Chapter 3

Ecosystem Responses to Warming and Interacting Global Change Factors

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3.1 The Multiple Factor Imperative in Global Change Research

Increases in atmospheric CO_2 concentration in the coming decades will be accompanied by other global changes. Higher air temperatures, altered precipitation patterns, increased tropospheric ozone concentrations, and N deposition are among the most prominent of the predicted changes that, along with elevated CO_2, have a high potential to affect ecosystem structure and function. Although the effect of elevated atmospheric CO_2 on ecosystem function was the primary focus of much of the GCTE effort in ecosystem physiology, each of these additional factors presents the possibility of altering the response of ecosystems to elevated CO_2 – perhaps negating the CO_2 response, enhancing it, or completely changing the nature of the response. Predictions of future ecosystem metabolism based solely on changes in a single factor are likely to be misleading. Hence, in addition to the elevated CO_2 network, GCTE fostered the development of a network to stimulate and coordinate research on ecosystem responses to climatic warming. Through all of its activities, GCTE promoted an agenda that embraced the mandate for understanding multi-factor interactions.

In the past, many model simulations of ecosystem response to global change were based on changes in climate alone, in part because the effects of elevated CO_2 were considered insignificant or too uncertain (Solomon 1986). Now, ecosystem and global models include multiple factors, particularly climate and CO_2, and the predicted responses can differ significantly from predictions based on changes in a single factor (Melillo et al. 2001; Cramer et al. 2001). It is important to the international global change research agenda that progress in experimental approaches keeps pace with model development. While many of the fundamental relations between ecosystem processes and temperature are well known, it is more difficult to have confidence in predictions of the combined responses to temperature and CO_2. Some interactions have a strong theoretical and empirical foundation: the optimum temperature for photosynthesis increases with increasing CO_2 (Long 1991). Temperature affects all biological processes, however, and the net response of an ecosystem to the combined effects of warming and elevated CO_2 are not so simply described (Norby and Luo 2004). Furthermore, ecosystem responses to CO_2 and temperature are likely to be modified by other environmental factors, especially the availabilities of water and nitrogen, which in turn are modified by CO_2 and temperature (Medlyn et al. 2000; McGuire et al. 2001).

Here, we explore recent experimental approaches to understanding ecosystem responses to global change, focusing on approaches that span an increasing range of complexity. First we will consider warming as a single factor, followed by an example of an experiment investigating interactions between warming and elevated CO_2 (Sect. 3.3). Temperature is more difficult to manipulate in field experiments than is CO_2, and the difficulties – both conceptual and operational – increase when temperature and CO_2 treatments are combined (Norby and Luo 2004). Hence, experiments on CO_2-temperature interaction have been at a smaller scale and in less complex biological systems than larger-scale FACE experiments, particularly those in forest ecosystems. Smaller stature systems, however, do permit more ambitious, whole-ecosystem, multi-factor experiments, such as the Jasper Ridge Global Change Experiment, which is discussed in the Sect. 3.4. Results from such studies can be complex and perplexing, and there is a strong need for experimental results to be linked to ecosystem models so that the responses can be better understood and projected over longer time frames, as will be described in the fourth section.

3.2 Ecosystem Responses to Experimental Warming

It is now widely accepted that human-induced increases in greenhouse gas concentrations have already raised mean global temperature by ~0.6 °C during the last century, and unless these emissions are significantly curtailed, will likely result in a continued increase in mean global temperature of ~1.4 to 5.8 °C during the next century (IPCC 2001). Because temperature is one of the fundamental regulators of all chemical and biological processes, climatic warming in combination with other global change drivers – elevated atmospheric CO_2, changes in the quantity and timing of precipitation, and alterations in the global N cycle – is likely to have profound effects on the structure and function of terrestrial ecosystems (Rustad and Norby 2002). For example, in undisturbed systems, temperature is a key factor that regulates many terrestrial biogeochemical processes, such as soil respiration (Raich and Nadelhoffer 1989; Raich and Schlesinger 1992; Raich and Potter 1995; Kirschbaum 1995), litter decomposition (Meentemeyer 1978; Jansson and Berg 1985; Hobbie 1996), N mineralization and nitrification (MacDonald et al. 1995), denitrification (Malhi et al. 1990), CH_4 emission (Crill et al. 1988, 1991; Johnson et al. 1996), fine root dynamics (Boone et al. 1998; Pregitzer et al. 2000; Gill and Jackson 2000), plant productivity (Warren-Wilson 1957; Morison and Lawlor 1999), and plant nutrient uptake (BassiriRad et al. 2000). However, despite this extensive literature, the longer-term response of whole ecosystems to warming remains elusive. This is due, in part, to the complex array of direct and indirect responses of ecosystem processes to changes in temperature, the variable time-scale of response of different ecosystem processes and components to changes in temperature, and the importance of initial conditions (Shaver et al. 2000).

To help disentangle these complex issues and to establish cause-and-effect relationships between warming and ecosystem effects, a growing number of ecosystem warming experiments have been initiated around the world over the past few decades. The accumulating evidence from these experiments has greatly increased our understanding of short-term (i.e., 1–10 yr) responses of terrestrial ecosystems and their components to experimental warming. In this section we highlight results from two syntheses of experimental results (the GCTE-NEWS synthesis, Rustad et al. 2001; and the ITEX synthesis, Arft et al. 2000) and one longer-term study (the Harvard Forest soil warming experiment, Melillo et al. 2002).

3.2.1 The GCTE-NEWS Synthesis

Rustad et al. (2001) used meta-analysis to synthesize results on the response of soil respiration, net organic horizon N mineralization, and aboveground plant productivity to experimental warming from 32 ecosystem warming experiments, representing four broadly defined biomes – high arctic, low arctic (including a Minnesota bog and fen and a Colorado alpine dry tundra), forest, and grassland – associated with the GCTE Network of Ecosystem Warming Studies (GCTE-NEWS). GCTE-NEWS was established in 1999 in response to a perceived need for better synthesis and integration of results from ecosystem warming experiments. The goals of this network are to integrate and foster research on ecosystem-level effects of rising temperature, both alone and in combination with other vectors of global change. Warming methods used in the studies in the meta-analysis included electrical heat-resistance ground cables (Peterjohn et al. 1994; Rustad and Fernandez 1998), infrared heaters (Harte et al. 1995; Bridgham et al. 1999), greenhouses (Shaver et al. 1998; Jonasson et al. 1999), open-top chambers (Marion et al. 1997; Norby et al. 1997), climate-controlled chambers (Tingey et al. 1996), and passive night-time warming (Alward et al. 1999). The relative merits of these different approaches have been discussed (Shaver et al. 2000). The duration of the experimental studies in the meta-analysis ranged from 2 to 9 years, and the experimental increases in soil or air temperature ranged from 0.3 to 6.0 °C, with a mean increase of 2.4 °C across all 32 studies.

