

# Predicting Ecosystem Responses to Elevated CO<sub>2</sub> Concentrations

*What has been learned from laboratory experiments on plant physiology and field observations?*

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One of the many changes occurring in the biosphere due to human activities is the increase in the carbon dioxide concentration of the atmosphere. This change is due both to the burning of fossil fuels, which is ejecting approximately 5–6 gT of carbon into the atmosphere yearly, and to deforestation, which may account for another 1–2 gT (Moore and Bolin 1986/87, Detwiler and Hall 1988). The preindustrial atmospheric CO<sub>2</sub> concentration has been estimated at 280 cm<sup>3</sup>m<sup>-3</sup> (Gammon et al. 1985), increasing to 350 cm<sup>3</sup>m<sup>-3</sup> today (Keeling et al. 1989). This rise is an increase of 21% in 170 years, with the most rapid increase occurring since 1950, when the concentration was 310 cm<sup>3</sup>m<sup>-3</sup>.

We do not yet know how these changes are affecting terrestrial ecosystems. This ignorance is partly because we have relatively poor records of the functional and structural response of any ecosystem through

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**It is urgent that we soon initiate bold and innovative large-scale experiments**

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time. Even with better records, it might be difficult to attribute any changes noted to CO<sub>2</sub> effects alone.

First, there are large errors in measurements of ecosystem properties. Second, ecosystems respond in a quantitative manner to naturally fluctuating climatic conditions, and there is considerable year-to-year variation in productivity, for example, due to changes in precipitation patterns and temperature regimes alone. Third, these systems may have large responses to changing pest cycles, which are in turn driven in part by the varying climate. Finally, not only is the CO<sub>2</sub> concentration of the atmosphere increasing, but so too are the concentrations of a number of pollutants that have adverse effects on system productivity. For example, there is evidence that ozone concentrations in the troposphere have increased to the extent that they are reducing crop productivity in the United States as much as 5–10% (Heck et al. 1983) and are affecting forests (Miller 1983, Wang et al. 1986).

In this article, we indicate what can be predicted about the CO<sub>2</sub> response of plants from physiological measurements and what has been learned from field observations. We then

show results from direct tests of the CO<sub>2</sub> response of whole ecosystems and indicate the promise and problems of these approaches. We also discuss the need for new ecosystem-level experiments and identify some of the challenges. The responses of plants and ecosystems to rising atmospheric CO<sub>2</sub> have been reviewed previously (e.g., Kramer and Sionit 1987, Morison 1990, Strain and Bazzaz 1983, Strain and Cure 1985).

## Physiological responses to CO<sub>2</sub> enrichment

There have been many demonstrations of enhanced rates of photosynthesis in C<sub>3</sub> plants with elevated atmospheric CO<sub>2</sub> levels (Acock and Allen 1985, Cure and Acock 1986, Oechel and Strain 1985). These rates are the result of two opposing effects of CO<sub>2</sub>, one on stomata and the other on the enzyme ribulose biphosphate carboxylase/oxygenase (rubisco). A doubling of CO<sub>2</sub> decreased stomatal conductance by approximately 36% in 16 herbaceous species (Morison and Gifford 1984); however, lower stomatal conductance has a minor effect on photosynthesis, because the gas diffusion is more rapid than the photochemical uptake of CO<sub>2</sub>. Thus, with elevated CO<sub>2</sub>, internal CO<sub>2</sub> concentration increases, providing an enhanced CO<sub>2</sub> gradient to chloroplasts and enhanced activity of rubisco, leading to increased sucrose formation.

The effect of CO<sub>2</sub> on photosynthesis increases with temperature. Elevated CO<sub>2</sub> increases the temperature

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optimum of photosynthesis, a response consistent with current concepts of the effects of CO<sub>2</sub> on the carboxylating enzyme, rubisco, and on the control over the flow of carbon through the photosynthetic reductive cycle or the photosynthetic oxidation pathway (Gutteridge and Keys 1985, Lorimer 1981, Pearcy and Bjorkman 1983). High levels of sucrose in leaves promote phloem loading and sucrose translocation, as well as starch formation in leaves (Huber et al. 1984). Inhibition of photosynthesis associated with carbohydrate accumulation may also be dependent on temperature. Recent research by Sage and Sharkey (1987) has shown that enhanced photosynthesis with CO<sub>2</sub> enrichment is precluded below approximately 18° C; however, this interacting temperature effect is species dependent.

Based on this analysis, one would predict that elevated CO<sub>2</sub> will have a large amplifying effect on the productivity of ecosystems where the daytime vegetation temperature is above 30° C, as in middle-latitude grasslands. The relative effects of CO<sub>2</sub> are also strongly influenced by other stress factors, such as salinity (Bowman and Strain 1987) and nutrient stress (Cure 1985). In fact, the most important effect of CO<sub>2</sub> on vegetation may be to relieve stress; however, examples given below indicate that CO<sub>2</sub> enhancement can amplify stress effects through leaf energy balance.

