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RESEARCH ARTICLE

Response of Root Respiration to Warming and Nitrogen Addition Depends on Tree Species

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ABSTRACT

Roots contribute a large fraction of CO_2 efflux from soils, yet the extent to which global change factors affect root-derived fluxes is poorly understood. We investigated how red maple (*Acer rubrum*) and red oak (*Quercus rubra*) root biomass and respiration respond to long-term (15 years) soil warming, nitrogen addition, or their combination in a temperate forest. We found that ecosystem root respiration was decreased by 40% under both single-factor treatments (nitrogen addition or warming) but not under their combination (heated × nitrogen). This response was driven by the reduction of mass-specific root respiration under warming and a reduction in maple root biomass in both single-factor treatments. Mass-specific root respiration rates for both species acclimated to soil warming, resulting in a 43% reduction, but were not affected by N addition or the combined heated × N treatment. Notably, the addition of nitrogen to warmed soils alleviated thermal acclimation and returned mass-specific respiration rates to control levels. Oak roots contributed disproportionately to ecosystem root respiration despite the decrease in respiration rates as their biomass was maintained or enhanced under warming and nitrogen addition. In contrast, maple root respiration rates were consistently higher than oak, and this difference became critical in the heated × nitrogen treatment, where maple root biomass increased, contributing significantly more CO_2 relative to single-factor treatments. Our findings highlight the importance of accounting for the root component of respiration when assessing soil carbon loss in response to global change and demonstrate that combining warming and N addition produces effects that cannot be predicted by studying these factors in isolation.

1 | Introduction

Soil respiration releases 83–108 Pg C $year^{-1}$ globally, an amount that exceeds CO_2 fluxes from fossil fuel combustion by an order of magnitude (Hanson et al. 2000). As such, factors that influence the magnitude of soil respiration can potentially affect the pace of climate change (Janssens et al. 2010; Melillo et al. 2017). Root respiration, which makes up 40%–60% of total soil respiration (K. Savage, Davidson, and Tang 2013; Schindlbacher, Zechmeister-Boltenstern, and Jandl 2009), frequently influences soil respiration rates observed under warming (Burton, Melillo, and Frey 2008; Jarvi and Burton 2020; Melillo et al. 2011) and simulated atmospheric nitrogen (N) deposition (Zhang et al. 2019; Zogg et al. 1996). While numerous studies and syntheses have been done to look at warming or N addition effects on total soil respiration, we know far less about how the plant root component of respiration will respond, making this a critical research priority for understanding the true potential of soil CO_2 flux.

Prior studies have shown that decreases in fine root biomass due to soil warming (Melillo et al. 2011) and N addition (Mo et al. 2008) result in decreased ecosystem root respiration (i.e., takes into account both mass-specific root respiration and root biomass). For example, under long-term soil warming in temperate forests, fine root biomass typically decreases (Melillo et al. 2011; Parts et al. 2019) while rates of mass-specific respiration may acclimate to warmer temperatures (Burton, Melillo, and Frey 2008; Jarvi and Burton 2013, 2020), resulting in substantive reductions in overall root respiration. Several studies predict that increases in soil respiration from warming could add over 190 Pg of soil carbon (C) to the atmosphere over the 21st century, equivalent to the past two decades of fossil fuel combustion (Melillo et al. 2017), owing to greater microbial respiration. Thus, the decrease in root respiration serves as a moderating force against the warming-induced acceleration of microbial respiration, dampening the potential soil CO_2 flux (Tjoelker 2018). On the other hand, simulated atmospheric N deposition can reduce total soil respiration by up to 22% by suppressing microbial respiration (Bowden et al. 2004; Frey et al. 2014; Zhang et al. 2019).

The effects of soil warming and N enrichment on roots may be linked since warming typically increases N availability by stimulating microbial-mediated N mineralization. The shift in N availability could alter the C economy of trees, leading to changes in root activity and overall soil respiration rates by alleviating both temperature (Saxe et al. 2001) and N constraints (E. Bai et al. 2013; Butler et al. 2012; Melillo et al. 2011) on plant growth when combined. Warming combined with N addition could undermine the ability of roots to mitigate soil respiration, potentially amplifying C release (T. Bai et al. 2023; Knorr et al. 2024). For example, Knorr et al. (2024) report that the combined effects of soil warming and N addition lead to soil respiration rates that are 1.6 times greater than warming alone and appear to negate the plant root processes that decrease root respiration under warming and N addition in isolation. This suggests that roots may be exacerbating soil respiration rates induced by warming under increased N availability.

Fine roots of trees have distinct functional roles in tree nutrition and because their primary function is to acquire and store nutrients, they are prone to changes in soil nutrient cycling imposed by soil warming and N addition. Absorptive roots, typically first-, second-, and third-order roots (McCormack et al. 2015), are the most active fraction of root systems and are essential for acquiring soil N directly by increasing the total volume of soil explored by roots (they account for over 75% of fine root length; Guo, Mitchell, and Hendricks 2004; Ostonen et al. 2007) and indirectly through mycorrhizal colonization (Tibbett 2000). Likewise, absorptive roots are responsible for most root respiration (Jia et al. 2013; Pregitzer et al. 1998), and because absorptive roots are sensitive to changes in both N availability (Liu et al. 2015) and temperature (Zogg et al. 1996), they may be an overlooked mediator of the temperature sensitivity of soil respiration under differential soil N availability. On the other hand, transport roots are longer lasting and are essential in relocating and storing the nutrients that absorptive roots acquire (Freschet and Roumet 2017; McCormack et al. 2015). Thus, expanding the absorptive fine root system in response to warming and N addition could amplify total soil respiration more than an expansion of the transport root system would, due to the inherently higher respiratory activity associated with absorptive fine roots.

Changes in absorptive root biomass in response to soil N availability can vary depending on tree species, such as the *Acer* spp. (maple) and *Quercus* spp. (oak), which are commonly found in the Eastern United States (Bergmann et al. 2020; Keller and Phillips 2019; McCormack et al. 2015). Maples are typically associated with arbuscular mycorrhizal (AM) fungi, while oaks are predominantly colonized by ectomycorrhizal (EM) fungi, with these two tree species having contrasting strategies for acquiring soil nutrients. Maples efficiently scavenge inorganic N that is made available through N mineralization by other soil microbes (Eissenstat et al. 2015), and tend to have greater fine root production and turnover to maximize foraging under variable N availability relative to oaks (Chen et al. 2016; Chen, Koide, and Eissenstat 2018). In contrast, oaks rely more on their fungal symbionts to access organic N sources directly from organic matter, often reducing the need for extensive fine root growth. Consequently, oaks may invest less C in fine root production and rely more heavily on the foraging of EM fungi to acquire N from organic sources (Chen et al. 2016; Jevon and Lang 2022). Soil inorganic N availability may interact with tree species to control plant C allocation belowground, which, in turn, could modulate the response of soil respiration to long-term warming and soil N addition. If warming and N addition increase inorganic N availability, oaks may be disadvantaged (Jo et al. 2019), leading them to acquire soil organic N by expanding their absorptive root system (Cheng et al. 2016), thereby increasing root respiration.

Despite the critical role of root respiration in soil C dynamics, most studies generalize fine root system responses to environmental changes, often neglecting functional responses and species-specific variation. This oversight can obscure how different species adjust their root systems to soil warming and N addition. In the present study, we hypothesized that N addition and warming would decrease root respiration but only when the treatments were applied alone and not in combination. To address this, our study at the Harvard Forest Long-Term Ecological Research (LTER) site focused on maples and oaks to systematically evaluate the effects of warming, N addition, or their combination on the biomass of absorptive and transport fine roots at the species level. By measuring these root types, assessing mycorrhizal colonization, and evaluating mass-specific respiration rates, we aimed to elucidate how tree species with distinct root dynamics influence soil respiration and ecosystem C fluxes.

2 | Methods

2.1 | Study Area and Sample Collection

Soil samples were collected in July 2020 from the Soil Warming × Nitrogen Addition Study located on the Prospect Hill Tract of the Harvard Forest LTER site in Petersham, Massachusetts, USA (42°50′ N, 72°18′ W). The forest is categorized as an ectomycorrhizal (EM)-dominated temperate deciduous forest (> 70% EM-associated trees by basal area; Keenan et al. 2012) and is composed of even-aged, mixed hardwoods, including red oak (*Quercus rubra*), black oak (*Q. velutina*), and red maple (*Acer rubrum*). Within the stand, the most dominant EM tree is *Q. rubra* (52% of the basal area) and the most dominant AM tree is *A. rubrum* (22% of the basal area). Soils are of the Gloucester series (fine loamy, mixed, mesic typic Dystrochrepts) and are shallow, with rocky glacial deposits starting within ~20–30 cm of the soil surface. Mean annual air temperature is 7°C and average total annual precipitation (including snowfall) is 1100 mm (Boose and Gould 2021). Mean annual air temperature has increased by +0.02°C year^{-1} and total annual precipitation by +6.9 mm year^{-1} when considering the past 52-year record at Harvard Forest (1964–2015; Finzi et al. 2020).

The experiment is a full factorial design composed of twenty-four 3 × 3 m plots randomly assigned to one of four treatments: control, N addition, heated, and heated × N, with six replicates per treatment (Contosta, Frey, and Cooper 2011). Soil temperature in all heated plots is continuously elevated 5°C above ambient conditions using buried heating cables placed 10 cm below the soil surface and spaced 20 cm apart. Heating cables were buried in 2005 and turned on in 2006. N additions were initiated in 2006, with N being applied in equal monthly doses during the growing season (May–October) as aqueous NH_4NO_3 at a rate of 50 kg N $\text{ha}^{-1}\,\text{year}^{-1}$.

Two individual soil samples were taken per treatment plot, starting with a 10 cm × 10 cm organic horizon "brownie" followed by 0–10 and 10–20 cm of mineral soil sampled using a Giddings slide hammer coring tool (5.7 cm inner diameter; Giddings Machine Co., Windsor, CO). Plot replicates were not bulked, and all samples were processed and analyzed separately. Thus, the full sampling design was four treatments × six replicates per treatment × two plot replicates × three depth increments, with the exception that one heated plot has been nonfunctional since 2009 and was excluded, leading to a total of 138 samples. Samples were stored at 4°C and processed within 1 week.

