Root standing crop and chemistry after six years of soil warming in a temperate forest

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RUNNING HEAD: ROOT MASS AND CHEMISTRY

Summary Examining the responses of root standing crop (biomass and necromass) and chemistry to soil warming is crucial for understanding root dynamics and functioning in the face of global climate change. We assessed the standing crop, total nitrogen (N) and carbon (C) compounds in tree roots and soil net N mineralization over the growing season after six years of experimental soil warming in a temperate deciduous forest in 2008. Roots were sorted into four different categories: live and dead fine roots (≤ 1 mm in diameter) and live and dead coarse roots (1-4 mm in diameter). Total root standing crop (live plus dead) in the top 10 cm of soil in the warmed area was 42.5% (378.4 vs. 658.5 g m^{-2}) lower than in the control area, while the live root standing crops in the warmed area was 62% lower than in the control area. Soil net N mineralization over the growing season increased by 79.4% in the warmed relative to the control area. Soil warming did not significantly change the concentrations of C and carbon compounds (sugar, starch, hemicellulose, cellulose, and lignin) in the four root categories. However, total N concentration in the live fine roots in the warmed area was 10.5% (13.7 vs. 12.4 mg g^{-1}) higher and C:N ratio was 8.6% (38.5 vs. 42.1) lower than in the control area. The increase in N concentration in the live fine roots could be attributed to the increase in soil N availability due to soil warming. Net N mineralization was negatively correlated to both live and dead fine roots in the mineral soil that is home to the majority of roots, suggesting that soil warming increases N mineralization, decreases fine root biomass, and thus decreases carbon allocation belowground.

Keywords: *carbon, nitrogen, root biomass, root diameter, root necromass*.

Introduction

Tree roots generally constitute between 15 and 30% of the total tree biomass and consume large portions of annual net primary production in forest ecosystems (Bowden et al. 1993, Janssens et al. 2002, Persson 2002). Since tree roots play a critical role in nutrient and water uptake, carbon and nutrient cycling, storage of carbohydrates, and synthesis of growth regulators (Jackson et al. 1997, López et al. 2001), the climate change impact on tree roots may in turn influence the structure and function of entire ecosystems.

Previous studies have found that climate warming can change the root function (Pregitzer et al. 2000), dynamics (Hendrick and Pregitzer 1993, Forbes et al. 1997, Fitter et al. 1999, King et al. 1999, Gill and Jackson 2000, Tierney et al. 2003, Majdi and Öhrvik 2004, Wan et al. 2004), morphology, mass and distribution (Björk et al. 2007, Bronson et al. 2008). For example, higher soil temperature increased the root production and mortality associated with soil nitrogen (N) availability (King et al. 1999; Pregitzer et al. 2000; Majdi and Ohrik 2004). In contrast to root production, root standing crop showed different responses to elevated temperature depending on species, research site, heating methods. In a black spruce plantation, live fine root biomass (< 2 mm diameter) in the soil warming plots was decreased by 24% to 46% (Bronson et al. 2008). Elevated temperature decreased fine root mass of maple trees by 34%, 53% and 43% for size class

< 0.5 mm, 1.0-2.0 mm, and < 2.0 mm (Wan et al. 2004). The root biomass of *Agrostis scabra* and *A. stolonifera* grown at elevated temperature decreased by 8% and 15%, respectively (Lyons et al. 2007). Inconsistently with above studies, it was reported that the fine roots (< 4 mm diameter) and total root biomass either increased slightly with increasing temperature (Allen and Vu 2009), or indicated no significant change with temperature (Kandeler et al. 1998).

While changes in root productivity and biomass have been correlated to changes in temperature, another factor also influences root productivity and biomass, that is, soil N availability, which also responds to temperature. Multiple studies have shown that fine root biomass decreases with increasing soil N (Nadelhoffer 2000, Powers et al. 2005, Lee et al. 2007). It has been observed that warming increases the rate of N mineralization in the soil, affecting soil N availability (Peterjohn et al. 1994, Lükewille and Wright 1997, Melillo et al. 2002, 2011, Strömgren and Linder 2002). In a meta-analysis of soil warming experiments, Rustad et al. (2001) found that warming increased net N mineralization rate by 46%. In a decade-long soil warming experiment at the Harvard Forest, Melillo et al. (2002) reported that constant soil warming at 5 °C above ambient resulted in a cumulative increase in N availability of 41 g m^{-2}. Therefore, we expect that root biomass decreases with warming-induced increases in soil N availability. Besides temperature and N availability, soil moisture is also a key factor that has been found to affect root mass (Meier and Leuschner 2008). For example, Dijkstra and Cheng (2007) found that root biomass increased with increased soil moisture content in a European forest. The study observing a decrease in the fine root biomass in the drier stands simultaneously found decreased fine root diameter, which may indicate that fine roots may compensate for the loss in root biomass by increased uptake area or uptake rate (Meier and Leuschner 2008).

In addition to biomass and productivity of fine roots, soil warming will likely affect carbon and nitrogen composition of fine roots. Root tissue chemistry plays a key role in controlling metabolic and decomposition dynamics of roots (McClaugherty et al. 1982, King et al. 2005), regulating soil microbial activity (Zak et al. 2000), and determining carbon inputs into soil (Brown et al. 2007). Root N concentration has been emphasized more than other chemical compounds because it is significantly correlated with root growth (Valverde-Barrantes et al. 2007), root respiration (Pregitzer et al. 1998, Burton et al. 2002), and potential decomposition dynamics (Hendricks et al. 2000). Increased soil temperatures are linked to increased N concentration of roots due to the kinetic increase of root activities and greater N availability at higher temperature (Zogg et al. 1996, BassiriRad 2000, Wan et al. 2004). A higher root N concentration is required for enzyme synthesis and activity, resulting in more nutrient uptake (Nadelhoffer 2000).

