

OPINION

Coordinated approaches to quantify long-term ecosystem dynamics in response to global change

YIQI LUO*, JERRY MELILLO†, SHULI NIU*, CLAUS BEIER‡, JAMES S. CLARK§, AIMÉE T. CLASSEN¶, ERIC DAVIDSON||, JEFFREY S. DUKES**, R. DAVE EVANS††, CHRISTOPHER B. FIELD‡‡, CLAUDIA I. CZIMCZIK§§, MICHAEL KELLER¶¶, BRUCE A. KIMBALL|||, LARA M. KUEPPERS***, RICHARD J. NORBY†††, SHANNON L. PELINI‡‡‡, ELISE PENDALL§§§, EDWARD RASTETTER†, JOHAN SIX¶¶¶, MELINDA SMITH|||, MARK G. TJOELKER**** and MARGARET S. TORN††††

*Department of Botany and Microbiology, University of Oklahoma, Norman, OK 73069, USA, †The Ecosystems Center, Marine Biological Laboratory, Woods Hole, MA 02543, USA, ‡Risø National Laboratory for Sustainable Energy, Biosystems Department, Technical University of Denmark – DTU, DK-4000 Roskilde, Denmark, §Department of Biology & Nicholas School of the Environment, Duke University, Durham, NC 27708, USA, ¶Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, TN 37996, USA, ||Woods Hole Research Center, Falmouth, MA 02540, USA, **Purdue University Department of Forestry and Natural Resources and Department of Biological Sciences, Purdue University, West Lafayette, IN 47907-2061, USA, ††School of Biological Sciences, Washington State University, Pullman, WA 99164, USA, ‡‡Department of Global Ecology, Carnegie Institution of Washington, Stanford, CA 94305, USA, §§Department of Earth System Science, University of California, Irvine, CA 92697, USA, ¶¶National Ecological Observatory Network Inc., Boulder, CO 80301, USA, |||U.S. Arid-Land Agricultural Research Center, Agricultural Research Service, US Department of Agriculture, Maricopa, AZ 85018, USA, ***School of Natural Sciences, University of California, Merced, CA 95343, USA, †††Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, TN 37831, USA, ‡‡‡Harvard Forest, Harvard University, Petersham, MA 01366, USA, §§§Department of Botany, University of Wyoming, Laramie, WY 82071, USA, ¶¶¶Department of Plant Sciences, University of California, Davis, CA 95616, USA, |||Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT 06520, USA, ****Department of Ecosystem Science and Management, Texas A & M University, College Station, TX 77843-2138, USA, ††††Earth Sciences Division, Lawrence Berkeley National Laboratory, Berkeley, CA 94720, USA

Abstract

Many serious ecosystem consequences of climate change will take decades or even centuries to emerge. Long-term ecological responses to global change are strongly regulated by slow processes, such as changes in species composition, carbon dynamics in soil and by long-lived plants, and accumulation of nutrient capitals. Understanding and predicting these processes require experiments on decadal time scales. But decadal experiments by themselves may not be adequate because many of the slow processes have characteristic time scales much longer than experiments can be maintained. This article promotes a coordinated approach that combines long-term, large-scale global change experiments with process studies and modeling. Long-term global change manipulative experiments, especially in high-priority ecosystems such as tropical forests and high-latitude regions, are essential to maximize information gain concerning future states of the earth system. The long-term experiments should be conducted in tandem with complementary process studies, such as those using model ecosystems, species replacements, laboratory incubations, isotope tracers, and greenhouse facilities. Models are essential to assimilate data from long-term experiments and process studies together with information from long-term observations, surveys, and space-for-time studies along environmental and biological gradients. Future research programs with coordinated long-term experiments, process studies, and modeling have the potential to be the most effective strategy to gain the best information on long-term ecosystem dynamics in response to global change.

Keywords: climate change, data assimilation, earth system, experimentation, global change, process study, terrestrial ecosystems

Received 1 April 2010; revised version received 13 May 2010 and accepted 13 May 2010

Introduction

The ultimate goal of global change research is to project future states of ecosystems and climate at decadal,

century, or even longer time scales. IPCC assessments for the fifth assessment report, for example, will be done with models that simulate ecosystem responses and feedback to global change at a time frame of 300 years from 1800 to 2100. The models used for long-term assessments are typically built upon knowledge of

Correspondence: Y. Luo, tel. +1 405 325 1651, e-mail: yluo@ou.edu

ecosystem processes and parameterized by short-term data. However, ecosystem responses to global change are strongly regulated by long-term, slow processes (Rastetter, 1996). Those processes include species replacement and composition changes in plant and microbial communities, soil carbon dynamics, the growth and death of long-lived plants, and accrual of nitrogen capital in ecosystems. Thus, knowledge on long-term processes is essential to test and constrain models in order to realistically project ecosystem dynamics at decadal to century time scales.

One approach to gain knowledge on long-term ecosystem dynamics is to perturb ecosystems using manipulative experiments and observe their responses over long time periods. Hundreds of global change experiments have been conducted in a wide range of managed and natural ecosystems (Rustad, 2008). Most of them lasted only for a few years and have effectively characterized short-term, fast processes whereas longer term dynamics and responses are less understood and much more difficult to predict. Some experiments have been conducted for a decade or longer to address long-term issues in global change research (Shaver & Jonasson, 1999; Niu *et al.*, 2010). Of those experiments, findings have transitioned from short-term physiological and biogeochemical changes to intermediate and long-term shifts in soil nutrient availability, the recalcitrance of organic matter, and species dominance (Mack *et al.*, 2004). The long-term experimental results are also critical to challenge existing hypotheses and models and to develop new conceptual frameworks for studying ecosystem responses and feedback to global change (McKane *et al.*, 1997).

Those decadal experiments alone are, however, not adequate to address long-term issues because some of the ecological processes have characteristic time scales of decades to millennia, well beyond experimental horizons. For example, the 17-year CO₂ enrichment on sour orange trees would have led to a great overestimation of CO₂ stimulation of plant growth if the experiment was terminated after 3 or 5 years – typical time scales of ecological experiments (Fig. 1) (Kimball *et al.*, 2007). Even this relatively long experiment offers no conclusions about the CO₂ effect on the longevity of the trees. As argued by May (1999), many of the most intellectually challenging and practically important problems of contemporary ecological science are on much longer time scales than are currently being investigated. Without the understanding of global change impacts on long-term processes and their feedbacks, we will face huge uncertainties in predicting future states of ecosystems and climate.

To develop effective approaches to long-term issues in global change research, we held a workshop in Washington, DC in August 2009 to review extant long-term

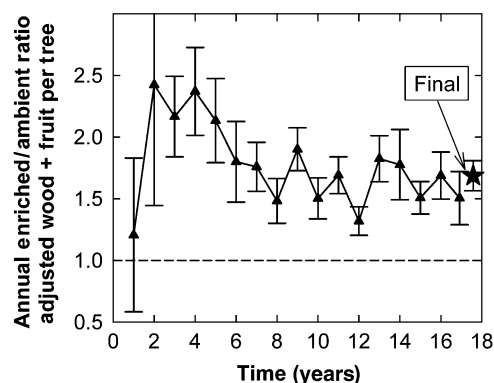


Fig. 1 Ratios of enriched to ambient sums of annual wood plus fruit biomass increments in sour orange trees (*Citrus aurantium* L.) subjected to +300 ppm of CO₂ enrichment for 17 years in open-top chambers (from Kimball *et al.*, 2007). If the experiment had been terminated after year 4, one would conclude the growth rate of the CO₂-enriched trees would continue to be about 2.3 times that of the ambient-CO₂ trees.

research efforts on global change impacts, to identify key long-term issues, and to examine effectiveness of long-term experiments. This paper summarizes our collective analysis and proposes a coordinated, multifaceted approach to long-term global change studies. This paper first examines processes and variables that determine long-term ecosystem dynamics. Then, we discuss major challenges to understand long-term processes. We also propose a coordinated approach that integrates long-term global change experiments, process studies, and information gained from other sources via modeling synthesis. Finally, we outline essential elements for future research programs to address long-term issues in ecology and global change research.

