Plant Ecology (2006) 182:43–62
DOI 10.1007/s11258-005-9030-2

From transient to steady-state response of ecosystems to atmospheric CO_2-enrichment and global climate change: conceptual challenges and need for an integrated approach

Lindsey E. Rustad*
*USDA Forest Service, 271 Mast Road, Durham, NH, UK; *Author for correspondence (e-mail: rustad@maine.edu; phone: +1-207-829-6817; fax: +1-207-829-6817)*

Received 1 September 2004; accepted in revised form 15 December 2004

Key words: Climate change, CO_2 enrichment, Ecosystem modeling, Global change, Temporal scaling

Abstract

Evidence continues to accumulate that humans are significantly increasing atmospheric CO_2 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 theoreticists, experimentalists and modelers.

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 CO_2 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 CO_2 concentrations will double in the next century, inducing an additional 1.4–5.8 °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 CO_2 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 CO_2, warming and changes in water availability (for syntheses, see Curtis and Wang 1998; Peterson et al. 1999; Medlyn et al. 1999, 2001; Norby et al. 2001a,b; Rustad et al. 2001; Zak et al. 2003; Badeck et al. 2004; Pendall et al. 2004; Nowalk et al. 2004; Ainsworth and 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., Potter et al. 1993; Running and Hunt 1993; Aber and Driscoll 1997; 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 and 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 CO_2 (Norby and 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 CO_2 and global climate change, and (b) presents an integrated approach to future work in this field.

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 component 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 equal 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

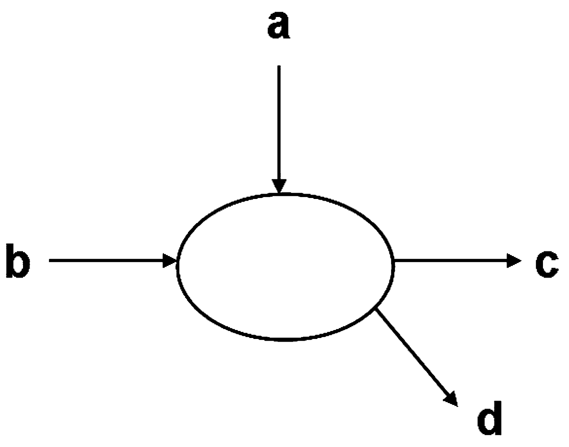

Figure 1. System states. Arrows represent flux of material and energy going into and out of a system.

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.

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 (Lamontagne 1998; Kristensen et al. 2000; Jefts et al. 2004) or the initial rapid increase in soil respiration following a step increase in soil warming (Peterjohn et al. 1994; Rustad and 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 and 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.

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 CO_2 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.

Direct vs. indirect effects

The direct effects of CO_2 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 and 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 16 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).

Interestingly, soil carbon also declined over time in the heated plots compared to the controls at the

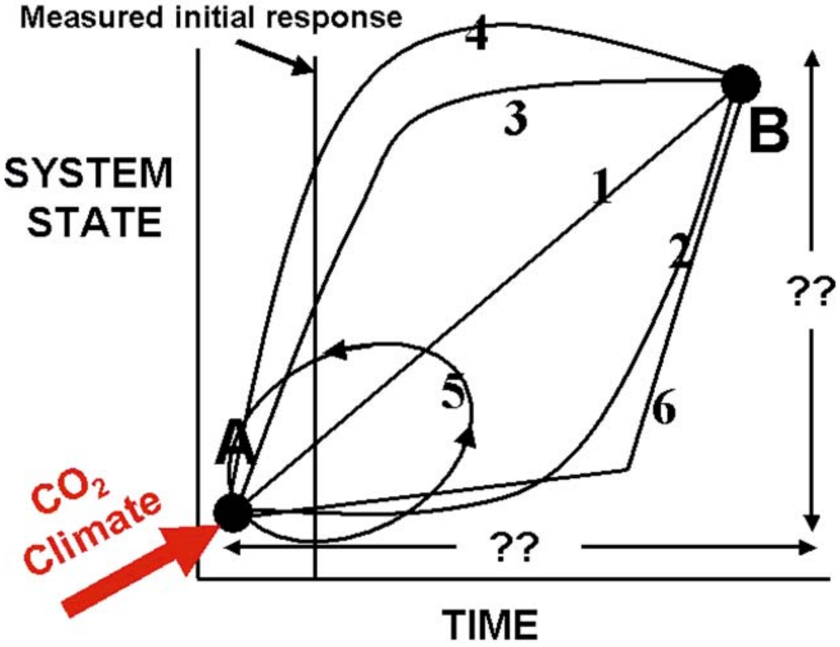

Figure 2. Hypothetical trajectories as a system moves from state A to state B. The lines represent the following hypothetical responses: 1 = a linear response, 2 = lag, 3 = acclimation, 4 = resource limitation, 5 = homeostasis, and 6 = threshold. (Diagram courtesy of Gus Shaver, TERACC Workshop, 2002.)

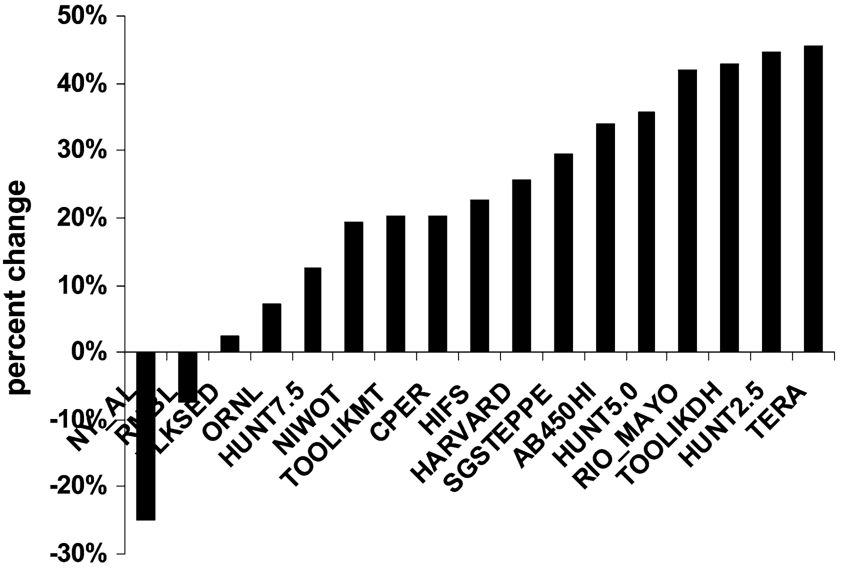

Figure 3. Percent change in soil respiration at 16 ecosystem warming experiments (from Rustad et al. 2001).

