

IMPACT OF CLIMATE CHANGE ON SOIL PROCESSES AND SOIL BIOLOGICAL ACTIVITY

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ABSTRACT

It is well known that elevated atmospheric carbon dioxide (CO₂) increases the potential for plant growth. At the ecosystem level, increased root production, changes in root demography, exudation of carbon into the soil, litter quality and the production of secondary metabolites may all influence carbon gain, feedback relationships and system stability. The increased flux of carbon from roots into the soil will probably have a positive influence on nitrogen availability as time goes on. On the other hand, increased soil temperature will accelerate both root and soil respiration and this could result in a substantial flux of CO₂ back to the atmosphere. The impact of higher level ecological interactions (such as elevated CO₂ combined with higher temperatures) on soil biological processes is very poorly understood.

INTRODUCTION

The composition of the Earth's atmosphere is changing due to the combustion of fossil fuels and human land use patterns. There is no doubt that carbon dioxide (CO₂) in the atmosphere is increasing and this increase will continue for at least several decades. An increase in global temperature has also been predicted, although the certainty of this is still somewhat debatable. Least certain are global changes in precipitation, but at a minimum, both managed agroecosystems and natural vegetation will grow in an increasingly CO₂ enriched atmosphere well into the future.

It is well known that elevated CO₂ increases the potential for plant growth. High levels of CO₂ stimulate photosynthesis *per se*, since both CO₂ and O₂ compete for the same site on the catalyzing enzyme rubisco (Goudriaan et al. 1990). Research has shown that for agricultural crops, elevated CO₂ increases photosynthesis, dry matter production and economic yield, substantially in C₃ species like soybean, but less in C₄ species such as maize. It also decreases stomatal conductance and transpiration and generally improves water-use efficiency in almost all plants (Lawlor and Mitchell 1991). On the whole, elevated CO₂ will very likely increase the productivity of the Earth's vegetation. However, experiments indicate that nutrient availability, water stress, and temperature can all influence plant response to elevated CO₂, and of course, climatic and edaphic factors vary from one field situation to the next in terms of controlling ecosystem function.

At the ecosystem level, the distribution of carbon within tissues (particularly roots and leaves), the demography of plant organs (rates of birth and death), exudation of carbon into the soil, litter quality (carbon:nitrogen ratio), and the production of defense compounds may all influence carbon gain, feedback relationships and system stability. Up to this point in time, most of the CO₂ experiments have been done in

controlled environments. Work has concentrated on a few crops, and the major research emphases have been leaf-level physiological responses (Bazzaz 1990). Very little is known about how temperature, water and nutrients interact to regulate plant responses to inevitable increases in atmospheric CO₂. As usual, the below-ground portion of the ecosystem is the least understood. The goal of this communication is to summarize some of what is known about the impact of global climate change on the below-ground processes. The greatest emphasis will be on plant-soil responses to elevated CO₂, for this aspect of global change is bound to occur and there is more empirical evidence to work from. Below-ground responses to an increase in soil temperature will also be briefly reviewed. Finally, some of the complex interactions between climatic and edaphic factors will be examined to demonstrate the difficulty in predicting how ecosystems will respond to global change.

ELEVATED CARBON DIOXIDE

Plant growth and carbon partitioning to roots

Carbon dioxide is the first molecular link from atmosphere to biosphere and the products of photosynthesis provide the energy for most heterotrophic activity in the soil. Virtually all literature (87% of the articles reviewed by Rogers *et al.* 1993) reports that root dry weight increases under elevated atmospheric CO₂, regardless of species or study conditions. For example, Del Castillo *et al.* (1989) report an increase in the number of actively growing soybean roots and greater exploration of the soil under elevated CO₂. Roots of winter wheat penetrated to depth faster and numbers were greater when plants were grown in an enriched CO₂ atmosphere in the field (Chaudhuri *et al.* 1990). Roots often exhibit the greatest relative dry weight increase among plant organs under high CO₂ (Zak *et al.* 1993), and root to shoot ratio sometimes increases, although such a response has been quite variable among species and life forms (Rogers *et al.* 1993). Recent studies have also demonstrated a strong correlation between pot size and photosynthetic capacity (Arp 1991, Thomas and Strain 1991). These results suggest that roots are an important sink for photosynthate and that rooting volume has the potential to constrain plant growth response to an enriched atmosphere.

