

Winter in northeastern North America: a critical period for ecological processes

John L Campbell¹, Myron J Mitchell², Peter M Groffman³, Lynn M Christenson^{2,3}, and Janet P Hardy⁴

Ecological research during winter has historically been a low priority in northeastern North America, an oversight that stems from the commonly accepted notion that there is little biological activity when temperatures drop below freezing. However, recent research has shown that winter can be an especially important period for ecological processes, providing evidence that "dormant season" is a misnomer. Uncertainties about the effects of climate change on ecosystems are highlighting the need for a more thorough understanding of winter ecology. The failure to collect winter data in northeastern North America has meant that researchers are ill-equipped to make predictions about how ecosystems will respond to future climate change. A more focused, integrative ecological winter monitoring and research effort will enable us to better prepare for, and respond to, future climate change.

Front Ecol Environ 2005; 3(6): 314–322

In northern regions, winter is often referred to as the "dormant season", based on the belief that biological activity ceases during this period. While it is true that trees harden off, some animals migrate, hibernate, or die, and the landscape is typically covered in snow and ice, there is more activity during this period of "dormancy" than previously thought. Many ecological processes can persist at temperatures near or below freezing, even though optimal temperatures may be higher (Table 1). Much of this winter activity occurs in soil, where an insulating layer of snow can keep temperatures warm enough to support a wide range of biotic activities, such as root growth and microbial respiration. Despite the harsh climate, winter processes can contribute substantially to annual nutrient budgets (Table 2), and should be included in ecological studies. The failure to collect winter data may result in an inability to fully understand ecological processes and long-term trends.

A number of reasons have been cited for the lack of

enthusiasm for conducting ecological studies during winter (see Marchand 1996). The omission is due not only to the misconception that there is little biological activity during this period, but also to the inherent difficulties associated with winter sampling; for instance, cold temperatures and snow cover can make sampling especially difficult and challenging in winter. Moreover, winter sampling conflicts with the academic calendar, thereby limiting the availability of students and academic scientists to conduct such research.

Much of our current understanding of winter processes, particularly research on hydrology and biogeochemistry, is based on research conducted in arctic and alpine regions. Numerous studies on winter ecology have occurred at high elevation sites in the western US, such as the Rocky Mountains (eg Colorado's Niwot Ridge Long Term Ecological Research site [LTER] and Rocky Mountain Biological Laboratory) and the Sierra Nevada Mountains of California (eg Emerald Lake, Sierra Nevada Aquatic Research Laboratory). Winter research has been a higher priority in these areas because runoff is generally dominated by snowmelt, which plays a critical role in water supply and quality. A more thorough understanding of cold weather processes has also been gained by examining arctic ecosystems, mainly because of the characteristic temperature extremes and sensitivity to climate change in these regions (Chapin *et al.* 1992). Far less ecological research has been carried out during winter in northeastern North America, despite prolonged periods of cold and heavy snow cover. This oversight has resulted in a gap in our understanding of ecological processes in these ecosystems.

There is a pronounced climate gradient of winter conditions across northeastern North America, varying from approximately 100 days of air temperatures below freezing in coastal southern New England to greater than 150 days

In a nutshell:

- Snow and other winter conditions in northeastern North America have a major effect on ecological processes
- Spatial and temporal patterns of snow cover are likely to change in response to future global warming
- Reductions in snow depth are expected to increase soil frost occurrence and severity
- Climate change interactions and feedback mechanisms during winter are complex, requiring an integrated research approach

¹USDA Forest Service, Northeastern Research Station, Durham, NH (jlcampbell@fs.fed.us); ²SUNY College of Environmental Science and Forestry, Syracuse, NY; ³Institute of Ecosystem Studies, Millbrook, NY; ⁴Cold Regions Research and Engineering Laboratory, Hanover, NH

