

Global Warming and Terrestrial Ecosystems: A Conceptual Framework for Analysis

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Emissions of greenhouse gases are expected to raise global mean temperature over the next century by 1.0–3.5 °C (Houghton et al. 1995, 1996). Ecologists from around the world have begun experiments to investigate the effects of global warming on terrestrial ecosystems, the aspect of global climate change that attracts the most public attention (Woodwell and McKenzie 1995, Walker and Steffen 1999). The effort to understand response to warming builds on a history of investigations of the effects of elevated CO₂ on plants and ecosystems (Koch and Mooney 1996, Schulze et al. 1999). There are important differences, however, between increases in atmospheric CO₂ and temperature change, both in the temporal and spatial patterns of change and in how they affect ecosystems. The scientists involved in temperature change research have had to face new technical and conceptual challenges in designing and interpreting their experiments (Schulze et al. 1999). In this paper we describe these challenges and present a conceptual framework for interpreting experimental results and predicting effects of warming on ecosystems.

ECOSYSTEM RESPONSES TO GLOBAL WARMING WILL BE COMPLEX AND VARIED. ECOSYSTEM WARMING EXPERIMENTS HOLD GREAT POTENTIAL FOR PROVIDING INSIGHTS ON WAYS TERRESTRIAL ECOSYSTEMS WILL RESPOND TO UPCOMING DECADES OF CLIMATE CHANGE. DOCUMENTATION OF INITIAL CONDITIONS PROVIDES THE CONTEXT FOR UNDERSTANDING AND PREDICTING ECOSYSTEM RESPONSES.

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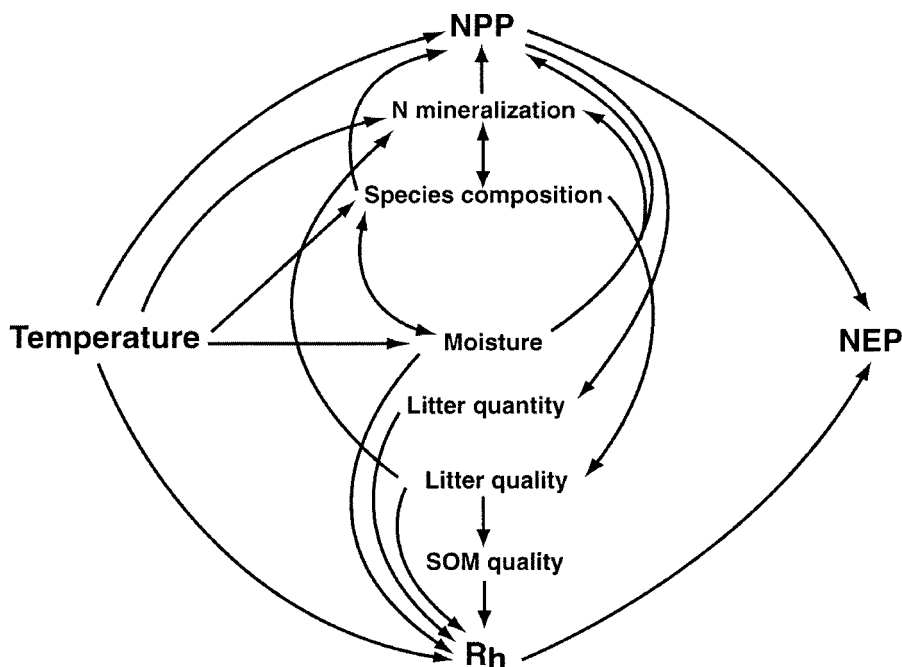


Figure 1. Direct and indirect effects of temperature on net primary production (NPP), heterotrophic respiration (R_h), and net ecosystem production (NEP), the major components of carbon exchange between terrestrial ecosystems and the atmosphere (Woodwell and Whittaker 1968). NPP removes carbon from the atmosphere, whereas R_h returns carbon to the atmosphere. NEP is the sum of these two opposing fluxes and represents the net exchange of carbon between an ecosystem and the atmosphere. From the perspective of the ecosystem, NEP is positive when NPP is larger than R_h and is negative when NPP is smaller than R_h . In this diagram, arrows represent chains of cause and effect by which temperature affects NPP and R_h but are not intended to indicate the magnitude or sign of an effect. Their purpose is simply to show that temperature influences NPP and R_h directly and indirectly, whereas changes in NEP are the net result of the effects on NPP and R_h . (SOM, soil organic matter.)

Projections of global warming from General Circulation Models (GCMs) are now familiar to both scientists and nonscientists. Knowing, however, that the mean global temperature will increase by 1.0–3.5 °C tells us little about how temperatures will change in a particular location or how the ecosystems in that location will respond. For instance, temperature increases are likely to be greater at higher latitudes (Houghton et al. 1995, 1996), where initial conditions are below 0 °C most of the year and growing season temperatures are only a few degrees higher. Even a small increase in average temperature at higher latitudes could increase both the length of the unfrozen period and degree-day accumulations by large percentages (Billings 1987). The implications of a given increase in temperature will also depend on the initial temperature at a specific location because the rate of many biological processes in relation to temperature typically peaks at some intermediate temperature. An increase from an initially low temperature may cause an increase in photosynthesis, for example, while an increase from an initially high

temperature might cause photosynthesis to decrease (Larcher 1995). Finally, even as the average temperature increases, some parts of the globe are actually expected to experience cooling (Houghton et al. 1995, 1996). The complexities of these patterns of change in temperature contrast with the increase in atmospheric CO_2 , for which there is no large temporal or spatial variation either in current levels or in the rate or pattern of increase.

