Available online at www.sciencedirect.com
SCIENCE DIRECT®
Forest Ecology and Management 200 (2004) 335–345
Forest Ecology and Management
www.elsevier.com/locate/foreco

Intensive management modifies soil CO_2 efflux in 6-year-old *Pinus taeda* L. stands

Lisa J. Samuelson[a,*], Kurt Johnsen[b], Tom Stokes[a], Weinlang Lu[a]

[a]*School of Forestry and Wildlife Sciences, Auburn University, 108 M. White Smith Hall, Auburn, AL 36849-5418, USA*
[b]*USDA Forest Service, Southern Research Station, P.O. Box 12254, Research Triangle Park, NC 27606, USA*

Received 5 May 2004; received in revised form 2 July 2004; accepted 6 July 2004

Abstract

Intensive forestry may reduce net CO_2 emission into atmosphere by storing carbon in living biomass, dead organic matter and soil, and durable wood products. Because quantification of belowground carbon dynamics is important for reliable estimation of the carbon sequestered by intensively managed plantations, we examined soil CO_2 efflux (S_{CO_2}) in a 6-year-old loblolly pine (*Pinus taeda* L.) plantation in response to weed control (W), weed control plus irrigation (WI), weed control plus irrigation and fertigation (addition of fertilizer to the irrigation water) (WIF), and weed control plus irrigation, fertigation and pest control (WIFP) since plantation establishment. Average S_{CO_2} ranged from 1.27 to 5.59 μmol m^{-2} s^{-1}, and linear models indicated that soil temperature explained up to 56% of the variation in S_{CO_2}. Plot position explained an additional 2–11% of the variation in S_{CO_2}. Soil moisture was only weakly correlated with S_{CO_2} in the W treatment, and S_{CO_2} was not significantly correlated to fine root mass. Predicted carbon loss from forest floor respiration ranged between 778 and 966 g C m^{-2} $year^{-1}$ and was 20% lower in the WIF treatment relative to the W treatment. Annual soil carbon loss through soil respiration declined linearly with increasing carbon content in total root biomass (tap + coarse + fine) at age 6.

Keywords: Loblolly pine; Fertilization; Carbon sequestration; Soil respiration

1. Introduction

Management of southern pine forests continues to intensify resulting in increased forest productivity (Borders and Bailey, 2001), but mechanisms contributing to increased productivity are not always understood. For instance, forest fertilization clearly increases leaf area but often does not increase carbon gain per unit leaf area (Samuelson, 1998; Samuelson et al., 2001; Maier et al., 2002; Gough et al., 2004). Fertilization can also modify the allocation of carbon. Decreased partitioning to fine root but not coarse root biomass has been reported in response to increased nutrient availability (Maier and Kress, 2000). Carbon allocated belowground also provides substrate for soil CO_2 efflux, the largest component of total ecosystem

* Corresponding author. Tel.: +1 334 844 1040;
fax: +1 334 844 1084.
E-mail address: samuelj@auburn.edu (L.J. Samuelson).

0378-1127/$ – see front matter
doi:10.1016/j.foreco.2004.07.002

respiration (Law et al., 1999; Boldstad et al., 2004). Recently, Högberg et al. (2002) estimated that, in 45–55-year-old Scots pine (*Pinus sylvestris* L.) stands, approximately 40% of soil CO_2 efflux originated from recently photosynthetically fixed carbon. Thus, reallocation of carbon from belowground processes might greatly impact forest productivity.

There is still ambiguity concerning the influence of intensive management on belowground carbon dynamics, because of the numerous factors that may influence soil CO_2 efflux (S_{CO_2}) such as soil moisture (Raich and Schlesinger, 1992), litterfall and net primary productivity (Nadelhoffer et al., 1985; Raich and Schlesinger, 1992), soil nutrient balance (Smolander et al., 1994; Maier and Kress, 2000), the activity and composition of microbe and soil fauna (Söderström and Landgren, 1983; Ågren et al., 2001), and carbon allocation between various tree components, especially the amount and activity of fine roots (Hanson et al., 2000). Several studies report that S_{CO_2} is negatively related to soil nutrient availability. For example, annual S_{CO_2} was greater in unfertilized than in fertilized 11-year-old (Maier and Kress, 2000) and 17-year-old (Butnor et al., 2003a) loblolly pine stands, and greater S_{CO_2} was also reported for unfertilized than fertilized 31-year-old red pine (*Pinus resinosa* Ait) (Haynes and Gower, 1995). In contrast, no response and/or accelerated S_{CO_2} in response to fertilization have been observed for both pine seedlings and mature plantations (Brumme and Beese, 1992; Vose et al., 1995; Pangel and Seiler, 2002). In two separate studies, no influence of fertilization on S_{CO_2} from mature slash pine (*Pinus elliottii* Engelm.) stands was detected (Castro et al., 1994; Shan et al., 2001). Contrasting response of S_{CO_2} to silvicultural manipulation of site resources likely reflects differences in stand age, climate, site, and the amount, frequency and timing of fertilizer application (Johnsen et al., 2001). Variation also originates from the measurement system employed and interactions with site attributes such as soil porosity and litter depth (Butnor and Johnsen, in press).

To better understand the effects of intensive silviculture on S_{CO_2}, we examined S_{CO_2} in a 6-year-old loblolly pine plantation subjected to different levels of management intensity since plantation establishment. Very high productivity has been achieved in this study: maximum aboveground net primary production was 25 Mg ha^{-1} year^{-1} and at age 6 total biomass was 93 Mg ha^{-1}, of which belowground was 21 Mg ha^{-1} (Samuelson et al., 2004). The objectives of this study were to quantify S_{CO_2} in response to management intensity and examine factors controlling S_{CO_2} such as soil temperature, soil moisture, spatial position and fine root biomass. We hypothesized that increasing availability of water and nutrients would decrease S_{CO_2} because of reduced fine root mass.