2.2 | Fine Root Biomass

Fine roots (< 2 mm diameter) were separated from fresh soil using forceps following the classification proposed by McCormack et al. (2015). Briefly, soil samples were placed onto a clean 2 mm sieve. Roots were picked gently from the soil, separating live root tissues into either absorptive (first, second, and third order) or transport root (fourth and fifth order) functional types based on branching order. Absorptive roots were further divided into tree species (maple or oak) based on color, morphology, and presence of EM or AM associations. Specifically, oak roots (*Quercus* spp.) were separated based on their darker color, root branching, and number of root tips. In contrast, maple roots (AM-associated) were identified based on lighter color and larger diameter characteristics. A stereomicroscope was used to aid the visualization and sorting of fine roots and confirm mycorrhizal status. Roots were picked in 5-min intervals, recording the mass returned after each interval until a period of stabilized diminishing returns was reached. Dead roots were identified and discarded based on their dark discoloration, poor adhesion between the stele and cortex, and brittleness (Persson and Stadenberg 2009). Fine roots from each functional pool (absorptive vs. transport) and species (oak vs. maple) combination were cleaned with deionized water to remove soil and organic debris, dried at 60°C, and weighed. Absorptive roots were finely ground using a stainless-steel ball mill grinder, and N concentrations were determined using a Perkin Elmer 2400 Series II CHN Elemental Analyzer.

2.3 | Mycorrhizal Colonization and Biomass

To evaluate the response of EM and AM fungi to soil warming, N addition, or their combination, we employed distinct methodologies reflective of their unique biological characteristics. We used visual morphotyping to enumerate the number of root tips colonized by EM fungi based on their physical traits. During root processing, a random subsample of oak (EM-associated) absorptive fine roots from the organic horizon was collected, washed gently with D.I. water, and stored in 2× CTAB solution (100 mM Tris–HCl (pH 8.0), 1.4 M NaCl, 20 mM EDTA, 2% cetyltrimethylammonium bromide). EM colonized root tips were visually morphotyped based on color, ramification, and hyphal color (Agerer 2001). At least 100 root tips were counted per sample, and the number of root tips colonized was divided by the total number of root tips counted to determine EM colonization rate. Phospholipid fatty acid (PLFA) analysis using the $16{:}1\omega5$ biomarker was selected to detect changes in AM fungal biomass. Briefly, 1 g of organic horizon soil was extracted using a mixture of citrate buffer, methanol, and chloroform and shaken for 24 h. Extracts were converted to fatty acid methyl esters and transferred to 2-mL glass vials prior to analysis via gas chromatography–mass spectrometry. Specific details on the method used to determine AM fungal biomass and the full PLFA data set are available in Stoica et al. (2023). While it is recognized that some bacteria also possess this lipid biomarker (Olsson and Lekberg 2022), potentially complicating its use as a definitive metric of AM biomass, our application of this method aims to provide a general indication of root-fungal response to global change. Here, we combined the PLFA approach with the examination of fine root associations to discern patterns of tree root response to soil warming and N addition and focus less on the PLFA biomarker as an absolute metric of AM biomass.

2.4 | Root Respiration

Starting in spring 2021, fine roots were collected the first week of each month during the growing season (May–October) from the organic horizon of each plot to measure root respiration using a standard approach (Burton, Melillo, and Frey 2008; Paradiso, Jevon, and Matthes 2019). This process involved removing the litter layer until one maple and one oak absorptive root system were identified. Roots (at least 10 cm long) were collected within 2–5 cm of the soil surface, severed, immediately transported to an onsite field facility, and confirmed for species identity. Roots were then carefully cleaned to remove organic debris, and respiration rates were determined within 15 min of collection. Previous work on fine roots has indicated that rates of root physiological traits attenuate after 2 h (Bloom and Caldwell 1988), and specifically, root respiration in temperate forests has been shown to remain stable for up to 4 h following removal from soil (Burton et al. 2002). To measure root respiration, absorptive roots were individually inserted into a sealed glass chamber (175 mL) connected using polyethylene tubing (19 mL) to a LICOR 8100a field infrared gas analyzer (LI-COR Biogeosciences) that measured CO_2 concentrations every second for a 5-min interval. Each interval contained a 15-s chamber prepurge and a 15-s chamber postpurge. We focused our measurements on absorptive fine roots to standardize the process between tree species (Freschet and Roumet 2017; McCormack et al. 2015). Upon returning to the laboratory, roots were stored at 4°C for up to 1 week before being dried at 60°C for 48 h for determination of dry mass.

We calculated specific root respiration by fitting a linear model to the relationship between time and CO_2 concentration (ppm) within the glass chamber using Soil Flux Pro (v4.0; Li-COR, Lincoln, Nebraska) and then converting the slope of this linear model to CO_2 respiration flux in nmol $CO_2\,s^{-1}$. We divided root respiration measurements by dry root biomass to quantify mass-specific root respiration (nmol $CO_2\,g^{-1}\,s^{-1}$). Mass-specific root respiration was scaled to the ecosystem level (hereafter "ecosystem root respiration") as the product of specific fine-root respiration (nmol $CO_2\,g^{-1}\,s^{-1}$) and absorptive root biomass ($g\,m^{-2}$), expressed as nmol $CO_2\,g^{-1}\,m^{-2}\,s^{-1}$ for each tree species (Jarvi and Burton 2020; Melillo et al. 2011; Tunison et al. 2024).

2.5 | Statistical Analysis

Analysis of variance (ANOVA) was used to determine the effects of treatment (heat, N addition, heat × N), soil depth (organic horizon and 0–10 and 10–20 cm mineral soil), root type (absorptive or transport), tree species (oak or maple), and their interactions on measured response variables. A second ANOVA model was used to test the effects of treatment, tree species, sample date, and their interactions on specific and ecosystem root respiration. Per plot replicates were averaged to obtain one plot measure for each response variable sampled. All model assumptions of the ANOVA were evaluated, and a square root transformation of variables was used to improve model fit when ANOVA model assumptions failed. Additional post hoc comparisons were made between groups by using Tukey's honest significant difference test using the "emmeans" package in R (R Core Team 2022). Finally, we performed Pearson's correlations for each treatment to test the relationship between soil temperature and mass-specific root respiration rates. Soil temperature data were obtained from Knorr et al. (2024). We also tested the relationship between biotic (absorptive root biomass, mycorrhizal colonization, biomass, and respiration rates) and soil nutrient availability. In all cases, we assessed significance at $\alpha = 0.05$ and reported any significant relationships.

3 | Results

Total fine root biomass across the soil profile was significantly reduced when soils were heated, regardless of N fertilization status (Figure 1). This result was driven by a significant interaction between heat × sample depth ($p = 0.011$; Table S1) such that total fine root biomass in the organic horizon was 45% lower in heated relative to control plots (Figure S1). Additionally, the depth of the organic horizon significantly decreased with warming (Table S5) and was the only edaphic property to vary between treatments, reducing the total volume available for roots in the organic horizon of heated plots.

We observed a significant interaction between heat × root functional type ($p < 0.0001$; Table S1). This was driven by a decline in total transport root biomass in all heated plots (heated and heated × N) relative to the control and N-only treatments (Figure 2). In contrast, total absorptive root biomass was not significantly altered. Transport root biomass was significantly greater than absorptive root biomass in control and N addition treatments; however, absorptive root biomass was equal to the transport root biomass in all heated plots (Figure 2; heated-only and heated × N). These overall patterns were driven by changes in the organic horizon which contained more than half of absorptive (55%–68%) and transport (49%–53%) fine root biomass ($p < 0.0001$; Figure S2). Thus, more root biomass is stored as transport fine roots under ambient temperature conditions (i.e., control and N addition treatments). When heat is added to the

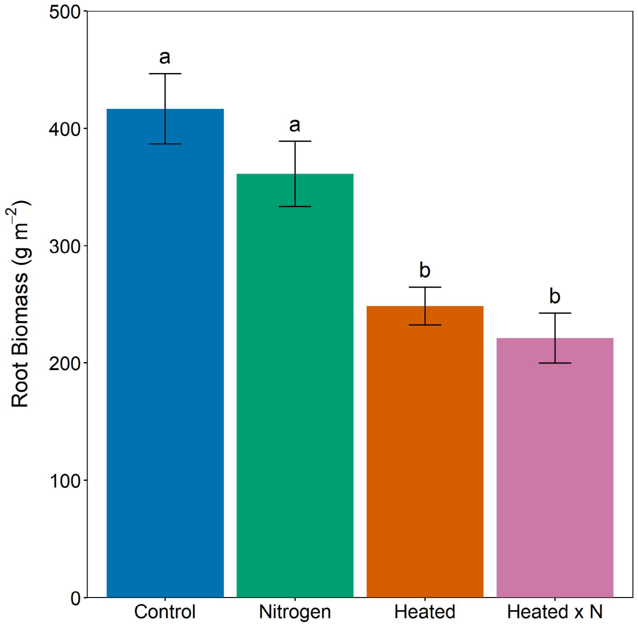

FIGURE 1 | Total fine root biomass in response to N addition (Nitrogen), soil warming (Heated), or their combination (Heated × N). Total root biomass is the sum of absorptive and transport roots across the depths sampled (organic horizon, 0–10 and 10–20 cm of mineral soil). Different letters indicate significant differences across treatments ($\alpha < 0.05$). Reported values represent the mean ± one standard error.

