

CARBON DIOXIDE LIMITATION AND POTENTIAL DIRECT EFFECTS OF ITS ACCUMULATION ON PLANT COMMUNITIES

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The burning of fossil fuels has caused the atmospheric concentration of CO₂ to increase, from 280 ppmv to 350 ppmv during the Industrial Revolution, with a current rate of increase of about 4 percent per decade (Siegenthaler et al., 1987). This increase may have a profound effect on global climate (e.g., Schneider, 1989), and thus, indirectly, on plant communities (e.g., Huntley, 1991; Webb and Wigley, 1985; Schneider, this volume). In addition, CO₂ accumulation may have a direct impact on plant communities because CO₂ is an essential nutrient for plant growth.

The potential effects of elevated atmospheric CO₂ might be inferred from other cases of nutrient enrichment. Phosphate is a major limiting nutrient in freshwater lakes, rivers, and streams. Increased rates of phosphate loading have led to dramatic changes in aquatic habitats (e.g., Edmondson, 1961, 1969; Edmondson and Lehman, 1981). As a result of phosphate inputs, many previously unproductive lakes have become highly productive, with diatoms and green algae being replaced by cyanobacteria (blue-green algae), which often form dense surface scums. In another ex-

ample, many heathlands in the Netherlands have been replaced by grasslands or forest, apparently as a result of increased rates of atmospheric nitrogen deposition (Berendse and Aerts, 1984; Aerts and Berendse, 1988). Nutrient additions have also been shown to change grassland species composition and decrease grassland diversity (Tilman, 1982). In the Park Grass Experiments of Rothamsted, England, for instance, many plots that initially contained over 40 species have become virtual monocultures following long-term, heavy fertilization.

In general, the addition of a limiting nutrient is thought to cause a shift in the composition and diversity of a plant community because each plant species responds to the addition in a different manner. All plants require carbon, nitrogen, phosphorus, potassium, calcium, magnesium, sulfur, and other elements for growth, but different species require these nutrients in different ratios (Tilman, 1982). A species is predicted to become competitively dominant if the ratio of supply rates of its limiting nutrients corresponds to the ratio in which that species uses them. An increased supply of any one limiting nutrient changes the ratios of nutrient supply and thus can have profound effects on competitive interactions and community composition (Tilman, 1982). If CO_2 limits growth in terrestrial or aquatic habitats, then the increased atmospheric CO_2 concentrations produced by anthropogenic global change will cause species to be limited by a resource other than CO_2 . The best competitor for that newly limiting resource would displace other species limited by it.

Thus, if CO_2 is a growth-limiting resource, both experimental evidence and theory suggest that CO_2 accumulation might have a direct effect on the composition and diversity of plant communities. However, existing theory regarding resource competition includes several critical assumptions that may not apply to CO_2 . This chapter proposes some alternative theories that may provide insights into the possible effects of CO_2 accumulation on the composition of plant communities. Although such resource-based theory may eventually be able to predict the outcome of CO_2 -dependent interactions, its most immediate contribution is to lay bare critical assumptions and processes, and thus to guide field experiments.

IS CO_2 LIMITING?

Before developing this theory, it is important to ask whether CO_2 is a limiting resource in terrestrial or aquatic habitats. If CO_2 were not limiting, changes in the supply of CO_2 would not have any direct effect on resource-dependent interactions among plant species. An essential plant nutrient is considered limiting if increases (or decreases) in the abundance of the resource cause changes in the specific growth rate of a species. For plants, the specific growth rate is usually best measured as $dB/dt \cdot 1/B$, where B is

biomass per unit of habitat area. A resource is considered limiting in a habitat if one or more of the species in the habitat are limited by it.

