

# Elevated CO<sub>2</sub> studies: past, present and future

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**Summary** Increasing concentrations of atmospheric CO<sub>2</sub> are predicted to impact both current and future ecosystems. Elevated CO<sub>2</sub> is also predicted to affect biological processes at many levels of organization. In this overview, we summarize the responses of plants to elevated CO<sub>2</sub> 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 CO<sub>2</sub> research, (c) generalize patterns arising from past research, and (d) list critical areas of research for the future.

*Keywords:* carbon sequestration, decomposition, elevated carbon dioxide, evolution, GCTE, global change, growth, IGBP, photosynthesis, respiration, species distribution, water relations.

## Introduction

Global change factors, particularly increases in atmospheric CO<sub>2</sub> concentration and temperature, changes in the mean and variance of regional precipitation, and land-use changes, are predicted to have profound effects on ecosystem functioning in the future. There is evidence that some global change factors are already affecting current ecosystems. For example, there is strong evidence that plants have already responded to the 25% increase in atmospheric CO<sub>2</sub> concentration that has occurred since the onset of the Industrial Revolution (Woodward 1987, Overdieck et al. 1988, Dippery et al. 1995, Duquesnay et al. 1998). Furthermore, atmospheric CO<sub>2</sub> concentrations are projected to double from the current concentration of 350 ppm to 700 ppm within the next 80 years, which will further stimulate ecosystem responses. In contrast to nonuniform water availability and temperature among ecosystems, CO<sub>2</sub> concentrations are similar among ecosystems as a result of more thorough atmospheric mixing (Schlesinger 1997). In addition, similar increases in CO<sub>2</sub> are expected to occur in all ecosystems, making this change unique among global change factors.

Because the predicted increase in atmospheric CO<sub>2</sub> concentration may affect biological processes at many levels of organization (Mooney et al. 1999), it is important to continue studying the direct effects of increasing CO<sub>2</sub> at levels ranging from the molecular to the global. Physiological and ecological controls on carbon sequestration in ecosystems were reviewed more than a decade ago by Strain (1985). That review included both primary physiological controls and ecological controls on carbon sequestration. Here we update those areas and also include a section on molecular controls on carbon sequestration (Table 1), because many advances have been made in this area since the mid-1980s.

The specific objectives of this paper are to: (a) overview the studies in this journal issue that were presented at the 1997 International Geosphere Biosphere Program-Global Change and Terrestrial Ecosystems (IGBP-GCTE) meeting, “Critical Assessment of the Response of Forest Ecosystems to Elevated Atmospheric Carbon Dioxide” that was held in Durham, North Carolina, USA, (b) review areas of recent progress in CO<sub>2</sub> research, (c) generalize patterns arising from past research, and (d) list critical areas of research for the future. Much research has been conducted on CO<sub>2</sub> enrichment during the past decade, and many excellent studies (and even whole areas of research) could not be included in this overview because of space constraints. Therefore, this paper is not a comprehensive review of the field, rather it is intended to serve as a guide for assessing areas that have been well studied relative to areas that deserve further investigation.

## Molecular and physiological controls on carbon sequestration

### *Primary molecular and physiological responses*

Effects of elevated CO<sub>2</sub> on C<sub>3</sub> photosynthetic rates have been the subject of many CO<sub>2</sub> enrichment studies and have been reported in hundreds of papers. Most of these studies show that photosynthetic rate is increased following initial exposure to elevated CO<sub>2</sub> (hours to days). Increases in photosynthetic rate are brought about by increased availability of CO<sub>2</sub> at the chloroplasts and reductions in photorespiration resulting from an increased ratio of CO<sub>2</sub> to O<sub>2</sub> (Farquhar and Sharkey 1982, Pearcy et al. 1987). However, many studies report that high

Table 1. Molecular, physiological and ecological controls on carbon sequestering in ecosystems. Modified from Strain (1985).

I. Molecular and physiological controls on carbon sequestering	
A. Molecular responses	1. Gene transcription
B. Primary physiological responses	1. Photosynthesis 2. Photorespiration 3. Dark respiration 4. Stomatal regulation
C. Secondary physiological responses	1. Photosynthate concentration 2. Photosynthate translocation 3. Plant water status a. Transpiration b. Tissue water potential c. Water-use efficiency d. Leaf temperature
D. Tertiary whole plant responses	1. Growth rate a. Mass b. Height c. Leaf area d. Node formation 2. Growth form a. Height b. Branch number c. Leaf area and number d. Root architecture e. Root versus shoot mass f. Leaf specific mass 3. Reproduction a. Flower number and size b. Fruit number and size c. Nectar production d. Seed size and number e. Seed germination 4. Phenology (development rate) a. Time to germinate b. Time to reproduction c. Time to leaf senescence d. Time to whole-plant senescence
II. Ecological controls on carbon sequestering	
A. Primary organism interaction	1. Plant-plant a. Competition 2. Plant-animal a. Herbivory b. Pollination c. Shelter 3. Plant-microbes a. Disease b. Decomposition c. Symbiosis
B. Secondary organism interaction	1. Evolutionary responses and genetic differentiation
C. Tertiary ecosystem responses	1. Integration of all effects through time

