

Soil CO₂ efflux in loblolly pine (*Pinus taeda* L.) plantations on the Virginia Piedmont and South Carolina Coastal Plain over a rotation-length chronosequence

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Abstract. We measured soil surface CO₂ efflux (F_s) in loblolly pine stands (*Pinus taeda* L.) located on the Virginia Piedmont (VA) and South Carolina Coastal Plain (SC) in efforts to assess the impact climate, productivity, and cultural practices have on F_s in the managed loblolly pine ecosystem. The effect of stand age on F_s was examined using a replicated chronosequence approach in which stands ranging from 1 to 25 years since planting were investigated. Soil CO₂ efflux was measured on both VA and SC sites for over a year using a closed dynamic system. Multiple linear regression was used to evaluate F_s correlates and examine the relationship between candidate explanatory variables and F_s . Soil temperature (top 10 cm) was the major correlate with F_s on both locations. We observed a positive age effect on F_s in VA stands and no relationship between age and F_s in SC stands. Annual soil C efflux declined with stand age in SC due to both reductions in soil temperatures as crown closure occurs and a diminishing heterotrophic C substrate pool. Annual estimated efflux ranges from 16.7 to 13.2 Mg C ha⁻¹ for 1 and 20-year-old stands, respectively. In contrast, annual soil C efflux increased with age in VA stands as a result of the positive relationship between stand age and F_s , which appears to be related to an increase in the contribution of root respiration to total F_s over time. In VA stands, efflux estimates range from 7.6 to 12.3 Mg C ha⁻¹ for 1 and 20-year-old stands, respectively. These results demonstrate the need to further consider the impact forest management and within-region variability have on soil C efflux over time when estimating C budgets.

Introduction

Intensively managed loblolly pine (*Pinus taeda* L.) stands comprise over 13 million hectares of forested land in the southeastern United States (Wear and Greis 2002) and represent a considerable carbon (C) store. However, the impact forest management has on belowground C dynamics across extensive spatial and temporal scales remains uncertain despite the fact that soils may

store over 70% of the total ecosystem C (Schlesinger and Andrews 2000). In loblolly pine forests, carbon accumulation and turnover in soils has been shown to be impacted by stand age, disturbance history, and soil properties (Richter et al. 1999). However, C efflux from managed loblolly pine forest soils has not been widely investigated despite a rapid increase in plantation management of these systems and forested ecosystems worldwide (FAO 2001; Wear and Greis 2002). Other evidence suggests that soil in intensively managed forests may sequester and store more soil C than natural forests, and that differences in belowground carbon sink capacity are related to soil C efflux (Valentini et al. 2000; Liski et al. 2002). Quantitative assessments of C fluxes will better define the role forest management has in altering terrestrial C dynamics.

Soil surface CO₂ efflux (F_s) or soil respiration includes respiration from roots (autotrophic respiration), and soil microorganisms (heterotrophic respiration). Carbon dioxide emissions from soils constitute a key source of CO₂ in terrestrial ecosystems and an important component of the global C cycle (Raich and Schlesinger 1992; Raich and Tufekcioglu 2000; Rustad et al. 2000; Schlesinger and Andrews 2000). The rate of F_s is affected by several environmental factors that are both inherent to a given site and may also be influenced by practices common to intensive loblolly pine management. To a large extent, temporal (i.e. seasonal) and spatial (i.e. latitudinal and intersite) variation in F_s and its components is driven by differences in soil temperature and moisture. Numerous studies have discussed the high correlation between F_s and temperature (e.g. Pajari 1995; Buchmann 2000; Maier and Kress 2000; Pangle and Seiler 2002). Low soil moisture also limits F_s in loblolly pine stands (Maier and Kress 2000; Pangle and Seiler 2002).

Researchers have cited a continued need for better understanding and quantifying the impact forest management has on F_s and soil C turnover over a range of stand ages (Woodwell et al. 1983; Turner et al. 1995; Field and Fung 1999; Banfield et al. 2002; Liski et al. 2002). Previous investigators observed an increase (Gordon et al. 1987; Lytle and Cronan 1998; Londo et al. 1999), decrease (Striegl and Wickland 1998), or no change (Edwards and Ross-Todd 1983; Fernandez et al. 1993; Toland and Zak 1994) in F_s rates following clear-cut harvesting. Differences among ecosystems and experimental designs may account for inconsistencies in the literature; however, the distinct differences found among investigators support the idea that generalizations across all forest types are not appropriate. Frequently, F_s and soil C turnover have been shown to increase with harvest intensity (Edwards and Ross-Todd 1983; Londo et al. 1999; Lee et al. 2002). Mallik and Hu (1997) showed that F_s corresponded to the amount of organic matter tilled into the soil during site preparation in boreal mixedwood forest. Further, prescribed burning, which is a common tool in loblolly pine management, may impact F_s by altering the quality and quantity of C substrate available to microorganisms and by changing the soil microclimate (Fritze et al. 1993; Pietikainen and Fritze 1993,

1995; Hernandez et al. 1997). Stand age may also impact F_s rates and therefore is an important consideration when developing C budgets for forest stands (Ewel et al. 1987a; Klopatek 2002; Pypker and Fredeen 2003).

Across the southeastern United States, loblolly pine is managed on sites varying in productivity, climate, and common cultural practices. Therefore, it is crucial to investigate multiple locations within the region over time in efforts to quantify F_s over the range of managed loblolly pine. We present an extensive examination of trends in F_s observed on Virginia Piedmont (VA) and the South Carolina Coastal Plain (SC) sites across a range of stand age classes. We also present expected trends in yearly soil C efflux for each study location over the course of a 20-year rotation. Finally, we discuss how within-region differences in loblolly pine forest management may impact F_s .

