Bazzaz, 1993). If elevated CO₂ generally increases variability in reproductive output, this could operate to greatly accelerate the selection process.

Elevated CO₂, Biodiversity and Conservation Issues

The impacts of potential global warming on biodiversity have received considerable attention from researchers and conservationists (e.g. Peter and Lovejoy, 1992). In contrast, very little emphasis has been placed on potential direct effects of elevated CO₂ on biodiversity issues until very recently (Bazzaz *et al.*, 1996). It has been argued that some aspects of the direct effects of CO₂ on vegetation (particularly increased water use efficiency) may work to enhance biodiversity in natural systems (Woodward and Rochefort, 1991; Rochefort and Woodward, 1992). The logic behind the prediction is that elevated CO₂ may enhance water use efficiency, permitting the development of vegetation with a higher LAI. Across biomass, it is often the case that high LAI systems have a higher local diversity of plant species or higher taxonomic groups. Thus, for example, enhanced water use efficiency might favor rain forest over savanna vegetation, resulting in locally increased plant diversity (Bazzaz *et al.*, 1996). However, at a regional scale, existing rain forest species would displace existing savanna species, thus leading to a net loss in species diversity. In this scenario, extinction rates may well be enhanced by rising CO₂, while speciation rates would be little affected due to shortness of the time scale of interest (50-200 yrs) (Bazzaz *et al.*, 1996).

In many analyses of potential effects of rising CO₂ on biodiversity, it seems essential that CO₂ generally enhances the growth of individual plants, and that this growth enhancement is highly species-dependent. CO₂ fertilization of ecosystems will thus enhance the performance of responsive species in the system, probably at the expense of less responsive species (Bazzaz *et al.*, 1996). There is some evidence to suggest that growth responses to CO₂ are largest in species with high intrinsic growth rates early in ontogeny (Poorter, 1993); a characteristic common among early successional species (Bazzaz, 1979; EL Kohen *et al.*, 1993). Early successional species are also in many cases more tolerant of a broad range of environmental conditions (Bazzaz, 1987). In sum, CO₂ fertilization seems likely to accelerate plant competition for other resources, and in many systems relatively early successional species may be differentially favored. Such a pattern could contribute to a loss of biodiversity in many systems.

Conclusion

Elevated CO₂ may result in enhanced carbon sequestration to soil. However, it is not clear if an increased soil carbon pool will contribute to higher plant productivity. While the

effects of elevated CO₂ on plant water use efficiency and light compensation point in leaves are positive for effective photosynthesis, associated effects of extreme temperatures may damage plant tissues, and consequently limit the survival of certain plant species in some regions. However, an increased anthropogenic nitrogen deposition co-occurring with elevated CO₂ may constitute a large portion of the missing sink for carbon in the ecosystem thereby contribute to enhanced plant productivity. Although this may result in differential pattern of growth responses in different species, their competitive abilities during regeneration may be affected which would, therefore, affect future forest composition. Rapid changes in climate may result in substantial tree mortality as a consequence of which large expanses of forested regions may become increasingly dominated by early successional vegetation. These species will be of small size and may suppress saplings of dominant canopy tree species. High resource availability associated with elevated CO₂ may cause a smaller number of individuals to proportionately dominate biomass and reproductive output within a population that may act to reduce effective population size in genetic terms. Thus plant biodiversity will be affected due to rising CO₂. However, speciation rates would be little affected due to shortness of the time scale.

References

- Ackerly, D.D., Coleman, J.S., Morse, S.R. and Bazzaz, F.A., 1992. CO₂ and temperature effects on leaf area production in two annual plant species. *Ecology*, 73: 1260-1269.
- Arnone, J.A.I. and Gordon, J.C., 1990. Effect of nodulation, nitrogen fixation and carbon dioxide enrichment on the physiology, growth and dry mass allocation of seedlings of *Alnus rubra* Bong. *New Phytologist*, 116: 55-66.
- Arp, W.J., Drake, B.G., Pockman, W.T., Curtis, P.S. and Whigham, D.F., 1993. Interactions between C₃ and C₄ salt marsh species during four years of exposure to elevated atmospheric CO₂. *Vegetatio*, 104/105: 133-143.
- Bazzaz, F.A. and McConnaughay, K.D.M., 1992. Plant-plant interactions in elevated CO₂ environments. *Australian Journal of Botany*, 40: 547-563.
- Bazzaz, F.A. and Miao, S.L., 1993. Successional status, seed size, and response of tree seedlings to CO₂ light and nutrients. *Ecology*, 74: 104-112.
- Bazzaz, F.A., 1979. The physiological ecology of plant succession. *Annual Review of Ecology and Systematics*, 10: 351-371.
- Bazzaz, F.A., 1987. Experimental studies on the evolution niche in successional plant populations: a synthesis. In: A.J. Gray, M.J. Crawley and P.J. Edwards (eds.), *Colonisation, Succession and Stability*, British Ecological Society Symposium, Vol. 26, pp. 245-272.
- Bazzaz, F.A., 1990. The response of natural ecosystems to the rising global CO₂ levels. *Annual Review of Ecology and Systematics*, 21: 167-196.
- Bazzaz, F.A., Ackerly, D.D., Woodward, F.I. and Rochefort, L., 1992. Growth responses of seven major co-occurring tree species of the northeastern United States to elevated CO₂. *Canadian Journal of Forest Research*, 20: 1479-1484.
- Bazzaz, F.A., Bassow, S.L., Bernston, G.M. and Thomas, S.C., 1996. Elevated CO₂ and terrestrial vegetation for and beyond the global carbon budget. In: B. Walker and W. Steffen (eds.), *Global Change and Terrestrial Ecosystems*, Cambridge University Press, pp. 43-76.

