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Colder soils in a warmer world: A snow manipulation study in a northern hardwood forest ecosystem

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Abstract. In this special section of *Biogeochemistry*, we present results from a snow manipulation experiment in the northern hardwood forest ecosystem at the Hubbard Brook Experimental Forest in the White Mountains of New Hampshire, U.S.A. Snow is important as an insulator of forest soils. Later development of snowpacks, as may occur in a warmer climate, may result in increases in soil freezing (i.e. colder soils in a warmer world) and could cause changes in fine root and microbial mortality, hydrologic and gaseous losses of nitrogen (N), and the acid-base status of drainage water. In our study, we kept soils snow free by shoveling until early February during the mild winters of 1997/1998 and 1998/1999. The treatment produced mild, but persistent soil freezing and induced surprisingly significant effects on root mortality, soil nitrate (NO_3^-) levels and hydrologic fluxes of C, N and P. In this special section we present four papers addressing, (1) soil temperature and moisture response to our snow manipulation treatment (Hardy et al.), (2) the response of fine root dynamics to treatment (Tierney et al.), (3) the response of soil inorganic N levels, *in situ* N mineralization and nitrification, denitrification and microbial biomass to the treatment (Groffman et al.) and (4) soil solution concentrations and fluxes of C, N and P (Fitzhugh et al.). In this introductory paper we: (1) review the literature on snow effects on forest biogeochemistry, (2) introduce our manipulation experiment and (3) summarize the results presented in the other papers in this issue.

Introduction

One of the most important recent developments in 'global change' research has been recognition of the importance of indirect effects of climate change on the structure and function of ecosystems. There is an emerging consensus that changes in fire frequency, hydroperiod, extreme temperature and precipitation events and snowpack accumulation may have more important effects on ecosystems than overall changes in temperature and precipitation (Vitousek 1994; Watson et al. 1998; Tilman 1998; Walker et al. 1999). These interrelated effects are difficult to study because they are highly variable in time and space and result in complex responses.

A reduction in snow cover associated with global warming may be an important effect of global climate change on northern forests. Because snow is important as an insulator of soils, reductions in snow cover may lead to increases in soil freezing, i.e. colder soils in a warmer world. Soil freezing stresses fine roots and soil microbial populations. Thus, increases in freeze events may affect root and microbial mortality, the cycling and loss of nutrients, the chemistry of drainage waters and soil-atmosphere trace gas fluxes. Over the long-term, differential resistance to freezing stress may be a key regulator of species composition in northern forests under a warmer climate condition.

In this special section of *Biogeochemistry*, we present results from a field manipulation experiment that examined the biogeochemical consequences of decreases in snowpack accumulation at the Hubbard Brook Experimental Forest (HBEF), a northern hardwood-dominated forest located in the White Mountains of New Hampshire. In this experiment, we quantified the effects of decreases in snowpack accumulation on soil temperature and moisture, root dynamics of two important tree species in this forest (sugar maple, yellow birch), microbial biomass, N cycling activity, soil solution chemistry and soil-atmosphere trace gas fluxes. In this special section we present four papers addressing: (1) soil temperature and moisture response to our snow manipulation treatment (Hardy et al.), (2) the response of fine root dynamics to treatment (Tierney et al.), (3) the response of soil inorganic N levels, *in situ* N mineralization and nitrification, denitrification and microbial biomass to the treatment (Groffman et al.), and (4) soil solution chemistry and fluxes of C, N and P (Fitzhugh et al.). In this introductory paper we: (1) review the literature on snow effects on forest biogeochemistry, (2) introduce our manipulation experiment and (3) present a brief overview of the results presented in the other papers in this issue.

Snow and ecosystems

While there has long been interest in the importance of snow as a regulator of the nature and extent of water dynamics in forest ecosystems, there has been a recent increase in interest in snow and winter biogeochemistry in temperate ecosystems. This interest has been stimulated by research showing that root and microbial processes are active in cold (0 to 5 °C) and even frozen soils (Vogt et al. 1986; Coxson & Parkinson 1987; Taylor & Jones

1990; Sommerfeld et al. 1993; Clein & Schimel 1995; Melloh & Crill 1995; Brooks et al. 1996, 1997, 1998, 1999; Alm et al. 1999) and that 20–50% of annual ecosystem C and N cycling and soil-atmosphere trace gas fluxes can occur during winter. Recent studies have investigated the factors that regulate variation in overwinter processes, their response to perturbation and climate change, and their influence on biogeochemical processes during the growing season (Mitchell et al. 1996; Brooks et al. 1998; Williams et al. 1998; Groffman et al. 1999; Hardy et al. 1999).

