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Source: *Annual Review of Ecology and Systematics*, Vol. 21 (1990), pp. 167-196

Published by: [Annual Reviews](#)

Stable URL: <http://www.jstor.org/stable/2097022>

Accessed: 25/08/2011 14:48

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THE RESPONSE OF NATURAL ECOSYSTEMS TO THE RISING GLOBAL CO₂ LEVELS

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KEY WORDS: carbon dioxide, global change, ecosystems, growth, competition

INTRODUCTION

Evidence from many sources shows that the concentration of atmospheric CO₂ is steadily rising (61, 17). This rise is strongly correlated with the increase in global consumption of fossil fuels (104). There are also significant contributions from the clearing of forests, especially in the tropics (136, 55). Controversy continues, however, as to whether the biosphere is presently a source or a sink for carbon (see 52, 54, 56).

Despite this controversy, most scientists agree that rising CO₂ levels will have substantial direct and indirect effects on the biosphere (80). Because CO₂ is a greenhouse gas, its increase in the atmosphere may influence the earth's energy budget. Several climatologists have used general circulation models to predict changes in mean annual global temperature (58, 108). While these models differ in detail, they all predict increased global warming and substantial shifts in precipitation patterns. Recently, some scientists (60) have questioned the predictions of these models. But regardless of changes in global temperature and other climate variables, rising CO₂ can influence world ecosystems by direct effects on plant growth and development.

The large body of literature on the response of crops and intensively managed forests to elevated CO₂ is not treated in this review because there are

several excellent and recent reviews of it (e.g. 2, 28, 62, 127, 132 for crops, and 37, 65, 111 for trees). Instead, this review concentrates on the response of natural vegetation to elevated CO_2 and some of the predicted climate change. The review addresses the CO_2 response of individuals at the physiological level and the consequences of that response to population, community, and ecosystem levels. It must, however, be emphasized that most of the findings on the physiological and allocational response to CO_2 were first discovered in agricultural crops, and that much of the initial work on plants from natural ecosystems (69) tests the variation among species in these responses.

PLANT RESPONSES AT THE PHYSIOLOGICAL LEVEL TO ELEVATED CO_2

Plant biologists have long known some of the effects of high CO_2 levels on plants, and greenhouse growers have used CO_2 fertilization to increase plant yield. Work on plants from natural ecosystems has lagged behind that on crops but, over the last few years, has produced a large body of information (see 120 for extensive reviews). The major emphases have been on individual physiological traits, but the consequences of these responses for the whole plant, population, and ecosystem are less understood and, in some cases, counter-intuitive. Many plant and ecosystem attributes will directly or indirectly be influenced by elevated CO_2 (118). Therefore, after briefly addressing physiological responses at the leaf level, I concentrate on growth and allocation, reproduction, plant-plant interactions, plant-herbivore interactions, and some ecosystem level attributes.

CO_2 and Photosynthesis

When other environmental resources and factors are present in adequate levels, CO_2 can enhance photosynthesis of C_3 plants over a wide range of concentrations. High CO_2 reduces competition from O_2 for Rubisco, increases its activation (95), and reduces photorespiration. In contrast, in plants with the C_4 metabolism net photosynthetic rates rise steeply with increased CO_2 and level off at external CO_2 concentrations slightly above ambient (122).

Early studies on the response of plants to elevated CO_2 examined short-term responses and used tissues that were grown in near-ambient but likely quite variable CO_2 levels of glasshouses and growth chambers. More recent studies use plants grown under controlled CO_2 levels. All these studies showed an increase of photosynthetic rates with increased CO_2 concentrations. Measurements of photosynthetic rates of these plants grown under ambient and elevated CO_2 levels have shown that after a period of time some species adjust their photosynthetic rates to the CO_2 levels during growth

(become acclimated) whereas other species show little or no adjustment (see 22, 87, 115, 121, 130, 141). The degree to which a species can adjust is probably influenced by the levels of other environmental variables and the timing of their availability (see later). Several investigators have also observed that with time plants grown at elevated CO₂ show a decline in photosynthetic rates. Although the reasons for this decline are not fully understood, several reasons for it have been proposed. They include: decline in carboxylation efficiency which may be caused by a decrease in the amount and activity of Rubisco (43, 105, 106); suppression of sucrose synthesis by an accumulation of starch (51, 128); inhibition of the triose-P carrier; reduction in the activity of sucrose-phosphate synthase; limitation of daytime photosynthate export from sources to sinks (36) or insufficient sinks in the plant (63). Because with acclimation there may be little overall increase in plant photosynthesis and growth, understanding acclimation to a high CO₂ environment is critical in assessing the long-term response of plants to the high CO₂ environments of the future.

From the extensive literature on the response of photosynthesis to elevated CO₂, the following patterns emerged: (a) Elevated CO₂ reduces or completely eliminates photorespiration; (b) C₃ plants are more responsive than C₄ plants to elevated CO₂ levels, especially those above ambient concentrations; (c) photosynthesis is enhanced by CO₂ but this enhancement may decline with time; (d) the response to CO₂ is more pronounced under high levels of other resources, especially water, nutrients, and light; (e) adjustment of photosynthesis during growth occurs in some species but not in others, and this adjustment may be influenced by resource availability; and (f) species even of the same community may differ in their response to CO₂ (Figure 1).

Dark Respiration

Little information is available on the effects of elevated CO₂ concentration on dark respiration rates. Enhancement of photosynthesis may lead to increased respiration because of the increased availability of substrate for respiration. Several arctic tundra species show a substantial increase in dark respiration (88). However, there was no influence of elevated CO₂ on dark respiration or on light compensation in *Desmodium paniculatum* (141). There is evidence in the agronomic literature that respiration may decline at high CO₂ levels (4). For species from natural communities, it is not known whether the change in dark respiration is proportional to the rise in net daytime photosynthesis. Furthermore, it is unknown if both growth and maintenance respiration respond to the same degree to elevated CO₂. These issues are important to the understanding of the response of whole plants to the CO₂ rise, especially in regard to carbon gain and biomass accumulation, and they require much attention.

