

Consequences of climate change for biogeochemical cycling in forests of northeastern North America¹

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Abstract: A critical component of assessing the impacts of climate change on forest ecosystems involves understanding associated changes in the biogeochemical cycling of elements. Evidence from research on northeastern North American forests shows that direct effects of climate change will evoke changes in biogeochemical cycling by altering plant physiology, forest productivity, and soil physical, chemical, and biological processes. Indirect effects, largely mediated by changes in species composition, length of growing season, and hydrology, will also be important. The case study presented here uses the quantitative biogeochemical model PnET-BGC to test assumptions about the direct and indirect effects of climate change on a northern hardwood forest ecosystem. Modeling results indicate an overall increase in net primary production due to a longer growing season, an increase in NO_3^- leaching due to large increases in net mineralization and nitrification, and slight declines in mineral weathering due to a reduction in soil moisture. Future research should focus on uncertainties, including the effects of (1) multiple simultaneous interactions of stressors (e.g., climate change, ozone, acidic deposition); (2) long-term atmospheric CO_2 enrichment on vegetation; (3) changes in forest species composition; (4) extreme climatic events and other disturbances (e.g., ice storms, fire, invasive species); and (5) feedback mechanisms that increase or decrease change.

Résumé : Une composante critique de l'estimation de l'impact des changements climatiques sur les écosystèmes forestiers implique la compréhension des changements associés au cycle biogéochimique des éléments. Une recherche conduite dans les forêts du nord-est de l'Amérique du Nord montre clairement que les effets directs des changements climatiques entraîneront des changements dans le cycle biogéochimique en altérant la physiologie des plantes, la productivité forestière et les processus impliqués dans la physique, la chimie et la biologie des sols. Les effets indirects engendrés surtout par des changements dans la composition en espèces, la longueur de la saison de croissance et le régime hydrique seront aussi importants. Une étude de cas est présentée ici à l'aide du modèle quantitatif biogéochimique PnET-BGC pour tester des hypothèses au sujet des effets directs et indirects des changements climatiques sur un écosystème forestier de feuillus nordiques. Les résultats des simulations permettent d'anticiper une augmentation générale de la production primaire nette causée par l'allongement de la saison de croissance, une augmentation du lessivage de NO_3^- due à de fortes augmentations de la minéralisation et de la nitrification nettes ainsi qu'une légère diminution de l'altération des minéraux due à une réduction de l'humidité du sol. Les recherches futures devraient être concentrées sur les incertitudes, lesquelles incluent les effets (1) des interactions multiples et simultanées des facteurs de stress (p. ex. : les changements climatiques, l'ozone, les dépôts acides), (2) de l'enrichissement à long terme en CO_2 atmosphérique sur la végétation, (3) des changements de la

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composition en espèces forestières, (4) des événements climatiques extrêmes et des autres perturbations (p. ex. : les verglas, le feu, les espèces invasives) et (5) des mécanismes de rétroaction qui augmentent ou diminuent ces changements.

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Introduction

Human activity has increased atmospheric greenhouse gas concentrations since preindustrial times, which, in turn, has led to a positive radiative forcing of climate. Observed changes in climate include a 0.75 °C increase in mean global temperature as well as shifts in global precipitation patterns (IPCC 2007). In northeastern North America, regional climatic, hydrological, and biophysical indicators are consistent with the global climatic trends. For example, Hayhoe et al. (2007) recently synthesized and analyzed historical records to show that surface air temperature in the northeastern United States has warmed by 0.8 °C over the twentieth century, with greater increases in winter temperature (1.2 °C) than summer temperature (0.7 °C). Precipitation has been more variable, with an overall increase of 100 mm for the twentieth century. Using a new statistical downscaling technique and simulations of twenty-first century climate from atmosphere–ocean general circulation models (AOGCMs) from the Intergovernmental Panel on Climate Change Fourth Assessment Report, Hayhoe et al. (2007, 2008) developed climate change projections for the northeastern United States (see www.northeastclimateimpacts.org). These projections suggest that temperature will continue to increase by 2.1–5.3 °C by 2100, depending on whether a lower (i.e., B1) or higher (e.g., A1FI) greenhouse gas emission pathway is followed. While precipitation is more uncertain, projections indicate that annual and winter precipitation will increase by 7%–14% and 12%–30%, respectively, while summer precipitation is expected to show little change. Plummer et al. (2006) computed similar increases in air temperature and precipitation for eastern North America (including Canada) using the Canadian Regional Climate Model.

Climate is a key regulator of most terrestrial biogeochemical processes and has the potential to markedly modify the function and services of forest ecosystems. Despite this critical role of climate, we lack a comprehensive understanding of potential ecosystem-level responses because of complex interactive effects and associated feedbacks. Undoubtedly, climate change will alter biogeochemical cycling, with potentially dramatic effects on forest productivity; soil physical, chemical, and biological processes; and stream-water quantity and quality. The goal of this review is to summarize the existing state-of-knowledge on how climate change affects cycles of elements at the ecosystem scale. This review draws largely on knowledge gained from long-term observations, experimental manipulations, and gradient and modeling studies. Additionally, we present a case study where the biogeochemical model, PnET-BGC, was run with newly generated climate predictions for the Hubbard Brook Experimental Forest (HBEF) in New Hampshire, USA. This example enables us to quantitatively estimate how ecological processes may respond to shifts in climate during the twenty-first century.

Although aspects of this analysis may apply to other regions, we focus on northeastern North America, defined for

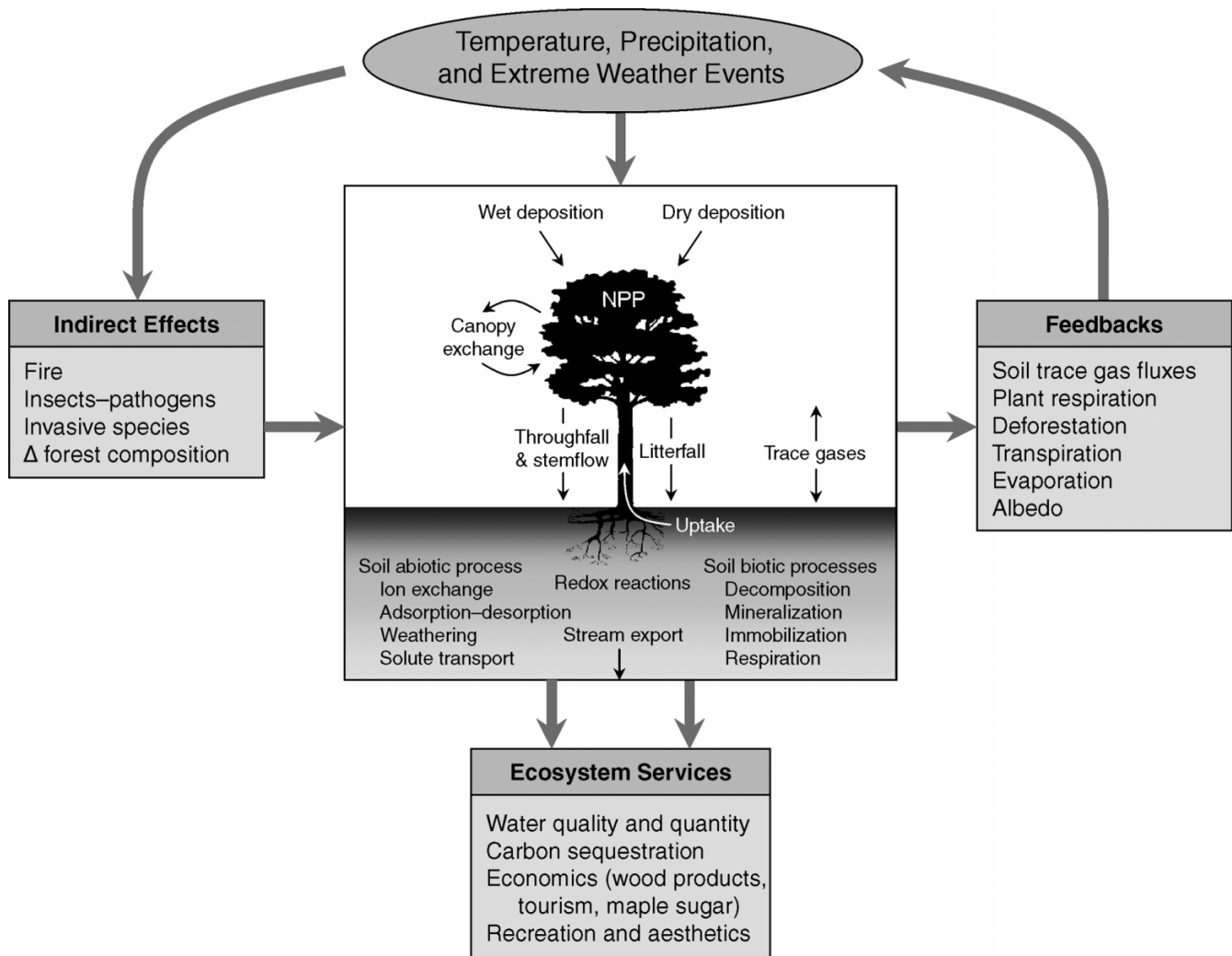
our purpose as the six New England states, New York, and eastern Canada (Quebec and the four Atlantic provinces). Understanding the consequences of climate change in this relatively populated region is important because there is an active effort to develop policies aimed at reducing carbon dioxide (CO₂) emissions. The governors of New England and premiers of eastern Canada approved a climate change action plan in 2001, which calls for a reduction in greenhouse gas emissions to 10% below 1990 levels by 2020. In a parallel effort, 10 northeastern states, with input from Canadian provinces, are implementing a CO₂ cap-and-trade program as part of the Regional Greenhouse Gas Initiative. This market-based approach is designed to reduce CO₂ emissions from electric power generators in participating states. Providing timely information on the effects of climate change is a necessary step in furthering regional strategies to reduce greenhouse gas emissions in the United States and Canada. This review and analysis will lead to a more comprehensive understanding of the ecological consequences of climate change and will help provide a foundation for future decision making about climate change policy.