References

- Chardard D, Desvages G, Pieau C, and Dournon C. 1995. Aromatase activity in larval gonads of *Pleurodeles waltl* (Urodele Amphibia) during normal sex differentiation and during sex reversal by thermal treatment. *Gen Comp Endocrinol* 99: 100–7.
- Conover DO and Heins SW. 1987. The environmental and genetic components of sex ratio in *Menidia menidia* (Pisces: Atherinidae). *Copeia* 1987: 732–47.
- Crews D. 1996. Temperature-dependent sex determination: the interplay of steroid hormones and temperature. *Zool Sci* 13: 1–13.
- Crisp TM, Clegg ED, Cooper RL, et al. 1998. Environmental endocrine disruption: an effects assessment analysis. *Environ Health Perspect* (Suppl) 106: 11–56.
- Du W-G and Ji X. 2003. The effects of incubation thermal environments on size, locomotor performance and early growth of hatchling soft-shelled turtles, *Pelodiscus sinensis*. *J Thermal Biol* 28: 279–86.
- Greenbaum E. 2002. A standardized series of embryonic stages for the emydid turtle *Trachemys scripta*. *Can J Zool* 80: 1350–70.
- Hayes TB. 1998. Sex determination and primary sex differentiation in amphibians. *J Exp Zool* 281: 373–99.
- Hayes T, Chan R, and Licht PJ. 1993. Interactions of temperature and steroids on larval growth, development, and metamorphosis in a toad (*Bufo boreas*). *J Exp Zool* 266: 206–15.
- Hayes TB, Collins A, Lee M, et al. 2002. Hermaphroditic, demasculinized frogs after exposure to the herbicide atrazine at low ecologically relevant doses. *Proc Nat Acad Sci* 99: 5476–80.
- Heinz GH, Percival HF, and Jennings ML. 1991. Contaminants in American alligator eggs from Lake Apopka, Lake Griffin, and Lake Okeechobee, Florida. *Environ Mon Assess* 16: 277–85.
- Janzen FJ. 1995. Experimental evidence for the evolutionary significance of temperature-dependent sex determination. *Evolution* 49: 864–73.
- Janzen FJ and Paukstis GL. 1991. Environmental sex determination in reptiles: ecology, evolution, and experimental design. *Quart Rev Biol* 66: 149–79.
- Rhen T and Crews D. 2000. Organization and activation of sexual and agonistic behavior in the leopard gecko, *Eublepharis macularius*. *Neuroendocrinology* 71: 252–61.
- Rhen T and Lang J. 1999. Temperature during embryonic and juvenile development influences growth in hatchling snapping turtles, *Chelydra serpentina*. *J Therm Biol* 24: 33–41.
- Rhen T, Willingham EJ, Sakata JT, et al. 1999. Incubation temperature influences sex-steroid levels in juvenile red-eared slider turtles, *Trachemys scripta*, a species with temperature-dependent sex determination. *Biol Reprod* 61: 1275–80.
- Tousignant A and Crews D. 1995. Incubation temperature and gonadal sex affect growth and physiology in the leopard gecko (*Eublepharis macularius*), a lizard with temperature-dependent sex determination. *J Morphol* 224: 159–70.
- Welshons WV, Thayer KA, Judy BM, et al. 2003. Large effects from small exposures. I. Mechanisms for endocrine disrupting chemicals with estrogenic activity. *Environ Health Persp* 111: 994–1006.
- Wibbels T, Bull JJ, and Crews D. 1994. Temperature-dependent sex determination: a mechanistic approach. *J Exp Zool* 270: 71–78.
- Willingham EJ. 2002. Embryonic exposure to low-dose pesticides: effects on fitness parameters in the hatchling red-eared slider turtle. *J Toxicol Environ Health* 64: 257–72.
- Willingham EJ. 2004. Different incubation temperatures result in differences in mass in female red-eared slider turtle hatchlings. *J Thermal Biol* 30: 61–64.
- Willingham EJ and Crews D. 1999. Sex reversal effects of environmentally relevant xenobiotic concentrations on the red-eared slider turtle, a species with temperature-dependent sex determination. *Gen Comp Endocrinol* 113: 429–35.
- Willingham EJ and Crews D. 2000. The red-eared slider turtle: an animal model for the study of low doses and mixtures. *Amer Zool* 40: 421–29.
- Willingham EJ, Rhen T, Sakata JT, and Crews D. 1999. Embryonic treatment with xenobiotics disrupts sex-steroid profiles in hatchling red-eared slider turtles, *Trachemys scripta*. *Environ Health Persp* 108: 329–32.

Table 1. Lower temperature limits of selected ecological processes

Ecological process	Temperature (°C)	Reference
Photosynthesis (conifer trees)	-6 (air)	Parker (1953); Hadley (2000)
Woody vegetation root growth	0 to 5 (soil)	Kozłowski <i>et al.</i> (1991); Burke and Raynal (1994)
Soil microbial growth (metabolic activity)	-20 (soil)	Rivkina <i>et al.</i> (2000)
Soil respiration (CO ₂ production)	-5 to -6 (soil)	Coxson and Parkinson (1987); Clein and Schimel (1995); Brooks <i>et al.</i> (1997)
Soil net N mineralization	-2 to -5 (soil)	Dorland and Beauchamp (1991); Clein and Schimel (1995)
Extracellular soil enzyme activity	-20 (soil)	Bremner and Zanuta (1975)

in southern Quebec, Canada (US National Weather Service, National Climatic Data Center; Environment Canada, National Climate Archive). Across this same gradient, annual snowfall typically ranges from 75 cm to greater than 300 cm, with 115 to 150 days of snow cover. Since air temperatures remain near freezing during much of the winter, small fluctuations in temperature can drastically alter the type of precipitation that occurs (eg snow, sleet, freezing rain, rain), which in turn can have dramatic impacts on ecosystems in the region.

The importance of understanding winter ecology is accentuated by concerns about how ecosystems will respond to climate change. Because we do not have a thorough understanding of ecological processes during winter, it is difficult to predict future responses to climate change with any certainty. This lack of understanding is a concern, since winter climates have the potential to affect ecological processes in far-reaching, complex ways. The objectives of this paper are to highlight the importance of ecological processes during winter and to provide an overview of some potential effects of climate change on winter ecology in northeastern North America. This information will identify gaps in our understanding and will help focus future winter research in the region.

■ The changing winter climate

There is ample evidence to suggest that climate has changed over the past century and will continue to change in the future. The Intergovernmental Panel on Climate Change (IPCC) estimates that average global near-surface air temperatures have increased by 0.6 °C (± 0.2 °C) during the 20th century and are expected to increase by 1.4–5.8 °C over the next century, based on various modeled estimates (IPCC 2001). In the northeastern US, temperature increases of 3–5 °C are predicted during this same time period (NERA 2001). Historical

increases in temperature in northeastern North America have been linked to changes in the timing of climate indicators such as lilac blooms (Schwartz and Reiter 2000), ice cover on lakes (Hodgkins *et al.* 2002), and the return of migratory birds (Oglesby and Smith 1995).

Changes in precipitation are expected to accompany air temperature increases, yet there is still a great deal of uncertainty about the direction and extent of change. Climate simulations generally indicate that precipitation will increase in northeastern North America, especially during winter (IPCC 2001). Modeled estimates project an increase in precipitation of as much as 10–30%, together with a greater frequency of intense storms and droughts (NERA 2001). Climate change may differentially affect precipitation patterns in northeastern North America, due to local geographic influences. In leeward regions of the Laurentian Great Lakes, an increase in lake-effect snowfall during the 20th century was a result of warmer surface water temperatures and decreased ice cover (Leathers and Ellis 1996; Burnett *et al.* 2003).