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 and 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).

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; Lynch and 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.

'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 and 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.

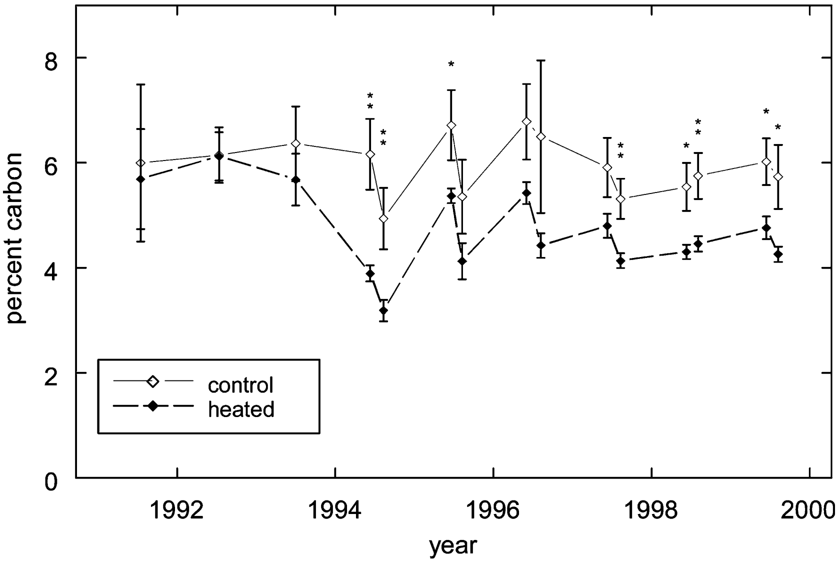

Figure 4. Percent carbon in heated and control plot soils at the Rocky Mountain Biological laboratory (RMBL) (from Saleska et al. 2002b; reproduced by permission of the American Geophysical Union).

Acclimation

Acclimation is the often misused term that refers to a non-heritable, reversible change in the physiology or morphology of an organism in response to changing environmental conditions (Ricklefs 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; Kozlowski and Pallardy 2002; Horacio 2003; Matsuki et al. 2003), or changes in phenology (e.g., Campbell and Sorensen 1973; Adam et al. 2001). Evidence is accumulating that many ecosystem processes acclimate to elevated CO_2 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 CO_2, the acclimation of photosynthesis to elevated temperature, and the acclimation of autotrophic respiration to elevated temperature. Photosynthetic down regulation in response to elevated CO_2 was initially reported in dozens of CO_2 enrichment studies (e.g., Gunderson and Wullscheleger 1994; Luo et al. 1994; Drake et al. 1997; Egli et al. 1998; Rey and Jarvis 1998; Ziska 1998; Medlyn et al. 1999; Sims et al. 1999; Hymus et al. 2002b; Rogers and 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 and 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 and Bjorkman 1980; Ferrar et al. 1989; Read 1990; 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 and Orcutt 1996). The acclimation of autotrophic respiration to elevated temperature has also been demonstrated (e.g., Kirshbaum and 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 and 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 and 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 and Nadelhoffer 1989; Raich and Schlesinger 1992; Raich and Potter 1995; Kirschbaum 1996; Rustad et al. 2001), and soil respiration is typically and effectively modeled with an exponential or Arrehenius 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 × grazing experiment in a tall grass prairie in Oklahoma, USA using overhead infra-red 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 CO_2 enrichment and global warming. Even slight changes in the direction and or magnitude of these fluxes could equal or exceed the annual input of CO_2 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 CO_2, with consequent feedbacks to climate change.

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 CO_2-enrichment then 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

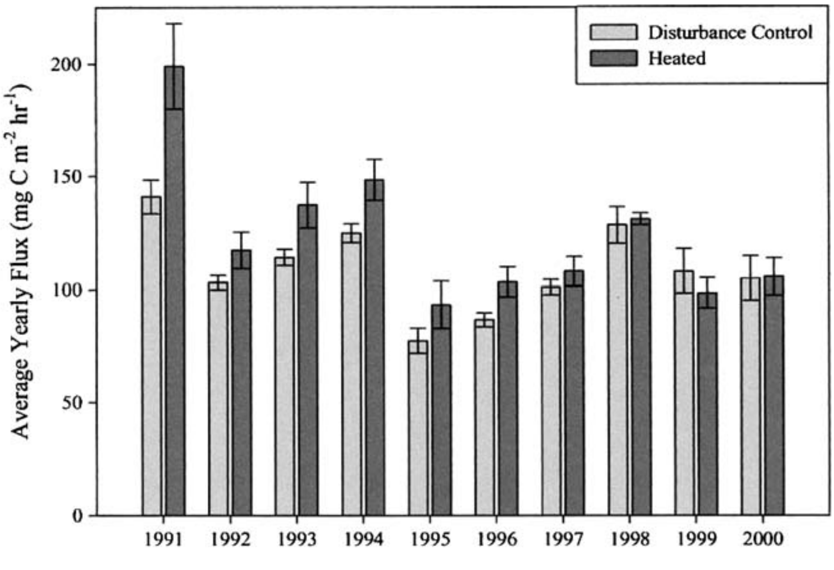

Figure 5. Annual soil respiration at the Harvard Forest soil warming experiment (reprint with permission from Melillo et al. SCIENCE 298: 2173–2176 (2002)).

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 and Ryan 2000; Melillo et al. 2002; Gu et al. 2004).

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 CO_2 and the global carbon cycle. Within limits, as atmospheric CO_2 increases, leaf level photosynthesis and NPP should increase, thereby removing CO_2 from the atmosphere and stabilizing atmospheric CO_2 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.

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 CO_2 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 and 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 and Li 1997; Walker et al. 1999; Chapin et al. 2000; Ives and Cardinale 2004)].

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 CO_2-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.

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 and 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 CO_2 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).

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 CO_2 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 CO_2 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 CO_2 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).