photosynthetic rates are not maintained over long time periods and substantial reductions in photosynthesis (down-regulation) may occur within days to weeks after initial exposure to elevated CO<sub>2</sub> (Long et al. 1993, Sims et al. 1998). Therefore, short-term measurements of photosynthetic rate may overestimate the potential for carbon assimilation of plants subjected to long-term exposure to elevated CO<sub>2</sub> (Oechel and Strain 1985).

At the physiological level, down-regulation of photosynthesis is most often related to reduced sink strength (processes that consume photosynthate, Stitt 1991) and low nutrient availability. For example, Myers et al. (1999, this issue) showed that reduced sink strength (experimentally induced by excising developing needles and by girdling of branches) resulted in reductions in leaf photosynthetic rate and carbohydrate storage in *Pinus taeda* L. within several days. Photosynthetic down-regulation in response to elevated CO<sub>2</sub> is also common in habitats characterized by nutrient-poor soils, and it is well known that nutrient (particularly nitrogen) availability in soil can affect production of photosynthetic enzymes. Li et al. (1999, this issue) reported that Florida scrub-oak species in a nutrient-limited system showed initial increases in photosynthetic rate in response to elevated CO<sub>2</sub>, and later exhibited photosynthetic down-regulation that varied among species. The authors attributed the interspecific differences in down-regulation to possible variation in nutrient acquisition by roots of the different species. We note that photosynthetic down-regulation does not always reduce photosynthesis to current rates. For example, Tissue et al. (1999, this issue) observed strong responses of photosynthetic down-regulation in *Pinus ponderosa* Dougl. ex Laws., but photosynthetic rates were still 53% higher in plants grown at elevated CO<sub>2</sub> for six years relative to plants grown at current ambient CO<sub>2</sub>. Photosynthetic down-regulation may also be maintained over long time scales by selection, as indicated by reduced photosynthetic capacity of *Nardus stricta* L. growing near a CO<sub>2</sub> spring (that has emitted CO<sub>2</sub> for hundreds to thousands of years) relative to plants of the same species growing at a distance from the spring (Cook et al. 1998).

Over the last decade, progress has been made in determining the biochemical and molecular mechanisms by which photosynthesis is down-regulated in response to elevated CO<sub>2</sub>. Photosynthetic down-regulation is characterized at the biochemical and leaf levels by reduced chlorophyll content, reduced Rubisco (ribulose-1,5-bisphosphate carboxylase-oxygenase) content and activity, limitations in RuBP and P<sub>i</sub> regeneration, higher leaf mass/leaf area ratios and decreased leaf nitrogen concentration on a leaf mass basis (Sage 1994, Tissue et al. 1995). These down-regulation responses are often associated with increased accumulation of carbohydrate in leaves that may result in feedback inhibition of photosynthesis at the molecular level. Strain and Thomas (1995) present a conceptual model of controls on CO<sub>2</sub> acquisition. On a molecular basis, glucose and other sugars are known to suppress the transcription of photosynthetic genes (Sheen 1990), and genes encoding D1 and D2 of photosystem II, cyt *f*, Rubisco small subunit and Rubisco activase, and carbonic anhydrase appear

to be most affected (van Oosten and Besford 1995, Griffin and Seemann 1996).

Studies of the direct effects of elevated CO<sub>2</sub> on plant respiration have become increasingly important as attempts are made to scale the physiological effects of elevated CO<sub>2</sub> from the biochemical to whole-plant level. González-Meler and Siedow (1999, this issue) point out that a doubling of atmospheric CO<sub>2</sub> concentration results in an average 15–20% reduction in mitochondrial respiration that varies both within and among species (some crops may show as much as a 20% increase in respiration). The direct effects of CO<sub>2</sub> on respiration also vary among leaves of different ages (Thomas and Griffin 1994) and between developmental stages (pre-reproductive versus post-reproductive, Griffin et al. 1999). The exact mechanisms that account for inhibition of respiration by elevated CO<sub>2</sub> have not been fully elucidated, in part because responses have been highly variable. Possible mechanisms include inhibition of enzymes involved in mitochondrial electron transport (González-Meler et al. 1996) and reduced activity of other enzymes in response to dissolved inorganic carbon (Amthor 1991). Furthermore, González-Meler and Siedow (1999, this issue) provide evidence that other mechanisms besides inhibition of mitochondrial enzymes may be associated with reductions in respiration in response to elevated CO<sub>2</sub>. Because many studies have demonstrated direct effects of CO<sub>2</sub> on respiration, it is important that high concentrations of CO<sub>2</sub> are maintained during both daytime and nighttime hours in elevated CO<sub>2</sub> studies in order to predict accurately the effects of elevated atmospheric CO<sub>2</sub> concentration on the carbon balance of plants (Griffin et al. 1999).

