

Research review

Evaluating ecosystem responses to rising atmospheric CO₂ and global warming in a multi-factor world

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Summary

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Analyses of ecosystem responses to global change must embrace the reality of multiple, interacting environmental factors. Ecosystem models demonstrate the importance of examining the combined effects of the gradually rising concentration of atmospheric CO₂ and the climatic change that attends it. Models to forecast future changes need data support to be useful, and data–model fusion has become essential in global change research. There is a wealth of information on *plant* responses to CO₂ and temperature, but there have been few *ecosystem*-scale experiments investigating the combined or interactive effects of CO₂ enrichment and warming. Factorial experiments to investigate interactions can be difficult to design, conduct, and interpret, and their results may not support predictions at the ecosystem scale – in the context of global change they will always be case studies. An alternative approach is to gain a thorough understanding of the modes of action of single factors, and rely on our understanding (as represented in models) to inform us of the probable interactions. Multifactor (CO₂ × temperature) experiments remain important, however, for testing concepts, demonstrating the reality of multiple-factor influences, and reminding us that surprises can be expected.

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Introduction

Terrestrial ecosystems are constantly responding to an ever fluctuating variety of biotic and abiotic influences. Daily and seasonal changes in light, temperature and humidity are obvious features of any natural environment, and they define the distribution of species and biomes. Ecosystems persist (usually) through drought years and wet years, unusually cool and unusually warm years. Insects and disease can alter the structure of ecosystems, sometimes with predictable regularity

but often with no warning. Superimposed on this complex suite of influences are the gradually rising concentration of CO₂ in the atmosphere and the climatic change that attends it. Sorting out the myriad natural influences from those caused by human activities is an extraordinary challenge.

Increasing atmospheric CO₂ concentration and rising average global temperature are well documented changes in the global environment, and their origin in human activity is clear (IPCC, 2001a). Understanding how ecosystems respond to simultaneous increases in atmospheric CO₂ and temperature,

Table 1 Principal mechanisms of plant and soil responses to CO₂ and temperature used in three biogeochemical models

	Biome-BGC	CENTURY	TEM
Plant responses			
CO ₂	Ci ↑ Production ↑ Canopy conductance ↑ Leaf N ↑	Potential production ↑ Transpiration ↓ Leaf N ↓	Ci ↑ Production ↑
Temperature	Pn optimum Rm ↑ Rg ↑ with Pn	Production optimum	GPP optimum Rm ↑ Rg ↑ with GPP
Soil responses			
CO ₂	Soil moisture ↑ Litter N ↓	Soil moisture ↑ Decomposition ↓ with leaf N ↓	Decomposition ↓ with leaf N ↓
Temperature	Decomposition ↑ Soil moisture ↓ N mineralization ↑	Decomposition ↑ Soil moisture ↓ N mineralization ↑	Decomposition ↑ Soil moisture ↓ N mineralization ↑

Ci, internal leaf CO₂ concentration; Pn, net photosynthesis; Rm, maintenance respiration; Rg growth respiration; GPP, gross primary productivity. Adapted from Melillo *et al.* (2001).

and how they will respond in the future, is imperative. 'The ecosystems of the world are critical foundations of human society' (Committee on Global Change Research, 1999). Ecosystems deliver goods and services to humankind that are critical for our survival – food, materials, energy, water and less tangible qualities. Maintaining the flow of those goods and services requires maintaining healthy ecosystems in the face of human-caused changes in the global environment. Furthermore, ecosystems play key roles in regulating the cycling of carbon (C) and the flow of energy, and hence they participate in the shaping of weather, climate, atmospheric composition and climate change.

Forecasting how rising CO₂ and temperature will affect ecosystems in the future has been the subject of many modeling exercises over a wide range of detail and sophistication. Most early efforts considered only one factor at a time, leading to seemingly incompatible conclusions: 'The projected climatic changes will destroy forests over large areas' (Woodwell, 1986) and 'In fact, if the air's CO₂ content were ever to double or triple, the productivity of the planet's trees may possibly rise severalfold' (Idso & Kimball, 1993). Clearly, ecosystems will not experience global warming without the co-occurrence of elevated CO₂, and how they respond will be a function of the combined effects of CO₂ and temperature. As recognized in the third assessment report of the IPCC (2001b), it is no longer useful to examine the impacts of climate change without including their interactions with rising atmospheric CO₂. Hence, both CO₂ and temperature effects were incorporated into the projections that were conducted as part of the comprehensive National Assessment of Climate Change Impacts on the United States (Melillo *et al.*, 2001), as well as in retrospective analyses of global vegetation responses to climatic change since the last glacial maximum (Harrison & Prentice, 2003).

These efforts have illustrated the importance of including CO₂ fertilization effects in estimating responses to both past and future climate change, despite the uncertainty in the magnitude of the response.

The predictions of future responses depend on how the effects of rising temperature and CO₂ are represented in the models, and the three models used in the National Assessment differ in some of their assumptions (Table 1). Several questions arise: Are the representations of CO₂ and temperature effects in the models reasonable and in agreement with what is known from direct observations and experimentation? Do the results of experiments in which CO₂ and temperature are manipulated agree with model projections (and is this a reasonable question)? Do experiments inform us about interactions between CO₂ and temperature that are missing from models?

These questions highlight an important principle: forecasting future changes relies on models as tools, but a model that has not been adequately evaluated against real data is almost useless. Hence, data–model fusion, or the introduction of diverse data sets into models to optimize constraints, has become essential in global change research. Here, we examine some of the issues and concepts that are important in bringing together experimental data and modeling approaches to address ecosystem responses to CO₂ and temperature interactions.

