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Soil CO_2 efflux across four age classes of plantation loblolly pine (*Pinus taeda* L.) on the Virginia Piedmont

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Abstract

Soil CO_2 efflux resulting from microbial and root respiration is a major component of the forest C cycle. In this investigation, we examined in detail how soil CO_2 efflux differs both spatially and temporally with respect to stand age for loblolly pine (*Pinus taeda* L.) plantations on the Virginia Piedmont. Throughout a 12-month period, efflux rates were measured both near the base of trees and midway between planting rows in stands of four age classes. Mean soil CO_2 efflux rates measured during the 12-month study were 1.72, 2.58, 2.84, and 2.90 μmol/m^2/s for 1- to 2-year-old, 4- to 6-year-old, 8- to 12-year-old, and 20- to 25-year-old stands, respectively. Time series analysis revealed that stand age had a significant effect on soil CO_2 efflux rate. Additionally, mean efflux rates were consistently higher near the tree and time series analysis revealed that measurement position had a significant effect on soil CO_2 efflux rate. Mean soil CO_2 efflux rates, by position, for the 12-month study were 2.72 and 2.28 μmol/m^2/s for the near and away measurement positions, respectively. Regression analysis was used to examine the influence of soil and climatic factors on seasonal changes in soil CO_2 efflux. The most influential factors affecting soil CO_2 efflux during the 12-month study were soil temperature, soil moisture, stand age, and measurement position. We believe respiring roots significantly influence soil CO_2 efflux of plantation loblolly pine and account for differences observed between stands of different ages as well as spatial differences observed within a given stand.

Keywords: Soil CO_2 efflux; Soil respiration; Pine root respiration; Loblolly pine

1. Introduction

The world's forests contain an estimated 618 Pg C (1 Pg = 10^{15} g) in the mineral soil and O horizon (Brown, 1996). This figure represents roughly 41% of global soil C and is similar in magnitude to the atmospheric C pool of 750 Pg C (Rustad et al., 2000). Soil C accounts for approximately 70% of total forest C in temperate regions (Huntington, 1995). In temperate evergreen forests, an estimated 20.4 kg C/m^2 resides in the top 3 m of soil (Jobbagy and Jackson, 2000).

Forest soil may act as either a sink or a source for atmospheric C, depending on ecosystem type, successional stage, geographic location, and land-use history (Klopatek, 2002). Photosynthesis accounts for the majority of C input to the soil through litter-fall, root exudates, and root mortality (Van Veen et al., 1991). Faunal mortality also contributes to the soil C pool. The majority of soil C output occurs as CO_2 efflux

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resulting from the metabolic activities of soil organisms (Mielnick and Dugas, 1999). Both autotrophic (e.g. roots) and heterotrophic (e.g. bacterial and fungal detritivores) organisms contribute to soil CO_2 efflux through respiration. In temperate forests, root respiration accounts for an estimated 40–50% of total soil CO_2 efflux (Epron et al., 1999; Ohashi et al., 2000). Mair and Kress (2000) found that root respiration accounted for 52 and 73% of total soil CO_2 efflux in non-fertilized and fertilized loblolly pine (*Pinus taeda* L.) stands, respectively.

Soil temperature and moisture are considered the most influential environmental factors affecting soil CO_2 efflux (Schlesinger, 1977; Singh and Gupta, 1977; Raich and Schlesinger, 1992). These factors interact to influence the productivity of terrestrial ecosystems and the decomposition rate of soil organic matter, thereby driving seasonal variation in soil CO_2 efflux. In temperate regions, soil CO_2 efflux is typically higher in summer and lower in winter, corresponding to changes in ambient temperature. In Florida slash pine (*Pinus elliottii* Engelm.) plantations, average soil CO_2 efflux rates during the summer season were approximately twice as fast as average rates during the winter season (Ewel et al., 1987). The influence of soil temperature on soil CO_2 efflux is modified by soil moisture. Both soil saturation and drought suppress soil CO_2 efflux (Londo et al., 1999) and weaken efflux response to changes in soil temperature.

The management of forests for timber production can have a significant impact on soil C flux. Harvesting and site preparation have been observed to both increase and decrease soil CO_2 efflux compared to undisturbed sites (Ewel et al., 1981; Edwards and Ross-Todd, 1983; Toland and Zak, 1994). Changes in soil temperature and moisture are often observed following timber harvest, and this may result in either higher or lower soil CO_2 efflux rates, depending on other site variables (Pypker and Fredeen, 2003). Following harvest of a 65-year-old bottomland hardwood forest in Texas, clear-cut efflux rates were higher than both partial-harvest and non-harvest control plots (Londo et al., 1999). Higher rates were attributed to increased microbial activity, decaying root biomass, and herbaceous species germination. Conversely, slash burning and soil compaction due to machinery may reduce soil respiration by altering microbial activity and hampering root growth (Chang et al., 1995). Root death and reduction in microbial activity were cited as the cause of a 40% decrease in soil respiration one year after clear-cutting of jack pine (*Pinus banksiana* Lamb.) woodland in Saskatchewan, Canada (Striegl and Wickland, 1998). Approximately 20% of total soil C may be lost during intensive site preparation following harvest of southern pine plantations (Hoover et al., 2000).

Understanding temporal and spatial variation in soil CO_2 efflux is critical to accurately predicting the impact of forests on the global C cycle. Few studies have examined long-term changes in forest soil CO_2 efflux. In managed forests, soil CO_2 efflux appears to increase with stand maturation, most likely due to greater root and microbial biomass (Bauhaus et al., 1998; Makkonen and Helmisaari, 2001). Due to variability in root proliferation, significant spatial variability in soil CO_2 efflux likely exists in managed forests and spatial patterns may change with stand maturation.

Intensively managed loblolly pine stands account for over 13 million hectares of forested land in the southeastern United States (Schultz, 1997). C sequestration by southern forests is an important ecosystem service (Schlesinger, 1995) and has the potential to offset accumulation of CO_2 in the earth's atmosphere due to combustion of fossil fuels. Due to its importance in the southern forest and its simpler biological and physical diversity relative to natural systems, a loblolly pine plantation provides an appropriate setting for modeling soil CO_2 efflux.

In this study, we investigated the effect of stand age on temporal and spatial patterns of soil CO_2 efflux for plantation loblolly pine on the Virginia Piedmont. Over a 12-month period, soil CO_2 efflux rate was repeatedly measured in loblolly pine stands ranging in age from 1 to 25 years. We also quantified specific site and environmental variables thought to influence the temporal and spatial variability of soil CO_2 efflux. We hypothesized that soil CO_2 efflux rate would increase with stand age and would exhibit a consistent pattern of spatial variability within a stand. We also hypothesized that soil temperature, soil moisture, soil coarse mineral fragment content, and pine root biomass would explain temporal and spatial variability observed in soil CO_2 efflux.