Transpiration rate is a complex function of several factors, including leaf temperature and stomatal conductance, and CO<sub>2</sub> effects on plant water loss are strongly dependent on the exposure conditions. The ratio of carbon gain to water loss, or water-use efficiency (WUE), is increased with elevated CO<sub>2</sub>; this effect has been demonstrated with instantaneous determinations and cumulative measurements. Increased WUE is a consistently observed response of plants to elevated CO<sub>2</sub>, although Morison (1987) notes that instantaneous WUE responses to high CO<sub>2</sub> can become muted by feedback effects at the whole-plant level and by acclimation adjustments over time.

Changes in physiological responses of plants to CO<sub>2</sub> enrichment occur with increasing exposure duration. This acclimation process generally re-

sults in a reduction in the maximal light-saturated photosynthetic rate (Acock and Allen 1985). Fetcher et al. (1988) demonstrated reduced biochemical rates of photosynthesis in sweetgum leaves (*Liquidamber styraciflua*) after 15 months' growth at 500 cm<sup>3</sup>m<sup>-3</sup> of CO<sub>2</sub>. This effect can be explained by reduced rubisco activity, as has been observed for soybean (*Glycine max*) in the studies of Vu et al. (1983). Reversible deactivation of rubisco with increase in CO<sub>2</sub> has been shown during short exposure periods (10 min) in herbaceous species

(Sage et al. 1987), but it seems that reversibility can be lost with long-term CO<sub>2</sub> enrichment (DeLucia et al. 1985). Nevertheless, rates of photosynthesis in plants acclimated to elevated CO<sub>2</sub> are almost always higher than in plants grown in normal ambient CO<sub>2</sub>, and many plants show no acclimation (Percy and Bjorkman 1983).

Plants with active growth or with active sinks for photosynthate show strong responses to CO<sub>2</sub> enrichment. Production of citrus fruit (Downton et al. 1987) and soybean yield (Ackerson et al. 1984) were enhanced

