Soil respiration, fine root production, and microbial biomass in cottonwood and loblolly pine plantations along a nitrogen fertilization gradient

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Abstract

It is well known that carbon storage capacity of forests will change in response to management practices such as fertilization. However, the influence of fertilization on belowground processes such as soil respiration, fine root production, and microbial biomass is still unclear. We measured soil respiration, fine root biomass production, and microbial biomass along a fertilization gradient (0, 56, 112, and 224 kg N ha^{-1} per year) in 7-year-old cottonwood and loblolly pine plantations, established on a well-drained, Redbay sandy loam (a fine-loamy, siliceous, thermic Rhodic Paleudlt), in northwest Florida. Soil respiration was measured monthly from June 2001 to May 2002 using the soda-lime technique. Fine root biomass production was quantified using the ingrowth core method during the same period. In addition, microbial biomass, soil temperature, moisture, soil pH, and organic matter were also measured along the same gradient for both species. Annual soil respiration rate was significantly greater (781 g C m^{-2} per year) in cottonwood than that (692 g C m^{-2} per year) in loblolly pine. Nitrogen fertilization had a significant negative effect on soil respiration in cottonwood, but no effect was observed in loblolly pine stands. Mean daily soil respiration rates exhibited significant exponential relationships with soil temperature both in cottonwood ($R^2 = 0.81$) and loblolly pine ($R^2 = 0.51$). Annual soil respiration rates in cottonwood stands were positively correlated with fine root production ($r = 0.64$) and soil microbial biomass C ($r = 0.87$) and negatively correlated with soil pH ($r = -0.81$). Annual soil respiration in loblolly pine stands was correlated positively with fine root production ($r = 0.54$) and with organic matter content ($r = 0.74$). Annual fine root production was significantly greater in cottonwood (221 g m^{-2} per year) than that in loblolly pine (144 g m^{-2} per year). Fertilization did not affect fine root production in both species. Microbial biomass, however, was significantly reduced by nitrogen fertilization in both species. We also observed an optimum range of soil pH (6.0 ± 0.4), where highest microbial activity could be expected. Multiple regression analysis indicated that microbial biomass, soil organic matter, and soil pH were the major factors affecting soil respiration in cottonwood, while fine root production and soil organic matter were the major factors affecting soil respiration in loblolly pine. These results suggest that belowground responses to fertilization can vary widely between conifers and hardwoods.
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1. Introduction

The potential response of aboveground biomass growth to fertilization is nearly always positive.

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However, belowground response to fertilization is often unclear in plantations and natural forests because of the uncertainty involved in quantifying root biomass. In addition to altering root growth and turnover rates, fertilization could also affect soil processes such as respiration, microbial activity, and soil pH. A complete understanding of belowground response to fertilization is critical in assessing soil carbon dynamics and long-term sustainability of forest soils (Fox, 2000).

Fertilization of forest plantations has become increasingly important as an intensive management tool in recent years (Allen et al., 1990; Fox, 2000). And, it has been speculated that intensive forest management may lead to a reduction in soil carbon, due partially to increased soil respiration (Hermon et al., 1990). However, the effects of fertilization on forest soil carbon fluxes have received little attention. The few existing studies have found conflicting results, with one reporting an increase (Gallardo and Schlesinger, 1994) and the other reporting a decrease (Haynes and Gower, 1995). For example, Gallardo and Schlesinger (1994) found an increase in soil respiration when nitrogen was added experimentally to forest soils in central North Carolina. Haynes and Gower (1995), however, reported that soil respiration was significantly lower for fertilized plots than for unfertilized plots in red pine plantations in northern Wisconsin. Since soil respiration results from two main sources, root respiration and the decomposition of organic matter and associated respiration of soil fauna, the conflicting results reported could be the result of fertilizer-induced differences in carbon fixation and allocation patterns among different tree species (Raich and Tufekcioglu, 2000).

Belowground carbon input through fine root production and turnover and associated microbial activity are well-documented processes in the carbon and nutrient cycling of forest ecosystems (Keyes and Grier, 1981; McClaugherthy et al., 1982). Majdi and Kangas (1997) reported that a high input of nitrogen increased fine root mortality and decreased production and longevity, while addition of nitrogen-free fertilizer extended fine root longevity. In many western conifers, the amount of carbon allocated to fine root production is inversely related to soil quality (Keyes and Grier, 1981; Vogt et al., 1987). For example, Gower et al. (1992) found that increased nutrient availability decreased fine root production in a Douglas-fir forest in New Mexico. Haynes and Gower (1995) also reported decreased fine root production with fertilization. Nadelhoffer et al. (1985), however, reported that belowground carbon allocation was positively correlated to nitrogen availability and aboveground productivity.

