16

Interactive Effects of Carbon Dioxide and Environmental Stress on Plants and Ecosystems: A Synthesis

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I. Introduction

There is now a clear understanding of the multiple-driver nature of global change, and the need to address complex and nonlinear responses as we try to predict the future function and structure of the world's biomes. Furthermore, as we prepare to meet the demands of the Framework Convention on Climate Change, and particularly of the Kyoto Protocol, a sound understanding of the carbon cycle at the ecosystem, regional, and global level is urgently needed. In this respect, there is a necessity for improving our knowledge on the temporal and spatial dynamics of sources and sinks of carbon. It is even more important to understand the controls of source–sink dynamics and how they may change in the future as global change keeps progressing (e.g., increase of atmospheric CO_2, N deposition, air temperature).

The effects of carbon dioxide on plants and ecosystems have been extensively studied in the past two decades. These studies have provided great insights into potential changes in plant and ecosystem functions and structure in the next century when atmospheric CO_2 increases to twice the current CO_2 concentration. How the CO_2 effects on plants and ecosystems are regulated by stresses has not been carefully examined. In the real world, rising atmospheric CO_2 concentration is always interacting with other environmental and biological stresses in determining actual changes in material and energy fluxes in ecosystems. It is critical to evaluate the interactive responses of plants and ecosystems to rising atmospheric CO_2 and environmental stress. This chapter summarizes and synthesizes major knowns and unknowns presented in the chapters compiled in this book. Built upon the synthesis, we propose future research needs in order to improve our predictive understanding of the interactive effects of rising atmospheric CO_2 and environmental stress.

II. Interactive Effects of Carbon Dioxide and Stresses on Plants and Ecosystems

Research on CO_2 and stress interactions is needed to address one question in two ways. One is whether or not elevated CO_2 ameliorates or exacerbates environmental stresses. The other is how environmental stress moderates the direct effect of elevated CO_2 on plants and ecosystems. Results from plant-level studies have suggested that elevated CO_2 is likely to ameliorate mild drought, salinity, UV-B, and ozone stresses, to exacerbate nutrient stress, and to interact with temperature in a complex fashion. Accordingly, direct effects of elevated CO_2 on plants are likely to be amplified under mild drought and salinity stresses but dampened by nutrient stress. At the ecosystem scale, we have very limited evidence to suggest one way or another on impacts of CO_2 and stress interactions because major feedback mechanisms have not been evaluated using multifactorial experiments (Table I).

A. Water and CO_2

Extensive experimental data have generally supported a conclusion that rising atmospheric CO_2 directly reduces stomatal conductance and then transpiration per unit leaf area (Chapter 1). The magnitude of reduction in stomatal conductance varies with species and growth environments, by 36% on average for 11 crop and herb species and 23% for 23 tree species when growth CO_2 increases from ambient to twice ambient levels. Stomatal conductance is generally reduced more for plants grown in growth chambers than in fields utilizing open-top chambers (OTC) or free-air CO_2 enrichment (FACE) facilities. Reduced stomatal conductance in elevated CO_2 is almost always associated with a decrease in water loss via leaf transpiration and an increase in leaf water potential and expansive growth (Chapter 1).

Translation of reduced stomatal conductance and leaf transpiration to plant and canopy levels is complicated by numerous factors, including leaf area growth (Chapter 1), root growth, canopy structure and closure, canopy water interception and loss, soil surface evaporation, and species replacement (Chapter 2) (Table I). Elevated CO_2 generally results in larger leaves and higher leaf area growth (Chapter 1) and more root growth (Chapter 8) than ambient CO_2 does. Increased leaf growth counteracts the reduced stomatal conductance in determining water loss, whereas increased root growth explores more soil water resource. Both lead to more water consumption. Interactions of these physical and biological processes are site specific, leading to diverse responses of ecosystem hydrological cycling to elevated CO_2. Ecosystem-level measurements indicated that soil water content increased in agricultural forb ecosystems and in annual and perennial grasslands (Chapters 2 and 10). Results from FACE studies, however, did not indicate much change in soil water content in the elevated CO_2 plots compared to that in the ambient CO_2 plots (Oren *et al.*, 1998) (Table I). Even if the ecosystem water consumption is similar between the two CO_2 treatments, gross primary productivity is expected to increase in elevated CO_2 due to increased water use efficiency (Chapter 1). Whether or not net primary productivity will consequently increase in elevated CO_2 depends on feedback processes of carbon allocation, carbon loss via respiration, leaf and root turnover, and carbon use efficiency associated with changes in nonstructural carbohydrate storage and leaf and root mass per unit area (Luo *et al.*, 1997).

