Soil CO_2 evolution and root respiration in 11 year-old loblolly pine (*Pinus taeda*) plantations as affected by moisture and nutrient availability

C.A. Maier and L.W. Kress

Abstract: We measured soil CO_2 evolution rates with (S_{ff}) and without (S_{ms}) the forest floor litter and root respiration monthly in 11-year-old loblolly pine (*Pinus taeda* L.) plantations during the fourth year of fertilization and irrigation treatments. Values of S_{ff} ranged from less than 1 $\mu mol \cdot m^{-2} \cdot s^{-1}$ during the winter to greater than 5 $\mu mol \cdot m^{-2} \cdot s^{-1}$ in late spring. Average S_{ff} was significantly greater in unfertilized relative to the fertilized stands; however, there was no difference in average S_{ms} among treatments. Soil temperature and the mass of the forest floor (litter) explained most of the difference in S_{ff} among treatments. Soil temperature and volumetric water content accounted for 70% of the seasonal variation in S_{ff}. Annual carbon efflux from the soil averaged 14.1 $Mg \cdot ha^{-1}$ per year for all treatments. Most of the evolved carbon was derived from root respiration (50–73%). Net ecosystem productivity was –1.1 and 6.9 Mg $C \cdot ha^{-1}$ per year for the unfertilized and fertilized stands, respectively. At age 11, the unfertilized stands were functioning as a net carbon source, while fertilized stands were a strong carbon sink. It was concluded that fertilization could decrease the time for a young pine plantation to change from a carbon source to a carbon sink.

Résumé : Nous avons mesuré mensuellement le taux d'évolution du CO_2 du sol avec (S_{ff}) et sans (S_{ms}) la couverture morte ainsi que la respiration racinaire dans des plantations de pin à encens (*Pinus taeda* L.) âgés de 11 ans, durant la quatrième année des traitements de fertilisation et d'irrigation. Les valeurs de S_{ff} allaient de moins de 1 $\mu mol \cdot m^{-2} \cdot s^{-1}$ durant l'hiver à plus de 5 $\mu mol \cdot m^{-2} \cdot s^{-1}$ tard au printemps. La moyenne de S_{ff} était significativement plus élevée dans les peuplements non fertilisés que dans les peuplements fertilisés, mais il n'y avait pas de différence dans la moyenne de S_{ms} entre les traitements. La température du sol et la masse de la couverture morte (litière) expliquent la majeure partie de la différence de S_{ff} entre les traitements. La température du sol et le contenu volumétrique en eau expliquait 70% de la variation saisonnière de S_{ff}. La perte annuelle de carbone du sol a été en moyenne de 14,1 $Mg \cdot ha^{-1}$ par année pour l'ensemble des traitements. La majorité du carbone dégagé provenait de la respiration racinaire (50–73%). La productivité nette de l'écosystème était de –1,1 et de 6,9 Mg $C \cdot ha^{-1}$ par année pour les peuplements non fertilisés et fertilisés, respectivement. À l'âge de 11 ans, les peuplements non fertilisés fonctionnaient comme une source nette de carbone tandis que les peuplements fertilisés constituaient un fort puits de carbone. Nous en avons conclu que la fertilisation pourrait réduire le temps nécessaire pour qu'une jeune plantation de pin évolue d'une source à un puits de carbone.

[Traduit par la Rédaction]

Introduction

Tans et al. (1990) suggested that temperate forest ecosystems are important for sequestering carbon from the atmosphere for long-term storage. In addition, fast-growing intensively managed plantation forests may be more effective sinks for CO_2 than native forests (Delcourt and Harris 1980; Gladstone and Ledig 1990). Intensive management (i.e., harvesting, site preparation, vegetation control, and fertilization) has the potential to increase carbon sequestration by greatly increasing net primary productivity (NPP) over that of natural forests. Research over the last several decades has expanded our knowledge of the processes that control aboveground productivity (Landsberg and Gower 1997). Comparatively, much less is known about the mechanisms that link above- and below-ground NPP and the effects of forest management on soil carbon. Thus at present, we cannot predict the direction and magnitude of management practices on the carbon sequestration potential of plantation forests.

Net ecosystem production (NEP) reflects the annual change in carbon storage (vegetation + aboveground detritus + belowground detritus + soil carbon) and indicates whether an ecosystem functions as a source or sink for atmospheric CO_2. Net ecosystem productivity is the difference between NPP (carbon accumulated by vegetation over time) and heterotrophic respiration (R_H, carbon loss from decomposition)

$$[1] \quad NEP = NPP - R_H$$

Heterotrophic respiration in soils is difficult to measure but is often defined in terms of soil CO_2 evolution (S):

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[2] $S = R_H + R_A$

where R_A is autotrophic respiration associated with root metabolism. Soil CO_2 evolution is the second largest carbon flux in the ecosystem carbon budget (Raich and Schlesinger 1992).

The relative contribution of R_H and R_A to S changes with time of year and stand age. During stand development, root processes may have the largest impact on S. However, heterotrophic respiration (decomposition) will determine the long-term potential for soil to store carbon (Schlesinger 1997). In addition, many abiotic and biotic factors regulate the pools and fluxes of carbon within the soil profile and consequently S will vary greatly within and across ecosystems (Raich and Tufekcioglu 2000). Temperature and moisture account for much of the diurnal and seasonal variation in S (Witcamp 1969; Garret and Cox 1973; Edwards 1975; Schlentner and Van Cleve 1985; Weber 1990; Davidson et al. 1998). Soil CO_2 evolution is also proportional to root growth and biomass (Ewel et al. 1987*b*; Behera et al. 1990), and the amount and type of organic matter (Wander et al. 1994). Changes in soil fertility may also influence S, but the direction and magnitude of the change is unclear. Soil fertility may differentially affect R_H and R_A making it difficult to develop general response mechanisms.

Loblolly pine (*Pinus taeda* L.) is the most important economic tree species in the United States occupying over 13×10^6 ha of commercial forest lands from Virginia to eastern Texas and Oklahoma (Schultz 1997). Much of this forest grows on severely degraded soils that are low in organic matter and nutrient poor. Management of loblolly pine plantations is increasingly relying on the use of fertilizer to increase productivity (Allen et al. 1990); however, the long-term effects of increased nutrient input on stand carbon cycling is unknown. Knowledge of the physical and biological factors that regulate above- and below-ground carbon cycling in loblolly pine is required to determine how management activities, climate change, and disturbance will impact long-term soil carbon storage and carbon carrying capacity.

We measured soil CO_2 evolution and root respiration in loblolly pine plantations that were maintained for 4 years under a range of nutrient and moisture availability. At the beginning of this study, improved nutrition had doubled leaf area index (LAI) and stand NPP (Albaugh et al. 1998). The objectives of this study were to (*i*) measure the magnitude and variability in seasonal soil CO_2 evolution, (*ii*) quantify the influence of abiotic and biotic driving variables on soil CO_2 evolution, and (*iii*) partition soil CO_2 evolution into root and heterotrophic respiration. Lastly, we developed annual carbon budgets to determine whether these stands were functioning as a source or a sink for atmospheric CO_2.