2. Materials and methods

2.1. Experimental design and treatments

The study was conducted in a loblolly pine plantation located in the Upper Coastal Plain approximately 22 km west of Bainbridge, Georgia (30.82°N, 84.76°W). Soils were classified as well-drained Grossarenic Paleudults and depth to the argillic horizon was 102 cm. The 15-ha research site was established in January 1995 by International Paper Company and described by Samuelson et al. (2004). The study was arranged using a randomized complete block design with three blocks and four treatments. Each treatment plot was quartered and four half-sibling, second-generation families of loblolly pine were each assigned to a different quarter subplot. One family was examined over the course of this study. Trees were planted using a 2.4 m × 3.7 m spacing, and excluding buffer rows the measurement plot was 0.026 ha with 28 sample trees (planting density 1070 trees ha^{-1}). The following four treatments were randomly assigned to treatment plots within a block:

W: complete weed control. Weed control was maintained using a broadcast application of sulfometuron (0.1 kg active ingredient ha^{-1}) and several directed applications of glyphosate (1.5% solution in water) throughout the summer.
WI: weed control plus drip irrigation (Netafim Irrigation, Inc., Altamonte Springs, FL). Drip lines ran along tree rows on the south side of each tree. In 2000, drip irrigation was applied all 12 months at a monthly rate of 46–173 mm with an annual total of 1127 mm. Yearly addition was 1128 mm in 2001.
WIF: weed control plus irrigation and fertigation (drip irrigation with a fertilizer solution of NH_4NO_3 and

urea (79 kg N ha^{-1} in 2000 and 79 kg N ha^{-1} in 2001), H_3PO_4 (20 kg P ha^{-1} in 2000 and 20 kg P ha^{-1} 1 in 2001) and K_2O (79 kg K ha^{-1} in 2000 and 79 kg K ha^{-1} in 2001)). Addition of fertilizer to the irrigation water began in May and continued through October.

WIFP: weed control plus irrigation, fertigation, and pest control. Fusiform rust (*Cronartium qurecuum* f. sp. *fusiforme*) was controlled with applications of triadimefon fungicide beginning in March. Nantucket pine tip moth (*Rhyacionia frusrtana* Comstock) was controlled with permethrin or acephate insecticides.

2.2. Procedures

Instantaneous S_{CO_2} was measured approximately monthly from July 2000 to July 2001 (13 dates). Measurements were made by block between 800 and 1400 h and 1 day was needed to complete all measurements. Blocks and treatment plots within a block were randomly selected for measurement each session. S_{CO_2} of the intact forest floor was measured with a soil chamber (LI-6400-09, Li-Cor, Inc., Lincoln, NE) connected to a portable infrared gas analyzer (IRGA, LI-6400, Li-Cor, Inc., Lincoln, NE). In order to minimize disturbance to S_{CO_2} caused by the insertion of the soil chamber, soil collars (diameter 10 cm, height 5 cm, made from PVC pipe) were installed 1 day before measurements. Soil temperature at a 15-cm depth was recorded concomitantly by a soil probe thermocouple inserted within 5 cm of the measurement collar.

Two different transects within a treatment plot were randomly selected each month. The 1.8-m transect was positioned equidistant between trees and perpendicular to rows. Three collars were inserted 4 cm into the soil along the linear transect at 92.5-cm intervals beginning between two trees within a row. The three positions were 0, 0.9 and 1.8 m, respectively, according to the relative distance from the row center. A measurement for each position was usually finished within 3 min.

Soil moisture of the top 15 cm of soil was measured using a Time Domain Reflectometer (Soilmoisture Equipment Co., Santa Barbara, CA) positioned vertically through the mineral soil within 5 cm of the collar immediately following each S_{CO_2} measurement. Because of machine failure, soil moisture data were not collected for the February–May 2001 measurements. An on-site weather station recorded precipitation.

In September 2000, March 2001 and June 2001, mineral soil under the respiration chambers in one of the two transects in each plot was excavated to a depth of 15 cm using a corer of 10 cm diameter (three soil cores per treatment per block, 36 cores collected in total). Roots were separated into fine ($\leq$2 mm) and coarse (>2 mm). Soils were washed through 2-mm mesh steel screen and roots picked by hand. Sorted roots were weighed after dried at 70 °C to a constant mass.

2.3. Statistical analyses

Data were averaged by plot and position across the two transects. Treatment effects on soil moisture averaged across all measurement dates were tested using a randomized complete block design and means were separated with Duncan's multiple range test. Multivariate repeated measures analyses (von Ende, 1993) were used to test main and interaction effects between treatment and season on soil temperature averaged over a 3-month period (July–August 2000; December 2000–February 2001; May–July 2001).

Based on the nine measurement periods for which soil moisture data were available, multiple linear regression models between S_{CO_2} and soil temperature, soil moisture, and distance from row center were selected using the stepwise procedure (Neter and Wasserman, 1974). Pearson's correlation coefficient was used to test for correlation between S_{CO_2} and distance from row center, fine root mass and total root mass.

To model annual forest floor carbon efflux, nonlinear regression analyses were used to describe the exponential relationship between S_{CO_2} and soil temperature for each treatment–block combination using data from all 13 measurement periods (n = 13 per block-treatment). Data were averaged across plot position because distance from the row center explained only a small amount of variability in S_{CO_2}. Parameterized models were used to estimate hourly and then annual S_{CO_2} from 1 July 2000 to 30 June 2001 by block and treatment. Hourly soil temperature was predicted from air temperature using linear relationships between soil and air temperature derived for each block–treatment combination from instantaneous measures of S_{CO_2} (n = 13; R^2 ranged from 0.59 to 0.81; $P < 0.01$ for each slope). Hourly air temperature data were obtained for Bainbridge, Georgia, from the National Climate Data Center (National Oceanic and Atmospheric Administration, Asheville, NC). Treatment effects on model coefficients and annual carbon loss were tested using a randomized complete block design and means were separated with Duncan's multiple range test. Because a factorial experiment was not used, the individual and interactive effects of nutrients, water, and pest control could not be tested.