Long-term ecosystem dynamics in response to global change

Long-term ecosystem responses to global change are interactively determined by three components (1) climate variability, (2) disturbances, and (3) internal long-term processes. Climatic variability includes variation in the means and extreme values of temperature and precipitation across seasons, among years, and along decadal trends. An example where this variation is critical at all three of these temporal scales is the Amazon Basin, where the annual dry season ranges from 1 to 6 months (Malhi *et al.*, 2009), where the El Niño Southern Oscillation (ENSO) causes droughts of 2–4 years once or twice per decade, and where a trend towards increasing drought episodes and seasonal water deficits has been predicted for the remainder of the 21st century (Cox *et al.*, 2004; Li *et al.*, 2006). In addition, there is a 28-year cycle of variation in precipitation, causing the biggest

floods when its wet phase coincided with an La Niña event in mid-1970s and the worst droughts when its dry phase coincided with an El Niño event in 1992 (Coe *et al.*, 2002; Marengo, 2004). When climate variability affects transient processes, such as trace gas emissions under varying soil aeration, observations during a few years may be sufficient to capture the most important variability (Davidson *et al.*, 2008). However, when climate variability and/or extreme events trigger transformative changes in species composition, forest structure, and/or fire susceptibility, longer studies are needed to observe those transformations and their consequences on ecosystem dynamics (Brando *et al.*, 2008).

Disturbances have the potential to fundamentally alter the direction, magnitude, and rates of changes in ecosystem structure and function. Disturbances that alter the patterns of succession and geographic ranges of vegetation include fire, hurricanes, ice storms, drought, herbivory, insect outbreaks, and pathogens. Disturbance effects on ecosystem dynamics are mediated in the short term by species differences in physiological limitations, such as shade and drought tolerance (Valladares & Niinemets, 2008; Volder *et al.*, 2010), and in the long term through demographic effects linked to population dynamics and species composition (Dietze & Clark, 2007), and through mortality and recruitment of long-lived tree (Sankaran *et al.*, 2004; Purves, 2009) and soil development. Disturbance effects on ecosystem functions are strongly regulated by global change as shown by Beier *et al.* (2004) with herbivory-induced N leaching under warming.

Long-term ecosystem responses to global change and disturbance involve changes in species composition, soil processes, and soil–plant–microbial interactions. Plant community compositional changes can be more important than the physiological responses of individuals in influencing long-term ecosystem dynamics (Fig. 2) (Smith *et al.*, 2009). Understanding plant performance, establishment, vulnerability, and persistency is important for long-term prediction of ecosystem functions in the future (Clark *et al.*, 2010). Similarly, long-term soil system functions, such as nitrogen accrual and carbon storage, are affected by a wealth of interactions between short- and long-term changes in microbial composition and processes, and plant–soil–microbial feedbacks. Climate change can alter these complex interactions and over time affect new generations of soil microbes and plants (Wardle *et al.*, 2004).

Challenges in quantifying long-term ecosystem processes

To project ecosystem dynamics in response to global change over decades and centuries, we have to carefully

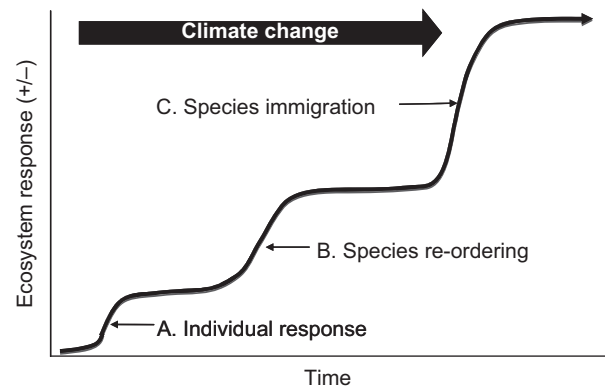


Fig. 2 Long-term ecosystem responses to global change as regulated by hierarchical mechanisms. Physiological processes of existing plants, animals, and microbes likely regulate initial ecosystem responses to global change (a). Reordering of species in the community may occur over time under global change, resulting in large shifts in ecosystem response (b). Global change may induce immigration of new species that are better suited for the new environment, leading to the largest change in ecosystem response (c). (Adopted from Smith *et al.*, 2009.)

examine key long-term processes, such as carbon dynamics in soil, nutrient regulation, and shifts in species composition. However, quantifying these processes is difficult because of their slowness in change, small signal:noise ratios, limited knowledge of key mechanisms, impediment in identifying generalizable properties, their interactive responses to multiple global change factors, and other aspects of complexity (e.g., nonlinearity, thresholds, and tipping points) (Table 1).

Long-term processes are by definition slowly changing. Most modeling and observational studies suggest that carbon turnover times in slow and passive soil pools are hundreds to thousands of years (Trumbore, 2000). Increases in organic matter during soil development are at a rate of approximately $2 \text{ g C m}^{-2} \text{ yr}^{-1}$ for soil at age of 3000–10 000 years (Schlesinger, 1990). Similarly, nitrogen accrual rates in ecosystems are typically small and become detectable only over decadal and century time scales. For example, recovery time of N stock following disturbance took more than half century throughout the course of secondary forest succession at a site in Georgia (Maloney *et al.*, 2008), 45–100 years in upland forests in Mississippi (Switzer *et al.*, 1979), and 180 years following old-field abandonment in Minnesota (Knops & Tilman, 2000). Nevertheless, some of those long-term processes could be abruptly altered in response to extreme climate events.

The small signal:noise ratio poses another common challenge in studying long-term processes. For instance,

Table 1 Challenges of and approaches to elucidating, detecting and predicting long-term ecosystem processes

Challenge	Example	Approaches
Slow in change	Soil nitrogen accrual	Long-term experiments, measurement along gradients, process studies
Small signal : noise ratio	Change in soil carbon input at elevated CO ₂ relative to soil carbon content and its variability	Isotope tracing, signal analysis from multiple information sources, isolation to more sensitive subcomponents
Lack of mechanistic understanding	Carbon allocation	Process studies, synthesis and analysis to identify mechanisms
Lack of generalizable patterns	Change in species composition	Multisite experiments, synthesis to identify generalizable patterns
Multifactor interaction	Evapotranspiration under rising CO ₂ , warming, and altered precipitation	Multifactor experiments and modeling analysis
Nonlinearity, threshold, tipping point	Vegetation die-off in response to drought	Gradient studies, experimental studies, and modeling analysis

changes in soil carbon stock are very difficult to assess partly because the changes over short and medium terms are small compared with the total pool size and partly because its spatial and temporal variability is high. An analysis with a first-order model of soil carbon dynamics indicated that it takes 5 and 9 years to reach a detectable level of increase in soil carbon pool due to a respective 70% and 35% CO₂-induced increases in carbon input into soil in a Californian grassland (Hungate *et al.*, 1996). The small changes relative to the great variability of soil carbon content require a large number of samples to reduce uncertainties and to detect a small change (Goidts & van Wesemael, 2007).