Chapter 2 pointed out that plot-level studies using OTCs and FACE facilities may not capture hydrological processes that operate at landscape, regional, and continent scales. These processes include CO_2-induced change in regional precipitation, within-continent water cycling between the biosphere and the atmosphere, and planetary boundary layer. Experimental studies by manipulating atmospheric CO_2 at the landscape or larger scales are beyond our technical capability. It may be a viable, alternative approach to analyze long-term watershed hydrological data. Chapter 2 analyzed 40-yr watershed hydrological data during the 1956–1996 period from the Hubbard Brook Experimental Forest in the White Mountain National Forest, New Hampshire, and concluded that watershed evapotranspiration may have slowed with rising atmospheric CO_2 in only one of five forested watersheds. That approach deserves more exploration in addressing large-scale, long-term impacts resulting from CO_2 and water interactions.

B. Temperature and CO_2

Temperature affects numerous physiological and ecological processes at several hierarchical levels and thus interacts with CO_2 in a complex fashion (Chapters 3 and 4). At the biochemical level, temperature regulates membrane permeability, enzyme kinetics, synthesis, and stability. For example, temperature differentially affects carboxylation and oxygenation kinetics of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) and then

Table I Plant and Ecosystem Responses to Environmental Stress That Interacts with Elevated CO_2[a]

	Plant response		Ecosystem response	
Stress	Direct mechanism	Experimental results	Feedback mechanisms	Experimental results
Water	Stomatal conductance	Reduced stomatal conductance Increased WUE and leaf expansive growth	Leaf area growth Canopy closure Interception/evaporation	Extended growing seasons in annual and perennial grasslands Little change in Duke and Arizona FACE
Temperature	Numerous biochemical and physiological processes	Increased CO_2 stimulation of photosynthesis with temperature Little leaf temperature increases observed in CO_2 experiments	Nutrient mineralization Migration/colonization Water balance C_3/C_4 competition	Accelerated nutrient cycling and increased respiratory C loss as indicated from soil warming experiments Decreased primary productivity
Salinity	Reduced water uptake	No effect on salt accumulation and turgor pressure Increased growth of salt-affected plants	Soil salinity Community structure Groundwater recharge	Increased productivity in salt marsh Altered community structure (more C_3 plants)
UV-B	Plant growth Secondary metabolites	No interactive effects on photosynthesis, productivity Change in allocation and morphogenesis	Decreased litter quality Photodegradation of litter Changes in community of decomposers	Changed herbivory by UV-B but not by elevated CO_2 in the tundra Increased mycorrhizal infection, lignin content Reduced decomposition in litter bags
Ozone	Stomatal conductance Antioxidant synthesis	Declined O_3 damage symptoms Increased carbohydrate and metabolite pools Decreased Rubisco	Plant protein content Soil nutrient availability	
Nutrients	Carbon and nutrient coupling in plant tissues	Reduced tissue N concentration Increased root growth Little downward regulation in photosynthesis across field studies	Altered C:N ratio Short-circuit C cycling Increased N supply	Variable changes in N mineralization Increased soil exploration Increased N fixation Increased carbon input into soil

[a] Direct interactions of elevated CO_2 with stress first take place through plant processes (direct mechanisms). The direct effects at the plant level are translated to ecosystem responses through a variety of feedback mechanisms. Also listed is evidence related from experimental studies on plant and ecosystem responses to the stress and CO_2 interactions. Note that results at the ecosystem level are based on a limited set of field experiments. Even fewer of them were in factorial design to study specifically the CO_2 and stress interactions.

controls the responsiveness of photosynthesis to elevated CO_2. As a consequence, the magnitude of the stimulation of C_3 plant photosynthesis and growth by elevated CO_2 tends to increase with temperature (Chapter 3) (Table I). At the plant level, temperature affects water relations, development, carbon partitioning, morphology, phenology, and reproduction. High temperature stress, for example, impairs reproductive development, exacerbating downward regulation of photosynthesis and growth limitation in CO_2-enriched plants.

