BELOWGROUND CARBON FLUXES RESPOND TO NUTRIENT AVAILABILITY IN A NORTHERN HARDWOOD FOREST

by

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Abstract

Soil respiration is a major flux of carbon to the atmosphere in terrestrial ecosystems. If belowground carbon cycling processes are disrupted, as by N deposition in northern hardwood forests, there could be feedbacks to atmospheric CO_2. Despite its importance in the global carbon budget, soil respiration is not widely studied across different levels of nutrient availability in soils. In this study, we measured soil respiration across northern hardwood forest sites of differing fertility and age in the White Mountains of New Hampshire.

Across the range of soil nutrient availability, soil respiration and belowground carbon allocation were lower in sites with relatively low nutrient availability compared with sites categorized as medium or high fertility. Soil respiration and belowground carbon allocation did not differ significantly with forest age.

Summer soil respiration rate was not correlated to soil P and Ca availability, but was low in soils with high N availability. This result suggests that greater N availability in soils may contribute to less belowground carbon allocation in northern hardwood forests.

To further study single and synergistic nutrient effects on soil or microbial respiration, nitrogen and phosphorus were applied in treatments of: N-only, P-only, N+P, and control. There were no significant N or P fertilization effects on soil or microbial respiration after two years of fertilization treatment.

To study microbial respiration alone, five stands (4 plots in each stand) were selected in which living roots were severed by digging trenches. Although total soil respiration did not change after fertilization, the contribution of microbial respiration to soil respiration increased significantly in N+P plots compared to N-only and control plots with trenches. Microbial respiration in laboratory incubations also suggested that there were no discernible changes in Oe and Oa horizons after fertilization.

Data from this study suggest that nutrient availability, particularly N, can affect soil respiration. The two-year study period was not long enough to detect fertilization effects on soil and microbial respiration, hence long-term tracking of the fertilization treatments in this study will be necessary to determine if belowground carbon flux changes in response to increased N and P availability in soils.

Keywords: Soil respiration, belowground carbon allocation, fine root biomass, Bartlett Experimental Forest, Hubbard Brook Experimental Forest, Jeffers Brook,

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Chapter 1. Introduction

1. 1 Review of studies on soil respiration

Soil respiration refers to the production of CO_2 from soils when soil organisms and roots respire during their metabolic activities (Luo and Zhou 2006). Soil respiration represents the combined respiration from autotrophic and heterotrophic organisms. When plants fix carbon through photosynthesis, some of the fixed carbon then returns to the atmosphere by respiring CO_2 to grow or maintain roots. Heterotrophic organisms (microbes and fauna) release CO_2 when they decompose soil organic matter and detritus (i.e., litter, roots, and root exudates).

Global CO_2 flux from soils is large. Global soil respiration was estimated to be 68 - 77 Pg (Petagram) C yr^{-1} (Schlesinger 1977, Raich and Schlesinger 1992, Raich and Potter 1995). The soil respiration rate in forests differs according to vegetation type (Raich and Schlesinger 1992, Raich and Potter 1995, Raich and Tufekciogul 2000). Among vegetation types, soil respiration is high in warm and wet forests (Raich and Schlesinger 1992) and in broadleaf and evergreen forests (Raich and Potter 1995) (Table 1.1).

In forests of North America, mean annual soil respiration (Table 2) was 733 g C m^{-2} yr^{-1}, which is similar to the soil respiration in temperature forests (647 – 681 g C m^{-2} yr^{-1}) (Table 1.1) based on the study by Raich and Schlesinger (1992). Within North American forests, annual soil respiration varies by abiotic and biotic factors such as climate (temperature and moisture), forest age, dominant tree species, and soil characteristics (Table 1.2).

Soil respiration differs with geographical characteristics such as soil physical properties, elevation, and topography, which may be due to different productivity. Across soil drainage classes, soil respiration can be low in poorly-drained soils which was shown under

different drainage environments in 60-year-old mixed forests at Harvard forests, Massachusetts (Davidson et al. 1998b) and also shown across 3 to 71-year-old chronosequence, black spruce stands in Manitoba, Canada (Wang et al. 2002). Soil respiration can be low at high elevation. In Olympic National Park in Washington, soil respiration decreased with increased elevation from 480 to 1450 m (Kane et al. 2003). Topographically, soil respiration also can be low at north-facing aspects, where the sun exposure is shorter than south-facing (Kane et al. 2003) and at valleys compared to on ridges (Hanson et al. 1993).

Correlation results based on data in Table 2 show that soil respiration in forests increases as mean annual temperature increases (n = 26, $p < 0.01$), but soil respiration is not correlated to annual precipitation (n = 15, $p = 0.36$) (Figure 1.1). In temperate forests, the high annual temperature means long growing seasons and short snow cover time, which can lead to increased productivity. No correlation of precipitation and soil respiration can be explained by the water condition being adequate for tree growth in this area.

Correlation results also supported the finding that soil respiration increases as forests age increases from 1 to 350 years, as shown in Table 2 (n = 56, $p < 0.01$) (Figure 1.2). As forests develop after disturbances, it is likely that soil respiration increases with increased forest productivity and litter production (Chapin and Matson 2011). However, the age pattern was not always clear within stand in some of the northern hardwood forests (Ryan 1991b, Wang et al. 1995, Irvine and Law 2002, Tang et al. 2008). Unclear age patterns within stands can be probably from natural variation, and the changes of tree species and environmental conditions across forest successions make it hard to interpolate the soil respiration patterns across forest ages.

Based on the data in Table1.2, soil respiration was slightly higher in deciduous

forests (687 g C m^{-2} yr^{-1}) than in coniferous forests (637 g C m^{-2} yr^{-1}). Tree species may have different plant productivity (Raich and Tufekciogul 2000). The lower soil respiration in coniferous forests than in deciduous forests is probably because of differences in net primary productivity and carbon inputs (Davidson et al. 1998b).

1.2 Belowground carbon allocation

Belowground carbon allocation (BCA) is carbon allocation to fine roots, exudates, and mycorrhizae. BCA is one of the most important carbon fluxes in forest ecosystems (Davidson et al. 2002, Giardina et al. 2005), and BCA is nearly 2/3 of soil respiration (Raich and Nadelhoffer 1989). BCA cannot be measured directly (Ryan 1991a, Hanson et al. 2000). Raich and Nadelhoffer (1989) suggest that BCA could be estimated by measuring the difference between annual rates of soil respiration and aboveground litterfall when the forest soil carbon storage is near a steady state (equation 1).

$$\text{BCA} = \text{soil respiration} - \text{literfall} \pm \Delta C \quad \text{(equation 1)}$$

where ΔC equals change in belowground carbon storage.

Soil respiration is CO_2 flux from the forest floor and soil including root respiration and microbial respiration from above- and below-ground litter. If the belowground carbon storage does not change, the amount of litterfall in equation 1 is the same as the aboveground production respired from soil, and BCA can be estimated using soil respiration minus litterfall (Davidson et al. 2002). The assumption, $\Delta C = 0$ in equation 1, is that annual changes in soil carbon and root biomass are negligible (Raich and Nadelhoffer 1989).

Table 1.3 shows that, in forests of North America, the mean BCA was 650 g C m^{-2} yr^{-1} when using Raich and Nadelhoffer (1989) approach, and BCA was 79 % of soil respiration (Table 1.2). Like soil respiration, BCA is also influenced by climate, soil properties, or soil nutrients. Several studies show that BCA is low where temperature is low due to low plant productivity (Schlesinger 1977, Vogt et al. 1986, Gower et al. 1995).

1.3 Environmental factors affecting soil respiration.

Soil respiration can be influenced by several environmental factors including soil temperature, moisture, and nutrients in soil. Since soil respiration results from metabolic activity, environmental factors can affect soil respiration.

1.3.1 Soil temperature

Modeling soil respiration is often based on the relationship between soil respiration and soil temperature. One of the most commonly used strategies for modeling soil respiration using soil temperature is an exponential model, which was proposed by Van't Hoff (1884).

$$\text{Soil respiration rate} = a\, e^{bT} \quad \text{(equation 2)}$$

where a and b are coefficients and T is soil temperature

To describe the sensitivity of soil respiration to temperature, Q_{10} is used. Q_{10} is a temperature coefficient where Q_{10} is the ratio of respiration rates over a 10℃ soil temperature interval (Drobnik 1962, Davidson et al. 1998a).

$$Q_{10} = 10^{b} \quad \text{(equation 3)}$$

where b is a coefficient of equation 2.

Although Q_{10} may not be the best model to predict soil respiration based on soil temperature, Q_{10} has been used to compare temperature sensitivity on soil respiration (Schlesinger and Andrews 2000, Qi et al. 2002). The literature suggests that the median Q_{10} value is 2.4 (between 1.3 to 3.3), which means that soil respiration increases about 2.4 times as soil temperature increases 10℃ (Schlesinger and Andrews 2000, Qi et al. 2002).

Both root and microbial respiration also correlate with soil temperature. First, root respiration increases as soil temperature increases up to 35 - 40 ℃ because metabolic activities and photosynthetic products (like sugar) increase at high temperatures (Palta and Nobel 1989, Atkin et al. 2000). Increasing root growth under high soil temperature can also influence root respiration (Tryon and Chapin III 1983). Microbial respiration increases as temperature increases but the correlation is less strong than for root respiration (Boone et al. 1998). Increased soil temperature contributes to enhanced microbial activities (Bunnell et al. 1977, Gill and Jackson 2000), leading to increased microbial respiration. Temperatures in the range of 30 - 40 ℃ restrict root or microbial respiration; however, this is not likely to happen in northern hardwood forest areas.

1.3.2 Soil moisture

Soil moisture is another important factor affecting soil respiration, in the short term because of effects on microbial metabolim and in the long term because of effects on primary productivity (Raich and Potter 1995, Davidson et al. 1998b, Qi and Xu 2001, Xu et al. 2004). Soil respiration is often high under wet soil conditions where precipitation is high or when precipitation increases in a specific year (Skopp et al. 1990, Liu et al. 2002, Xu et al. 2004, Harper et al. 2005). However, under the very wet conditions like saturated and anaerobic

conditions, soil respiration decreases as aerobic metabolisms of roots and microbes are restricted (Bridgham and Richardson 1992).

1.3.3 Nutrients

Human activities have increased nutrient availability in soils. For example, N availability in soil has increased through post-industrial deposition by anthropogenic activities including fossil fuel combustion and high-intensity agriculture (Davidson 2009). Forest ecosystems are often limited by nutrients (Aber and Melillo 2001), especially N and P. Nitrogen is one of the most important and often limiting nutrients in temperate forests (Chapin 1980) and many studies have focused on N. The P is much less studied than N in temperate forests, but P is also one of the most limiting nutrients (Vitousek et al. 2010). Increased N and P can affect forest productivity and related biological processes, leading to the potential for positive or negative feedback on the global carbon budget (Janssens et al. 2010, Vitousek et al. 2010). Nutrient input has been shown to increase forest productivity, reduces carbon allocation belowground by trees, and to changes decomposition rates directly through effects on decomposing organisms or indirectly through substrate quality (Fog 1988, Melillo et al. 1993) Meta-analysis shows that nutrient addition generally suppresses soil respiration (Janssens et al. 2010), though increased nutrients can enhance soil respiration by increasing plant productivity under nutrient limited soils. For example, N fertilization in 11 year-old loblolly pine plantations in North Carolina increased root respiration by 42 % and soil respiration by 13 %, which probably resulted from doubling standing litter biomass and increasing coarse roots (Maier and Kress 2000). N fertilization also increased soil respiration by 19 % in mixed hardwoods at Harvard Forest, Massachusetts, as plant productivity increased (Contosta et al. 2011). However, responses to fertilization may be transient. For

example, Burton et al. (2004) found in 90-year-old sugar maple dominant stands in Michigan that soil respiration increased after N fertilization during the first year, but decreased 6 years later. Similarly, Bowden et al. (2004) found that in 55-year-old mixed hardwood forests in Massachusetts that soil respiration increased in the first year, but was less 2 and 13 years after fertilization.

Nutrient additions can increase plant respiration per unit biomass. Experimental N addition increased root N concentration and root specific respiration in northern hardwood forests in Michigan (Burton et al. 2011) and in larch and ash plantations in China (Jia et al. 2010). Microbial respiration per unit biomass was also higher in multi-nutrient addition plots compared to control plots in young northern hardwood forests in New Hampshire (Fisk and Fahey 2001).

However, N effects on soil respiration may vary depending on site conditions and the amount of nutrient addition (Luo and Zhou 2006, Janssens et al. 2010). For example, in temperate forest ecosystems, meta-analysis based on over 200 studies showed the negative effects of N on soil respiration in 75 % of studies (Janssens et al. 2010). The meta-analysis showed 10 % reduction of soil respiration following N additions with decreases in both autotrophic and heterotrophic respiration. There were few studies using other nutrients such as P and Ca to study nutrient effects on soil respiration.

Nutrient additions can reduce BCA due to negative effects on root or microbial respiration. Several studies report that increased nutrient availability decreased fine root production in a 65-year-old sugar maple plantation in New York, an 85-year-old yellow birch stand in New Hampshire (Phillips and Fahey 2007), a Douglas-fir forest in New Mexico (Gower et al. 1992), a 31-year-old red pine plantations in northern Wisconsin (Haynes and

Gower 1995), and an 11 year-old loblolly pine plantations in North Carolina (Maier and Kress 2000). Nutrient additions were also found to decrease root activity in a 13-year-old *Eucalyptus pauciflora* forest in Australia (Giardina et al. 2003). Diminished root production and activity can lead to reduced root respiration and associated microbial respiration. Nutrient addition also decreased microbial biomass production in a 65-year-old red oak and sugar maple plantations in New York, an 85-year-old yellow birch stand in New Hampshire (Phillips and Fahey 2007), a sugar maple dominated forest in northern Michigan (Saiya-Cork et al. 2002), and a 7-year-old cottonwood and loblolly pine plantations in northwest Florida (Lee and Jose 2003a). Likewise, nutrient addition decreased microbial activity in 55-year-old mixed hardwood forests and 70-year-old red pine plantations at Harvard Forest, Massachusetts (Bowden et al. 2004) and both microbial biomass and microbial activities in sugar maple and northern red oak plots in New York and yellow birch plots in New Hampshire (Phillips and Fahey 2008).

N additions can alter decomposition rates of litter and soil organic matter. Decomposition rate is often higher when nutrient concentration of litter or roots is high (Melillo et al. 1982, Silver and Miya 2001), and it can be expected that the decomposition rate should increase with increased nutrient concentration in plant tissues after fertilization. However, several fertilization studies found no clear pattern of decomposition rate after fertilization because variations among tree species offset the fertilization effects on their decomposition rates (Hobbie 2005, Knorr et al. 2005). Nutrient addition also affects microbes involved in decomposition. Nutrient addition not only alters microbial biomass and activities, as mentioned above, but nutrient addition can also change microbial community composition (Compton et al. 2004, Allison et al. 2008). In a 40-year-old pine stand in northern Sweden, NPK additions reduced the decomposition rate probably due to changed microbial

community and litter quality (Franklin et al. 2003). Since each microbial community has different structure and function for nutrients, the changed microbial community can also affect soil respiration.

There are a few studies adding not only N, but P or other elements to study the nutrient effects on soil respiration. In a mature black spruce forest in Alaska, N and P did not change soil respiration, while N addition changed microbial community composition (Allison et al. 2008). In 2-year-old loblolly pine clones in Virginia, soil respiration did not change after N+P additions; increased root respiration was offset by decreased microbial respiration (Tyree et al. 2008). These two studies show that N is more limiting than P and P is correlated to N since a single P addition did not differ with controls (no nutrient addition). In a 13-year-old *Eucalyptus pauciflora* forest in Australia, P additions reduced soil respiration by 8 % due to low root activity (Keith et al. 1997).

1.4 Separating root and microbial respiration

Soil respiration is the sum of autotrophic (root) and heterotrophic (microbial) respiration. Root respiration is the CO_2 produced during the process of living root tissue, and microbial respiration is the CO_2 produced by the decomposition of litter and soil organic matter. Root and microbial respiration can be influenced differently by environmental factors (e.g., the climate, soil type, or soil properties) or human disturbances (e.g., climate change, N deposition, or forest management). Therefore, separating soil respiration into root and microbial respiration is critical to understanding the response of soil respiration to environment changes. To separate soil respiration into root and microbial respiration, Hanson et al. (2000) describe three common methods: 1) direct measurements of components (litter,

roots, soils) in situ, 2) measurements in the presence of roots versus in the absence of roots, and 3) measurements using isotopes.

1) Measurement of each component requires measuring the CO_2 flux in roots, soils without roots, and litter. This method is simpler than root exclusion or isotope methods. However, measurements from disturbing components (by pulling out roots, sieving soils, and removing litter) may not represent the natural ecosystems.

2) Root exclusion is used to estimate microbial respiration by excluding roots, and root respiration is estimated as the total soil respiration minus the estimated microbial respiration. In forests, roots are removed by trenching (Bowden et al. 1993, Drake et al. 2012), clear-cutting, or girdling. The root exclusion method disturbs soils less than the sum of each component methods. However, after killing roots, dead roots remain (Epron et al. 1999), and starch reserves of roots can increase after girdling trees (Högberg et al. 2001), which can make microbial respiration overestimated or underestimated. To minimize this problem, soil respiration should be measured several months after roots are excluded (Ewel et al. 1987, Bowden et al. 1993). Also, the root exclusion method could change the environment by increasing soil moisture after trenching (Hart and Sollins 1998) or increasing soil temperature after clear-cutting (Toland and Zak 1994).

3) Isotope method can determine the component sources of soil respiration by tracing an isotope through photosynthetic pathways. The most commonly used isotope methods are stable isotope techniques (growing a C3 plant on a C4 soil or C4 plot on C3 soil), using Bomb ^{14}C, and free air CO_2 enrichment using ^{13}C (Hendrey et al. 1993, Hanson et al. 2000). The isotope method is costly and

requires highly technical approaches; however the advantage is that the isotope method is not accompanied by environmental disturbances.

The average microbial respiration contribution to soil respiration was 50 %, ranging from 10 to 96 % in North American forests (Table 1.4). The sum of components method was used the most (n = 20), followed by root exclusion (n = 9) and isotope (n = 4) methods. If it is assumed that the isotope method is the most accurate among these three methods, the contribution of microbial respiration to soil respiration was overestimated using root exclusion methods (62 %) compared to isotope (53 %), and the sum of components (45 %) was underestimated (Table 1.4).

The ratio of microbial respiration to soil respiration can be affected by environmental conditions. Based on the data in Table 4, as soil respiration increases, a portion of microbial respiration to soil respiration decreases (n = 19, $p = 0.06$). Deciduous stands (n = 13, 54 %) had a little larger microbial portion of soil respiration than conifer stands (n = 20, 46 %), in agreement with an early analysis of respiration in deciduous and conifer forests (Subke et al. 2006). Microbial respiration contributed less to soil respiration in high N stands than low N stands in sugar-maple dominated stands in Michigan (Burton et al. 2004). Microbial respiration was 24 - 40 % less in high elevation than in mid and low elevation in black spruce stands in Alaska (Vogel et al. 2005).

1.5 Overview and objectives

Soil respiration is a key ecosystem process that releases carbon from the soil in the form of CO_2. Soil respiration is the 2nd greatest flux in the global carbon cycle after gross

primary productivity, and it is greater than CO_2 emissions from fossil fuels (Schlesinger 1977, Raich and Schlesinger 1992). The carbon flux between plants and soils are closely balanced before disturbances (Schlesinger 1977). If belowground carbon cycling processes are disrupted, there could be important feedback to atmospheric CO_2.

N availability in soil has increased through post-industrial deposition in northern hardwood forests (Aber et al. 2003). Anthropogenic N deposition has an influence on plants and soils, through soil acidification, leaching cations, and changing tree species composition (Aber et al. 1993, Lovett and Rueth 1999). The added N can also affect other nutrients, such as P (Braun et al. 2010, Crowley et al. 2012) and Ca (Lawrence et al. 1995). Changed nutrient availability in forest soil has the potential for providing positive or negative feedback on the global carbon budget (Janssens et al. 2010) by altering decomposition rates (Matson et al. 2002, Knorr et al. 2005), plant growth (Pregitzer et al. 2008, Thomas et al. 2009), or carbon allocation amounts and the partitioning of allocation above- and below-ground (Poorter and Nagel 2000, Matson et al. 2002).

The overall aim of this study was to understand how soil respiration differs with soil nutrient availability.

1) The first objective was to investigate differences in soil respiration, BCA, and fine root biomass in northern hardwood forests. This study was conducted across forest ages (20 years old, 30-40 years old, and 80-120 years old) in site differing in fertility including N, P, and Ca availability (Bartlett: infertile, Hubbard Brook: intermediate, and Jeffers Brook: fertile site)

2) The second objective was to understand N, P, and NP fertilization effects on soil respiration and microbial respiration across forest ages in stands with inherently different site fertility.

Table 1.1. Average soil respiration rates based on literature studies in different vegetation types in forests

	Vegetation type	**Soil respiration rate (g C m^{-2} yr^{-1})**
Raich and Potter (1995)	Broadleaf evergreen	1050-1185
	Broadleaf deciduous	463-566
	Broadleaf and needleleaf	421-505
	Needleleaf evergreen	314-364
	Needleleaf deciduous	161-245
Raich and Schlesinger (1992)	Tropical moist	1260
	Tropical dry	673
	Temperate deciduous	647
	Temperate coniferous	681
	Boreal	322

* 68 literature studies for Raich and Potter (1995) and 59 literature studies for Raich and Schlesinger (1992) were used in their estimates of soil respiration.