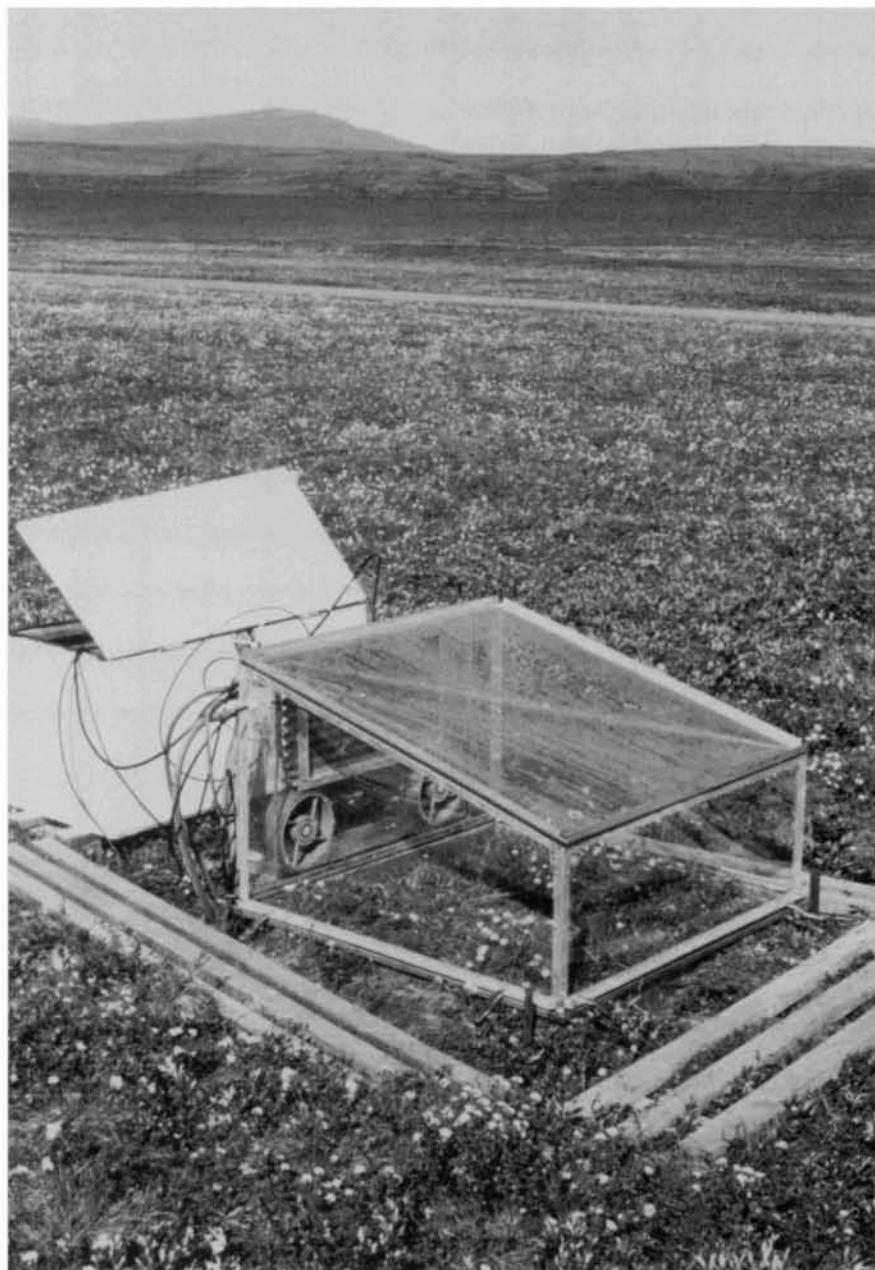


Figure 1. Null balance and CO<sub>2</sub> and temperature-controlled greenhouse system used in arctic tundra at Toolik Lake, Alaska.

when elevated CO<sub>2</sub> levels were provided during the reproductive and fruit-development period. Sink strength has an important bearing on plant response to CO<sub>2</sub> enrichment.

Most of the available data on the effects of elevated CO<sub>2</sub> on vegetation have been derived from short-term treatments (i.e., days to weeks) in controlled environments (Acock and Allen 1985, Cure and Acock 1986). These data show that the response to CO<sub>2</sub> varies widely among species, with most C<sub>4</sub> plants responding less than C<sub>3</sub> species, and the response is coupled to environmental factors (Cure and Acock 1986). In contrast, almost nothing is known about the field effects of long-term exposure of wild vegetation to elevated CO<sub>2</sub> and on ecosystem processes, such as carbon sequestering, decomposition, nutrient balance, and species competition (Oechel and Strain 1985).

### Forest response to a rise in CO<sub>2</sub>

Forests may account for as much as two-thirds of global photosynthesis (Kramer 1981) and thus play a dominant role in the conversion of atmospheric CO<sub>2</sub> to fixed forms of carbon that have slow decomposition rates. The potential effects that changes in CO<sub>2</sub> and climate have on forest ecosystems are of global significance; however, the complexity of forest ecosystems and the technical challenges of quantifying their behavior necessitates the implementation of a range of investigation methods. A number of studies have been conducted with CO<sub>2</sub> enrichment of small trees and seedlings (Eamus and Jarvis 1989, Jarvis 1989, Kramer and Sionit 1987), whereas, with mature trees, tree ring chronologies have been evaluated for forest responses to the historical rise in atmospheric CO<sub>2</sub>.

**Growth responses of forest species to changes in CO<sub>2</sub>.** The response of evergreen and deciduous species to elevated atmospheric CO<sub>2</sub> has been investigated for a range of exposure periods (hours, weeks, and months) primarily in growth chambers (Eamus and Jarvis 1989). Short-term exposure experiments have shown increased leaf photosynthesis in several evergreen species grown under CO<sub>2</sub>-enriched

conditions for up to 2 days (Bryan and Wright 1976, Green and Wright 1977, Wong and Dunin 1987).

An increase in short-term photosynthesis does not necessarily translate into an increase in dry-matter production (Dutton et al. 1988). Nevertheless, Purohit and Tregunna (1976) demonstrated increased growth of Douglas fir (*Pseudotsuga menzeii*) seedlings exposed to CO<sub>2</sub> at 1000 cm<sup>3</sup>m<sup>-3</sup> for 90 days. Similarly, the seedling growth of lodgepole pine (*Pinus contorta*) and Sitka spruce (*Picea sitchensis*) increased with CO<sub>2</sub> enrichment up to 1320 μl/l during a 20-week exposure (Canham and McCavish 1981). Conroy et al. (1986) and Luxmoore et al. (1986) showed an in-

crease in the growth of *Pinus radiata* and *Pinus virginiana* with CO<sub>2</sub> enrichment under low-nutrient conditions in experimental periods of 22 and 16 weeks, respectively. Conroy et al. (1986) also demonstrated that CO<sub>2</sub> enrichment increased growth at low phosphorus levels under water-stress conditions, but not under conditions of adequate water supply (Conroy et al. 1988). Thus, under many water- and nutrient-stress conditions, seedling growth may be enhanced with elevated levels of atmospheric CO<sub>2</sub>.