Experimental Approaches to CO₂ × Temperature Interaction

The effects of elevated CO₂ have been investigated in many experiments with different species and over a range of scales from the chloroplast to the ecosystem. Most of these have been single-factor experiments; other environmental variables (e.g. temperature, soil moisture, N availability) were either constant

(as in a growth chamber experiment) or uncontrolled. Some insights into $\text{CO}_2 \times$ temperature interaction might be gleaned from analysing the responses to CO_2 in relation to diurnal or seasonal variation in temperature (Naumburg *et al.*, 2004), but temperature variation will inevitably be confounded by other plant and environment factors. Air temperature is more difficult to manipulate than CO_2 in experiments outside of growth cabinets, and there have been far fewer ecosystem-scale experiments (Rustad *et al.*, 2001). Many warming experiments have elevated only soil temperatures (using buried heating cables) or primarily canopy temperatures (using infrared heaters), making interpretation of results difficult (Rustad *et al.*, 2001). Whole-ecosystem warming experiments have been conducted in grasslands (Luo *et al.*, 2001a; Saleska *et al.*, 2002), but existing technologies (and financial resources) essentially preclude similar experiments in intact forests. Hence, available data on forest responses come from soil warming experiments (Melillo *et al.*, 2002; Stromgren & Linder, 2002), treatment of individual trees (Peltola *et al.*, 2002), small assemblages of young trees (Norby *et al.*, 2000; Olszyk *et al.*, 2003; Turnbull *et al.*, 2004), or unreplicated enclosures over intact ecosystems (Wright, 1998). It is not surprising, then, that despite the wealth of information on plant responses to the interaction of CO_2 and temperature (Morison & Lawlor, 1999), there have been few ecosystem-scale experiments investigating the combined or interactive effects of CO_2 enrichment and warming.

Factorial experiments can be difficult to implement. Inevitable limitations on the number of experimental units, due to financial constraints or space availability, often require a trade-off between the number of treatments and the number of replications. The number of different treatment combinations and possible outcomes often leads to vague hypotheses and confusing results. With limited replication there is often insufficient statistical power to detect interactions, defeating the primary purpose of conducting factorial experiments. (By 'interaction' we mean the situation in which the direction or magnitude of the response to one variable depends on the value of one or more other variables; in this case, the combined effect of the two variables is not simply the sum of the responses to the two variables alone.) It might well be more efficient to gain a thorough understanding of the modes of action of single factors, and rely on our understanding (as represented in models) to inform us of the probable interactions. Before we adopt such a strategy, we should explore the benefits and pitfalls of $\text{CO}_2 \times$ temperature factorial experiments.

Experimental evidence

A fundamental basis for expecting interactions between CO_2 and temperature effects comes from the response of photosynthesis, which has been revealed by experimental research and supported by a strong, mechanistic framework (Long, 1991; Morison & Lawlor, 1999). The rate of leaf photosynthesis increases as leaf temperature increases to an optimum, and then

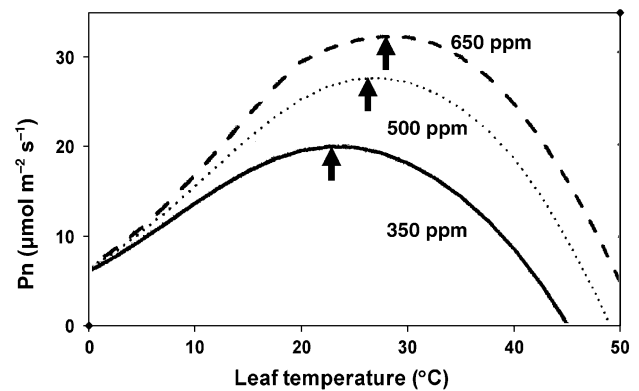


Fig. 1 The response of light-saturated net photosynthesis to changes in leaf temperature at different atmospheric CO_2 concentrations. Arrows indicate the shift in optimum temperature with increasing CO_2 concentration. Redrawn from Long (1991), with permission of Blackwell Science.

decreases as temperature rises further (Fig. 1). At any given temperature, photosynthesis increases with increasing CO_2 concentration, $[\text{CO}_2]$, but in addition the optimum temperature increases. Hence, $[\text{CO}_2]$ can alter the magnitude or even the direction of response to temperature increases, depending on the relationship between current temperature and the temperature optimum. The mechanistic foundation of this response is in the biophysics and biochemistry of photosynthesis and photorespiration (Long, 1991). Ecosystem models that represent C assimilation using equations based on Farquhar *et al.* (1980) will automatically include an interaction between CO_2 and temperature.

The question arises, however, as to whether the expression of $\text{CO}_2 \times$ temperature interaction on leaf photosynthesis translates to whole-plant or ecosystem properties. Short-term responses of photosynthesis to environmental variables do not predict longer-term responses of plant productivity (Lloyd & Farquhar, 1996; Drake *et al.*, 1997; Morison & Lawlor, 1999). Internal feedback, such as through the nitrogen (N) cycle, can limit the responsiveness of photosynthesis, and acclimatization of photosynthesis and other processes to elevated CO_2 and temperature can occur. Structural changes, such as leaf area index or leaf display, can alter the relationship between leaf photosynthesis and canopy photosynthesis. Allocation patterns can change such that increases in C uptake do not result in a concomitant increase in biomass (Norby *et al.*, 2002). Ecosystem response to CO_2 and temperature will be a function of a large suite of processes involved in biogeochemical cycles, energy fluxes between soil, plant and atmosphere, and changes in community composition. Characterization of effects at larger scales must come from the incorporation of additional mechanisms into models, from observations of CO_2 responses in relation to natural variations in temperature (e.g. diurnal or seasonal variation, or changes along a latitudinal gradient), or from experimental manipulation of CO_2 and temperature