#### *Secondary physiological responses*

Many studies have shown that regulation of stomata by guard cells can be directly affected by CO<sub>2</sub> concentration, but the exact mechanism underlying this response remains controversial (Zhu et al. 1998). With few exceptions, studies have shown that stomatal conductance of C<sub>3</sub> plants is initially reduced in response to elevated CO<sub>2</sub> (higher C<sub>a</sub>), resulting in reduced transpiration and increased conservation of water (higher carbon assimilation per water lost); however, these responses are short-lived in some species (Bunce 1992). Elevated CO<sub>2</sub> has also been shown to ameliorate the negative effects of drought stress (Tolley and Strain 1985). Although most drought studies have been conducted in small pots where water was withheld and dry down of soil was rapid, these studies are useful for understanding short-term physiological responses to severe droughts that do not allow for long-term physiological adjustments. However, open-top chamber sites, free air carbon dioxide enrichment (FACE) sites, and CO<sub>2</sub> springs now provide excellent systems for studying long-term effects of drought under elevated CO<sub>2</sub> conditions with non-limiting soil volume. For example, Tognetti et al. (1999a, this issue) showed that, in *Quercus pubescens* Willd., water flux (relative to cross-sectional area) was reduced in trees that occurred near a CO<sub>2</sub> spring relative to trees that occurred far from the spring. However, they found that transpiration responses to elevated CO<sub>2</sub> showed strong seasonal effects, and the beneficial effects of

elevated CO<sub>2</sub> were lowest during the most severe periods of drought (periods of highest vapor pressure deficit). Furthermore, Tognetti et al. (1999b, this issue) reported that there were interspecific differences in the hydraulic conductivity of Mediterranean tree species, but trees of the same species did not differ in their responses at a CO<sub>2</sub> spring site compared to a non-spring site, indicating that long-term exposure to elevated CO<sub>2</sub> may not result in differentiation of xylem hydraulic properties. Furthermore, Pataki et al. (1998) found that water flux per unit sapwood did not vary between current ambient and elevated CO<sub>2</sub> concentrations in *Pinus taeda*, but elevated CO<sub>2</sub> increased absolute water loss by increasing leaf and sapwood areas. In addition, Ellsworth et al. (1995) found that *P. taeda* generally did not undergo adjustments in stomatal conductance after 80 days of exposure to elevated CO<sub>2</sub> at a FACE site in the southeastern United States, although plants in elevated CO<sub>2</sub> did exhibit transient adjustments in stomatal conductance and reductions in water loss during cloudy conditions.

#### *Tertiary whole-plant responses*

It is well known that elevated CO<sub>2</sub> stimulates biomass production of C<sub>3</sub> plants, and plants with indeterminate growth show higher growth enhancements in response to elevated CO<sub>2</sub> than plants with determinate growth, presumably because of differences in sink strength (Oechel and Strain 1985). Furthermore, plants often show higher growth responses to elevated CO<sub>2</sub> when other resources such as nutrients and water are not limiting (Curtis and Wang 1998). With respect to light, however, higher relative growth enhancements are sometimes observed under low light conditions than under high light conditions because elevated CO<sub>2</sub> increases the quantum yield (photosynthetic carbon gain per photons absorbed) of C<sub>3</sub> species (Ehleringer and Björkman 1977, Ehleringer and Pearcy 1983, Long and Drake 1991, Ehleringer et al. 1997). However, Lewis et al. (1999, this issue) point out that increases in irradiance may increase, decrease, or have no effect on the growth of plants under elevated CO<sub>2</sub> conditions.