A similar range of responses has been identified for seedlings of deciduous species exposed to CO<sub>2</sub> enrichment (Rogers et al. 1983, Tolley and Strain 1984). Under nutrient-stress

**Table 1.** Effects of doubling CO<sub>2</sub> on several plant and ecosystem properties and processes. In the arctic, all species are C<sub>3</sub>. Salt marsh communities are monospecific stands of the sedge *Scirpus olneyi* (C<sub>3</sub>) and the grass *Spartina patens* (C<sub>4</sub>). The symbols indicate the response to elevated compared to normal ambient CO<sub>2</sub> as an increase (+), decrease (-), or no change (0). Blanks represent no data available. (Data derived from Curtis et al. 1989a,b, 1990, Grulke et al. 1990, Oberbauer et al. 1986, Tissue and Oechel 1987, Ziska et al. 1990.)

Effects	Arctic	Salt marsh	
		C <sub>3</sub>	C <sub>4</sub>
<b>Plant effects</b>			
Carbon exchange			
Photosynthesis	0	+	0
Acclimation of photosynthesis	+	0	0
Plant respiration	0	-	-
Decomposition of dead shoots		-	-
Growth			
Shoot expansive growth	0	0	0
Root biomass	-/0	+	0
Number of shoots	+	+	0
Size of shoots	0	0	0
Root/shoot ratio	-/0	+	0
Tissue composition			
N tissue concentration	-	-	0
Carbon/nitrogen	+	+	0
Starch content	+		
Tissue density/specific weight	+	0	0
Salt content		-	
Development/reproduction			
Senescence	-	-	0
Tillering	+	+	0
Number of flowers	-	0	0
Number of seeds/stem		0	0
Sexual/asexual reproduction	-		
Water use			
Transpiration	0	-	-
Water use efficiency	0	+	+
Leaf temperature	0	+	+
Leaf water potential		+	+
<b>Ecosystem</b>			
Evapotranspiration	0	-	-
Net carbon storage	+/0	+	0
Acclimation of net carbon exchange to CO <sub>2</sub>	+	0	0
Net ecosystem respiration		-	-
Species composition	+	+	0
Water use	0	-	-
Nitrogen content of canopy	-	0	0
Soil enzyme activity	+/-		
Soil solution nitrogen	-/0		



Figure 2. Open-top CO<sub>2</sub>-controlled chamber system used in the salt marsh on the Chesapeake Bay.

conditions, enhanced seedling growth of white oak (*Quercus alba*) was shown by Norby et al. (1986a) and of yellow poplar (*Liriodendron tulipifera*) by O'Neill et al. (1987). In addition, the relative growth response of woody species to CO<sub>2</sub> enrichment under environmental stress conditions, such as water limitation, may be greater than under nonstress conditions, as Idso (1988) demonstrated for several herbaceous species.

**Long-term CO<sub>2</sub> responses.** Long-term growth responses of woody perennial species to CO<sub>2</sub> enrichment remain speculative. It is not clear whether the short-term responses can be sustained in long-term perennial growth.

Long-term exposure experiments are necessary. One open-top-chamber experiment on relatively long-term CO<sub>2</sub> exposure was conducted with saplings of ponderosa pine (*Pinus ponderosa*) planted in native soil and lasted for 2.5 years (Surano et al. 1986). This unreplicated pilot study showed that tree growth was enhanced up to a CO<sub>2</sub> level of 500 cm<sup>3</sup>m<sup>-3</sup>, but at 650 cm<sup>3</sup>m<sup>-3</sup> growth

was inhibited, an effect attributed to heat stress. Higher leaf temperature has been consistently observed for plants exposed to elevated CO<sub>2</sub> (Morison and Gifford 1984).

It is possible to gain some insights into long-term responses of trees to CO<sub>2</sub> enrichment from short-term research. Norby et al. (1986b) suggested that the greater growth of white oak seedlings at high CO<sub>2</sub> levels could not be sustained unless nitrogen uptake also increased. Greater nitrogen-use efficiency occurred at high CO<sub>2</sub> levels, but less internal nitrogen was available for subsequent growth.

In the nutrient-cycling dynamics of forests, litter quality is another factor that could change with CO<sub>2</sub> enrichment. Litter produced at high CO<sub>2</sub> was predicted to be carbon rich and nitrogen poor (Melillo 1983), yet the initial findings of Norby et al. (1986b) suggest that leaf litter decomposition rates at elevated CO<sub>2</sub> may not be greatly altered. The forms of carbon in the litter from CO<sub>2</sub>-enriched plants contained higher amounts of soluble sugars and less lignin than control plants, so Pastor

and Post (1988) suggest that higher temperature (increasing decomposition rate) and higher CO<sub>2</sub> (decreasing litter quality) could work together to result in little change in nitrogen availability. It has been noted that elevated CO<sub>2</sub> increases feeding rates of insect larvae as the proportional nitrogen content of leaves is reduced (Lincoln and Couvet 1989).

Assessing the effects of CO<sub>2</sub> enrichment on the long-term growth of trees at sites low in nutrients involves quantitative estimation of internal and external nutrient cycling processes of forest ecosystems that must be understood in terms of the carbon and water dynamics of the stand. Simulation modeling provides a consistent framework for meeting this challenge, and it should provide valuable guidance in the design of efficient field experiments for effects that CO<sub>2</sub> enrichment has on the nutrition and growth of large trees.