Direct and indirect effects of warming on ecosystems

The direct effects of warming on ecosystems will also be more complex than the direct effects of increased CO_2 because temperature impacts virtually all chemical and biological processes, whereas the direct influence of CO_2 is almost entirely limited to leaves (photosynthesis, stomatal aperture, and perhaps respiration; Koch and Mooney 1996). For both warming and CO_2 , however, the greatest obstacles to understanding lie in the web of indirect effects resulting from interactions among processes affected directly by environmental change. These interactions lead to feedbacks that are sometimes positive and

sometimes negative, so the responses to temperature change or CO_2 can be expected to vary among ecosystems in both magnitude and direction depending on the properties of the dominant species, interactions among species, and the initial physical and chemical environment.

The effects of a temperature increase on the carbon budget of an ecosystem provides an example of this complexity (Figure 1). Net ecosystem production (NEP), defined as the overall carbon balance of an ecosystem over some time period (Woodwell and Whittaker 1968, Mooney et al. 1999), has two major components, net primary production (NPP) and heterotrophic respiration (R_h). NPP, the principal input of carbon to the ecosystem, is the net result of CO_2 fixation by photosynthesis and CO_2 loss by plant respiration. The product of NPP is new organic matter, which accumulates first in plants as living biomass and is eventually transferred to soils as litter and to animals and decomposer organisms as food. R_h represents the loss of carbon from the ecosystem by respiration of animals and decomposers; the products of R_h include

CO₂ and other inorganic carbon products (e.g., CH₄). Both NPP and R_h are affected directly by temperature change. Both are usually increased by warming, although R_h often increases more rapidly in the short term (Woodwell 1995). In addition, warming can affect NPP and R_h indirectly by altering the ecosystem's moisture regime, nitrogen availability, length of its growing season, or species composition (Figure 1). Warming-driven changes in moisture, nitrogen, or species composition may also have intermediate effects on other ecosystem processes or states (e.g., litter quality and quantity, which affect both R_h and nitrogen mineralization), leading to multistep indirect effects including losses of carbon through fire or leaching and changes in the balance of NPP and R_h (Melillo et al. 1990, Chapin et al. 1997).

For many ecosystems, the indirect effects of a temperature increase on carbon balance are likely to be more important than the direct effects. Nutrient-limited tundra and northern forest ecosystems, for example, are much more responsive in the short term (1–10 years) to changes in nutrient availability, which is likely to increase with soil warming, than to the direct effect of increased temperature (Clark and Rosswall 1981, Chapin 1983, Jonasson and Shaver 1999). In many dry ecosystems, increased evaporative water loss at higher temperatures, resulting in dryer soils, may strongly limit soil and plant processes so that potential temperature-driven increases in process rates are not achieved (Mooney et al. 1999, Saleska et al. 1999). Finally, changes in temperature may alter species' competitive interactions and the activity of herbivores and pathogens (Mooney et al. 1991, Smith et al. 1997, deValpine and Harte in press), leading to changes in light, water, and nutrient limitations with complex long-term effects on carbon turnover, NPP, and R_h (Herbert et al. 1999).

Variable time scales of responses to warming

Warming will affect essentially all ecosystem processes and organic matter pools but at different rates. Because the processes and pools are linked to each other through biogeochemical cycles, the magnitude and even the direction of the net change in the ecosystem may vary over time. For example, NPP is affected by processes operating over a wide range of time scales, from the very short-term responses of leaf-level photosynthesis to the long-term changes in storage and turnover of soil nitrogen stocks (Figure 2). Although in most ecosystems the immediate effect of warming may be to increase NPP through increased photosynthesis, in the longer-term the uptake and accumulation of nitrogen in plant biomass (particularly in forests) might reduce the possibility for further increases in NPP by reducing nitrogen availability. Eventually, changes in species composition or litter quality might lead to further increases or decreases in NPP through changes in plant biomass (and nutrient) turnover