Our understanding of key mechanisms underlying long-term ecosystem dynamics is extremely limited (Table 2). Carbon allocation within plants, for example, is an important process in determining ecosystem carbon, nutrient, and species dynamics. Plants allocate carbon to different organs to optimize acquisition of limiting resources and maximize growth rates. However, understanding carbon allocation is not trivial because carbon allocation changes over the lifetime of a plant, as allocation to structural growth is controlled by a species-dependent morphogenetic plan. Plant allocation is further influenced by resource limitations (light, water, and soil nutrients), microbial partners, and the respiratory demand of different plant organs (Morgan *et al.*, 2004; Lambers *et al.*, 2008). Although a variety of models have been developed to describe carbon allocation, mostly based on the concept of functional balance (e.g., Luo *et al.*, 1994), there is no mechanistic model that is applicable to different plants under varying environments.

One major challenge to studying responses of species composition to global change is to identify relationships and/or patterns that can be scaled from lower to higher

hierarchical levels within ecological systems. Plants, microbes, and animals individually respond to global change. For example, elevated CO₂ accelerated stem and root growth in a loblolly pine forest (Schäfer *et al.*, 2003) and increased fine-root production but not biomass growth in a sweetgum forest (Norby *et al.*, 1999). So far, few properties have been identified that allow extrapolation of species- and site-specific observations to regional and global scales. Predictions of species composition changes at larger scales are further complicated by biogeographical variation within species, especially for those with genetically distinct populations over large ranges (Pelini *et al.*, 2009; Tjoelker *et al.*, 2009). Disproportionate rates and magnitudes of climatic changes within species ranges and across biomes also confound the predictability of species compositional changes at larger spatial scales.

Predicting long-term ecosystem dynamics is also challenged by interactive and nonlinear responses to global change (Zhou *et al.*, 2008). Global change involves a series of simultaneous changes in atmospheric and climatic conditions, which are most often studied in isolation and up-scaled to the long term by dynamic ecosystem models. However, the few experimental studies involving multifactorial treatments have shown that even in the short term there are strong nonlinear interactions between the different global change factors, which are very difficult to predict (e.g., Dukes *et al.*, 2005). Since multifactorial studies have still only been run for relatively short term in almost all cases, we lack long-term data on their interactive and nonlinear effects on ecosystem processes. It is even more difficult to identify thresholds and tipping points beyond which ecosystems shift to alternative states. Realistically modeling these interactions, nonlinearity, and state shifts is a major challenge for the future.

Table 2 Samples of challenging issues related to long-term ecosystem processes

Processes	Description of challenging issues
Carbon dynamics	<ol style="list-style-type: none"> 1. To develop generalizable models of carbon allocation to biomass growth of plant parts, respiration, nonstructural carbon reserve, reproduction and defense 2. To quantify fraction of plant carbon being transferred to mycorrhizae and to the SOM pool via root exudates or litter transfer 3. To estimate lag times between plant carbon uptake and release from soil to the atmosphere 4. To partition relative contributions of carbon sources from dead biomass, exudates of plants, microorganisms, and soil animals, and their decomposition products to form stable SOM 5. To understand mechanisms underlying retention of organic carbon in soils as regulated by biochemical recalcitrance, physical protection within the soil matrix, association with minerals, anaerobiosis, and water limitations
Nutrient regulation	<ol style="list-style-type: none"> 1. To estimate relative effects of various global change factors on N mineralization, immobilization, plant uptake, fixation, and loss under various soil moisture regimes 2. To quantify long-term accrual and depletion of ecosystem N and P capital under multifactor global change 3. To define thresholds owing to temporal shifts in substrate and microbial stoichiometry to alter long-term responses of nutrient availability to global change 4. To test the postulation of progressive nutrient limitation under elevated CO₂ that more nutrients are sequestered in increased plant biomass and SOM as increased C:N and lignin:N reduce substrate quality and decrease decomposition 5. To understand microbial regulation of carbon and nitrogen processes via mineralization, priming, decomposition of old and new SOM 6. To examine the role of root exudates in releasing N from microbial pools via decomposition of SOM
Species composition	<ol style="list-style-type: none"> 1. To identify temporal and spatial scales of species compositional shifts under global change 2. To develop generalizable patterns across various studies that can be used to improve model prediction of species responses to global change 3. To understand mechanisms underlying species expansion or contraction of their geographic ranges 4. To quantify response rate, magnitude, and direction of population size, geographic location, phenology or even genetic composition of individual species to global change 5. To estimate disproportionate rates and magnitudes of climatic changes within species' ranges and across biomes 6. To delineate nonlinear shifts in species composition and consequent asymmetrical changes in ecosystem processes

SOM, soil organic matter.

Approaches to quantify long-term ecosystem responses to global change

To unravel the complexities of long-term ecosystem responses to global change, we need a coordinated approach that involves long-term experiments in high-priority regions, process studies of key ecosystem processes, measurements and observations of ecosystem processes across climatic and ecological gradients, and modeling synthesis (Fig. 3).

Long-term global change experiments

To maximize information gain on responses of the earth system to global change, long-term experiments should be conducted in ecosystems that are expected to critically regulate global change and about which there is minimal knowledge. Arguably ecosystems of the high-

est priority are tropical forests and arctic ecosystems underlain by permafrost. Wet tropical systems play a pivotal role in regulating both carbon and water feedbacks to the climate system. They transpire large volumes of water and thereby generate clouds, affecting atmospheric circulation across continents and hemispheres (Malhi *et al.*, 2008). A large-scale experiment has been conducted in an Amazon forest to exclude 35–40% of rainfall for five successive rainy seasons. The study has demonstrated drought impacts on many long-term processes, such as wood production and tree mortality (Nepstad *et al.*, 2007; Brando *et al.*, 2008). However, no *in situ* experiment has ever been done to examine the response of tropical forests to elevated CO₂ and warming, leaving many hypotheses (Körner, 2009) and model predictions, such as forest dieback (Cox *et al.*, 2004), untested. We urgently need to conduct such experiments to gain a mechanistic understanding of