2. Materials and methods

2.1. Study site

The study was conducted on industrial forestland in Buckingham County, Virginia (37°34′56″N, 78°26′55″W). The study area is typical of the Piedmont, with broad ridges and moderate slopes ranging from 5 to 25%. Average annual precipitation for this region is 107 cm. The average growing season temperature (April through September) is 20.7 °C and the average winter temperature (December to February) is 3.3 °C. A frost-free period lasts on average 180 days from mid-April through early October (MeadWestvaco Corporation, unpublished data).

Soils in the study area are predominantly derived from stratified, metasedimentary bedrock of the Western Piedmont geologic formation. Typical mineral content is metagraywacke, quartzose schist, and mélange. Soil textural class is typically a gravelly loam to gravelly sandy loam over 1:1 non-sticky clay or clay loam subsoil. Soil thickness averages 63 to 127 cm and site index averages 17.7 m at 25 years for loblolly pine (MeadWestvaco Corporation, unpublished data).

The loblolly pine stands chosen for this investigation had undergone similar management practices since their establishment. Site preparation prior to planting involved varying intensities of broadcast burning, chopping, and raking. All stands were established within 2 years of conventional harvesting of loblolly or Virginia pine (*Pinus virginiana* Mill.) plantations. Most stands were established by hand planting and all received herbicide treatment for control of herbaceous and hardwood competition at or shortly after establishment. Stands were typically established on 2 m × 3 m spacing, averaging approximately 1435 trees per hectare. Neither fertilization nor mid-rotation thinning was performed on the stands under investigation.

2.2. Experimental design

Four age classes of plantation loblolly pine were chosen for this study. Classes were based on the age of stands during the 2000 growing season. These included 1- to 2-year-old stands, 4- to 6-year-old stands, 8- to 12-year-old stands, and 20- to 25-year-old stands (hereafter referred to as classes one, two, three, and four, respectively). The study was designed as a split-plot in a randomized complete block where stand age class was the whole-plot factor and measurement position within the stand was the subplot factor. Each of the four stand age classes was replicated four times, represented by 16 stands dispersed across four geographical blocks. To account for within-stand variability, three sub-sampling locations were established in each replicate. Each sub-sampling location was split by proximity to a loblolly pine, with one point situated at the base of a tree and the other point situated halfway across the planting row. Thus, a total of six sampling points were established in each age class replicate (three near a tree and three away from a tree).

2.3. Study installation

In March 2000, 96 permanent measurement plots were installed. Three dominant or co-dominant loblolly pines were randomly chosen within each stand age class replicate. Trees exhibiting poor form, storm damage, disease or pest infestations were omitted from the selection process. Sample trees were selected well within the borders of each stand to minimize any edge effects. At each sample tree, a pair of permanent 1 m^2 plots was established. One plot was located at the base of the sample tree and the other plot was located midway (approximately 1.5 m) across the planting row. At plot establishment, a herbicide consisting of sulfometuron methyl (Oust®, DuPont, Wilmington, DE) and isopropylamine salt of imazapyr (Arsenal®, American Cyanamid Co., Wayne, NJ) was applied to the plots at rates of 2 and 4 oz/acre, respectively. Spot-treatment using glyphosate (Round-Up Pro®, Monsanto Co., St. Louis, MO) at a 6.25% volumetric concentration was also performed in May 2000. Herbicide applications were made to control competing woody and herbaceous vegetation within the plots, thereby preventing aboveground plant biomass from contributing to the efflux measurements.

2.4. Soil CO_2 efflux, soil temperature, and soil moisture measurements

Beginning in April 2000, soil CO_2 efflux, soil temperature, and soil moisture were measured one day per month for a period of 12 months. Measurements were taken only on days without precipitation and/or high winds to minimize equipment damage and measurement error. Beginning shortly after sunrise and continuing until late afternoon, each parameter was measured in each of the 96 permanent measurement plots. Measurements were made on a block-by-block basis to control for the effect of time of day.

Soil CO_2 efflux was measured using an LI-6250 infrared gas analyzer (Li-Cor Environmental Science Division, Lincoln, NE) linked to an LI-6200 portable photosynthesis console. A dynamic closed cuvette chamber was used to capture CO_2 diffusing from the soil surface and to circulate the gas to and from the analyzer (Janssens et al., 2000). The cuvette chamber was constructed using a PVC pipe end-cap (20.3 cm i.d.). A Plexiglas ring (0.32 cm thick, 21.6 cm i.d., 29.6 cm o.d.) was cemented to the lip of the end-cap. A 1.6 cm thick closed-cell foam gasket of the same inside/outside diameter was cemented to the Plexiglas ring. The foam gasket provided a reliable seal between the chamber and the soil surface. The total system volume was 4103 cm^3 and the soil diffusive area enclosed by the chamber was 368 cm^2. Upon arriving at each measurement plot, the chamber was allowed to equilibrate with the ambient CO_2 concentration near the soil surface for 30–60 s. The chamber was then pressed firmly on the ground at the plot center, and a 30 s sampling period was initiated when the CO_2 concentration was observed to be rising steadily. The gas analyzer then calculated flux rate to the nearest 0.01 $\mu mol/m^2/s$. Simultaneously, soil temperature was measured at each plot center using a 15 cm soil probe attached to a Digi-Sense® thermocouple thermometer (Cole-Parmer, Vernon Hills, IL). Soil moisture was measured to a depth of 30 cm using a Trase® 6050X1 time domain reflectrometer (Soil Moisture Equipment Corp., Golena, CA) connected to permanently installed, stainless steel wave guides (Topp and Davis, 1985).

2.5. *Final intensive sampling*

At the end of the study period in May 2001, intensive sampling was performed at each of the 96 permanent measurement plots. The normal regime of soil CO_2 efflux rate, soil temperature, and soil moisture measurements was made. In addition, litter samples and mineral soil samples were collected from each plot center. The entire O horizon (Oi, Oe, Oa) was collected from beneath the cuvette chamber location and a 382 cm^3 core was extracted from the exposed mineral soil to a depth of 10.2 cm. Live roots, coarse woody debris, and coarse mineral fragments were captured in the mineral soil sample.

2.6. *Laboratory analysis*

Litter samples were oven-dried at 65 °C until mass stabilization. Each sample was then ashed at 380 °C for 24 h to correct for mineral soil contamination and ash-corrected litter mass was calculated. Each mineral soil sample was sieved through 0.64 cm mesh to separate the soil from live roots, coarse woody debris, and coarse fragments. The sieved soil was then passed through an additional 0.2 cm sieve and analyzed with a Carlo Erba Nitrogen and Carbon Series II analyzer (CE Elantech Inc., Lakewood, NY) to determine C and N content. Coarse mineral fragments greater than 0.64 cm diameter were collected and weights recorded for each sample. Coarse woody debris greater than 0.64 cm diameter was collected and ash-corrected mass was calculated for each sample.