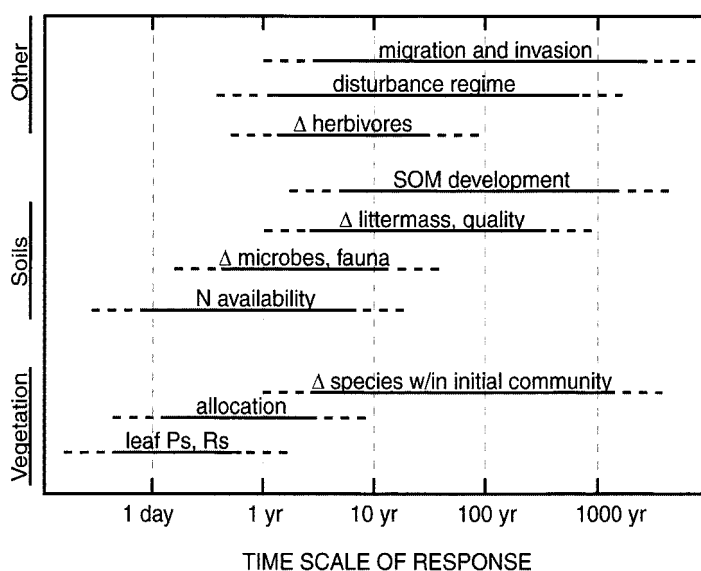


Figure 2. Time scales of response to temperature change by various ecosystem processes and components. Each of the processes or components shown in the figure affect net ecosystem production either directly or indirectly. For convenience, they are grouped into categories: vegetation, soils, and other. The intent is to show how different processes and components respond to temperature change at different rates; hence, the overall ecosystem response (the result of the individual responses and their interactions) may be very different in the long-term versus the short-term. Many other processes and components could be added to this figure. (Ps, photosynthesis; Rs, respiration; SOM, soil organic matter.)

or changes in litter decomposition and nitrogen mineralization. In some ecosystems (e.g., boreal forests), the increasing fuel load associated with biomass increase may increase the likelihood of fire and therefore the proportion of stands with low carbon storage on the landscape. Thus, the principal long-term mechanisms of regulation of NPP and overall carbon balance with respect to temperature may be very different from the short-term mechanisms (McKane et al. 1995, Braswell et al. 1997, Rastetter et al. 1997).

The time scales of response of individual processes should also vary among ecosystems, adding further complexity to long-term prediction of changes caused by warming (Figure 2). For example, in ecosystems where the dominant species in the vegetation are long-lived trees, changes in species composition might have relatively minor effects on NPP in the first few decades of warming, but changes in biomass allocation within the existing dominants might have major effects. Principal controls over nitrogen availability in such forests might lie in controls over turnover of existing large soil nitrogen pools. On the other hand, the changes in species composition in an annual grassland with a relatively small soil organic matter

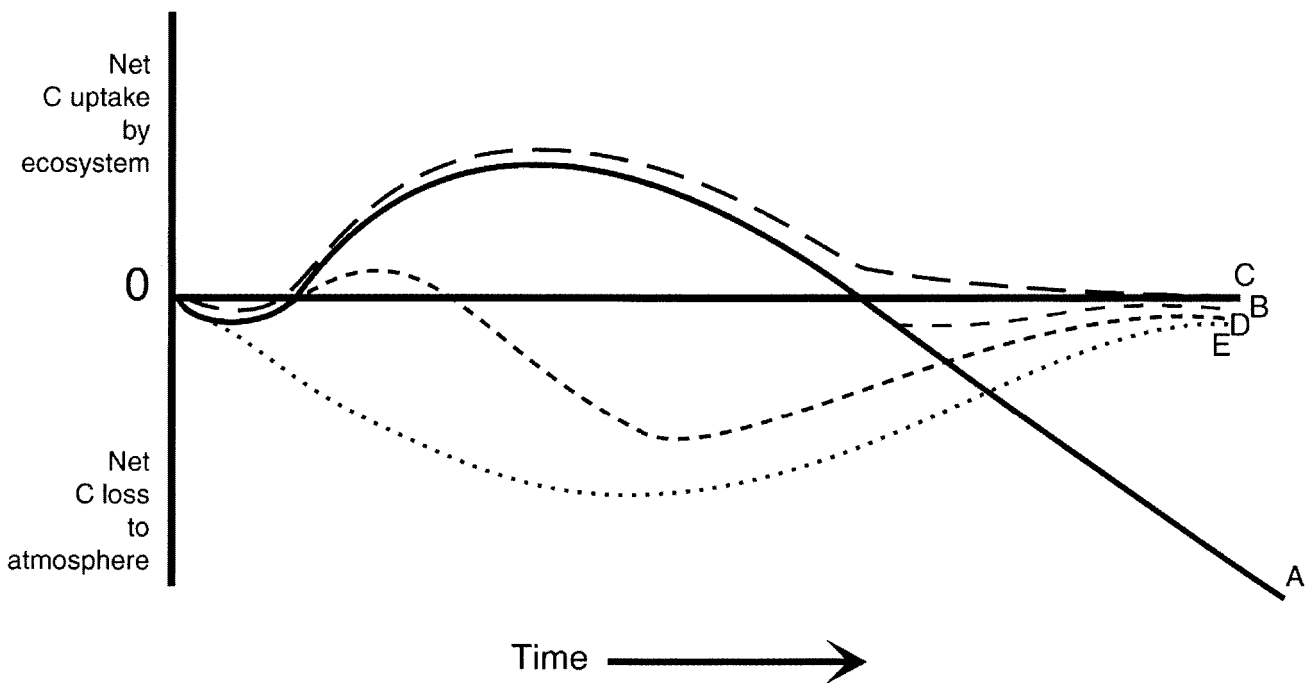


Figure 3. Changes in net ecosystem production (NEP, the net exchange of carbon between an ecosystem and the atmosphere) over time in response to warming. There is a net carbon uptake by the ecosystem when NEP is positive; when NEP is negative, there is a net carbon loss. The different lines represent qualitative differences in response (and predicted long-term responses) to experimental warming by different ecosystems, as discussed in the text. Harvard Forest, lines A, B; Toolik Lake, lines C, D; Great Dun Fell, lines D, E; Colorado subalpine meadow, line C; Abisko, line C.

pool could be more important to NPP, and changes in soil nitrogen turnover less important, within the first decades.