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 CO_2, 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 CO_2 enrichment experiments have shown that even a single species can dominate responses of an entire plant community. For instance, Grünzweig and Körner (2001) reported significant ecosystem-scale changes in aboveground biomass, reproduction, and plant nitrogen content in response to CO_2 enrichment in semi-arid grassland assemblages from Israel. Surprisingly, these ecosystem-scale responses were attributable to CO_2-induced changes in just one out of 32 plant species. Morgan et al. (2004a) also reported that CO_2-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 CO_2-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 CO_2-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 CO_2 often interact with resource availability (Smith et al. 2000; Poorter and 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 CO_2 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 CO_2 (Morse and 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 C_3 species will show greater photosynthetic response to CO_2 enrichment compared to C_4 species (Strain and Bazaaz 1983). In a higher CO_2 world, an increase in the ecosystem abundance of C_3 relative to C_4 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 CO_2 enrichment in C_3 compared to C_4 species (e.g., Bazaaz 1990; Bowes 1993; Ehrlinger and Monson 1993; Poorter 1993; Reich 2001a), 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 C_3 vs. C_4 functional group paradigm to manifest may be attributed, in part, to the fact that stomates of most herbaceous species close under elevated CO_2, which induces a water relations benefit that minimizes differences among photosynthetic functional groups. This is especially important in dry environments where CO_2-induced water relations responses often drive CO_2 responses (Morgan et al. 2004b). Legumes are another functional group that has been predicted to respond strongly to elevated CO_2, because of their capability to fix atmospheric N. While this has been confirmed in several studies (Hebeisen et al. 1997; Tissue et al. 1997; Lüscher et al. 1998; Grünzweig and Körner 2001), other experiments show little or advantage of N-fixing capability under elevated CO_2 (Niklaus et al. 1998; Stöcklin and Körner 1998; Nowak et al. 2004). In some cases, lack of a legume CO_2 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, C_3 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 CH_4 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 (Wand 1999; Reich et al. 2001a,b; Morgan et al. 2004a,b). Exceptions include the work on tree species response to (a) elevated CO_2 in a coastal scrub-oak community in Florida, USA (Hymus et al. 2002a,b), (b) elevated CO_2 and warming for two species of maple in Tennessee, USA (Norby et al. 1997, 2000), and (c) elevated CO_2 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).

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.

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 CO_2 concentrations from a low of ~160–200 μmol/mol in the Last Glacial Maximum (about 18,000 years ago) to the current high of ~360 μmol/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 (Wake and Markham 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. 2005). Similarly, in the southeastern United States, a dramatic increase in winter precipitation was documented for the period 1977–1992. 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 CO_2 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 CO_2 world to future ecosystem responses to possibly more rapid climate change in a higher CO_2 world.

Space-for-time substitutions

Observations across latitudinal or elevational 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 (Ineson et al. 1998; Saleska et al. 2002a,b), 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 CO_2 emission from hot springs, no comparable gradients exist for atmospheric CO_2 and thus it is not possible to use space-for-time substitutions for either CO_2 effects alone or the effects of simultaneous changes in CO_2, temperature, and precipitation. Despite these cautions, space-for-time substitutions remain a valuable approach to studying ecosystem response to changing conditions.

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 CO_2 (Keeling and 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 CO_2 enrichment 'experiment' unfold. The drawbacks to monitoring are that historic records rarely go back more then 100 years, and future responses are as yet unknown, making later validations of models of limited use to policy makers and land managers now.

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 CO_2 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 then two or three factors in any one ecosystem-scale experiment at any one time. An exception is the Jasper Ridge Experiment where four factors (CO_2, 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 CO_2, 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.

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 and Langeley 2005). 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.

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 and Luo 2004; Classen and Langeley 2005). 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 CO_2 enrichment and global climate change.

Acknowledgements

This paper summarizes themes leading to and expressed at the workshop on ‘From Transient to Steady State Response of Ecosystems to

Atmospheric CO_2 Enrichment and Global Climate Change, Durham, New Hampshire, April 28 to May 1, 2002. Special recognition goes to Gus Shaver, Ed Rastetter, and Jack Morgan for contributions and critical review of the manuscript. This workshop was sponsored by the Terrestrial Ecosystem Response to Atmospheric and Climatic Change (TERACC), a research coordination network supported by the National Science Foundation. This paper was prepared with support from the USDA Forest Service, and is based upon work supported by the National Science Foundation under Grant No. 0090238.

References

Aber J.D. and Driscoll C.T. 1997. Effects of land use, climate variation and N deposition on N cycling and C storage in northern hardwood forests. Global Biogeochem. Cycles 11: 639–648.

Aber J.D., Goodale C.L., Ollinger S.V., Smith M.-L., Magill A.H., Martin M.E. and Stoddard J.L. 2003. Is nitrogen deposition altering the nitrogen status of northeastern forests? BioScience 53: 375–390.

Adam N.R., Wall G.W., Kimball B., Pinter P. Jr., LaMorte R.L., Hunsaker D., Adamsen F.J., Thompson T.L., Matthias A.D., Leavitt S.W. and Webber A. 2001. Acclimation response of the photosynthetic apparatus in a wheat ecosystem under free-air CO_2 enrichment (FACE) and variable soil nitrogen regimes: leaf position and phenology determine acclimation response. Photosynth. Res. 66: 79–95.

Ainsworth E.A. and Long S.P. 2005. What have we learned from 15 years of free-air CO_2 enrichment (FACE)? A meta-review of the responses of photosynthesis, canopy properties and plant production to rising CO_2. New Phytol. 165: 351–372.

Ainsworth E.A., Davey P.A., Hymus G.J., Osborne C.P., Rogers A., Blum H., Nosberger J. and Long S.P. 2003. Is stimulation of leaf photosynthesis by elevated carbon dioxide concentration maintained in the long term? A test with *Lolium perenne* grown for 10 years at two nitrogen fertilization levels under free air CO_2 enrichment (FACE). Plant, Cell Environ. 26: 705.

Arnold S.S., Fernandez I.J., Rustad L.E. and Zibilske L.M. 1999. Microbial response of an acid forest soil to experimental soil warming. Biol. Fertil. Soils 30: 239–244.

Arp W.J., Drake B.G., Pockman W.T., Curtis P.S. and Whigham D.F. 1993. Interactions between C_3 and C_4 salt marsh plant species during four years of exposure to elevated atmospheric CO_2. Vegetatio 104(105): 133–143.

Atkin O.K. and Lambers H. 1998. Slow-growing alpine and fast-growing lowland species: a case study of factors associated with variation in growth rate among herbaceous higher plants under natural and controlled conditions. In: Lambers H., Poorter H. and VanVuuren M.M.I. (eds), Inherent Variation in Plant Growth: Physiological Mechanisms and Ecological Consequences, Backhuys Publishers, Leiden, pp. 259–288.

Atkin O.K., Holly C. and Ball M.C. 2000a. Acclimation of snow gum (*Eucalyptus pauciflora*) leaf respiration to seasonal and diurnal variations in temperature: the importance of changes in the capacity and temperature sensitivity of respiration. Plant Cell Environ. 23: 15–26.