In addition to the amount of belowground carbon, soil respiration could also be influenced by a number of other parameters, including the inherent and/or fertilizer-induced variation in soil physical and chemical properties, which may influence the quality and quantity of soil fauna. Microbial biomass has been shown to be a sensitive indicator responding quickly to environmental impacts. Zhang and Zak (1998) found that nitrogen fertilization increased microbial biomass and root growth. On the contrary, others have reported decreased soil microbial biomass in response to high rates of nitrogen fertilization (Söderström et al., 1983; Smolander et al., 1994). These conflicting results may be due to the differences in the initial status of the microbial communities, soil pH, organic matter, and soil nutrient contents. It is well known that the response of forest soils to nitrogen input may vary depending on soil pH (Binkley and Högberg, 1997). Microbial activity and microbial biomass of forest soils are strongly related to such soil chemical parameters as pH, cation exchange capacity, and nutrient availability. Decomposition of organic matter and transformation of nutrients by microorganisms are diminished by soil acidification (Persson et al., 1989). Further, acidification changes microbial community composition by promotion of fungi and reduction of bacteria (Bääth et al., 1980).

Though fairly large amount of information exists on how forest stands and individual trees respond to nutrient input, many uncertainties and controversies exist on the belowground responses and on the interactions among various processes such as soil respiration, fine root production and microbial biomass in response to long-term fertilization. We utilized a 7-year-old fertigation trial with cottonwood (*Populus deltoides* Marsh.) and loblolly pine (*Pinus taeda* L.) to investigate the effects of long-term nitrogen fertilization on belowground processes such as soil respiration, fine root production, and microbial biomass. The specific questions addressed through our study were:

1. How do soil respiration, microbial biomass, fine root production and soil pH vary for hardwood

vs. conifer stands (established on the same soil) along a fertilization gradient?

2. What are the interrelationships among the above-mentioned variables and how do they vary between species?

2. Materials and methods

2.1. Study site

This study was conducted in 7-year-old cotton-wood and loblolly pine plantations established in 1995 on an agricultural field (16.2 ha) located in northern Santa Rosa County, FL (30°50′N, 87°11′W). The climate is temperate with mild winters and hot, humid summers. The soil is characterized as a well-drained, Redbay sandy loam (a fine-loamy, siliceous, thermic Rhodic Paleudlt). The study included a completely randomized design with four plots per treatment for each species. Planting density was 229 trees ha^{-1} with 3.3 m (row) by 2.1 m (tree) spacing. A drip irrigation system was run to apply water and fertilizer in the treatment plots during growing seasons for eight consecutive years from 1995 to 2002. The fertilizer treatment was 0, 56, 112, 224 N kg ha^{-1} per year. The drip irrigation system operated for 2 h per day and N fertilizer was injected to the irrigation system only 2–8 min per day depending on N application rates. The stand characteristics are summarized in Table 1. Three plots in each treatment were selected for this experiment.

2.2. Soil respiration

We measured soil respiration monthly using the soda-lime technique (Edwards, 1982; Raich et al., 1990) from June 2001 through May 2002 at three randomly selected locations in each plot. The measurements were conducted at the same locations during the study year. Cylindrical plastic buckets, 20 cm tall and 27.5 cm in diameter, were used as measurement chambers. At least 1 day before the soil respiration measurement, a plastic collar with the same diameter as the bucket was inserted into the ground. The plastic collar was carefully replaced with the inverted plastic chamber under which was placed an uncovered tin cup containing 60 g of oven-dried soda-lime. Two bricks were placed on top of each chamber to make a tight seal between the chamber and soil. After 24 h CO_2 absorption period, the tin cups were removed and oven dried at 105 °C for 24 h to measure weight gain. Mass gain was multiplied by 1.69 to correct for the amount of water formed and lost during the bonding of CO_2 to soda-lime (Grogan, 1998). Eight blanks were used to account for CO_2 absorption during handling and drying (Raich et al., 1990). Soil temperature was measured at 12 cm depth adjacent to each chamber during installation and volumetric soil water content was measured at 12 cm depth using a Hydrosense soil moisture meter (Cambell Scientific, Inc. Logan, UT).