Cascading effects of climate change on biogeochemical cycling

Biogeochemical responses to projected climate change are likely to be profound and complex. Change that occurs in one component of the ecosystem (e.g., soil) will likely affect other components (e.g., vegetation, stream water), causing a cascading sequence of effects. Some of the more important impacts of climate change on forest ecosystems can be illustrated with a conceptual model showing the major processes and functions anticipated to be affected (Fig. 1). These impacts include the direct effects of altered temperature and precipitation on hydrology and biogeochemical processes as well as acute disturbances stemming from weather-related phenomenon such as hurricanes, ice storms, droughts, and floods. Impacts of climate change also include indirect effects of varying intensity and duration. While these disturbances already have an inherent influence on hydrology and biogeochemical processes, climate change may accelerate the frequency or increase the magnitude of disturbances. Indirect effects consist of transient events such as fire and insect outbreaks, and may also include sustained disturbances such as more permanent shifts in ecosystem structure and function associated with changes in tree species composition (see Mohan et al. 2009), pests and pathogens, and invasive species (see Dukes et al. 2009).

While the focus of this review is on forest ecosystems, it is important to recognize that humans are an integral part of the ecosystem in northeastern North America. Central to the conceptual diagram are the ecosystem services that forests provide (Fig. 1), including benefits for water quality and quantity, carbon (C) sequestration, forest products, recreational opportunities, wildlife habitat, and aesthetics. A key to maintaining ecosystem services is to understand how eco-

Fig. 1. Conceptual diagram showing the direct and indirect effects of changes in temperature and precipitation on biogeochemical processes in forests and on the services forests provide. Also shown are feedbacks that further influence climatological effects.



systems will respond to climate change. The complexity of responses is compounded by other concurrent types of human-induced global change such as atmospheric ozone (O_3) concentrations, nitrogen (N) and sulfur (S) deposition, invasive species, and land disturbance. Additionally, there will be a human behavioral response to climate change, which can exacerbate (e.g., increased energy and water consumption, development of forest lands) or mitigate (e.g., technological advances) the problem.

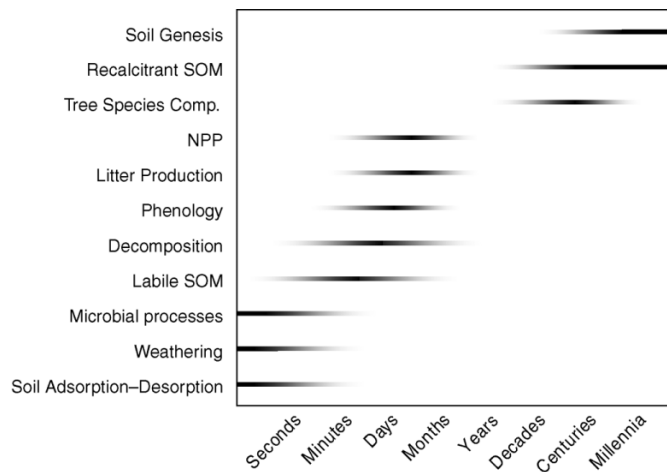
One of the most difficult factors to address in making predictions about biogeochemical responses to climate change is the importance of feedbacks that further influence climate (Fig. 1). For example, climate-induced ecosystem processes can either increase or decrease the release of trace gases (CO_2 , methane (CH_4), nitrous oxide (N_2O)) to the atmosphere. These gases, in turn, influence the amount of radiant energy trapped near the Earth's surface, causing further warming or cooling. Other feedbacks arise from changes in energy and water balances (e.g., albedo of snow and forest canopy, aerosol reflectance, transpiration, cloud cover, soil moisture). Compared with atmospheric trace gases, interactions of atmospheric aerosols and water vapor have received less attention, even though they can be substantial climate

drivers. While there has been much conjecture on the importance of feedbacks to the climate system, accurately quantifying responses remains a formidable task.

Time scales

Climate change is generally considered a slow process, involving relatively small changes in temperature and precipitation over long periods of time relative to natural variability. Despite these slow changes in climate, large variation exists in the response times of biogeochemical processes (Shaver et al. 2000; Fig. 2). For example, the reaction times of biogeochemical responses to changes in climate range from nearly instantaneous processes such as soil adsorption-desorption and microbial activity, to intermediate responses involving changes in vegetation that range from years to centuries, to much slower processes such as changes in recalcitrant soil organic matter (SOM) pools and soil genesis that occur over the millennia. During the past several decades, an increasing number of short-term and small spatial scale climate change experiments have provided useful information on ecosystem responses to climate, as well as valuable input to conceptual and empirical ecosystem, re-

Fig. 2. Timeline indicating when the initial effects of climate change are expected for selected ecological processes.



gional, and global-scale models (as reviewed by Rustad 2008). However, much less is known about direct and indirect responses to climate change over the long-term and at large spatial scales. Future environmental monitoring will be critical for documenting these fundamental changes over time (Lovett et al. 2007).

Overarching climate-induced controls of forest biogeochemistry

Changes in regional climate will likely result in changes in forest species composition, length of the growing season, and forest hydrology, which together exert significant controls on forest biogeochemistry.

Changes in species composition

Forests of northeastern North America include both northern hardwood and boreal and subboreal spruce–fir forests. Model results indicate that warmer temperatures will result in a general loss of more cold-tolerant boreal coniferous species, such as spruce and fir, as northern hardwood cover types move northward (Iverson and Prasad 1998; Mohan et al. 2009; Iverson et al. 2008). Additionally, areas that are now occupied by northern hardwood species may become more suitable for oak–hickory species that are currently found to the south of these areas. Related changes in species composition may also occur along elevational gradients, and tree lines may shift upslope (Walther et al. 2005). Since conifer and hardwood forests differ markedly in their structure and function, shifts in species composition within the region would impact nutrient cycling. For instance, conifer species have a greater leaf area index, which generally results in higher transpiration rates and dry deposition capture (Swank and Douglass 1974; Johnson and Lindberg 1992; Weathers et al. 2000). Additionally, coniferous litter decomposes more slowly and supports less biotic activity than deciduous litter (e.g., Pastor et al. 1984). There are also major differences in nutrient cycling among specific tree species. For example, watersheds dominated by sugar maple (*Acer saccharum* Marsh.) typically have higher rates of nitrification and N export than those dominated by oak and beech

(Finzi et al. 1998; Lovett et al. 2004; Christopher et al. 2006). Models indicate that sugar maple could be replaced by other species (Mohan et al. 2009), thereby offsetting increases in nitrification commonly associated with warmer temperatures. These examples demonstrate that the indirect effect of a change in species composition could be potentially quite important and could outweigh the direct effects of changes in climate alone.

Length of the growing season

The growing season is typically defined as the length of time between the last spring freeze and the first hard freeze of autumn when daily temperatures decrease to or below 2.2 °C (Schwartz et al. 2006). The length of the growing season has increased across the United States for roughly the last half century (Schwartz et al. 2006) and is expected to continue to increase in the northern hemisphere in the future (Tebaldi et al. 2006). For the northeastern United States and eastern Canada, the average growing season length was 184 days for the period 1961–1990 and is projected to increase by 29–43 days by the end of the twenty-first century (Hayhoe et al. 2007). Such an increase in the length of growing season would have a profound effect on many hydrologic and biogeochemical processes, including mean annual productivity, plant nutrient uptake, evapotranspiration, soil moisture, and streamflows with both potentially positive (e.g., increased net primary productivity (NPP)) and negative (increased pressure on water resources) impacts. In addition, some phenological events, such as bud break in spring and senescence and dormancy in fall, are controlled by a complex suite of environmental signals including photoperiod that are not subject to anthropogenic perturbation. Climatic warming can create a disjunction between the temperature and photoperiodic influences on phenology, and surprises such as insufficient winter chilling or untimely frosts could decrease NPP (Norby et al. 2000).

Changes in hydrology

Much like climate-induced changes in species composition, an altered hydrologic cycle also will affect biogeochemical cycling at many different levels. Drainage is a major pathway of element transport (Likens and Bormann 1995). As a result, future projected changes in the quantity and temporal distribution of precipitation could have a major impact on biogeochemical cycling in all ecosystem compartments.

Since air temperatures remain near freezing throughout winter across northeastern North America, small changes in climate could have a large impact on snow, an important component of the hydrologic cycle in this region. Snow insulates soils from cold winter air and can prevent the formation of soil frost, which alters physical and biological processes in soils (e.g., Groffman et al. 2001a). Additionally, the pulsed release of ions to streams during spring snowmelt can result in episodic acidification in acid-sensitive areas (e.g., Schaefer et al. 1990; Mitchell 2005). Acidic episodes can be caused also by rain-on-snow events (MacLean et al. 1995; Eimers et al. 2007), which are expected to become more prevalent in a warmer winter climate. The impact of climate change on the snowpack is unclear. Although warmer air temperatures would decrease snowpack depth and duration, these declines could be offset by increases in snowfall

due to greater amounts of winter precipitation projected with most model scenarios (Hayhoe et al. 2007, 2008). Additionally, for areas affected by large water bodies including the Great Lakes, increases in lake water temperatures can cause significant increases in snowfall (Leathers and Ellis 1996; Burnett et al. 2003).

Even though summer precipitation amounts are not expected to change significantly, the temporal distribution of precipitation will likely change. More specifically, rainstorms will be characterized by intense storms of shorter duration with intermittent droughty periods (Hayhoe et al. 2007, 2008; IPCC 2007). Higher air temperatures may also increase the frequency and severity of droughts by increasing the amount of water loss to the atmosphere via evapotranspiration. Other factors such as changes in vegetation biomass and species composition, as discussed previously, could alter evapotranspiration (Aber et al. 1995). Many biogeochemical processes are affected by drought, most notably rates of soil illuvial processes and oxidation–reduction reactions that are regulated by wet–dry cycles in soil. Other solutes, including nitrate (NO_3^-), dissolved organic carbon (DOC), and aluminum (Al), also can be readily mobilized during rainfall events (Watmough et al. 2004; Mitchell et al. 2006). Climatic conditions alter hydrologic flow paths that are known to have a marked impact on drainage-water solute concentrations and fluxes (McHale et al. 2002; Schiff et al. 2002; Christopher et al. 2008). The overall wetness and hence connectivity of a watershed to both soil water and groundwater sources also can affect solute chemistry in surface waters (Inamdar and Mitchell 2006; Inamdar et al. 2006). Overall, any change in climate that alters watershed hydrology also will influence solute dynamics in soil, ground, and surface waters.