Results for individual sites showed considerable variation in response to warming, as illustrated by the range in effect sizes [*d*] (Fig. 3.1). However, when all sites were considered together, results from the meta-analysis showed that experimental warming significantly increased rates of soil respiration by a weighted mean average of 20% (with a 95% confidence interval of 18 to 22%; $n = 17$), O horizon net N mineralization by a weighted mean average of 46% (with a 95% confidence interval of 30 to 64%; $n = 12$), and plant productivity by a weighted mean average of 19% (with a 95% confidence interval of 15 to 23%; $n = 20$) (Fig. 3.1). Although the number of studies was limited, the response of soil respiration to warming was generally greater in forested ecosystems compared to low arctic and grassland ecosystems ($P < 0.10$), and the response of plant productivity was generally greater in low arctic ecosystems than in forest and grassland ecosystems ($P < 0.01$). With the exception of aboveground plant productivity, which showed a greater positive response to warming in colder ecosystems, meta-analysis did not reveal any other significant relationships between the magnitude of the response of these three ecosystem processes to experimental warming and the other geographic (latitude, longitude), climatic (mean annual and growing season temperature and precipitation, mean frost-free days), or environmental (soil and foliar chemical properties, dominant vegetation type, soil classification, successional status) variables evaluated in this analysis.

These results appear to be consistent with the hypothesis that warming, at least in the short term, directly increases rates of microbial processes including litter decomposition and N mineralization, thereby increasing the availability of nutrients, and, particularly in nutrient-limited ecosystems, increasing plant productivity. Unfortunately, the observations of increased N mineralization and increased plant productivity largely came from different experiments; few experiments took a whole-ecosystem approach with integrated analysis of both above- and belowground responses. Hence, available experimental data cannot be used to evaluate a hypothesis linking warming, nutrient availability, and productivity.

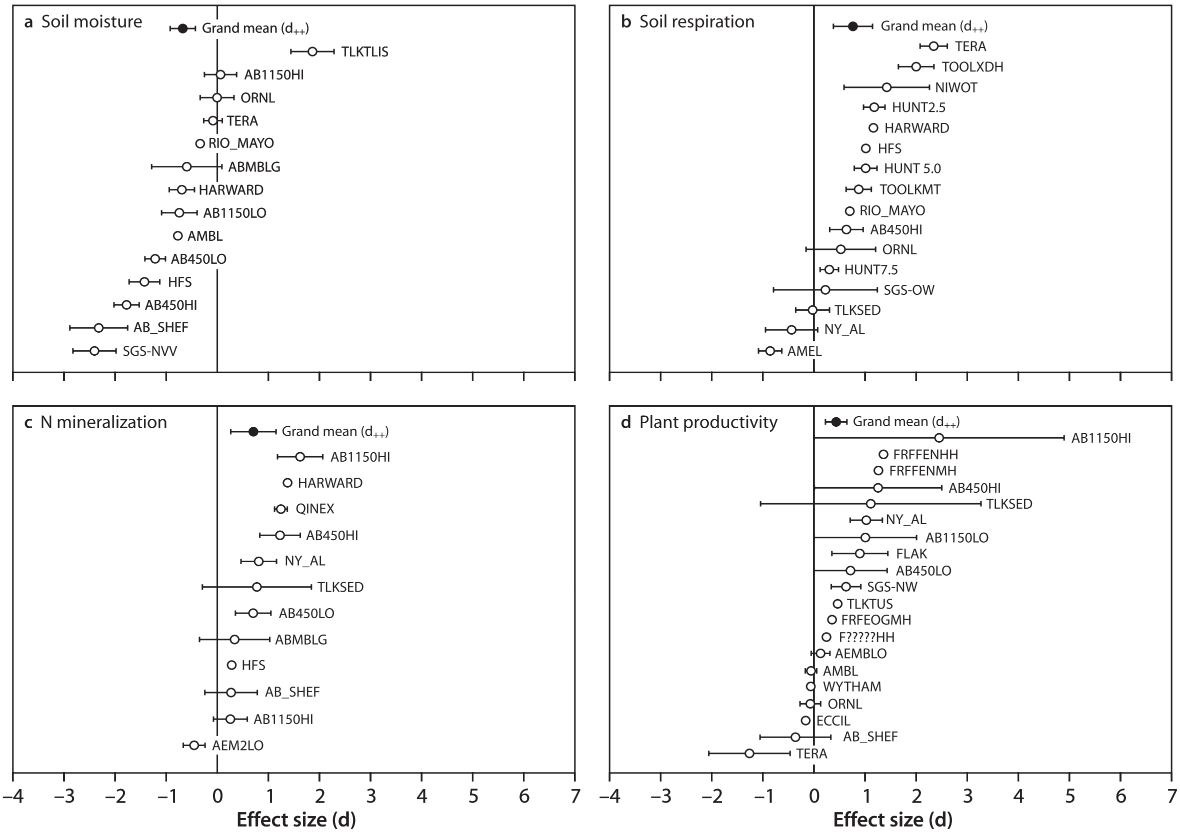

Fig. 3.1. Mean effect size, *d*, and 95% confidence intervals for different experimental sites used in a meta-analysis of responses to ecosystem warming. Measures of response are soil moisture, N mineralization, soil respiration, and plant productivity. If the 95% confidence interval of the grand mean does not include $d = 0$, the effect is considered statistically significant. The key to the different sites and a full analysis of the data are presented in Rustad et al. (2001) (reprinted with permission from Fig. 2 in Rustad et al. 2001)

The stimulation of plant productivity may also be a direct effect of warming on rates of photosynthesis (Lewis et al. 2001) or a warming-induced extension of the growing season (Dunne et al. 2002). However, the absence of strong relationships between the magnitude of the effect size of warming on the soil respiration, O horizon net mineralization, and aboveground plant productivity and the various geographic, climatic, and environmental variables considered in this analysis underscores the need to better understand the relative importance of specific factors (such as temperature, moisture, site quality, vegetation type, successional status, land-use history, etc.) at different spatial and temporal scales.

3.2.2 The ITEX Synthesis

Arft et al. (2000) also used meta-analysis to examine the response of plant phenology, growth, and reproduction to 1–4 years of experimental warming at 13 circumpolar sites associated with the International Tundra Experiment (ITEX). ITEX is a collaborative, multi-site experiment using a common open-top chamber experimental design to evaluate variability in species response to warming in tundra ecosystems. Results showed that (1) key phenological events including leaf bud burst, flowering, and seed dispersal generally occurred earlier in warmed plots compared to control plots throughout the four years of the study; (2) plant productivity was greater in the warmed plots than the control plots only during the first 2–3 years of the experiments (probably due to a depletion of belowground resources); (3) reproductive effort and success increased in later years, particularly in year 4 (probably due to the fact that flower buds are typically formed from one to several seasons before flowering); (4) the vegetative response to warming differed among plant life forms, with the response being generally greater in herbaceous than in woody species; (5) warmer, low arctic sites showed the strongest growth response to warming, and (6) colder, high arctic sites showed the strongest reproductive response to warming. Overall, the responses to warming observed at the ITEX study sites were consistent with those observed in the GCTE-NEWS study sites, and the two syntheses reinforce the observation that although terrestrial ecosystem processes are very sensitive to warming, the magnitude and even direction of response can be highly variable in time and space.