Despite potentially greater amounts of winter precipitation, reductions in snowpack depth are projected, due to a

Table 2. Winter versus annual values for selected ecological processes at the Hubbard Brook LTER site

Ecological process	Winter*	Annual	Reference
Net N mineralization (g N m ⁻²)			Groffman <i>et al.</i> (2001)
Forest floor	0.8	9.7	
Mineral soil	0.9	7.3	
Net nitrification (g N m ⁻²)			
Forest floor	0.3	3.8	
Mineral soil	0.6	6.0	
Soil N ₂ O flux (ng N cm ⁻² h ⁻¹)	0.7	4.9	Groffman <i>et al.</i> (submitted)
Soil methane flux (mg CH ₄ m ⁻² d ⁻¹)	-0.6	-4.9	
Total soil respiration (mg C m ⁻² h ⁻¹)	11	144	
Streamwater export (kg ha ⁻¹)			Likens and Bormann (1995)
NO ₃ ⁻	3.9	17.2	
SO ₄ ²⁻	9.9	54.0	
Cl ⁻	0.9	4.7	
Ca ²⁺	2.7	13.8	

*Defined as Dec–Mar, except for streamwater export (Dec–Feb).



Courtesy of USDA Forest Service

Figure 1. Tree damage following an ice storm in January 1998 that affected much of the northeastern United States and southern Quebec, Canada.

greater occurrence of thaws, sleet, and rain-on-snow events. These events also alter the physical properties of the snowpack and hence alter snow density and ice lens formation. Reductions in the duration and depth of snow cover can have a marked impact on soil temperature, since snow provides an insular layer that protects soils from exposure to aboveground winter temperatures. An insulating snow layer may prevent soil frost formation at the onset of winter, and may also reduce the incidence of soil freeze–thaw cycles. If early winter snowpack formation is delayed, then soils typically freeze and remain frozen underneath the snow throughout the winter (Goodrich 1982).

■ Ecological responses to a changing winter climate

The effects of a changing winter climate may be extensive and complex, with positive and negative feedbacks to a variety of ecological processes.

Vegetation

Vegetation can be affected by climate change both directly and indirectly. In January of 1998, an ice storm severely damaged forests in northeastern North America, impacting 8.9 million hectares of forestland in New York, Vermont, New Hampshire, Maine, and Quebec (Figure 1; Miller-Weeks and Eagar 1999; Irland 2000). The creation of forest gaps and the increase in available light due to canopy damage caused the subsequent release and rapid growth of shade-tolerant understory species, such as American beech (*Fagus grandifolia*; Rhoads *et al.* 2002).

Warmer winter temperatures have been shown to trigger phenological phases earlier (eg spring bud burst), resulting in a loss of cold hardiness. The widespread decline of red spruce (*Picea abies*) in northeastern North America has been attributed to winter injury caused by cold air temperatures combined with a reduction in frost hardiness caused by acidic deposition (Schaberg and

DeHayes 2000). Winter injury to vegetation may also occur belowground. Soil frost heaving due to ice expansion can sever fine roots, impairing water and nutrient uptake by plants (Tierney *et al.* 2001).

Microbial processes

Rates of soil microbial activity are surprisingly high in winter, comprising a significant percentage of annual activity (Table 2; Brooks *et al.* 1996; Groffman *et al.* 2001b). Trace gas concentration gradients within the snowpack are well documented (eg Sommerfeld *et al.* 1993) and provide evidence of microbial processing during winter. Experiments at high elevation sites in the Rocky Mountains of Colorado have shown that heterotrophic respiration in soils at temperatures below 0 °C is limited by carbon, and that CO₂ efflux during winter depends on the availability of carbon substrates (Brooks *et al.* 2004). Microbial respiration is an exothermic reaction that generates heat, potentially causing soil temperatures to rise. It has been suggested that soil respiration reactions during winter in arctic regions may warm soils enough to promote further respiration, creating a positive feedback (Zimov *et al.* 1996).

Soil freeze–thaw cycles enhance litter decomposition, mineralization rates, nutrient leaching, and trace gas fluxes, and therefore have important effects on the cycling of nutrients such as carbon and nitrogen. Freeze–thaw cycles can also destabilize soil aggregates, exposing substrates and stimulating microbial growth. Laboratory experiments have shown that microbial populations may increase following initial freeze–thaw cycles, fueled by a pulse of dead cells released from biological material in soil (Skogland *et al.* 1988). However, multiple freeze–thaw cycles may eventually cause a reduction in microbial populations and their respective processes as the supply of available substrates diminishes (Schimel and Clein 1996; Schimel *et al.* 2004). Recent studies have shown that freezing and thawing do not significantly affect microbial biomass when measured in situ (Groffman *et al.* 2001b) or in laboratory experiments with realistic rates of freezing and thawing, such as those that occur in the field (Lipson *et al.* 2000). Microbial communities appear to tolerate freezing temperatures, provided that the freezing occurs slowly.

Water

Soil freezing strongly influences watershed hydrology by affecting runoff patterns. When soil frost forms in open areas, such as agricultural ecosystems, it is typically continuous and highly impermeable (Hart 1963). This “concrete” frost causes snowmelt and rainwater to run off the soil surface directly into surface waters, bypassing soil and

groundwater flowpaths (Shanley and Chalmers 1999). In contrast, forest ecosystems are more likely to have granular frost, characterized by higher infiltration rates and negligible surface runoff.

Soil and groundwater reservoirs store great quantities of water and therefore serve as buffers against flooding during the snowmelt period. A large amount of water is also stored in the snowpack during winter. Under a warmer winter climate scenario, snowpack water storage would be reduced and the water flux distributed more evenly throughout the year. Because there is less spring snowmelt when temperatures are warmer, high river flows are dampened and occur earlier (Hodgkins *et al.* 2003). Despite a reduction in snowmelt runoff, climate change may increase the frequency of rain-on-snow events and intense storms, often resulting in high river flows and flooding, particularly when the snowpack has a high water content and soils are saturated.