Soluble carbohydrates, holocellulose (hemicellulose and cellulose) and lignin represent three root carbon pools that are associated with specific root functions. Uselman et al. (2000) found that warmer temperature significantly increased root exudation of organic carbon. This indicates that warming might alter the carbon compounds of roots and soil carbon storage. Furthermore, increased root respiration and root turnover rates due to soil warming might potentially change root carbon compounds and the relationship between carbon and nitrogen. Burton et al. (2008) reported that root respiration rates increased with rising soil temperatures, consequently leading to decreases in carbon available for biomass construction. If it is true that fine root turnover rates and soil N availability increase with increased temperature, more carbon will be consumed in growth and respiration and less will be allocated to structural costs (Nadelhoffer 2000).

Our knowledge in understanding the interactions between root standing crop, soil N mineralization and root chemistry in response to warming is very limited. Here we use an in situ experimental warming to study the effects of soil warming on biomass and necromass of hardwood forest roots with different diameters, and changes in carbon compounds and N concentration in the four different root fractions, including live fine roots (≤ 1 mm in diameter), live coarse roots (1-4 mm in diameter), dead fine roots and dead coarse roots. We also examine the relationships between changes in fine roots, N availability, soil temperature and moisture. We hypothesize that 1) soil warming decreases root standing crop; 2) the soil N mineralization is negatively correlated with root mass; and 3) the N concentration in roots is increased mainly due to increased soil N availability.

Materials and Methods

Site description

The study was conducted in a warmed area and an adjacent control area, each 30 by 30 meters, established in 2002 with heating commencing in May 2003 in the Barre Woods tract of Harvard Forest, Petersham, Massachusetts, USA (Melillo et al 2011). The highest mean weekly air temperature is about 20 °C and occurs in July, and the lowest, about -6 °C, occurs in January. The average annual precipitation is approximately 1080 mm (Melillo et al. 2002). Each area is divided into 5-by-5 meter subplots. The soil is warmed by resistance heating cables buried at a 10 cm depth and spaced 20 cm apart. The soil temperature in the warmed area is maintained at 5 °C above the adjacent control area. For a detailed description of the soil warming system, see Melillo et al. (2002, 2004). The study areas are within a mixed hardwood stand dominated by *Quercus rubra* and *Acer rubrum*, with lesser components of *Quercus velutina* and *Fraxinus Americana*. The majority of trees in the study area have naturally regenerated after a major hurricane in 1938. The average tree diameter at breast height was 19.3 cm and the stand had a basal area of approximately 31 m^2 ha^{-1} in 2008.

This larger warming experiment (30 m by 30 m) follows an earlier warming experiment established in 1991 in the Harvard Forest with multiple small (6 m by 6 m) warmed plots, disturbance control plots (with buried cables but no warming), and undisturbed control plots (no buried cable, no warming) (Melillo et al. 2002). Results from the smaller warming experiment indicated that soil disturbance caused by the installation of heating cables had no significant effects on soil temperatures and only minor and insignificant impacts on soil moisture, shrub growth, and nitrogen mineralization. This larger warming experiment has an advantage against the previous smaller one in that the plot can be large enough to include all roots from trees inside the warmed area. Due to the high installation and maintenance costs of this large-scale warming experiment, we do not have replicate areas, and nor disturbance control areas. However, we made pre-treatment measurements in the present warmed and control areas in 2002, and found that there were no significant differences in tree characteristics and key soil processes between the two areas such as tree biomass, woody increment, stand basal area, species composition, soil respiration, and nitrogen mineralization rates. The soil temperature at 5 cm depth measured during the sampling period is shown in Figure 1, indicating a consistent increase in soil temperature in the warmed area. For the 2008 growing season, the average gravimetric soil moisture in the organic layer was 56% in the heated and 66% in the control horizon. However, in the mineral horizon, the soil moisture was 36% in the heated and 37% in the control areas.

Figure 1 here

Separation and classification of roots

Soil cores were collected six times at approximately monthly intervals during the growing season from April to November 2008 (April 29, May 27, June 25, July 28, September 2 and November 4) from eight subplots within the warmed area and nine subplots within the control area. Soil cores of 10 cm in diameter were taken to a 10 cm depth to cover the most active tree roots in the organic layers and upper mineral layers. The average organic layer depth was 1.4 cm, so the average depth of mineral soil layer sampled in each core was 8.6 cm. Gravimetric moisture content was measured for each soil core. The average bulk density was 0.373 g cm^{-3} in the organic layer and 0.781 g cm^{-3} in the mineral layer. After weighing, deionized water was put in each bag, and the bags were stored between 0 and 4°C until sorting.

We used a 1 mm diameter threshold to define fine roots ($\leq$ 1 mm) and coarse roots (1 to 4 mm). Only a small amount of root material was over 3 mm in diameter and roots > 4 mm in diameter were not found in this study. Root diameter was measured using a digital caliper. The soil was put into a small tub with some water and roots were separated from the soil with forceps. By frequently changing water and rinsing, we were able to pick up almost all of the roots by hand. When small roots were connected to a larger root, they were cut out and separated into different size classes.