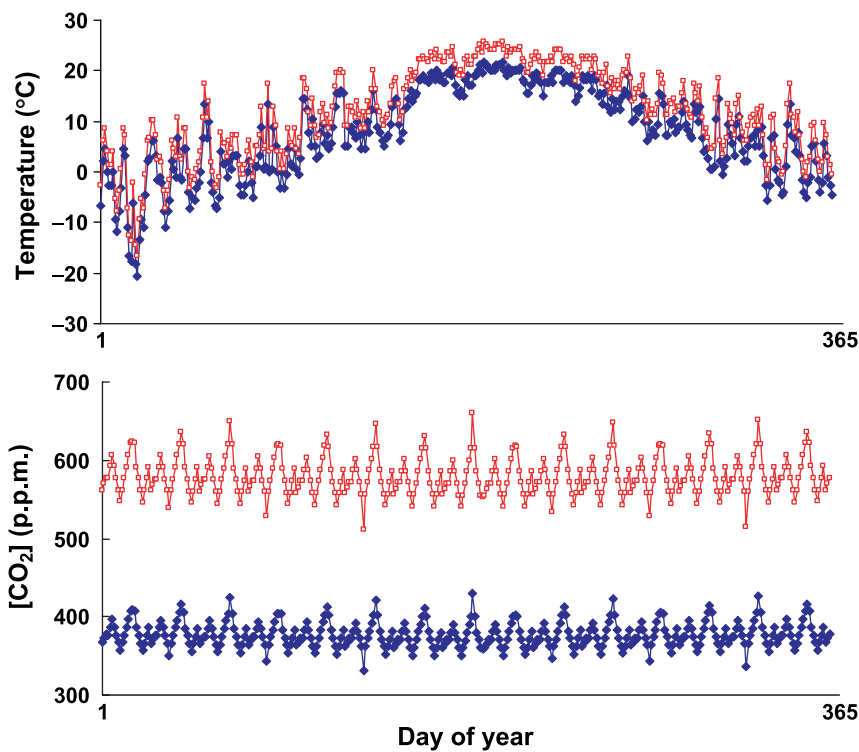


Fig. 2 Variation in air temperature (upper panel) and atmospheric CO₂ concentration (lower panel) that typically occur diurnally and seasonally, and the relationship of that variation to treatments (squares) typically imposed in warming and CO₂ enrichment experiments compared with the ambient or control condition (diamonds).

in intact or model ecosystems. The difficulty in implementing large-scale warming treatments has precluded many CO₂ × temperature interaction experiments in intact ecosystems (Rustad *et al.*, 2001).

Characteristics of the variables

The specification of the variables to be used in experiments on CO₂ × temperature interaction is an important consideration in experimental design if the results are to be used to address larger-scale questions about ecosystem responses to global change. The challenge is that experiments are necessarily constrained in time, space, and biological complexity, and the CO₂ and temperature treatments must also be constrained, yet we want to interpret the experiments over much broader scales with much wider variation in CO₂ and temperature. Some of the issues involved can be seen by examining the characteristics of the variables. Elevated [CO₂] primarily stimulates photosynthesis and reduces stomatal conductance. Other responses, including accelerated growth, changes in allocation and transpiration, and reduced foliar N concentration, are secondary, deriving from the increase in C supply and its interaction with water loss. Temperature, however, affects all biological processes – photosynthesis, respiration, cell division, transport, phenology and so on. Even small amounts of warming can have cumulative effects over time, significantly affecting growth and ontogenetic development (Morison & Lawlor, 1999). Furthermore, changing temperature implies changing water regime. The nature of temporal and spatial variation of CO₂ and temperature is

markedly different. Atmospheric CO₂ does vary diurnally and seasonally, but the amount of variation (especially during daylight hours) is much smaller than the multidecadal change that is simulated in experiments. Temperature can vary over a very wide range over the course of a single day, much larger than the increase in average temperature that is simulated in experiments (Fig. 2). Spatial variation also differs considerably: variation in CO₂ concentration across the globe is much less than the wide range in temperature regimes. Furthermore, projected increases in CO₂ will generally be spatially uniform, but temperature is projected to rise more in the high latitudes than in low latitudes (IPCC, 2001a).

An important aspect of analyses of ecosystem responses to warming is the dependency on initial conditions (Shaver *et al.*, 2000). Biological processes have a temperature optimum, with reaction rates increasing from *c.* 0°C to the optimum, and then declining rapidly with further increases in temperature. Hence, temperature increases can have either positive or negative effects on a given process depending on the current relationship to the optimum curve. An assemblage of species that are near the northern limit of their ranges (from a northern hemisphere perspective) might be expected to respond favorably to an increase in temperature, whereas those at the southern limit may be adversely affected. In a meta-analysis of warming experiments, the response of above-ground productivity varied inversely with the mean annual temperature of the experimental site (Fig. 3). Hence, it will be difficult, if not impossible, to generalize from the responses of an individual warming experiment. It is also impossible to specify with

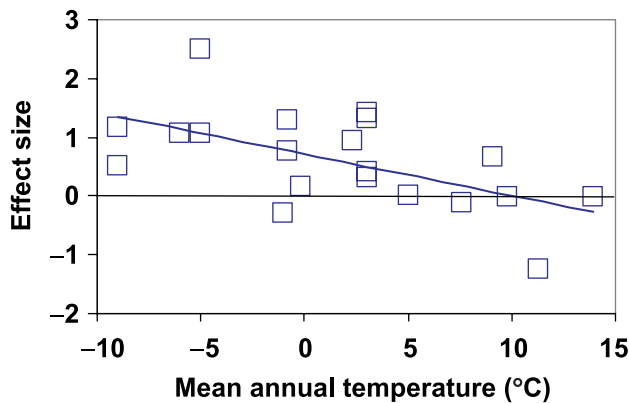


Fig. 3 The response of above-ground plant productivity to experimental warming at 20 different research sites in relation to the mean annual temperature (MAT) at the site. The 'effect size' summarizes the magnitude of response using Hedges' *d* index, or standardized mean difference; an effect size of 0.8 is considered to be large. The data are from Rustad *et al.* (2001). The linear regression is: $\text{effect} = 0.71 - 0.071 \times \text{MAT}$, $R^2 = 0.33$, $P < 0.003$.