In northeastern North America, snowmelt and rain-on-snow events may result in episodic acidification, since the region receives relatively high acidic deposition and soils often have little acid buffering capacity (Schaefer *et al.* 1990). During acidic episodes, the low pH of water acting in combination with a high concentration of inorganic aluminum is toxic to acid-sensitive aquatic species. Winter temperatures may influence the degree of surface water acidification. Several studies have shown a relatively strong positive relationship between winter temperatures and nitrate (NO_3^-) in surface water; this is attributed to enhanced nitrification resulting from earlier snowmelt and greater soil temperature fluctuations (Figure 2; Murdoch *et al.* 1998; Park *et al.* 2004). Winter is a critical period for the export of biologically important nutrients such as NO_3^- , since uptake by vegetation and microbial immobilization are lower during the winter months (Mitchell *et al.* 1996). A large proportion of the export of these nutrients occurs during winter and is greatly affected by changes in winter climate (Table 2).

Wildlife

Animals are also responsive to winter climate change, since winter is often a critical period for their survival (Pruitt 1960; Merritt 1984). Warmer winters and decreased snow depth may be beneficial to some species, such as white-tailed deer (*Odocoileus virginianus*) and moose (*Alces alces*), although increased reproduction and survival of these species following a warmer winter may exhibit a 2–3 year time lag (Post and Stenseth 1999). In contrast, animals that overwinter in surface soils, such as some insects, reptiles, amphibians, and mammals, may become inactive or perish as a result of low temperatures caused by a lack of insulating snow. Deep snow has a positive effect on the energy economy of subnivean (under the snow) animals, often resulting in increased survival and shifts in population dynamics (Merritt *et al.* 2001; Lima *et al.* 2002). Many ectothermic animals have adaptations

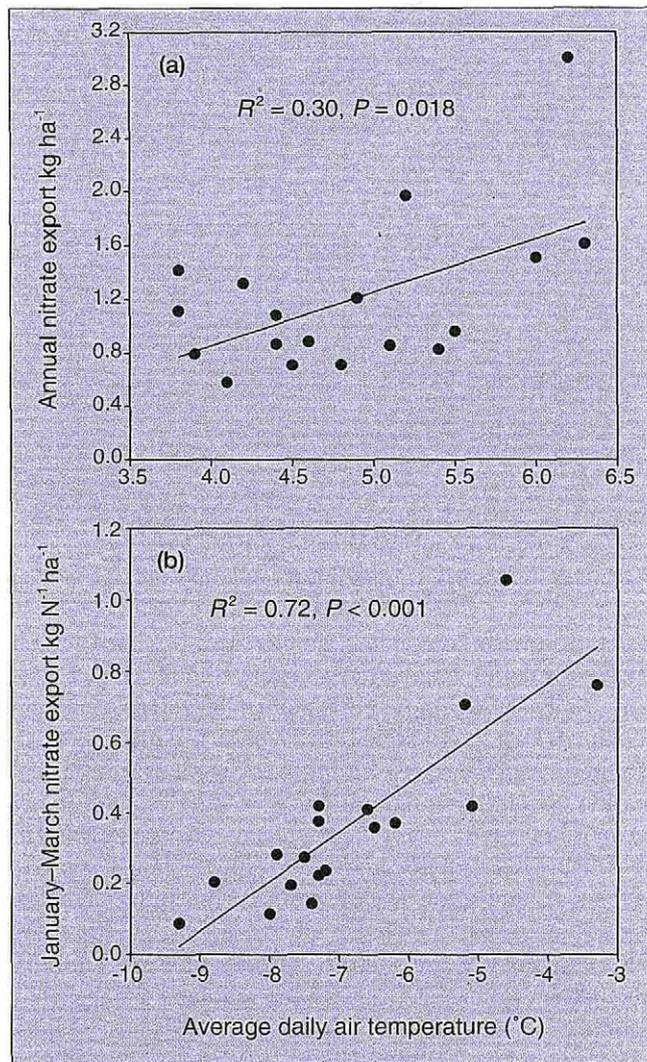


Figure 2. Relationship between air temperature and nitrate export for (a) the entire year and (b) January–March at the Arbutus Lake outlet, Huntington Forest, New York, 1984–2001. Adapted from Park *et al.* (2004).

that make them freeze tolerant or that prevent their cells from freezing (Schmid 1982; Storey and Storey 1996). Endothermic animals exposed to excessively low temperatures may increase their metabolic rates, ultimately leading to starvation when food supplies are inadequate.

Behavioral patterns, including hibernation and migration, may be delayed or disrupted as a result of changes in temperature, and habitats may become unsuitable, resulting in a shift in population ranges (eg Johnston and Schmitz 1997; Blumstein *et al.* 2004). Changes in patterns of herbivory associated with winter climate affect the distribution and type of vegetation present. A reduction in snow depth increases the amount of available browse by making the lower branches more accessible. The removal of understory vegetation by herbivores during winter leads to changes in the structure of the forest, and reduced snow depth may improve animal survival, further increasing herbivore populations and browsing.

During winter, some herbivores (such as moose) prefer



CH Wiley

Figure 3. Changes in climate and snow depth may alter the browsing behavior of animals such as moose, affecting forest health and composition.

vegetation with favorable characteristics (eg large winter buds, succulent evergreen vegetation; Shipley *et al.* 1998), potentially causing more unpalatable vegetation to prevail (Figure 3; Pastor and Naiman 1992). Consequently, selective herbivory may cause a shift in the composition of vegetation towards a predominance of species with more recalcitrant, lower quality litter, ultimately reducing available N and net primary production. These changes may be offset to some extent by increases in urine and fecal pellet inputs deposited by a greater abundance of herbivores. Further complicating factors, such as increases in soil freeze–thaw cycles associated with climate change, may enhance decomposition of both litter and fecal pellets. These examples of complex interactions and feedback mechanisms suggest the need for a more integrative approach to studying winter ecology.

■ Approaches to winter research

Researching the effects of winter climate on ecosystem processes is challenging but necessary in order to make predictions about ecological responses to future climate change. Long-term data are often used to address these issues, based on relationships between historical climate and response patterns. While long-term data may provide valuable insight into winter climate change effects, there are complications associated with this approach. Historically, events such as deep soil frost and ice storms are relatively rare and vary in severity, making interannual comparisons difficult. An additional complication is that responses are obfuscated by other long-term changes (eg increased atmospheric CO₂, acidic deposition, introduction of exotic species) and short-term disturbances (eg insect defoliations, extreme climatic events).