Figure 4. Harvard Forest Soil Warming Experiment, Massachusetts, showing early spring greening of forest floor. In this experiment, electric heating cables are buried 10 cm beneath the soil surface and 10 cm apart, along lines indicated by the string laid out on the surface. Photo: Kathy Newkirk.

Ecosystem warming experiments, if continued over several years, can capture much but not all of this changing sequence of responses to temperature change (Figure 2). Changes in basic metabolism (such as photosynthetic acclimation to temperature) may take place over less than 1 year and will be missed by annual sampling schedules, but these short-term responses may have less net impact on long-term change in ecosystem properties than the warming-induced rearrangement of ecosystem carbon and nutrient stocks and species composition, which takes place on a time scale of 1–100 years. Some changes, especially those occurring over very long time scales (e.g., soil profile development and organic matter accumulation) or large spatial scales (changes in fire regime or long-distance movements of large herbivores or timberlines) will not be picked up by experiments and must be investigated in other ways.

Examples of warming responses: Case studies

Despite the complexities of ecosystem responses to warming, an important goal of ecosystem science should be to predict which *kinds* of ecosystems are more or less responsive to warming, and to identify the characteristics of ecosystems that cause them to be more or less responsive. Our present ability to do so is limited, but evidence indicates that ecosystem responses to warming are strongly affected by initial conditions, including:

- Stocks and initial turnover rates of labile carbon in the soil
- Stocks and initial turnover rates of labile nitrogen in the soil
- Relative size of the carbon pools of plants and soil
- Dominant form of available nitrogen in the soil (e.g., organic nitrogen, ammonium, nitrate)
- Soil water and precipitation regime
- Chemical composition and turnover rates of live plant tissues and litter
- Longevity of individuals and population turnover rates of dominant plant species

The effects of these initial conditions on the response of ecosystems to warming can be illustrated by comparing changes in NPP, NEP, or R_h over time in contrasting ecosystems that have been manipulated experimentally. This approach has already led to useful insights, as shown by the following examples and illustrated in Figure 3.

Nitrogen redistribution model (Harvard Forest, Massachusetts, United States). At Harvard Forest in central Massachusetts (a temperate deciduous forest ecosystem), a long-term soil warming experiment used electric heating cables buried in the soil to elevate soil temperatures at a depth of 10 cm by 5 °C above ambient (Figure 4; Peterjohn et al 1994, Melillo et al. 1995). At this site, the important initial conditions include:

- Relatively small labile soil carbon pool
- Large, slow-turnover vegetation carbon pool
- Relatively large soil nitrogen pool
- Ammonification-dominated nitrogen mineralization sequence

These initial conditions constrain how the Harvard Forest ecosystem responds to soil warming over time, such that a three-phase transient pattern of changes in carbon storage results (Figure 3, line A; Melillo et al. in press). During Phase I, the labile carbon pool is rapidly oxidized by decomposing organisms, leading to a short period of net carbon loss. In Phase II, nitrogen is transferred from the soil, which has a low C:N ratio, to the vegetation, which has a high C:N ratio. This redistribution of nitrogen results in net carbon storage at the ecosystem level, although there is a loss of soil carbon (Rastetter et al. 1991, 1997). During Phase II there is no significant loss of nitrogen from the ecosystem because the system has an ammonium economy. If the system had a nitrate economy or a mixed ammonium–nitrate economy, nitrogen could be lost from the system by leaching or denitrification and so reduce the nitrogen available to promote carbon storage. Eventually, the labile and metastable nitrogen pools in the soil decrease to the point where very little nitrogen can be redistributed from the soil to the plants. At this point, the ecosystem may begin to lose carbon overall (i.e., NEP becomes negative) because of increased respiratory losses from plants and soils (Figure 3, line A). This decline may



Figure 5. The Toolik Lake Field Greenhouse Experiment in moist tussock tundra vegetation, Alaska, showing moderately increased abundance of deciduous shrubs and total vegetation mass. The photograph was taken in 1999, after 11 summers of warming. Photo: Gus Shaver.

be reversed if external nitrogen inputs (deposition or fixation) are available or if plant biomass is lost due to disturbance such as a hurricane or insect attack and is decomposed, releasing nitrogen once again (Figure 3, line B).

Nitrogen redistribution with variable moisture regime (Toolik Lake, Alaska, United States). In a moist tundra ecosystem at Toolik Lake in northern Alaska, responses to warming were studied using small greenhouses to increase air temperature during the growing season by 3–5 °C (Figure 5). The soil organic matter pool of this ecosystem is larger and contains even more labile carbon and nitrogen than the soils of many northern temperate forests (Giblin et al. 1991). Decomposition and nitrogen mineralization in tundra is strongly limited by low soil temperatures and high soil moisture (Nadelhoffer et al. 1992). Thus, if soil organic matter turnover is increased due to warming, there is a high potential for redistribution of nitrogen from soils (with low C:N ratio) to vegetation (with high C:N ratio), resulting in net carbon storage with little or no net change in ecosystem nitrogen stocks (Shaver et al. 1992). This response, however, is strongly interactive with soil moisture, with a relatively small temperature response if the soil is saturated (Nadelhoffer et al. 1992).