3.2.3 The Harvard Forest Soil Warming Experiment

Results from the aforementioned syntheses and individual warming experiments have greatly increased our understanding of the short-term responses of terrestrial ecosystems and their components to experimental warming. Nevertheless, concern exists that the majority of the existing or completed ecosystem warming experiments are of relatively short duration (i.e., <10 years) and that the initial reported responses may differ in magnitude and even direction compared to longer-term responses, thereby invalidating our ability to extrapolate short-term results to infer longer-term responses. An example of such a shift in response patterns over time is provided by the Harvard Forest soil warming experiment. Peterjohn et al. (1994) initially reported an approximately 40% increase in soil respiration during the first 6 months of the experiment. However, the magnitude of this initial 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 from rates in the control plots, probably due to depletion over time of temperature-sensitive, labile soil C (Fig. 3.2; Melillo et al. 2002). Net nitrogen mineralization rates, however, remained elevated for the duration of the experiment, resulting in a cumulative release of 41 g N m^{-2}. Assuming that 12.7% of this added N would be taken up by woody tissue (based on results from an associated long-term nitrogen fertilization experiment) and that C/N ratios of woody tissue are ~300/1, then warming-induced nitrogen mineralization could have resulted in a sequestration of ~1 560 g C m^{-2} during the course of the experiment, thereby off-setting the estimated 944 g m^{-2} of labile soil C lost from the upper 60 cm of the soil profile. Results from this study underscore the needs for (1) long-term (i.e., >10 year) studies to evaluate changes in response patterns over time, and (2) understanding both direct and indirect effects of warming on ecosystem processes.

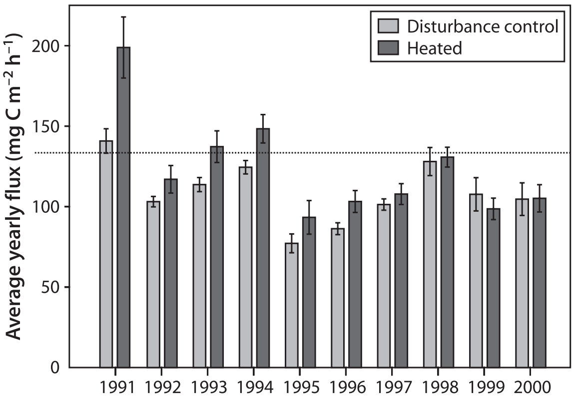

Fig. 3.2. Average yearly fluxes of CO_2 from the heated and disturbance control plots of the Harvard Forest soil warming experiment. Electrical resistance heating cables were buried 20 cm apart at 10 cm depth in the 6 × 6 m plots, and average soil temperature in the heated plots was maintained at 5 °C above ambient. Measurements were made from April through November for the period from 1991 through 2000. *Error bars* represent the standard error of the mean ($n = 6$ plots) between plots of the same treatment (reprinted with permission from Melillo et al. 2002)

An additional consideration should be how the results would have differed in the presence of an elevated atmospheric CO_2 concentration, given that the warming scenario being simulated in this experiment will in reality be associated with a significantly CO_2-enriched atmosphere. CO_2 enrichment of deciduous forests can significantly enhance the flux of C below ground (Norby et al. 2004) and soil respiration (King et al. 2004). Pendall et al. (2004) speculated that the effects of elevated CO_2 and warming on C substrate availability would moderate each other. In the Harvard Forest soil warming experiment the depletion of labile soil C and diminution of the soil respiration response (Melillo et al. 2002) might well not have occurred under a more realistic scenario combining warming and elevated CO_2.

3.3 Temperature and CO_2 Interactions in Trees: the TACIT Experiment

As discussed above, the climatic warming that is predicted for the future will be associated with increased atmospheric CO_2 concentrations, and there are strong reasons to suggest that CO_2 will alter the response of plants to temperature. The response of trees to a warmer, CO_2-enriched atmosphere is an important component of integrated analyses of forest response to global change and, therefore, of analyses of the feedbacks between the terrestrial biosphere, the global carbon cycle, and the climate system. Hence, it is important to understand not just the separate effects of elevated CO_2 and warming, but their combined effects and interactions as well.

3.3.1 Experimental Design

A 4-year experiment on temperature and CO_2 interactions in trees (TACIT) was designed to describe the effects of elevated CO_2 and temperature on ecosystem-level processes that control or influence C sequestration in ecosystems and to test specific hypotheses about the differential response of related species in relationship to their geographic ranges and ecological characteristics. TACIT explored the responses to a 4 °C increase in air temperature and a 300 ppm increase in CO_2 concentration in young *Acer rubrum* and *A. saccharum* trees growing in open-top chambers.

The experimental trees were grown in small stands for four growing seasons in open-top field chambers on the Oak Ridge National Environmental Research Park in Roane County, Tennessee (35°54' N; 84°20' W). Twelve

3-meter diameter chambers were modified to control air temperature to be the same as ambient air or to maintain a constant 4 °C elevation in air temperature (Norby et al. 1997). The temperature treatments were combined with ambient or elevated (+300 ppm) CO_2 concentrations. The temperature treatments were maintained throughout the year, but the CO_2 treatments were suspended during the winter (November–March) when the trees were leafless. The four treatments, comprising a 2 × 2 factorial arrangement of the two levels of temperature and CO_2 concentration, were replicated three times in a randomized complete block design. One-year-old seedlings were planted into the soil within the chambers in spring, 1994, and additional seedlings were planted in spring, 1995, for a total of 10 plants per species per chamber. The trees were harvested in September, 1997, ending the experiment. More details about the research site, chamber operation, and environmental conditions were provided by Norby et al. (1997, 2000).

3.3.2 Growth Responses

When the trees were harvested after four growing seasons (3.5 years) in the different combinations of CO_2 and temperature, they were in dense stands 4 m tall and with a leaf area index between 5 and 7 (Fig. 3.3). Elevated CO_2 enhanced growth: stem dry mass was increased by CO_2 enrichment by 34% in ambient temperature and 88% in elevated temperature. Warming, however, retarded growth by 35% in ambient CO_2 but only 9% in elevated CO_2 (Fig. 3.4). The main effects of CO_2 and temperature were statistically significant ($P = 0.001$ and $P = 0.025$, respectively), but the interaction between CO_2 and temperature was not ($P = 0.198$) (Norby and Luo 2004). Fine root biomass at the end of the experiment showed a similar pattern: a 60% reduction caused by the warming treatment in ambient CO_2 and a 27% reduction in elevated CO_2, but the CO_2–temperature interaction was not statistically significant (Wan et al. 2004).