* Soil respiration was estimated using two exponential models using log-transformed and untransformed data (Raich and Potter, 1995)

Table 1.2. Annual soil respiration in forests in North America

Location	Mean annual temperature (°C)	Mean annual precipitation (mm)	Age (yr)	Tree species	Treatment	Soil respiration (g C m^{-2} yr^{-1})	References
Alaska	-3.3	269	110	*Picea mariana*	High elevation	496	Vogel et al. (2005)
			75	*Picea mariana*	Mid elevation	415	
			120	*Picea mariana*	Low elevation	377	
Alaska	4.6		160-200	*Picea mariana*	—	470	Ruess et al. (2003)
Florida	21.3	1300	6	*Pinus elliottii*	—	850	Ewel et al. (1987)
			6	*Pinus elliottii*	—	1123	
Florida			7	*Hibiscus tiliaceus*	—	858	Lee and Jose (2003a)
			7	*Pinus taeda*	—	647	
Indiana	11	1000	60-80	*Acer* spp., *Fagus* spp., *Quercus* spp.	—	1050	Ehman et al. (2002)
Maine	5.5	1000	45-130	*Picea* spp., *Tsuga* spp., *Populus* spp., *Betula* spp.	—	753	Savage and Davidson (2001)
Maine			4-6	*Acer rubrum*	Control	645	Fernandez et al. (1993)
			4-6	*Acer rubrum*	Clearcut	765	
Manitoba, Canada	-3.4	536	3	*Picea mariana*	Well drained	226	Wang et al. (2002)
			6	*Picea mariana*	Well drained	412	

			12	*Picea mariana*	Well drained	357	
			20	*Picea mariana*	Well drained	413	
			37	*Picea mariana*	Well drained	350	
			71	*Picea mariana*	Well drained	274	
			131	*Picea mariana*	Well drained	244	
			3	*Picea mariana*	Poorly drained stands	146	
			6	*Picea mariana*	Poorly drained stands	380	
			12	*Picea mariana*	Poorly drained stands	300	
			20	*Picea mariana*	Poorly drained stands	303	
			37	*Picea mariana*	Poorly drained stands	256	
			71	*Picea mariana*	Poorly drained stands	233	
			131	*Picea mariana*	Poorly drained stands	264	
Massachusetts	8.5	1100	mixed	*Quercus* spp., *Acer* spp.	—	371	Bowden et al. (1993)
Massachusetts			60	mixed hardwood	Well drained	780	Davidson et al. (1998b)
			60	mixed hardwood	Moderately well drained	720	
			60	*Tsuga spp.*	Moderately well drained	670	
			60	mixed hardwood, *Tsuga* spp.	Poorly drained	840	
			60	*Acer* spp.	Poorly drained	530	
Massachusetts			50-70	*Quercus* spp., *Acer* spp., *Tsuga* spp.	—	647	Savage and Davidson

							(2001)
Massachusetts			mixed	mixed hardwood	—	442	Contosta et al. (2011)
Massachusetts	7	2800	100>	mixed hardwood	—	840	Gaudinski et al. (2000)
Michigan	6.2	750	90	*Populus grandidentata, P. tremuloides, Quercus alba, Fagus grandifolia, Acer saccharum*	—	1132	Curtis et al. (2002)
Michigan			mixed	*Acer saccharum, Quercus rubra*	Intact	487	Toland and Zak (1994)
			mixed	*Acer saccharum, Quercus rubra*	Clearcut	467	
			mixed	*Acer saccharum, Tilia 17mericana*	Intact	469	
			mixed	*Acer saccharum, Quercus rubra*	Clearcut	474	
Michigan	4.8	821	94	*Acer saccharum*	Low N availability	1627	Burton et al. (2004)
	6.1	828	88	*Acer saccharum*	High N availability	1824	
	6.9	856	89	*Acer saccharum*	High N availability	1801	
	7.6	793	93	*Acer saccharum*	Low N availability	2176	
New Hampshire	-9~18	1400	40>	mixed hardwood	—	660	Fahey et al. (2005b)
North Carolina	17	1200	11	*Pinus taeda*	—	1263	Maier and Kress (2000)
North Carolina			<20	*Pinus taeda* forest and mixed deciduous	—	994	Andrews and Schlesinger (2001)
North Carolina				*Pinus taeda*	—	1183	Andrews et al. (1999)
Oregon	8.7	2400	old	*Pseudotsuga menziesii, Tsuga heterophylla*	—	800	Sulzman et al. (2005)
Oregon	7.5	552	14	*Pinus ponderosa*	—	484	Irvine and Law

							(2002)
	8.1	524	50~250	*Pinus ponderosa*	—	526	
Oregon	7.5	552	14	*Pinus ponderosa*	—	780	Law et al. (2001)
	8.1	524	50~250	*Pinus ponderosa*	—	654	
Tennessee	14	1400	50-120	*Populus* spp., *Acer saccharum, Tilia Americana, Fraxinus pennsyvanica*	—	950	Curtis et al. (2002)
Tennessee	15	1400	50-100	mixed hardwood	Valleys	736	Hanson et al. (1993)
				mixed hardwood	NE slopes	818	
				mixed hardwood	SW slopes	845	
				mixed hardwood	Ridges	927	
Washington				*Pseudotsuga menziesii*	—	490	Vogt et al. (1980)
				Tsuga heterophylla	—	650	
				Abies alba	—	620	
				Alnus rubra	—	570	
Washington			23	*Pinus contorta, Abies amabilis*	—	590	Ryan (1991b)
			180	*Pinus contorta, Abies amabilis*	—	616	
Washington	5.8		79	*Pseudotsuga menziesii, Tsuga heterophylla*	SE 33% slope, 710 elevation (m)	1230	Kane et al. (2003)
	5.3		78	*Pseudotsuga menziesii, Tsuga heterophylla*	N 14% slope, 669 elevation (m)	1090	
	6.6		221	*Pseudotsuga menziesii*	SW 35% slope, 955 elevation (m)	890	
	5.7		205	*Pseudotsuga menziesii, Tsuga heterophylla*	N 52% slope, 898 elevation (m)	1020	
	4.4		76	*Pseudotsuga menziesii, Pinus*	S 71% slope,	870	

				contorta	1423 elevation (m)		
	3.4		73	*Abies lasiocarpa, Tsuga heterophylla*	N 58% slope, 1450 elevation (m)	740	
	6.4		216	*Pseudotsuga menziesii, Tsuga heterophylla*	N 23% slope, 568 elevation (m)	1310	
	5.1		302+	*Pseudotsuga menziesii, Tsuga heterophylla*	SE 60% slope, 940 elevation (m)	1080	
	3.9		206	*Abies lasiocarpa, Pseudotsuga menziesii*	SE 37% slope, 1383 elevation (m)	610	
	7.1		183	*Pseudotsuga menziesii*	SW 47% slope, 480 elevation (m)	1210	
	7.2		216	*Pseudotsuga sitchensis, Thuja plicata*	0% slope, 175 elevation (m)	1000	
Wisconsin	4.8	780	31	*Pinus resinosa*	—	858	Haynes and Gower (1995)
Wisconsin	4.6	3200	66	*Quercus alba, Q. prinus, Acer rubrum, A. saccharum*	—	810	Curtis et al. (2002)
Wisconsin to Michigan	3.9	896	1	-	Clearcut and repeated burns	513	Tang et al. (2008)
			1	-	Blowdown and partial salvage	680	
			1	*Populus tremuloides*	Clearcut with residual trees	747	
			3	*Populus tremuloides*	Regeneration from clearcut	747	
			10	*Populus tremuloides*	Young aspen	794	
			26	*Populus tremuloides*	Intermediate aspen	802	
			73	*Acer saccharum*	Mature northern hardwood	690	
			~350	*Acer. Saccharum*	Old-growth northern hardwood	571	
				Mean		**733**	

Table 1.3. Belowground carbon allocation (BCA) in forests in North America

Location	Age (yr)	Tree species	Treatment	BCA (g C m^{-2} yr^{-1})	Litterfall (g C m^{-2} yr^{-1})	% of BCA to annual soil respiration	References
Indiana	60-80	*Acer* spp. *Fagus* spp. *Quercus* spp.		810	240	77	Ehman et al. (2002)
Maine	45-130	*Picea* spp. *Tsuga* spp. *Populus* spp. *Betula* spp.		595	158	79	Savage and Davidson (2001)
Massachusetts	50-70	*Quercus* spp., *Acer* spp., *Tsuga* spp.		459	188	71	Savage and Davidson (2001)
Massachusetts	100>	mixed hardwood		620	220	74	Gaudinski et al. (2000)
Michigan	90	*Populus* spp and hardwoods		1012	148	87	Curtis et al. (2002)
New Hampshire	40>	mixed hardwood		478	200	71	Fahey et al. (2005)
Oregon	old	*Pseudotsuga menziesii, Tsuga heterophylla*		650	150	81	Sulzman et al. (2005)
Oregon	mixed	*Pinus ponderosa*	Semi-arid	648	132	83	(Law et al. 2000, Law et al. 2001)
		Pinus ponderosa	not	602	52	92	
Tennessee	50-100	mixed hardwood	Valleys	597	139	81	Hanson et al. (1993)
		mixed hardwood	NE slope	642	176	78	
		mixed hardwood	SW slope	634	212	75	
		mixed hardwood	Ridges	748	179	81	
Wisconsin	66	*Pinus resinosa*	Control	722	136	84	Haynes and Gower (1995)
		Pinus resinosa	Fertilized	377	171	69	
Wisconsin	80	mixed hardwood		763	182	81	Bolstad
			Mean	**650**	**169**	**79**	

Table 1.4. Microbial respiration (MR) as a portion of soil respiration (SR) in forests

Location	**Age (yr)**	**Tree species**	**Treatment**	**MR/SR (%)**	Method	**References**
Alaska	160-200	*Picea mariana*		43	Component integration	Ruess et al. (2003)
		Pinus ponderosa		10	Component integration	Johnson (1993)
Alaska	110	*Picea mariana*	high elevation	42	Root exclusion	Vogel et al. (2005)
	75	*Picea mariana*	mid elevation	59	Root exclusion	
	120	*Picea mariana*	low elevation	52	Root exclusion	
Florida	9	*Pinus elliottii*		49	Component integration	Ewel et al. (1987)
	29	*Pinus elliottii*		38	Component integration	
Massachusetts		*Quercus* spp. *Acer* spp.		67	Component integration	Bowden et al. (1993)
Massachusetts	100>	northern hardwoods		42	Isotope	Gaudinski et al. (2000)
Michigan	94	*Acer saccharum*	Low N availability	45	Component integration	Burton et al. (2004)
	88	*Acer saccharum*	High N availability	29	Component integration	
	89	*Acer saccharum*	High N availability	46	Component integration	
	93	*Acer saccharum*	Low N availability	65	Component integration	
Michigan	2	*Populus euramericana*		80	Isotope	Horwath et al. (1994)
New Hampshire	40>	northern hardwoods		61	Component integration	Fahey et al. (2005)

North Carolina	mid age	*Pinus taeda*		45	Isotope	Andrews et al. (1999)
North Carolina		*Pinus taeda*		45	Isotope	
North Carolina	11	*Pinus taeda*	Control	48	Component integration	Maier and Kress (2000)
		Pinus taeda	N fertilization	27	Component integration	
North Carolina		*Pinus taeda*	Control	44	Root exclusion	Drake et al. (2012)
		Pinus taeda	N fertilization	91	Root exclusion	
Oregon	14	*Pinus ponderosa*		52	Component integration	Law et al. (2001)
	50~250	*Pinus ponderosa*		49	Component integration	
Oregon	old	*Pseudotsuga menziesii*, *Tsuga heterophylla*		77	Root exclusion	Sulzman et al. (2005)
Tennessee	1	*Pinus taeda*	Dec	33	Component integration	Edwards (2006)
		Pinus taeda	Mar	22	Component integration	
		Pinus taeda	May	46	Component integration	
		Pinus taeda	Aug	33	Component integration	
Wisconsin	31	*Pinus resinosa*	Control	58	Root exclusion	Haynes and Gower (1995)
		Pinus resinosa	N fertilization	96	Root exclusion	
France	35	*Fagus sylvatica*		39	Root exclusion	Epron et al. (1999)
Ontario, Canada	mature	*Pinus strobus, Populus tremuloides, Betula papyrifera, Acer rubrum*	mineral soils	50	Component integration	Hendrickson and Robinson (1984)

	Pinus strobus, Populus tremuloides, Betula papyrifera, Acer rubrum	litter layer Oe/Oa	80	Component integration
		Mean	**50**	

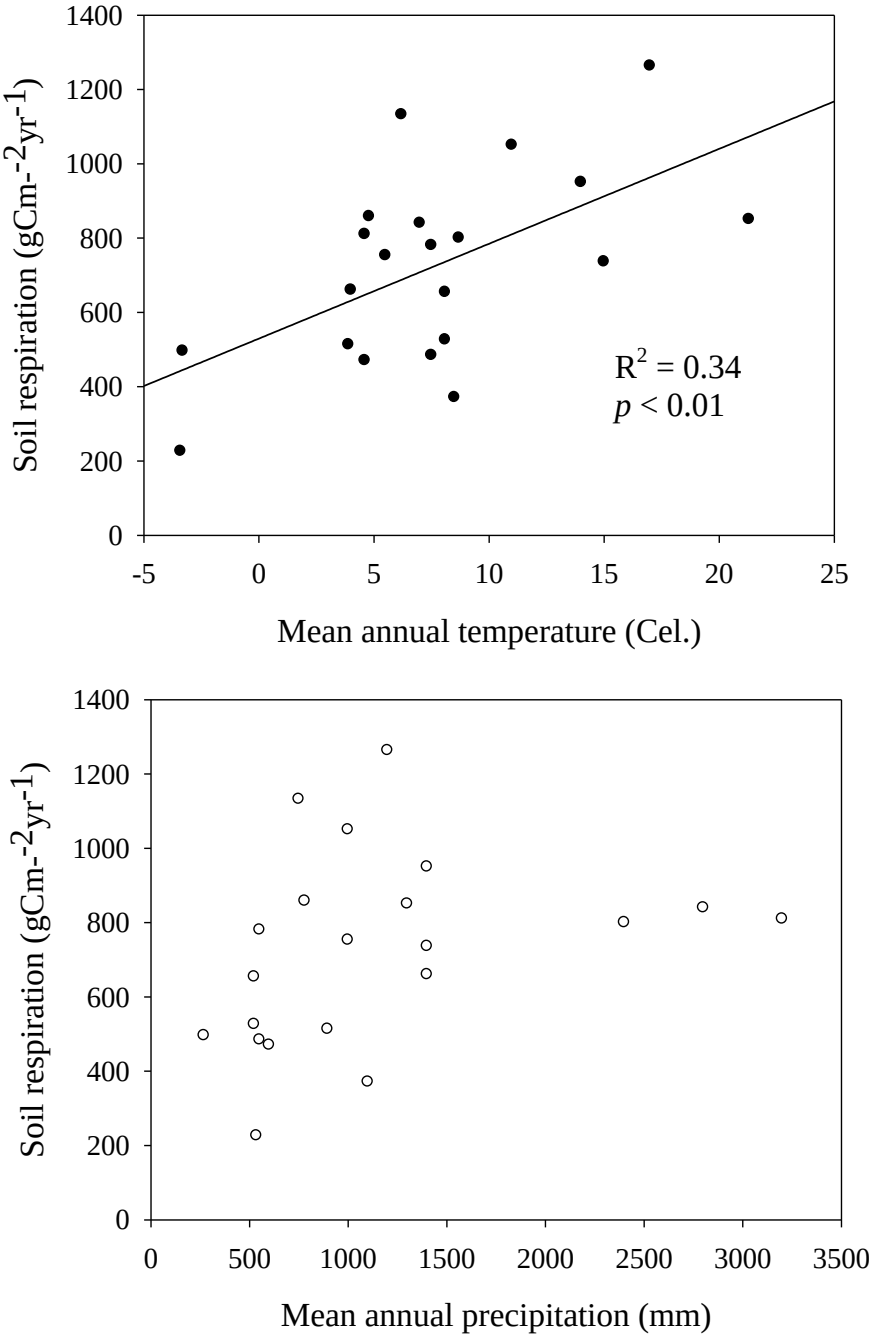

Figure 1.1. Relationship between soil respiration and climate (mean annual temperature and mean annual precipitation)

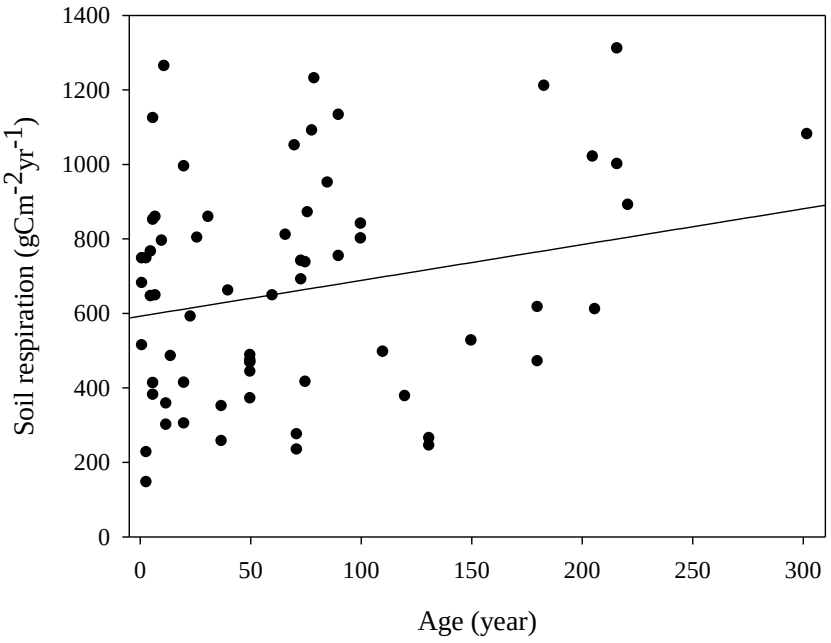

Figure 1.2. Relationship between soil respiration and forest age.

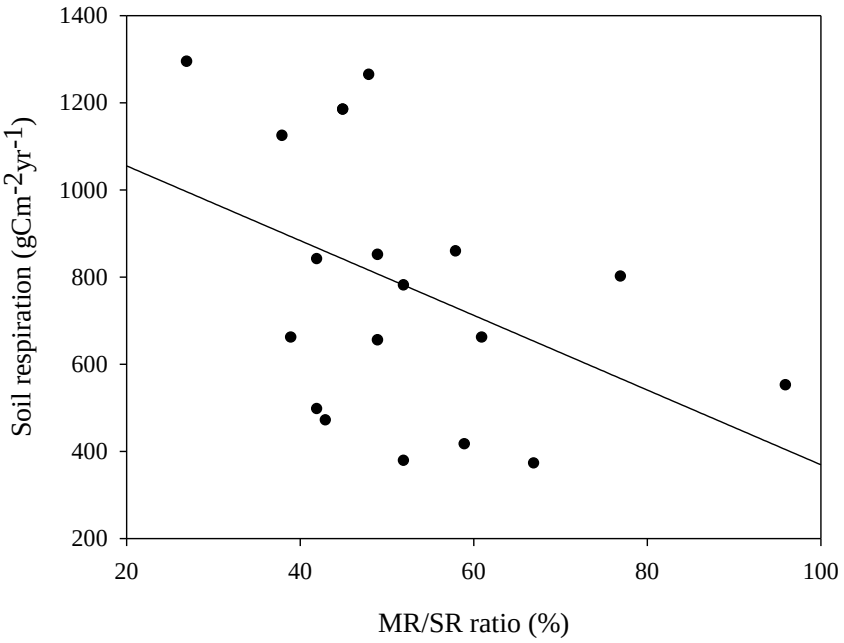

Figure 1.3. Relationship between soil respiration and the ratio of microbial respiration to soil respiration (MR/SR ratio).

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Chapter 2. Inherent nitrogen availability in soils affects belowground carbon allocation and soil respiration in northern hardwood forests of New Hampshire

2.1 Abstract

Nutrient acquisition in forests requires respiration by roots and associated mycorrhizae. Belowground carbon allocation and soil respiration should thus reflect effort allocated to nutrient uptake, for example in conditions of different nutrient availability controlled by site quality or stand history. Soil respiration, belowground carbon allocation, and fine root biomass were measured in three sites of different nutrient availability in the northern hardwood forests of the White Mountains of New Hampshire. Annual soil respiration was lowest at Jeffers Brook, the site with highest nutrient availability, and higher at Hubbard Brook and Bartlett Experimental Forests ($p < 0.01$). Comparing mid-aged (31-45 yr) and old (>80 yr) stands within each site, annual soil respiration was slightly but not significantly higher (3-9 %) in old stands than in mid-aged stands ($p = 0.14$ - 0.46). Fine root biomass did not differ across the three sites ($p = 0.79$), but it was higher in old stands than mid-aged stands ($p < 0.01$). Belowground carbon allocation, calculated by subtracting annual leaf litter production from total soil respiration and assuming no change in soil carbon storage, was lowest at Jeffers Brook ($p = 0.02$), like soil respiration, because there was little variation in leaf litter production across stands. There was no significant difference in belowground carbon allocation between forest ages ($p = 0.19$). During the growing season, soil respiration was low where net N mineralization and net nitrification were high across thirteen stands. However, available P and exchangeable Ca were not related to soil respiration. The relationship between N availability and soil respiration rate supports the claim that forests allocate more carbon belowground in ecosystems with low nutrient availability.

2.2 Introduction

Plants deploy assets to maximize the acquisition of limiting soil resources (Bloom et al. 1985, Rastetter et al. 2013). In forest ecosystems with low nutrient availability, plants allocate more carbon (C) belowgound to increase nutrient acquisition (Chapin 1991, Phillips and Fahey 2008). One of the key responses to increased soil nutrient availability is lower C allocation belowground (Haynes and Gower 1995), which allows proportionally higher aboveground production. Belowground C allocation (to roots, rhizosphere, and mycorrhizae) is one of the most important components of forest productivity (Litton et al. 2007), but it is difficult to quantify directly. Soil respiration reflects both root and microbial respiration, including the decomposition of above- and belowground litter. Subtracting aboveground litter production from total soil respiration provides an indirect estimate of belowground C allocation, assuming that there is no change in belowground C storage (Raich and Nadelhoffer 1989).

In forest ecosystems, nutrient addition reduced soil respiration in 75 % of >200 studies (Janssens et al. 2010), even though enhanced productivity could increase both aboveground litter production and the availability of C for allocation belowground. The causes of decreased soil respiration after nutrient addition include reduced fine root biomass (Lee and Jose 2003b, Olsson et al. 2005) and the supression of the decomposition of soil organic matter (Bowden et al. 2004). However, it is not clear whether differences in soil respiration in sites with differing native fertility will follow the pattern predicted by nutrient manipulation experiments.

In northern hardwood forests, soil respiration also can vary with stand age (Ryan et al.

1997, Tang et al. 2008). Soil respiration increases with stand age as fine root biomass and aboveground litter production also increase. For example, in northern hardwood forests of the White Mountain in New Hampshire, both litter and root production increased rapidly until canopy closure, which takes about 10 years, and then stabilized (Fahey et al. 1998). Yanai et al. (2012) observed that leaf litter production increased up to 50 years, and Claus and George (2005) and Yanai et al. (2006) reported that root production increased in temperate hardwood stands up to age 30 years. Some of the variation in soil respiration with stand age may reflect differences in nutrient availability during stand development (Vitousek and Farrington 1997).

The objective of this study is to quantify the variation in soil respiration, fine root biomass, and belowground C allocation in northern hardwood stands differing in soil fertility and age. We hypothesized that soil respiration, fine root biomass, and belowground C allocation would be higher in the less fertile sites. We also expected variation in soil respiration, fine root biomass, and belowground C allocation across stands of different ages. Finally, we tested the relative importance of N, P, and Ca availability in explaining variation in soil respiration across stands of different ages.

2.3 Methods

2.3.1 Study site

This study was conducted at three sites in the White Mountain National Forest, NH, USA: Bartlett Experimental Forest (BEF: 44° 02-04’ N, 71° 16-19’ W and 330 - 570 m elevation), Hubbard Brook Experimental Forest (HBEF: 43° 56’ N, 71° 44’ W and 500 m elevation), and Jeffers Brook (JB: 44° 02’ N, 71° 53’ W and 730 m elevation) (Table 2.1). The

soils are predominantly Spodosols derived from glacial till. Annual precipitation ranges from 1270 to 1400 mm (www.fs.fed.us/ne/durham/4155/bartlett.htm and www.hubbardbrook.org/overview/site_description.htm#Climate). The three sites have inherent differences in soil fertility: JB has the highest and BEF has the lowest nitrogen mineralization and calcium availability (Table 2.2). The BEF site included nine stands: three young (19 – 24 years old), three mid-aged (31 – 45 years old), and three old (119 – 126 years old). The HBEF and JB sites each included one mid-aged (35 – 45 years old) stand and one old (80 – 98 years old) stand. Four plots (30 x 30 m) (Figure 2.1) were located in each stand making a total of 52 plots in 13 stands.

Six stands, one mid-aged and one old stand at each site (Stand C6 and C9 for BEF), were selected for "intensive" measurements of total soil respiration, fine root biomass, litter production, and soil nutrient availability. An additional seven stands at BEF were included in less frequent measurements of soil respiration, referred to as the "extensive" portion of the study.

2.3.2 Soil respiration

In each plot, one soil respiration collar was located in each of five sub-plots (Figure 2.1), avoiding tree boles, boulders and big roots. The collars were made from 10-cm slices of 20-cm inside-diameter PVC and were inserted 2 to 4 cm into the soil.

In the intensively studied stands, soil respiration was measured every three to four weeks during the summer (June – August) and every four to five weeks during spring (March – May) and fall (September – November) from June 2009 to November 2010 (total of 15 dates). In the extensive stands, soil respiration was measured two to four times during the growing season (June – August) in 2010. Soil respiration measurements were made between

09:30 AM and 2:30 PM using an infrared gas analyzer system (LI-8100 survey system; Li-Cor Biosciences, Lincoln, NE, USA). The rate of soil C efflux was calculated based on the increase in chamber CO_2 concentration over two minutes. If a soil respiration measurement differed by more than 50 % from other measurements in the stand, that point was re-measured and the second measurement was used. Hereafter, these data are designated "measured soil respiration" to distinguish them from estimated annual soil respiration.

Temperature at 10 cm depth and soil moisture at 5 cm depth were sometimes measured concurrently with soil respiration at each collar, but sometimes temperature and moisture of the air in the chamber were recorded instead, due to operator error. We used the measured temperature and moisture to compare stands and sites, assuming that they were indicative of soil conditions, though not always accurate. We did not use these data in modeling soil respiration (Figure 2.2).

To estimate annual soil respiration, we used daily (average of all hours) soil temperature monitored near our study sites. At BEF, continuous soil temperature data were taken near a gas exchange tower by the North American Carbon Program (Andrew Richardson, unpublished data). At HBEF, soil temperature was monitored by the Soil Climate Analysis Network (www.wcc.nrcs.usda.gov/nwcc/site?sitenum=2069&state=nh). At JB, continuous soil temperature data were not available, and soil temperatures at BEF were used because static measurements of soil temperature at these two sites were similar.

Three approaches were used to estimate annual soil respiration. For all of these approaches zero C efflux was assumed for the soil area covered by rocks and tree root crowns, as measured in each plot using the line intercept method (Table 2.1). In the first approach the mean measured soil respiration was calculated for each of three seasons: 1) winter (day 340

to day 100) (Campbell et al. 2005); 2) the growing season (day 140 to day 280) (Richardson et al. 2006); and 3) spring and fall (day 100 – 140 and day 280 to day 340). There were 9 – 10 measurements for the growing season and 5 – 6 measurements for spring and fall. There was only one date measurement (across 8 plots, 12 measurements per plot) for winter (November 2010, 0.66 *u*mol m^{-2} sec^{-1}), which was very similar to the mean winter value used by Fahey et al. 2005 (0.64 *u*mol m^{-2} sec^{-1}) using LI-6400 at HBEF. The mean values were applied to the corresponding season length and summed to estimate plot-level annual soil respiration.

In the second approach, we used linear interpolation between all pairs of measurements, with the exception of the winter period, where we used the winter estimate, as above.

