

Terrestrial Carbon–Cycle Feedback to Climate Warming

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Key Words

global change, net ecosystem production, photosynthesis,
respiration, soil carbon pools, temperature sensitivity

Abstract

The coupled carbon-climate models reported in the literature all demonstrate a positive feedback between terrestrial carbon cycles and climate warming. A primary mechanism underlying the modeled positive feedback is the kinetic sensitivity of photosynthesis and respiration to temperature. Field experiments, however, suggest much richer mechanisms driving ecosystem responses to climate warming, including extended growing seasons, enhanced nutrient availability, shifted species composition, and altered ecosystem-water dynamics. The diverse mechanisms likely define more possibilities of carbon-climate feedbacks than projected by the kinetics-based models. Nonetheless, experimental results are so variable that we have not generated the necessary insights on ecosystem responses to effectively improve global models. To constrain model projections of carbon-climate feedbacks, we need more empirical data from whole-ecosystem warming experiments across a wide range of biomes, particularly in tropic regions, and closer interactions between models and experiments.

1. INTRODUCTION

Human activities, such as fossil-fuel burning and deforestation, have resulted in a gradual increase in the atmospheric CO₂ concentration from 280 ppm volumetrically in pre-industrial time to ~380 ppm at present and potentially to 700 ppm toward the end of the twenty-first century (Intergov. Panel Clim. Change 2007). As a consequence of the buildup of CO₂ and other greenhouse gases in the atmosphere, Earth's surface temperature has increased by 0.74°C since 1850 and is expected to increase by another 1.1°C ~ 6.4°C by the end of this century (Intergov. Panel Clim. Change 2007). Because temperature affects almost all aspects of terrestrial carbon (C) processes, increasing Earth's surface temperature likely enhances ecosystem C fluxes, potentially feeding back to a buildup of atmospheric CO₂ concentration and climate dynamics. Will climate warming trigger terrestrial carbon-cycle feedback that leads to warmer climate? This is a central question in global-change research that urgently needs to be addressed in the coming years.

Terrestrial feedbacks to climate change involve several greenhouse gases (e.g., CO₂, CH₄, N₂O, and O₃) and are modulated by changes in precipitation, land uses, and nitrogen (N) deposition and invasive species (Field et al. 2007). This review does not cover all those aspects; rather it focuses on ecosystem C uptake and release processes in response to changes in Earth's surface temperature. This review will include neither wetlands and/or peatlands, nor the issues involved in destabilization of peat deposits. First, I critically examine mechanisms that have been incorporated to capture temperature feedback within global models. The models are effective tools to evaluate carbon-climate feedbacks. The accuracy of their projections, however, depends on how closely the models represent the real-world processes of C uptake and release. Second, I review experimental evidence to show that the responses of C uptake and release processes to temperature changes are extremely variable. Third, this article illustrates that several mechanisms underlie the variable responses of major C processes to climate warming. Those mechanisms include changes in phenology and the length of growing seasons, species composition, nutrient dynamics, and ecohydrological processes. The last section of this review briefly discusses various approaches to improve the model representation of terrestrial C processes. I conclude that there is an urgent need for more empirical knowledge from experiments and observations that will permit the quantification of temperature sensitivity at the ecosystem scale and fundamentally improve our ability to predict feedbacks of the terrestrial carbon cycle to climate warming.

2. MODELED POSITIVE FEEDBACK

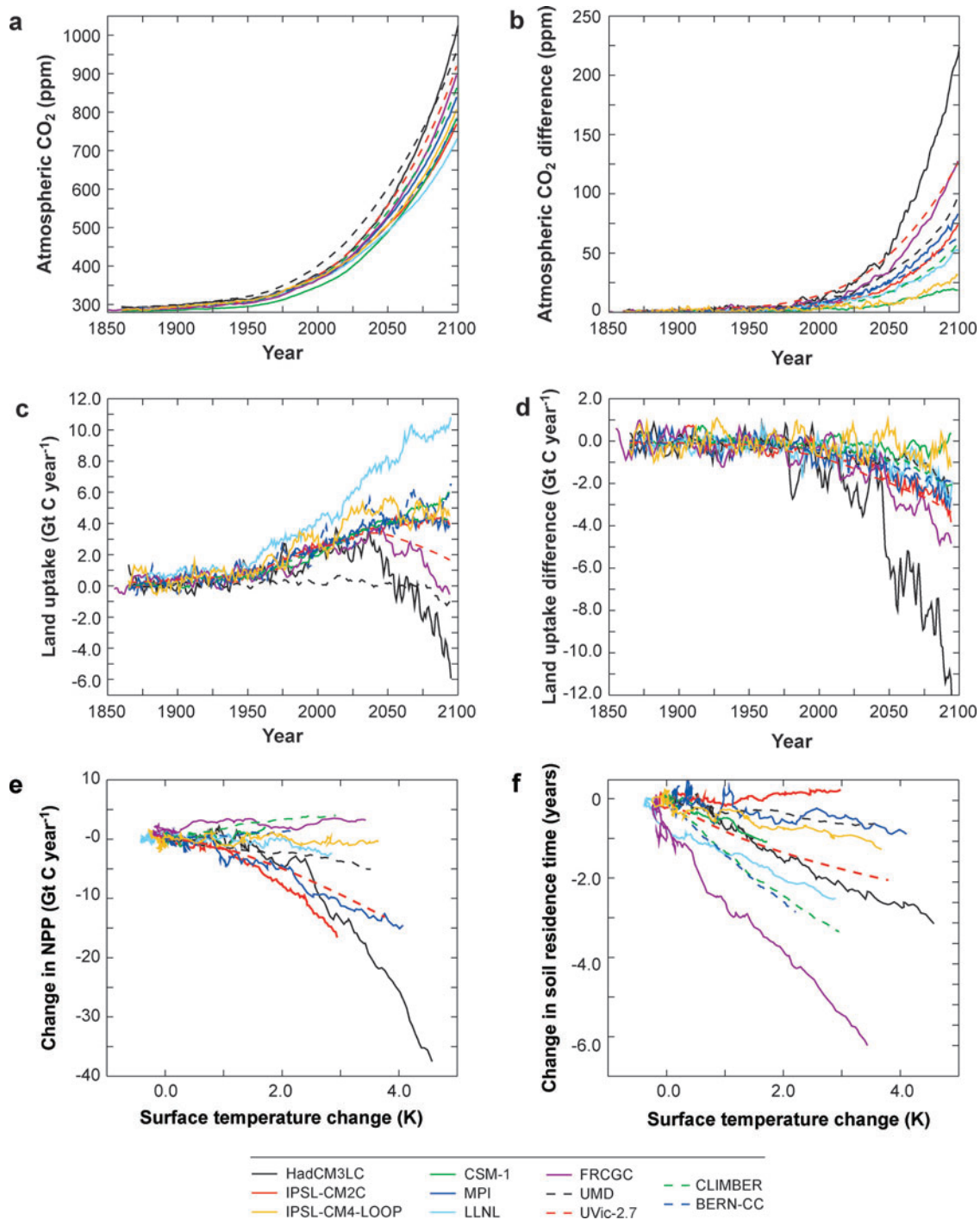
All global models that have sought to couple climate dynamics and carbon cycles have predicted a positive feedback between carbon cycling and climate warming (Friedlingstein et al. 2006). Cox et al. (2000) evaluated this feedback issue first with three simulations. The first simulation examined the effects of rising atmospheric CO₂ concentration on the land C sink. The model prescribed atmospheric CO₂ concentrations according to the Intergovernment Panel for Climate Change 1992 "Business-as-Usual" scenario (IS92a) (Alcamo et al. 1995) and projected that land