Atkin O.K., Edwards E.J. and Loveye B.R. 2000b. Response of root respiration to changes in temperature and its relevanc to global warming. New Phytol. 147: 141–154.

Badeck F.W., Bondeau K., Bottcher D., Doktor D., Lucht W., Schaber J. and Sitch S. 2004. Responses of spring phenology to climate change. New Phytol. 162: 295–310.

Barry J. and Bjorkman O. 1980. Photosynthetic temperature response and adaptation to temperature in higher plants. Annu. Rev. Plant Physiol. 31: 491–543.

Bazzaz F.A. 1990. The response of natural ecosystems to the rising global CO_2 levels. Annu. Rev. Ecol. Systemat. 21: 167–196.

Belote R.T., Weltzin J.F. and Norby R.J. 2003. Response of an understory plant community to elevated [CO_2] depends on differential responses of dominant invasive species and is mediated by soil water availability. New Phytol. 161: 827–835.

Berbet M.L.C. and Costa M.H. 2002. Climate change after tropical deforestation: seasonal variability of surface albedo and its effects on precipitation change. J. Climate 16: 2099–2104.

Betts R.A. 2000. Offset of the potential carbon sink from boreal forestation by decreases in surface albedo. Nature 408: 187–190.

Betts R.A., Cox P., Lee S.E. and Woodward F.I. 1997. Contrasting physiological and structural vegetation feedbacks in climate change simulations. Nature 387: 796–799.

Bolstad P.V., Reich P. and Lee T. 2003. Rapid temperature acclimation of leaf respiration rates in *Quercus alba* and *Quercus rubra*. Tree Physiol. 23: 969–976.

Bowes G. 1993. Facing the inevitable: plants and increasing atmospheric CO_2. Annu. Rev. Plant Physiol. Plant Mol. Biol. 44: 309–332.

Brown J.H., Valone T.J. and Curtin C.G. 1997. Reorganization of an arid ecosystem in response to recent climate change. Proceed. Natl. Acad. Sci. 94: 9729–9733.

Campbell R.K. and Sorensen F.C. 1973. Cold-acclimation in seedling Douglas-Fir related to phenology and provenance. Ecology 54: 1148–1151.

Chapin F.S. III and Starfield A.M. 1997. Time lags and novel ecosystems in response to transient climate change in arctic Alaska. Climatic Change 35: 449–461.

Chapin F.S. III, Zavaleta E.S., Eviners V.T., Naylor R.L., Vitousek P.M., Reynolds H., Hooper D.U., Lavorel S., Sala O.E., Hobbie S.E., Mack M. and Diaz S. 2000. Consequences of changing biodiversity. Nature 405: 234–242.

Classen A.T. and Langley J.A. 2005. Data-model integration is not magic: Modeling ecosystem responses to global change: techniques and recent advances. New Phytol. 166: 367–370.

Collins H.P., Paul E.A., Paustian K. and Elliott E.T. 1997. Characterization of soil organic matter relative to its stability and turnover. In: Paul E.A., Paustian Elliott E.T. and Cole C.V. (eds), Soil Organic Matter in Temperate

Agroecosystems: Long-term Experiments in North America, CRC Press, Boca Raton, FL, pp. 51–72.

Curtis P.S. and Wang X. 1998. A Meta-analysis of elevated CO_2 on woody plant mass, form, and physiology. Oecologia 113: 299–313.

Davidson E.A., Belk E. and Boone R. 1998. Soil water content and temperature as independent or cofounded factors controlling soil respiration in a temperate mixed hardwood forest. Global Change Biol. 4: 217–227.

Derner J.D., Johnson H.B., Kimball B.A, Pinter P.J. Jr., Polley H.W., Tischler C.T., Boutton T.W., Lamorte R.L., Wall G.W., Adam N.R., Leavitt S.W., Ottman M.J., Matthias A.D. and Brooks T.J. 2003. Above- and belowground responses of C_3-C_4 species mixtures to elevated CO_2 and soil water availability. Global Change Biol. 9(3): 452–460.

deValpine P. and Harte J. 2001. Plant responses to experimental warming in a montane meadow. Ecology 82: 637–648.

Drake B.G., Gonzalez-Meler M.A. and Long S.P. 1997. More efficient plants: a consequence of rising atmospheric CO_2? Annu. Rev. Plant Physiol. Plant Mol. 48: 609–639.

Egli P., Maurer S., Gunthardt-Goerg M.S. and Korner C. 1998. Effects of elevated CO_2 and soil quality on leaf gas exchange and aboveground growth in beech-spruce model ecosystems. New Phytol. 140: 185–196.

Ehleringer J.R. and Monson R.K. 1993. Evolutionary and ecological aspects of photosynthetic pathway variation. Annu. Rev. Ecol. Systemat. 24: 411–439.

Equiza M., Mirave J. and Tognett J. 2001. Morphological, anatomical, and physiological responses related to differential shoot vs root growth inhibition at low temperature in spring and winter wheat. Ann. Bot. 87: 67–76.

Farage P.K., McKee I.F. and Long S.P. 1998. Does a low nitrogen supply necessarily lead to acclimation of photosynthesis to elevated CO_2? Plant Physiol. 118: 573–580.

Ferrar P.J., Slatyer R.O. and Vranjic J.A. 1989. Photosynthetic temperature acclimation in *Eucalyptus* species from diverse habitat, and comparison with *Nerium oleander*. Aust. J. Plant Physiol. 16: 199–217.

Fitzhugh R.D., Likens G.E., Driscoll C.T., Mitchell M.J., Groffman P.M., Fahey T.J. and Hardy J.P. 2003. The role of soil freezing events in interannual patterns of stream chemistry at the Hubbard Brook Experimental Forest. Environ. Sci. Technol. 37: 1575–1580.

Gesch R.W., Vu J.C.V., Boote K.J., Allen L.H. Jr. and Bowes G. 2002. Sucrose-phosphate synthase activity in mature rice leaves following changes in growth CO_2 is unrelated to sucrose pool size. New Phytol. 154: 77–84.

Giardina C.P. and Ryan M.G. 2000. Evidence that decomposition rates of organic carbon in mineral soil do not very with temperature. Nature 404: 858–861.

Gregory J.M., Huybrechts P. and Raper S.C.B. 2004. Climatology: threatened loss of the Greenland ice-sheet. Nature 428: 616.

Griffin K.L., Turnball M. and Murphy R., , 2002. Leaf respiration is differentially affected by leaf vs stand night-time warming. Global Change Biol. 8: 479–485.