Experimental results (Chapin et al. 1995, Shaver et al. 1998) and modeling (McKane et al. 1997a, 1997b, Rastetter et al. 1997) indicate a multiphase response of NEP to warming in this tundra ecosystem that is quite similar to that at Harvard Forest, as long as soil moisture does not change greatly (Figure 3, line C). Similar results have also been obtained in the long-term monitoring and modeling



Figure 6. Infrared heaters in place above subalpine meadow vegetation, Colorado. Photo: Taylor Ricketts.

studies by Oechel and coworkers (e.g., Vourlitis and Oechel 1997, 1999, Waelbroeck et al. 1997). The initial response to warming is a large increase in R_h , leading to a decrease in NEP for the first 1–3 years (Phase I). Increased soil respiration, however, is accompanied by increased



Figure 7. Smaller plastic greenhouses and burlap-covered shade frames at the subarctic heath site, Abisko, Sweden. Photo: Sven Jonasson

nitrogen mineralization, leading to increased plant nitrogen uptake and increased NPP after 3–10 years (Phase II). Further increases in NPP are limited by other factors (e.g., light). Increased NPP leads to increased litter production, which eventually leads to higher R_h , and NEP returns to near zero (Phase III) after approximately 50–100 years.

Changes in NEP in response to warming of moist tundra may be very different if there is an interaction between

warming and soil moisture (Billings 1987, McKane et al. 1997b, Vourlitis and Oechel 1999). Warming combined with decreased soil moisture will cause a long-term loss of both carbon and nitrogen because of large increases in R_h combined with losses of mineralized nitrogen by drainage from the system, especially in areas where thaw depth increases greatly. (In such areas nitrogen losses may include large amounts of dissolved organic nitrogen, the product of incomplete mineralization.) In this scenario, increases in nitrogen uptake and NPP in Phase II are insufficient to compensate for nitrogen and carbon losses in leaching and respiration, so that even though the ecosystem eventually returns to an equilibrium where NPP equals R_h (NEP = 0), over 50–100 years there is a net loss of carbon to the atmosphere (Figure 3, line D).

Partial decay of large carbon pool (Great Dun Fell, United Kingdom).

In an upland grassland system at Great Dun Fell in the United Kingdom, a combination of approaches was used to assess the impact of global warming on ecosystem carbon stores and soil water quality. In one, intact vegetation/soil monoliths were moved down an altitudinal gradient (Ineson et al. 1998a); in another, *in situ* warming using electric heating cables (Ineson et al. 1998b) was applied. Both approaches were tested in several different vegetation/soil systems, including a mineral acidic brown earth and a peaty stagnohumic gley. Results after 3 years of the heating treatments were qualitatively similar to those predicted for the arctic tundra under warming combined with reduced soil moisture (Figure 3, line D), but the net carbon losses were even larger.

All systems at Great Dun Fell showed an increase in plant biomass under the warmer conditions, but major reductions in the total carbon content of the peaty gley (approximately 10% reduction in 3 years) demonstrated the vulnerability of the carbon stored in this particular soil. The increases in temperature, which stimulated the mineralization of organic matter and release of nutrients, significantly improved plant growth, but these increases in carbon fixation were insufficient to replace the carbon lost through increased decomposition. These increases in decomposition were caused by generally greater soil biological activity and, in particular, by population increases and changes in vertical distribution of the enchytraeid worm *Cognettia sphagnetorum* (Briones et al. 1998). These large losses in total soil carbon stocks clearly cannot continue; eventually, the soils are expected to stabilize at a lower carbon content analogous to the pattern shown in Figure 3 (line E) and by the native soils at the lower end of the same altitudinal gradient.

Species changes affect ecosystem carbon storage (subalpine meadow, Colorado, United States).

In a subalpine meadow ecosystem in Colorado, Harte and colleagues have used overhead infrared heaters to warm both soil and vegetation year-round since 1991 (Figure 6), causing significant changes in NPP and NEP (Harte et al. 1995,

Saleska et al. 1999). In contrast to the previous examples, a principal mechanism driving the changes in Colorado is the effect of the vegetation on species growth rates and functional type composition (Harte and Shaw 1995, deValpine and Harte in press). A 12% loss of soil carbon in the top 15 cm of the heated plot soils was observed after 4 years of treatment (Scott Saleska and John Harte, University of California–Berkeley, unpublished data). This initial loss of soil organic matter was not driven by a warming-induced increase in heterotrophic respiration because the positive effect of a temperature increase on R_h was cancelled by the negative effect of soil drying. Instead, this initial loss of soil organic matter was driven mainly by the effect of warming on the rate of litter input to the soil. In particular, warming induced a shift from more productive forbs to less productive shrubs. However, litter produced by forbs is more easily decomposed than litter produced by the shrubs, which has a higher lignin:nitrogen ratio. Thus, the loss of soil organic matter is likely to be a transient effect, with the recalcitrant litter input from shrubs causing an increase in soil organic matter over the long term, and ultimately in an overall pattern of change in NEP similar to that in Figure 3 (line C).