The third approach was a a composite of regression and linear interpolation, as used by Aulenbach and Hooper (2006) for interpolating stream chemistry. For this approach, soil respiration was modeled as an exponential function of the daily soil temperature: $Rs = ae^{bT}$ (Van't Hoff 1884), where Rs is soil respiration (umol m^{-2} s^{-1}), a and b are coefficients, and T is daily soil temperature at 10 cm depth. Because the relationships differed significantly by year and season, this model was applied to the average of the five collars in each plot for the growing season in 2009 (n = 5 dates) and 2010 (n = 6), and for the dormant season of 2009 - 2010 (n = 5 to 7).

In the intensive stands, there was a strong relationship between mid-summer (Jun – Aug) soil respiration rate and annual soil respiration rate (n = 24 plots, $R^2 = 0.86$, $p < 0.01$). Therefore, across the extensive stands, the mid-summer soil respiration rate was used to explore the wider relationship between soil respiration and factors such as fine root biomass, litter production, and nutrient availability.

2.3.3 Fine root biomass

To estimate fine root biomass, ten 5-cm diameter soil cores were taken to the depth of 30 cm in each plot at HBEF and JB in July 2008 and at BEF in August 2010. Root samples were frozen until they could be processed. Soil samples were thawed and roots were wet-sieved with tap water in a 0.05 mm sieve. Roots less than 5 mm diameter (divided visually into 0-1 and 1-5 mm classes) were separated in the sieve, cleaned with tap water, oven-dried at 60 ℃ to a constant weight, and weighed. Dead roots and herbaceous roots were excluded, distinguished by their color, brittleness, and resiliency.

2.3.4 Litter production

Leaf litterfall was collected in five litter baskets (each 0.23 m^2) at each plot (Figure 2.1). We collected litter from August 2008 to August 2009 at HBEF and JB, and from July 2009 to July 2010 at BEF. In each plot at HBEF and JB, the litter from all five baskets was composited, mixed, weighed moist, and a 20 % subsample was analyzed for moisture content. At BEF, all the litter (100 %) was dried and weighed. The collected litter at three sites was weighed after drying at 60 ℃. Woody litter production was not included in this study; woody litter constituted <10 % of total litter production at HBEF (Fahey et al. 2005a). Aboveground leaf litter production was calculated as 50 % of the leaf litter mass.

2.3.5 Soil properties

Soil samples were collected in late June, 2009, to evaluate soil pH, texture, and fertility in the intensive and extensive stands. Approximately 30 soil cores (2 cm diameter) were collected in each plot and separated into Oe, Oa, and the upper 10 cm of the mineral soil. Cores were pooled by horizon, giving one composite sample per horizon per plot.

Soil pH in 0 - 10 cm mineral soil was measured electrometrically in a 2:1 mixture

with water and 10 g of soil (Robertson et al. 1999). Soil texture was quantified using the hydrometer method (Sheldrick and Wang 1993).

Net N mineralization was estimated from laboratory incubations in sealed Mason jars for 21 days at 20 ℃. Subsamples were extracted before and after incubation by shaking in 40 mL of 2 M KCl for 1 hr, waiting for 18 hrs, and filtering through Whatman #1 filter paper. Concentrations of NH_4^+ and NO_3^- in extracts were measured using a phenolate-hypochlorite method (351.2, US EPA 1983) and a cadmium reduction method (353.2, US EPA 1983). Net N mineralization was calculated as the difference in $NH_4^+ + NO_3^-$ between the initial and final extracts and net nitrification was calculated as the difference in NO_3^- between initial and final extracts.

Resin-extractable P was measured by shaking soil subsamples for 18 hr in 100 mL of distilled water with nylon mesh bags containing bicarbonate-form anion exchange-resins (JT Baker Anion Exchange Resin, 325 NA-38, OH- Form, Type I, 16-50 Mesh). The bags were washed in distilled water to remove soil particles and resin-extractable P was recovered from ion-exchange resins by shaking bags for 1 hr in 100 mL 0.5 M HCl. Inorganic P in HCl extracts was analyzed using the ammonium molybdate-ascorbic acid method (Murphy and Riley 1962).

Soil extractable Ca was determined by shaking 10-g soil samples for 30 minutes with 100 mL of 1 M NH_4Cl. After waiting 18 hrs, soil samples were shaken again for 45 minutes and the extract was filtered through Whatman #1 paper. The Ca concentration was analyzed using a Varian Spectra Atomic Absorption Spectrometer (Mulgrave, Victoria, Australia) with a 10,000 ppm (1 %) lanthanum chloride solution as a releasing agent to eliminate chemical interferences.

2.3.6 Statistical analysis

We used a randomized block design with four replicate plots blocked by stand. The number of stands depended on the analysis. There were six "intensive" stands in which all variables were measured; in eleven stands, litterfall was measured; and in all 13 stands, respiration was measured, at least in the growing season. In the intensive stands, we analyzed measured soil respiration, temperature, and moisture as a function of stand age (mid-aged and old) and site (BEF, HBEF, and JB) using repeated-measures analysis of variance (ANOVA). We also analyzed the effects of stand age and site on estimated annual soil respiration, litter production, fine root biomass (0 – 1, 0 – 5 mm), belowground C allocation, and soil nutrient availability in the Oe, Oa, and 0 – 10 cm mineral soil horizons; these effects were analyzed by ANOVA using the GLM procedure using Minitab v.10.

In the intensive plus the extensive stands, Pearson's product moment correlations based on individual plot values blocked by each stand in SAS (SAS Inc, 2003) were calculated between observed soil respiration rate in summer (mean of June to August 2010) and fine root biomass (0 – 1 mm and 0 - 5 mm), leaf litter production, and soil nutrient availability. In the intensive stands, correlations were calculated between belowground C allocation and fine root biomass (0 – 1 mm and 0 – 5 mm), leaf litter production, and soil nutrient availability. Statistically significant differences are reported at $\alpha = 0.05$.

2.4 Results

2.4.1 Soil respiration, fine root biomass, and belowground C allocation in

the intensively studied stands

Measured soil respiration was lower at JB than at BEF or HBEF ($p < 0.01$; Figure 2.4), consistent with expectations based on generally higher fertility at JB (Table 2.2). Mid-aged stands at BEF and JB had significantly lower measured soil respiration rate than old stands ($p < 0.05$), but the difference with stand age was not significant at HBEF ($p = 0.28$).

Measured soil respiration increased with temperature; daily soil temperature measured at HBEF and at BEF explained 72 – 97 % of the variation in soil respiration measurements within plots over time. However, soil temperature did not explain differences between years (2009 and 2010) or sites (BEF and HBEF) in annual soil respiration. For example, the average soil temperature was only 0.7 °C higher in 2010 than in 2009 at both BEF and HBEF, but annual soil respiration in 2009 was 35 – 58 % higher than in 2010 across six stands.

Fine root biomass did not differ significantly among the sites ($p \geq 0.14$) (Table 2.3), but within sites, it was about 40% higher in old stands than in mid-aged stands ($p < 0.001$) (Table 2.3). Leaf litter production in these stands did not differ significantly with stand age ($p = 0.45$) or site ($p = 0.34$) (Table 2.3).

Estimated annual soil respiration, interpolated between measurement dates using the composite method was significantly lower at JB than at BEF or HBEF ($p < 0.01$). Within sites, estimated annual soil respiration in mid-aged stands was lower than in old stands by 9 % at BEF, 3 % at HBEF and 5 % at JB ($p = 0.10$). The effect of interpolation method in estimating annual soil respiration ranged from 0.01 – 4 % of estimated annual respiration, depending on the stand (Figure 2.3). The conclusion of lower annual soil respiration at JB

than at BEF and HBEF ($p < 0.01$) was consistent for all three methods.

Belowground C allocation was calculated as the difference between estimated annual soil respiration minus annual aboveground leaf litter production. Like estimated annual soil respiration, belowground C allocation varied more by site ($p = 0.02$) than by stand age ($p = 0.19$), being lower at JB than at BEF and HBEF ($p = 0.05$) (Table 2.3). Belowground C allocation accounted for 77 – 83 % of annual soil respiration, which is why annual soil respiration and belowground C allocation show similar patterns.

2.4.2 Soil properties

Soil pH and soil texture did not differ among sites ($\alpha = 0.05$) (Table 2.2). Measured temperature and moisture did not differ among sites or ages across two years, either ($p > 0.47$) (Figure 2.2). However, soil nutrient availability differed significantly among sites. In the mineral soil, net N mineralization, nitrification, and exchangeable Ca were highest at JB and lowest at BEF (Table 2.2). In the forest floor horizons (Oe and Oa), JB had higher net nitrification and exchangeable Ca than BEF and HBEF (Table 2.2).

Across the 13 stands, soil respiration during summer was significantly higher where net N mineralization and nitrification were lower in most of the soil horizons assayed ($p = 0.05$) (Figure 2.5). In contrast, soil respiration did not show any relationship with available P or exchangeable Ca. In the six intensively studied stands, belowground C allocation was low where soil N availability and Ca availability were high (Figure 2.6), supporting the hypothesis that soil fertility influences belowground allocation in these northern hardwood forests. Leaf litter production did not show any correlation with net N mineralization, net nitrification, available P or exchangeable Ca ($r < 0.30$; $p > 0.20$).

2.5 Discussion

2.5.1 Soil respiration across stand age

Estimated annual soil respiration (678 – 864 g C m^{-2} $year^{-1}$) across the six intensive stands was similar to or slightly higher than nearby hardwood forests at Hubbard Brook (80 years old; 541 – 801 g C m^{-2} $year^{-1}$) (Fahey et al. 2005b) and at Harvard Forest (60 – 100 years old; 530 – 850 g C m^{-2} $year^{-1}$) (Davidson et al. 1998b). In this study, annual soil respiration did not differ significantly between mid-aged and old stands even though fine root biomass was 40% higher in the older stands (Table 2.3). Fine roots usually account for approximately half of the total soil respiration (Hanson et al. 2000), so the lack of a difference in soil respiration between forest ages was surprising given the difference in fine root biomass.

Other studies of soil respiration in temperate forests have found relationships with stand age that were attributed to differences in root biomass. For instance, soil respiration increased with stand age across four loblolly pine stands aged 1 – 25 years in Virginia; this increase was attributed to greater root biomass in older stands (Wiseman and Seiler 2004). Decreases in soil respiration with stand age were reported in 8 – 26 year-old aspen forests in northern Wisconsin (Martin and Bolstad 2005) and in 10 – 47 year-old Sitka spruce forests in central Ireland (Saiz et al. 2006); in these cases, fine root biomass was lower in the older stands. The lack of a significant effect on soil respiration of differing fine root biomass between mid- and old-age stands in our study might be explained by variation in specific root respiration rates, root turnover, or rhizosphere C flux or by compensating differences in heterotrophic respiration.

2.5.2 Belowground C allocation

Estimating belowground C allocation as the difference between annual soil respiration flux and aboveground leaf litter C flux depends on the assumption that the C contents of the forest floor, mineral soil, and living and dead roots are at steady state (Raich and Nadelhoffer 1989). Measuring changes in these pools is difficult because of high spatial variability and imperfect sampling methods (Yanai et al. 1999, Yanai et al. 2003, Ryzhova and Podvezennaya 2008). The uncertainty in change over time of forest floor C at Hubbard Brook has been estimated at 83 g C m^{-2} yr^{-1} and uncertainty in measurements of mineral soil C stocks are much larger (Yanai et al. 2012).

Could the differences observed in belowground C allocation among sites be attributed to differences in C accumulation rates in some of these pools? Changes in forest floor C content over 15 years in several young and mid-aged northern hardwood stands in and around BEF were up to ~30 g C m^{-2} yr^{-1} (Yanai et al. 1999) which is relatively small compared to 70 - 130 g C m^{-2} yr^{-1}difference in belowground C allocation between JB and other sites. Long term study on watershed 6 at HBEF suggested that the C pools of root biomass, forest floor, and mineral soils were near steady state in the mature forest (Fahey et al. 2005a). Nevertheless, some of the between-stand differences in belowground C allocation in this study might be attributed to deviations from the assumption of constancy in the belowground C pools.

There was weak evidence that belowground C allocation increased with increasing 0-1 mm fine root biomass across six intensive stands (p = 0.12) consistent with a high proportion of belowground C allocation supplying fine root respiration (Hogberg et al. 2002). However, across stands only about 38 % of the variation in belowground C allocation was

explained by fine root biomass. Some of the residual variation is probably associated with measurement error; however, according to Giardina and Ryan (2002), differences across stands in specific root respiration rates and rhizosphere C flux may also contribute to residual variation.

2.5.3 Soil respiration, belowground C allocation and soil properties

As hypothesized, soil respiration was lower in stands with higher soil N availability, assayed by net N mineralization and nitrification potential in upper soil horizons (Figure 2.5). Lower soil respiration under high N conditions is common in temperate forests and can be attributed to lower heterotrophic respiration or root-associated respiration (Janssens et al. 2010). Lower soil respiration in fertile soil is consistent with theory of plant resource allocation (Bloom et al. 1985), if N is a limiting nutrient for northeastern US forests (Finzi 2009, Vadeboncoeur 2010).

There was no significant relationship between soil respiration and P and Ca availability across sites. However, belowground C allocation decreased with increasing Ca availability (Figure 2.5). Across a much larger (30 fold) Ca availability gradient, Park et al. (2008) observed that root production was higher where Ca was high, in direct contrast to what the data from this study show. In this study, availability of N and Ca were significantly correlated ($R^2 = 0.53$ for N mineralization and Ca availability and $R^2 = 0.67$ for nitrification and Ca availability in mineral soil), so it is difficult to distinguish the effect of soil Ca from that of soil N on belowground C allocation.

The relationship between soil respiration and N availability was similar to net N mineralization and nitrification, but varied by soil horizons, especially in organic horizons (Figure 2.5). The development and properties of surface organic horizons in these forests vary

markedly for reasons that are not well understood (Lützow et al. 2006) and this source of variation certainly contributes to differences in the measurements of N availability and respiratory activity. Since a high proportion of soil respiration in northern hardwood forests has been attributed to forest floor organic horizons (e.g., 58%; Fahey et al. 2005b), separating soil respiration of organic and mineral soils would be helpful to understand the relationship between soil respiration and soil nutrient availability.

Why is it that soil respiration and belowground C allocation are low at high N availability, as predicted, whereas fine root biomass is not? The relationship between fine root dynamics and nitrogen availability can be complex and many factors could contribute to this finding. Respiration per unit mass of root may increase with root tissue N (Burton et al. 2002), suggesting that the same fine root biomass should exhibit higher respiration in high N sites. However, root biomass or root turnover (Burton et al. 2011) may be reduced by addition of N, which could contribute to declining root respiration across our N availability gradient. Reduced rhizosphere C flux (Phillips and Fahey 2008) and allocation to mycorrhizal fungi (Högberg et al. 2003, Treseder 2004) with increasing N could also contribute to reduced root-associated respiration.

Concerns have been expressed that reductions of P and Ca availability caused by decreased soil pH due to acid deposition could cause reductions in forest health and productivity (Paré and Bernier 1989, Likens et al. 1998). If P or Ca were limiting in the study sites, then one might expect to see greater investment belowground, and hence greater soil respiration, in stands with low P or Ca. The study result showing reduced soil respiration where N availability was high, but no (or less) relationship with P or Ca, suggests that greater effort is allocated to N acquisition in the study stands of this project. In the future, N, P, and

Ca will be added to the study plots, with the objective of determining whether soil respiration and belowground C allocation are related to nutrient limitation as defined by productivity response to nutrient additions.

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Table 2.1. Northern hardwood stands used in this study. The young and mid-aged stands were naturally regenerated after clear-cutting

Site	Stand	Year cut	Elevation (m)	Basal area (m^2 ha^{-1})	Dominant species based on basal area
Bartlett, C1	Young	1990	570	25.2	*Betula papyrifera, Prunus pensylvanica, Fagus grandifolia*
C2	Young	1988	340	23.4	*Acer rubrum, F. grandifolia, B. papyrifera*
C3	Young	1985	590	30.5	*P. pensylvanica, F. grandifolia,A. rubrum*
C4	Mid-aged	1978	410	32.9	*B. papyrifera, Populus grandidentata,P. pensylvanica*
C5	Mid-aged	1976	550	27.2	*B. papyrifera, P. pensylvanica,A. rubrum*
C6*	Mid-aged	1975	460	30.1	*A. rubrum, B. papyrifera,F. grandifolia*
C7	Old	About 1890	440	32.1	*F. grandifolia, A. saccharum,Tsuga canadensis*
C8	Old	1883	330	35.2	*F. grandifolia, A. saccharum,B. alleghaniensis*
C9*	Old	1890	440	32.7	*A. saccharum, F. grandifolia,B. alleghaniensis*
Hubbard Brook*	Mid-aged	1966	500	29.5	*B. alleghaniensis, B. papyrifera,A. rubrum*
	Old	1911 - 1913	500	33.9	*B. alleghaniensis, F. grandifolia,A. saccharum*
Jeffers Brook*	Mid-aged	About 1974	730	27.9	*B. alleghaniensis, B. papyrifera,A. saccharum*
	Old	1915 - 1929	730	35.7	*A. saccharum, B. alleghaniensis,F. grandifolia*

* means intensive stands

Table 2.2. Nutrient availability (plot mean ± standard error) in Oe, Oa, and mineral (0 – 10 cm) horizon at intensive stands of BEF, HBEF, and JB. Different superscript letters are significantly different from one another at the $\alpha = 0.05$

Soil horizon	Site	Soil pH	Soil texture		Net N mineralization ($ug\ g^{-1}\ day^{-1}$)	Net nitrification ($ug\ g^{-1}\ day^{-1}$)	Available P ($ug\ g^{-1}\ day^{-1}$)	Exchangable Ca ($ug\ g^{-1}\ day^{-1}$)
			Sand (%)	Clay (%)				
Oe	BEF				19.79 ± 3.04a	-0.71 ± 0.32b	16.32 ± 0.88a	4372 ± 304b
	HBEF				19.52 ± 2.03a	3.26 ± 1.53ab	17.91 ± 1.16a	3339 ± 254b
	JB				20.96 ± 2.44a	6.25 ± 0.69a	16.11 ± 0.95a	5339 ± 532a
Oa	BEF				7.41 ± 0.68a	1.17 ± 0.36b	11.80 ± 0.73ab	1326 ± 127b
	HBEF				7.69 ± 0.31a	3.44 ± 0.56ab	14.07 ± 2.49a	762 ± 137b
	JB				6.46 ± 0.90a	5.11 ± 0.68b	9.79 ± 0.34b	1578 ± 83a
Mineral	BEF	4.7 ± 0.2a	54 ± 2a	15 ± 1a	0.38 ± 0.02b	0.25 ± 0.03c	2.03 ± 0.16a	86 ± 9b
	HBEF	4.4 ± 0.2a	56 ± 3a	19 ± 3a	0.57 ± 0.03ab	0.51 ± 0.06b	3.20 ± 0.74a	135 ± 50b
	JB	4.8 ± 0.2a	56 ± 2a	15 ± 1a	0.64 ± 0.06a	0.68 ± 0.03a	3.09 ± 0.64a	320 ± 8a

Table 2.3. Fine root biomass (plot mean ± standard error), leaf litter production, average annual soil respiration, and belowground C allocation at mid-aged and old at BEF, HBEF, and JB in six intensive stands

Forest age	Site	Fine root biomass ($g\ m^{-2}$)			Leaf litter	Average annual soil respiration	Belowground C allocation
		0 – 1 mm	1 – 5 mm	0 – 5 mm	($gC\ m^{-2}$)	($gC\ m^{-2}$)	($gC\ m^{-2}$)
Mid-aged	BEF	299 ± 37	264 ± 41	563 ± 37	135 ± 8	790 ± 36	655 ± 29
	HBEF	270 ± 12	181 ± 21	451 ± 34	182 ± 6	790 ± 23	608 ± 25
	JB	195 ± 24	248 ± 20	443 ± 28	153 ± 51	678 ± 34	525 ± 47
Old	BEF	416 ± 73	316 ± 23	732 ± 65	174 ± 10	864 ± 19	690 ± 17
	HBEF	406 ± 19	377 ± 20	783 ± 53	161 ± 11	812 ± 26	651 ± 22
	JB	432 ± 16	273 ± 12	706 ± 22	133 ± 14	714 ± 42	581 ± 45

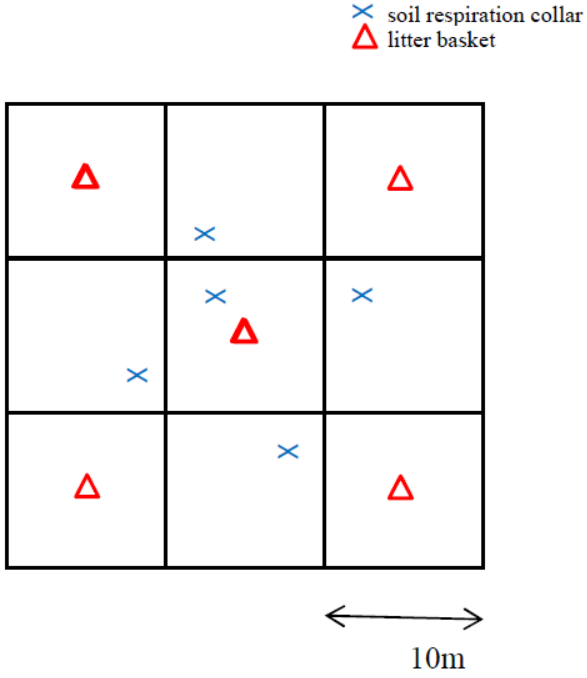

Figure 2.1. Field plot layout (30 x 30 m). Five soil respiration collars and five litter baskets were located in each plot.

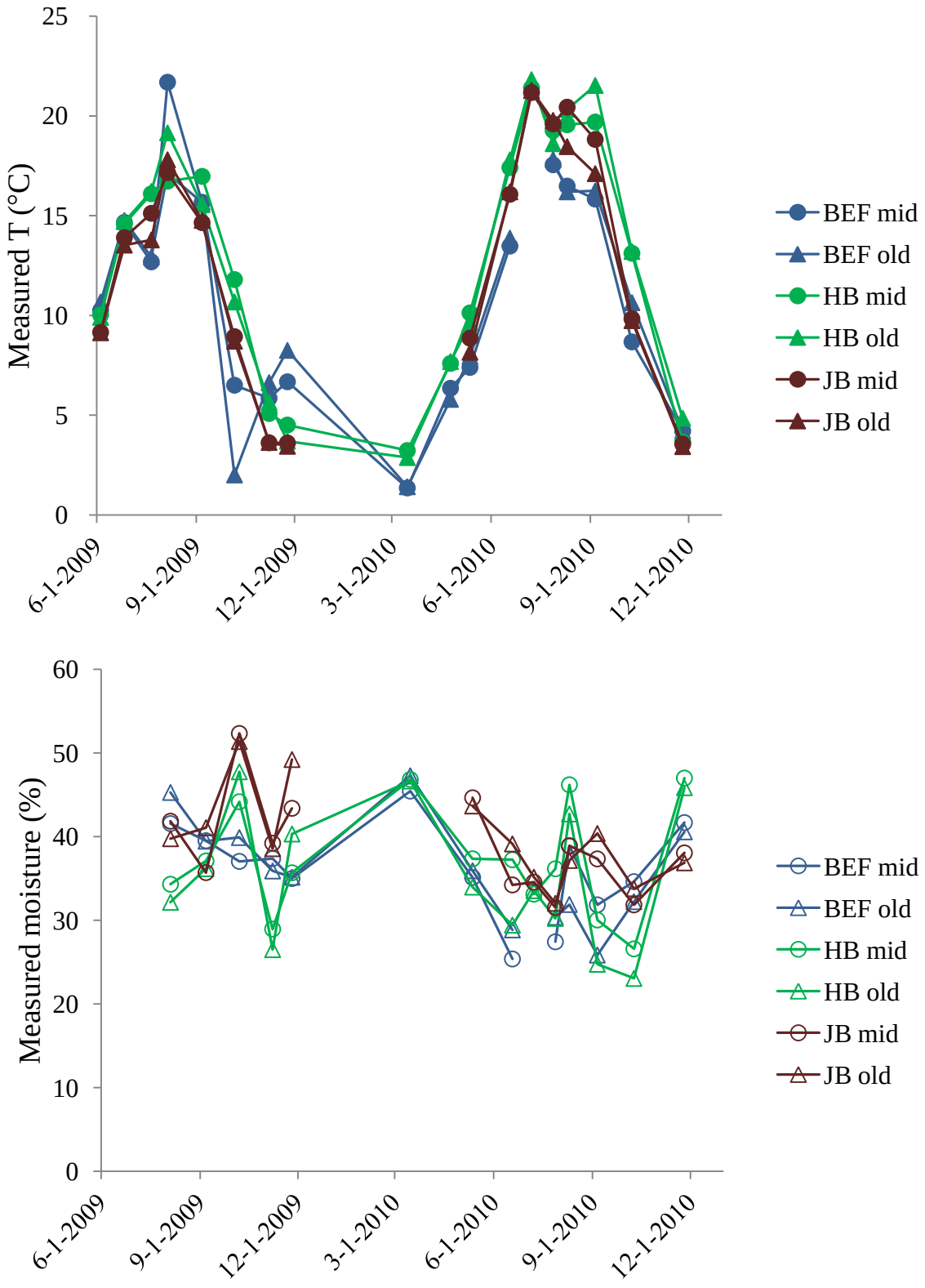

Figure 2.2. Stand mean of plots measured temperature and moisture using Li-cor in 2009 and 2010 across six stands.