Literature reviews by Bazzaz (1990) and by Strain and Cure (1985) show that many wild terrestrial plants can be limited by CO₂; at least when grown in greenhouses or environmental chambers. Crop plants also can be CO₂-limited under controlled conditions (Acock and Allen, 1985; Cure and Acock, 1986). The underlying physiological causes of such limitation are complex because CO₂ influences numerous processes, including photosynthesis, dark respiration, stomatal conductance, transpiration, allocation, nutrient conservation, phenology, and reproduction (Bazzaz, 1990). Because plant species may differ in their growth responses to CO₂, CO₂ enrichment may influence the composition of plant communities. Zangerl and Bazzaz (1984) showed that different CO₂ concentrations changed species composition in laboratory communities of annual plants, especially on fertile soils or at high light intensity. In a greenhouse experiment, Wray and Strain (1987) showed that CO₂ levels increased the growth rate of a C₃ relative to a C₄ species, but did not alter their competitive interactions. Hunt et al. (1991) compared the responses of 25 native British plants to CO₂ in a greenhouse study in which all resources other than CO₂ were amply provided. They found major interspecific differences in the degree to which plant growth was influenced by CO₂ concentrations. Plants that they classified as "competitive" (generally taller pasture species that do well in short-term competition experiments in fertile soils) had the greatest growth response to CO₂.

Under controlled laboratory conditions, CO₂ limitation is more prevalent when water, other nutrients and light are provided at high levels (Bazzaz, 1990), as would be expected for any essential resource (Tilman, 1982; Bloom et al., 1986). These results suggest that CO₂ limitation might be more common in productive than in unproductive ecosystems. This prediction is in accord with the small growth responses to CO₂ enrichment observed in unproductive arctic ecosystems (Oberbauer et al., 1986; Billings et al., 1983; Peterson et al., 1984), and with the greater growth increases observed in *Scirpus* (but not in *Spartina*) in a more productive estuarine marsh ecosystem in Chesapeake Bay (Curtis et al., 1989a,b). Shapiro (1973) found that injection of CO₂ into a lake caused more pronounced changes in the abundances of the dominant species when the treatments also included other nutrients.

However, there have been few field experiments in which CO₂ has been added to natural plant communities and the responses of individual plant species observed (see Bazzaz, 1990; Woodward et al., 1991). Thus, at present, it is impossible to determine whether CO₂ limitation is more prevalent in particular types of habitats, or even whether many natural plant communities have a significant number of CO₂-limited species. Although the available evidence suggests the plausibility of CO₂ limitation for many plant

species, it is imperative to test this experimentally in the field. By definition, essential plant nutrients affect plant growth; therefore it is not at all surprising that CO₂, or any plant nutrient, can influence interspecific competitive interactions under appropriate laboratory conditions. However, for an essential nutrient to influence the dynamics or structure of natural plant communities, that nutrient must be limiting under field conditions (Tilman, 1982, 1988). Future research must go beyond laboratory demonstrations by directly observing the effects of CO₂ enrichment in natural communities.

SHOULD CO₂ BE LIMITING?

My emphasis on demonstrating limitation in nature as a prerequisite for further work on CO₂ is also based on the empirical observation that sometimes the addition of essential resources does not produce any change in plant growth rates or community composition. In particular, when a resource is not limiting (and is not brought to toxic levels), supplementing that resource will have little, if any, direct impact on a plant community. For instance, for the past decade I have added phosphorus, potassium, calcium, magnesium, and sulfur, singly and in combination, to replicated plots in three successional grasslands and a stand of native prairie. There has never been a significant effect of any of these nutrients, singly or in combination, on the aboveground biomass either of individual species or of the total community (Tilman, 1990). In contrast, other plots that received nitrogen showed significant increases in total community biomass and significant shifts in species abundances and diversity (Tilman, 1988). In numerous aquatic and terrestrial habitats, nutrient addition experiments have produced similar results: Only one or a few nutrients are limiting, and only these nutrients influence community structure (e.g., Milton, 1934; Thurston, 1969; Spect, 1963; Shaver and Chapin, 1980; Tilman, 1982; Chapin and Shaver, 1985; Tamm, 1985).

This finding seems inconsistent with a growing body of theory on plant optimal foraging (Rappart, 1971; Tilman, 1982, 1988; Bloom et al., 1986; Chapin et al., 1987). One prediction from this theory can be called the "equal limitation hypothesis," which states that a plant should forage for essential resources so as to become equally limited by all of them. The premise underlying "equal limitation" is the presence of allocation plasticity in plants, which can be based on physiological and/or genetic variation. If a plant is limited by one essential resource and not limited by some other one, it could gain fitness by allocating more to the structures or functions involved in the acquisition or efficient use of its limiting resource and allocating less to acquiring or using nonlimiting resources. The optimal outcome of such shifts in allocation is the morphology and physiology that leads a plant to be limited simultaneously by all essential resources.

