Nutrient Dynamics in a Warmer World: Nitrogen Uptake by Trees

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Abstract:

Climate models project a reduced snowpack depth and delay of the onset of its seasonal formation in the northeastern United States. Reduction of the snowpack leaves soils exposed to freezing air temperatures that can induce soil frost and inhibit soil biotic activity. Increased soil frost may affect nutrient cycling by damaging fine roots and increasing root mortality. Repeated freezing damage and subsequent heightened production of fine roots in the following growing season may deplete nutrient and carbon reserves within trees. This may leave fine roots more susceptible to frost damage in the following winter, which could decrease nutrient uptake by trees in future years.

In order to assess the effects of increased soil frost on nutrient uptake by trees in Northeastern forests, I measured nitrogen uptake by excised fine roots from a snow removal experiment at Harvard Forest. Fine roots from snow removal plots had higher mean rates of NH_4^+ and NO_3^- uptake than fine roots from reference plots. Uptake of NH_4^+ was significantly greater than NO_3^- uptake in reference (p=0.011) and snow-removal plots (p=0.003). However, there were no significant differences in soil freezing depth between reference and snow removal plots for the mild winter of 2011-2012.

Differences in nutrient uptake by fine roots could be occurring for multiple reasons. Soil frost may have damaged fine roots, diminishing nutrient uptake capacity. Furthermore, trees in the snow removal plots may be nutrient deficient from regenerating fine roots that died the previous winter when soil frost was greater. Increased fine root necromass and subsequent nutrient release through decomposition may increase nutrient availability in soils of the snow removal plots. However, increased soil nitrogen pools may lead to greater nutrient leaching from the ecosystem and change nutrient dynamics of northeastern forests.

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Introduction:

The winter season in northern temperate forests has been historically regarded as a dormancy period based on the misconception that biological activity ceases during this time (Campbell et al. 2005). However, studies have shown that many ecological processes can continue at temperatures near or below freezing (reviewed in Kreyling 2010). Much of this biological activity occurs in soil, where a sufficiently deep layer of snow provides insulation, maintaining temperatures warm enough to support a range of biotic activities (Edwards and Cresser 1992). These processes include mineralization and nitrification (Groffman et al. 2001), microbial growth (Rivkina et al. 2000), and soil respiration (Groffman et al. 2006). Additionally, a deep insulating snowpack maintains water availability in soils by reducing freezing allowing animals that overwinter in surface soils such as arthropods (Templer et al. 2012b) and small mammals (Pruitt 1957) to survive winter.

Winter ecological processes can substantially contribute to annual forest nutrient budgets (Groffman et al. 2001; 2006). Yet for a number of reasons, such as inherent difficulties associated with winter sampling, ecological processes during the winter have not been studied to the same extent as growing season (summer) processes in northern forest ecosystems.

Climate change effects on the Northeast

The Intergovernmental Panel on Climate Change estimates that mean global near-surface air temperatures have increased by 0.6°C during the 20th century and are projected to increase by 1.1-6.4 °C in the next century (IPCC 2007). Climate models project a warming of 2.8 to 4.3°C for the northeastern United States (Hayhoe et al. 2006). Air temperatures in this region remain near freezing during a large part of the winter and small fluctuations in air temperature can affect whether precipitation occurs as rain, sleet or snow (Campbell et al. 2005). Climate change is predicted to differentially affect precipitation patterns in northern latitudes as temperatures increase (IPCC 2007). Most of the predicted 10-30% increase in precipitation will occur during the winter and it is more likely to be in the form of rain or sleet (New England Regional Assessment Group 2001). Warmer temperatures combined with greater occurrences of snow thaws and rain-on-snow events will reduce snow pack depth and duration and delay the onset of its seasonal formation (Campbell et al. 2005). Absence or reduction of the snowpack leaves soils exposed to the freezing air temperatures that can induce soil frost. Soils may freeze early in the winter and remain frozen throughout the season, diminishing biotic activity (Goodrich 1982). Decreased snow cover may also lead to increases in severity and frequency of soil freeze/thaw cycles, which can affect important ecological processes by disrupting microbial activity (Gilliam et al. 2010), decreasing arthropod diversity and abundance (Templer et al. 2012b), increasing export of carbon and nutrients (Matzner and Borken 2008), and causing fine root injury (Tierney et al. 2001).

Nutrient cycling and fine root dynamics

Hardwood forests in the northeastern United States are a net carbon sink and store more than 15% of the U.S. forest carbon pool (Heath et al. 2003). However, forests' ability to store carbon is likely being altered by changes in air temperature and the resulting indirect effects on nitrogen availability. A meta-analysis of 32 sites found that increases in soil temperature might result in increased nitrogen availability for plants via increased rates of mineralization (Rustad et al. 2001). Fine roots (≤ 2 mm diameter) are responsible for most plant nutrient uptake and are a substantial sink for carbon acquired in terrestrial net primary productivity; as much as 33% of global annual net primary production is used for fine root production (Jackson et al. 1997).