Materials and methods

Site description

The study was established in a loblolly pine plantation located at the Southeast Tree Research and Education Site (SETRES), 17 km north of Laurinburg, N.C., (34°48′N, 79°12′W). The site is located on a flat, infertile, excessively well drained, sandy, siliceous, thermic Psammentic Hapludult soil (Wakulla series) with a water-holding capacity of 4 cm in a 50 cm profile. The climate is mild. Average annual temperature is 17°C (30-year average). Annual rainfall is 1210 mm (300-year average) evenly distributed throughout the year. The site was hand planted on a 2 m × 3 m spacing with 10 improved North Carolina Piedmont loblolly pine families in 1985 after harvesting of the previous natural longleaf pine (*Pinus palustris* Mill.) stand.

In January 1992, sixteen 50 m × 50 m treatment plots with 30 m × 30 m (0.9 ha) measurement plots centered in the treatment plot were established in the 8-year-old stand. Before treatment application, all plots were thinned to a similar initial tree height, diameter, basal area, volume, LAI, and density (1260 stems/ha). All nonpine vegetation in the treatment plots was eliminated since 1992 through chemical (glyphosphate) and mechanical means (Albaugh et al. 1998). The study has a randomized complete block design with a 2 × 2 factorial combination of nutrition (no addition and complete nutrition) and water (no addition and well watered) replicated four times. In brief, the nutrition treatment objective was to maintain optimum foliar nutrition of 1.3% N with all other macro- and micro-nutrients held in balance (Allen 1987). All nitrogen additions were applied as urea. The irrigation treatment objective was to maintain a soil water content > 40% field capacity. Nutrition treatments began in the March 1992 and irrigation treatments began in April 1993. Albaugh et al. (1998) provides full details on treatment application, monitoring, and efficacy.

Monthly measurements of soil CO_2 evolution and root respiration began in April 1995 and continued through March 1996. Four or five randomly selected sample sites were measured in each treatment in all replicate blocks. Each months' sample consisted of 64 or 80 measurements for all variables. The coefficient of variation for soil CO_2 evolution, averaged for all measurement days, ranged between 27 and 36% for individual treatment plots.

Measurement of soil CO_2 evolution

We measured soil CO_2 evolution using a chamber and an infrared gas analyzer (IRGA) in an open, flow through design. The chamber consisted of a 15 cm diameter PVC pipe cap (surface area 177 cm^2, volume 2032 cm^3) with the open end fitted with a 4 cm long aluminum pipe. The aluminum pipe extended 2 cm below the cap edge and provided a good seal between the PVC cap and the soil surface. A small fan installed in the roof of the cap stirred chamber air. All tubing to and from the chamber and IRGA was Bev-a-line. Air was cycled through the chamber using two pumps (Spec-Trex Corp., Redwood, Calif.) in a push–pull fashion, where air flow entering was slightly greater than exiting the chamber. Excess air vented through a 1 cm diameter port located on the side of the chamber and ensured that the air pressure within the chamber was held near ambient and any leaks were pushing outward. Pressure effects on soil CO_2 flux were tested by varying the input airflow between 700 and 2000 $cm^3 \cdot min^{-1}$ while keeping output airflow constant at 700 $cm^3 \cdot min^{-1}$ allowing the excess airflow to escape out the chamber vent. Varying the input airflow had no effect on CO_2 flux. Typical airflow rates during measurements ranged between 700 and 1500 $cm^3 \cdot min^{-1}$ giving a chamber turnover rate between 0.3 and 0.75 volumes per minute. The carbon dioxide concentration entering and exiting the chamber was measured with an IRGA (LI-COR 6262, LI-COR Inc., Lincoln, Neb.). All data were recorded with a data logger (Campbell 21x, Campbell Scientific, Logan, Utah). A computer attached to the data logger allowed real-time monitoring of chamber CO_2 differentials. Soil CO_2 flux ($\mu mol \cdot m^{-2} \cdot s^{-1}$) were calculated using the difference between entering and exiting CO_2 concentration, air flow rate, and chamber surface area.

Soil surface CO_2 evolution with the litter in place (S_{ff}) was measured by inserting the chamber through the litter and into the mineral soil and allowing the CO_2 flux rate to stabilize (8–10 min). The chamber was then lifted, the litter material enclosed within the chamber removed, and the chamber replaced back over the

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exposed mineral soil. The CO_2 flux was again allowed to stabilize (10–20 min) giving a measure of mineral soil CO_2 evolution (S_{ms}). Positioning the chamber on the soil surface disturbs the litter and soil sometimes causing a short-term flush of CO_2. Test measurements made over a 45- to 60-min period showed that the initial CO_2 flush dissipated within 10–20 min. Soil temperature at 2 and 7 cm and chamber air temperature were recorded concurrently during each CO_2 flux measurement using copper–constantan thermocouples. Water content of the top 15 cm of mineral soil at each sample point was measured using time-domain reflectrometry (TDR) and a Tektronix 1502-C cable tester (Tektronix, Inc., Beaverton, Oreg.) in the morning prior to CO_2 flux measurements. Moisture content, fresh mass, and dry mass of the litter material within the chamber was determined.

Immediately after soil CO_2 flux measurements, a soil core (15-cm diameter × 15-cm depth) was collected and brought back to the laboratory, where all dead and live root material was sieved from the soil by hand. The sandy texture of the soil allowed easy separation of roots with minimal loss. While dry sieving may have missed some of the smaller roots and associated mycorrhizae, this method produced similar biomass estimates to wet sieving using root elutriation (Mignano 1995). The CO_2 flux of the root mass was measured using an open gas exchange system identical to that described for soil CO_2 evolution measurement except the entire root mass could be sealed within a modified PVC chamber. The CO_2 flux from the root mass (all roots) was measured within 5–10 min after separation from the soil. The time between root coring and measurement of root respiration was typically less than an hour. Prestudy tests showed that respiration from a typical mass of roots was within 10% of the initial measurement up to 24 h after removal from the soil. These measurements were performed by measuring root respiration immediately after separation from the soil core and then periodically thereafter. In between measurements, roots were refrigerated in a plastic bag containing a wet paper towel. Root respiration was measured at room temperature at ambient CO_2 concentrations (350–380 umol·(mol CO_2)$^{-1}$) and was corrected to soil temperature at the time of coring using a $Q_{10} = 2$ (Amthor 1989). Root respiration was expressed per unit ground area (R_A, μmol·m^{-2}·s^{-1}) to facilitate comparisons to S_{ff} and S_{ms}. After measuring R_A, the roots were separated into four size classes (diameters <2, 2–5, 5–15, and >15 mm), stored on dry ice, and freeze-dried for determination of dry mass, carbohydrate content, and nutrient content.

A small subsample from each soil core was used to determine soil organic matter by loss-on-ignition. Soil carbon and nitrogen content were determined on a 10- to 20-g sample of oven-dried soil using a Carlo-Erba Model 1500 (Carlo Erba Instruments/Fison Instruments, Danvers, Mass.). Stand level values were calculated using a bulk density of 1.3 g·cm^{-3}, an average value for the upper 25 cm of soil at SETRES (Abrahamson et al. 1998).

Data analysis

Statistical significance of fertilization and irrigation and interaction effects on S_{ff}, S_{ms}, and R_A were determined using analysis of variance on treatment plot means (the average of four or five measurements per plot). Analyses were performed for individual sampling periods and for data pooled across the year. In the pooled analysis, sampling period (month) was included as an independent variable. The general linear models procedure was used for all analyses (SAS Institute Inc. 1987). Regression analysis was used to quantify the relationship between S_{ff}, S_{ms}, and R_A and independent variables.