There is an apparent marked contrast between this prediction and the

empirical observation that only one or a few resources are demonstrably limiting to plant species in most habitats. However, Gleeson and Tilman (1992) have shown that optimal foraging by plants does not necessarily result in equal growth responses to the addition of all essential resources. In particular, modifications that add biological realism to plant optimal foraging models lead to the prediction that some essential resources may not be limiting in a habitat. There are two major reasons for this. First, a plant's growth response to the addition of a resource should be proportional to the allocation that can be saved because of the higher abundance of that resource. If there is plasticity for patterns of allocation within the plant, then this savings could be reallocated to the acquisition of other resources. If a resource is relatively inexpensive for a plant to obtain, the savings caused by resource enrichment should be small, and therefore the growth response to its addition would be small, perhaps immeasurable. Second, many essential plant resources are acquired simultaneously by a single foraging structure. Roots, for instance, forage for nitrogen, phosphorus, potassium, calcium, magnesium, water, and other soil resources. Leaves forage for light and CO₂. Such simultaneous foraging can cause growth to be limited by a single resource (Gleeson and Tilman, 1992). The root mass of a plant, for instance, might be determined mainly by its requirement for nitrogen. Given enough root mass to equalize nitrogen versus light limitation, a plant might have coincidentally produced sufficient root mass to preclude limitation by phosphorus, potassium, calcium, or other soil resources. In this case, adding PO₄ would not decrease the amount of root mass needed to forage for nitrogen, so there would be no growth response to the added phosphate. The only potential savings to the plant from the addition of phosphate might be from the plant decreasing allocation to the actual enzyme systems (or mycorrhizal fungi) involved in active uptake of phosphorus by root hairs. This, however, probably would be a minor savings that would convert into a small growth response.

What, then, is the potential for limitation by CO₂? Because CO₂ is required in large amounts (carbon being the major constituent of dry plant mass), it seems plausible that CO₂ could limit the growth of many plant species. However, it is not obvious whether wild plants would experience major allocation shifts in response to CO₂ addition. CO₂ is obtained through stomata on leaves. If the major function of leaf area is light capture, plants may have more leaf area than they need for CO₂ capture. In this case, the addition of CO₂ would not result in smaller leaf area, but might provide some minor savings to a plant from decreased production of stomata. The energy saved, however, would probably have an immeasurably small impact on growth rates. Second, there may be a trade-off between leaf area and biochemical photosynthetic capacity. In productive habitats, CO₂ uptake by leaves may be limited by the rate of its diffusion through the boundary layer, and plants with greater total leaf area or different leaf shape or

placement may have an advantage. In this case, increased CO_2 concentrations could increase growth and favor a shift in allocation to roots. However, predicting field responses to CO_2 elevation is complicated by the water cost associated with CO_2 uptake. Water diffuses out of open stomata as CO_2 diffuses in; therefore plants living in a high- CO_2 environment need less water. If the root mass of a plant were determined by its demand for water, a plant living in elevated CO_2 could allocate less to roots, and thereby increase its growth rate. The relative importance of the root and leaf costs associated with CO_2 uptake should depend on environmental conditions and plant traits. Perhaps CO_2 will be most limiting in dry habitats with rich soils (which are rare habitats in nature, at least before global warming) and in moist, fertile habitats. Alternatively, the confounding of both above- and below-ground costs, and the aspects of simultaneous uptake by both below- and aboveground structures, may mean that CO_2 is rarely limiting in nature. Answers to these questions await appropriate field experiments.

THEORY OF CO_2 -DEPENDENT INTERSPECIFIC INTERACTIONS

For any individual plant, CO_2 may function in one of two ways: as a depletable resource or as a nondepletable physical factor. Different theories are needed for each case.

There is evidence of CO_2 depletion by plants on a variety of temporal and spatial scales. The uptake of CO_2 by leaves causes a CO_2 concentration gradient around each leaf. CO_2 is lowest near the stomata and in the boundary layer around a leaf, and higher further from the leaf surface. The steepness of this gradient depends on the rate of CO_2 uptake and the thickness of the boundary layer, which in turn depends on wind speed and leaf shape. Thus, CO_2 uptake by a leaf can decrease the amount of CO_2 locally available for further uptake by that leaf. On a larger scale, the CO_2 concentration inside the canopy of a stand of plants is lowered during photosynthesis. On a global scale, the atmospheric CO_2 concentration at Mauna Loa Observatory has an annual depression corresponding with peak terrestrial photosynthesis (Keeling, 1986). Such annual depressions suggest that plants can affect global CO_2 concentrations.