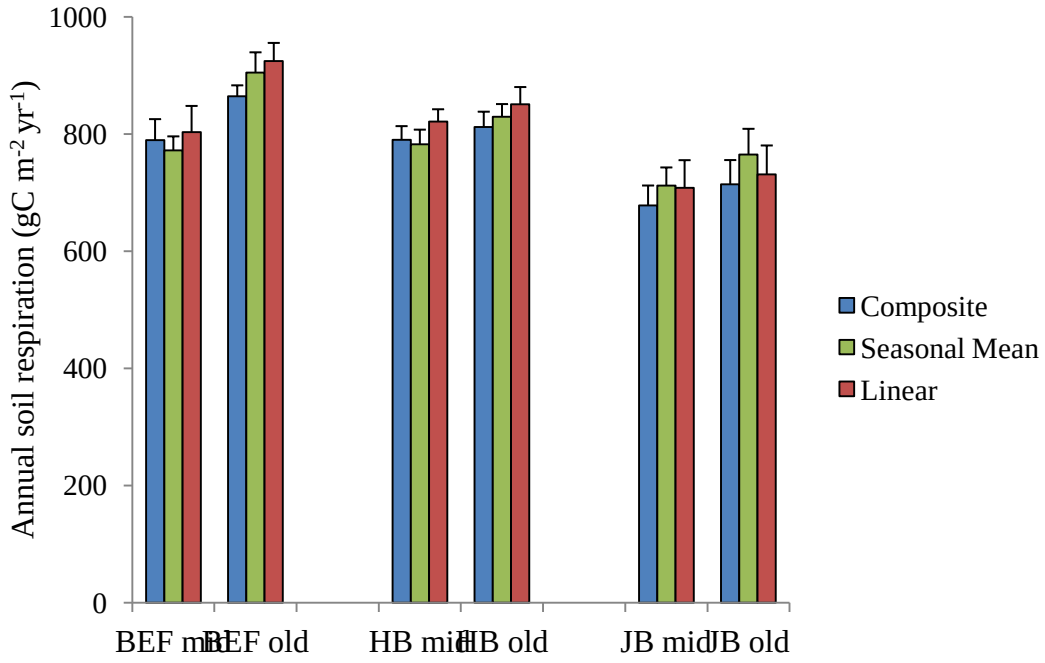

Figure 2.3. Estimates of annual soil respiration by composite method, seasonal mean method, and linear interpolation method in each stand. Bars are standard error of the mean (n = 4 plots per stand).

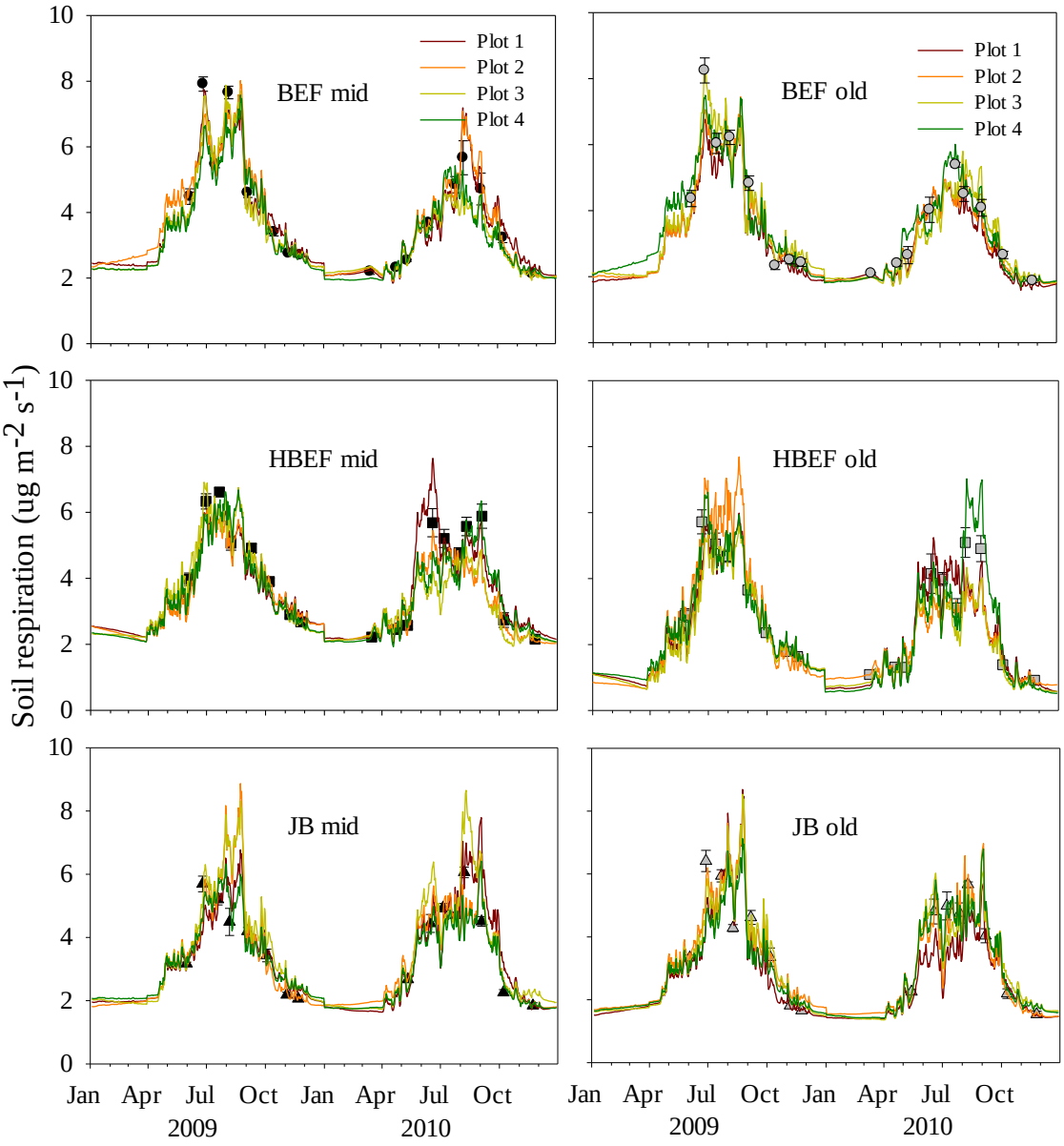

Figure 2.4. Daily estimated soil respiration in four plots in mid-aged and old stands in Bartlett (BEF, with circles), Hubbard Brook (HBEF, with squres), and Jeffer's Brook (JB, with triangles). Bars are standard error of the mean (n = 4 plots per stand). Daily respiration between measurement dates was estimated based on measured soil temperature from nearby locations.

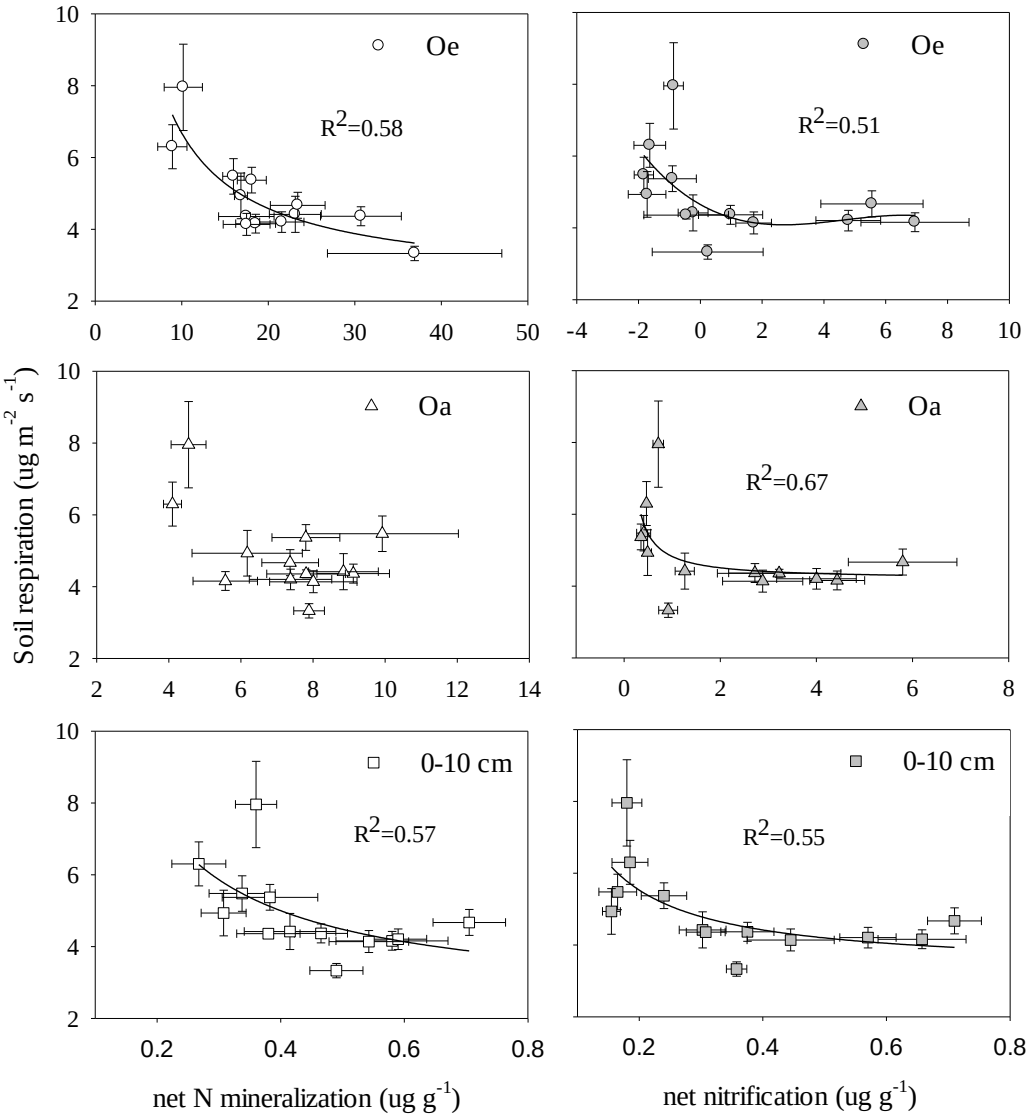

Figure 2.5. Relationship between soil respiration in summer (mean of Jun to Aug) and N availability in 13 stands at Bartlett, Hubbard Brook, and Jeffers Brook. Data are displayed for three soil horizons; Oe, Oa, and 0 – 10 cm in the mineral soil. Points represent the mean and bars the standard error of the mean (n = 4 plots per stand); and lines show relationships significant at $\alpha = 0.05$.

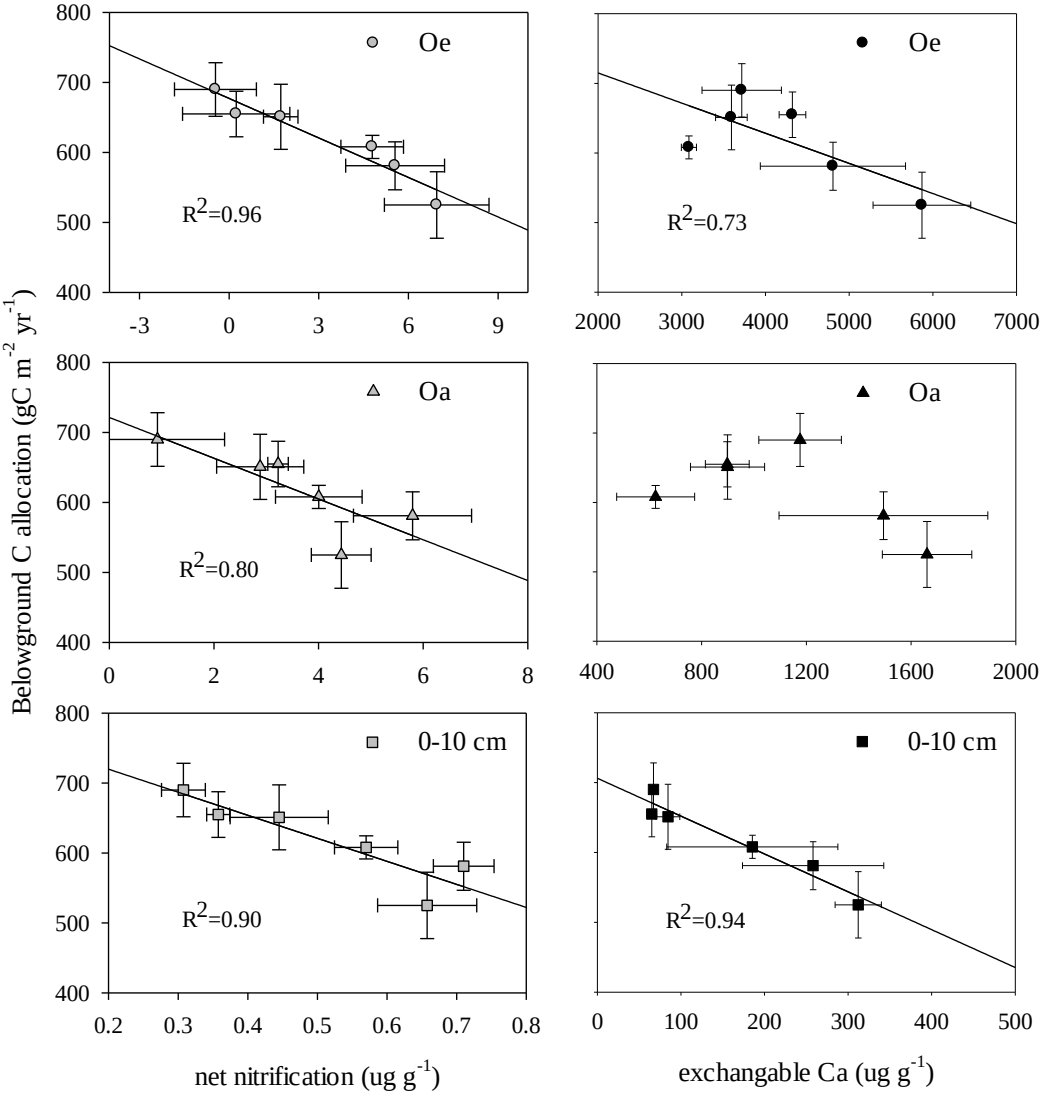

Figure 2.6. Relationship between belowground C allocation and N and Ca availability in the 6 intensive stands at Bartlett, Hubbard Brook, and Jeffers Brook. Data are displayed for three soil horizons; Oe, Oa, and 0 – 10 cm in the mineral soil. Points represent the mean and bars the standard error of the mean (n = 4 plots per stand) and lines show relationships significant at $\alpha = 0.05$.

2.7 Appendix

Table 1. Coefficient constants for exponential model and Q10 of each plot in six stands in 2009 and 2010.

		2009				2010			
Stand	Plot	a	b	R^2	Q10	a	b	R^2	Q10
C6	1	0.87	0.10	0.81	1.25	0.48	0.11	0.82	1.28
	2	0.74	0.11	0.87	1.28	0.44	0.11	0.88	1.29
	3	0.67	0.12	0.89	1.30	0.49	0.09	0.81	1.24
	4	0.68	0.11	0.93	1.29	0.40	0.11	0.97	1.29
C9	1	0.58	0.13	0.91	1.34	0.55	0.10	0.72	1.24
	2	0.77	0.11	0.90	1.30	0.58	0.10	0.79	1.26
	3	0.92	0.11	0.83	1.29	0.60	0.10	0.90	1.27
	4	0.84	0.11	0.82	1.29	0.66	0.09	0.78	1.24
HBEF mid	1	1.08	0.07	0.84	1.18	0.61	0.09	0.88	1.24
	2	1.07	0.07	0.84	1.19	0.49	0.10	0.89	1.26
	3	0.80	0.10	0.95	1.25	0.54	0.09	0.84	1.23
	4	0.84	0.09	0.94	1.23	0.53	0.10	0.92	1.26
HBEF old	1	1.02	0.08	0.92	1.20	0.48	0.11	0.88	1.29
	2	0.74	0.11	0.81	1.29	0.70	0.08	0.91	1.20
	3	1.00	0.08	0.90	1.20	0.50	0.09	0.89	1.24
	4	1.03	0.08	0.88	1.21	0.43	0.11	0.89	1.30
JB mid	1	0.38	0.13	0.97	1.35	0.23	0.15	0.93	1.41
	2	0.23	0.17	0.96	1.48	0.24	0.14	0.86	1.39
	3	0.45	0.14	0.94	1.37	0.37	0.12	0.75	1.32
	4	0.50	0.12	0.91	1.30	0.21	0.15	0.88	1.40
JB old	1	0.14	0.21	0.96	1.60	0.11	0.18	0.82	1.52
	2	0.33	0.16	0.97	1.45	0.11	0.19	0.87	1.56
	3	0.26	0.17	0.96	149	0.31	0.14	0.81	1.37
	4	0.29	0.16	0.95	1.44	0.24	0.16	0.88	1.43

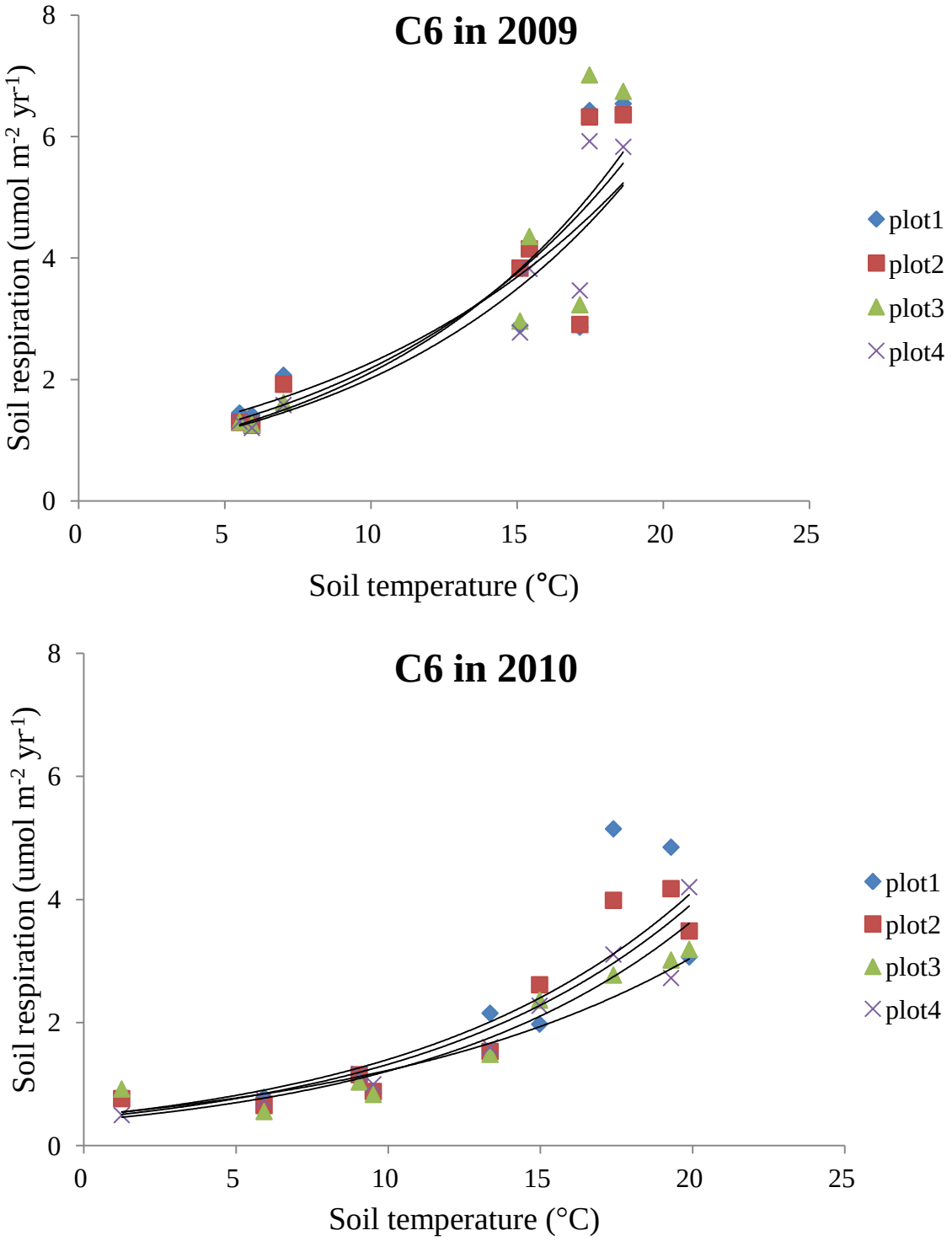

Figure 1. Relations between soil respiration in each plot and daily soil temperature in each site at a depth of 10 cm fitted with an exponential model at C6 in 2009 and in 2010.

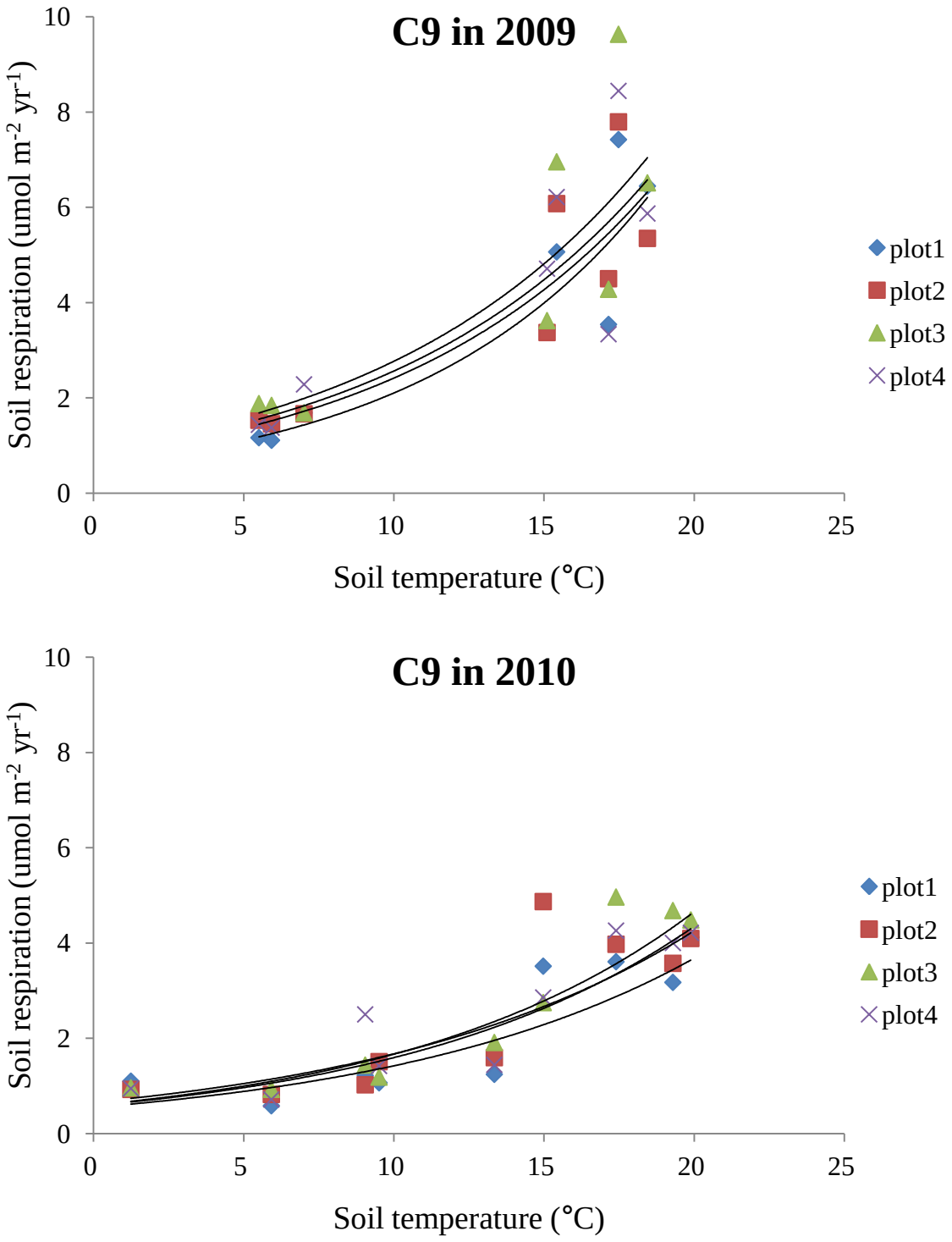

Figure 2. Relations between soil respiration in each plot and daily soil temperature in each site at a depth of 10 cm fitted with an exponential model at C9 in 2009 and in 2010.