Pastor and Post (1988) recently presented insights into the effects that differences in water availability in clay loam and sandy soils have on forest succession of boreal and north-

ern temperate ecosystems subjected to CO<sub>2</sub>-induced climate warming. Although the direct physiological effects of CO<sub>2</sub> on forests were not included in their analysis, changes in biome distributions were predicted, based largely on the effects of drought-stress effects in a warmer and drier climate. However, effects of elevated CO<sub>2</sub> on transpiration and water use efficiency are expected to alter these relationships.

**Historical evidence.** Because trees in temperate zones form distinct annual growth rings and are generally long-lived, they provide a biological record of past environmental changes. It is reasonable to expect that the historical change in CO<sub>2</sub> is recorded in tree-ring chronologies, because there is extensive evidence that tree growth responds to CO<sub>2</sub> enrichment.

Findings from modern tree-ring records indicate increases in growth that correlate with the increase in atmospheric CO<sub>2</sub> in recent decades (Graybill 1986, Hari et al. 1984, LaMarche et al. 1984, Parker 1986). Nevertheless, the evaluation by Kienast and Luxmoore (1988) for conifer species suggests that some of the observed growth responses may exceed that expected from CO<sub>2</sub> enrichment alone.

Statistically rigorous methods have been developed to identify the stand age and climate components of variation in tree-ring chronologies so that residual patterns of ring variation may be evaluated (Cook et al. 1987). Association of these residual patterns with environmental stress or atmospheric CO<sub>2</sub> enrichment, nevertheless, remains a difficult task. For example, Kienast and Luxmoore (1988) estimated a 4% increase in annual increment as an expected response to atmospheric CO<sub>2</sub> enrichment (from 312 to 332 cm<sup>3</sup>m<sup>-3</sup>) during a 20-year period beginning in 1955, based on experiments with tree seedlings. The equivalent response for a CO<sub>2</sub> increase from 260 to 340 cm<sup>3</sup>m<sup>-3</sup> is a 16% increase in annual increment, which may be detectable in chronologies dating back to the early 1800s.

### Direct tests of natural ecosystem response to CO<sub>2</sub>

At the level of communities and ecosystems, our knowledge of the effects

of CO<sub>2</sub> enrichment, and hence our predictive ability, is poor. There have been, however, two recent experiments on intact ecosystems that provide important insights into the kinds of effects on natural systems that we might see in a CO<sub>2</sub>-enriched world. These experiments were conducted on relatively low-stature, mainly herbaceous, perennial communities. The differing results provide a framework for predicting the possible responses of diverse ecosystem types.

The two natural ecosystems for which we have extensive field information on the effects of elevated CO<sub>2</sub> on plant- and ecosystem-level effects are the coastal salt marsh on the Chesapeake Bay (Curtis et al. 1989a,b, 1990, Drake 1989, Drake et al. 1989, Ziska et al. in press) and the moist tussock tundra at Toolik Lake in the foothills of the Brooks Range in Alaska (Oechel and Riechers 1986, Tissue and Oechel 1987).

The tussock tundra experiments used temperature-controlled greenhouses, which also could control atmospheric CO<sub>2</sub> concentration and monitor net CO<sub>2</sub> flux (Figure 1). Experimental manipulations included ambient CO<sub>2</sub> and temperature conditions, elevated CO<sub>2</sub> (510 and 680 cm<sup>3</sup>m<sup>-3</sup> CO<sub>2</sub>), and elevated CO<sub>2</sub> and temperature to simulate predicted summer conditions in the next century (680 cm<sup>3</sup>m<sup>-3</sup> CO<sub>2</sub> and 4° C temperature above ambient; Manabe and Wetherald 1980, Schlesinger and Mitchell 1985). Humidity was maintained near ambient, and rainfall occurred in amounts and with timing approximating that occurring naturally. The system maintained excellent temperature and CO<sub>2</sub> control (Oechel and Riechers 1986, Tissue and Oechel 1987). The control system was operated from before snowmelt to after soil freezing.

In Chesapeake Bay wetlands, open-top chambers were used to create test atmospheres of normal ambient and elevated CO<sub>2</sub> (normal ambient + 340 cm<sup>3</sup>m<sup>-3</sup>; Drake et al. 1989; Figure 2). Chambers were placed on the marsh when plants emerged in spring (23 April 1987; 15 April 1988) and removed in the fall when no green tissue remained (15 November 1987; 1 December 1988). At appropriate intervals, the following measurements were made: shoot density, biomass

production, nitrogen and carbon content of plant tissue, photosynthesis and respiration in individual leaves and the plant canopy, evapotranspiration water use efficiency, and shoot water potential.