To control some of the problems associated with the use of long-term data, scientists have carried out field experiments involving “climate manipulations”. Examples of winter climate manipulations include a number of soil

warming experiments that have been conducted around the world, using various techniques (Rustad *et al.* 2001). In arctic and alpine sites, snow depth has been altered by installing snow fences to examine the long-term effects of changing winter snow conditions (Walker *et al.* 1999). The effect of snow depth on ecological processes is examined by comparing processes that occur in deep snow plots on the leeward side of the fence to shallower snow plots on the windward side. Similar winter climate manipulation experiments have been conducted in the northeastern US. At the Harvard Forest in Massachusetts, a long-term experiment was conducted to determine ecosystem responses to increased soil warming (Melillo *et al.* 2002). Soil temperatures in treatment plots were maintained at 5°C above control plots throughout the year, using buried heating cables. The treatment successfully warmed the soil during winter and decreased the duration of snow cover. Increases in soil temperature had a number of effects, including increased methane uptake in soils, increased N mineralization and net nitrification, and a reduction in the soil carbon pool available for decomposition (Melillo *et al.* 2004). However, field measurements of ecosystem processes in this study were mostly restricted to April through November, making it difficult to assess the ecological effects of soil warming during winter. The extent to which this type of soil warming experiment can be used as a surrogate for warming as a result of global climate change is not fully understood, particularly during winter, since warming the soil is not the same as warming the air above the soil.

A paradox of soil temperature responses to climate change in northeastern North America is that warmer winter air temperatures may result in colder soil temperatures. This prediction is demonstrated in snow removal experiments, where snow accumulation on treated plots is controlled by manually shoveling plots (Figure 4; Groffman *et al.* 2001a; Decker *et al.* 2003) or constructing shelters above plots (Boutin and Robitaille 1994). Surface soil temperatures in snow-covered control plots, remain close to 0°C and increase with depth (Figure 5). Snow removal eliminates the thermal buffer between soil and air, resulting in soil temperatures that are more closely coupled to air temperatures. Surface soils, which are the most biologically active, have the greatest temperature fluctuations and are consequently more susceptible to freezing and thawing. In a 4-year snow removal experiment in Vermont, the surface soil (upper 15 cm) of snow-free plots was colder than control plots, even during winters that were considered “warm” (Decker *et al.* 2003). Since there is generally less snow accumulation during comparatively “warm” winters, soil temperatures are often lower because air temperatures are still below 0°C

during most of the winter, even with the expected increases due to climate change.

Beyond soil temperature responses to winter climate variability, snow removal experiments have, more importantly, provided an understanding of plot-scale ecosystem responses. Vegetation health and soil-water chemistry responses to soil temperature treatments were examined in a snow removal study at the Duchesney Experimental Forest in southern Quebec (Boutin and Robitaille 1994). Treatment plots surrounding individual sugar maple trees were kept free of snow by installing shelters around the trunks of trees that extended beyond the circumference of the canopy. Compared to control plots and plots with superficial frost, plots with deep frost had greater soil-water losses of NO_3^- and base cations below the rooting zone, and higher soil-water content during June through August. These results suggest that soil frost caused a reduction in plant uptake of nutrients and water by impairing the functionality of the root system, ultimately increasing tree canopy dieback and transparency.

In a similar snow removal experiment at the Hubbard Brook Experimental Forest in New Hampshire, treatment plots were kept snow free by shoveling (Figure 4). Just as in the snow removal experiment in Quebec, the treatment caused an increase in soil-water NO_3^- and increased leaching losses of N, P, and C, even though the treatment produced what was considered a mild frost (Groffman *et al.* 2001a). The snow removal treatment had no effect on microbial N mineralization, nitrification, denitrification, and microbial biomass (Groffman *et al.* 2001b); however, overwinter fine root mortality was greater in treatment plots (Tierney *et al.* 2001). These results indicate that leaching of excess nutrients was due to reduced plant uptake rather than an increase in nutrient production through mineralization and other microbial processes.

Snow depth manipulations have provided valuable information on ecosystem function, but are not flawless and have been criticized on a number of fronts. A common criticism of shoveling as a method of snow removal is that it can create a disturbance effect, which is not duplicated in reference plots. Another potential problem is that water, in the form of snow, is removed; this can alter the water balance and hydrology of the plots. Perhaps the greatest limitation of snow manipulation experiments is that they are only practical to conduct at the small plot scale due to the intensive labor (eg shoveling) or infrastructure (eg shelters, buried heating cables) requirements. This precludes scientists from using these experiments to



Figure 4. A snow removal experiment (10 m x 10 m plots) was conducted at the Hubbard Brook Experimental Forest, New Hampshire, to investigate the effects of changing winter climate on ecosystem processes.

examine responses over greater spatial scales, such as those involving large animals with an extensive range.

■ Recent advances

Winter ecology is increasingly recognized as an important area of research, and there has been much recent progress in this field. Major advances in measuring snow cover extent, snow water equivalent, soil frost, and related winter climate variables at regional to global scales have occurred in recent years. The greater availability and use of airborne and satellite remote sensing data have contributed to this progress (Groisman and Davies 2001). Remote sensing methodology, such as passive microwave measurements of snow cover extent and snow water equivalent, have improved, and these data have aided in the examination of trends in winter climate at large spatial scales. These remotely sensed data have been incorporated into climate change models, greatly increasing their utility. Our ability to model future climate change has improved over the past decade, enabling us to better predict ecological responses. Reconstructions of past winter climate have also improved, and weather proxies such as tree-ring dating have been used to hindcast the winter weather of past centuries (Bégin and Boivin 2001).