Snow is a critical regulator of soil processes in temperate forests during winter, acting as an insulator, preventing soil from freezing in many cases and providing moisture to support biological processes (Marchand 1987; Jones 1999). Snowpack dynamics and ice features also influence the overwinter exchange of gases, water and solutes and are a major regulator of nutrient outputs at spring melt (Likens & Bormann 1995; Rascher et al. 1987; Williams & Melack 1991; Stottlemyer & Toczydlowski et al. 1996, 1999; Brooks et al. 1999). Although the physics and chemistry of snow have been well studied in relation to water quantity and quality issues, the role of snow as a regulator of soil and ecosystem processes is poorly understood.

Interest in snow as a regulator of ecosystem biogeochemical processes has accelerated in recent years due to concerns about global climate change (Moore & McKendry 1996), and more importantly, due to observations of marked biogeochemical changes at the regional scale associated with low snow years. Snow 'drought' has been linked to sugar maple decline in Canada (Auclair et al. 1992; Pilon et al. 1994) and to changes in watershed nitrate (NO_3^-) outputs in the northeastern U.S. (Mitchell et al. 1996). A lack of mechanistic understanding of these events, coupled with predictions that global warming is expected to be most dramatic at high latitudes, during winter, has heightened interest in ecosystem processes during winter and how they respond to environmental change (Murdoch et al. 1998). While there are no detailed predictions of snow depth changes with global warming, existing studies and models have suggested that snowpacks respond very dynamically to climate change (van Katwijk et al. 1993; Giorgi et al. 1994; Williams et al. 1996; Moore & McKendry 1996).

Effects of soil frost and freeze/thaw on roots

There is increasing evidence that overwinter climate can substantially affect fine root processes, but the impact of freezing on fine root dynamics has not previously been studied under field conditions. In many northern forests, snowpack normally insulates soil from cold air temperatures and inhibits soil freezing (Stadler et al. 1996; Shanley et al. 1999), and winter fine root mortality is lower than other times of the year (Hendrick & Pregitzer 1992; Fahey & Hughes 1994). In contrast, minirhizotron observations in the boreal conifer forest of Alaska suggest that root mortality is concentrated in the winter months as concrete frost permeates the rooting zone (Reuss et al. 1998). Boutin and Robitaille (1995) induced soil freezing in a Canadian sugar maple forest by experimentally removing snow. They did not measure fine root dynamics, but suggested that extensive fine root mortality may have caused the resulting canopy dieback and elevated loss of nutrients from the system. Nor have fine root dynamics been observed during the rare winters when extensive soil freezing has occurred in temperate hardwood forests (e.g. 1969–1970, 1973–1974 and 1988–1989 at HBEF, Fahey & Lang 1975).

While the survival of temperate plants depends upon their ability to survive sub-freezing temperatures, fine roots may be more susceptible to freeze injury than other plant tissues. Fine roots normally experience less temperature variation than aboveground parts, and consequently exhibit freeze injury at milder temperatures than leaves or twigs (Sakai & Larcher 1987). Roots undergo winter-hardening later in the dormant season than aboveground parts (Sakai & Larcher 1987; Bigras & D'aoust 1993; Calme et al. 1994); thus, plants may be particularly susceptible to winter injury of root stock in years when snowpack is sparse or late in accumulating. Furthermore, the susceptibility of fine roots to freeze injury might differ by species within the northern hardwood forest. In this forest type, yellow birch occupies higher elevations and more extreme environmental conditions than sugar maple, and birch is a common associate of red spruce and balsam fir in the lower subalpine zone of northeastern mountains (Battles et al. 1995). A laboratory study of the frost hardiness of seedling fine roots found yellow birch to exceed sugar maple (Calme et al. 1994).

