Biogeochemistry **56:** 175–190, 2001.

Soil freezing alters fine root dynamics in a northern hardwood forest

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Key words: belowground production, global change, minirhizotron, plant-soil interactions, winter

Abstract. The retention of nutrients within an ecosystem depends on temporal and spatial synchrony between nutrient availability and nutrient uptake, and disruption of fine root processes can have dramatic impacts on nutrient retention within forest ecosystems. There is increasing evidence that overwinter climate can influence biogeochemical cycling belowground, perhaps by disrupting this synchrony. In this study, we experimentally reduced snow accumulation in northern hardwood forest plots to examine the effects of soil freezing on the dynamics of fine roots (< 1 mm diameter) measured using minirhizotrons. Snow removal treatment during the relatively mild winters of 1997–1998 and 1998–1999 induced mild freezing temperatures (to -4 °C) lasting approximately three months at shallow soil depths (to -30 cm) in sugar maple and yellow birch stands. This treatment resulted in elevated overwinter fine root mortality in treated compared to reference plots of both species, and led to an earlier peak in fine root production during the subsequent growing season. These shifts in fine root dynamics increased fine root turnover but were not large enough to significantly alter fine root biomass. No differences in morality response were found between species. 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, suggesting that the marked response recorded in our forest plots was caused indirectly by mechanical damage to roots in frozen soil. Elevated fine root necromass in treated plots decomposed quickly, and may have contributed an excess flux of about 0.5 g N/m^2·yr, which is substantial relative to measurements of N fluxes from these plots. Our results suggest elevated overwinter mortality temporarily reduced fine root length in treatment plots and reduced plant uptake, thereby disrupting the temporal synchrony between nutrient availability and uptake and enhancing rates of nitrification. Increased frequency of soil freezing events, as may occur with global change, could alter fine root dynamics within the northern hardwood forest disrupting the normally tight coupling between nutrient mineralization and uptake.

Introduction

Elucidating the complex role of fine root dynamics in regulating biogeochemical cycles is critical to understanding ecosystem function, including nutrient retention, and the potential impacts of global change. However, investigation of this role has been hindered by the difficulty of studying fine roots and their relationships with soil and microbes *in situ*. In forest ecosystems, more than half of the annual carbon gain may be allocated belowground to grow and maintain fine roots (< 1 mm diameter) and support their mycorrhizal symbionts (Harris et al. 1977, Raich & Nadelhoffer 1989). Unlike coarse roots, these fine roots turnover quickly (typically < 1 year; Hendrick & Pregitzer 1992a; Fahey & Hughes 1994) and contain high concentrations of nitrogen (N) which make them a readily decomposable substrate (Pregitzer et al. 1997). Nutrient uptake by fine roots is essential for retention of nutrients in many forest ecosystems (Vitousek et al. 1982), and fine roots compete intensely with microbes for N in N-limited systems (Zak et al. 1990; Norton & Firestone 1996).

The retention of nutrients within an ecosystem depends on temporal and spatial synchrony between nutrient availability and nutrient uptake (Bormann & Likens 1979), and disruption of fine root processes can have dramatic impacts on nutrient retention. 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 forest ecosystems often leads to losses of nutrient elements, most notably N in the form of nitrate (NO_3^-), and the magnitude of nutrient loss varies with the extent and nature of the disturbance (e.g. herbivory, harvest) and characteristics of the site (e.g. forest cover type, soil type, topography; 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 resulted in nutrient loss from a variety of forest types. Application of herbicide to a harvested northern hardwood forest prevented regrowth of vegetation and thus uptake by fine roots, and led to increased nutrient losses compared to 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 in temperate systems is high.