Annual carbon budget

Seasonal trends in S_{ff} were modeled using an equation adapted from Hanson et al. (1993):

$$[3] \qquad S_{ff} = \frac{kW_s R_{max}}{(mW_s) + R_{max}} Q^{T/10}$$

where W_s is the volumetric soil water content, T is the temperature at 7 cm, k is the rate of change in S_{ff} with W_s, R_{max} is maximum S_{ff} when W_s = 100%, and Q is the rate of change in S_{ff} with a 10°C change in soil temperature. The model was parameterized for each treatment plot (16 models) using nonlinear regression (SAS Institute Inc. 1987), and treatment effects on parameter estimates were tested using ANOVA. The parameterized models developed for each treatment were used to estimate annual carbon loss from January 1 through December 31, 1995, using individual plot environmental data. Soil temperature (5 cm) was continually monitored in each treatment plot as part of the site environmental monitoring. Soil moisture was measured in each treatment plot on a weekly basis during the growing season (March–October) and biweekly during the dormant period. Soil moisture between measurement days was estimated by interpolation. Annual S_{ff} estimates were calculated by summing daily values. The portion of annual carbon loss due to root respiration in the top 15 cm ($R_{A,<15}$) was calculated using the relationship between R_A and S_{ff} for each treatment. Summing daily values gave an annual estimate of $R_{A,<15}$.

Recent sampling completed after this study (January 1998) revealed substantial root biomass down to 200 cm, far deeper than previously reported in the literature (Shultz 1997). The ratio of surface (0–15 cm) to deep root biomass (15–200 cm) was 0.34, 0.30, and 0.44 for the <2, 2–5, and >5 mm root size classes, respectively (B. Ewers, Duke University, Durham, N.C., personal communication). Thus, we have modified our approach for estimating stand root respiration to include deep root respiration ($R_{A,>15}$). These ratios were used to estimate deep root biomass during our study. Deep root maintenance respiration was calculated using temperature-response curves derived for each size class (C.A. Maier, unpublished data). Construction respiration was calculated from annual productivity estimates for fine and coarse roots (Albaugh et al. 1998) assuming 0.25 g C were released as CO_2 for every gram C in new tissue (Amthor 1989). Taproot respiration (R_{TR}) was calculated using equations for taproot biomass (Albaugh et al. 1998) and woody tissue respiration (Maier et al. 1998) assuming that taproot respiration is similar to stem respiration.

Heterotrophic respiration (R_H, decomposition) was calculated as the difference between annual S_{ff} and total root respiration ($R_T = R_{A,<15} + R_{A,>15} + R_{TR}$). Annual S_{ff}, R_T, and R_H were then compared with total NPP (Albaugh et al. 1998). Values for NEP were calculated as the difference between NPP and R_H. All values are in grams C per square metre.

Results

Treatment effects on soil C, N, litter, and root biomass

Four years of fertilization had a significant impact on soil nitrogen, carbon, and organic matter in the top 15 cm of soil (Table 1). While soil nitrogen concentration was generally low in both unfertilized and fertilized stands, fertilization resulted in 22% more soil nitrogen in the fertilized stands. Total soil nitrogen content averaged 53 and 65 g N·m^{-2} in unfertilized and fertilized stands, respectively. Similarly, soil carbon concentration was 14% greater in fertilized stands. Fertilized stands contained 2661 g C·m^{-2} compared with 2340 g C·m^{-2} for the unfertilized controls. There was little seasonal variation in soil carbon or nitrogen, however, levels were generally higher during the dormant season (December–February) (data not shown). Soil organic matter concentration was also elevated in the fertilized treatments. Fertilized treatments contained 5330 g·m^{-2} compared with

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Table 1. Amounts of soil carbon, nitrogen, and organic matter and forest floor litter in 11-year-old loblolly pine plantations after 4 years of fertilization and 3 years of irrigation treatment.

Treatment	Soil carbon		Soil nitrogen		Soil organic matter		Litter
	($mg \cdot g^{-1}$)	($g \cdot m^{-2}$)	($mg \cdot g^{-1}$)	($g \cdot m^{-2}$)	($mg \cdot g^{-1}$)	($g \cdot m^{-2}$)	($g \cdot m^{-2}$)
Unirrigated	13.4 (0.40)*a*	2616	0.31 (0.01)*a*	60	26.4 (0.79)*a*	5132	1003 (53)*a*
Irrigated	12.2 (0.33)*a*	2384	0.29 (0.01)*a*	56	25.4 (0.88)*a*	4949	966 (49)*a*
Unfertilized	12.0 (0.28)*a**	2340	0.27 (0.01)*a**	53	24.4 (0.76)*a*†	4751	669 (29)*a*
Fertilized	13.7 (0.42)*b*	2661	0.33 (0.01)*b*	65	27.4 (0.87)*b*	5330	1300 (48)*a*

Note: Values are annual means with SE given in parentheses. Means within column and treatment comparison followed by a different letter are significantly different ($\alpha = 0.05$).

*Differences between means for fertilized and unfertilized treatments are significant at $\alpha = 0.05$.

†Differences between means for fertilized and unfertilized treatments are significant at $\alpha = 0.10$.

Table 2. Probability values for season and treatment effects on live root biomass in the top 15 cm of soil.

Size class (mm)	Month	Fertilized	Irrigated	Interaction
<2	<0.01	<0.01	0.67	0.70
2–5	0.13	0.03	0.88	0.52
5–15	0.29	0.77	0.89	0.08
>15	0.12	<0.01	0.86	0.63

Note: Size class refers to root diameter.

4751 $g \cdot m^{-2}$ in unfertilized controls. Litter dry mass was generally low for all treatments, but increased foliage production and litterfall in fertilized stands had doubled litter dry mass over a 4-year period. Irrigation had no significant effect on soil carbon, nitrogen, organic matter, or litter mass; however, note that mean values for all variables were lower in the irrigated versus unirrigated stands (Table 1).

The effects of treatment and sampling period (month) on root biomass in the top 15 cm of soil differed with root size class. Root biomass for the <2 and 2–5 mm size classes were decreased in the fertilized treatments (Table 2). Root biomass for these small roots (<2 + 2–5 mm) was 24% lower in the fertilized versus unfertilized stands (Table 3). In contrast, fertilization had no effect on 5–15 mm diameter roots but greatly increased large root (>15 mm) biomass. Root biomass of the >15 mm size class was 4.7 times greater in the fertilized stands (Table 3). Thus, total root biomass was 30% larger in the fertilized than in unfertilized stands. Standing dead root biomass (all roots) was relatively small ranging from 8 to 21% of the total live root pool. Dead root pool sizes were similar between treatments, although the fertilized treatments had lower mean values. There were no irrigation or irrigation by fertilization interaction effects on live or dead root biomass for any size class. There were month-to-month differences in the standing biomass for small roots (<2 mm) (Table 2); however, there was no clear seasonal pattern (Fig. 1). The month-to-month variations in small root biomass were similar for both the fertilized and unfertilized stands. There was no significant seasonal variation in root biomass for the larger roots (Table 2).

Soil CO_2 evolution and root respiration

Average soil temperature at 7 cm varied seasonally from 5°C in the winter to greater than 25°C in the summer (Fig. 2*a*). Soil temperature was similar in each treatment during most measurement periods except for July, August and March when soil temperature was significantly greater in the control (C) versus the irrigated (I), fertilized (F), and irrigated + fertilized (IF) treatments. Averaged over the year, soil temperature at 7 cm was significantly greater in unfertilized (17.8°C) than in fertilized (16.5°C) stands. Volumetric soil water content in the unirrigated treatments varied seasonally from less than 3% to greater than 11% (Fig. 2*b*). Irrigation significantly elevated soil water content in April, May, July, and August.

