

From Transient to Steady-State Response of Ecosystems to Atmospheric CO₂-Enrichment and Global Climate Change: Conceptual Challenges and Need for an Integrated Approach

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ABSTRACT

Evidence continues to accumulate that humans are significantly increasing atmospheric CO₂ concentrations, resulting in unprecedented changes in the global climate system. Experimental manipulations of terrestrial ecosystems and their components have greatly increased our understanding of short-term responses to these global perturbations and have provided valuable input to ecosystem, dynamic vegetation, and global scale models. However, concerns exist that these initial experimental responses may be transitory, thereby limiting our ability to extrapolate short-term experimental responses to infer longer-term effects. To do these extrapolations, it will be necessary to understand changes in response patterns over time, including alterations in the magnitude, direction, and rate of change of the responses. These issues represent one of our largest challenges in accurately predicting longer-term changes in ecosystems and associated feedbacks to the climate system. Key issues that need to be considered when designing future experiments or refining models include: linear vs. non-linear responses, direct vs. indirect effects, lags in response, acclimation, resource limitation, homeostasis, buffers, thresholds, ecosystem stoichiometry, turnover rates and times, and alterations in species composition. Although experimental and landscape evidence for these response patterns exist, extrapolating longer-term response patterns from short-term experiments will ultimately require a unified multidisciplinary approach, including better communication and collaboration between theoreticians, experimentalists and modelers.

I. INTRODUCTION

An overwhelming consensus exists that 20th century human activities have induced dramatic and unprecedented changes in the global chemical and physical environment, including a ~33% increase in atmospheric CO₂ concentrations, a ~0.6°C increase in mean annual temperature and changes in both the magnitude and degree of variability of precipitation (IPCC 2001). Current predictions indicate that, unless greenhouse gas emissions are significantly curtailed, atmospheric CO₂ concentrations will double in the next century, inducing an additional 1.4 to 5.8°C increase in mean global temperature, and further alterations in the amount, timing, and intensity of regional and global patterns of precipitation (IPCC 2001).

The response of terrestrial ecosystems to these predicted alterations in atmospheric CO₂ and climate has been the subject of intense scientific scrutiny over the past several decades, and the focus of a growing number of single and multi-factor ecosystem-scale manipulation experiments. The accumulating evidence from these experiments has greatly increased our understanding of short-term responses of terrestrial ecosystems and their components to elevated atmospheric CO₂, warming and changes in water availability (for syntheses, see Curtis & Wang 1998, Peterson *et al.* 1999, Medlyn *et al.* 1999, 2001, Rustad *et al.* 2001, Norby *et al.* 2001a,b, Zak *et al.* 2003, Badeck *et al.* 2004, Pendall *et al.* 2004, Nowalk *et al.* 2004, and Ainsworth & Long 2005), and has provided valuable input for dozens of ecosystem and global scale models that are allowing us to better understand and predict future response patterns (e.g., Parton *et al.* 1993, Potter *et al.* 1993, Running & Hunt 1993, Aber & Driscoll 1997, and Tian *et al.* 1999). Concern exists, however, that these initial responses may be transitory, and caution should be used when attempting to extrapolate short-term experimental responses from a limited number of experiments to infer longer-term effects (Norby & Luo 2004). To do these extrapolations and to better construct

conceptual and empirical models of ecosystem response to global change, it will be necessary to improve our understanding of the *change in response patterns over time*, including alterations in the magnitude, direction, and rate of change of the response. These issues represent one of the biggest challenges in accurately predicting long-term changes in ecosystems and associated feedbacks to the atmospheric and climate system.

Previous papers have explored conceptual challenges in evaluating ecosystem response to global warming (Shaver *et al.* 2000) and global warming in combination with elevated atmospheric CO₂ (Norby & Luo 2004). This paper (a) focuses on current and emergent issues that are important to guide our conceptual understanding of the *temporal patterns of response* of ecosystems to elevated CO₂ and global climate change, and (b) presents an integrated approach to future work in this field.

II. DEFINITIONS

The terms ‘steady state’, ‘transient state’, and ‘transient response’ have been loosely defined in the ecological literature. Here the term ‘steady state’ is used to describe a system where the sum of all fluxes of material and energy going into any individual component of the system equals the sum of all fluxes of material and energy going out of that same component of the system, or $a+b=c+d$ (Figure 1). A ‘static steady state’ describes a system where there is no flux of material and energy going into or out of any of the components of the system, or $a=b=c=d = 0$. Biological systems, by definition, are never in a static steady state as life is defined by the flow of materials and energy. A ‘dynamic steady state’ describes a system where the fluxes of material and energy going into each component of the system equal the fluxes going out of each components of the system, or $a+ b \neq 0, c+d \neq 0, a+b=c+d$. For example, soil carbon is considered to be in a dynamic steady state when biotic and abiotic carbon inputs into the soil system equals biotic and abiotic

carbon exports from the soil system. A 'cyclic steady state' describes a system where the cumulative flux of material and energy going into each individual component of the system over the period of the cycle equals the cumulative flux of material and energy going out of each component of the system over the same period. For example, annual cycles of leaf area index (LAI) in mature hardwood forest ecosystems and annual hydrologic cycles can be considered in cyclic steady states if they return to the same value or stage year after year. A cyclic steady state can either be externally driven (e.g., diel, monthly, or annual temperature or radiation cycles), or can arise from interactions of the internal components of the system (e.g., lynx-hare cycle). The failure to recognize these cycles could lead to erroneous conclusions about the trajectory of the system.

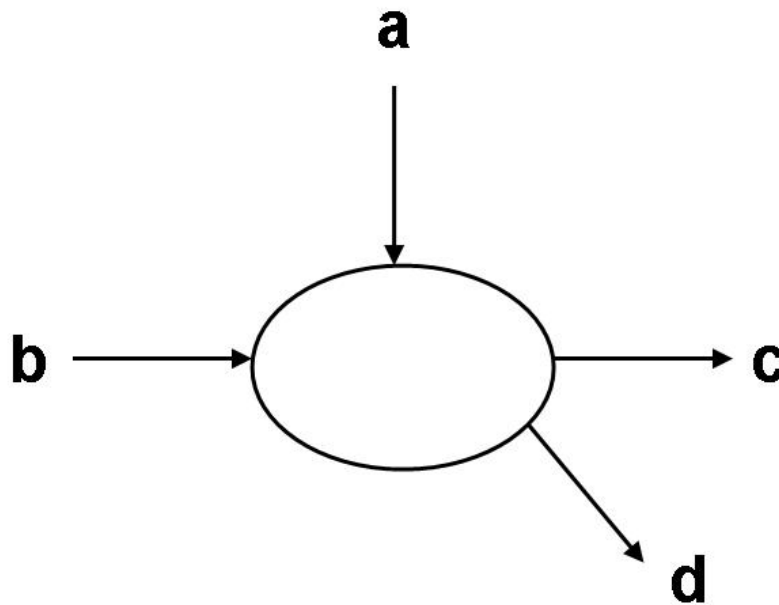


Figure 1. System states. Arrows represent flux of material and energy going into and out of a system.