At the community scale, temperature governs the success of migration and colonization of different plant species, inducing changes in species distribution and vegetation movement. Chapter 3 provided case studies in Arctic and alpine regions to illustrate that temperature and CO_2 interactive effects may be primarily exhibited by potentially adverse factors that result from a prolonged winter. A warmer winter is a major component of current climatic change. Winter warming that is greater than summer warming may cause remarkable changes in species distribution. But other factors, including a high degree of polymorphism, gene migration between adjacent populations in contrasting microsites, a genetic memory in the seed bank and in hybrid population, and longevity, contribute to the capacity of plant populations to withstand the impacts of climate change. It is a challenge for modelers to incorporate these processes when predicting the impacts of both rising atmospheric CO_2 and temperature on vegetation distribution in the arctic and alpine regions while manipulative studies of these processes are yet beyond experimental reality.

At the ecosystem scale, temperature alters primary productivity, water balance, nutrient availability, and fire (Table I). However, few studies, either experimental or simulation based, have addressed the combined effects of elevated CO_2 and temperature stress on ecosystem processes. Chapter 4 synthesized our knowledge on effects of temperature and CO_2 on these key ecosystem processes and made substantial inferences about potential ecosystem responses to temperature and CO_2 interactions. Elevated CO_2 is predicted to stimulate primary production most in water-limited ecosystems due to a substantial enhancement of plant water use efficiency though this may be offset by higher leaf area production (Chapters 1 and 2). In contrast, higher temperature could have markedly negative effects on plant production in water-limited ecosystems due to higher evapotranspiration rates and/or more temperature stress. In cold ecosystems, warming might stimulate ecosystem production by increasing nutrient availability. Overall ecosystem responses will probably vary widely across different ecosystem types because elevated CO_2 and global warming seem to have opposite effects on primary production, ecosystem water dynamics, and nutrient availability. Thus, regional predictions will be difficult with any level of precision.

C. Salinity, UV-B, Ozone, and CO_2

The total area of saline, sodic, or alkaline land counts up to 7% of the world land area, approximately 950 million hectares. Most of the salt-affected land is man-made, resulting from irrigation and clearing of perennial vegetation. Understanding how elevated CO_2 might mitigate the salinity problem has important applications for world food production. Chapter 5 provided a comprehensive overview of this issue. Salinity inhibits plant growth primarily through reduced water uptake from saline soil solution and excessive amount of salts in live cells causing damage. Elevated CO_2 enhances growth of plants in saline soil due to reduced water uptake (Table I). Possible mechanisms involved in CO_2 amelioration of salt-affected plants include decreased salt accumulation in leaves, increased turgor, or increased carbon supply to growing tissues. Results from numerous experimental studies have provided little evidence for increased turgor and decreased salt accumulation in elevated CO_2 in comparison to that in ambient CO_2. Thus, increased carbohydrate supply to growing tissues may be the primary mechanism of increased growth of salt-affected plants. Although elevated CO_2 may have ameliorating effects on salt-affected plants, its impact on soil salinity is much less clear. Chapter 5 discussed a variety of mechanisms at the ecosystem scale, including increased canopy closure, ecosystem water loss, CO_2-induced global warming, and increased groundwater recharge (Table I). The only evidence available from the field experiment in a salt marsh in Chesapeake Bay is that community structures shifted to have more C_3 plants and fewer C_4 plants in elevated CO_2.