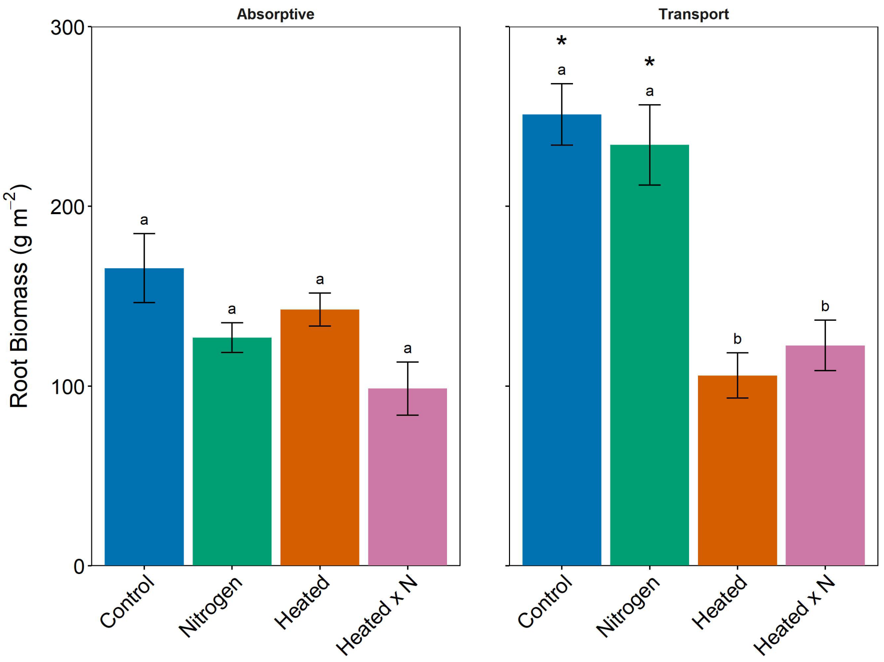

FIGURE 2 | Absorptive and transport root biomass in response to N addition (Nitrogen), soil warming (Heated), or their combination (Heated × N). Absorptive and transport root biomass is the sum of each functional root class (absorptive vs. transport) across the depths sampled (organic horizon, 0–10 and 10–20 cm of mineral soil). Different letters indicate significant differences across treatments, whereas an asterisk (*) indicates significant differences between root types within a treatment ($\alpha < 0.05$). Reported values represent the mean ± one standard error.

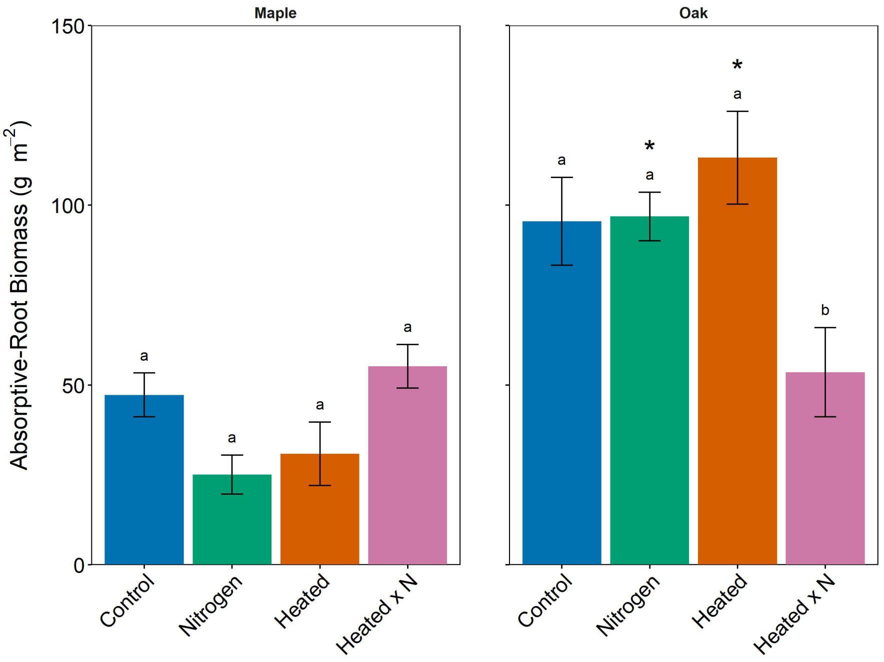

FIGURE 3 | Absorptive root biomass of maple (AM) versus oak (EM) trees in response to N addition (Nitrogen), soil warming (Heated), or their combination (Heated × N). Absorptive and root biomass maple and oak is the sum of each root species (maple vs. oak) across the depths sampled (organic horizon, 0–10 and 10–20 cm of mineral soil). Letters indicate significant differences between treatments and tree species, whereas an asterisk (*) indicates significant differences between tree species within a treatment ($\alpha < 0.05$). Reported values represent the mean ± one standard error.

system, a greater proportion of fine root biomass is allocated to absorptive roots at the cost of decreased transport root biomass.

The overall lack of change in the absorptive root biomass fraction was due to the differential effects of heat and N addition on the two predominant tree species (oak vs. maple). There was a significant depth × tree species interaction ($p < 0.0001$; Table S2) such that the majority of oak absorptive root biomass was found in the organic horizon (67%–88%), whereas greater than half of the maple root biomass (45%–64%) was found in the mineral soil layers (Figure S2). We observed a three-way interaction between heat × N addition × species indicating a restructuring of species composition of absorptive root systems ($p < 0.0001$; Figure 3, Table S2). Under control conditions, oak and maple trees maintained equal root biomass ($p = 0.1128$). This was reversed in the single-factor treatments (Figure 3) whereby the heated or N addition-only treatments had greater oak root biomass relative to maple root biomass ($p < 0.0001$; Figure 3). However, when heat and N addition were applied simultaneously, oak root biomass significantly decreased such that the combination treatment (heated × N) stored equal amounts of oak and maple absorptive fine roots ($p = 0.2830$). Taken together, oak absorptive root biomass is maintained or enhanced under heat or N additions only. However, the combination of heat and N simultaneously interact to decrease oak root biomass while increasing the proportion of maple root biomass.

Metrics of mycorrhizal associations varied between treatments and tree species. There was a significant interaction between heat and N addition on EM root tip colonization rates ($p < 0.0001$), with EM colonization declining in response to the single-factor treatments (heat or N only). In contrast, the combination treatment (heated × N) returned EM colonization rates to control levels (Figure 4a). AM fungal biomass was unaffected by heat or N addition alone, but their combination (heated × N) led to a significant decrease in AM fungal biomass relative to the control (Figure 4b). We observed a significant positive correlation between maple absorptive root biomass and EM root tip colonization rates (Figure S4; $p = 0.0017$, $r^2 = 0.38$).

Finally, we observed changes in mass-specific and ecosystem fine-root respiration that were mediated by tree species. Maple roots had greater respiration rates compared to oak roots ($p = 0.001$; Table 1, Table S3). For both tree species, there was a significant interaction between heat and N addition ($p = 0.0002$) such that specific root respiration was significantly reduced by warming relative to the control and heated × N treatments. Similarly, root N content was significantly reduced in single-factor treatments but only compared to roots found in heated × N (Figure S3). Root N content was not significantly correlated with specific root respiration rates ($p = 0.0716$). Sampling date significantly influenced mass-specific root respiration, with the greatest rates occurring during the summer (June–August). However, we did not observe a significant interaction between sample date and treatments ($p = 0.6660$). The separation between the heated and heated × N treatment was apparent throughout the duration of the study (Figure 5a, $p < 0.0001$). There was a significant positive relationship between soil temperature and mass-specific root respiration rates that was apparent in the heated (Figure 5b, $p = 0.0388$) and heated × N plots ($p = 0.0174$), although these relationships have low predictive power ($R^2 = 0.08$).

We scaled mass-specific respiration to the ecosystem level by accounting for the relative biomass of maple and oak absorptive fine roots within each plot. The cumulative contribution of ecosystem fine-root respiration from maple and oak tree roots in control plots was 50.4 mg CO_2-C $g^{-1}\,m^{-2}\,h^{-1}$ (Table 1). Ecosystem root respiration was reduced by 40% in both heated-only and N-only treatments. There was a significant interaction between heat × N addition × species ($p = 0.0177$; Table S3) that returned ecosystem root respiration to control conditions in the combination treatment (heated × N). Absorptive root respiration of oak roots accounted for over 60% of ecosystem root respiration ($p < 0.0001$; Table S3). For both tree species, ecosystem root respiration was reduced in the single-factor treatments (heat or N addition alone), although this was most pronounced in the maple roots (Table 1) which accounted for 60% of the reduction in CO_2 flux from roots.

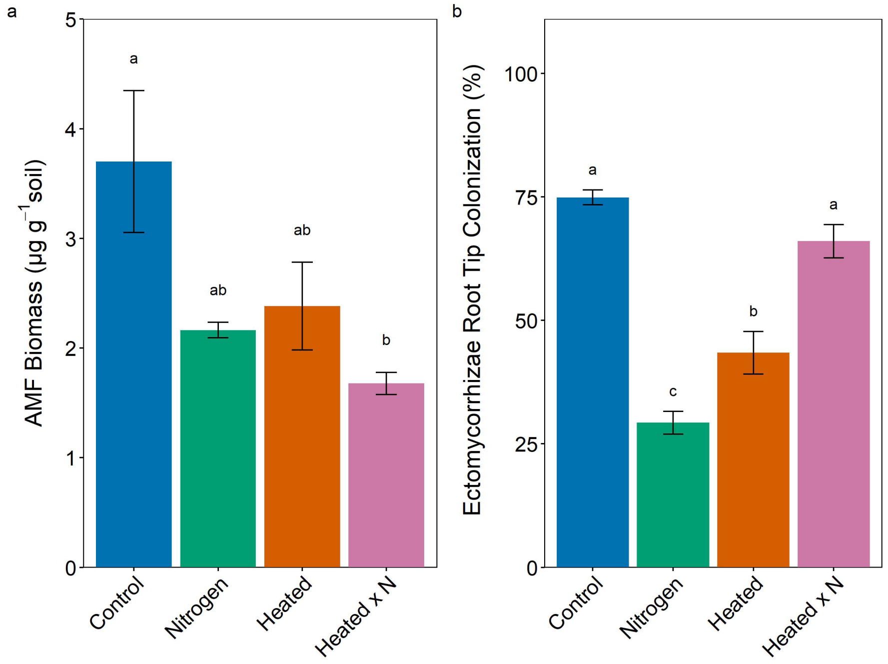

FIGURE 4 | Effects of N addition (Nitrogen), soil warming (Heated), or their combination (Heated × N). (a) Arbuscular mycorrhizal fungal (AMF) biomass assessed via phospholipid fatty acid (PLFA) analysis, and (b) ectomycorrhizal colonization rates. Letters indicate significant differences between treatments ($\alpha < 0.05$). Reported values represent the mean ± one standard error.

TABLE 1 | Mass-specific and ecosystem root respiration rates for maple and oak trees. Total ecosystem root respiration rates represent the sum of maple and oak ecosystem root respiration. Significant differences ($\alpha < 0.05$) between treatments are indicated by different letters. Reported values represent the mean ± one standard deviation.