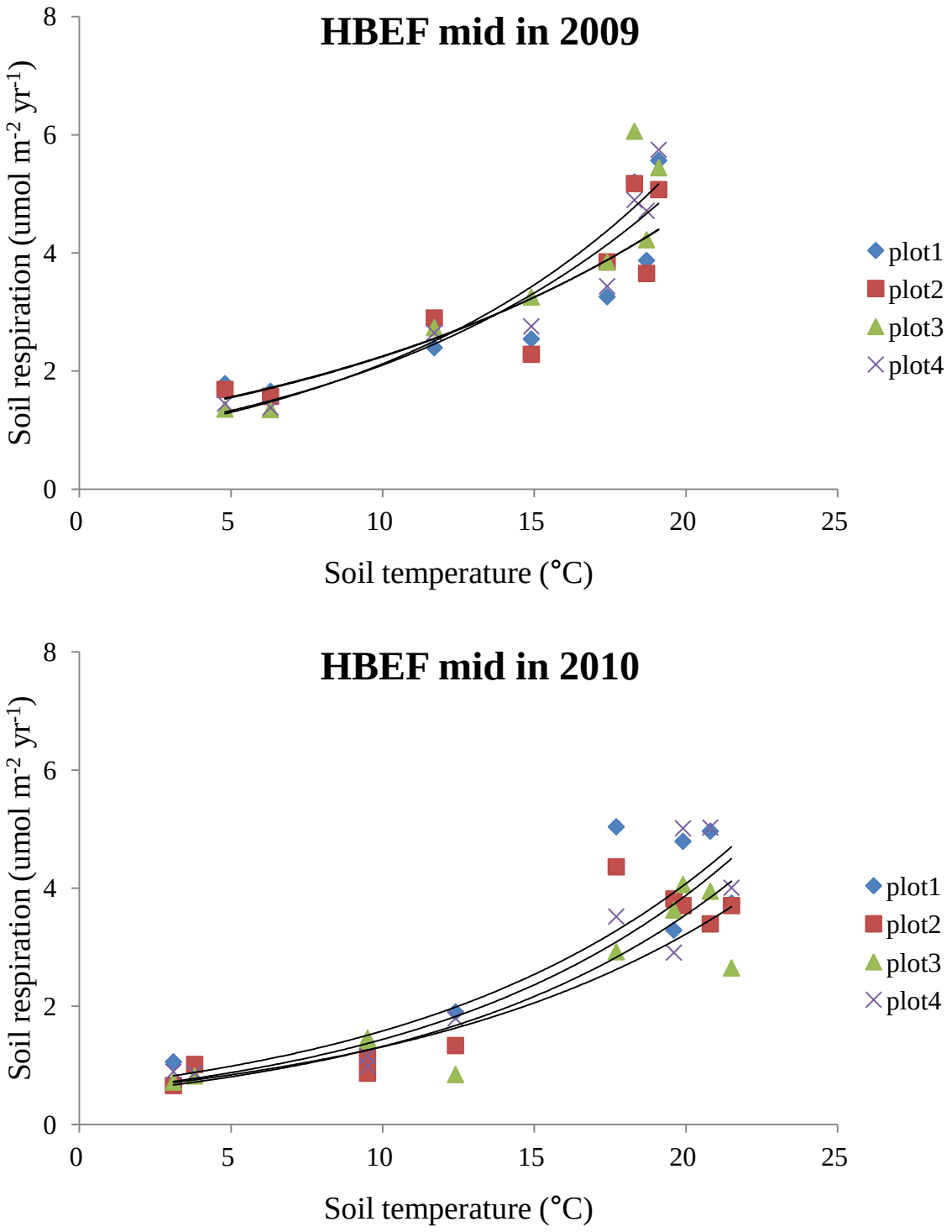

Figure 3. Relations between soil respiration in each plot and daily soil temperature in each site at a depth of 10 cm fitted with an exponential model at HBEF mid-aged in 2009 and in 2010.

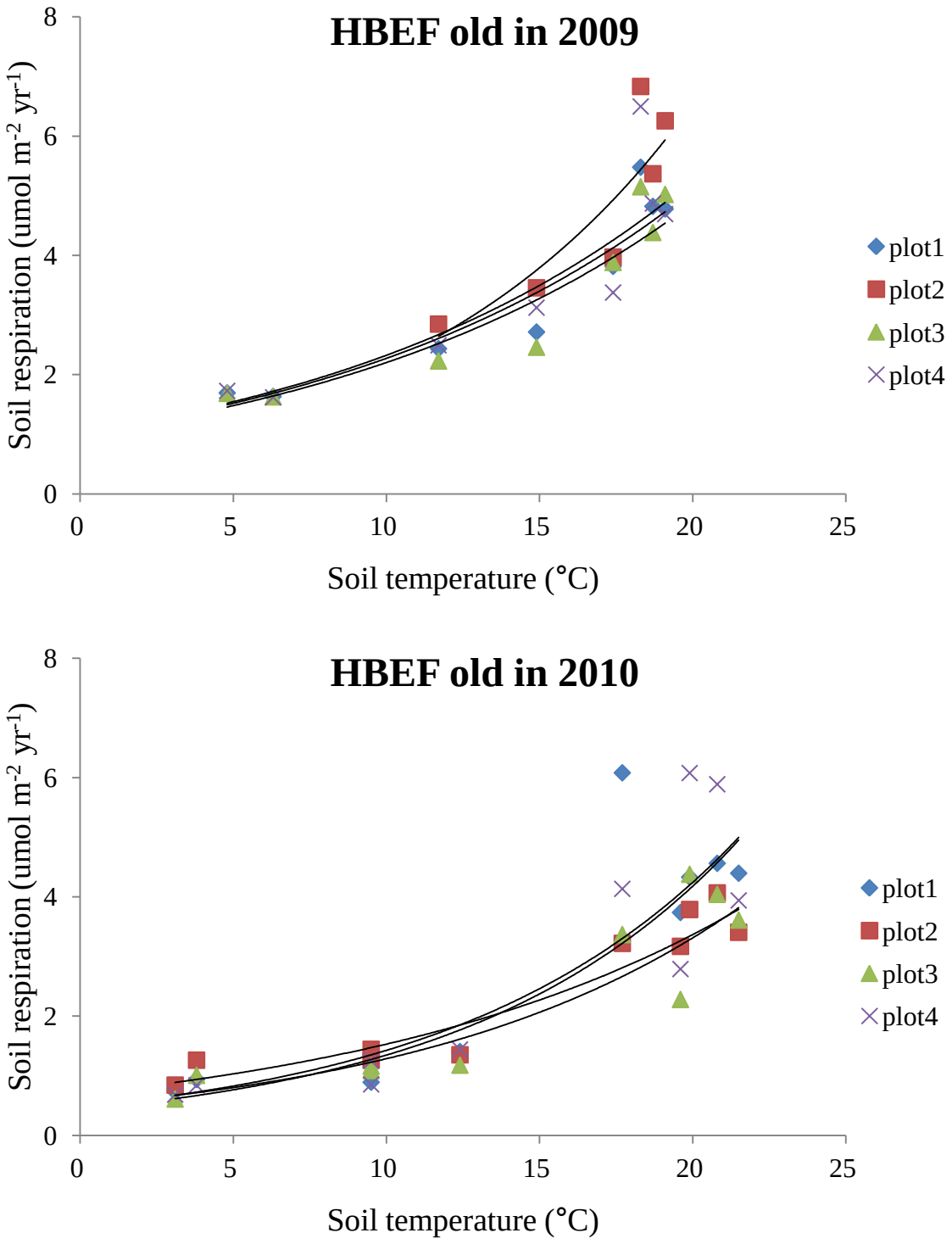

Figure 4. Relations between soil respiration in each plot and daily soil temperature in each site at a depth of 10 cm fitted with an exponential model at HBEF old in 2009 and in 2010.

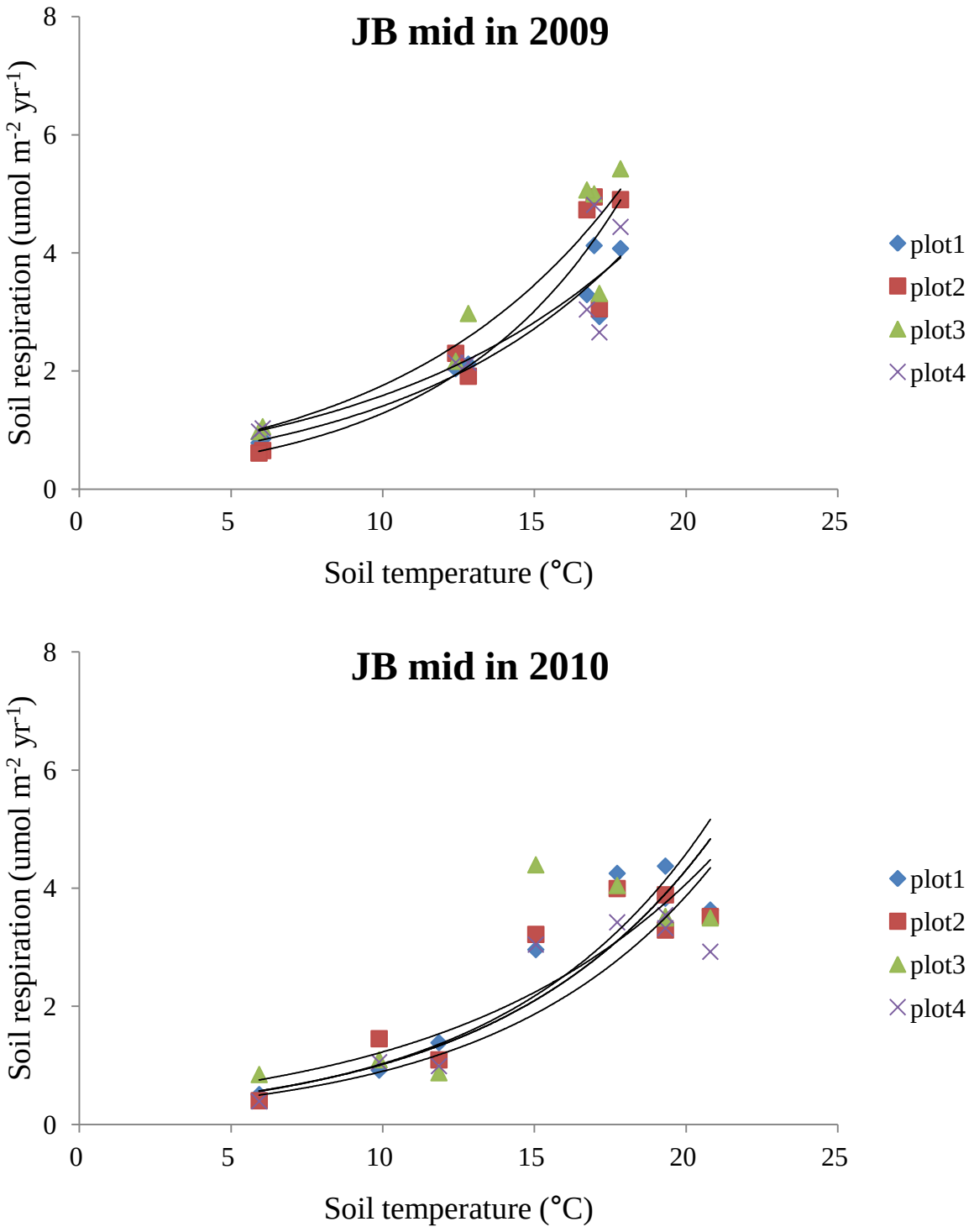

Figure 5. Relations between soil respiration in each plot and daily soil temperature in each site at a depth of 10 cm fitted with an exponential model at JB mid-aged in 2009 and in 2010.

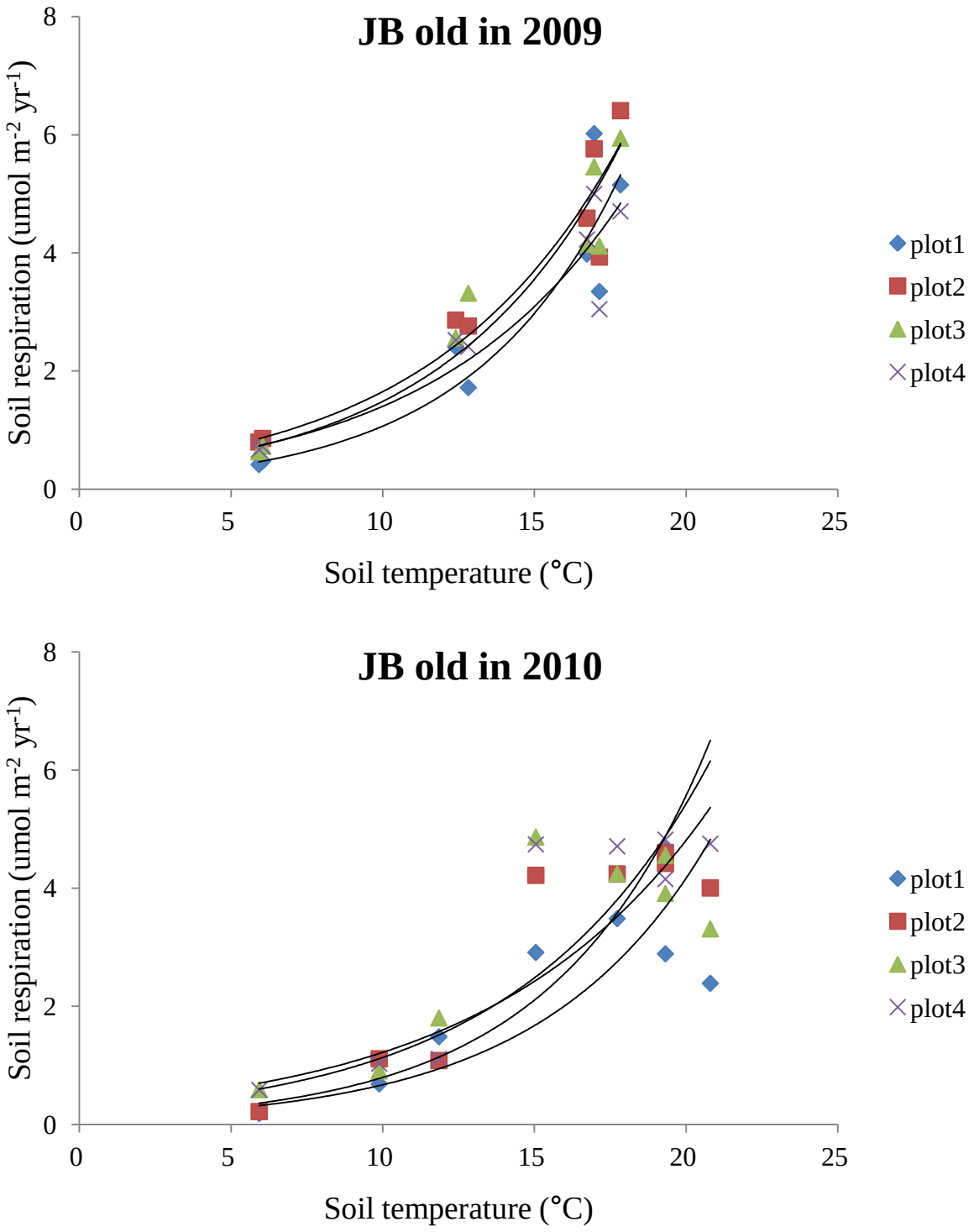

Figure 6. Relations between soil respiration in each plot and daily soil temperature in each site at a depth of 10 cm fitted with an exponential model at JB old in 2009 and in 2010.

Chapter 3. Response of soil respiration and microbial respiration to N and P addition in northern hardwood forests of New Hampshire

3.1 Abstract

Nutrient additions to forest ecosystems can affect soil respiration by altering microbial or root respiration. Soil respiration and microbial respiration were measured using field trenching and laboratory incubations after nitrogen (N), phosphorus (P), and nitrogen plus phosphorus (N+P) fertilization in forests of different age and site quality. Treatments were carried out in three northern hardwood sites in central New Hampshire (Bartlett Experimental Forest, Hubbard Brook Experimental Forest, Jeffers Brook).We hypothesized that soil respiration and microbial respiration would decrease after fertilization, and the reduction would be more significant in infertile soils regardless of treatment, in young stands in N plots, and in old stands in P plots. Contrary to the expectation, there was no general response of soil respiration or microbial respiration two years after the fertilizer treatments were initiated ($p \geq 0.37$). Contribution of microbial respiration to total soil respiration was higher in N+P plots than N and control plots. The fertilization responses varied among stands. Within an individual stand, soil respiration decreased in fertilized plots in two young stands at Bartlett (C1 and C2), but soil respiration increased in the N plot in one mid-aged stand at Hubbard Brook. Soil respiration in the trenched plots decreased for all fertilization plots in one young stand at Bartlett, but increased in N and P plots in one old stand at Bartlett. Fertilization effects on microbial respiration measured by lab incubation varied by soil horizon. In the Oe horizon, microbial respiration increased in P plots at Hubbard Brook and in N+P plots at Jeffers Brook, and increased in P plots in young stands across three sites. In

the Oa horizon, microbial respiration decreased in N plots at Hubbard Brook, and increased in P plots in young stands. Fertilization effects differed in relation to natural soil fertility. N stimulated microbial respiration in Oe horizon more in high N availability soil. P decreased microbial respiration in Oa and Oe+Oa horizons in low P availability soil. Inconsistent responses of fertilization within stand support the conclusion that soil and microbial respiration may increase or decrease in different site environmental conditions, but two years of modest nutrient additions may have been too brief to elicit consistent responses.

3.2 Introduction

Soil resources are one of the major determinants of forest productivity (Chapin 1980). Global change drivers such as CO_2, temperature, precipitation, and nitrogen (N) deposition can alter forest productivity in part by direct and indirect effects on soil resource availability (Melillo et al. 1993, Boisvenue and Running 2006, Bonan 2008). If soil resource availability changes, ecosystem carbon (C) flux will respond with consequences for ecosystem C storage. In northern hardwood forests, for example, anthropogenic N deposition has greatly increased N availability in forested ecosystems (Aber et al. 2003). Since temperate forest ecosystems are generally N limited, increased N availability in soils can positively impact forest productivity and C storage; however, high levels of N deposition can result in dysfunction with possible reductions in forest production and C storage (Aber et al. 1998). As N limited ecosystems become saturated with N, nutrient limitation may shift to other elements, such as P (Braun et al. 2010, Crowley et al. 2012).

Soil respiration in terrestrial ecosystems releases 75 Pg C yr^{-1} (Schlesinger and Andrews 2000), one of the largest fluxes in the global C cycle (Schlesinger 1977). If

belowground C cycling processes in these systems are disrupted, there could be important feedbacks to atmospheric CO_2 and global climate change. A recent meta-analysis suggested that soil respiration was decreased by nutrient additions in general, especially N in temperate forests (Janssens et al. 2010). When nutrients are added, root respiration may decrease because of reduced C allocation belowground (Keyes and Grier 1981, Nadelhoffer et al. 1985, Axelsson and Axelsson 1986), reduced root production (Gower et al. 1992, Haynes and Gower 1995) or root-associated mycorrhizae (Johnson 1993). Also, microbial respiration may decrease by reduced decomposition rates of litter and soil organic matter by changing litter quality and associated microbial composition and activity (Fog 1988, Compton et al. 2004) or by reduced microbial biomass (Treseder 2008). Most studies of nutrient effects on soil respiration have focused on N in temperate forests, and not P. However, P can also affect the belowground C cycle by, for example, reducing C allocation belowground (Keith et al. 1997) or limiting the decomposition rate of organic matter (Cleveland et al. 2002, Kaspari et al. 2008). Further studies are necessary for P effects on soil respiration.

Since root and microbial respiration may be affected differently by changes in nutrient availability (Vogel et al. 2005), it is necessary to understand whether an effect of nutrient addition on soil respiration is caused by root or microbial responses, or both. Separating root and microbial respiration after fertilization could clarify the mechanisms of soil respiration response to nutrient additions. In northern hardwood forests, several studies have reported that the proportion of microbial respiration to soil respiration is between 42 - 80 % (Bowden et al. 1993, Haynes and Gower 1995, Gaudinski et al. 2000, Fahey et al. 2005b). These estimates were developed by integration of component measurements, root exclusion, or isotope methods, as categorized by Hanson et al. (2000). One difficulty with estimating the contribution of root and microbial respiration to soil respiration is trying to measure each

component separately. Since the component integration method is often associated with problems such as soil environment disturbance, or the difficulty in clearly separating affects attributable to each component (Bond- Lamberty et al. 2004, Kuzyakov 2006), it has been hard to accurately estimate root and microbial respiration.

Although nutrient effects on forest soil respiration have been characterized (Janssens et al. 2010), how soil respiration varies by forest age and site fertility in response to N and P is not known in northern hardwood forest ecosystems. The Multiple Element Limitation (MEL) model uses resource optimization theory, including N and P, to predict ecosystem responses in northern hardwood forests (Rastetter et al. 2013). The MEL model predicts that N is more limiting in young stands and P is more limiting in old stands. This means that N may be a major controller on soil respiration in young stands and P in old stands. Regarding site fertility, under the resource optimization theory of the MEL model, N and P fertilization effects on soil respiration can depend on natural soil N and P availability. In a previous study (Bae et al. in review), it was determined that soil respiration in the most fertile site, Jeffers Brook, was lower than at either Bartlett or Hubbard Brook. It was also determined that soil respiration was higher in old stands compared to young stands at these sites. In theory, soil respiration may be less affected by fertilization in fertile soils than in infertile soils probably because nutrients in fertile soils are not limiting (Aber et al. 1998). Also, if one element is originally more limited than the other between N and P, when nutrients are added, the limiting element could affect soil respiration more than the other.

The objective of this study is to test the response of soil respiration and microbial respiration to N, P, or N+P additions in forest sites of different ages and different soil fertility. In view of resource optimization theory, it was hypothesized that total soil respiration and

microbial respiration would be decreased by adding nutrients regardless of nutrient elements. Also, it was hypothesized that soil respiration and microbial respiration would decrease more in infertile sites than in fertile sites, and decrease more in N plots in young stands and in P plots in old stands within site. Microbial respiration was measured using laboratory incubations and field trenches, and we expected the two methods would reveal similar responses.

3.3 Methods

3.3.1 Study site

This study was conducted at three sites in the northern hardwood forest type in the White Mountains, NH, USA: Bartlett Experimental Forest (BEF), Hubbard Brook Experimental Forest (HBEF), and Jeffers Brook (JB) (Table 3.1). The BEF site has three young (21 – 26 years old), three mid-aged (33 – 47 years old in 2009), and three old (121 – 128 years old in 2009) stands. The HBEF and JB sites each have one mid-aged (37 – 47 years old in 2009) and one old (82 – 100 years old in 2009) stand (Table 3.1).

The three sites have different N availability: BEF is the lowest, HBEF intermediate, and JB is the highest in net N mineralization and net nitrification in mineral soils (Table 3.2). Four plots (50 m x 50 m, 10 m buffer around the inside 30 m x 30 m) were established in each stand, treated with N (30 kg N ha^{-1} yr^{-1} as NH_4NO_3), P (10 kg P ha^{-1} yr^{-1} as NaH_2PO_4), N+P, and control. The fertilization began in spring 2011, and plots were fertilized in mid May and in early July in 2011 and 2012. Total soil respiration and microbial respiration (laboratory incubations) were measured in each plot before and after treatment. At BEF

(infertile site) and JB (fertile site) one stand in each age class per site (total five stands: one of each young, mid-aged, and old stand at BEF (C2, C6, and C7) and one mid-aged and one old stand at JB) (Table 3.1) were selected for trenching as an alternative approach for estimating microbial respiration response to treatment.

3.3.2 Soil respiration

To measure soil respiration, five polyvinyl chloride (PVC) collars (20 cm inside diameter) in each plot were installed in June 2009. Soil respiration was measured every three to four weeks from May to November in 2009 - 2012 in six stands (C6, C9 at BEF, mid-aged and old at HBEF, mid-aged and old at JB) (Table 3.1). Beginning in 2010 seven additional stands were added at BEF. Soil respiration was measured every three to four weeks from May to October in 2010 - 2012 in three of these stands (C1, C2, and C7) and during mid-summer 2010 - 2012 in four of these stands (C3, C4, C5, C8) (Table 3.1). Soil respiration was measured between 09:30 AM and 2:30 PM by an infrared gas analyzer system (LI-8100 survey system; Li-Cor Biosciences, Lincoln, NE, USA). The rate of soil C efflux was calculated based on the increase in chamber CO_2 concentrations over 120 seconds.