2.3. Fine root production

Monthly fine root (<2 mm) production was determined by means of ingrowth core method (Persson, 1983)

Table 1
Stand characteristics of 7-year-old cottonwood and loblolly pine plantations along a N fertilization gradient (0, 56, 112, and 224 kg N ha^{-1} per year) in northwest Florida[a]

Treatment	Cottonwood				Loblolly pine			
	Height (m)	DBH (cm)	SOM[b] (%)	Soil pH[c]	Height (m)	DBH (cm)	SOM[b] (%)	Soil pH[c]
Control	11.7 b	11.3 b	2.4 a	5.7 b	9.0 b	15.7 ab	2.2 a	5.7 a
56 N	15.4 a	14.1 a	1.7 a	6.0 ab	10.0 a	16.4 a	1.7 a	6.1 a
112 N	14.3 a	13.7 a	1.7 a	6.5 a	9.8 ab	16.7 a	2.1 a	5.9 a
224 N	15.3 a	13.7 a	2.1 a	6.3 ab	9.1 b	14.6 b	1.6 a	5.5 a
Average	14.2[*]	13.3[*]	2.0	6.1[*]	9.5[*]	15.9[*]	1.9	5.8[*]

[a] Different letters within a column denote significantly different (Tukey's HSD test, $\alpha = 0.05$).
[b] Soil organic matter.
[c] Soil:water (1:2).
[*] Significantly different between cottonwood and loblolly pine at $P < 0.05$.

at three randomly selected locations in each plot from June 2001 through May 2002. The ingrowth core method consists of removing a core to a depth of 30 cm by a sharp-edge steel corer with an internal diameter of 5.1 cm and refilling the hole with root-free soil, which was taken from the same site and sieved through a 2 mm screen. The core was resampled after a month and the roots that had grown into the core counted as fine root production. The same hole was used for ingrowth sampling during the entire study year. Weed-free condition was maintained around the holes throughout the study period. Soil cores were wet sieved through a fine mesh screen, and all hand-sorted root fragments were considered fine root production. There was no root bigger than 2 mm in diameter for any sampling period. Roots were dried at 65 °C for 48 h and weighed to ±0.1 mg.

2.4. Microbial biomass C

Soil microbial biomass C was measured by chloroform fumigation–extraction procedure (Vance et al., 1987). Three soil cores (10 cm deep) were taken near the location for soil respiration measurement in each plot in September 2001. These soil samples were used for microbial biomass C, soil organic matter, and soil pH measurements. Soil was passed through a 2 mm mesh sieve to separate roots and debris. Sieved 50 g soil samples were placed in a 100 ml beaker and a 250 ml HDPE bottle for the fumigated and control samples, respectively. The fumigated samples were incubated in ethanol-free chloroform in evacuated desiccators for 24 h at 25 °C. Fumigated and control samples were extracted with 100 ml of 0.5 M K_2SO_4, shaken for 1 h, and filtered through Whatman No. 42 filter paper into 60 ml HDPE bottles. The extracted samples were acidified with phosphoric acid and frozen for overnight shipping to the soil analysis lab of the Department of Forestry at Iowa State University where the analysis was conducted. Dissolved organic carbon (DOC) was analyzed using a Phoenix 8000 autoanalyzer (Tekmar-Dormann, Cincinnati, OH). Microbial biomass C was calculated as follows:

$$\text{Microbial biomass C } (\text{mg C kg}^{-1} \text{ dry soil})$$
$$= \frac{[(\text{DOC in fumigated sample} - \text{DOC in control})/0.33]}{\text{Soil dry weight}}$$

A correction factor (0.33) was used to convert DOC to microbial biomass C, which also accounts for the efficiency of extracting DOC and lysis by fumigation (Dictor et al., 1998). Soil organic matter was determined by the ignition method using a 5 g dried soil and soil pH was measured using a 1:2 soil-deionized water paste.

2.5. Statistical analysis

The effect of treatments (species and fertilization) on soil respiration rate and fine root production was tested using an unequal two-way ANOVA, and on microbial biomass C, soil organic matter and pH was tested using the general linear model procedure of SAS (SAS Institute, 1990). If significant treatment effects were revealed ($\alpha = 0.05$), Tukey's studentized range test was used for mean separation. Possible effects of soil microbial biomass C, fine root production, soil organic matter, and soil pH on annual soil respiration rates were evaluated using a stepwise variable selection procedure using R^2 and C_p criteria and Pearson correlation analysis (SAS Institute, 1990).