Biogeochemical responses

Atmospheric deposition

Atmospheric aerosols and gases are deposited on forests in wet (rain, snow, cloud, fog) and dry (gas and particulate) forms. These materials serve as both sources of nutrients and pollutants in forest ecosystems. For instance, base cations and other elements in eolian dust add to the fertility of some ecosystems (Reynolds et al. 2006), and atmospheric S has been long recognized as an acidifying pollutant in many industrialized regions of the world (Likens and Bormann 1974; Galloway et al. 1984). Atmospheric N can cause both eutrophication and acidification (Driscoll et al. 2003), and can also stimulate forest growth and C sequestration (Magnani et al. 2007). Most research on climate effects on atmospheric deposition has focused on how tropospheric aerosols serve as feedbacks to the climate system. For example, sulfate aerosols scatter solar radiation, thereby creating a cooling effect (e.g., Myhre et al. 1998). Less is known about how climate change will affect atmospheric deposition. Since atmospheric chemical deposition is largely influenced by climatic variables (e.g., air mass movement, precipitation, clouds, relative humidity), changes in weather patterns will undoubtedly influence the transfer of atmospherically derived materials to forested landscapes. However, human impacts on atmospheric emissions will likely have a much greater influence than climate on atmospheric deposition.

Wet deposition

Wet deposition flux is calculated as the product of precipitation volume and associated solute concentrations. As such, the projected increase in precipitation amounts in northeastern North America is expected to increase wet deposition, provided that precipitation solutes are not diluted. Three-dimensional atmospheric chemical transport models have been used to predict how changes in climate will affect atmospheric deposition. In general, chemical transport model projections show that wet deposition is concordant with precipitation amounts (Langner et al. 2005). Similarly, the greatest inputs of major ions in northeastern North America occur during high-precipitation years, and concentrations of major ions are not negatively correlated with precipitation amounts, suggesting that limited dilution is associated with increases in precipitation quantity (Ollinger et al. 1993). Along with overall increases in the amount of annual precipitation, projected changes in the timing and intensity of precipitation events will influence the flux of atmospheric inputs. For example, mobile anions (i.e., NO_3^- and SO_4^{2-}) from atmospheric deposition will be transported more readily from soil during intense storms, thereby reducing opportunities for immobilization and ultimately increasing the potential for surface-water acidification (Chen et al. 1984).

During winter, decreases in chemical inputs in wet deposition will likely arise from a decrease in the ratio of snowfall to rainfall due to warmer temperatures (Huntington et al. 2004). Snowflakes have a greater surface area than raindrops and hence have a higher scavenging efficiency (Topol 1986; Dasch 1987). Consequently, the incorporation of atmospheric particles and gases in raindrops is lower than that in snowflakes, resulting in lower amounts of chemical inputs in wet deposition under a warmer climate scenario.

In addition to rain and snow, cloud and fog water also can be an important form of deposition in some areas, such as mountainous regions of northeastern North America, where it can exceed the sum of wet and dry inputs (Baumgardner et al. 2003). Cloud formation is a poorly understood process and has received recent attention because of the potential feedbacks to climate (IPCC 2007). While highly uncertain, changes in cloud cover due to climate change (see Huntington et al. 2009) may affect acidic deposition and deposition of other dissolved ions. Cloud water is characterized by high concentrations of cations, anions, and trace metals (Weathers et al. 1986), which may adversely affect forests through foliar loss of cations and other acidification processes (Joslin et al. 1988).

Dry deposition

Dry deposition is inherently difficult to measure directly. Estimates of this flux are typically calculated by multiplying atmospheric concentrations by modeled deposition velocities. Deposition velocities depend on the nature of the depositing substance, meteorological factors, and characteristics of the vegetation (Lovett 1994). As noted previously, climate change will likely alter tree species composition, which may, in turn, influence deposition velocities. A greater proportion of hardwood trees would cause a reduction in dry deposition, since broadleaf deciduous species have a lower leaf area index and are less efficient at scavenging airborne particulates compared with coniferous species (Weathers et al. 2000).

Climate change also is expected to cause changes in tree phenology. Numerous studies have demonstrated that the growing season is being extended in both spring and autumn as a result of recent warming trends, resulting in an earlier spring leaf-out date for hardwood species (e.g., Schwartz et al. 2006; Hayhoe et al. 2007). Consequently, even though deciduous species capture less dry deposition, there would likely be an extended period of dry deposition capture owing to an increase in canopy duration.

Throughfall and stemflow

As wet deposition passes through the forest canopy, its chemical composition can be altered considerably by exchange processes. Either throughfall ion enrichment or depletion can occur depending on the reactivity of ions and characteristics of the canopy (Houle et al. 1999). Consequently, an extended duration of deciduous green canopy would result in a reduction in inputs that are readily absorbed by the canopy (e.g., NH_4^+) and an increase in inputs that are readily leached by the canopy (e.g., DOC, potassium (K^+)). Shifts in tree species composition also will affect throughfall inputs (Houle et al. 1999). In much the same way, stemflow also would be affected by changes in tree species composition. However, stemflow generally accounts for a small percentage of incident precipitation (<5%) in northeastern North American forests (Eaton et al. 1973; Rustad et al. 1994); therefore, the effect of changes in stemflow will be small relative to the effects of changes in throughfall.

Vegetation

Aboveground biomass

Climate change will have marked impacts on forest vegetation, with broad ecological, economic, and social implications. Aforementioned changes in tree species composition and phenology, in addition to physiological changes, are addressed more thoroughly in the companion review paper by Mohan et al. (2009). For brevity, only a short synopsis of climate change effects on aboveground biomass is provided.

Aboveground plant biomass is influenced by climate at scales ranging from leaf to landscape. Difficulties in predicting the effect of climate change on forest productivity arise from the complexity of interactions associated with simultaneous changes in air temperature, atmospheric CO_2 , and the availability of water and nutrients. Photosynthesis is regulated by the exchange of water vapor and CO_2 transfer through leaf stomates. Increases in air temperatures increase stomatal water vapor losses and lower the water use efficiency of plants (i.e., moles of CO_2 fixed through photosynthesis per moles of water lost through transpiration). In contrast, increases in atmospheric CO_2 restrict the stomatal aperture of leaves, thereby limiting transpirational losses (Gedney et al. 2006) and increasing water use efficiency. This balance in the availability of CO_2 and water is a fundamental factor that controls the rate of photosynthesis.

Increases in atmospheric CO_2 and temperature should stimulate photosynthesis; however, other factors may become limiting such as nutrients or genetic restrictions. Single and multifactor field experiments have shown variable responses in NPP, but generally indicate an increase for woody plants (Norby et al. 2005). Past experiments have been limited in

scope because the high costs (especially for CO_2 enrichment) make it difficult to examine whole-forest responses over the long term. Consequently, it is uncertain how useful these experimental results are for extrapolating effects at more extensive spatial and temporal scales. One of the most vexing questions about the response of aboveground biomass to changes in climate and CO_2 is how effectively and rapidly plants will acclimate to changing conditions. Physiological acclimation can include the response of photosynthesis to increasing CO_2 , the response of photosynthesis to increasing temperature, and the response of autotrophic respiration to increasing temperature (see review by Rustad 2006).

Despite these uncertainties, forest ecosystem models have generally shown that future changes in climate will increase NPP in northeastern North America and that CO_2 growth enhancement effects can be nearly equal to or greater than the effects of climate change alone (e.g., Ollinger et al. 2008). Other global change processes can further increase (e.g., N deposition) or decrease (e.g., tropospheric O_3) forest productivity (Ollinger et al. 2002). Additional complexity results from forest disturbances associated with climate change such as catastrophic winds (Peterson 2000), insect outbreaks (Cooke et al. 2006), and ice storms (Rhoads et al. 2002) that cause physical damage to aboveground biomass (e.g., windthrow, defoliation, breakage) as well as invasion of exotic species (Lovett et al. 2006). These changes in aboveground biomass ultimately affect other biogeochemical processes, such as throughfall, litterfall, and root functioning.

Fine roots

Fine roots (<2 mm diameter) play a fundamental role in water and nutrient cycling in terrestrial ecosystems and serve as a sink for C, N, and other nutrients. For example, an estimated 33% of global annual NPP is used for the production of roots (Jackson et al. 1997), the global fine root C pool is approximately 5% of the size of the atmospheric C pool (Jackson et al. 1997), and root respiration constitutes ~50% of total soil respiration (Högberg et al. 2001), making it one of the largest fluxes in the global C cycle. Given their central role in water and nutrient dynamics, fine roots (and their mycorrhizal symbionts) will undoubtedly play a pivotal role in determining ecosystem response to a changing climate.

Temperature and moisture are fundamental mediators of belowground physiology. Temperature directly influences the timing of the initiation of root growth in the spring (Arft et al. 1999), the growth and metabolism of roots during the growing season (Burton et al. 1998), and the cessation of growth at the end of the growing season (Wells and Eissenstat 2001). Water directly affects soil aeration and redox status and nutrient availability through microbial and diffusive processes.

The overall effects of the projected warmer and drier summers and warmer and wetter winters on fine root dynamics are difficult to predict because of conflicting anticipated responses. Given that (1) the rate of extension of root length is generally positively related to soil temperature (up to a temperature optimum) (Pregitzer et al. 2000); (2) fine root respiration and fine root turnover tend to increase with increasing temperature (Zogg et al. 1996); and (3) the total production of fine roots is, in part, a function of the length of the growing season (Majdi and Öhrvik 2004), total grow-

ing season belowground C allocation and root production could be expected to increase under future climate scenarios. However, warmer temperatures (in the absence of severe moisture limitation) also increase rates of net N mineralization (Rustad et al. 2001) and thus increase N availability. Increased N availability has been, in turn, linked to reductions in fine root biomass (Nadelhoffer 2000).