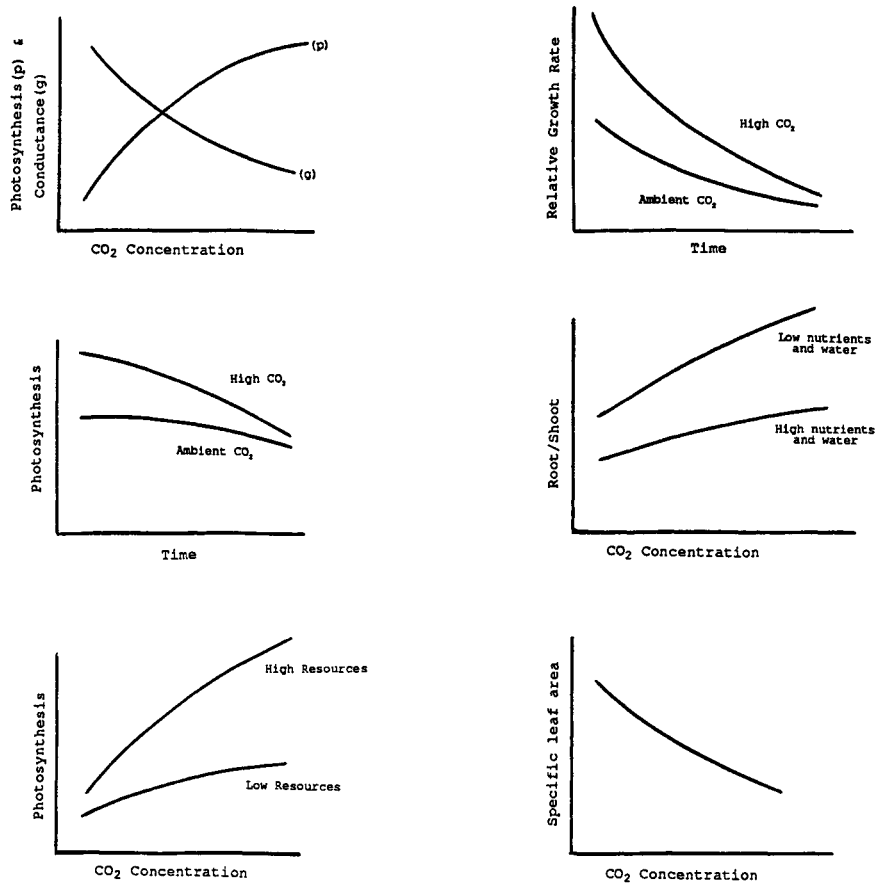


Figure 1 General trends of response of plants to CO₂ concentrations.

Stomatal Conductance, Transpiration, and Water Use

There is now some evidence that growth in high CO₂ environments causes a change in stomatal density in some species (e.g. 86). Woodward (134) has shown that stomatal density and stomatal index increased markedly as the CO₂ partial pressure is reduced below 340 $\mu\text{l l}^{-1}$. Above 340 $\mu\text{l l}^{-1}$ there is a slight decrease in stomatal density in several species studied (135).

Most studies have shown a decline in stomatal conductance with an increase in CO₂ concentrations (Figure 1). Stomatal response to CO₂ varies greatly among species and may be influenced by other environmental factors such as soil moisture and light levels (e.g. 125). Although strong evidence suggests that stomata respond more to internal CO₂ concentration than to

external concentrations (e.g. 78), the mechanism by which CO₂ controls stomatal activities is not known (95). Therefore, explanation of the differential response of stomata to the CO₂ rise is not possible at this time. Transpiration rates decline as a result of decreased stomatal conductance. This decline has been shown in several studies to lead to a favorable instantaneous water use efficiency, improved plant water status, higher carbon gain and biomass accumulation, and lower season-long water consumption rate (e.g. 100). Enhancement of plant water use efficiency was observed also in plants grown in the field (102). Drought stress in plants grown at elevated CO₂ levels may be also ameliorated by osmo-regulation and the maintenance of higher turgor pressure (112). Lower transpiration rates should lead to higher leaf temperature under high irradiance and low windspeed conditions (57). This increase, coupled with the anticipated rise in air temperature, may have significant effects on photosynthesis and plant growth.

Growth and Allocation

The critical issues that ought to be examined with regard to the effect of the rising CO₂ on plant growth are: (a) how long does the enhancement of growth continue; (b) how do the allocational relationships in the plant change with time under elevated CO₂ levels; and (c) how will tissue quality change over time and what are the consequences of this to herbivores, pathogens, and symbionts?

Most studies on the effects of elevated CO₂ show an initial enhancement in growth, and like photosynthesis, this enhancement is especially large when other resources are plentiful. In many species, however, this enhancement may decline or completely disappear in time (11, 47, 114, 123–125). Most studies have shown that there is generally an increase in allocation to roots, especially when nutrients and water are limiting (68, 75, 79, 82–84, 114, 125). There is also strong evidence that specific leaf areas (SLA) decrease with increasing CO₂ levels (e.g. 47). Decreased SLA in high CO₂-grown plants is often associated with increased starch levels in leaves and decreased N concentration. Furthermore, the concentrations of C-based secondary chemicals (e.g. phenolics) usually show no change in levels in leaves from CO₂-enriched plants even though the plants have greater carbon availability. Several studies (e.g. 114), especially with woody seedlings, have shown that branching increases with elevated CO₂. Some evidence from tree ring analysis suggests that growth in natural vegetation has been enhanced by the rising global CO₂ concentrations (66).

Phenology and Reproductive Biology

Despite its great importance to understanding the future impact of CO₂ and climate change as possible agents on natural selection, there is very limited

information on the effects of the rising CO₂ on plant reproductive biology. Most of the studies on the effects of CO₂ on plants of natural communities were terminated before reproduction. Because of the well-established effects of elevated CO₂ on plant growth, it is expected that aspects of reproduction such as flowering phenology, allocation to reproduction and to various components of reproduction, seed and flower abortion, and seed quality will also be influenced (10). Studies have shown that depending on the species, flowering time could be earlier or later under elevated CO₂ (24, 46). In some species these changes are only evident under unusually high levels of CO₂ (e.g. 117). When plants are grown in competition, significant CO₂ effects on flowering among the species were found only under high nutrient conditions (143), or the effects became less pronounced than when the plants were grown separately (E. G. Reekie, F. A. Bazzaz, unpublished). Differences in flower birth rate, flower longevity, and total floral display have been observed among species in the same community as well as among populations of the same species (e.g. *Phlox drummondii*) (46).

Reekie & Bazzaz (unpublished) examined the relation between CO₂ level and reproduction in four species from the annual community of disturbed ground in Texas. Four insect pollinated forbs with showy flowers were used. In *Gallardia pulchella*, doubling CO₂ reduced the time required for flowering by six days, though plant size at the time of flowering remained unchanged. In *Gaura brochycarpa*, doubling CO₂ also reduced time to flowering; however, these reductions do not appear to be related to increased growth at elevated CO₂. The response of *Lupinus texensis* was the reverse: elevated CO₂ increased rather than decreased the time to flowering except when the plants were given much underground space. No clear trends were found in *Oenothera laniculata*. Shifts in flowering phenology caused by CO₂ rise could have marked effects on community structure and regeneration, especially in communities where pollination is dependent upon animals or when the growing season could be short, as is the case in this community where drought can suddenly terminate the growing season. The combined effects of elevated CO₂ and other aspects of climate change, such as rising temperature, may cause large shifts in phenology such that the activities of the plants and their pollinators become decoupled.

