



Reduced Winter Snowpack and Greater Soil Frost Reduce Live Root Biomass and Stimulate Radial Growth and Stem Respiration of Red Maple (*Acer rubrum*) Trees in a Mixed-Hardwood Forest

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ABSTRACT

Northeastern U.S. forests are currently net carbon (C) sinks, but rates of C loss from these ecosystems may be altered by the projected reduction in snowpack and increased soil freezing over the next century. Soil freezing damages fine roots, which may reduce radial tree growth and stem respiration. We conducted a snow removal experiment at Harvard Forest, MA to quantify effects of a reduced winter snowpack and increased soil freezing on root biomass, stem radial growth and respiration in a mixed-hardwood forest. The proportion of live fine root biomass during spring (late-April) declined with increasing soil frost severity ($P = 0.05$). Basal area increment index was positively correlated with soil frost severity for *Acer rubrum*, but not *Quercus rubra*. Rates of stem respiration in the growing season correlated positively with soil frost duration in the previous winter, ($R^2_{\text{LMM(m)}} = 0.15$ and

0.24 for *Q. rubra* and *A. rubrum*, respectively). Losses of C from stem respiration were comparable to or greater than C storage from radial growth of *Q. rubra* and *A. rubrum*, respectively. Overall, our findings suggest that in mixed-hardwood forests (1) soil freezing has adverse effects on spring live root biomass, but at least in the short-term could stimulate aboveground processes such as stem respiration and radial growth for *A. rubrum* more than *Q. rubra*, (2) stem respiration is an important ecosystem C flux and (3) the increasing abundance of *A. rubrum* relative to *Q. rubra* may have important implications for C storage in tree stem biomass.

Key words: *Acer rubrum* (red maple); Forest carbon storage and loss; Harvard Forest; *Quercus rubra* (red oak); Snow; Winter climate change.

Received 21 May 2015; accepted 7 August 2015;
published online 6 October 2015

Electronic supplementary material: The online version of this article (doi:10.1007/s10021-015-9923-4) contains supplementary material, which is available to authorized users.

Author contributions ABR conceived of the measurements, analyzed the data, and wrote the paper. PHT conceived of the experimental design and contributed to the writing of the paper.

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INTRODUCTION

Forests of the northeastern U.S. contain more than 15% of the total carbon (C) stored in U.S. forests (Heath and others 2003) and are typically considered to be net C sinks (Turner and others 1995; Fan and others 1998; Houghton and others 1999; Zheng and others 2011; Lu and others 2013).

Ecosystem respiration can be an important determinant of the C sink strength in forest ecosystems (Valentini and others 2000). In temperate forests, autotrophic respiration accounts for approximately two-thirds of total C losses from respiration (Malhi and others 1999). Therefore, environmental perturbations that affect autotrophic respiration can have important implications for C storage in temperate forests. In the northeastern U.S., winter air temperatures have increased and snowpack duration and maximum depth have declined over the last several decades (Burakowski and others 2008; Campbell and others 2010). These trends are expected to continue and climate models project further winter warming of 1.7–5.4°C and further reduction in the depth and duration of snowpack by the end of the 21st century, compared to 1961–1990 means (Hayhoe and others 2007). A reduced snowpack can increase soil exposure to freezing air temperatures and result in greater soil freezing during winter and early spring (Boutin and Robitaille 1994; Hardy and others 2001).

Projected reductions in winter snowpack and greater severity of soil frost in temperate hardwood forests of the northeastern U.S. have been shown to damage roots of maple trees (Tierney and others 2001; Comerford and others 2013) and diminish their ability to take up nitrogen (N; Campbell and others 2014), leading to increased NO_3^- losses in soil solution (Campbell and others 2014; Groffman and others 2001). Furthermore, soil freezing has been shown to reduce terminal shoot elongation, foliar Ca:Al ratios and concentrations of foliar non-structural carbohydrates during the growing season (Comerford and others 2013) in the same forests. Although these studies illustrate the damaging effects of soil freezing on the health and functioning of trees, we are unaware of studies examining the extent to which reduced snowpack and increased soil freezing alter aboveground C storage in tree stems and autotrophic losses of C from sources such as stem respiration.

Radial growth of tree stems is the primary mechanism for aboveground C storage in trees and tree stem and branch respiration is an important pathway for C losses from forest ecosystems, with losses equivalent to 10–40% of gross primary productivity (GPP; see review by Litton and others 2007). Across forest ecosystems, stem respiration is positively correlated with GPP (Litton and others 2007) and is closely coupled with rates of photosynthesis and wood production (Acosta and others 2008; Wertin and Teskey 2008; Maier and others 2010). In temperate hardwood forests where rates have been

quantified, the combined C losses from tree stem and branch respiration are equivalent to 40% of aboveground net primary production and comprise approximately 13–17% of total ecosystem respiration (Malhi and others 1999; Tang and others 2008).

Acer rubrum (red maple) and *Quercus rubra* (red oak) are two common tree species in forests of the Northeastern USA, but the relative abundance of these species at the regional scale has been shifting in favor of red maples (Thompson and others 2013). In contrast, at the local scale of Harvard Forest in MA, USA, an increase in the biomass of red oaks compared to red maples has been linked to the strengthening forest C sink over the past two decades (Urbanski and others 2007). In light of these changes in forest composition and their potential implications for future C storage, it is important to quantify the effects of projected reductions in winter snowpack on the C dynamics of both red oaks and red maple trees.

We conducted a snowpack removal experiment in a mixed-hardwood forest at Harvard Forest in Massachusetts, USA to quantify the effects of a reduced snowpack and increased soil freezing on root biomass, stem radial growth, and stem respiration of red oaks and red maples. A companion study examining laboratory rates of microbial activity found that soil respiration decreases with greater soil freezing in these soils (unpublished manuscript). We hypothesized that snow removal and increased soil freezing diminish root biomass and rates of stem radial growth in red maples and red oaks, resulting in a decline in aboveground C storage in tree stems, but some of the declines in C storage are offset by reductions in rates of stem respiration in both tree species. We expected the effect of soil frost to be stronger in red maples than red oaks due to the shallower root systems of maple trees (Lyford and Wilson 1964; Lyford 1980) and therefore greater exposure to soil freezing.