There is increasing evidence that overwinter climate can influence biogeochemical cycling belowground and ecosystem nutrient loss (Rascher et al. 1987; Stottlemeyer & Toczydlowski 1996; Brooks et al. 1999), perhaps by disrupting the synchrony of mineralization and uptake (Likens & Bormann

1995). In many northern forests, snowpack normally insulates soil from cold air temperatures and inhibits soil freezing (Stadler et al. 1996; Shanley & Chalmers 1999), and recent research has indicated that lack of a snowpack can cause soil freezing and alter biogeochemical cycling in northern hardwood forests. Snow removal experiments in a Canadian sugar maple forest caused soil freezing, resulting in canopy dieback and elevated loss of nutrients (Boutin & Robitaille 1995; Robitaille et al. 1995). Likens and Bormann (1995) have suggested that elevated NO_3^- fluxes from the Hubbard Brook Experimental Forest (HBEF) in 1970 and 1974 were due to natural soil freezing events associated with low snowpack accumulation during the those winters. On a larger scale, Mitchell et al. (1996) found that elevated NO_3^- losses from four forest watersheds across the northeastern United States were correlated with cold overwinter temperatures. Soil freezing events may become more common if snow cover at northern latitudes is reduced due to anthropogenic global climate change (Cooley 1990).

While none of the studies mentioned above measured effects on fine roots, it is likely that disruption of fine root processes by soil freezing is an important mechanism contributing to the biogeochemical response. Fine roots normally experience less temperature variation than aboveground plant tissues, and consequently exhibit freeze injury at milder temperatures than leaves or twigs (Sakai & Larcher 1987). In far northern ecosystems where concrete soil frost permeates the rooting zone, fine root morality is high in winter (Ruess et al. 1998), while in temperature forests where snow normally insulates the soil, the rate of fine root mortality is lower during winter than other times of the year (Hendrick & Pregitzer 1992a). 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. While recent studies of fine root dynamics using minirhizotrons have characterized patterns of fine root dynamics during the growing season in many ecosystems (Aerts et al. 1992; Hendrick & Pregitzer 1992a; Majdi & Kangas 1997; Ruess et al. 1998), the impact of freezing on fine root dynamics has not previously been studied under field conditions.

Our goal in this study was to explore the effects of reduced snow cover and subsequent soil freezing, as may occur with global change, on the fine root dynamics of a northern hardwood forest ecosystem at the HBEF in the White Mountains of New Hampshire. This study was a component of a larger, integrated study based on a snow removal manipulation designed to investigate the biogeochemical response to decreases in snow cover (see Hardy et al. this issue; Groffman et al. this issue; Fitzhugh et al. this issue). Thus, we had an exceptional opportunity to observe the effects of a disturbance on fine root dynamics within the larger context of nutrient cycling, and to compare effects on fine roots with related effects on soil microbes, soil solution chemistry, and nutrient cycling and fluxes. Our primary objective was to test the hypothesis that snow removal would increase overwinter mortality of fine roots. A second objective was to determine if there were differences in the freeze tolerance of fine roots between two dominant tree species in the northern hardwood forest. In this forest type, yellow birch occupies higher elevations and more extreme environmental conditions than sugar maple, and we hypothesized that the fine roots of yellow birch would be more frost tolerant than those of sugar maple (Calme et al. 1994). A final objective was to improve understanding of the environmental conditions which cause freeze injury to fine roots of northern hardwood tree species.

Methods

Site

This study was conducted at the HBEF in central New Hampshire, U.S.A. (43°56′ N 71°45′ W) (Likens 1985). This site is a second-growth northern hardwood forest dominated by American beech (*Fagus grandiflora*), sugar maple (*Acer saccharum Marsh.*) and yellow birch (*Betula alleghaniensis Brit.*) with a patchy understory of shrubs and herbs (Siccama et al. 1970). Soils are shallow, well-drained Spodosols (Haplorthods) of sandy loam texture developed from unsorted basal tills, with a thick (2–20 cm) forest floor (Johnson et al. 1991). Climate at the HBEF is characterized by long, cold winters and short, cool summers, with annual average precipitation of about 140 cm distributed relatively evenly throughout the year (Federer et al. 1990). Mean air temperatures range from -10 °C in January to 17 °C in July, and a continuous snowpack typically covers the ground from December until April.

Forest experiment

The experimental design at our forest sites consisted of two 10×10 m plots at each of four sites, with one plot at each site designed for snow manipulation and the other as reference. In order to test for differential response between dominant tree species, we selected two sites dominated by sugar maple (> 80% basal area; referred to as SM1 and SM2 herein), and two by yellow birch (YB1 and YB2). In Fall 1996, these plots were equipped with minihizotron tubes as described below, in addition to thermistors to monitor soil temperature, lysimeters to measure soil solution chemistry, water content reflectometers to measure soil moisture, and trace gas flux chambers. Additional details on site characteristics and instrumentation can be found in Hardy et al. (this issue).