3. Results

Average yearly precipitation and temperature for the region are 1257 mm and 18.9 °C, respectively (Ruffner, 1980). Mean soil temperature at 15 cm during instantaneous measurements ranged from a minimum of 9.4 °C in December 2000 to a maximum of 29.6 °C in July 2000, and monthly precipitation ranged from 25 to 290 mm (Fig. 1). Repeated measures analyses indicated that treatment effects on soil temperature varied with season. In the warmer months of both years, average soil temperature was highest in the W treatment and significantly decreased with irrigation and fertiga-

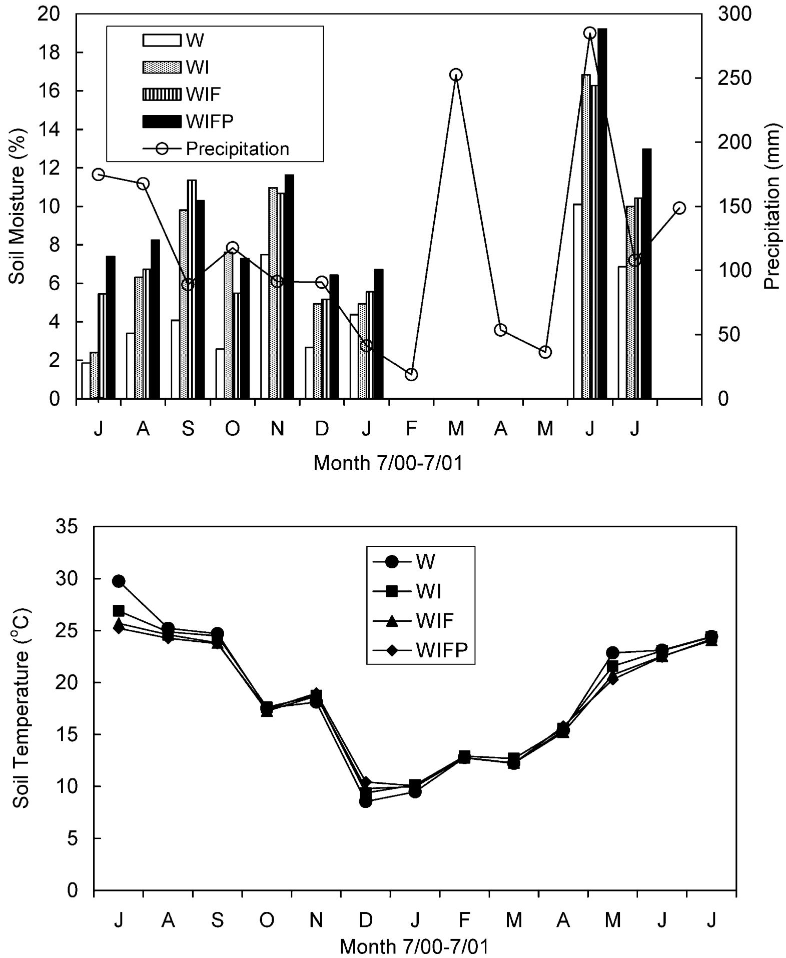

Fig. 1. Seasonal variation in soil temperature at 15 cm and volumetric soil moisture to 15 cm during soil CO_2 efflux measurements and monthly total precipitation in a 6-year-old loblolly pine plantation in response to weed control (W), weed control plus irrigation (WI), weed control plus irrigation and fertigation (WIF), and weed control plus irrigation, fertigation and pest control (WIFP).

Table 1
Average (S.E.) soil temperature at 15 cm averaged over a 3-month period and soil moisture averaged over all soil CO_2 efflux measurements in a 6-year-old loblolly pine plantation in response to weed control (W), weed control plus irrigation (WI), weed control plus irrigation and fertigation (WIF), and weed control plus irrigation, fertigation and pest control (WIFP)

Treatment	July–August 2000 soil temperature (°C)	December 2000–February 2001 soil temperature (°C)	May–July 2001 soil temperature (°C)	Soil moisture (%)
W	25.9 a	10.2 b	23.5 a	4.2 b
WI	25.1 b	11.0 a	23.0 b	7.7 a
WIF	24.4 c	10.8 a	22.4 c	8.5 a
WIFP	24.4 c	11.1 a	22.3 c	9.5 a

Different letters indicate differences between treatments at $\alpha = 0.05$.

tion (Table 1). In winter, soil temperature was significantly lower in the W treatment relative to the other treatments. In general, soil moisture was higher in treatments receiving irrigation relative to the control treatment (Fig. 1), and soil moisture averaged across all dates was significantly lower in the W treatment compared with the other treatments (Table 1).

Average S_{CO_2} was as low as 1.27 μmol m^{-2} s^{-1} in December and as high as 5.59 μmol m^{-2} s^{-1} in July 2001 (Fig. 2). Multiple linear regression models (Table 2) between S_{CO_2} and soil temperature, soil moisture, and distance from row center were fit to evaluate factors related to S_{CO_2}. Soil temperature was consistently the first variable to enter the model for each treatment and depending on treatment explained 38–56% of the variability in S_{CO_2}. Although distance from row center was significant in models for all treatments, plot position explained only 2–11% of variability in S_{CO_2}. When data were pooled across all treatments, soil temperature and distance accounted for 48% of the variation in S_{CO_2}. Although average soil moisture increased in response to irriga-