The arctic tundra ecosystem is floristically diverse and comprised of C<sub>3</sub> species. The coastal marsh system studied was comprised of two higher plants, *Scirpus olneyi*, which is C<sub>3</sub>, and *Spartina patens*, which is C<sub>4</sub>, both often occurring in monospecific stands. The plant and ecosystem responses in these two systems (Table 1) generally follow predictions based on the environmental factors (e.g., temperature limitations) and resource availabilities (nutrient and water) discussed above. The responses given in Table 1 for the arctic ecosystem represent the general response for the majority of individuals and for the ecosystem. The results given for the salt marsh are for single species or for monospecific salt marsh stands comprised of *S. olneyi* and *S. patens*.

**Photosynthesis.** There was little effect of elevated CO<sub>2</sub> on photosynthesis rates in the arctic after a period of acclimation. Cotton grass, *Eriophorum vaginatum*, which is the dominant plant, showed complete homeostatic adjustment to elevated CO<sub>2</sub> within two to three weeks (Tissue and Oechel 1987). Other species showed some continued enhancement of leaf photosynthesis, but often not of canopy photosynthesis.

The lack of long-term photosynthetic response to elevated CO<sub>2</sub> may be due, at least in part, to the photosynthate accumulation (Azcon-Bieto 1983) induced by nutrient limitation effects on growth. Also, low temperatures may have further limited growth responses to elevated CO<sub>2</sub>. Although there was little positive effect of elevated CO<sub>2</sub> on growth rate in the arctic, there was a strong stimulation on tillering. In the long term, this stimulation could have major effects on composition and ecosystem functioning. Surprisingly, root biomass and root/shoot ratios generally decreased at elevated CO<sub>2</sub>.<sup>1</sup>

In the salt marsh, the C<sub>4</sub> *S. patens* showed no significant photosynthetic

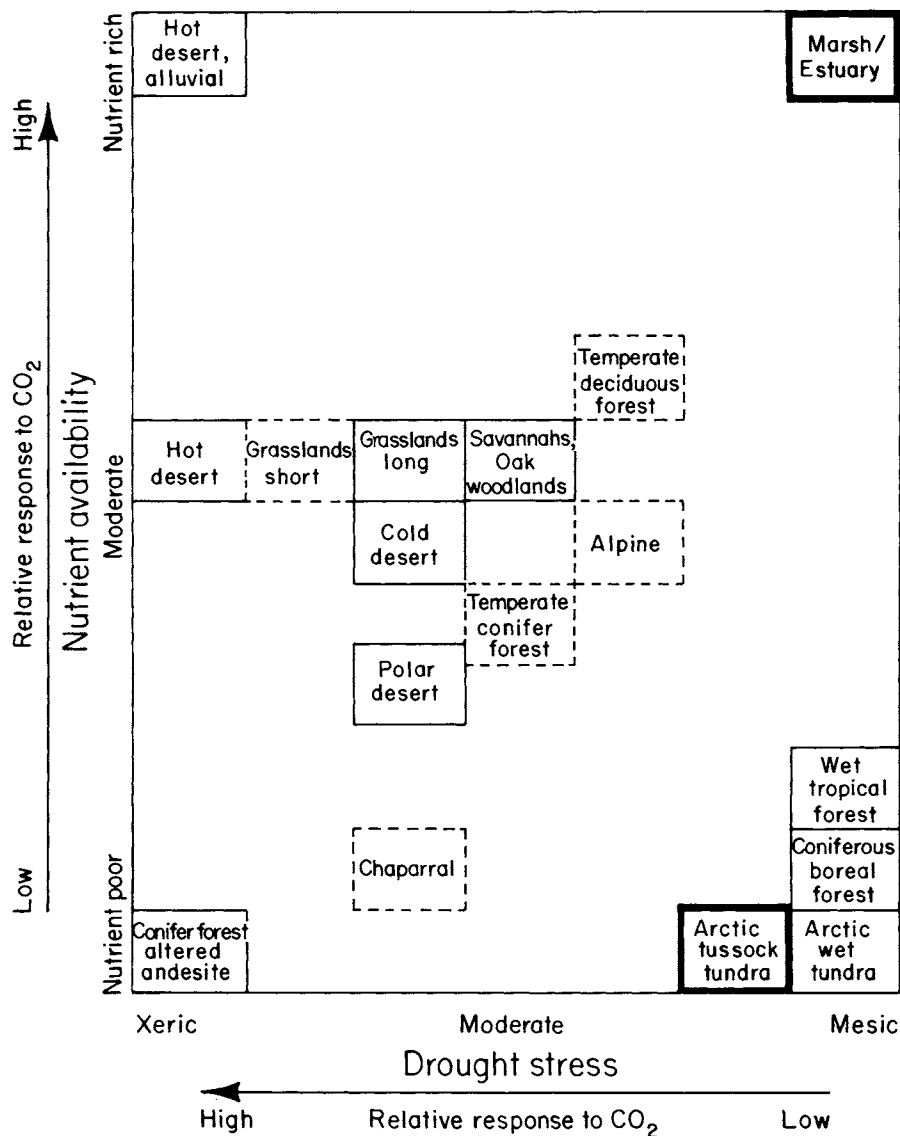
<sup>1</sup>W. C. Oechel, 1990, unpublished data.