Live root samples were washed and then digitized using a flatbed scanner. WinRhizo® 5.0A software (Regent Instruments Inc., Que., Canada) was used to analyze the images and quantify total root length, root surface area, root projected area, root volume, and average root diameter. The root samples were also divided into fine (<2 mm), medium (2–5 mm), and coarse (>5 mm) diameter classes using the software. No attempt was made to separate pine roots from other roots, but very few non-pine roots were observed in the samples. After scanning, root samples were oven-dried at 65 °C and weighed.

2.7. *Statistical analysis*

To gauge the general effect of stand age and measurement position within each month, an analysis of variance was performed using the general linear model (GLM) procedure of SAS® (SAS Institute, Cary, NC). Effects and the interaction between effects were tested against the null hypothesis at the $\alpha = 0.05$ significance level. A time series analysis was also performed on the entire 12-month data set by testing month as an independent variable in the GLM procedure. When main effects were significant, differences in means for each dependent variable were tested using Tukey's studentized range test (HSD) at the $\alpha = 0.05$ significance level. When interactions were significant, the slicing option within the GLM procedure was used to test for differences between measurement positions within each age class at the $\alpha = 0.05$ significance level. Multiple linear regression analyses were used to examine the relationship between soil CO_2 efflux rate and continuous site variables (e.g. soil temperature and moisture) and the effects of discrete variables (e.g. position) were included using dummy variables. Significant model variables were first screened using the SAS stepwise procedure and then the models were examined for fit.

3. Results

3.1. Stand age, measurement position, and soil CO_2 efflux

Time series analysis of the 12-month data set revealed a significant stand age effect ($P = 0.0026$) on soil CO_2 efflux rate (Table 1). When sampling dates were examined individually, stand age class had a significant ($P < 0.05$) effect on soil CO_2 efflux rate on 10 of the 12 monthly sampling dates. Mean soil CO_2 efflux rate by age class ranged from a high of 6.50 μmol/m^2/s for class four during June 2000 to a low of 0.31 μmol/m^2/s for class one during December 2000 (Fig. 1). There was not a significant difference between mean efflux rates for classes two, three, and four on any sampling date. However, class one had a significantly ($P < 0.05$) lower mean efflux rate compared to the other classes on a consistent basis.

During the period from June to September 2000, efflux rates were at their highest and the classes were clearly ordered from youngest to oldest in terms of efflux rate magnitude. At other times, the three older classes changed ranking with no discernible trend. All four classes followed a similar pattern of changing efflux rates during the year.

Time series analysis also revealed a significant measurement position effect ($P = 0.0221$) on soil CO_2 efflux rate. Mean soil CO_2 efflux rates were higher at the near position throughout the investigation, and were significantly ($P < 0.05$) higher on eight of the 12 sampling dates when examined individually. Efflux rate at the near position ranged from 77% higher during January 2001 to 9% higher during July 2000. The interaction between stand age and measurement position was non-significant ($P = 0.2047$) in the time series analysis. There was a significant ($P < 0.05$) interaction between stand age and measurement position during August, September, and December 2000 when months were examined individually. With the exception of age class two, higher mean efflux rates tended to occur near the tree during most months of the investigation (Fig. 2). From July through October 2000, class two showed a trend of higher efflux rates away from the tree.

Table 1
Results of time series ANOVA testing of the effects of stand age, measurement position, month, and the age × position interaction on soil CO_2 efflux, soil temperature, and soil moisture

Source	d.f.	Mean square	P-value
Soil CO_2 efflux			
Stand age	3	27.18	0.0026
Measurement position	1	18.30	0.0221
Month	11	108.11	0.0001
Age × position	3	10.63	0.2047
Error	98	0.40	
Soil temperature			
Stand age	3	30.50	0.0514
Measurement position	1	0.64	0.6051
Month	11	1912.77	0.0001
Age × position	3	0.70	0.3971
Error	97	0.20	
Soil moisture			
Stand age	3	863.30	0.0110
Measurement position	1	132.32	0.0858
Month	10	680.28	0.0001
Age × position	3	18.74	0.4954
Error	89	0.97	

Data were collected through a 12-month period from April 2000 to April 2001 in four age classes of plantation loblolly pine on the Virginia Piedmont.

3.2. Soil temperature, moisture, and CO_2 efflux

CO_2 efflux rates were highest during the growing season and lowest during the winter months, closely paralleling soil temperatures (Figs. 1 and 2). Monthly mean soil temperature ranged from a high of 27.2 °C for class one during July 2000 to a low of 0.5 °C for

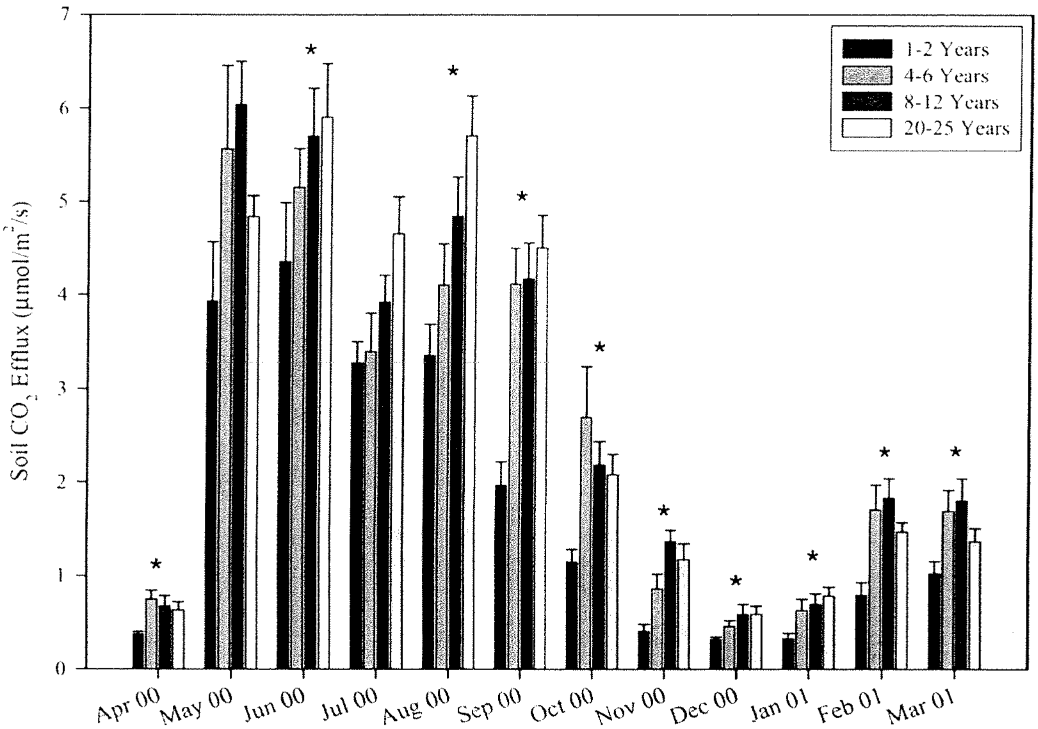

Fig. 1. Mean soil CO_2 efflux rates measured during monthly sampling periods in four age classes of plantation loblolly pine on the Virginia Piedmont. *Significant main effect ($P < 0.05$) for stand age class in ANOVA. Error bars represent ± 1 S.E. ($n = 8$).

class one during December 2000 (Table 2). Class one tended to have the highest soil temperatures during the growing season and lowest soil temperatures during the winter months. Conversely, class four tended to have the lowest soil temperatures during the growing season and highest soil temperatures during the winter months.