Moreover, fine roots have high nutrient concentrations and relatively rapid turnover rates making them disproportionately important for nutrient cycling and carbon allocation (Gordon & Jackson 2000). Yet compared to our understanding of aboveground dynamics, much less is known about how fine roots contribute to ecosystem function and how they may be altered by climate change (Kreyling 2010). Two main scenarios of how forest ecosystems may respond to climate change have been postulated: one where nutrient uptake and carbon sequestration in northern forest ecosystems increase (Melillo et al. 2011) and another where they decrease (Groffman et al. 2001, Figure 1).

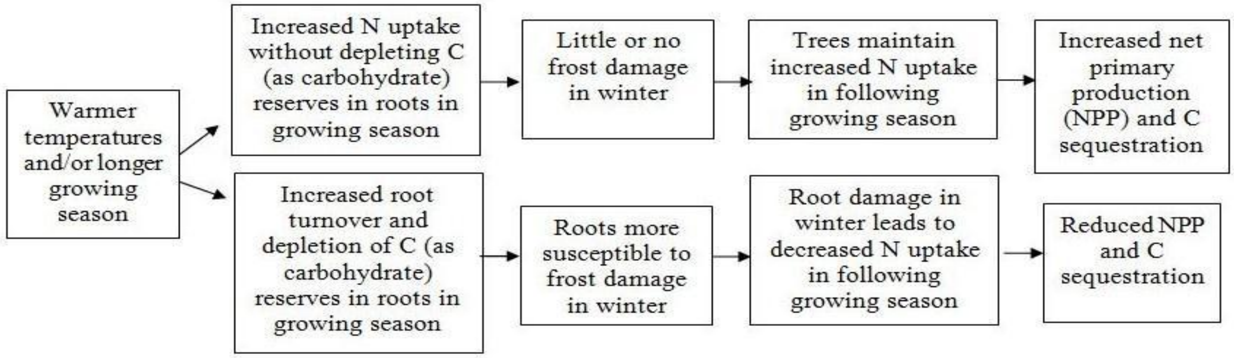

Figure 1: Potential responses of nitrogen and carbon cycles to combined effects of warming during the growing season and increased frequency of freeze/thaw cycles in winter. Diagram by Pamela Templer.

Increased nitrogen uptake and carbon sequestration

In a warmer world, increased supply of inorganic nitrogen in the soil via heightened rates of mineralization may lead to increased carbon sequestration by trees in northern forest ecosystems (Melillo et al. 2011). Results of a soil warming experiment in a northern hardwood forest demonstrated that short-term ecosystem losses of soil carbon from increased respiration were compensated by increased plant carbon gains in the woody tissues of trees over time (Melillo et al. 2011). The researchers attribute the increases in vegetation carbon storage in the experimental plot to a relative increase of about 45% in net nitrogen mineralization. The study also found that soil warming resulted in consistently higher soil respiration rates per unit of root mass, but also lead to decreased fine-root mass (62% reduction in top 10 cm of soil over 7 years). The primary function of fine is the uptake of nutrients and thus this marked decrease in fine root biomass is thought to be a response to increased nitrogen availability. As nitrogen becomes more readily available via warming-induced mineralization, trees do not have to allocate as much carbon belowground to acquire nitrogen resulting in decreased fine root biomass. Researchers also observed an increased growing season of about 3-4% in the warmed plot, indicating that in a warmer world, a longer growing season may combine with the benefits of greater nitrogen availability to enhance plant productivity and carbon storage in vegetation.

Colder soils in a warmer world

Contrastingly, nutrient uptake and carbon sequestration by northern hardwood forests may decrease as the formation of snowpacks is delayed due to warmer climate, resulting in increases in soil freezing i.e. colder soils in a warmer world (Groffman et al. 2001). Overwinter fine root mortality is normally lower than during other times of the year and this is mostly due to the insulating effect of the snowpack (Hendrick and Pregitzer 1992). However, delayed formation of the snowpack – as may occur in a warmer world – diminishes the snowpack's insulating effect and exposes soils to freezing air temperatures, causing soils to freeze (Hardy et al. 2001). Increased soil frost causes elevated overwinter fine root mortality and increased fine root injury (Tierney et al. 2001). Plants normally avoid freezing damage via intra-cellular crystallization by undergoing an acclimation process triggered by shorter day lengths and decreasing temperature, a process termed winter hardening. During hardening, plant cells pump out water and accumulate carbohydrates to store for the winter season. The soluble sugars act as antifreeze, reducing the temperature at which liquid solutions inside the cells freeze. Fine roots typically experience less temperature variation than the aboveground tissues and consequentially exhibit freeze injury at milder temperatures (Sakai and Larcher 1987)**.** They also may be more susceptible to freeze injury than aboveground plant tissues because they undergo winter hardening later in the winter season than the aboveground parts (Sakai and Larcher 1987)**.** Ice formation in soil may also damage fine roots in several ways including via desiccation, abrasion of root tissue, severing of root segments, or disruption of mycorrhizal associations (Sutinen et al. 1996; Bray et al. 2000)