Soil CO_2 evolution measured with the litter in place (S_{ff}) ranged from less than 1 $\mu mol \cdot m^{-2} \cdot s^{-1}$ in January to greater than 5 $umol \cdot m^{-2} \cdot s^{-1}$ in June for all treatments (Fig. 2*c*). Individual measurements were as high as 12 $\mu mol \cdot m^{-2} \cdot s^{-1}$. The seasonal trend closely followed the seasonal pattern in soil temperature at 7 cm (Fig. 2*a*), although maximum soil temperatures were recorded in July. The S_{ff} was generally lower in the fertilized than in the unfertilized stands from late spring through fall; however, these differences were only significant ($p \leq 0.10$) in September (C, I vs. F, IF), October (C, I vs. F, IF) and November (C vs. IF) (Fig. 2*c*). Annual average S_{ff} was 13% higher in unfertilized (3.22 $\mu mol \cdot m^{-2} \cdot s^{-1}$) versus fertilized stands (2.80 $\mu mol \cdot m^{-2} \cdot s^{-1}$). Soil CO_2 evolution, measured with litter removed (S_{ms}), followed the same seasonal pattern as S_{ff}. In contrast to S_{ff}, S_{ms} was similar between unfertilized and fertilized treatments except during winter when S_{ms} was greater in the fertilized treatments. These differences were significant ($p < 0.10$) between F and C treatments in December and January (Fig. 2*d*). Interestingly, within a treatment plot, S_{ms} was generally greater than S_{ff}. The difference between S_{ms} and S_{ff} was directly related to the mass of fresh litter. For example, in February, when large differences existed between S_{ff} and S_{ms}, the differences were strongly and negatively correlated with fresh litter mass (Fig. 3). This relationship was significant for 9 of the 12 months measured (slope $-4.82 \times 10^{-4} \pm 0.72 \times 10^{-4}$; mean ± SE). Low soil moisture appeared to reduce S_{ff} and S_{ms} in early spring and summer especially in the fertilized only treatment; however, differences between unirrigated and irrigated treatments were only significant in August, when soil moisture in the unirrigated treatments was below 4% (Fig. 2*b*).

Respiration of the root mass in the top 15 cm of soil ($R_{A,<15}$, $\mu mol \cdot m^{-2} \cdot s^{-1}$) generally followed the same seasonal pattern as S_{ff} with maximum rates in the late spring and low

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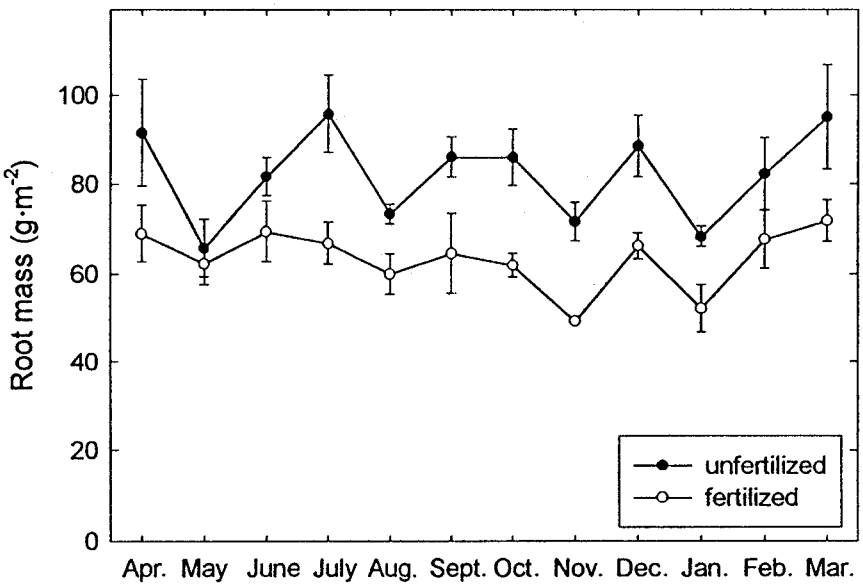
Table 3. Annual live root biomass ($g \cdot m^{-2}$) in the top 15 cm of soil in 11-year-old loblolly pine stands.

	Root mass ($g \cdot m^{-2}$) by size class				Total	
Treatment	<2 mm	2–5 mm	5–15 mm	>15 mm	live	Dead
Unirrigated	73.6 (2.2)*a*	72.4 (2.4)*a*	111.4 (7.5)*a*	133.1 (27.0)*a*	391	62.3 (8.1)*a*
Irrigated	72.1 (2.1)*a*	73.5 (3.0)*a*	109.9 (8.1)*a*	138.8 (31.4)*a*	394	48.4 (5.7)*a*
Unfertilized	82.2 (2.2)*a*	83.2 (2.7)*a*	108.5 (6.7)*a*	47.8 (10.1)*a*	322	62.7 (6.6)*a*
Fertilized	63.5 (1.5)*b*	62.7 (2.4)*b*	112.9 (8.8)*a*	224.1 (38.1)*b*	463	48.0 (7.3)*a*

Note: Values are means with SE given in parentheses. Means within column and treatment comparison followed by a different letter are significantly different ($\alpha = 0.05$).

Fig. 1. Mean live fine root (<2 mm diameter) biomass (±1SE) in unfertilized and fertilized 11-year-old loblolly pine stands. Biomass is for the top 15 cm of soil. Each point is the mean of four observations.



rates during the winter (Fig. 2*e*). Neither fertilization nor irrigation affected R_A except in May when R_A in the fertilized only treatment was significantly greater than in the control. The root mass in this shallow soil layer appears to contribute a relatively large amount of CO_2 to S_{ff}. The relative contribution of R_A to S_{ff} varied seasonally from <30% in the summer to >50% in January.

Response to environmental variables

Within a sampling period (month), S_{ff} was rarely significantly correlated ($\alpha = 0.05$) with soil temperature. This was likely due to the small range in soil temperature experienced within a measurement cycle (2 days). When treatment means were pooled across all months, soil temperature at 7 cm explained 70% of the variation in S_{ff} (Fig. 4*a*). S_{ff} was significantly related to volumetric soil moisture when soil moisture in the unirrigated plots was low (April, August, November, and February). For example, in August when soil moisture varied significantly across treatment plots, S_{ff} was linearly related to moisture content (Fig. 4*b*). There was no significant relationship between S_{ff} and soil carbon, nitrogen, or organic matter. S_{ff} was linearly but weakly related to the total root biomass in the top 15 cm ($R^2 = 0.20$, $p < 0.001$). However, R_A of the root mass in the top 15 cm was a significant component of S_{ff} (Fig. 5).

Annual carbon budget

The seasonal trend in S_{ff} for each treatment plot was modeled using eq. 3 with model fits (R^2) ranging from 0.72 to 0.85 (Table 4). Parameter estimates did not differ by treatment. Q_{10} values ranged from 2.2 to 2.4. The model slightly overestimated the minimum values and underestimated maximum values but did a good job predicting the mean S_{ff}. The percent absolute deviation, an estimate of model accuracy, overestimated S_{ff} by 15–20%. Model precision (root mean square error) was within 10%.