It is often reported that sustaining a positive response to increased CO₂ requires an increase in plant uptake of the total amount of essential nutrients, and that in some natural situations, where available minerals may be exhausted by stimulated plant growth, nutrient availability in the soil may impose a severe constraint on further plant growth. However, Long (1991) has pointed out that even if plants grown at elevated CO₂ show a 40% loss of their active Rubisco, net photosynthetic rates will still be enhanced at elevated CO₂ when temperatures exceed 22.5 degrees C. It would seem that except in cases of extreme nutrient deficiency or in cold environments, plant growth will likely be stimulated by elevated CO₂ in most field situations. This certainly seems to be the case with temperate crops (Rogers *et al.* 1993). Furthermore, the partitioning of carbon to the root systems of plants growing in a CO₂ enriched atmosphere will probably depend directly upon mineral nutrition, especially nitrogen availability.

In experimental situations where nutrition has been adequate to optimal, increased CO₂ has resulted in a decrease or no change in the

root:shoot ratio (Tolley and Strain, Sionit *et al.* 1985, Koch *et al.* 1986, Conroy *et al.* 1986, Brown and Higginbotham *et al.* 1985, Hollinger 1987). In contrast, in experiments in which no nutrients were added or plants were grown in a nutrient deficient medium, an increase in atmospheric CO₂ resulted in an increase in the root:shoot ratio and small diameter roots were particularly responsive to an increase in CO₂ (Norby *et al.* 1986, Luxmore *et al.* 1986, Norby *et al.* 1987, Zak *et al.* 1993). A number of whole-plant growth and physiological models suggest that plants allocate resources to balance the relative uptake of nitrogen and carbon as a function of the relative availability of these resources in the environment (Thornley 1972, Hunt 1975, Reynolds and Thornley 1982, Agren and Ingestad 1987, Hilbert 1990, Gleeson 1993). Essentially, the response of a plant to a low rate of N supply is to increase the amount of roots, whereas the response to a low rate of C supply is to increase leaf area (Eamus and Jarvis 1989). Nutrient uptake is often not simply proportional to root weight but rather to root length (Nye and Tinker 1977). In perennial plants where structural roots serve important anchorage and storage functions, simple root:shoot ratios may not be a very meaningful way to understand plant response to elevated CO₂. In summary, it appears that root growth in response to elevated CO₂ is in general accordance with carbon/nutrient balance models. We should expect allocation to roots to be a function of nitrogen availability in the soil and, in most cases, an increase in total plant growth. Since in a relative sense plants have more carbon to spend on the production of various plant organs at elevated CO₂, the common reports of increased root growth at a given level of nutrient availability might be expected. Factorial experiments that vary nitrogen availability in the soil and CO₂ in the atmosphere should provide a more generalized answer to questions of carbon partitioning under elevated CO₂.

Increased root growth under elevated CO₂ has the potential to influence plant respiration. Respiration of roots is significantly greater than the above-ground portion of the plant on a dry weight basis (Farrar 1981). In rapidly growing crop plants, maintenance respiration is generally a small percentage of net assimilation and the rate of respiration is often assumed to be directly related to growth rate (Agren and Ingestad 1987). If root growth is increased, increases in root respiration are sure to follow and the overall flux of CO₂ from the soil should exhibit an increase proportional to increased fine root respiration.

A question that is as yet unanswered is whether or not elevated CO₂ changes the nature of the plant itself or if it simply speeds ontogenetic development. There seems to be very little information on this topic. Coleman *et al.* (1993) recently reported that elevated CO₂ accelerated plant growth rate and that tissue nitrogen concentration was a function of plant size. Their results indicate a simple acceleration of ontogeny. There seem to be no growth curves for fine roots in the literature comparable to those that exist for leaf area and the questions of whether or not elevated CO₂ alters root system aging, the rates of exudation of carbon, sloughing of tissue, or the rate of root turnover seem to be more or less totally unanswered in any kind of conclusive way. Root turnover is a very critical process to understand because this is one of the major pathways for carbon flux to the soil.

Altered root growth may also influence host-pathogen interactions in the soil. Rogers *et al.* (1993) report that since elevated CO₂ generally increases carbon gain and plant growth potential, plants may be able to sustain a higher level of infection without a reduction in yield. Plants

which are more vigorous should also be able to resist infection from weak pathogens, such as facultative parasites, resulting in lower disease incidence and severity. Such generalities are sure to be too simple, and all that seems certain is that the quantity and quality of metabolic products in the rhizosphere will very likely change under an enriched atmosphere. This may have an impact on the incidence and severity of soil-borne disease.