Models of competition for resources assume that species interact only through their effects on the concentrations of shared, depletable resources (e.g., Leon and Tumpson, 1975; Petersen, 1975; Taylor and Williams, 1975; Tilman, 1977, 1982). Such theory seems to apply to many cases of interspecific plant competition (Tilman, 1982, 1990; Tilman and Wedin, 1991a,b), and may apply to competition for CO_2 , if it functions as a depletable resource.

However, it is not clear whether such CO_2 depletion by any one plant

is sufficient to allow interspecific competition for CO₂. Because the atmosphere is relatively well mixed, it seems likely that CO₂ consumption by one individual plant might have little, if any, effect on neighboring plants (Begon et al., 1986: 85). In this case there would be no direct competition for CO₂. However, even if plants did not compete directly for CO₂, ambient CO₂ levels could influence plant growth rates, allocation patterns, nutrient conservation, and other plant traits. These traits could, in turn, influence the outcome of competition for a different resource, or the outcome of plant-herbivore interactions (Ayres, this volume), and thus influence the abundances of species in natural communities. In this case, the concentration of CO₂ would influence growth rates and other traits, much as might temperature, pH, or some other physical factor. I refer to this possibility as the case of "CO₂ as a physical factor."

Let us now consider two alternative theories. In one it is assumed that CO₂ is not depletable but acts as a physical factor; in the other, it is assumed that CO₂ is a limiting, depletable essential plant nutrient. First, though, we need to review the concept of competition for a single limiting resource (Tilman, 1982). Consider a plant species that is limited by a single nutrient resource, such as soil nitrogen (i.e., nitrate and ammonium). The growth rate of such a population will depend on the concentration of this resource. The population will also experience losses from herbivory, senescence, mortality, and other sources. As the population grows, its resource consumption will reduce the concentration of its limiting resource. At some point the population will attain a size at which it has reduced the concentration of the resource sufficiently that the resource-dependent growth rate of the population balances its loss rate, and the rate of resource supply balances consumption. At this point, a monoculture of this species will have reached equilibrium, and will have reduced the resource concentration down to a level R^* (Tilman, 1982). R^* represents the lowest concentration of available resource at which the species can survive. Now consider two plant species competing only for this same limiting resource. The plant with the lower R^* for the resource will be able to reduce the resource concentration to a point below that required for the survival of the other species, and should thereby competitively displace it from the habitat (Tilman, 1977, 1982). This theory has been tested for various combinations of five species of grasses competing for soil nitrogen (Tilman and Wedin, 1991a, b). Monocultures of the grasses differed in their R^* values for dissolved soil ammonium plus nitrate. When grown together in various pairwise combinations, the species with significantly lower R^* values displaced all others from unproductive, low-nitrogen field plots within 3 to 5 years. Such displacement occurred independent of the initial relative densities or initial life history stages of the competing plant species. Thus, experimentally observed R^* values can predict the outcome of interspecific resource competition among terrestrial plants.

CO₂ as a physical factor

Consider a simple case in which there is a single limiting, depletable resource. Let us assume that this resource is available soil nitrogen (i.e., nitrate and ammonium). How might CO₂, acting as a physical factor, influence the outcome of nitrogen competition? Several studies have shown that higher concentrations of CO₂ can lead to increased biomass allocated to roots, to higher C:N ratios in leaves, to higher photosynthetic rates, and to lower dark respiration rates (Bazzaz, 1990). All of these traits are predicted to influence the R^* of a plant for nitrogen (Tilman, 1990). The R^* of a species is a summary variable that incorporates the effects of physiology, allocation pattern, and nutrient conservation ability on competition. Indeed, five models that differed in their physiological and morphological complexity all predicted that a single number, R^* , was the only appropriate way to summarize the total effect of plant traits on nutrient competitive ability (Tilman, 1990). The most complex of these models predicted that the greater biomass a plant allocated to roots (as long as it still had enough leaf to meet root and leaf respiration needs), the greater its rate of photosynthesis and the greater its nutrient conservation ability (i.e., higher C:N ratios), the lower should be its R^* for a limiting nutrient (Tilman, 1990). Consistent with this, Tilman and Wedin (1991b) found that the observed nitrogen R^* values of five grass species were inversely correlated with root mass. Thus, R^* for nitrogen is likely to be a decreasing function of the atmospheric CO₂ concentration, if increased CO₂ leads to increased root allocation and high leaf C:N ratios.