3. Results

3.1. Soil respiration

Annual soil respiration rates differed significantly ($P = 0.002$) between cottonwood and loblolly pine stands (Table 2). N fertilization significantly affected soil respiration in cottonwood stands ($P = 0.008$), but had no effect in loblolly pine stands (Fig. 1A and B). In cottonwood stands, annual soil respiration rates during the study year were higher in control (858 g C m^{-2} per year) and 56 N treatment (814 g C m^{-2} per year) than in 112 N (725 g C m^{-2} per year) and 224 N (726 g C m^{-2} per year) treatments. In loblolly pine stands, annual soil respiration rates ranged from 647 g C m^{-2} per year in 56 N to 720 g C m^{-2} per year in control, with no significant treatment effect (Fig. 1A and B). Temporal variation in soil respiration rates was closely related to soil temperature fluctuation in both species (Fig. 2). Mean daily soil respiration rates displayed a significant exponential relationship with soil temperature and the exponential

Table 2
Means of soil respiration, fine root production, and microbial biomass in cottonwood and loblolly pine plantations in northwest Florida[a]

Variable	Cottonwood	Loblolly pine
Soil respiration (g C m^{-2} per year)	780.8 (19.3) a	691.5 (24.2) b
Fine root production (g m^{-2} per year)	220.8 (28.5) a	144.2 (23.4) b
Microbial biomass (mg C kg^{-1} dry soil)	144.3 (19.5) a	122.2 (25.7) a

[a] Numbers in parenthesis are the standard error of the mean ($n = 12$). Different letters within a row indicate significant differences (Tukey's HSD test, $\alpha = 0.05$).

relationship was stronger in cottonwood stands ($R^2 = 0.81$) than in loblolly pine stands ($R^2 = 0.51$) (Fig. 3). Annual soil respiration rate in cottonwood stands was positively correlated with fine root biomass production ($r = 0.64$) and soil microbial biomass C ($r = 0.87$) and negatively correlated with soil pH ($r = -0.81$). In loblolly pine stands, however, annual soil respiration was positively correlated to fine root
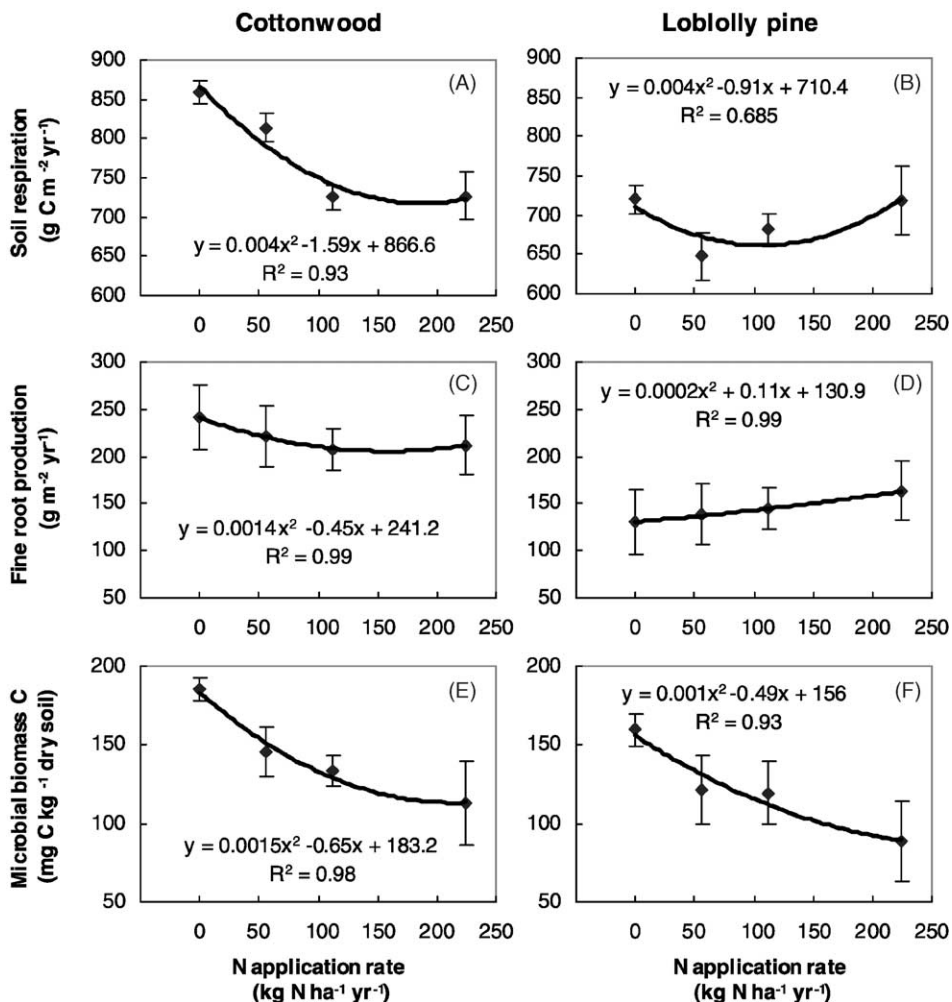