Materials and methods

Study sites

The SC Coastal Plain study sites were located approximately 40 km northwest of Charleston, SC in Berkeley County (33.18°N, 79.95°W) on managed industrial forestlands. Stands were even-aged and ranged in age from 1 to 24 years-old at the beginning of the study (Table 1). The average annual temperature in Berkeley County is 17.7 °C, with an average daily maximum of 28.2 °C and an average daily minimum of 9.89 °C. Average annual rainfall is 1250 mm. Flooding is relatively common; however, severe droughts frequently occur during the summer and fall seasons. Precipitation for the months coinciding with measurements was on average 15.5% lower than the 30-year average (SRCC 2003). Elevation ranges from 1.5 to 4.6 m above sea level with mild slopes of less than 2%. Inter-beds are frequently submerged during the

Table 1. Stand age, site index (base age 25 years), soils description, and common site preparation methods associated with SC Coastal Plain and VA Piedmont study plots

Location	Stand age (Years)	Site index ₂₅ (m)	Soils description	Site preparation
SC Coastal Plain	1, 1, 1, 1	24, 23, 18, 21	Deep, poorly drained,	Bedding
	5, 7, 6, 5	22, 22, 21, 20	acidic, low P, sandy to	
	9, 11, 13, 11	22, 21, 24, 21	sandy-loam derived	
	24, 20, 19, 20	20, 20, 20, 20	from marine sediment	
VA Piedmont	1, 1, 1, 1	14, 15, 15, 20	Deep, moderately	Chop and burn
	4, 4, 4, 4	19, 18, 16, 18	well-to well-drained,	
	8, 8, 8, 12	18, 19, 18, 18	loam to sandy-loam	
	21, 24, 25, 24	19, 18, 16, 18	derived from sedimentary bedrock	

Individual stand ages and corresponding site indexes are presented in sequence for each plot by age class in replication order. See text for more detailed site and soils description.

cooler, wetter winter months. Soil parent material is Wicomico or Penholoway backbarrier flats, former shoreline, or offshore deposits. Soils are deep to very deep, acidic, and low in phosphorus. Common soil series and taxonomic classifications are: (1) Coxville series: fine, kaolinitic, thermic Typic Paleaquults, (2) rains series: fine-loamy, siliceous, semiactive, thermic Typic Paleaquults, (3) Bonneau series: loamy, siliceous, thermic Arenic Paleudults, and (4) Lynchburg series: fine-loam, siliceous, semiactive, thermic Aeric Paleaquults. All sites were bedded prior to planting. Site indexes, which provide a measure of site productivity in terms of stand height for a given age, range from 20.0 to 22.3 m at 25 years for loblolly pine. The native forest cover type is a loblolly pine-hardwood mix. The degree of competing vegetation within a stand is highly variable. However, understory competition is generally minimal following crown closure. Common associated species include *Quercus marilandica*, *Acer rubrum*, *Sassafras albidum*, and *Liquidambar styraciflua* (MeadWestvaco Corporation, unpublished data).

The VA Piedmont sites were located on managed industrial forestland in Buckingham County, VA (37.34°N, 78.26°W). Stands were even-aged and ranged from 1 to 25 years of age at the beginning of the study (Table 1). Average annual precipitation for this region is 1070 mm. Precipitation during the measurement months on the VA sites averaged 9.0% lower than the 30-year average (SRCC 2003). Elevation ranges from approximately 40–55 m above sea level with broad ridges and moderate slopes ranging from 5 to 25%. The average annual temperature is 13 °C, with an average daily maximum of 23.9 °C and an average daily minimum of 2.0 °C. In general, soil parent material is derived from stratified, metasedimentary bedrock of the western Piedmont geologic formation. Soils are moderately well-drained to well-drained and deep. Major soil series and associated taxonomic descriptions found on the study sites include: (1) Cecil series: fine, kaolinitic, thermic Typic Kanhapludult (moderately well-drained), and (2) Appling series: fine, kaolinitic, thermic Typic Kanhapludult (well-drained). Site indexes range from 15.8 to 18.4 m at 25 years for loblolly pine. Site preparation prior to planting involved varying intensities of broadcast burning, chopping, and raking. As with SC sites, competing vegetation levels vary and understory vegetation is generally predominant only prior to crown closure. Common associated species include *Quercus alba*, *Nyssa sylvatica*, *Acer rubrum*, *Sassafras albidum*, and *Liquidambar styraciflua* (MeadWestvaco Corporation, unpublished data).

Study design

Four replications of four chronosequences were selected from each study location (SC and VA) from existing loblolly pine stands. The average stand age across replications was 1, 6, 11, 21 (SC) and 1, 4, 9, 24 (VA) years-old since planting at beginning of the data collection. A replicate included one stand from each age class. Stands comprising a replicate had similar soil and drainage

characteristics. This design allowed for the replication of four chronosequences on multiple soil types common to each location within the region. All stands within a replicate were in close proximity (<1 km) to each other. All stands were accessible via roads and measurements were taken at least three planting rows from the stand perimeter in efforts to avoid edge effects. Within each study plot, F_s , temperature, and moisture measurements described below were taken near the base of the tree and between rows (two measurement positions) in order to account for spatial variability within a loblolly pine stand as described by Pangle and Seiler (2002). Three sets of measurements, considered subsamples, were taken at each replication $\times$ age class $\times$ measurement position combination. Subsamples were averaged for analyses. Measurements began in April 2000 on the VA location and continued monthly through March 2001. Measurements in SC began in August 2001 and continued bimonthly through the following August. An additional SC measurement date in January 2003 was added in order to cover the range in temperature variability that is representative of the study location. A total of 96 measurements (on each parameter described below) were collected on a sampling date (4 replications $\times$ 4 age classes $\times$ 2 measurement positions $\times$ 3 subsamples). The resulting datasets for the SC and VA locations include 768 and 1152 soil CO_2 efflux measurements, respectively.