Grünzweig J.M. and Körner C. 2001. Growth, water and nitrogen relations in grassland model ecosystems of the semiarid Negev of Israel exposed to elevated CO_2. Oecologia 128: 251–262.

Gu L., Post W.M., King A.W. 2004. Fast labile carbon turnover obscures sensitivity of heterotrophic respiration from soil to temperature: a model analysis. Global Biogeochem. Cycles 18, GB1022, doi:10.1029/2003GB002119.

Gunderson C.A. and Wullschleger S.D. 1994. Photosynthetic acclimation in trees to rising atmospheric CO_2: a broader perspective. Photosynth. Res. 39: 369–388.

Gunderson C.A., Norby R.J. and Wullschleger S.D. 2000. Acclimation of photosynthesis and respiration to simulated climatic warming in northern and southern populations of *Acer saccharum*: laboratory and field evidence. Tree Physiol. 20: 87–96.

Hebeisen T., Löscher Zanetti S., Fischer B.U., Hartwig U.A., Frehner M., Hendrey G.R., Blum G. and Nrger J. 1997. Growth response of *Trifolium repens* L. and *Lolium perenne* L. as monocultures and bi-species mixture to free air CO_2 enrichment and management. Global Change Biol. 3: 149–160.

Horacio H. 2003. Root/shoot allocation and root architecture in seedlings: variation among forest sites, microhabitats, and ecological. Biotropica 35: 318–332.

Hungate B.A., Dukes J.S., Shaw M.R., Luo Y. and Field C.B. 2003. Nitrogen and climate change. Science 302: 1512–1513.

Hymus G.J., Pontailler J.Y., Li J., Stiling P., Hinkle C.R., Drake B.G. 2002a. Seasonal variability in the effect of elevated CO_2 on ecosystem leaf area index in a scrub-oak ecosystem. Global Change Biol. 8: 931–940.

Hymus G.J., Snead T.G., Johnson D.P., Hungate B.A. and Drake B.G. 2002. Acclimation of photosynthesis and respiration to elevated atmospheric CO_2 in two scrub oaks. Global Change Biol. 8: 318.

Ineson P, Taylor K., Harrison A.F., Poskitt J., Benham D.G., Tipping E. and Woof C. 1998. Effects of climate change on nitrogen dynamics in upland soils I A transplant approach. Global Change Biol. 4: 143–152.

Ingram W.J., Wilson C.A. and Mitchell J.F.B. 1989. Modeling climate change: an assessment of sea ice and surface albedo feedbacks. J. Geophys. Res. 94: 8609–8622.

Intergovernmental Panel on Climate Change 2001. In: Houghton J.T., Ding Y., Griggs D.J., Noguer M., van der Linden P.J. and Xiaosu D. (eds.), Climate Change 2001: The Scientific Basis. University Press, Cambridge, United Kingdom.

Ives R.A. and Cardinale B.J. 2004. Food-web interactions govern the resistance of communities after non-random extinctions. Nature 429: 174–177.

Jefts S., Fernandez I.J., Rustad L.E. and Dail D.B. 2004. Decadal responses in soil N dynamics at the Bear Brook Watershed in Maine, USA. Forest Ecol. Manage. 189: 189–205.

Karnosky D.F., Zak D.R., Pregitzer K.S., Awmack C.S., Bockheim J.G., Dickson R.E., Hendrey G.R., Host G.E., King J.S., Kopper B.J., Kruger E.L., Kubiske M.E., Lindroth R.L., Mattson W.J., McDonald E.P., Noormets A., Oksanen E., Parsons W.F.J., Percy K.E., Podila G.K., Riemenschneider D.E., Sharma P., Thakur R.C., Sober A., Sober J., Jones W.S., Anttonen S., Vapaavuori E., Mankovska B., Heilman W.E. and Isebrands J.G. 2003. Tropospheric O_3 moderates responses of temperate hardwood forests to elevated CO_2: A synthesis of molecular to ecosystem results from the Aspen FACE project. Funct. Ecol. 17: 289–304.

Keeling C.D., Whorf T.P. 2004. Atmospheric CO_2 records from sites in the SIO air sampling network. In: Trends: A Compendium of Data on Global Change. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, US Department of Energy, Oak Ridge, Tennessee, USA.

Kirscbaum M.U.F. and Farquhar G.D. 1984. Temperature dependence of whole-leaf photosynthesis in *Eucalyptus pauciflora* Sieb ex Spreng. Plant Physiol. 11: 519–538.

Klickoff L.G. 1966. Temperature dependence of the oxidative rates of mitochondria in *Danthonia intermedia*, *Penstemmon davidsonii* and *Sitanion hystrix*. Nature 212: 529–530.

Körner Ch. 2000. Biosphere responses to CO_2 enrichment. Ecol. Appl. 10: 1590–1619.

Kozlowski T.T. and Pallardy S.G. 2002. Acclimation and adaptive responses of woody plants to environmental stresses. Bot. Rev. 68: 270–334.

Kristensen H.L., McCarty G.W. and Meisinger J.J. 2000. Effects of soil structure disturbance on mineralization of organic soil nitrogen soil. Sci. Soc. Am. J. 64: 371–378.

Kubiske M.E., Zak D.R., Pregitzer K.S. and Takeuchi Y. 2002. Photosynthetic acclimation of overstory *Populus tremuloides* and understory *Acer saccharum* to elevated atmospheric CO_2 concentration: interactions with shade and soil nitrogen. Tree Physiol. 22: 321–329.

Lambers H., Atkin O.K. and Scheurwater I. 1996. Respiratory patterns in roots in relation to their functioning. In: Waisel Y., Eschel A. and Kafkaki U. (eds), Plant Roots: The Hidden Half, Marcel Dekker, New York, pp. 323–362.

Lamontagne S. 1998. Nitrogen mineralization in upland Precambrian Shield catchments: contrasting the role of lichen-covered bedrock and forested areas. Biogeochemistry 441: 53–69.

Likens G.E., Bormann F.H. and Johnson N.M. 1972. Acid rain. Environment 14: 33–40.

Liski J., Ilvesniemi H., Makela A. and Westman C.J. 1999. CO_2 emissions from soil in response to climatic warming are overestimated - the decomposition of old soil organic matter is tolerant to temperature. Ambio 28: 171–174.

Lukewille A. and Wright R. 1997. Experimentally increased soil temperature causes release of nitrogen at a boreal forest catchment in southern Norway. Global Change Biol. 3: 13–21.

Luo Y., Field C.B. and Mooney H.A. 1994. Predicting responses of photosynthesis and root fraction to elevated CO_2: interaction among carbon, nitrogen and growth. Plant, Cell Environ. 17: 1195–1204.