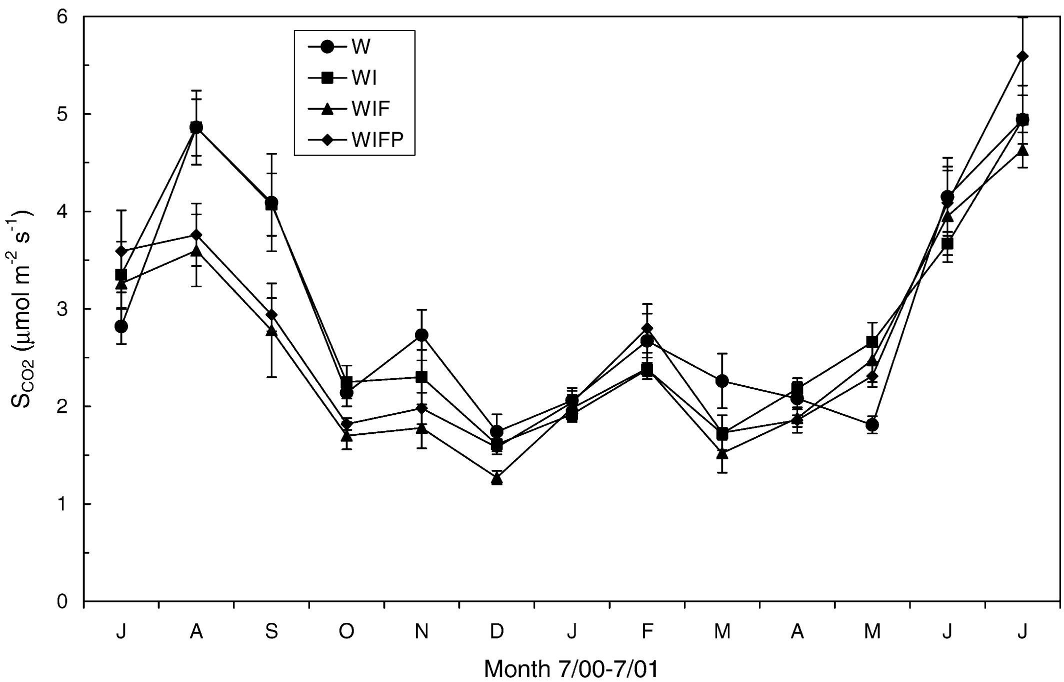

Fig. 2. Monthly instantaneous soil CO_2 efflux (S_{CO_2}) with the forest floor in place from July 2000 to July 2001 in a 6-year-old loblolly pine plantation in response to weed control (W), weed control plus irrigation (WI), weed control plus irrigation and fertigation (WIF), and weed control plus irrigation, fertigation and pest control (WIFP).

Table 2
Parameters for multiple regression models for forest floor soil CO_2 efflux rate (S_{CO_2}) from a 6-year-old loblolly pine plantation in response to weed control (W), weed control plus irrigation (WI), weed control plus irrigation and fertigation (WIF), and weed control plus irrigation, fertigation and pest control (WIFP)

Treatment	Variable	Parameter estimate	Partial R^2	$P > F$
W, WI, WIF, WIFP	Temperature	0.145	0.44	<0.001
	D	−0.374	0.04	<0.001
W	Temperature	0.112	0.38	<0.001
	Moisture	0.123	0.07	0.003
	D	−0.362	0.04	0.019
WI	Temperature	0.160	0.56	<0.001
	D	−0.222	0.02	0.096
WIF	Temperature	0.145	0.43	<0.001
	D	−0.590	0.11	<0.001
WIFP	Temperature	0.163	0.42	<0.001
	D	−0.355	0.03	0.0322

All equations are of the form S_{CO_2} =intercept + a(temperature) + b(D) + c(moisture), where temperature is the soil temperature (°C) at 15 cm, D the distance from row center (m), and moisture the soil moisture to 15 cm (%). Variables entered the model at the 0.15 significance level.

Table 4
Mean (S.E.) values of coefficients a and b of the exponential equation ($S_{CO_2} = a * e^{b*\mathrm{Temp}}$) between soil CO_2 efflux from the forest floor (S_{CO_2}) and soil temperature (temperature) at 15 cm, and predicted annual carbon loss from forest floor respiration in a 6-year-old loblolly pine plantation in response to weed control (W), weed control plus irrigation (WI), weed control plus irrigation and fertigation (WIF), and weed control plus irrigation, fertigation and pest control (WIFP)

Treatment	Coefficient a	Coefficient b	g C m^{-2} $year^{-1}$
W	1.488 (0.164) a	0.0357 (0.0043) b	966 (48) a
WI	0.909 (0.023) b	0.0594 (0.0023) a	893 (35) ab
WIF	0.805 (0.056) b	0.0606 (0.0039) a	778 (6) b
WIFP	0.817 (0.144) b	0.0647 (0.0087) a	857 (20) ab

Different letters indicate differences between treatments at $\alpha = 0.05$.

tion, soil moisture did not account for variation in S_{CO_2} when data were pooled across treatments. Soil moisture was significant only in the model for the W treatment and explained only 7% of the variability in S_{CO_2}. While distance from row center was negatively correlated to fine root mass for most treatments and when data were pooled across treatments, S_{CO_2} was not significantly correlated to fine root mass within a treatment or across all treatments (Table 3).

Exponential models ($S_{CO_2} = a * e^{b*\mathrm{Temp}}$) describing the relationship between S_{CO_2} and soil temperature explained more than 80% of the variation in S_{CO_2}, and coefficients of the models (Table 4) were similar to coefficients (a = 0.864, b = 0.091) used to model annual soil carbon loss for an older loblolly pine stand by Butnor et al. (2003a). Coefficient a was significantly higher and coefficient b was significantly lower in the W treatment compared with the other treatments. Predicted 24-h soil temperature was lowest in the W treatment during winter (Fig. 3), but carbon loss from the forest floor was highest in the W treatment during winter months (Fig. 4). On an annual basis, carbon loss was 966 g C m^{-2} $year^{-1}$ in the W treatment

Table 3
Pearson's correlation coefficient and associated observed probability values (in parentheses) for correlation between soil CO_2 efflux rate (S_{CO_2}) and distance from row center (D), fine root mass or total root mass beneath measurement collars, and between D and root mass in a 6-year-old loblolly pine plantation in response to weed control (W), weed control plus irrigation (WI), weed control plus irrigation and fertigation (WIF), and weed control plus irrigation, fertigation and pest control (WIFP)

Variable	Treatment	D	Fine root	Total Root
S_{CO_2}	W, WI, WIF, WIFP	−0.212 (0.029)	0.098 (0.316)	0.039 (0.694)
	W	−0.349 (0.074)	0.270 (0.173)	0.083 (0.680)
	WI	−0.048 (0.812)	0.297 (0.133)	0.416 (0.031)
	WIF	−0.165 (0.430)	0.227 (0.275)	−0.043 (0.840)
	WIFP	−0.311 (0.114)	−0.168 (0.402)	−0.027 (0.895)
D	W, WI, WIF, WIFP	–	−0.328 (<0.001)	−0.200 (0.038)
	W	–	0.129 (0.520)	0.155 (0.440)
	WI	–	−0.398 (0.040)	−0.161 (0.423)
	WIF	–	−0.423 (0.028)	−0.458 (0.016)
	WIFP	–	−0.488 (0.010)	−0.230 (0.249)