Soil CO_2 efflux measurements

Soil CO_2 efflux was measured using a LiCor 6200 (LiCor Inc., Lincoln, Nebraska) closed dynamic system with a LiCor 6250 infrared gas analyzer (IRGA) and a self-built chamber. The chamber allowed us to extensively monitor F_s across the landscape without disturbing or severing vegetation prior to sampling. The chamber was constructed from a 20.3 cm internal diameter PVC end cap assembled with a 1 cm thick foam gasket around the base to provide a seal with the ground. The chamber height at the center was approximately 10 cm. A single gas sampling port was located at the top of the chamber. Circulated air (coming from the IRGA) was redistributed evenly in the chamber through circular perforated plastic tubing that lined the top inner perimeter of the chamber. The internal chamber volume was 4105 cm^3 with an area of 368 cm^2 . Paired field F_s measurements taken with our self-built chamber and an automated open dynamic system described by Butnor et al. (2003) yielded similar results in a 1-year-old SC stand. Mean rates between systems differed by only 2.5% within an efflux range of $\sim 3\text{--}8 \mu\text{mol m}^{-2} \text{ s}^{-1}$.

The LiCor was calibrated to a CO_2 standard and zeroed prior to field measurements. Prior to measurements, the chamber was flushed with ambient atmospheric air close to the soil surface and then placed firmly on the ground to maintain a seal with the forest floor. After a steady rise in CO_2 concentration was observed (usually within 1 min), soil CO_2 efflux rates were determined by measuring CO_2 evolution over a 30 s period and calculating the respiration rate

per unit land area from the following equation:

$$F_s = [(\Delta C / \Delta t)(PV_t / RT)] / SA_s,$$

where C , $[CO_2]$; t , time; P , atmospheric pressure; V_t , system volume; R , universal gas constant; T , temperature; and SA_s , soil surface area. Measurements were taken on the surface of the forest floor where living plant material was not present. This was an effort to eliminate the measurement of CO_2 efflux from aboveground plant tissues and respiring senescent tissue.

Soil temperature and moisture measurements

Concurrent with F_s measurements, soil temperature at 10 cm was measured upon stabilization using a digital thermometer (model no. 8528-20, Cole-Parmer Instrument Co., Niles, Illinois). Volumetric soil moisture was determined to a depth of 10 cm using a time domain reflectometer (Soil Moisture Equipment Corporation, 6050X1, Golenia, CA).

Soil excavation

In SC, a cylindrical corer was used to extract a 0.0157 m^3 soil sample from beneath the measurement location on each measurement date in order to evaluate soil parameters after F_s , temperature, and moisture measurements were completed. The O horizon (L, F, H layers) was removed prior to the excavation of the mineral soil and associated roots to a 20 cm depth. No roots were apparent in the removed O layer. In VA, a 0.003814 m^3 soil sample was collected below the measurement area following F_s , temperature, and moisture measurements only on the last measurement date. Mineral soil and roots were excavated to a depth of 10 cm as described above.

Laboratory analyses

In efforts to examine trends in belowground root dynamics over the chronosequence, soils were sampled for root volume density and coarse woody debris (CWD) content. Soil samples were sieved through a 6.4 mm screen to separate soil from live roots and CWD. Visible fine roots that passed through the sieve were removed from the soil and added to the collection of live roots. No attempt was made to separate pine from non-pine roots. Live roots were scanned, digitized, and surface area and root volume were determined using the WinRhizo 5.0A software (Regent Instruments Inc., Quebec, Canada). Coarse woody debris (CWD) was oven-dried at 65°C for 48 h, weighed, and then ashed in a muffle furnace (Sybron/Thermolyne F-A1740, Debuque, IA) at

500 °C for 24 h. The ash weight was subtracted from the pre-ashed mass to correct for mineral content.

Assessing soil CO₂ efflux correlates

Multiple linear regression analyses were used to assess the relationship between F_s and candidate explanatory variables including soil temperature, soil moisture, stand age, site index, and measurement position. A linear regression approach was taken for three reasons. First, a linear regression approach allowed us to assess and compare the significance of explanatory variables and determine which variables explain the most variance in F_s across our sites. Second, using linear regression we were able to determine if the relationship between F_s and explanatory variables differed between sites by testing for statistical differences among coefficients. Lastly, we were able to use regression equations to examine trends in soil C efflux across stand ages (Schabenberger and Pierce 2002).

Regression analyses initially were performed using the SAS stepwise procedure (SAS Inst., Cary, NC) in order to identify the primary variables driving F_s across our sites. In the stepwise selection procedure, datasets for SC and VA sites were examined together and separately. Main effects, two-way, and three-way interaction terms initially were included in the stepwise model selection procedure. Standardized residuals and normality plots were examined and variable transformations were applied to minimize bias in models when appropriate. Parameter coefficients (i.e. slopes) calculated for SC and VA models were compared statistically using indicator variables to determine whether the relationship between F_s and explanatory variables differed between locations. All statistical analyses were performed using PROC REG and PROC GLM in SAS.

A seven-parameter model requiring 5 input variables explained the greatest amount of variance in F_s across both SC and VA sites when data from both study locations were combined ($R^2 = 0.60$). Note that the term ‘parameter’ includes the y -intercept. The model contains all of the five possible input variables including soil temperature, soil temperature, soil moisture, stand age, site index, and measurement position. The model form is as follows:

$$F_s = \beta_0 + \beta_1(T_s) + \beta_2(\ln[T_s]) + \beta_3[(\ln[A]) \times T_s] + \beta_4(P) + \beta_5(M_s) + \beta_6(A \times SI_{25}) + \varepsilon_i$$

where T_s is the soil temperature (°C) at 10 cm; A the stand age in years; P the measurement location (dummy variable where 1 = near the base of tree and 2 = between rows); M_s the soil moisture at 10 cm; SI_{25} the site index in meters at 25 years; and ε_i is the error associated with estimate of F_s . When SC and VA sites were modeled separately, slope comparisons revealed that the relationship between T_s , $[(\ln[A]) \times T_s]$, M_s and F_s differed between the two locations