Fine roots and coarse roots were separated into live and dead categories based on visible morphological characteristics, mainly color and strength. Detailed information on how to judge live roots and dead roots has been described in the literature (Vogt and Persson 1991, Matamala and Schlesinger 2000, John et al. 2002, Persson and Stadenberg 2009). Roots from different tree species were not distinguished, but herbaceous roots were excluded. Herbaceous roots are white, light and succulent, while tree roots are slightly brown or yellow and well branched. After sorting, live and dead roots of different size classes were dried at 60 °C for at least 48 h and then weighed.

Chemical measurements

Since the amount of root material in each sample class was too small for chemical analysis, we pooled roots from all subplots after sorting and weighing. This gave us monthly chemical composition data of four categories (live fine roots, live coarse roots, dead fine roots, and dead coarse roots) from each area.

Root samples were analyzed for total soluble sugars, starch, hemicellulose, cellulose, lignin, total C and total N. Total C and N were determined by combustion in a CHN analyzer (PerkinElmer 2400 Series, Waltham, Massachusetts 02451, USA). The concentrations of the carbon compounds were measured in a sequential extraction process with anthrone-sulfuric acid method (Gao 2006). Samples submerged in deionized water were extracted in a boiling water bath twice. The supernatant was used to analyze the concentration of total soluble sugars, and then the residues were extracted with hot deionized water and hydrolyzed with perchloric acid to determine starch concentration. After sugars and starch were removed, the residues were hydrolyzed with hydrochloric acid for three hours in a boiling water bath to analyze hemicellulose concentration. The residues in the extraction tubes were washed twice with ethanol and acetone to remove lipids and pigments. Then the residues were dried and digested with concentrated sulfuric acid in boiling water bath for five hours to determine cellulose concentration. All final reducing sugar was measured colorimetrically using the anthrone-ethyl acetate method with a spectrophotometer at 630 nm (Shimadzu UV-1201, Shimadzu Scientific Instruments, Columbia, MD, USA). Lignin, an acid-insoluble structural component, was assessed by the weight difference.

N mineralization

We measured net nitrogen mineralization rates using the standard *in situ* buried bag method (Eno 1960) approximately every five weeks from April through November 2008. We took two 10 cm deep soil cores from each of the ten subplots per treatment during each sampling period. We designated one core as the “initial” sample, which was split into organic and mineral horizons and each horizon was transported to the laboratory for analysis. The second core, designated as the “final” sample, was placed intact inside a gas-permeable polyethylene bag and positioned back in the ground. The ‘final’ bags were incubated during April-November and then transported to the lab for analysis.

In the laboratory, soils were separated into organic and mineral layers and sieved through a 5.6 mm screen to remove rocks and roots. Approximately 10 grams of soil was placed in 100 ml of 2M KCl, incubated for 36 hours, and filtered. The extracts were analyzed for nitrite/nitrate (NO_2^-/ NO_3^--N) and ammonium (NH_4^+-N) using a Lachat

QuikChem FIA+ 8000 Series Flow Injection Analyzer with Omnion 3.0 software (Lachat Instruments Inc., Loveland, CO, USA). Using these techniques, the detection limit for NO_2^-/ NO_3^--N was 0.02 mg L^{-1} and the detection limit for NH_4^+-N was 0.005 mg L^{-1}.

Statistical Analyses

The statistical analysis was conducted with SPSS 13.0 (SPSS Inc. Chicago, IL, USA). Effects of soil temperature, soil depth and sample dates on root mass were tested using three-way ANOVA. The effect of soil temperature on the ratio of biomass to necromass from different soil fractions was analyzed using a one-way ANOVA. We used paired-sample T-tests to analyze the difference in total N, total C and all carbon compounds between warming and control areas. We conducted Spearman's correlation between root mass, net mineralization and soil moisture data across each sample location after these data were averaged over the growing season.

Results

Changes in root mass

Warming decreased live plus dead root mass in the upper 10 cm of soil compared with the control (Tables1, 2). Significant decreases in both live and dead root mass between warmed and control areas were confined to the mineral soil (*P* < 0.001) (Table 1). No significant seasonal change in total root mass and four root categories was found from April to November (Table 2, Figure 2).

Table 1 here

Table 2 here

Figure 2 here

Live root mass – Relative to the control, soil warming resulted in a significant decrease in live root biomass, with a 61.9% decline in fine root biomass and a 61.1% decrease in coarse root biomass (Table 1).

Dead root mass – The necromass in the warmed area was significantly lower than in the control area (242.3 g m^{-2} vs. 304.6 g m^{-2}) (Table 1). The fine root necromass in the warmed area was 22.7% lower than in the control area. Coarse root necromass was not significantly affected by soil warming (Table 2).

Ratio of live to dead fine roots - When we aggregated all live roots into one pool and dead roots into another (regardless of root diameter) and examined the ratios of live to dead roots, soil warming led to significantly lower ratios in the organic layer, mineral layer, and organic plus mineral layer relative to the control (Table 3). No significant differences were found in the ratios of root biomass to necromass of fine roots in the organic layer, but there was a trend toward a decreased ratio in the warmed area relative to the control (Table 3). Soil warming significantly decreased the ratios of fine root biomass to necromass by 61.5% in the mineral soil and 50.0% in the organic plus mineral soil relative to the control area (Table 3). The ratios of coarse root biomass to necromass were not significantly affected by higher soil temperature.

Table 3 here

Changes in C and N

Soil warming significantly increased the total N concentration in live fine roots by 10.5% (13.7 vs. 12.4 mg g^{-1}) compared with the control area ($P < 0.05$, Table 4). With no change in C concentration, this led to a significant decline in C:N ratio (-8.6%) (38.5 vs. 42.1) ($P < 0.05$, Table 4) since there was no significant difference in total C concentration in live fine roots between the warmed and control areas. There were no significant effects of soil warming on total N concentration and C:N ratio in the other root classes.