Recent field experiments have provided evidence that an elevated UV-B level does not affect photosynthesis but reduces plant elongation growth, and alters production of plant secondary metabolites, for example, flavonoids, tannins, and lignin, leading to changes in primary productivity (Chapter 6). Thus, significant interaction between CO_2 and UV-B is generally manifested by changes in biomass allocation and feedback processes through, for example, litter decomposition (Table I). Plant morphogenesis, including height, shoot and leaf length, leaf thickness and area, and auxiliary branching, is often altered under elevated UV-B. But limited data are available concerning the influence of CO_2 and UV-B interaction on those characteristics. Increased production of secondary metabolites, which are complex polyphenolics, influences plant–animal, plant–microorganism interactions, and litter decomposition (Table I). Both elevated CO_2 and enhanced UV-B reduce the quality of plant tissues and litter, leading to reduced insect herbivory and litter decomposition.

Chapter 7 suggested that a decline in O_3 sensitivity due to elevated CO_2 is probably an integration of multiple processes, including reduction in stomatal conductance, possible anatomical changes in the leaf, and flexibility to induce antioxidants when needed. When plants are grown in elevated CO_2, O_3-induced foliage symptoms are reduced. Biochemical mechanisms for the CO_2 and O_3 interaction can be complicated. Plants grown in elevated CO_2 result in increased carbohydrate and decreased content of enzymes, such as Rubisco. Data presented in Chapter 7 indicated that plants grown in elevated CO_2 have greater flexibility to shift carbohydrates to increase pools of antioxidants as needed. On the other hand, the O_3 target is protein, like Rubisco. Reduction of Rubisco concentrations in elevated CO_2 could have an adverse interaction with O_3 because each Rubisco molecule has a higher chance of being damaged by O_3 in elevated than in ambient CO_2. Thus, responses of plants to elevated CO_2 and O_3 interactions are influenced substantially by nutrient availability. If nutrients are not limiting, as in agricultural situations, CO_2 could have an ameliorating effect on O_3 toxicity. In natural ecosystems, where nutrients are more limiting, elevated CO_2 may render the plant less flexible to synthesizing protective compounds and as a result offer less protection from O_3.

D. Nutrients and CO_2

The interactive effects of nutrients and elevated CO_2 on plants have been extensively studied. It is a consistent conclusion across numerous experiments that growth in elevated CO_2 almost always results in lower nutrient concentration in plant tissues than in ambient CO_2. Despite the decrease in tissue nutrient concentration, three recent reviews, conducted by Curtis and Wang (1998), Drake *et al.* (1997), and Mooney *et al.* (1999), have found little reduction in photosynthetic capacity for plants grown in elevated CO_2 relative to that in ambient CO_2 (also see Chapter 12). In addition, factorial experiments with multiple levels of nitrogen and CO_2 concentration have suggested that plants responded to elevated CO_2 even at low nutrient supply levels (Johnson *et al.*, 1996). Responsiveness of plants to elevated CO_2 usually increases with nutrient supply levels. Thus, it is critical to understand how ecosystems regulate nutrient availability and then influence CO_2 effects on plant and ecosystem carbon processes (Fig. 1). Several chapters in this book are devoted to various aspects of ecosystem nutrient dynamics.

There is no doubt that elevated CO_2 generally stimulates root growth (Chapter 8), which extends the potential to increase carbon deposition into rhizosphere and nutrient uptake by plants (Chapters 8–10, 12–15) (Fig. 1). Elevated CO_2 tends to increase rhizodeposition either through increased root growth and turnover, or increased deposition per unit of root mass (e.g., root exudation), or both. Although root exudation is critical for predicting soil carbon and nutrient dynamics in ecosystems, virtually no report is available on the amount of root exudates in elevated CO_2. Continuous ^{14}C-labeling studies have shown that plants grown in elevated CO_2 allocated more carbon to total rhizosphere respiration, suggesting a substantial amount of short-term carbon influx into the rhizosphere through fast pathways such as exudation (Chapter 9). Root growth and turnover have also been found to increase considerably in elevated CO_2 (Chapter 8), leading to increased medium-term carbon influx to the rhizosphere (Fig. 1).