Luo Y., Wan S., Hui D. and Wallace L.L. 2001. Acclimation of soil respiration to warming in a tall grass prairie. Nature 413: 622–625.

Lüscher A., Hebeisen T., Zanetti S., Hartwig U.A., Blum H., Hendrey G.R., Nösberger J. 1996. Differences between legumes and non-legumes of permanent grassland in their responses to free air carbon dioxide enrichment. In: Körner C. and Bazzaz (eds), Carbon Dioxide, Populations and Communities, Academic Press, San Diego, pp. 287–299.

Lüscher A., Hendry G.R. and Nösberger J. 1998. Long-term responsiveness to free air CO_2 enrichment of functional types, species and genotypes of plants from fertile permanent grassland. Oecologia 113: 37–45.

Lynch A.H. and Wu W. 1999. Impacts of fire and warming on ecosystem uptake in the boreal forest. J. Climate 13: 2334–2338.

Maroco J.P., Edwards G.E. and Ku M.S.B. 1999. Photosynthetic acclimation of maize to growth under elevated levels of carbon dioxide. Planta 210: 115–125.

Matsuki S., Ogawa K., Tanaka A. and Hara T. 2003. Morphological and photosynthetic responses of *Quercus crispula* seedlings to highlight conditions. Tree Physiol. 23: 769–775.

McNulty S.G., Aber J.D., McLellan T.M. and Katt S.K. 1990. Nitrogen cycling in high elevation forests of the northeastern US in relation to nitrogen deposition. Ambio 19: 38–40.

McNulty S.G., Aber J.D. and Boone R.D. 1991. Spatial changes in forest floor and foliar chemistry in spruce-fir forests across New England. Biogeochemistry 14: 13–26.

Medlyn B.E., Badeck F.W., De Pury D.G.G., Barton C.V.M., Broadmeadow M., Ceulemans R., De Angelis P., Forstreuter M., Jach M.E., Kellomäki S., Laitat E., Marek M., Philippot S., Rey A., Strassemeyer J., Laitinen K., Liozon R., Portier B., Roberntz P., Wang K. and Jstbid P.G. 1999. Effects of elevated [CO_2] on photosynthesis in European forest species: a meta-analysis of model parameters. Plant, Cell Environ. 22: 1475–1495.

Medlyn B.E., Barton C.V.M., Broadmeadow M.S.J., Ceulemans R., De Angelis P., Forstreuter M., Freeman M., Jackson S.B., Kellomäki S., Laitat E., Rey A., Roberntz P., Sigurdsson B.D., Strassemeyer J., Wang K., Curtis P.S. and Jarvis P.G. 2001a. Stomatal conductance of forest species after long-term exposure to elevated CO_2 concentration: a synthesis. New Phytol. 149: 247–264.

Medlyn B.E., Barton C.V.M., Broadmeadow M.S.J., Ceulemans R., De Angelis P., Forstreuter M., Freeman M., Jackson S.B., Kellomäki S., Laitat E., Rey A., Roberntz P., Sigurdsson B.D., Strassemeyer J., Wang K., Curtis P.S. and Jarvis P.G. 2001b. Stomatal conductance of forest species after long-term exposure to elevated CO_2 concentration: a synthesis. New Phytol. 149: 247–264.

Melillo J.M., Steudler P.A., Aber J.D., Newkirk K., Lux H., Bowles F.P., Catricala C., Magill A., Ahrens T. and Morrisseau S. 2002. Soil warming and carbon-cycle feedbacks to the climate system. Science 298: 2173–2176.

Miroslavov E.A. and Kravkina I.M. 1991. Comparative analysis of chloroplasts and mitochondria in leaf chlorenchyma from mountain plants grown at different altitudes. Ann. Bot. 68: 195–200.

Morgan J.A., Mosier A.R., Milchunas D.G., LeCain D.R., Nelson J.A. and Parton W.J. 2004a. CO_2 enhances productivity, alters species composition, and reduces forage digestibility of shortgrass steppe vegetation. Ecol. Appl. 14: 208–219.

Morgan J.A., Pataki D.E., Körner C., Clark H., Del Grosso S.J., Grünzweig J.M., Knapp A.K., Mosier A.R., Newton P.C.D., Niklaus P.A., Nippert J.B., Nowak R.S., Parton W.J., Polley H.W. and Shaw M.R. 2004b. Water relations in grassland and desert ecosystems exposed to elevated atmospheric CO_2. Oecologia 140: 11–25.

Morse S.R. and Bazzaz F.A. 1994. Individuals vs stands: differential responses to elevated CO_2 and temperature. Ecology 75: 966–975.

Nadelhoffer K.J., Emmet B.A., Gundersen P., Kjonaaas O.J., Koopsman C.J., Schleppi P., Tietma A. and Wright R.F. 1999. Nitrogen deposition makes a minor contribution to carbon sequestration in temperate forests. Nature 398: 145–148.

Naeem S. and Li S. 1997. Biodiversity enhances ecosystem reliability. Nature 390: 507–509.

National Academy Committee on Abrupt Climate Change 2001. In: Abrupt Climate Change: Inevitable Surprises, Alley R.B., Chair, National Academy Press, Washington, DC.

New England Regional Assessment Group (NERA) 2001. Preparing for a chancing climate: the potential consequences of climate variability and change. New England Overview; U.S. Global Change Research Program, University of New Hampshire, 96 p.

Nielsen E.T. and Orcutt D.M. 1996. Physiology of Plants Under Stress: Abiotic Factors. John Wiley and Sons, New York, p. 689.

Niklaus P.A., Leadley P.W., Stöcklin J. and Körner Ch. 1998. Nutrient relations in calcareous grassland under elevated CO_2. Oecologia 116: 67–75.

Niklaus P.A., Leadley P.W., Schmid B. and Kr Ch. 2001. A long-term field study on biodiversity X elevated CO_2 interactions in grassland. Ecol. Monogr. 71: 341–356.

Norby R.J., Cotrufo M.F., Ineson P., O'Neill E.G. and Canadell J.G. 2001. Elevated CO_2, litter chemistry, and decomposition: a synthesis. Oecologia 127: 153–165.

Norby R.J., Edwards N.T., Riggs J.S., Abner C.H. and Wullschleger S.D. 1997. Temperature-controlled open-top chambers for global change research. Global Change Biol. 3: 259–267.

Norby R.J., Kimball B.A., Kobayashi K. (eds.) 2001b. Rising CO_2 - Future Ecosystems. New Phytol. Special Issue 150(2).