A 'transient state' refers to a system where the sum of all the fluxes of material and energy going into all components of a system do not equal the sum of all fluxes of material and energy going out of all components of a system, or $a + b \neq 0$, $c + d \neq 0$, $a + b \neq c + d$. Although theoretically the distinction between a transient state and a steady state is clear, in practice it can be difficult to distinguish whether a system is in a transient state, a part of a cyclical steady state, or truly in a steady state.

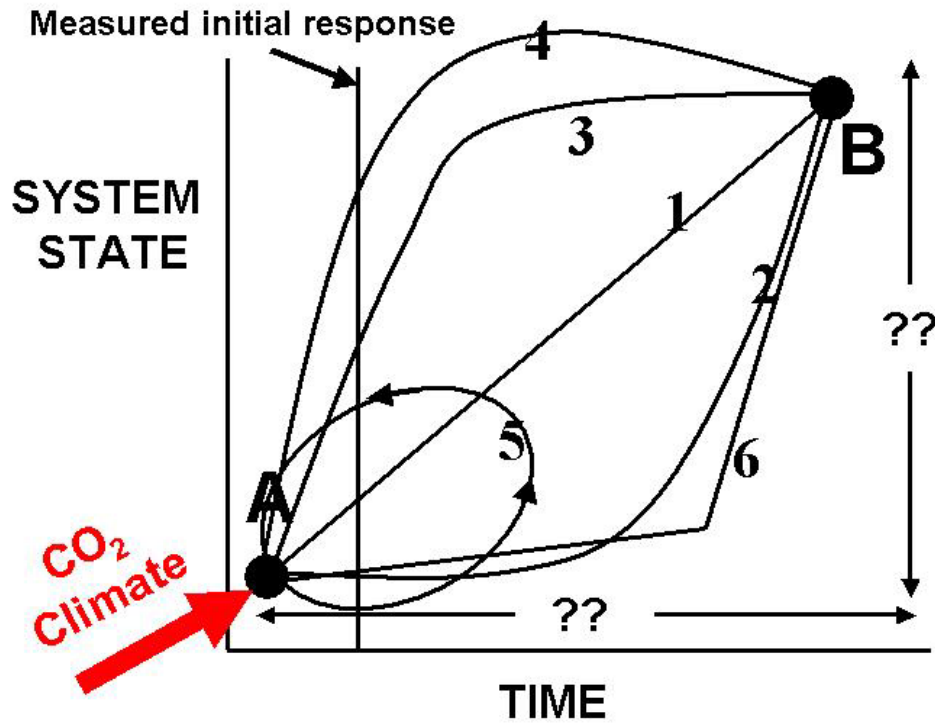
A 'transient response' describes the dynamics of a system as it approaches a steady state following a perturbation. Examples include increased N mineralization following the physical disturbance of a soil system (Kristensen *et al.* 2000, Jefts *et al.* 2004, Lamontagne 1998) or the initial rapid increase in soil respiration following a step increase in soil warming (Peterjohn *et al.* 1994, Rustad & Fernandez, 1998). The magnitude of both of these responses typically decreases over time as the systems come into a new equilibrium (Kristensen *et al.* 2000, Melillo *et al.* 2002). Questions have been raised as to whether transient responses such as these are important, and this term has increasingly been used to describe an undesired artifact at the beginning of an experiment (Lukewille & Wright 1997). These initial 'transient' responses are now often disregarded, with greater emphasis placed on understanding the longer-term responses at time scales of years or decades. By definition, however, even these "longer-term" responses remain transitory until a new steady state is reached, and short-term transient responses can be important in determining the trajectory of the longer-term response. This would occur if, for example, the transient response resulted in changes in key nutrients or resources, or if the transient response displaced the system onto a trajectory leading to an alternate steady state.

III. TEMPORAL RESPONSE PATTERNS: CONSIDERATIONS AND CONTROLS

Understanding temporal response patterns and the underlying mechanisms that control them will be fundamental to making longer-term predictions of ecosystem response to a changing environment. As illustrated in Figure 2, a perturbation, such as elevated CO₂ or a change in climate can move a system from one state (A) to another state (B), but the trajectory of the response may vary.

If the response is assumed to be approximately linear (i.e., a change in the perturbation results in a uni-directional change in the response over time; hypothetical line 1 in Figure 2), when, in fact, the response is non-linear or cyclic (hypothetical lines 2-6 in Figure 2), then extrapolations from measurements of the initial response may lead to false conclusions concerning the future state of the system. The following sections describe issues that should be considered when evaluating and modeling temporal patterns of ecosystem response to global change.

Figure 2. Hypothetical trajectories as a system moves from state A to state B. The lines represent the following hypothetical responses: 1 = a linear response, 2 = lag, 3 = acclimation, 4 = resource limitation, 5 = homeostasis, and 6 = threshold. (Diagram courtesy of Gus Shaver, TERACC Workshop, 2002).