Alteration of fine root processes by freezing might have dramatic impacts on nutrient cycling and retention of forest ecosystems by disrupting the temporal and spatial synchrony between nutrient availability and nutrient uptake. In northern hardwood forests, nutrient loss typically peaks in early spring when microbial mineralization and nitrification can precede tree uptake by fine roots (Muller & Bormann 1976; Likens & Bormann 1995). Disturbance to vegetation in forested systems often leads to losses of nutrient elements, most notably nitrogen in the form of NO_3^-, and the magnitude of nutrient loss varies with magnitude and nature of the disturbance (e.g. herbivory, harvest) and characteristics of the site (e.g. forest cover type, soil type; Vitousek et al. 1982; Likens & Bormann 1995). Disruption of fine root processes has been shown to play an important role in these losses. Vitousek et al. (1982) showed that trenching of root systems in forested plots resulted in nutrient loss from a variety of forest types. Application of herbicide to a harvested northern hardwood forest at HBEF prevented regrowth of vegetation and thus uptake by fine roots, and led to increased nutrient losses over harvests in which herbicide was not applied (Likens & Bormann 1995). Hence, disruption of fine root processes can have substantial effects on biogeochemical cycling, particularly during springtime when nutrient loss is often highest.

In sum, regional climate changes that influence snowpack accumulation might affect the structure and function of northeastern forests by altering fine root dynamics. Even if there are no differential effects of soil freezing on root mortality of northern hardwood tree species, increased overwinter mortality of fine roots will undoubtedly alter the magnitude and timing of substrate availability to the decomposer community. Fine roots are a labile resource for decomposers (Fahey et al. 1988), and the large increase in NO_3^- leaching following cutting of northern hardwood forests is linked to the mineralization of fine roots and consequent increases in substrate availability to nitrifying bacteria (Vitousek et al. 1982; Aber et al. 1989; Fahey & Arthur 1994).

Effects of soil frost and freeze/thaw on soil microbial biomass and activity

While it is generally recognized that soil frost and freeze/thaw events have important effects on soil microbial biomass and activity, this disturbance is not well characterized due to the complexity of the soil ecosystem and to the multiple effects that freezing has on different biological, physical and chemical variables. Many studies have suggested that freeze/thaw cycles stress and/or kill off a portion of the soil microbial biomass (Ross 1972; Morely et al. 1983; Skogland et al. 1988; Christensen & Christensen 1991; DeLuca et al. 1992; Clein & Schimel 1995; Schimel & Clein 1996). This partial sterilization leads to a marked increase in C and N mineralization as the growth and activity of the surviving microbes are stimulated by the input of substrate (i.e. the killed microbial cells). While this response has been well demonstrated in laboratory studies, its relevance to field conditions remains a critical question. There is also uncertainty relating to the duration of enhanced mineralization and the response to repeated freeze/thaw events. It is likely that the response of mineralization to freezing will vary with soil temperature, the size of the microbial biomass and other soil conditions (Edwards & Cresser 1992). Freeze/thaw events also affect soil structure, which influences C availability, aeration and water and nutrient movement, all of which have important effects on microbial biomass and activity (Tisdall & Oades 1982).

The partial sterilization effect, combined with disruption of soil structure and input of labile organic matter from root mortality may enhance N mineralization and nitrification in ecosystems affected by freeze/thaw events (DeLuca et al. 1992; Edwards & Cresser 1992; Boutin & Robitaille 1994; Clein & Schimel 1995; Brooks et al. 1998). In many temperate forest soils, nitrification is regulated by intense competition for ammonium (NH_4^+) between plants, heterotrophic microbes and nitrifiers (Aber et al. 1989). Disruption of this competition at the ecosystem scale by clear-cutting, blowdowns and other major disturbances stimulates nitrification and NO_3^- loss (Vitousek et al. 1982; Aber et al. 1989). Freeze/thaw events can be viewed in this context (i.e. as disturbances of the soil/plant system that allow for nitrification to proceed). Changes in freeze/thaw events could thus be an important disturbance, influencing ecosystem N loss, acidification of drainage waters (driven by nitrification), N_2O fluxes (nitrifiers can produce N_2O) and CH_4 fluxes (there are links between soil NH_4^+, nitrifiers and methanotrophs).