- Bonan, G.B. and Sirois, L., 1992. Air temperature, tree growth, and the northern and southern range limits to *Picea mariana*. *Journal of Vegetation Science*, 3: 495-506.
- Bowes, G., 1991. Growth at elevated CO₂: photosynthetic responses mediated through Rubisco. *Plant, Cell and Environment*, 14: 795-806.
- Brown, K and Higginbotham, K.O., 1986. Effects of carbon dioxide enrichment and nitrogen supply on growth of boreal tree seedlings. *Tree Physiology*, 2: 223-232.
- Burns, R.M. and Honkala, B.H., 1990. *Silvics of North American Trees, Vol. 2*. US Department of Agriculture, Washington DC.
- Coleman, J.S. and Bazzaz, F.A., 1992. Effects of CO₂ and temperature on growth and resource use of co-occurring C₃ and C₄ annuals. *Ecology*, 73: 1244-1259.
- Coleman, J.S., McConnaughay, K.D.M. and Ackerly, D.D., 1994. Interpreting phenotypic variation in plants. *Tree*, 9: 187-191.
- Coleman, J.S., Rochefort, L., Bazzaz, F.A. and Woodward, F.I., 1991. Atmospheric CO₂, plant nitrogen status and the susceptibility of plants to an acute increase in temperature. *Plant, Cell and Environment*, 14: 667-674.
- Cure, J.D., 1985. Carbon dioxide doubling responses: a crop survey. In: B.R. Strain and J.D. Cure (eds.), *Direct Effects of Increasing Carbon Dioxide on Vegetation*, US Department of Energy, Washington DC, pp. 99-116.
- Curtis, P.S., Drake, B.G., Leadley, P.W., Arp, W.J and Whigham, D.F., 1989. Growth and senescence in plant communities exposed to elevated CO₂ concentrations on an estuarine marsh. *Oecologia*, 78: 20-26.
- Curtis, P.S., Snow, A.A. and Miller, A.S., 1994. Genotype-specific effects of elevated on fecundity in wild radish (*Raphanus raphanistrum*). *Oecologia*, 97: 100-105.
- Davis, M.B. and Zabinski, C., 1992. *Changes in Geographical Range Resulting from Greenhouse Warming: Effects on Biodiversity in Forests*. Yale University Press, New Haven.
- Davis, M.B., 1989. Insights from paleoecology on global change. *Ecological Society of America Bulletin*, 70: 222-228.
- DeLucia, E.H., Sasek, T.W., and Strain, B.R., 1985. Photosynthetic inhibition after long-term exposure to elevated leaves of atmospheric carbon dioxide. *Photosynthesis Research*, 7: 175-184.
- Eamus, D. and Jarvis, P.G., 1989. The direct effects of increase in the global atmospheric CO₂ concentration on natural and commercial temperate trees and forests. *Advances in Ecological Research*, 19: 1-55.
- Eamus, D., 1991. The interaction of rising CO₂ and temperature with water use efficiency. *Plant, Cell and Environment*, 14: 843-852.
- Ehret, D.L. and Joliffe, P.A., 1985. Photosynthetic carbon dioxide exchange of bean plants grown at elevated carbon dioxide concentrations. *Canadian Journal of Botany*, 63: 2026-2030.
- El Kohen, A., Venet, L., and Mousseau, M., 1993. Growth and photosynthesis of two deciduous forest species at elevated carbon dioxide. *Functional Ecology*, 7: 480-486.
- Enoch, H.Z., Rylski, I. and Spiegelman, M. 1976. Enrichment of strawberry and cucumber plants grown in unheated greenhouse in Israel. *Scientific Horticulture*, 5: 33-41.
- Farrar, J.F. and Williams, M.L., 1991. The effects of increased atmospheric carbon dioxide and temperature on carbon partitioning, source-sink relations and respiration. *Plant, Cell and Environment*, 14: 819-830.
- Ford, H., 1982. Leaf demography and the plastochron index. *Biological Journal of the Linnean Society*, 17: 361-373.
- Gahrooe, F.R. 1998. Impacts of elevated atmospheric on litter quality, litter decomposability and nitrogen turnover rate of two oak species in a Mediterranean forest ecosystem. *Global Change Biology*, 4: 667-677.