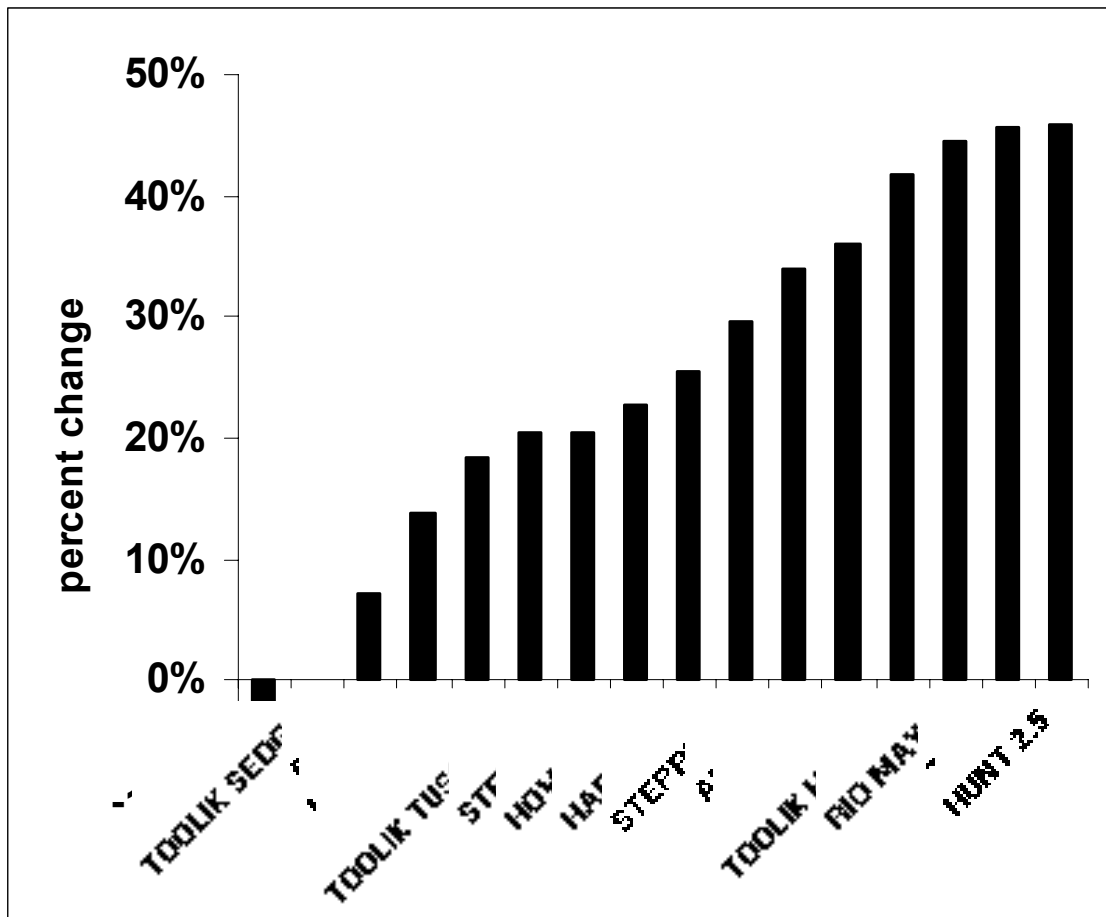


III.A. Direct vs indirect effects

The direct effects of CO₂ enrichment, warming, and changes in moisture on ecosystem processes are relatively well understood. Indirect effects, which will likely regulate long-term changes in ecosystem response, are more complex and will require considerably more effort to accurately predict and model because they can involve a complex web of interactions (Shaver *et al.* 2000). An example of direct vs indirect effects is the influence of warming on soil respiration. In general, and up to a temperature optima, warming directly increases both autotrophic and heterotrophic soil respiration (Rustad & Norby 2002). However, if higher temperatures increase evapotranspiration and thereby reduce soil moisture, then warming can indirectly result in a decrease in soil respiration. This was demonstrated by Rustad *et al.* (2001) who showed that experimental soil warming (either with electrical heating cables, infra-red heaters, or glasshouses) at sixteen

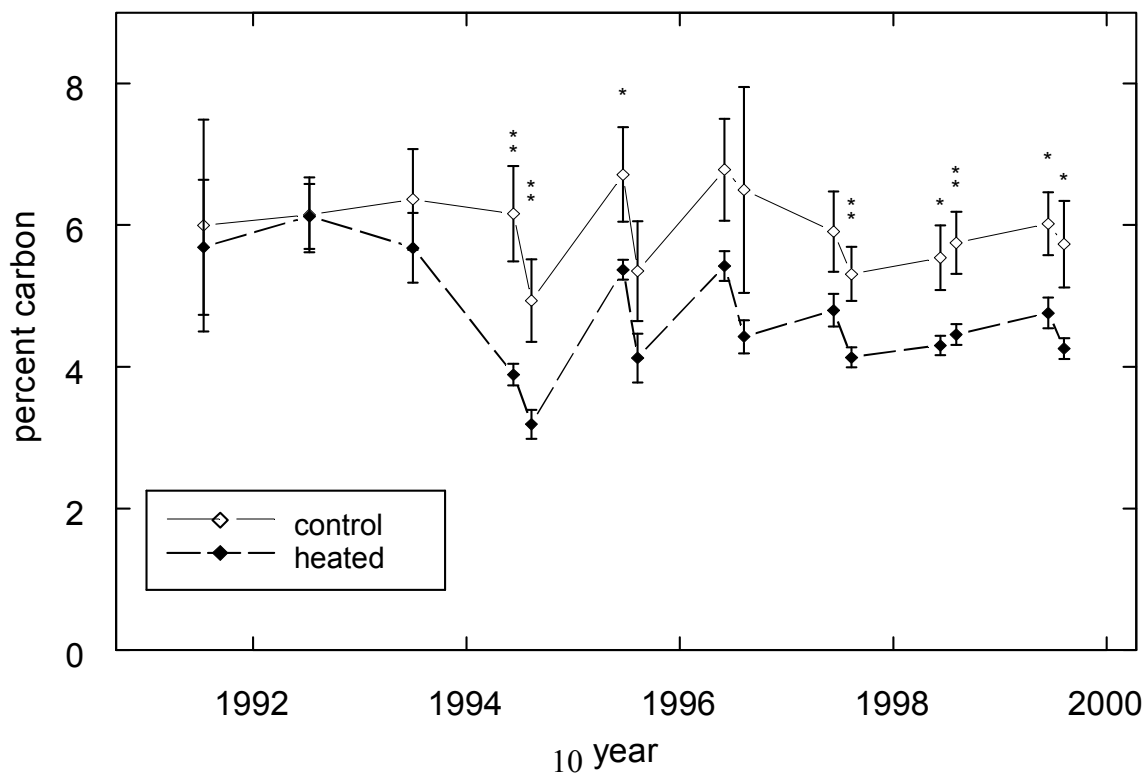
different research sites generally increased soil respiration (Figure 3). However, at one site (The Rocky Mountain Biological Laboratory, or 'RMBL' in Figure 3), a warming-induced decline in soil moisture resulted in lower rates of soil respiration in the heated plots compared to the controls (Rustad *et al.* 2001; Figure 3).

Figure 3. Percent change in soil respiration at sixteen ecosystem warming experiments. From Rustad *et al.* (2001).



Interestingly, soil carbon also declined over time in the heated plots compared to the controls at the RMBL (Saleska *et al.* 2002b, Figure 4). This decline in soil carbon was not due to an increased loss of carbon through soil respiration (since soil respiration had declined) but rather was due indirectly to a change in plant community dynamics, with a shift from forbs (characterized by high productivity) to shrubs (characterized by low productivity), and consequent declines in above and belowground plant detrital quantity and quality (deValpine & Harte 2001). Results from observations across an associated climate gradient, however, suggest that the temporal response patterns for this study will be even more complicated, and that the observed decline in soil carbon is a transient response that will eventually be reversed as lower quality detrital inputs from the increasingly dominant shrub species reduce soil respiration losses (Saleska *et al.* 2002a).

Figure 4. Percent carbon in heated and control plot soils at the Rocky Mountain Biological laboratory (RMBL) (from Saleska *et al.* 2002b).



At a larger scale, direct effects of warming on snow and/or ice cover, LAI, and/or changes in disturbance frequency such as fire may alter local, regional, or even global albedo, or the fraction of incoming solar radiation that is reflected back to the atmosphere (Ingram *et al.* 1989, Betts *et al.* 1997, Murphy & King 1997, Lynch & Wu 1999, Betts 2000). Decreases in albedo will increase the radiation absorbed by the region which will amplify warming whereas increases in albedo will cause a greater amount of radiation to be reflected back to the atmosphere, and will thus have a negative feedback to warming.