Ecosystem nutrient retention

Soil freezing is linked to elevated fine root mortality and pulses of nitrate in stream waters suggesting that soil frost may decrease the ability of forest ecosystems to retain nitrogen (Cleavitt et al. 2008). Soil nitrogen concentrations increase with soil frost as nitrogen is released through decomposition of fine root necromass (Groffman et al. 2001). This leads to increased nitrogen leaching in early spring when the snowpack and soil frost melt (Boutin and Robitaille 1995). Nitrate (NO_3^-) is the dominant N species mobilized from the forest floor but ammonium (NH_4^+) and dissolved organic nitrogen (DON) are leached out as well (Fitzhugh et al. 2001). Nitrate losses are likely caused by reduced nutrient uptake due to frost damage to roots and increased fine root mortality (Matzner and Borken 2008).

The retention of nutrients within an ecosystem depends on temporal and spatial synchrony between nutrient availability and nutrient uptake (Bormann & Likens 1979). Nutrient loss in northern hardwood forests typically peaks in early spring when microbial mineralization and nitrification precede uptake by fine roots (Likens and Borman 1995). Increased soil frost in northern forest ecosystems results in earlier and sharper peaks in fine root production in the following growing season (Tierney et al. 2001). This shift in fine root dynamics is believed to be a compensatory response to reduced nutrient uptake as the tree requires quick replacement of fine roots to take up nutrients to support aboveground growth (Cleavitt et al. 2008). The elevated rates of fine root mortality and of fine root production in the early spring following winters with increased soil frost translate into increased root turnover rates for the forest ecosystem (Tierney et al. 2001). The combined effects of elevated mineralization due to increase in fine root necromass and decreased nutrient uptake result in increased loss of nutrients from forest ecosystems (Fitzhugh et al. 2001).

Fine root dynamics and carbon sequestration

Increased soil frost may affect carbon allocation of trees via its effects on root growth and production (Côté et al. 2003). Repeated freeze damage and resulting heightened production of fine roots could represent a significant carbon and nutrient drain on the tree (Cleavitt et al. 2008). Carbon reserves are important for survival and growth especially during the winter when resources are limited (Bloom et al. 1985). Therefore, depletion of carbon reserves may leave fine roots more susceptible to frost damage in the winter following increased fine root production. Although the mechanisms through which soil frost damages fine roots are still unknown, there is evidence that it impairs cell membrane integrity and decreases nutrient uptake by fine roots (Murray et al. 1989, Tierney et al. 2001). For example, decreases in aboveground growth and nutrient uptake capacity of fine roots, accompanied by increased tree mortality in the growing season have been observed in forests stands with increased soil frost (Weih and Karlsson 2002). Soil frost has also been shown to result in a significantly later recovery of whole-tree carbon fixation and reduced canopy carbon uptake (Comerford et al. 2012). A reduction in carbon uptake in combination with depletion of carbon reserves could significantly decrease forest net primary production and lead to reduced uptake of nitrogen and carbon sequestration by northern hardwood forest ecosystems, thus further elevating atmospheric concentrations of CO_2. Overall, the positive feedback cycle described here indicates that the growing season nitrogen gains caused by warming in the northeast might be offset by increased root turnover decreased net primary productivity.

Thesis Statement:

In order to assess the effects of increased soil frost as result of delayed snowpack formation on nutrient uptake by trees, I measured uptake of nitrogen – NH_4^+ and NO_3^- – by excised fine roots from Harvard Forest where snow-removal experimental plots have been established. I predicted that increased soil frost would lead to decreased uptake of NH_4^+ and NO_3^- by fine roots but NH_4^+ uptake would be greater than NO_3^- uptake regardless of field treatment.

Methods:

Study site

Harvard Forest is located in Petersham, Massachusetts, USA and is also a Long Term Ecological Research (LTER) site (Figure 2). It is a deciduous forest dominated by red maple (*Acer rubrum*), red oak (*Quercus rubra*), black oak (*Quercus velutina*), and some white ash (*Fraxinus americana*). The climate is cool and moist with an annual precipitation of 110 cm distributed evenly throughout the year. The mean annual air temperature in January is -7°C and the snowpack typically lasts from late December to early April. The soils are mainly sandy loam glacial till, with some alluvial and colluvial deposits.