ecosystems would sequester nearly 400 Gt (10^{15} g) C owing to CO₂ fertilization in the twenty-first century. The second simulation explored the effects of climate warming on the carbon cycle. Rising atmospheric CO₂ concentration induced climate warming by 5.5°C over Earth's land surface. This warming stimulated C loss, resulting in a net source of 60 Gt C from land ecosystems to the atmosphere over the twenty-first century. The third simulation coupled the climate model with the carbon-cycle model, causing the projected atmospheric CO₂ to be 980 ppm in 2100, 40% higher than the 700 ppm predicted by IS92a. The land ecosystems became a net source of 170 Gt C in the coupled carbon-climate simulation. The coupled carbon-climate model projected the temperature to increase by 8.0°C over land, 2.5°C greater than the climate-model simulation alone.

Friedlingstein et al. (2006) recently examined the climate-carbon feedback using 11 coupled climate change-carbon cycle models with a common protocol. All 11 models unanimously displayed a positive climate warming-carbon cycle feedback (**Figure 1**). By the end of the twenty-first century, the predicted feedback caused additional CO₂ buildup in the atmosphere, from a low of 20 ppm in the Lawrence Livermore National Laboratory climate-carbon model (Thompson et al. 2004) to a high of 200 ppm in the Hadley Center Climate Model coupled with a land-surface model (HadCM3LS). The majority of models projected additional CO₂ buildup between 50 and 100 ppm (**Figure 1a,b**). The additional CO₂ buildup in the atmosphere triggered by the climate-carbon feedback led to an additional climate warming of 0.1°C–1.5°C. All the 11 models except the University of Maryland model (Zeng et al. 2004) exhibited stronger sensitivities to climate warming for land C storage compared with ocean C storage. For example, the HadCM3LS model projected a loss of 177 Gt C per degree Celsius of warming from land ecosystems, whereas other models projected losses of 20–112 Gt C per degree Celsius of warming (**Figure 1c,d**).

Similarly, a variety of terrestrial ecosystem models that are not coupled with climate dynamics have ubiquitously projected the loss of C from land ecosystems in response to climate warming (Berthelot et al. 2005, Cao & Woodward 1998, Cramer et al. 2001, Ito 2005) regardless of the model structure or climate-change scenario. The high degree of uniformity among model projections stems from the similar representation of carbon-climate relationships among models. The primary mechanism incorporated into these uncoupled and coupled carbon-climate models is the kinetic sensitivity of photosynthesis and respiration to temperature. The temperature sensitivity of photosynthesis is primarily described by either empirical equations (Cox 2001) or biochemical processes in the Farquhar model (Cao & Woodward 1998). The temperature-respiration relationship is usually described by exponential or Arrhenius functions (Luo & Zhou 2006). The sensitivity of photosynthesis and respiration influences net primary productivity (NPP) and ecosystem respiration, respectively, and ultimately determines net changes in land ecosystem C storage in response to climate warming.

In an intercomparison study with the 11 coupled carbon-climate models, two models simulated minor increases in NPP, five models showed little change, and four models simulated large decreases in NPP with global-scale climate warming (Friedlingstein et al. 2006) (**Figure 1e**). Variations in modeled responses of NPP can



have substantial effects on the strength of the carbon-climate feedback (Matthews et al. 2005). At regional scales, most models simulated a climate-induced increase of NPP at high latitudes at which warming considerably decreased the duration of snow cover and increased the length of the growing season. In tropical regions, the majority of the models simulated a decrease of NPP, although the degree of decrease varied greatly among models. In a perhaps extreme simulation by HadCM3LS, the excess heating under climate warming induced marked soil drying and dieback of the rainforest in the Amazon basin (Cox et al. 2004), causing dramatically decreased atmospheric CO₂ uptake by vegetation and increased C loss from soil. In fact, HadCM3LS simulated the largest NPP sensitivity to climate warming—a global decrease of 8 Gt C in NPP per degree Celsius of warming.

The other major contribution to the modeled C loss in response to climate warming is the decomposition of soil organic matter. In fact, practically all models assume that the decomposition rate of organic matter increases with temperature. When decomposition rates increase under climate warming, the residence time of C pools decreases because the residence time is an inverse of a specific decomposition rate (Luo et al. 2003). In Friedlingstein et al.'s (2006) intercomparison, all models except one simulated a decrease in soil C residence time (**Figure 1f**), indicating that most models assume that specific respiration rates increase with climate warming. The Frontier Research Center for Global Change model (Ito & Oikawa 2002), for example, simulated a decrease in soil C residence time by approximately 2 years per degree Celsius of warming (**Figure 1f**). Most of the models used a temperature-sensitivity index of Q₁₀—a quotient of change in respiration caused by a change in temperature of 10°C—equaling 2. In contrast, the University of Maryland model has Q₁₀ ranging from 1.1 for the slow soil C pool to 2.2 for the fast turnover soil C pool. Carbon loss under climate change is also regulated by the residence time itself. HadCM3LC, which has one single pool with a residence time of 25 years (Jones et al. 2004), projected a strong ecosystem response to climate warming. The National Center for Atmosphere Research—Climate System Model 1 coupled carbon-climate model, which has nine pools, projected a decrease in C sink at low latitudes that nearly canceled an increase at high latitude (Fung et al. 2005).

Overall, the modeled positive feedback between climate warming and global carbon cycling is attributable primarily to stimulated net C release from land ecosystems in response to climate warming. The net land C release results from decreased NPP in most models and increased respiratory C release by all the models under climate warming. Major uncertainties remain about both the direction and degree of the

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Figure 1

(a) Atmospheric CO₂ concentration (ppm) as simulated by 11 coupled carbon-climate models (see Friedlingstein et al. 2006 for detailed description of the 11 models). (b) Atmospheric CO₂ difference between the coupled and uncoupled simulations (ppm). (c) Land C fluxes for the coupled runs (Gt C year⁻¹). (d) Differences between coupled and uncoupled land C fluxes (Gt C year⁻¹). (e) Simulated net primary productivity (NPP) sensitivity to climate (coupled run – uncoupled run). (f) Simulated soil C turnover time sensitivity to climate (coupled run – uncoupled run). Figure adopted from Friedlingstein et al. 2006.

response of NPP and soil respiration, as well as the possibility of vegetation dieback and soil drying, especially in tropical forests.