- Harper, J.L. and White, J., 1974. The demography of plants. *Annual Review of Ecology and Systematics*, 5: 419-463.
- Hesketh and Hellmers, H., 1973. Floral initiation in four plant species growing in CO₂ enriched air. *Environmental Control in Biology*, 11: 51-53.
- Heywood, J.S., 1986. The effect of plant size variation on genetic drift in populations of annuals. *American Naturalist*, 127: 851-861.
- Hogan, S.P., Smith, A.P. and Ziska, L.H., 1991. Potential effects of elevated CO₂ and changes in temperature on tropical plants. *Plant, Cell and Environment*, 14: 763-778.
- Hollinger, D.Y., 1987. Gas exchange and dry matter allocation responses to elevation of atmospheric CO₂ concentrations in seedlings of three tree species. *Tree Physiology*, 3: 193-202.
- Houghton, J.T., 1991. The role of forests in affecting the greenhouse gas composition of the atmosphere. In: R.L. Wyman (ed.), *Global Climate Change and Life on Earth*, Chapman and Hall, New York, pp. 43-56.
- Houghton, J.T., Jenkins, J.G. and Ephraums, J.J., 1990. *Climate Change: The IPCC Scientific Assessment* Cambridge University Press, Cambridge.
- Hovland, A.S. and Dybing, C.D., 1973. Cyclic flowering patterns in flax as influenced by environment and plant growth regulators. *Crop Science*, 13: 380-384.
- Hudson, R.J.M., Gherini, S.A., and Goldstein, R.A., 1994. Modeling the global carbon cycle: Nitrogen fertilization of the terrestrial biosphere and the missing CO₂ sink. *Global Biochemical Cycles*, 8: 307-333.
- Idso, S.B. and Kimball, B.A., 1989. Growth responses of carrot and radish to atmospheric CO₂ enrichment. *Environmental and Experimental Botany*, 29: 135-139.
- Idso, S.B., Kimball, B.A. and Mauney, J.R., 1987. Atmospheric carbon dioxide enrichment effects on cotton midday foliage temperature: implications for plant water use and crop yield. *Agronomy Journal*, 79: 667-672.
- Imazu, T., Yabuki, K. and Oda, Y., 1967. Studies on the influence of carbon dioxide concentration on the growth, flowering and fruit setting of eggplant (*Solanum melongena* L.). *Journal of Japanese Society for Horticultural Science*, 36: 222-227.
- Johnson, D.W., Ball, J.T., and Walker, R.F., 1992. Effects of CO₂, nitrogen, and phosphorus on *Ponderosa* pine seedlings. II. Nutrient uptake and soil interactions. *Bulletin of the Society of America*, 73: 224.
- Jones, H.G., 1992. *Plants and Microclimate- A Quantitative Approach to Environmental Plant Physiology*. 2nd Edition, Cambridge University Press, Cambridge.
- Körner, Ch., 1993. Fertilization: the great uncertainty in future vegetation development. In: A.M. Solomon and H.H. Shugart (eds.), *Vegetation Dynamics and Global Change*, Chapman and Hall, New York, pp. 53-70.
- Körner, Ch., 1996. The response of complex multispecies systems to elevated CO₂. In: B. Walker and W. Steffen (eds.), *Global Change and Terrestrial Ecosystems*, Cambridge University Press, Cambridge, pp. 20-42.
- Körner, Ch., and Miglietta, F., 1994. Long-term effects of naturally elevated CO₂ on Mediterranean grasslands and forest trees. *Oecologia*, 99: 343-351.
- Körner, Ch., Pelaez-Riedl, S. and van Bel, A.J.E., 1995. CO₂ responsiveness of plants: a possible link to phloem loading. *Plant, Cell and Environment*, 18: 595-600.
- Leith, J.H., Reynolds, J.F. and Rogers, H.H., 1986. Estimation of leaf area of soybeans grown under elevated carbon dioxide levels. *Field Crops Research*, 13: 193-203.
- Lekkerkerk, L.J.A., Van de Geijn, S.C. and van Veen, J.A., 1990. *Effects of Elevated CO₂ Atmospheric Levels on the Carbon Economy of a Soil Planted with Wheat*. John Wiley & Sons, New York.