Elevated CO₂ can also affect other reproductive parameters, such as seed number and size and seed nutrient content. In *Datura stramonium*, total fruit weight was higher in plants grown in elevated CO₂ than in plants grown in ambient CO₂. Plants grown in high CO₂ produced thicker fruit walls, which may prevent insects from laying eggs in these seeds, but, seed size was not affected (46). In *Abutilon theophrasti* grown at elevated CO₂ levels, total seed production did not increase, but flower number, capsule number, and seed number decreased (Figure 2). Individual seed weight was higher in plants

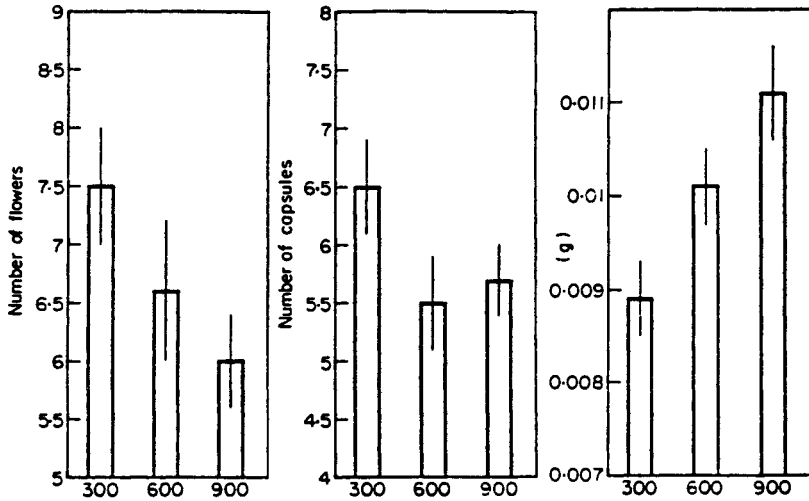


Figure 2 The influence of CO₂ concentrations during growth on flower number, seed number, and mean weight of individual seed in *Abutilon theophrasti*. From (46).

grown at high CO₂ (46). In some species (e.g. *Ambrosia artemisiifolia*) there was also much higher N concentration in seeds from plants grown at elevated CO₂ concentrations (47). Because of the well-established relationship between individual seed size and nutrient content, and seedling success in nature, the effects of rising CO₂ and associated climate change may have great impact on the demography and evolution of natural populations.

INTERACTION OF CO₂ WITH OTHER ENVIRONMENTAL FACTORS

The interaction of CO₂ with other plant resources has been amply demonstrated (Figure 1). The response of plants to elevated CO₂ is contingent upon light levels (e.g. 95, 110, 113), soil moisture (7, 138), and nutrient availability (2, 20, 93, 103, 133). Several investigators have shown that the enhancing effects of CO₂ disappear under nitrogen and phosphorus limitation (20, 50, 133, 143). Light saturation is usually higher under elevated than under ambient CO₂ (126), and high CO₂ may compensate for low light (2). Plant response to elevated CO₂ is usually more strongly expressed under higher levels of these resources, in a manner consistent with predictions about the response of plants to multiple environmental resources (16, 25).

Elevated CO₂ may modify the effects of stress factors on plant growth. Such elevation has been shown to ameliorate effects of high salinity (19) by

supplying extra energy for maintenance respiration and by the reduction in the entry of salt into the plant due to reduced transpirational pull (39, 44, 45). High CO₂ levels may influence the plant response to gaseous pollutants as well. Coyne & Bingham (27) have shown that reduction in stomatal conductance caused by high CO₂ reduces both the amount of O₃ entering the leaves and the resulting damage. Similarly, decreased stomatal conductance caused by high CO₂ reduces entry of SO₂ into leaves and lessens its damage in C₃ plants (23). SO₂ reduced the growth of the C₃ species at the ambient but not at the elevated CO₂ concentration. In contrast, in the C₄ species, SO₂ increased growth at the ambient CO₂ concentration and reduced at a high CO₂. The results of this experiment support the notion that C₃ species are more sensitive to SO₂ than are C₄ species (131). This study shows that CO₂ reversed the effect of SO₂ on C₃ but not C₄ plants, results which correlated with differences in sensitivity of stomatal conductance.

The interaction of CO₂ with temperature is critical to the response of plants to climate change. Acock (1) and Acock & Allen (2) present a model for the response of photosynthesis to temperature and CO₂. They show that at high CO₂ levels the optimal temperature for photosynthesis is higher than at ambient CO₂ and the range of optimal temperature for photosynthesis is narrower. There are, however, only a few studies that consider their joint effects. J. Coleman & F. A. Bazzaz (unpublished) examined growth and resource acquisition and allocation in response to temperature and CO₂ in a C₃ and a C₄ species that occur together in the field. The results show significant interactive effects on these parameters, but the strength and direction differed between the two species. In the C₄ species (*Amaranthus*), final biomass was increased by CO₂ at 28°C but was depressed at 38°C. In the C₃ species (*Abutilon*), CO₂ enhanced initial biomass at both temperatures, but the final biomass was not different in the two temperatures. These somewhat surprising results were explained by the amount of standing leaf areas and changed photosynthetic rates in the two species under these conditions. It was clear from this model system that the interaction between factors may be complex but could be understood by studying patterns of carbon gain and allocation.

Several of the climate models also predict that in addition to the global rise in mean annual temperature there can be an increase in temperature extremes. Furthermore, because of the generally reduced stomatal conductance under elevated CO₂ conditions, transpirational cooling of plant tissues will be reduced. Few studies have addressed the joint effects on plant growth of unusually high and unusually low temperature in conjunction with elevated CO₂. When the C₄ weedy grasses *Echinochloa crus-galli* and *Elusine indica* were grown in a range of temperatures and then subjected to one night of chilling at 7° C, the decline in both conductance and photosynthesis was less

in plants grown under elevated CO₂ than in plants grown under ambient CO₂ levels (97). Preliminary results with *Abutilon* suggest that individuals grown at high CO₂ concentrations are more sensitive to heat shock than are individuals grown at ambient CO₂ (F. A. Bazzaz, unpublished).

SUBSPECIFIC DIFFERENCES IN RESPONSE TO CO₂

Populations of the same species respond differently to CO₂, and these differences may be related to the CO₂ environment in which the plants grow (e.g. 140). However, differences among individuals of a population in response to CO₂ have rarely been investigated. Clearly, genetic differences among individuals in response to atmospheric CO₂ can affect the future of the genetic structure of the population in a changing CO₂ atmosphere. The studies that have examined variation among individuals have detected differences among them in response to CO₂. For example, Wulff & Miller (142) found that families of *Plantago lanceolata* differed in their response to CO₂ enrichment and to combinations of CO₂ and temperature treatments. They suggested the presence of genetic variability in this species in response to CO₂ enrichment. F. A. Bazzaz & G. Carlton (unpublished) found differences in CO₂ response in growth and architecture among several genotypes of *Polygonum pensylvanicum* from a single population. Garbutt & Bazzaz (46) found differences in the time of flowering, the number of flower births, and the maximum flower display among four populations of the annual *Phlox drummondii* from central Texas (Figure 3). Significant effects were also seen on plant final biomass and in the number of flowers produced per unit of plant dry weight. These responses may have significant implications for pollination success, dispersal, and establishment.

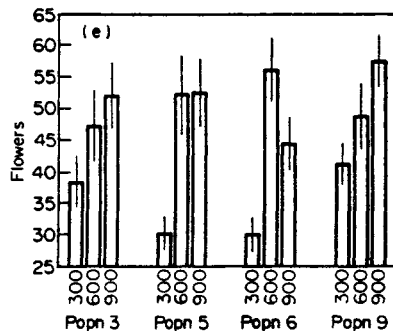


Figure 3 Differences in floral display among natural populations of *Phlox drummondii* in response to CO₂ concentration. From (46).

PLANT RESPONSE TO CO₂ AT THE POPULATION LEVEL

Almost no information is available on the response to elevated CO₂ at the population level. But because elevated CO₂ affects growth, allocation, and reproduction, undoubtedly there are some effects on populations. Using our model system of the annuals *Abutilon theophrasti* and *Amaranthus retroflexus*, we investigated how the simultaneous changes in CO₂ and temperature affect the recruitment of seeds into the population (S. Morse, F. A. Bazzaz, unpublished). Although no differences appear in survivorship with respect to ambient CO₂ concentrations for either species, stand productivity was significantly affected by both CO₂ and temperature. In general, stand productivity increased with both CO₂ and temperature and was inversely proportional to the number of survivors. CO₂ magnified the intensity of plant-plant interactions and enhanced the growth of the remaining dominant individuals.