3. EXPERIMENTAL EVIDENCE

Models that couple the carbon cycle and climate change are essential for examining biosphere-atmosphere feedbacks at the global scale. Field experiments cannot be used to quantify the global-scale sensitivity of terrestrial ecosystems to climate warming over time spans of decades or centuries. However, models are necessary abstractions of reality, and the accuracy of their projections depends on how well the models represent the mechanisms responsible for the real-world feedback. As Moorcroft (2006) argues, model-assisted “understanding of biosphere-atmosphere feedbacks is a collection of interesting, but largely untested, hypotheses for the future state of terrestrial ecosystem and climate.” It is therefore imperative to critically examine experimental evidence about key C uptake and release processes that determine the terrestrial carbon feedback to climate warming.

3.1. Carbon Uptake Under Warming

Most C uptake processes, such as photosynthesis, plant growth, and primary production, are sensitive to changes in temperature. Their responses to climate warming are regulated by other factors and processes, leading to diverse changes observed in warming experiments.

Photosynthesis. Temperature influences the rate of photosynthetic CO₂ uptake through changes in the ratio of [CO₂]:[O₂] dissolved in solution, the specificity of Rubisco for CO₂ and O₂, and rates of carboxylation and oxygenation (Brooks & Farquhar 1985, Long 1991). For C₃ plants, net photosynthesis increases with temperature at its low range, reaches a maximum at optimal temperature, and then declines (**Figure 2a**). The optimal temperature usually varies broadly depending on the local adaptation of different species to their habitats and thermal acclimation over seasons (Percy & Ehleringer 1984).

Experiments have shown the diverse effects of warming on photosynthesis, including increases (Bergh & Linder 1999, Loik et al. 2004), decreases (Callaway et al. 1994, Gunderson et al. 2000, He & Dong 2003, Roden & Ball 1996), and no apparent change (Llorens et al. 2004, Loik et al. 2000, Nijs et al. 1996, Starr et al. 2000). Warming air temperature by 3°C–5°C, for example, increased photosynthesis in four vascular species in arctic tundra (Chapin & Shaver 1996) and two dominant tree species and a shrub species in a boreal forest (Beerling 1999). In contrast, a 3.5°C increase in air temperature did not significantly impact the photosynthesis of *Polygonum viviparum* in arctic polar semidesert (Wookey et al. 1994). Leaf photosynthesis increased in spring, decreased in early fall, and did not change in summer and late fall for four species exposed to an air warming of 0.5°C–2.0°C in the southern Great Plains of the United States (Zhou et al. 2007a) (**Figure 3**). The variable responses may result from different methods and/or levels of warming and may reflect diverse

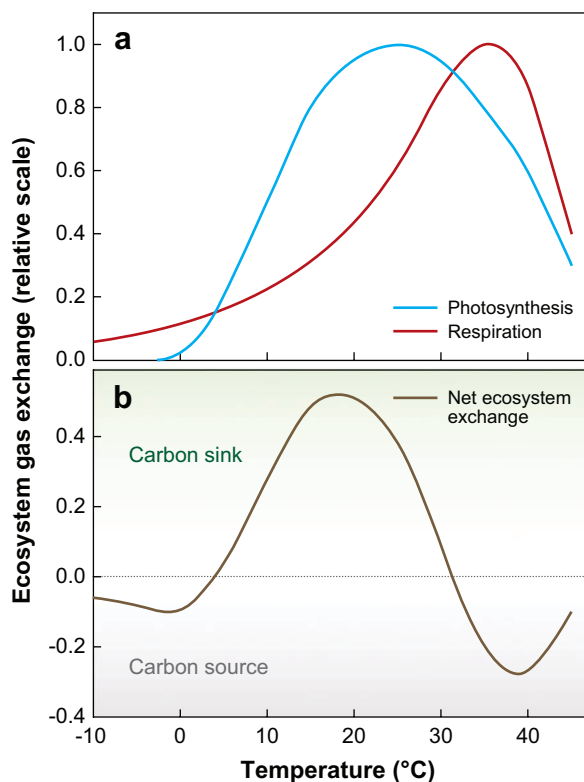


Figure 2

Idealized response functions of (a) plant photosynthesis and ecosystem respiration and (b) net ecosystem exchange to temperature, illustrating that climate warming can result in either net C release or net C uptake by terrestrial ecosystems purely on the basis of kinetic sensitivity. In the very low or very high temperature ranges in which respiration is higher than photosynthesis, ecosystems have net C release. In an intermediate temperature range, photosynthesis is higher than respiration, leading to net C uptake in terrestrial ecosystems.

temperature sensitivities and optimal temperatures of photosynthesis among species and ecotypes (Chapin et al. 1995, Llorens et al. 2004, Shaw et al. 2000). In addition, other factors may influence the results, such as drought, leaf age, and nutrient availability (Gunderson et al. 2000).

Plant growth. The effects of warming on plant growth are highly variable. Experimental warming increased leaf production by 50% and shoot production by 26% for *Colobanthus quitensis* but decreased leaf production by 17% for *Deschampsia antarctica* in Antarctica (Day et al. 1999). Warming stimulated growth of C₄ plants in a tallgrass prairie over a 6-year experiment, whereas the growth of C₃ plants increased in the first 2 years and then decreased in the last 2 years (Luo et al. 2007). Field soil-warming experiments showed that herbs and grass were more responsive to elevated temperature than shrubs, whereas tree species were less sensitive in a temperate forest (Farnsworth et al. 1995). A meta-analysis of 13 tundra experiments similarly showed that the vegetative growth of herbaceous species was more responsive to warming than woody species (Arft et al. 1999). However, Chapin & Shaver (1985) observed that evergreen species generally responded more strongly to warming than deciduous species (except for *Betula nana*), whereas the growth of graminoid species did not change or decreased under greenhouse warming in