Initial stimulations in growth in response to elevated CO<sub>2</sub> may diminish over time, possibly because of down-regulation of photosynthesis or modifications in biomass allocation and phenology. For example, Jach and Ceulemans (1999, this issue) observed that three-year-old *Pinus sylvestris* L. seedlings showed enhanced relative growth rates during the first season of exposure to elevated CO<sub>2</sub>, but showed similar growth rates to control plants during the second season. Similarly, Tissue et al. (1997b) reported that, after four years of exposure to elevated CO<sub>2</sub> in open-top chambers, *Pinus taeda* plants exhibited 90% more biomass than control plants grown at the current ambient CO<sub>2</sub> concentration. However, the greater final biomass production was attributed to the large increases in growth and leaf area that occurred only during the first season that compounded growth responses over time. This study indicates that long-term measurements of growth in response to elevated CO<sub>2</sub> are necessary for predicting the potential for carbon sequestration by terrestrial forest ecosystems.

The rate of height growth and branching increase in some tree species exposed to elevated CO<sub>2</sub> (Curtis and Wang 1998).

Increased height growth by some genotypes and species may give certain individuals a competitive advantage over others if light is a limiting resource. Furthermore, increased branching has been correlated with increases in leaf number (Oechel and Strain 1985). As leaf number increases, leaf area index (leaf area/land area) may also increase, resulting in higher carbon assimilation on an ecosystem level. Jach and Ceulemans (1999, this issue) found evidence for these responses in *Pinus sylvestris* seedlings grown at elevated CO<sub>2</sub> and they predicted that the increase in leaf area index would result in more rapid canopy closure. These results indicate that changes in growth form in response to elevated CO<sub>2</sub> may have a substantial effect on light interception.

Plants are generally predicted to allocate biomass to structures that are involved in the uptake of limiting resources. Therefore, relative limitations in nitrogen and other soil nutrients at elevated CO<sub>2</sub> were initially predicted to increase the allocation of biomass to roots. In the early CO<sub>2</sub> studies, conclusions about allocation of biomass were often based on measurements of root-to-shoot ratio (root biomass/shoot biomass); however, this measurement only relates information on growth form at one point in time and does not include information on allocation of biomass over time (Samson and Werk 1986). Plants grown at different CO<sub>2</sub> concentrations and even plants within the same CO<sub>2</sub> treatment are likely to differ in size and this may result in differences in root-to-shoot ratio that are independent of the effects of CO<sub>2</sub> treatment, and are only related to shifts in allometry during development. To remove the effects of plant size when testing for effects of CO<sub>2</sub> on biomass allocation, allometric statistical techniques (primarily analysis of covariance) can be used. The majority of studies based on the allometric technique have shown that elevated CO<sub>2</sub> rarely alters the allocation of biomass between roots and shoots when size effects are removed (Gebauer et al. 1996, Tissue et al. 1997b). However, more studies are needed to determine if differences in biomass allocation occur between fine and course root fractions in response to elevated CO<sub>2</sub> (King et al. 1996).

Most elevated CO<sub>2</sub> studies on reproductive output have been conducted on herbaceous species. However, the mechanisms underlying these responses are probably similar in tree species, although they may occur over a longer life cycle. Reproductive output is associated with fitness (more so than any of the previously discussed measurements) and may influence the effects of elevated CO<sub>2</sub> on long-term evolutionary processes. Changes in reproduction in response to elevated CO<sub>2</sub> are important for quantifying effects on crop yields, for determining changes in the fitness of genotypes in natural systems, and for predicting changes in species composition that may be manifested through differences in reproduction. Most studies have shown that elevated CO<sub>2</sub> increases reproductive output (flower number, fruit number, and seed production) of herbaceous species (Garbutt and Bazzaz 1984, Curtis et al. 1994, Curtis et al. 1996, Ward and Strain 1997). However, Billings and Billings (1983) found that the highly determinate alpine and arctic annual, *Saxifraga flagellaris* Willd., exhibited decreased reproduction in response to elevated CO<sub>2</sub>. Reproduction is often increased at elevated CO<sub>2</sub> as a result of increased allocation of

resources to reproduction and a higher number of nodes (and branches) that increase available sites for flower and fruit production. However, increased reproductive output at elevated CO<sub>2</sub> can also be a function of increased plant size rather than increased allocation to reproductive structures (Ward and Strain 1997). Furthermore, if the reproductive structures themselves provide a portion of the carbon allocated to reproduction, this would also affect the interpretation of carbon allocation between vegetative and reproductive structures (Bazzaz et al. 1979).