Table 2. Model R^2 values, y-intercepts, and parameter coefficients associated with models developed for loblolly pine stands located on the SC Coastal Plain and the VA Piedmont

Model	Site	R^2	Parameters						
			Y-int.	T_s	$\ln(T_s)$	$\ln(A) \times T_s$	P	M_s	$A \times SI_{25}$
Seven-parameter	SC	0.54	1.48	0.320 ^{†*}	-0.655	-8.74E ^{-3*}	-0.875 [†]	-1.35E ^{-3*}	8.48E ⁻⁵
	VA	0.77	-0.934	0.166 ^{†*}	-0.281 [†]	0.0649 ^{†*}	-0.560 [†]	0.0833 ^{†*}	-5.14E ^{-5†}
Four-parameter	SC	0.50	0.341	0.324 [†]	-0.752	-6.75E ^{-3*}			
	VA	0.70	7.25E ⁻³	0.198 [†]	-0.432 [†]	0.0403 ^{†*}			

Coefficients are presented for the seven-parameter and the four-parameter models. Cruciform (†) indicates that the parameter is significant to the model ($p < 0.05$). Stars (*) indicate a significant difference between alike parameter coefficients (i.e. slopes) calculated for each location ($p < 0.05$). Y-intercepts were not evaluated statistically since we did not monitor efflux at or below 0 °C and therefore represent extrapolated value outside the range of data. Abbreviations: Y-int, y-intercept; T_s , soil temperature (°C); A , stand age in years; P , measurement location; M_s , soil moisture; SI_{25} , site index in meters at 25 years.

($p < 0.05$), indicating a need for location-specific models (Table 2). Separate modeling of each location improved the amount of variance in F_s explained on the VA Piedmont sites (R^2 VA = 0.77) and reduced the variance explained on the SC Coastal Plain (R^2 SC = 0.54).

We developed a simpler four-parameter model that reduced the number of input variables from five to two without greatly compromising the amount of variance in F_s explained. The model developed has the following form:

$$F_s = \beta_0 + \beta_1(T_s) + \beta_2(\ln[T_s]) + \beta_3[(\ln[A]) \times T_s] + \varepsilon_i$$

where symbols are identical to the seven-parameter model presented above. The four-parameter modeling results indicate that soil temperature and stand age alone explained 50 and 70% of the variance in F_s in the SC and VA stands, respectively.

Assessing annual soil C efflux trends across stand ages

Using regression models and meteorological data, we estimated annual soil C efflux for each stand age ranging from 1 to 20 years-old. This exercise allowed us to compare expected trends in soil C efflux over time on both the SC and VA study locations, and to relate these trends to site characteristics. However, our estimations are only representative of the sites, and the time period and conditions during which we measured soil CO₂ efflux. Interannual climate variability, stochastic weather events, changes in management, and other potential driving forces will alter the annual estimates. However, our analyses provide a reasonable ‘snapshot’ of soil C efflux across stand ages within the range of conditions we monitored.

Soil CO₂ efflux was scaled up using the simpler, four-parameter model developed for each study location, which requires soil temperature and stand

age inputs. Since we did not continuously monitor soil temperature on our study sites, we developed regression models for each study location in an effort to predict soil temperature based on air temperature and stand age. To do this, we acquired daily air temperature averages from onsite meteorological stations. Daily temperature averages were regressed against average soil temperature data collected from study sites on the same measurement date. Since canopy cover moderates soil temperature, stand age was also included in the model. Air temperature and stand age explained 94 and 95% of the variability in soil temperature at 10 cm in the SC and VA study sites, respectively. The following common model allowed us to estimate soil temperatures for both measurement locations within the region across the range of air temperatures and stand ages examined in the current study:

$$\text{South Carolina : } T_s = -0.153 + 1.04T_a + 0.196A - 0.103(T_a * \ln A) + \varepsilon_i$$

$$\text{Virginia : } T_s = 1.58 + 0.988T_a + 0.0784A - 0.0812(T_a * \ln A) + \varepsilon_i$$

where T_s is the estimated soil temperature at 10 cm, T_a the average daily air temperature, and A is the stand age.

In order to scale up soil C efflux to the stand level, we obtained daily temperature averages from onsite meteorological stations corresponding to the time period during which we measured F_s . Using the above location-specific regression equations, air temperature and stand age inputs were used to estimate average daily soil temperature at 10 cm for stands ranging from 1 to 20 years-old. Daily soil temperature estimates for each location were then input into the location-specific four-parameter F_s model along with stand age to estimate average daily F_s rates for stand ages 1–20 years. To obtain year-long soil C efflux estimates for each stand age, daily F_s was summed over each 1-year stand age increment. Efflux estimates were expressed in terms of grams of C rather than CO_2 .

Results

Ranges in soil CO_2 efflux, soil temperature, and soil moisture

Soil CO_2 efflux rates on the SC Coastal Plain ranged from a mean high of $8.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ in 1-year-old stands on the August 2001 measurement date to a mean low of $1.1 \mu\text{mol m}^{-2} \text{s}^{-1}$ in 1-year-old stands on the January 2003 measurement date (Figure 1). On the VA Piedmont, F_s ranged from an average high of $6.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the 24-year-old age class on the June 2000 measurement date to a low of $0.31 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the 1-year-old stands on the December 2001 measurement date. Soil CO_2 efflux rates generally paralleled soil temperature values, which ranged from 6.0 to 28.3 °C in 1-year-old SC stands and 0.5 to 27.3 °C in 1-year-old VA stands. The range in observed soil temperatures covers the average range in air temperature for