These biomass values at the end of the experiment mask a great deal of complexity. The final harvest data are the net result of both positive and negative effects that changed through time. Although elevated temperature suppressed instantaneous rates of photosynthesis (Gunderson et al. 2000), it also lengthened the growing season by 2–3 weeks (Norby et al. 2003). Relative growth rates were depressed in elevated temperature only during the second year of treatment when a severe hot period caused heat stress, but since the trees were undergoing exponential growth during the course of the experiment, this negative effect on dry matter accumulation during the stress period had a continuing effect on absolute growth rate for the remainder of the experiment despite a recovery in relative growth rate. Similarly, observations of fine root production and mortality during the third year of treatment did not predict fine root biomass at the final harvest. Both production and mortality were significantly increased by CO_2 enrichment and warming. The discrepancy between these observations of root dynamics and the harvest data are probably associated with drought-induced differential responses of productivity and mortality during the latter half of the growing season (Wan et al. 2004).

Fig. 3.3. *Acer saccharum* and *A. rubrum* trees in an open-top chamber at the conclusion of the TACIT experiment. The plastic panels of the chambers and lower portions of the shade cloth, which were present throughout the four growing seasons of the experiment, have been removed to facilitate harvesting of the trees

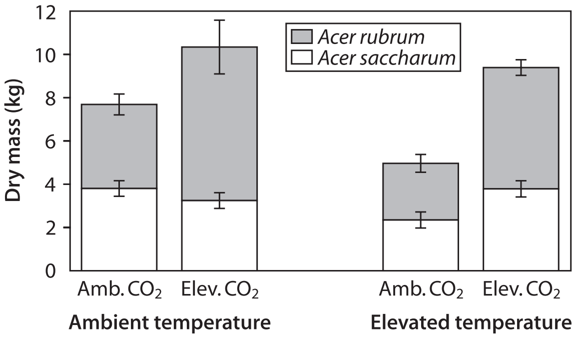

Fig. 3.4. Aboveground woody dry mass of *Acer saccharum* and *A. rubrum* trees after exposure for four growing seasons in open-top chambers with ambient or elevated CO_2 (+300 ppm) in combination with ambient or elevated (+4 °C) air temperature. The data are presented as biomass per chamber and are the means of three chambers per treatment ±SE (reprinted from Norby and Luo 2004 with the permission of New Phytologist Trust)

3.3.3 Higher-Order Responses

Higher-order responses also were addressed in this experiment. A premise of the experiment was that the two species would respond differently based on their presumed adaptations to temperature. The experimental site was close to the southern limit of the range of *A. saccharum*, whereas the range of *A. rubrum* extends much farther to the south. Although temperature effects were similar in the two species, *A. rubrum* was stimulated by CO_2 enrichment much more than *A. saccharum*. This observation is consistent with the premise that when temperatures are close to optimal, the relative biomass increase caused by increases in CO_2 enrichment is greater than when temperatures are sub- or supra-optimal (Poorter and Pérez-Soba 2001). The species also differed with regard to biotic interactions. Elevated CO_2 reduced growth of gypsy moth larvae feeding on *A. rubrum*, but not *A. saccharum* leaves (Williams et al. 2000). Warming shortened insect development but had no effect on pupal weight (Williams et al. 2003).

3.3.4 TACIT Summary

This relatively simple experiment illustrated many of the issues that must be considered when addressing multi-factor interactions, as well as many of the difficulties in taking up those issues in experimental studies (Norby and Luo 2004). Temperature affects many processes in plants and the net effect of a warmer atmosphere on tree growth will be difficult to predict when both negative and positive responses can occur together. Stochastic events, such as a late-spring frost that altered normal phenology (Norby et al. 2003) and the period of especially hot and dry weather that altered the growth trajectory, can play an important role in the integrated response. The duration of the experiment is an important consideration in this regard: the influence of a single unusual event should decrease with time, but the likelihood of an event occurring at all should increase. The specific combination of factors that influenced final dry mass in this experiment are not likely to be reproduced exactly in another experiment or in the real world, making it more difficult to extrapolate these results directly to an ecosystem scale. Different species – even closely related ones – may respond differently to global change factors, although some of those differences may be predictable based on the species' characteristics. In this experiment the effects of CO_2 and warming were additive; hence, their combined effects were predictable from knowledge of their single-factor effects. However, as will be apparent in the next section, unexpected interactions can also occur.

3.4 More Than Two Factors: the Jasper Ridge Global Change Experiment

Few ecosystem experiments have examined responses to more than two global change factors. Results from a four-factor study, the Jasper Ridge Global Change Experiment (JRGCE), demonstrate the need for this approach if we are to develop a comprehensive understanding of community and ecosystem responses to global environmental changes.

3.4.1 Experimental Design

Starting in 1998, the JRGCE exposed grassland plots in the San Francisco Bay Area (California, USA) to a factorial combination of warming, elevated CO_2, increased precipitation, and increased nitrogen deposition (Fig. 3.5). Circular grassland plots (2 m diameter) experienced either ambient conditions, ~1 °C of warming from infrared heat lamps, CO_2 enhancement of ~300 ppm via a FACE system, or warming and CO_2 enrichment together. Each plot was divided into four quadrants, which received am-

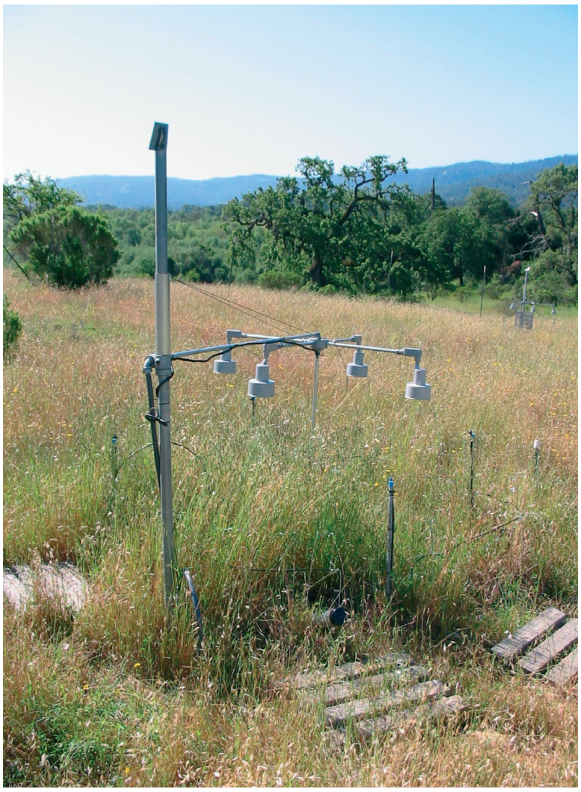

Fig. 3.5. An experimental plot in the Jasper Ridge Global Change Experiment. Four infrared heat lamps suspended over the 2-m diameter plot increase the canopy temperature by ~1 °C. Pure CO_2 is released from a circle of tubing surrounding the plot, enriching the CO_2 concentration in the air by about 300 ppm. Subplots comprise different combinations of precipitation and N deposition

bient or increased precipitation (+50%, including a 20-day extension of the growing season) combined with ambient or increased nitrogen deposition (+7 g N $m^{-2} yr^{-1}$ as $CaNO_3$). Fiberglass barriers below the soil surface prevented roots and resources from escaping the quadrants. Because annual grasses and forbs dominate the grassland, species composition and standing biomass can respond quickly to the step changes in environmental variables. In addition, evolutionary responses to the treatments can occur within the course of a relatively short-term experiment.