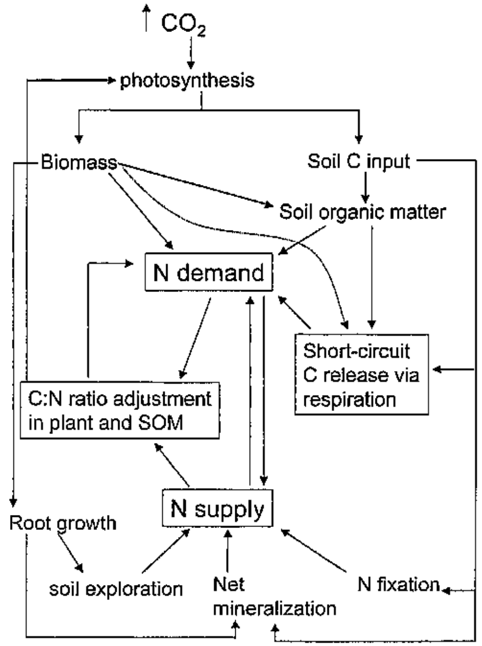


Figure 1 A conceptual model of ecosystem carbon and nitrogen interactions as affected by elevated CO_2. Elevated CO_2 generates additional nitrogen demand primarily through increased plant biomass growth and soil carbon storage. To meet the additional nitrogen demand, three general mechanisms are used: adjustment of C:N ratios in plant biomass and soil organic matter (SOM), short-circuit dissipation of additional carbon, and additional nitrogen supply through soil exploration, net mineralization, and nitrogen fixation.

Increased carbon input to soil in elevated CO_2 has been reported to increase, decrease, and have no effect on nitrogen availability to plants. These idiosyncratic results may be partly explained by differences in the timescales of experimental measurements and plant species involved in the experiments and partly explained by different measurement techniques (Chapters 9 and 10). Elevated CO_2 tends to increase rhizosphere symbiants such as mycorrihizae and rhizobia across several types of associations. N fixation has generally been found to increase in elevated CO_2. Inputs of nitrogen through N fixation may not be quantitatively significant in the short term, but merit attention for their effects on nitrogen stocks in the long term (Chapter 10) (Fig. 1). Whether or not the structure of rhizosphere communities will be changed in elevated CO_2 is not clear yet. Most of the data, however, are from growth chamber experiments under highly disturbed and highly controlled conditions. Rhizosphere dynamics urgently need to be studied in field experiments (Chapter 9).

Chapter 10 offered compelling experimental data as well as comprehensive conceptual models to support a notion that soil nitrogen cycling is not only altered directly by increased carbon input to soil but also indirectly by increased soil moisture. Soil moisture content has been found to be significantly altered in several ecosystems, including annual and perennial grasslands, agricultural fields, and microcosm experiments in elevated CO_2. CO_2-induced change in soil water content resulted in changes in soil microbial activities and nitrogen transformation (Chapter 10). Because ecosystem hydrological cycling depends on leaf area growth (Chapters 1 and 2), the indirect effects of elevated CO_2 through changed soil moisture content on nitrogen cycling are likely to vary among ecosystems. Elevated CO_2 may cause the largest reduction in evapotranspiration in ecosystems where aboveground growth responses to elevated CO_2 are the smallest, leading to a large change in N cycling.

Long-term impacts of various mechanisms of nitrogen supply as well as C:N ratio adjustment in plant and soil organic matter (SOM) on ecosystem carbon and nitrogen dynamics were quantitatively evaluated in Chapters 12–14. Examined also were implications of three-way interactions among carbon dioxide, nitrogen, and water for ecosystem productivity and carbon sequestration (Chapter 14). Soil respiratory carbon release has often been found to increase substantially (Chapter 9), leading to short-circuit carbon cycling (Fig. 1). The short-circuit carbon release reduces nitrogen demand in elevated CO_2 and thus may mitigate nitrogen stress in natural ecosystems. It may also be partly responsible for little photosynthetic down-regulation observed from most of the OTC and FACE experiments in natural ecosystems. The impact of the short-circuit mechanism, however, has not been evaluated using either experimental or modeling approaches.