MATERIALS AND METHODS

Site Description

This study was conducted in the Prospect Hill Tract of Harvard Forest in central Massachusetts (42°30' N, 72°10' W, 380 m above sea level), which is a mixed-hardwood forest dominated by red oak and red maple. The site was a pasture until about the year 1900, after which the forest began to regenerate naturally until a stand-replacing hurricane in 1938. The forest today is the product of natural regeneration and the few trees that survived the

hurricane. Soils are of the Montauk series (coarse-loamy, mixed, mesic Oxyaquic Dystrudepts) and Whitman series (loamy, mixed, mesic, shallow Typic Humaquepts). The climate is cool temperate and humid with mean temperatures of 20°C in July and -7°C in January. Mean annual precipitation is 1100 mm, distributed evenly throughout the year.

Experimental Design and Stand Characteristics

During the summer of 2010, we established six 13 m × 13 m plots (3 reference and 3 snow removal plots) each including a 1.5 m buffer on each side from which no data were collected. Plots were centered on two red oaks and two red maples. Snow was removed from the treatment plots via shoveling within 24 h of snowfall for the first 5 weeks of the 2010/2011 and 2011/2012 winters to reduce snowpack and induce soil frost. A compacted 3–5 cm base of snow was left to prevent damage and to maintain wintertime albedo of the forest floor. Snow accumulated naturally in the reference plots throughout the winter and in the treatment plots after the snow removal period.

Tree species composition, tree diameter at breast height (DBH), basal area, and stem surface area (0–10 m height, which is below the canopy) were quantified in each plot for trees >10 cm DBH. Stem surface area was calculated following:

$$SA = \pi * (D_{\text{Base}} + D_{10\text{m}})/2 * \text{Height}, \quad (1)$$

where SA is the stem surface area, D_{Base} is the diameter just above the buttressing of the root collar, $D_{10\text{m}}$ is the diameter at 10 m height, and Height is the height to which SA was calculated. Tree diameter at 10 m height was estimated from the linear rate of taper quantified for each canopy tree in each plot from four diameter measurements between just above the root collar and 3 m height. Trees aside from red maples and red oaks were

categorized as ‘other species’ and were comprised mostly of American beech (*Fagus grandifolia*). We calculated plot-level stem surface area index (SAI), which is the ratio of SA to ground surface area, for red maples, red oaks, other species, and their sum (hereafter referred to as ‘total’). Red oaks were larger than red maples ($P < 0.05$; Table 1) and these two species together comprised 80–90% of the basal and stem area to a stem height of 10 m. Tree DBH, basal area, stem area, and SAI were not significantly different between reference and snow removal plots ($P > 0.05$ for all measurements).

Snow, Soil Frost and Temperature Measurements

Weekly measurements of snow and soil frost depth in four locations within each plot were used to characterize snowpack and soil frost conditions during the winters of 2010/11 and 2011/12. Snow depth was measured using meter sticks that were permanently affixed to stakes. Soil frost depth was measured using frost tubes constructed from flexible PVC tubing (1.3 cm diameter) filled with methylene blue dye (Ricard and others 1976). The solution is clear when frozen, enabling visual assessment of soil frost depth. Each frost tube was inserted into a rigid PVC pipe to a soil depth of 50 cm and frost depth was determined by measuring the length of clear, frozen solution beneath the surface. Snow cover duration was defined as the number of days with measureable snow on the ground. The depth and duration of soil frost were integrated into the parameter ‘Area Under the Curve’ (AUC; Duran and others 2014), which was calculated by plotting weekly measurements of soil frost depth (Y-axis) against time (X-axis) and using a trapezoidal approach to calculate the area between the soil frost depth line and the x-axis (at a y-intercept of 0). The unit for AUC is ‘cm days,’ which increases with greater depth and/or duration of soil frost.

Table 1. Stand Characteristics of the Reference and Snow Removal Plots

| Stand parameter | Component | Reference | Snow removal |
|---|-----------|--------------------------|---------------------------|
| Diameter at breast height (cm) | Red oak | 38.6 ^a ± 2.1 | 34 ^a ± 4.8 |
| | Red maple | 21.5 ^b ± 2.0 | 18.3 ^b ± 2.7 |
| Stem area index (m ² m ⁻²) | Red oak | 0.14 ^a ± 0.02 | 0.13 ^a ± 0.02 |
| | Red maple | 0.15 ^a ± 0.03 | 0.12 ^{ab} ± 0.01 |
| | Other | 0.03 ^b ± 0.01 | 0.05 ^b ± 0.02 |
| | Total | 0.32 ± 0.04 | 0.31 ± 0.03 |

Diameter at breast height is for trees with stem respiration collars. Values represent the mean with standard error. Distinct letters indicate statistically significant differences between species within a plot type for a given parameter. There were no significant differences between plot types for either stand parameter ($P > 0.05$).

Soil temperature was measured in one location at the center of each plot using CS107 temperature probes (Campbell Scientific, Logan, UT, USA) buried at 5 cm depth. One Campbell Scientific HMP45C-L was used to measure air temperature at 2 m height in one location central to all plots. All sensors were connected to CR1000 dataloggers (Campbell Scientific) and the average of measurements scanned at 30-s intervals was recorded every 30 min. One of the reference plots was not instrumented until spring 2011; therefore, soil temperature data presented for winter 2010/2011 represent the mean of three snow removal plots and two reference plots.

We measured sapwood temperature on all trees equipped with respiration collars. Sapwood temperature was measured just below and offset approximately 3 cm horizontally from the stem respiration collars using 15-mm-long thermocouples constructed from copper constantan (type T) thermocouple wire. Thermocouples were connected to CR 1000 dataloggers and the average of measurements scanned at 30-s intervals was recorded every 30 min. Gaps in stem temperature data (for example, from power outages, malfunctioning probes, and so on) were filled using the relationship between the stem temperature of a tree with missing data and another tree if data were available or using the relationship between stem temperature and air temperature measurements collected in our plots or the Fisher Meteorological Station at Harvard Forest (Boose 2001).

Root Biomass

During both the spring (late-April) and fall (early-December) of 2011, we collected five soil cores at evenly spaced intervals along a diagonal transect that bisected each plot. Soils were sampled to a depth of 15 cm using a 5-cm diameter soil corer and slide hammer. Each sample was stored in a sealed plastic bag at 4°C until processed for root sorting when live fine roots (≤ 2 mm in diameter) were separated from dead roots based on tensile strength and color (McClougherty and others 1982) and dried at 65°C to a constant weight.