Elevated CO<sub>2</sub> can affect seed germination, seed quality, and seedling viability. Studies of the effects of CO<sub>2</sub> enrichment on germination have been inconsistent, with some showing significant effects of CO<sub>2</sub> enrichment (Wulff and Alexander 1985, Andalo et al. 1996) and others showing no effect (Garbutt et al. 1990). Concentrations of CO<sub>2</sub> within soil and on the surface of soil may be several times that of the atmosphere because of the high rates of microbial respiration. Consequently, seeds are often exposed to very high CO<sub>2</sub> concentrations under field conditions, and may not show changes in germination in response to the relatively small increases in CO<sub>2</sub> concentration predicted for the next 50–100 years (Andalo et al. 1998). Interestingly, however, Andalo et al. (1996) found that the germination percentage of field-collected *Arabidopsis thaliana* (L.) Heynh. seeds was unaffected by high CO<sub>2</sub> concentrations unless the seeds were borne by mother plants that had developed at high CO<sub>2</sub>, in which case, germination was reduced and was slower. The authors later reported that this response may be a result of increases in the C:N ratio of seed tissue induced by a maternal effect at elevated CO<sub>2</sub> that reduced growth of the radical (Andalo et al. 1998). If these effects occur in tree species and vary among species, the impact on reproductive success may result in progressive changes over successive generations in the species composition of forest communities.

Relatively few studies have measured the effects of elevated CO<sub>2</sub> on seedling survival. Increases in atmospheric CO<sub>2</sub> concentration may have direct effects on the carbon balance of seedlings and may affect early seedling survival, because respiration often exceeds photosynthesis during the early stages of growth (Larcher 1995). Polley et al. (1996) showed that, under drought-stress conditions and low plant density, the survival of *Prosopis glandulosa* Torr. seedlings was increased from 0 to 40% as a result of increases in CO<sub>2</sub> concentration above the current ambient concentration, suggesting that increased CO<sub>2</sub> reduced the negative effects of drought stress on seedling survival. However, when *Abutilon theophrasti* Medic. was grown at high density, elevated CO<sub>2</sub> reduced survival because it increased the intensity of competition (Bazzaz et al. 1992). Therefore, differences in microhabitats may alter the effects of high CO<sub>2</sub> on seedling survival. Variations in the effects of elevated CO<sub>2</sub> on survival have also been documented between closely related species. For example, Rochefort and Bazzaz (1992) found that, of four birch species, only *Betula alleghaniensis* Britt. showed increased survival when the concentration of CO<sub>2</sub> was increased from 350 to 700 ppm. This result suggests that shifts in community composition may result from the effects of increasing CO<sub>2</sub> on seedling survival.

Elevated CO<sub>2</sub> can alter plant phenology (development rate) and time to senescence at both the leaf and whole-plant levels. For example, Jach and Ceulemans (1999, this issue) observed that, in *Pinus sylvestris*, needle fall occurred earlier at elevated CO<sub>2</sub> than at current ambient CO<sub>2</sub>, which the authors attributed to possible changes in transpiration rate or earlier translocation of nutrients away from leaves. In addition, *Nardus stricta* growing near a CO<sub>2</sub> spring exhibited earlier leaf senescence compared to plants growing far from the spring, indicating that long-term exposure to elevated CO<sub>2</sub> may decrease the life span of leaves (Cook et al. 1998). In contrast, delayed leaf senescence in response to elevated CO<sub>2</sub> occurred in *Glycine max* (L.) Merrill (Hardy and Havelka 1975), and leaves of *Eriophorum vaginatum* L. maintained high photosynthetic rates later in the season when grown at elevated CO<sub>2</sub> compared to current ambient CO<sub>2</sub> (Tissue and Oechel 1987). These studies demonstrate that effects of elevated CO<sub>2</sub> on leaf phenology may alter leaf-level carbon assimilation throughout the growing season in ways that may be difficult to predict.

Elevated CO<sub>2</sub> can also affect whole-plant development rate (most often measured as time to reproduction). Species may exhibit slower (Carter and Peterson 1983), faster (St. Omer and Horvath 1983, Garbutt and Bazzaz 1984), or similar (Garbutt and Bazzaz 1984) rates of development in response to elevated CO<sub>2</sub>. In some species, changes in time to reach reproduction were caused by faster growth rates that resulted in earlier attainment of the minimum size required for reproduction. In other species, however, elevated CO<sub>2</sub> altered the size at which plants initiated reproduction (Reekie and Bazzaz 1991). Changes in the timing of reproduction may have implications at the community level by disrupting the timing of plant–pollinator interactions (Garbutt and Bazzaz 1984). Alterations in flowering time may also affect the reproductive output of both herbaceous species and tree species, particularly in regions where frost or drought events limit seed production at the end of the growing season.