Symbiotic relationships and soil biological activity

Luxmoore (1981) suggested a scenario whereby increased photosynthesis in a high CO₂ environment would increase the amount of carbon allocated to roots, resulting in increased root exudation, mycorrhizal infection, and N-fixation. In some trees, an increase in fine root production under elevated CO₂ has been associated with an increase in the rate of establishment and density of mycorrhizal symbiosis (C'Neill et al. 1987, Norby et al. 1987). It has also been hypothesized that, since respiration rates of fungi are higher than for vascular plants, increased mycorrhizal colonization of plant roots under elevated CO₂ may increase whole-plant respiration (Lamborg et al. 1983). If both root growth and mycorrhizal colonization increase under elevated CO₂, this would compound the respiratory costs of the root system. There are also reports that legume nitrogen fixation increases with higher CO₂ concentrations by increased levels of nodulation (Norby 1987). From a very simple perspective, intuition suggests that increased root growth at elevated CO₂ should provide additional carbon substrate for heterotrophic activity in the soil, and preliminary experimental evidence suggests that this is in fact the case (Zak et al. 1993).

Changes in the rhizosphere and soil structure may be important phenomenon in a world with a CO₂ enriched atmosphere. Although there seems to be very little information on sloughing and exudation of carbon from fine roots under elevated CO₂ (Norby et al. 1987), it must increase in many situations simply due to increased fine root proliferation. Increased inputs of carbon might have a positive influence on the formation of desirable soil structure.

Changes in the placement of litter may also have a significant impact on soil processes and soil biological activity. In field studies using ¹⁴C-labeled wheat straw, Holland and Coleman (1987) showed that a greater proportion of added ¹⁴C was retained in the surface-straw treatment compared to when straw was incorporated into the soil. When litter was distributed on top of the soil it was decomposed to a greater extent by fungi compared to when it was mixed into the soil. The lesson here is that microbial community structure is influenced by both the quality and placement of litter and that if root:shoot ratios or litter quality shifts under elevated CO₂, microbial community structure is bound to respond.

Carbon and nitrogen cycling

The impact of elevated CO₂ on nitrogen cycling is a key issue since nitrogen limits the growth of many terrestrial ecosystems. Several authors have predicted that the rate of litter decomposition may be slower under elevated CO₂. These predications are based on the finding in many studies that the carbon-to-nitrogen ratio of tissues grown under elevated CO₂ declines and on evidence that tissue high in carbon (and lignin) and low in nitrogen decays slowly. Schimmel (1990) has actually

suggested that at the ecosystem level a longer-term effect of climate change will be decreased availability of nitrogen, negating the atmospheric fertilization effect.

My colleagues and I have not been operating under these assumptions (Zak et al. 1993). Because plant production regulates the magnitude of C input to the soil, and because microbial populations within the soil are often C limited (Smith and Paul 1990), we believe increases in litter production, especially fine root production, in response to elevated CO₂ should elicit a concomitant increase in microbial populations. Although soil microorganisms are limited by physical factors (e.g. soil temperature and water potential), microbial biomass is correlated to soil organic C content over a range of conditions (Insam and Domsch 1988, Insam et al. 1989). At elevated atmospheric CO₂, the extent to which C availability and microbial populations increase should be dependent, at least in part, on the increase in fine root production and the rate at which root-derived C enters the soil. Changes in soil C availability related to elevated CO₂ may first be apparent in microbial activity and nutrient dynamics within the rhizosphere, and some preliminary evidence supports this assumption (Zak et al. 1993).

Increased C availability, resulting from relatively greater rates of plant production under elevated CO₂, could then produce positive feedback effects on N transformations and lead to greater N availability for plant growth. This hypothesis is outlined in Figure 1. The metabolism of plant-derived C undoubtedly influences N transformations, because soil microorganisms require both C and N for growth and maintenance. When the quantity of labile C within the soil is high, inorganic N is assimilated for maintenance, or to form new microbial cells. In turn, N is liberated from microbial cells when C availability limits growth and populations decline. However, theoretical analysis and experimental evidence suggest that N mineralization could increase in response to labile C inputs from root production (Clarholm 1985, Robinson et al. 1989, Kuikman et al. 1990). The amount of C available for microbial maintenance or biosynthesis should therefore be a key regulator of soil N dynamics. We believe that labile C in the soil will increase under elevated CO₂ and that this will eventually have a positive influence on soil N availability (Figure 1). The resolution of the ecosystem feedback effect of elevated CO₂ on N availability is critical in terms of understanding how natural vegetation will respond to atmospheric enrichment.