3.3.3 Trenches

To estimate root and microbial respiration, one trench was excavated to 50 cm depth around a 1.8 x 1.8 m sub-plot in each treatment plot at five stands at BEF and two at JB in summer 2010 (total 20 trenches). Soils inside of the trenches were not disturbed. Around the trenches, plastic was put down to prevent root in-growth, and the trenches were back-filled with soil after installing the plastic barriers. One PVC collar was installed in each trenched plot. Soil respiration in the trenched plots was measured beginning in 2011 concurrent with other soil respiration measurements. Soil respiration in the trenched plots provided an

estimate of microbial respiration, and root respiration was estimated by difference between soil respiration and microbial respiration.

3.3.4 Microbial respiration in organic horizons in laboratory incubation

The effect of fertilization on microbial respiration was tested in laboratory incubations of organic horizons. 16 soil cores (5 cm diameter) were collected in each plot in July 2012. Cores were separated into Oe and Oa horizons and pooled, for one Oe and one Oa sample per plot. Samples were refrigerated at 2 - 4 ℃, and processed within 24 hours of collection. Samples were sorted to remove roots and coarse fragments and were gently homogenized by hand. Moisture content was measured for subsamples of approximately 5 g for Oe and 8 g for Oa horizon.

Subsamples (approximately 10 g) were incubated for 72 hours in Mason jars at room temperature (~21 ℃). Microbial respiration was estimated by quantifying CO_2 evolution in Mason jars using a NaOH-trap method. 20-mL glass vials containing 10 mL 0.1 M NaOH were sealed inside of Mason jars for 24 hours to remove CO_2 from all jars. These vials were replaced at 24 hour intervals with new vials containing 10 mL 0.1 M NaOH. All NaOH was titrated with 0.1 M HCl in the presence of approximately 0.33 ml 2 M $BaCl_2$ to determine how much NaOH had reacted with CO_2.

3.3.5 Nutrient availability in soils

Soil samples were collected in late June 2009 to determine natural soil fertility before fertilization. In each plot, about 30 soil cores (2 cm diameter) were collected and composited within Oe, Oa, and 0-10 cm mineral soils.

Net N mineralization was measured using before and after incubations at 20 ℃ for

21 days. Soils from soil cores were subsampled and incubated in 40 mL of 2 M KCl for 1 hour, and filtering through Whatman #1 filter paper after 18 hrs. Using subsamples, concentrations of NH_4^+ and NO_3^- in extracts were measured using phenolate-hypochlorite (351.2, US EPA 1983) and cadmium reduction (353.2, US EPA 1983). Net N mineralization and net nitrification were estimated using the difference of $NH_4^+ + NO_3^-$ and NO_3^- between the initial and final extracts for 21 days.

Extractable PO_4^{3-} was measured by bicarbonate-form anion exchange-resins (JT Baker Anion Exchange Resin, 325 NA-38, OH- Form, Type I, 16-50 Mesh). In this method, soil subsamples were shaken for 18 hour in 100 mL of distilled water with nylon mesh bags containing the resins. After washing the bags in distilled water to remove soil particles, resin-extractable P was recovered from ion-exchange resins by shaking bags for 1 hour in 100 mL 0.5 M HCl. Inorganic P in HCl extracts was analyzed using the ammonium-molybdate-ascorbic acid method (Murphy and Riley 1962)

Extractable Ca was measured in 10 g soil samples by shaking for 30 minutes with 100 mL of 1 M NH_4Cl. After waiting 18 hours, soil samples were shaken again for 45 minutes and the extract was filtered through Whatman #1 paper. The Ca concentration was analyzed using a Varian Spectra Atomic Absorption Spectrometer (Mulgrave, Victoria, Australia) with a 10,000 ppm (1%) lanthanum chloride solution as a releasing agent to eliminate chemical interferences.

3.3.6 Statistical analysis

To determine the fertilization effects on soil respiration and soil respiration in the trenched plots among four treatments (control, N, P, and NP plots), field measurements of soil respiration from 2009 to 2012 and soil respiration in the trenched plots in 2011 to 2012 were

analyzed using repeated-measure analysis of variance (ANOVA) to look at interaction of treatment and year (including all years before and after fertilization for total soil respiration (TSR), randomized-blocked by stand. Experimental unit was treatment plot and sampling units were five collars. To determine if the fertilization effects differed by site or by age, we included site or age in the repeated-measure ANOVA using proc mixed in SAS (SAS Inc, 2005).

To determine the fertilization effects on soil- and microbial- respiration, analyses were performed on: the differences of incubated microbial respiration in Oe, Oa, and Oe+Oa weighted by soil mass of each organic horizon between 2009 and 2012 and the mean of soil respiration from June to August between 2009 - 2010 to 2012. We calculated the difference between fertilization plots and control plots within 2009 (or mean of 2009 and 2010) and 2012. There were no pretreatment data for soil respiration in the trenched plots, and therefore calculations were limited to the difference between fertilization plots and control plots in 2012. Fertilization effects were analyzed across all 13 stands, to include the effects of stand age and site on incubated microbial respiration in Oe, Oa, and Oe+Oa, soil respiration in the trenched plots, and TSR. The fertilization effect was analyzed by the General Linear Models procedure in SAS (SAS Inc, 2005).

To understand which factors affect microbial respiration (trenches and incubation) and soil (annual and summer) respiration, a Factor analysis was performed on variables including nutrient availability, roots, and litterfall (Minitab ver.14). To understand the relationship between incubated microbial- and total summer- soil respiration and nutrient availability in soils, Pearson's product moment correlations were determine using SAS (SAS Inc, 2005). For the correlations, microbial and summer soil respiration during June to August

in the fields and incubated microbial respiration at 72 hour were used. The correlation analysis was blocked by treatment plot if there was no fertilization effect among plots, but if soil respiration or microbial respiration differed by fertilization treatment, the correlation was conducted in each treatment. All the significant differences are reported at $\alpha = 0.10$.

3.4 Results

The responses of soil and microbial respiration to nutrient additions in these northern hardwood forest stands were highly variable. In many cases, responses were not statistically significant. Moreover, the responses varied among stands, between soil horizons and between methods. Both significant increases and decreases in respiration component responses to fertilization were observed. Following is a summary of the most important observed responses.

3.4.1 Fertilization effects on TSR

TSR did not respond consistently to the fertilization treatments, in an overall repeated ANOVA results across all stands ($p = 0.81$) (Table 3.3). The fertilization effects did not differ among sites ($p = 0.68$) or among ages ($p = 0.70$) either (Table 3.3).

Within individual stands, TSR responded significantly to fertilization in some cases (Figure 3.1), but the responses were variable among stands. In particular, fertilization reduced TSR in the two young stands at BEF in 2012: N plots ($p = 0.03$) in 2012 at C1 and P ($p = 0.09$) and NP ($p = 0.09$) plots in 2012 at C2; whereas fertilization increased TSR in mid-aged stands, especially in N plots ($p < 0.01$), at HBEF in 2012. No effects were observed for the

other stands.

3.4.2 Fertilization Effects on Microbial Respiration in Trenched Plots

Because there was no replication (one trench in each plot) in each treatment plot in five stands, only the overall model provided statistical comparisons of treatment effects. Similar to TSF, soil respiration in the trenched plots did not respond significantly to the fertilization treatments ($p = 0.48$). The fertilization effects did not differ among sites ($p = 0.72$) or ages ($p = 0.42$) (Table 3.3). Among the individual stands at BEF, the response of soil respiration in the trenched plots to the fertilization treatments was highly variable (Figure 3.2).

The contribution of microbial respiration to TSR was calculated as the difference between rates measured in trenched and un-trenched plots at each site. This value differed between control and fertilization treatments across the five stands: The N+P plots had the highest proportion (73 %) of microbial respiration, and control and N plots had the lowest portion (61 – 62 %) ($p = 0.05$) (Figure 3.3).

3.4.3 Laboratory incubations for Microbial Respiration

Fertilization effects on incubated microbial respiration varied by soil horizon, site, and forest age. In the Oe horizon, incubated microbial respiration was not significantly different among treatments across all 13 stands ($p = 0.37$). Between sites in the Oe horizon, P plots were 37 – 56 % higher than others at HBEF ($p = 0.02$), and N+P plots were 127 – 190 % higher than others at JB ($p < 0.01$) (Figure 3.5, Table 3.4). For stand age in Oe horizon, P plots were 34 - 77 % higher than others in young stands ($p < 0.01$) (Figure 3.6, Table 3.5). In Oa horizon, like Oe horizon, incubated microbial respiration was not significantly different among treatments across 13 stands ($p = 0.53$). Between sites in Oa horizon, N plots were 34 –

64 % lower than others at HBEF (p = 0.01) (Figure 3.5, Table 3.4). For stand age in Oa horizon, P plots were 23 – 89 % higher than others in young stands (p = 0.05) (Figure 3.6, Table 3.5). In Oe+Oa horizon, calculated by weighted soil mass in each horizon, incubated microbial respiration was not different among treatments across 13 stands, and there was no consistent pattern by sites or stand age (Figure 3.5 and 3.6, Table 3.4 and 3.5).

Finally, the incubated microbial respiration in the organic horizons was correlated to the trenched soil respiration ($p < 0.01$, $R^2 = 0.45$), but not to TSR (p = 0.32) (Figure 3.4).

3.4.4 Natural nutrient availability effects on the changes of soil respiration and microbial respiration after fertilization

Generally, factor analysis suggested that N availability explains a large amount of the variability in soil and microbial respiration. Particularly, correlation results suggested that nutrient availability in specific horizons is related to soil and microbial respiration. In 2009, summer soil respiration and incubated microbial respiration in organic horizons were low in high N availability soils (Ch 2). These negative correlations between both soil and incubated microbial respiration vs. soil N availability in 2009 were no longer present, or had changed to positive correlations by 2012 (Table 3.6).

The natural fertility gradient across the 13 stands appeared to be related to the response of microbial respiration to the N and P treatments. In particular, when N was added, incubated microbial respiration in Oe horizons increased more in stands with high N availability than low N availability (Table 3.6). When P was added, incubated microbial respiration in Oa and Oe+Oa horizon decreased more in stands with high P availability than low P availability (Table 3.6).

3.5 Discussion

Measurements were taken to document the response of TSR and microbial respiration to additions of N, P and N+P in a series of northern hardwood forest stands of different ages across a soil fertility gradient in NH. As shown in a previous study, TSR and belowground C allocation declined significantly with increasing soil N availability across the fertility gradient. It was hypothesized that nutrient additions would reduce TSR with the greatest reductions occurring in the low fertility sites. Also expected was a greater response of TSR to N addition in younger than older stands in accordance with predictions of a resource optimization theory model (MEL, Rastetter et al 2013) that indicated a switch from N to P limitation over forest succession in northern hardwoods.

Soil respiration: There was no effect of fertilization treatment on TSR over two years of treatment. The lack of an overall response across all 13 stands can be explained by three principal factors: 1. The relatively short duration of this study and probable delay in the treatment response, 2. The relatively low level of nutrient additions, and 3. Variation in the direction of TSR responses among stands.

Long-term fertilization studies in northern hardwood forests show that it may take several years to find a fertilization effect on soil respiration. For example, in mixed deciduous stands in Massachusetts, soil respiration did not change in the first two years but decreased by about 40 % after 13 years N addition (50 - 150 kgN ha^{-1} yr^{-1}) (Bowden et al. 2004). In sugar maple-dominated sites in Michigan, soil respiration did not change the first year of fertilization, but decreased about 15 % after 6 years of fertilization (Burton et al. 2004). Although Phillips and Fahey (2007) observed reductions in TSR in a northern hardwood

forest in the second year of treatment, the level of nutrient addition in that study was about five times higher than in the present study. Other N addition studies in temperate forests also applied N at higher rates (50 - 150 kg N ha^{-1} yr^{-1}) than N deposition level in North America (3 - 32 kg N ha^{-1} yr^{-1} (Fenn et al. 1998), like our study, 30 kg N ha^{-1} yr^{-1}) and TSR was reduced (Haynes and Gower 1995, Bowden et al. 2004, Drake et al. 2012). The delayed responses of soil respiration after fertilization suggests that long term study is important for assessing the impact of fertilization effects on reducing soil CO_2 flux.

In this study significant responses of TSR to fertilization treatments in some of the stands were observed, but the responses were not uniform in direction. For example, significant decreases in TSR were observed in C1 and C2 at BEF, whereas significant increases occurred in the mid-aged stand at HBEF. Although these variable responses may support the transient effects noted above, there are some reasons to expect variable responses of TSR to nutrient additions in different forests. Most studies report reduced TSR in fertilized forests but some have noted no response or an increase in TSR. Increased soil respiration after N fertilization may be explained by increased plant productivity including litter and roots in nutrient limited soils (Maier and Kress 2000, Contosta et al. 2011). The TSR response can be complex because TSR includes root respiration, root-associated microbial respiration and heterotrophic respiration, and each of these may respond differently to changes in nutrient availability (Haynes and Gower 1995, Maier and Kress 2000). Moreover, some microbial populations may be suppressed by increasing nutrient availability (e.g., white-rot fungi by N fertilization, (Waldrop et al. 2004)) whereas others may be stimulated (Carreiro et al. 2000, Knorr et al. 2005).

Microbial respiration: Consistent with soil respiration, there was no general pattern

of soil respiration in the trenched plots after fertilization (Table 3.4 and 3.5). However the proportion of TSR attributed to microbial respiration did respond significantly to N+P treatments. In control plots, the ratio of 0.61 of microbial respiration to TSR was similar with another study in Hubbard Brook (0.60) estimated using TSR minus detached root respiration (Fahey et al. 2005b). The high ratio of soil respiration in the trenched plots to TSR in N+P plots (73 %) resulted from the combination of relatively low soil respiration (6 % lower than control plots) and high soil respiration in the trenched plots (15 % higher than control plots) in N+P plots. The high contribution of soil respiration in the trenched plots when N and P were added could suggest that, for stands in this study response to N and P could be co-dependent. In August 2011, soil N and P availability increased more in N+P plots than in N or P only plots at BEF (Fisk, not published), which would support the NP co-limitation theory (Elser et al. 2007) in our stands. The increase of N and P availability in soils may increase decomposition rates, microbial biomass, or microbial activities, leading to enhanced microbial respiration.

The laboratory incubation measurements of microbial respiration potentials provided further insights into the effects of nutrient additions across the 13 stands. Although the evidence did not support the simple interpretation of the theory provided by the MEL model – i.e. a switch from N to P limitation across stand ages – there were significant treatment effects on microbial respiration potential in several of the sites. Most consistent was the stimulation of respiration in the young stands at BEF. Notably, the BEF site is the most infertile among the three sites (Ch 2), and the response to P additions strongly suggests that low P availability limits microbial activity in these infertile stands at BEF. However, based on MEL, greater response to treatment might have been expected in older stands at BEF, but treatment effects in the older stands were not statistically significant.

It has commonly been observed that N additions can suppress microbial respiration through effects on phenol oxidize activity of white-rot fungi (Kirk and Farrell 1987, Waldrop et al. 2004). A decrease in microbial activity was observed in N addition plots in the Oa horizon only at the HBEF. Inconsistent responses of microbial respiration to N addition might be explained by variable responses of different microbial populations. Also, the N suppression of fungal activity appears to vary across forests of different tree species composition as decay of high quality litter increases whereas low quality litter decreases (Carreiro et al. 2000, Hobbie 2005, Phillips and Fahey 2007). Meta-analysis results also showed that decomposition rate was stimulated more in high N availability soil and in a short period after fertilization (Knorr et al. 2005).

Some striking inconsistencies were observed between the lab and the trenching responses of microbial respiration. Microbial respiration was low in fertilized plots at C2 in trenches, but microbial respiration from incubation was high in fertilized plots, especially P plot, compared to control. Microbial respiration in trenches at C7 (old stand at BEF) and at JB old was high in N plots, but incubated microbial respiration was relatively low in N plots in old stands. Field and incubated soil and microbial respiration did not always agree in other studies, which has been explained by the disturbance associated with sieving soils for incubation (Fierer et al. 2003) or different soil conditions between two methods (Curiel Yuste et al. 2007).

The inconsistent microbial respiration between the two different methods in this study might be explained by the different fertilization effects on two horizons (organic and mineral soils) or by methodological differences. First, the microbial respiration method using trenches cannot distinguish changes between organic and mineral soil horizons and the

laboratory incubations included only the organic horizons. In forest soils in North Carolina, USA, N fertilization increased microbial biomass leading to increased soil respiration in the forest floor but not in upper 10cm mineral soils (Gallardo and Schlesinger 1994). Also, in a 50- year old *Pinus sylvestris* stand, increased C and N concentration only in organic horizons, but not in mineral soil horizons is consistent with the enhanced microbial respiration only in organic layer as reported by (Nohrstedt 1992). N and P availability were not measured in soils after fertilization in the present study, but large amounts of fertilizer may be still retained in the upper part of the soil profile without being mobilized to greater depths (Mälkönen et al. 1990), and this fertilizer retention may contribute to increases in microbial respiration only in the organic horizons.

Another cause of differential response of microbial respiration between incubation and trenching could be methodological effects. In the trenching, microbial respiration could be overestimated if residuals of fine and coarse roots are still decaying in trenched plots (Epron et al. 1999, Ngao et al. 2007) even though it is known this problem can be minimized by measuring soil respiration after several months (Ewel et al. 1987, Bowden et al. 1993). Or higher moisture during summer in the trenched plots (Hart and Sollins 1998, Tang et al. 2005) can alter the microbial activities. Also, the laboratory incubated soils are more disturbed. The inherent problems of each method for estimating microbial respiration complicate interpretation of the fertilization effects on microbial respiration between two methods.

The fertilization effects on soil respiration and microbial respiration differed by inherent soil fertility. We hypothesized that after fertilization; belowground C flux would decrease, especially in infertile sites where nutrients are more limiting. However, in Oe horizon, when N was added, microbial respiration even increased more in stands with high N

availability than in low N stands across 13 stands. In Oa and Oe+Oa horizons, when P was added, the microbial respiration increased in low P stands, supporting the idea that the limited P probably inhibited microbial activities. Regarding inherent soil fertility, there was no clear pattern in soil respiration across 13 stands after fertilization. In a previous study before fertilization in these stands, it was found that soil respiration was high in stands with low N availability (Ch 2). In this study, after fertilization, nutrient availability did not affect belowground C flux in soils during the first two years.

This study indicated that two years of modest nutrient addition was not long enough to result in consistent overall effects of N and P on soil respiration and microbial respiration. Long term study is necessary to understand the response of fertilization on belowground C flux.

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Table 3.1. Northern hardwood stands used in this study. Tree species are listed as dominant species based on basal area

Site	Age	Basal Area (m^2 ha^{-1})	Dominant species based on basal area
BEF, C1[b]	Young	25.2	*Betula papyrifera, Prunus pensylvanica, Fagus grandifolia*
C2 [b†]	Young	23.4	*Acer rubrum, F. grandifolia,B. papyrifera*
C3[c]	Young	30.5	*P. pensylvanica, F. grandifolia,A. rubrum*
C4 [c]	Mid-aged	32.9	*B. papyrifera, Populus grandidentata,P. pensylvanica*
C5 [c]	Mid-aged	27.2	*B. papyrifera, P. pensylvanica,A. rubrum*
C6[a†]	Mid-aged	30.1	*A. rubrum, B. papyrifera,F. grandifolia*
C7 [b†]	Old	32.1	*F. grandifolia, A. saccharum,Tsuga canadensis*
C8 [c]	Old	35.2	*F. grandifolia, A. saccharum,B. alleghaniensis*
C9[a]	Old	32.7	*A. saccharum, F. grandifolia,B. alleghaniensis*
HBEF[a]	Mid-aged	29.5	*B. alleghaniensis, B. papyrifera,A. rubrum*
	Old	33.9	*B. alleghaniensis, F. grandifolia,A. saccharum*
JB[a†]	Mid-aged	27.9	*B. alleghaniensis, B. papyrifera,A. saccharum*
	Old	35.7	*A. saccharum, B. alleghaniensis,F. grandifolia*

[a] means soil respiration measured every 3 - 4 weeks from May to November in 2009 - 2012.

[b] means soil respiration measured every 3 - 4 weeks from May to October in 2010 - 2012.

[c] means soil respiration measured every 3 - 4 weeks from May to August in 2010 - 2012.

† means having trenching.

Table 3.2. Nutrient availability in upper 10 cm of mineral soil at BEF, HBEF, and JB. Different superscript letters are significantly different from one another at the $\alpha = 0.05$

	BEF	HBEF	JB
Latitude and Longitude	44° 02-04' N, 71° 16-19' W	43° 56' N, 71° 44' W	44° 02' N, 71° 53' W
Elevation (m)	330-570	500	730
net N mineralization ($ug\ g^{-1}\ day^{-1}$)	0.38 ± 0.02b	0.57 ± 0.03ab	0.64 ± 0.06a
net nitrification ($ug\ g^{-1}\ day^{-1}$)	0.25 ± 0.03c	0.51 ± 0.06b	0.68 ± 0.03a
available P ($ug\ g^{-1}\ day^{-1}$)	2.03 ± 0.16a	3.20 ± 0.74a	3.09 ± 0.64a
exchangable Ca ($ug\ g^{-1}\ day^{-1}$)	86 ± 9b	135 ± 50b	320 ± 8a

Table 3.3. Repeated measure ANOVA for fertilization effects on field soil respiration in 2009 -2012 and trenched soil respiration in 2011 - 2012

Source	Field soil respiration in 2009 - 2012			Trenched soil respiration in 2011 – 2012		
	Df	F	*P* value	df	F	*P* value
Treatment	3	0.15	0.20	3	0.24	0.87
Year	3	5.04	<0.01	1	4.59	0.03
Site	2	1.92	0.14	1	3.84	0.05
Age	2	11.0	<0.01	2	0.78	0.46
Treatment x Year	6	0.49	0.81	3	0.83	0.48
Treatment x Site	6	0.54	0.78	3	0.24	0.87
Treatment x Age	6	0.82	0.55	6	1.00	0.43
Year x Site	4	12.8	<0.01	1	3.90	0.05
Year x Age	5	3.81	<0.01	2	2.59	0.08
Treatment x Year x Site	12	0.77	0.68	3	0.44	0.72
Treatment x Year x Age	15	0.78	0.70	6	1.01	0.42

Table 3.4. Soil respiration, soil respiration in trenched plots, and incubated microbial respiration in Oe and Oa horizon (mean±standard error of stands) before and after fertilization by site at BEF, HBEF, and JB

Belowground C flux (umol m^{-2} sec^{-1})	Site	Control		N			P			N+P		
		Before	After	Before	After	Difference (%)	Before	After	Difference (%)	Before	After	Difference (%)
Soil respiration	BEF	5.9±0.5	4.2±0.4	5.1±0.7	3.8±0.4	12	4.9±0.3	3.8±0.2	9	4.9±0.5	3.8±0.3	10
	HBEF	4.0±0.3	3.2±0.2	4.0±0.2	3.9±0.2	19	4.4±0.3	3.5±0.3	0	4.3±0.5	3.4±0.1	2
	JB	4.8±0.0	4.5±0.4	4.4±0.2	3.9±0.3	-4	4.5±0.7	4.0±0.4	-4	4.0±0.2	3.9±0.1	5
Soil respiration in trenched plots	BEF		2.2±0.0		2.4±0.1	10		2.6±0.2	19		2.4±0.2	10
	JB		2.0±0.1		2.2±0.0	10		2.2±0.2	7		2.5±0.3	23
Oe microbial respiration	BEF	3.7±0.2	16±1.1	3.7±0.2	16±1.0	-6	3.5±0.2	19±1.8	29	3.8±0.5	16±1.4	-1
	HBEF	2.5±0.0	18±2.7	2.6±0.2	21±3.1	15	2.6±0.0	28±0.1	56	1.7±0.6	16±3.4	19
	JB	2.8±0.6	18±2.8	2.5±0.1	26±1.2	51	3.0±0.2	18±1.7	-12	2.4±0.3	44±5.3	178
Oa microbial respiration	BEF	1.1±0.1	7.9±0.8	1.0±0.0	8.1±0.6	9	1.0±0.1	8.8±0.9	27	0.8±0.1	7.3±0.8	18
	HBEF	0.5±0.1	6.8±0.6	0.7±0.0	5.9±0.2	-64	0.8±0.2	9.4±1.5	-15	0.7±0.1	7.6±1.0	-30
	JB	0.5±0.0	8.1±3.1	0.5±0.0	6.7±1.3	-6	0.5±0.0	7.1±1.5	-13	0.5±0.1	7.0±1.9	-19
Oe+Oa microbial respiration	BEF	0.7±0.1	1.5±0.1	0.7±0.1	1.3±0.1	-4	0.8±0.1	1.5±0.1	15	0.7±0.1	1.4±0.1	1
	HBEF	0.9±0.2	1.9±0.2	0.4±0.0	1.3±0.2	-24	0.7±0.1	1.6±0.4	24	0.8±0.1	1.4±0.2	-14
	JB	0.6±0.2	1.4±0.1	0.8±0.1	2.5±0.4	13	0.8±0.2	1.9±0.2	4	0.6±0.0	1.5±0.2	43

* Difference (%) means that relative % of fertilization plots to control plot in 2009 minus the relative % in 2012.