III.B. 'Lags' in response

Lags in response occur when some responses take longer to come to a new equilibrium with the environment than others because of either internal (e.g., life span, seed dispersal, vegetative propagation, etc) or external (e.g., fire, pathogens, etc) factors (hypothetical line 2 in Figure 2). For example, Vetaas (2002) showed that although mature individuals of long-lived *Rhododendron* species were not able to survive outside the cold limit of their realized niche, they could survive and continue to reproduce vegetatively when planted outside their natural high temperature range. The future distribution of this species may thus show a lag in response to gradual increases in mean annual temperature. 'Lags' due to limitations to seed dispersal and changes in disturbance regimes have been suggested by Chapin & Starfield (1997) who modeled a lag of 150-250 years in forestation of an arctic tundra following climatic warming due to (1) slow tree establishment and growth under slow climatic warming and (2) higher frequencies of fire and insect attack under more rapid climatic warming.

III.D. Acclimation

Acclimation is the often misused term that refers to a nonheritable, reversible change in the physiology or morphology of an organism in response to changing environmental conditions

(Rieleys 1990; hypothetical line 4 in Figure 2). Plants, for example, can acclimate to changing conditions by various mechanisms including changing enzyme concentrations (e.g., Maroco *et al.* 1999, Watling *et al.* 2000, Gesch *et al.* 2002), altering shoot:root ratios (e.g., Equiza *et al.* 2001, Kozłowski & Pallardy 2002, Horacio 2003, Matsuki *et al.* 2003), or changes in phenology (e.g., Campbell & Sorensen 1973, Adam *et al.* 2001). Evidence is accumulating that many ecosystem processes acclimate to elevated CO₂ and warming at the physiological level, thereby reducing their sensitivity to these perturbations, and invalidating many predictions of future responses. Considerable effort must be made to (a) understand the mechanisms underlying physiological acclimation at the organism level and (b) incorporate acclimation into existing ecosystem models.

Three examples of physiological acclimation that have received considerable attention in recent years are the acclimation, or down regulation, of photosynthesis in response to elevated CO₂, the acclimation of photosynthesis to elevated temperature, and the acclimation of autotrophic respiration to elevated temperature. Photosynthetic down regulation in response to elevated CO₂ was initially reported in dozens of CO₂ enrichment studies (e.g., Gunderson & Wullscheleger 1994, Luo *et al.* 1994, Drake *et al.* 1997, Egli *et al.* 1998, Ziska 1998, Rey and Jarvis 1998, Medlyn *et al.* 1999, Sims *et al.* 1999, Hymus *et al.* 2002b, Rogers & Ellsworth 2002) and was generally attributed to decreases in leaf nitrogen and ribulose 1,5-biphosphate carboxylase/oxygenase (Rubisco) which lead to declines in photosynthesis (Rogers & Humphries 2000). More recently, however, the role of photosynthetic down regulation has been questioned, and its prevalence, particularly in earlier pot or chamber studies has been attributed, in part, to root restriction within experimental pots (e.g., Stitt 1991, Farage *et al.* 1998), inadequate N

supply (e.g. Webber *et al.* 1994, Drake *et al.* 1997, Kubiske *et al.* 2002, Ainsworth *et al.* 2003), or the age class of needles in conifers (Medlyn *et al.* 1999).

Photosynthetic acclimation to increased temperature including both shifts in temperature optima and uniform shifts across all temperatures, has been long recognized (e.g., Barry & Bjorkman 1980, Ferrar *et al.* 1989, Read 1990, and Gunderson *et al.* 2000), and has been attributed to various factors including different thermal properties of key photosynthetic enzymes, different temperatures at which membranes are damaged, and differential thermal stability of photochemical reactions (Nilsen & Orcutt 1996). The acclimation of autotrophic respiration to elevated temperature has also been demonstrated (e.g., Kirshbaum & Farquhar 1984, Tjoelker *et al.*, 1999, 2001, Atkin *et al.* 2000a,b, Will 2000, Griffin *et al.* 2002, Bolstad *et al.* 2003), and has been attributed variously to decreased number of mitochondria (Miroslavov & Kravkina 1991), decreased respiratory capacity per mitochondria (Klikoff 1966), limitations in substrate supply (Lambers *et al.* 1996), changes in the concentration of plant soluble sugars (Atkin *et al.* 2000a), changes in demand for respiratory energy (Atkin & Lambers 1998), and/or changes in enzymatic capacity (Atkin *et al.* 2002).

Although the acclimation of both photosynthesis and autotrophic respiration to warming is well established, the potential acclimation of ‘soil respiration’ (i.e., the combined respiration of roots and soil micro- and macro-biota) to warming is more controversial. Historically, dozens of studies have demonstrated strong positive relationships between soil respiration and temperature (for syntheses see Raich & Nadelhoffer 1989, Raich & Schlesinger 1992, Raich and Potter 1995, Kirschbaum 1996; Rustad *et al.* 2001), and soil respiration is typically and effectively modeled with an exponential or Arrhenius function (Rustad *et al.* 2000). Recently, however, the temperature dependence of soil respiration has been challenged by Luo *et al.*

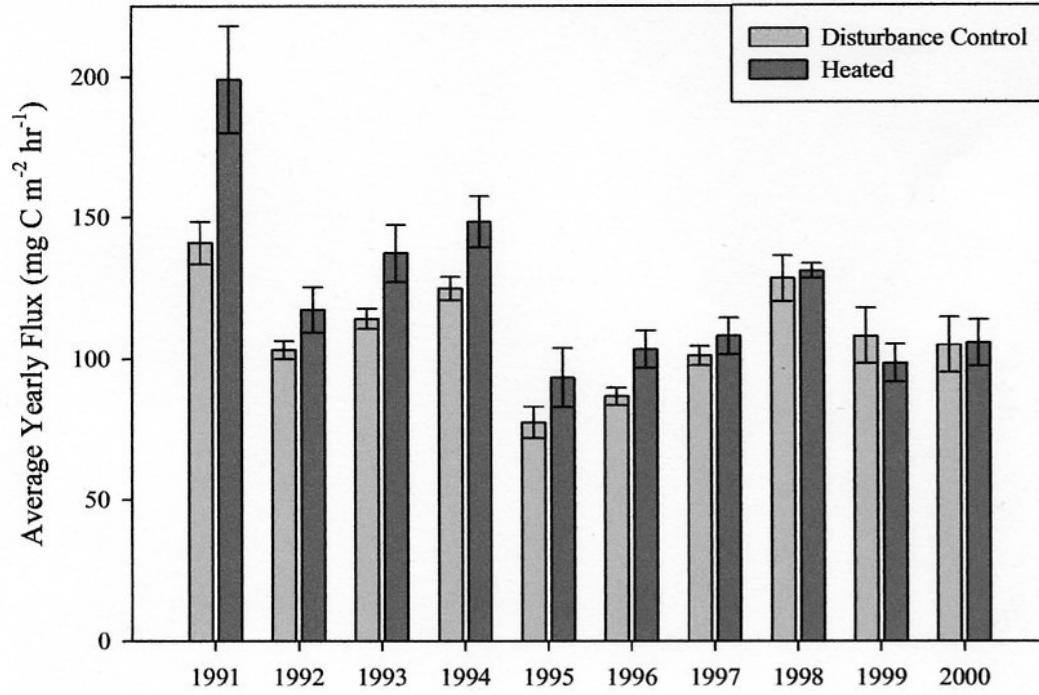
(2001) who suggested that soil respiration ‘acclimates’ to elevated temperature. They conducted a warming x grazing experiment in a tall grass prairie in Oklahoma, USA using overhead infrared lamps and clipping, and reported a decline in the respiration quotient Q_{10} from 2.70 in the unheated, unclipped plots to 2.43 in the heated, unclipped plots, and from 2.25 in the unheated, clipped plots to 2.10 in the heated, clipped plots. However, a physiological mechanism for the acclimation of soil respiration to temperature has yet to be elucidated. This is in part because, unlike photosynthesis, soil respiration is not a single process but is instead the sum of the combined respiration of plants and the complex community of micro- and macro-heterotrophic soil organisms, and includes several alternate chemical pathways. In addition, the direct effect of warming on soil respiration is complicated by a host of indirect effects, including warming-induced changes in above and belowground biomass, soil moisture, N mineralization, substrate quality and/or quantity, and microbial community activity, biomass, and composition.