	Mass-specific root respiration ($\mathrm{nmol\ CO_2\ g^{-1}\ s^{-1}}$)		Ecosystem root respiration ($\mathrm{mg\ CO_2\text{-}C\ m^{-2}\ h^{-1}}$)		
Treatment	**Maple**	**Oak**	**Maple**	**Oak**	**Total**
Control	15.9 ± 7.2 a	12.1 ± 6.7 a	15.8 ± 15.1 a	34.6 ± 24.7 a	50.4 ± 39.8 a
Nitrogen	14.0 ± 6.6 ab	10.5 ± 5.7 ab	5.6 ± 3.8 b	24.7 ± 14.4 a	30.3 ± 18.2 b
Heated	11.2 ± 7.0 b	8.3 ± 4.4 b	5.4 ± 7.36 b	24.6 ± 15.1 a	30.0 ± 22.7 b
Heated × N	16.0 ± 14.6 a	13.7 ± 7.5 a	16.3 ± 16.8 a	28.9 ± 22.7 a	45.2 ± 39.4 ab

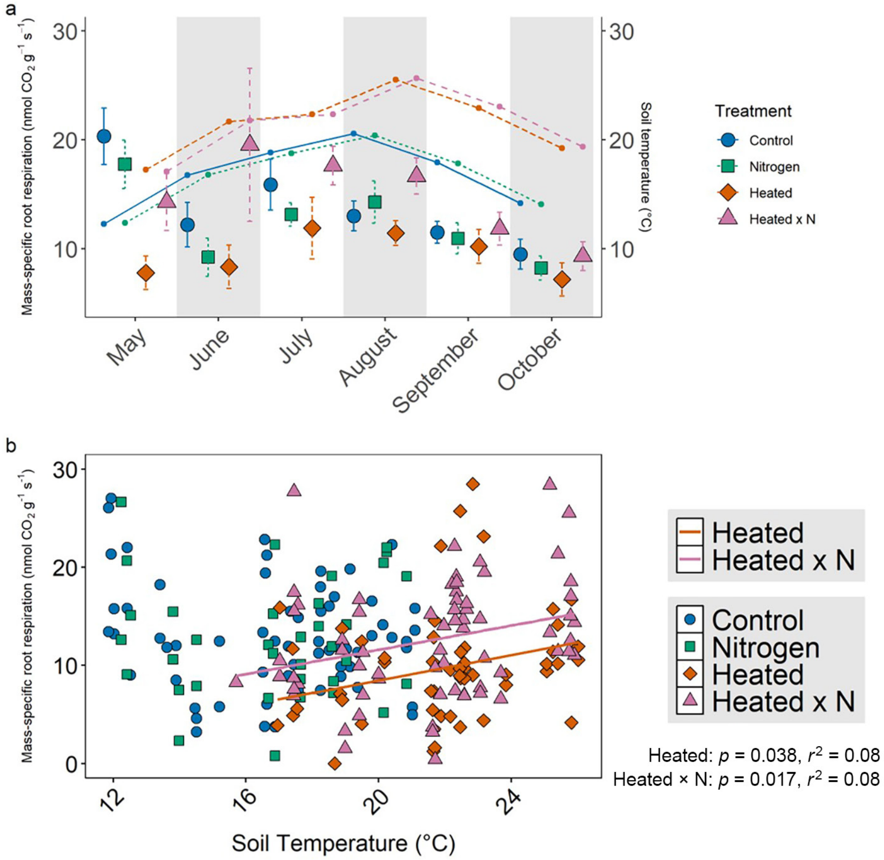

FIGURE 5 | Mass-specific root respiration over the growing season and its relationship with soil temperature. (a) Temporal dynamics of mass-specific root respiration between May and October (points) and average soil temperature in unwarmed and warmed plots (lines). *p*-values indicate the effects of sample date, treatment, and their interaction on mass-specific root respiration rates. Reported values represent the mean ± one standard error. (b) Relationships between soil temperature and mass-specific root respiration rates over the duration of the growing season by treatment. *p*-values indicate the significance of the relationship between soil temperature and root respiration.

4 | Discussion

Fine roots of trees make up 40%–60% of total soil respiration, yet the extent to which global change factors can interactively affect root respiration and ecosystem C fluxes is poorly understood. In this study, we showed that soil warming significantly reduced root biomass due to the loss of transport roots. Although absorptive root biomass remained stable, there was a treatment × species interaction where the single-factor treatments supported greater oak absorptive root biomass while their combination (heated × N) was not significantly different from control levels. Consistent with previous studies (Jarvi and Burton 2013, 2020; Tunison et al. 2024; Zogg et al. 1996), we found that mass-specific respiration rates were significantly reduced when soils were warmed. However, we show that when N is added to warmed soils (heated × N), a synergistic interaction occurs (Table S4), returning fine-root respiration to control levels. This was attributed to two key factors: (1) an interaction between treatment × species on root biomass allocation, and (2) the mitigation of the warming effect on specific root respiration. Our results only partially supported our hypothesis that the plant root component of respiration would be significantly enhanced under simultaneous warming and N addition, exacerbating the temperature sensitivity of soil respiration. Instead, maple root respiration in the heated × N treatment was significantly greater than warming alone, partially helping to explain the elevated respiration found in the combination treatment at our site (Knorr et al. 2024). Our results demonstrate that the interactions among global change factors yield species-specific ecosystem responses that are unique to those found in isolation (i.e., warming or N addition alone).

We observed stable fine root biomass under N addition and decreased fine root biomass under warming (Figure 1). Previous research at our field site found increased NH_4^+ concentrations in N addition plots and increased N mineralization rates in heated plots, which also increased inorganic N concentrations (Contosta, Frey, and Cooper 2011). In temperate forests, N limitation of plant growth can be alleviated by N addition (Aber et al. 1998; Magill et al. 2000; Nadelhoffer, Aber, and Melillo 1985; Nadelhoffer and Raich 1992) or soil warming (Dawes et al. 2017). In our study, the decrease in fine root biomass was driven by the main effect of heat on transport fine roots (Figure 2), which aligns with a previous study that reported that transport (but not absorptive) roots decreased under warming (Parts et al. 2019). In contrast to previous studies (W. Li et al. 2015), we found no effect of N addition on fine root biomass, indicating that increased N availability due to long-term warming may not be an important factor controlling standing root biomass. However, because we did not measure fine root production and turnover, it is unclear whether overall belowground C allocation changed. While both N addition (X. Li et al. 2021; Nadelhoffer 2000; Nadelhoffer, Aber, and Melillo 1985) and warming (Kwatcho Kengdo et al. 2022; Majdi and Öhrvik 2004) can increase fine root growth by alleviating N limitation, soil warming also introduces other stresses that may increase root mortality, including water stress, embolism (Sperry, Stiller, and Hacke 2002; Wang et al. 2021), and exposure to freeze–thaw cycles (Sanders-DeMott et al. 2018). At the time of our root sampling, no differences in soil moisture content or soil nutrient availability were observed (Table S5). However, a nearby soil warming experiment demonstrated a reduced capacity of soils to maintain moisture (Werner, Sanderman, and Melillo 2020), suggesting that water stress in our plots may have gone undetected. Increased mortality associated with warming would be more apparent in long-lived transport fine roots (> 8 years) compared to absorptive roots (0–1.5 years) and would affect overall patterns of belowground C flux. Evaluating fine root production and mortality could address these gaps and refine our understanding of root dynamics on soil C in the context of global change factors.

The lack of change in total absorptive fine root biomass across treatments in our study resulted from contrasting responses of maple and oak absorptive roots to N addition and warming (Figure 3), potentially due to differences in the suite of belowground traits these trees use to acquire soil N (Bergmann et al. 2020; Cheng et al. 2016; Phillips, Brzostek, and Midgley 2013). Belowground nutrient acquisition strategies of oaks rely on the slow mineralization of soil organic N that can be accessed by some EM fungi, along with the suppression of saprotrophs (Van Nuland et al. 2023). In contrast, nutrient acquisition of maples favors scavenging N mineralized by other soil microbes (Chen et al. 2016; Chen, Koide, and Eissenstat 2018). We observed a strong influence of N addition and warming on the root biomass of oak. Under the single-factor treatments in our study (N addition or warming alone), the biomass of oak absorptive roots increased at the expense of maple absorptive roots (Figure 3). Enhanced oak root biomass under warming may signal belowground overyielding of oak trees to compensate for greater N competition with maple (Schuster et al. 2022; Valverde-Barrantes et al. 2015). At the same time, EM fungal colonization of oak roots was significantly reduced in the single-factor treatments. The competition between oaks and maples is highlighted in the relationship between maple absorptive root biomass and EM colonization rate on oak roots (Figure S4; $p = 0.0017$, $r^2 = 0.38$). Thus, oak may increase fine root biomass as an inorganic N acquisition mechanism while reducing EM fungal colonization, owing to absorptive root efficiency in scavenging inorganic N mineralized by other soil microbes (Cheng et al. 2016). The absence of a similar response in maple suggests less responsiveness to N addition and soil warming, at least in terms of fine root biomass. The simultaneous increase in microbial activity (DeAngelis et al. 2015; J. Li et al. 2019; Pold, Melillo, and DeAngelis 2015; Pold et al. 2017), shifts in saprotrophic fungal community composition (Anthony et al. 2021; Pec et al. 2021), and enhanced N mineralization rates (Contosta, Frey, and Cooper 2011) in response to long-term soil warming at our study site likely enhance soil inorganic N sufficiently to alleviate N demand for maple trees while imposing greater N competition on oak trees as their nutrient acquisition strategy become less efficient under enhanced soil inorganic N availability.