response to elevated CO<sub>2</sub>. The C<sub>3</sub> *S. olneyi*, however, showed substantial response to doubled CO<sub>2</sub>, ranging up to a doubling of photosynthesis (Ziska et al. 1990). Plant respiration and decomposition of dead shoots was decreased with elevated CO<sub>2</sub>. Although reduced respiration in elevated CO<sub>2</sub> has been noted by others (Bunce 1990, Ludwig et al. 1976, Reuveni and Gale 1985), there is no physiological explanation for this effect. In the marsh, although growth in the C<sub>4</sub> plant was unaffected by elevated CO<sub>2</sub>, root biomass was increased 85% and aboveground primary production increased 16% (Curtis et al. 1989a,b, Drake et al. 1989).

**Nitrogen content and water use.** In the arctic, elevated CO<sub>2</sub> tended to decrease carbon:nitrogen content and increase carbon:nitrogen ratio, starch content, and specific leaf weight. Similar effects, along with a decrease in tissue salt content, were noted in the marsh with *S. olneyi*. No effects on tissue nutrient or salt content were noted for *S. patens*.

As expected, there were no effects on water use and WUE in the arctic species, but significant effects were noted in the physiologically xeric salt marsh. Interestingly, similar effects on water relations were found in the marsh in both the C<sub>3</sub> and C<sub>4</sub> species: evapotranspiration decreased 30%, WUE increased 80–100% in both communities, and midday water potentials increased 0.5 Mpa (Drake 1989).

**Ecosystem effects.** Significant ecosystem-level effects were noted in both the arctic and the salt marsh. In the arctic, there was little long-term effect on evapotranspiration, water use, or production. However, there were effects on short-term (1–2 years) carbon storage, nutrient relations, and soil enzyme activity. Homeostatic adjustment of whole-ecosystem carbon flux was complete within three years. The combination of elevated CO<sub>2</sub> and temperature rise resulted in a stimulation of net carbon uptake that lasted for the three years of observations (Oechel and Riechers 1986). In stands of the C<sub>3</sub> *S. olneyi*, there were improvements in water relations and the marsh increased carbon storage,



**Figure 3.** Hypothesized response of ecosystems to enhanced CO<sub>2</sub> in relation to prevailing nutrient and water availability. Those ecosystems that have been studied in the field are marked with heavy outlines; those where aspects of the system have been studied under controlled environmental conditions are shown using broken outlines. The remaining ecosystems are largely unstudied. (Modified from Strain and Bazzaz 1983.)

but no changes in nutrient relations were observed. The C<sub>4</sub> *S. patens* showed results similar to *S. olneyi*, except there was no increase in ecosystem carbon storage.

### A research framework

The above results indicate that ecosystems are likely to vary in their response to elevated CO<sub>2</sub>. Studies over a range of ecosystem types are required before credible generalizations and predictions can be made. Laboratory and field experiments in-

dicate that nutrient availability, water stress, and temperature affect response to elevated CO<sub>2</sub>, and natural ecosystems vary to the degree that these factors control system function.

Response to elevated CO<sub>2</sub> can be constrained where possible sinks for increased photosynthate are unavailable due to nutrient limitation. In controlled environment studies on plants, the absolute response to elevated CO<sub>2</sub> is usually greater with elevated nutrient availability (Larigauderie et al. 1988, Oberbauer et al. 1986). Where sinks are limited, pho-

tosynthetic response appears to be limited (Cave et al. 1981, Sasek et al. 1985). Ecosystem response to elevated atmospheric CO<sub>2</sub> may also be greater in warmer environments, because plant-growth response seems to be greater at higher temperature (Idso et al. 1987).

Also, it is expected that relative ecosystem response to CO<sub>2</sub> will be greatest in drought-stressed ecosystems. Increases in stomatal resistance and increases in WUE are greatest with water stress. In moist conditions, elevated CO<sub>2</sub> causes less increase in stomatal resistance. Therefore, in areas where water limits productivity, there will be a double benefit: productivity will be boosted directly by increased CO<sub>2</sub> exchange rates and indirectly by increased WUE.

A diverse sampling of ecosystems with different resource limitations that include nutrient availability, drought stress (Figure 3), and temperature is appropriate. Such experiments are expected to enhance the results' applicability to ecosystems not studied.