INVESTIGATIONS AT THE COMMUNITY AND ECOSYSTEM LEVELS

Productivity

Predictions about the changes in productivity of ecosystems are also based on the generally observed increase in plant growth under high CO₂ conditions. A physiologically based graphical model (Beam 82) was proposed by a group of scientists (see 119) to represent possible changes in productivity of ecosystems. To address the relationship between elevated CO₂ and productivity, Gates (48) suggested a modification of the B factor, described by Bacastow & Keeling (5), and proposed B' (the biotic growth factor), based on the Michaelis-Menton equation. B' is the fractional increase in net primary productivity (NPP) with a fractional increase in CO₂ concentration. Using data on single leaves, Gates (48) calculated B' factors for several deciduous forest tree species and showed that they could be high, ranging from 0.33–0.53. However, he also found that, depending on environmental limitations, the B' values could be small (between 0.05–0.25). Using high B' values, Gifford (49) estimated high carbon storage in the biosphere (1.65 Gt y⁻¹ for B' = 0.60). Several other authors (e.g. 18, 48, 54, 64, 73) have pointed out that because of the limits on plant growth already set by water and nutrient deficiency, and temperatures at the northern limits of distribution, primary productivity in natural ecosystems may not be enhanced much by the rising global CO₂. Furthermore, even in systems that have the potential for an increase in production, Oechel & Strain (88) show that negative feedbacks may soon lead to the elimination of any enhancement by the rising CO₂. For

example in the chaparral, a water-limited system, increased water use efficiency may lead to enhanced productivity. However, the chaparral is a fire-prone system, and the increased accumulation of living and dead biomass may increase the frequency of fire, which in turn would reduce biomass accumulation. In contrast, Luxmoore (74) suggests a different scenario, where increased photosynthesis in a high CO₂ environment would increase the amount of carbon allocated to roots, resulting in increased root exudation, mycorrhizal proliferation, and increased N-fixation. Evidence also suggests increased nitrogenase activity at high CO₂ levels (81). These factors in turn can lead to increased water and nutrient supply to the plants and increased phytomass even in somewhat infertile habitats. The very limited evidence from field studies shows both an increase in productivity with elevated CO₂, especially during the first year or two (e.g. 29, 90), and no change (121). Thus, these responses to elevated CO₂ remain very poorly understood despite their great importance in predicting future productivity. Accurate predictions about the response of natural ecosystems to global increase in CO₂ levels still require much additional data on the mechanistic bases of the responses of several ecosystems (31).

RESPONSE OF SPECIFIC ECOSYSTEMS TO ELEVATED CO₂

Graminoid-Dominated Ecosystems

CO₂ AND ARCTIC TUNDRA Arctic ecosystems may be the ecosystems most sensitive to climate change (see 119). All climate models show a greater increase in mean annual temperature in these regions, compared to lower latitudes. Arctic ecosystems possess several properties that make them of particular interest to the study of CO₂ response (12). Because of permafrost, the active layer of the soil is shallow, and the top 10 cm of the soil contain most of the root and rhizome systems, which constitute by far most of the living biomass in this ecosystem. Up to 90% of the CO₂ which evolves from soil comes from root and rhizome respiration (12). Tundra soils also contain large quantities of organic matter which, being mostly in the permafrost, is normally unavailable to decomposers.

In a series of experiments with microcosms of intact cores of turf and soil of coastal arctic tundra, W. D. Billings and associates (13–15, 96) examined the effects on ecosystem carbon balance of doubling CO₂, increasing temperature, lowering the water table, and applying N-fertilizer. They concluded that increasing summer temperature by 4°C would reduce net ecosystem CO₂ uptake by half. Lowering the water table by only 5 cm and increasing temperature greatly lowered ecosystem carbon storage. In contrast, doubling CO₂ concentrations per se had very little effect. They suggest that warmer

temperatures would extend the growing season into the short days of autumn, expose much more peat to decomposers (which become more active in the higher temperatures and the longer season), and lower the water table by high transpiration under the warm conditions. Enhanced ecosystem carbon gain caused by the release of nutrients would be more than offset by decreased insulation and the resultant lowering of the permafrost table and increased soil erosion. From these studies Billings reaches the dramatic conclusion that doubling CO_2 would convert the wet tundra ecosystem from a CO_2 sink to a CO_2 source.

W. Oechel and coworkers have been studying the response of arctic ecosystems to the increase in CO_2 and temperature using environmentally controlled greenhouses placed in situ in the tundra near Barrow, Alaska (99, 88, 121). Contrary to most results obtained on the response of single individuals, *Eriophorum* plants in situ showed little response to high levels of CO_2 . Plants grown at the high CO_2 adjusted their photosynthetic rates within three weeks so that their rates were similar to those grown under ambient CO_2 when both were measured at CO_2 levels of their growth. Although there was no seasonal pattern of growth, a significant increase occurred in tillering under the high CO_2 conditions. When responses to elevated CO_2 under controlled conditions of six arctic tundra species of different growth forms were compared (in 88), most of the species had increased their photosynthetic rates on a leaf area basis, but they varied in the degree of response, and that was influenced by nutrient level. All species except *Eriophorum* had increased leaf dark respiration as well. Surprisingly, and contrary to the results from the in situ measurements, the photosynthetic rate of *Eriophorum vaginatum* was enhanced, especially under high nutrient conditions, and that enhancement was still high after 2 months of exposure to the high CO_2 level. Oberbauer et al (87) found that *Carex bigelowii*, *Betula nana*, and *Ledum palustre* responded to elevated CO_2 and nutrient levels. They found that nutrients enhanced growth much more than did CO_2 and concluded that CO_2 with or without nutrient limitation has little effect on the production of these species. These results point out the importance of in situ measurements to accurately assess plant response to elevated CO_2 concentration. Analysis of whole ecosystem response to elevated CO_2 and temperature from the in situ measurements shows that net CO_2 uptake by tussock tundra was higher at elevated CO_2 than at ambient CO_2 . But, net CO_2 uptake was reduced by temperatures 4°C higher than ambient (53). Although the higher temperature increased conductance and consequently gross photosynthesis, higher temperatures also increased respiration to a degree that resulted in lower net CO_2 uptake. These authors conclude that nutrient limitation in this system lowers the ability of tundra plants to make full use of the elevated CO_2 concentrations.

The following conclusions emerge from work on this ecosystem: (a) in *Eriophorum*, the dominant species in this system, only tillering increases dramatically with rise in CO₂; (b) photosynthetic acclimation to high CO₂ occurs; (c) nutrients enhance the response to increasing CO₂; (d) species differ in the degree to which growth is enhanced by CO₂; (e) different life forms do not seem to respond differently to increase in CO₂; (f) conductance and respiration increase; and (g) temperature rise lowers the CO₂ enhancement effects. Therefore, while some general responses are similar to those observed in other ecosystems, the tundra ecosystem differs in some quite surprising ways, particularly the increase in conductance.