3.4.2 Net Primary Productivity

Shaw et al. (2002) described responses of grassland net primary productivity (NPP) to the global change treatments after three years of exposure. At this time, warming, precipitation, and nitrogen all tended to stimulate NPP. The authors did not present a direct test of whether treatment responses were additive, but qualitatively described the interactions. NPP responses to some treatment combinations appeared approximately additive (warming and N deposition), while others were intermediate between treatments (warming and precipitation). The response to elevated CO_2 was even more complex. CO_2 enrichment increased aboveground biomass when all other factors were at ambient levels (paired *t*-test, $P = 0.0003$), but significantly suppressed NPP responses to other global change factors (paired *t*-test, $P = 0.048$). Much of this suppression occurred in the root biomass, which declined by 22% in response to CO_2 across all treatments.

Although this strong interaction appeared in the 2001 season, interactions involving CO_2 or warming were less common in other years. Dukes et al. (2005) found that, over the first five years of the experiment, the only consistent interaction occurred between increased precipitation and N deposition, with each treatment making the response to the other more positive in annual-dominated grassland (repeated measures mixed-model ANOVA, precipitation–N interaction, $P < 0.01$). NPP and aboveground biomass increased significantly in response to N deposition in four of the five years (by 21–42%, mixed-model ANOVA, $P < 0.05$). Precipitation tended to increase shoot growth, but decreased root growth, causing a shift in allocation but no net effect on NPP across the five years. Effects of CO_2 and warming were not significant, with warming tending to slightly increase NPP on average and CO_2 tending to increase NPP in two years and decrease it in three.

In this Mediterranean-climate system, plants germinate in October or November and senesce during May and June, after which they no longer use soil moisture. Zavaleta et al. (2003a) found that warming accelerates this senescence, leaving wetter soils in late spring and early summer. Elevated CO_2 also increased soil moisture during late spring, and the individual effects of warming and CO_2 were approximately additive over the first two years of the experiment (CO_2 effect on volumetric spring soil moisture: 1.6 ±1.0%; warming effect: 1.1 ±0.95%; combined warming and CO_2 effect: 2.7 ±1.0%).

3.4.3 Community Composition

Zavaleta et al. (2003b) found that some of these global changes affected the species richness of the grassland over the first three years of the JRGCE. Elevated CO_2 and nitrogen deposition both decreased species richness by reducing the number of forb species present in the plots, while more forb species were present in the plots receiving increased precipitation. In this case, treatment effects on species richness were almost perfectly additive, as indicated by both a lack of significant interactions in the ANCOVA model and by a "striking" correspondence between observed responses to treatment combinations and predicted responses based on the effects of single factors.

Global change treatments also affected the production and relative abundance of grasses and forbs (Zavaleta et al. 2003c). Although individual species responses were weak, responses of these groups could be more clearly characterized. Few responses were consistently strong across the first three years of the experiment, but a split-plot ANCOVA model identified some general patterns. Nitrogen deposition favored grasses at the expense of forbs. Forbs benefited from increased precipitation and from warming, but grass production was unresponsive to these treatments. Finally, elevated CO_2 had little effect on production of either functional group. Interactions among the treatment effects were even less consistent than the main effects. The treatment combination that featured warming, elevated CO_2, and increased precipitation caused the greatest change in relative abundance of the functional groups, a 50% increase in forbs.

Because these functional groups differ in their chemical makeup, shifts in community composition can affect litter quality. Henry et al. (2005) found that global change treatments affected lignin and nitrogen concentrations in litter, but that some of these direct effects were counteracted by the shifts in community composition. Direct effects included CO_2-induced increases in lignin (which were attenuated by warming in grasses and increased precipitation in forbs) and increases in litter nitrogen concentration in response to nitrogen deposition. This latter effect was dampened by increased precipitation. Although litter quality responded predictably to the global change treatments, the effects on litter quality did not markedly affect decomposition rates over the short term.

Litter decomposition and many other ecosystem functions could be altered by shifts in microbial community structure. Horz et al. (2004) observed shifts in the abundance and community composition of ammonia-oxidizing bacteria in response to some global change treatments. In this case, all responses depended on the level of other factors. Nitrogen deposition affected community structure, but only at ambient temperature and precipitation, and elevated CO_2 affected bacterial abundance, but only under increased precipitation.

3.4.4 JRGCE Summary

Thus far, results from the JRGCE suggest that treatment responses of production, community composition, and other measured variables are not tightly linked. Supplemental nitrate deposition has affected more of these variables than other factors, consistently increasing NPP, decreasing species richness by favoring grasses over forbs, and, under certain background conditions, influencing litter quality and bacterial community structure. The modest warming treatment has had few effects, most notably an acceleration of phenology that led to a small and unexpected increase in spring soil moisture. The precipitation treatment caused shifts in biomass allocation (from belowground to aboveground) and plant species composition (increasing forb diversity and abundance), and had interactive effects on litter quality and bacterial communities. Elevated CO_2 has had small, mostly nonsignificant effects on biomass production (with exceptions in 2001), and positive effects on spring soil moisture. Responses of plant and microbial community composition to elevated CO_2 have mostly been subtle, and CO_2-driven increases in litter lignin concentration were sometimes ameliorated by other treatments. Overall, the complexity of responses in the JRGCE confirms that multifactor, multi-year experiments are critical to forecasting global change responses, and highlights the challenge of determining the mechanisms behind such responses.

3.5 Modeling Temperature, CO_2 and N Interactions in Trees and Grass

The complexity of the ecosystem- and community-level responses to multiple changes in environmental conditions as observed in the JRGCE increases the need for a modeling framework to assist in drawing useful generalizations that are applicable to different ecosystems and over longer time frames. Models are needed to explore questions that cannot be addressed in experiments. Whereas climate-change experiments impose step changes in CO_2 concentration and temperature over periods of several years, models can be used to simulate either a step change or gradual change on the longer (decadal) timescales that are of primary relevance to policy makers.