Increased nitrification following freeze/thaw events may not result in increased NO_3^- availability and loss if denitrification increases as a NO_3^- sink. Several studies have demonstrated increases in denitrification following freeze/thaw events in forest soils (Edwards & Killham 1986; Groffman & Tiedje 1989; Christensen & Christensen 1991). In temperate forest ecosystems, denitrification tends to be most vigorous in the late winter/early spring period when soils are wet (anaerobic) and soil NO_3^- concentrations are relatively high (Groffman & Tiedje 1989). However, it is likely that stimulation of nitrification will overwhelm enhanced denitrification because denitrifiers are more sensitive to freezing stress than nitrifiers (Cooke 1990) and more importantly, denitrification occurs only during the period of very wet soil conditions immediately following soil thaw, while enhanced nitrification persists for several months following soil disturbance (Aber et al. 1989; Boutin & Robitaille 1994).

Effects of soil frost and freeze/thaw on soil solution chemistry and nutrient loss

Acidic deposition has impacted soil and drainage waters in forested regions of the northeastern U.S. and eastern Canada (Jeffries et al. 1986; Landers et al. 1988). Chronic acidification of surface waters is largely due to elevated inputs of SO_4^{2-}. Surface waters also exhibit episodic acidification associated with hydrologic events. In the northeast U.S., episodic acidification of surface waters is generally associated with increases in concentrations of NO_3^- and dilution of concentrations of basic cations during spring snowmelt and storm events (Schaefer et al. 1990; Wigington et al. 1990). Emissions of SO_2 peaked in 1970 and concentrations of SO_4^{2-} in precipitation and surface waters have decreased since that time (Likens et al. 1996). However, these changes have not been accompanied by increases in acid neutralizing capacity (ANC) in surface waters (Dillon et al. 1988; Driscoll & van Dreason 1993; Stoddard et al. 1999; Driscoll et al. 2001). The recovery of surface waters from inputs of acidic deposition has been restricted due to depletion of basic cations in soil (Bailey et al. 1996; Likens et al. 1996) and increases in concentrations of NO_3^- (Driscoll & van Dreason 1993; Murdoch & Stoddard 1993). There is concern that forests in the Northeast U.S. may be susceptible to a condition of 'nitrogen saturation' (Aber et al. 1989; Kahl et al. 1993; Stoddard 1994; Foster et al. 1997; Fenn et al. 1998; Lovett et al. 2000). Due to elevated inputs of N from atmospheric deposition and decreasing uptake of N by vegetation associated with increasing stand age, forested watersheds are exhibiting increased leaching losses of NO_3^- (Hedin et al. 1995). Unfortunately, due to large pools of N in forest ecosystems and the strong biotic control of the terrestrial N cycle, it is difficult to discern 'real' long-term trends in N cycling and loss.

In addition to atmospheric deposition, climate and biotic disturbances such as soil freezing may influence acidification and N loss in terrestrial ecosystems. For example, Mitchell et al. (1996) reported a pattern of elevated NO_3^- concentrations and loss from forested watersheds across the northeastern U.S. in response to a soil freezing event. Very low air temperature and limited snow cover during early winter in 1989 were suggested to result in a soil freezing event that likely contributed to very high concentrations of NO_3^- during the spring of 1990. For sites in the Adirondack and Catskill regions of New York, the period of elevated NO_3^- loss persisted during summer baseflow conditions. Given the effects of soil freezing on root and microbial processes described above, it is likely that this regional soil freezing event resulted in elevated NO_3^- losses. This event also resulted in short-term (2-yr) increases in the acidity of surface waters. It is likely that soil freezing events also result in elevated concentrations of DOC in drainage waters. Elevated export of DOC from soil enhances acidification and the transport of trace metals to downstream surface waters (Driscoll et al. 1993, 1995).

A snow manipulation experiment at Hubbard Brook

Over the past three years, we have investigated the consequences of decreases in snow cover on biotic functions and biogeochemical processes at the HBEF, a northern hardwood-dominated forest in the White Mountains of New Hampshire (www.hbrook.sr.unh.edu). The HBEF has been the site of numerous biogeochemical studies, primarily focused on whole northern hardwood forest watershed ecosystem element budgets. While the importance of snowpack dynamics and winter climate on these budgets has been noted (Likens & Bormann 1995), there have been few detailed studies or experimental manipulations focused on overwinter processes.