There were no significant differences in the concentrations of total C or any of the carbon compounds analyzed in four root categories in the warmed area compared with the corresponding chemistry observed in the control area ($P > 0.05$). Although soil warming resulted in lower concentrations of total soluble sugars in four different root categories and higher starch concentrations in live roots compared with control, the differences were not statistically significant. The total nonstructural carbohydrate content

(TNC, the sum of soluble sugars and starch) of live roots, especially live coarse roots, was significantly higher than that of dead roots, regardless of treatment (Table 4). Since the absolute concentration of hemicellulose in roots was very low (less than 10 mg g^{-1}) and hemicellulose and cellulose have similar structure, we combined hemicellulose and cellulose. The holocellulose (hemicellulose plus cellulose) concentrations in live roots in the warmed area were very close to those in the control area. However, soil warming resulted in a decreased trend in holocellulose concentration in dead roots relative to the control. Soil warming caused a slight increase in the lignin concentrations in live fine, live coarse and dead coarse roots compared with the control area although the difference was not statistically significant.

Table 4 here

Soil N mineralization

Soil net N mineralization showed pronounced seasonal patterns during the sampling period in both warmed and control areas, with highest values in July and lowest values in November (Table 2, Figure 3). Net N mineralization was also affected by warming treatment and soil layer (Table 2, Figure 3). Net N mineralization in the upper mineral soil was over four times higher than that in the organic layer for both warmed and control areas from April to November. Soil warming increased soil net N mineralization by

60.9% (13.3 vs. 8.3 kg N ha^{-1}) in the organic layer, by 83.7% (65.2 vs. 35.5 kg N ha^{-1}) in the mineral layer and 79.4% (78.5 vs. 43.7 kg N ha^{-1}) in the organic plus upper mineral layer compared with control area.

Figure 3 here

Relationship among soil N mineralization, root mass, soil temperature and moisture

Soil net nitrogen mineralization was significantly correlated (negatively) to both fine root biomass (*P* = 0.0018, correlation coefficient = -0.70) and fine root necromass (*P* = 0.0093, correlation coefficient = -0.61) in the mineral soil that is home to the majority of root mass. In the mineral soil, moisture was significantly correlated to fine root necromass (*P* = 0.0467, correlation coefficient = 0.49), but not to other root categories. The soil net N mineralization in the warmed and control areas was linearly correlated with soil temperature, and the slope of the net mineralization against temperature was higher in the warmed area than that in the control area (Figure 4).

Figure 4 here

Discussion

Effects of warming on root mass and net N mineralization

Fine roots (≤ 1 mm) made up a majority of the root biomass in the heated and control areas to a depth of 10 cm. We did not find any roots greater than 4 mm in diameter due to shallow depth of our sampling. Our results indicate that soil warming does not alter seasonal patterns of root biomass and necromass.

The root mass in this study is within the range of global estimations of root mass in other forest ecosystems. Jackson et al. (1997) estimated that the average total and live fine root (≤ 2 mm in diameter) mass in the upper 30 cm of soil of global temperate deciduous forest were 780 g m^{-2} and 440 g m^{-2}. The two values are a little higher than the values in the control area (658.5 and 354.0 g m^{-2}) because the sampling depth was only 10 cm in our study. However, the percentage of live roots to total root mass is similar, 56% for global average and 54% in the control area. In the warmed area, the absolute values of total and live fine roots and the percentage of live roots are significantly lower than the average global values or our control. Soil warming resulted in a more than 60% decrease in fine root or coarse root biomass, while fine root and coarse root necromass decreased by less than 23%, consistent with previous research (Bronson et al. 2008).

Results from our study support the first hypothesis that soil warming leads to a decrease in root standing crop, but the decline is probably not the direct effect of elevated soil temperature. Correlation analysis shows that decreased fine root mass is mainly attributed to the increase in soil N mineralization rates and thus soil N availability, and therefore support our second hypothesis. The carbon allocation theory indicates that plants maximize growth rates by partitioning carbon to optimize the capture of limiting resources (Tilman 1988, Cannell and Dewar 1994, McConnaughay and Coleman 1999). When soil N availability increases by warming, the demand for carbon allocation to roots decreases, leading to a decline in fine roots, the functional tissue for N uptake. Here we used net N mineralization rates to indicate soil N availability, but we acknowledge that plant roots and associated mycorrhizal fungi may directly use organic N such as amino acid (Schimel and Bennett 2004). Given the difficulty in directly measuring total N availability, N mineralization remains a useful index to indicate N availability (Schimel and Bennett 2004). In addition, the seasonal pattern of soil N mineralization in the warmed and control areas is positively correlated with soil temperature, which is consistent with many previous publications (Hill and Shackleton 1989, Tietema and Verstraten 1992, Owen et al. 2003, Zak et al. 1999, Rustad et al. 2001, Strömgren and Linder 2002, Pajuste and Frey 2003) and this research site at Harvard Forest (Melillo et al. 2002, 2011).

Compared with N availability changed by soil warming, soil moisture does not strongly affect live fine root mass. Although gravimetric soil moisture was lower in the organic horizon in the warmed area compared to the control (56% in the warmed area versus 66% in the control), there was little difference between the soil moistures measured in the upper mineral horizon in the warmed and control areas (36% and 37% respectively). Since significant decreases in live and dead root mass between warmed and control areas were confined to the mineral soil, we have concluded that the warming-induced change in soil moisture had little effect on root mass in this temperate forest with average annual precipitation of 1080 mm. However, it has been found in other studies that root mass decreases with soil water availability (Cavelier et al. 1999; Metcalfe et al. 2008; Vanguelova et al. 2005).