We observed a general pattern of declining mycorrhizal biomass and colonization in single-factor treatments but a mycorrhizal type-specific response under their combination (Figure 4). This aligns with prior research indicating that soil inorganic N enrichment can reduce mycorrhizal fungal biomass (Lilleskov et al. 2019; Suz et al. 2021) and alter community composition (Anthony et al. 2021; Frey et al. 2004; Morrison et al. 2016; Pec et al. 2021). The mechanisms behind this response include the direct effect of N on fungal growth (Morrison et al. 2018), indirect effects through changes in host plant physiology (Fleischer et al. 2013; Magill et al. 2000) or localized changes in soil chemistry (Grandy et al. 2008; Magill et al. 1997). For example, elevated levels of available N can reduce plant reliance on mycorrhizal fungi for nutrient acquisition (Brzostek, Fisher, and Phillips 2014), thereby diminishing the C allocated to these fungi. Interestingly, the addition of N to warmed soils further reduced AM fungal biomass but returned EM colonization rates back to control levels (Figure 4). The contrasting response of AM and EM fungi to the combination treatment may be due to the affinity these differing mycorrhizal fungi have for high levels of inorganic nutrients (Ma et al. 2021). Although the heated × N treatment increased colonization back to control levels, previous research at our site documented that EM fungal communities are less diverse in the heated × N plots compared to the control (Anthony et al. 2021). Thus, the differential shifts in belowground nutrient acquisition strategies of maple versus oak observed in our study may reflect broader ecological patterns between trees and their associated mycorrhizal fungal partners in response to global change factors.

Our study identified a reduction in mass-specific root respiration that mitigates the increase in oak fine root biomass in warmed plots. Specifically, we observed that mass-specific respiration decreased under warming but returned to control levels when N was applied simultaneously, regardless of tree species. This pattern was consistent across the months when root respiration was sampled (Figure 5a). The reduction in respiration under warming, contrary to expectations of increased respiration due to temperature sensitivity (Tjoelker, Oleksyn, and Reich 2001), may be attributed to long-term thermal acclimation (Sun et al. 2023; Tjoelker 2018). Over time, root metabolic processes may adjust to maintain efficiency at elevated temperatures, resulting in downregulated respiration rates despite higher soil temperatures. This response aligns with previous findings of acclimation of root respiration in response to soil warming (Burton, Melillo, and Frey 2008; Jarvi and Burton 2013, 2020; Wang et al. 2021), where the root-level metabolic response was observed not to be species specific (Jarvi and Burton 2018). Thermal acclimation may help prevent excessive C loss from roots in heated plots, as indicated by a weak but positive relationship between soil temperature and mass-specific root respiration in heated plots (Figure 5b). However, the relationship suggests that while acclimation has occurred, further temperature increases could still elevate CO_2 emissions from roots.

Interestingly, the observed respiratory acclimation was alleviated when N was added to warmed soils. We hypothesize that this may be due to interactions with mycorrhizal fungi, as EM colonization rates declined under both N addition and warming but were comparable to control levels when both factors were applied together. The higher respiratory costs in the control and heated × N treatments could reflect a greater demand for nutrient acquisition compared to the single-factor treatments. Additionally, the pattern of root respiration mirrored root N concentrations, which in the heated × N combination treatment was not significantly different from the control, but higher than in either single-factor treatment. Since root N content has been shown to be positively correlated with respiration (Burton et al. 2002; Han and Zhu 2021; Pregitzer et al. 1998), this relationship could explain the alleviation of acclimation in the combined treatment. However, because roots used for respiration and N measurements were collected at different times, their relationship was not fully captured as we did not find a strong relationship between the two ($p = 0.0716$, $r^2 = 0.22$).

After scaling up from root- to ecosystem root respiration (by accounting for the respective biomass of maple and oak absorptive roots in each treatment), we found a decrease in ecosystem fine-root respiration for both the N addition and warming single-factor treatments (Table 1). In the present study, we anticipated that increased N availability due to both N addition and warming would lead oak trees to increase fine root biomass, potentially increasing ecosystem root respiration. Indeed, oak fine root biomass significantly increased relative to maple roots under N addition and warming. Nevertheless, the observed physiological reduction in mass-specific root respiration in oak was sufficient to offset the expected increase in ecosystem-level respiration, leading to no significant differences in ecosystem respiration despite the rise in absorptive root biomass. Contrary to our expectations, the largest increase in root respiration was due to the proliferation of maple roots in the combination treatment (heated × N plots). Because maple roots had greater mass-specific respiration rates, a smaller change in maple root biomass yielded a proportionally larger effect when scaled to the ecosystem level relative to the contribution of oak roots. Both the relative biomasses of maple and oak roots and the acclimation of mass-specific respiration rates that constrained ecosystem root respiration in single-factor treatments were ameliorated when N was applied simultaneously to heated soils, thus returning ecosystem root respiration to control levels in the combination treatment (Table 1).

We acknowledge that our root respiration measurements, particularly after excising, sorting, and cleaning roots, may have introduced variability in respiration rates. This potential alteration of respiration rates, along with the extrapolation of measured rates to the ecosystem level, presents a limitation of our study. To contextualize our findings, we compared our estimates of fine root respiration with previously published ecosystem soil respiration measurements made at our study site. Total soil respiration under control conditions is estimated to be 125–156 mg CO_2-C m^{-2} h^{-1} (Contosta, Frey, and Cooper 2011; Knorr et al. 2024). Nitrogen addition decreased soil respiration by 4%, whereas warming increased it by 15%. Using our measures of ecosystem root respiration (Table 1), we estimate that the relative contribution of roots to total soil respiration is approximately 32% in control plots, while being 16%, 25%, and 24% in the N addition, heated, and heated × N plots, respectively. Our estimates of the root contribution to total soil respiration in control plots align closely with earlier estimates taken under ambient conditions at Harvard Forest where it was determined that roots accounted for 33% of total soil respiration in a deciduous forest stand (Bowden et al. 1993). Likewise, root respiration composed 26% of soil respiration under ambient conditions, decreasing to 17% in the heated plots of a single-factor soil warming experiment at Harvard Forest (Melillo et al. 2011).

To assess the potential influence of plot size on our results, we compared our data with those collected the same year at a nearby soil warming experiment consisting of 900 m^2 plots that encompass entire trees and where soils had been warmed for 20 years at the time of sample collection (Chari et al. 2024). Observations from the two experiments (small vs. large plots) are comparable, with both studies showing a decrease in fine root biomass under warming driven by a maple-specific reduction in absorptive roots. Ecosystem root respiration in the larger plots was 73.3 and 50.2 mg CO_2-C m^{-2} h^{-1} in the control and warmed treatments, respectively, consistent with previous data from this experiment (Melillo et al. 2011) and a similar reduction in response to warming (Table 1). Thus, our findings, reinforced by both previous and new estimates of root respiration at Harvard Forest, validate the reliability of our small plots in capturing the nuanced dynamics of root changes under global change scenarios.

The similarity between root respiration measurements across plot size and experiment may be more closely associated with an individual root trait rather than tree responses (Paradiso, Jevon, and Matthes 2019). Under ambient conditions, roots are exposed to spatially variable pressures that shape overall tree nutrient foraging. Thus, our small plots distributed across the forest floor are consistent with the patchy nutrients and abiotic gradients already imposed on tree roots. Numerous studies demonstrate that leaf litter or fertilizer additions, even at the spatial scale of ingrowth cores or root bags, affect root foraging traits independent of aboveground tree changes (Adams, McCormack, and Eissenstat 2013; Caplan et al. 2017; Chen et al. 2016; Cheng et al. 2016; Eissenstat et al. 2015; Liu et al. 2015). For example, specific root respiration in stands at Harvard Forest was shown to be more closely associated with localized root traits than tree species identity (Paradiso, Jevon, and Matthes 2019), suggesting that shifts in root traits to localized conditions drive root respiratory responses. Furthermore, a meta-analysis of root trait responses to warming (Wang et al. 2021) and N addition (W. Li et al. 2015; Ma et al. 2021) documented consistent patterns across various experimental designs, including both large and small plots.

While our results provide strong evidence that N addition and soil warming influence root respiration, it is important to recognize that nutrient availability and C assimilation are complex processes. In plant physiology, nutrient availability influences photosynthesis, which, in turn, impacts C transport from source organs (leaves) to sink organs (roots) (Bloom et al. 2010; Paul and Foyer 2001). However, C allocation to roots can also be regulated by internal plant mechanisms that may not always align with nutrient levels in the soil (Keller and Phillips 2019). This raises the possibility of decoupling between soil nutrient availability and C substrate allocation to roots (Ehtesham and Bengtson 2017). Such decoupling has been observed when plants prioritize stress responses or when internal hormonal signals override external nutrient conditions (J. A. Savage et al. 2016; Smith and Stitt 2007), and this could be especially relevant in global change scenarios. For example, plants under nutrient stress may allocate more C to root growth to enhance nutrient acquisition, but this can reduce C availability for root respiration (Bloom, Chapin III, and Mooney 1985; Poorter and Nagel 2000). This suggests that substrate availability for root respiration may not be directly tied to soil nutrient conditions but may instead reflect a combination of internal plant responses, root–microbe interactions, and environmental conditions. The decoupling between soil nutrients and root respiration may help explain why we did not observe significant correlations between soil nutrients and root respiration. Overall, these dynamics highlight the uncertainty in predicting root respiration solely based on soil conditions. Simultaneously, evaluating photosynthetic rates, plant growth, and root respiration across environmental conditions could address these gaps in source-sink dynamics and improve our understanding of the exchange of C between the atmosphere and soil.

5 | Conclusion and Future Directions

Our study aimed to more fully understand the soil C response to global change by addressing the uncertainty of root contributions to soil CO_2 flux. We do not know the true magnitude of soil feedback on the climate system because root contributions to respiration have been overlooked. The observations made in our study, alongside previous research at our site, reveal that the temperature sensitivity of soil respiration depends on the availability of N and is mediated by root–microbe–soil interactions. For instance, 16 years of data from our site suggest that soil warming leads to a loss of soil organic C while increasing soil respiration (Knorr et al. 2024). In contrast, N enrichment suppresses soil respiration, resulting in a gain in soil organic C. Combining warming and N enrichment results in soil respiration rates that are 1.6 times greater than warming alone but elicit no change in soil organic C (Knorr et al. 2024) suggesting that the autotrophic component of respiration and/or fresh plant C inputs in the heated × N treatment is greater than warming alone. Our results indicate that root respiration is reduced in single-factor treatments but returns to control levels when in combination (heated × N). As such, the root component of soil respiration is partially responsible for the increase in total soil respiration observed in combination treatment at our site. Taken together, the additive effects of root and microbial respiration in heated × N on total soil respiration are far greater than those observed under warming alone.