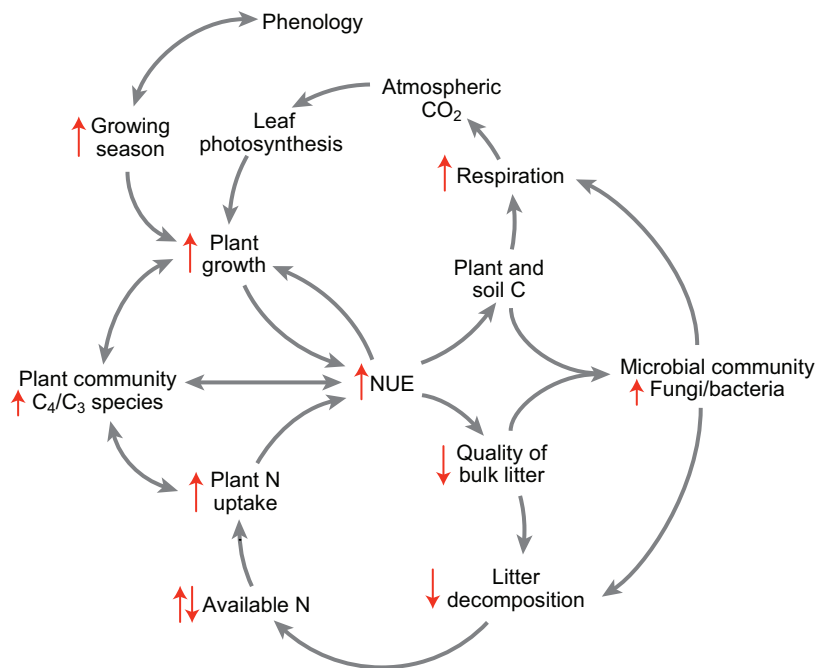


Figure 3

Illustration of regulatory mechanisms of ecosystem temperature sensitivity using results from an Oklahoma warming experiment. Major carbon (C) and nitrogen (N) processes are affected by warming in complex ways. Warming extended growing seasons, shifted species composition toward C₄ plants, and increased plant biomass growth. The increased growth was associated with increased plant N uptake and N use efficiency (NUE). Warming also increased soil respiration, which was roughly balanced by increased C uptake via plant growth, leading to little change in soil C storage, although warming accelerated almost all the rate processes. Owing to the increased dominance of C₄ plants in the grassland, the quality of bulk litter decreased under warming, which likely leads to diminished or even decreased soil N availability over time, although warming may initially increase N availability.

tundra. The individualistic responses to warming reflect differences in optimum growth temperatures across species, as well as the limitations on growth by other factors than temperature.

The effects of warming on primary production are also diverse. Soil warming increased the yields of crops by 19%–50% and vegetables by 19%–100% (Rykboest et al. 1975), primarily owing to enhanced growth in early spring. Experimental warming increased NPP by up to 25% in a tallgrass prairie (Luo et al. 2007) (**Figure 3**). Soil warming in a Norway spruce forest at Flakaliden in northern Sweden increased the stem-wood growth of trees in heated plots by 50% relative to controls after 5 years (Bergh et al. 1999, Jarvis & Linder 2000). A synthesis of data from 20 field warming experiments indicates that warming, on average, stimulated aboveground plant productivity by 19% (Rustad et al. 2001). In contrast, the aboveground biomass of sugar maples decreased in response to warming in open top chambers (Norby et al. 1995).

Total aboveground biomass was largely unresponsive to temperature manipulation in tundra (Hobbie & Chapin 1998; Shaver et al. 1986, 1998).

Along a gradient of increasing infrared heating, shrub production increased, whereas graminoid production decreased in a bog. In a fen, graminoids were most productive at high infrared heating, and forbs were most productive at medium infrared heating (Weltzin et al. 2000). In both the bog and fen communities, ratios of belowground to aboveground NPP increased with warming, indicating shifts in C allocation.

3.2. Carbon Release Under Warming

Terrestrial ecosystems release C to the atmosphere through autotrophic (i.e., plant) and heterotrophic (primarily by microbes) respiration. Both autotrophic and heterotrophic respiration is very sensitive to changes in temperature. Since most measurements were made on plant tissues (e.g., leaf or root) to quantify plant respiration and at soil surface to quantify soil respiration, I discuss plant respiration and soil respiration separately although soil respiration includes both root and microbial respiration.

Plant respiration. Actively growing plants respire approximately 50% of the C available from photosynthesis (after photorespiration), with the remainder available for growth and reproduction (Law et al. 1999, Ryan 1991). Respiration increases with temperature in its low range when the respiration rate is mainly limited by biochemical reactions (Atkin et al. 2000). At high temperatures, the transport of substrates and products of the metabolism (e.g., sugar, oxygen, CO₂) mainly via diffusion processes becomes a limiting factor. At very high temperatures, the protoplasm system may start to break down. As a result, respiration usually follows a general temperature-response curve, increasing exponentially with temperature in its low range, reaching a maximum at an optimal temperature, and then declining (**Figure 2a**). During the exponential increase phase, respiration often doubles in response to a 10°C temperature increase ($Q_{10} = 2$) (Amthor 1989, Ryan et al. 1995).

Although leaf respiration is usually stimulated by experimental warming (Zhou et al. 2007a), the acclimation of plant respiration to temperature (Atkin et al. 2006) reduces C loss over extended periods. Based on short-term studies indicating that warming stimulates plant respiration more than photosynthesis, many plant-growth models predict an increase in respiration:photosynthesis ratio at elevated temperatures. Long-term experiments (Gifford 1994, 1995) suggest that respiration:photosynthesis ratio is often remarkably insensitive to growth temperature (Arnone & Körner 1997, Gunn & Farrar 1999, Lambers 1985) because plants acclimate to a new temperature environment over a few days. This acclimation may be controlled by carbohydrate status, the demand for ATP, and/or the reduced production of reactive oxygen species (Atkin et al. 2005). A simple substrate-based model of plant acclimation to temperature shows that respiration is effectively limited by carbohydrate supply from photosynthesis (Dewar et al. 1999). The short-term, positive temperature response of respiration:photosynthesis ratio therefore reflects the transient dynamics

of nonstructural carbohydrate and protein pools, whereas the insensitivity of respiration/photosynthesis ratio to temperature on a longer time scale reflects the state behavior of the pools.

Soil respiration. Soil respiration accounts for approximately two-thirds of C loss from terrestrial ecosystems and is generally responsive to temperature changes (Luo & Zhou 2006). Its sensitivity to climate warming has been identified as one of the major sources of uncertainty in model projections of future climate change (Cox et al. 2000, Friedlingstein et al. 2006). As a consequence, scientists have conducted extensive research on the sensitivity of soil and/or ecosystem respiration to climate warming (Davidson & Janssens 2006). When natural ecosystems have been exposed to experimental warming, soil CO₂ efflux generally increases (Melillo et al. 2002, Mertens et al. 2001, Zhou et al. 2007b) (**Figure 3**). A meta-analysis of data collected at 17 sites from tundra, grassland, and forest shows that soil respiration under experimental warming increased at 11 sites, decreased at 1 site, and did not change at 5 sites (Rustad et al. 2001). An increase in soil temperature by 5°C above ambient temperature using buried heating cables, for example, caused additional C release of 538 g m⁻² year⁻¹ from soil in Harvard Forest (Peterjohn et al. 1994). In contrast, infrared heating slightly decreased soil respiration in a Rocky Mountain meadow in Colorado (Saleska et al. 1999) and a grassland in Oklahoma in the first year of the experiment (Luo et al. 2001).

Warming-induced increases in soil respiration likely result from changes in multiple processes (Shaver et al. 2000). Global warming extends the length of growing seasons (Lucht et al. 2002, Norby et al. 2003), alters plant phenology (Dunne et al. 2003, Sherry et al. 2007), stimulates plant growth (Wan et al. 2005), increases mineralization and soil N availability (Melillo et al. 2002, Rustad et al. 2001), reduces soil water content (Harte et al. 1995, Wan et al. 2002), and shifts species composition and community structure (Harte & Shaw 1995, Saleska et al. 2002, Weltzin et al. 2003). Responses also differ across locations. The magnitude of response in soil respiration to soil warming is greater in cold, high-latitude ecosystems than in warm, temperate areas (Kirschbaum 1995). Recent warming has likely caused a great loss of C in tundra and boreal soils (Goulden et al. 1998).