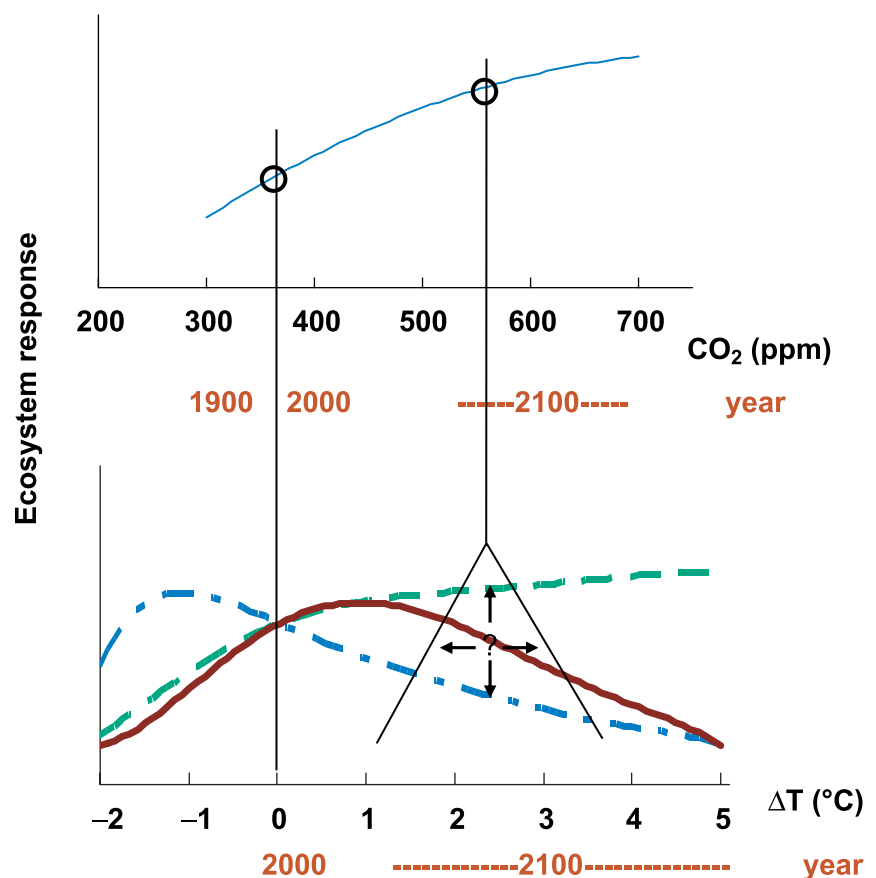
confidence a temperature scenario to correspond with a given CO₂ concentration (Fig. 4). As a consequence of these manifold sources of variation and uncertainty, any experiment with a CO₂ × temperature interaction will necessarily be a case study

in a model system. The observed responses to the combination of elevated CO₂ and warming would likely be different with a different choice of treatments levels, or with a different assemblage of species, or with the same species in a different climatic zone. Specific projections from the net response to elevated CO₂ and elevated temperature must be avoided.

A case study

As an example, consider the 4-yr CO₂ × temperature experiment with maple trees in Oak Ridge, TN, USA, called the TACIT experiment (Temperature and CO₂ Interaction in Trees). Sugar maple (*Acer saccharum*) and red maple (*Acer rubrum*) trees were grown from seedlings in open-top chambers that had been modified to control air temperature at ambient or ambient +4°C, combined with ambient or ambient +300 ppm CO₂ (Norby *et al.*, 1997). A premise of the experiment was that the two species would respond differently based on their presumed adaptations to temperature. The experimental site was close to the southern limit of the range of sugar maple, whereas the range of red maple extends much further to the south. Typical of such experiments, a wide range of processes were measured, including photosynthesis, leaf optical characteristics (Carter *et al.*, 2000), above-ground growth and phenology (Norby *et al.*, 2003), root dynamics (Wan *et al.*, 2004), soil

Fig. 4 Illustration of the issues involved in designing a treatment scenario for a CO₂ × temperature interaction experiment. A hypothesized ecosystem response to increasing CO₂ concentration (upper panel) is relatively straightforward, although there is uncertainty about the CO₂ concentration that will occur in any given future year. The uncertainty in the amount of warming (lower panel) that will correspond to the chosen CO₂ concentration is much larger (horizontal arrows), and ecosystem response will depend on the current relationship between the ecosystem and temperature regime (vertical arrows). As a result of these sources of uncertainty, CO₂ × temperature experiments must be considered case studies and not a representation of a future reality.



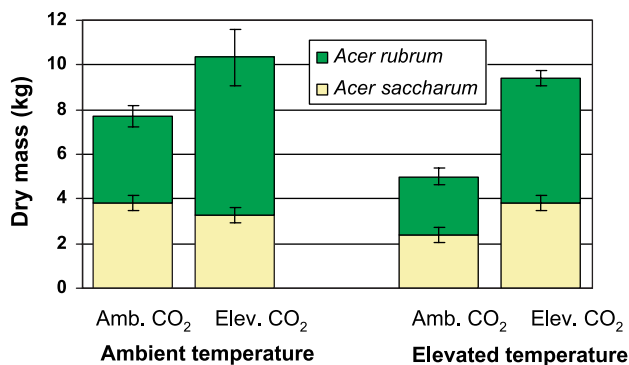


Fig. 5 Above-ground woody dry mass of *Acer saccharum* and *Acer rubrum* trees after exposure for four growing seasons in open-top chambers with ambient or elevated CO₂ (+300 ppm) in combination with ambient or elevated (+4°C) air temperature. The data are presented as biomass per chamber and are the means of three chambers per treatment ± SE. Experimental details are given in Norby *et al.* (2000).

respiration (Edwards & Norby, 1998), N dynamics (Norby *et al.*, 2000), and insect interactions (Williams *et al.*, 2000, 2003). When the trees were harvested after four growing seasons (3.5 years) in the different combinations of CO₂ and temperature, they were in a dense stand 4 m tall and with a leaf area index between 5 and 7. As is generally expected, growth was enhanced in a CO₂-enriched atmosphere: total stem dry mass was increased by CO₂ enrichment by 34% in ambient temperature and by 88% in elevated temperature (Fig. 5). Warming, however, retarded growth by 35% in ambient CO₂ but only by 9% in elevated CO₂. Hence, we can conclude that the stimulation of plant growth by CO₂ enrichment is greater at elevated temperature, or alternatively, that the negative effect of warming in this experiment was ameliorated by CO₂ enrichment. Any such conclusion must be tempered by the qualification that although the main effects of CO₂ and temperature in this study were statistically significant ($P = 0.001$ and $P = 0.025$, respectively), the interaction term was not ($P = 0.198$). Hence, in a statistical sense, the effects of CO₂ and temperature were additive and no new information was gained by studying them together. Productivity responses were additive (no significant CO₂ × temperature interaction) in other multiyear field chamber experiments with *Pseudotsuga menzeisii* (Olszyk *et al.*, 2003), *Pinus sylvestris* (Peltola *et al.*, 2002) and clover-phalaris swards (Lilley *et al.*, 2001).