Some of the most prominent recent contributions in the field of winter ecology have addressed biogeochemical processes within and under snow. Recent results in this area of research, particularly in arctic and alpine areas, have provided much needed information on cold weather processes. The results of this work show that winter weather plays an important role in the retention and loss of biologically important nutrients such as C and

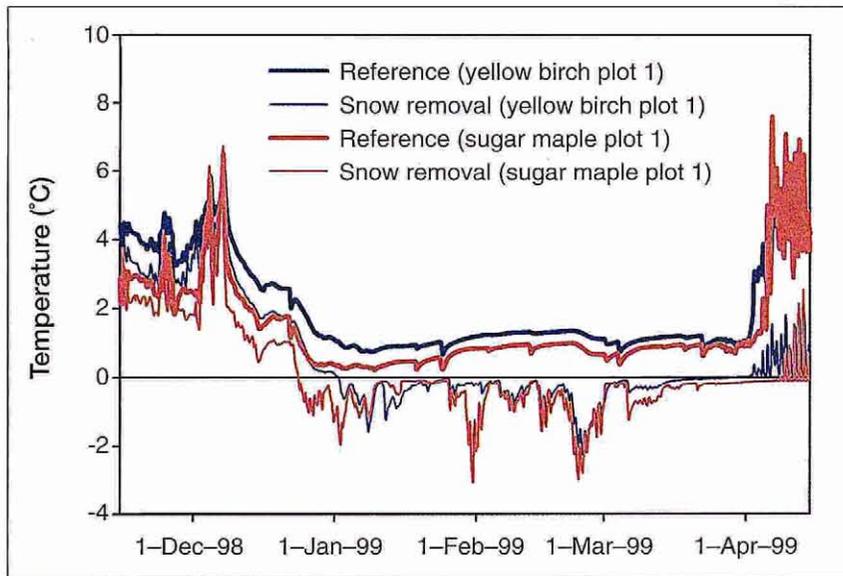


Figure 5. Soil temperatures at a depth of 10 cm in reference and snow removal plots at the Hubbard Brook Experimental Forest, New Hampshire.

N (eg Brooks *et al.* 1999; Schimel *et al.* 2004). In recent years, a number of studies have documented substantial microbial activity beneath the snow, despite low soil temperatures (eg Schadt *et al.* 2003), an important finding which counters previous assumptions that soil processes in winter were negligible.

Recent findings on the interconnectedness among ecological processes during winter are important. Historically, winter processes were examined in individual studies, and scientists rarely attempted to integrate the results across disciplines. More recently, scientists have begun to synthesize studies on winter processes and to examine complex interactions, particularly in response to climate change. An example of this higher level of analysis is occurring in arctic Alaska, where warmer weather is causing a shift in vegetation from tundra to shrubland (Sturm *et al.* 2005). The increasing shrub abundance leads to deeper snow, which results in warmer soil temperatures, greater soil microbial activity, and increased N available to plants. Greater N availability promotes additional shrub growth, resulting in a positive feedback loop. Understanding the interactions between organisms and their changing winter environment is moving the field of winter ecology forward.

■ Future research

Despite recent advances in our understanding of winter ecology, there are still research areas that warrant further investigation. While there have been several winter climate manipulations in northeastern North America, the approaches have been relatively similar. There is a need for experiments that use innovative methods, such as snow additions or different warming or cooling techniques. Studies conducted at multiple spatial scales and across climatic gradients should also be undertaken.

As soil frost is a critically influential factor in many aspects of winter ecology, a better understanding of soil frost dynamics should be a high research priority. Although soil frost is difficult to measure and characterize, it should be included in long-term monitoring programs and incorporated into relevant models. A more thorough understanding of soil frost would also improve our understanding of hydrological flowpaths and water routing during winter. This information might help establish sources of surface-water pollutants, which could be used to guide clean air and water policy.

Existing winter data are from disparate sources and are consequently spotty and lacking in uniformity and consistency in terms of collection methodology. The establishment of a snow, and related climate data network in northeastern North

America, equivalent to the SNOTEL network (SNOpack TElemetry, Natural Resources Conservation Service) in the western United States would provide much needed baseline data for winter research in the region. Similarly, networks such as LTER and the proposed National Ecological Observatory Network could benefit from standardizing winter sampling protocols, thereby facilitating cross-site comparisons and syntheses. Data produced by these types of networks would enable researchers to look at broader spatial scales and would facilitate the development of predictive climate change models.

The complexity of winter ecology requires an integrative research approach that should include different facets of ecology (eg soils, animals, vegetation, hydrology). This integrative approach is crucial because of the many winter climate interactions and climate change feedback mechanisms. Past experimental winter climate manipulations in northeastern North America have focused primarily on small plot scale biogeochemical responses; far less is known about responses to winter climate change at larger spatial scales. Future research should focus on developing spatially explicit models to capture large-scale phenomena, such as shifts in population dynamics. Advances in this area would help refine current models by capturing the effect of winter climate on ecological processes that occur throughout the year, and would improve our ability to scale up results to broader regions.

Historically, there have been many noteworthy studies of winter ecology conducted around the world; however, these studies have typically been treated as a separate type of ecology. Too often the influences of ecological processes in winter are not interpreted in the context of annual nutrient budgets and long-term trends. While winter research has provided much insight into ecological processes, it becomes far more valuable when it is considered as part of the whole.

While it may be more logistically challenging for scientists to conduct ecological research during winter compared to other seasons, the knowledge gained often outweighs the difficulties encountered. This knowledge will improve our ability to predict how ecosystems will respond to acute and chronic disturbances, such as climate change, and will enable us to make more informed policy decisions.