Norby R.J., Long T.M., Hartz-Rubin J.S. and O'Neill E.G. 2000. Nitrogen resorption in senescing tree leaves in a warmer, CO_2-enriched atmosphere. Plant Soil 224: 15–29.

Norby R.J. and Luo L. 2004. Evaluating ecosystem responses to rising CO_2 and warming in a multi-factor world. New Phytol. 162: 281–293.

Nowak R.S., Ellsworth D.S. and Smith S.D. 2004. Functional responses of plants to elevated atmospheric CO_2 - do photosynthetic and productivity data from FACE experiments support early predictions? New Phytol. 162: 253–280.

Park J., Mitchell M.J., McHale P.J., Christopher S.F. and Myers T.P. 2003. Interactive effects of changing climate and atmospheric deposition on N and S biogeochemistry in a forested watershed of the Adirondack Mountains, New York State. Global Change Biology 9: 1602–1619.

Paustian K., Collins H.P. and Paul E.A. 1997. Management controls on soil carbon. In: Paul E.A., Paustian K., Elliott E.T. and Cole C.V. (eds), Soil Organic Matter in Temperate Agroecosystems: Long-term Experiments in North America, CRC Press, Boca Raton, FL, pp. 15–49.

Paustian K., Elliott E.T., Six J. and Hunt H.W. 2000. Management options for reducing CO_2 emissions from agricultural soils. Biogeochemistry 48: 147–163.

Pendall E., Bridgham S., Hanson P.J., Hungate B., Kicklighter D.W., Johnson D.W., Law B.E., Luo Y., Megonigal J.P., Olsrud M., Ryan M.G. and Wan S. 2004. Belowground process response to elevated CO_2 and temperature: a discussion of observations, methods, and models. New Phytol. 162: 311–322.

Peterjohn W.T, Melillo J.M., Steudler P.A., Newkirk K.M., Bowles S.T. and Aber J.D. 1994. Responses of trace gas fluxes and N availability to experimentally elevated soil temperatures. Ecol. Appl. 4: 617–625.

Peterson A.G., Ball J.T., Luo Y., Field C.B., Reich P.B., Curtis P.S., Griffin K.L., Gunderson C.A., Norby R.J., Tissue D.T., Forstreuter M., Rey A.A., Vogel C.S., Cmeal participants 1999. The photosynthesis - leaf nitrogen relationship at ambient and elevated atmospheric carbon dioxide: a meta-analysis. Global Change Biol. 5: 331–346.

Poorter H. 1993. Interspecific variation in the growth response of plants to an elevated ambient CO_2 concentration. Vegetatio 104(105): 77–97.

Poorter H. and Perez-Soba M. 2001. The growth response of plants to elevated CO_2 under non-optimal environmental conditions. Oecologia 129: 1–20.

Poorter H., Roumet C. and Campbell B.D. 1996. Interspecific variation in the growth response of plants to elevated CO_2: a search for functional types. In: Kr C.H. and Bazzaz F.A. (eds), Carbon dioxide, Populations, and Communities, Academic Press, San Diego, pp. 375–412.

Potter C.S., Randerson J.T., Field C.B., Matson P.A., Vitousek P.M., Mooney H.A. and Klooster S.A. 1993. Terrestrial ecosystem production: a process model based on global satellite and surface data. Global Biogeochem. Cycles 7(4): 811–841.

Rahmstorf S. 2002. Ocean circulation and climate during the past 120,000 years. Nature 419: 207–214.

Raich J.W. and Nadelhoffer K.J. 1989. Belowground carbon allocation in forest ecosystems: global trends. Ecology 70: 1346–1354.

Raich J.W. and Potter C.S. 1995. Global patterns of carbon dioxide emissions form soils. Global Biogeochem. Cycles 9: 23–36.

Raich J.W. and Schlesinger W.H. 1992. The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. Tellus 44: 81–89.

Rastetter E.B. 1996. Validating models of ecosystem response to global change. BioScience 46(3): 190–198.

Read J. 1990. Some effects of acclimation temperature on net photosynthesis in some tropical and extra-tropical Australasian *Nothofagus* species. J. Ecol. 78: 100–112.

Reich P.B., Tilman D., Craine J., Ellsworth D., Tjoelker M.G., Knops J., Wedin D., Naeem S., Bahauddin D., Goth J., Bengtson W. and Lee T.D. 2001a. Do species and functional groups differ in acquisition and use of C, N and water under varying atmospheric CO_2 and N availability regimes? A field test with 16 grassland species. New Phytol. 150: 435–448.

Reich P.B., Knops J., Tilman D., Craine J., Ellsworth D., Tjoelker M., Lee T., Naeem S., Wedin D., Bahauddin D., Hendrey G., Jose S., Wrage K., Goth J. and Bengston W. 2001b. Plant diversity enhances ecosystem responses to elevated CO_2 and nitrogen deposition. Nature 410: 809–812.

Rey A. and Jarvis P.G. 1998. Long-term photosynthetic acclimation to increased atmospheric CO_2 concentration in young birch (*Betula pendula*) trees. Tree Physiol. 18: 441–450.

Ricklefs R.E. 1990. Ecology 3. W.H. Freeman and Company, New York, NY.

Rogers A. and Ellsworth D.S. 2002. Photosynthetic acclimation of *Pinus taeda* (Loblolly Pinte) to long-term growth in elevated pCO_2 (FACE). Plant, Cell, and Environment 25: 851–858.

Rogers A. and Humphries S.W. 2000. A mechanistic evalution of Photosynthetic acclimation at elevated CO_2. Global Change Biol. 6:105.

Running S.W. and Hunt E.R. Jr. 1993. Generalization of a forest ecosystem process model for other biomes, BIOME-BGC and an application for global-scale models. In: Ehleringer J.R. and Field C. (eds), Scaling Processes Between Leaf and Landscape Levels, Academic Press, San Diego, pp. 141–158.

Rustad L.E. and Fernandez I.J. 1998. Experimental soil warming effects on CO_2 and CH_4 flux from a low elevation spruce fir forest soil in Maine, USA. Global Change Biol. 4: 597–607.

Rustad L.E. and Norby R.J. 2002. Effects of increased temperature on terrestrial ecosystems. In: Mooney H.A. and Canadell J. (eds), Encyclopedia of Global Environmental Change, Vol. 2: Biological and Ecological Dimensions of Global Environmental Change, John Wiley & Sons Ltd, Chichester, pp. 575–581.