The projected increased occurrence of short- and medium-term droughts also will likely affect fine root dynamics and nutrient uptake. Drought affects various physiological activities of roots, typically resulting in reduced root respiration and reduced water and nutrient uptake (Bryla et al. 2001; Rey et al. 2002; Borken et al. 2006a). Drought also reduces water films on soil particles, creating barriers to diffusion of nutrients. Although trees respond to longer-term drought by increasing fine root biomass and increasing rooting depth, evidence also indicates that shorter-term severe droughts can locally decrease fine root biomass owing to decreased root elongation, cavitation, and mortality (Jackson et al. 2000; Joslin et al. 2000). Root systems already reduced by warming-induced nutrient mineralization or elevated inputs of atmospheric N deposition may not be able to withstand reductions in water availability. Only a few studies, however, have evaluated consequences of the possible positive feedbacks between elevated nutrient availability and drought stress. Palatova (2002), for example, studied the response of Scots pine (*Pinus sylvestris* L.) saplings to drought (60% reductions in precipitation), N additions (100 kg-ha⁻¹·year⁻¹), and the combination of the two. Although all treatments resulted in significant declines in fine root biomass, the largest response was observed in the combined drought and N treatment, with a 30% decline in fine root biomass after 2 years.

Projected climate changes during winter will also likely impact root systems. Warmer winter temperatures, coupled with a greater amount of precipitation as rain versus snow, could, paradoxically, increase the risk of freezing injury because snow insulates soils (and roots) from cold winter air temperatures. For example, a snow removal experiment at the HBEF in New Hampshire caused increased soil freezing (Groffman et al. 2001a; Hardy et al. 2001), elevated overwinter fine root mortality (Tierney et al. 2001), and elevated leaching of N and P (Fitzhugh et al. 2001). Elevated nutrient leaching was attributed to the rapid decomposition of fine root necromass, decreased nutrient uptake by roots, and increased physical disruption of soil aggregates (Fitzhugh et al. 2001).

Mycorrhizal fungi

Mycorrhizal fungi form symbiotic associations with roots whereby they obtain carbon from plants and in return provide plants with water and nutrients. Both ectomycorrhizal and arbuscular mycorrhizal fungi are ubiquitous in forests of northeastern North America and their importance in plant health is widely recognized. Numerous studies have demonstrated that mycorrhizal colonization typically decreases with increasing nutrient availability (Wallenda and Kottke 1998; Hobbie and Colpaert 2003). Fewer studies have evaluated responses to shifts in temperature and moisture, and the limited results have been contradictory. For example, Rillig et al. (2002) reported increases in mycorrhizal root colonization with a 1–2 °C increase in temperature in an annual grassland community in California, USA, but Monz et

al. (1994) reported either a decrease or no change in mycorrhizal colonization with a 4 °C increase in temperature for two species in a perennial grassland community in Colorado, USA. Similarly, Palatova (2002) found that drought decreased mycorrhizal colonization in a coniferous stand in the Czech Republic, whereas other studies reviewed by Staddon et al. (2002) showed that drought promoted more colonization. An inherent problem in these and related studies of global change effects on mycorrhizae is separating direct effects on mycorrhizal fungi from indirect effects mediated by changes in plant community composition and structure (Staddon et al. 2002). Moreover, much of the research on climate effects on mycorrhizae has focused on grassland and agricultural ecosystems, often with short-term pot or mesocosm studies. Long-term field experiments in mature forest ecosystems are generally lacking. Future work is needed in these ecosystems to unravel the complex effects of climate change on plant–mycorrhizal interactions, and to better understand the implications of these interactions for forest nutrient cycling.

Soils

Climate plays a central role in the paradigm of pedogenesis, serving as one of the key “state factors” as originally defined by the Russian soil scientist Dokuchaiev and further developed by Jenny (1980). Climate change effects on soil processes are of great interest, as soils contain large and dynamic pools of C, N, and other nutrients. For example, soils contain about twice as much C as the atmosphere (Raich and Potter 1995), and in forests, soil N organic reservoirs are orders of magnitude higher than either annual atmospheric N deposition or internal fluxes within and between soil, plant, and atmospheric pools (Bormann et al. 1977; Schlesinger 1997). Even small changes in these large pools could therefore provide substantial positive feedback to climate warming.

Soil microbiological processes

In general, soil biological processes increase with temperature with a Q_{10} of ~ 2 (i.e., activity doubles for every 10 °C change in temperature). However, multiple interacting factors, including water and nutrient availability, and tree species, make predictions of soil changes in response to temperature problematic (Paul and Clark 1996; Lovett et al. 2004; Davidson and Janssens 2006). Changes in both soil moisture conditions and dynamics (e.g., drying and rewetting, freezing and thawing) have been shown to be important drivers of soil microbial processes (Nielsen et al. 2001; Fierer and Schimel 2003; Borken et al. 2006b). In the following sections we highlight the climatic impacts on key processes relative to C and nutrient cycling dynamics: litter decomposition, soil respiration, methane oxidation and reduction, N mineralization, and denitrification.

Litter decomposition and soil organic matter (SOM) dynamics

The decomposition of litter releases C and nutrients. The net balance between the rates of litter inputs and decomposition has a major influence on the accumulation (or depletion) of SOM. Litter quality, temperature, and moisture have been historically recognized to play critical roles in

regulating rates of litter decay, with decay rates generally greater in litter with lower lignin and higher N concentrations (Melillo and Aber 1982), and decay rates generally increasing with increasing temperature (Meentemeyer 1978; Jansson and Berg 1985). Recent studies have refined our understanding of the temperature sensitivity of decomposition showing that (1) the labile fraction of SOM is subject to temperature-sensitive decomposition; but (2) the more recalcitrant fraction of SOM is subject to environmental constraints that may obscure the intrinsic temperature sensitivity of its decomposition. These constraints include physical and chemical protection of organic matter, freezing, drought, and flooding (see review by Davidson and Janssens 2006).

The effects of warming on rates of litter decomposition have been studied in two soil warming experiments in the northeastern United States: one in a low-elevation spruce–fir stand at the Howland Forest, Maine (Rustad and Fernandez 1998b), and the other in an even-aged mixed-hardwood stand at the Huntington Forest near Newcomb, New York (McHale et al. 1998). The response to a 5 °C increase in soil temperature varied both by site and species. At the Howland Forest, red maple (*Acer rubrum* L.) litter lost 27% more mass and 33% more C during the first 6 months of decay in the heated plots than in the reference plots. After 30 months of decay, significant treatment effects were no longer evident for red maple litter. Red spruce (*Picea rubens* Sarg.) litter at the Howland Forest showed few treatment effects during the initial 18 months of decay. However, after 30 months, red spruce litter in the heated plots had lost 19% more mass and C than that in the reference plots. At the Huntington Forest, American beech (*Fagus grandifolia* Ehrh.) litter lost significantly more mass (19%) and C (16%) in the heated plots than in the reference plots after 1 year of decay, and significantly more C (19%) after 2 years of decay. Red maple litter, however, decayed at comparable rates in both the heated and reference plots. These and other experimental warming studies (e.g., Robinson et al. 1995; Verburg et al. 1999) demonstrate that a 3–5 °C increase in mean annual soil temperature can affect decomposition, but the response is species dependent.

Overall, expected changes in species composition (softwood to hardwood, Mohan et al. 2009) with an associated increase in litter quality and quantity, increases in temperature, and increases in the frost-free period will all favor increased rates of litter decomposition. Potential decreases in summer soil moisture and increased occurrence of short- and medium-term droughts may, however, decrease decomposition. Thus, the overall effect of climate change on litter decomposition is difficult to predict.

Soil respiration

Soil respiration represents the combined respiration of roots (autotrophic) and the soil microflora and fauna (heterotrophic). On a global scale, soil respiration is estimated to range from 68 to 100 Pg C·year⁻¹, making this process second only to gross primary productivity in the global C budget (Raich and Schlesinger 1992). Even a small increase in soil respiration could thus equal or exceed the estimated 8 Pg C released annually from the combination of land-use change

and fossil-fuel combustion (IPCC 2007), and could significantly exacerbate atmospheric increases in CO₂. Historically, many studies have demonstrated that soil temperature is a primary driver of soil respiration (e.g., Raich and Schlesinger 1992; Kirchbaum 1996; Rustad et al. 2001), with biological Q_{10} 's typically ranging from 2.0 to 2.5 (Raich and Schlesinger 1992; Davidson and Janssens 2006). However, higher and lower Q_{10} 's have been reported and can be attributed, in part, to the direct effects of temperature on substrate supply, substrate quality, and moisture stress, and the indirect effects of temperature and water content on substrate diffusion and availability (Davidson and Janssens 2006).

Direct evidence for the effect of temperature and moisture on rates of soil respiration is available from a range of climate change experiments and gradient studies in the northeastern United States. For example, experimental increases of 5 °C in soil temperature resulted in mean increases in soil respiration of 25%, 26%, and 33% during the first 2–3 years of experimental warming at the Howland Forest, Maine (Rustad and Fernandez 1998a), the Huntington Forest, New York (McHale et al. 1998), and a third soil warming experiment in an even-aged mixed-hardwood stand at the Harvard Forest in Petersham, Massachusetts (Melillo et al. 1995), respectively. Similar results were reported in a synthesis by Rustad et al. (2001) for 8 of 14 other ecosystem warming studies, where 2–9 years of experimental warming in the range of 0.3 to 6.0 °C significantly increased respiration rates by a mean of 20%. Note that soil respiration increased during the first 5 years of warming at the Harvard Forest. However, by the end of 10 years of warming, soil respiration rates in the heated plots had declined, likely reflecting a warming-induced depletion of labile soil organic C pools (Melillo et al. 2002). A weakness of this type of soil warming study is that ecosystems are warmed from belowground rather than aboveground. In a warmer world with elevated CO₂, NPP may increase, resulting in greater aboveground and belowground detrital inputs, which would replenish labile soil organic C pools and fuel a sustained increase in soil respiration.

Increases in soil respiration with temperature also have been reported across both latitudinal and elevational climate gradients in Maine and New Hampshire (Simmons et al. 1996; Groffman et al., submitted³). Decreases in soil respiration under low moisture stress has been reported for a precipitation-exclusion drought experiment at the Harvard Forest (Borken et al. 2006a). Taken together, these studies provide strong evidence that an increase in temperature will increase the efflux of CO₂ from the soil through soil respiration. The extent and duration of this increase will be influenced by soil moisture, the availability of labile C, soil N, and (or) other limiting nutrients, and will likely be at least initially greater in northern hardwood stands than in softwood stands because the latter produces more recalcitrant litter.