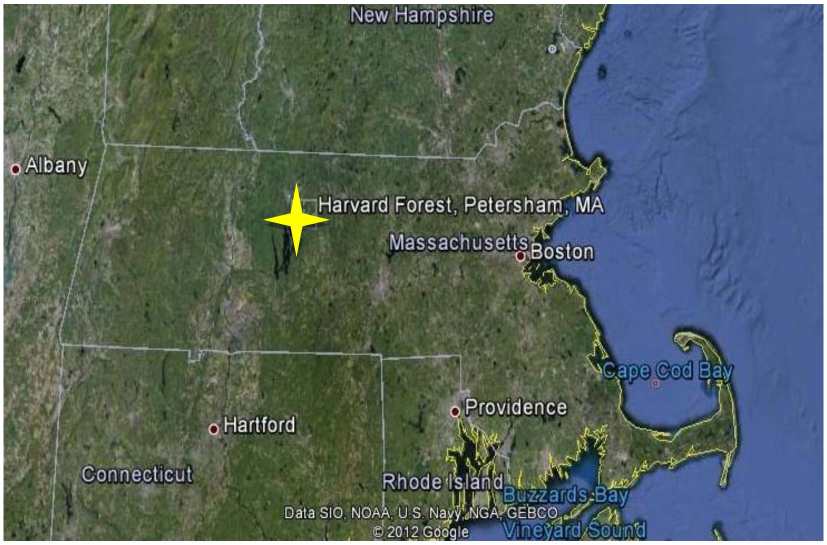

Figure 2: Google Earth aerial view of location of Harvard Forest in Petersham, Massachusetts, U.S.A. (42.5°N; 72°W**)**

Snow-removal plots

Snow removal plots (n=3) and reference plots (n=3) were established in the winter of 2009-2010 at Harvard Forest. All plots measured 13m x 13m. There were two red maple (*Acer rubrum)* and two red oak (*Quercus rubra)* trees of similar size in each plot. Snow was removed via shoveling from the treatment plots for the first 4-5 weeks of snowfall in each winter and then allowed to accumulate throughout the remainder of winter. During the snow removal period, a 3 cm base of snow was maintained on the snow removal treatment plots to preserve albedo of a snow-covered forest floor and to avoid disturbing the soil and litter during snow removal. Snow removal did not result in compaction of soils (Templer et al. 2012b).

Nutrient uptake by excised roots

Rates of NH_4^+ and NO_3^- uptake were quantified using the nutrient uptake by excised fine roots method as established by Epstein et al. (1963), an *ex situ* ^{15}N tracer method that utilizes enriched isotopic tracers to measure nitrogen uptake.

A total of 6 soil cores (5-10 cm in depth) were collected from each snow removal and reference plot at randomly located points. Collections were made from 8:30-9:30 am on August

3rd, 2012. Each field sample contained three bulked soil cores for a total of n=2 per plot (average weight= 328 g). Soil cores were stored on ice in a cooler during transport and refrigerated at 4°C upon arrival to the lab. Soil cores were homogenized and sieved through 8 mm brass mesh to remove rocks and coarse roots. Fine roots (<2mm diameter, 2-4 cm in length) were picked from the homogenized soils and placed into a pre-labeled weigh boat.

Fine roots from each plot were divided to create 3 subsamples of 200 mg of fine roots per field sample. The roots for each subsample were then inserted into 25 cm^2 cheesecloth teabags, which were then placed in specimen cups indicating their nutrient solution treatment: $^{15}NH_4Cl$, $K^{15}NO_3$, or a control treatment with no added nutrients. All the fine roots were soaked in 60 mL of 0.5 mmol/L $CaCl_2$ for 20 minutes to preserve membrane integrity prior to nutrient incubations. $CaCl_2$ solution was discarded and roots were incubated for 30 minutes in 75 mL of one of three solutions: 100 μmol N/L solutions of 98-atom%-enriched $^{15}NH_4Cl$ or $K^{15}NO_3$ containing 0.5 mmol/L $CaCl_2$, and 0.01 mol/L sucrose as an energy source (Jackson et al. 1990). Solutions contained either $^{15}NH_4Cl$ or $K^{15}NO_3$ since the source of tracer ^{15}N taken up by roots could not be determined if both form of inorganic nitrogen were present in the incubation solution. Additionally, this concentration of ^{15}N was chosen due to the difficulty of detecting uptake by roots at lower concentrations (Templer and Socci, personal communication). The 3rd control teabags were incubated for 30 minutes in Milli-Q water containing 0.5 mmol/L $CaCl_2$, and 0.01 mol/L sucrose to determine natural abundance of ^{15}N. Throughout the incubation process, we took care to make sure that all of the roots were submerged in solution.

Following the incubation period, the incubation solutions were discarded and the fine root teabags were soaked in four separate solutions of 1 mmol/L KCl for 10 minutes at a time to remove any ^{15}N adsorbed to the root surface (Jackson & Reynolds 1996). The fine roots were removed from the cheesecloth teabags using forceps and placed into glass vials. All processing was completed within 12 hours of root excision.