The objective of our experiment was to quantify the effects of decreases in snowpack accumulation on soil freezing, root dynamics of two key tree species (sugar maple, yellow birch) at HBEF, microbial biomass and activity, the chemistry of drainage water, and soil-atmosphere trace gas fluxes. In addition to the experimental work, Jordan et al. (in preparation) developed a model (SOILTHERM) of snow depth and soil frost dynamics that we use to analyze field data and to evaluate climate scenarios. A long-term (36 yr) database on streamwater chemistry is used in concert with this model to examine the effects of past natural freezing events on nutrient loss and to forecast possible future response under changing climatic conditions.

In this special section of *Biogeochemistry*, we present four papers addressing, (1) soil temperature and moisture response to our snow manipulation treatment (Hardy et al.), (2) response of fine root dynamics to treatment (Tierney et al.), (3) the response of soil inorganic N levels, *in situ* N mineralization and nitrification, denitrification and microbial biomass to the treatment (Groffman et al.) and (4) soil solution losses of C, N and P (Fitzhugh et al.).

Hardy et al. (this issue, 'Snow depth, soil frost and water dynamics in a northern hardwood forest') describe our experimental design and plot installations for quantifying snow characteristics, soil temperature and moisture dynamics and present detailed data on these dynamics for the period from fall 1997–spring 2000. Included are analysis of relationships between snow depth and soil frost and evaluation of the effects of soil freezing on soil water dynamics.

Tierney et al. (this issue, 'Soil freezing alters fine root dynamics in a northern hardwood forest') evaluate the effects of the snow manipulation treatment on fine root mortality and production. Minirhizotrons were used to quantify fine root dynamics throughout the year. Estimates of nutrient release associated with root mortality were also presented.

Groffman et al. (this issue, 'Effects of mild winter freezing on soil nitrogen and carbon dynamics in a northern hardwood forest') present data on soil inorganic N levels, in *situ* rates of N mineralization and nitrification, denitrification (intact core, C_2H_2-based method), microbial biomass C and N content and potential net N mineralization and nitrification. Treatment and species effects and seasonal as well as annual variation in N cycling processes were analyzed.

Fitzhugh et al. (this issue, 'Effects of soil freezing disturbance on soil solution N, P, and C chemistry') characterize and quantify losses of inorganic and organic N and C as well as inorganic P induced by the snow manipulation treatment. Zero-tension lysimeters were used to sample soil solutions draining from the forest floor and mineral soil horizons throughout the year.

A brief summary of our findings

During the mild winters of 1997/1998 and 1998/1999, our snow removal manipulation produced relatively mild freezing events (soil temperatures seldom decreased below –4 °C). Previous laboratory studies suggest that significant biogeochemical effects should only occur with a severe freeze that directly causes root and microbial mortality (Nielsen et al. 2001; Clein & Schimel 1995). Surprisingly, our treatment caused significant increases in fine root mortality, soil NO_3^- concentrations and leaching of N, P and C, and a shift in the timing of fine root production. No significant increase in rates of N mineralization and nitrification were detected even though the increase in root mortality represented a significant input of labile N to the soil microbial community.

Our initial hypothesis was that snow is an important insulator of the forest soil so that reduced snowpack induces soil freezing, causing fine root and microbial mortality. This mortality subsequently results in increased hydrologic and gaseous N losses as the dead root and microbial cells are decomposed, mineralized and nitrified. While our treatment increased N losses as expected, the detailed results raised important mechanistic questions about the response of the soil ecosystem to freezing disturbance. The marked response of fine root dynamics within the forest plots to such mild freezing temperatures was unexpected and raises important questions about the mechanism whereby soil freezing affects fine root dynamics. Laboratory tests on potted tree seedlings exposed to controlled freezing regimes confirmed that mild freezing temperatures (to –5 °C) were insufficient to directly injure winter-hardened fine roots of these species (Tierney et al. this issue). Unlike typical lab studies which are limited to short-term, sustained freezing, our controlled freezing treatments attempted to create freezing conditions similar to those in our forest plots including a long-duration freeze (ten weeks) and a freeze-thaw scenario; yet our results show that neither treatment significantly affected fine root dynamics in potted seedlings. While the mechanism of injury acting in our forest plots will only be determined by further study, these results provide evidence that the mechanism is indirect and difficult to replicate in pots. Thus, it seems plausible that fine root injury in our forest plots was caused indirectly by the physical nature of freezing and root anchorage in forest soils. Pressure on fine roots caused by soil movement and ice lens formation during freezing would be greater in a forest soil than in a pot and could result in significant mechanical damage. These effects would not be replicable in laboratory studies of potted trees.