The ratio of live to dead root mass is considered as a useful index of root turnover (Persson and Stadenberg 2009). The biomass:necromass ratio of fine roots has been reported to be 0.4-3.0 in a beech and Norway spruce stand (Stober et al. 2000), 1.4-2.2 in a coniferous forest (Persson and Stadenberg 2009), and 0.3-2.9 collected from various natural stands (Persson 2000). In the present study, we found that the biomass:necromass of fine roots ranged from 1.0-1.3 in the control area and 0.5-0.7 in the warmed area, within the range of previous studies. If the low biomass:necromass ratio indicates reduced fine root longevities (Leuschner et al. 2004, Persson and Stadenberg 2009), the significant decrease in the biomass:necromass ratio in the warmed area implies that fine roots at elevated temperature have a higher turnover rate relative to the control. As expected, we also found that the biomass:necromass ratios of fine roots were lower than those of coarse roots for both warming and control areas, since coarse roots have a longer life span or a lower turnover rate (Gill and Jackson 2000, Gill et al. 2002, King et al. 2002).

Effects of warming on root chemistry

The most pronounced changes in the chemical composition of roots in the warmed area are the increased N concentration and the decreased C:N ratio in the live fine roots. It has been observed in some forests that fine root N concentration increases with increased soil N availability (Majdi and Rosengren-Brinck 1994, Zogg et al. 1996, Högberg et al. 1998, Burton et al. 2000). In addition to inorganic N, trees also have capability to directly take up organic N such as amino acid (Schimel and Bennett 2004, Finzi and Berthrong 2005). If warming stimulates root activity, we reason organic N uptake via live fine roots will be increased. Thus, our third hypothesis is supported only for the live fine roots.

In contrast to nitrogen, total C of roots were not significantly changed with soil warming. The ratio of C:N is an important predictor of root longevity or decomposition rates (Müller et al. 1988, Entry et al. 1998, Hishi and Takeda 2005, Withington et al. 2006). In the current study, only the C:N ratios of live fine roots were decreased by soil warming (-8.6%) compared to the control area due to the significant increases in total N and no change in total C. The decrease in C:N ratios with warming, indicating an increase in root mortality (Withington et al. 2006), is consistent with our earlier discussion that soil warming decreases root longevity based on the biomass:necromass ratio. The C:N ratios found in our study are between 38 and 92, a range consistent with previously published values. For example, Jackson et al. (1997) reported that the global average is 42 for live roots less than 2 mm in diameter. The C:N ratio is 22 to 32 in tropical tree species (Valverde-Barrantes et al. 2007). Gordon and Jackson (2000) found the C:N was 43 in live roots < 2 mm in diameter and 79 in live roots 2-5 mm in diameter by analyzing 56 published studies. Relatively higher C and lower N concentrations in coarse roots resulted in higher C:N ratios (63 in dead coarse roots and 92 in live coarse roots) in our study. In the control area, we found no difference in the C:N ratio of live and dead fine roots, which is consistent with the results of Valverde-Barrantes et al. (2007).

There are no significant changes in nonstructural and structural carbon concentrations of roots due to soil warming. Thus, the lack of change in chemical composition of roots suggests that the intrinsic decomposition rate of dead roots may not be affected by warming. However, kinetic theory indicates that higher soil temperature increases the decomposition rate as an external driver (Fierer et al. 2005, Davidson and Janssens 2006). A confirmed conclusion on temperature sensitivity of root decomposition in response to warming cannot be reached by our study since soil moisture, carbon availability, microbial community and other conditions may also influence temperature sensitivity of decomposition (Tang et al. 2005, Tang and Baldocchi 2005, Davidson and Janssens 2006).

Long-term soil warming experiments show that soil respiration increases over the first few years of soil warming, and then the stimulatory effect decreases due to the decrease in the labile soil carbon pool or microbial acclimation to warming (Luo et al. 2001, Melillo et al. 2002). Our results of an approximately 40% decline in root standing crop and previous reports of decreased root metabolic capacity (Burton et al. 2008) due to soil warming suggest that the contributions of root respiration to total soil respiration decreases in response to warming. To understand the mechanisms underlying the belowground dynamics in response to warming, root respiration, root production and turnover, microbial decomposition using various pools of carbon, and microbial community composition should be further studied. Future soil warming experiments could involve manipulation of soil moisture as well because these two environmental factors are so closely related.

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Figure 1 Averaged daily soil temperature in the warmed and control areas from April to November, 2008. The data from April to July were recorded every six hours. After July, the data were collected hourly. The arrows indicated the period of root sampling.

Figure 2 Monthly root mass of (a) live fine roots, (b) live coarse roots, (c) dead fine roots and (d) dead coarse roots in the organic and upper mineral layer in the warmed and control areas from April to November, 2008. (Mean values ± SE) (n = 8)

WO = organic layer in the warmed area; WM = mineral layer in the warmed area; CO = organic layer in the control area; CM = mineral layer in the control area

Figure 3 The seasonal change of net N mineralization in the organic layer, upper mineral layer and the organic plus upper mineral layer for both warmed and control areas from April to November, 2008 (Mean values ± SE) (n = 10).