The annual carbon evolved from the soil surface ranged from 1263 to 1576 $g \cdot m^{-2}$ (Table 5). Soil carbon flux was 17% greater for irrigated versus unirrigated stands reflecting the seasonal effect of irrigation on S_{ff}. Total root respiration ranged from 663 to 1062 g $C \cdot m^{-2}$. Root respiration in the 0- to 15-cm layer ($R_{A,<15}$) accounted for 52% of total root respiration in the unfertilized stands but only 38% of the total flux in the fertilized stands. Respiration of deeper roots (15–200 cm, $R_{A,>15}$) was more important in the fertilized treatments because of the much greater coarse root biomass in this zone. Taproot respiration accounted for only 5–12% of total root respiration. $R_{A,<15}$ contributed 26% of the annual soil carbon flux. Considering all root respiration in the 200-cm profile ($R_{A,<15} + R_{A,>15} + R_{TR}$), root metabolism contributed 50–73% of the annual soil carbon loss. Heterotrophic

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Fig. 2. Seasonal variation in (*a*) soil temperature, (*b*) volumetric soil moisture, (*c*) soil CO_2 evolution (S_{ff}) with the litter layer intact, (*d*) soil CO_2 evolution (S_{ms}) with the litter layer removed, and (*e*) root respiration (R_A) in 11-year-old loblolly pine stands. Root respiration rate is the CO_2 flux of all roots and is expressed per unit of ground area to facilitate comparison to S_{ff} and S_{ms}. Each point is the mean of four observations. An asterisk shows a significant difference ($p \leq 0.05$) for at least one treatment.

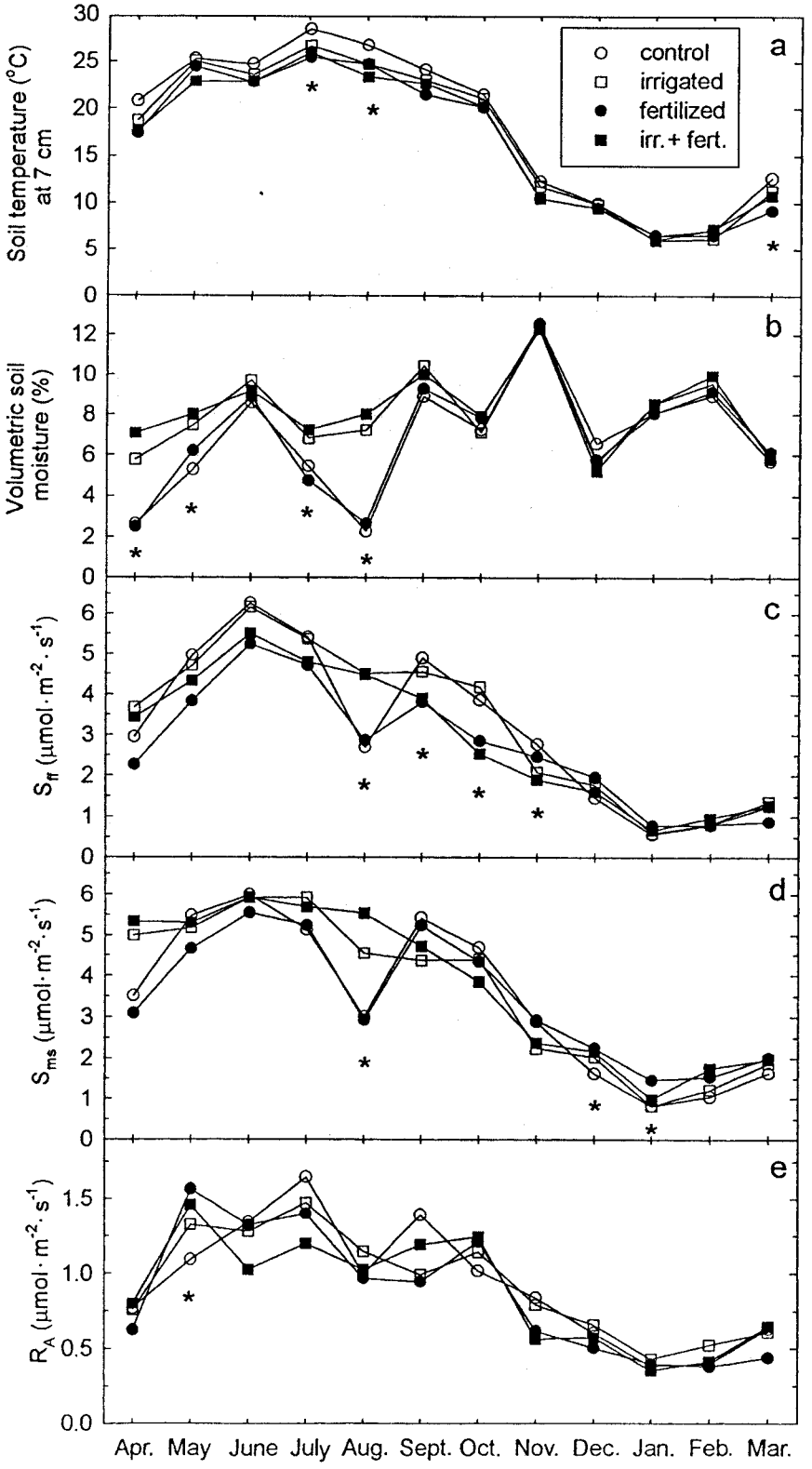

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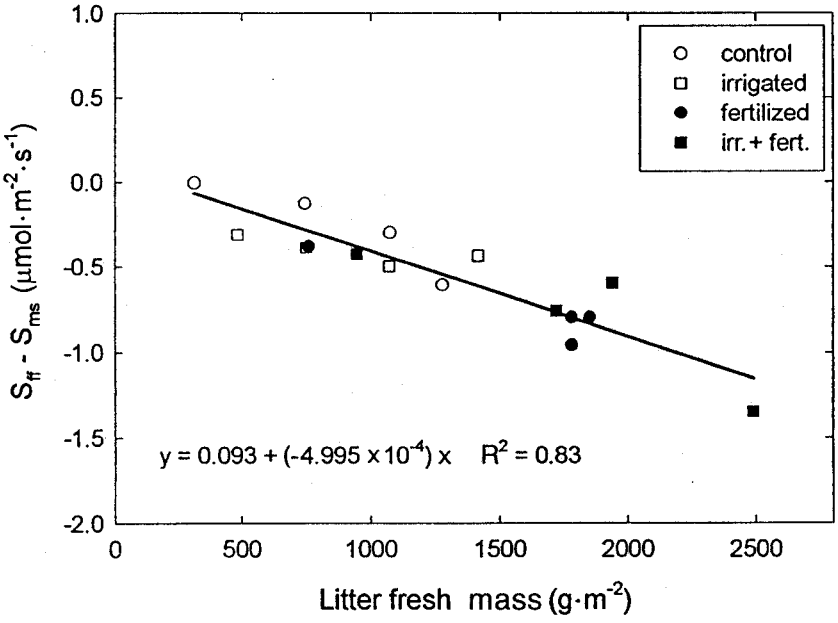
Fig. 3. The effect of litter mass on soil CO_2 evolution. The y axis is the difference between soil CO_2 evolution with (S_{ff}) and without (S_{ms}) the litter layer in place. Data are for measurements made in February; each point is the mean of four observations in each treatment plot.



respiration, calculated as the difference between S_{ff} and total root respiration, was slightly greater than NPP in the unfertilized stands. NEP (from eq. 1) was therefore negative indicating that the unfertilized stands are likely net carbon sources. In contrast since R_H was only 34 to 42% of NPP in the fertilized stands, NEP was positive, and these stands were functioning as a strong carbon sinks.