Stand age had a marginally significant ($P = 0.0514$) effect on soil temperature in the time series analysis (Table 1). Soil temperature significantly ($P < 0.05$) differed among stand age classes on nine of the 12 monthly sampling dates when examined individually. Measurement position did not have a significant ($P = 0.6051$) effect on soil temperature in the time series analysis. Soil temperature significantly ($P < 0.05$) differed between measurement positions only on the October 2000 sampling date when examined individually, at which time it was higher at the near position.

Time series analysis also revealed a significant stand age effect ($P = 0.0110$) on volumetric soil moisture (Table 1), which significantly ($P < 0.05$) differed among stand classes on eight of the 11 monthly sampling dates when examined individually. Classes one and two tended to have the highest soil moistures while classes three and four tended to have the lowest (Table 3). The highest monthly mean soil moisture was 28.1% (classes one and two during May 2000 and March 2001, respectively), and the lowest monthly mean soil moisture was 8.8% (class three during July 2000). Interestingly, a depression in CO_2 efflux rates occurred in all classes during July 2000 when soil moisture values were extremely low due to a period of prolonged drought.

The effect of measurement position on volumetric soil moisture was marginally significant ($P = 0.0858$) in the time series analysis. Mean volumetric soil moisture was lower at the near position during the entire investigation and was significantly ($P < 0.05$) lower on six of the 11 sampling dates when examined individually. Three of these dates occurred consecutively from July through September 2000. Soil moisture at the near position ranged from 11% lower during July 2000 to 2% lower during November 2000.

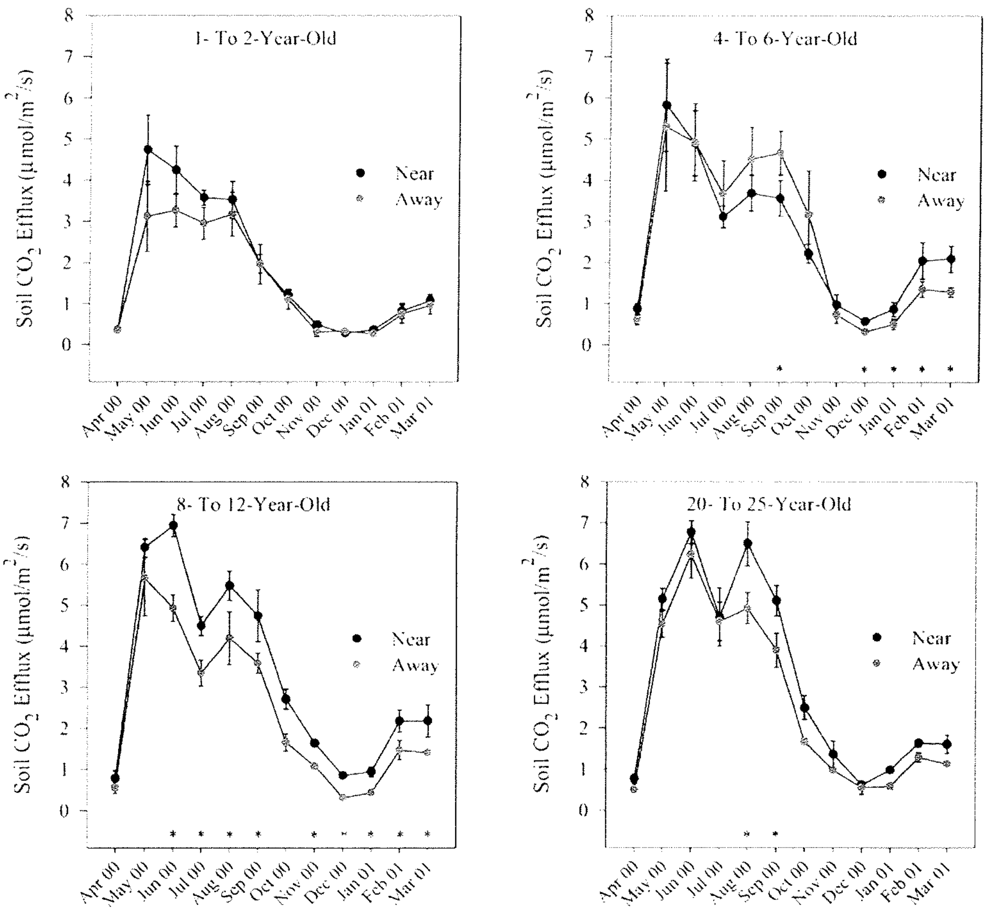

Fig. 2. Mean soil CO_2 efflux rates, by tree proximity, measured during monthly sampling periods in four age classes of plantation loblolly pine on the Virginia Piedmont. *Significant difference ($P < 0.05$) in mean efflux rates between near and away plots using SLICE option of PROC GLM. Error bars represent $\pm$ 1 S.E. ($n = 4$).

The interaction between stand age and measurement position was non-significant ($P = 0.4954$) in the time series analysis.

3.3. Regression analysis

Regression analyses revealed that soil temperature and soil moisture, along with stand age, tree proximity, and soil coarse fragments, explain a large percentage of the seasonal variability in soil CO_2 efflux rates (Table 4). Seven significant parameters were identified, explaining 55% of soil CO_2 efflux variation observed during the 12-month study. Soil temperature proved to be the most influential parameter tested for the data set. The most significant parameter in the model, explaining 23.2% of efflux variation, was the interaction term soil temperature × soilmoisture × stand age. Soil temperature alone was the second most significant parameter, explaining 14.0% of efflux variation.

The effects of stand age and soil temperature on soil CO_2 efflux are demonstrated by using the model to predict values for soil CO_2 efflux rate across a range of observed soil temperatures (Fig. 3). Holding all other variables in the model constant at mean values for the 12-month study period, predicted curves were computed for each stand age class. As soil temperature increases, predicted soil CO_2 efflux rate also increases; furthermore, at a given soil temperature, predicted efflux rate increases with increasing stand age.