It is commonly observed that the magnitude of response in soil respiration to warming decreases over time (Rustad et al. 2001). The yearly flux of CO₂ from heated plots at the Harvard Forest was ~40% higher than control plots in the first year but gradually declined to the level in the control plots after the 6-year warming treatment (Melillo et al. 2002). This decline can be attributable to acclimatization (Luo et al. 2001) and/or depletion of substrates (Eliasson et al. 2005, Gu et al. 2004, Niinistö et al. 2004, Pajari 1995). In addition, warming caused a shift in the soil microbial community toward more fungi (Zhang et al. 2005), which are more tolerant to high soil temperature and dry environments than bacteria owing to their filamentous nature (Holland & Coleman 1987). Shifted microbial community structure may partially explain observed decreases in the temperature sensitivity of soil CO₂ efflux.

3.3. Net Ecosystem Production

Changes in plant production and ecosystem respiration together determine the long-term effects of warming on ecosystem C balances. If C uptake and release are primarily determined by the kinetic properties of photosynthesis and respiration, respectively, net ecosystem production (NEP) should be negative at high and low temperature ranges and positive (i.e., sink) at an intermediate range along a temperature variation over a season or latitude (**Figure 2b**). In addition, NEP is also regulated by many processes other than photosynthesis and respiration kinetics, leading to complex responses to climate warming. Buried heating cables only warm soil and have generally caused net C loss, such as in experiments at Harvard Forest (Melillo et al. 2002) and the arctic tundra (Billings et al. 1982). Ineson et al. (1998) also showed a net C reduction of approximately 10% after 3 years of heating an upland grassland ecosystem at Great Dun Fell in the United Kingdom.

Whole-ecosystem warming using infrared heaters or greenhouse chambers may decrease, increase, or cause no changes in net ecosystem exchange. Using infrared heating, Marchand et al. (2004) found a 24% increase in canopy C uptake and a nearly 50% increase in net C sink under warming in comparison with that under control in high-arctic tundra. After 8 years of experiment, an average increase of 5.6°C in air temperature with field greenhouse warming did not cause much change in canopy photosynthesis, ecosystem respiration, and net ecosystem C exchange in arctic tundra (Johnson et al. 2000), although warming stimulated early canopy development and extended the length of growing seasons by 3 weeks. The warming experiment at the southern Great Plains did not cause significant changes in soil C stocks or NEP (Luo et al. 2007) (**Figure 3**). Saleska et al. (2002), however, observed a decrease of soil organic carbon by $\sim 200 \text{ g C m}^{-2}$ ($\sim 8.5\%$ reduction) in warmed plots relative to control plots in a Rocky Mountain meadow.

If warming primarily stimulates the decomposition of litter and the oxidation of soil organic matter, soil C pools will decline over time. If increased temperature strongly stimulates NPP, climate warming may lead to increased terrestrial C storage (Smith & Shugart 1993). There are several mechanisms (e.g., increased N mineralization, extended growing seasons, and shifted species composition) that may enhance NPP.

In summary, warming experiments have not produced many clear and consistent patterns across ecosystems. Warming caused increases, decreases, or no change in photosynthesis, plant growth, primary production, soil respiration, and NEP. There are several reasons for these highly variable responses. First, the levels of temperature increases are not consistent among warming experiments. Second, warming methods vary among experiments, ranging from the infrared heating of whole ecosystems to heating cables for soil warming and passive heating systems using open top chambers and/or nighttime cover. Third, measured variables and measurement methods differ among investigators. Fourth, plants and ecosystems are inherently diverse in their responses to warming. Overall, the highly variable results from field experiments may not have generated the necessary insights on ecosystem responses to climate warming to the detriment of model improvement. Nevertheless, experiments have suggested that the kinetic sensitivities of photosynthesis and respiration, although fundamental

to models, are usually overridden by other processes. The latter processes strongly regulate ecosystem responses to climate warming.

4. REGULATORY MECHANISMS OF ECOSYSTEM TEMPERATURE SENSITIVITY

Both carbon release and uptake processes in intact ecosystems are affected by complex mechanisms such as phenology and the length of growing seasons, nutrient dynamics, species composition, and water availability in addition to the kinetic sensitivities of photosynthesis and respiration (Figures 3 and 4). It is essential to understand such regulatory mechanisms to develop terrestrial ecosystem models capable of predicting changes in C uptake and release in response to climate warming.

4.1. Changes in Phenology and Length of Growing Seasons

Plant phenology is responsive to environmental cues such as temperature, photoperiod, and moisture (Rathcke & Lacey 1985) and has been used as a sensitive indicator of climate change in Earth's system (Peñuelas & Filella 2001, Walther et al. 2002). Long-term ground-based and remote-sensing measurements indicate that plant phenology has been advanced by 2–3 days in spring and delayed by 0.3–1.6 days in autumn

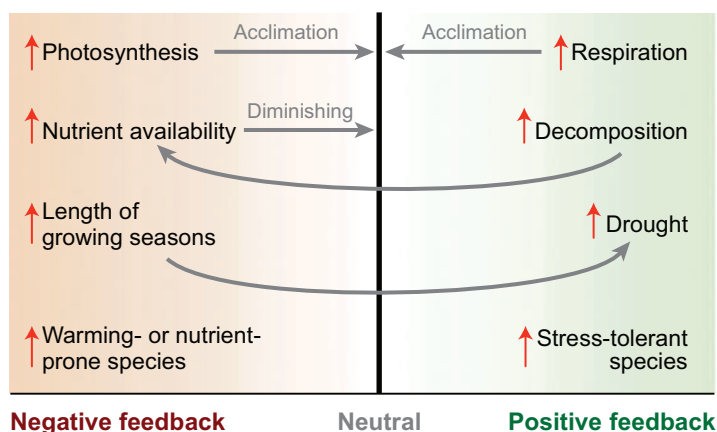


Figure 4

Schematic summary of major regulatory mechanisms that lead to either positive or negative feedbacks of terrestrial C cycles to climate warming. Climate warming instantaneously stimulates photosynthetic C uptake and respiratory release. Acclimation can neutralize their kinetic responses. Warming-stimulated decomposition of soil organic matter is associated with respiratory C release and increases nutrient availability that stimulates plant growth and ecosystem C uptake. The warming-induced increases in nutrient availability may be diminishing over time. Warming extends growing seasons and lengthens C uptake periods. Extended growing seasons and warming in combination can exacerbate drought stress and limit net ecosystem C uptake in some regions. Warming-induced changes in species composition can result in either positive or negative feedbacks of C cycles to climate warming, depending on which species adapt to the new environment.

per decade (Myneni et al. 1997, Parmesan & Yohe 2003) over the past 30–80 years, probably owing to recent climatic warming (Parmesan & Yohe 2003).