WO = organic layer in the warmed area; WM = mineral layer in the warmed area; CO = organic layer in the control area; CM = mineral layer in the control area

Figure 4 The linear relationship of net N mineralization to soil temperature in the warmed and control areas. (n=8)

Figure 1

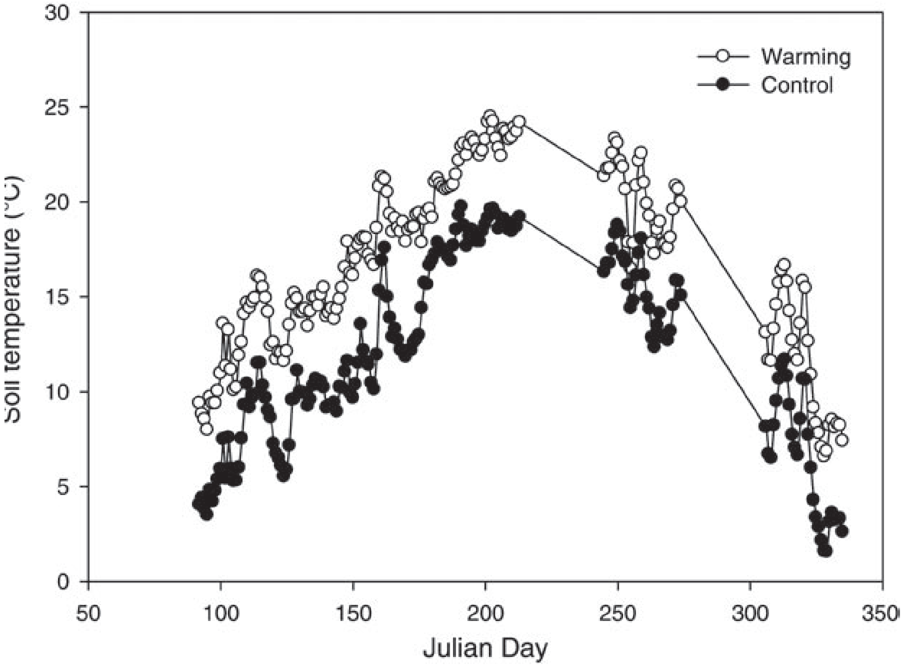

Warming
Control
Soil temperature (°C)
Julian Day
0
5
10
15
20
25
30
50
100
150
200
250
300
350

Figure 2

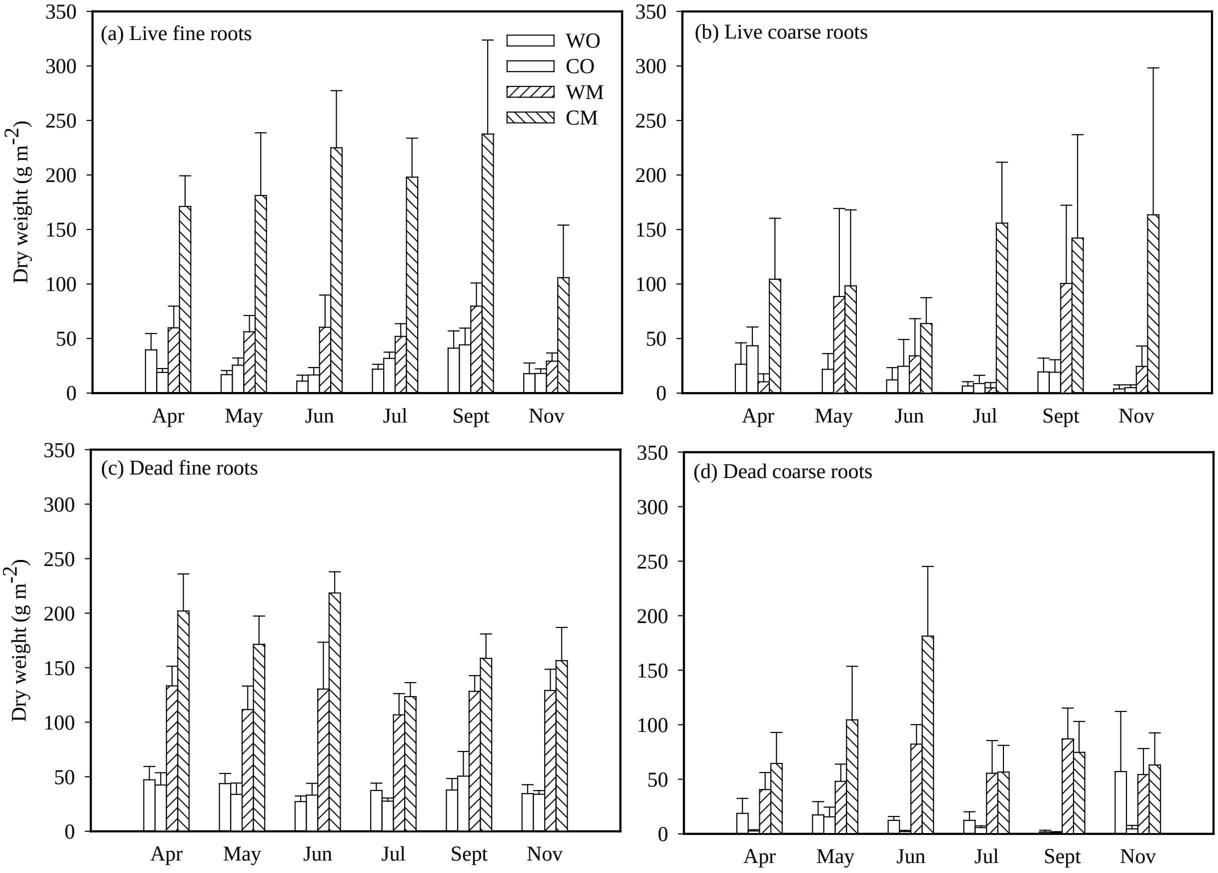
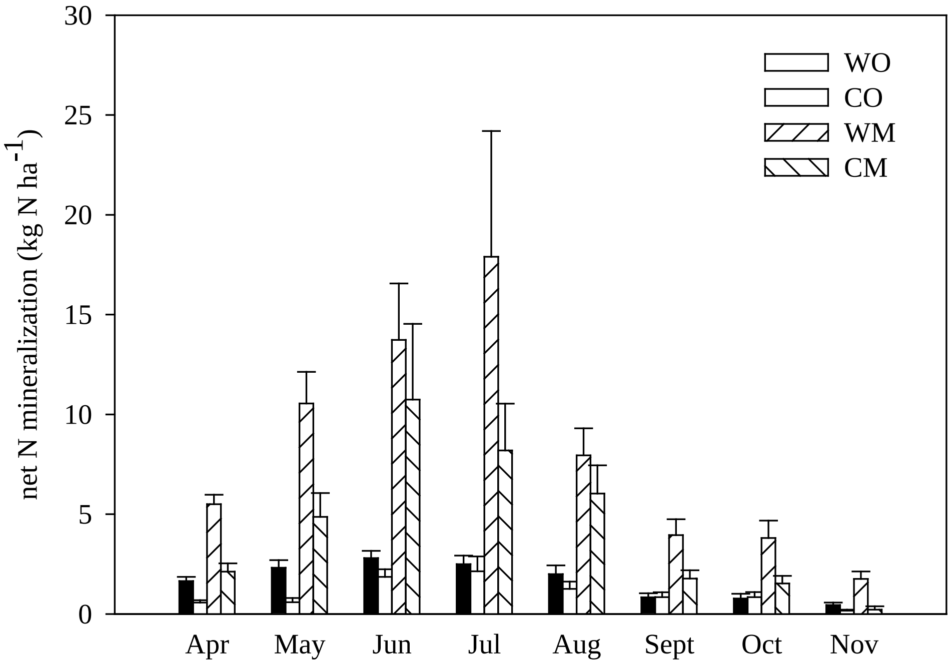