Fig. 1. Effects of nitrogen fertilization rates on soil respiration (A and B), fine root production (C and D), and microbial biomass C (E and F) in cottonwood and loblolly pine plantations in northwest Florida. Vertical bars indicate standard error of the mean ($n = 12$).
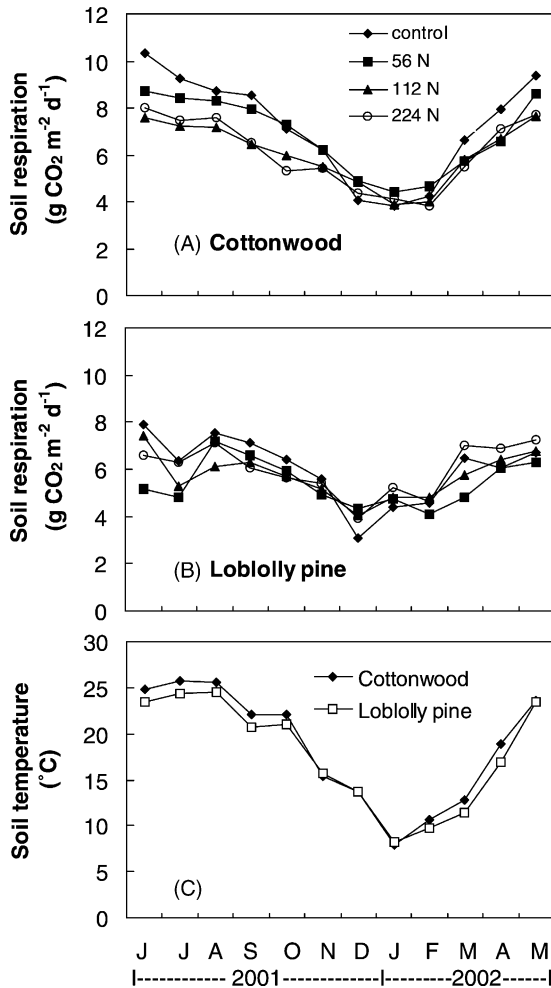
Fig. 2. Mean monthly soil respiration rates in 7-year-old cotton-wood (A) and loblolly pine (B) plantations along a fertilization gradient (0, 56, 112, and 224 kg N ha^{-1} per year), and average soil temperature (C) at 12 cm depth under both species.

biomass production ($r = 0.54$) and soil organic matter content ($r = 0.74$) (Table 3). Average volumetric soil water content was about 15% at 12 cm depth during the measurement period and changes in soil water did not have a significant effect on soil respiration in this study.

3.2. Fine root production, microbial biomass C, organic matter and pH

Annual fine root production in cottonwood stands was 35% greater ($P < 0.0001$) than that in loblolly
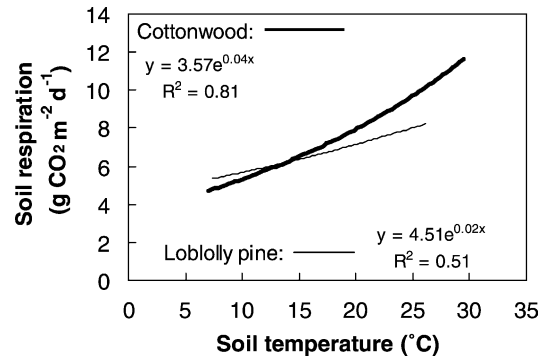

Fig. 3. Relationship between soil respiration and soil temperature in 7-year-old cottonwood and loblolly pine plantations in northwest Florida.

pine stands (Table 2 and Fig. 4). No significant effect of N fertilization on fine root production was found in either cottonwood or loblolly pine stands. Annual fine root production ranged from 208 to 241 g m^{-2} per year in cottonwood stands, and from 131 to 163 g m^{-2} per year in loblolly pine stands (Fig. 1C and D).