The glass vials with the roots were placed into a 60°C oven for at least 48 hours to dry. Once the roots dried, they were ground using a mortar and pestle and liquid nitrogen to homogenize the samples until they became a consistent powder. Roots were combusted in a Euro EA Elemental Analyzer to analyze ^{15}N content at the Stable Isotope Laboratory at Boston University. The combustion gases were separated on a GC column, passed through a GV Instruments diluter and reference gas box, and analyzed for 15N content on a GVI IsoPrime isotope ratio mass spectrometer. Continuous flow analysis also reported N content of each sample.

Gross uptake of $^{15}NH_4Cl$ and $K^{15}NO_3$ using the nutrient uptake by excised roots method was calculated as:

$$N_{up} = Mass_{root}^{-1} \times [(N_{root} \times \text{atom } \%^{15}N_{\ root}) - (N_{root} \times \text{atom } \%^{15}N_{NA})] \times \text{atom}\% \ ^{15}N_s^{-1} \times T^{-1} \qquad [1]$$

where N_{up} is the rate of nutrient ($^{15}NH_4^+$ or NO_3^-) taken up by roots; $Mass_{root}$= dry root mass, N_{root}=mass of N in the roots post-incubation, atom% $^{15}N_{\ root}$= atom percent ^{15}N of the roots post-incubation, atom% $^{15}N_{\ NA}$= atom percent of reference roots (roots that did not receive ^{15}N tracer), $^{15}N_s$=atom percent ^{15}N of treatment solutions, and T = incubation time. Results were compared using independent samples t-test on SPSS.

Results:

Soil frost

Soil frost depth in snow removal plots was significantly greater ($p<0.001$, mean= 3.84 cm) than in reference plots (mean=11.58 cm) for winter 2010-2011. The snowpack was present in reference plots from mid-December to late March (mean=25.86 cm) and from early February to early March (mean= 3.17 cm) in snow removal plots (Figure 3). There were no significant differences ($p>0.05$) in soil frost depth between snow removal plots (mean=4.08) and reference plots (mean=5.25 cm) for winter 2011-2012. The snowpack was present for 3 weeks in January and 2 weeks in February in both snow removal (mean snow depth=1.65 cm) and reference plots (mean snow depth=2.31 cm) (Figure 4).

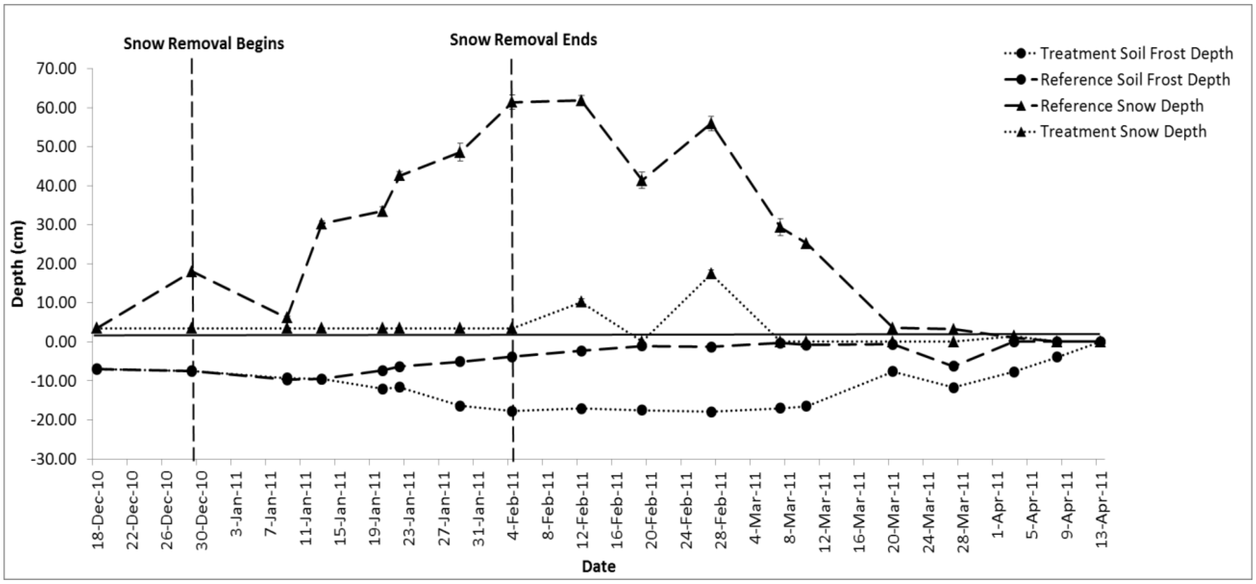

Figure 3: Mean soil frost and snow pack depth at snow removal and reference plots for winter of 2010-2011.Soil frost was significantly greater ($p<0.001$) in snow removal plots than in reference plots.