From the available data, the following scenario emerges: As CO₂ and temperature rise, thaw of permafrost increases, the growing season lengthens, decomposition of organic matter increases sharply, nutrient availability increases, net CO₂ uptake increases, and transpiration increases because of higher temperature and increased conductance. After a while, however, the water table recedes, photosynthesis and net ecosystem productivity decrease, and the system becomes a CO₂ source and a positive feedback loop would be established.

THE ESTUARINE MARSH Another in situ study of the response of graminoid ecosystem to elevated CO₂ has been underway in the estuarine marsh of Chesapeake Bay, Maryland, USA. Open top chambers were used by B. Drake and his associates to enclose stands of *Scirpus olneyi* (C₃), *Spartina patens* (C₄), and a combination of both species and to expose them to ambient ($350 \pm 22 \mu\text{l l}^{-1}$) and elevated ($686 \pm 30 \mu\text{l l}^{-1}$) CO₂ concentrations. Elevated CO₂ increased shoot density, delayed senescence, and increased biomass in *Scirpus*, the C₃ species, but there was no effect on *Spartina*, the C₄ species (30). Furthermore, *Scirpus* responded positively to elevated CO₂ both in pure and in mixed stands. Carbon-nitrogen relations were also examined for these species (29). While carbon percentage did not change with elevated CO₂ in green leaves of *Scirpus*, nitrogen was reduced by as much as 40%. Furthermore, aboveground tissue content of nitrogen on a per leaf area basis was not influenced by CO₂, indicating that nitrogen was allocated from storage pools. Surprisingly, litter C/N ratio was not affected by CO₂ level, and the authors suggested that CO₂ rise will not influence the rate of decomposition or N mineralization. Because of the continued input of nutrients in water from the adjacent creek into this already highly productive marsh, the authors conclude that continued exposure to high CO₂ levels may cause a continued increase in *Scirpus* productivity and increased dominance in this system. Thus, this situation contrasts sharply with that observed in the nutrient-limited tundra ecosystem discussed previously.

OTHER GRASSLANDS Information about the response of grasslands to elevated CO_2 is very limited. Smith et al (115) compared the response of four grass species from the Great Basin. High CO_2 resulted in increased growth, especially basal stem production, in the C_3 but not in the C_4 species. This enhancement was particularly strong for *Bromus tectorum*, an introduced weed. Since *Bromus* predisposes rangelands to burning, the authors speculated that this enhancement by high CO_2 levels in the future may increase the number and the severity of wildfires in this region, which could result in a change in ecosystem function. Work with Blue grama (*Bouteloua gracilis*), an important native perennial in the same region, showed that biomass and leaf area were greatly enhanced at elevated CO_2 levels, which is unusual for a C_4 plant (101).

When plants were grown individually, CO_2 concentration differentially influenced the growth of six species from the short annual grasslands found on serpentine soil in California (129). In competition, however, these species did not differ in their growth response to CO_2 . The species are of small stature and presumably adapted to low nitrogen and calcium availability and to heavy metals such as Ni and Mg. Apparently, the potential for these species to respond to increased CO_2 concentrations may be constrained by physiological traits that enable these annuals to grow in their native, nutrient-limited environment. Furthermore, in this low-stature community with a very short growing season and nutrient limitation, competitive networks and adaptation can develop and dampen the CO_2 effects.

Regenerating Ecosystems

The speed of the rise in CO_2 concentrations and the associated temperature rise will far exceed the regeneration time of many woody species in the world and their migration to new habitats (32). Thus, this rapid change would likely result in the death of many individual plants and their replacement with early successional species that, in general, are adapted to live in an environment with initially high resource levels (6). Regenerating ecosystems may be the dominant ones over much of the landscape in a high CO_2 world. Thus, the study of regenerating ecosystems is crucial to assessing the possible impact of global change. Our extensive knowledge of their behavior at the physiological, populational, and community levels under ambient and more recently elevated CO_2 may allow some predictions about their future.

The Early Successional Community: A Model System

NONCOMPETITIVE RESPONSE Work in our laboratory has focused mainly on community level, using individual species responses to interpret communi-

ty level responses. A major premise of the research is that the response of individuals is highly modified by the presence of other individuals in a population or a community, and that these relationships themselves would be modified by other factors in the natural environment.

Community-level investigations of CO₂ effects on plant growth were reported by Carlson & Bazzaz (22). The annual community of postagricultural succession and the flood plain forest community in the midwestern United States were studied. The experiments also included three crop species (corn, soybean, and sunflower) in order to compare results with the published agronomic literature. The results confirmed that species from natural communities have physiological responses similar to those of the agronomic species studied thus far. The degree of variation in response of different species even of the same community was enormous. Based on these findings, and without consideration of the associated climate change, three hypotheses about the effects of elevated CO₂ on plants were put forward: (a) Because of increased water use efficiency, plant species will be able to expand their ranges into drier habitats; (b) competitive interactions among species in a community may change and will result in a change in community composition and function; and (c) competitive interaction between crops and weeds may change. The latter hypothesis was also proposed by Patterson & Flint (92) and was later confirmed (94).

Further work with individually grown plants established the fundamental physiological and morphological basis of the response of plants to CO₂ and its interactions with other environmental factors. Most of these studies involved growing several species individually and studying differences among them in their photosynthetic response, growth and allocation, or some other indicator of their potential competitive success. These results were used to infer competitive outcome among species (e.g. 8). The results have also been useful in interpreting the response of communities to the rising CO₂ levels. We chose as a model system an early successional community of annual plants to investigate in detail aspects of the CO₂ response at the individual, population, and community levels. Depending on the questions asked we sometimes used all dominant species of the community and sometimes a subset of these species. This community was chosen because annual plants can be grown to maturity, so that the effects of CO₂ on all phases of the life cycle, including reproduction, could be studied, and also because we have accumulated much background information on this community over two decades. The community is dominated by a small number of species (five to six) and has both C₃ and C₄ plants. Comparing the response of the major species in this community to elevated CO₂ when the plants were grown individually (47), we found:

1. CO₂ concentration had little effect on the timing of seedling emergence;
2. Photosynthetic rates increased and stomatal conductance decreased with increased CO₂;
3. The levels of CO₂ during growth had no effect on photosynthetic rates;
4. Shoot water potential was less negative in plants grown at high CO₂;
5. Relative growth rates were enhanced by CO₂ early in the growth period but declined later;
6. Specific leaf area (SLA) consistently decreased with increased CO₂;
7. High CO₂ caused one species to flower earlier and one to flower later, while the rest showed no change;
8. There were significant species x CO₂ interactions for leaf area, leaf weight, weight of reproductive parts, and seed weight indicating species-specific response to CO₂; and
9. Carbon/nitrogen ratios increased with increasing CO₂.

The results of this experiment and others also suggest that the commonly suggested C₃/C₄ dichotomy does not fully explain the responses of plants to CO₂. For example, *Amaranthus* (C₄) often shows a greater increase in biomass as a result of elevated CO₂ than does the C₃ species *Abutilon theophrasti* (8, 47).