Methane oxidation and reduction

Estimates of global flux of CH₄ to the atmosphere range from 503 to 582 Tg·year⁻¹ (IPCC 2007). Although this amount is less than the flux of CO₂, CH₄ is an important greenhouse gas because it can absorb 25 times more radiant

³Groffman, P.M., Hardy, J.P., Fisk, M.C., Fahey, T.J., and Driscoll, C.T. Climate variation and soil carbon and nitrogen cycling processes in a northern hardwood forest. Submitted to *Ecosystems*.

energy than CO₂ on a molar basis (IPCC 2007). Most of the atmospheric methane produced from natural sources is thought to originate from biological processes in anoxic soils. Recent evidence suggests that terrestrial vegetation also may be an important source of methane (Keppler et al. 2006; Wang et al. 2008), although there is not a clear consensus on this issue (Dueck et al. 2007; Ferretti et al. 2007). Soils serve as both a source and a sink for atmospheric CH₄, with the direction of flux depending largely on the O₂ status of the soils. Under anaerobic conditions, typical of wetland soils, methanogenic bacteria use CO₂ as an electron acceptor, reducing CO₂ to CH₄. Under aerobic conditions that are more typical of well-drained upland forest soils, methanotrophic bacteria use CH₄ as a substrate for growth, converting CH₄ to CO₂ (Alexander 1977).

Methane flux from forest soils is largely regulated by soil moisture (Castro et al. 1993, 1995; Torn and Harte 1996). Soil moisture affects both soil O₂ status as well as the diffusion of atmospheric CH₄ into the soil (King 1997). The positive relationship between temperature and N availability and CH₄ production and oxidation also has been recognized (Crill et al. 1988; Castro et al. 1995; Yavitt et al. 1995) and is attributed to the effects of both of these factors on microbial biomass and activity.

The effects of temperature on CH₄ dynamics were evaluated at the three soil warming experiments in the northeastern United States. Mean CH₄ fluxes in reference plots were negative at all three sites, showing that oxidation is the primary process controlling CH₄ flux in these aerobic forest soils. At the Harvard Forest, a significant positive correlation between CH₄ uptake and soil temperature was found ($r^2 = 0.46$; Peterjohn et al. 1994). A weaker but still significant correlation between CH₄ flux and soil temperature was found at the Huntington Forest for the heated plots ($r^2 = 0.12$; McHale et al. 1998). No relationship between CH₄ flux and soil temperature was found at the Howland Forest (Rustad and Fernandez 1998a). The 5 °C increase in soil temperature resulted in a ~14% greater uptake of CH₄ in the heated plots compared with the controls at the Harvard Forest (Peterjohn et al. 1994) and no significant differences in CH₄ uptake at either the Huntington or Howland Forest experiments. Relationships between CH₄ uptake and moisture were typically stronger than relationships between CH₄ uptake and temperature at all three sites (Peterjohn et al. 1994; McHale et al. 1998; Rustad and Fernandez 1998a). These studies suggest that an increase in mean annual temperature can increase the consumption of atmospheric CH₄ in freely drained, aerobic forest soils if warming is accompanied by decreases in summer precipitation.

Although not the focus of this review, wetlands account for an estimated 24% of global CH₄ emissions (IPCC 2007). Despite this high proportion, only a few experimental studies have examined temperature and water-table effects on CH₄ emissions from wetlands. Updegraff et al. (2001) evaluated warming effects in bog and fen microcosms in Minnesota. They found that CH₄ emissions were strongly correlated with N availability, plant productivity, soil temperature, and water-table height. These results are consistent with field observations linking warmer temperature to greater CH₄ emissions from wetlands (Chapman and Thurlow 1996; Christensen et al. 2003).

N mineralization

Nitrogen mineralization is the process by which organic N is oxidized first to NH₄⁺ (ammonification) and then to NO₂⁻ and NO₃⁻ (nitrification) by soil microorganisms. As with many other microbial processes, temperature has a major influence on N mineralization (Rustad et al. 2001), although other factors such as soil water, total N, labile C, soil texture, and overstory vegetation are also important (Pastor et al. 1984; Gower and Son 1992; Reich et al. 1997). Temperature-induced increases in N mineralization could increase the availability of N, thereby alleviating N limitation for microorganisms and trees and enhancing forest productivity (Magnani et al. 2007). Given that aboveground plant tissues, especially wood, have higher C/N ratios than SOM (25 to >300 vs. 10 to 12), this temperature-driven process of transferring N from SOM pools to woody biomass pools can be an important mechanism for C sequestration (Melillo et al. 2002). However, increased internal production of mineral N, coupled with elevated atmospheric inputs of reactive N, also can increase the potential for some forested ecosystems to become "N saturated" (Aber et al. 1989). Nitrogen saturation has been associated with declines in forest health and productivity (Likens et al. 1996), increases in soil acidification, Al mobilization, and base cation depletion (Likens et al. 1996; Rustad et al. 1996; Fernandez et al. 2003), and accelerated leaching of N from soils with consequent declines in surface water quality (Stoddard 1994).

Direct evidence for the effect of temperature and moisture on rates of N mineralization is also available from a range of climate change experiments and gradient studies in the northeastern United States. For example, experimentally warming soils by 5 °C resulted in a near doubling of N mineralization rates in both the O and Ap horizons at the Harvard Forest (Melillo et al. 1995). Unlike the respiratory response, this increase was sustained throughout the next decade of the experiment (Melillo et al. 2002). At the Howland Forest, no treatment effects were observed on N mineralization rates in the B horizon. In the O horizon, no treatment response was observed during the first year of manipulation, but the O horizon mineralization rates increased by 20% in the heated plots in both the second and third years of the study (Rustad et al. 2000). This lag could reflect an initial immobilization of excess available N at this N-limited coniferous site. The general increase in N mineralization with increasing temperature is consistent with results from eight other ecosystem warming experiments (Rustad et al. 2001) where experimental warming increased net N mineralization rates by ~50%. Note that net in situ N mineralization rates published for 55 sites in the region during the period 1980–2000 range from <1 to upward of 180 kg·ha⁻¹·year⁻¹, with a mean of 56 kg·ha⁻¹·year⁻¹ (Rustad et al., unpublished data). A 50% increase in mineralization could add 1 to 83 kg·ha⁻¹·year⁻¹ of N, potentially greatly exceeding total atmospheric N deposition for the region (<5 to ~10 kg·ha⁻¹·year⁻¹).

Unexpectedly, latitudinal and elevational gradient studies within the region show the reverse pattern, with increased N mineralization under colder climates. For example, forest floor samples were collected from 16 hardwood stands across a climatic gradient in Maine in 1995 and were analyzed for potential N mineralization and nitrification using a 28 day laboratory incubation. Hardwood sites in the northern region

had two to four times the potential net N mineralization compared with central, southern, and coastal regions (mean 57.9 mg·kg⁻¹·day⁻¹ compared with means of 30.7, 20.5, and 15.1 mg·kg⁻¹·day⁻¹, respectively) (Fernandez et al. 2000). These results are consistent with the significantly higher rates of in situ net N mineralization observed for hardwood sites in northern Maine (mean 7.0 mg·kg⁻¹·day⁻¹) compared with other regions in Maine (mean 2.9–3.8 mg·kg⁻¹·day⁻¹) during the 2 year period 1993–1994 (Fernandez et al. 2000). Results from an elevational gradient study also suggested higher rates of N mineralization at higher elevations and colder temperatures (Groffman et al., submitted³). These results indicate that other factors, such as soil moisture, site quality, species composition, and the size of the total N pool, could be more important than soil temperature in controlling N mineralization rates at the regional scale.

Denitrification

Although atmospheric N₂O concentrations are considerably lower than either CO₂ or CH₄ concentrations, N₂O is also an important greenhouse gas because of its long atmospheric lifetime (~120 years) and because it has the ability to absorb ~200 times more radiant energy than CO₂ on a molar basis (IPCC 2007). Soils are the primary source of N₂O to the atmosphere. Nitrous oxide is produced during both nitrification and denitrification. The rate of denitrification is primarily controlled by NO₃⁻, O₂, and labile C supply. Soil moisture content is important in affecting O₂ supply. Warmer, wetter conditions increase mineralization and nitrification, lower soil O₂, and increase the potential for gaseous losses associated with both nitrification and denitrification. Drier soil conditions could lead to higher soil O₂ and declines in gaseous N losses. An increase in episodic drying and rewetting events, however, will result in an increase in gaseous losses, as these events produce bursts of both nitrification and denitrification (McClain et al. 2003).

Direct evidence for climate change effects on denitrification processes in forest soils is available from both the Harvard Forest and Huntington Forest soil warming experiments (Peterjohn et al. 1994; McHale et al. 1998) and the snow removal experiment at the HBEF. At the Harvard Forest, a weak positive correlation was observed between soil temperature and N₂O flux ($r = 0.14$; $P < 0.05$), but warming the soils by 5 °C had no significant effect on N₂O flux rates. At the Huntington Forest, no relationship was observed between soil temperature and N₂O flux during the first year of the study (McHale et al. 1998). However, in the second year of the study, the flux of N₂O was significantly correlated with soil temperature ($r = 0.67$; $P < 0.0001$), and the 5.0 °C increase in soil temperature resulted in significantly higher rates of N₂O flux in the heated plots than in the control plots. The stronger relationship between N₂O flux and soil temperature in the second year of the study can be attributed either to an increase in N mineralization and thus an increase in the supply of NH₄⁺ and NO₃⁻ (the precursors to both nitrification and denitrification), or to an increase in soil moisture during the second year of the study (McHale et al. 1998).

A clear linkage between N mineralization and N₂O flux was not apparent at the snow removal experiment at the HBEF. Although mild soil freezing resulted in significantly elevated soil NO₃⁻ leaching (Fitzhugh et al. 2001) and in-

creases in N₂O flux (Groffman et al. 2006), the response was likely due to a physical disruption of the soil ecosystem and not a direct stimulation of microbial activity, as N mineralization, nitrification, denitrification, and soil respiration showed no response to the treatments (Groffman et al. 2001b). The increased N₂O flux also could have been due to altered product ratios among, NO, N₂O, and N₂ during denitrification, resulting in increased N₂O flux with no concomitant increase in mineralization rates (Groffman et al. 2006).