Despite the increased total soil respiration observed with simultaneous warming and N addition, soil organic C stocks remained unchanged (Knorr et al. 2024), suggesting that root-derived inputs may offset C losses. However, the mechanisms behind this balance remain poorly understood, particularly the role of root–microbe interactions specific to different tree species (e.g., maple vs. oak) in regulating soil organic matter formation and turnover. This uncertainty highlights the need to investigate how species-specific interactions contribute to soil C stabilization under global change. In particular, understanding how root inputs from maple or oak contribute to soil C stocks, even as respiration rates increase. Clarifying this balance is essential, as the relationship between soil C sequestration and atmospheric C release will determine the net carbon flux between these major C sinks under warming and N addition.

Author Contributions

T. J. Muratore: conceptualization, formal analysis, investigation, methodology, validation, visualization, writing – original draft, writing – review and editing. **M. A. Knorr:** investigation, supervision, writing – review and editing. **M. J. Simpson:** investigation, methodology, writing – review and editing. **R. B. Stephens:** methodology, visualization, writing – review and editing. **R. P. Phillips:** validation, visualization, writing – review and editing. **S. D. Frey:** funding acquisition, methodology, project administration, resources, supervision, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in the Harvard Forest Data Archive at https://harvardforest1.fas.harvard.edu/exist/apps/datasets/showData.html?id=HF045.

References

Aber, J. D., W. McDowell, K. Nadelhoffer, et al. 1998. "Nitrogen Saturation in Temperate Forest Ecosystems: Hypotheses Revisited." *Bioscience* 48, no. 11: 921–934. https://doi.org/10.2307/1313296.

Adams, T. S., M. L. McCormack, and D. M. Eissenstat. 2013. "Foraging Strategies in Trees of Different Root Morphology: The Role of Root Lifespan." *Tree Physiology* 33, no. 9: 940–948. https://doi.org/10.1093/treephys/tpt067.

Agerer, R. 2001. "Exploration Types of Ectomycorrhizae." *Mycorrhiza* 11, no. 2: 107–114. https://doi.org/10.1007/s005720100108.

Anthony, M. A., M. Knorr, J. A. M. Moore, M. Simpson, and S. D. Frey. 2021. "Fungal Community and Functional Responses to Soil Warming Are Greater Than for Soil Nitrogen Enrichment." *Elementa: Science of the Anthropocene* 9, no. 1: 000059. https://doi.org/10.1525/elementa.2021.000059.

Bai, E., S. Li, W. Xu, W. Li, W. Dai, and P. Jiang. 2013. "A Meta-Analysis of Experimental Warming Effects on Terrestrial Nitrogen Pools and Dynamics." *New Phytologist* 199, no. 2: 441–451. https://doi.org/10.1111/nph.12252.

Bai, T., P. Wang, Y. Qiu, Y. Zhang, and S. Hu. 2023. "Nitrogen Availability Mediates Soil Carbon Cycling Response to Climate Warming: A Meta-Analysis." *Global Change Biology* 29, no. 9: 2608–2626. https://doi.org/10.1111/gcb.16627.

Bergmann, J., A. Weigelt, F. van der Plas, et al. 2020. "The Fungal Collaboration Gradient Dominates the Root Economics Space in Plants." *Science Advances* 6, no. 27: eaba3756. https://doi.org/10.1126/sciadv.aba3756.

Bloom, A. J., M. Burger, J. S. R. Asensio, and A. B. Cousins. 2010. "Carbon Dioxide Enrichment Inhibits Nitrate Assimilation in Wheat and Arabidopsis." *Science* 328, no. 5980: 899–903. https://doi.org/10.1126/science.1186440.

Bloom, A. J., and R. M. Caldwell. 1988. "Root Excision Decreases Nutrient Absorption and Gas Fluxes 1." *Plant Physiology* 87, no. 4: 794–796.

Bloom, A. J., F. S. Chapin III, and H. A. Mooney. 1985. "Resource Limitation in Plants-An Economic Analogy." *Annual Review of Ecology, Evolution, and Systematics* 16: 363–392. https://doi.org/10.1146/annurev.es.16.110185.002051.

Boose, E., and E. Gould. 2021. *Harvard Forest Climate Data Since 1964 ver 3*. Environmental Data Initiative. https://doi.org/10.6073/PASTA/305455801DB84257FD4A5FBDB1350BD6 (Accessed (2024).

Bowden, R. D., E. Davidson, K. Savage, C. Arabia, and P. Steudler. 2004. "Chronic Nitrogen Additions Reduce Total Soil Respiration and Microbial Respiration in Temperate Forest Soils at the Harvard Forest." *Forest Ecology and Management* 196, no. 1: 43–56. https://doi.org/10.1016/j.foreco.2004.03.011.

Bowden, R. D., K. J. Nadelhoffer, R. D. Boone, J. M. Melillo, and J. B. Garrison. 1993. "Contributions of Aboveground Litter, Belowground Litter, and Root Respiration to Total Soil Respiration in a Temperate Mixed Hardwood Forest." *Canadian Journal of Forest Research* 23, no. 7: 1402–1407. https://doi.org/10.1139/x93-177.

Brzostek, E. R., J. B. Fisher, and R. P. Phillips. 2014. "Modeling the Carbon Cost of Plant Nitrogen Acquisition: Mycorrhizal Trade-Offs and Multipath Resistance Uptake Improve Predictions of Retranslocation." *Journal of Geophysical Research: Biogeosciences* 119, no. 8: 1684–1697. https://doi.org/10.1002/2014JG002660.

Burton, A. J., J. M. Melillo, and S. D. Frey. 2008. "Adjustment of Forest Ecosystem Root Respiration as Temperature Warms." *Journal of Integrative Plant Biology* 50, no. 11: 1467–1483. https://doi.org/10.1111/j.1744-7909.2008.00750.x.

Burton, A. J., K. Pregitzer, R. Ruess, R. Hendrick, and M. Allen. 2002. "Root Respiration in North American Forests: Effects of Nitrogen Concentration and Temperature Across Biomes." *Oecologia* 131, no. 4: 559–568. https://doi.org/10.1007/s00442-002-0931-7.

Butler, S. M., J. M. Melillo, J. E. Johnson, et al. 2012. "Soil Warming Alters Nitrogen Cycling in a New England Forest: Implications for Ecosystem Function and Structure." *Oecologia* 168, no. 3: 819–828. https://doi.org/10.1007/s00442-011-2133-7.

Caplan, J. S., B. W. G. Stone, C. A. Faillace, et al. 2017. "Nutrient Foraging Strategies Are Associated With Productivity and Population Growth in Forest Shrubs." *Annals of Botany* 119, no. 6: 977–988. https://doi.org/10.1093/aob/mcw271.

Chari, N., T. J. Muratore, S. Frey, and B. Taylor. 2024. "Long-Term Soil Warming Drives Different Belowground Responses in Arbuscular Mycorrhizal and Ectomycorrhizal Trees." *Global Change Biology* 30, e17550. https://doi.org/10.1111/gcb.17550.

Chen, W., R. T. Koide, T. S. Adams, J. L. DeForest, L. Cheng, and D. M. Eissenstat. 2016. "Root Morphology and Mycorrhizal Symbioses Together Shape Nutrient Foraging Strategies of Temperate Trees." *Proceedings of the National Academy of Sciences of the United States of America* 113, no. 31: 8741–8746. https://doi.org/10.1073/pnas.1601006113.

Chen, W., R. T. Koide, and D. M. Eissenstat. 2018. "Nutrient Foraging by Mycorrhizas: From Species Functional Traits to Ecosystem Processes." *Functional Ecology* 32, no. 4: 858–869. https://doi.org/10.1111/1365-2435.13041.

Cheng, L., W. Chen, T. S. Adams, et al. 2016. "Mycorrhizal Fungi and Roots Are Complementary in Foraging Within Nutrient Patches." *Ecology* 97, no. 10: 2815–2823. https://doi.org/10.1002/ecy.1514.

Contosta, A. R., S. D. Frey, and A. B. Cooper. 2011. "Seasonal Dynamics of Soil Respiration and N Mineralization in Chronically Warmed and Fertilized Soils." *Ecosphere* 2, no. 3: art36. https://doi.org/10.1890/ES10-00133.1.

Dawes, M. A., P. Schleppi, S. Hättenschwiler, C. Rixen, and F. Hagedorn. 2017. "Soil Warming Opens the Nitrogen Cycle at the Alpine Treeline." *Global Change Biology* 23, no. 1: 421–434. https://doi.org/10.1111/gcb.13365.

DeAngelis, K. M., G. Pold, B. D. Topçuoğlu, et al. 2015. "Long-Term Forest Soil Warming Alters Microbial Communities in Temperate Forest Soils." *Frontiers in Microbiology* 6: 104. https://doi.org/10.3389/fmicb.2015.00104.

Ehtesham, E., and P. Bengtson. 2017. "Decoupling of Soil Carbon and Nitrogen Turnover Partly Explains Increased Net Ecosystem Production in Response to Nitrogen Fertilization." *Scientific Reports* 7, no. 1: 46286. https://doi.org/10.1038/srep46286.

Eissenstat, D. M., J. M. Kucharski, M. Zadworny, T. S. Adams, and R. T. Koide. 2015. "Linking Root Traits to Nutrient Foraging in Arbuscular Mycorrhizal Trees in a Temperate Forest." *New Phytologist* 208, no. 1: 114–124. https://doi.org/10.1111/nph.13451.

Finzi, A. C., M.-A. Giasson, A. A. Barker Plotkin, et al. 2020. "Carbon Budget of the Harvard Forest Long-Term Ecological Research

Site: Pattern, Process, and Response to Global Change." *Ecological Monographs* 90, no. 4: e01423. https://doi.org/10.1002/ecm.1423.

Fleischer, K., K. T. Rebel, M. K. van der Molen, et al. 2013. "The Contribution of Nitrogen Deposition to the Photosynthetic Capacity of Forests." *Global Biogeochemical Cycles* 27, no. 1: 187–199. https://doi.org/10.1002/gbc.20026.

Freschet, G. T., and C. Roumet. 2017. "Sampling Roots to Capture Plant and Soil Functions." *Functional Ecology* 31, no. 8: 1506–1518. https://doi.org/10.1111/1365-2435.12883.

Frey, S. D., M. Knorr, J. L. Parrent, and R. T. Simpson. 2004. "Chronic Nitrogen Enrichment Affects the Structure and Function of the Soil Microbial Community in Temperate Hardwood and Pine Forests." *Forest Ecology and Management* 196, no. 1: 159–171. https://doi.org/10.1016/j.foreco.2004.03.018.