Discussion

Soil carbon, soil organic matter, and root biomass

We observed a slight but significant increase in mineral soil carbon and soil organic matter in the top 15 cm of soil in the fertilized stands after 4 years of treatment. This increase in soil carbon was likely due to an increase in belowground carbon allocation and to a doubling of forest floor litter. While increased nutrient availability decreased small root biomass (<2 and 2–5 mm) in the fertilized stands, it had the opposite effect on large root biomass (>15 mm). Consequently, on average, there was 30% more roots in the 0–15 cm soil layer in the fertilized stands. Total belowground NPP was 25% higher in fertilized (2.0 Mg $C \cdot ha^{-1}$ per year) than in unfertilized (1.5 Mg $C \cdot ha^{-1}$ per year) stands (Albaugh et al. 1998) in 1995. The observed response of fine and coarse root biomass and productivity to fertilization is consistent with that reported for other coniferous forests (Axelsson and Axelsson 1986; Vogt et al. 1986; Gower et al. 1992, 1994).

Root respiration

Our approach to measuring root respiration assumes that ex situ measurements on excised roots are a good approximation of in situ root respiration rates. Severed roots often exhibit increased respiration rates immediately after cutting (Rakonczay et al. 1997*b*), a response attributed to traumatic respiration (Sprugel and Benecke 1991). However, Rakonczay et al. (1997*a*) demonstrated that fine root respiration in several tree species stabilized within 30 min after excision and that the stabilized ex situ rates were similar to in situ measurements. Our root respiration measurements were made 30–60 min after excision, and we likely missed the initial high respiration rates reported by Rakonczay et al. (1997*b*). Another concern with measuring detached roots is the effect of CO_2 concentration on apparent respiration rates. Root respiration rates were measured under ambient air CO_2 concentrations (≅400 $\mu mol \cdot mol^{-1}$). The rhizosphere CO_2 concentration is typically much higher (e.g., 1000 $\mu mol \cdot mol^{-1}$ in April). Recent evidence suggests that apparent root respiration rates decrease with increasing CO_2 concentration surrounding the root (Qi et al. 1994; Clinton and Vose 1999). Clinton and Vose (1999) demonstrated that in situ fine root respiration in white pine trees declined 90% as ambient CO_2 concentrations increased from 400 to 1000 $\mu mol \cdot mol^{-1}$. Based on their results, we may have greatly over estimated the proportion of soil CO_2 evolution derived from root respiration especially during the summer, when soil CO_2 concentrations are likely to be high. Since we calculated R_H as the difference between S_{ff} and R_A, adjusting down R_A for elevated soil concentration would significantly reduce our estimates of NEP. However, not all studies show an inhibition of root respiration with elevated soil concentration (Nobel and Palta 1989; Bouma et al. 1997). McDowell et al. (1999) showed that root maintenance respiration was strongly controlled by concentration, while construction respiration was unaffected; thus, small fast growing roots and larger coarse roots may respond differently to soil concentration.

Surprisingly, there was no treatment effect on R_A. The lack of a treatment effect on R_A may be a result of measuring CO_2 flux on the root mass in each core (all size classes together) rather than measuring each size class independently. This is

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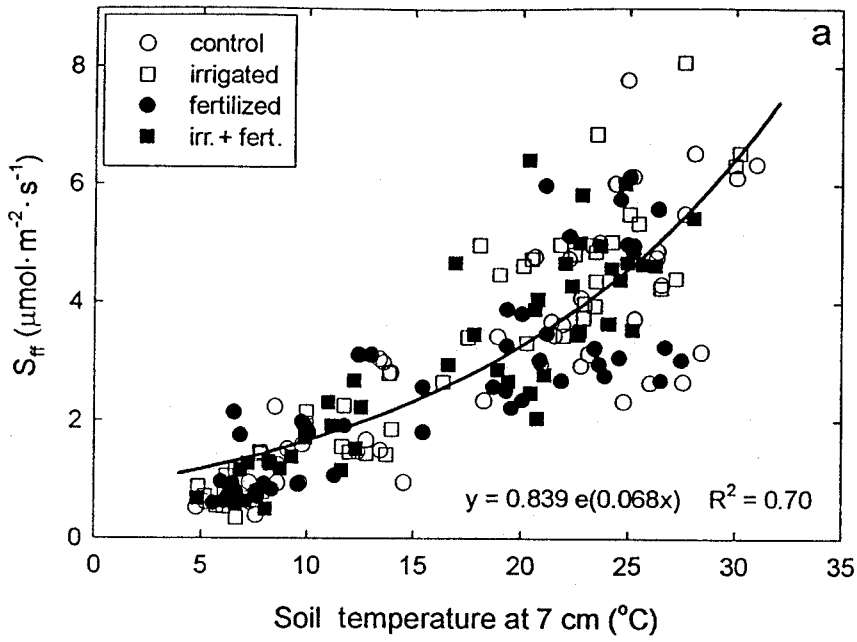
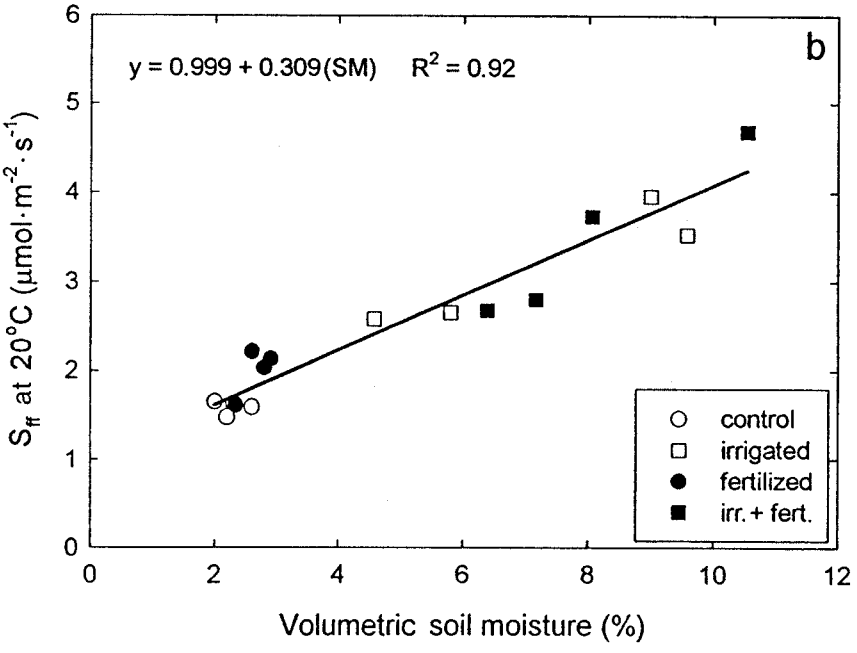
Fig. 4. The relationship between soil CO_2 evolution and (*a*) soil temperature at 7 cm, (*b*) volumetric water content. In Fig. 4*a*, data are treatment plot means for each sampling period. In Fig. 4*b*, data are treatment plot means measured in August.





because, although fertilization decreased fine root biomass, it increased course root biomass relative to the unfertilized stands. In addition, woody tissue respiration is often correlated with tissue nitrogen concentration (Ryan 1991; Maier et al. 1998), and fertilized fine and coarse roots had significantly higher tissue nitrogen concentrations than unfertilized roots. The relationship between root respiration and nitrogen is likely tissue specific. Preliminary evidence suggests that specific root respiration increases with nitrogen content in coarse roots but not for fine roots (C.A. Maier, unpublished data). Thus, while stand level root respiration associated with fine root growth and maintenance would decrease in fertilized stands, coarse root respiration would increase owing to more biomass and increased specific respiration rates.