Soil abiotic processes

Soil abiotic processes have received considerably less attention than biological processes in the global change literature. Although probably not as sensitive as many biological processes, changes in soil temperature and moisture will influence soil abiotic processes. These processes fall across a spectrum of time scales and include adsorption–desorption reactions, primary and secondary mineral weathering, oxidation–reduction reactions, and physical perturbations.

Adsorption–desorption reactions

Adsorption–desorption reactions, including cation exchange, are perhaps the fastest of the major chemical reactions in soils. Although they are minimally sensitive to small changes in soil temperature, they are strongly dependent on soil moisture. Soil moisture influences solute concentration and therefore proportioning of cations between soil solutions and soil organic and mineral colloidal surfaces (Kelley 1948; Bolt and Bruggenwert 1976). For example, drier soils influence the balance between cations of lower valence (e.g., calcium (Ca²⁺)) and those of higher valence (e.g., Al³⁺), potentially favoring Al on soil exchange sites and in soil solutions owing to cation exchange equilibria. These factors could lead to an increase in soil solution Al³⁺ activity that could have negative effects on forest biota (Cronan and Grigal 1995). Increased leaching of strong acid anions such as NO₃⁻ resulting from increased rates of nitrification would lead to accelerated losses of cations, which could magnify the concerns for base cation depletion in forest soils in northeastern North America (Fernandez et al. 2003; Huntington 2005; Watmough et al. 2005). Increased rates of autotrophic and heterotrophic respiration may lead to higher soil CO₂ concentrations, which could influence soil acidity. However changes in soil acidity may not be evident if soils are drier, as gas exchange with the atmosphere will be more rapid, or if soil pH was already highly acidic because bicarbonate acidity would not be functional.

Primary and secondary mineral weathering

Along with atmospheric deposition, mineral weathering can be an important source of nutrients, particularly base cations (Ca, K, magnesium (Mg), and sodium (Na)) that contribute to exchangeable soil pools. Higher weathering rates generally lead to higher soil base saturation and pH, and thus to lower concentrations of toxic elements such as Al (see Driscoll and Schecher 1990) and manganese (Mn) (Kogelmann and Sharpe 2006; Houle et al. 2007). The supply of Ca²⁺ is particularly important in northeastern North America because evidence exists that acidic deposition has depleted exchangeable soil Ca²⁺ and other base cations in forest soils (Likens et al. 1996; Houle et al. 1997). In areas where Ca²⁺ is limiting, projected increases in NPP due to a

warmer, wetter climate may not occur if the Ca^{2+} exchangeable pool does not increase. In this context, the response of mineral weathering to a warmer climate could be a key issue for predicting future forest growth.

Weathering is strongly influenced by both soil temperature (White et al. 1999) and soil moisture, as well as other intrinsic characteristics such as the mineral type and surface area. Indirect effects of soil temperature and moisture on “rock-eating” mycorrhizae could also affect weathering rates (van Breemen et al. 2000; van Schöll et al. 2008). Increased rates of mineral weathering associated with a warming climate represent an important new input of nutrients to the ecosystem. Note that the solubility of Al secondary minerals is highly temperature dependent (Schecher and Driscoll 1987). As a result, increases in solution temperature will decrease Al mobilization in drainage waters, with potential ecosystem effects.

Oxidation–reduction (redox) reactions

Redox reactions include all chemical reactions involving a change in oxidation number (oxidation state). Biologically mediated redox reactions already have been discussed and include the oxidation and reduction of C during photosynthesis and respiration; oxidation and reduction of CH_4 ; and the oxidation and reduction of N during mineralization, nitrification, and denitrification. Common abiotic redox reactions in forest soils include the oxidation and reduction of S, iron (Fe), and Mn. The abiotic reduction of NO_3^- to nitrite by Fe^{2+} and consequent immobilization by soil organic matter also has been proposed as an important abiotic mechanism in forest soils (Davidson et al. 2003), although methodological concerns exist in demonstrating the existence of such a mechanism (Colman et al. 2007).

Redox reactions are largely controlled by soil moisture and the availability of decomposable organic matter. Increases in temperature coupled with static summer precipitation are expected to reduce soil moisture in the summer, which should favor oxidation. Greater periods between extreme precipitation events and the expected greater frequency of droughts also will promote more favorable conditions for oxidation. In wetlands, these drying conditions could allow O_2 to penetrate formerly anaerobic portions of the soil, resulting in the oxidation of reduced S compounds and the release of SO_4^{2-} , and consequent acidification of soils and solutions (Warren et al. 2001; Eimers and Dillon 2002; Mitchell et al. 2006).

Physical perturbations

Changes in the frequency, intensity, and timing of precipitation also will have consequences for the physical perturbation of soils. For example, lower frequency but more intense rainfall events can increase surface runoff and erosion (Pruski and Nearing 2002), and increased episodes of freezing and thawing can lead to increased physical disruption of aggregates (Bullock et al. 1988). Changes in SOM, root exudates, and microbial activity also can affect soil aggregate stability and structure (Brady and Weil 2007).

Modeling biogeochemical responses

We used the biogeochemical model PnET-BGC to test our assumptions about how forest ecosystems in northeastern North America could respond to future climate change.

PnET-BGC is a comprehensive forest–soil–water model that links a C, N, and water balance model, PnET-CN (Aber et al. 1997), with a biogeochemical model, BGC (Gbondo-Tugbawa et al. 2001). PnET-BGC extends the simulations of PnET-CN to include the cycling of major elements (i.e., C, N, phosphorus (P), S, Ca, Mg, K, Na, Al, chloride (Cl), silicon (Si)). Both biotic and abiotic processes are represented in PnET-BGC, including canopy interactions, hydrology, photosynthesis, respiration, SOM dynamics, mineral weathering, chemical reactions involving solid and solution phases, and surface-water processes. A thorough description of the model including the processes depicted and a detailed sensitivity analysis of parameters is provided in Gbondo-Tugbawa et al. (2001).

Model application

PnET-BGC was run using data from the HBEF in North Woodstock, New Hampshire. The HBEF has a long history of ecosystem research and is one of the most extensively studied forests in northeastern North America. Consequently, it is an ideal candidate site for modeling applications because there are adequate data for establishing parameters, as well as long-term field measurements for comparison with modeled values.

The results of PnET-BGC simulations reported here spanned the period from 1950 through the end of the twenty-first century (150 years total). The model was run as a single soil layer, and spatial variations across the watershed were not considered (i.e., run as a one-dimensional model). Monthly minimum and maximum air temperature, precipitation, and solar radiation were used as input data. Future climate simulations were generated using monthly output from two of the latest AOGCMs (Hadley Centre Coupled Model, version 3 (HadCM3) and Parallel Climate Model (PCM)) available from the Intergovernmental Panel on Climate Change Fourth Assessment Report database (IPCC 2007). Additionally, two future greenhouse gas emission scenarios were used (B1 and A1FI), for a total of four climate simulations. These scenarios approximate potential lower and upper bounds (respectively, 550 and 970 ppm by 2100) of projected atmospheric CO_2 . The monthly ensemble AOGCM forecasts were bias corrected, downscaled to $1/8^\circ$ horizontal resolution, and disaggregated to a daily time step (Hayhoe et al. 2007, 2008).

In addition to climate input, PnET-BGC also requires wet and dry deposition values for major elements. Wet to dry deposition ratios were estimated following the procedure of Chen and Driscoll (2004). Estimates of future atmospheric deposition were based on a “business-as-usual” deposition scenario developed for the northeastern United States (CMAQ 2008), which is representative of current average trends and thus assumes no change in emissions. Atmospheric deposition fluxes were calculated using precipitation amounts specific to each scenario. Direct effects of CO_2 fertilization on NPP are currently not accounted for in PnET-BGC because of the uncertainties discussed previously.

Trends in model output were assessed using the Mann–Kendall statistical test, which is commonly used for analyses of hydrological and ecological time series data (Kendall 1938; Helsel and Hirsch 1992). One of the advantages of this test is that it is rank based, making it suitable for non-

Table 1. Projected changes in temperature and hydrological values for the Hubbard Brook Experimental Forest.

	Units	1990–1999	2000–2099			
		Reference	PCM low CO ₂	PCM high CO ₂	HadCM3 low CO ₂	HadCM3 high CO ₂
Temperature						
Annual	°C	4.5	+1.8 (<0.001)	+4.1 (<0.001)	+3.5 (<0.001)	+8.2 (<0.001)
Winter	°C	-7.3	+2.8 (<0.001)	+4.6 (<0.001)	+3.6 (<0.001)	+7.7 (<0.001)
Summer	°C	16.4	+1.5 (<0.001)	+4.2 (<0.001)	+3.8 (<0.001)	+9.0 (<0.001)
Precipitation						
Annual	cm	146.7	+17.5 (0.001)	+16.2 (0.002)	+15.0 (0.006)	+28.9 (<0.001)
Winter	cm	33.9	+7.3 (0.014)	+5.8 (0.028)	+3.4 (0.211)	+14.3 (<0.001)
Summer	cm	38.3	+4.7 (0.087)	+3.5 (0.136)	+5.8 (0.028)	+3.6 (0.268)
Evaporation	cm·year ⁻¹	16.0	+1.9 (0.001)	+1.8 (0.002)	+1.7 (0.006)	+3.2 (<0.001)
Transpiration	cm·year ⁻¹	30.6	+9.8 (<0.001)	+15.9 (<0.001)	+16.1 (<0.001)	+27.9 (<0.001)
Mean soil water content	cm	138.0	+0.4 (0.796)	-4.4 (0.007)	-4.5 (0.009)	-8.7 (<0.001)
Streamflow	cm·year ⁻¹	100.1	+6.0 (0.207)	-0.5 (0.929)	-1.6 (0.632)	+0.33 (0.953)

Note: Winter is December, January, and February; summer is June, July, and August. For the reference period (1990–1999), temperature and precipitation are measured values, whereas other values are from PnET-BGC simulations. Future PnET-BGC simulations (2000–2099) were run using climate inputs from two different models (PCM and HadCM3) with two CO₂ scenarios (550 and 970 ppm by 2100). For 2000–2099, *p* values are given in parentheses; *p* < 0.05 indicates significant increases (+) or decreases (-) determined with a Mann-Kendall test for trend.

normally distributed data, data containing outliers, and non-linear trends, such as those commonly encountered in long-term environmental data. Increasing and decreasing trends for 2000–2099 were evaluated at the 0.05 level of significance.