There appear to be several areas of future study that will make critical contributions to our understanding of elevated CO<sub>2</sub> effects on physiological and molecular responses that control carbon sequestration. Thus, studies linking physiological and developmental processes that influence whole-plant responses to elevated CO<sub>2</sub> will be crucial for making long-term predictions about the potential for carbon sequestration of trees in response to elevated CO<sub>2</sub>. For example, long-term FACE sites will allow us to study the effects of elevated CO<sub>2</sub> on the rate of photosynthesis relative to respiration throughout the development of trees. Additional information on the effects of elevated CO<sub>2</sub> on the transcription of photosynthetic genes may allow us to explain why some genotypes and species exhibit strong down-regulation responses. Furthermore, knowledge of the interactive effects of CO<sub>2</sub> with other environmental factors (such as temperature, light, and nutrient availability) on molecular processes that control photosynthetic and respiration rates will enable us to predict physiological responses to global change factors more accurately.

## Ecological controls on carbon sequestering

### *Primary organism interaction*

It is important to understand the effects of elevated CO<sub>2</sub> on plant–plant interactions, because plants grown as individuals are likely to show different responses to elevated CO<sub>2</sub> compared with plants grown in competition (Bazzaz et al. 1995). Bazzaz and McConnaughay (1992) pointed out that CO<sub>2</sub> may not be a direct limiting resource because of its gaseous state and high diffusion capacity, except within dense canopies where CO<sub>2</sub> drawdown can be substantial. However, it should be noted that CO<sub>2</sub> may have been a limiting resource for some C<sub>3</sub> species before the Industrial Revolution (125 years ago, 23% lower CO<sub>2</sub> concentration), which spans the lifetime of some extant trees. Because relatively few studies have focused on the competitive interactions of trees, most information on elevated CO<sub>2</sub> effects on competition must be abstracted from studies with herbaceous species. However, one study demonstrated that seedlings of a perennial grass species (C<sub>3</sub>, *Calamagrostis epigejos* L. (Roth)) may become more competitive against *Picea abies* (L.) Karst. seedlings at elevated CO<sub>2</sub> as a result of higher absolute growth rates of the grass relative to the tree (Gloser 1996). Most competition studies have demonstrated that C<sub>3</sub> species have an advantage over C<sub>4</sub> species with increasing CO<sub>2</sub>, although exceptions have been reported (Owensby et al. 1993). Furthermore, the effects of elevated CO<sub>2</sub> on competition vary greatly depending on the ecosystem under consideration. In estuarine marsh systems, C<sub>3</sub> and C<sub>4</sub> species occur in close proximity and elevated CO<sub>2</sub> was shown to alter species composition and biomass production in favor of C<sub>3</sub> species (Curtis et al. 1989). However, in a dry, tallgrass prairie system, a dominant C<sub>4</sub> species was favored over a dominant C<sub>3</sub> species in response to elevated CO<sub>2</sub> (Owensby et al. 1993) because of higher drought tolerance in the C<sub>4</sub> species relative to the C<sub>3</sub> species. Therefore, predictions regarding the effects of elevated CO<sub>2</sub> on competitive interactions of C<sub>3</sub> and C<sub>4</sub> species must be made in an ecosystem context.

There have been few studies on the effects of elevated CO<sub>2</sub> on higher trophic levels. Increases in the C:N ratio of plant tissue may increase herbivore consumption (Lincoln et al. 1993). Furthermore, increases in leaf carbohydrates induced by elevated CO<sub>2</sub> may lead to the accumulation of carbon-based secondary compounds (Bryant et al. 1983). Kinney et al. (1997) grew several tree species in current ambient and elevated CO<sub>2</sub> in open-top chambers and found that, as predicted, carbon-based starch concentrations of leaves increased in response to elevated CO<sub>2</sub>, and nitrogen-based compounds (protein) decreased. The concentration of condensed tannins, which are carbon-based secondary compounds, also increased in elevated CO<sub>2</sub>. The authors found that gypsy moth larvae (*Lymantria dispar* L.) that were fed high C:N leaf material responded differently depending on the source of the leaf material. For *Acer saccharum* Marsh., the consumption rate of gypsy moths only increased by 7% with high C:N material, and growth rates, final mass, and digestion efficiency were reduced. For *Populus tremuloides* Michx., however, consumption rates increased by 86% on high C:N material, but

conversion efficiencies decreased, and growth rates of the larvae were not affected by elevated CO<sub>2</sub>. Excess tannins in aspen had little effect on gypsy moth performance. This study illustrates the importance of measuring specific changes in plant chemistry in response to elevated CO<sub>2</sub> rather than measuring only C:N, because plant species may vary in their specific biochemical responses, leading to differential effects on herbivores. In a unique study, Runion et al. (1999, this issue) measured changes in root chemistry in *Pinus palustris* Mill. in response to elevated CO<sub>2</sub> and water availability. They found that the taproots of plants developed in elevated CO<sub>2</sub> had lower concentrations of structural compounds such as cellulose and lignin and higher concentrations of starch (nonstructural), whereas fine roots had lower starch concentrations, which may have been a transient response. These changes in tissue chemistry were predicted to have large effects on herbivores that consumed roots and on the severity of fungal infection. Taken together, these studies of plant-herbivore interactions show the importance of studying changes in tissue chemistry of both leaves and roots in response to elevated CO<sub>2</sub>.