Whether one takes a rigorous statistical approach to declare no interaction between CO₂ and temperature or ignores the statistics to make broad generalizations about temperature effects on CO₂ response and CO₂ amelioration of temperature effects, the data presented here on total dry matter production mask a great deal of complexity. For example, the two species responded differently to CO₂: red maple was stimulated by CO₂ enrichment much more than sugar maple (Fig. 5). This observation is consistent with the premise that when temperatures are close to optimal, the relative biomass increase caused

by increases in CO₂ enrichment is greater than when temperatures are sub- or supra-optimal (Poorter & Pérez-Soba, 2001). The responses varied with time: elevated temperature depressed relative growth rate only during the second year of treatment. The realized response was the net result of the effects on different processes, some negative (elevated temperature suppressed photosynthesis; C. A. Gunderson, pers. comm.) and some positive (growing season was usually longer at elevated temperature; Norby *et al.*, 2003). There also was an important role for stochastic events: a late-spring frost that altered normal phenology (Norby *et al.*, 2003) and a severe hot period that caused heat stress. The combination of factors that influenced final dry mass in this experiment are unlikely to be reproduced in another experiment or in the real world, making it more difficult to apply these results to an ecosystem context.

Value of experiments

This experiment and others suggest that, at levels of organization higher than a single leaf or in the field environment with multiple, fluctuating and interacting variables, CO₂ and temperature effects are usually additive. This apparent discrepancy with the observed response of photosynthesis under controlled conditions (Fig. 1) might be related to lack of statistical power, offsetting process-level effects, or scale considerations. However, additivity is not always the rule, and surprises may well occur as in the multifactor manipulation in an annual grassland at Jasper Ridge, CA, USA. Here, the single factor effect of elevated CO₂ on net primary productivity (NPP) was positive, but when combined with other global change factors, elevated CO₂ suppressed the positive effects of warming, N deposition or increased precipitation, apparently by decreasing allocation to roots (Shaw *et al.*, 2002). Hence, the interactive effects of CO₂ and temperature differed greatly from the simple, additive combinations of the single factors. By contrast, the effects on biodiversity in this ecosystem were strictly additive: elevated CO₂ and N deposition reduced diversity (primarily through the loss of forbs), increased precipitation increased diversity, warming had no effect, and there were no significant interactive effects (Zavaleta *et al.*, 2003). Regardless of the presence or absence of interactions, factorial experiments provide the opportunity to investigate two or more variables simultaneously on the same ecological system and under the same climatic and edaphic conditions. They can illustrate areas of uncertainty, and they can be used to test whether models are appropriately characterizing interactions.

Modeling Approaches

A model is particularly useful when we have to deal with multiple processes with complex feedbacks and interactions. A contemporary model is supposed to function as a deposit of knowledge, reflecting our current understanding of a subject. Deficiencies in model predictions and explanation often

reflect gaps in our knowledge, and for that reason models can be useful in generating questions for future research. However, advances in scientific understanding rely on experimental evidence to support or falsify modeling inferences. While a well-validated and calibrated model can generate policy-relevant scenarios or projections of future change, experimental data occasionally reveal novel phenomena, leading to new discovery.

A model represents a system by its structure and parameter values. For example, to study the C cycle in terrestrial ecosystems, dozens of biogeochemical models have been developed (Parton *et al.*, 1987; Rastetter *et al.*, 1991, 1997; Comins & McMurtrie, 1993; Luo & Reynolds, 1999; Thompson & Randerson, 1999; Cramer *et al.*, 2001; McGuire *et al.*, 2001). Most of those models share a common structure that partitions photosynthetically fixed C into several pools, although the number of C pools in each model may vary. In general, C transfers between pools are driven by donor pools. That is, the amount of C leaving a pool is proportional to the pool size. The parameter values that are related to partitioning and transfer coefficients of photosynthate determine how fast C cycles within an ecosystem and regulate the capacity of an ecosystem to sequester C (Luo & Reynolds, 1999; Thompson & Randerson, 1999). To simulate the hydrological cycle of an ecosystem, a model has to describe energy balance that drives evapotranspiration, soil surface wetness and stomatal conductance.

Model structure and parameterization

In this section, we examine both model structure and parameterization in terms of modeling studies of ecosystem responses to rising atmospheric CO₂ and temperature. Research has demonstrated that direct effects of elevated CO₂ are primarily on C influx into ecosystem, through stimulation of leaf and canopy photosynthesis, and secondarily on ecosystem water loss through reduction of stomatal conductance. The direct effects of CO₂ on photosynthesis and stomatal conductance can be simulated well by the Farquhar photosynthesis model (Farquhar *et al.*, 1980) and the Ball–Berry stomatal conductance model (Ball *et al.*, 1987), respectively.

Warming could directly affect almost all ecosystem processes because all the chemical, physical, and biological processes are sensitive to temperature. Experimental evidence has shown that there are consistent direct effects of warming on phenology and both plant and microbial respiration. Plant and microbial respiration can be described well by either an exponential or an Arrhenius equation (Lloyd & Taylor, 1994). Phenological responses to temperature can be represented by empirical equations based on degree-day accumulation, but this approach may not be accurate under the new conditions brought on by climatic warming (Hänninen, 1995).

The direct effects of CO₂ and temperature set the initial responses. The long-term changes in ecosystem properties in response to CO₂ enrichment and warming are largely regulated

by indirect, interactive, and feedback effects. The noticeable indirect effect of warming is through soil drying, which affects a suite of soil and plant processes, such as litter decomposition and N availability. A widely discussed indirect effect of elevated CO₂ is through soil nutrient availability (Luo *et al.*, 2004). It is still challenging to incorporate mechanisms in models to predict those indirect and feedback effects. We need data sets from long-term experiments and to conduct data–model fusion to help improve our predictive understanding of those feedbacks.

To improve predictions from models, we have to estimate parameter values from measurements. According to the ease with which these values can be derived, we can divide parameter estimation into five scenarios, starting with the simplest case: 1 *Experimental data can be directly converted to parameter values.* For example, specific rates of litter decomposition can usually be derived directly from laboratory and field studies of litter decomposition (Parton *et al.*, 1987), and C allocation to leaf and other plant parts is generally estimated from measured biomass (Wang *et al.*, 1998).