Given that gross primary productivity (GPP), aboveground respiration, and soil respiration represent three of the largest fluxes in the terrestrial global carbon cycle (estimated at ~120, 60, and 60 Pg C yr⁻¹, respectively; Schlesinger 1997), it is imperative to understand if and to what degree these processes will acclimate to changing environmental conditions such as CO₂ enrichment and global warming. Even slight changes in the direction and or magnitude of these fluxes could equal or exceed the annual input of CO₂ to the atmosphere via combined fossil fuel combustion and land-use changes (estimated at ~ 6 Pg C yr⁻¹), and could therefore significantly accelerate-or decelerate-the rate of atmospheric build-up of CO₂, with consequent feedbacks to climate change.

III. E. Resource limitation/Initial Conditions

The sustainability of the magnitude and even direction of a response may be governed by the availability of resources which will be governed in part by initial conditions. For example, ecosystems with large stocks of relatively labile C may show a larger and more sustained increase in soil respiration in response to warming than an ecosystem with low initial labile C stocks, or an N-rich ecosystem may show a more sustained increase in photosynthesis and NPP under CO₂-enrichment than a N-poor ecosystem. In either case, if the systems receive no new inputs of labile C or atmospheric or fertilizer N, the magnitude of the response will decline over time as either labile C or N are depleted (hypothetical line 2 in Figure 2). For example, at the Harvard Forest soil warming experiment, Peterjohn *et al.* (1994) initially reported an approximately 40% increase in soil respiration during the first six months of the experiment. However, the magnitude of this increase diminished over time such that after 10 years of warming soils at 5°C above ambient, soil respiration rates in the heated plots were not significantly different than rates in the control plots (Figure 5; Melillo *et al.* 2002). One explanation is that labile C supplies were depleted during the course of the experiment suggesting resource limitation. The lack of a treatment effects in the latter years of the experiment also lend support to the hypothesis that different carbon fractions have different temperature sensitivities, with labile carbon fractions (consistently predominantly of simple sugars and amino acids) being highly temperature sensitive but recalcitrant carbon fractions (consisting of more complex aromatic compounds) being relatively temperature insensitive (Liski *et al.* 1999, Giardina & Ryan 2000, Melillo *et al.* 2002, Gu *et al.* 2004).

Figure 5. Annual soil respiration at the Harvard Forest soil warming experiment (from Melillo *et al.* 2002).



III. F. Homeostasis

Homeostasis is the "maintenance of" or "return to" constant internal conditions in the face of a varying external environment (Ricklefs 1990). Classic examples include (a) the thermal regulation of homeotherms despite external fluctuations in temperature, (b) the ability of organisms to maintain their internal chemical composition despite fluctuations in the chemical content of their environment or food source, and (c) predator-prey cycles where as the population of prey increases so does the population of predators, thereby decreasing the population of prey and consequently the population of predators (hypothetical line 5 in Figure 2). Local, regional, and even global ecological systems also exhibit homeostatic behavior. An example is elevated atmospheric CO₂ and the global carbon cycle. Within limits, as atmospheric CO₂ increases, leaf

level photosynthesis and NPP should increase, thereby removing CO₂ from the atmosphere and stabilizing atmospheric CO₂ concentrations. Concerns exist, however, that the current anthropogenic input of carbon to the atmosphere from fossil fuel combustion and land-use changes, particularly in combination with possible positive (rather than negative) feedbacks from warming-induced increases in the release of soil carbon to the atmosphere or decreases in albedo, may exceed the capacity of the earth's systems to maintain this homeostatic balance.

III. G. Buffers

Buffers are mechanisms or attributes that allow systems to resist change in response to external perturbation or impact. In chemistry, solutions that contain a weak acid and its salt or a weak base and its salt, and which thereby can resist changes in pH, are called buffers. Similarly, ecological systems have certain attributes that allow them to resist moderate changes in environmental variables. Examples of ecosystem properties that may provide 'buffers' against impacts of CO₂ fertilization and climate change may include soil C quality and quantity (i.e., systems with more protected, chemically stable C will be less vulnerable to soil C loss than systems with less stable C [e.g., Collins *et al.* 1997, Paustian *et al.* 1997, 2000, Six *et al.* 2000]), soil depth and water holding capacity (i.e., ecosystems with deeper soils with better water holding capacity will be less sensitive to fluctuations in precipitation than those with shallower soils with limited water holding capacity), albedo (i.e., ecosystems with higher albedo will reflect more solar radiation back to the atmosphere and will thus be less sensitive to warming than systems with lower albedo [e.g., Betts *et al.* 1997, Betts 2000, IPCC 2001, Berbet & Costa 2002]) and biodiversity (i.e., ecosystems with greater species or functional group diversity may be more resistant and resilient to environmental change than those with lower diversity [e.g., Naeem & Li 1997, Walker *et al.* 1999, Chapin *et al.* 2000, Ives & Cardinale 2004]).

III. H. Thresholds

A process is said to have a threshold if below that threshold there is either no change or proportionate change in the response of the process to a perturbation and above that threshold there is a dramatic, non-proportional response (hypothetical line 6 in Figure 2). Arnold *et al.* (1999) provide an example of the former, where, using laboratory incubations under controlled temperature and moisture conditions, they showed no difference in microbial biomass at gravimetric soil moisture contents between 120 and 320%, but a dramatic reduction of almost 95% of the microbial biomass when gravimetric soil moisture was decreased to 20%. They suggest a soil moisture threshold exists between 20 and 120% for their soils above which moisture is not limiting and temperature largely controls microbial biomass dynamics, and below which moisture is too low to sustain viable microbial biomass, regardless of temperature.

At a larger scale, thresholds also appear to exist in the climate system. Reconstruction of past climates, for example, show gradual changes in climate over geologic time scales, punctuated by dramatic changes in temperature and precipitation on time scales as small as decades (IPCC 2001). Examples include a 5-10°C increase in temperature and a doubling of snowfall that occurred in Greenland over a period of 40 years following the last glaciation and the rapid transition from shrubland to desert that occurred in the Sahara approximately 5500 years ago (Rahmstorf 2002). The causes of these rapid changes are uncertain but may be associated with thresholds in ocean circulation and sea ice dynamics, or vegetation-induced changes in albedo (Rahmstorf 2002). Concerns exist, including those expressed by the National Academy of Science Committee on Abrupt Climate Change (2001) and by Gregory *et al.* (2004), that similar mechanisms will come into play such that CO₂-induced global warming will lead to increased precipitation in high northern latitudes, which, combined with melting of the polar ice sheets, will

increase freshwater input to the North Atlantic Ocean, leading to a precipitous reduction in the global ocean's thermohaline circulation, thereby shutting down the Gulf Stream, and resulting in decreases in temperature, particularly over much of Europe.