By comparing responses observed in the warming experiment to changes in microclimate, soil organic matter, and vegetation species composition along a natural elevation gradient, Harte and colleagues have shown that the combined use of manipulations and gradient studies can provide a unified picture, partitioned into short and long-term components, of how climate change influences soil organic matter. The research shows how the impacts of warming on carbon cycling can be dominated by the indirect effect of a warming-induced shift in relative species composition on the quantity (short term) and quality (longer term) of litter input to the soil.

Exploitation of available space (Abisko, Sweden).

In low-biomass ecosystems where the surface of the soil is partially bare, warming brought about by increasing plant cover may cause increases in NEP. In tundra heath and fell field ecosystems at Abisko, Sweden, warming with small plastic-covered greenhouses caused such an increase in plant cover (Figure 7). Plant biomass, driven in part by temperature-related increases in plant nitrogen uptake, increased almost twofold within 5 years (Jonasson et al. 1999).

The response of biomass to warming at Abisko was similar to that in the tussock tundra at Toolik Lake, although the response at Abisko was greater and NPP increased without any pronounced changes in species composition. Overall, the response followed the curve represented in Figure 3 (line C); initial declines in carbon stocks were not observed because the experiment was not sampled immediately. The longer term (more than 10 years) response is expected to level off and reach an equilibrium at a net carbon accumulation rate close to zero when the available space has been occupied by plants.

Initial increases in biomass in response to warming need not be a continuous process over time, particularly not in the northernmost ecosystems where the plants operate close to the limit of their cold tolerance. For instance, an increase in biomass similar to that at Abisko took place over several years in a poorly vegetated high arctic semi-desert; however, after an unusually mild and rainy growing season, much of the increase was lost in warmed and watered plots. The loss in biomass presumably occurred because winter hardening in the experimental plots was delayed and the plants suffered frost damage when the winter set in (Robinson et al. 1998), reflecting a possible effect of stochastic “extreme events.” Such events are likely to be of great importance in climatic regimes close to the tolerance limits of plants. Under such regimes, carbon pools in the living plant biomass may fluctuate between phases of accumulation and abrupt decline, never stabilizing at zero net accumulation, while soil organic matter is built up stepwise during the periods of plant die-back.

Experiments, data, and synthesis needs

Past warming experiments have used a variety of heating methods, including electric resistance heating, infrared irradiation, reciprocal transplants, and open- and closed-top field greenhouses (Table 1). Some experiments have warmed only portions of the ecosystem. Others have warmed the ecosystem for only part of each day or year. In most cases, the choice of warming method is constrained by logistical and engineering considerations (e.g., availability of electric power, difficulty of enclosing an entire forest, and the initial interests of the investigators). No one method perfectly simulates the expected climatic changes, but all have yielded useful results that, with cautious interpretation, have begun to reveal similarities, differences, and patterns of response among the ecosystems studied. Although there is considerable intellectual appeal to designing future experiments that use a common methodology and realistic simulation of expected change, it also is true that different warming methods illuminate different aspects of the overall warming response. To optimize intercomparisons, future research should include a mix of common manipulations in diverse ecosystem types. Future research should also include manipulations designed to provide focused insights into individual ecosystems or key processes.

Several networks and consortia are already working to meet the need for a global understanding of ecosystem responses to climate change (Ingram et al. 1999). The International Tundra Experiment (ITEX) uses passively warmed, open-top chambers in 26 different arctic and alpine tundras to compare the effects of warming on plant growth and flowering (Henry and Molau 1997, Arft et al. 1999). A broader-based Network of Ecosystem Warming Studies (NEWS) is being developed as part of the Global Change and Terrestrial Ecosystems (GCTE) Core Project of the International Geosphere–Biosphere Program

(IGBP). Most warming experiments to date, however, have taken place in north temperate, boreal, and arctic ecosystems, which are cool and moist and where NPP is strongly nutrient-limited. Although the processes that dominate the warming responses of these ecosystems are important everywhere, they may not dominate in other ecosystem types. In warm and dry regions, including Mediterranean or desert ecosystems, and in tropical, humid ecosystems, indirect warming effects acting through changes in evapotranspiration and soil dryness will play a major regulatory role. We also might expect the direct effects of warming on NPP to be relatively smaller in these warm systems because temperatures are already near optimum for photosynthesis. NPP might even decrease due to overheating in the warmest ecosystems or microenvironments. Additional experiments and networks are needed to expand the range of ecosystems studied, including studies of vegetation with contrasting plant life histories (e.g., annual versus perennial grasslands, woodlands, and evergreen versus deciduous vegetation).