III. Evolutionary, Scaling, and Modeling Studies of CO_2 and Stress Interactions

Rising CO_2 concentration in the atmosphere is a long-term, large-scale phenomenon. It not only affects short-term physiological and ecological processes such as those described in Chapters 1–10, but also regulates evolutionary courses as well as large spatial scale processes. Several chapters in this book offer approaches to place physiological and ecological research in broad evolutionary and scaling perspectives.

Most of the research addressing biological responses to variation in atmospheric CO_2 has focused on physiological responses of plants to doubling of the present CO_2 level. But much less has been considered on evolutionary responses of plants to the long-term CO_2 change in the atmosphere. Chapter 11 explored the latter issues and argued that the world's flora may be adapted to the preindustrial CO_2 level under which plants are selected for stress-tolerant mechanisms in order to survive under carbohydrate deficiency. These mechanisms include low growth potential, conservative allocation patterns, and storage investment. At optimal environmental conditions, plant performance modestly decreases with declining CO_2. As CO_2 levels decline, the inhibitory range of environmental conditions broadens substantially. Many conditions that are currently nonstressful may have been stressful during past episodes of low CO_2, and conditions that are now moderately stressful may have been lethal at low CO_2. Thus, strong selection pressure may have favored stress-tolerant mechanisms at low CO_2. The hypothetical evolutionary mechanism provides an alternative explanation of imbalances between sources and sinks or between nutrient supply and carbon availability often observed in experiments. If evolutionary processes do correct the imbalances and reestablish a shared control among multiple resources, a gradual increase of atmospheric CO_2 over a time frame of a century could lead to substantial enhancement of CO_2 responsiveness. Chapter 11 also urged incorporation of stress and low CO_2 interactions in experimental studies of plant evolutionary responses to rising atmospheric CO_2.

Scaling has become one of the major scientific activities in global change research partly because plant and ecosystem studies are primarily driven by large-scale issues and partly because we are unable to make direct measurements at regional and global scales (Chapters 2 and 12). Our predictions of large-scale terrestrial carbon sinks and sources rely on the scaling up of our knowledge from leaf, plant, and small ecosystem studies. Conventional scaling-up schemes include summation, averaging, and aggregation in association with gridded geographical information systems of world vegetation, soil, and climate conditions. Chapter 12 argued that a scaling-up study fundamentally has to cope with two general factors: environmental variability and biological diversity. The challenge in scaling-up studies is to reduce uncertainties associated with these two general factors. In addition to the conventional approaches, Chapter 12 also suggested that scaling studies can be accomplished by identifying scaleable parameters. Such a parameter characterizes intrinsic properties of a system in question and thus reduces extrapolation uncertainties caused by environmental and biological variability. For example, quantum yield of CO_2 uptake, that is, a physiological parameter, has been successfully used to delineate relative distribution of C_3 and C_4 plants in terrestrial ecosystems over the globe. In addition, identification of scaleable parameters may provide a unique approach to deal with the complexity of CO_2 and stress interactions. An invariant leaf-level function, for instance, that describes photosynthetic sensitivity to a small increment in atmospheric CO_2 is powerful in extrapolating leaf-level studies to predict marginal increments in carbon influx and storage caused by rising atmospheric CO_2.