2 *Process-level measurements cannot easily be converted into parameter value.* For example, fine root biomass is a net product of growth and death, which are two simultaneous but counteracting processes. A given level of root biomass can be produced by numerous combinations of root growth and death rates (Luo *et al.*, 1995). Similarly, microbial biomass is determined by the counteracting growth and death processes. Parameter estimation for such processes depends on ancillary information (e.g. isotope tracing; Matamala *et al.*, 2003) or assumptions.

3 *Parameter values are not measurable in experiments because of limited technology.* In this scenario, parameters cannot be derived directly from process-level measurements. For example, root exudation, which is suspected to be an important pathway transferring C to the rhizosphere (Norby *et al.*, 1987; Ineson *et al.*, 1996; Paterson *et al.*, 1997; Hu *et al.*, 1999), is not readily measurable in natural ecosystems. As a consequence, this C-transfer pathway has rarely been included in any of the biogeochemical models. Where we have to incorporate root exudation into a modeling study, parameters for the process are usually based on multiple constraints with some degree of educated guess.

4 *A measurable quantity is a convolution of several processes with distinguishable characteristics.* For example, soil respiration is regulated by multiple processes, including root exudation, root respiration, root turnover, and decomposition of litter and soil organic matter. Those processes have distinctive response times to C perturbation which can be used in a deconvolution study to derive parameter values (Luo *et al.*, 2001b).

5 *Multiple parameters need to be derived from multiple data sets.* In this case, inverse analysis is an effective approach for parameter estimation. The inverse analysis is usually based on a process-oriented model with a given model structure and a set of parameters to be estimated. Parameter estimation is realized by defining a cost function, which measures goodness

of fit between data and the model, and by applying an optimization algorithm. For example, Luo *et al.* (2003) estimated seven C-transfer coefficients among plant and soil pools from six data sets (i.e. soil respiration, woody biomass, foliage biomass, soil C content, litter C content and litterfall) from the Duke free-air CO₂ enrichment (FACE) experiment. The estimated transfer coefficients help indicate CO₂ effects on plant and soil C processes.

It should now be clear that analysis of ecosystem responses to CO₂ × temperature interaction requires a combination of mechanistic understanding derived from experimental results and an appropriate modeling framework to integrate those responses under the desired global change scenario. A particular challenge is to make appropriate use of experimental data in models that operate over much longer time-scales than is possible to simulate in a manipulative experiment. While such a framework is already in place and is being used to address ecosystem-scale questions, projections of future ecosystem changes still will not be credible unless we substantially advance our understanding of indirect, interactive and feedback effects of elevated CO₂ and warming.

Model projections

As part of the comprehensive National Assessment of Climate Change Impacts on the USA (Melillo *et al.*, 2001), NPP of the continent was projected by three models of ecosystem biogeochemistry: Biome-BGC (Running & Hunt, 1993), Century (Parton *et al.*, 1993), and TEM (Tian *et al.*, 1999). These models simulate the cycles of C, water and nutrients in terrestrial ecosystems, which are parameterized according to life form. The influences of environmental variables, including CO₂ and temperature, are incorporated through general algorithms describing plant and soil processes (Melillo *et al.*, 2001; Table 1). Two different simulations of the climate in 2025–34 were coupled with the projected average CO₂ concentration (425 ppm) for those years. All three ecosystem models predict small increases in NPP for both climate simulations when both climate change and CO₂ effects are considered (Fig. 6). The increases are smaller when only climate change effects are considered, and both Biome-BGC and TEM suggest that without CO₂ fertilization, average annual NPP for the period 2025–34 would decline relative to current annual average.

Cramer *et al.* (2001) evaluated the response of highly integrative measures of ecosystem function (NPP, biomass, runoff, net ecosystem production (NEP) and soil C) to rising CO₂ and temperature at the global scale using six dynamic global vegetation models, driven by a mid-range projection of atmospheric CO₂ concentration (IS92a) and a coupled atmosphere-ocean general circulation model (HadCM2-SUL). Global NPP in these simulations increased monotonically in the simulations with increased CO₂ only, but showed little response to climate change; in combination, climate change depressed the response to CO₂ by about 12% in 2100. The response of NEP, which includes more temperature-sensitive

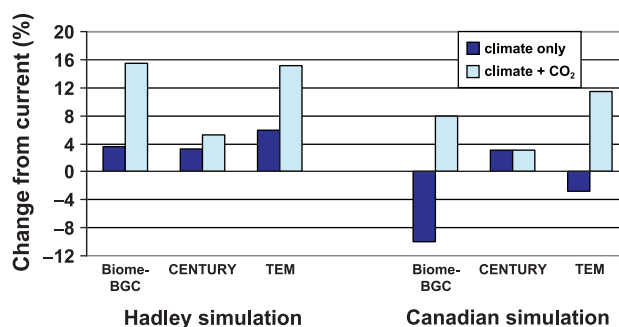


Fig. 6 Projected change in net primary productivity of the coterminous USA in response to climate change with or without concurrent changes in atmospheric CO₂. Three different biogeochemistry models (Table 1) were run using climate input from two general circulation model (GCM) experiments, one conducted at the Hadley Centre for Climate Prediction and Research of the Meteorological Office of the UK and the other at the Canadian Centre for Climate Modelling and Analysis. The simulations are for the period 2025–34 (with 425 ppm CO₂) and results are compared with the modeled net primary productivity (NPP) for 1990 (with 354 ppm CO₂). Data are from Melillo *et al.* (2001). Closed bars, climate only; open bars, climate + CO₂.

processes, was more complicated. Higher [CO₂] increased NEP, but unlike the response of NPP, the response tended to saturate. Climate change reduced NEP and the combined response was somewhat less than additive, although the different models varied substantially. The impacts of climate change on vegetation were associated with the occurrence of regional droughts in the simulations. Drought-induced forest dieback in tropical regions was associated with a loss of C, a reduction in NPP, and a change in vegetation composition toward C₄-dominated grasslands, which further reduced the capacity to respond to increased CO₂ (Cramer *et al.*, 2001). Although these large-scale changes are beyond the scope of experiments, they do suggest that experimental approaches to interactions between CO₂ and water may be more important than CO₂ × temperature.