### The need for experiments on ecosystems

There is an urgent need for additional research on terrestrial ecosystem response to elevated CO<sub>2</sub> and climate change. The potential complexity of responses calls for direct experimentation on intact ecosystems. For these experiments to be useful in answering the critical questions concerning the feedbacks between biotic systems and atmospheric properties, each experimental treatment or plot must be large enough to encompass these feedbacks and to allow for the measurement of critical fluxes and parameters, without excessive disturbance to the system.

The time required to get meaningful results from whole-ecosystem manipulations vary with ecosystem type and the carbon-turnover rates within the system. Responses to elevated CO<sub>2</sub> do not occur on a single time scale. Photosynthesis can respond to elevated CO<sub>2</sub> in seconds. Acclimation of photosynthesis to elevated CO<sub>2</sub> can occur in days, and complete adjustment to a doubling of CO<sub>2</sub> has been observed within two to three weeks (Tissue and Oechel 1987).

Because of the number of processes and species involved, adjustment of net ecosystem CO<sub>2</sub> flux to elevated CO<sub>2</sub> is slower than adjustment of leaf photosynthesis. Even so, homeostatic adjustment of net ecosystem CO<sub>2</sub> flux begins within a season, and complete adjustment to doubled CO<sub>2</sub> can occur within three seasons (Oechel and Riechers 1987).

However, even this time scale may not reflect the true effect of a change in atmospheric CO<sub>2</sub> on net ecosystem CO<sub>2</sub> flux. Because of differential effects of elevated CO<sub>2</sub> or other factors on species and genotypes, we expect changes in ecosystem composition to occur over weeks to decades. Further, selection of genotypes best adapted to new conditions is expected to occur over even longer time scales—decades to centuries, depending on the life-spans of the component species.

Changes in some processes can be observed directly during the course of the experimental manipulation (e.g., leaf photosynthesis and initial ecosystem flux), whereas in other cases we must work with initial trajectories and simulation modeling, extrapolating the final result based on subjective understanding of system dynamics. Evolution and gene-frequency changes are expected to be even more difficult to evaluate and may not be tractable in an ecosystem field experiment.

The technology for ecosystem experimentation using CO<sub>2</sub> enrichment is available or currently being developed (Mooney et al. in press). However, the size and number of experiments that are needed is unprecedented in ecology. Past ecosystem-level experiments have typically involved few treatments and no replications (e.g., Bormann et al. 1974, Wright et al. 1988), but the CO<sub>2</sub>/climate problem dictates a more complex approach. We need to evaluate the effects of rising CO<sub>2</sub> and temperature change both alone and in combination. Additionally, changes in precipitation or nutrient availability may be important variables in some systems.

At minimum, these experiments should be undertaken in each of the world's six major biomes (tundra, boreal forest, temperate forest, tropical forest, grassland, and desert). Factors to be considered in site selection

might include: likely importance in affecting atmospheric composition and global climate, potential sensitivity to rising CO<sub>2</sub> or climate change, socioeconomic value, geographic extent, and existing knowledge base. The boreal forest should have a high priority because of its extent, potential sensitivity, and likely feedbacks on climate if it responds to change.

The experiments that have examined low-stature marsh and tundra systems required treatment plots smaller than those that the other ecosystem types will require to estimate accurately all the energy and element fluxes. In addition, larger plots are needed if all essential measurements are to be conducted without excessive disturbance to the system. Small watersheds would be ideal units for experimentation, but the requirement for numerous treatments with replication would be difficult to achieve with the use of watersheds. Treatment plots at least 5 m × 5 m in size will be required in grassland or tundra systems. In forests, even larger experimental plots will be essential if the plots are to be representative. Even a single-species tree plantation may require plots at least 10 m × 20 m. In some cases, an option may be to study lower-stature regenerating forests that can feasibly be contained. Any ecosystem experiment must run for at least a decade to allow a response trajectory to be determined.

CO<sub>2</sub> enrichment on plots as large as those needed to evaluate ecosystem responses, with the exception of those described for tundra and marsh, have not been attempted, although the technology is available. Chamberless, or free-air fumigation facilities, have been developed for use in research on effects of air pollutants on crops and forest trees (McLeod and Baker 1988). These facilities could be scaled up for use on larger experimental units and could be modified to allow for an elevated temperature treatment (Mooney et al. in press). A major cost would be CO<sub>2</sub>, but experimental sites close to inexpensive CO<sub>2</sub> sources, such as cement plants, could be selected. Another approach would be to use large enclosed or semienclosed greenhouses, in which conditions can be controlled more easily.

The cost of bold and innovative experiments would far exceed the

amounts spent addressing past ecological problems. But given the seriousness of the threats posed by global atmospheric and climate change and the important role terrestrial ecosystems will play if climate change proceeds, it is urgent that we begin the experiments necessary to understand the role and responses of terrestrial ecosystems on our changing planet.

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