SOIL TEMPERATURE

Fine roots

The relationship between soil temperature and fine root longevity (i.e. mortality rates) is unclear. Root mortality can occur at any sublethal soil temperature if resources like moisture are in short supply (Bevington and Castle 1985, Deans 1979, Kuhns et al. 1985). But, optimal soil temperatures for root growth approach 30° C for some species, and field soil temperatures are unlikely to reach lethal levels in a globally warmed world. High soil temperatures do appear to accelerate the rate at which roots "age" (Rogers 1939, Atkinson 1980, Kuhns et al. 1985) but, to our knowledge, the effect of soil temperature on fine root lifespan has not yet been determined.

Despite the lack of empirical data, inferences about the relationship between soil temperature and fine root longevity can be made

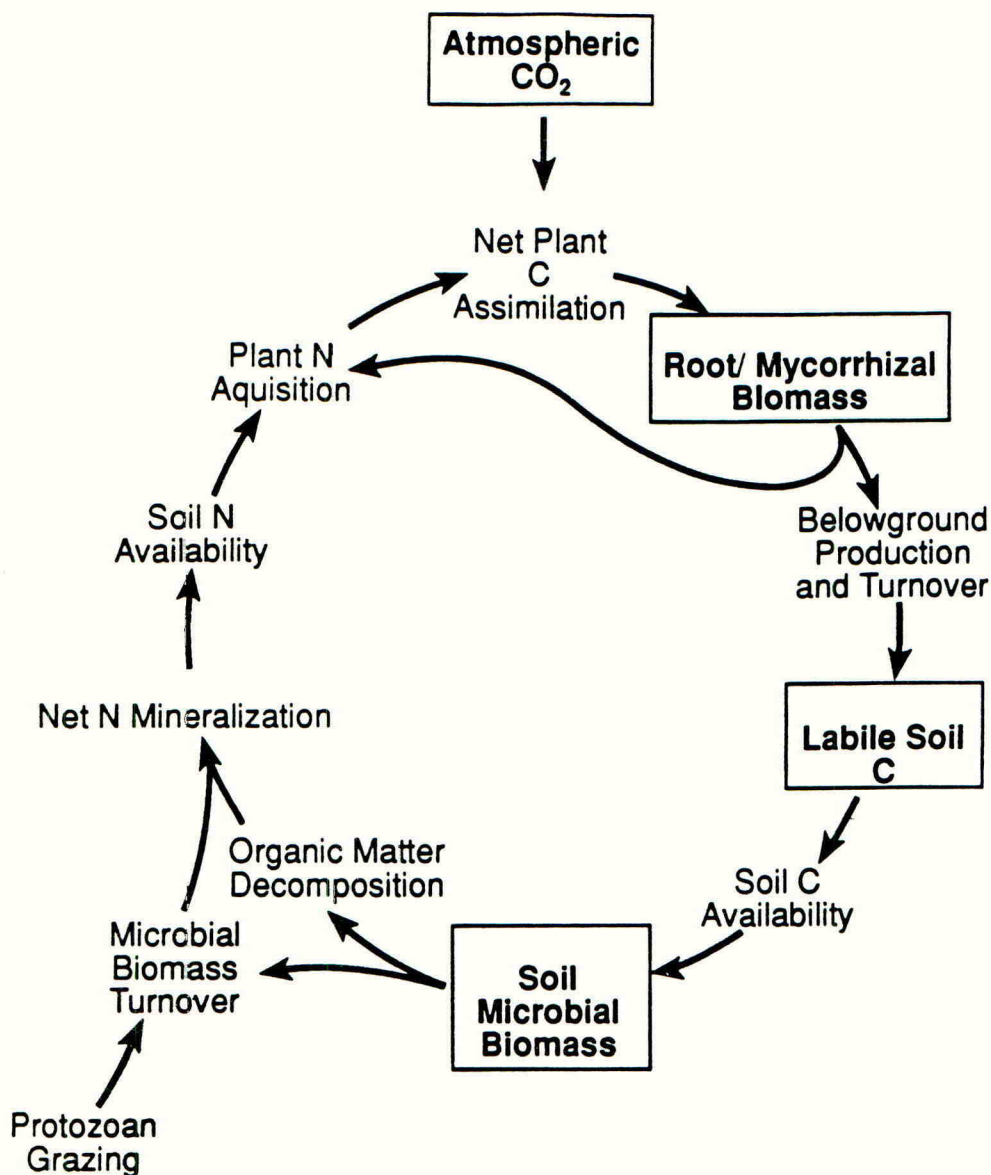


Figure 1. A conceptual model depicting the influence of elevated atmospheric CO₂ on plant production, microbial activity, and the cycling of carbon and nitrogen. The model is characterized by a series of positive feedbacks in which increased net carbon assimilation under elevated CO₂ results in increased fine root/mycorrhizal growth, microbial biomass, and rates of N mineralization. Negative feedbacks could occur if below-ground litter C:N ratios widen to the point where gross rates of microbial immobilization surpass gross rates of N mineralization. Input of leaf and stem litter is also significant but is not illustrated here. (Figure modified from Zak et al. 1993).

based upon our knowledge of how soil temperatures affect root respiration. It is well known that root maintenance respiration rates increase as soil temperatures increase (Cox 1975, Billings et al. 1977, Lawrence and Oechel 1983). Q_{10} values ranging from less than 2 to 2.7 have been reported in the literature (Billings et al. 1977, Lawrence and Oechel 1983, Marshall and Waring 1985). Warmer soil temperatures have also been shown to accelerate the depletion of carbohydrate supplies in fine roots (Marshall and Waring 1985). Hendrick and Pregitzer (1993) have recently reported that soil temperature may be responsible for shorter root lifespan in temperate deciduous forests. One mechanism for this relationship may simply be a more rapid rate of carbohydrate depletion due to higher respiration rates.

If root longevity decreases as soil temperature increases, then fine root construction costs will escalate because fine root absorbing area will need to be replaced more frequently. However, the observation that roots "age" faster at warmer soil temperatures is significant regardless of the degree to which longevity is affected. Roots typically lose some of their capacity for water and nutrient absorption as they age and become suberized. Thus, the cost of maintaining sufficient absorbing area, and therefore construction costs, will increase as the rate of root aging increases. All the evidence points to the fact that warmer soil temperatures will increase the carbon costs of the root system. However, it should be noted that acclimation to moderate changes in temperature can occur (Amthor 1991). Nonetheless, it seems likely that higher temperatures will modify plant developmental processes, resulting in changes in many aspects of plant metabolism, including root respiration.