Now consider two species whose nutrient-dependent growth is influenced by CO₂ concentration (Figure 1A). This is not a purely hypothetical case, since Bazzaz (1990) has found that different species do respond differently to CO₂ enrichment. Carrying through our specific example, it can be seen in Figure 1 that species A will be competitively dominant (will have lower R^* for nitrogen) if CO₂ concentration is less than 350 ppmv, and species B will be competitively dominant for higher CO₂ concentrations. Thus, if CO₂ acts as a physical factor, and if two species respond differently to CO₂, it is possible for changes in atmospheric CO₂ to tip the competitive balance from one species to another. This occurs even though the plants do not compete for CO₂. Different magnitudes of physiological responses to CO₂ are the norm (Bazzaz, 1991), and thus this case seems plausible. Similarly, if numerous species differ in the dependence of their R^* values on CO₂, increasing CO₂ can lead to a successional sequence of species dominance (e.g., dominance first by species A, then by B, C, and D, as in Figure 1B).

The scenarios in Figure 1 assume an interspecific trade-off between competing well for nutrients at one CO₂ level versus competing well at some other level. If no trade-off exists, atmospheric CO₂ levels would have

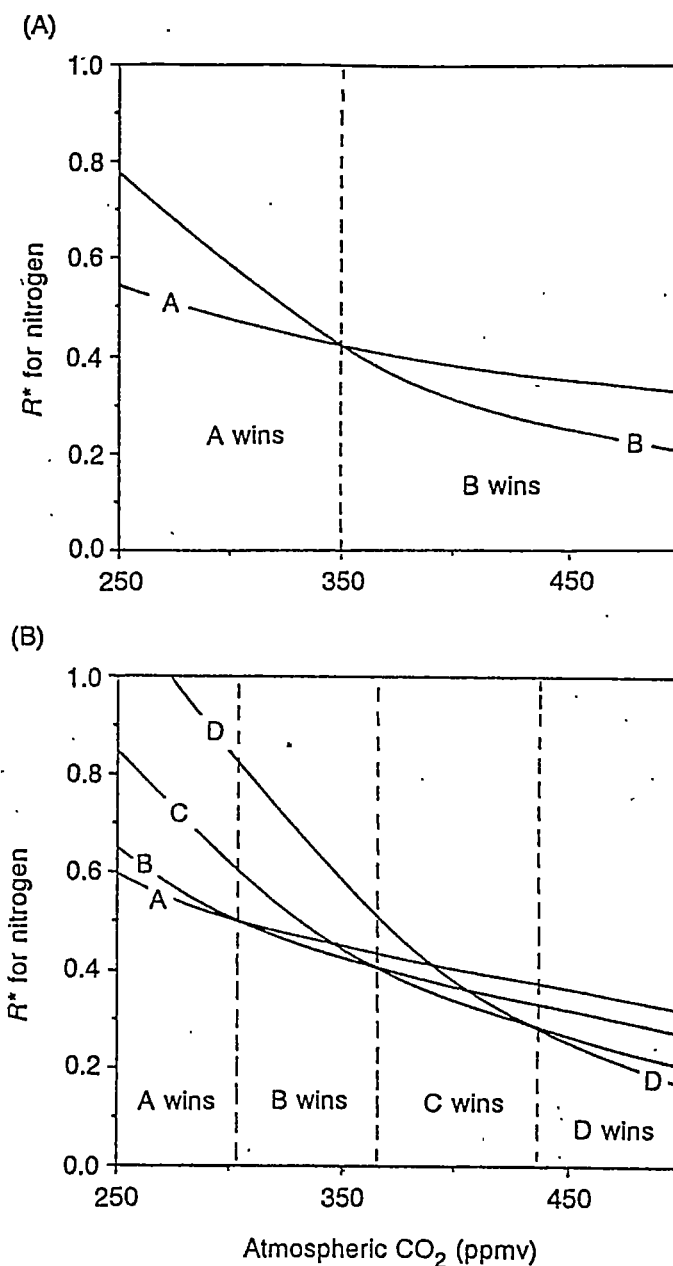


FIGURE 1. Hypothetical dependence of nitrogen-competitive ability on atmospheric CO₂ concentration, assuming that CO₂ acts as a nondepletable physical factor. The Curves show the R^* for dissolved soil nitrogen (ammonium plus nitrate) for species A, B, C, and D. At any given CO₂ concentration, the species with the lowest R^* for nitrogen is predicted to competitively displace all other species.

little direct effect on plant competition. Thus, it is important to determine whether such trade-offs exist, or whether morphological or physiological allocation patterns might make such trade-offs unavoidable. If trade-offs are unavoidable, then CO₂ enrichment could have profound direct effects on