COMPETITIVE RESPONSE IN THE MODEL SYSTEM Under competitive conditions the interaction between CO₂ concentration and soil moisture showed that total community biomass increased with increasing CO₂ at both moist and dry soil moisture conditions. The contribution of each species to total community biomass was greatly influenced by CO₂. For example, *Polygonum pennsylvanicum* contributed more at high CO₂ and moisture levels. In contrast, *Amaranthus retroflexus* declined under these conditions (7). These results are commensurate with the response of these species individually to CO₂ and moisture separately. Work on the interaction of CO₂ with light and nutrients (143) using all six species from this community showed that total community production reached its peak at 450 μl l⁻¹ CO₂. While total community biomass was higher under high light, relative to low light, and under high nutrients, relative to low nutrients, the response of the community to elevated CO₂ was affected by light level but not by nutrient availability. The relative success of some species, particularly in terms of seed biomass and reproductive allocation, was significantly altered by CO₂. The contribution of the C₃ species in this community to total production increased with CO₂ enrichment.

Competitive interactions and CO₂ have been examined in more detail using one C₃ and one C₄ plant from this community. Detailed growth analysis, patterns of leaf display, and N allocation were used to understand the mechanisms of interaction and to begin to model these interactions (11). The species were grown both individually and in competition with each other. At

ambient CO₂ levels *Abutilon* was competitively superior to *Amaranthus* because the latter was unable to overcome the initial difference in starting capital (larger seeds and seedling). But, at elevated CO₂ that difference disappeared, largely because of the enhanced relative growth rate (RGR) of *Amaranthus* in high CO₂ (especially earlier in the growth period) which overcame the seed size advantage that *Abutilon* has over *Amaranthus*. High CO₂ caused an increase in root/shoot ratio in *Abutilon* and a decrease in *Amaranthus*. But *Amaranthus* had a much higher rate of N uptake per unit of root relative to *Abutilon*. Thus, the results of this experiment show that: (a) the response to high CO₂ is limited to early stages of growth; (b) elevated CO₂ greatly increased RGR in *Amaranthus*; and (c) although, when compared with C₃ plants, C₄ plants show a lesser enhancement of photosynthesis and net assimilation rate (NAR) with increased CO₂ levels, they did not "lose out" in competition with C₃ plants at elevated CO₂ concentrations.

Bazzaz & Garbutt (8) studied the influence of the identity of competing species and that of neighborhood complexity on the interaction between CO₂ and competition. Four species of the annual community were grown in monoculture and in all possible combinations of two, three, or four species at levels of CO₂. Overall, the species responded differently to CO₂ levels. In mixtures the species interacted strongly, and in some cases these interactions cancelled out the effects of CO₂. For example, there were clear differences in the responses of species in different competitive neighborhoods. All competitive arrays that had C₃ species in them depressed the growth of the C₄ species (Figure 4). The interactions between CO₂ and the identity of the competing species were particularly strong at the intermediate CO₂ level (500 $\mu\text{l l}^{-1}$). These findings suggested that competitive outcome will be modified by CO₂ and by the interaction of CO₂ with other environmental factors. They show that different species will behave differently in a high CO₂ world and that their response will depend on the identity of the competing species and perhaps on community diversity.

Early Perennial Stage

The interaction between *Aster pilosus* (C₃) and *Andropogon virginicus* (C₄), important species in old-field succession, was studied by Wray & Strain (137, 138, 139). They grew the two species both separately and in competition in ambient and high CO₂ levels, while half of them were subjected to a drought cycle. In *Aster*, droughted plants grown at high CO₂ had greater leaf water potential and greater photosynthetic rates and total dry weight than did plants grown at ambient CO₂. In contrast, in *Andropogon* no differences appeared among CO₂ treatments in response to drought. In competition the differences between the species in response to elevated CO₂ were accentuated, and *Aster* strongly dominated *Andropogon*. These authors suggested that CO₂ enrich-

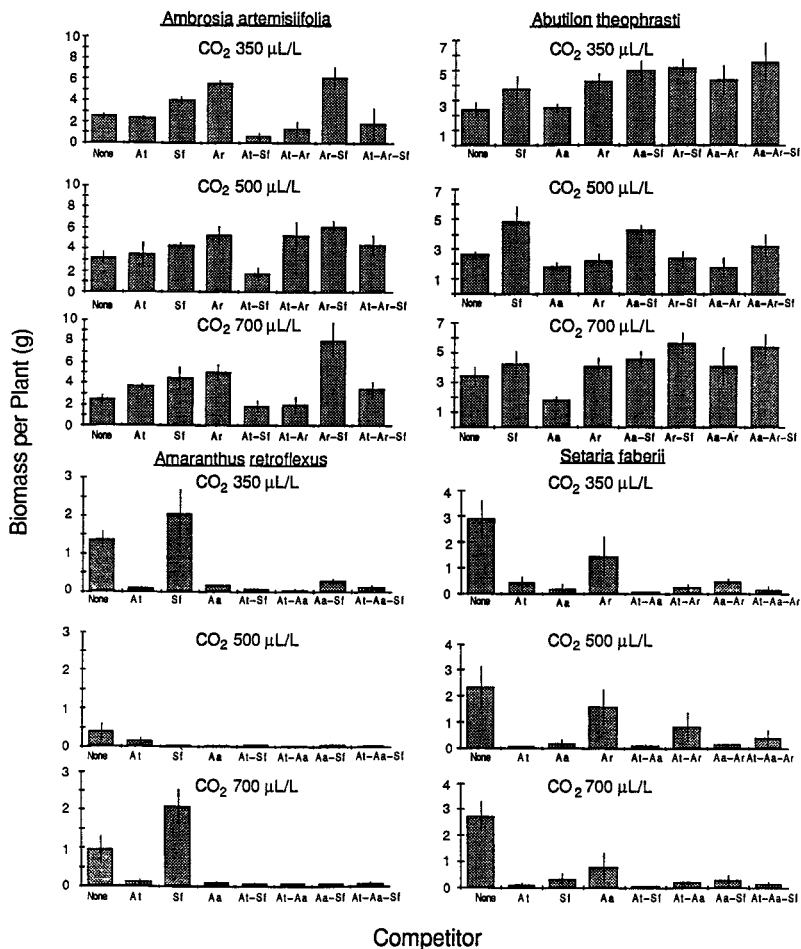


Figure 4 The relationship between plant growth, identity and diversity of competitors, and CO₂ concentrations during growth in a community of annuals made up of two C₃ species (*Ambrosia artemisiifolia* (Aa), and *Abutilon theophrasti* (At)) and two (C₄) species (*Amaranthus retroflexus* (Ar), and *Setaria faberii* (Sf)) From (8).

ment may increase the competitive ability of *Aster* relative to *Andropogon*, allowing *Aster* to persist for longer periods during old-field succession.

Early Successional Trees

Tolley & Strain (123–125), Sionit et al (114), and Fetcher et al (43) studied the response of Sweetgum (*Liquidambar styraciflua*) and loblolly pine (*Pinus taeda*), two midsuccessional tree species, to elevated CO₂. They found that elevated CO₂ increased components of growth more in sweetgum than in loblolly pine, especially at high irradiance. Sweetgum developed more rapid-

ly, reached maximum size earlier, and maintained height dominance relative to loblolly pine. Under drought stress high CO₂-grown sweetgum individuals developed internal water deficits more slowly than did those grown under ambient CO₂, and the seedlings maintained higher photosynthetic rates over the drying cycle. In contrast, loblolly pine seedlings had a more severe internal water deficit than did sweetgum, irrespective of CO₂ level. The authors concluded that sweetgum seedlings should tolerate longer exposure to low moisture, especially under high CO₂ conditions, and that these conditions would result in greater seedling survival on drier sites in successional fields in the piedmont. Furthermore, the height dominance and shading that sweetgum presently exerts on pine may be intensified in a high CO₂ environment. In the climate of the future, with high CO₂, the authors suggest that sweetgum could displace loblolly pine.