References

- Bégin Y and Boivin S. 2001. Tree-ring dating of past snow regimes. In: Jones HG, Pomeroy JW, Walker DA, and Hoham RW (Eds). *Snow ecology: an interdisciplinary examination of snow-covered ecosystems*. New York, NY: Cambridge University Press.
- Blumstein DT, Im S, Nicodemus A, and Zugmeyer C. 2004. Yellow-bellied marmots (*Marmota flaviventris*) hibernate socially. *J Mammal* 85: 25–29.
- Boutin R and Robitaille G. 1994. Increased soil nitrate losses under mature sugar maple trees affected by experimentally induced deep frost. *Can J Forest Res* 25: 588–602.
- Bremner JM and Zantua MI. 1975. Enzyme activity in soils at sub-zero temperatures. *Soil Biol Biochem* 7: 383–87.
- Brooks PD, Campbell DH, Tonnessen KA, and Heuer K. 1999. Natural variability in N export from headwater catchments: snow cover controls on ecosystem N retention. *Hydrol Process* 13: 2191–2201.
- Brooks PD, McKnight D, and Elder K. 2004. Carbon limitation of soil respiration under winter snowpacks: potential feedbacks between growing season and winter carbon fluxes. *Glob Change Biol* 11: 231–38.
- Brooks PD, Schmidt SK, and Williams MW. 1997. Winter production of CO₂ and N₂O from alpine tundra: environmental controls and relationship to inter-system C and N fluxes. *Oecologia* 110: 403–13.
- Brooks PD, Williams MW, and Schmidt SK. 1996. Microbial activity under alpine snowpacks, Niwot Ridge, Colorado. *Biogeochemistry* 32: 93–113.
- Burke MK and Raynal DJ. 1994. Fine root growth phenology, production and turnover in a northern hardwood forest ecosystem. *Plant Soil* 162: 135–46.
- Burnett AW, Kirby ME, Mullins HT, and Patterson WP. 2003. Increasing Great Lake-effect snowfall during the twentieth century: a regional response to global warming? *J Climate* 16: 3535–42.
- Chapin FS, Jefferies RL, Reynolds JF, *et al.* 1992. *Arctic ecosystems in a changing climate: an ecophysiological perspective*. New York, NY: Academic Press.
- Clein JS and Schimel JP. 1995. Microbial activity of tundra and taiga soils at sub-zero temperatures. *Soil Biol Biochem* 27: 1231–34.
- Coxson DS and Parkinson D. 1987. Winter respiratory activity in aspen woodland forest floor litter and soils. *Soil Biol Biochem* 19: 49–59.
- Decker KLM, Wang D, Waite C, and Sherbatskoy T. 2003. Snow removal and ambient air temperature effects of forest soil temperatures in northern Vermont. *Soil Sci Soc Am J* 67: 1234–42.
- Dorland S and Beauchamp EG. 1991. Denitrification and ammonification at low soil temperatures. *Can J Soil Sci* 71: 293–303.
- Goodrich LE. 1982. The influence of snow cover on the ground thermal regime. *Can Geotech J* 19: 421–32.
- Groffman PM, Driscoll CT, Fahey TJ, *et al.* 2001a. Colder soils in a warmer world: a snow manipulation study in a northern hardwood forest ecosystem. *Biogeochemistry* 56: 135–50.
- Groffman PM, Driscoll CT, Fahey TJ, *et al.* 2001b. Effects of mild winter freezing on soil nitrogen and carbon dynamics in a northern hardwood forest. *Biogeochemistry* 56: 191–213.
- Groffman PM, Hardy JP, Driscoll CT, and Fahey TJ. Snow depth, soil freezing, and trace gas fluxes in a northern hardwood forest. Submitted to *Glob Change Biol*.
- Groisman PY and Davies TD. 2001. Snow cover and the climate system. In: Jones HG, Pomeroy JW, Walker DA, and Hoham RW (Eds). *Snow ecology: an interdisciplinary examination of snow-covered ecosystems*. New York, NY: Cambridge University Press.
- Hadley JL. 2000. Effect of daily minimum temperature on photosynthesis in eastern hemlock (*Tsuga canadensis* L) in autumn and winter. *Arct Antarct Alp Res* 32: 368–74.
- Hart G. 1963. Snow and frost conditions in New Hampshire, under hardwoods and pines and in the open. *J Forest* 61: 287–89.
- Hodgkins GA, Dudley RW, and Huntington TG. 2003. Changes in the timing of high river flows in New England over the 20th century. *J Hydrol* 278: 244–52.
- Hodgkins GA, James IC, and Huntington TG. 2002. Historical changes in lake ice-out dates as indicators of climate change in New England. *Int J Climatol* 22: 1819–27.
- IPCC (Intergovernmental Panel on Climate Change). 2001. *Climate change 2001: the scientific basis*. Cambridge, UK: Cambridge University Press.
- Irland LC. 2000. Ice storms and forest impacts. *Sci Total Environ* 262: 231–42.
- Johnston CA and Schmitz OJ. 1997. Wildlife and climate change: assessing the sensitivity of selected species to simulated doubling of atmospheric CO₂. *Glob Change Biol* 3: 531–44.
- Kozłowski TT, Kramer PJ, and Pallardy SG. 1991. *The physical ecology of woody plants*. New York, NY: Academic Press.
- Leathers DJ and Ellis AW. 1996. Synoptic mechanisms associated with snowfall increases to the lee of lakes Erie and Ontario. *Int J Climatol* 16: 1117–35.
- Likens GE and Bormann FH. 1995. *Biogeochemistry of a forested ecosystem*. New York, NY: Springer-Verlag.
- Lima M, Merritt JF, and Bozinovic F. 2002. Numerical fluctuations in the northern short-tailed shrew: evidence of non-linear feedback signatures on population dynamics and demography. *J Anim Ecol* 71: 159–72.
- Lipson DA, Schmidt SK, and Monson RK. 2000. Carbon availability and temperature control the post-snowmelt decline in alpine soil microbial biomass. *Soil Biol Biochem* 32: 441–48.
- Marchand PJ. 1996. *Life in the cold: an introduction to winter ecology*. Hanover, NH: University Press of New England.
- Melillo JM, Steudler PA, Aber JD, *et al.* 2002. Soil warming and carbon cycle feedbacks to the climate system. *Science* 298: 2173–76.
- Melillo JM, Steudler PA, Aber JD, *et al.* 2004. Soil warming: a major consequence of global climate change. In: Foster DR and Aber JD (Eds). *Forests in time – the environmental consequences of 1000 years of change in New England*. New Haven, CT: Yale University Press.
- Merritt JF. 1984. *Winter ecology of small mammals*. Pittsburgh, PA: Carnegie Museum of Natural History.
- Merritt JF, Lima M, and Bozinovic F. 2001. Seasonal regulation in fluctuating small mammal populations: feedback structure and climate. *Oikos* 94: 505–14.
- Miller-Weeks M and Eagar C. 1999. *The northeastern 1998 ice storm: a forest damage assessment for New York, Vermont, New Hampshire and Maine*. Concord, NH: North East State Foresters Association Report.
- Mitchell MJ, Driscoll CT, Kahl JS, *et al.* 1996. Climatic control of nitrate loss from forested watersheds in the northeast United States. *Environ Sci Technol* 30: 2609–12.
- Murdoch PS, Burns DA, and Lawrence GB. 1998. Relation of climate change to the acidification of surface waters by nitrogen deposition. *Environ Sci Technol* 32: 1642–47.
- NERA (New England Regional Assessment). 2001. *Preparing for a changing climate: the potential consequences of climate variability and change*. New England Regional Overview.