Modeling results

Projected trends in climate for the HBEF (Table 1) generally reflect trends across the broader northeastern region of North America (Hayhoe et al. 2008). Results from the downscaled AOGCM output indicate that annual mean air temperatures at HBEF will increase by 1.8 to 8.2 °C by the end of the century, with greatest increases occurring under the higher CO₂ scenario. Both the PCM and HadCM3 models project significant increases in air temperature during both summer and winter. The PCM model projections indicate slightly greater increases in winter temperatures than in summer temperatures, consistent with regional trends (Hayhoe et al. 2007, 2008). In contrast, the HadCM3 model predicted slightly lower increases in winter temperatures compared with summer temperatures, illustrating the site-to-site variability inherent in these model projections.

In addition to air temperature increases, significant increases in annual precipitation also were projected under all scenarios. These increases ranged from 10% to 20% above the precipitation mean for 1990–1999. Increases in precipitation were projected for both winter and summer; however, differences were only significant during winter under the PCM low CO₂ and HadCM3 high CO₂ scenarios. Consistent with warmer temperatures and greater precipitation, hydrological fluxes modeled with PnET-BGC indicate that both evaporation and transpiration are projected to increase significantly by the end of the century, although increases in transpiration (9.8 to 27.9 cm·year⁻¹) are expected to far exceed increases in evaporation (1.7 to 3.2 cm·year⁻¹). These greater amounts of water loss to the atmosphere are projected to cause a reduction in soil water content. Interestingly, there was no significant change in streamflow amounts for any of the scenarios because projected increases in precipitation were offset by higher transpiration rates.

The combination of higher air temperatures and greater precipitation resulted in a longer and more productive growing season. The model indicated that total NPP (above-ground and belowground) increased by 8% to 15% from 1999 to 2099 (Fig. 3). These overall increases in NPP were relatively small compared with changes in the distribution of NPP among tissue types. Under all scenarios, wood production increased significantly by 34% to 70%, whereas root and foliage production declined (-4% to -39% and -3% to -42%, respectively) from 1999 to 2099. The decline in foliar mass (and related decline in roots, which are linked to foliar growth in the model) was caused by an increase in midsummer drought stress owing to low soil moisture and higher vapor pressure deficits under the climate change scenarios. These moisture deficits were driven by increases in temperature and evapotranspiration rather than declines in summer precipitation. In the model, repeated midsummer drought stress reduces the maximum leaf area index that can be achieved by the canopy even though higher leaf area index values could be attained during other months. This process serves to bring temporal variation in canopy mass to realistic levels and minimizes the need for premature leaf drop (Aber and Federer 1992). The increases in wood growth occurred despite the decrease in leaf production and were driven by longer growing seasons and higher canopy photosynthetic rates during the nonstressed time periods.

The decline in foliar biomass resulted in a precipitous decline in litterfall C and, to a lesser extent, litterfall S, whereas responses of litterfall Ca²⁺ and N were inconsistent across the various model scenarios (Table 2). These inconsistencies in litterfall Ca²⁺ and N suggest that other processes represented in the model, such as canopy uptake, retranslocation, and uptake from soil, balanced declines in litterfall mass. The reduction in litterfall C inputs resulted in lower C mineralization rates under the warmest scenario (HadCM3 high CO₂). However, there were no significant reductions under the other model scenarios because they were offset by enhanced C mineralization arising from more favorable soil climatic conditions. Nitrogen mineralization showed a strong positive response to climate change, with

Fig. 3. Projected changes in foliage, wood, root, and total net primary productivity (NPP) (megagrams per hectare per year) determined with PhET-BGC at the Hubbard Brook Experimental Forest. Simulations before 2000 were run using measured climate input data. Future simulations were run using climate input data from two different models (HadCM3 and PCM) with two CO₂ scenarios (550 and 970 ppm by 2100).

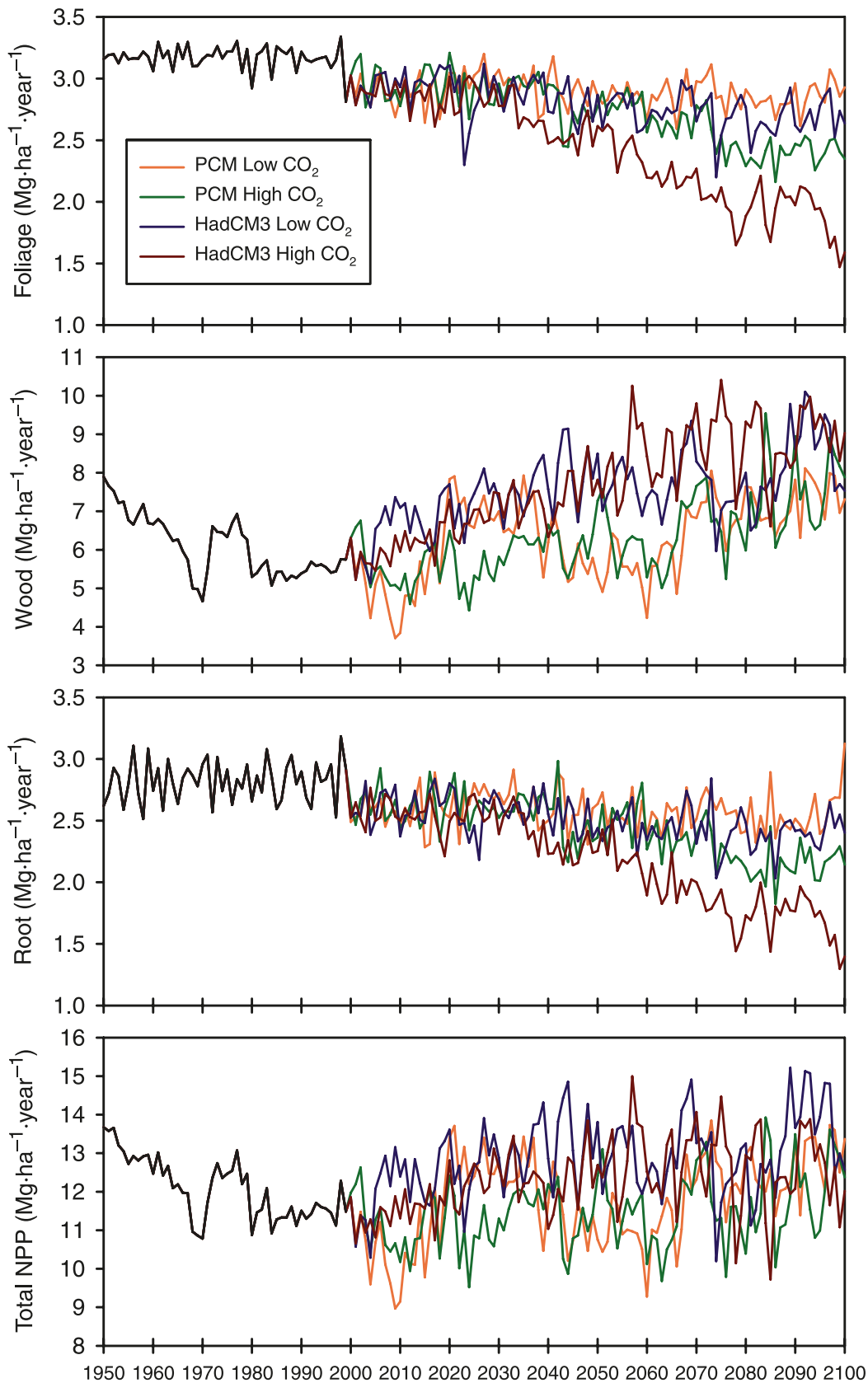


Table 2. Projected changes in biogeochemical fluxes (kilograms per hectare per year) of selected elements for the Hubbard Brook Experimental Forest.

	1990–1999	2000–2099			
	Reference	PCM low CO ₂	PCM high CO ₂	HAD low CO ₂	HAD high CO ₂
Litterfall					
C	7102.8	-137.8 (0.064)	-1222.0 (<0.001)	-274.3 (0.003)	-1975.0 (<0.001)
Ca	39.0	-4.8 (<0.001)	+3.2 (0.002)	-1.0 (0.278)	+0.9 (0.181)
S	21.7	-2.3 (<0.001)	-1.8 (<0.001)	-1.5 (<0.001)	-4.0 (<0.001)
N	93.1	+5.5 (<0.001)	+1.5 (0.269)	+8.1 (<0.001)	-12.8 (<0.001)
Mineralization					
C	990.6	+0.3 (0.983)	-47.8 (0.088)	-40.8 (0.094)	-188.4 (<0.001)
Ca	41.5	-6.9 (<0.001)	+1.3 (0.271)	-3.4 (0.002)	+3.8 (0.012)
S	23.3	-3.9 (<0.001)	-2.3 (<0.001)	-3.8 (<0.001)	-3.8 (<0.001)
N	89.0	+13.8 (<0.001)	+30.5 (<0.001)	+15.6 (<0.001)	+20.3 (<0.001)
Nitrification	3.5	+30.7 (<0.001)	+107.8 (<0.001)	+63.6 (<0.001)	+122.8 (<0.001)
Weathering					
Ca	4.9	+0.02 (0.796)	-0.16 (0.007)	-0.16 (0.009)	-0.31 (<0.001)
S	1.5	+0.01 (0.791)	-0.05 (0.007)	-0.05 (0.009)	-0.09 (<0.001)
Stream water					
DOC	20.3	-0.9 (0.435)	-3.4 (0.001)	-3.1 (0.005)	-6.2 (<0.001)
Ca ²⁺	8.1	+1.2 (0.006)	+4.8 (<0.001)	+0.5 (0.190)	-0.1 (0.896)
SO ₄ ²⁻ -S	14.0	-4.0 (<0.001)	-3.7 (<0.001)	-4.1 (<0.001)	-2.2 (<0.001)
NO ₃ ⁻ -N	1.6	+4.8 (<0.001)	+15.5 (<0.001)	+6.6 (<0.001)	+16.1 (<0.001)

Note: Values for the reference period (1990–1999) are from PnET-BGC simulations using measured climate input data. Future values (2000–2099) are from PnET-BGC simulations using climate inputs from two different models (PCM and HadCM3) with two CO₂ scenarios (550 and 970 ppm by 2100). For 2000–2099, *p* values are given in parentheses; *p* < 0.05 indicates significant increases (+) or decreases (-) determined with a Mann-Kendall test for trend.

rates increasing by 16% to 34%, which, in turn, greatly increased nitrification rates (Table 2). Weathering rates of Ca²⁺ and S declined slightly, but significantly in all scenarios except for the least extreme PCM low CO₂ scenario. These declines were caused by significant decreases in soil moisture and hence reduced leaching losses of weathering products (Table 1).