Table 2
Mean soil temperature observed in four age classes of plantation loblolly pine on the Virginia Piedmont over a 12-month period from April 2000 to April 2001

Mean[a] soil temperature (°C) at 15 cm depth						
Measurement date	Stand age class				Position[b]	
	1	2	3	4	Near	Away
April 2000	10.5 ab[c]	10.8 a	10.0 b	10.1 ab	10.3 a	10.4 a
May 2000	22.5 a	21.9 a	18.5 b	17.8 b	20.1 a	20.2 a
June 2000	24.3 a	23.1 a	20.5 b	19.8 b	21.9 a	21.9 a
July 2000	27.2 a	26.9 a	22.5 b	21.5 b	24.6 a	24.5 a
August 2000	25.la	24.3 a	21.3 b	21.0 b	22.8 a	23.0 a
September 2000	16.8 a	17.5 a	16.4 a	16.5 a	16.8 a	16.7 a
October 2000	11.9 a	13.5 a	13.1 a	13.5 a	13.2 a	12.8 b
November 2000	5.2 c	7.1 b	8.2 a	9.0 a	7.4 a	7.3 a
December 2000	0.5 b	1.3 b	2.8 a	3.4 a	2.2 a	2.0 a
January 2001	1.8 c	3.4 b	4.5 ab	5.0 a	3.7 a	3.5 a
February 2001	7.3 a	7.9 a	7.5 a	7.6 a	7.7 a	7.5 a
March 2001	8.7 a	8.6 ab	7.9 bc	7.7 c	8.2 a	8.2 a
Overall mean	13.5	13.9	12.7	12.7	13.3	13.2

[a] Means for age classes based on $n = 8$. Means for positions based on $n = 16$.
[b] Position refers to at the tree base or 1.5 m away from the tree base.
[c] For age class and position, means within a month followed by the same letter are not significantly different at the 0.05 level using Tukey's HSD and the SLICE option, respectively.

Table 3
Mean volumetric soil moisture observed in four age classes of plantation loblolly pine on the Virginia Piedmont over a 12-month period from April 2000 to April 2001

Mean[a] soil moisture (vol.%) to 30 cm depth						
Measurement date	Stand age class				Position[b]	
	1	2	3	4	Near	Away
April 2000	NA[c]	NA	NA	NA	NA	NA
May 2000	28.1 a[d]	25.8 ab	21.3 c	22.3 bc	23.6 b	25.2 a
June 2000	25.1 a	22.8 ab	17.3 b	16.8 b	19.8 a	21.2 a
July 2000	18.0 a	15.2 ab	8.8 b	9.6 b	12.2 b	13.6 a
August 2000	18.6 a	16.7 a	11.8 a	11.7 a	14.1 b	15.3 a
September 2000	26.1 a	24.3 ab	21.4 b	21.2 b	22.4 b	24.1 a
October 2000	20.2 a	16.4 ab	9.7 c	10.3 bc	13.6 a	14.7 a
November 2000	24.4 a	20.5 ab	15.4 b	15.6 b	18.8 a	19.2 a
December 2000	22.1 a	23.3 a	20.0 a	20.5 a	20.8 a	22.2 a
January 2001	25.2 a	25.6 a	21.8 a	22.5 a	23.4 a	24.3 a
February 2001	26.8 a	27.3 a	23.1 a	21.9 a	24.0 b	25.6 a
March 2001	27.5 a	28.1 a	24.2 a	23.8 a	25.3 b	26.4 a
Overall mean	23.8	22.4	17.7	17.9	19.8	21.1

[a] Means for age classes based on $n = 8$. Means for positions based on $n = 16$.
[b] Position refers to at the tree base or 1.5 m away from the tree base.
[c] Measurements were not taken due to equipment malfunction.
[d] For age class and position, means within a month followed by the same letter are not significantly different at the 0.05 level using Tukey's HSD and the SLICE option, respectively.

Table 4
Significant parameters influencing mean annual soil CO_2 efflux rates in plantation loblolly pine on the Virginia Piedmont over a 12-month period from April 2000 to April 2001

Parameter	Parameter estimate	Partial R^2	F-value	$P > F$
Soil temperature × soil moisture × stand age (years)	0.000379	0.232	82.18	<0.0001
Soil temperature	0.446520	0.140	49.70	<0.0001
Soil moisture × stand age (years) × measurement position (near or away)[a]	−0.001330	0.049	17.33	<0.0001
(Soil temperature)^2	−0.006250	0.047	16.71	<0.0001
Natural log soil temperature	−0.731760	0.041	14.55	0.0001
Soil temperature × soil moisture x mineral coarse fragment mass	−0.000008	0.026	9.12	0.0026
Soil temperature × measurement position (near or away)	−0.017390	0.018	6.53	0.0108
Model R^2 = 0.553	Intercept = −0.05195		175.23	<0.0001

[a] Measurement position refers to at the tree base (1) or 1.5 m away (2) from the tree base.

Also, the magnitude of difference in efflux rates between stand age classes increases as soil temperature increases. The shape of the predicted efflux curves suggests that extremely high soil temperatures, which slow the respiratory function of soil microbes and plant roots, inhibit soil CO_2 efflux. Furthermore, high temperature inhibition of efflux is likely exacerbated by a concomitant decrease in soil moisture.

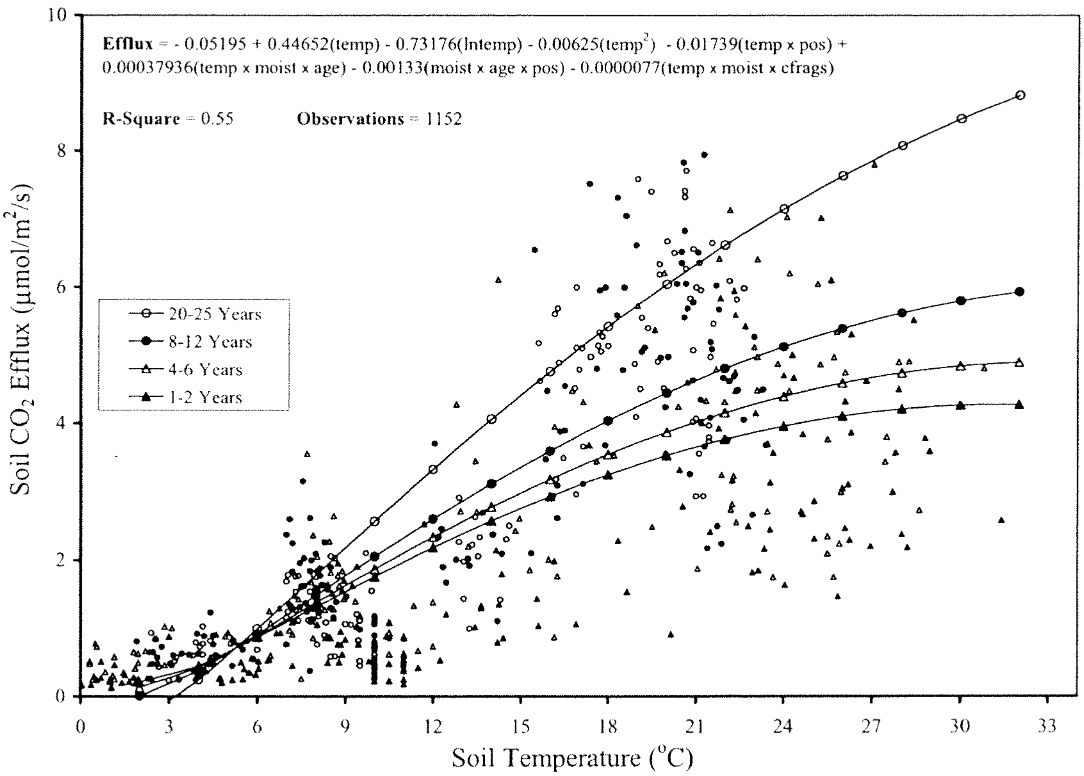

Fig. 3. Actual and predicted soil CO_2 efflux rates over a range of observed soil temperatures for four age classes of plantation loblolly pine on the Virginia Piedmont (n = 1152). Observations were collected from April 2000 to April 2001. Predicted rates were calculated using an empirical model and mean parameter values for the 12-month study. Soil temperature measured at 15 cm depth. Percent volumetric soil moisture measured at 30 cm depth. Soil coarse fragment mass measured in a 382 cm^3 soil core to 10.2 cm depth. Position refers to measurement either near (1) or 1.5 m away (2) from the tree base.