Modeling has been an essential tool in studying plant and ecosystem responses to stress and CO_2 interactions because of a critical need to synthesize and extrapolate plot-level measurements to predict long-term, large-scale ecosystem responses to global change. Various modeling approaches have been developed in the literature. Most of the models have been built on the fundamental basis of stoichiometry that carbon dynamics in terrestrial ecosystems are strongly coupled with nitrogen cycling (Chapter 13). Increased input of carbon resulting from rising atmospheric CO_2 should result in changes in the total amount of nitrogen in the ecosystem while maintaining C:N ratios, or changes in the C:N ratios of ecosystem components, or changes in the distribution of nitrogen among ecosystem components. This basic stoichiometrical relationship leads to the theory of nitrogen productivity that the relative plant growth rate is determined by plant nitrogen concentration. When the concept is applied to the whole ecosystem net primary productivity, it is crucial to consider whether the ecosystem is open or closed in terms of nitrogen input. Because the availability of mineral nutrients cannot be expected to increase in proportion to the carbon increase, changes in the relative availability of elements are predicted to cause changes in root fraction, C:N ratio of litter and soil organic matter, and immobilization of nitrogen (Fig. 1).

It is a common practice to utilize the minimum limitation notion or the multiplicity concept to simulate multiple stresses in interacting with rising atmospheric CO_2. Using the former notion, Chapter 14 extended the G'DAY (General Decomposition And Yield) model to predict interactive effects of nitrogen and water with elevated CO_2 on forest ecosystems. The model predicted that the CO_2 fertilization effect is likely to be amplified under water limitation, but reduced under long-term nitrogen limitation. The amplification of the CO_2 fertilization effect by water limitation is primarily due to enhanced water use efficiency, which has a large, direct effect on carbon uptake, and smaller, indirect effect due to stimulation of soil decomposition.

IV. Future Research Needs

A. Experiments

The primary goal of experimentation is to identify and quantify the mechanisms underlying ecosystem responses. The challenge here is to provide relevant ecophysiological data to develop and test models, and to incorporate ecosystem and biosphere metabolic processes that are not currently well understood.

Abundant research on plant physiological responses to various environmental factors has taken place during the last two decades. However, if one of the main goals of our research is to predict ecosystem or larger-scale responses to global change, there is a critical need for research on processes relevant at the ecosystem and landscape levels. In this respect, great progress has been made during the past 6 yr in understanding ecosystem-level responses to elevated CO_2, particularly in grassland systems (Mooney *et al.*, 1999). However, as we begin recognize the multifactorial nature of global change, it becomes obvious that single-factor experiments will provide limited information to predict the consequences of several simultaneously occurring environmental changes. Therefore, multifactorial experiments, in which interactions among factors can be tested, are critically important. Among many of the global changes that are already occurring, special attention should be paid to air and soil warming, nitrogen deposition, and changes in water availability in addition to elevated CO_2, ozone, and UV-B. They are all major controls of net ecosystem exchange and, therefore, of the ecosystem and global carbon cycle.

There are still important technical difficulties associated with setting up such multifactorial experiments in the field, particularly for the interaction between elevated CO_2 and warming in large stature systems (e.g., forests). Although various techniques are available to increase atmospheric CO_2 at the stand level and each has a unique strength, the free-air carbon dioxide enrichment (FACE) experiments are the least environmentally disturbing technique and, therefore, the preferred one. Natural CO_2 springs also offer excellent opportunities for studying undisturbed systems exposed to long-term elevated CO_2.

There is no one technology for warming experiments that can be clearly considered the best, although convective heating should be preferred over other types of heating. In addition, natural experiments using thermal gradients can provide us, as in the case of natural CO_2 springs, with unique opportunities to study long-term adaptations and community dynamics, which cannot be studied in short-term studies (<5 yr). Soil/vegetation transplant experiments can equally provide valuable information.

A list of recommendations follows for whole ecosystem experiments to better address responses to global change (see also Canadell *et al.*, 1999; Schulze *et al.*, 1999):