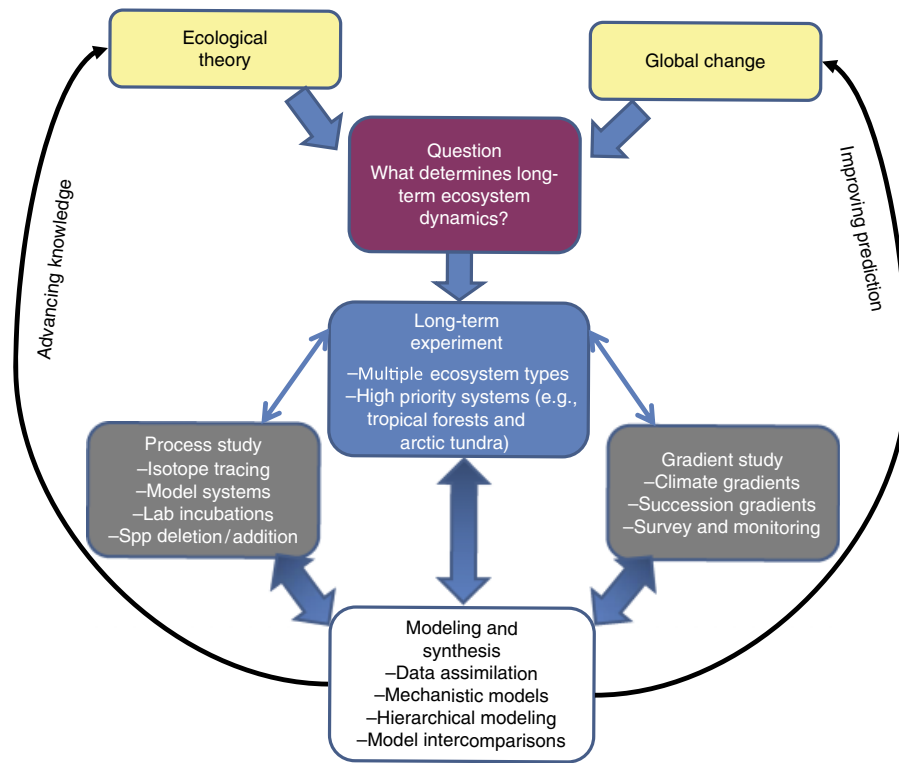


Fig. 3 Schematic illustration of the coordinated approaches to study long-term ecosystem dynamics in response to global change. Ecologists define long-term global change questions according to ecological theory and global change scenarios. The questions help guide design of long-term global change experiments, which will be supported by process studies and observations along environmental and ecological gradients. Modeling can help experimental design in terms of the necessary duration of the project and help prioritizing measurements. Modeling can also synthesize data of multiple sources toward improved predictions of global change and advancing ecological understanding spp, species.

tropical forest responses to global change and to provide critical tests of global models.

Permafrost in the high latitude regions of the northern hemisphere contains an estimated 1672 Pg of organic carbon or ~50% of the global belowground organic carbon pool (Tarnocai *et al.*, 2009). Land surface temperatures are projected to increase by up to 7–8 °C in arctic regions by the end of this century, which will result in permafrost melting over much of the Arctic. The loss of permafrost will result in substantial carbon loss and potentially become one of the most significant feedbacks from terrestrial ecosystems to the atmosphere (Schuur *et al.*, 2008). Global change is also likely to induce shifts in the disturbance regimes of the Arctic. For example, lightning strikes, once rare, are becoming common in northern Alaska and have increased the incidence of tundra wildfires (Jones *et al.*, 2009). Hill-slopes, once held in place by permafrost, are thawing and sliding downhill (thermokarst slumps). Fire and thermokarst can trigger the release of large amounts of soil carbon. Furthermore, permafrost melting and the development of thermokarst may result in large areas of saturated soil and thereby increase methane produc-

tion. Therefore, long-term global change experiment should be conducted to address these key issues in arctic regions.

Hundreds of global change experiments have been conducted in many types of ecosystems in temperate regions, such as croplands, grasslands, forests, deserts, and wetlands (Rustad, 2008). While these experiments have advanced our understanding of ecosystem responses to global changes, there are reasons to continue some of the existing experiments and initiate new ones. For example, croplands and forests, which may be intentionally subjected to manipulations to provide food, fuel, and fiber for human use, require long-term experiments to evaluate sustainability of not only their commodities but also other ecosystem services under global change (Ainsworth *et al.*, 2008; Calfapietra *et al.*, 2010). Current interests in the use of terrestrial land surfaces for the production of biofuels mandate the evaluation of tradeoffs between energy production and environmental impacts using global change experiments (Luo *et al.*, 2009). Moreover, long-term experiments across a range of ecosystems in which multiple global change factors are manipulated in similar ways

should be coordinated to develop generalizable knowledge on ecosystem responses across scales (Smith *et al.*, 2009).

Process studies

Well-designed process studies can complement field experiments to elucidate mechanisms underlying long-term ecosystem response to global change. For example, species removal or addition experiments in field, laboratory, and greenhouse settings help understand impacts of species composition on ecosystem processes. Wardle & Zackrisson (2005) used a series of islands to experimentally remove combinations of both plant functional groups and plant species. They found that some islands were, within 7 years of the removal, affected very little whereas others were much more affected by these removals. This study clearly indicated that effects of species loss on ecosystem functions greatly depend on abiotic and biotic characteristics of the system. The large Biosphere II in Arizona was used to grow a tropical plant community to show strong CO₂ stimulation of the ecosystem light compensation point (Lin *et al.*, 1999).

Laboratory incubations and isotope tracing have been used to understand responses of soil carbon and litter decomposition, microbial activity, and community structure to global change (Trumbore, 2000; Pendall & King, 2007; Karhu *et al.*, 2010). The potential mechanisms for carbon retention in soils include chemical recalcitrance, physical protection within the soil matrix, association (e.g., sorption) to minerals, anaerobiosis, and water limitations (Six *et al.*, 2002). Understanding responses of decomposition of soil organic matter to changing climate requires differentiating between these environmental constraints to decomposition and the intrinsic susceptibility of soil carbon substrates to decomposition as temperature varies (Davidson & Janssens, 2006). Recently, compound-specific isotope analyses greatly improved our understanding of soil organic matter composition and turnover, such as the persistence of lignin in mineral soils (Hofmann *et al.*, 2009).

Gradient studies

Decadal-long manipulative experiments may provide information on transient soil carbon dynamics from the control to treatment environments. The transient responses to treatments may be quite different from the steady-state dynamics observed along environmental gradients. For example, soil organic carbon increased with temperature along a gradient but decreased in a warming experiment (Saleska *et al.*, 2002). The experi-

mental warming induced a shift in species composition from high to low production and consequently decreased soil inputs from plant litter, resulting in the decrease of soil carbon in the manipulative experiment. However, the experimentally induced decline in soil carbon is transient and may be eventually reversed as lower quality litter inputs from the less productive species reduce decomposition (Saleska *et al.*, 2002). Thus, results from either of the methods could not be simply used to predict responses of soil organic carbon to temperature whereas the methods are complementary for understanding underlying mechanisms (Dunne *et al.*, 2004).

A manipulative experiment usually has two or more levels of treatments at one site within a narrow range of environmental variation, making it difficult to detect thresholds of ecosystem response. A linear positive relationship between precipitation and aboveground net primary production (ANPP), for example, was observed from an experiment with four levels of rainfall treatments (30%, 55%, 80%, and a control) in Patagonian steppe in southern Argentina (Yahdjian & Sala, 2006). However, over a large gradient study (500–5500 mm), ANPP showed a threshold near 2000 mm, below which ANPP linearly increases with precipitation but declines above the threshold (Austin, 2002). Root biomass, soil carbon and nitrogen contents were observed to be constant while shoot biomass linearly increased and community structure considerably differed along a precipitation gradient from 430 to 1200 mm in southern Great Plains (Zhou *et al.*, 2009). To understand the contrasting patterns among root and shoot biomass, soil carbon and nitrogen contents, and plant community structure along the gradient, we need manipulative experiments to examine underlying mechanisms. Overall, information extracted from naturally occurring space-for-time gradients studies is useful for the evaluation of ecosystem response to gradual changes in climate and highly complementary to long-term experiments (Rustad, 2008).