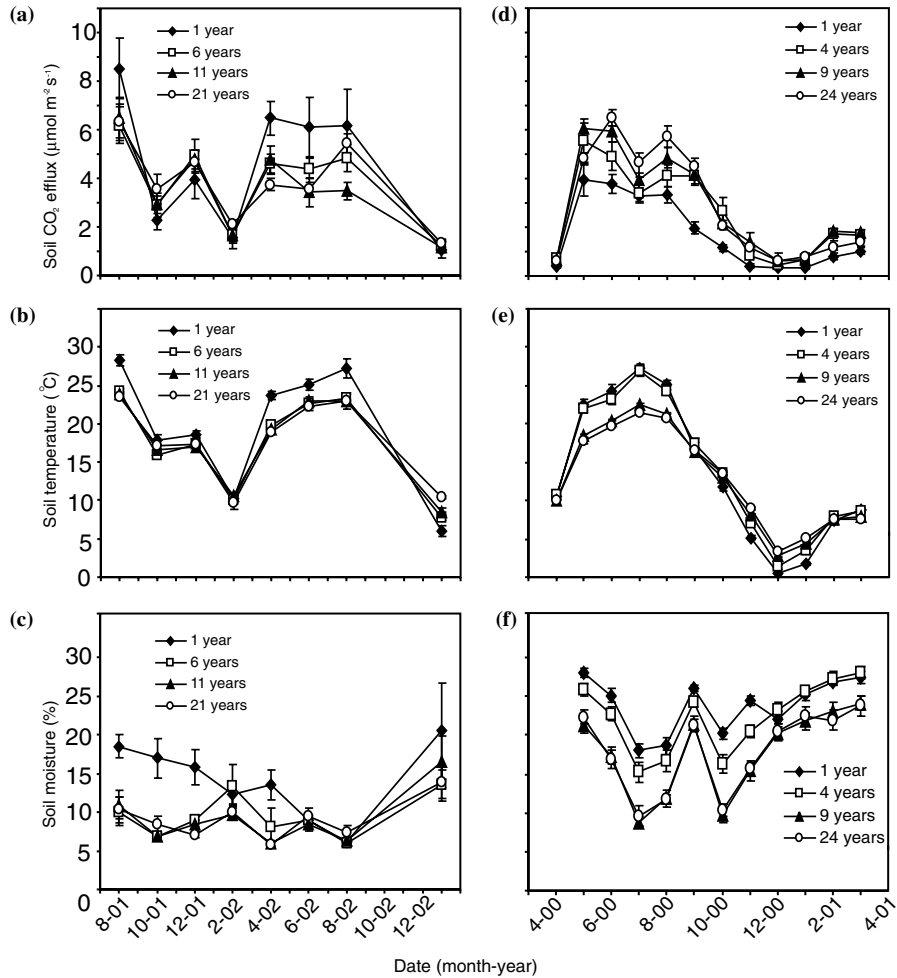


Figure 1. Mean soil surface CO₂ efflux rates (a,d), soil temperatures (top 10 cm; b,e), and soil moistures (top 10 cm; c,f) of loblolly pine stands during measurement days on the SC Coastal Plain (a–c) and the VA Piedmont (d–f). Means are presented for each age class investigated. Bars associated with means illustrate one standard error.

both locations, demonstrating that our measurements captured a range of soil temperature conditions that are typical of each location. Mean soil moisture at 10 cm ranged from 5.8% volumetric water content in the 21-year-old age class to 20.5% water in 1-year-old SC stands. In contrast, volumetric water content was a low of 8.8% in 9-year-old stands to 28.1% in 1-year-old stands in VA.

Soil CO₂ efflux correlates

In the seven-parameter model, only T_s and P were significantly related to F_s on SC Coastal Plain sites ($p < 0.05$), explaining 49 and 3.8% of the variance in F_s , respectively (Table 2). Soil surface CO₂ efflux in SC was positively correlated with T_s . The negative relationship between P and F_s indicates that efflux rates were greater near the base of trees compared with rates between rows. We did not discard the non-significant variables from the common model since all parameters were highly significant in explaining variance in F_s on the VA Piedmont location ($p < 0.05$) and we wished to compare how relationships differed between SC and VA sites. However, non-significant parameter coefficients should be interpreted with caution since they do not express a statistically meaningful relationship with F_s . In contrast, on the VA sites where all model parameters explained a significant amount of variance in F_s ($p < 0.05$), partial R^2 values for each parameter were $T_s = 59.3\%$, $\ln[T_s] = 0.28\%$, $[(\ln[A]) \times T_s] = 11.9\%$, $P = 1.78\%$, $M_s = 3.05\%$, $A \times SI_{25} = 0.80\%$. Once again, parameter coefficients imply a positive relationship between F_s and temperature and higher efflux rates near the base of trees. Note that the negative sign associated with the $\ln[T_s]$ coefficient is responsible for the mild curvilinear relationship between F_s and temperature (Figure 2), but does not negate the overall positive relationship between the variables within the range of temperatures we observed. Additionally, the positive $[(\ln[A]) \times T_s]$ term implies that the F_s response to temperature is increasingly greater with stand age. Soil moisture (M_s) had a positive impact on F_s and site index was negatively related to F_s with increasing stand ages ($A \times SI_{25}$) in VA plots. In the four-parameter model, T_s explained the greatest variance in F_s on both locations. All parameters explained a significant amount of variance in F_s on the VA sites ($p < 0.05$) and had similar partial R^2 -values and relationships with F_s as in the seven-parameter model. Only T_s was significant in explaining variance in SC stands however.

Trend lines generated for the SC and VA locations using the four-parameter model illustrate the distinctly different relationship between stand age and F_s across temperatures observed on the two locations (Figure 2). On the SC Coastal Plain, the effect of age on F_s was not significant or apparent when plotted. In contrast, there was a positive relationship between stand age and F_s on VA sites. Overall, F_s rates across soil temperatures were higher on the SC Coastal Plain relative to the VA Piedmont, except in the oldest age class.