Snow was removed manually by shoveling treatment plots from November to early February during winters 1997–1998 and 1998–1999. In order to protect the forest floor and equipment during shoveling and to preserve normal wintertime albedo, a few centrimeters of snow were allowed to remain on treatment plots throughout the winter. After treatment ended in February each year, snow was allowed to accumulate on treatment plots in a normal fashion for the duration of the winter. Additional details on this treatment can be found in Hardy et al. (this issue).

Laboratory experiment

In order to more closely examine the relationship between freezing regime and fine root injury at mild freezing temperatures similar to those occurring in our forest plots, we examined the effects of mild freezing on fine root dynamics of potted sugar maple and yellow birch seedlings under controlled conditions. Forty- to sixty-cm tall seedlings with intact root systems were removed from the forest at HBEF and installed into one meter diameter pots with reconstructed root profiles. Twelve sugar maple trees were obtained in July 1998 and sixteen yellow birch were obtained in July 1999. Each pot was equipped with two horizontal minirhizotron tubes to measure fine root dynamics.

Seedlings were exposed to experimental freezing regimes which varied in temperature and duration. During winter 1998–1999, the sugar maple seedlings were divided equally into two treatments of varying intensity (−1 °C and −5 °C) and a control (3 °C) for five weeks beginning November 18. During winter 1999–2000, the yellow birch seedlings were divided equally into three mild freezing treatments (−4 °C) of varying duration beginning December 6 and including a medium duration freeze of five weeks, a long duration freeze of ten weeks, a freeze-thaw treatment which included a one week thaw to 3 °C (beginning 13 December) within a five week freeze treatment, and a control (3 °C). The seedlings were maintained indoors at the control temperature for the remainder of the winter and maintained outdoors during the growing season.

Fine root dynamics

We used minirhizotrons to monitor dynamics of fine roots (< 1 mm diameter) (Fahey et al. 1999). Four clear plastic minirhizotron tubes (5 cm diameter) were installed at a 45-degree angle in each of the eight forest plots during fall 1996. Tubes were installed to depth of obstruction by rocks, which varied from site to site with a mean of 21 +/− 5 cm standard error. Additionally, two tubes were installed horizontally into each seedling pot when the seedlings were potted. Portions of the tubes exposed at the surface were covered with several layers of duct tape and the ends were capped to prevent entry of water and light. An index handle and a hole on each tube allowed positioning of the minirhotron camera (Bartz Technology, Inc., Santa Barbara, CA) in exactly the same location on each measurement day. Styrofoam insulation was placed in each tube to minimize temperature differences between the tube environment and the bulk soil.

Images were collected at 25-mm intervals along each tube approximately monthly during the snow-free season in the forest plots from July 1997 to October 1999. Measurements began before tubes had one full year for installation effects to subside (Joslin & Wolfe 1999), but disturbance due to installation should be similar between treated and reference plots. Winter conditions prevented measurements from late November until mid-April; thus, overwinter mortality and production are reflected in data from April, the first collection after snowmelt. On each date, from 30 to 38 images were collected from each tube along four axes filmed at about 45 degrees from the vertical along the upper and lower surfaces of each tube. In total our analysis included over 3,500 cm fine root length from the four forest plots. Images were collected in a similar fashion from each tube in the seedling pots for one month prior to treatment, and for three months in the spring following treatment.

Video images were captured to digital media and subsequently analyzed using RooTracker software (Craine & Tremmel 1995). Each month, the location, length, diameter and appearance of all new roots growing within each frame were recorded. Roots were considered ‘dead’ when they appeared extremely faint or transparent, became discontinuous, shriveled to a fraction of their previous width, or disappeared altogether. ‘Dead’ roots were subsequently tracked until disappearance to yield a measure of time for root decomposition. Roots which became obstructed from view by other roots, condensation, debris, or subtle shifts in MR tube position were classified as ‘obscured’ and were not included in calculations of root death or decomposition.