Litter decomposition and soil carbon

Temperature increases will allow increased rates of microbial activity for mineralization of organic matter and denitrification. Soil microbial activity generally responds in an exponential manner to temperature with, approximately, a doubling of activity for every 10 degrees of temperature increase. Consequently, a projected 2-3 degree C temperature increase associated with climate change is calculated to increase microbial activity by 15-23% (Sinclair 1992).

Increased microbial activity due to global warming will accelerate the decomposition of soil organic matter, thereby releasing CO_2 to the atmosphere, which may further enhance the warming trend (Jenkinson et al. 1991). Jenkinson et al. (1991) calculate that such a feedback mechanism could be quantitatively important, because CO_2 is thought to be responsible for about 55% of the increase in radiative forcing arising from anthropogenic emissions of gases to the atmosphere, and there is about twice as much carbon in the top meter of soil as in the atmosphere.

Release of CO_2 from the soil can be a very important source of atmospheric CO_2 on a global basis. Land use practices can also greatly influence soil carbon storage. If agriculture moves north in the northern hemisphere as the climate warms, then soil carbon may become an even greater source of atmospheric C (Jenkinson et al. 1991). In a very interesting story, Billings et al. (1982, 1983) have suggested that the Arctic tundra will change from a CO_2 sink to a CO_2 source if global temperatures increase, and Schlesinger (1990) makes the point that stable soil carbon is stored so slowly that the soil will probably not become a significant sink for atmospheric carbon in the coming decades. Clearly the respiration of soil carbon is an important source that may accelerate the accumulation of CO_2 in the atmosphere if the climate warms.

HIGHER LEVEL ECOLOGICAL INTERACTIONS

Although the effects of increasing CO₂ and temperature on plant productivity and soil processes have received separate consideration, the interaction among factors has received little attention. It is in the context of complex interactions and variable field environments that the effects of global change must be judged (Bazzaz 1990, Lawlor and Mitchell 1991).

On current evidence, it is striking that certain of the effects of increasing CO₂ and temperature are opposite (Bazzaz 1990). At warmer temperatures, plants have less storage carbohydrate to maintain fine roots; plants in high CO₂ have more. At warmer temperatures, plants have a lower root:shoot ratio; plants at elevated CO₂ often have a higher one. Conversely, the increased supply of assimilate provided by high CO₂ and the increased sink metabolism permitted by soil warming should combine to produce larger root systems, with less feedback inhibition of photosynthesis, and a higher flux of carbon to the soil via exudation, sloughing and fine root mortality.