The metabolism of near surface roots and associated mycorrhizae appears to contribute a disproportionate amount of CO_2 to S_{ff} than deeper roots. Root respiration in the surface layer (top 15 cm) accounted for 20–50% of S_{ff}, depending on time of year. Considering all of the roots in the 200-cm profile, 50–73% of the annual S_{ff} was derived from root respiration. These estimates are in line with those reported by Ewel et al. (1987*b*) for slash pine (*Pinus elliottii* Engelm.)

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Fig. 5. The correlation between root respiration (R_A) of the root mass in a 15 cm diameter by 15 cm deep soil core and soil CO_2 evolution (S_{ff}). Data are treatment plot means for each sampling period.

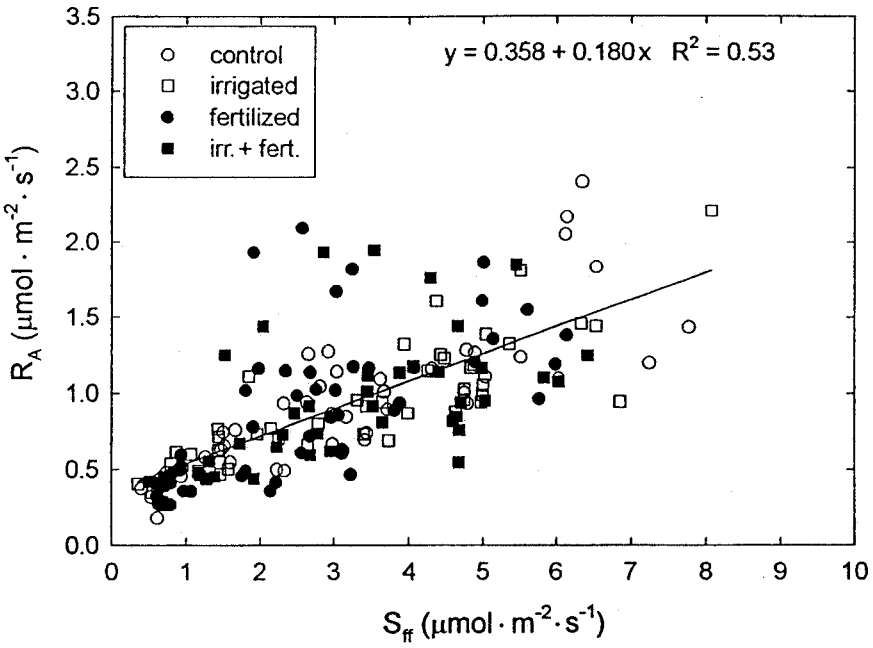

Table 4. Parameter estimates for eq. 3 and model fit statistics for soil CO_2 evolution (S_{ff}) as a function of soil temperature and volumetric water content.

Treatment	R_{max}	Q	k		Mean	Minimum	Maximum	R^2	RMSE (%)	AD (%)
Control	1.289 (0.130)	2.370 (0.133)	0.187 (0.040)	Model	3.155	1.143	6.850	0.85	5.70	20.06
				Observed	3.161	0.395	7.773			
Irrigated	1.195 (0.189)	2.245 (0.163)	0.307 (0.083)	Model	3.240	1.152	7.420	0.83	5.44	15.21
				Observed	3.292	0.353	8.072			
Fertilized	1.088 (0.241)	2.395 (0.210)	0.278 (0.078)	Model	2.717	1.171	5.749	0.72	4.26	14.39
				Observed	2.684	0.605	6.141			
Irrigated and fertilized	2.268 (0.746)	2.191 (0.071)	0.197 (0.057)	Model	3.064	1.114	6.227	0.77	4.62	19.59
				Observed	2.923	0.509	6.419			

Note: Values in parentheses are the standard error of the parameter estimates.

plantations but are much higher than in other forest types (Landsberg and Gower 1997). The variation between studies may be due in part to differences in root biomass, rates of root growth and respiration, decomposition rates, and soil type but could also be attributed to the various methods used to partition soil CO_2 evolution into root and heterotrophic respiration (Bowden et al. 1993). Root distribution in the soil profile is also important. Pregitzer et al. (1998) found that respiration of roots at deeper depths was lower than similar size shallow roots. As mentioned earlier, our root respiration rates may be inflated owing to the low measurement [CO_2] (Qi et al. 1994; Clinton and Vose 1999).

Soil CO_2 evolution

The S_{ff} rates observed in this study (0.5–6.0 $\mu mol \cdot m^{-2} \cdot s^{-1}$) are comparable with those reported for temperate pine (Witkamp and Frank 1969; Ewel et al. 1987*a*; Haynes and Gower 1995) and hardwood ecosystems (Garret and Cox 1973; Edwards and Harris 1977; Hanson et al. 1993; Bowden et al. 1993). The seasonal trend in S_{ff} was generally higher in the unfertilized than fertilized stands. The reported responses of soil CO_2 evolution to fertilization vary. Fertilization can decrease (Mattson 1995; Haynes and Gower 1995), increase (Salonius and Mahendrappa 1979; Brumme and Beese 1992), or have no discernable effect on soil surface CO_2 flux (Vose et al. 1995; Castro et al. 1994). Changes in soil fertility may have a differential effect on root growth biomass, root maintenance respiration, and heterotrophic respiration (Kowalenko et al. 1978; Fog 1988). However, King et al. (1997) found no effect of fertilization on coarse root decomposition rates in these stands. Although the averaged S_{ff} in the unfertilized treatments was significantly greater than in the fertilized treatments (13%), there was no difference in S_{ms}. This indicates that any direct effects of fertilization on root or heterotrophic respiration were not responsible for the differences in S_{ff}.

The slightly higher soil temperatures in the unfertilized stands compared with fertilized stands accounted for about 60% of the difference in S_{ff} between treatments. In addition, fertilized stands had almost twice the amount of litter than

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Table 5. Summary of annual carbon fluxes for midrotation loblolly pine plantations.

Component	Control	Irrigated	Fertilized	Fertilized and irrigated
Soil CO_2 evolution*	1263	1489	1293	1576
Root respiration†				
0–15 cm	350	386	354	400
15–200 cm (maintenance)	183	230	353	392
15–200 cm (construction)	98	98	124	140
Taproot	32	31	111	130
Total root respiration	663	745	942	1062
Heterotrophic respiration	600	744	351	514
NPP	500	635	1020	1235
NEP	−100	−109	669	721

Note: Soil CO_2 evolution (S_{ff}) is from eq. 3. Total root respiration (R_T) was partitioned into root respiration in the 0- to 15-cm and 15- to 200-cm soil layer (see footnotes) and taproot. Heterotrophic respiration (R_H) is the difference between soil CO_2 evolution and R_T. Net primary productivity (NPP) is from Albaugh et al. (1998) assuming carbon is 50% of biomass. Net ecosystem productivity (NEP) is the difference between NPP and R_H. All values are g $C \cdot m^{-2}$.

*Total carbon released from the soil in the form of CO_2.