III.I. Ecosystem stoichiometry

Ecosystem stoichiometry is based on principals of (1) the conservation of matter, (2) the stoichiometry of chemical reactions, and (3) the observation that plants, animals and even ecosystems are constructed of multiple elements in relatively fixed forms (Sterner & Elser 2002). Ratios between elements are therefore also relatively fixed, which puts constraints on element distribution and cycling, and implies that a change or disruption in the ecosystem- or global-scale cycle of one element, such as C, N, or P, will necessarily impact the cycling of other elements. For example a CO₂ enrichment-induced increase in photosynthesis and NPP will require an increase in belowground nitrogen acquisition in order to maintain leaf C:N ratios within a relatively fixed range, and will thereby impose a change in the nitrogen cycle. Or, as pointed out by Nadelhoffer *et al.* (1999) and Hungate *et al.* (2003), the amount of C that can be sequestered by an ecosystem with increasing N deposition will depend largely on whether the N is immobilized in bacteria (C:N ratios typically between 5 and 15) or soil organic matter (C:N ratios typically between 10 and 50), or whether the added N is taken up and stored in foliage (C:N ratios typically 30-100) or wood (C:N ratios typically > 300). Results from the decadal-scale N fertilization experiment at the Bear Brook Watershed in Maine and the decadal-scale soil warming experiment at the Harvard Forest in Massachusetts both show that most of the added or warming-induced mineralized N is stored in soil organic matter with relatively low C/N ratios, thus limiting the potential for these systems to sequester large amounts of additional carbon (Nadelhoffer *et al.* 1999, Melillo *et al.* 2002).

III. J. Turnover Rates and Times

The concepts of turnover rates and turnover times are fundamental to understanding and modeling ecosystem response to global change. Assuming a steady state, turnover ‘rate’ is defined as the net mass of a material entering or leaving a system or reservoir in a given time period (i.e., flux) divided by the total mass of the material present in that system or reservoir (i.e., pool; units are percent/time period). Turnover ‘time’ is the inverse, or the total mass of a material in a system or reservoir (i.e., pool) divided by the net mass of the material going into or out of that system or reservoir over a given time (i.e., flux; units are time). Turnover times can also be interpreted as the mean life span of a system or component of a system (e.g. mean tree or root lifespans) or the mean residence time of material in a system or component of a system (e.g., mean residence times for greenhouse gases in the atmosphere and for the amount of carbon in a particular soil carbon pool).

Within the global change literature, concepts of turnover rates and times have been most frequently applied to greenhouse gas concentrations, above- and below-ground biomass pools, and carbon and nutrient cycles, and questions have arisen as to whether global change will alter the *fluxes* of material into or out of atmospheric, biomass or nutrient pools, or the *pool sizes* themselves. For example, over the long term, the amount of carbon that can be sequestered by an ecosystem will depend on both the size of the carbon pool in that system and its turnover time. More carbon can be stored in an ecosystem only if either the same amount of carbon is retained for a longer time (longer turnover times) or more carbon is added to the total pool than is lost from the pool (larger pool size). Elevated CO₂ and warming will generally increase photosynthesis and will thus increase the flux of carbon going into an ecosystem. However, if this carbon is stored in labile carbon pools with fast turnover times, and if elevated CO₂ and temperature directly or indirectly increase the turnover time of these labile carbon pools, then

little or no carbon will be sequestered. Mitigation efforts to reduce the rise in atmospheric CO₂ must therefore be focused not just on stabilizing or increasing terrestrial or oceanic carbon pool sizes but also either decreasing or slowing turnover rates of existing pools (for example, by increasing the chemical and physical protection of soil carbon through better soil management practices) or transferring carbon from pools with short turnover times to pools with longer turnover times (for example, converting pasture land to forest and forest to wood products).

III. K. Community Composition, Biodiversity and Ecosystem Function

It is widely accepted that species composition and community dynamics will be strongly affected by the combined effects of elevated CO₂, warming, and changes in precipitation, and that these community changes will, in turn, have significant feedbacks on ecosystem function. However, despite this consensus, the underlying mechanisms driving plant community responses to global change are not well understood, and it has been difficult to accurately predict both community response to global change and the ecosystem consequences of these responses. This is due, in part, to the variable influence in time and space of global change on individual species, functional groups, and/or entire communities.

The responses of plant communities to simulated global change can be strongly influenced by individual plant species. A few CO₂ enrichment experiments have shown that even a single species can dominate responses of an entire plant community. For instance, Grünzweig & Körner (2001) reported significant ecosystem-scale changes in aboveground biomass, reproduction, and plant nitrogen content in response to CO₂ enrichment in semi-arid grassland assemblages from Israel. Surprisingly, these ecosystem-scale responses were attributable to CO₂-induced changes in just one out of 32 plant species. Morgan *et al.* (2004a) also reported that CO₂-induced increases in aboveground biomass in native Colorado shortgrass steppe were driven primarily by one of 36

plant species, and that enhanced seedling recruitment appeared to be an important mechanism behind this response. How would these plant communities have responded without the CO₂-responsive species, and what would have been the long-term implications for the ecosystems? These questions are difficult to answer, since species interact complexly in plant communities where microclimatic feedbacks and competition for resources occur. Absence of the CO₂-sensitive plant species would not necessarily result in a non-responsive plant community since more resources would be available to the remaining plants, and the reaction of individual species to CO₂ often interact with resource availability (Smith *et al.* 2000, Poorter & Perez-Soba 2001, Belote *et al.* 2003, Zavaleta *et al.* 2003). While a single species may drive a plant community response, plant community production and related responses to CO₂ are generally enhanced by plant species diversity (Niklaus *et al.* 2001, Reich *et al.* 2001b). Species-rich plant communities are thus more likely to exhibit strong reactions to global changes. Greater responsiveness of species-rich over species-poor communities can involve one of several forms of synergy whereby the presence of one species enhances the capability of another species to respond to CO₂ (Morse & Bazzaz 1994, Lüscher *et al.* 1996, Reich *et al.* 2001b), or may simply be attributed to the greater likelihood of having global change-sensitive species in a community with more species.

Less work has been done on the role of belowground biological diversity in global change experiments (Pendal *et al.* 2004). Linkages of aboveground and belowground biota indicate that global change may indirectly affect a number of belowground biological activities that will have powerful potential to feedback on plant communities, invoking both positive and negative responses (Wardle *et al.* 2004). Belowground biotic diversity will likely be important in determining the long-term reactions of plant communities to global change which are expected to be strongly conditioned by soil nutrient cycling (Zak *et al.* 2000).