Rustad L.E., Campbell J., Marion G.M., Norby R.J., Mitchell M.J., Hartley A.E., Cornelissen J.H.C. and Gurevitch J.GCTE-NEWS 2001. A meta-analysis of the response of soil respiration, net N mineralization, and aboveground plant growth to experimental ecosystem warming. Oecologia 126: 543–562.

Saleska S., Shaw M.S., Fischer M., Dunne J., Holman M., Still C., Harte J. 2002a. Plant community composition mediates both large transient decline and predicted long-term recovery of soil carbon under climate warming. Global Biogeochem. Cycles 16(4).

Saleska S., Shaw M., Fischer M., Dunne J., Shaw M., Holman M., Still C., Harte J. 2002b. Carbon-cycle feedbacks to climate change in montane meadows: results from a warming experiment and a natural climate gradient. Global Biogeochem. Cycles 16, 2001gb001573.

Schlesinger W.H. 1997 Carbon balance in terrestrial detritus. Annu. Rev. Ecol. Syst. 8: 51–81.

Shaver G.R., Canadell J., Chapin F.S. III, Gurevitch J., Harte J., Henry G., Ineson P., Jonasson S., Melillo J., Pitelka L. and Rustad L. 2000. Global warming and terrestrial ecosystems: a conceptual framework for analysis. BioScience 50: 871–882.

Shaw M.R., Zavaleta E.S., Chiarello N.R., Cleland E.E., Mooney H.A. and Field C.B. 2002. Grassland responses to global environmental changes suppressed by elevated C. Science 298: 1987–1990.

Sims D.A., Cheng W., Luo Y. and Seeman J.R. 1999. Photosynthetic acclimation to elevated CO_2 in a sunflower canopy. J. Exp. Bot. 50: 645–653.

Six J., Elliott E.T. and Paustian K. 2000. Soil macroaggregate turnover and microaggregate formation: A mechanism for C sequestration under no-tillage agriculture. Soil Biol. Biochem. 32: 2099–2103.

Smith S.D., Husman T.E., Zitzer S.F., Charlet T.N., Houseman D.C., Coleman J.S., Fenstermaker L.K., Seemann J.R. and Nowak R.S. 2000. Elevated CO_2 increases productivity and invasive species in an arid ecosystem. Nature 408: 79–82.

Sterner R.W. and Elser J.J. 2002. Ecological Stoichiometry: The Biology of Elements form Molecules to the iosphere. Princeton University Press, Pinceton, NJ, p. 584.

Stitt M. 1991. Rising CO_2 levels and their potential significance for carbon flow in photosynthetic cells. Plant Cell Environ. 14: 741–762.

Stöcklin J. and Körner Ch. 1998. Interactive effects of elevated CO_2, P-availability, and legume presence on calcareous grassland: results of a glasshouse experiment. Funct. Ecol. 13: 200–209.

Strain B.R., Bazzaz F.A. 1983. Terrestrial plant communities. In: Lemon E. (ed.), CO_2 and Plants: the Response of Plants to Rising Levels of Atmospheric Carbon dioxide, AAAS Selected Symposium 8, Washington, DC, pp. 177-222.

Tian H., Melillo J.M., Kicklighter D.W., McQuire A.D., Moore B. III and Vorosmarty C.J. 1999. Parameters for global ecosystem models. Nature 399: 536.

Tissue D.T., Megonigal J.P. and Thomas R.B. 1997. Nitrogenase activity and N_2 fixation are stimulated by elevated CO_2 in a tropical N_2-fixing tree. Oecologia 109: 28–33.

Tjoelker M.G., Oleksyn J. and Reich P.B. 2001. Modeling respiration of vegetation: evidence for a general temperature-dependent Q_{10}. Global Change Biol. 7: 223–230.

Tjoelker M.G., Reich P.B. and Oleksyn J. 1999. Changes in leaf nitrogen and carbohydrates underlie temperature and CO_2 acclimation of dark respiration in five boreal tree species. Plant, Cell Environ. 22: 767–778.

Updegraff K., Bridgham S.D., Pastor J., Weishampel P. and Harth C. 2001. Response of CO_2 and CH_4 emissions from peatlands to warming and water table manipulation. Ecol. Appl. 11: 311–326.

Vetaas O.R. 2002. Realized and potential climate niches: a comparison of four Rhododendron tree species. J. Biogeogr. 29: 545–554.

Wake C. and Markham A. 2005. Indicators of climate change in the northeast 2005. Clean Aiv-Cool Planet, portsmouter, NH. http://inhale.unh.edu/Publications/wake_2005_indicators.pdf.

Walker B., Kinzig A. and Langridge J. 1999a. Plant attribute diversity, resilience, and ecosystem function: the nature and significance of dominant and minor species. Ecosystems 2: 95–113.

Wand J.K., Tissue D.T., Thomas R.B. and Strain B.R. 1999. Comparative responses of model C3 and C4 plants to drought in low and elevated CO_2. Global Change Biol. 5: 857.

Wolfe D.W., Lakso A.N., Otsuki Y., Poole R.M. and Shaulis N.J. 2005. Climate change and shifts in the spring phenology of three horticultural woody perennials in the Northeastern U.S. Int. J. Biometeorol. 49: 303–309.

Wardle D.A., Bardgett R.D., Klironomos J.N., Setälä H., van der Putten W.H. and Wall D.H. 2004. Ecological linkages between aboveground and belowground biota. Science 304: 1629–1633.

Watling J.R., Press M.C. and Quick W.P. 2000. Elevated CO_2 induces biochemical and ultrastructural changes in leaves of the C4 cereal sorghum. Plant Physiol. 123: 1143–1152.

Webber A.N., Nie G.-Y. and Long S.P. 1994. Acclimation of photosynthetic proteins to rising atmospheric CO_2. Photosynth. Res. 39: 413–425.

Zak D.R., Holme W.E., Finzi A.C., Norby R.J. and Schlesinger W.H. 2003. Soil nitrogen cycling under elevated CO_2: a synthesis of the forest face experiments. Ecol. Appl. 13: 1508–1514.

Zak D.R., Pregitzer K.S., King J.S. and Holmes W.E. 2000. Elevated atmospheric CO_2, fine roots and the resonse of soil microorganisms: a review and hypothesis. New Phytol. 147: 201–222.

Zavaleta E.S., Shaw M.R., Chiariello N.R., Thomas B.D., Cleland E.E., Field C.B. and Mooney H.A. 2003. Grassland responses to three years of elevated temperature, CO_2, precipitation, and N deposition. Ecol. Monogr. 73: 585–604.

Ziska L.H. 1998. The influence of root zone temperature on photosynthetic acclimation to elevated carbon dioxide concentrations. Ann. Bot. 81: 717–721.