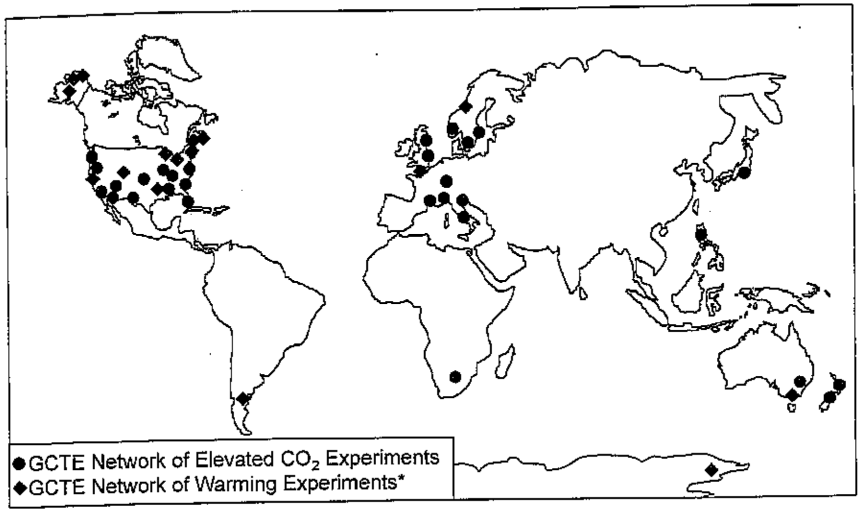
1. Experiments with either elevated CO_2, or warming, or both should investigate the interactions with other factors such as nitrogen deposition and water availability. If possible, it is desirable to include ozone, salinity, and UV-B.
2. As we learn more about the existence of thresholds and nonlinearity of plant and ecosystem responses, multifactorial treatments with more than two levels in each factor (e.g., ambient concentration, 500 ppm, 700 ppm in CO_2 treatments) are recommended.
3. Experiments should run long enough to allow, if possible, at least one life cycle of the dominant species. Such an experiment will allow inter- and intraspecific competition and feedback processes (e.g., litter decomposition and nutrient availability changes) to manifest. This recommendation may be feasible only for herbaceous systems.
4. The study of mature systems is encouraged over young, expanding systems. The latter is more prone to show unsustainable large responses that are likely to be quite different from those revealed from the mature systems.
5. Field experiments that have coupled plant–soil systems and undisturbed soils are recommended in order to characterize more realistic belowground processes (e.g., rhizosphere dynamics).

Finally, a major effort should be directed at setting up experiments in biomes that have been studied insufficiently or not at all but are critical for understanding the global carbon cycle (Fig. 2). These include such major ecosystems as boreal forests, savanna, and both humid and dry tropical forests. However, even with a major scientific guided effort (both for funding and personnel), it may not be possible to study enough sites to cover the basic ecosystem types. This makes the use of model ecosystems (e.g., annual grasslands) an essential tool in understanding the basic operating mechanisms involved in response to global changes.

B. Modeling

Whole ecosystem experiments will be closely linked to the development and operation of dynamic ecosystem models. This linkage will help to guide the interpretation of the results, sharpen the focus on understanding the mechanisms underlying the observed responses, and ensure the broader applicability of the results to other systems.

At the regional and global levels, ecosystem and biospheric models have shown to be very valuable. However, they do not account for important landscape processes such as disturbances (e.g., fire) and biome shifts that are known to occur under climate change. To account for these important landscape processes, which have major impacts on the regional and global carbon cycle, new modeling approaches are needed. One exemplary approach is to couple vegetation movement with biogeochemical cycling. Such models account for disturbances and biome shifts as well as changes in ecosystem functioning and they also quantify changes in carbon pools in a more realistic way.



(*Under Development)

Figure 2 Global distribution of GCTE (global change and terrestrial ecosystem) networks of elevated CO_2 experiments and warming experiments. This global map is also indicative of where future efforts should be placed in biomes that have not been studied or have been less studied.

V. Conclusions

Global change is a multifactorial process, involving not only rising atmospheric CO_2 concentration but also increases in nitrogen deposition, global warming, ozone, UV-B radiation, and salinity in association with variations in precipitation. Research on the effects of elevated CO_2 on plants and ecosystems in the past two decades has provided a great foundation for developing a predictive ability with regard to terrestrial responses to global change. However, our understanding of stress and CO_2 interactions in determining actual changes in plant and ecosystem structure and function is extremely limited. This book, while providing the most up-to-date knowledge and thinking on multistress interactions, is designed to stimulate future research on that matter.

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