Strain (1987) has discussed the physiological and ecological aspects of plant response to elevated atmospheric CO₂. His argument is that if primary shifts in physiological processes such as photosynthesis, respiration, carbon allocation and water use efficiency occur in response to elevated CO₂, then higher level ecological interactions in competition, plant-animal relationships and biotic-abiotic interactions will take place. Such changes will very likely aggregate to alter local ecosystem function and might even alter some aspects of the global environment (see, for example, Jenkinson et al. (1991). Bazzaz (1990) concluded that impacts on ecosystem productivity would result primarily from changes in species composition brought about by differential species response to elevated CO₂. Plant density, species composition, the availability of essential resources, and the influence of herbivores, pathogens, and symbionts will all interact with a changing global environment in complex ways to determine community response to future global conditions. With the knowledge that ecosystems are interactive, complex, dynamic and still relatively poorly understood, decision makers must decide how humans will alter their behavior in order to promote their own well-being and the integrity of the planetary environment. Clearly, we have only scratched the soil surface in terms of our fundamental knowledge of those below-ground processes that will partly determine what the future will be like.

ACKNOWLEDGEMENTS

Support from the NSF, DOE and USDA Competitive Grants Programs to study global climate change, and the continual support of the Michigan Agricultural Experiment Station and The University of Michigan Biological Station is gratefully acknowledged. I would like to thank co-workers David Atkinson, Peter Curtis, Robert Fogel, Ronald Hendrick, John Lussenhop, James Teeri and Donald Zak for my continuing education on the topic of global change.

REFERENCES

- Agren, G.I.; T. Ingestad. (1987) Root:shoot ratio as a balance between nitrogen productivity and photosynthesis. *Plant, Cell and Environment* **10**:579-586.
- Amthor, J.S. (1991) Respiration in a future, higher-CO₂ world. *Plant, Cell and Environment* **14**:13-20.
- Arp, W.J. (1991) Effects of source-sink relations on photosynthetic acclimation to elevated CO₂. *Plant, Cell and Environment* **14**:869-875.
- Atkinson, D. (1980) The distribution and effectiveness of roots of tree crops. *Horticulture Review* **2**:425-490.
- Bazzaz, F.A. (1990) The response of natural ecosystems to the rising global CO₂ levels. *Annual Review of Ecology and Systematics* **21**:167-196.
- Bevington, K.B.; W.S. Castle. (1985) Annual root growth pattern of young citrus trees in relation to shoot growth, soil temperature and soil water content. *Journal American Society Horticultural Science* **110**:840-845.
- Billings, W.D.; J.O. Luken; D.A. Mortensen; K.M. Peterson. (1983) Increasing atmospheric carbon dioxide: possible effects on Arctic tundra. *Oecologia* **58**:286-289.
- Billings, W.D.; J.O. Luken; D.A. Mortensen; K.M. Peterson. (1982) Arctic tundra: a source or sink for atmospheric carbon dioxide in a changing environment? *Oecologia* **53**:7-11.
- Billings, W.D.; K.M. Peterson; G.R. Shaver; A.W. Trent. (1977) Root growth, respiration and carbon dioxide evolution in an Arctic tundra soil. *Arctic and Alpine Research* **9**:129-137.
- Brown, K.; K.O. Higginbotham. (1986) Effects of carbon dioxide enrichment and nitrogen supply on growth of boreal tree seedlings. *Tree Physiology* **2**:223-232.
- Chaudhuri, U.N.; M.B. Kirkham; E.T. Kanemasu. (1990) Root growth of winter wheat under elevated carbon dioxide and drought. *Crop Science* **30**:853-857.
- Clarholm, M. (1985) Interactions of bacteria, protozoa and plants leading to mineralization of soil nitrogen. *Soil Biology and Biochemistry* **17**:181-187.
- Coleman, J.S.; K.D.M. McConnaughay; F.A. Bazzaz. (1993) Elevated CO₂ and plant nitrogen use: is reduced tissue nitrogen concentration size-dependent? *Oecologia* **93**:195-200.
- Conroy, J.; E.W.R. Barlow; D.I. Bevege. (1986) Response of *Pinus radiata* seedlings to carbon dioxide enrichment at different levels of water and phosphorus: growth, morphology and anatomy. *Annals of Botany* **57**:165-177.
- Cox, T.L. (1975) Seasonal respiration rates of yellow poplar roots by diameter class. *Forest Science* **21**:185-188.