plant community composition and diversity. CO_2 , acting as a physical factor, could also influence interspecific interactions in habitats in which there are two or more limiting resources. This would occur if one or a few of the species in a community benefitted more than the others from a CO_2 increase.

CO_2 as a depletable resource

Alternatively, plants may compete directly for CO_2 through either local or global depression of atmospheric CO_2 concentrations. If such competition were to occur, it would likely be a slow, weak process. However, even slow and weak processes can have major long-term implications for the dynamics and structure of communities. Consider first the highly hypothetical case in which it is assumed that CO_2 is the only resource limiting plant growth worldwide. If this were so, plants would eventually reduce atmospheric CO_2 down to a quasi-equilibrium level, R^* . At R^* , CO_2 -dependent growth would just balance biomass loss (when viewed on an annual or longer time scale). Increased rates of CO_2 release, such as from the burning of fossil fuels, would lead to higher equilibril plant biomass on the earth, but, once a quasi-equilibrium was reattained, would not change equilibril CO_2 concentrations, assuming that loss rates remained constant. In this case, global plant biomass would directly regulate CO_2 (Figure 2), albeit with an as yet

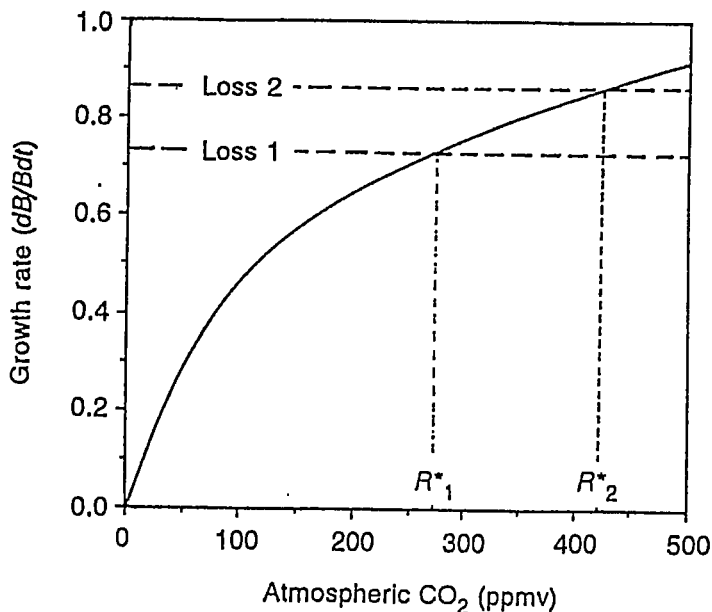


FIGURE 2. Here it is assumed that CO_2 is a depletable, essential plant resource. The solid curve is the CO_2 dependence of plant growth. The two dashed lines show different plant biomass loss rates, and the two dotted lines show the equilibril CO_2 concentration associated with each loss rate.

unknown time lag following atmospheric enrichment. Habitat destruction, biomass harvesting, and other actions that increased loss or mortality rates for plants would increase the quasi-equilibrium atmospheric CO₂ concentration (Figure 2).