- Lemon, E.R., 1983. *CO₂ and Plants- the Response of Plants to Rising Levels of Atmospheric Carbon Dioxide*. Westview Press, Boulder.
- Lincoln, D.E., Fajer, E.D. and Johnson, R.H., 1993. Plant-insect herbivore interactions in elevated CO₂ environments. *Tree*, 8: 64-84.
- Long, S.P. and Drake, B.G., 1991. Effect of the long-term elevation of CO₂ concentration in the field on the quantum yield of photosynthesis of C₃ sedge, *Scirpus olneyi*. *Plant Physiology*, 96: 221-226.
- Long, S.P. and Drake, B.G., 1992. Photosynthetic CO₂ assimilation and rising atmospheric CO₂ concentrations. In: N.R. Baker and H. Thomas (eds.), *Crop Photosynthesis: Spatial and Temporal Determinants*, Elsevier, Amsterdam, pp. 69-109.
- Long, S.P., 1991. Modification of the response of photosynthetic productivity to rising temperature atmospheric CO₂ concentrations: has its importance been understood. *Plant Cell and Environment*, 14: 729-739.
- Lovelock, C.E., Kyllö, D and Winter, K., 1996. Growth responses to vesicular arbuscular mycorrhizal inoculation and elevated CO₂ in seedlings of a tropical tree, *Belischemedia pendula*. *Functional Ecology*, 10: 662-667.
- Lovelock, C.E., Winter, K., Marsits, R., and Popp, M., 1998. Responses of communities of tropical tree species to elevated CO₂ in a forest clearing, *Oecologia*, 116: 207-218.
- Marc, J. and Gifford, R.M., 1984. Floral initiation in wheat, sunflower, and sorghum under carbon dioxide enrichment. *Canadian Journal of Botany*, 62: 9-14.
- Mooney, H.A., 1996. Ecosystem physiology: overview and synthesis. In: B. Walker and W. Steffen (eds.), *Global Change and Terrestrial Ecosystems*, Cambridge University Press, Cambridge, pp. 13-19.
- Norby, R.J. and O'Neill, E.G., 1989. Growth dynamics and water use of seedlings of *Quercus alba* L. in CO₂-enriched atmospheres. *New Phytology*, 111: 491-500.
- Norby, R.J. and O'Neill, E.G., Hood, W.G., and Luxmoore, R.J., 1987. Carbon allocation, root exudation and mycorrhizal colonization of *Pinus echinata* seedlings grown under elevated CO₂ enrichment. *Tree Physiology*, 3: 203-210.
- Norby, R.J., Gunderson, C.A., Wullschlegel, S.D., O'Neill, E.G. and McCracken, M.K., 1992. Productivity and compensatory responses of yellow-poplar trees in elevated CO₂. *Nature*, 357: 322-324.
- Palloix, A., Herve, Y., Knox, R.B. and Dumas, C., 1985. Effect of carbon dioxide and relative humidity on self-incompatibility in cauliflower, *Brassica oleracea*. *Theoretical and Applied Genetics*, 70: 628-633.
- Pastor, J., 1993. Northward march of spruce. *Nature*, 361: 208-209.
- Peters, R.H., 1991. *A Critique for Ecology*. Cambridge University Press, Cambridge.
- Peters, R.L. and Lovejoy, T.E., 1992. *Global Warming and Biological Diversity*. Yale University Press, New Haven, USA.
- Phillips, O.L. and Gentry, A.H., 1994. Increasing turnover through time in tropical forests. *Science*, 263: 954-958.
- Poorter, H., 1993. Interspecific variation in the growth response of plants to an elevated ambient CO₂ concentration. *Vegetatio*, 104/105: 77-79.
- Prentice, I.C., 1993. Process and production. *Nature*, 363: 209-210.
- Reekie, E.G. and Bazzaz, F.A., 1991. Phenology and growth in four annual species grown in ambient and elevated CO₂. *Canadian Journal of Botany*, 69: 2475-2481.
- Rey, A., Jarvis, P.G. and Proctor, J., 1997. An overview of long-term effects of elevated atmospheric CO₂ concentration on the growth and physiology of birch (*Betula pendula* Roth.).
- Rocheffort, L and Bazzaz, F.A., 1992. Growth response to elevated CO₂ in seedlings of four co-occurring birch species. *Canadian Journal of Forest Science*, 22: 1583-1587.