Researchers have consistently observed across experiments that plant phenology is responsive to warming (e.g., Cleland et al. 2006). Field experiments via heating and snow removal in alpine ecosystems reveal that a 3°C increase in temperature advances flowering time by 4.5 days (Dunne et al. 2003, Price & Waser 1998). *Maianthemum canadense* and *Uvularia sessilifolia*, the herbaceous dominants, emerged 7–10 days earlier in the growing season under soil-warming conditions (Peterjohn et al. 1993). Leaf bud burst and flowering phenology occurred earlier in warmed plots compared with control plots at 13 different tundra sites (Arft et al. 1999). Sherry et al. (2007) observed that early flowering species advanced phenology by 3–17 days in spring, whereas late flowering species delayed phenology up to 12 days in the Oklahoma warming experiment (**Figure 3**).

Shifts in phenology result in a growing-season extension, with earlier greenness in spring and later senescence in autumn. The divergence of phenology toward early spring and late autumn under experimental warming (Sherry et al. 2007) extended the growing seasons by more than 2 weeks (Wan et al. 2005). Intact field greenhouse warming in arctic tundra extended growing seasons for 3 weeks. Analysis of remote-sensing data has also shown that climate warming has extended the growing season in the past decades (Myneni et al. 1997, Nemani et al. 2003, White et al. 1999).

Those changes in phenology and growing-season length directly affect ecosystem C processes (**Figure 3**). In a deciduous forest, for example, the timing of leaf expansion and senescence influenced interannual shifts in photosynthesis (Goulden et al. 1996). Analysis of satellite data suggested that extending the growing season earlier in the spring and/or later in the autumn increased primary production in terrestrial ecosystems (Nemani et al. 2003). Analysis of data from eddy-flux networks showed that NEP and gross C assimilation increase with decreasing latitude (Falge et al. 2002). Measured NEP from eddy-flux sites is strongly correlated with the length of the C uptake period for temperate broad-leaved forests (Baldocchi & Wilson 2001) and other vegetation types (Churkina et al. 2005) (**Figure 4**).

Changes in phenology and growing-season length also affect C cycling indirectly via changes in species composition, water balance, and nutrient processes (see discussion below). For example, experimental warming in a tallgrass prairie in Oklahoma stimulated the availability and plant uptake of soil N in spring, causing higher leaf N concentration in *Schizachyrium scoparium* compared with the control. The effect was reversed in summer owing to increased soil drying, decreased soil N availability, and increased plant growth (Y. An & Y. Luo, unpublished data).

4.2. Changes in Species Composition

Species composition in ecological communities reflects interactions among organisms under a set of environmental conditions. Climate warming alters essential environmental conditions (such as temperature and soil nutrient and water availabilities) and results in changes in species composition (Peñuelas & Boada 2003). Under experimental warming, for example, species composition changed to favor shrubs over

graminoid species in a bog and graminoids over forbs in a fen in northern Wisconsin peatland (Weltzin et al. 2000). Experimental warming differentially affected the growth of C₃ and C₄ species and shifted species composition in favor of C₄ plants in the southern Great Plains (Luo et al. 2007, Wan et al. 2005). In a Rocky Mountain meadow, warming stimulated the relative abundance of shrub species, but depressed forb species (Harte & Shaw 1995). Experimental warming at 11 locations across the tundra biome rapidly altered a whole plant community by increasing the height and cover of deciduous shrubs and graminoids and decreasing the cover of mosses and lichens (Walker et al. 2006). As a consequence, species diversity and evenness decreased in the warming plots in comparison with that in the control. Climate warming also altered the geographical distribution of plants (Parmesan & Yohe 2003, Peñuelas & Boada 2003).

Shifts in species composition result from changes in the competitive balance among species. A shift of species composition occurred in a montane meadow toward shrubs (De Valpine & Harte 2001, Harte & Shaw 1995) because warming lowered leaf water potential (Loik & Harte 1997) and increased photosynthetic rates and water-use efficiency for *Artemisia tridentata* (Shaw et al. 2000). In contrast, warming stimulated mineralization, increased N availability, and favored fast-growing and N-rich species in a moist tundra ecosystem near Toolik Lake, Alaska (Chapin et al. 1995). Mesic sites in tundra had higher species diversity and were more responsive than xeric sites to warming (Walker et al. 2006). In the tallgrass prairie, experimental warming stimulated C₄ plant growth but depressed C₃ plant growth (Luo et al. 2007) because C₄ plants have competitive advantages in a warm and dry environment.

Changes in plant community composition have long-term effects on ecosystem C balance. A shift from forbs to shrubs resulted in decreased litter inputs and decreased soil organic C in an alpine meadow ecosystem (Saleska et al. 2002). Because the decomposition of woody litter is slower than forb litter, increased C residence time potentially leads to long-term recovery of SOC in the warming plot (Saleska et al. 2002). A modeling study that was calibrated to tussock vegetation at Toolik Lake, Alaska, suggested that warming stimulates soil respiration and N availability, thus favoring high-productivity forbs over the shrubs (McKane et al. 1997) and leading to the partial recovery of the initial SOC loss in the long run (Herbert et al. 1999). In an Oklahoma grassland, warming increased C₄ plant growth, causing increased primary production and litter input to the soil (Luo et al. 2007). Increased C₄ litter production with a low C:N ratio slowed down decomposition and increased C accumulation in the litter layers (**Figure 3**). Decreased litter quality in response to warming resulted in a shift in the soil microbial community composition toward a fungi dominance (Zhang et al. 2005). Fungi dominance, in turn, could favor soil aggregation and C storage in ecosystems (Rillig 2004), thus reinforcing physical and biochemical protection of soil C storage (Jastrow 1996, Six et al. 2002).

4.3. Nutrient-Mediated Feedbacks

Many warming experiments have showed that increased temperature causes faster microbial decomposition of organic matter (Grogan & Chapin 2000), increased N

mineralization (Chapin et al. 1995, Johnson et al. 2000, Shaver et al. 1998), and increased N uptake by plants (Ineson et al. 1998, Jarvis & Linder 2000, Rustad et al. 2001, Welker et al. 2004). Soil warming in Harvard Forest stimulated the net N mineralization rate for a decade (Melillo et al. 2002). A meta-analysis of net N mineralization rates from 12 ecosystem warming experiments showed a large stimulation by 46% (Rustad et al. 2001). However, Jonasson et al. (1999) did not find any significant change in total soil N and phosphate contents over 5 years of greenhouse warming at Abisko, Sweden, possibly owing to the microbial immobilization of gross mineralized N or small temperature increases.

Warming-induced changes in soil N transformations can trigger long-term feedbacks on ecosystem C balances because N strongly regulates terrestrial C sequestration. Stimulated N mineralization and plant N uptake under warming resulted in increased biomass production in arctic tundra (Gough & Hobbie 2003, Hobbie et al. 2002, Welker et al. 2004). Over time, accelerated decomposition under warming may lower soil organic pools, leading to declines in mineral N availability and constraints on plant N uptake in the long-term (**Figure 4**). Ultimately, this feedback may reduce the stimulation of biomass growth by warming. Furthermore, warming has been shown to decrease bulk litter quality in a tallgrass ecosystem (An et al. 2005) (**Figure 3**), leading to the reduced release of soil N over time. Thus, the increased N demand due to faster plant growth under warming may not be met by the N supply in the long-term, possibly leading to progressive N limitation (Luo et al. 2004).