(a) Live fine roots
(b) Live coarse roots
(c) Dead fine roots
(d) Dead coarse roots
WO
CO
WM
CM
Dry weight (g m^{-2})
0
50
100
150
200
250
300
350
Apr
May
Jun
Jul
Sept
Nov

Figure 3



30
25
20
15
10
5
0
net N mineralization (kg N ha^{-1})
WO
CO
WM
CM
Apr
May
Jun
Jul
Aug
Sept
Oct
Nov

Figure 4

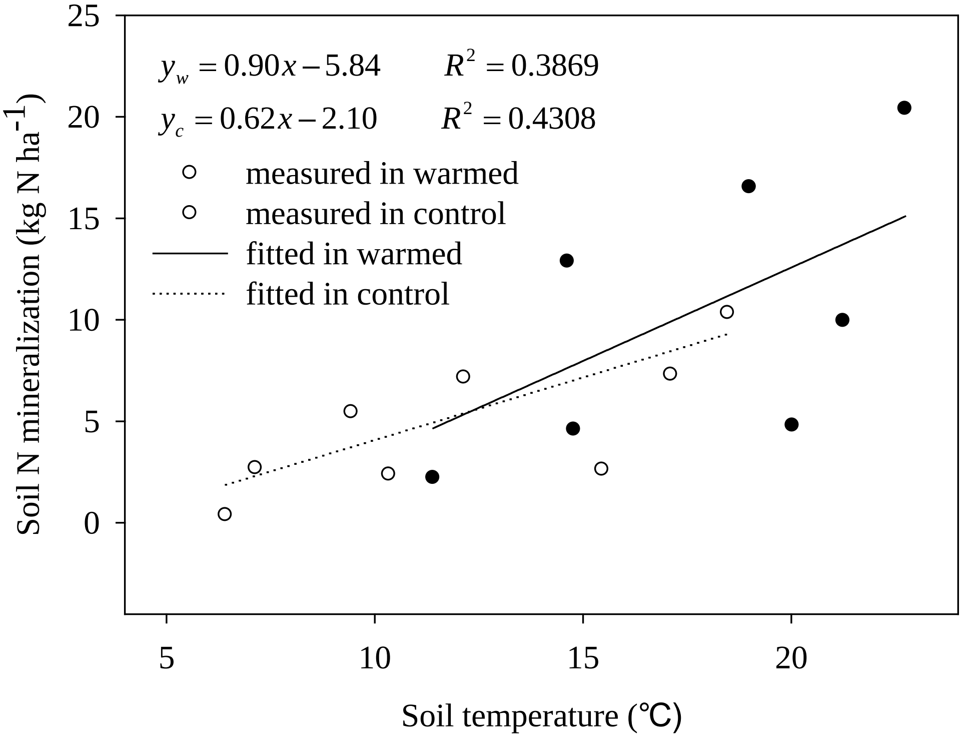

$y_w = 0.90x - 5.84$ $R^2 = 0.3869$
$y_c = 0.62x - 2.10$ $R^2 = 0.4308$
measured in warmed
measured in control
fitted in warmed
fitted in control
25
20
15
10
5
0
5
10
15
20
Soil N mineralization (kg N ha^{-1})
Soil temperature (℃)

Table 1 The averaged mass of live fine roots (LF), live coarse roots (LC), dead fine roots (DF) and dead coarse roots (DC) in the organic layer, upper mineral layer and the organic plus upper mineral layer in the warmed and control plots across all sample dates (Mean values ± SE) (g m^{-2}) (n=8).