Frey, S. D., S. Ollinger, K. Nadelhoffer, et al. 2014. "Chronic Nitrogen Additions Suppress Decomposition and Sequester Soil Carbon in Temperate Forests." *Biogeochemistry* 121, no. 2: 305–316. https://doi.org/10.1007/s10533-014-0004-0.

Grandy, A. S., R. L. Sinsabaugh, J. C. Neff, M. Stursova, and D. R. Zak. 2008. "Nitrogen Deposition Effects on Soil Organic Matter Chemistry Are Linked to Variation in Enzymes, Ecosystems and Size Fractions." *Biogeochemistry* 91, no. 1: 37–49. https://doi.org/10.1007/s10533-008-9257-9.

Guo, D., R. J. Mitchell, and J. J. Hendricks. 2004. "Fine Root Branch Orders Respond Differentially to Carbon Source-Sink Manipulations in a Longleaf Pine Forest." *Oecologia* 140, no. 3: 450–457. https://doi.org/10.1007/s00442-004-1596-1.

Han, M., and B. Zhu. 2021. "Linking Root Respiration to Chemistry and Morphology Across Species." *Global Change Biology* 27, no. 1: 190–201. https://doi.org/10.1111/gcb.15391.

Hanson, P. J., N. T. Edwards, C. T. Garten, and J. A. Andrews. 2000. "Separating Root and Soil Microbial Contributions to Soil Respiration: A Review of Methods and Observations." *Biogeochemistry* 48, no. 1: 115–146. https://doi.org/10.1023/A:1006244819642.

Janssens, I. A., W. Dieleman, S. Luyssaert, et al. 2010. "Reduction of Forest Soil Respiration in Response to Nitrogen Deposition." *Nature Geoscience* 3, no. 5: 315–322. https://doi.org/10.1038/ngeo844.

Jarvi, M. P., and A. J. Burton. 2013. "Acclimation and Soil Moisture Constrain Sugar Maple Root Respiration in Experimentally Warmed Soil." *Tree Physiology* 33, no. 9: 949–959. https://doi.org/10.1093/treephys/tpt068.

Jarvi, M. P., and A. J. Burton. 2018. "Adenylate Control Contributes to Thermal Acclimation of Sugar Maple Fine-Root Respiration in Experimentally Warmed Soil." *Plant, Cell & Environment* 41, no. 3: 504–516. https://doi.org/10.1111/pce.13098.

Jarvi, M. P., and A. J. Burton. 2020. "Root Respiration and Biomass Responses to Experimental Soil Warming Vary With Root Diameter and Soil Depth." *Plant and Soil* 451, no. 1: 435–446. https://doi.org/10.1007/s11104-020-04540-1.

Jevon, F. V., and A. K. Lang. 2022. "Tree Biomass Allocation Differs by Mycorrhizal Association." *Ecology* 103, no. 6: e3688. https://doi.org/10.1002/ecy.3688.

Jia, S., N. B. McLaughlin, J. Gu, X. Li, and Z. Wang. 2013. "Relationships Between Root Respiration Rate and Root Morphology, Chemistry and Anatomy in Larix Gmelinii and Fraxinus Mandshurica." *Tree Physiology* 33, no. 6: 579–589. https://doi.org/10.1093/treephys/tpt040.

Jo, I., S. Fei, C. M. Oswalt, G. M. Domke, and R. P. Phillips. 2019. "Shifts in Dominant Tree Mycorrhizal Associations in Response to Anthropogenic Impacts." *Science Advances* 5, no. 4: eaav6358. https://doi.org/10.1126/sciadv.aav6358.

Keenan, T. F., E. Davidson, A. M. Moffat, W. Munger, and A. D. Richardson. 2012. "Using Model-Data Fusion to Interpret Past Trends, and Quantify Uncertainties in Future Projections, of Terrestrial Ecosystem Carbon Cycling." *Global Change Biology* 18, no. 8: 2555–2569. https://doi.org/10.1111/j.1365-2486.2012.02684.x.

Keller, A. B., and R. P. Phillips. 2019. "Relationship Between Belowground Carbon Allocation and Nitrogen Uptake in Saplings Varies by Plant Mycorrhizal Type." *Frontiers in Forests and Global Change* 2: 81. https://doi.org/10.3389/ffgc.2019.00081.

Knorr, M. A., A. R. Contosta, E. W. Morrison, et al. 2024. "Unexpected Sustained Soil Carbon Flux in Response to Simultaneous Warming and Nitrogen Enrichment Compared to Single Factors Alone." *Nature Ecology & Evolution*, 1–9. https://doi.org/10.1038/s41559-024-02546-x.

Kwatcho Kengdo, S., D. Peršoh, A. Schindlbacher, et al. 2022. "Long-Term Soil Warming Alters Fine Root Dynamics and Morphology, and Their Ectomycorrhizal Fungal Community in a Temperate Forest Soil." *Global Change Biology* 28: 3441–3458. https://doi.org/10.1111/gcb.16155.

Li, J., G. Wang, M. A. Mayes, et al. 2019. "Reduced Carbon Use Efficiency and Increased Microbial Turnover With Soil Warming." *Global Change Biology* 25, no. 3: 900–910. https://doi.org/10.1111/gcb.14517.

Li, W., C. Jin, D.-X. Guan, et al. 2015. "The effects of simulated nitrogen deposition on plant root traits: A meta-analysis [Dataset]." *Soil Biology and Biochemistry* 82: 112–118.

Li, X., C. Zhang, B. Zhang, et al. 2021. "Nitrogen Deposition and Increased Precipitation Interact to Affect Fine Root Production and Biomass in a Temperate Forest: Implications for Carbon Cycling." *Science of the Total Environment* 765: 144497. https://doi.org/10.1016/j.scitotenv.2020.144497.

Lilleskov, E. A., T. W. Kuyper, M. I. Bidartondo, and E. A. Hobbie. 2019. "Atmospheric Nitrogen Deposition Impacts on the Structure and Function of Forest Mycorrhizal Communities: A Review." *Environmental Pollution* 246: 148–162. https://doi.org/10.1016/j.envpol.2018.11.074.

Liu, B., H. Li, B. Zhu, R. T. Koide, D. M. Eissenstat, and D. Guo. 2015. "Complementarity in Nutrient Foraging Strategies of Absorptive Fine Roots and Arbuscular Mycorrhizal Fungi Across 14 Coexisting Subtropical Tree Species." *New Phytologist* 208, no. 1: 125–136. https://doi.org/10.1111/nph.13434.

Ma, X., B. Zhu, Y. Nie, Y. Liu, and Y. Kuzyakov. 2021. "Root and Mycorrhizal Strategies for Nutrient Acquisition in Forests Under Nitrogen Deposition: A Meta-Analysis." *Soil Biology and Biochemistry* 163: 108418. https://doi.org/10.1016/j.soilbio.2021.108418.

Magill, A. H., J. D. Aber, G. M. Berntson, et al. 2000. "Long-Term Nitrogen Additions and Nitrogen Saturation in Two Temperate Forests." *Ecosystems* 3, no. 3: 238–253. https://doi.org/10.1007/s100210000023.

Magill, A. H., J. D. Aber, J. J. Hendricks, R. D. Bowden, J. M. Melillo, and P. A. Steudler. 1997. "Biogeochemical Response of Forest Ecosystems to Simulated Chronic Nitrogen Deposition." *Ecological Applications* 7, no. 2: 402–415. https://doi.org/10.1890/1051-0761(1997)007[0402:BROFET]2.0.CO;2.

Majdi, H., and J. Öhrvik. 2004. "Interactive Effects of Soil Warming and Fertilization on Root Production, Mortality, and Longevity in a Norway Spruce Stand in Northern Sweden." *Global Change Biology* 10, no. 2: 182–188. https://doi.org/10.1111/j.1365-2486.2004.00733.x.

McCormack, L., I. A. Dickie, D. M. Eissenstat, et al. 2015. "Redefining Fine Roots Improves Understanding of Below-Ground Contributions to Terrestrial Biosphere Processes." *New Phytologist* 207, no. 3: 505–518. https://doi.org/10.1111/nph.13363.

Melillo, J. M., S. Butler, J. Johnson, et al. 2011. "Soil Warming, Carbon–Nitrogen Interactions, and Forest Carbon Budgets." *Proceedings of the National Academy of Sciences* 108, no. 23: 9508–9512. https://doi.org/10.1073/pnas.1018189108.

Melillo, J. M., S. D. Frey, K. M. DeAngelis, et al. 2017. "Long-Term Pattern and Magnitude of Soil Carbon Feedback to the Climate System in a Warming World." *Science* 358, no. 6359: 101–105. https://doi.org/10.1126/science.aan2874.

Mo, J., W. Zhang, W. Zhu, et al. 2008. "Nitrogen Addition Reduces Soil Respiration in a Mature Tropical Forest in Southern China." *Global Change Biology* 14, no. 2: 403–412. https://doi.org/10.1111/j.1365-2486.2007.01503.x.

Morrison, E. W., S. D. Frey, J. J. Sadowsky, L. T. A. van Diepen, W. K. Thomas, and A. Pringle. 2016. "Chronic Nitrogen Additions Fundamentally Restructure the Soil Fungal Community in a Temperate Forest." *Fungal Ecology* 23: 48–57. https://doi.org/10.1016/j.funeco.2016.05.011.

Morrison, E. W., A. Pringle, L. T. A. van Diepen, and S. D. Frey. 2018. "Simulated Nitrogen Deposition Favors Stress-Tolerant Fungi With Low Potential for Decomposition." *Soil Biology and Biochemistry* 125: 75–85. https://doi.org/10.1016/j.soilbio.2018.06.027.

Nadelhoffer, K. J. 2000. "The Potential Effects of Nitrogen Deposition on Fine-Root Production in Forest Ecosystems." *New Phytologist* 147, no. 1: 131–139. https://doi.org/10.1046/j.1469-8137.2000.00677.x.

Nadelhoffer, K. J., J. D. Aber, and J. M. Melillo. 1985. "Fine Roots, Net Primary Production, and Soil Nitrogen Availability: A New Hypothesis." *Ecology* 66, no. 4: 1377–1390. https://doi.org/10.2307/1939190.