There was no difference in soil microbial biomass C between cottonwood and loblolly pine stands
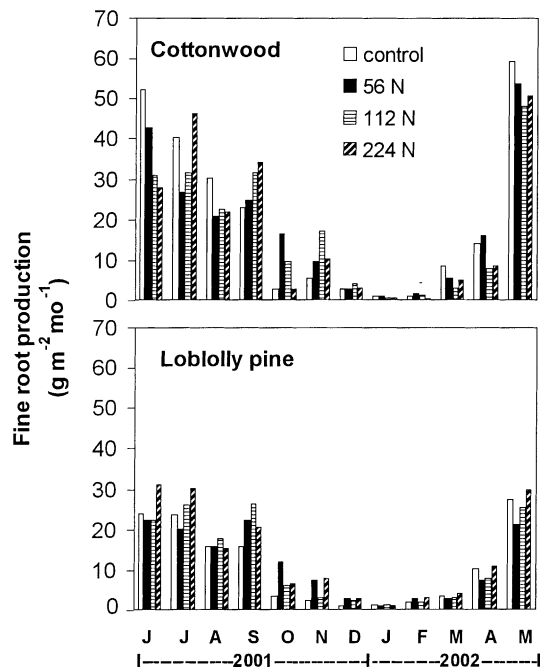

Fig. 4. Monthly pine root production in cottonwood and loblolly pine plantations along a fertilization gradient (0, 56, 112, and 224 kg N ha^{-1} per year) in northwest Florida.

Table 3

Pearson correlation coefficients among measured variables ($n = 12$) in cottonwood and loblolly pine plantations in northwest Florida

Species	Variables	FRP[a]	MB[b]	SOM[c]	Soil pH
Cottonwood	SR[d]	0.64[***]	0.87[****]	0.47	−0.81[***]
	FRP		0.71[***]	0.57[**]	−0.54[*]
	MB			0.57[**]	−0.57[**]
	SOM				−0.51[*]
Loblolly pine	SR	0.54[*]	0.32	0.74[***]	0.10
	FRP		−0.23	−0.11	0.15
	MB			0.60[**]	0.53[*]
	SOM				0.17

[a] Fine root (<2 mm) production (g m^{-2} per year).
[b] Microbial biomass (mg C kg^{-1} dry soil).
[c] Soil organic matter (%).
[d] Soil respiration (g C m^{-2} per year).
[*] $P < 0.1$.
[**] $P < 0.05$.
[***] $P < 0.01$.
[****] $P < 0.001$.

(Table 2); however, soil microbial biomass C was affected negatively by N fertilization ($P = 0.048$) in both species (Fig. 1E and F). Positive correlation ($r = 0.71$) was observed between fine root production and microbial biomass C in cottonwood stands. Similarly, microbial biomass C was positively correlated with soil organic matter ($r = 0.57$) and negatively correlated with soil pH ($r = -0.57$). In loblolly pine stands, microbial biomass C was positively correlated with soil organic matter ($r = 0.60$) and soil pH ($r = 0.53$) with no significant correlation with fine root production (Table 3).

Mean soil organic matter content was not different between cottonwood and loblolly pine stands and N

fertilization effect on soil organic matter was not significant (Table 1). Soil pH was significantly higher in cottonwood than that in the loblolly pine stand and N fertilization effect on soil pH was found only in the cottonwood stands ($P = 0.023$), as soil pH increased with N fertilization. The pH in mineral soil under cottonwood was 0.3 units higher than that under loblolly pine (Table 1).

Soil microbial biomass C, organic matter, and pH were the best predictors of soil respiration in cottonwood stands and 93% of the variability in soil respiration could be explained with the multiple regression model. In loblolly pine stands, fine root biomass production and soil organic matter were the best predictors

Table 4

Soil respiration models based on selected variables among soil organic matter, fine root production, microbial biomass, and soil pH using a stepwise variable selection procedure with R^2 and C_p criteria[a]

Species	Model	R^2	C_p	F	P
Cottonwood	SR = 1250 + 1.2 (MB) − 29.7 (SOM) − 94.9 (pH)	0.93	3.1	36.5	<0.0001
	SR = 1150 + 1.1 (MB) − 85 (pH)	0.91	3.5	45.2	<0.0001
	SR = 1192 − 0.16 (FRP) + 1.16 (MB) − 88.7 (pH)	0.91	4.9	28.3	<0.0001
	SR = 1266 − 0.1 (FRP) + 1.2 (MB) − 28.2 (SOM) − 96 (pH)	0.93	5.0	24.3	0.0003
Loblolly pine	SR = 419.4 − 0.8 (FRP) + 80.4 (SOM)	0.77	1.7	14.8	0.0014
	SR = 501.5 − 0.8 (FRP) + 82.1 (SOM) − 15.3 (pH)	0.78	3.4	9.2	0.0057
	SR = 416.8 − 0.8 (FRP) − 0.03 (MB) + 78.1 (SOM)	0.77	3.6	8.8	0.0065
	SR = 568.4 − (FRP) − 0.2 (MB) + 69.6 (SOM) − 30.7 (pH)	0.79	5.0	6.5	0.0168

[a] SR: soil respiration (g C m^{-2} per year); MB: microbial biomass (mg C kg^{-1} dry soil); SOM: soil organic matter (%); pH: soil pH; FRP: fine root (<2 mm) production (g m^{-2} per year).

of soil respiration with 77% of the variability explained (Table 4).