Stem Radial Growth

Prior to leaf-out in April 2014 one 5 mm diameter tree core was collected from each of the two red maples and two red oaks in each plot that were equipped with a stem respiration collar (see below). Each tree core was collected from within the area of the stem that was sampled for stem respiration to quantify rates of tree growth and stem respiration

for the same location on the tree. Tree cores were air-dried, mounted, and sanded to a smooth, flat surface. Rings were measured to the nearest 0.01 mm using a Velmex measurement system (Velmex, East Bloomfield, New York, USA) and MeasureJ2X software (v.4.2, VoorTech Consulting, Holderness, New Hampshire, USA). Cores were crossdated with the assistance of COFECHA (Holmes 1983; Grissino-Mayor 2001). To estimate radial wood production, basal area increment (BAI) was calculated for each of the 5 years prior to the start of the experiment (that is, 2006–2010) and each year following snow removal (that is, 2011 and 2012) by back-calculating tree diameters from each year's growth increment. A basal area increment index (BAII) was calculated for each tree sampled by dividing the BAI of each year after the start of the experiment (2011 and 2012) by the mean BAI of the 5 years prior to the start of the experiment (2006–2010). This index quantifies the relative change in growth of each tree (for example, BAII < 1 indicates reduced growth). Plot-level mean BAII was calculated for each species.

Rates of C storage in stem wood were calculated for the 2011 and 2012 growing seasons for comparison with C losses from stem respiration (see below). Briefly, the two-dimensional BAIs of each tree for 2011 and 2012 were converted to a three-dimensional wood volume increment following the equation for the volume of a cylinder. Biomass was then calculated from wood volume increment using stem wood densities of 590 kg biomass m^{-3} for red oaks and 602 kg biomass m^{-3} red maples (Gonzalez 1990). Carbon storage in stem wood was calculated per unit stem area by multiplying biomass by 0.5. Using rates of C storage in stem wood and rates of C loss through stem respiration (described below), we estimated the carbon use efficiency (CUE) of stem wood production for both red oaks and red maples. Carbon use efficiency is defined here as the ratio of the rate of C storage in stem wood to the rate of C loss through stem respiration.

Stem Respiration

One stem respiration collar was attached to each of the center two red oaks and two red maples in each plot in April 2011. Collars were constructed from PVC pipe (10 cm inside diameter) with an arch cut into the end attached to the tree to conform to the curvature of the tree stem. Each collar was attached to the north side of each tree at 1.4 m height using silicone sealant (General Electric Silicone II Sealant) and allowed to dry for at least 24 h prior to

measurement. We attached collars only to the north side of each tree to avoid possibly confounding effects of interactions between insolation and the collar on stem temperature. To ensure secure attachment, loose bark, moss, and lichen were gently removed from an area the size of the collar prior to collar installation. Laboratory measurements confirmed that the cured silicone sealant does not produce any detectable CO₂. Briefly, a PVC collar 10-cm wide and 5-cm deep was attached to a piece of Plexiglas using silicone sealant. The CO₂ flux was measured following the protocol described below, but no flux could be detected (detection limit <0.3 ppm change).

Stem respiration was measured using a LI-6400 Infrared Gas Analyzer with a soil respiration chamber (LI-COR Biosciences, Lincoln, NE, USA) that was attached horizontally to stem respiration collars using compression straps (*sensu* Xu and others 2000). Measurements were made twice per month during the growing season (May–Oct) in 2011 and 2012. Exceptions were August of 2011 and 2012 when only one measurement was made and July 2012 when no measurements were made because of technical issues with the LI-6400. We include only growing season measurements here because winter fluxes were too low (that is, often surrounding zero) to be reliably measured.

We scaled up measurements of stem respiration from per unit stem area to per unit ground area for its utility in estimating ecosystem C fluxes. Stem respiration per unit ground area was calculated for red oaks, red maples, other species, and the total from:

$$\text{Stem}_{\text{forest}} = \text{SAI} * \text{Stem}_{\text{collar}}, \quad (2)$$

where $\text{Stem}_{\text{forest}}$ is the stem respiration per unit ground area and $\text{Stem}_{\text{collar}}$ is the stem respiration per unit stem area.

Previous work suggests that rates of stem respiration do not change consistently with stem height up to the base of the crown (Araki and others 2010). Similarly, we did not find significant differences vertically along the bole of the tree up to 5 m height (maximum height accessible) along stems in trees adjacent to our plots (that is, measured on 3 red oaks and 3 red maples; $P = 0.28$ for red oaks and $P = 0.09$ for red maples). Therefore, we scaled our measurements made at 1.4 m height of target trees in each experimental plot up to 10 m stem height, which is just below the canopy.

We used stem surface area to extrapolate stem respiration to the ecosystem scale (Chambers and others 2004). Our scaled-up estimates of stem respiration for 0–10 m stem height for red oaks and

red maples were calculated using the mean respiration of the two red oaks and two red maples measured in each plot, respectively. Stem respiration for other tree species was calculated using the mean respiration rate of the two red oaks and the two red maples measured in each plot and scaled up using our measurements of total stem surface area of these individual trees.

Losses of C from stem respiration of all trees in each plot during the growing season were quantified using the relationship between the natural logarithm of stem respiration and sapwood temperature using the following:

$$\ln(\text{Stem}_{\text{collar}}) = \beta_0 + \beta_1 T_{\text{sapwood}}, \quad (3)$$

where $\text{Stem}_{\text{collar}}$ is the instantaneous stem respiration measurement per unit stem area, β_0 and β_1 are the regression coefficients and T_{sapwood} is the sapwood temperature at the time stem respiration was measured. This relationship was quantified for each species (that is, not individual red oaks or red maples) in each plot using the mean respiration rate and mean stem temperature of the two trees per species at each sampling period. A natural logarithm transformation was used to linearize the otherwise exponential relationship between stem efflux and sapwood temperature. The lag time in the response of stem respiration to sapwood temperature was determined by comparing models with sapwood temperatures at the time stem respiration was measured, as well as 1, 2 and 3 h earlier. Cumulative C losses from respiration for the growing season were quantified using the model with the highest coefficient of determination (r^2).

Statistical Analyses

All statistical analyses were conducted in R version 3.0.2 (R Core Team). We used analysis of variance (ANOVA) to examine potential differences among snow and soil frost depth, soil temperature, and site characteristics (for example, DBH, stem area, fine root biomass) between reference and snow removal plots. Interannual differences in snow depth and soil freezing were examined using repeated measures ANOVA and posthoc tests were conducted with Tukey's HSD. Effects of soil frost on fine root biomass, BAIL, and stem respiration were quantified using linear mixed effects models (LMM; lme function, Pinheiro and others 2012) with plot as the random effect to account for the lack of independence among repeated measures from each plot. AUC for soil frost, soil frost duration, and maximum soil frost depth were used as continuous fixed effects. A LMM coefficient of determination

(R^2) proposed by Nakagawa and Schielzeth (2013) was used as an absolute estimator of model fit. Marginal R^2 ($R^2_{\text{LMM}(m)}$) was calculated to quantify variability explained by the fixed effects (Nakagawa and Schielzeth 2013). LMM were used to quantify the relationship between tree radial growth increment and stem respiration, respectively.