Model as an inference tool for assessment of global change impacts

Models are an essential inference tool to understand long-term ecosystem dynamics in response to global change for several reasons. First, global change experiments usually involve step changes in treatment factors to perturb ecosystems to generate responses, which are completely different from the responses to gradual increases in atmospheric CO₂ concentration and temperature (Luo & Reynolds, 1999; Shen *et al.*, 2009). Modeling is an essential tool to extract information from measurements at the experimental sites toward

predictive understanding via data assimilation (Luo *et al.*, 2003). Second, no experiment is long enough to fully quantify slow processes with response times of decades, centuries, or longer (Rastetter, 1996). However, modeling can examine the ecosystem dynamics far beyond the lifetimes of any experiments. Third, models are useful to assist synthesis of information not only from ecosystem experiments but also from process studies, from patterns in ecosystem function and structure along gradients, from historical and paleontological records, and from long-term monitoring measurements (Rastetter, 1996). Fourth, models can help generate hypotheses to guide the next generation of experiments and observations. Models can be manipulated to isolate and analyze responses to individual components of global change and to help identify the most effective experimental approaches to answer particular questions. Such manipulations may be difficult and expensive in a real world setting. Finally, models can help examine potential impacts and interactions among simultaneous drivers that may be difficult or expensive to test in experiments.

Several modeling approaches are available to improve understanding of and predict long-term ecosystem dynamics in response to global change. First,

mechanistic simulation models that have been used in ecology for several decades are still very effective for incorporating process understanding, integrating experimental results, making sensitivity analysis to examine long-term ecosystem dynamics under different assumptions. Second, data assimilation or data-model fusion is an emerging approach that extracts information from data to improve models via estimating parameter values, selecting alternative model structures, and analyzing uncertainties (Williams *et al.*, 2009; Rastetter *et al.*, 2010). Data assimilation can also be used to help design experimental, monitoring, and survey efforts to maximize constraints on models by data. For example, Weng & Luo (2010) have evaluated that the information contribution of eight sets of 10-year data to constraints of forecasted carbon sink dynamics in fast and slow pools at the century time scale (Fig. 4). Third, model intercomparisons have been frequently used to analyze ecosystem responses to global change (Hanson *et al.*, 2004). Such intercomparisons do not constitute a definitive test of the models but can be enlightening with regard to identifying important processes and constraints that need to be accounted for and investigated further (Rastetter, 1996). Fourth, hierarchical modeling provides a framework for synthesis of

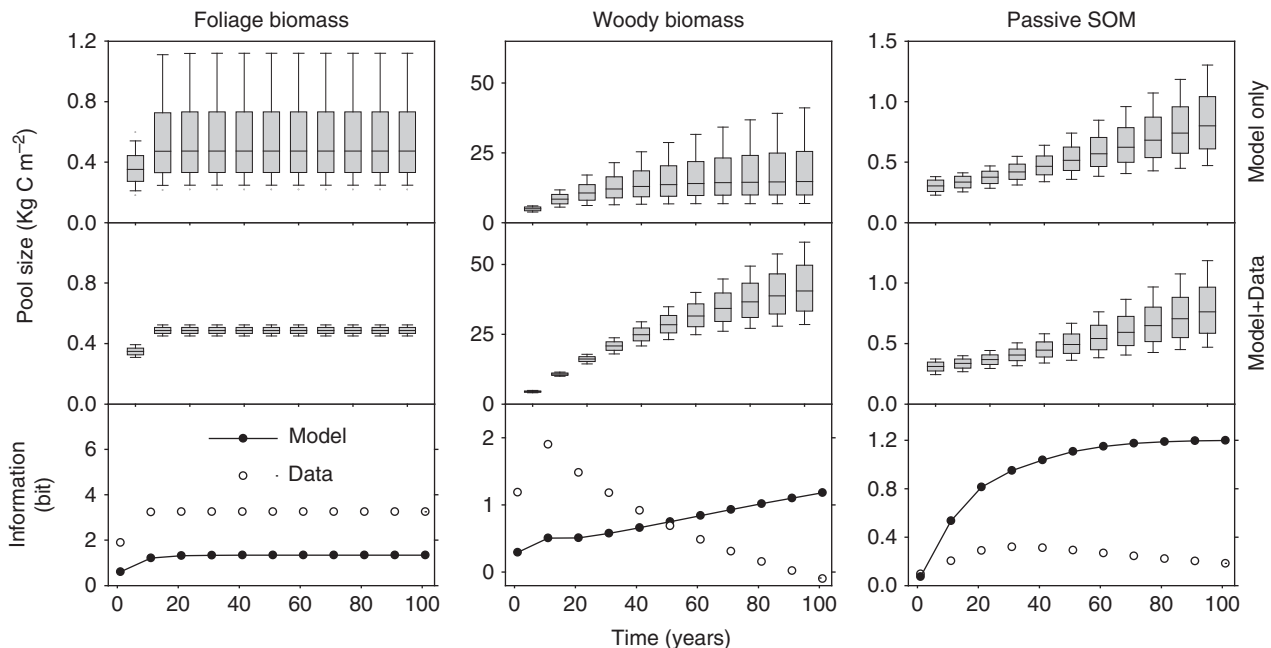


Fig. 4 Relative information contribution by model and data to long-term projection of ecosystem carbon storage in Duke Forest, NC. Box plot in the upper (model only without data) and middle rows (model plus data) shows projected carbon content distributions in the 5% (bottom bar), 25% (bottom hinge of the box), 50% (the lined across the box), 75% (upper hinge of the box), and 95% (upper bar) intervals. Closed circles with solid lines are the information contribution of the model; open circles with dotted lines are the additional information provided by data. Eight 10-year data sets contribute information to constrain carbon sink dynamics in the foliage biomass pool substantially, the woody biomass pool in the first several decades, and little in the passive soil organic matter (SOM) pool (Weng & Luo, 2010). Uncertainty in projected carbon content grows with time because forecasting becomes less constrained farther in time.

multiple sources of information from experiments, observations, and theory in a coherent fashion. For example, By applying a coherent synthesis of 5- to 18-year observations of tree census plots, increment core data, maturation, gender, and crown status observations, and seed traps, Clark *et al.* (2010); J.S. Clark, D.M. Bell, M.H. Hersh & L. Nichols (unpublished results) determined effects of climate variation and its interaction with light availability on growth and fecundity of individual trees. The increasing capacity of models to integrate multiple sources of information will give them a prominent role in the global change experiments of the next decade.

Future research programs for long-term global change experiments

Global change acts globally and on long time scales and involves simultaneous impacts from multiple drivers. Therefore, future experiments are likely to be conducted at large scales and to explore complex ecosystem responses to global change. Successful research programs for future experiments must consider composition of research teams, experimental facilities, measurement schemes, and research durations.

Research team

Future long-term global change programs need multidisciplinary research teams, consisting of scientists in relevant and disparate fields of study as well as highly skilled technicians, engineers, instrumentation specialists, and data managers to keep an experiment operating efficiently. In order to embrace the complexity and understand the interactions among the multitude of ecosystem responses, scientists from many different disciplines are needed to make measurements in the realms of plant biochemistry and physiology, growth and allocation, biogeochemistry and water relations, soil chemistry and microbiology, community and ecosystem ecology. In addition to these classic scientific disciplines, it is important to be aware that long-term ecosystem experiments involving great complexities requires advanced technology, facilities and long-term commitments. Thus, highly skilled technicians and engineers are needed to design, build, run, and maintain the experiments (Mikkelsen *et al.*, 2008).

Management and coordination of such long-term experiments are essential. With many researchers from different disciplines, with many different foci, and most likely from different institutions, it is essential that project management ensures coordinated activities to avoid duplication of effort or forgotten measurements, ensure efficient use of resources, minimize impacts on the site, and facilitate sharing of data and information.