Statistical analysis

To allow for statistical comparison between treatments despite high small-scale heterogeneity belowground, data from all four minirhizotrons within each plot were pooled for analysis (Hendrick & Pregitzer 1992b). Similarly, data from both minirhizotrons in a seedling pot were pooled. To allow comparison of root dynamics between plots or pots with differing fine root length sampled, proportional production and mortality values were calculated. For each plot or pot, proportional production was calculated each month as the ratio of new fine root length to existing live fine root length, while proportional mortality was calculated as the fraction of live fine root length which died within a sample period.

Data were analyzed for treatment, date, species, and interaction effects in a multi-factor ANOVA using SAS Proc Mixed with repeated measures to account for correlation between successive measurements on the same tubes (SAS 1989). We used linear contrasts to test specific hypotheses and least squares means to test for differences between reference and treatment means on all dates. Response variables tested were proportional production, proportional mortality (as described above) and fine root length.

Differences in fine root survivorship and decomposition rate between treatment and reference plots were evaluated using the Wilcoxon test with a Kaplan-Meier survivorship function in SAS PROC LIFETEST. This survivorship statistic is more appropriate for analyzing lifetime data than traditional statistical analyses such as ANOVA because survivorship analysis appropriately incorporates data from individuals which remain alive at the end of the study (i.e. censored data values) (Allison 1995).

Results

Snow removal enhanced overwinter mortality of fine roots in this northern hardwood forest (Figure 1). Mortality in treated plots was significantly higher than reference plots in both April 1998 ($p = 0.002$) and April 1999 ($p < 0.001$). We were unable to sample plots during the winter months and therefore the April data include all overwinter mortality. High early season mortality in response to treatment continued into May after the first year's treatment but not the second; mortality was higher in treated vs. reference plots in May 1998 ($p < 0.05$). Prior to treatment, mortality was similar between plots, and no significant differences in fine root mortality between reference and treatment plots were found on other post-treatment dates.

Snow removal caused a marked shift in fine root production during the subsequent growing season, with new fine root production peaking earlier in the growing season in the treated plots (Figure 2). In treated plots, fine root production peaked in June then decreased substantially in July and August, while in reference plots a lower, broad peak of fine root production was maintained throughout the summer. Production was marginally significantly higher in the treated plots than the reference plots in June of both years ($p =$

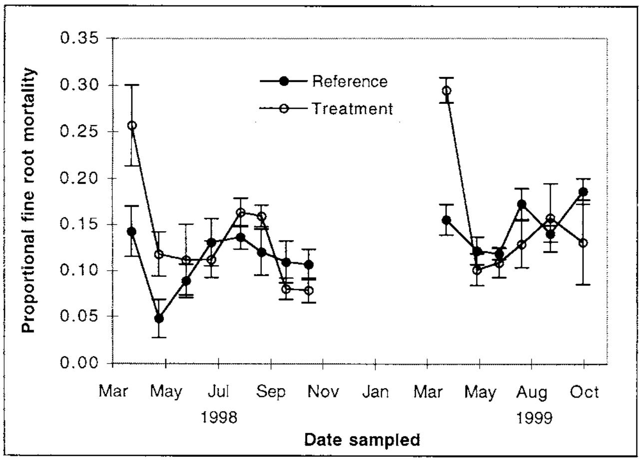

Figure 1. Morality of the fine roots (< 1 mm diameter) in 4 treated and 4 reference plots in a northern hardwood forest, New Hampshire U.S.A. Plots were treated with snow removal from mid-November to early February during the winters of 1997–1998 and 1998–1999. Proportional mortality is the fraction of live fine root length which died within a sample period, and error bars are standard errors.

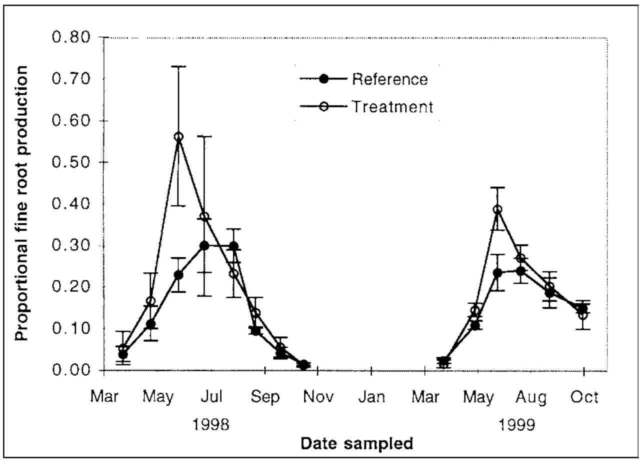

Figure 2. Production of fine roots (< 1 mm diameter) in 4 treated and 4 reference plots in a northern hardwood forest, New Hampshire U.S.A. Plots were treated with snow removal from mid-November to early February during the winters of 1997–1998 and 1998–1999. Proportional production is the ratio of new fine root length on a sample date to existing live fine root length, and error bars are standard errors.