4.4. Feedbacks Through Hydrological Cycling

Warming usually happens in concert with drought. The 2003 summer heat wave occurred in Europe with combined drought and high temperature, resulting in net release of C from terrestrial ecosystems (Ciais et al. 2005) (**Figure 4**). In general, the influences of climate warming on large-scale hydrological processes (such as precipitation, runoff, tropospheric water vapor, and evaporation) have been extensively studied using modeling and observation approaches (Huntington 2006). Both theoretical analysis and observational evidence suggest that climate warming likely results in increases in evaporation and precipitation at the global scale. Many regions may experience severe drought or moisture surplus (Dai et al. 1998).

The indirect effects of climate warming on C dynamics via changes in ecosystem-scale hydrological cycling have not been carefully studied. In general, climate warming accelerated evapotranspiration, leading to soil drying (Harte et al. 1995, Llorens et al. 2004, Wan et al. 2002) and decreased soil- and leaf-level water potentials. However, Zavaleta et al. (2003) found that experimental warming increased spring soil moisture by 5%–10% in an annual grassland in California owing to the accelerated decline of canopy greenness by inducing earlier plant senescence. Warming-induced increases in soil surface evaporation and plant transpiration accelerate soil water depletion. With an increased soil water deficit, water replenishment in soil may increase, and water runoff decreases after precipitation events as shown in a modeling study (E.S. Weng and Y. Luo, submitted manuscript). If precipitation occurs at such a frequency that soil water is replenished before the soil water content is lowered to such an

extent that plant growth is influenced severely, the portion of precipitation water used for plant growth increases under warming in comparison with that in control. However, in years when precipitation is evenly distributed and largely partitioned for evapotranspiration without much surplus for runoff at ambient conditions, warming substantially decreases soil water content (Zhou et al. 2007b) and may not change precipitation partitioning to runoff.

In response to warming and soil drying, plants may adjust ecophysiological processes so as to influence C balance. Warming and associated drought, for example, may stimulate belowground growth, increase the root/shoot ratio, and result in shifts of the plant community to C₄ species, shrubs, and other drought-tolerant species. Warming-induced extension of growing seasons to early spring and late fall can increase ecosystem-level water-use efficiency and production in regions in which winter precipitation does not contribute to plant growth (Luo et al. 2007). Early spring warming in an alpine forest of Colorado, however, was usually related to shallow late-spring snow pack and resulted in low springtime and annual net CO₂ uptake (Monson et al. 2005). Thus, warming may decrease ecosystem productivity in regions in which either summer plant growth depends on winter soil water storage or there is no winter water surplus (**Figure 4**).

5. QUEST FOR PREDICTIVE UNDERSTANDING

One ultimate goal of global-change research is to project future states of climate and ecosystems. Although research over the past years has established a modeling framework that can be used to evaluate feedbacks between climate change and global C cycles, the model assumption that kinetics of photosynthetic and respiratory biochemistry underlie terrestrial carbon-cycle feedback to climate warming is not fully in accordance with experimental results. Conversely, results from experiments and observation have great uncertainties owing to the nature of perturbation experiments (Luo & Reynolds 1999), different experimentation methods, scales of studies, and other issues. A search for predictive understanding from imperfect models and uncertain experimental evidence therefore represents a great challenge. Here I discuss a few approaches that are not mutually exclusive but may simultaneously contribute to our predictive understanding of terrestrial carbon-cycle feedback to climate warming.

5.1. Fundamental Approach

Potential feedbacks of terrestrial ecosystems to climate warming originate from temperature-sensitive processes at biochemical and physical levels. The primary processes include enzyme kinetics involved in photosynthesis, plant respiration, decomposition of litter, and oxidation of soil organic matter. Temperature regulation of enzymatic activities is usually described by an exponential or Arrhenius equation (Luo & Zhou 2006) in most coupled carbon-climate or stand-alone ecosystem models. However, declining phases of photosynthesis and respiration in the high temperature range (**Figure 2**), which are usually observed in laboratory studies but rarely in field, are usually not represented in models (but see Parton et al. 1997). Moreover,

although the fundamental nature of these biochemical processes is independent of the hierarchical level (from cellular to global), scaling up of biochemical kinetics to project carbon-climate feedback at the global scale is challenging because many indirect processes (e.g., those discussed in Section 4) can easily override the lower-level biochemical processes. Nevertheless, it is essential to understand and more accurately model kinetics of biochemical processes (Davidson & Janssens 2006, Davidson et al. 2006) to project carbon-climate feedback.

Temperature also directly affects plant development and growth via cell division and differentiation, the occurrence of fires and insects, and water-temperature relationships in permafrost ecosystems. Cell differentiation determines phenological responses to warming and directly regulates the dynamics of leaf area over growing seasons at local scales, whereas temperature effects on fire and insect infestation alter C balance at landscape and regional scales. Most of the processes are regulated by other factors and cannot be described easily by simple temperature functions. For example, phenology is regulated by photoperiod, temperature, and moisture (Peñuelas & Filella 2001, Rathcke & Lacey 1985, Walther et al. 2002). Fire occurrence is determined by fuel loading, moisture content, and temperature (Weise et al. 2005). Most models simulate temperature effects on phenology and fire occurrence based on empirical relationships.

5.2. Pragmatic Approach

Although there are variable responses of all C uptake and release processes to climate warming, two globally coherent patterns have emerged across warming experiments and observations. Global coherence is a common term in economics and refers to a process or event that has a similar effect across multiple systems at different locations throughout the world, even though the mechanisms underlying the coherent process may be different (Parmesan 2006). One globally coherent pattern observed across warming experiments is a consistent response of phenology to warming, leading to the extension of growing seasons. The other commonly observed ecosystem response to climate warming is a shift in species composition. The development of reliable models that can more accurately simulate the globally coherent patterns is a critical step toward improving model projections of future carbon-cycling feedback to climate warming.

Phenology consistently responds to climate warming (Parmesan 2006), although the degree of the response and the mechanisms underlying it may differ (see Section 4.1). To account for such coherent responses, several phenology models have been developed to predict leafing out, senescence, and reproductive events. Leafing out, for example, can be predicted by growing degree days, a combined chilling and forcing temperature (Chuine et al. 1999), a moisture index in water-limited ecosystems (Kramer et al. 2000, White et al. 1997), the timing of the first heavy precipitation in deserts (Beatley 1974), or the occurrence of soil thawing in arctic ecosystems (van Wijk et al. 2003). Jolly et al. (2005) proposed a growing season index to predict foliar phenology at the global scale based on daily temperature, the vapor pressure deficit, and photoperiod. Leaf senescence has been predicted by a frost index (Kramer

et al. 2000), environmental fluctuations (Arora & Boer 2005), and specific thresholds for different plant functional types in a dynamic global vegetation model (Sitch et al. 2003).