Long-term experiments have been valuable opportunities for collaborators from outside the core research teams to conduct novel measurements or test out new methods; the project leader must ensure that external collaborators do not compromise the integrity of the experiment or duplicate ongoing efforts, and that they have access to other project data.

We emphasize here the importance of including modeling experts in the research teams for planning, experimental design, and project management. Modeling analysis that is conducted before an experiment is set up can provide insight on the necessary duration of the project and estimate information gain from different sets of measurements to constrain long-term patterns and responses. A model prediction of ecosystem response to proposed manipulations often generates specific hypotheses to be tested in the experiment, thereby identifying critical measurements that must be made (Parton *et al.*, 2007). Nonsensical model results might identify spurious measurements or problems in data analysis. Likewise, experimental observations can suggest improvements to be made in model structure.

Infrastructure

A variety of facilities have been developed in the past decades to manipulate carbon dioxide concentration, temperature, and precipitation at ecosystem scales. The facilities to fumigate CO₂ include free-air CO₂ enrichment (FACE) and open-top chamber (OTC) (Norby *et al.*, 1999; Lewin *et al.*, 2009). The commonly used facilities to increase temperature in ecosystems include OTC and infrared radiator (Kimball, 2005; Walker *et al.*, 2006). The facilities to alter precipitation include rainout-shelter and throughfall displacement (Knapp *et al.*, 2002; Fröberg *et al.*, 2008). The next generation of global change experiments may further challenge the facility development by involving new materials, more advanced computer steering, and less environmental impacts.

Global change research needs facilities that are affordable and can manipulate multiple global change factors for high stature ecosystems and for long-term studies. With increasing stature comes a need to increase plot sizes to capture relevant ecological processes, and therefore, greater challenges. Treatments need to be applied uniformly across plot areas, which can prove more difficult as stature increases. Especially challenging is the fact that treatment costs generally scale with the square of the plot diameter. On the positive side, with greater plot sizes, economies of scale and equipment efficiency exist (Kimball, 1992; B.A. Kimball, M.M. Conley, K.F. Lewin, unpublished results), which can significantly reduce costs on a per unit area basis. Research programs involving long-term experiments

can greatly benefit from combinations with facilities for process studies. Traditionally, greenhouse, growth chamber, lab incubation, and model ecosystems have been successfully used to understand mechanisms underlying long-term ecosystem dynamics.

Data management is a particular important and often neglected area of concern. Global change experiments have over time collected vast amounts of valuable information. Such data will be of great value to the scientific community. In particular, when data from many different projects are combined new dimensions of knowledge may become clear and the value of individual projects may increase. However, the true value only becomes clear if the data are stored, quality checked and documented in a way that other researchers can get access to these. Future global change research programs should strive to develop facilities for such comprehensive data storage to ensure data access and at the same time protect the ownership of the data. A policy for open data access should be in place to support synthesis and modeling from broader research communities. Finally, long-term experimental facilities should also include model frameworks to test hypotheses, evaluate results, advance process- and system-level understanding, and project results in time and space. We need to develop infrastructure to allow for data assimilation to facilitate real- and near-time forecasting.

Lifetime of long-term experiments

The lifetime of a long-term global change experiment is a critical factor to be considered at planning because it affects the design of the experiment, infrastructure, and potential cost. The lifetime of an experiment is primarily determined by the core questions that are to be addressed. To examine how global change induces alternations in species composition, soil carbon dynamics, and nutrient regulation, experiments usually should last at least a decade or more. For a particular question, models can be used to examine response time of various variables and thus to estimate when particular responses may be large or consistent enough to be reliably quantified so as to estimate, at least roughly, how long an experiment might need to run. Lifetimes of experiments are specific to the system of interest. Most processes operate much faster in tropical rainforests, for instance, than in boreal forests and their pool sizes differ dramatically. So, the time necessary to detect a given response might be quite different between tropical, temperate, and boreal systems.

During the lifetime of an experiment, measurements should be planned to remain consistent across years and to capture the data necessary to understand pro-

cesses of interest over time. Measurements before any manipulation is started are very useful to assess treatment effects because the controls and treatments are often different. In addition, investigator-caused disturbance to the experimental plots can become a major problem as the time length of the experiment increases. Measurements and sampling have to be planned in order to not jeopardize the integrity of future measurements or otherwise limit future opportunities for study. For instance, intensive soil coring will potentially affect many important processes in the ecosystem (e.g., soil, plant, and hydrology, etc.) and will have to be planned in accordance with the soil processes being examined (i.e., the size of the core) as well as the size of the plot, and the total number of cores to be removed from the plot over the lifetime of the experiment. This also requires careful planning of destructive harvesting and use of stable and/or radioactive isotopes, which potentially affects future investigations. As a long-term experiment progresses, research teams may gradually shift from studying fast response processes in its first few years to addressing long-term issues using long time-series data. Many long-term questions listed in Table 2 can potentially become research topics for new cohorts of students and postdocs who join the projects in later stages.

Ideally, experiments should last long enough to be able to identify important 'surprise' responses. By definition, the ideal duration to accomplish this task is unknowable. Nevertheless, records of past disturbance events or landscape-scale patterns around the area of study can suggest what important thresholds might be reached in the system and can help researchers estimate when an environmental change might drive the system past these thresholds. Surprise responses that only occur once a system has passed some threshold may cause far greater changes to the system than the direct responses to environmental changes.

Summary

To gain a predictive capacity for long-term ecosystem responses to global change, future experiments must be designed to reveal responses of many component processes at a broad range of time scales and their relative contributions to whole-ecosystem responses over time. Long-term field experiments, process studies, and modeling each provide insights into ecosystem responses to global change in different but complementary ways. Combining these approaches is essential for better understanding and improving our predictive capacity of long-term responses to global change. The data-model fusion and model intercomparisons would be greatly beneficial for identifying model gaps and

experimental priorities to improve our understanding of long-term ecosystem responses.

Acknowledgements

We thank Ding Guo for his help with references. The work was financially supported by DOE through Oak Ridge for Science and Education and NSF EF 0938795. The preparation of the manuscript by Y. L. and S. N. was also financially supported by NSF DBI 0850290, DEB 0840964, DEB 0743778; by the Office of Science (BER), Department of Energy, Grant No.: DE-FG02-006ER64319 and through the Midwestern Regional Center of the National Institute for Climatic Change Research at Michigan Technological University, under Award Number DE-FC02-06ER64158. The participation of C. B. was financially supported by the CLIMAITE project.

