TEMPORAL AND SPATIAL PATTERNS OF SOIL CO_2 EFFLUX, SOIL CARBON, AND ROOT BIOMASS ASSOCIATED WITH BEDDING IN YOUNG LOBLOLLY PINE PLANTATIONS

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Abstract—We measured soil CO_2 efflux (Fs) in four loblolly pine plantations in the coastal plain of South Carolina in an effort to understand how site preparation, drainage, and microclimate affect Fs, root biomass, and soil carbon pools during early stand development. All plantations were site prepared: sheared, raked, and bedded. Soil CO_2 efflux, temperature (Ts), moisture (θ), root biomass (Rb), coarse (COF) and fine (FOF) organic fragments, and mineral soil carbon (Cs) were measured quarterly during the first two years of stand growth. Mean daily Fs were similar between sites and ranged from 0.5 to 12 mmol m^{-2} s^{-1} during the winter and summer, respectively. Soil CO_2 efflux, COF, FOF, and Cs were significantly greater in the beds than inter-rows on wet sites, but not on the dry site. Soil temperature accounted for 26-55 percent of the variation in Fs across all sites. Soil θ and Cs explained a significant, but small amount (6-22 percent) of variance in Fs. Annual soil carbon efflux ranged from 12 to19 Mg C ha^{-1} yr^{-1}. We conclude that bedding during site preparation can have significant effects on the spatial variation in Fs and associated drivers, with some site-specific caveats.

INTRODUCTION

Managed pine plantations in the Southeastern United States play a prominent role in the regional and global carbon cycle (Turner and others 1995). Net ecosystem productivity (NEP), a measure of carbon sequestration, reflects the change in carbon stored in vegetation and soil and is the small difference between carbon uptake in photosynthesis and loss through autotrophic and heterotrophic respiration (Chapin and others 2002). Intensively managed pine plantations have the potential to increase NEP by increasing net primary productivity (NPP; Maier and others 2004). However, factors regulating the soil carbon cycle, i.e. soil carbon inputs, transformations, and decomposition may be more important for determining NEP (Janssens and others 2001, Valentini and others 2000). Regenerating pine plantations are a net carbon source (-NEP) immediately after harvest because heterotrophic respiration exceeds NPP. The recovery time for a new plantation to become a net carbon sink (+NEP) will differ with site and depends on the degree of soil disturbance during site preparation (e.g. burning, disking, and bedding), site fertility, and NPP of the regenerating stand (Sampson and others 2008).

Soil CO_2 efflux (Fs) is comprised of autotrophic (root and associated fungi) and heterotrophic (microbial decomposition of soil organic matter) respiration (Hanson and others 2000). Soil temperature and moisture greatly influence the component processes of Fs (see Hanson and others 2000 and references therein); however, following a disturbance such as harvesting and site preparation, soil organic matter and nitrogen content are important factors regulating F_s (Rustad and others 2000). Soils in the Coastal Plain of the Southeastern United States are some of the most productive sites for intensive pine management (Allen and Campbell 1988). These soils are often carbon and nutrient rich and have the potential for significant releases of carbon when disturbed. A common management practice is whole-tree harvesting followed by intensive site preparation that includes stump shearing, raking, and bedding. Bedding mixes surface organic layers into the mineral soil, enriches soil carbon and nutrients, increases soil aeration, and improves drainage (Haines and others 1975, McLaughlin and others 2000, Trettin and others 1996). This heavy soil disturbance can increase decomposition and Fs (Ewel and others 1987a, Mallik and Hu 1997) potentially leading to a net loss in soil carbon (Henderson 1995).

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Quantifying the effects of site preparation on the carbon dynamics during early stand growth is fundamental to understanding both the carbon cycle and the role of intensive management in sequestering carbon.

We examine the spatial and temporal variation in Fs in loblolly pine (*Pinus taeda* L.) plantations during the first two years of stand growth. Ancillary measurements of soil temperature, moisture, organic matter, and root biomass were made to determine their importance in explaining variability in Fs. Plantations were growing on four soil types that differed in drainage class. All sites received standard site preparation protocols that included bedding. Our objectives were to 1) measure the temporal and spatial variability in Fs, 2) develop empirical models of Fs based on site-specific factors, and 3) estimate annual soil carbon efflux.