Functional groups may also show differential responses to global change, and may be useful in streamlining approaches to understanding plant community responses to global change. However, contradictory results from field studies show that more work is needed to elucidate these differences (Morgan *et al.*, 2004b, Nowak *et al.*, 2004). For example, it has generally been predicted that C₃ species will show greater photosynthetic response to CO₂ enrichment compared to C₄ species (Strain & Bazaaz 1983). In a higher CO₂ world, an increase in the ecosystem abundance of C₃ relative to C₄ species over time would thus be accompanied by increased ecosystem productivity (Arp *et al.* 1993). Although numerous studies have demonstrated the greater photosynthetic response to CO₂ enrichment in C₃ compared to C₄ species (e.g., Bazaaz 1990, Poorter 1993, Bowes 1993, Ehrlinger & Monson 1993, Reich 2001), other studies have shown few differences between species with these very different photosynthetic pathways, particularly under conditions of water or nutrient stress (e.g., Wand *et al.* 1999, Derner *et al.* 2003). Failure of the C₃ vs C₄ functional group paradigm to manifest may be attributed, in part, to the fact that stomates of most herbaceous species close under elevated CO₂, which induces a water relations benefit that minimizes differences among photosynthetic functional groups. This is especially important in dry environments where CO₂-induced water relations responses drive CO₂ responses (Morgan *et al.* 2004b). Legumes are another functional group that has been predicted to respond strongly to elevated CO₂, because of their capability to fix atmospheric N. While this has been confirmed in several studies (Tissue *et al.* 1997, Hebeisen *et al.* 1997, Lüscher *et al.* 1998, 2000, Grünzweig & Körner 2001), other experiments show little or advantage of N-fixing capability under elevated CO₂ (Niklaus *et al.* 1998, Stöcklin & Körner 1998, Nowak *et al.* 2004). In some cases, lack of a legume CO₂ response may be attributable to insufficient soil P levels such that N fixation capacity is impaired (Körner 2000), or to super-optimal N levels (Poorter *et al.*

1996). However, in many cases, failure of legumes, C₃ plants and other functional groups to respond simply indicates that one response mechanism may be insufficient to account for a species response in a plant community and other factors may need to be considered (e.g. water relations, nutrition, plant morphology, phenology). The temporal and spatial variability of the environment, which can interact with species and plant communities in complex ways, may also be important to determine species responses.

Different plant communities are also expected to show different responses to global change. Updegraff *et al.* (2001), for example, reported greater seasonal CH₄ emissions, aboveground net primary productivity, and dissolved N retention in bog compared to fen mesocosms under conditions of warming and water table manipulation. All of these examples underscore the linkage between species composition and ecosystem function, and illustrate that temporal patterns of ecosystem response to global change will be determined, in part, by the changing assemblages of species within that ecosystem.

For pragmatic reason, much of the experimental work on the effects of global change on species diversity has been done on species with short life spans such as annuals and short-lived perennials (Ward 1999, Reich *et al.* 2001a,b, Morgan *et al.* 2004a,b). Exceptions include the work on tree species response to (a) elevated CO₂ in a coastal scrub-oak community in Florida, USA (Hymus *et al.* 2002a,b), (b) elevated CO₂ and warming for two species of maple in Tennessee, USA (Norby *et al.* 1997, Norby *et al.* 2000), and (c) elevated CO₂ and ozone in a northern forest ecosystem in Wisconsin, USA (Karnosky *et al.* 2003). The time scale of response will vary directly with the life span of the biota, with changes occurring on the scale of days to months for soil microbes, to years for annual plants, to decades and even centuries for longer-lived perennials and woody species. Although experimental manipulations will continue to be useful to evaluate

the effects of changes in species composition on ecosystem function for short-lived species, alternative approaches, using space-for-time substitutions such as gradients and chronosequences, along with ecosystem- and regional-scale models may be necessary to elucidate species change and ecosystem consequences over time for species with longer life spans (e.g. decade or greater).

IV. OBSERVATIONS, EXPERIMENTS, AND MODELS: TOWARDS AN INTEGRATED APPROACH

The foregoing discussion underscores some of the complexities involved in understanding short and longer-term responses of ecosystems to global change. A challenge remains to better integrate these concepts into current and future global change research, particularly those efforts aimed at understanding and predicting longer-term responses. As discussed by Rastetter (1996), these efforts include (1) reconstructions of past events, (2) observations across existing elevational and/or latitudinal gradients (space-for-time substitutions), (3) long-term monitoring, (4) experimental manipulations, and (5) modeling. All five approaches have their strengths and weaknesses.

IV. A. Reconstruction of past events

Over the last 20,000 years, regional and global environments have experienced dramatic shifts in their physical and chemical environments. Examples include the approximate doubling of atmospheric CO₂ concentrations from a low of ~160 to 200 micromol/mol in the Last Glacial Maximum (about 18,000 years ago) to the current high of ~ 360 micromol/mo, and the relatively regular oscillations in temperature and moisture between cool/dry and warm/moist periods on an ~ 1500 yr cycle (IPCC 2001). More subtle changes, including a 0.6°C increase in mean global temperature and alterations in the timing and magnitude of precipitation, have also been

documented during the more recent past (i.e., past 100-150 yrs) (IPCC 2001). Reconstructing temporal response patterns of terrestrial ecosystems to these past changes have provided valuable insights on predicting temporal patterns of response to future changes in these same factors. For example, in the northeastern United States, the mean annual temperature has increased by 1.0°C and the mean length of the growing season has increased by an average of 8 days since 1899 (Markham & Wake 2005). Recent evidence documents a decrease of 4-8 days in Julian date of bloom for three horticultural woody perennial species in New England during this same time period (Wolfe *et al.* 2004). Similarly, in the southeastern United States, a dramatic increase in winter precipitation was documented for the period 1977 to 1992. This increase was accompanied by a 3-fold increase in the density of woody shrubs, and the gain and loss of several species of small mammals (Brown *et al.* 1997). However, because (a) the rate and magnitude of climatic change predicted for the 21st century is likely to be greater and more rapid than any experienced during the last 20,000 yrs (IPCC 2001; NERA 2001) and (b) atmospheric CO₂ concentrations are likely to be higher in the 21st century than at any time in the past, caution must be exercised when making extrapolations from past ecosystem responses to relatively slow changes in climate in a low CO₂ world to future ecosystem responses to possibly more rapid climate change in a higher CO₂ world.