Root volume and CWD densities

We hypothesized that changes in F_s over a rotation might be due to variation over time in respiring root volume and C substrate available to microbes. Although we are unable to make direct comparisons between measurement

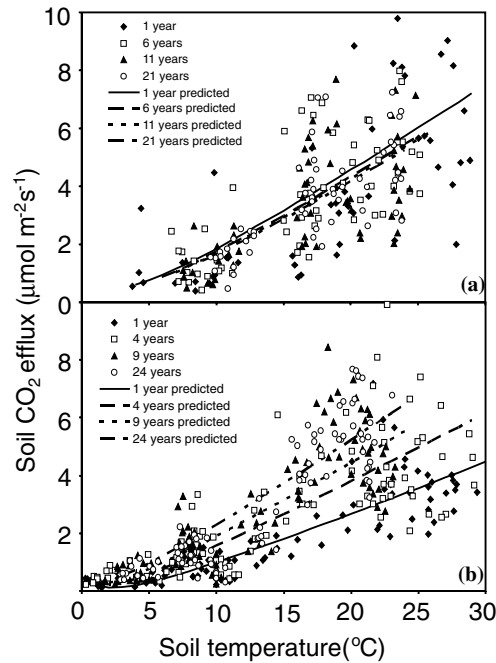


Figure 2. Relationship between soil temperature (10 cm depth) and soil CO₂ efflux in four age classes of loblolly pine stands located on the SC Coastal Plain (a) and the VA Piedmont (b). Trend lines were generated for each age class using the four-parameter linear regression model, which requires soil temperature and stand age inputs.

locations due to different sampling depths at each location, we wished to observe qualitative trends across stand ages in SC and VA. In a survey of root volume and CWD below F_s measurement locations, mean root volume density, although highly variable, increased with age in both the SC and VA soils sampled (Figure 3). Conversely, mean CWD density in the mineral soil fell with increasing stand age on the SC Coastal Plain and the VA Piedmont sites sampled.

Annual soil C efflux trends across stand ages

Using the four-parameter model and soil temperature estimates for each site location, we estimated annual C fluxes for stands ranging in age from 1 to 20 years-old. Two distinctly different trends across stand ages are apparent for the two study locations (Figure 4). On the SC Coastal Plain, soil C efflux was greatest in young stands, followed by a decline and a steadier trend in soil C efflux from age 8–20 years. In contrast, VA Piedmont stands show a trend of increasing annual soil C efflux as stands age. As stand age increases, annual soil

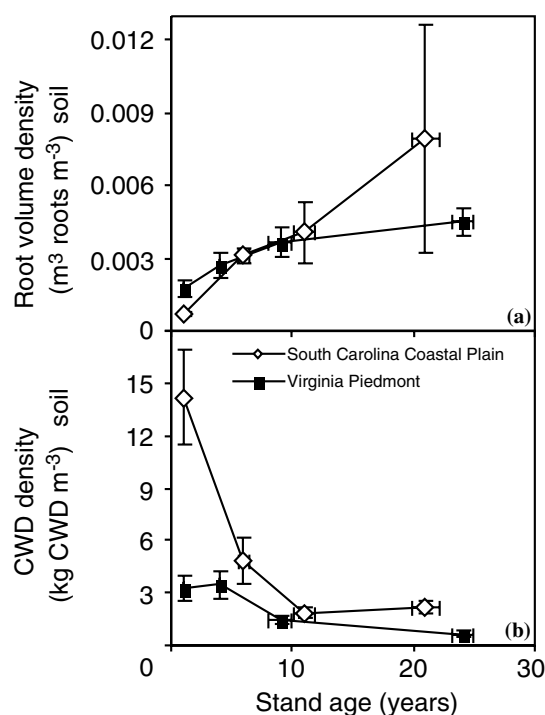


Figure 3. Mean root volume density and mean CWD density in the mineral soil of loblolly pine stands on the SC Coastal Plain and the VA Piedmont for each age class investigated. A mineral soil core was taken in the top 20 cm on the SC Coastal Plain and top 10.2 cm on the VA Piedmont. Densities shown were calculated for the soil depths sampled at each location. Bars illustrate one standard error from the mean.

C efflux from the SC and VA sites nearly converges. Soil C efflux estimates in 1-year-old SC stands were $16.7 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ compared to an estimated annual rate of $7.6 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ for VA Piedmont sites. In 10-year-old stands, an estimated 12.9 and $11.0 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ are respired from soils in SC and VA stands, respectively. In 20 year-old stands, C efflux was most comparable between the two locations with an estimated flux of 13.2 and $12.3 \text{ Mg C ha}^{-1}$ from the soil in SC and VA stands, respectively.

Discussion

Soil CO₂ efflux correlates

Regression modeling results indicate that soil temperature explains the greatest fraction of variance in F_s across each location within the region (Table 2), which is consistent with previous findings (Pajari 1995; Buchmann 2000; Maier and Kress 2000; Pangle and Seiler 2002). Soil surface CO₂ efflux was consis-

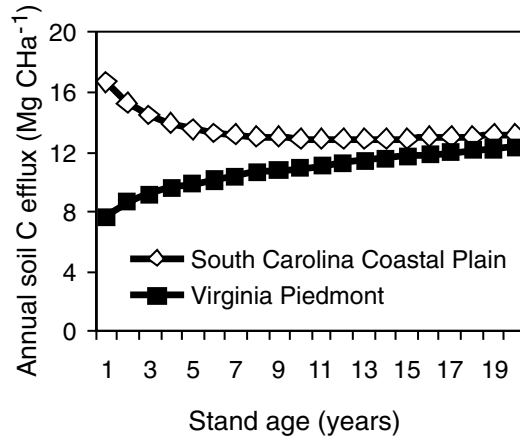


Figure 4. Annual trends in soil surface C efflux across loblolly pine stands ranging in age from 1 to 20 years-old. Trends are presented for SC Coastal Plain and VA Piedmont sites. Estimates were derived by scaling up chamber-based measurements using a four-parameter regression model requiring soil temperature and stand age inputs. Soil temperature inputs were estimated using air temperature data collected from onsite meteorological stations.

tently higher adjacent to trees in comparison to measurements taken between rows. Pangle and Seiler (2002) attributed higher rates near the base of a tree to respiring root biomass in recently planted loblolly pine stands. We found no significant interaction between stand age and position indicating a similar spatial trend in F_s exists in older stands as well as recently planted stands.