$\alpha = 0.05$ was used to denote significance. Assumptions of normality and constant variance were assessed by visual inspection of residuals and Shapiro–Wilk normality test and response variables were log transformed as necessary.

RESULTS

Effect of Snow Removal Treatment on Soil Frost and Temperature

The winter of 2010/2011 had a deep, persistent snowpack (Figure 1) and was colder (average Dec–Mar air temperature = -3.7°C) than the long-term average for Harvard Forest. Snow removal induced greater maximum frost depth in the treatment (18.0 ± 0.5 cm) compared to the reference (9.7 ± 0.6 cm) plots in 2011 ($P < 0.01$). The soils remained frozen for 2 weeks longer in the treatment than reference plots in 2011. Surprisingly, the average and minimum winter soil temperatures

(5 cm depth) were not significantly colder ($P = 0.65$ and $P = 0.81$; respectively) in the snow removal plots (-0.16 ± 0.3 and $-2.7 \pm 0.3^\circ\text{C}$ for average and minimum soil temperatures, respectively) than the reference plots (0.6 ± 0.6 and $-0.8 \pm 0.6^\circ\text{C}$, respectively), likely due to large variability among the plots. Although the snow removal treatment prolonged the duration of soil frost, there were no differences in soil temperature after April 15th (that is, before the start of the growing season and measurement of stem respiration; see Reinmann 2014). Additionally, images from phenology cameras in each plot did not reveal any discernable differences in leaf-out time across plot types (data not shown).

In contrast, the winter of 2011/12 was warmer (average Dec–Mar air temperature = 0.5°C) and the snowpack was present for a significantly shorter period (Figure 1). Because little snow fell, snow was removed only twice and in both storms less than 10 cm of snow fell. Despite the average air temperature being above freezing, the presence of some below freezing air temperatures and the lack of an insulating snowpack allowed soil frost to develop in all plots and last from late-December through mid-March. The average (1.7 ± 0.4 and $1.5 \pm 0.6^\circ\text{C}$ in reference and treatment plots, respectively; $P = 0.82$) and minimum winter

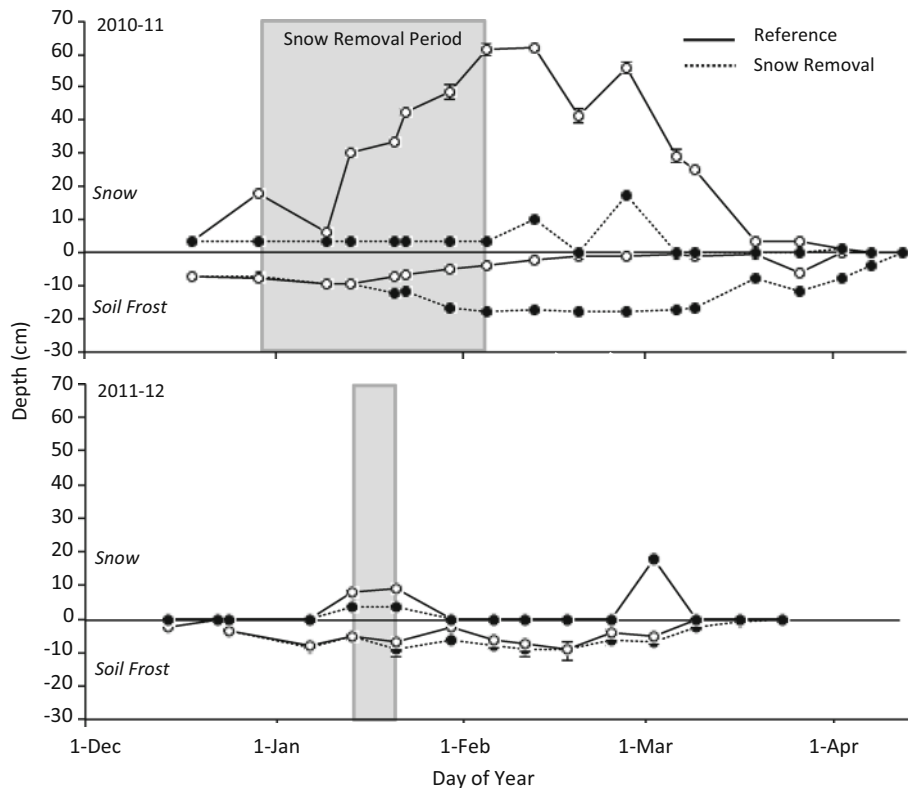


Figure 1. Snow depth and soil frost depth during the winters of 2010/11 and 2011/12. Lines above the solid zero line indicate snow depth and lines below indicate soil frost depth. Open symbols represent reference plots and closed symbols represent snow removal plots. The gray-shaded area indicates the snow removal period. Measurements of snow depth and soil frost depth ceased earlier in 2011/12 than 2010/11 because of the earlier snowmelt and soil thaw dates. Error bars represent standard error of the mean.

(-1.1 ± 1.0 and $-0.8 \pm 0.7^\circ\text{C}$, respectively; $P = 0.81$) soil temperatures (5 cm depth) overlapped between reference and treatment plots.

Effects of Soil Frost on Root Biomass

Across plots, total fine root biomass in the top 15 cm of the soil ranged from 417 to 699 g m⁻² in spring and from 281 to 455 g m⁻² in fall, but was not significantly affected by AUC, maximum soil frost depth, or soil frost duration (across variables, spring $P > 0.24$; fall $P > 0.47$). The proportion of live fine roots in the spring declined from 0.95 to 0.74 with increasing AUC, maximum soil frost depth and soil frost duration, but soil frost depth was the only statistically significant predictor of live root biomass ($P = 0.05$; $r^2 = 0.76$; Supplemental Figure 1). In contrast, there were no significant effects of soil frost depth, duration or AUC on live fine roots in the fall (early-December; $P > 0.56$).