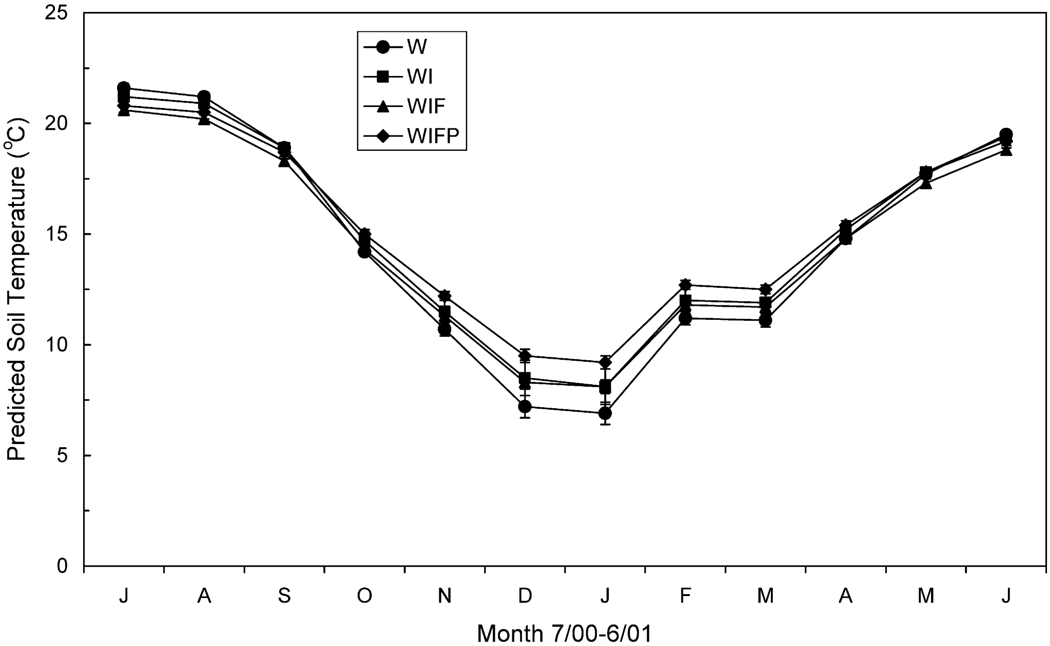

Fig. 3. Predicted 24-h average monthly soil temperature at 15 cm in a 6-year-old loblolly pine plantation in response to weed control (W), weed control plus irrigation (WI), weed control plus irrigation and fertigation (WIF), and weed control plus irrigation, fertigation and pest control (WIFP).

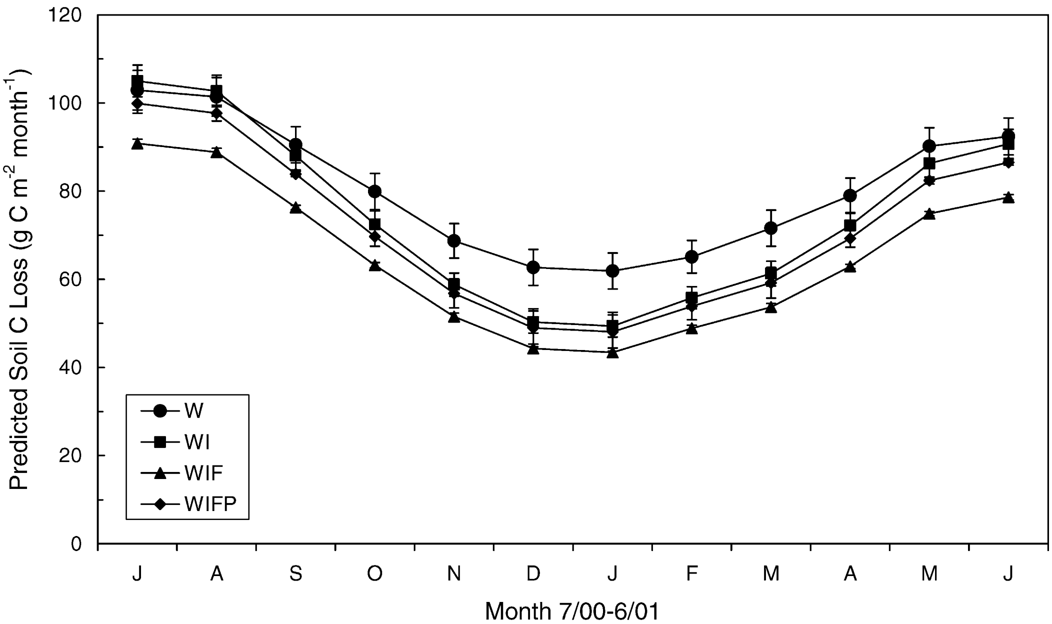

Fig. 4. Predicted monthly soil carbon (C) loss with the forest floor in place from July 2000 to June 2001 in a 6-year-old loblolly pine plantation in response to weed control (W), weed control plus irrigation (WI), weed control plus irrigation and fertigation (WIF), and weed control plus irrigation, fertigation and pest control (WIFP).

and was significantly higher than 778 g C m^{-2} $year^{-1}$ from the WIF treatment (Table 4).

4. Discussion

The range of S_{CO_2} observed in this study (1.27–5.59 μmol m^{-2} s^{-1}) is comparable to rates reported for other conifers including Monterey pine (*Pinus radiata* D. Don., 1.83–7.08 μmol m^{-2} s^{-1}) (Carlyle and Than, 1988), slash pine (0.70–5.75 μmol m^{-2} s^{-1}) (Fang et al., 1998), loblolly pine (0.5–6.0 μmol m^{-2} s^{-1}) (Maier and Kress, 2000), and ponderosa pine (*Pinus ponderosa* Dougl. ex Laws., 1.67–5.87 μmol m^{-2} s^{-1}) (Xu and Qi, 2001). Similarly, S_{CO_2} ranged from 0.57 to 7.05 μmol m^{-2} s^{-1} in a mixed tropical forest (Behera et al., 1990) and from 0.8 to 5.7 μmol m^{-2} s^{-1} in deciduous forests of the eastern United States (Hanson et al., 1993).