References

- Ainsworth EA, Beier C, Calfapietra C *et al.* (2008) Next generation of elevated [CO₂] experiments with crops: a critical investment for feeding the future world. *Plant, Cell and Environment*, **31**, 1317–1324.
- Austin AT (2002) Differential effects of precipitation on production and decomposition along a rainfall gradient in Hawaii. *Ecology*, **83**, 328–338.
- Beier C, Schmidt IK, Kristensen HL (2004) Effects of climate and ecosystem disturbances on biogeochemical cycling in a semi-natural terrestrial ecosystem. *Water, Air and Soil Pollution: Focus*, **4**, 191–206.
- Brando PM, Nepstad DC, Davidson EA, Trumbore SE, Ray D, Camargo P (2008) Drought effects on litterfall, wood production and belowground carbon cycling in an Amazon forest: results of a throughfall reduction experiment. *Philosophical Transactions of the Royal Society B-Biological Sciences*, **363**, 1839–1848.
- Calfapietra C, Ainsworth EA, Beier C *et al.* (2010) Challenges in elevated CO₂ experiments on forests Source. *Trends in Plant Science*, **15**, 5–10.
- Clark JS, Bell D, Chu C *et al.* (2010) High dimensional coexistence based on individual variation: a synthesis of evidence. *Ecological Monographs*, in press.
- Coe MT, Costa MH, Botta A, Birkett C (2002) Long-term simulations of discharge and floods in the Amazon Basin. *Journal of Geophysical Research-Atmospheres*, **107**, doi: 10.1029/2001JD000740.
- Cox PM, Betts RA, Collins M, Harris PP, Huntingford C, Jones CD (2004) Amazonian forest dieback under climate-carbon cycle projections for the 21st century. *Theoretical and Applied Climatology*, **78**, 137–156.
- Davidson EA, Janssens IA (2006) Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature*, **440**, 165–173.
- Davidson EA, Nepstad DC, Ishida FY, Bando PM (2008) Effects of an experimental drought and recovery on soil emissions of carbon dioxide, methane, nitrous oxide, and nitric oxide in a moist tropical forest. *Global Change Biology*, **14**, 2582–2590.
- Dietze M, Clark JS (2007) Changing the gap dynamics paradigm: vegetative regeneration control on forest response to disturbance. *Ecological Monographs*, **78**, 331–347.
- Dukes JS, Chiariello NR, Cleland EE *et al.* (2005) Responses of grassland production to single and multiple global environmental changes. *PLoS Biology*, **3**, 1829–1837.
- Dunne JA, Saleska SR, Fischer ML, Harte J (2004) Integrating experimental and gradient methods in ecological climate change research. *Ecology*, **85**, 904–916.
- Fröberg M, Hanson PJ, Todd DE, Johnson DW (2008) Evaluation of effects of sustained decadal precipitation manipulations on soil carbon stocks. *Biogeochemistry*, **89**, 151–161.
- Goidts E, van Wesemael B (2007) Regional assessment of soil organic carbon changes under agriculture in Southern Belgium (1955–2005). *Geoderma*, **141**, 341–354.
- Hanson PJ, Amthor JS, Wullschlegel SD *et al.* (2004) Oak forest carbon and water simulations: model intercomparisons and evaluations against independent data. *Ecological Monographs*, **74**, 443–489.
- Hofmann A, Heim A, Christensen BT, Miltner A, Gehre M, Schmidt MWI (2009) Lignin dynamics in two ¹³C-labelled arable soils during 18 years. *European Journal of Soil Science*, **60**, 250–257.
- Hungate BA, Jackson RB, Field CB, Chapin FS (1996) Detecting changes in soil carbon in CO₂ enrichment experiments. *Plant and Soil*, **187**, 135–145.
- Jones BM, Kolden CR, Jandt R, Abatzoglou JT, Urban F, Arp CD (2009) Fire behavior, weather, and burn severity of the 2007 Anaktuvuk River tundra fire, North Slope, Alaska. *Arctic, Antarctic, and Alpine Research*, **41**, 309–316.
- Karhu K, Fritze H, Tuomi M, Vanhala P, Spetz P, Kitunen V, Liski J (2010) Temperature sensitivity of organic matter decomposition in two boreal forest soil profiles. *Soil Biology and Biochemistry*, **42**, 72–82.
- Kimball BA (1992) Cost comparisons among free-air CO₂ enrichment, open-top chamber, and sunlit controlled-environment chamber methods of CO₂ exposure. *Critical Reviews in Plant Sciences*, **11**, 265–270.
- Kimball BA (2005) Theory and performance of an infrared heater for ecosystem warming. *Global Change Biology*, **11**, 2041–2056.
- Kimball BA, Idso SB, Johnson S, Rillig MC (2007) Seventeen years of carbon dioxide enrichment of sour orange trees: final results. *Global Change Biology*, **13**, 2171–2183.
- Knapp AK, Fay PA, Blair JM *et al.* (2002) Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. *Science*, **298**, 2202–2205.
- Knops JMH, Tilman D (2000) Dynamics of soil nitrogen and carbon accumulation for 61 years after agricultural abandonment. *Ecology*, **81**, 88–98.
- Körner C (2009) Responses of humid tropical trees to rising CO₂. *Annual Review of Ecology, Evolution and Systematics*, **40**, 61–79.
- Lambers H, Raven JA, Shaver GR, Smith SE (2008) Plant nutrient-acquisition strategies change with soil age. *Trends in Ecology and Evolution*, **23**, 95–103.
- Lewin KF, Nagy J, Nettles WR, Cooley DM, Rogers A (2009) Comparison of gas use efficiency and treatment uniformity in a forest ecosystem exposed to elevated [CO₂] using pure and prediluted free-air CO₂ enrichment technology. *Global Change Biology*, **15**, 388–395.
- Li WH, Fu R, Dickinson RE (2006) Rainfall and its seasonality over the Amazon in the 21st century as assessed by the coupled models for the IPCC AR4. *Journal of Geophysical Research-Atmospheres*, **111**, D02111, doi: 10.1029/2005/JD006355.
- Lin G, Adams J, Farnsworth B, Wei Y, Marino BDV, Berry JA (1999) Ecosystem carbon exchange in two terrestrial ecosystem mesocosms under changing atmospheric CO₂ concentrations. *Oecologia*, **119**, 97–108.
- Luo Y, Field CB, Mooney HA (1994) Predicting responses of photosynthesis and root fraction to elevated CO₂: interaction among carbon, nitrogen and growth. *Plant, Cell and Environment*, **17**, 1195–1204.
- Luo YQ, Reynolds JF (1999) Validity of extrapolating field CO₂ experiments to predict carbon sequestration in natural ecosystems. *Ecology*, **80**, 1568–1583.
- Luo YQ, Sherry R, Zhou XH, Wan SQ (2009) Terrestrial carbon-cycle feedback to climate warming: experimental evidence on plant regulation and impacts of biofuel feedstock harvest. *Global Change Biology Bioenergy*, **1**, 62–74.
- Luo YQ, White LW, Canadell JG *et al.* (2003) Sustainability of terrestrial carbon sequestration: a case study in duke forest with inversion approach. *Global Biogeochemical Cycles*, **17**, 1021, doi: 10.1029/2002GB001923.
- Mack MC, Schuur EAG, Bret-Harte MS, Shaver GR, Chapin FS (2004) Ecosystem carbon storage in arctic tundra reduced by long-term nutrient fertilization. *Nature*, **431**, 440–443.
- Malhi Y, Aragão LEOC, Galbraith D *et al.* (2009) Exploring the likelihood and mechanism of a climate-change-induced dieback of the Amazon rainforest. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 20610–20615.
- Malhi Y, Roberts JT, Betts RA, Killeen TJ, Li WH, Nobre CA (2008) Climate change, deforestation, and the fate of the Amazon. *Science*, **319**, 169–172.
- Maloney KO, Garten CT, Ashwood TL (2008) Changes in soil properties following 55 years of secondary forest succession at Fort Benning, Georgia, USA. *Restoration Ecology*, **16**, 503–510.
- Marengo JA (2004) Interdecadal variability and trends of rainfall across the Amazon basin. *Theoretical and Applied Climatology*, **78**, 79–96.
- May RM (1999) The dimensions of life on earth. In: *Nature and Human Society: The Quest for a Sustainable World* (eds Raven RH, Williams T), pp. 30–45. National Academy of Sciences Press, Washington, DC.
- McKane RB, Rastetter EB, Shaver GR, Nadelhoffer KJ, Giblin AE, Laundre JA, Chapin FS (1997) Climatic effects on tundra carbon storage inferred from experimental data and a model. *Ecology*, **78**, 1170–1187.
- Mikkelsen TN, Beier C, Jonasson S *et al.* (2008) Experimental design of multifactor climate change experiments with elevated CO₂, warming and drought: the CLIMATE project. *Functional Ecology*, **22**, 185–195.
- Morgan JA, Pataki DE, Körner C *et al.* (2004) Water relations in grassland and desert ecosystems exposed to elevated atmospheric CO₂. *Oecologia*, **140**, 11–25.
- Nepstad DC, Tohver IM, Ray D, Moutinho P, Cardinot G (2007) Mortality of large trees and lianas following experimental drought in an Amazon forest. *Ecology*, **88**, 2259–2269.
- Niu SL, Sherry RA, Zhou XH, Wan SQ, Luo YQ (2010) Nitrogen regulation of the climate-carbon feedback: evidence from a long-term global change experiment. *Ecology*, in press.