New methods are also needed for the quantitative synthesis of data from different studies of temperature effects on ecosystems. Comparisons among different simulation models have also yielded important insights (Schimel et al. 1997). Some relatively new simulation models are

designed to facilitate comparisons among ecosystems and to predict their responses to temperature change within a common model structure (e.g., Rastetter et al. 1991, Williams et al. 1997). New statistical methods can also be used to search for and explain general patterns in diverse data sets. For example, we might want to know the average effects of experimental warming treatments on NPP across a group of studies and the extent to which those effects differ in biomes at different latitudes or with different moisture regimes. Ecologists have begun to use meta-analysis statistics to synthesize experimental data from many independent studies to answer these kinds of questions (Arnqvist and Wooster 1995, Gurevitch and Hedges 1999), including plant responses to warming in ITEX (Arft et al. 1999).

Finally, there is a need to extrapolate experimental results over longer time scales and over larger landscapes and regions. An excellent way to do so is to combine experimentation with measurement of ecosystem properties and processes along environmental transects such as the IGBP-GCTE Terrestrial Transects (Steffen et al. 1999). The transects are assumed to mirror longer-term (decades to centuries) responses of vegetation and soils to environmental conditions, whereas warming experiments reflect responses over the shorter-term (years to decades).

Table 1. Comparison of currently used methods for experimental warming of terrestrial ecosystems

Method	Mechanism of warming	Advantages	Disadvantages	Examples
Field greenhouse	"Greenhouse warming" (i.e., reflection of reradiated infrared energy and reduced advective energy loss)	Simple and inexpensive; requires no electrical power	Little or no temperature control and large temperature variability; other artifacts include altered light, wind, humidity, and precipitation regimes	Chapin et al. 1995, Shaver et al. 1998, Jonasson et al. 1999
Passive Open-top Chamber (OTC)	Same as above	Same as above	Little or no temperature control; altered wind and humidity; only small areas can be manipulated uniformly	Marion et al. 1997, Arft et al. 1999
Active Open-top Chamber (OTC)	Same as above plus warming by advection of electrically heated, forced warm air	Precise control of air temperature or temperature difference; may be combined with CO ₂ control	Altered wind regime, humidity, and evapotranspiration	Norby et al. 1997
Active Soil Warming	Warming by conduction from buried electrical resistance cables	Precise control of soil temperature or temperature difference; may be combined with greenhouses or OTCs	Altered soil moisture regime; no effect on aboveground temperatures	Peterjohn et al. 1994, Ineson et al. 1998b, Hartley et al. 1999
Electric infrared heat	Warming by increased infrared radiation	Precise control of energy input; direct simulation of global change in energy balance	Warming depends entirely on radiation; no change in advective energy inputs	Harte et al. 1995, Harte and Shaw 1995
Reciprocal or one-way transplantation 1999	Transplantation of plants, soils, or whole plant-soil locations	Comparison of relatively natural temperature gradient systems to warmer or cooler	Disturbance effects; multiple environmental changes make it difficult to assign specific causes to responses observed	Ineson et al. 1998a, Grogan and Chapin

Combined information from experiments and transects may thus be useful in distinguishing relatively short-term, transient changes in the experiments from longer-term, near-equilibrium changes. For example, global analyses of primary production (NPP; Figure 1) and litter (the major contributor to R_h ; Figure 1) have shown that both are reasonably well-predicted by actual evapotranspiration (Lieth and Whittaker 1975, Meentemeyer 1984). Although short-term responses of NPP and R_h to experimental warming may not have the same relationships with actual evapotranspiration as do undisturbed ecosystems, convergence toward the predicted relationship might be a useful measure of expected future change in the experiments.

Ultimately, experimental and analytical approaches should be combined with large-scale monitoring of variables and processes that experimental studies have identified as critical indicators of ecosystem change. The combination of global monitoring with ongoing experimental data acquisition, meta-analysis, modeling, and other data synthesis efforts would provide an early warning system to detect and potentially mitigate these ecosystem responses.

Field stations, long-term ecological research sites, and nature reserves already exist in many relatively unmanaged landscapes. Collecting simple baseline data and monitoring annually or even less frequently would not be very expensive, although data quality may be highly variable (e.g., Stohlgren et al. 1995). Efforts to coordinate data and establish protocols for data sharing might be daunting, but the resulting information would be immensely valuable: responses of species, communities, and biogeochemical processes to climate change could potentially be detected decades earlier than they would be otherwise.

Interactions with other drivers of global change

Changes in temperature are now occurring simultaneously with other types of global change. It will not be possible to fully understand and predict ecosystem responses to temperature change without taking into account the interactions with the other components of global environmental change (Koch and Mooney 1996, Sellers et al. 1997, Vitousek et al. 1997, Luo and Mooney 1999). For example, increases in atmospheric CO_2 may modify plant tissue chemistry and ecosystem water balance, both of which may in turn modify responses to warming. Length of the growing season may increase with warming, or it may decrease as drought duration increases, altering NPP, NEP, and other processes. Many regions of the globe are experiencing increased levels of nitrogen deposition, and the nature of the nitrogen economy of an ecosystem is an important factor in determining responses to other environmental factors (Aber et al. 1998).

Changes in land use and disturbance regime may also influence responses to warming. For instance, land clearing over very large areas may modify local temperature or

precipitation regimes beyond what would happen with climate change alone. Similarly, changes in fire regimes could be caused by and affect ecosystem responses to warming. The spread of invasive species will also be affected by both warming and land use change.