4. Discussion

Annual soil respiration rates in this study ranged from 725 to 858 g C m^{-2} per year (average of 781 g C m^{-2} per year) under cottonwood to 647–720 g C m^{-2} per year (average of 692 g C m^{-2} per year) under loblolly pine stands (Table 2). Similar range has been reported in a number of studies from temperate forests (Edwards and Ross-Todd, 1983; Weber, 1990; Raich and Schlesinger, 1992; Hudgens and Yavitt, 1997) to tropical rain forests (Raich, 1998). For example, Raich and Schlesinger (1992) reported a mean soil respiration of 647 and 695 g C m^{-2} per year from a wide array of temperate deciduous forests and coniferous forests, respectively. Annual soil respiration rate in loblolly pine was approximately 11% lower than that in cottonwood stands in our study, similar to a 10% reduction observed by Raich and Tufekcioglu (2000), while comparing deciduous and coniferous stands on identical soils.

While fertilization decreased soil respiration in cottonwood, no significant effect was detected in loblolly pine stands. Since fine root respiration and associated microbial activity are two major sources of soil respiration (Keyes and Grier, 1981; McClaugherthy et al., 1982), it is not surprising that soil respiration decreased along an increasing N gradient in cottonwood. Both fine root production and microbial biomass exhibited a decreasing trend along the same gradient in cottonwood (Fig. 1). The multiple regression models (Table 4) and strong correlation coefficients (Table 3) also reveal the interdependency of these variables in controlling soil respiration rates. Though microbial biomass was significantly reduced by fertilization, fine root production tended to increase along the N fertilization gradient in loblolly pine. It is obvious that these two processes were counteracting each other in loblolly pine stands, resulting in no net change in soil respiration across the treatments.

Increased belowground carbon allocation under nutrient stress and/or water stress (Cromer and Jarvis, 1990; Kolb et al., 1990; Jose et al., in press) has been commonly reported, especially in seedlings. Gower et al. (1992) reported a significant decrease in Douglas-fir (*Pseudostuga menziesii* var. *glauca*) fine root production in response to fertilization. Despite having a decreasing trend of fine root production in cottonwood and increasing trend in loblolly pine along an increasing soil N gradient, no significant differences among the fertilization treatments were observed in either species (Fig. 1).

Seasonal variation in fine root production was detected for both species as expected. We observed high levels of fine root production during late spring and early summer for both species, consistent with other published reports (Van Praag et al., 1988; Kummerow et al., 1990). In comparison to other average fine root production estimates by ingrowth core methods, our estimation, 144.2 g m^{-2} per year in 7-year-old loblolly pine stands was within the range of 120–200 g m^{-2} per year reported by Nadelhoffer et al. (1985) and Aber et al. (1985) for red pine plantations in Wisconsin. Fine root production (221 g m^{-2} per year) in cottonwood stands was also within the range of 147–254 g m^{-2} per year reported for temperate deciduous forests (Fahey and Hughes, 1994; Hertel and Leuschner, 2002).

The greater fine root production observed in cottonwood stands compared to loblolly pine stands agrees with results from others as well. For example, Aber et al. (1985) and Steele et al. (1997) have shown that hardwood forests have greater fine root biomass production compared to pine forests of similar age. In a recent study, Usman et al. (2000) reported that fine root production was 44.6% higher in oak forests than in nearby pine forests in central Himalaya.