Effects of Soil Frost on Tree Stem Growth

For the 5 years prior to the start of the snow removal experiment (that is, 2006–2010), red oaks were growing four times faster (mean BAI = 17.4 ± 2.8 cm² y⁻¹) than red maples (mean BAI = 4.3 ± 1.2 cm² y⁻¹) across all plots ($P < 0.01$). BAI of red oaks ranged from 0.75 to 1.04 across plots and both years of snow removal and tended to decline with increasing soil frost severity, but was not significantly correlated with any metrics of soil frost ($P \geq 0.10$; Figure 2). In contrast, red maple BAI ranged from 0.54 to 1.19 and was positively correlated with the AUC, duration of soil frost and maximum soil frost depth ($P < 0.05$, $R^2_{\text{LMM(m)}} > 0.44$), but the logarithm of maximum soil frost depth was the most closely correlated predictor of BAI ($P < 0.01$, $R^2_{\text{LMM(m)}} = 0.66$; Figure 2).

Annual rates of C storage across plots and both years of snow removal ranged from 138 to 481 g C m⁻² stem for red oaks and from 12.2 to 94 g C m⁻² stem for red maples. Because C storage in stems scales with BAI the effects of soil frost on relative changes in C storage (that is, comparing individual trees to themselves) mirror those of BAI (see above). Reflecting their larger size and faster radial growth rates (that is, BAI), red oaks stored C at significantly higher rates than red maples ($P < 0.01$; Figure 3).

Effects of Soil Frost on Stem Respiration

Stem respiration throughout the growing season was significantly and positively correlated with the dura-

tion of soil frost, which explained more of the variability in stem respiration of red maples ($P < 0.01$; $R^2_{\text{LMM(m)}} = 0.24$) than red oaks ($P < 0.01$; $R^2_{\text{LMM(m)}} = 0.14$; Figure 4). Growing season losses of C from stem respiration ranged from 114.5 to 347.1 g C m⁻² stem for red oaks and from 104.7 ± 20.1 to 256.9 g C m⁻² stem for red maples. Across the range in soil frost duration (44 days), growing season losses of C from stem respiration increased by 1.7 and 2.0% per day of soil frost for red maples and red oaks, respectively (from LMM coefficients). Total growing season losses of C from stem respiration were significantly and positively correlated with annual rates of radial tree growth, but explained more variability in stem respiration of red maples ($P = 0.02$; $R^2_{\text{LMM(m)}} = 0.55$) than red oaks ($P = 0.03$; $R^2_{\text{LMM(m)}} = 0.47$; Figure 5).

Rates of stem respiration across sampling dates were correlated positively with sapwood temperature for red oaks (mean $r^2 = 0.81$; $P < 0.05$) and red maples (mean $r^2 = 0.71$; $P < 0.05$). Sapwood temperatures for both species overlapped and mirrored patterns of air temperature, but with a narrower amplitude and a lag time of approximately 3 h. Following patterns in temperature, rates of stem respiration tended to be highest during the middle of the growing season (Figure 6).

Growing season rates of C loss through stem respiration of red oaks were not significantly different than rates of C storage in stem wood (Figure 3; 2011 $P = 0.59$; 2012 $P = 0.95$). In contrast, growing season rates of C loss through stem respiration of red maples were 2.5 to 4 times higher than rates of C storage in stem wood, and these differences were significant (see values above; 2011 $P < 0.01$; 2012 $P = 0.03$). These data indicate a CUE of wood production of 0.95 ± 0.16 for red oaks, which is significantly higher than the CUE of 0.39 ± 0.08 for red maples ($P < 0.01$). The CUE of red oak wood production was significantly higher than for red maples even within the range in which there was overlap in the DBH of these two species ($P < 0.01$; data not shown).

We used the averaged fluxes from all six plots to estimate ecosystem losses of C from tree stems. Total growing season losses of C from stem respiration ranged from 41.8 to 85.9 g C m⁻² forest and were significantly and positively correlated with duration of soil frost ($P < 0.01$; $R^2_{\text{LMM(m)}} = 0.29$), but not AUC or maximum frost depth ($P > 0.05$).

DISCUSSION

Similar to findings from previous studies (for example, Hardy and others 2001), snow removal in