Now consider a more realistic case in which CO₂ is a limiting, depletable resource and there are other limiting resources. If soil nitrogen were also limiting, and if species were different in their abilities to compete for CO₂ versus nitrogen, changes in the supply of either resource would change the composition of the community (Figure 3). For instance, if the equilibrium concentrations of soil nitrogen and CO₂ in a habitat before the Industrial Revolution were at point 1, species A and B would be competitively dominant. An increase in the CO₂ supply rate could shift concentration to point 2, where species B and C are dominant. Further increases could lead to dominance by other combinations of species.

In this case, as CO₂ increases there is a progression of dominance from species that are better CO₂ but poorer nitrogen competitors toward species that are better nitrogen but poorer CO₂ competitors (Figure 3). As this

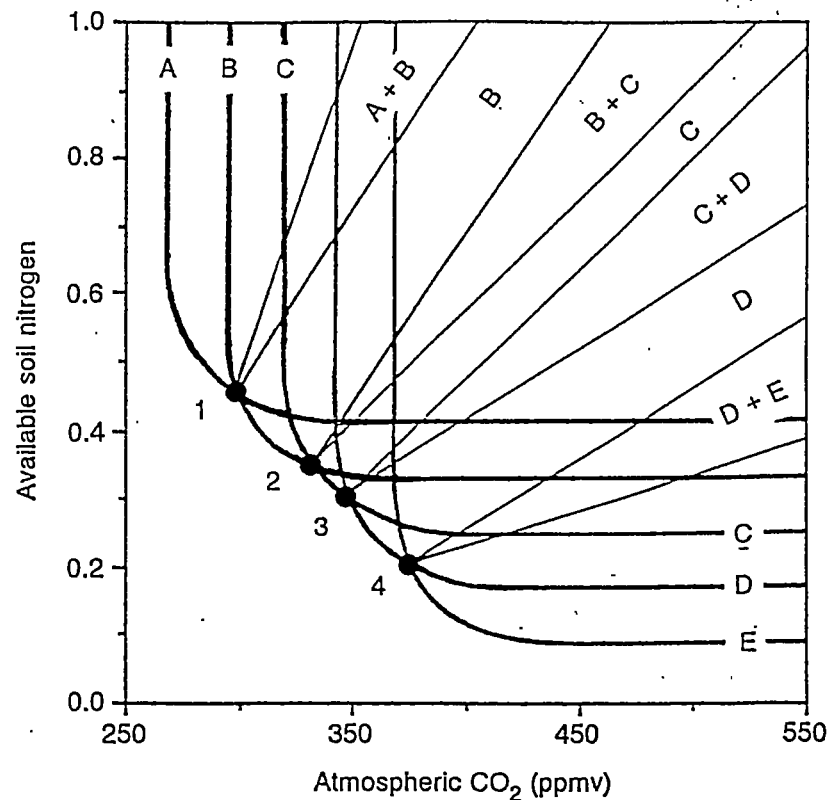


FIGURE 3. CO₂ is assumed to be a depletable, essential plant nutrient. The bold curves are resource-dependent growth isoclines for species A through E. These isoclines, along with the consumption vectors (straight lines), define regions in which a species or species pair is dominant. See Tilman (1982) for a detailed explanation.

occurs, the average environmental concentration of CO_2 increases and average soil nitrogen concentrations (dissolved ammonium plus nitrate) decrease. Each of these concentrations represents a potential quasi-equilibrium between the supply rate of CO_2 and its rate of consumption. A similar argument could be made in which the two limiting resources were CO_2 and light. If the best CO_2 competitors were the poorest light competitors, they would be replaced, as CO_2 accumulated, by taller, leafier species that were better light competitors, but poorer CO_2 competitors. These processes could occur on any spatial scale over which there was significant CO_2 depletion.

Biotic regulation of global CO_2 would occur because of shifts in the relative abundances of species that were different in their abilities to compete for CO_2 versus other limiting resources. At equilibrium, the species that were better competitors for CO_2 would be held in check by their high requirement for some other limiting resource. This would prevent them from further depleting atmospheric CO_2 levels. The species that were better competitors for the other resource would be held in check by their high requirement for CO_2 . This would prevent them from reducing the availability of the other resource to a level below that required by the better competitors for CO_2 . Thus, the processes hypothesized in Figures 2 and 3 could act to regulate global CO_2 concentration.