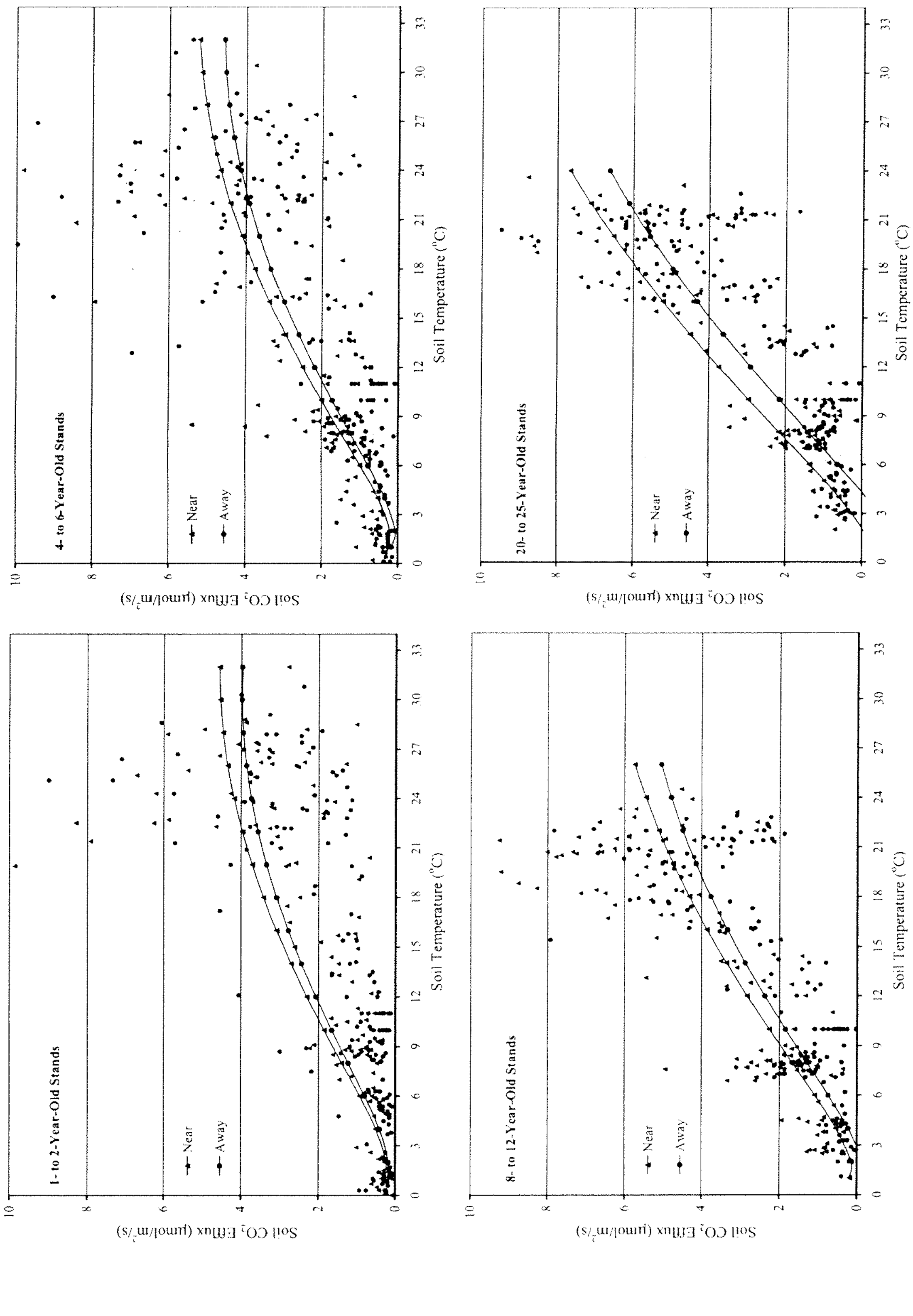

Fig. 4. Actual and predicted soil CO_2 efflux rates, by position, over a range of observed soil temperatures for four age classes of plantation loblolly pine on the Virginia Piedmont. Observations were collected from April 2000 to April 2001. Predicted rates were calculated using an empirical model and mean parameter values for the 12-month study. Measurement proximity refers to near (1) or away (2) from the tree base. For each age class, $n = 288$.

To demonstrate the effect of measurement position on soil CO_2 efflux rate, separate graphs were constructed for each age class using the model (Fig. 4). Predicted soil CO_2 efflux rates were computed across a range of expected temperatures while all other variables in the model were held constant. Within a given age class, separate curves were computed for the near and away measurement positions. For each class, soil CO_2 efflux rate increases as soil temperature increases. The divergent nature of the near and away position curves suggests two notable phenomena. Within a given class, the effect of position on soil CO_2 efflux rate increases as soil temperature increases. Also, this position effect appears to increase with stand age, i.e. the difference between the near and away position curves becomes stronger as stand age increases.

3.4. *Influence of soil, root, and environmental parameters on soil CO_2 efflux rates*

Pine root volume, as estimated from the intensive sampling of May 2001, significantly ($P = 0.0169$) differed among stand age classes (Fig. 5). Mean root volumes showed a clear ranking by age for the four classes, with root volume steadily increasing with stand age class. Measurement position had a marginally significant ($P = 0.0649$) effect on pine root volume, indicating a strong probability of greater root volume near than away from the tree. There was not a significant interaction between stand age and measurement position for root volume ($P = 0.6103$).