Table 3.5. Soil respiration, soil respiration in trenched plots, and incubated microbial respiration in Oe and Oa horizon (mean±standard error of stands) before and after fertilization by age at BEF, HBEF, and JB

Belowground C flux (umol m^{-2} sec^{-1})	Age	C		N			P			N+P		
		Before	After	Before	After	Difference (%)	Before	After	Difference (%)	Before	After	Difference (%)
Soil respiration	Young	5.8±0.5	4.5±1.0	4.0±0.2	3.7±0.7	12	5.1±0.3	4.2±0.6	7	4.8±0.6	3.8±0.8	2
	Mid-aged	4.6±0.4	3.5±0.4	4.4±0.4	3.5±0.3	5	4.2±0.4	3.3±0.4	2	4.0±0.3	3.2±0.6	3
	Old	6.1±0.7	4.4±1.3	5.7±1.2	4.3±1.2	15	5.1±0.2	4.1±0.7	9	5.2±0.7	4.2±0.7	16
Soil respiration in trenched plots	Young		2.2±0.0		2.2±0.0	2		3.0±0.0	38		2.7±0.0	25
	Mid-aged		2.0±0.1		2.4±0.1	17		2.3±0.1	13		2.1±0.0	5
	Old		2.2±0.1		2.4±0.2	6		2.3±0.4	4		2.7±0.2	21
Oe microbial respiration	Young	4.2±0.2	13±1.7	3.5±0.1	16±3.4	30	3.9±0.1	23±1.8	77	3.4±0.2	17±5.8	43
	Mid-aged	3.0±0.3	16±3.7	3.5±0.5	18±5.5	-4	3.2±0.2	17±6.3	-12	3.9±1.0	23±14	24
	Old	3.3±0.4	19±2.8	3.2±0.3	19±4.8	2	3.0±0.2	23±4.1	36	2.4±0.4	20±8.8	29
Oa microbial respiration	Young	1.3±0.2	6.7±1.5	0.9±0.1	6.8±1.1	32	1.1±0.1	11±2.8	89	0.8±0.2	8.0±2.0	66
	Mid-aged	0.8±0.1	5.8±1.0	0.8±0.1	6.6±1.6	2	0.8±0.1	6.3±1.7	6	0.7±0.1	5.5±1.8	0
	Old	0.8±0.1	10±1.9	0.9±0.1	8.9±1.8	-33	0.9±0.1	9.7±1.0	-21	0.8±0.1	8.6±1.6	-27
Oe+Oa microbial respiration	Young	1.0±0.1	1.5±0.2	0.7±0.1	1.5±0.2	15	0.7±0.2	1.5±0.3	54	0.6±0.0	1.2±0.3	47
	Mid-aged	0.7±0.	1.5±0.2	0.6±0.1	1.3±0.5	-2	0.8±0.1	1.5±0.3	-8	0.7±0.0	1.5±0.2	-9
	Old	0.6±0.1	1.6±0.3	0.7±0.2	1.7±0.8	-20	0.8±0.1	1.6±0.5	15	0.8±0.2	1.4±0.2	-6

* Difference (%) means that relative % of fertilization plots to control plot in 2009 minus the relative % in 2012.

Table 3.6. Relationship between 2009 soil nutrient availability and changes between 2009 and 2012 of soil and microbial respiration

Soil nutrient availability in 2009	Horizon	Changes between 2009 and 2012 (%)			
		Soil respiration in Jun-Aug	Microbial respiration in Oe	Microbial respiration in Oa	Microbial respiration in Oe+Oa
Nitrification	Oe	P↘	N↗		
	Oa		N↗, NP↗		
	0-10cm		N↗, NP↗		
N mineralization	Oe			P↗	
	Oa				
	0-10cm		N↗, NP↗		
available P	Oe				P↘
	Oa	N↗, NP↗		N↘, NP↘	N↘, NP↘
	0-10cm		N↗	P↘	
exchangable Ca	Oe			N↗	
	Oa			N↗	N↗
	0-10cm	NP↘			

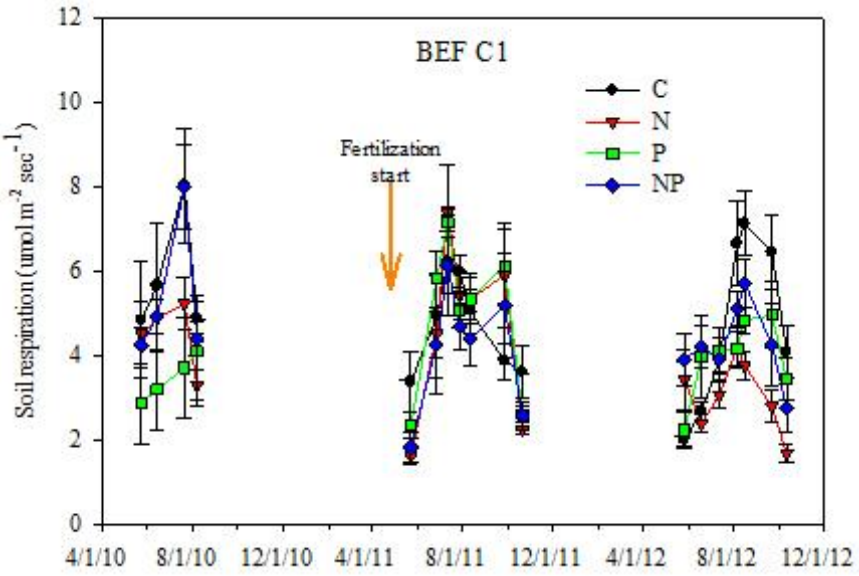

Figure 3.1 (a) Soil respiration (mean ± standard error of five collars) in four treatment plots at C1.

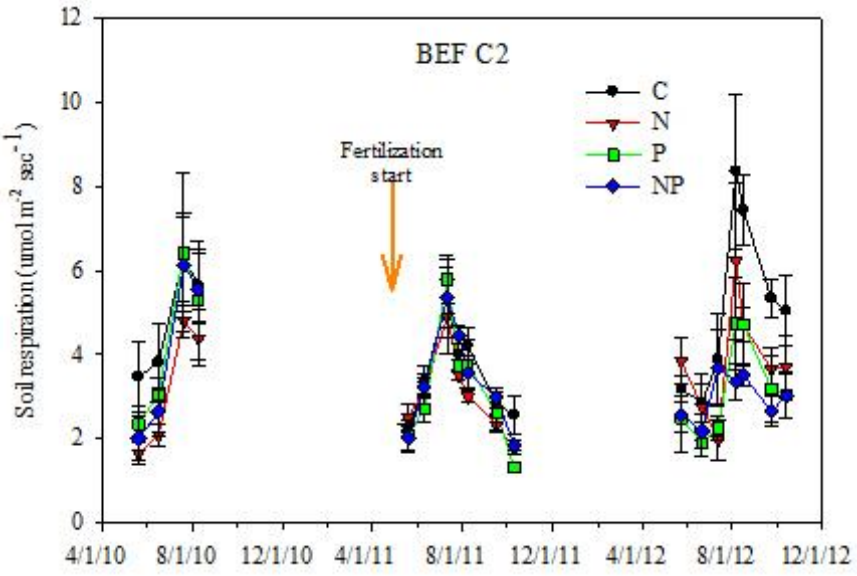

Figure 3.1 (b) Soil respiration (mean ± standard error of five collars) in four treatment plots at C2.

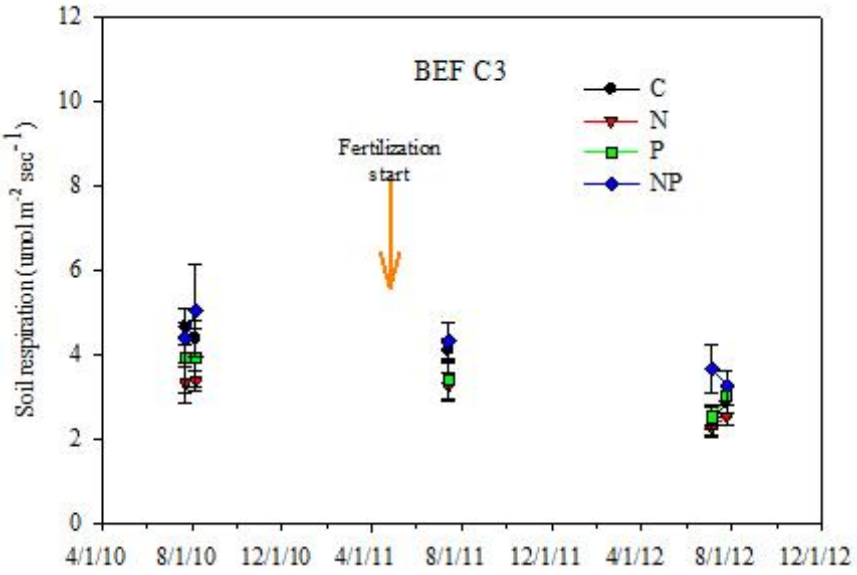

Figure 3.1 (c) Soil respiration (mean ± standard error of five collars) in four treatment plots at C3.

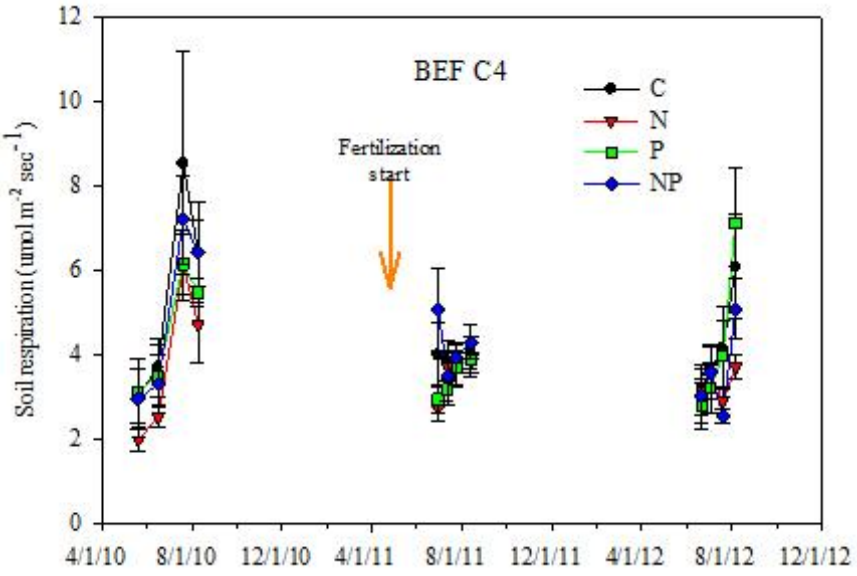

Figure 3.1 (d) Soil respiration (mean ± standard error of five collars) in four treatment plots at C4.

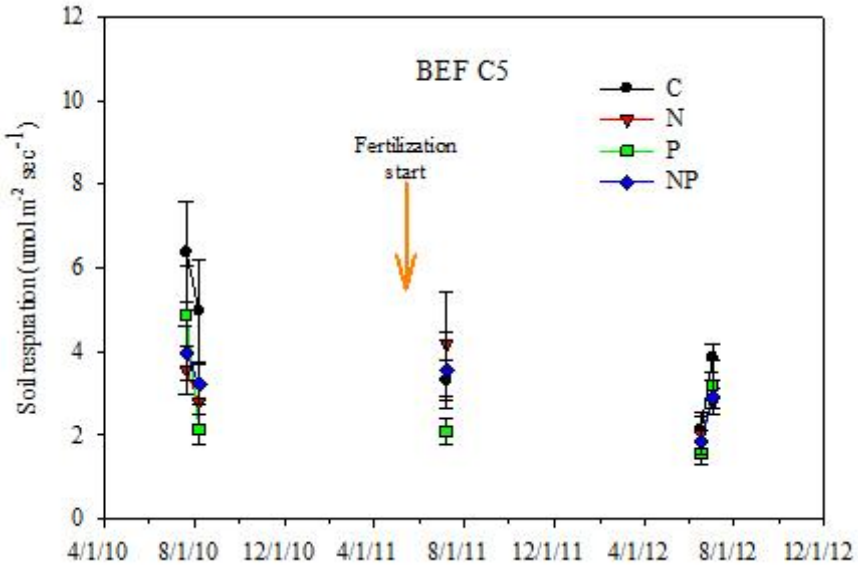

Figure 3.1 (e) Soil respiration (mean ± standard error of five collars) in four treatment plots at C5.

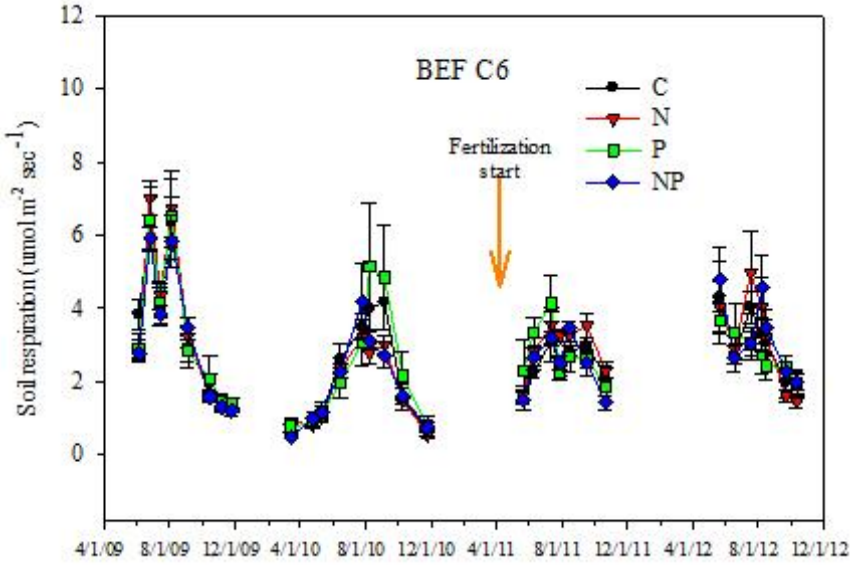

Figure 3.1 (f) Soil respiration (mean ± standard error of five collars) in four treatment plots at C6.

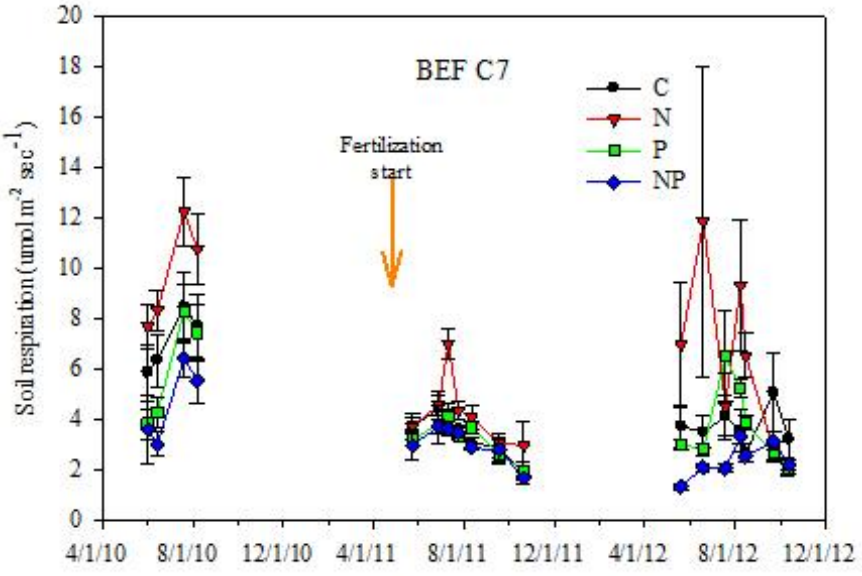

Figure 3.1 (g) Soil respiration (mean ± standard error of five collars) in four treatment plots at C7.

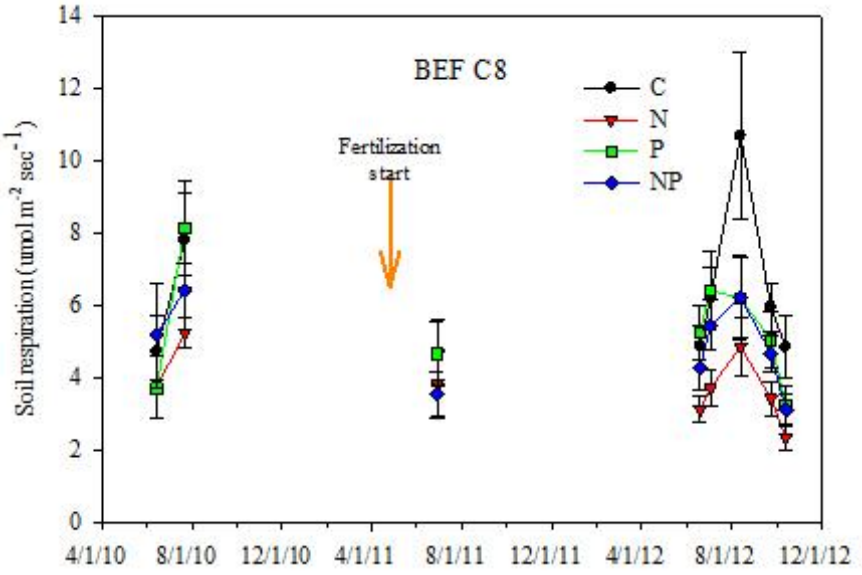

Figure 3.1 (h) Soil respiration (mean ± standard error of five collars) in four treatment plots at C8.

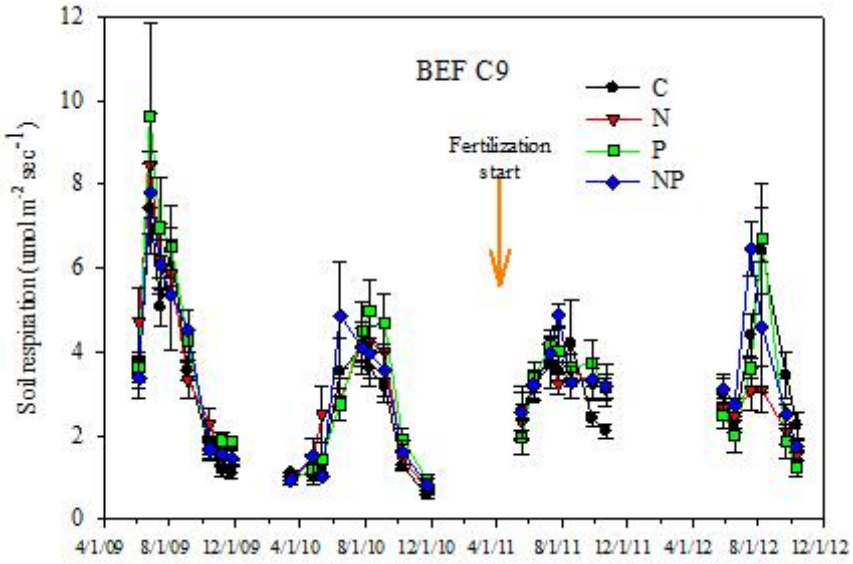

Figure 3.1 (i) Soil respiration (mean ± standard error of five collars) in four treatment plots at C9.

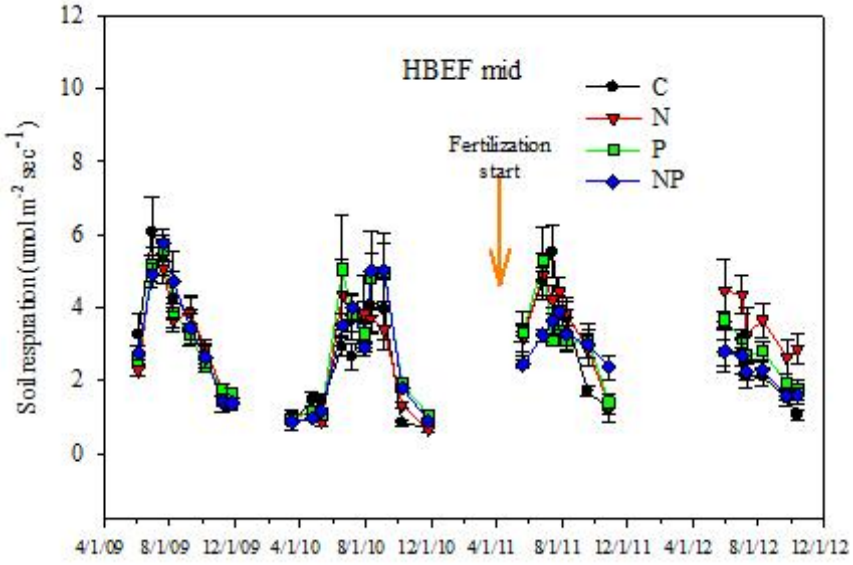

Figure 3.1 (j) Soil respiration (mean ± standard error of five collars) in four treatment plots at HBEF mid-aged.

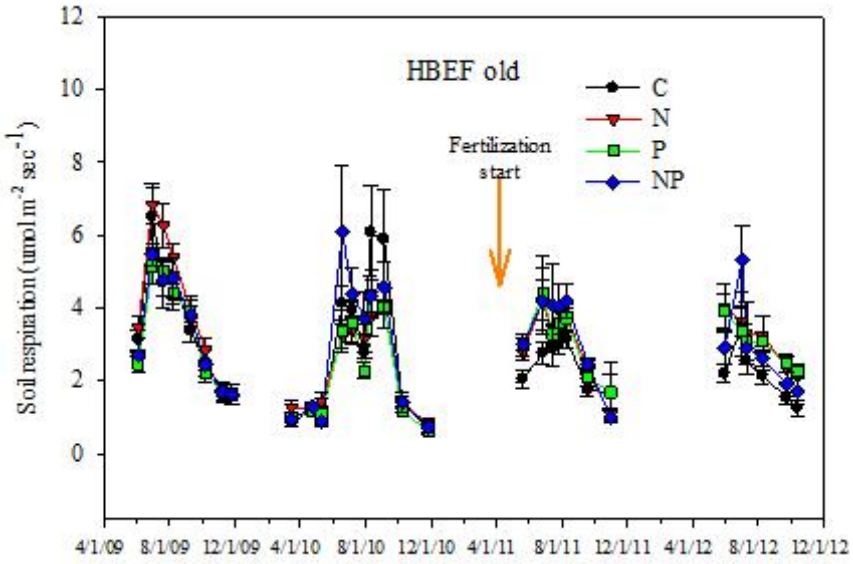

Figure 3.1 (k) Soil respiration (mean ± standard error of five collars) in four treatment plots at HBEF old.

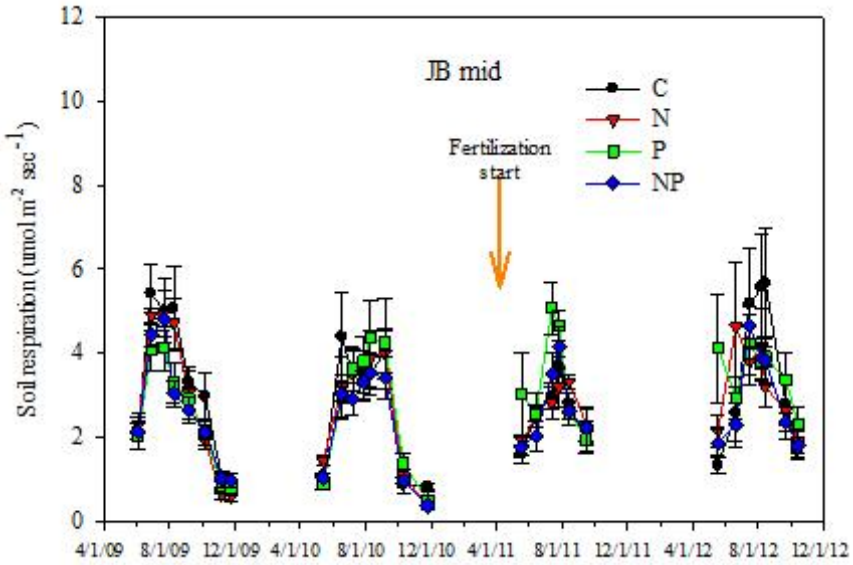

Figure 3.1 (l) Soil respiration (mean ± standard error of five collars) in four treatment plots at JB mid-aged.