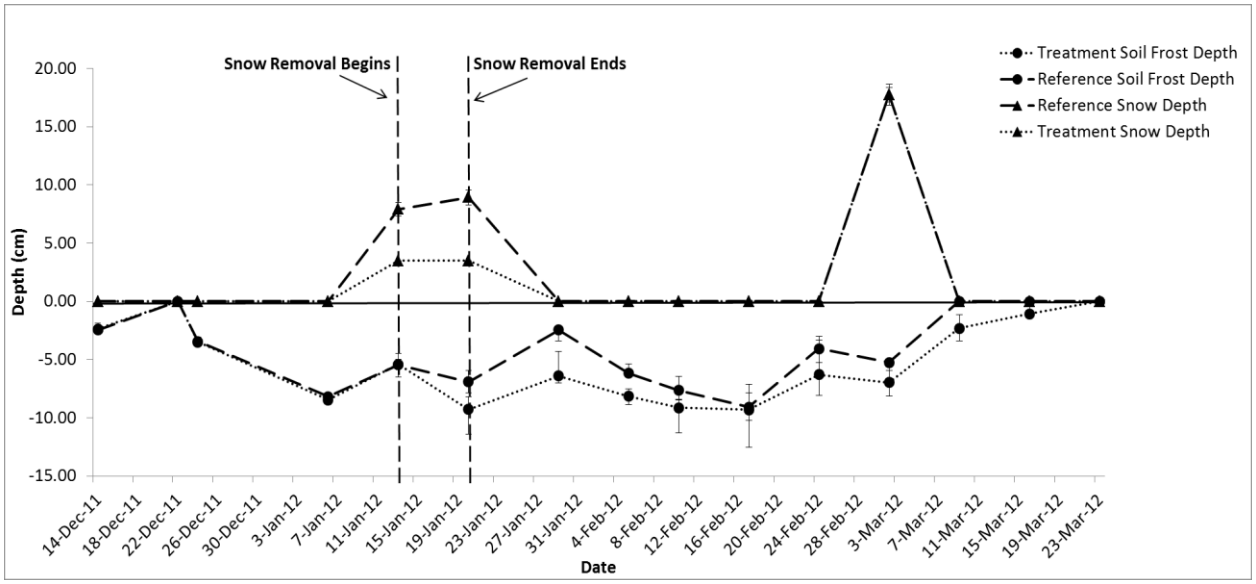

Figure 4: Mean soil frost and snow pack depth at snow removal and reference plots for winter of 2011-2012. There were no significant differences in soil frost depth between plots.

Nutrient uptake

Fine roots from snow removal plots had greater mean rates of uptake of both NH_4^+ and NO_3^- than fine roots from reference plots but differences in uptake were not statistically significant ($p>0.025$) (Figure 5). Uptake of NH_4^+ was significantly greater than NO_3^- uptake in both reference ($p=0.011$) and snow-removal plots ($p=0.003$) (Figure 6).

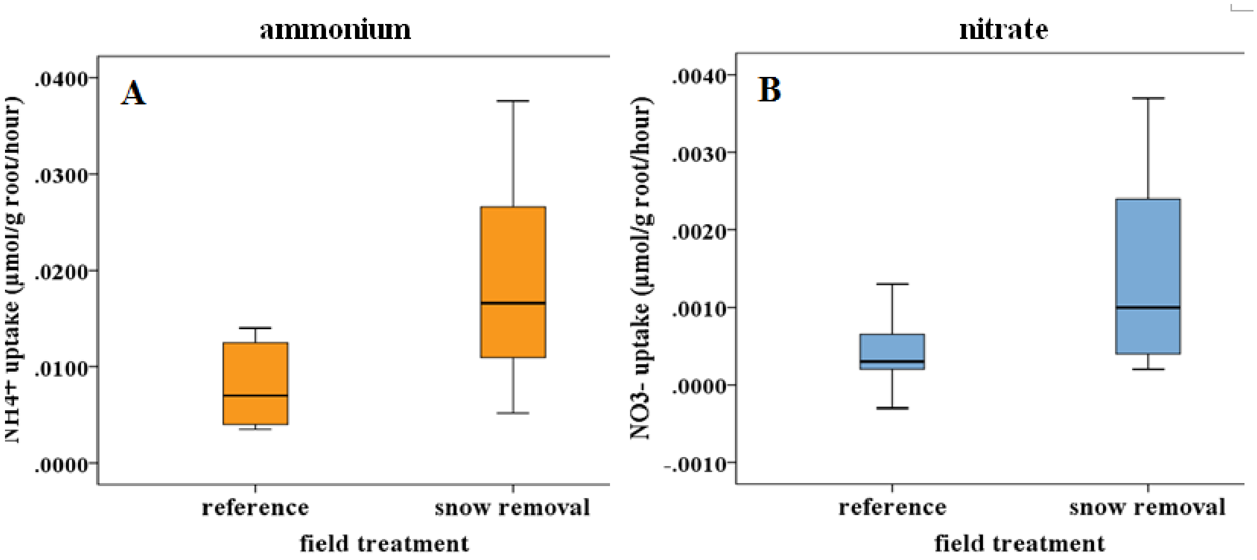

Figure 5: NH_4^+ (A) and NO_3^- (B) uptake by fine roots in reference and snow removal plots