High correlation between S_{CO_2} and soil temperature in intensively managed loblolly pine is consistent with previous reports for terrestrial systems (Raich and Schlesinger, 1992; Lloyd and Taylor, 1994), and when soil moisture availability is low, S_{CO_2} is often positively correlated with soil moisture (Carlyle and Than, 1988). For instance, in an intensively managed 11-year-old loblolly pine plantation, soil temperature accounted for 70% of the seasonal variation in S_{CO_2}, and positive correlation between S_{CO_2} and soil moisture was observed when soil moisture in non-irrigated plots was low (Maier and Kress, 2000). Because rainfall was evenly distributed throughout the year, soil moisture did not explain variability in S_{CO_2} in a 17-year-old loblolly pine plantation under ambient or elevated CO_2 or with varying nutrient availability (Butnor et al., 2003a). However, no influence of soil water content on S_{CO_2} of northern hardwood, mature aspen (*Populus tremuloides* Michx.) and intermediate age aspen forests was observed, although soil water content varied between sites (Boldstad et al., 2004). In our study, although the W treatment had the lowest average soil moisture content, soil moisture explained only 7% of the variability in S_{CO_2} in the W treatment and no variability was attributed to soil moisture when data were pooled across treatments, perhaps because S_{CO_2} was not measured at either extremely high or low soil moisture levels that may limit S_{CO_2} (Pangel and Seiler, 2002; Gough and Seiler, 2004). In addition, at low soil water content, matric potential may be a more appropriate expression of soil water content in relation to S_{CO_2} (Davidson et al., 1998).

The significance of distance from row center in the multiple regression models indicates that spatial variation accounted for a small amount of the variation in S_{CO_2}. The negative effect of distance from the tree on S_{CO_2} is in agreement with Wiseman and Seiler (2004), who observed higher S_{CO_2} and live root volume near the base of loblolly pine trees but only a small influence of soil position and root volume on S_{CO_2}. Because respiration from deeper coarse roots and taproots (below 15 cm soil) may account for as much as 62% of total root respiration (Maier and Kress, 2000), higher S_{CO_2} near the tree is likely a function of overwhelming contributions from tap and coarse roots rather than root mass immediately below the collars.

The range in carbon loss from forest floor respiration reported in this study (778–966 g C m^{-2} $year^{-1}$) is similar to the 994 g C m^{-2} $year^{-1}$ reported for an older loblolly pine forest in North Carolina (Andrews and Schlesinger, 2001), but lower than 1400 g C m^{-2} $year^{-1}$ reported for fertilized and irrigated 11-year-old loblolly pine (Maier and Kress, 2000) and higher than the 692 g C m^{-2} $year^{-1}$ reported for 7-year-old loblolly pine in northwest Florida (Lee and Jose, 2003). Lack of a significant difference between the W and WIFP treatments in annual carbon loss may be explained by differences in predicted temperature between the WIF and WIFP treatments during winter months. From November to March, predicted 24-h soil temperature was on average 1 °C higher in the WIFP than WIF treatment (Fig. 3), possibly in response to greater LAI (5.5 versus 4.5, respectively) (Samuelson et al., 2004).

Numerous studies report that S_{CO_2} is negatively related to nutrient availability (Haynes and Gower, 1995; Maier and Kress, 2000), and a 16% reduction in carbon loss via soil respiration over a 220-day period in response to fertilization was observed in older loblolly pine stands (Butnor et al., 2003a). The 20% reduction in annual carbon loss from the forest floor in WIF stands was not likely in response to a smaller contribution of fine root respiration to total respiration, as fine root biomass was not reduced by WIF and WIFP treatments compared with the W treatment (Butnor et al., 2003b; Samuelson et al., 2004) and

S_{CO_2} was not correlated to fine root biomass. Recent studies also report little relationship between fine root mass and S_{CO_2} in loblolly pine (Pangel and Seiler, 2002; Gough and Seiler, 2004), but positive correlation between S_{CO_2} and fine root production has been observed (Lee and Jose, 2003).

During winter months, average soil temperature during instantaneous measurements and predicted average 24-h temperatures were lower but S_{CO_2} was greater in the W treatment compared with the water and nutrient augmented treatments. Differences in the coefficients of the exponential models indicated that S_{CO_2} at low temperature was highest in the W treatment, but the increase in S_{CO_2} with increasing temperature was lowest in the W treatment. Thus, although treatment differences in predicted annual carbon loss were a function of model coefficients, other factors in addition to soil temperature likely contributed to differences in carbon loss between treatments. For example, fertilization has been shown to reduce microbial activity and microbial biomass (Smolander et al., 1994; Vose et al., 1995; Fog, 1988), and the temperature sensitivity of heterotrophic respiration may be less than for root respiration (Boone et al., 1998). Greater microbial biomass and/or activity in the W treatment and a lower Q_{10} for microbial respiration compared with root respiration as well as seasonal changes in the relative contribution of heterotrophic and root respiration (Hanson et al., 2000) may be important in understanding differences in model slope coefficients. Given the large increase in aboveground and belowground growth with increasing management intensity (Samuelson et al., 2004), ontogeny-related shifts in autotrophic versus heterotrophic components of S_{CO_2} may also be significant (Gough and Seiler, 2004).