FEEDBACK EFFECTS

There are several additional ways that CO_2 enrichment could influence plant community structure. Optimal foraging theory predicts that CO_2 enrichment should favor traits that increase the ability of a plant to deal with limitation by resources other than CO_2 . Many plant species increase root biomass and decrease leaf nitrogen concentration in response to CO_2 enrichment, suggesting that they become more limited by nitrogen (Bazzaz, 1990). In contrast, in habitats with fertile soils, CO_2 enrichment could cause a plant to become more limited by light. In this case, increased allocation to stem and leaf would be expected.

These CO_2 -induced changes could affect nutrient cycling within the ecosystem, since the rate of nitrogen mineralization is influenced by the C:N ratio of litter. Litter with a higher C:N ratio, such as that produced by some CO_2 -enriched species, will have a lower decay rate (Woodward et al., 1991). Low decay rates can lead to decreased availability of nitrogen. Wedin and Tilman (1990) observed that initially identical soils diverged as much as tenfold in their rate of nitrogen mineralization after 3 years, depending on the C:N ratio of the resident grass species. CO_2 -induced changes in litter C:N ratios could potentially cause major shifts in nitrogen dynamics. The rate of nitrogen supply, in turn, could have a long-term impact on community structure. The impact would be the greatest if CO_2

were a depletable resource and if there were interspecific trade-offs, as illustrated in Figure 3. In this case, CO₂ enrichment would favor better nutrient competitors, and this would in turn favor nutrient conservation, which would lead to lower rates of nutrient supply, and thus further favor better nutrient competitors. Such a positive feedback loop could magnify the effect of CO₂ enrichment on changes in community composition.

There could be similar feedback effects mediated by herbivory (see Fajer et al., 1989; Bazzaz, 1990; Ayres, this volume). For instance, if CO₂ enrichment were to favor lower tissue nitrogen content in some species, herbivory on these species might decline in the long term, because herbivores might shift their food preferences or suffer population reduction due to the poorer food source. The decreased rates of herbivory experienced by these species would provide an advantage in their interactions with other plant species. Such herbivory shifts could further complicate the effects of CO₂ enrichment on competitive interactions and community structure.

CONCLUDING QUESTIONS

Both the known effects of CO₂ on plant physiology and a variety of theories regarding the effects of CO₂ on plant competition raise many more questions than they answer. The most important of these questions is the extent to which CO₂ is a limiting resource. Field studies are needed to investigate this question in a wide variety of natural terrestrial and aquatic habitats. Such field studies should simultaneously observe the responses of herbivore populations and soil nutrient concentrations and mineralization rates.

If it is found that CO₂ is frequently limiting in nature, it will then be important to determine whether there are observable interspecific trade-offs between responses to CO₂ concentration and other environmental constraints. For instance, are there unavoidable physiological or morphological costs associated with increased efficiency of CO₂ utilization? What are the traits of plants favored by elevated CO₂? If there are broad, underlying trade-offs that define the possible ranges of all plants, then the description of these trade-offs could provide a framework (as outlined in Tilman, 1988) that would eliminate the necessity of studying the response of each species separately. Rather, a species could be considered as a point or a region on a trade-off curve or trade-off surface. The general effects of an environmental change could then be predicted by knowing how it mapped onto the trade-off response surface. To focus on unavoidable trade-offs, if they exist, is to lift ecology from the study of the peculiarities of millions of species into a simpler, more general, predictive science.

Another question raised by the foregoing discussion is which plant traits should be studied to understand the effects of CO₂ on plant communities. The answer depends on the level of mechanistic detail desired. Currently there are no simple, logically consistent ways to extrapolate from a few

measures of physiological parameters to the effects of CO_2 on competition or community structure. An approach that seeks an abstracted variable, such as R^* , and develops and tests theory that relates R^* to underlying physiological processes (see Tilman, 1990), is thus needed to provide a logical link between physiological mechanisms and their impact on community-level patterns.

Conservation and resource management in the face of global change require simple models that can give robust qualitative predictions of the effects of CO_2 enrichment, as well as those of other environmental perturbations, on the composition and diversity of plant communities. Such models will likely be resource-based, and thus will share some qualitative features with the models presented here. The level of complexity needed in such models is unclear at this time, as is whether they should assume that CO_2 is a depletable resource or that CO_2 is a physical factor.