These model results can be compared with a few experimental results, albeit with a clear recognition of the vast difference in scale between the two. The global NPP response to CO₂ in these simulations (19% increase between 2000 and 2050) is generally consistent with that observed in two forest FACE experiments in the south-eastern USA, in which NPP has increased by about 24% in response to a similar increase in CO₂ concentration (Hamilton *et al.*, 2002; Norby *et al.*, 2002). The lack of NPP response to climate change in the Cramer *et al.* (2001) simulation, however, is not consistent with the result of a meta-analysis of above-ground productivity in experimental warming studies (Rustad *et al.*, 2001), in which productivity increased by 19% in response to an average of 2.4°C of experimental warming. However, in the meta-analysis, the relative productivity response decreased with increasing mean annual temperature (Fig. 3), and there were no data from warm, tropical and subtropical sites where productivity might

be expected to decrease with experimental warming. Furthermore, the experiments do not simulate the regional droughts that were a dominant influence in the model simulations. The sparse data set on ecosystem response to experimental warming and the inevitable restriction in scale that can be addressed in experiments limit the confidence we might otherwise have in broad-scale predictions. The observation that the combined effects of climate change and CO₂ were close to additive is generally consistent with experimental results, although there are few relevant ecosystem-scale CO₂ × temperature experiments with which we can compare.

A Conceptual Framework

The difference in response of NPP and NEP to CO₂ and temperature in the simulations of Cramer *et al.* (2001) illustrate the need to explore the primary responses in more detail and with a more complete mechanistic understanding, as well as to find ways to connect experimental data realistically to processes that operate over larger scales and with much longer response times. Specific ecosystem-scale hypotheses should be developed and tested experimentally. As we have seen, the design, execution, and interpretation of experiments exploring ecosystem responses to CO₂ × temperature interaction can be difficult. It may often be more efficient and more revealing to conduct single-factor experiments and analyse and interpret their results in a model that can predict responses to the combined effects of CO₂ and warming. Shaver *et al.* (2000) illustrated the direct and indirect effects of temperature on ecosystem C exchange (Fig. 7), consistent with the previously discussed assumptions in models. Temperature could alter ecosystem C cycling through its direct effects on NPP, N mineralization, species composition, soil moisture, or heterotrophic respiration. Not shown here are the multiple mechanisms at the physiological scale whereby temperature might alter NPP, including photosynthesis, autotrophic respiration, plant development, and phenology (Morison & Lawlor, 1999). Within this same framework, we can ask where elevated CO₂ is most likely to have significant effects. The primary effect of elevated CO₂ in most ecosystems will be on NPP through a direct effect on photosynthesis. Secondary effects of CO₂ on soil moisture via its effects on stomatal conductance and transpiration can also influence ecosystem processes (e.g. Hungate *et al.*, 1997). These responses could ramify through the ecosystem, as indicated in Fig. 7, and combine with the responses to elevated temperature. In addition, interactive effects might be expected to occur such that warming alters the relationship between CO₂ and NPP, or CO₂ alters the effect of temperature on species composition.

Other environmental factors can be expected to alter how CO₂ and temperature interact and complicate the framework considerably. For example, models without N feedback generally have GPP responses to CO₂ and temperature change that are additive, while those with N feedback have interactive

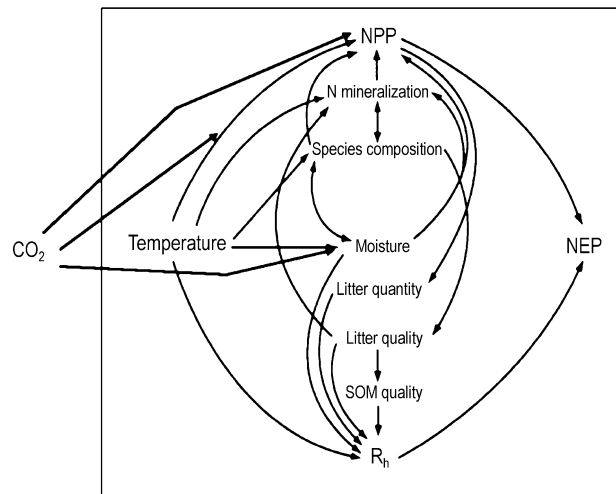


Fig. 7 A conceptual scheme for analysing the interactions between atmospheric CO₂ concentration and temperature on ecosystem processes. The portion within the box showing the influences of temperature comes from Shaver *et al.* (2000), and is used with permission of the American Institute of Biological Sciences. Temperature is shown to have direct effects on several different processes, and indirect effects follow. Enrichment of CO₂ will alter these relationships primarily through its effect on net primary productivity (NPP) (through stimulation of photosynthesis), moisture (through stomatal effects) and the relationship between NPP and temperature (alteration of the optimum balance between photosynthesis and respiration).

effects (McGuire *et al.*, 2001). Hungate *et al.* (2003) questioned the validity of models without N feedback. Most experiments, however, especially those in forests, have not been of long enough duration to support comprehensive studies of N cycling and feedback, and FACE experiments have drawn different conclusions about the likelihood of an eventual N limitation to CO₂ response (Finzi *et al.*, 2002; Johnson *et al.*, 2004). Ecosystem models include a feedback on productivity resulting from CO₂-induced changes in litter quality, decomposition, and N availability (Table 1), and the experimental evidence for this proposition has been discussed (Norby *et al.*, 2001). The more important litter quality feedback may occur at scales beyond the reach of experiments – the change in litter quality associated with the change in species composition brought on by elevated CO₂ and climate change (Pastor & Post, 1988).

From this framework emerge a number questions about CO₂ × temperature interactions, or more specifically, the interaction of CO₂ enrichment and warming. These questions can help in our interpretation of experimental data and provide a more mechanistic explanation for the broad system-level response, such as NPP and NEP.

- *How long must an experiment run to provide clues to the long-term equilibration between the competing responses of increased C influx and increased C loss?* Experiments have shown that NPP increases in response to CO₂ enrichment (Hamilton *et al.*, 2002; Norby *et al.*, 2002), and under some circumstances

C can accumulate in the soil, depending in part on the allocation and dynamics of the C (Matamala *et al.*, 2003). However, if elevated temperature increases heterotrophic respiration, the increased C input could simply be returned to the atmosphere. The rate of C loss depends on the fluxes of C between pools with different turnover rates and their responses to a sudden influx of C, as occurs in a FACE experiment. This response will likely be different from the response to a gradual rise in atmospheric CO₂ (Luo, 2001).