In conclusion, we hypothesized that increasing availability of water and nutrients would decrease S_{CO_2} because of reduced fine root mass. Annual soil carbon loss was decreased and belowground carbon

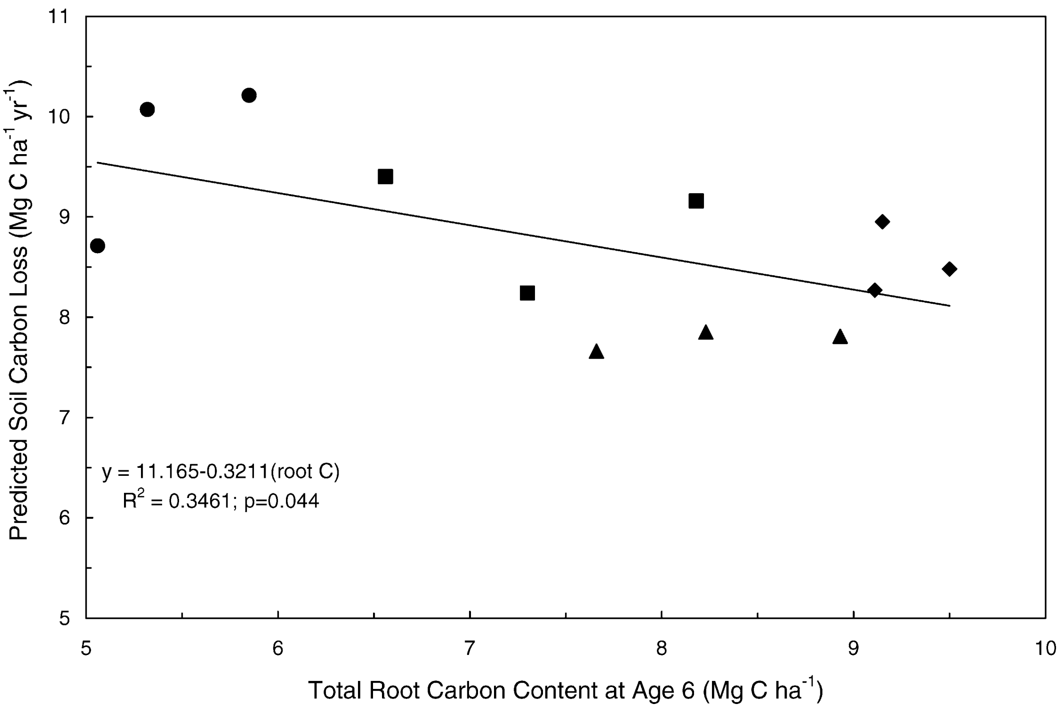

Fig. 5. Total belowground carbon (C) content in root mass (fine + coarse + tap) (from Samuelson et al., 2004) vs. predicted annual soil C loss in a 6-year-old loblolly pine plantation in response to weed control (circles), weed control plus irrigation (squares), weed control plus irrigation and fertigation (triangles), and weed control plus irrigation, fertigation and pest control (diamonds). Root biomass was converted to C content by multiplying by 0.44 (Oren et al., 2001).

sequestration was greatly increased by irrigation plus fertigation relative to the control, but S_{CO_2} was not correlated to fine root mass. Total belowground biomass was increased up to 70% with increasing management intensity, primarily in response to large increases in taproot biomass (Samuelson et al., 2004). As shown in Fig. 5, annual soil CO_2 efflux declined linearly with increasing belowground carbon content in root biomass at age 6. We suggest that the influence of intensive management on belowground carbon sequestration in southern pine ecosystems is considerable and a better understanding of controls on soil respiratory activity in these systems is needed.

Acknowledgements

This project was supported by funds provided by the USDA Forest Service, Southern Research Station, Asheville, NC, International Paper Company, and the Center for Forest Sustainability at Auburn University.

References

Ågren, G.I., Bosatta, E., Magill, A.H., 2001. Combining theory and experiment to understand effects of inorganic nitrogen on litter decomposition. Oecologia 128, 94–98.

Andrews, J.A., Schlesinger, W.H., 2001. Soil CO_2 dynamics, acidification, and chemical weathering in a temperate forest with experimental CO_2 enrichment. Global Biogeochem. Cyc. 15, 149–162.

Behera, S.K., Joshi, S.K., Pati, D.P., 1990. Root contribution to total metabolism in a tropical forest soil from Orissa, India. For. Ecol. Manage. 36, 125–134.

Boldstad, P.V., Davis, K.J., Martin, J., Cook, B.D., Wang, W., 2004. Component and whole-system respiration fluxes in northern deciduous forests. Tree Physiol. 24, 493–504.

Boone, R.D., Nadelhoffer, K.J., Canary, J.D., Kaye, J.P., 1998. Roots exert a strong influence on the temperature sensitivity of soil respiration. Nature 396, 570–572.

Borders, B.E., Bailey, R.L., 2001. Loblolly pine-pushing the limits of growth. South. J. Appl. For. 25, 69–74.

Brumme, R., Beese, F., 1992. Effects of liming and nitrogen fertilization on emissions of CO_2 and N_2O from a temperate forest. J. Geophys. Res. 97, 12851–12858.

Butnor, J.R., Johnsen, K.H., Oren, R., Katul, G.G., 2003a. Reduction of forest floor respiration by fertilization on both carbon dioxide-enriched and reference 17-year-old loblolly pine stands. Global Change Biol. 9, 849–861.

Butnor, J.R., Doolittle, J.A., Johnsen, K.H., Samuelson, L., Stokes, T., Kress, L., 2003b. Utility of ground-penetrating radar as a root biomass survey tool in forest systems. Soil Sci. Soc. Am. J. 67, 1607–1615.

Butnor, J.R., Johnsen, K.H., in press. Dynamic flux apparatus using artificial soil media of varying diffusivity for calibrating soil respiration measures. Eur. J. Soil Sci.

Carlyle, J.C., Than, U.B., 1988. Abiotic controls of soil respiration beneath an eighteen-year-old *Pinus radiata* stand in Southeastern Australia. J. Ecol. 76, 654–662.

Castro, M.S., Peterjohn, W.T., Melillo, J.M., Steudler, P.A., 1994. Effects of nitrogen fertilization on the fluxes of N_2O, CH_4, and CO_2 from soils in a Florida slash pine plantation. Can. J. For. Res. 24, 9–13.

Davidson, E.A., Belk, E., Boone, R.D., 1998. Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. Global Change Biol. 4, 217–227.

Fang, C., Moncrieff, J.B., Gholz, H.L., Clark, K.L., 1998. Soil CO_2 efflux and its spatial variation in a Florida slash pine plantation. Plant Soil. 205, 135–146.