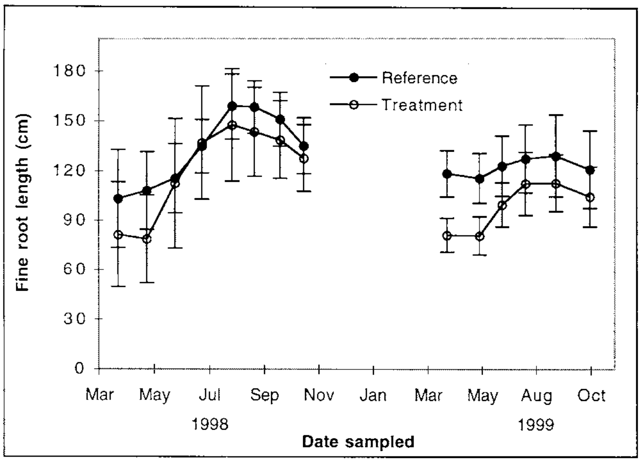

Figure 3. Length of fine roots (< 1 mm diameter) visible in 3 treated and 3 reference plots in a northern hardwood forest, New Hampshire U.S.A. Plots were treated with snow removal from mid-November to early February during the winters of 1997–1998 and 1998–1999. Error bars are standard errors.

0.06). Furthermore, a paired t-test showed that production in treated plots was significantly ($p < 0.05$) higher in June than August during both years, while production in reference plots was similar throughout June, July and August.

The elevated rates of fine root mortality in early spring and of fine root production in early summer in treated plots translated into higher annual rates of turnover in treated plots. An analysis of fine root survivorship showed that survivorship was significantly decreased in treatment vs. reference plots ($p = 0.002$).

Fine roots killed during treatment decomposed quickly. For example, the median decomposition time (i.e. time between visible death and complete disappearance) of all fine roots over the course of this experiment was 35 days; however, the majority of roots that died overwinter in the treatment plots had completely disappeared by the first post-treatment sample date in mid-April.

While patterns of fine root dynamics shifted substantially in response to treatment, this perturbation was not large enough to cause differences in overall mean fine root length between treatment and reference plots (Figure 3). There were no statistically significant differences in fine root length visible within tubes in reference compared to treatment plots during any month of the study. For this comparison it was necessary to exclude one of the sugar maple plots (SM2) because substantially greater fine root length was visible within tubes in treated plots at this site throughout the pre-treatment phase and most of the post-treatment phase of this experiment.

Contrary to initial expectations, the treatment response did not differ between dominant tree species. Neither mortality nor production showed significant interaction effects of species and treatment factors. Elevated overwinter mortality was similar in magnitude within sugar maple and yellow birch plots, and was followed by a similar shift in production in both species. The treatment response also did not vary in a predictable manner in response to the intensity of the soil freezing treatment at different sites. Climatic conditions varied among the four sites, creating a gradient in duration, depth and magnitude of freeze treatment from YB2 (the coldest site) to SM1 (the warmest; Hardy et al. this issue). However, no pattern was evident in magnitude or timing of the root response to freezing along this gradient.

In contrast to the forest plots, fine root dynamics of potted tree seedlings were not affected by mild freezing temperatures under controlled conditions. Fine root mortality of potted sugar maple seedlings exposed to −1 °C or −5 °C did not differ from that of control pots for three months after treatment ($p = 0.34$). Fine root mortality of potted yellow birch seedlings exposed to mild freezing temperatures of −4 °C for five weeks, ten weeks, or under a freeze-thaw scenario did not differ from that of control pots for three months after treatment ($p = 0.66$).