Nadelhoffer, K. J., and J. W. Raich. 1992. "Fine Root Production Estimates and Belowground Carbon Allocation in Forest Ecosystems." *Ecology* 73, no. 4: 1139–1147. https://doi.org/10.2307/1940664.

Olsson, P. A., and Y. Lekberg. 2022. "A Critical Review of the Use of Lipid Signature Molecules for the Quantification of Arbuscular Mycorrhiza Fungi." *Soil Biology and Biochemistry* 166: 108574. https://doi.org/10.1016/j.soilbio.2022.108574.

Ostonen, I., Ü. Püttsepp, C. Biel, et al. 2007. "Specific Root Length as an Indicator of Environmental Change." *Plant Biosystems—An International Journal Dealing with all Aspects of Plant Biology* 141, no. 3: 426–442. https://doi.org/10.1080/11263500701626069.

Paradiso, E., F. Jevon, and J. Matthes. 2019. "Fine Root Respiration Is More Strongly Correlated With Root Traits Than Tree Species Identity." *Ecosphere* 10, no. 11: e02944. https://doi.org/10.1002/ecs2.2944.

Parts, K., L. Tedersoo, A. Schindlbacher, et al. 2019. "Acclimation of Fine Root Systems to Soil Warming: Comparison of an Experimental Setup and a Natural Soil Temperature Gradient." *Ecosystems* 22, no. 3: 457–472. https://doi.org/10.1007/s10021-018-0280-y.

Paul, M. J., and C. H. Foyer. 2001. "Sink Regulation of Photosynthesis." *Journal of Experimental Botany* 52, no. 360: 1383–1400. https://doi.org/10.1093/jexbot/52.360.1383.

Pec, G. J., L. T. A. Diepen, M. Knorr, et al. 2021. "Fungal Community Response to Long-Term Soil Warming With Potential Implications for Soil Carbon Dynamics." *Ecosphere* 12, no. 5: e03460. https://doi.org/10.1002/ecs2.3460.

Persson, H. Å., and I. Stadenberg. 2009. "Spatial Distribution of Fine-Roots in Boreal Forests in Eastern Sweden." *Plant and Soil* 318, no. 1: 1–14. https://doi.org/10.1007/s11104-008-9811-1.

Phillips, R. P., E. Brzostek, and M. G. Midgley. 2013. "The Mycorrhizal-Associated Nutrient Economy: A New Framework for Predicting Carbon–Nutrient Couplings in Temperate Forests." *New Phytologist* 199, no. 1: 41–51. https://doi.org/10.1111/nph.12221.

Pold, G., A. S. Grandy, J. M. Melillo, and K. M. DeAngelis. 2017. "Changes in Substrate Availability Drive Carbon Cycle Response to Chronic Warming." *Soil Biology and Biochemistry* 110: 68–78. https://doi.org/10.1016/j.soilbio.2017.03.002.

Pold, G., J. M. Melillo, and K. M. DeAngelis. 2015. "Two Decades of Warming Increases Diversity of a Potentially Lignolytic Bacterial Community." *Frontiers in Microbiology* 6: 480. https://doi.org/10.3389/fmicb.2015.00480.

Poorter, H., and O. Nagel. 2000. "The Role of Biomass Allocation in the Growth Response of Plants to Different Levels of Light, CO_2, Nutrients and Water: A Quantitative Review." *Functional Plant Biology* 27, no. 12: 1191. https://doi.org/10.1071/pp99173_co.

Pregitzer, K. S., M. J. Laskowski, A. J. Burton, V. C. Lessard, and D. R. Zak. 1998. "Variation in Sugar Maple Root Respiration With Root Diameter and Soil Depth." *Tree Physiology* 18, no. 10: 665–670. https://doi.org/10.1093/treephys/18.10.665.

R Core Team. 2022. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/.

Sanders-DeMott, R., P. O. Sorensen, A. B. Reinmann, and P. H. Templer. 2018. "Growing Season Warming and Winter Freeze–Thaw Cycles Reduce Root Nitrogen Uptake Capacity and Increase Soil Solution Nitrogen in a Northern Forest Ecosystem." *Biogeochemistry* 137, no. 3: 337–349. https://doi.org/10.1007/s10533-018-0422-5.

Savage, J. A., M. J. Clearwater, D. F. Haines, et al. 2016. "Allocation, Stress Tolerance and Carbon Transport in Plants: How Does Phloem Physiology Affect Plant Ecology?" *Plant, Cell & Environment* 39, no. 4: 709–725. https://doi.org/10.1111/pce.12602.

Savage, K., E. A. Davidson, and J. Tang. 2013. "Diel Patterns of Autotrophic and Heterotrophic Respiration Among Phenological Stages." *Global Change Biology* 19, no. 4: 1151–1159. https://doi.org/10.1111/gcb.12108.

Saxe, H., M. G. R. Cannell, Ø. Johnsen, M. G. Ryan, and G. Vourlitis. 2001. "Tree and Forest Functioning in Response to Global Warming." *New Phytologist* 149, no. 3: 369–399. https://doi.org/10.1046/j.1469-8137.2001.00057.x.

Schindlbacher, A., S. Zechmeister-Boltenstern, and R. Jandl. 2009. "Carbon Losses Due to Soil Warming: Do Autotrophic and Heterotrophic Soil Respiration Respond Equally?" *Global Change Biology* 15, no. 4: 901–913. https://doi.org/10.1111/j.1365-2486.2008.01757.x.

Schuster, M. J., L. J. Williams, A. Stefanski, et al. 2022. "Patterns of belowground overyielding and fine-root biomass in native and exotic angiosperms and gymnosperms." *Oikos* 2023, no. 1. e08877. https://doi.org/10.1111/oik.08877.

Smith, A. M., and M. Stitt. 2007. "Coordination of Carbon Supply and Plant Growth." *Plant, Cell & Environment* 30, no. 9: 1126–1149. https://doi.org/10.1111/j.1365-3040.2007.01708.x.

Sperry, J. S., V. Stiller, and U. G. Hacke. 2002. "Soil Water Uptake and Water Transport Through Root Systems." In *Plant Roots: The Hidden Half*, edited by Y. Waisel, A. Eshel, and U. Kafkafi, 3rd ed., 663–681. New York: Marcel Dekker, Inc.

Stoica, I., M. Tabatabaei Anaraki, T. Muratore, M. Knorr, S. D. Frey, and M. J. Simpson. 2023. "Chronic Warming and Nitrogen-Addition Alter Soil Organic Matter Molecular Composition Distinctly in Tandem Compared to Individual Stressors." *ACS Earth and Space Chemistry* 7, no. 3: 609–622. https://doi.org/10.1021/acsearthspacechem.2c00380.

Sun, H., J. Li, H. Liu, C. Fang, B. Li, and M. Nie. 2023. "Global Change Factors Regulate the Apparent Thermal Acclimation of Soil Respiration: A Meta-Analysis." *Applied Soil Ecology* 183: 104741. https://doi.org/10.1016/j.apsoil.2022.104741.

Suz, L. M., M. I. Bidartondo, S. van der Linde, and T. W. Kuyper. 2021. "Ectomycorrhizas and Tipping Points in Forest Ecosystems." *New Phytologist* 231, no. 5: 1700–1707. https://doi.org/10.1111/nph.17547.

Tibbett, M. 2000. "Roots, Foraging and the Exploitation of Soil Nutrient Patches: The Role of Mycorrhizal Symbiosis." *Functional Ecology* 14, no. 3: 397–399.

Tjoelker, M. G. 2018. "The Role of Thermal Acclimation of Plant Respiration Under Climate Warming: Putting the Brakes on a Runaway Train?" *Plant, Cell & Environment* 41, no. 3: 501–503. https://doi.org/10.1111/pce.13126.

Tjoelker, M. G., J. Oleksyn, and P. B. Reich. 2001. "Modelling Respiration of Vegetation: Evidence for a General Temperature-Dependent Q10." *Global Change Biology* 7, no. 2: 223–230. https://doi.org/10.1046/j.1365-2486.2001.00397.x.

Tunison, R., T. E. Wood, S. C. Reed, and M. A. Cavaleri. 2024. "Respiratory Acclimation of Tropical Forest Roots in Response to In Situ Experimental Warming and Hurricane Disturbance." *Ecosystems* 27, no. 1: 168–184. https://doi.org/10.1007/s10021-023-00880-y.

Valverde-Barrantes, O. J., K. A. Smemo, L. M. Feinstein, M. W. Kershner, and C. B. Blackwood. 2015. "Aggregated and Complementary: Symmetric Proliferation, Overyielding, and Mass Effects Explain Fine-Root Biomass in Soil Patches in a Diverse Temperate Deciduous Forest Landscape." *New Phytologist* 205, no. 2: 731–742. https://doi.org/10.1111/nph.13179.

Van Nuland, M. E., P.-J. Ke, J. Wan, and K. G. Peay. 2023. "Mycorrhizal Nutrient Acquisition Strategies Shape Tree Competition and Coexistence Dynamics." *Journal of Ecology* 111, no. 3: 564–577. https://doi.org/10.1111/1365-2745.14040.

Wang, J., C. Defrenne, M. L. McCormack, et al. 2021. "Fine-Root Functional Trait Responses to Experimental Warming: A Global Meta-Analysis." *New Phytologist* 230, no. 5: 1856–1867. https://doi.org/10.1111/nph.17279.

Werner, W. J., J. Sanderman, and J. M. Melillo. 2020. "Decreased Soil Organic Matter in a Long-Term Soil Warming Experiment Lowers Soil Water Holding Capacity and Affects Soil Thermal and Hydrological Buffering." *Journal of Geophysical Research: Biogeosciences* 125, no. 4: e2019JG005158. https://doi.org/10.1029/2019JG005158.

Zhang, H., Y. Liu, Z. Zhou, and Y. Zhang. 2019. "Inorganic Nitrogen Addition Affects Soil Respiration and Belowground Organic Carbon Fraction for a *Pinus tabuliformis* Forest." *Forests* 10, no. 5: Article 5. https://doi.org/10.3390/f10050369.

Zogg, G. P., D. R. Zak, A. J. Burton, and K. S. Pregitzer. 1996. "Fine Root Respiration in Northern Hardwood Forests in Relation to Temperature and Nitrogen Availability." *Tree Physiology* 16, no. 8: 719–725. https://doi.org/10.1093/treephys/16.8.719.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.