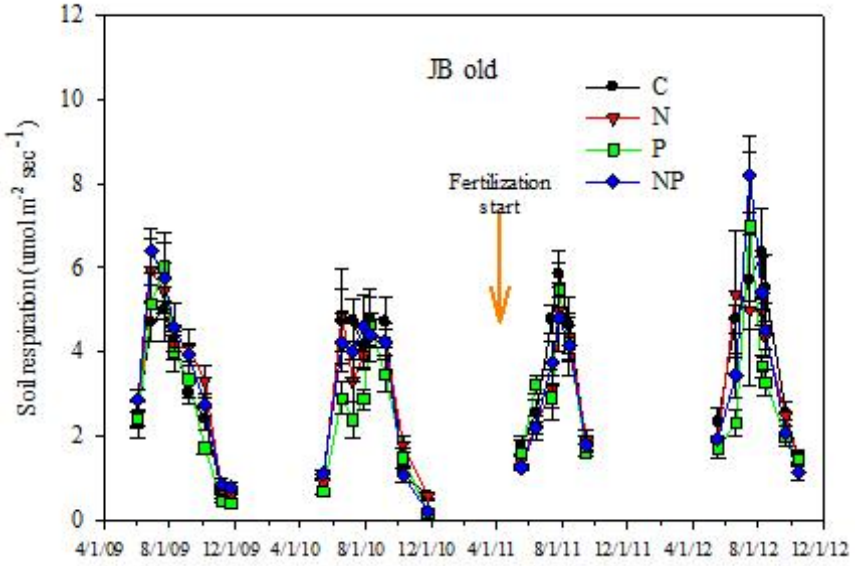

Figure 3.1 (m) Soil respiration (mean ± standard error of five collars) in four treatment plots at JB old.

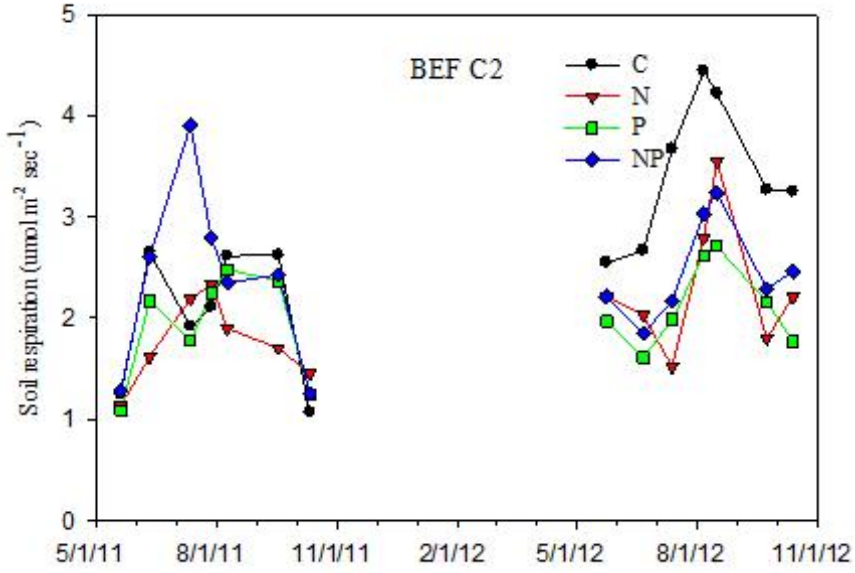

Figure 3.2 (a) Soil respiration in four trenched plots at C2.

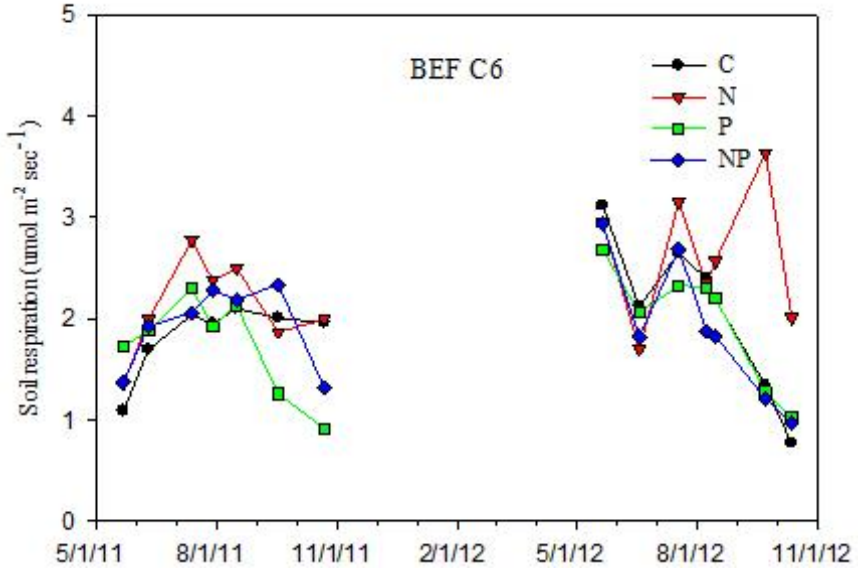

Figure 3.2 (b) Soil respiration in four trenched plots at C6.

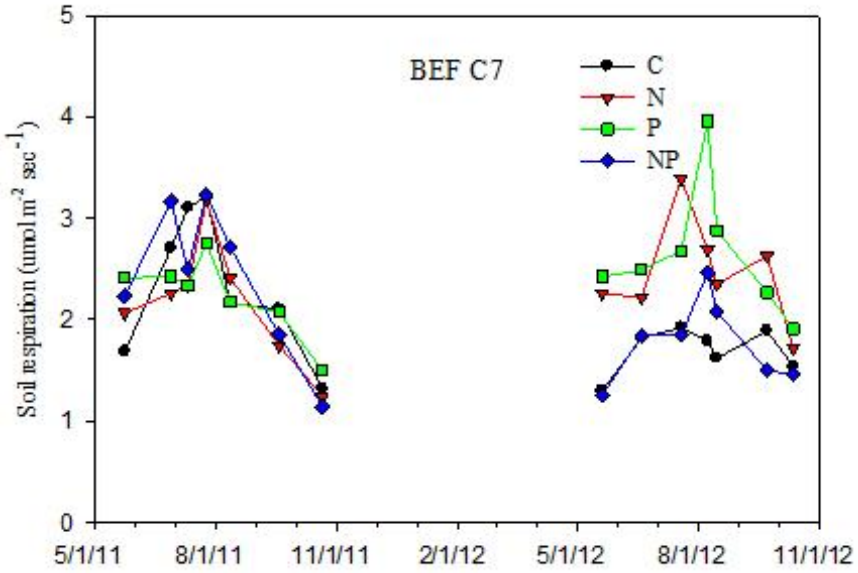

Figure 3.2 (c) Soil respiration in four trenched plots at C7.

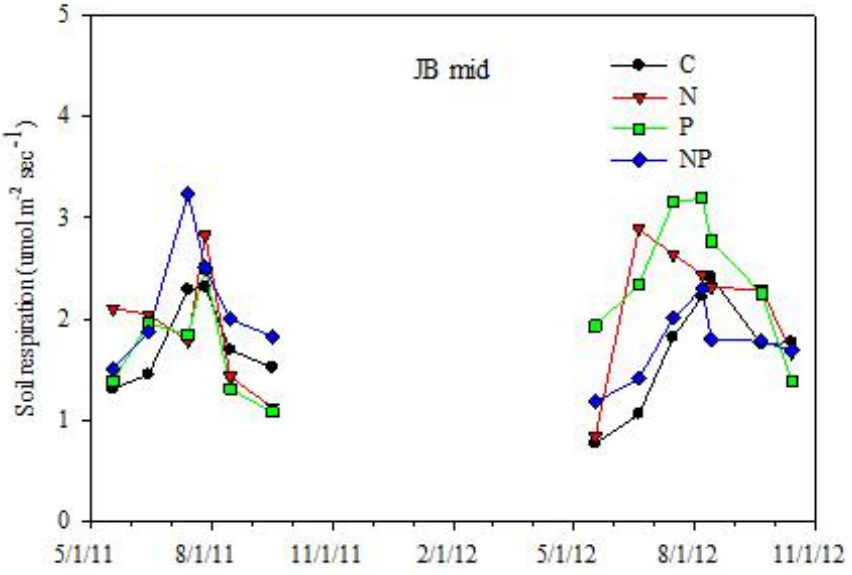

Figure 3.2 (d) Soil respiration in four trenched plots at JB mid-aged.

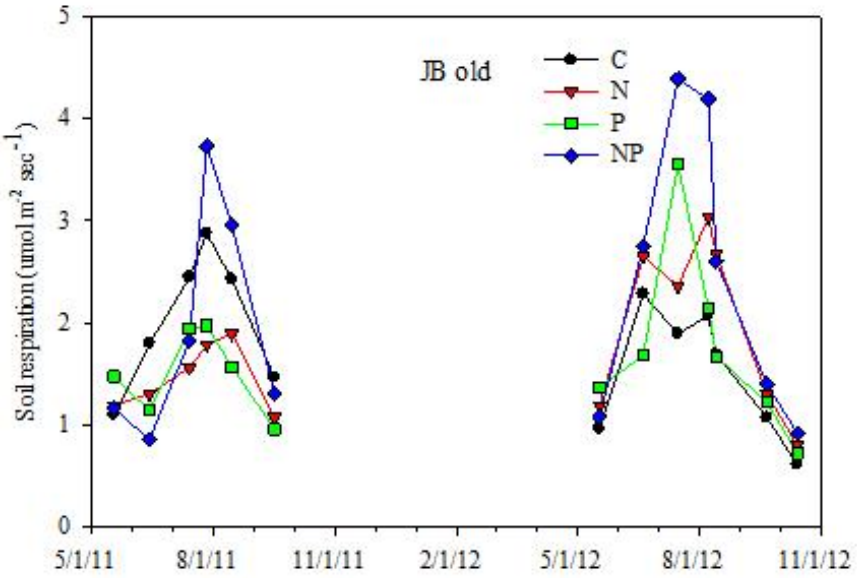

Figure 3.2 (e) Soil respiration in four trenched plots at JB old.

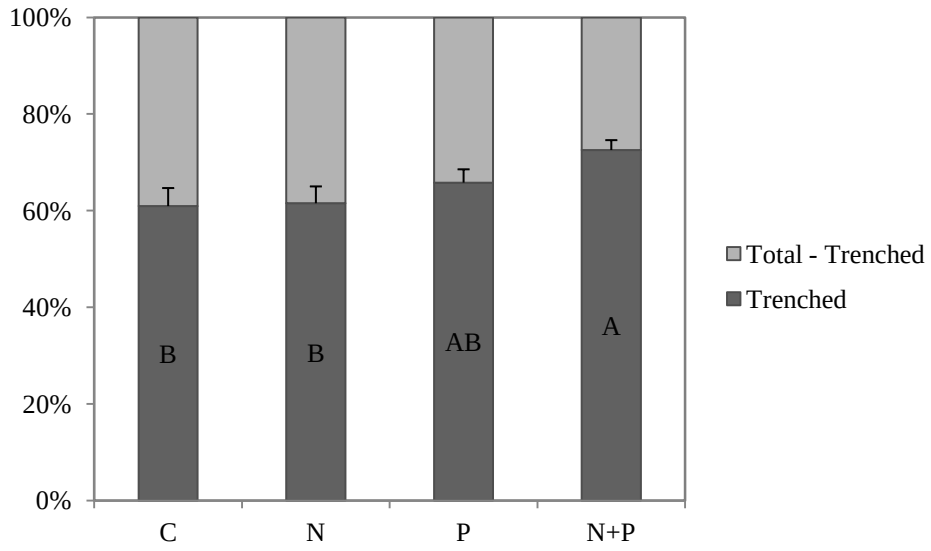

Figure 3.3. The contribution of microbial respiration on soil respiration by treatments. Error bars represent the standard error across five stands.

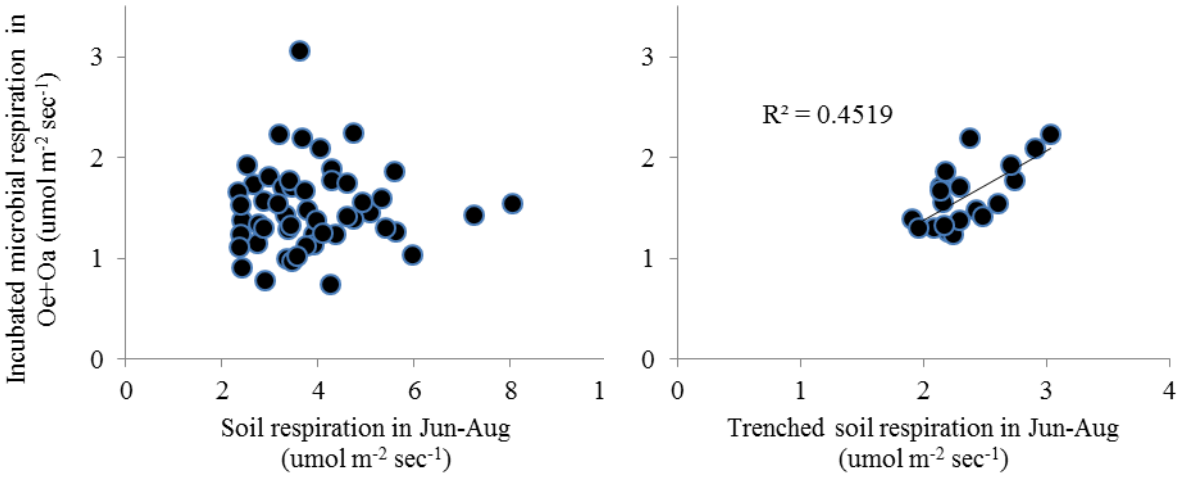

Figure 3.4. Correlations between incubated microbial respiration and summer soil respiration (left) and summer soil respiration in trenched plots (right).

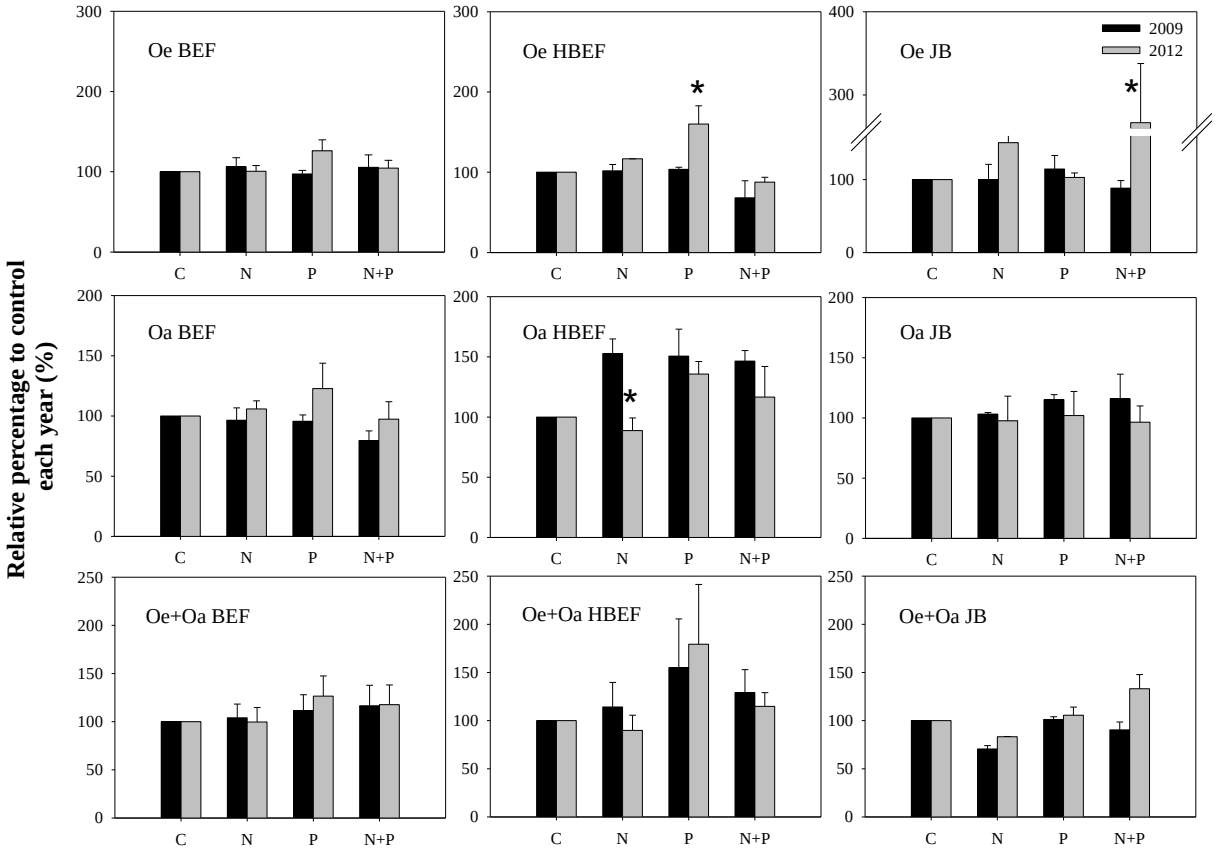

Figure 3.5. Relative percentage of incubated microbial respiration to control plot within 2009 and in 2012 in each of Oe, Oa, Oe+Oa horizon by site.

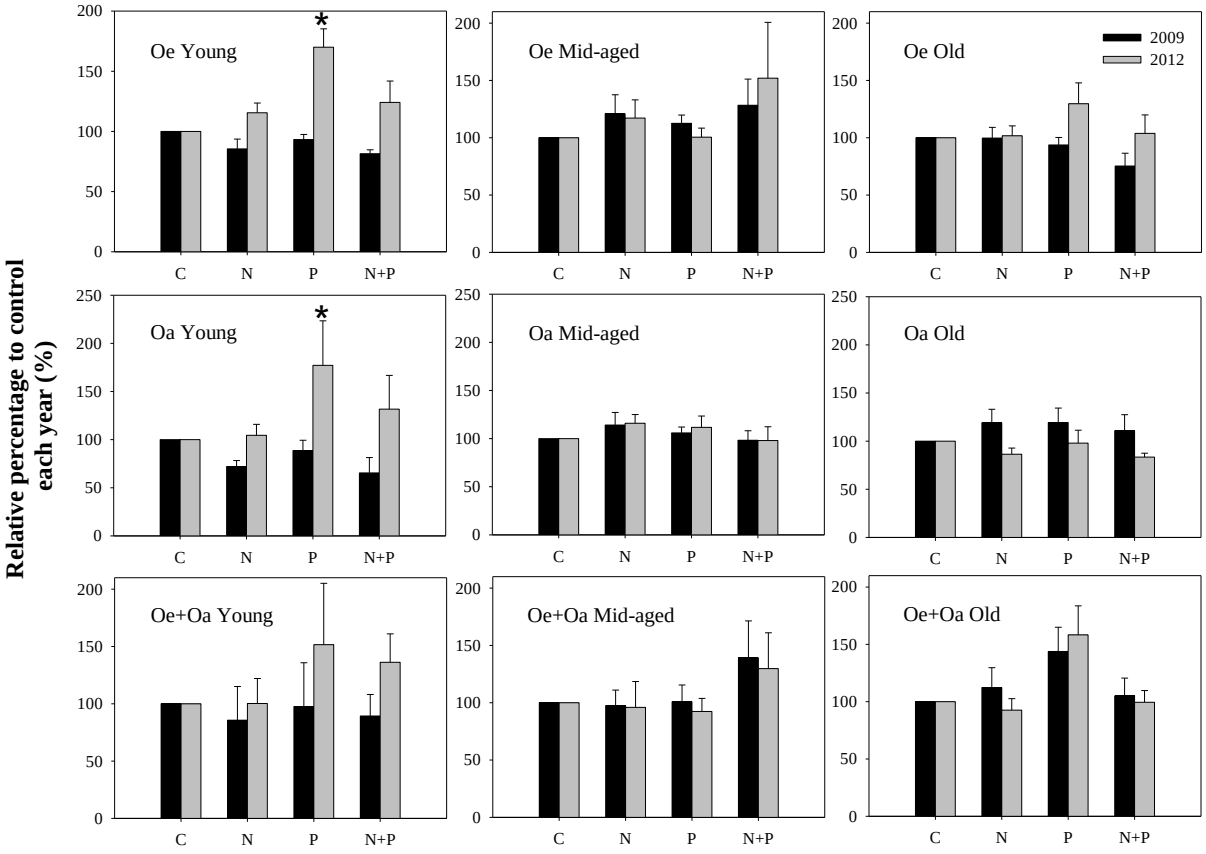

Figure 3.6. Relative percentage of incubated microbial respiration to control plot within 2009 and 2012 in each of Oe, Oa, Oe+Oa horizon by forest age.

Chapter 4. Summary and recommendations

4.1 Summary

This study showed that soil nutrient availability by natural variation or by anthropogenic fertilization can affect soil respiration across different sites and ages in the northern hardwood forests of the White Mountains of New Hampshire.

In 2009 and 2010, across the natural variation of soil nutrient availability, annual soil respiration was lower at Jeffers Brook (735 g C m^{-2} in mid-aged and 763 g C m^{-2} in old stand), the site with the highest nutrient availability, than at either Hubbard Brook (868 g C m^{-2} in mid-aged and 924 g C m^{-2} in old stand) or Bartlett (807 g C m^{-2} in mid-aged and 938 g C m^{-2} in old stand) ($p = 0.02$).

Belowground C allocation, calculated by subtracting annual litter production from annual soil respiration and assuming there was no change in belowground C storage, was also lower at Jeffers Brook (582 g C m^{-2} in mid-aged and 630 g C m^{-2} in old stand) than at Hubbard Brook (686 g C m^{-2} in mid-aged and 763 g C m^{-2} in old stand) or Bartlett (672 g C m^{-2} in mid-aged and 764 g C m^{-2} in old stand) ($p = 0.05$).

Soil respiration and below ground C allocation did not differ between mid-aged and old stands ($p \geq 0.11$), but fine root biomass was about 40 % higher in old stands (406 – 432 g C m^{-2}) than middle-aged stands (195 – 299 g C m^{-2}) ($p < 0.01$).

During the growing season in June to August, soil respiration was high in stands with low soil N availability (net N mineralization and net nitrification). Available P and exchangeable Ca were not related to soil respiration. These results suggest that greater N availability in soils can reduce belowground C allocation in northern hardwood forests.

After fertilization in 2011 and 2012, there was no consistent N or P fertilization effect on soil or microbial respiration. Fertilization responses of soil and microbial respiration were highly variable among stands between soil horizons and between measurement methods.

Soil respiration did not change after two years of fertilization across all 13 stands ($p = 0.81$), and the fertilization effects did not differ among sites ($p = 0.68$) or among ages ($p = 0.70$). Soil respiration in the trenched plots, representing microbial respiration, did not differ before and after fertilization across five stands (C2, C6, C7, mid-aged and old stand of Jeffers Brook) ($p = 0.48$), and the fertilization effects did not differ between BEF and JB ($p = 0.72$), or among ages ($p = 0.42$).

Although there were no general responses of fertilization on soil respiration or soil respiration in the trenched plots (microbial respiration), the contribution of microbial respiration to soil respiration was higher in N+P plots than N or control plots across the five trenched stands ($p = 0.05$).

Microbial respiration measured in laboratory incubations showed inconsistent responses of fertilization that varied by soil horizon, site, and age. In Oe, Oa, and Oe+Oa horizons, microbial respiration did not change after fertilization across 13 stands ($p \geq 0.37$).

This study suggested that the availability of nutrients, especially N, can affect soil respiration. The long-term fertilization treatment in this study will improve our understanding of how belowground C flux adjusts under increased N and P availability in soils.

4.2 Recommendations for future research

After fertilization, in general, we did not find any significant changes in soil and microbial respiration due to trenching in 2011. We found that soil respiration and microbial

respiration increased after fertilization in a few stands, which was not expected based on results reported in the literature. A longer-term study is necessary to clarify these short-term trends.

In this study, before treatment in 2009, detectable difference of soil respiration in June to August across 13 stands with four treatments was 21 – 47 %. The detectable difference of microbial respiration from incubation was 21 – 59 % in Oe horizons and 29 – 52 % in Oa horizons. Like some of the long term studies showed that the fertilization effects on soil respiration occurred more than five years later (Bowden et al. 2004, Burton et al. 2004), it would take longer than two years to see significant fertilization effects on soil respiration in the range of 21 – 47 %. Since it is very unlikely that large changes (21 – 47 %) in soil respiration will occur in the next two years, we recommend that the existing experimental design be maintained and that soil respiration be monitored for up to ten years to determine fertilization effects on soil respiration in the long term.

Even though two years was not long enough to determine the effects of fertilization on soil respiration, the differences of incubated microbial respiration in organic horizons between 2009 and 2012 were enough to detect the differences. However, to understand the long term responses of fertilization along with soil respiration, microbial respiration would be important to continue to measure to explain the soil respiration mechanisms.

Soil respiration and microbial respiration from trenches was measured from May to October (or November) to be consistent with soil respiration studies for estimating annual soil respiration budget in 2009 and 2010. For the objective of fertilization effects on soil respiration, we recommend measuring soil respiration only during the growing season, probably June to September. The relatively small variation in soil respiration among

treatments during the non-growing season is probably not important for understanding fertilization effects. Reducing sampling intensity in the non-growing season would decrease the cost and time required to continue the study.

4.3 References

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**:43-56.

Burton, A. J., K. S. Pregitzer, J. N. Crawford, G. P. Zogg, and D. R. Zak. 2004. Simulated chronic NO3− deposition reduces soil respiration in northern hardwood forests. Global change biology **10**:1080-1091.

Vita

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