Discussion

Snow removal in this northern hardwood forest during the relatively mild winters of 1997–1998 and 1998–1999 caused modest soil freezing (to − 4°C) at shallow depths (0 to −30 cm) lasting several months each winter (Hardy et al. this issue). The treatment reduced infiltration and soil moisture by about 15% during snowmelt, but did not affect these variables during the growing season (Hardy et al. this issue). Despite the mild temperatures, this treatment caused a significant shift in fine root dynamics within forest plots, increasing overwinter fine root mortality, altering the temporal pattern of subsequent fine root production, and increasing fine root turnover. In contrast, no effects of freezing on microbial biomass were found (Groffman et al. this issue). Accompanying this biotic response, the treatment caused a cascade of biogeochemical effects including elevated levels of nitrification and NO_3^- in the soil (Groffman et al. this issue) and increased loss of N and phosphorus (P) leachate (Fitzhugh et al. this issue). Our data suggest that the shift in fine root dynamics may have caused these changes in N cycling and loss by disrupting the temporal synchrony of nutrient availability and uptake.

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. While

Boutin and Robitaille (1995) suggested that soil freezing temperatures of −6 °C may have caused extensive fine root mortality in Canadian sugar maple stands, the potted seedling experiments reported herein concur with the literature from laboratories and tree nurseries in demonstrating that mild freezing temperatures up to −5 °C are insufficient to cause direct mortality of winter-hardened fine roots (Sakai & Larcher 1987; Calme et al. 1994; McEvoy & McKay 1997). 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.

It is unlikely that shifts in the position of the minirhizotron tubes in treatment plots was a significant problem; our careful root tracing protocol was designed to avoid this potential problem. Roots were only classified as decomposed if we had an unobstructed view of their previous location, as verified by at least two visual markers in the frame (e.g. other roots or soil features). We maintained a separate category for roots which became lost from view due to visual obstruction or minor shifts in tube position, and roots in this ‘obscured’ category were not included in calculations of fine root mortality or decomposition.

The patterns of fine root production and mortality reported here generally correspond with those reported in the literature for northern hardwood forests. Fine root production at the HBEF typically begins in late spring, peaks in mid-summer, and tapers off in early fall (Fahey & Hughes 1994). Fine root mortality at the HBEF occurs throughout the growing season, and the rate decreases during the winter as in other temperature ecosystems (Hendrick & Pregitzer 1992a).

The magnitude, depth and duration of soil freezing were roughly similar between the two winters of experimental treatment, but varied from site to site due to differences in elevation, aspect and topography at the four sites (Hardy et al. this tissue). Accordingly, the magnitude of the root mortality response was similar between years, but the shift in fine root production was more pronounced during the first year of the study (Figure 2). This difference may have been in part a residual effect of minirhizotron tube colonization (Joslin & Wolfe 1999). The response of fine root dynamics did not vary with the freeze intensity between sites, probably because the freezing temperatures at all plots were relatively mild.

In order to ascertain the potential role of these fine responses in altering biogeochemical cycling, and in particular of driving the dramatic changes in soil solution chemistry measured in these plots by Fitzhugh et al. (this issue), we estimated the magnitude of the increased nutrient flux from elevated fine root mortality in response to this treatment. For this comparison, we estimated N flux because N is an important and often limiting nutrient in this ecosystem. N is readily lost from the system following disturbance (Vitousek et al. 1982). Fitzhugh et al. (this issue) have reported large increases of N in soil solution in response to this treatment. In 1999, the magnitude of elevated overwinter mortality in response to treatment was similar among plots in this study: overwinter fine root mortality roughly doubled from about 14% to 28% of existing fine root length in treated over reference plots. Assuming fine root biomass within the forest floor of this system is 200 g/m^2 (Fahey & Hughes 1994), this corresponds to an influx of about 30 g/m^2 more fine root necromass in early spring after treatment. Fine roots in the forest floor contain approximately 2% nitrogen (Fahey et al. 1988); thus, this necromass would yield an excess flux of about 0.5 g N/m^2 from fine root morality. This is a substantial portion of the enhanced flux observed in drainage waters in response to the treatment (Fitzhugh et al. this issue) and is similar to annual N deposition at this site (Lovett & Rueth 1999).