In one modeling study, six dynamic global vegetation models were used to simulate future global terrestrial net primary production (NPP) and net ecosystem production (NEP) (Cramer et al. 2001). Under gradual CO_2 change alone NPP was predicted to increase by 60% on average by 2100, and NEP was predicted to increase to an average value of approximately 6 Pg C yr^{-1} by the end of the century, with little evidence of terrestrial carbon-sink saturation. Under rising CO_2 plus climate change, the models still predicted a sustained carbon sink, but with smaller increases in NPP (+50%) and NEP. There were, however, wide discrepancies among the six models. Explaining model discrepancies was difficult because of the models' complexity and the global scale of simulations with dynamic vegetation distributions and complicated climate-change scenarios. One factor contributing to discrepancies was that only two of the six models included soil nutrient feedbacks.

It is more straightforward to interpret results from models of individual stands that use simplified climate-change scenarios and simulate ecosystem processes, but not vegetation dynamics. Two ecosystem models that have been used in stand-scale simulations of experimental sites are DAYCENT (Del Grosso et al. 2001; Kelly et al. 2000; Parton et al. 1998) and G'DAY (Comins and McMurtrie 1993; Medlyn et al. 2000). The responses of NPP, NEP, and C storage to gradually increasing CO_2, temperature, and nitrogen input have been simulated for grasslands and forests.

3.5.1 Global Change Simulations for a California Annual Grassland

The Jasper Ridge experiment provided a unique opportunity to compare model results with field data for a complex situation with multiple global change drivers. To have confidence in model projections that are unconstrained by data, it is important that the models can adequately recreate observed responses. Here, we describe how the DAYCENT model was used to simulate responses to increased atmospheric CO_2 concentration, N deposition temperature and precipitation for this site and compare the simulations with data collected during 1999–2002.

3.5.1.1 *DAYCENT Model Description*

DAYCENT is the daily time-step version of the CENTURY model (Parton et al. 1994). DAYCENT simulates exchanges of carbon, nutrients, and trace gases among the atmosphere, soil, and vegetation (Fig. 3.6). The model is of intermediate complexity and requires relatively simple inputs. Site-specific model input data include climate (daily maximum and minimum temperature and precipitation), soil texture and physical properties, vegetation

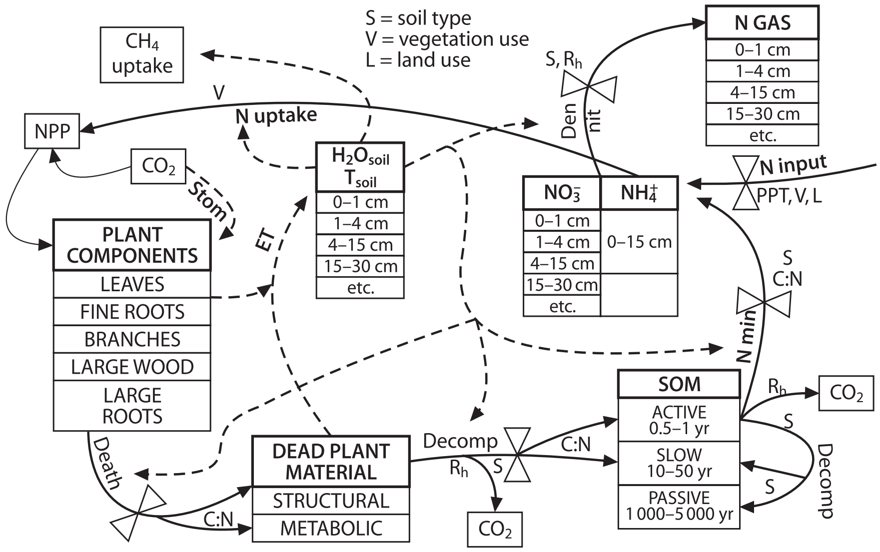

Fig. 3.6.
Pools and fluxes simulated in the DAYCENT model (Parton et al. 1998; Kelly et al. 2000; Del Grosso et al. 2001)

cover, and land management. Maximum plant growth rate is a function of vegetation type and solar radiation, which is calculated from latitude and day of year. Maximum NPP is down-regulated to account for nutrient, water, and temperature limitation. C allocation patterns, C/N ratios of biomass components, and senescence of plant components are functions of plant type, phenology and nutrient and water stress. Decomposition of dead plant material and SOM are driven by the amount of material and C/N ratios of different pools, as well as water and temperature limitation. Decomposition results in N mineralization, which makes N available for plant uptake, NO_3 leaching, and the processes (nitrification and denitrification) that result in N gas losses. DAYCENT includes a fairly complex soil water and temperature submodel (Parton et al. 1998) and also simulates CH_4 uptake in non-saturated soils. The effects of increased CO_2 concentration are implemented in three ways in DAYCENT. Maximum potential NPP rates can increase, C/N of above ground biomass can increase, and transpiration demand can decrease.

3.5.1.2 *DAYCENT Simulations and Results*

DAYCENT was used to investigate the effects of changes in precipitation, temperature, CO_2 concentration, and N deposition on plant growth and soil water content at the Jasper Ridge annual grassland. Model drivers (CO_2 concentration, precipitation, air temperature, and N inputs) were varied to mimic the experiments conducted at this site. Effects of elevated CO_2 were operationally defined for this site as a 10% increase in maximum NPP and C/N of leaf biomass, and a 50% decrease in transpiration demand. To better match observed NPP data, parameters had to be adjusted to decrease late-season belowground C allocation.

These effects capture the major biogeochemical interactions between CO_2, rainfall, heat and N fertilization. The experimental analysis and the model simulations indicate the role that water use and nitrogen availability have in affecting the net response to global change factors. Comparisons between mean simulated and observed changes in ANPP showed that the model did well for the single factor treatments but not for the interactions (Fig. 3.7a). The data showed a larger positive response for CO_2 alone than when CO_2 interacted with the other factors, whereas the model showed an additive response between CO_2 and the other factors.

Both simulated and observed aboveground productivity at the Jasper Ridge study was more dynamic relative to belowground productivity. The observed and simulated interannual and treatment variability tended to be much higher in the aboveground biomass. However, model results for mean BNPP did not agree with the data (Fig. 3.7b). In contrast to the data that showed a negative BNPP response for some treatments, DAYCENT showed a positive BNPP effect for all of the treatments because the model assumes that increased ANPP leads to higher nutrient and water demand so BNPP is enhanced. This indicates that ecosystem responses to global change are sensitive to environmental conditions modifying the belowground allocation, and the model needs improvement in how it represents allocation. Variability in observed data also contributes to the difficulty in modeling this system. Figure 3.7c shows the 4 years of data points that were averaged to obtain the bars in Fig. 3.7a along with the standard errors of the observed data. Both the spatial and temporal variability in the observed data are large and the model shows substantial error for some treatments during some years.