Warming causes shifts in the species composition of plant communities across many experimental sites (see Section 4.2). Prediction of species shifts at individual levels, however, has been difficult owing to species-specific responses (Chapin & Shaver 1985), whereas responses at the level of plant functional type may be more predictable. Researchers have developed several models to simulate species response to climate change. Herbert et al. (1999) used a multiple-element limitation model to simulate changes in species composition in response to climate change. Increased temperature stimulated N release and therefore favored fast-growing species with low N use efficiency. Peters (2002) developed a mixed life-form, individual plant-based gap dynamics model to examine the consequences of differences in recruitment, resource acquisition, and mortality to patterns in species dominance and composition under a variety of soils and climate conditions. The model predicted that a grass, *Bouteloua eriopoda*, will dominate the Chihuahuan desert if climate change leads to increased summer water availability. If climate change leads to increased winter precipitation, a C₃ shrub, *Larrea tridentata*, may dominate. The major challenge of the individual-based modeling approach is scaling up the simulation of local-level species dynamics to landscape-level changes. Epstein et al. (2001) used a regional-scale model to examine warming effects on species dynamics in arctic tundra at four levels of aggregation—individual species, functional types, life forms, and vegetation types. The level of aggregation affected simulation results of community composition, total community biomass, and NPP.

As we accumulate more experimental evidence, some other ecosystem properties may emerge to be globally coherent so as to assist our predictive understanding of ecosystem responses to climate warming. Results from numerous experiments have demonstrated that ecosystem respiration is tightly coupled with plant photosynthesis. It will be useful to examine how warming affects such coupling between soil respiration and NPP and if the coupling between photosynthesis and respiration leads to any predictive relationships (e.g., relative constant ratio) under different warming regimes. At the leaf level, the ratio of instantaneous respiration to photosynthesis has been found to be relatively constant, even in plants exposed to contrasting growth temperature (Gifford 1995, Ziska & Bunce 1998). When individual plants are exposed to growth temperature within a range plants experienced in the natural habitat, plants adjust biomass allocation to maintain a homeostatic respiration to photosynthesis ratio (Atkin et al. 2007). This constancy, if held for the majority of plant species, offers a potential to account for photosynthetic and respiratory acclimation in coupled carbon-climate models (Gifford 2003).

5.3. Probabilistic Approach

Carbon processes and regulatory mechanisms are inherently variable. The variations stem from many sources, including genetic differences between organisms, environmental variability over time and space (e.g., climate dynamics and heterogeneity in the

physical and chemical processes in soil), and diversity in plant and microbial responses to environmental change. Observations on the responses of ecosystem C uptake and release processes to climate warming are also subject to errors in measurement and disparities in experimental methods and treatment levels. Synthesis of experimental data across sites, experiments, and studies all shows great variations in C processes (e.g., Arft et al. 1999, Luo et al. 2006, Rustad et al. 2001). Although it is exceedingly desirable to discover invariant functions that cut across scales or globally coherent patterns to fundamentally improve models, high variability in ecosystem processes within and between studies poses a significant challenge for the development of our predictive understanding of carbon-climate feedbacks. To realistically reflect variability in ecosystem processes, probabilistic approaches such as stochastic modeling and ensemble analysis may be effective tools to assess uncertainty. Stochastic modeling has been widely used in other disciplines (Zhang 2002) and applied to global-change research (e.g., Moorcroft et al. 2001). Ensemble results from the intercomparison of multiple models (e.g., Friedlingstein et al. 2006) can account for variations among model structure and parameters but may not identify systematic bias if some of the key processes have not been integrated into any of the models.

Most simulation models assume that there are some intrinsic constants of parameters for each vegetation type, which are modified by environmental scalars such as temperature and moisture functions to model spatial and temporal variations in ecosystem processes. However, analyses by Hui et al. (2003) and Richardson et al. (2007) indicate that parameters need to vary with years to account for interannual variability in net ecosystem exchange of C. It is also likely that intrinsic parameter values may vary with space. Spatial and temporal variations in parameters propagate to variability in projections of future states of terrestrial ecosystems as quantified by stochastic approaches to data-model assimilation (Xu et al. 2006). We need extensive studies of spatial and temporal variability in parameter values and their propagation to model projections of future states of ecosystems and climate.

6. CONCLUDING REMARKS

The global-modeling community has established a quantitative framework over the past years to evaluate feedbacks between climate change and global C cycles. The coupled carbon-climate models reported in the literature all simulate a positive feedback between terrestrial C cycle and climate warming. The high degree of uniformity among projections by various models results from a similar mechanism underlying the modeled changes in C fluxes. That mechanism is the kinetic sensitivity of photosynthesis and respiration to temperature. Experimental results suggest much richer mechanisms than kinetic sensitivity that drive ecosystem responses to climate warming. Climate warming, for example, consistently affects phenology, leading to extended growing seasons and enhanced biomass growth and C sequestration from the atmosphere. Experiments often show that species composition changes in response to climate warming. Altered species composition can lead to either the net source or net sink of C, depending on the ecophysiology of altered species. Experimental warming also consistently stimulates mineralization and nutrient availability, favoring plant

growth. The increase in nutrient availability may be transient, and its impact on plant growth and ecosystem C storage may diminish over time. Climate warming modifies ecosystem–water balance as well, via changes in precipitation, evapotranspiration, and other ecohydrological processes. Diverse mechanisms likely delineate more possibilities of carbon–climate feedbacks than projected by the current, kinetics-based global models.

Experimental evidence on the temperature sensitivity of ecosystem C uptake and release processes is extremely variable. Climate warming causes increases, decreases, and no change in photosynthesis, plant growth, primary production, soil respiration, and NEP although trends of warming-induced changes exist for some variables. The highly variable experimental results have not provided the necessary insights on model improvement to realistically simulate ecosystem responses to climate warming. To improve our understanding of ecosystem temperature sensitivities, we need to improve experimental studies in several aspects. First, we need whole-ecosystem warming experiments to examine the integrated responses of entire ecosystems to climate warming. Second, we need to establish common research protocols among experiments (e.g., levels of temperature increases) to facilitate direct comparison and data synthesis. Third, we need experiments with multiple levels of temperature increases to investigate nonlinear responses of ecosystems to climate warming. Fourth, we need experiments in underrepresented and/or critical biomes (e.g., ecosystems in tropic regions) to develop global views of the temperature sensitivities of ecosystem C uptake and release processes. Fifth, we need long-term experiments to identify ecosystem responses at different timescales. Finally, we need multifactor global-change experiments to investigate the interactive effects of temperature, elevated CO₂, precipitation, N deposition, and invasive species on carbon–climate feedbacks.

To effectively constrain the model projections of future states of climate and ecosystems, we have to not only continue the model representation of fundamental processes (e.g., kinetics of photosynthesis and respiration) but also use pragmatic and probabilistic approaches to model improvement. The pragmatic approach is to develop empirical modules to simulate globally coherent patterns that have consistently emerged from experiments and observations such as phenology and species shifts. The probabilistic approach is to account for variations in ecosystem processes, spatial and temporal variability in model parameters, and the propagation of variations in parameter values and observations to model projections.

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