IV. B. Space-for-time substitutions

Observations across latitudinal or elevation gradients also allow for the evaluation of ecosystem response to gradual changes in climate, and have added to our understanding of ecosystem response to changes in temperature (Saleska *et al.* 2002a,b, Ineson *et al.* 1998), moisture (Davidson *et al.* 1998), and other global change factors such as atmospheric N deposition (McNulty *et al.* 1990, 1991, Aber *et al.* 2003). However, three drawbacks exist for space-for-time

substitutions. First, even with the greatest attention to detail in site selection, it is impossible to hold all ecosystem properties constant, and thus differences between ecosystems at different positions along the gradient may not reflect the same changes that might occur in a single ecosystem over time. Second, the characteristics of ecosystems at different positions along the gradient have typically evolved over the millennia time scale providing sufficient time for different short and longer-term processes to operate and for the ecosystems to come into equilibrium with their local climate. The characteristics of ecosystems responding to rapid changes in temperature and precipitation, such as those predicted to occur over the next 50-200 years, may be different. Third, spatial gradients can be identified for temperature, precipitation, and combinations of temperature and precipitation. However, with the exception of a few studies on CO₂ emission from hot springs, no comparable gradients exist for atmospheric CO₂ and thus it is not possible to use space-for-time substitutions for either CO₂ effects alone or the effects of simultaneous changes in CO₂, temperature, and precipitation. Despite these cautions, space-for-time substitutions remain a valuable approach to studying ecosystem response to changing conditions.

IV. C. Long-term monitoring

Long-term monitoring, or the methodical collection of environmental data at single or multiple sites over time, has provided a wealth of data and invaluable insights on changes in vectors such as atmospheric CO₂ (Keeling & Whorf 2004), climate (IPCC 2001), and atmospheric sulfur and nitrogen deposition (Likens *et al.* 1972). These measurements also provide insights on ecosystem responses to daily, seasonal, annual, and decadal climatic variability (e.g., NERA 2001, Fitzhugh *et al.* 2003, Park *et al.* 2003). Results from long-term monitoring studies will also, eventually, provide the ultimate validation for ecosystem and global scale models, as the results of humankind's global CO₂ enrichment 'experiment' unfold. The drawbacks to monitoring are that

historic records rarely go back more than 100 years, and future responses are as yet unknown, making later validations of models of limited use to policy makers and land managers now.

IV. D. Experimental manipulations

Experimental manipulations of whole ecosystems or ecosystem components are powerful tools that allow for the elucidation of cause-and-effect relationships and provide for a mechanistic understanding of short-term (typically < 20 years) responses of ecosystems to single or multiple vectors of global change. These experiments further provide a much needed means to validate (or not) current ecosystem models of global change, both highlighting processes that are well understood and those that need further study. Experimental manipulations also provide the opportunity for ‘surprises’ that might not be anticipated based on the current understanding of ecosystem dynamics. These anomalies can point to areas where more work is needed and can lead to new directions and discoveries. Experimental manipulations have several drawbacks. First, experimental manipulations typically involve a step increase in state factors such as CO₂ or temperature. Global change will involve gradual changes in these factors over time, and the response to a step change may be different than the response to a gradual change. Second, because of financial, logistical, and intellectual constraints, few manipulations vary more than two or three factors in any one ecosystem-scale experiment at any one time. An exception is the Jasper Ridge Experiment where four factors (CO₂, temperature, water, nutrients) were varied in a full factorial design (Shaw *et al.* 2002). Although single factor experiments provide critical information on the response to single vectors of change, and two or three-factor experiments provide some insight on the nature of interactions, it is recognized that these single or few factor experiments can not directly inform us on ecosystem response to simultaneous changes in multiple factors, including atmospheric CO₂, temperature, moisture, N deposition, UVB radiation, ozone, and a host of other

factors, some of which may not have been identified yet. Third, even decadal-scale experiments still only generate short-term data. Concern exists that short term data are only useful for testing short-term mechanisms, and that long-term mechanisms will likely dominate the longer-term response. For example, understanding the short-term response of soil respiration to increasing temperature sheds little light on longer-term effects of elevated temperature on the turnover of soil organic matter, which will ultimately be controlled by longer term changes in plant productivity and the quantity and quality of litter inputs, or stochastic events such as fire.

IV. E. Models

Models are essential tools for conceptually and empirically integrating existing knowledge and for making longer-term predictions of ecosystem response to multiple interacting vectors of global change at multiple spatial scales. Models can also be used to generate testable hypotheses, and because they integrate the current understanding of ecosystem processes, their failure highlights gaps or errors in that knowledge. For example, due to a strong mechanistic understanding of leaf photosynthesis and canopy radiation interception, most models work well at predicting ecosystem carbon uptake. Conversely, due to a lack of a theoretical foundation, they typically do not work well at predicting carbon loss through respiration or plant carbon allocation to leaves, stems, and roots, pointing to the need for more empirical work in these areas (Classen *et al.* in press). Further, the current generation of models needs to better incorporate (a) spatial heterogeneity within the existing structures, (b) the ecological ramifications of extreme events, and (c) the temporal scaling issues discussed in the preceding section. Finally, as pointed out by Rastetter (1996), a fundamental drawback of using models to make longer-term predictions, is that it is not possible in the short term to validate models of longer-term effects. Despite these drawbacks, the field of ecological modeling has seen major advances during the past several decades and these models

remain critical tools for continuing to integrate our understanding of ecosystem response to global change and making projections of how ecosystems will continue to evolve under projected future global change scenarios.

V. CONCLUSIONS

Considerable progress has been made during the past several decades to better understand and model short and longer-term responses of ecosystems to global change. A growing consensus, however, exists, that in order to more rapidly advance this field of inquiry, it will be necessary to better integrate observational, experimental and modeling techniques into a *unified multidisciplinary approach* to evaluate ecosystem response to global change (Norby & Luo 2004, Classen & Adams in review). For example, combining experimental studies with gradient studies or superimposing experiments across gradients would provide powerful tools to bracket the decadal to century-scale response (which is of most interest to policy-makers) between the short-term experimental response and the longer-term response that has developed over the millennia across a landscape. Improved communication between experimentalists and modelers and closer data-model integration will also help move the global change research agenda forward more rapidly. A better match, for example, between empirical data from observation, gradient or experimental studies and model requirements could be achieved if empirical scientists and modelers interacted more closely during the design stage of experiments or studies. The empiricists could thus better understand what types of data are needed and at what temporal and spatial scales for models, and modelers could better understand what types of data are available to be used in model construction. Models also can be used more advantageously to (a) help generate testable hypotheses for observational, gradient and experimental studies, (b) scale-up empirical

results in time and space, and (c) extrapolate results from single- or few-factor experiments to a better understanding of ecosystem response to multiple interacting vectors of global change. Communication efforts should also focus on identifying processes that are poorly represented in models, such as respiration and carbon allocation, and designing empirical studies to help develop a better mechanistic understanding of these processes that can then be incorporated into models. Finally, if we are truly committed to understanding longer-term responses of terrestrial ecosystems to global change, it is imperative to increase the number of decadal and longer term experiments and to provide more stable funding for long-term monitoring.

All of these considerations, along with more frequent and extensive data-model comparisons and model-model comparisons, will require increased communication and information exchange amongst scientists from the theoretical, experimental, and modeling communities. Research coordination networks, such as the NSF funded TERACC (Terrestrial Ecosystem Response to Atmospheric and Climatic Change) network of global change scientists, are an effective mechanism to bring multidisciplinary communities of scientists together. It is this larger community of scientists that will ultimately move our understanding of, and ability to effectively model, transient and steady state responses of ecosystems to CO₂ enrichment and global climate change.

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