Simulation results indicate that environmental conditions and allocation patterns interact and have indirect effects on N mineralization and N-use efficiency,

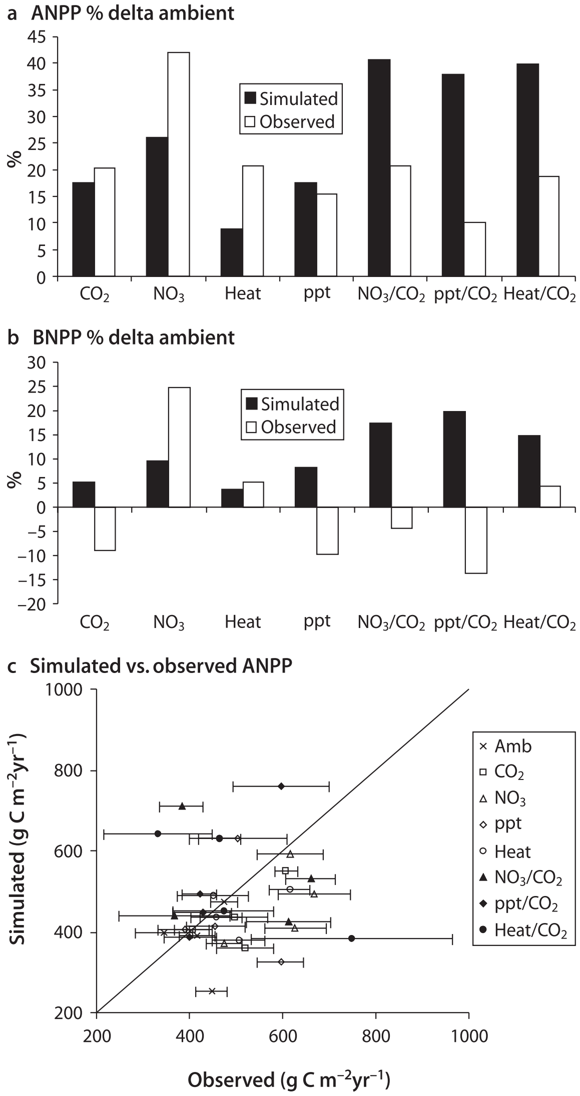

Fig. 3.7. Simulations and measurements of the relative effect of elevated CO_2, rainfall, heat and N fertilization on mean **a** aboveground and **b** belowground net primary productivity (ANPP and BNPP) during 4 years of the Jasper Ridge Global Change Experiment. The relative effect was calculated as (treatment – ambient) / ambient. **c** Simulated vs. observed annual ANPP, standard errors of observations, and the 1–1 line

which alter root-to-shoot allocation of new production. This effect has both short-term and long-term impacts on carbon biogeochemistry of these systems. The long-term storage of carbon will depend on the amount structural carbon formed, and changes in N-use efficiency may favor formation of less labile carbon materials and promote sequestration of carbon.

3.5.2 Comparing Forest and Grassland with G'DAY

DAYCENT and G'DAY were used to simulate responses of NPP, NEP, and C storage to gradually increasing CO_2, temperature, and nitrogen input for a short-grass steppe and a boreal forest site (Pepper et al. 2005). Here we will discuss NPP and NEP results from the G'DAY model. G'DAY (Comins and McMurtrie 1993; Medlyn et al. 2000) is a mechanistic model of C and N cycling and water balance in plant ecosystems. The model simulates plant physiological and soil processes: canopy photosynthesis, respiration, C and N allocation within the plant, and soil N feedbacks associated with decomposition of litter and soil organic matter. Processes included in the water-balance model are canopy interception and soil-surface evaporative water loss, drainage, runoff and transpiration modified by the CO_2 effect on water-use efficiency.

The sites considered are a short-grass steppe in Colorado, USA (40°8' N, 104°45' W; 1 625 m a.s.l.) where the perennial C_4-dominant grassland is strongly water- and N-limited (Uresk et al. 1996), receiving 320 mm mean annual precipitation with a 4-month growing season. The forest plantation site is located at Flakaliden, Sweden (64°7' N, 19°27' E; 310 m a.s.l.) where stands of Norway spruce, planted in 1963, are N-limited but not water-limited (Bergh et al. 1999), receiving approx. 600 mm annual precipitation with a 4-month growing season. Both ecosystems are the subject of major long-term (>8 yr) climate-change experiments with CO_2-enrichment treatments at both sites and soil-warming at Flakaliden.

G'DAY was parameterized for each site and then simulated to equilibrium under current climate. Treatments simulated at each site were: gradually (linearly) increasing $[CO_2]$ from 350 to 700 ppm over 100 years (Treatment C); gradually (linearly) increasing daily maximum and minimum air temperatures and soil temperature by 1, 3, and 2 °C, respectively, over 100 years (T), and nitrogen addition that increases linearly from 0 to 1 g m^{-2} yr^{-1} over the century. The four treatments shown in Fig. 3.8 are denoted C, T, CT (rising CO_2 and temperature), and CTN (rising CO_2, temperature and N input). The CT treatment approximated the IS92a IPCC scenario (Houghton et al. 1995). Key results from multi-factor simulations are summarized below.

3.5.2.1 *Simulations with Rising Temperature and CO_2*

The NPP-response to treatment CT is similar in percentage terms at the grassland and forest, but comprises a large CO_2 effect and small negative T-effect at the water-limited grassland, compared with a small CO_2 effect and large temperature effect at the N-limited forest (Fig. 3.8). The explanation for these differences between grassland and forest is that the CO_2-effect is amplified under water limitation but diminished under N limitation, whereas warming enhances water stress at the grassland but stimulates N availability at the forest. NPP-responses to