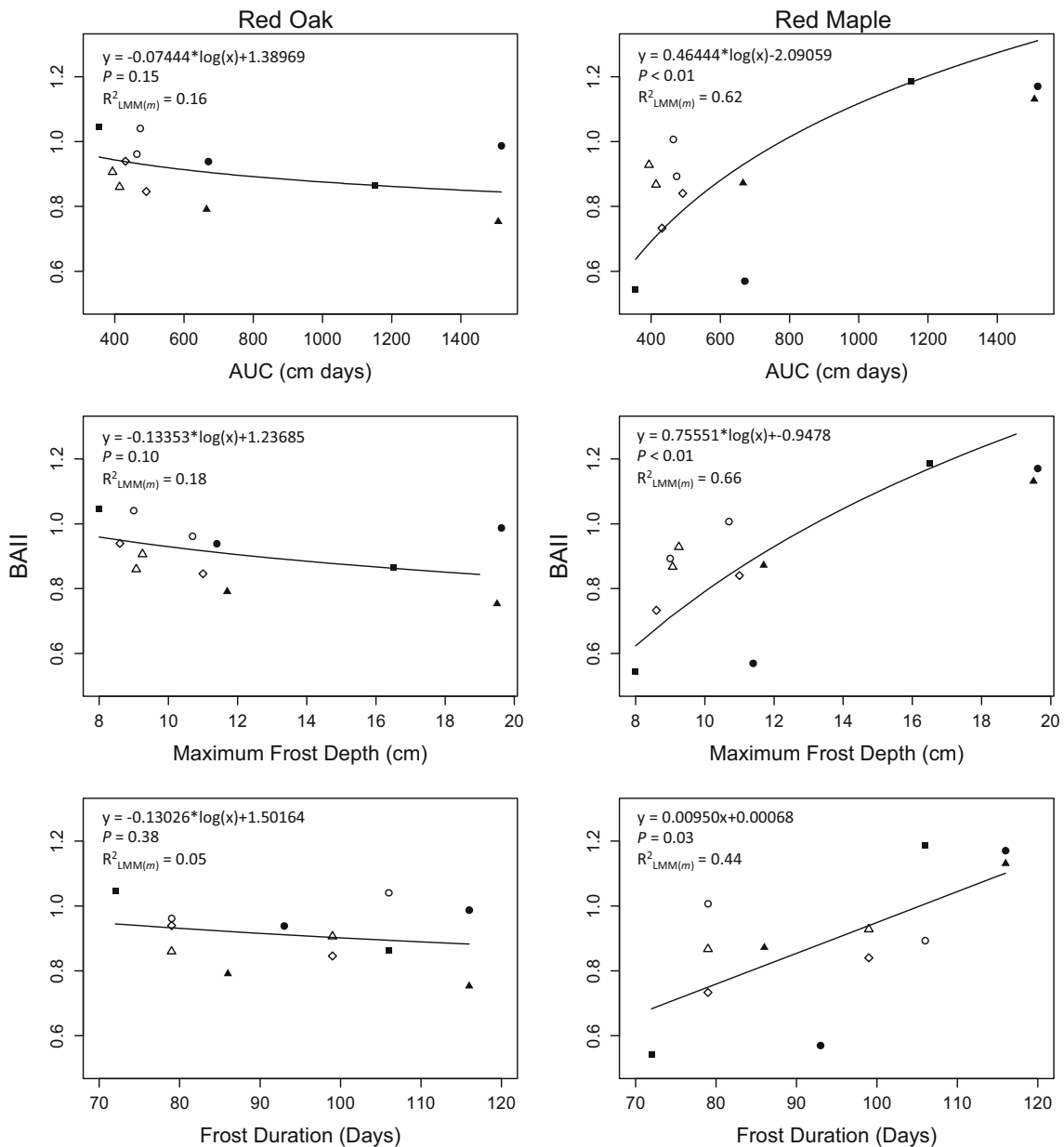


Figure 2. Relationships between basal area increment index (BAII) and AUC (*top*), maximum soil frost depth (*middle*) and soil frost duration (*bottom*) during the previous winter for red oaks (*left*) and red maples (*right*). The P -values, $R^2_{LMM(m)}$ values, coefficients and best-fit lines were derived from the linear mixed models. Symbols of the *same shape and color* correspond to the same plot and indicate the trajectory of individual plots from lower to higher severities of soil frost (that is, from 2010/2011 to 2011/2012 winter).

this study increased the depth and duration of soil frost. However, the winter of 2011/12 had below average snowfall and above average air temperatures (Rasche 1958; Fitzpatrick and others 2012) precluding any effect of snow removal on soil temperatures and frost depth that winter. The difference in air temperature between the two winters (4.2°C) was within the range of winter warming

projected by the end of the 21st century for the region (Hayhoe and others 2007).

Results from this study highlight the importance of understanding the effects of a projected decrease in winter snow and increased soil freezing on root biomass, stem growth, and respiration. Despite reductions in the live fraction of fine root biomass with increasing maximum soil frost depth, BAI of

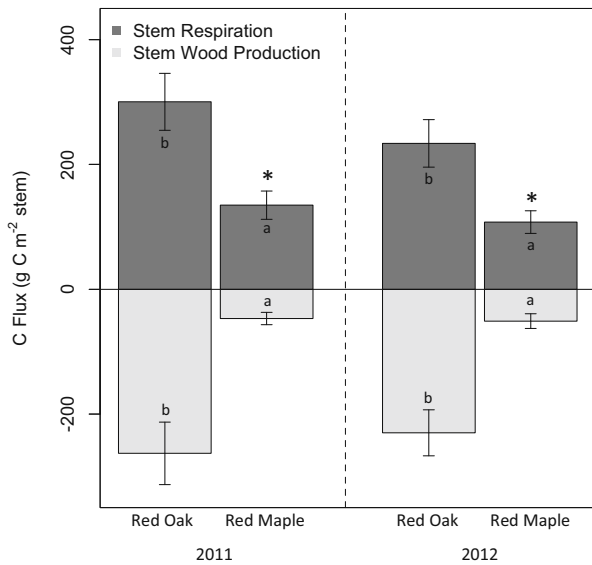


Figure 3. Carbon fluxes per square meter of stem surface area for the 2011 and 2012 growing seasons, averaged across all plots. Positive values represent losses of C to the atmosphere through stem respiration and negative values indicate removal of C from the atmosphere through stem wood production. *Error bars* represent standard error of the mean. Different *letters* indicate statistically significant ($P < 0.05$) differences between species within a year. *Asterisks* indicate statistically significant ($P < 0.05$) differences between stem respiration and wood production within a species and year.

red maples increased while there was no effect on BAI of red oaks. Soil frost duration was positively correlated with stem respiration of both tree species studied, but explained a smaller amount of the variability in red oaks (14%) than red maples (24%). Losses of C from stem respiration were comparable to or greater than rates of C storage in the stem wood of red oaks and red maples, respectively. To the best of our knowledge, this is the first study to document an increase in tree growth and autotrophic respiration in response to increased soil freezing. These results show that the adverse effects of soil freezing on belowground live root biomass observed in this study do not translate into similar trends for aboveground growth and respiration of red maple and red oak trees. Rather, our results demonstrate that at least in the short-term, a reduced winter snowpack and increased soil freezing could enhance rates of aboveground growth and C storage for red maple trees in mixed-hardwood forests. However, at the landscape scale increasing abundance of red maples in mixed-hardwood forests of the northeastern U.S. (Thompson and others 2013) could reduce C stor-

age of these forests because their CUE of wood production and rates of C storage in stem biomass are less than half those of red oaks.

Effects of Soil Frost on Root Biomass, Stem Radial Growth, and Stem Respiration

Similar to studies examining the effects of a reduced snowpack and increased soil freezing on sugar maple (*A. saccharum*) dominated stands in northern hardwood forests (Tierney and others 2001; Comerford and others 2013), our results show that increased soil freezing reduces early-growing season live fine root biomass of a red maple-red oak forest. However, in contrast to the adverse effects of soil freezing found for shoot elongation of sugar maples (Comerford and others 2013), we found that soil freezing stimulates radial tree growth of red maples, but has no impact on radial growth of red oaks. Although we measured a different metric of tree growth (that is, radial growth) and tree species (that is, red maple and red oak) than Comerford and others (2013; that is, shoot elongation of sugar maple), the opposite direction of the response to soil frost of red maples could be due to the shallower depth of soil frost observed in our study (20 cm) compared to those measured by Comerford and others (2013; 50 cm). Corroborating findings of previous studies (Acosta and others 2008; Werten and Teskey 2008; Maier and others 2010), we found that rates of stem respiration are positively correlated with rates of radial growth.