- Deans, J.D. (1979) Fluctuations of the soil environment and fine root growth in a young Sitka spruce plantation. *Plant and Soil* **52**:195-208.
- Del Castillo, D.; B. Acock; V.R. Reddy; M.C. Acock. (1989) Elongation and branching of roots on soybean plants in a carbon dioxide enriched aerial environment. *Agronomy Journal* **81**:692-695.
- Eamus, D.; P.G. Jarvis. (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.
- Farrar, J.F. (1981) Respiration rate of barley roots: Its relation to growth, substrate supply and the illumination of the shoot. *Annals of Botany* **48**:53-63.
- Gleeson, S. (1993) Optimization of tissue nitrogen and root-shoot allocation. *Annals of Botany* **71**:23-31.
- Goudriaan, J.; R.J. Bijlsma. (1987) Effect of CO₂ enrichment on growth of faba beans at two levels of water supply. *Netherlands Journal of Agricultural Science* **35**:189-191.
- Hendrick, R.L.; K.S. Pregitzer. (1993) Patterns of fine root mortality in two sugar maple forests. *Nature* **361**:59-61.
- Hilbert, D.W. (1990) Optimization of plant root:shoot ratios and internal nitrogen concentration. *Annals of Botany* **66**:91-99.
- Holland, E.A.; D.C. Coleman. (1987) Litter placement effects on microbial and organic matter dynamics in an agroecosystem. *Ecology* **68**:425-433.
- Hollinger, D.Y. (1987) Gas exchange and dry matter allocation responses to elevation of atmospheric CO₂ concentration in seedlings of three tree species. *Tree Physiology* **3**:193-202.
- Hunt, R. (1975) Further observations on root-shoot equilibria in perennial ryegrass (*Lolium perenne* L.). *Annals of Botany* **39**:745-755.
- Insam, H.; K.H. Domsch. (1988) Relationship between soil organic carbon and microbial biomass on chronosequences of reclaimed sites. *Microbial Ecology* **15**:177-188.
- Insam, H.; D. Parkinson; K.H. Domsch. (1989) Influence of macroclimate on soil microbial biomass. *Soil Biology and Biochemistry* **21**:211-221.
- Jenkinson, D.S.; D.E. Adams; A. Wild. (1991) Model estimates of CO₂ emissions from soil in response to global warming. *Nature* **351**:304-306.
- Koch, K.E.; P.H. Jones; W.T. Avigne; L.H. Allen. (1986) Growth, dry matter partitioning, and diurnal activities of RuBP carboxylase in citrus seedlings maintained at two levels of CO₂. *Physiologia Plantarum* **67**:477-484.
- Kuhns, M.R.; H.E. Garrett; R.O. Teskey; T.M. Hinckley. (1985) Root growth of black walnut trees related to soil temperature, soil water potential and leaf water potential. *Forest Science* **31**:617-629.