To investigate the relationship between soil/root parameters and soil CO_2 efflux of plantation loblolly pine, regression analyses were performed using data

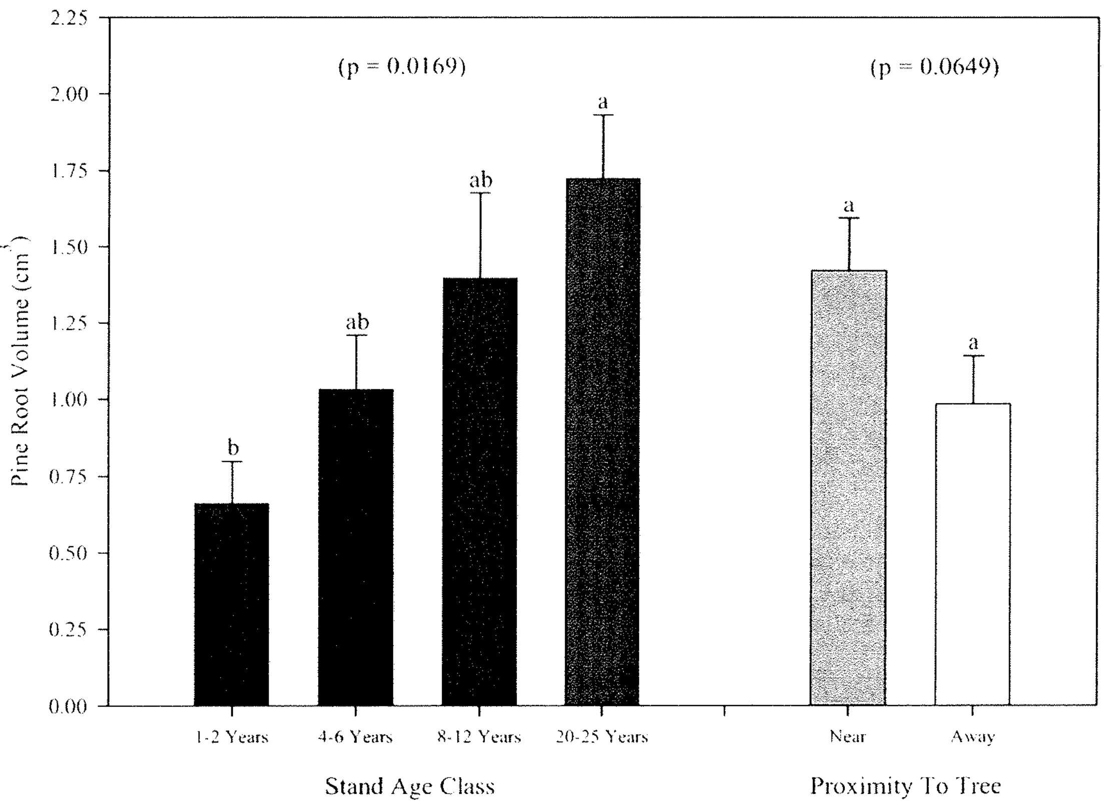

Fig. 5. Mean pine root volume collected in a 382 cm^3 soil core from the top 10.2 cm of the A horizon of four age classes of plantation loblolly pine on the Virginia Piedmont on 15 and 16 May 2001. Near and away means are overall means for the four age classes. P-values are stand age and position effects from ANOVA. Different letters within each category denote significant differences using Tukeys's HSD at $P = 0.05$. Error bars represent $\pm$ 1 S.E. ($n = 8$ for stand age; $n = 16$ for position).

Table 5
Significant parameters influencing mean soil CO_2 efflux rates in plantation loblolly pine on the Virginia Piedmont during intensive sampling on 15 and 16 May 2001

Parameter	Parameter estimate	Partial R^2	F-value	$P > F$
Soil temperature × soil moisture × stand age	0.003320	0.087	13.37	0.0004
Soil moisture × stand age (years)	−0.046640	0.077	11.77	0.0009
Soil carbon content	0.345650	0.064	9.75	0.0024
Soil temperature × soil moisture x measurement position (near or away)[a]	0.013310	0.053	8.07	0.0056
Soil moisture × measurement position (near or away)	−0.240910	0.050	7.73	0.0067
Root volume	0.329830	0.048	7.32	0.0082
Soil temperature × stand age (years)	−0.005430	0.031	4.78	0.0314
Natural log soil temperature	−6.615990	0.030	4.60	0.0347
Model R^2 = 0.439	Intercept = 20.12534		8.42	<0.0001

[a] Measurement position refers to at the tree base (1) or 1.5 m away (2) from the tree base.

collected during intensive sampling of May 2001. Parameters evaluated were soil temperature, soil moisture, stand age, mineral corrected litter mass, mineral corrected coarse woody debris mass, coarse mineral fragment mass, soil C content, soil N content, dry root mass, root length, root volume, average root diameter, root surface area, root surface area by diameter class, and root length by diameter class. Eight significant parameters were identified, explaining 44% of soil CO_2 efflux variation observed during the intensive sampling of May 2001 (Table 5). Due to the much narrower range in observations for the single sampling date, soil temperature did not explain as large a percentage of soil CO_2 efflux variation as in the full-year model. However, soil temperature was a significant ($P < 0.05$) parameter with a natural log transformation and in four interaction terms (20.1% total variation explanation). With exception of soil temperature and moisture, soil C content and total root volume were the only soil and root parameters measured in May 2001 that proved to be significant variables, explaining 6.4 and 4.8% of efflux variation, respectively.

4. Discussion

4.1. Stand age influence on soil CO_2 efflux

Based on our results, it is clear that soil CO_2 efflux increases with stand age for plantation loblolly pine on the Virginia Piedmont. Few studies have examined the effect of stand age on forest soil CO_2 efflux rates. Whereas the influence of stand maturation varies among studies, researchers generally agree that roots make a significant contribution to soil CO_2 efflux and that root biomass tends to increase with stand maturation. Ewel et al. (1987) found soil CO_2 efflux rates for a 29-year-old Florida slash pine plantation were 35% higher than the observed rates for a 9-year-old plantation. The investigators attributed the higher efflux rate to the nearly threefold increase in live root biomass observed in the older plantation. In Douglas-fir (*Pseudotsuga menziesii* Mirb.), soil CO_2 efflux rates from a 40-year-old stand were significantly lower than from both a 20-year-old stand and old growth stand during the growing season (Klopatek, 2002). Additionally, the 20-year-old stand and old-growth stand showed no consistent differences in soil CO_2 efflux rates. However, both young stands showed markedly less fine root growth than the old-growth stand. In hybrid spruce (*Picea glauca* × *Picea engelmannii*), comparisons among a mature stand and seven stands varying in age from 0 to 10 years showed similar cumulative belowground CO_2 fluxes for all stands during the growing season (Pypker and Fredeen, 2003). While belowground biomass was not measured, aboveground biomass increased significantly with stand age and the investigators asserted that proportional increases in belowground biomass were likely.