Effects of Soil Frost on Ecosystem C Losses from Stem Respiration

Our results suggest that soil freezing during the winter can result in a large increase in stem respiration during the following growing season. Given the positive correlation that we observed between stem respiration and radial wood growth, we suspect that woody respiration in tree branches also increases following soil frost. Rates of foliar respiration may also increase following soil freezing if greater radial wood growth is driven by higher rates of photosynthesis. Using species composition weighted rates of stem respiration, we found that ecosystem C losses from stem respiration increased by 79% across the observed 44-day range in soil frost duration. Additionally, C losses through stem respiration were comparable to or larger than the C sequestered through annual wood production and comprise an important ecosystem flux in mixed-

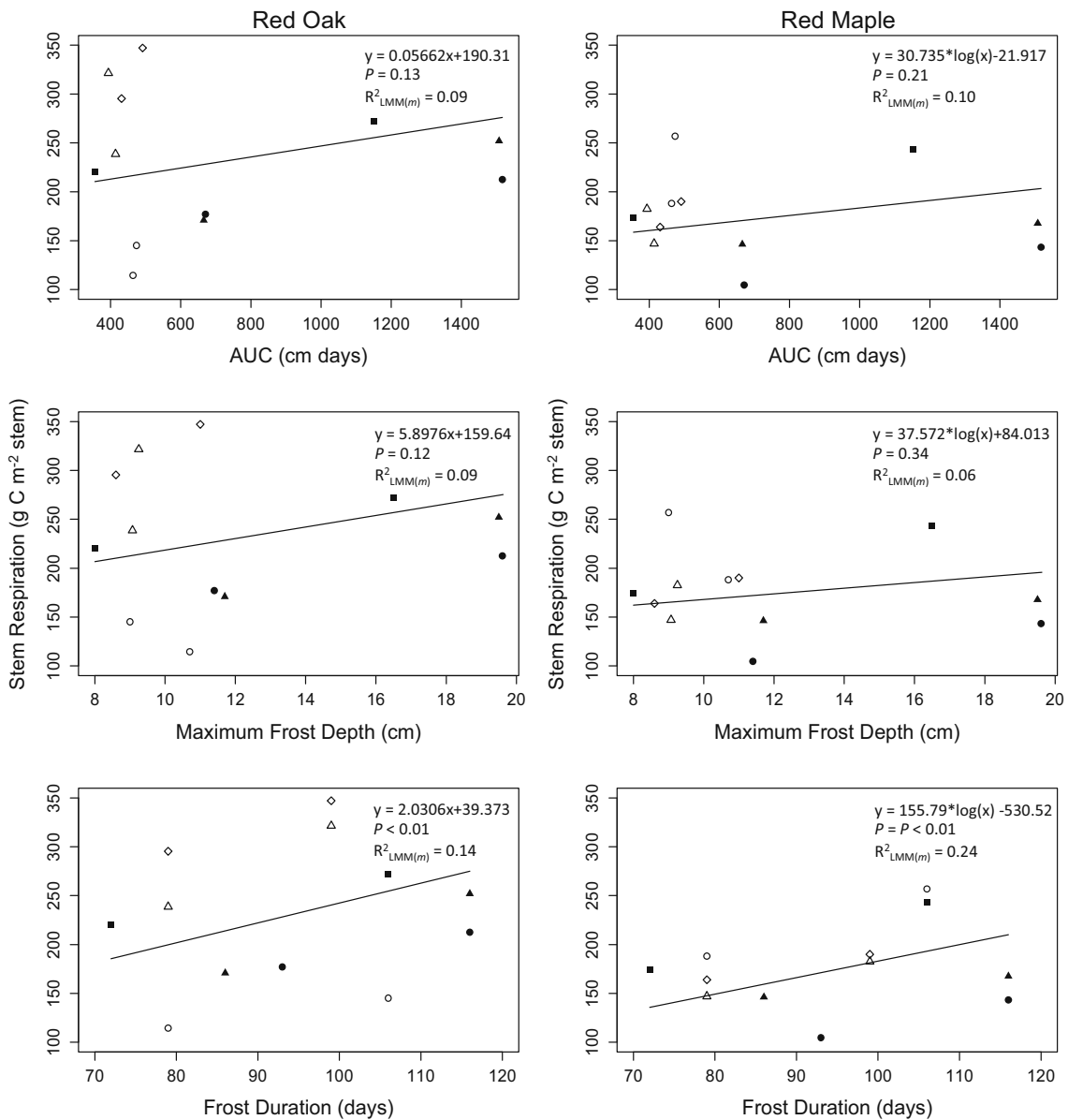


Figure 4. Relationships between stem respiration during the growing season and AUC (*top*), maximum soil frost depth (*middle*) and soil frost duration (*bottom*) during the previous winter for red oaks (*left*) and red maples (*right*). The *P*-values, $R^2_{LMM(m)}$ values, coefficients, and best-fit lines were derived from the linear mixed models. Symbols of the same shape and color correspond to the same plot and indicate the trajectory of individual plots from lower to higher severities of soil frost (that is, from 2010/2011 to 2011/2012 winter).

hardwood forests. Eddy flux data for whole ecosystem C exchange at Harvard Forest averaged from 1992 to 2004 (Urbanski and others 2007) suggest that stem respiration to a stem height of 10 m presented here (41.8–85.9 g C m⁻² forest y⁻¹, across plots and years) comprises 3–6% of GPP (mean = 1400 g C m⁻²), 17–36% of annual net C assimilation (mean = 242 g C m⁻²), and 5–10% of growing season ecosystem respiration (mean = 860 g C m⁻²) in these forests. These values are similar to those reported by Edwards and others

(2002) who estimated that stem respiration accounted for 5% of GPP in a young temperate hardwood forest (*Liquidamber styracilua* L. plantation) in Tennessee, USA. Using our cumulative growing season estimates of stem respiration to a height of 10 m (41.8–85.9 g C m⁻² forest y⁻¹) and annual rates of aboveground respiration (423 g C m⁻² y⁻¹) calculated as the difference between published values of ecosystem (1145 ± 142 g C m⁻² y⁻¹) and soil respiration (722 ± 62 g C m⁻² y⁻¹) at Harvard Forest from 1992 to 2009 (Giasson and