Calculation of the N release associated with the elevated fine root mortality induced by freezing indicated that it was a substantial fraction of the measured increase in hydrologic N loss, suggesting that fine root decomposition contributed significantly to the increased loss. However, the effects of the snow manipulation on N loss were likely more complex than a simple increase in mineralization associated with root mortality. Despite the root mortality, no significant increases in soil N mineralization and nitrification were detected, although soil NO_3^- levels were increased. These results suggest that reduced N uptake by fine roots was also important as a regulator of hydrologic loss. Fine root uptake may have been impaired directly by reduction in fine root length due to elevated mortality, and indirectly by sublethal effects on fine root physiology or severed mycorrhizal connections. Reduced fine root uptake could reduce competition for inorganic N, allowing soil NO_3^- to increase without a stimulation of mineralization and nitrification. Thus soil freezing altered fine root dynamics and disrupted the temporal and spatial synchrony between nutrient availability and nutrient uptake in the northern hardwood forest, causing nutrient loss (Bormann & Likens 1979).

Fluxes of N leaching from the soil freezing treatment plots ranged from 1,880 to 4,570 mol ha^{-1} yr^{-1} in the Oa horizon and from 488 to 1,340 mol ha^{-1} yr^{-1} in the Bs horizon which are significant in comparison to wet N deposition to the HBEF during 1992–1993 (525 mol ha^{-1} yr^{-1}; Mitchell et al. 1996) as well as stream NO_3^- export at watershed 6 of the HBEF during 1997 (25.1 mol ha^{-1} yr^{-1}). Accelerated mobilization of inorganic P from the forest floor, coupled with retention in occluded forms in the mineral soil horizons could affect the relative roles of N and P as limiting nutrients for forest growth. Amounts of inorganic P loss induced by freezing ranged 14.5 to 31.5 mol ha^{-1} yr^{-1} in the Oa horizon and from 0.41 to 7.1 mol ha^{-1} yr^{-1} in the Bs horizon, which are significant relative to available P pools (22 mol ha^{-1}) and P mineralization rates in the forest floor (182 mol ha^{-1}) in this ecosystem (Yanai 1992).

Our results have important implications for the function of forest ecosystems under changing climatic conditions. Mild freeze events are likely to become increasingly common if snowpacks develop later and melt earlier, as is predicted to occur as the climate warms due to increased atmospheric CO_2 levels (Cooley 1990). Increased freeze frequency may disrupt the spatial and temporal synchrony between nutrient availability and nutrient uptake, and lead to forests with higher root turnover, less ability to retain atmospheric N deposition and higher N_2O emissions. These changes could decrease timber production, increase delivery of N to receiving waters, affect competitive relationships among tree species and increase greenhouse forcing and stratospheric ozone depletion (Vitousek et al. 1997).

Our results suggest that forest species composition will be an important regulator of the response of forest ecosystems to increased freeze frequency. Sugar maple treatment plots had higher NO_3^- concentrations and drainage water acidity than yellow birch treatment plots. This contrasting response to treatment likely derives from differences in litter quality between these species. Litter quality has been shown to have strong effects on organic matter quality and N dynamics in soil (Pastor et al. 1984; Scott & Binkley 1997; Finzi et al. 1998). Differences in mycorrhizal associations (yellow birch is an ectomycorrhizal species, while sugar maple is endomycorrhizal) may also play a role in response to freezing stress. Our results are consistent with recent studies that suggest that natural or anthropogenic factors that influence species composition will be critical determinants of ecosystem response to environmental change (Tilman 1998; Lovett & Rueth 1999; Nielsen et al. 2001).

In a more basic sense, our study raises questions about the importance of freeze frequency as a regulator of the nature and extent of N cycling and loss in forest ecosystems. Perhaps freeze frequency should be considered in large-scale functional evaluations of ecosystems. Forests with soils that freeze frequently may have inherently different patterns of element cycling and loss than those that do not.

Our results also reinforce the idea that subtle changes in climate may have much more significant effects on ecosystem function than simple changes in mean temperature and precipitation (Vitousek 1994; Watson et al. 1998; Tilman 1998; Walker et al. 1999). In addition to snow cover, changes in factors such as seasonal drought, ice storms and extreme precipitation events likely need to be included in assessments of the effects of climate change on ecosystem function.

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