Other variables, including soil moisture, site index, and stand age were significantly related to F_s on the VA Piedmont, but not on the SC Coastal Plain. Soil moisture has been repeatedly shown to impact F_s , especially under extreme flooding or drought (Maier and Kress 2000; Pangle and Seiler 2002). While we observed a narrower range in mean volumetric moisture contents across measurement days on the SC Coastal Plain in comparison to VA, we observed individual volumetric moisture contents ranging from 2 to 69% in SC compared with a range from 2 to 35% in VA. Soil moisture was generally more variable on the SC sites, especially in 1-year-old bedded stands in which microtopography highly influenced soil water content. Despite the fact that soil moisture was not autocorrelated with temperature, we did not detect a relationship between F_s and soil moisture on the SC sites, suggesting that soil water status was not a major correlate with F_s over the range of soil moistures we recorded. Site index only slightly explained variance in F_s on the VA Piedmont ($A \times SI_{25}$; partial $R^2 = 0.008$) despite evidence that faster growing stands have greater respiring root biomass at an earlier age (Ewel et al. 1987b). However, we may not have captured an adequate range of site indexes within a given age class on each study location, which would prevent us from detecting a strong stand age by site index interaction.

Within-region differences in soil CO₂ efflux

Cultural practices on the Coastal Plain and Piedmont differ considerably, which likely provides some explanation for the inconsistent age effect we observed between the two locations. Generally, F_s and C turnover increase as management intensity and soil disturbances increase (Edwards and Ross-Todd 1983; Londo et al. 1999; Lee et al. 2002). For example, the intensity of site preparation and the amount of organic matter incorporated into the soil have been shown to affect F_s (Ewel et al. 1987a; Mallik and Hu 1997). Bedding, which was performed on our SC Coastal Plain sites prior to planting, incorporates slash into the soil and severely tills the mineral soil, disrupting soil structure. Bedding may have created a more favorable microenvironment for soil heterotrophs in part by providing accessible C substrate (Trumbore et al. 1996; Progar et al. 2000; Wang et al. 2002).

Our results indicate that the contribution of microbial respiration to total F_s is greater in young SC stands. Specifically, F_s was higher on SC sites relative to VA sites across temperatures in 1-year-old stands. The difference in F_s across soil temperatures between the two locations must primarily be the result of a greater contribution of microbial respiration in SC stands since residual pine roots from the previous rotation were not likely respiring and because live root biomass is at a minimum in young pine stands (Ewel et al. 1987b; Hogberg et al. 2001). Further, we found evidence that CWD incorporated into beds during site preparation is subjected to microbial decomposition early in the rotation since CWD density sharply declined with stand age on the SC sites. In contrast, the amount of F_s attributable to root respiration likely increases over time (Ewel et al. 1987b), which is consistent with the increase in root biomass we observed with stand age. Therefore, it is likely that inverse shifts in contributions from root respiration and microbial respiration resulted in no detectable change in F_s across stand ages in the SC stands. Our results are similar to those of previous authors who concluded that increases in microbial respiration following clear-cutting were offset by reductions in root respiration, resulting in no detectable difference in F_s between recently cut and intact stands (Edwards and Ross-Todd 1983; Toland and Zak 1994).

The strong positive relationship between F_s and stand age in VA was most likely the combined result of both a less intensive mineral soil disturbance and the use of burning during site preparation. Growth of respiring root biomass and recovering microbial populations impacted by burning may account for the positive trend in F_s we observed in VA stands with age (Ewel et al. 1987b; Chang et al. 1995; Litton et al. 2003). Investigators have shown that burning reduces microbial respiration in European coniferous forests by changing soil physical and chemical properties, by reducing C substrate availability, and also through surface sterilization (Fritze et al. 1993; Pietikainen and Fritze 1993, 1995; Hernandez et al. 1997). Further, the contribution of microbial respiration to F_s may be less in young VA stands relative to SC sites since the

mineral soil was less disturbed during site preparation. Relatively minor changes in CWD density across stand ages in VA stands is likely due to site preparation typical in the Piedmont region, which does not involve the incorporation of residual organic matter into the mineral soil. While CWD densities are not directly comparable between the two locations due to the fact that we sampled to a shallower depth in VA, we expect that deeper sampling would reduce our CWD density values for VA since total C tends to decrease with depth (Jobaggy and Jackson 2000) and because no tillage occurred during site preparation. Mean root volume density values for each location are less comparable due to the difference in sampling depth and because rooting depths may differ between locations. Rooting depths of pines vary according to genetics and the soil environment (Eisenstat and Van Rees 1994).

The distinct difference in the amount of variance in F_s explained on the SC and VA sites may be due to more intensive site preparation on the SC Coastal Plain, which appeared to result in high site heterogeneity relative to the VA Piedmont location. Further, variability in F_s decreased with increasing stand age, implying that high heterogeneity due to site disturbance diminishes over time. The coefficient of variation (CV) was highest in the SC 1-year-old age class with a value of 52.2% and lowest in the 21-year-old age class, which had a CV of 33.4%. In comparison, the 1- and 24-year-old VA age classes had CV values of 47.4 and 33.4%, respectively. Bedding on SC sites may have encouraged pockets of high microbial respiration in young stands. Localized pockets of high microbial activity might explain why we observed the highest variance in F_s across temperatures in 1-year-old stands. Again, previous reports attribute high site disturbance to a rise in F_s (Edwards and Ross-Todd 1983; Londo et al. 1999; Lee et al. 2002).