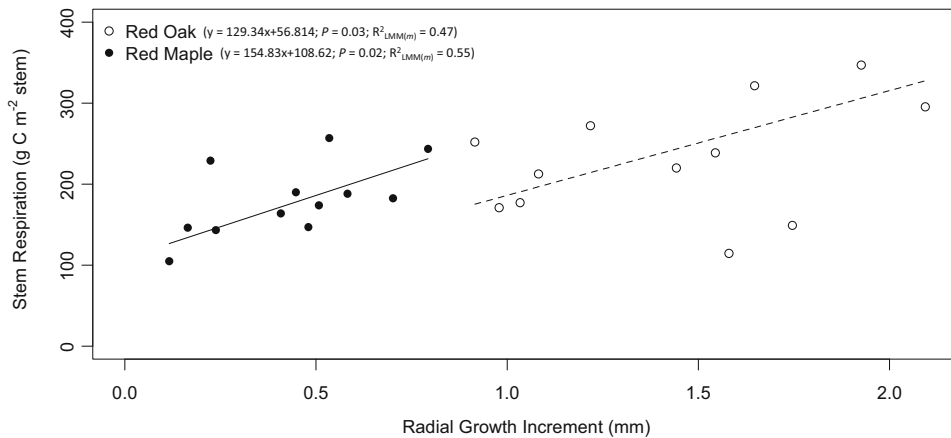


Figure 5. Relationship between plot-level mean rates of radial tree growth and stem respiration for red oaks and red maples. There are two data points for each plot and species reflecting data for 2011 and 2012 growing seasons. The best-fit lines were derived from the coefficients of the LME models.

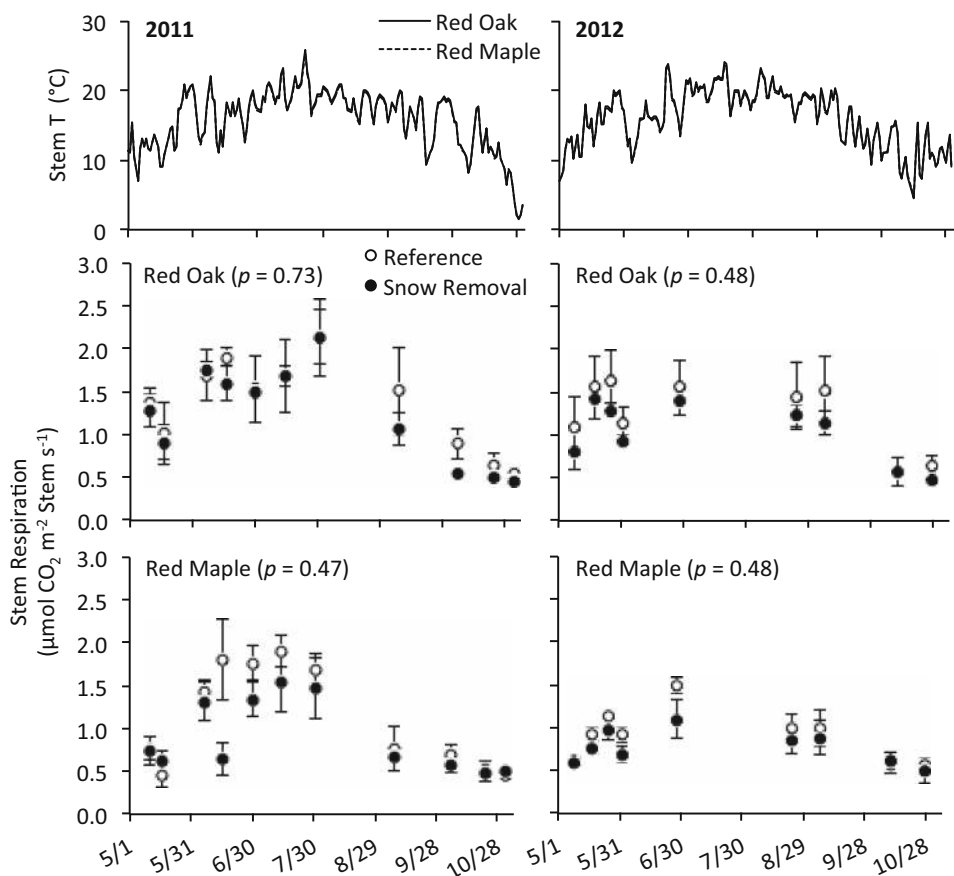


Figure 6. Stem temperature averaged across six plots ($n = 12$ for each species; plotted as a mean here for illustrative purposes as there was little deviation in stem temperature within a species or between plot types). Stem respiration for red oak and red maple during the growing season following the winters of 2010–2011 and 2011–2012 (right). Measurements are expressed per unit stem surface area. P -values show comparison between reference and snow removal plots within each tree species and year. Error bars represent standard error of the mean.

others 2013), we estimate that stem respiration during the growing season comprises 10–20% of annual aboveground respiration. Further understanding of stem respiration and its variability across species may be useful in reconciling the mechanisms driving the strengthening C sink at Harvard Forest associated with an increase in the biomass of red oaks (Urbanski and others 2007).

CONCLUSIONS

The results from this study provide insight into the relationships between soil frost severity and ecosystem pools and processes, including root biomass, stem growth, and respiration and their potential effects on ecosystem C storage and loss. We found that the projected decrease in the winter

snowpack and greater soil frost severity will lead to reduced live root biomass in mixed-hardwood forests. In contrast to the belowground response, we found that greater soil freezing leads to greater BAI of red maples with no effect on red oaks. The mechanisms driving the growth response of red maples to soil freezing remain unclear, and therefore we suggest that researchers examine the species-specific belowground response of co-occurring tree species to soil freezing. Our results show that increased soil freezing could increase aboveground C storage of red maples and their competitiveness relative to red oaks in mixed-hardwood forests. However, at the landscape scale, we suspect that increases in the relative abundance of red maples could reduce C storage of these forests due to their lower CUE of wood production and rates of C storage in stem biomass compared to red oaks.

ACKNOWLEDGEMENTS

We are grateful for the assistance of Audrey Barker-Plotkin, Christine Bollig, Keala Cummings, Dash Donnelly, Omar Gutiérrez del Arroyo Santiago, Adam Jacobs, Stephanie Juice, Eli Melaas, Trustees of Reservation, and the staff at Harvard Forest. We are appreciative of the thoughtful feedback on this manuscript provided by Ivan Fernandez, Adrien Finzi, Peter Groffman, Lucy Hutyra, Nathan Phillips, and Jim Tang. This project was supported by a US EPA Science to Achieve Results Graduate Fellowship to A. Reinmann and by the Northeastern States Research Cooperative through funding made available by the USDA Forest Service. The conclusions and opinions in this paper are those of the authors and not of the NSRC, the Forest Service, EPA, or the USDA.

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