- Kuikman, P.J.; J.A. Van Veen. (1989) The impact of protozoa on the availability of bacterial nitrogen to plants. *Biology and Fertility of Soils* **8**:13-18.
- Lamborg, M.R.; R.W.F. Hardy; E.A. Paul. (1983) Microbial effects. pp. 131-176. (E.R. Lemon, ed) In *CO₂ and plants: The response of plants to rising levels of atmospheric carbon dioxide*. AAAS Selected Symposium 84. Westview Press, Boulder, Colorado.
- Lawlor, D.W.; R.A.C. Mitchell. (1991) The effects of increasing CO₂ on crop photosynthesis and productivity: a review of field studies. *Plant, Cell and Environment* **14**:807-818.
- Lawrence, W.T.; W.C. Oechel. (1983) Effects of soil temperature on the carbon exchange of taiga seedlings. I. Root respiration. *Canadian Journal of Forest Research* **13**:840-849.
- Long, S.P. (1991) Modification of the response of photosynthetic productivity to rising temperature by atmospheric CO₂ concentrations: Has its importance been underestimated? *Plant, Cell and Environment* **14**:729-739.
- Luxmoore, R.J. (1981) CO₂ and phytomass. *BioScience* **31**:626.
- Luxmore, R.J.; E.G. O'Neil; J.M. Ellis; H.H. Rogers. (1986) Nutrient uptake and growth responses of Virginia pine to elevated atmospheric carbon dioxide. *Journal of Environmental Quality* **15**:244-251.
- Marshall, J.P.; R.H. Waring. (1985) Predicting fine root production and turnover by monitoring root starch and soil temperature. *Canadian Journal of Forest Research* **15**:791-800.
- Norby, R.J. (1987) Nodulation and nitrogenase activity in nitrogen-fixing woody plants stimulated by CO₂ enrichment of the atmosphere. *Physiologia Plantarum* **71**:77-82.
- Norby, R.J.; E.G. O'Neill; R.J. Luxmore. (1986) Effects of atmospheric CO₂ enrichment on the growth and mineral nutrition of *Quercus alba* seedlings in nutrient poor soil. *Plant Physiology* **82**:83-89.
- Norby, R.J.; E.G. O'Neill; W.G. Hood; R.J. Luxmore. (1987) Carbon allocation, root exudation and mycorrhizal colonization of *Pinus echinata* seedlings grown under CO₂ enrichment. *Tree Physiology* **3**:203-210.
- Norby, R.J.; J. Pastor; J. Melillo. (1986) Carbon-nitrogen interactions in CO₂ enriched white oak: physiological and long-term perspectives. *Tree Physiology* **2**:233-241.
- Nye, P.H.; P.B. Tinker. (1977) *Solute movement in the soil:root system*. Blackwell Scientific Publications, Oxford.
- O'Neill, E.G.; R.J. Luxmore; R.J. Norby. (1987) Elevated atmospheric CO₂ effects on seedling growth, nutrient uptake, and rhizosphere bacterial populations of *Liriodendron tulipifera* L. *Plant and Soil* **104**:3-11.
- Reynolds, J.F.; J.H.M. Thornley. (1982) A shoot:root partitioning model. *Annals of Botany* **49**:585-597.

- Robinson, D.; B. Griffiths; K. Ritz; R. Wheatly. (1989) Root-induced nitrogen mineralization: A theoretical analysis. *Plant and Soil* **117**:185-193.
- Rogers, H.H.; G.B. Runion; S. V. Krupa. (1993) Plant response to atmospheric CO₂ enrichment with emphasis on roots and the rhizosphere. *Environmental Pollution* (in press).
- Rogers, W.S. (1939) Root studies. VII. Apple root growth in relation to rootstock, soil, seasonal and climatic factors. *Journal Pomology* **17**:99-130.
- Schimmel, D. (1990) Biogeochemical feedbacks in the Earth system. pp. 68-82. In (J. Leggett, ed.) *Global Warming: The Greenpeace Report*. Oxford University Press, Oxford.
- Schlesinger, W.H. (1990) Evidence from chronosequence studies for a low carbon-storage potential of soils. *Nature* **348**:232-234.
- Sinclair, T.R. (1992) Mineral nutrition and plant growth response to climate change. *Journal of Experimental Botany* **43**:1141-1146.
- Sionit, N; B.R. Strain; H. Hellmers; G.H. Riechers; C.H. Jaeger. (1985) Long-term atmospheric CO₂ enrichment affects the growth and development of *Liquidambar styraciflua* and *Pinus taeda* seedlings. *Canadian Journal of Forest Research* **15**:468-471.
- Smith, J.L.; E.A. Paul. (1990) The significance of soil microbial biomass estimations. pp. 357-393. In (J. Bollag and G. Stotsky, eds.) *Soil Biochemistry*. Marcel Dekker, Inc. NY.
- Strain, B.R. (1987) Direct effects of increasing atmospheric CO₂ on plants and ecosystems. *Trends in Ecology and Evolution* **2**:18-21.
- Thomas, R.B.; B.R. Strain. (1991) Root restriction as a factor in photosynthetic acclimation of cotton seedlings grown in elevated carbon dioxide. *Plant Physiology* **96**:627-634.
- Thornley, J.H.M. 1972. A balanced quantitative model for root:shoot ratios in vegetable plants. *Annals of Botany* **36**:431-441.
- Tolley, L.C., and B.R. Strain. 1984. Effects of CO₂ enrichment and water stress on growth of *Liquidambar styraciflua* and *Pinus taeda* seedlings. *Canadian Journal of Botany* **62**:2135-2139.
- Zak, D.R., K.S. Pregitzer, P.S. Curtis, J.A. Teeri, R.F. Fogel, and D.L. Randlett. 1993. Elevated atmospheric CO₂ and feedback between the carbon and nitrogen cycles. *Plant and Soil* **151**:105-117.