Forest Ecosystems

TEMPERATE FORESTS Only a few studies have examined the response of tree species in a community context, and fewer still in competitive situations. Seedlings of the dominants of a floodplain forest community and of an upland deciduous forest community were grown as two groups in competition under ambient and elevated CO₂ concentrations (130). Photosynthetic capacity (rate of photosynthesis at saturating CO₂ and light) tended to decline as CO₂ concentration increased. Stomatal conductance also declined with an increase in CO₂. Nitrogen and phosphorus concentrations generally decreased as CO₂ increased. Overall growth of both communities was not enhanced by CO₂, but the relative contribution of species to the total community biomass changed in a complex way and was also influenced by light/CO₂ interactions.

In four cooccurring species of *Betula*, elevated CO₂ enhanced survivorship in yellow birch only, but nearly doubled total weight and root/shoot ratio in all species. However, differences among the species in growth response to elevated CO₂ were small despite the differences among the species in habitat preference (F. Bazzaz, unpublished). The response to CO₂ of seven co-occurring tree species from the Northern Hardwood forests in New England was studied by F. A. Bazzaz, J. Coleman, & S. Morse, (unpublished). Seedlings of *Fagus grandifolia*, *Acer saccharum*, *Tsuga canadensis*, *Acer rubrum*, *Betula papyrifera*, *Prunus serotina*, and *Pinus strobus* were grown under 400 $\mu\text{l l}^{-1}$ and 700 $\mu\text{l l}^{-1}$ CO₂. The species differed greatly in their responses; elevated CO₂ significantly increased the biomass of *Fagus*, *Prunus*, *Acer saccharum*, and *Tsuga*, but only marginally that of *Betula*, *Acer rubrum*, and *Pinus*. Under the conditions of this experiment—relatively low light (400–700 $\mu\text{mole mole}^{-1}$) and high nutrients—the species that are considered more shade tolerant and late successional (*Fagus*, *Acer saccharum*, and *Tsuga*) showed the largest biomass increase, with high CO₂ levels. Furthermore, *Betula* and *Acer rubrum* grown from seed did not exhibit

different responses to elevated CO₂ than did those individuals transplanted from the field while dormant. These results suggest that seedlings of the late successional trees in this system growing in the shade and with ample nutrients will do relatively better in a high CO₂ world than will early successional trees in open environments. This may be particularly important since young seedlings near the forest floor may experience a high CO₂ environment caused by the efflux of CO₂ from the soil (9). These findings, at first glance, differ from those of other studies (e.g. 86) which found that growth enhancement by elevated CO₂ in *Ochroma lagopus*, a fast growing pioneer species, was greater than that in *Pentaclethra macroloba*, a slower growing climax species. Furthermore, Tolley & Strain (123) found a greater enhancement of growth in the faster growing of two early successional tree species *Liquidambar styraciflua* and *Pinus taeda*. The findings of these two studies fit the general notion that early successional plants growing in open environments are able to take opportunistic advantage of available resources and that they have high growth rates (6). However, the results from the seven-species study point once again to the importance of other environmental resources in modifying the response of plants to elevated CO₂.

TROPICAL RAINFORESTS Reekie & Bazzaz (100) studied competition and patterns of resource use among seedlings of tropical trees under ambient and elevated CO₂ using five relatively fast growing early successional species from the rainforest of Mexico (*Cecropia obtusifolia*, *Myriocarpa longipes*, *Piper auritum*, *Senna multijuga*, and *Trichospermum mexicanum*). Elevated CO₂ only slightly affected photosynthesis and overall growth of the individually grown plants but greatly affected mean canopy height. Though stomatal conductance slightly declined with increased CO₂, leaf water potential and plant water use were relatively unaffected. However, in the competitive arrays there were marked effects of CO₂ on species composition, with some species decreasing and others increasing in importance. High CO₂ increased the mean canopy height in *Cecropia*, *Piper*, and *Trichospermum*, and decreased it in *Senna* (Figure 5). There were also some differences among species in allocation to roots and in the timing of that allocation. Stepwise regression analysis of several physiological and architectural measurements showed that canopy height (leaf display in the canopy) was the single most important variable determining competitive ability. Photosynthetic rates, especially in low light, and allocation to root early in the growth period were also significant. The results of this study suggest that competition for light was the major factor influencing community composition, and that CO₂ influenced competitive outcome largely through its effects on canopy architecture. Early in the experiment competition for nutrients was intense. This allowed *Piper*, with greater allocation to roots, to gain a competitive edge.

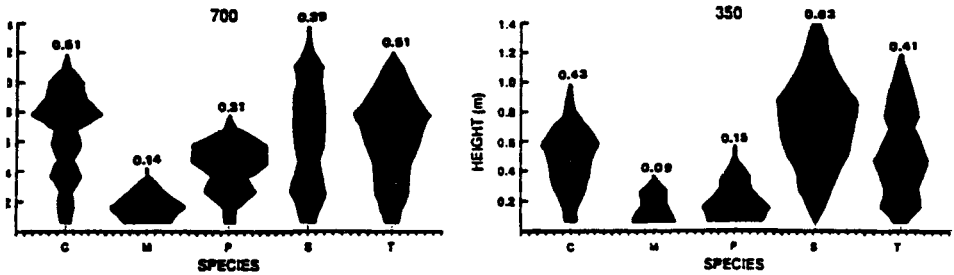


Figure 5 Leaf area profiles, and mean canopy height of seedling of 5 fast-growing tropical rainforest trees grown at 350 (left) and 700 $\mu\text{l l}$ (right) CO₂. Each unit on the horizontal axis represent 1 dm². The species are *Cecropia obtusifolia* (C), *Myriocarpa longipes* (M), *Piper auritum* (P), *Senna multijuga* (S), and *Trichospermum mexicanum* (T). From (100).

Very rapidly, however, the canopy closed and competition for light become more intense. Therefore, *Senna*, *Trichospermum*, and *Cecropia*, with their greater biomass allocation to shoots, were able to overtop the other species. *Senna* was particularly successful because of its high photosynthetic rate and tall shoot architecture. Thus, the major effect of elevated CO₂ on competition was through its modification of plant architecture.

CO₂ AND EFFECTS ON SOIL MICROORGANISMS/PLANT ROOT INTERACTIONS

It has been hypothesized that high CO₂ and the resulting high availability of photosynthate will enhance root growth and root exudation in the soil. These will in turn influence plant nutrition by enlarging soil volume explored by roots and by increasing mycorrhizal colonization (119), nodulation, and nitrogen-fixing capacities (67, 74). There have been only a few tests of these ideas with plants from natural ecosystems. In *Quercus alba* seedlings grown in nutrient-poor forest soil, elevated CO₂ increased growth, especially of the root system (83). Much of the nitrogen was in fine roots and leaves, and the plant's efficiency of N-use was enhanced. Furthermore, elevated CO₂ increased uptake of P which may have also been associated with a greater proliferation of mycorrhizae and rhizosphere bacteria. The weight of new buds of seedlings grown in elevated CO₂ was greater than of those of seedlings grown in ambient CO₂, suggesting that shoot growth in the subsequent year would be enhanced (84). Seedlings of *Pinus echinata* grown in elevated CO₂ allocated proportionally more photosynthate to fine roots, produced larger fine root mass, and had higher mycorrhizal density than plants grown in ambient CO₂ (85).