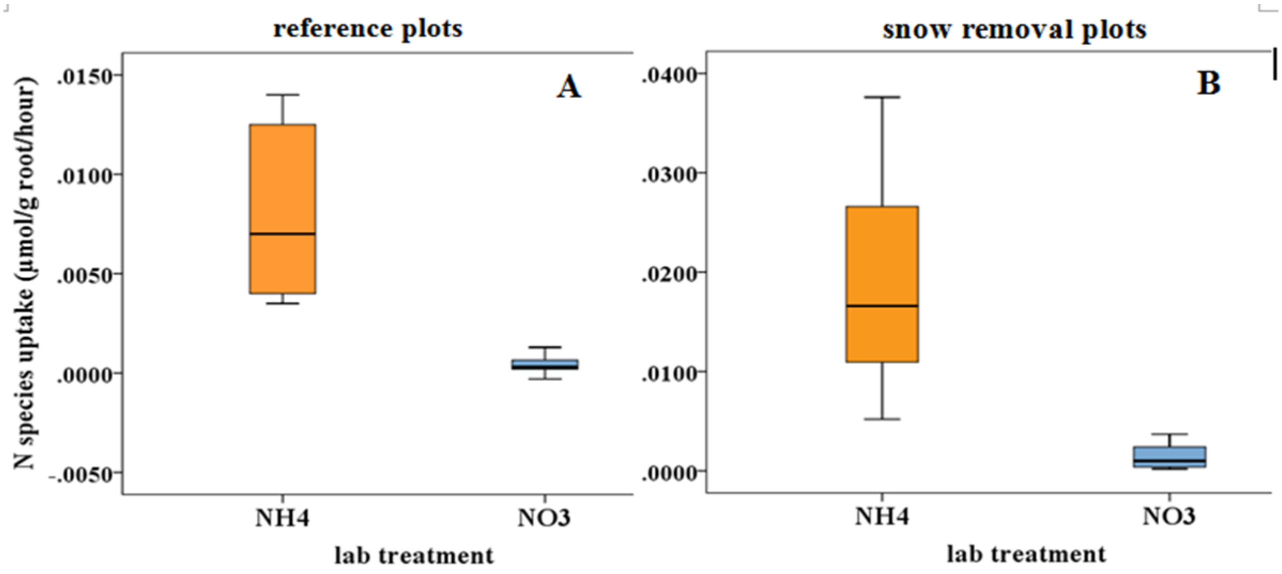

Figure 6: NH_4^+ and NO_3^- uptake by fine roots in reference (A) and snow removal plots (B). Mean NH_4^+ uptake by fine roots in snow removal and reference plots was 0.0192 µmol/g root/hour and 0.0082 µmol/g root/hour, respectively. Mean NO_3^- uptake by fine roots in snow removal and reference plots was 0.0001 µmol/g root/hour and 0.0004 µmol/g root/hour.

Discussion:

Increased soil frost was successfully induced in snow removal plots for the winter of 2010-2011 (Figure 3). However, due to mild conditions during the winter of 2011-2012 in the Northeast, differences in soil frost depth were not significant between snow removal and reference plots. This was due to an absence of a snowpack with snow only accumulating for a few weeks at a time in reference and snow removal plots. The absence of a developed snowpack indicates that fine roots from snow removal and reference plots experienced similar environmental conditions for the winter of 2011-2012. Differences in nutrient uptake by fine roots are likely explained by the impacts of increased soil frost on roots in snow removal plots that occurred in the winter of 2010-2011 rather than direct effects from the winter of 2011-2012.

Uptake of ammonium (NH_4^+) and nitrate (NO_3^-) by fine roots from snow removal plots was higher than those from the reference plots. Although differences in uptake were not statistically significant, this result is surprising as past studies have shown that increased soil decreases nutrient uptake by fine roots. Increased soil frost decreases nutrient uptake by heightening root mortality (Tierney et al. 2001) and inflicting frost damage to roots (Comerford et al. 2012). Roots in snow removal plots experienced increased soil frost during the winter of 2010-2011 and likely had higher rates of mortality and frost damage. Furthermore, increases in root production in the summers following a winter with increased soil frost have been observed (Cleavitt et al. 2008). It is possible that trees in snow removal plots are nutrient limited from regenerating fine roots in the following growing season. An increase in root turnover could cause a nutrient and carbon drain from trees. Trees from the snow removal plots may be in the process of replenishing nutrient sources, thus explaining the observed increases in nutrient uptake by fine roots when compared to those from the reference plots.