†Estimate of root respiration from 0–15 cm are from monthly measurements of root respiration in soil cores associated with soil CO_2 evolution measurements. Values from 15–200 cm are calculated from estimated root biomass.

unfertilized stands. This extra litter may act to restrict mineral soil CO_2 diffusion in the fertilized stands. The evidence supporting this hypothesis comes from comparing S_{ff} and S_{ms} within a treatment. Within a treatment, S_{ff} was usually less than S_{ms}, and the difference was well correlated with fresh litter mass. This relationship was also observed using dry litter mass, but the correlation was weaker indicating that not only the amount of litter is important for regulating CO_2 flux but also the moisture condition of the litter as well. The difference in litter biomass between unfertilized and fertilized stands accounted for 40–50% of the difference in S_{ff}. In a mixed hardwood forest, Edwards and Sollins (1973) measured higher CO_2 evolution on plots with the least amount of litter. However, they attribute these differences to variations in litter decomposition rates. At our site, litter decomposition rates were greater in the fertilized treatments (F. Sanchez, personal communication) and would not account for differences in S_{ff} between treatments.

Considering that the litter layer restricts S_{ff} in these stands, the litter mass should be a determinant of soil CO_2 concentration in the surface mineral soil. Preliminary measurements support this hypothesis. The CO_2 concentration in the top 15 cm of mineral soil in April was 950 ± 200 $\mu mol \cdot mol^{-1}$ in the unfertilized treatments compared with 1250 ± 220 $\mu mol \cdot mol^{-1}$ in the fertilized treatments (C.A. Maier, unpublished data). These values will likely vary with depth (Kiefer and Amey 1992) and time of year (Castelle and Galloway 1990; Clinton and Vose 1999). Changes in the soil CO_2 concentration will potentially alter soil-solution pH, nutrient cycling, and microbial and root respiration (Johnson 1995).

Annual carbon budgets

Our estimate of annual soil carbon flux (14.1 $Mg \cdot ha^{-1}$ per year) was high considering the small amount of organic matter in the soil. However, our values were within the range estimated for temperate coniferous forests at this latitude (Schlesinger 1977) and are similar to those reported for 9-year-old (8.2 Mg $C \cdot ha^{-1}$ per year) and 29-year-old (13 Mg $C \cdot ha^{-1}$ per year) slash pine plantations (Ewel et al. 1987*a*). The large soil carbon flux relative to the soil carbon pool suggests that most of the soil carbon input is released to the atmosphere with little accumulation in the mineral soil. This is consistent with turnover rates reported for loblolly pine forests (Kinerson et al. 1977; Richter et al. 1995). Richter et al. (1995) showed that, in a 34-year-old loblolly pine forest, annual soil carbon inputs could be as high as 3 $Mg \cdot ha^{-1}$ per year but that only 2 $Mg \cdot ha^{-1}$ had accumulated over 34 years of forest growth. An analysis of thermonuclear bomb originated ^{14}C over time corroborated these rapid turnover rates (Richter et al. 1999).

Although we did not directly measure the CO_2 evolution from the litter material, this source of CO_2 was likely a very small component of the annual carbon flux. Standing litter mass in our stands was low, and litter decomposition rates were less than 20% per year (F. Sanchez, personal communication). The open nature of the stands, void of understory vegetation, allowed litter material to dry quickly after rainfall (and irrigation) events, thus restricting decomposer activity. Based on the standing litter mass and decomposition rates, CO_2 evolution from decomposing aboveground litter contributed 50 and 115 g $C \cdot m^{-2}$ per year for unfertilized and fertilized stands, respectively, or less than 8% of the total carbon flux. Litterfall in 1995 was 305 and 625 $g \cdot m^{-2}$ per year (total biomass) (Albaugh et al. 1998), well within the range for foliage production of midrotation southern pine plantations (Gower et al. 1994). We expect that, as the forest floor and canopy continues to develop, the forest floor environment with respect to moisture will become more suitable for microbial activity, and litter decomposition should become a larger component of the S_{ff}. Ewel et al. (1987*b*) estimated that litter decomposition was about 7% total forest floor CO_2 flux in a 9-year-old slash pine stand but increased to 19% of the annual carbon flux in a 29-year-old stand.

The balance between annual NPP and decomposition (R_H) will determine whether a stand is a net source or sink for

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CO_2 (i.e., NEP). Forest management activities such as harvesting and site preparation (e.g., chopping slash residues, root raking, subsoiling, bedding etc.) represent a major disturbance and will likely drastically change soil carbon dynamics at least in the short term. The effects of disturbance on soil organic matter are hard to generalize but are probably related to site-specific soil and vegetative characteristics. Harvesting alone appears to have little effect on soil carbon levels, but post-harvest site preparation and silviculture can result in a sizable increase in soil carbon (Johnson 1992). The effects of these activities on soil CO_2 evolution are unclear. Post-harvest soil CO_2 evolution may decrease (Nakane et al. 1986; Striegl and Wickland 1998), not change (Mattson and Smith 1993), or increase (Gordon et al. 1987; Ewel et al. 1987*a*) from pre-harvest rates. These differences are likely due to the differential effects on autotrophic and heterotrophic respiration and to site specific soil physical (i.e., soil porosity) and chemical characteristics. Nevertheless, regenerating pine stands immediately after harvest will undoubtedly be a net carbon source because soil organic matter decomposition will exceed NPP of the new stand. The time needed for a regenerating forest to become a net sink for carbon depends on the degree of site disturbance, site microclimate, soil fertility, and initial soil carbon and plant productivity. Estimates range from 15 years for northeastern hardwood forests (Bormann and Likens 1979; Covington 1981) to as little as 3 years for slash pine plantations (Gholz and Fisher 1982). Nakane (1994) simulated the long-term carbon dynamics for temperate pine systems and showed that 7–15 years was required for the annual carbon budget to become positive and the stand to begin accumulating carbon. Our data indicate that, at age 11, the unfertilized stands were functioning as net carbon sources (NEP = −1.0 $Mg{\cdot}ha^{-1}$ per year) while the fertilized stands were strong carbon sinks (NEP = 6.9 $Mg{\cdot}ha^{-1}$ per year). This suggests that resource supply capacity plays a role in determining the rate at which a forest stand becomes a carbon sink after a disturbance.

Conclusions

Knowledge of the mechanisms controlling carbon loss from the soil surface is essential for understanding the impact of land-use changes, forest management practices, and climate change on net ecosystem productivity. Four years of fertilization decreased fine root biomass, increased coarse root biomass, and doubled standing litter biomass in fertilized stands. Soil CO_2 evolution was 13% higher in unfertilized versus fertilized stands; however, there was no difference in S_{ms} between treatments. Differences in S_{ff} were attributed to soil temperature and to the amount of litter mass restricting CO_2 diffusion. The annual soil carbon flux was 14.1 $Mg{\cdot}ha^{-1}$ per year. Root respiration, measured at ambient atmospheric concentration, accounted for more than half of this flux. Although the data used in this study are only for 1 year, they suggest that, at age 11, the unfertilized stands are net carbon source (NEP $\cong$ −1.0 $Mg{\cdot}ha^{-1}$). In contrast, NEP for the fertilized stands was large ($\cong$7.0 Mg $C{\cdot}ha^{-1}$). The fate of this large input of carbon is unknown; however, the increased concentration of mineral soil carbon in fertilized stands (12%) indicates the soil carbon pool in these stands may be in an aggrading phase. It appears that fertilization can accelerate the transition of a forest from a carbon source to a carbon sink especially on nutrient poor soils.

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