Although there have been no experimental tests of the hypothesis, several

authors have predicted that the rate of litter decomposition may be slower in high CO₂ environments (119, 130). These predictions are based on the finding in the majority of studies that the carbon-to-nitrogen ratio of tissues grown under elevated CO₂ levels declines and on experimental evidence that tissue with high lignin and low nitrogen content decays slowly (77).

CO₂ AND PLANT-HERBIVORE INTERACTIONS

Elevated CO₂ concentrations within the range predicted by global change scenarios are unlikely to influence herbivores directly (e.g. 42). However, several investigators (see 119) have suggested that the tissue quality of plants grown under high CO₂ environments could be altered, thereby indirectly affecting insect performance. Recent experimental evidence has supported this notion. For example, most studies have demonstrated that foliar nitrogen concentrations, a limiting nutrient for insect herbivores (76), decline with increased CO₂ (40–42, 59, 70, 71, 130, 133). Other important nutritional factors, such as foliar carbon-based allelochemical and fiber concentrations, do not seem to be affected by elevated CO₂ conditions (40–42, 70, 59), and foliar water content does not change in any consistent way in higher CO₂ atmospheres (e.g. 71, 41). Too few systems have been examined to make any general statements about these patterns.

Insect herbivore behavior and subsequent performance are affected when they are reared on low nitrogen, high CO₂ grown plants. To compensate for the lower nitrogen concentrations, insect herbivores feeding on high CO₂ grown foliage increase their consumption rate by 20%–80% compared to those larvae feeding on low CO₂ grown tissue (40, 59, 70, 72). Despite this increased consumption, insect herbivore performance on high CO₂ grown plants is often poorer than on low CO₂ grown plants. Lepidopteran larval mortality increases (3, 41), and growth is often slower for larvae reared on high CO₂-grown plants (40–42) (Figure 6). Slower growth might reduce insect herbivore fitness in the wild due to an increased exposure to predators and parasitoids (98) and a decrease in the likelihood of their completing development in seasonal environments (e.g. 26). Reduced population numbers have also been observed for foliage-feeding herbivores on plants in enriched CO₂ environments in open-top chambers (21). Interactions between plants and other plant-eating organisms, such as mammals, have yet to be investigated.

GLOBAL CHANGE AND PREDICTED CHANGES IN SPECIES RANGES

Various modelling results, based on changes in temperature caused by the increase in CO₂ and other greenhouse gases, have suggested a significant

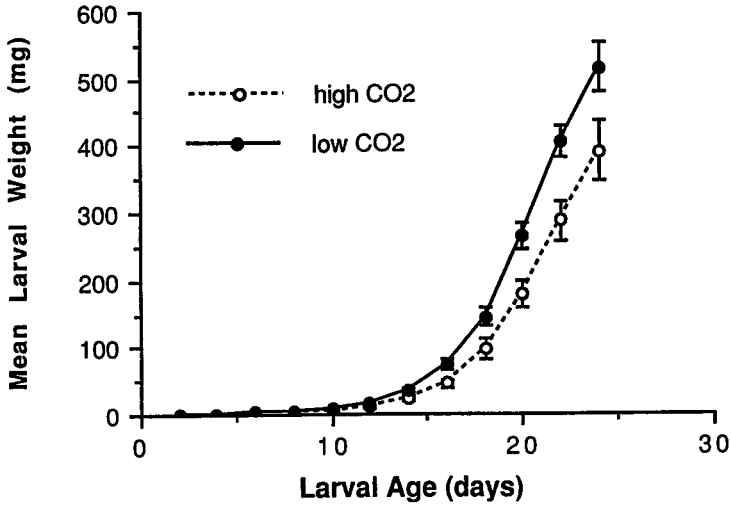


Figure 6 Growth of larvae of the Buckeye butterfly *Junonia coenia* on *Plantago lanceolata* grown at ambient and elevated CO₂ concentration. From (41).

change in patterns of regional plant productivity (109, 38, 116), in the distribution ranges of some plant species (34, 33), and in species composition on a regional scale (91). For example, the range of American beech (*Fagus grandifolia*) could drastically change, and its distribution could be several hundred miles north of its current position (33). Additionally, based on the direct response to increased CO₂ alone and the resultant decrease in water consumption, it was also predicted that the ranges of species can expand into drier habitats (22). Of course, neither of these approaches by itself would yield definitive conclusions; the influence of both the direct and indirect effects of the rising CO₂ should be jointly considered. Using growth and other physiological data on the response of the weedy vines Kudzu (*Pueraria lobata*), and honeysuckle (*Lonicera japonica*) to elevated CO₂, and considering the indirect effects of the CO₂-induced climate change, Sasek & Strain (107) concluded that elevated CO₂ levels and increased winter minimum temperatures may allow northward and westward migration of both species, but the decreased summer precipitation may minimize the westward spread. It must be pointed out that these predictions concern only the potential for range shifts in species and do not take into account the new and potentially very effective barriers to and corridors for dispersal of propagules, nor do they consider the important factors of the changed plant/plant interactions, plant/animal interactions, and plant/microbial interactions.

CONCLUSIONS

It is clear from this review that some general patterns of response of plants, especially at the physiological level, to the rising CO₂ and the associated climate change are beginning to emerge (Figure 1). Enhanced photosynthesis and growth, increased allocation to underground parts, and particularly water use efficiency have been strongly documented. However, photosynthesis and growth enhancement in some species can be of limited duration, perhaps because of shortages of sinks and the resulting simulation of photosynthates in leaves. It is also clear that CO₂ interacts strongly with other environmental factors, especially nutrients and temperature, to generate the response at the individual level.

Work at the community and ecosystem level has clearly shown that, in most situations, the response at the individual level may become highly modified and may not predict the response of communities. It is quite likely that the impact on productivity of ecosystems may result mainly from changes in species composition brought about by differential species response to elevated CO₂. The number and the identity of neighboring plants, the levels of environmental resources, the activities of herbivores, pathogens, and symbionts are crucial to the way plants respond to elevated CO₂. Because of the complexity of these interactions, and our limited knowledge of them, our predictions about the future impact of the rising CO₂ and associated climate change are very tenuous. In fact, for some ecosystems we cannot presently even predict the direction of the change that would result from increasing CO₂. Nevertheless, the work on a model system of annual plants, and with other assemblages, is giving us some insights into the mechanisms of the response to CO₂ at the community level. We are beginning to identify certain parameters that seem to explain significant amounts of the response to elevated CO₂. For example, initial relative plant growth rates and biomass allocation seem very important determinants of plant response to CO₂. Responses at the population level are essentially unknown, but that research in this area, particularly plant-animal interactions, will be of great importance in understanding the future of biological systems in a high CO₂ world.

ACKNOWLEDGEMENTS

I thank J. Coleman, E. Fajer, S. Morse, K. Norweg, A. Quinn, and D. Tremmel for much help in preparing this review. I also thank the U.S. Department of Energy for their support.

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