Changes in stream water chemical fluxes were driven by changes in concentrations rather than by stream water volume, since streamflow did not change significantly over the simulation period (Tables 1, 2). Stream water losses of DOC declined under all scenarios, reflecting declines in litterfall C and soil C mineralization rates. Lower S mineralization rates in soil caused by lower litterfall S also resulted in significant declines in stream water losses of SO₄²⁻-S. Calcium fluxes in stream water increased significantly under both PCM model scenarios, but showed no significant trends under the HadCM3 model scenarios. The most notable change in stream water was a significant increase in NO₃⁻-N export (4.8 to 16.1 kg·ha⁻¹·year⁻¹) due to the marked increase in soil nitrification rates, which are highly dependent on soil temperature and moisture.

Element mass balances were calculated as the difference between precipitation inputs and stream water outputs to examine patterns of net ecosystem retention and loss (Fig. 4). Both measured and modeled estimates show that dissolved inorganic N (DIN) has been retained in the forest ecosystem at the HBEF during the last 50 years. PnET-BGC simulations indicate that future shifts in climate will push the ecosystem from one that accumulates N to one that exhibits net N losses. Future DIN losses are driven primarily by high net mineralization and nitrification rates and resultant elevated

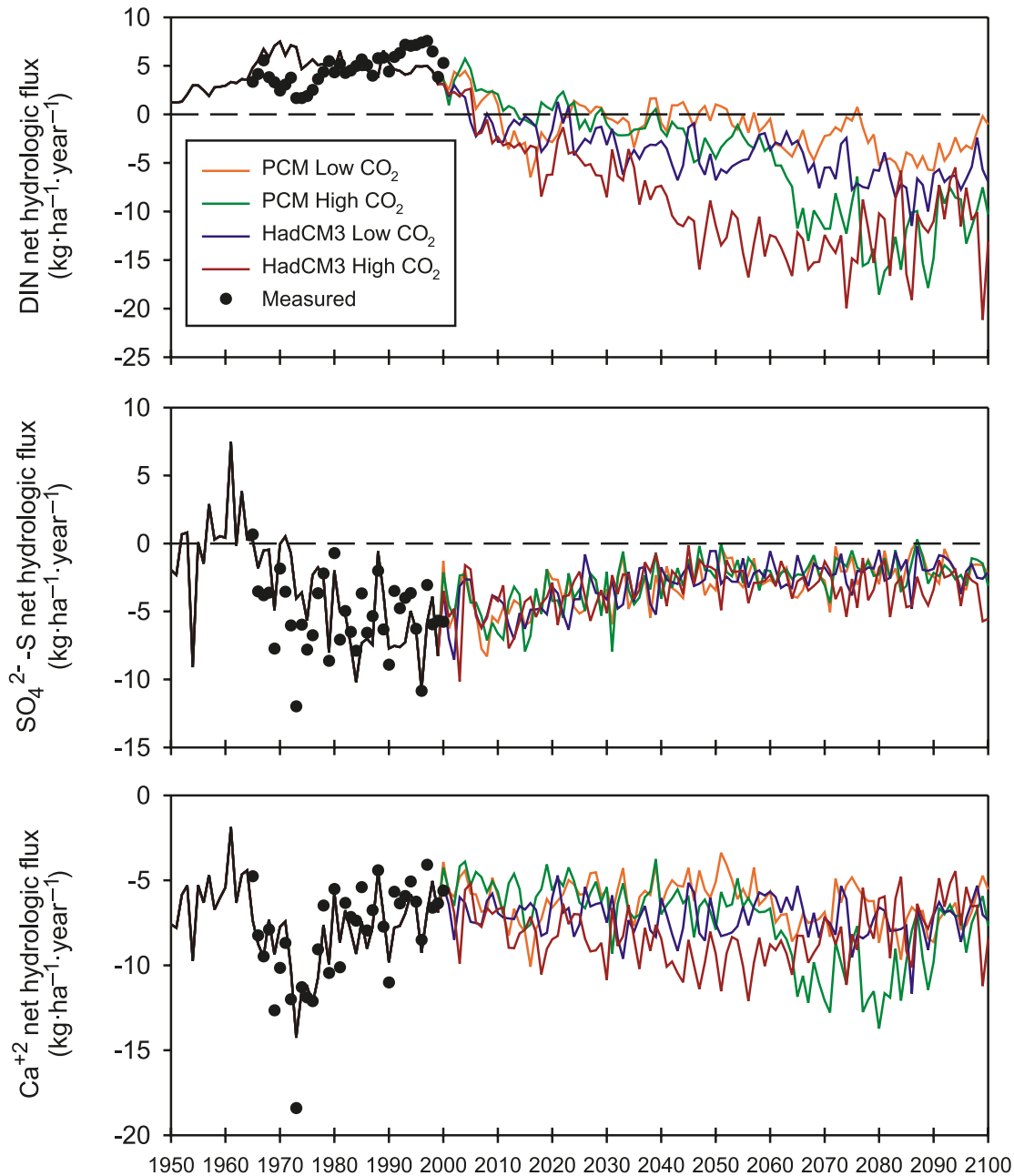
stream water NO₃⁻-N export. Sulfur showed an opposite trend with a shift toward greater retention of SO₄²⁻-S. However, the range in SO₄²⁻-S responses for all model scenarios is very narrow, indicating that climate is not a major driver of change for S in this upland forest ecosystem. The shift toward higher SO₄²⁻-S retention is due to a recovery response to declining atmospheric deposition of S, coupled with increased soil SO₄²⁻-S absorption associated with increased soil acidification (Gbondo-Tugbawa et al. 2002), rather than a specific response to climate. Shifts in Ca²⁺ retention varied more widely depending on which model and CO₂ scenario was used. However, in all cases the Ca²⁺ response was relatively minor and showed only slight declines in retention compared with the reference period (1990–1999).

Although these model simulations and analyses have limitations, they indicate the direction and magnitude of change that is expected by the end of the century for trends in important biogeochemical processes at the HBEF. The design of PnET-BGC is intentionally parsimonious and represents only the most important ecosystem processes to minimize the number of required parameters. Consequently, the model does not capture all the intricate responses to climate change discussed throughout this review. Future efforts should continue to evaluate what processes need to be included in the model. Additionally, the model should be applied over a broader range of landscape types within the region.

Future research directions

One of the most noteworthy predicted ecosystem responses to climate change is an increase in NPP and associated shifts in C storage within plants. Even though this

Fig. 4. Projected net hydrologic fluxes of dissolved inorganic nitrogen (DIN = NO_3^- -N + NH_4^+ -N), SO_4^{2-} , and Ca^{2+} determined with PnET-BGC at the Hubbard Brook Experimental Forest. Net hydrologic flux is calculated as stream water output minus bulk deposition input. Simulations before 2000 were run using measured climate input data. Future simulations were run using climate input data from two different models (HadCM3 and PCM) with two CO_2 scenarios (550 and 970 ppm by 2100).



response of vegetation to elevated atmospheric CO_2 concentrations, warmer temperatures, and a longer growing season seems obvious, the actual response is more complex because it has to be considered within the context of other global change processes, such as tropospheric O_3 and atmospheric N and S deposition (i.e., acidic deposition). In addition to direct effects of these factors, the interactive effects are also important but are often ignored because they are poorly understood and highly complex. An example is the interactive effect of changes in N deposition and climate change. Since N typically limits forest growth in northeastern North America, higher N deposition could increase C accumulation

in biomass, thereby creating a sink that could slightly suppress projected increases in atmospheric CO_2 . However, if the added N is sequestered mainly in soils or is exported in stream water or as N gases to the atmosphere, then the effect on C storage would be minor, resulting in higher atmospheric CO_2 (Nadelhoffer et al. 1999).

Models are particularly useful for addressing these interactions but are only able to represent processes to the extent that they are quantitatively understood. Many questions in climate change research remain unanswered, making it difficult to improve the predictive ability of models. Some of these questions can be addressed with short-term field experi-

ments; however, longer-term studies are needed to better understand how ecosystems could adapt to global change. For instance, even though experimental manipulations have generally shown that atmospheric CO₂ enrichment enhances NPP, it is uncertain whether growth can be sustained as plants acclimate to higher concentrations of atmospheric CO₂ (Gunderson and Wullschlegel 1994; Sage 1994; Wolfe et al. 1998). Another example is the effect of climate change on tree species composition. While the optimal range for tree species will likely shift northward, it is unclear when and how new species will displace established species. It is critical to understand how tree species composition will change because the implications for biogeochemical cycling are substantive.

In addition to disturbances that occur over longer periods of time, it is also unclear how biogeochemical processes are affected by shorter-term climatic disturbances, such as floods, hurricanes, ice storms, and soil frost events. One obvious need is to account for episodic events in biogeochemical monitoring and modeling efforts. Measuring these events in the field is challenging because they occur quickly and unpredictably, at varying spatial scales. These stochastic properties also make it difficult to incorporate them into models, especially those that produce results at large temporal and spatial scales, because disturbances are often transient and only of local importance. Other disturbances such as fire or insect and disease outbreaks are similarly challenging to model, yet may be central to mechanisms of transition in forest composition. Since multiple disturbances can occur simultaneously, it is also important to recognize how ecosystems respond to multiple events and how one event can influence the effect of subsequent events.

Perhaps the greatest weakness in our understanding of the consequences of climate change involves feedback loops between biogeochemical processes and the climate system. These feedbacks include more obvious examples involving climate-induced changes in biogeochemical processes that emit additional greenhouse gases and volatile organic compounds to the atmosphere. However, they also include more complex processes such as feedbacks associated with cloud formation and aerosol reflectance. Models can help address these issues, but also have limitations and require empirical data for comparison. Going forward, a continued mixture of models, long-term monitoring, manipulative experiments, and comparative studies will be necessary for building a comprehensive understanding of the complex response of biogeochemical processes to climate change.

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