We cannot attribute increasing soil CO_2 efflux with stand maturation solely to the proliferation of pine roots due to our inability to partition efflux between root and microbial respiration. Our sampling design and procedures were not developed to measure the contribution of these components to total soil CO_2 efflux. Likewise, no sampling procedure was utilized to quantify microbial biomass. Based on a review of the literature, it is difficult to surmise whether microbial activity increases or decreases with stand maturation/succession. Lundgren (1982) noted that clear-cutting of a 120-year-old Scots pine (*Pinus sylvestris* L.) forest in Sweden initially resulted in increases in bacterial biomass, but by the third year, bacterial biomass had decreased to levels lower than the uncut control plots. Hendrickson et al. (1985) observed that microbial respiration was significantly lower during the first year following harvest of a mixed conifer and hardwood forest in Ontario despite the observation of increased bacterial populations in both the forest floor and mineral soil of harvested plots compared to controls. Apparently, the microbial response depends heavily on the level of disturbance of the forest floor, the intensity of the harvest, and the resultant effects on soil microclimate and organic matter inputs.

4.2. Spatial trends of soil CO_2 efflux

We also observed significant spatial heterogeneity in soil CO_2 efflux of plantation loblolly pine on the Virginia Piedmont and believe that roots exert significant influence on these spatial patterns. We were not surprised to discover spatial differences in soil CO_2 efflux in the younger loblolly pine stands. In previous research, Pangle and Seiler (2002) observed significantly greater soil CO_2 efflux rates near the base of 2-year-old loblolly pine seedlings in comparison to rates measured away from the seedlings. The researchers reported that fine root biomass beneath cuvette chambers was a significant variable in explaining the observed spatial variability in soil CO_2 efflux.

Our observation of sustained positional differences in soil CO_2 efflux in older loblolly pine stands was unexpected. We expected that fine root biomass would become increasingly homogeneous with stand maturation, thereby, diminishing positional differences in efflux. However, we found that a marginally significant positional difference existed in pine root volume regardless of stand age class. At rotational maturity, the contribution of fine root respiration to total root respiration is likely similar near the tree and away from the tree. However, total root respiration is likely greater near the tree due to the presence of the taproot and large lateral roots, which are absent away from the tree.

Several studies have demonstrated that a large proportion of total root biomass exists in the taproot and large lateral roots residing at the base of loblolly pines. Van Lear and Kapeluck (1995) investigated above- and below-stump biomass of a mature loblolly pine plantation in the upper Piedmont of South Carolina. The investigators observed that 75% of below-stump biomass was contained in the taproot and lateral roots larger than 2.5 cm in diameter. Intuitively, the majority of roots in this size class are located near the base of the tree. Wells et al. (1975) reported similar findings for a 16-year-old loblolly pine plantation on the North Carolina Piedmont. These investigators estimated that the taproot and lateral roots greater than 4 cm in diameter accounted for approximately 74% of total root biomass. While the radial distribution of fine root biomass may become homogeneous with stand maturity, clearly a large proportion of total root biomass remains concentrated near the stem of the tree. It is apparent from our research and the research cited above that a radial gradient in total root biomass likely persists at least through a typical timber management rotation.

4.3. Environmental and edaphic parameters influencing soil CO_2 efflux

In this study, soil temperature and moisture were the main drivers of seasonal variation in soil CO_2 efflux. Previous investigators have observed a strong relationship between soil temperature and soil respiration in managed pine plantations of various ages (Ewel et al., 1987; Maier and Kress, 2000). A positive correlation between soil temperature and instantaneous below-ground CO_2 flux was observed in hybrid spruce (*Picea glauca* × *Picea engelmannii*) stands of various ages in sub-boreal British Colombia, yet the relationship to soil moisture was much weaker (Pypker and Fredeen, 2003). The investigators attributed the weak relationship to the absence of moisture-limiting conditions during the study.

Soil C content, pine root volume, and coarse mineral fragment mass were significant variables in explaining observed variability in soil CO_2 efflux. The model derived from observations made during May

2001 predicts an increase in soil CO_2 efflux with an increase in either soil C content or pine root volume. Increasing soil C could be indicative of either an increase in microbial biomass or detrital substrate, both of which could result in increased microbial respiration. Likewise, an increase in root volume equates to a larger respiring biomass.

Soil coarse mineral fragment mass was a significant variable in the full-year model. According to the model, a decrease in soil CO_2 efflux is predicted with an increase in coarse mineral fragment mass at a given soil temperature and moisture. This is an important observation because a negative relationship has been reported between coarse mineral fragment content and soil CO_2 efflux in previous studies. A significant portion of the soil organic C with short turnover periods resides in the top 10–20 cm of the soil profile (Pietikainen et al., 1999; Jobbagy and Jackson, 2000; Trumbore, 2000). Our sampling of coarse mineral fragment mass was from the upper 10.2 cm of the A horizon. As coarse mineral fragment mass increases in this portion of the A horizon, available volume for water, soil organic matter, and roots is diminished (Rustad et al., 2000). With less water, fewer roots, and a smaller detrital substrate, soil CO_2 efflux is diminished. On an extremely rocky site (15–35% coarse fragments by volume) on the Virginia Piedmont, Pangle and Seiler (2002) found a significant negative relationship between coarse fragment content and soil CO_2 efflux for a 2-year-old loblolly pine plantation. Regression analysis showed that 21.7% of efflux variation could be explained by coarse fragment content alone.

5. Conclusion

Stand age has a significant, positive influence on soil CO_2 efflux of plantation loblolly pine on the Virginia Piedmont. Specifically, we observed that soil CO_2 efflux increases with stand maturation and can be attributed, in part, to increasing root biomass. We have also demonstrated that significant spatial patterns exist for soil CO_2 efflux of plantation loblolly pine on the Virginia Piedmont. Observed efflux rates were generally higher when measured near a tree than when measured a short distance away. We attributed this spatial difference in efflux to differences in root biomass. Specifically, we assert that a radial gradient in root biomass exists around a tree and expands outward through the upper soil horizon. Within this radial gradient, greater root biomass exists near the tree than away from the tree. Initially, this gradient is driven by the near absence of fine root biomass away from the seedling. As the tree matures, however, positional differences in fine root biomass likely diminish and greater taproot and lateral root biomass near the tree may drive the radial gradient. This radial gradient likely persists through time as evidenced by the observed trend of higher efflux rates near the tree across all stand age classes in this study.

Soil temperature, soil moisture, stand age, and measurement position are variables that explain a large percentage of the observed variation in soil CO_2 efflux for plantation loblolly pine on a seasonal and annual basis. Observations of these variables and other site parameters were utilized in developing empirical models for soil CO_2 efflux of plantation loblolly pine. Soil C content and root volume were found to exert a minor, but significant, influence on soil CO_2 efflux. Based on our observations, an increase in soil C or root volume results in an increase in soil CO_2 efflux.

This research demonstrates that future efforts to predict C losses from intensively managed loblolly pine plantations will have to give consideration to the spatial and temporal trends of soil CO_2 efflux. Empirical modeling has proven that we can accurately describe the spatial and temporal characteristics of soil CO_2 efflux and their interaction with specific environmental/site variables. Yet the limited predictive ability of our models also shows that there is more to be learned about soil CO_2 efflux and the parameters that influence it. Greater confidence in soil CO_2 efflux models will be gained as larger data sets are compiled across regions of varying productivity, soil type, climate, and management intensity.

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