Fog, K., 1988. The effect of added nitrogen on the rate of decomposition of organic matter. Biol. Rev. 63, 433–462.

Gough, C.M., Seiler, J.R., 2004. The influence of environmental, soil carbon, root, and stand characteristics on soil CO_2 efflux in loblolly pine (*Pinus taeda* L.) plantations located on the South Carolina Coastal Plain. For. Ecol. Manage. 19, 353–363.

Gough, C.M., Seiler, J.R., Johnsen, K.H., Sampson, D.A., 2004. Seasonal photosynthesis in fertilized and nonfertilized loblolly pine. For. Sci. 50, 1–9.

Hanson, P.J., Wullschleger, S.D., Bohlman, S.A., Todd, D.E., 1993. Seasonal and topographic patterns of forest floor CO_2 efflux from an upland oak forest. Tree Physiol. 13, 1–15.

Hanson, P.J., Edwards, N.T., Garten, C.T., Andrews, J.A., 2000. Separating root and soil microbial contributions to soil respiration: a review of methods and observations. Biogeochemistry 48, 115–146.

Haynes, B.E., Gower, S.T., 1995. Belowground carbon allocation in unfertilized and fertilized red pine plantations in northern Wisconsin. Tree Physiol. 15, 317–325.

Högberg, P., Nordgren, A., Ågren, G., 2002. Carbon allocation between root growth and root respiration in a boreal pine forest. Oecologia 132, 579–581.

Johnsen, K.H., Wear, D., Oren, R., Teskey, R.O., Sanchez, F., Will, R., Butnor, J., Markewitz, D., Richter, D., Rials, T., Allen, H.L., Seiler, J., Ellsworth, D., Maier, C., Katul, G., Dougherty, P.M., 2001. Meeting global policy commitments: carbon sequestration and southern pine forests. J. For. 99, 14–21.

Law, B.E., Ryan, M.G., Anthoni, P.M., 1999. Seasonal and annual respiration of a ponderosa pine ecosystem. Global Change Biol. 5, 169–182.

Lee, K., Jose, S., 2003. Soil respiration, fine root production, and microbial biomass in cottonwood and loblolly pine plantations along a nitrogen fertilization gradient. For. Ecol. Manage. 185, 263–273.

Lloyd, J., Taylor, J.A., 1994. On the temperature dependence of soil respiration. Funct. Ecol. 8, 315–323.

Maier, C.A., Kress, L.W., 2000. Soil CO_2 evolution and root respiration in 11-year-old loblolly pine (*Pinus taeda*) plantations as affected by moisture and nutrient availability. Can. J. For. Res. 30, 347–359.

Maier, C.A., Johnsen, K.H., Butnor, J., Kress, L., Anderson, P., 2002. Effects of nutrients and CO_2 amendments on branch growth, phenology and gas exchange in 13-year-old loblolly pine (*Pinus taeda*) trees. Tree Physiol. 22, 1093–1106.

Nadelhoffer, K.J., Aber, J.D., Melillo, J.M., 1985. Fine roots, net primary production, and soil nitrogen availability—a new hypothesis. Ecology 66, 1377–1390.

Neter, J., Wasserman, W., 1974. Applied Linear Statistical Models, Richard D. Irwin, Inc., Homewood, IL.

Oren, R., Ellsworth, D.S., Johnsen, K.H., Liu, K., Phillips, N., Ewers, B.E., Maier, C., Schafer, K., Hendrey, G., McNulty, S., Katul, G.G., 2001. Soil fertility limits carbon sequestration by forest ecosystems in CO_2-enriched atmosphere. Nature 411, 469–472.

Pangel, R.E., Seiler, J., 2002. Influence of seedlings roots, environmental factors and soil characteristics on soil CO_2 efflux rates in a 2-year-old loblolly pine (*Pinus taeda* L.) plantation in the Virginia Piedmont. Environ. Pollut. 116, S85–S96.

Raich, J.W., Schlesinger, W.H., 1992. The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. Tellus 44B, 81–99.

Ruffner, J.A., 1980. Climates of the States. NOAA, Gale Research, Detroit, MI.

Samuelson, L.J., 1998. Influence of intensive culture on leaf net photosynthesis and growth of sweetgum and loblolly pine seedlings. For. Sci. 44, 308–316.

Samuelson, L.J., Stokes, T., Cooksey, T., McLemore III, P., 2001. Production efficiency of loblolly pine and sweetgum in response to four years of intensive management. Tree Physiol. 21, 369–376.

Samuelson, L.J., Johnsen, K., Stokes, T., 2004. Production, allocation, and stemwood growth efficiency of *Pinus taeda* L. stands in response to six years of intensive management. For. Ecol. Manage. 192, 59–70.

Shan, J., Morris, L.A., Hendrick, R.L., 2001. The effects of management on soil and plant carbon sequestration in slash pine plantations. J. Appl. Ecol. 38, 932–941.

Smolander, A., Kurka, A., Kitunen, V., Mälkönen, E., 1994. Microbial biomass C and N, and respiratory activity in soil of repeatedly limed and N- and P-fertilized Norway spruce stands. Soil Biol. Biochem. 26, 957–962.

Söderström, E., Landgren, B., 1983. Decrease in soil microbial activity and biomass owing to nitrogen amendments. Can. J. Microbiol. 29, 1500–1506.

von Ende, C.N., 1993. Repeated measures analysis, Design and Analysis of Ecological Experiments, Chapman & Hall, New York.

Vose, J.M., Elliott, K.J., Johnson, D.W., Walker, R.F., Johnson, M.G., Tingey, D.T., 1995. Effects of elevated CO_2 and N fertilization on soil respiration from ponderosa pine (*Pinus ponderosa*) in open-top chambers. Can. J. For. Res. 25, 1243–1251.

Wiseman, P.E., Seiler, J.R., 2004. Soil CO_2 efflux across four age classes of plantation loblolly pine (*Pinus taeda* L.) on the Virginia Piedmont. For. Ecol. Manage. 192, 297–311.

Xu, M., Qi, Y., 2001. Soil surface CO_2 efflux and its spatial and temporal variations in a young ponderosa pine plantation in northern California. Glob. Chang. Biol. 7, 667–677.