The severity of plant diseases may also be affected by elevated CO<sub>2</sub>. For example, *Triticum aestivum* L. grown at elevated CO<sub>2</sub> had lower shoot nitrogen concentrations and reduced severity of infection by the fungus causing powdery mildew (*Erysiphe graminis*) than plants grown at current ambient CO<sub>2</sub> (Thompson et al. 1993). Similarly, *Scirpus olneyi* Gray exhibited reduced nitrogen concentrations and frequencies of fungal infection at elevated CO<sub>2</sub> in a sub-estuary of the Chesapeake Bay (Thompson and Drake 1994). These results suggest that changes in tissue chemistry (particularly decreases in nitrogen) may inhibit parasitic infections on plants developed at elevated CO<sub>2</sub>.

Coûteaux et al. (1999, this issue) synthesized results from published studies of elevated CO<sub>2</sub> on the quality of live plant tissue and litter. The authors found that leaf material from many species showed decreased nitrogen concentrations following short-term exposure to elevated CO<sub>2</sub>, whereas the effects of elevated CO<sub>2</sub> on lignin concentration were more variable among species. However, trees exposed to elevated CO<sub>2</sub> over long time scales (at a CO<sub>2</sub> spring) did not differ in their nitrogen concentrations from trees growing at current ambient CO<sub>2</sub> (at a distance from the CO<sub>2</sub> spring). Studies on litter quality also revealed high variation in the effects of elevated CO<sub>2</sub> on decomposition as indicated by measurements of carbon mineralization. Norby and Cotrufo (1998) summarized recent studies on the effects of elevated CO<sub>2</sub> on decomposition in various ecosystems (forests, grasslands, salt marshes, and agricultural systems) and concluded that litter chemistry is rarely altered by elevated CO<sub>2</sub>, and decomposition rates are often unaffected. One explanation to account for this discrepancy is that live leaf material and litter vary in their chemical composition as a result of translocation of nutrients away from senescing leaves near the end of the growing season. Furthermore, retention of nutrients from senescing leaves at the end of the growing season is predicted to enhance growth responses to elevated CO<sub>2</sub> because nutrients will remain in vegetation rather than possibly being immobilized by microbes on the forest floor (Johnson 1999, this issue).

Symbiotic relationships between plants and mycorrhizal fungi and nitrogen fixing bacteria may be enhanced by elevated CO<sub>2</sub>. Mycorrhizal fungi in association with plant roots occur in over 80% of plant species and increase the uptake of soil nutrients (mainly phosphorus, Sage 1995). Production of higher amounts of carbohydrates by leaves exposed to elevated CO<sub>2</sub> may offset the costs (approximately 10–20% of photosynthate) associated with maintenance of mycorrhizal fungi. For example, in *Pinus echinata* Mill. and *Quercus alba* L. grown on unfertilized forest soil, elevated CO<sub>2</sub> enhanced both root growth and mycorrhizal colonization, which presumably contributed to higher nutrient uptake (Norby et al. 1987, O'Neill et al. 1987). Increases in root production and mycorrhizal colonization may increase nutrient uptake, reducing relative differences in carbon and nitrogen concentrations that may be induced by elevated CO<sub>2</sub>. Thomas et al. (1991) found that seedlings of a nitrogen fixing tree, *Gliricidia sepium* (Jacq.) Kunth ex Walp., that were supplied with nitrogen in the soil showed greater activity of nitrogen fixing bacteria (*Rhizobium*) and higher nodule production in elevated CO<sub>2</sub> than in current ambient CO<sub>2</sub>. This response contributed to increased foliar nitrogen concentration. Furthermore, Tissue et al. (1997a) showed that foliar carbon compounds were supplied to nodules at a faster rate under elevated CO<sub>2</sub> conditions that stimulated the activity of nitrogenase and increased nitrogen uptake by plants.