Soil layer	Treatment	LF	LC	DF	DC
Organic (O)	Warming	22.7±3.8	10.2±3.7	36.7±3.2	19.0±8.8
	Control	25.7±3.2	20.3±5.5	37.0±4.6	5.3±1.6
Mineral (M)	Warming	56.2±7.6	43.8±18.9	123.2±9.6	61.3±9.1
	Control	188.0±22.1	121.0±30.6	172.0±10.6	91.0±16.7
O+M	Warming	80.9±10.5	55.2±16.7	161.2±5.0	81.1±8.3
	Control	212.2±21.8	141.8±12.9	208.6±15.1	96.0±19.5

Table 2. Statistical results (*F*- and *P*-values are given) of the effects of soil warming (T), sample dates (M), soil layers (SL) and their interactions on total root mass, live fine roots (LF), live coarse roots (LC), dead fine roots (DF), dead coarse roots (DC) mass and net N mineralization.

	Total mass		LF		LC		DF		DC		N mineralization	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Treatment (T)	13.391	**<0.001**	20.196	**<0.001**	3.657	0.058	7.119	**0.008**	0.394	0.531	6.934	**0.012**
Soil layer (SL)	77.085	**<0.001**	43.185	**<0.001**	8.672	**0.004**	153.304	**<0.001**	28.699	**<0.001**	35.948	**<0.001**
Month (M)	0.479	0.792	1.105	0.360	0.192	0.965	1.154	0.335	0.906	0.479	13.277	**<0.001**
T×SL	14.449	**<0.001**	19.489	**<0.001**	2.286	0.133	7.762	**0.006**	3.464	0.065	3.495	0.070
T×M	0.133	0.984	0.297	0.914	0.255	0.937	0.503	0.774	0.708	0.618	1.052	0.395
SL×M	0.476	0.794	0.595	0.704	0.330	0.894	0.996	0.422	1.438	0.214	7.028	**<0.001**
T×SL×M	0.109	0.990	0.183	0.969	0.361	0.875	0.433	0.825	0.563	0.728	0.866	0.534

Significant differences ($P < 0.05$) were highlighted in bold.

Table 3 The ratios of fine root biomass to fine root necromass (FB:FN), coarse root biomass to coarse root necromass (CB:CN) and total biomass to total necromass (TB:TN) in the organic layer, upper mineral layer and the organic plus upper mineral layer for both warming and control plots across all sampling dates (mean value ± SE) (n=8).

Soil layer	Treatment	FB:FN	CB:CN	TB:TN
Organic	Warming	0.7±0.1	2.4±2.8	0.7±0.8
	Control	1.0±0.2	4.2±5.0	1.5±1.9
	P-value	0.063	0.294	**0.015**
Mineral	Warming	0.5±0.1	0.5±0.6	0.6±0.9
	Control	1.3±0.2	2.5±1.5	1.5±1.5
	P-value	**0.001**	0.248	**0.002**
O+M	Warming	0.6±0.2	1.4±1.3	0.7±0.3
	Control	1.2±0.4	3.4±3.2	1.5±0.3
	P-value	**0.008**	0.191	**0.032**

Significant differences ($P < 0.05$) are highlighted in bold.

Table 4 The concentrations of total N, total C and carbon compounds in the live fine, live coarse, dead fine and dead coarse roots from the warmed and control plots. Data were averaged across all sample dates with one standard error. Different letters (a and b) of total N and C:N indicated significant difference at 0.05 level between the warmed and control plots. (Mean values ± SE)

Treatment	Root categories	Total C (mg g^{-1})	Total N (mg g^{-1})	C:N	Sugars (mg g^{-1})	Starch (mg g^{-1})	Hemicellulose (mg g^{-1})	Cellulose (mg g^{-1})	Lignin (mg g^{-1})
Warming	Live fine roots	449.3±6.1	13.7±0. 3a	38.5±1.2a	49.9± 4.6	52.4±4.5	9.0±1.5	87.4±3.7	222.9±16.3
	Live coarse roots	474.5±4.2	6.1±0.3	91.7±5.0	64.8±9.6	61.3±7.1	6.8±1.8	168.5±4.1	173.4±16.8
	Dead fine roots	431.4±6.6	11.2±0.3	45.2±0.7	36.1±4.1	40.4±4.5	4.6±0.4	54.4±2.2	277.8±31.4
	Dead coarse roots	455.2±8.6	8.6±0.5	63.0±3.6	36.1±4.5	42.7±4.7	6.2±0.9	95.5±12.4	227.7±24.2
Control	Live fine roots	444.4±4.8	12.4±0.2b	42.1±1.13b	52.5±4.4	51.7±4.6	7.8±1.2	86.8±5.1	203.8±9.4
	Live coarse roots	469.8±5.4	6.8±0.5	83.6±7.4	67.6±5.5	60.6±4.2	9.3±1.6	164. 3±6.6	140.2±17.9
	Dead fine roots	425.1±7.2	11.4±0.2	43.6±0.5	37.3±3.1	44.7±4.4	4.7±0.4	62. 6±4.0	282.0±20.5
	Dead coarse roots	451.4±5.5	8.0±0.9	69.4±7.0	38.6±4.5	46.7±5.2	5.8±0.8	103.5±14.9	218.4±29.7