Although microbial biomass C did not differ significantly between cottonwood and loblolly pine stands, there was a trend of greater microbial C in soils under cottonwood (144.3 mg C kg^{-1} dry soil) than under loblolly pine (122.2 mg C kg^{-1} dry soil) (Table 2). Microbial biomass C was strongly correlated to soil organic matter and soil pH in both species, indicating direct (through organic matter addition) as well as indirect (modification of soil) effects of species. Although we do not know soil pH at the beginning of the fertigation trial, sampling in a nearby untreated soil showed an average pH of 5.7. It is reasonable to assume that addition of litter (both above and belowground) for the past 7 years has altered soil characteristics under both species (Priha and Smolander, 1999; Smolander and Kitunen, 2002),
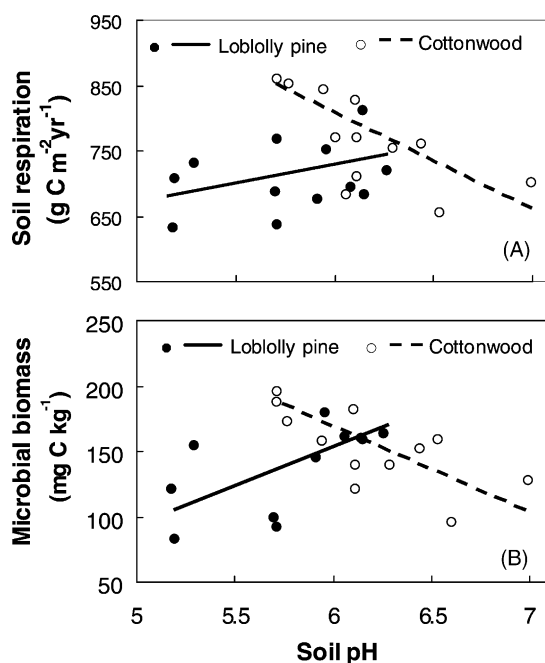
Fig. 5. Relationships between soil respiration and soil pH (A) and between microbial biomass and soil pH (B) in cottonwood and loblolly pine plantations along a fertilization gradient (0, 56, 112, and 224 kg N ha^{-1} per year).

making it more acidic under loblolly pine and less acidic under cottonwood. Soil pH ranged from 5.2 to 6.25 with a positive correlation ($R^2 = 0.53$) with microbial biomass C under loblolly pine, and 5.7–7.0 with a negative correlation ($R^2 = 0.57$) under cottonwood (Fig. 5). Given the relatively high soil respiration rate and microbial biomass C at soil pH 6.0 ± 0.4, it is likely that a range in soil pH exists where microbial activity and respiration could be high (Fig. 5).

As mentioned earlier, microbial biomass C decreased along an increasing soil N gradient in our study. Similar results have been reported from other long-term fertilization trials as well (Scott et al., 1998; Fisk and Fahey, 2001). For example, Fisk and Fahey (2001) reported that microbial biomass C was significantly reduced by 8 years of continued N fertilization in a temperate hardwood forest. In contrast, shorter-term N fertilization has been shown to increase microbial biomass (Gallardo and Schlesinger, 1994; Hart and Stark, 1997). The immediate increase in microbial biomass following N additions suggests that N could be limiting in the soil. However, there is no obvious

explanation for the decrease in microbial biomass over longer periods of treatment (Fisk and Fahey, 2001). Although soil acidification and subsequent reduction in microbial biomass C could be suspected (Anderson, 1998), we did not observe this for either species. However, there were strong positive correlations observed between microbial biomass C and soil organic matter (Table 3) for both species. The trend of decreasing soil organic matter along the increasing N gradient, perhaps, indicates faster C mineralization and subsequent loss from upper soil horizon. Overall, soils under both species were poor in organic C and ranged only from 0.9 to 1.4%.

5. Conclusions

Soil respiration decreased significantly along an increasing soil N gradient in cottonwood; however, it remained unchanged in loblolly pine. The speculation that fertilization might lower soil C due partially to increased soil respiration was found untenable in our experiment. Contrary to our expectation and some published reports, fine root production exhibited no significant differences among treatments in both species. There was a trend of decreasing fine root production in cottonwood and increasing production in loblolly pine along the increasing soil N gradient, which may become more pronounced in the future as stands get older. Averaged across all treatments, loblolly pine had 35% lower fine root production compared to cottonwood. Microbial biomass decreased along the increasing N gradient in both species and was correlated strongly to soil organic matter and pH. Although soil acidification was expected (due to annual N addition for 7 years), no significant decrease in soil pH was observed either in cottonwood or loblolly pine stands. Overall, soil under loblolly pine was more acidic than under cottonwood, an indication of the buffering capacity of hardwood litter. Since soil microbial biomass is an important indicator of long-term soil quality and site productivity, it is important to recognize that an optimum range of soil pH (6.0 ± 0.4) may exist where microbial activity could be the highest. In general, our results suggest that long-term N fertilization can modify belowground soil processes in both hardwood and coniferous stands, but not always in identical ways.

Acknowledgements

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