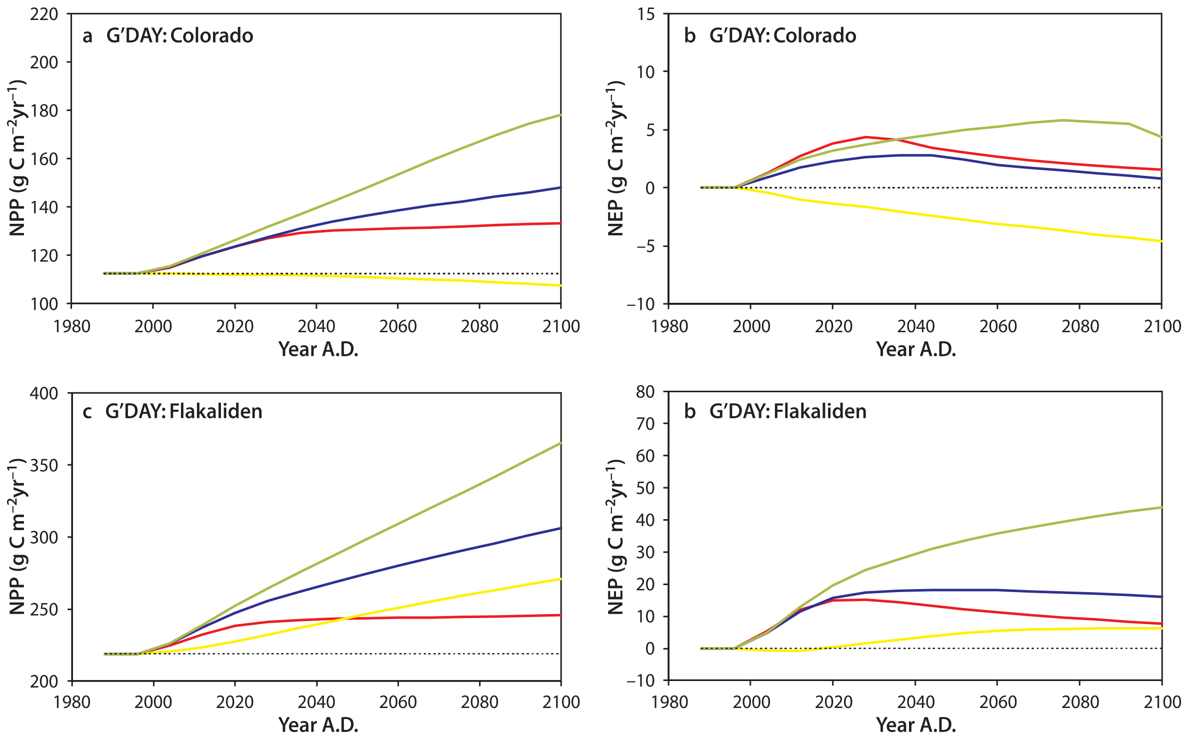

Fig. 3.8. Simulated **a** NPP and **b** NEP for Colorado short-grass steppe and **c** NPP and **d** NEP for Flakaliden boreal forest under single- and multi-factor treatments, where the *dotted line* denotes current equilibrium, *C* (*red*) denotes gradually increasing CO_2 concentration, *T* (*yellow*) denotes warming, *CT* (*blue*) the combination of *C* and *T*, and *CTN* (*green*) denotes the combination of *C* and *T* and increasing N inputs

CO_2 and T are approximately additive for forest, but not for grassland. The modeled CO_2–T interaction is strong at the grassland because of a synergistic effect whereby elevated CO_2 alleviates water-stress that is the major limitation on the grassland's temperature response.

Simulations of NEP under rising CO_2 show evidence of C-sink saturation (NEP declining towards zero) at both sites, probably because of developing N limitation. Under rising CO_2 and temperature, however, the forest shows little evidence of C-sink saturation because warming causes a gradual N transfer from soil with low C/N ratio to wood with high C/N ratio, which promotes C storage.

3.5.2.2 *Simulations with Increased N Input*

CTN simulations for both grassland and forest (Fig. 3.8) show that a relatively modest cumulative N fertilization (50 g m^{-2} over 100 years) is sufficient to sustain large NPP and NEP responses that are comparable in percentage terms to results of Cramer et al. (2001). This modest N addition overcomes the negative soil-N feedback that otherwise occurs at high CO_2 when increased litter input to the soil leads to increased N immobilization and reduced plant N availability. The CTN simulations show no evidence of C-sink saturation for at least 80 years (Fig. 3.8).

3.6 Conclusions

It is undeniable that ecosystems of the future will be subjected to multiple atmospheric and climatic changes. Research planning documents recognize this certainty and strongly promote the understanding of multi-factor interactions as a research imperative for the future (Committee on Global Change Research 1999). The research that we have highlighted here illustrates many of the challenges of addressing this imperative, but it also shows the importance of attempting to meet those challenges.

The net response to increased CO_2 concentration, warming, altered precipitation, N deposition, and other changes may be a simple additive effect of the separate influences, but experimental results also demonstrate the possibility of complex interactions. Single-factor experiments, such as those in the GCTE Elevated CO_2 network, are highly valuable for advancing understanding of the primary responses and how they are modified by other environmental factors. However, such experiments cannot be interpreted as providing predictions for ecosystem responses in a future climate. Single-factor ecosystem warming experiments are especially problematic, given the temporal and spatial variability of air temperature and the greater uncertainty (compared to CO_2) in future trajectories. Realistic warming treatments also are more difficult to carry out in experiments, especially in forests, and it has been harder to attain an integrated, ecosystem-scale understanding of all of the factors that will influence how ecosystems will respond to a warmer climate. Coupling the uncertain responses to warming to the simultaneous changes in other global change factors would seem to be a daunting task.

The experiments and modeling efforts highlighted in this chapter do not lead to a clear prediction of how ecosystems will be affected by various combinations of global change factors. They do, however, support several general principles about responses to climatic warming and multi-factor interactions:

1. Warming alone affects multiple pools and processes with different rate constants. Hence, responses are likely to change over time, as occurred in the response of soil respiration to soil warming at the Harvard Forest.
2. Whole-ecosystem warming experiments are necessary to address the complex interactions between belowground and aboveground responses. Without a whole-ecosystem perspective, critical hypotheses such as the linkage between warming effects on N availability and aboveground production cannot be evaluated.
3. Stochastic events can strongly alter the trajectory of response to warming. In the TACIT experiment a severe summer heat spell led to a loss in productivity after 4 years despite generally positive effects of warming. Short-term experiments may over emphasize the importance of such events while under representing the possibility of their occurrence.
4. Elevated CO_2 can sometimes ameliorate deleterious effects of warming, and since higher CO_2 concentrations are certain to be associated with future warming scenarios, it is imperative that their combined effects be considered when interpreting data. However, we cannot assume that the responses to elevated CO_2 always are positive, as evidenced by the Jasper Ridge experiment.
5. The responses to combinations of factors often equal the simple additive effects of the individual factors. That being the case, single-factor experiments continue to be very informative and can be the basis for model simulations. However, complex interactions do occur, and they may or may not be predictable. Multi-factor experiments are important for reminding us of this complexity.
6. Ecosystem models that incorporate our best understanding of the modes of actions of the individual factors will also capture many of the major biogeochemical interactions. Discrepancies between experimental data and model projections, such as for belowground productivity in the Jasper Ridge experiment, indicate areas where model improvement is needed. The influence of stochastic events and unexplained year-to-year variation in the nature of interactions suggest that simulations should be expected only to provide an envelope of possible future responses.
7. The long-term net effect of elevated CO_2 and temperature may be similar in different ecosystems, but the relative importance of the two global-change factors varies with site factors (e.g., water and N availability). Relatively modest N additions can overcome the soil-N feedback that can otherwise lead to C-sink saturation and loss of continued stimulation of NEP. These model results demonstrate why experiments must be conducted in a range of ecosystems under different conditions.

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