- Rocheffort, L and Woodward, F.I., 1992. Effects of climate change and a doubling of CO₂ on vegetation diversity. *Journal of Experimental Botany*, 43: 1169-1180.
- Ryan, M.G., 1991. Effects of climate change on plant respiration. *Ecological Applications*, 1: 157-167.
- Sanders, I.R., 1996. Plant-fungal interactions in CO₂-rich world. In: C. Körner and F.A. Bazzaz (eds.), *Carbon Dioxide Populations and Communities*, San Diego Academic Press, California.
- Solomon, A.M., 1986. Transient response of forests to CO₂-induced climate change: simulation modelling experiments in eastern North America. *Oecologia*, 68: 567-579.
- St Omer, L. and Horvath, S., 1983. Elevated carbon dioxide concentrations and whole plant senescence. *Ecology*, 64: 1311-1314.
- Staddon, P.L. and Fitter, A.H., 1999. Does elevated atmospheric carbon dioxide affect arbuscular mycorrhizas? *Trends in Ecology and Evolution*, 13: 455-458.
- Steffen, W.L., Walker, B.H., Ingram, J.S.I. and Koch, G.W., 1992. *Global Change and Terrestrial Ecosystems. The Operational Plan (21)*, The International Geosphere-Biosphere Programme, Stockholm.
- Strain, B.R. and Bazzaz, F.A., 1983. Terrestrial Plant Communities. In: E.R. Lemon (ed.), *The Response of Plants to Rising Levels of Atmospheric Carbon Dioxide*, Washington DC, pp. 177-222.
- Strain, B.R. and Cure, J.D., 1985. *Direct Effects of Increasing CO₂ on Vegetation*. US Department of Energy, Washington DC.
- Strain, B.R., 1987. Direct Effects of Increasing atmospheric CO₂ on plants and ecosystems. *Tree*, 2: 18-21.
- Tans, P.P. Fung, I.Y. and Takahashi, T., 1990. Observational constraints on the global atmospheric CO₂ budget. *Science*, 247: 1431-1438.
- Thomas, S.C. and Bazzaz, F.A., 1993. The genetic component in plant size hierarchies: norms of reaction to density in a *Polygonum* species. *Ecological Monographs* 63: 231-250.
- Tjoelker, M.G., Oleksyn, J. and Reich, P.B., 1998. Seedlings of five boreal tree species differ in acclimation of net photosynthesis to elevated CO₂ and temperature. *Tree Physiology*, 18: 715-726.
- Valle, R., Mishoe, J.W., Campbell, W.J., Jones, J.W. and Allen, L.H.Jr., 1985. Photosynthetic responses of bragg soybean leaves adapted to different CO₂ environments. *Crop Science*, 25: 333-339.
- Van Veen, J.A., Liljeroth, E., Lekkerkerk, L.J.A. and Van de Geijn, S.C., 1991. Carbon fluxes in plant-soil systems at elevated atmospheric CO₂ levels. *Ecological Applications*, 12: 175-181.
- Watson, R.T., Rodhe, H., Oeschger, H. and Siegenthaler, U., 1990. Greenhouse gases and aerosols. In: J. Houghton *et al.* (eds.), *Climate Change-The IPCC Scientific Assessment Cambridge*, Cambridge University Press, Cambridge.
- Weiner, J. and Thomas, S.C., 1986. Size variability and competition in plant monocultures. *Oikos*, 47: 211-222.
- Wong, S.C. and Dunin, F.X., 1987. Photosynthesis and transpiration of trees in a eucalypt forest stand: CO₂ light and humidity responses. *Australian Journal of Plant Physiology*, 14: 619-632.
- Wong, S.C., 1990. Elevated atmospheric partial pressure of CO₂ and plant growth. II. Non-structural carbohydrate content in cotton plants and its effects on growth parameters. *Photosynthesis Research*, 23: 171-180.
- Wong, S.C., Kreidermann, P.E. and Farquhar, G.D., 1992. CO₂ x nitrogen interactions on seedling growth of four species of eucalypt. *Australian Journal of Botany*, 40: 457-472.
- Woodward, F.I. and Rocheffort, L., 1991. Sensitivity analysis of vegetation diversity to environmental change. *Global Ecology and Biodiversity Letters*, 1: 7-23.
- Zak, D.R., Pregitzer, K.S., Curtis, P.S., Teri, J.A., Fogel, R. and Randlett, D.L., 1993. Elevated atmospheric CO₂ and feedback between carbon and nitrogen cycles. *Plant and Soil*, 151: 105-117.