Annual soil C efflux trends across stand ages

Differences in annual C efflux estimates are due to the variable effect of age on F_s described in detail above and in response to the changing relationship between stand age and soil temperature. Soil temperature was most variable in young stands, especially prior to crown closure, since less foliage is present to moderate soil temperatures. In SC, high annual soil C efflux in young stands was directly related to greater soil temperatures early in the rotation since we observed no effect due to stand age. In VA, where F_s was positively related to stand age, changes in soil temperature with stand age dampened the strong effect of age on estimated annual C efflux rates, explaining why annual C efflux values do not simply parallel the relationship between F_s and stand age shown in Figure 2. Gordon et al. (1987) attributed increases in F_s following a clear-cut in Alaska white spruce (*Picea glauca* Voss) forests mainly to higher soil temperatures, which supports our findings that changes in soil temperature associated with crown cover strongly influence annual estimates of soil C efflux.

Our findings suggest that forest management (e.g. bedding) and/or inherent site characteristics exert a considerable and lasting influence on the rate of C efflux from the soil and directly impact the relationship between soil C efflux and stand age. Litton et al. (2003) determined that fire disturbance and stand density altered both heterotrophic and autotrophic components of soil C efflux in lodgepole pine (*Pinus contorta* Dougl.) stands, which directly affected the relationship between soil C efflux and stand age. While Litton and coworkers observed a positive relationship between stand age and annual soil C efflux, most previous studies conducted in coniferous forests do not report a consistent trend in annual soil C efflux with increasing stand age (Ewel et al. 1987a; Irvine and Law 2002; Klopatek 2002; Pypker and Fredeen 2003). Further, there is no definitive consensus among reports in the literature relating changes in soil C efflux across stand age to abiotic or biotic soil processes. Concurrent monitoring of both root and microbial dynamics across extensive spatial and temporal scales is necessary to provide a more complete assessment of the processes responsible for trends in soil C efflux as forests age.

Annual estimates of soil C efflux reported in the current study are among the highest for North American coniferous forests, ranging from 7.6 to 16.7 Mg C ha⁻¹ yr⁻¹. Ewel et al. (1987a) reported the highest values for soil C efflux expressed in the literature to our knowledge, ranging from 8.2 to 22.7 Mg C ha⁻¹ yr⁻¹ in Florida slash pine (*Pinus elliotii* Englem.) stands. Maier and Kress (2000) determined that annual C efflux from a North Carolina loblolly pine site located in the Sandhills was 14.1 Mg C ha⁻¹ yr⁻¹, which is close to our estimated annual efflux of 12.9 Mg C ha⁻¹ yr⁻¹ from 11-year-old SC Coastal Plain stands. Other investigators report annual stand-level efflux rates ranging from 5.60 to 8.61 Mg C ha⁻¹ yr⁻¹ for hybrid spruce (*Picea glauca* × *engelmannii*) (Pypker and Fredeen 2003), 8.83 to 13.67 Mg C ha⁻¹ yr⁻¹ for Douglas-fir (*Pseudotsuga menziesii* Franco) (Klopatek 2002), 4.0 to 6.83 Mg C ha⁻¹ yr⁻¹ for ponderosa pine (*Pinus ponderosa* Dougl.) (Conant et al. 1998; Law et al. 1999; Irvine and Law 2002), 3.31 to 5.41 Mg C ha⁻¹ yr⁻¹ for red pine (*Pinus resinosa* Ait.) (Haynes and Gower 1995), and 1.56 to 4.60 Mg C ha⁻¹ yr⁻¹ for lodgepole pine (Litton et al. 2003).

While regional differences exist in annual soil C efflux largely due to distinct differences in climate and species composition (Raich and Schlesinger 1992), our results show that annual soil C efflux within the region varies considerably over time. The large differences in annual soil C efflux between SC and VA stands exemplify the need to include within-region trends in soil C efflux over time when estimating net ecosystem productivity (NEP) with ecophysiological data. Differences in annual soil C efflux between SC and VA are especially important to consider early in the rotation when microbial-mediated turnover of soil C is comparatively high and annual biomass-C increment is relatively low (Valentine 1999). Estimated annual efflux is 9.1 and 0.9 Mg C ha⁻¹ yr⁻¹ greater in 1 and 20 year-old SC stands, respectively, in comparison to VA stands of the same age. The considerable difference in early-rotation soil C

efflux from the two locations will have a profound influence on NEP calculated in part from gas fluxes by impacting the estimated time that a stand transitions from a C source to a sink and further by affecting integrated C storage estimates over the entire rotation.

Conclusions

We have shown that forest management practices along with inherent site and climate differences within a region have a considerable impact on temporal patterns of F_s and annual soil C efflux across stand ages. Our results agree with previous reports that cultural practices influence F_s (e.g. Lytle and Cronan 1998; Londo et al. 1999). With plantation forestry increasing in area worldwide by 31% from 1990 to 2000 and opposite trends occurring in natural forests (FAO 2001), the impact that management has on C sequestration is becoming increasingly relevant to global estimates of terrestrial C storage. The rise in managed forests has prompted several investigators to emphasize the need for continued study in managed systems (Field and Fung 1999; Richter et al. 1999; Valentini et al. 2000). Long-term investigations in managed forests remain a priority since a limited number of studies exist in these systems and mechanisms influencing changes in C cycling processes over time have not been thoroughly defined. Specifically, uncertainties regarding belowground shifts in autotrophic and heterotrophic processes over time reveal the need for integrated studies that monitor both source components of soil CO₂ simultaneously across a range of management intensities. Addressing the impact cultural practices have on C cycling and storage will remain essential in efforts to identify specific forest management practices that enhance or deplete C stores relative to less disturbed natural systems (Field and Fung 1999; Valentini et al. 2000).

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