- *Can the response of ecosystem respiration to warming be evaluated without concurrent changes in C input?* Some experiments show loss of soil C under elevated temperature (Melillo *et al.*, 2002), but if these are interpreted in the context of simultaneous increases in CO₂, it could be proposed that CO₂ stimulation of NPP will ameliorate the enhanced C losses caused by warming.
- *Does a longer growing season in a warmer climate provide an enhanced opportunity for CO₂ stimulation of NPP?* Elevated [CO₂] does not seem to have large or consistent effects on the phenology of perennial plants, but warming can accelerate spring phenology and extend the length of the growing season (Norby *et al.*, 2003; Badeck *et al.*, 2004). A 5-yr warming in a C₃/C₄ mixed grassland increased NPP and resulted in C accumulation in soil, primarily due to extended growing seasons in both early spring and late autumn (Y. Luo & S. Wan, unpubl. data).
- *Is the net effect of opposing influences of warming and CO₂ enrichment on ecosystem water balance predictable?* Elevated temperature leads to increased evapotranspiration; without commensurate increases in precipitation, water stress can result, affecting both plant and soil processes. Elevated [CO₂], however, often reduces stomatal conductance (Medlyn *et al.*, 2001), which can reduce transpiration and increase soil moisture in some ecosystems (Hungate *et al.*, 1997) but not in others (Wullschleger *et al.*, 2002).
- *Will temperature increases lead to sufficient N availability to support a sustained response of NPP to elevated CO₂?* Carbon dioxide fertilization is often thought to be constrained by N availability (Oren *et al.*, 2001; Hungate *et al.*, 2003). Although changes in microbial N cycling have not been seen in forest FACE experiments (Zak *et al.*, 2003), experimental warming generally increases N mineralization (Rustad *et al.*, 2001). Accordingly, a forest model (Medlyn *et al.*, 2000) predicts that increased N mineralization and plant uptake under elevated temperature support a long-term increase in NPP in response to warming, whereas increases due to elevated [CO₂] are not sustained. The N status of ecosystems could be a critical determinant of how CO₂ and temperature interact.
- *Over the longer-term, will vegetation patterns that are currently defined by temperature regimes be modified in the future by elevated [CO₂]?* Enrichment of CO₂ may slow succession in temperate pasture communities by facilitating the growth of early successional dicots relative to monocots (Potvin & Vasseur, 1997). Similarly, CO₂ enrichment has tended to shift

the composition of pasture communities to increased dominance by legumes (Clark *et al.*, 1997; Schenk *et al.*, 1997). Modeling and empirical studies suggest that the secondary effects of changes in species composition on ecosystem processes are as important as the direct effects of environmental perturbations on individual plants in determining the trajectory of ecosystem response (Pastor & Post, 1988; VEMAP, 1995; Hungate *et al.*, 1996; Reich *et al.*, 2001).

These and similar questions are based on our understanding of plant responses gained in many single-factor experiments. The questions can be framed as hypotheses to test in new manipulative experiments, and their longer-term implications of the results can be explored in ecosystem and dynamic vegetation models that incorporate mechanisms of response to CO₂ and temperature.

Conclusions

Projections of ecosystem and global responses to environmental changes must recognize and incorporate the reality of multiple factor influences. Clearly, there has been much progress in the sophistication of both models and experiments, and it is no longer considered acceptable to make projections about the responses to climate change without incorporating the likely effects of CO₂ fertilization. Similarly, analyses about the role of CO₂ fertilization in the global carbon cycle or as a perturbation to ecosystem goods and services should not be made in isolation from the likelihood of climate change, a secondary effect of rising CO₂.

Our understanding of the primary effects of CO₂ and temperature on plants and ecosystems provides clues about how the two factors might interact, and this understanding guides our development of testable hypotheses for experiments and model simulations. Enrichment of CO₂ will affect ecosystem metabolism primarily by increasing C input through photosynthetic stimulation and growth, as modified by N, water and other environmental factors. Warming will influence ecosystem metabolism through effects on C processing rates that regulate NPP, microbial respiration, and ecosystem structure (population and community responses). Enrichment of CO₂ will interact with warming, primarily by altering C supply, but alterations in water relations may also be important. Responses to increased temperature, and hence CO₂ × temperature interactions, are especially dependent on initial conditions and are the net result of multiple responses. Analyses of ecosystem responses to increased CO₂ and temperature must be sensitive to scale considerations, especially with regard to fluxes between pools with different rate constants. Even as we complicate analyses by looking at combined or interactive effects of CO₂ and temperature, this is still a simplified framework. It is likely that CO₂ × temperature interactions are modified by N or water feedbacks.

We cannot predict how the effects of CO₂ enrichment and global warming will interact at the ecosystem scale simply

from the results of experiments. It is impossible to duplicate a future ecosystem and the multiple influences on it. The net effect of elevated CO₂, warming, and their interaction on ecosystem structure and function is the result of many contributing processes, the response of which will vary in magnitude and direction depending on many site-specific factors. These factors include the species and their relationship to the prevailing climate, age or successional status of the plant community, soil conditions, the particular combination of CO₂ and warming treatment levels, and stochastic (unpredictable) events during the course of an experiment. Although in many experiments the net effect of CO₂ enrichment and warming are additive, interactions occur at finer scales, and surprising results can be expected. Hence, experiments are case studies, and it is difficult to generalize from their results or use the integrated response (e.g. NPP or NEP) to parameterize models.

Models can be informed by single-factor experiments that provide process-level information about CO₂ and temperature response surfaces, and in turn model outputs can provide testable hypotheses for experiments. Current models already have frameworks to incorporate direct CO₂ and temperature responses, but improvements in parameterization of uncertain processes should be a continuing objective in experimental design, particularly related to the indirect, interactive, and feedback effects of CO₂ and temperature. Multifactor (CO₂ × temperature) experiments are important for testing concepts (looking for nonadditivity), demonstrating the reality of multiple-factor influences, and reminding us that surprises can be expected. A continued dialog between experimentalists and modelers and an explicit program of model–data fusion, including data sharing, data synthesis, and transparency of model processes, are high priorities in the ongoing effort to understand how humans are altering the planet.

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