- Norby RJ, Wullschlegel SD, Gunderson CA, Johnson DW, Ceulemans R (1999) Tree responses to rising CO₂ in field experiments: implications for the future forest. *Plant, Cell and Environment*, **22**, 683–714.
- Parton WJ, Morgan JA, Wang GM, Del Grosso S (2007) Projected ecosystem impact of the Prairie heating and CO₂ enrichment experiment. *New Phytologist*, **174**, 823–834.
- Pelini SL, Dzurisin JDK, Prior KM, Williams CM, Marsico TD, Sinclair BJ, Hellmann JJ (2009) Translocation experiments with butterflies reveal limits to enhancement of poleward populations under climate change. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 11160–11165.
- Pendall E, King JY (2007) Soil organic matter dynamics in grassland soils under elevated CO₂: insights from long-term incubations and stable isotopes. *Soil Biology and Biochemistry*, **39**, 2628–2639.
- Purves DW (2009) The demography of range boundaries versus range cores in Eastern US tree species. *Proceedings of the Royal Society B-Biological Sciences*, **276**, 1477–1484.
- Rastetter EB (1996) Validating models of ecosystem response to global change. *Bioscience*, **46**, 190–198.
- Rastetter EB, Williams M, Griffin KL *et al.* (2010) Application of the ensemble Kalman filter to assimilate Eddy covariance flux data into a model of arctic carbon exchange. *Ecological Applications*, in press.
- Rustad LE (2008) The response of terrestrial ecosystems to global climate change: towards an integrated approach. *Science of the Total Environment*, **404**, 222–235.
- Saleska SR, Shaw MR, Fischer ML, Dunne JA, Still CJ, Holman ML, Harte J (2002) Plant community composition mediates both large transient decline and predicted long-term recovery of soil carbon under climate warming. *Global Biogeochemical Cycles*, **16**, doi: 10.1029/2001GB001573.
- Sankaran M, Ratnam J, Hanan NP (2004) Tree-grass coexistence in savannas revisited – insights from an examination of assumptions and mechanisms invoked in existing models. *Ecology Letters*, **7**, 480–490.
- Schäfer KVR, Oren R, Ellsworth DS *et al.* (2003) Exposure to an enriched CO₂ atmosphere alters carbon assimilation and allocation in a pine forest ecosystem. *Global Change Biology*, **9**, 1378–1400.
- Schlesinger WH (1990) Evidence from chronosequence studies for a low carbon-storage potential of soils. *Nature*, **348**, 232–234.
- Schuur EAG, Bockheim J, Canadell JG *et al.* (2008) Vulnerability of permafrost carbon to climate change: implications for the global carbon cycle. *Bioscience*, **58**, 701–714.
- Shaver GR, Jonasson S (1999) Response of Arctic ecosystems to climate change: results of long-term field experiments in Sweden and Alaska. *Polar Research*, **18**, 245–252.
- Shen WJ, Reynolds JF, Hui DF (2009) Responses of dryland soil respiration and soil carbon pool size to abrupt vs. gradual and individual vs. combined changes in soil temperature, precipitation, and atmospheric [CO₂]: a simulation analysis. *Global Change Biology*, **15**, 2274–2294.
- Six J, Conant RT, Paul EA, Paustian K (2002) Stabilization mechanisms of soil organic matter: implications for C-saturation of soils. *Plant and Soil*, **241**, 155–176.
- Smith MD, Knapp AK, Collins SL (2009) A framework for assessing ecosystem dynamics in response to chronic resource alterations induced by global change. *Ecology*, **90**, 3279–3289.
- Switzer GL, Shelton MG, Nelson LE (1979) Successional development of the forest floor and soil surface on upland sites of the East Gulf Coastal Plain. *Ecology*, **60**, 1162–1171.
- Tarnocai C, Canadell JG, Schuur EAG, Kuhry P, Mazhitova G, Zimov S (2009) Soil organic carbon pools in the northern circumpolar permafrost region. *Global Biogeochemical Cycles*, **23**, GB2023, doi: 10.1029/2008GB003327.
- Tjoelker MG, Oleksyn J, Lorenc-Plucinska G, Reich PB (2009) Acclimation of respiratory temperature responses in northern and southern populations of *Pinus banksiana*. *New Phytologist*, **181**, 218–229.
- Trumbore S (2000) Age of soil organic matter and soil respiration: radiocarbon constraints on belowground C dynamics. *Ecological Applications*, **10**, 399–411.
- Valladares F, Niinemets ü (2008) Shade tolerance, a key plant feature of complex nature and consequences. *Annual Review of Ecology and Systematics*, **39**, 237–257.
- Volder A, Tjoelker MG, Briske DD (2010) Contrasting physiological responsiveness of establishing trees and a C₄ grass to rainfall events, intensified summer drought, and warming in oak savanna. *Global Change Biology*, in press, doi: 10.1111/j.1365-2486.2009.02152.x.
- Walker MD, Wahren CH, Hollister RD *et al.* (2006) Plant community responses to experimental warming across the tundra biome. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 1342–1346.
- Wardle DA, Walker LR, Bardgett RD (2004) Ecosystem properties and forest decline in contrasting long-term chronosequences. *Science*, **305**, 509–513.
- Wardle DA, Zackrisson O (2005) Effects of species and functional group loss on island ecosystem properties. *Nature*, **435**, 806–810.
- Weng ES, Luo YQ (2010) Relative information contributions of model vs. data to constraints of short- and long-term forecasts of forest carbon dynamics. *Ecological Applications*, in press.
- Williams M, Richardson AD, Reichstein M *et al.* (2009) Improving land surface models with FLUXNET data. *Biogeosciences*, **6**, 1341–1359.
- Yahdjian L, Sala O (2006) Vegetation structure constrains primary production response to water availability in the Patagonian steppe. *Ecology*, **87**, 952–962.
- Zhou XH, Talley M, Luo YQ (2009) Biomass, litter, and soil respiration along a precipitation gradient in southern Great Plains, USA. *Ecosystems*, **12**, 1369–1380.
- Zhou XH, Weng ES, Luo YQ (2008) Modeling patterns of nonlinearity in ecosystem responses to temperature, CO₂, and precipitation changes. *Ecological Applications*, **18**, 453–466.