It is important to note that observed nutrient uptake rates are magnitudes smaller than ambient nutrient uptake despite amplification of nitrogen in the incubation solutions. Socci and Templer (2011) found that the ex situ excised root method may underestimate nutrient uptake as evidenced by in situ uptake rates up to 400-fold greater than those using the ex situ methodology. Differences in uptake are largely due to the effects of excision of roots. Carbohydrate supply will decrease over time upon excision, disrupting the active uptake of nutrients by roots (Bloom and Caldwell 1988). Although processing of fine roots was completed within 12 hours of excision to reduce its effect, it is likely that nutrient uptake rates are underestimated.

The observed trends in nutrient uptake documented are likely to be occurring in forest floor soils. Increased fine root necromass in snow removal plots increases soil nitrogen availability through release of nutrients via decomposition. Exposure to severe soil frost has been show to lead to earlier peaks in fine root production (Tierney et al. 2001). Fine root necromass decomposes relatively quickly after snowmelt but an earlier peak in fine root production may allow trees to take advantage of increased soil nitrogen pools (Tierney et al. 2001). Given that retention of nutrients within an ecosystem depends on temporal and spatial synchrony between nutrient availability and nutrient uptake, increased nutrient uptake and an earlier peak in fine root production may decrease nutrient leaching from the ecosystem (Bormann & Likens 1979). However, a very tight temporal coupling between these two processes would have to occur to prevent losses of nitrogen.

Ecosystem nutrient retention may be impaired by increased soil frost. Nutrient leaching following increased soil frost and snowmelt soil are common and are attributed to increased nitrogen availability in soils (Jaeger and Monson 1992, Matzner and Borken 2008). Additionally, forest ecosystem's ability to retain pulses of nitrogen are reduced when soils are nitrogen rich (Templer et al. 2012a). This change in nitrogen availability may have larger implications at an ecosystem scale given that the form of nitrogen taken up by plants can affect ecosystem nutrient retention. Ammonium is less energetically costly to assimilate than nitrate so it is preferentially taken up by fine roots (Gutschick 1981). Greater NH_4^+ uptake from reference and snow removal plots is consistent with other published studies (BassiriRad et al. 1999, Templer and Dawson 2004, Socci and Templer 2011). It is important to document nitrogen uptake dynamics because the form of nitrogen taken up by plants can significantly affect ecosystem nitrogen retention. Greater uptake of nitrogen as NH_4^+ may lead to decrease nitrification rates and reduce NO_3^- soil abundance. NO_3^- is of concern because it is a "leaky" nutrient, more easily leached from forest ecosystems (Templer et al. 2005).

Conclusion and Implications of Research:

Northeastern forests may be significantly affected by changes in climate. Decreases in the depth and duration of the snowpack led to increased soil frost and impacted nutrient dynamics. Damage to fine roots and increased fine root mortality likely resulted in nutrient deficient trees in snow removal plots. Nutrient deficient trees will exhibit increased nutrient uptakes to replenish their reserves. Trees in the snow removal plots were likely able to recuperate nutrients because winter conditions were mild 2011-2012 and soil frost was not severe. However, consistent increases in severity of soil frost as may occur in the future due to climate change may prevent trees from recovering from nutrient losses. Nutrient limitation of trees may have an ecosystem-scale effect as a result of positive feedback cycles that could decrease net primary productivity and lower the ability of forests to store carbon (Figure 1). It is therefore important to continue investigating how projected changes in climate may affect critical biotic processes such as nutrient cycling in northeastern forest ecosystems.

Future Directions:

Northeastern forests may not be well adapted to severe soil frost and climate change may bring upon a slew of changes in ecosystem processes. There is an important temporal component to nutrient cycling that may be impacted by changes in nitrogen dynamics in these forests. Increased fine root necromass resulting from increased soil frost may increase soil nitrogen pools. This nitrogen may be either taken up by nutrient limited trees or leached out of the ecosystem with snowmelt. In order to understand how nutrient cycling may be impacted by increased soil frost, it is necessary to document the timing of root production, snowmelt, and rates of decomposition of root necromass. It would also be beneficial to compare soil nitrogen availability through time and compare it to fine root a production. A relationship between these processes may indicate that root production is responding to soil nitrogen availability. There are inherent difficulties in documenting and measuring these processes but doing so could provide immense insight into how increased soil frost may affect nutrient retention in forest ecosystems.

There is evidence that tree species have different roles in nutrient retention in northeastern forests (Lovett et al. 2002, Templer and Dawson 2004, Socci and Templer 2011). Documenting species specific responses to soil frost would provide insight into how climate changes may affect different forest types found in the northeast. Additionally, different tree species have varying rooting depths and may exhibit different responses to increased soil frost. Trees with shallow rooting depths may be better adapted to soil frost which may indicate the possibility of trees to adapt to increased soil frost.

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