Some interactions between warming and other global changes are predicted more readily than others. For example, outbreaks of insects or pathogens that kill the dominant plants and increase fire probability would lead to dramatically different results than the phased changes in response to warming alone. We must expect some surprises.

Clearly, it will not be possible to incorporate all important dimensions of global change into experiments. It will rarely be feasible to include more than one or two factors in addition to temperature (e.g., CO_2 concentration or nitrogen level) as experimental factors (Schulze et al. 1999). However, through the use of combinations of experiments, gradient studies, remote sensing, and simulation modeling, it should be possible to make substantial progress toward developing a mechanistic understanding of the most important interactions (Canadell et al. 2000).

Although much current global change research focuses on feedbacks from terrestrial ecosystems to climate through greenhouse gases, important feedbacks also exist through changes in vegetation structure, surface energy balance, and water balance. Leaves in the canopy act as surfaces for energy and mass exchanges with the atmosphere, and changes in canopy density and transpiration in response to warming will change the energy and mass fluxes (McFadden et al. 1998). One of the most important and obvious effects of changes in the canopy is its albedo (i.e., the fraction of incoming solar radiation that is reflected). Decreasing albedo through increased leaf density will increase net radiation (solar radiation absorbed by the system). The increased net radiation must be dissipated through one or a combination of three major energy pathways or fluxes: sensible heat (actual warming of the air), latent heat (evapotranspiration), and ground heat (warming the soil). If increased evapotranspiration decreases soil moisture, and species changes result in better stomatal control of water loss, the result will be increased sensible heat flux to the atmosphere. Foley et al. (1994) illustrated the importance of such a change during the last temperature optimum in the Holocene approximately 6000 years ago. Latitudinal treeline advanced significantly, greatly reducing albedo. The increased soil temperature and sensible heat flux from this vegetation change was as great as the solar forcing believed to be responsible for initiating the climate change. Similarly, further loss of soil moisture in dry systems will decrease latent heat flux, with more energy dissipated as sensible heat. Current understanding of these types of feedbacks on climate change (i.e., those operating through changes in surface energy and water balance) is less advanced than that of feedbacks through greenhouse gas fluxes and should be a particularly high priority for future research.

Conceptual framework for analysis of ecosystem response to changing temperature

A. Complexity

- *Spatial and temporal variation:* Global temperature changes will not be uniform, with most regions warming by varying amounts but others cooling. These changes will occur over a range of natural temperature regimes and annual temperature variations that are greater than the expected average temperature change.
- *Direct and indirect effects:* Because temperature affects virtually all ecosystem processes, indirect temperature effects resulting from interactions among processes are likely to be very important, especially in the long term.
- *Variable time constants of response:* Diverse ecosystem processes have different time constants for response to temperature. Thus, initial, overall ecosystem responses to change are not reliable indicators of long-term responses because they represent only part of the total response.

B. Responses

- *Initial response a function of initial conditions:* The same temperature change applied to different ecosystems will elicit different responses depending on initial position on the temperature response surface (direct effects) and on initial biogeochemical conditions and composition (indirect effects).
- *Changing sequence of controls:* The dominant controls over ecosystem response to temperature will change over time, as different processes change at different rates. This changing sequence will not necessarily be the same in all ecosystems.
- *Changing direction as well as magnitude of response:* Initial losses or gains of carbon by the ecosystem may be reversed over time as indirect effects and slowly changing components of the ecosystem come into play.
- *Species changes can affect biogeochemistry:* Changes in species composition and abundance will affect ecosystem functions (net primary production, carbon and nutrient cycling, energy fluxes) through changes in tissue chemistry, demography (both parts and individuals), turnover rates, and vegetation structure (physiognomy, leaf area index).
- *Response is predictable (at least qualitatively) from initial conditions:* Key variables include initial temperature regime, initial carbon and nutrient pool sizes and turnover rates, and initial population dynamics of vegetation.

Conclusions

Because temperature has a direct effect on virtually all ecosystem processes, responses of terrestrial ecosystems to global warming will be even more complex and difficult to predict than responses to increased atmospheric CO₂ concentrations. Nonetheless, a useful conceptual framework for analysis, comparison, and prediction of responses to warming is beginning to emerge (see box this page). For now, the principal applications of this framework are as a statement of the major dimensions of complexity of the ecosystem warming response and as a reminder of the major constraints on long-term predictions based on relatively small-area, short-term experimental studies. A key need is to further develop our understanding of how initial climate, biogeochemical states, and species characteristics might be used to generate long-term predictions of relative sensitivity to climate change. Such a framework would serve as a heuristic guide to new research.

We also need improved models of the temporal sequence of ecosystem responses to temperature change because it is increasingly clear that long-term responses to warming and increased CO₂ may differ greatly in both magnitude and direction from initial responses. Ecosystem-level experiments are a useful tool for developing this understanding; a broader array of experiments in contrasting ecosystem types is needed, including both whole-system manipulations and more focused experimental treatments. Also needed are the transect studies, long-term monitoring, and the development of research networks that will allow spatial extrapolation and validation of predictions based on intensive experimental studies.

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