#### Secondary organism interaction

Over the last decade, much emphasis has been placed on predicting the degree to which terrestrial ecosystems will sequester or release carbon in future scenarios of increasing atmospheric CO<sub>2</sub> concentration. (Oechel et al. 1994, Hungate et al. 1997, Mooney et al. 1999). However, predictions about the effects of elevated CO<sub>2</sub> on the carbon uptake of C<sub>3</sub> plants have generally assumed that plant responses will remain stable over long time scales, and relatively little attention has focused on the consequences of increasing CO<sub>2</sub> on plant evolution. Recent studies have demonstrated that C<sub>3</sub> plants exhibit genetic variation in response to elevated CO<sub>2</sub> for photosynthesis (Curtis et al. 1996), stomatal characters (Case et al. 1998), growth (Norton et al. 1995, Zhang and Lechowicz 1995, Schmid et al. 1996), and reproduction (Curtis et al. 1994, Bazzaz et al. 1995). The existence of genetic variation in the responses to elevated CO<sub>2</sub> strongly suggests that plants may undergo rapid directional selection in response to increasing CO<sub>2</sub> concentration (Strain 1991). The effects of selection may result in phenotypic changes in development rate and biomass production that may alter the capacity for carbon sequestration by terrestrial systems. For example, Ward et al. (unpublished data) found that elevated CO<sub>2</sub> was a strong selective agent on a model C<sub>3</sub> species (*Arabidopsis thaliana*) that altered phenology and biomass accumulation. More specifically, selection for high seed number at elevated CO<sub>2</sub> over multiple generations resulted in plants that initiated reproduction at a younger age and had lower final biomass production as a result of earlier senescence relative to control plants. If such responses occur in tree species, evolutionary responses may not further

increase the capacity for trees to utilize increased CO<sub>2</sub> concentrations as has been suggested in the literature (Curtis et al. 1994). The results of future studies will improve our understanding of the effects of elevated CO<sub>2</sub> on the evolution of tree species.

#### *Tertiary ecosystem responses*

It is important that elevated CO<sub>2</sub> studies consider ecosystem responses over long time scales (Oechel et al. 1994). Changes in net primary production, carbon storage in soils, and nutrient cycling may occur during long-term exposure to elevated CO<sub>2</sub> that may alter the degree to which vegetation and soils sequester carbon. For example, Hungate et al. (1997) found that, following three years of exposure to elevated CO<sub>2</sub> in open-top chambers, serpentine and sandstone grasslands exhibited increased carbon uptake by vegetation. However, carbon was partitioned to soil pools with rapid turnover that reduced the potential for long-term carbon storage in these systems. In a modeling effort (FORDYN model) by Luan et al. (1999, this issue) for stands of *Pinus taeda* exposed to elevated CO<sub>2</sub>, carbon uptake by vegetation was predicted to be much greater during early stages of forest development relative to later stages. Following long-term exposure to elevated CO<sub>2</sub>, the model predicted relatively low carbon uptake by vegetation in response to elevated CO<sub>2</sub> because of reduced nitrogen availability and lower production of leaf biomass and fine root biomass in older stands. The model predicted that carbon storage would be increased by only 4% in trees and 9% in soils at the 10th year of exposure to elevated CO<sub>2</sub>. Despite these low values for carbon storage in vegetation and soils of old forests, long-term accumulation of carbon in soils was predicted to increase by 20% throughout forest development at elevated CO<sub>2</sub> relative to current ambient CO<sub>2</sub>. At a higher level, Pan et al. (1998) used a variety of models to determine that the USA may show increases in net primary production in response to a doubling of CO<sub>2</sub> concentration that range between 5 and 11% depending on the model used. Although these predictions are lower than those based on greenhouse studies involving high resources, stimulation of net primary production in natural systems (particularly forests) may still result in substantial sequestration of carbon emitted from the burning of fossil fuels.

Other areas of research that may make important contributions to our understanding of elevated CO<sub>2</sub> effects on ecological controls on carbon sequestration include determining whether elevated CO<sub>2</sub> invokes directional selection on a global basis and whether this phenomenon will reduce genetic diversity of plant species. Furthermore, modeling efforts and field studies focused on ecosystem-level responses to elevated CO<sub>2</sub> will be improved by further study of the interactions between carbon, water, and nutrient cycles (Pan et al. 1998), and further information on root and rhizosphere responses will aid in our understanding of elevated CO<sub>2</sub> effects on belowground processes (Cheng 1999, this issue). In addition, future studies should continue investigating the interactive effects of elevated CO<sub>2</sub> and higher atmospheric and soil temperatures on ecosystem functioning. Consideration of anthropogenic effects on

future ecosystems and climate requires a more complete understanding of the global carbon cycle. The studies presented in this volume represent contemporary research interests and suggest future directions for carbon-related global change research.

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