- Durham, NH: US Global Change Research Program, University of New Hampshire.
- Oglesby RT and Smith CR. 1995. Climate changes in the north-east. In: LaRoe ET, Farris GS, Puckett CE, et al. (Eds). Our living resources: a report to the nation on the distribution, abundance, and health of US plants, animals, and ecosystems. Washington, DC: US Department of the Interior, National Biological Service.
- Park J, Mitchell MJ, McHale PJ, et al. 2004. Impacts of changing climate and atmospheric deposition on N and S losses from a forested watershed of the Adirondack Mountains, New York State. *Glob Change Biol* 9: 1602–19.
- Parker J. 1953. Photosynthesis of *Picea excelsa* in winter. *Ecology* 34: 605–09.
- Pastor J and Naiman RJ. 1992. Selective foraging and ecosystem processes in boreal forests. *Am Nat* 139: 690–705.
- Post E and Stenseth NC. 1999. Climatic variability, plant phenology, and northern ungulates. *Ecology* 80: 1322–39.
- Pruitt WO. 1960. Animals in the snow. *Sci Am* 202: 60–68.
- Rhoads AG, Hamburg SP, Fahey TJ, et al. 2002. Effects of an intense ice storm on the structure of a northern hardwood forest. *Can J Forest Res* 32: 1763–75.
- Rivkina EM, Friedman EI, McKay CP, and Gilichinsky DA. 2000. Metabolic activity of permafrost bacteria below the freezing point. *Appl Environ Microb* 66: 3230–33.
- Rustad LE, Campbell JL, Marion GM, et al. 2001. A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental warming. *Oecologia* 126: 543–62.
- Schaberg PG and DeHayes DH. 2000. Physiological and environmental causes of freezing injury in red spruce. In: Mickler RA, Birdsey RA, and Hom J (Eds). Response of northern US forests to environmental change. New York, NY: Springer-Verlag.
- Schadt CW, Martin AP, Lipson DA, and Schmidt SK. 2003. Seasonal dynamics of previously unknown fungal lineages in tundra soils. *Science* 301: 1359–61.
- Schaefer DA, Driscoll CT, van Dreason R, and Yatsko CP. 1990. The episodic acidification of Adirondack Lakes during snowmelt. *Water Resour Res* 26: 1639–47.
- Schimel JP, Bilbrough C, and Welker JA. 2004. Increased snow depth affects microbial activity and nitrogen mineralization in two Arctic tundra communities. *Soil Biol Biochem* 36: 217–27.
- Schimel JP and Clein JS. 1996. Microbial response to freeze–thaw cycles in tundra and taiga soils. *Soil Biol Biochem* 8: 1061–66.
- Schmid WD. 1982. Survival of frogs in low temperatures. *Science* 215: 697–98.
- Schwartz MD and Reiter BE. 2000. Changes in North American spring. *Int J Climatol* 20: 929–32.
- Shanley JB and Chalmers A. 1999. The effect of frozen soil on snowmelt runoff at Sleepers River, Vermont. *Hydrol Process* 13: 1843–57.
- Shiple LA, Blomquist S, and Danell K. 1998. Diet choices made by free-ranging moose in northern Sweden in relation to plant distribution, chemistry, and morphology. *Can J Zool* 76: 1722–33.
- Skogland T, Lomeland S, and Goksoyr J. 1988. Respiratory burst after freezing and thawing of soil: Experiments with soil bacteria. *Soil Biol Biochem* 20: 851–56.
- Sommerfeld RA, Mosier AR, and Musselman RC. 1993. CO₂, CH₄, and N₂O flux through a Wyoming snowpack and implications for global budgets. *Nature* 361: 140–42.
- Storey KB and Storey JM. 1996. Natural freezing survival in animals. *Annu Rev Ecol Syst* 27: 365–86.
- Sturm M, Schimel J, Michaelson G, et al. 2005. Winter biological processes help convert arctic tundra to shrubland. *BioScience* 55: 17–26.
- Tierney GL, Fahey TJ, Groffman P, et al. 2001. Soil freezing alters fine root dynamics in a northern hardwood forest. *Biogeochemistry* 56: 175–90.
- Walker MD, Walker DA, Welker JM, et al. 1999. Long-term experimental manipulation of winter snow regime and summer temperature in arctic and alpine tundra. *Hydrol Process* 13: 2315–30.
- Zimov SA, Davidov SP, Voropaev YV, et al. 1996. Siberian CO₂ efflux in winter as a CO₂ source and cause of seasonality in atmospheric CO₂. *Climatic Change* 33: 111–20.