The altered patterns of fine root mortality and production caused by soil freezing in this northern hardwood forest probably disrupted the temporal synchrony between nutrient availability and uptake, and this perturbation was probably the cause of the enhanced nitrification rates, soil nitrate levels and leaching of nutrients from the treatment plots described by Groffman et al. (this issue) and Fitzhugh et al. (this issue). Soil freezing increased overwinter fine root mortality (Figure 1), which enhanced the amount of substrate available for nutrient mineralization in the early spring. Fine roots have high N concentration (Pregitzer et al. 1997) and minirhizotron studies have shown that they can decompose very quickly (Hendrick & Pregitzer 1992a). While this elevated mortality probably increased N mineralization rates in treated plots, no significant increase in soil N mineralization was detected. This suggests that the N mineralization due to overwinter fine root mortality was small relative to the high measured variation in N mineralization rates (Groffman et al. this issue).

The elevated overwinter mortality temporarily reduced the fine root length in the treatment plots which probably reduced plant uptake. In addition, the treatment may have caused sublethal effects on fine root physiology or severed mycorrhizal connections which could further reduce plant uptake of nutrients. The elevated rates of nitrification reported by Groffman et al. (this issue) indicate that reduced uptake by fine roots decreased competition for ammonium (NH_4^+) between roots and nitrifying bacteria. Finally, note that these factors were acting simultaneously in the early spring, which is a critical time for nutrient loss in the northern hardwood forest (Muller & Bormann 1976; Likens & Bormann 1995). The cumulative effect of increased mineralization from fine root necromass and decreased plant uptake represented a substantial disruption of the soil ecosystem and resulted in increased leaching losses of nutrients (Fitzhugh et al. this issue).

While the results of this study support our hypothesis that treatment would increase overwinter fine root mortality, we had not foreseen that this would be accompanied by such a large shift in fine root production during subsequent months. It is unclear whether this shift was triggered exogenously, by higher nutrient availability in treated plots, or endogenously, as a consequence of reduced plant uptake due to reduced fine length in treated plots. In either case, this shift represents an important alteration of fine root dynamics early in the growing season, and indicates that freeze stress may help explain variation in patterns of fine root production. Furthermore, fine roots are thought to be a lower priority destination for plant carbon allocation than leaves (Retzlaff et al. 1996). Thus, this strong early season production response may indicate that this mild treatment did not substantially reduce plant carbon storage. However, if mild freezing caused a doubling of overwinter fine root mortality and significant shifts in subsequent seasonal root production, more severe or more frequent freezing might be expected to affect plant carbon balance and fine root length.

Vogt et al. (1993) have suggested that fine roots could serve as sensitive indicators of environmental change belowground. Our findings that snow manipulation and subsequent soil freezing significantly changed fine root dynamics without substantially altering fine root length support their speculation that fine root dynamics might be useful early indicators of environmental change. Changes to fine root dynamics may signal that disturbance may be starting to effect ecosystem function (e.g. nutrient retention), before that disturbance becomes substantial enough to reduce plant carbon gain and fine root length, and perhaps impair ecosystem function.

In conclusion, this study demonstrated that a mild soil freezing treatment caused significant shifts in fine root dynamics that disrupted the temporal synchrony between nutrient mineralization and uptake and led to nutrient leaching. The freezing temperatures induced by treatment in this study were relatively mild, and thus provide a realistic scenario for soil freezing events that might occur with anthropogenic global change due to a combination of reduced snow cover and warmer winter temperatures. An increase in the frequency of mild freezing events could have important effects on fine root dynamics and nutrient retention in forest ecosystems.

Acknowledgments

The authors would like to thank Cindy Wood, Adam Welman, Jason Demers and the Fahey crew for their indispensable assistance with field collection and lab analysis, and Francoise Vermeylen for her excellent advice on statistical analysis of these data. This research was supported by National Science Foundation (NSF) Grant DEB-9652678 which was a product of the interagency program on Terrestrial Ecosystems and Global Change, and by the NSF Long Term Ecological Research program. This research was conducted at the Hubbard Brook Experimental Forest, which is owned and operated by the Northeastern Research Station, USDA Forest Service, Newtown Square, PA. This paper is a contribution to the Hubbard Brook Ecosystem Study.

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