MATERIAL AND METHODS

Study Sites

The study took place on commercial forestlands in the upper Coastal Plain of South Carolina, USA. Measurements were made on four sites: Andrews (A), Camphall (C), Oswald (O), and Watson Hill (W). The sites differed in soil type, drainage class, and soil physical characteristics (table 1). Sites were clear-cut harvested to remove the 20–25 year-old loblolly pine and then site-prepared (sheared, raked, and bedded). Bedding created three distinct microsites (bed, inter-row, and trough) with distinct soil temperature, moisture, organic matter, and physical characteristics. Beds were 1.83 m wide and were 25-30 cm and 30-40 cm higher than adjacent inter-rows (0.92 m wide) and troughs (0.45 m wide), respectively.
Seedlings were planted on beds at a 1.8 m spacing (1290 trees ha^{-1}) in the winter of 1999. On each site, three 50x50 m plots were selected for measurement. Each plot contained 12 rows with 27 seedlings per row (324 seedlings). Measurement plots were confined to the inner eight rows.

Measurement of Soil CO_2 Efflux (Fs)

Soil CO_2 efflux (Fs) was measured with the multi-chambered Automated Carbon Efflux System (ACES) developed at the USDA Forest Service, Southern Research Station Laboratory in Research Triangle Park, NC (Butnor and others 2003). Soil chambers were 25 cm in diameter (491 cm^2) and were equipped with air and soil (5 cm, Ts) thermocouples. The system has been shown to give consistent responses regardless of differences in soil and litter properties and has been calibrated to provide true efflux rates (Butnor and others 2005). Fifteen soil chambers were placed in groups of three in a diagonal transect across the plot. Transects were randomly located each measurement period. Within a group, the first chamber was placed on the bed 25 cm from a seedling (tree), the second on the bed equal distance between trees (between-tree), and the third on the adjacent inter-row. Occasionally, troughs were measured. Chambers were measured sequentially, six to nine times, over a 24 hour period and then averaged to compute daily average Fs. Volumetric soil moisture (θ) to a 30 cm depth was measured at each chamber location with time domain reflectometry (CS615; Campbell Scientific, Ogden, Utah).

Organic Matter, Carbon, Nitrogen and Root Measurements

Following Fs measurements, a 10 cm diameter by 20 cm depth soil core was taken at each chamber. The soil was sieved through a 6.4 mm mesh screen to remove large live roots and coarse organic fragments (COF). A 500 g subsample of sieved soil was washed with a hydropneumatic elutriator (Gillison's Variety Fabrication, Inc., Benzonia, MI) to separate fine organic fragments (FOF) and small live roots. Root biomass (Rb, large and small), COF, and FOF were dried at 65°C and weighed and expressed per unit surface area (kg m^{-2}). Soil carbon (Cs) and nitrogen (Ns) concentration (mg g^{-1}) were determined on a 20 g sample of oven-dried soil with a Carlo Erba NA 1500 Series II C/N/S Analyzer (Fison Instruments, Danvers, MA).

Table 1—Study site soil characteristics and site index of the previous stand

Site	Soil Series	Soil type	Description	Drainage	SI25[1]
Andrews	Bladen	thermic Typic Albaquults	Fine sandy loam (<35 cm), clay (>35cm)	Very poorly	25
Camphall	Rains	thermic Typic Paleaquults	Deep sandy loam	Poorly	24
Oswald	Ocilla/ Yemassee	thermic Aquic Arenic Paleudults	Deep loamy sand	Somewhat Poorly	22
Watson Hill	Alpin	thermic, coated Aquic Quartzipsamments	Fine sand	Well	22

[1]SI – site index at 25 years (meters)

Statistical Analysis

Soil CO_2 efflux, Ts, **θ**, COF, FOF, Cs, Ns, and Rb were measured quarterly over two years beginning in July 1999. Plot averages, the average of 4-5 measurements per plot, served as the experimental unit. Site and location within site (bed or inter-row) effects were tested by using a randomized complete block analysis of variance with repeated measures (PROC MIXED, SAS Institute Inc. 1987). Main or interactive effects were tested at $\alpha=0.05$. Tukey's adjustment was used for pair-wise comparison of site and site x location means.

Correlation analysis (PROC CORR) and linear regression (PROC REG) were used to assess the spatial and temporal variation in measured parameters and to quantify the response of Fs to environmental and site variables. Individual chamber measurements were used for these analyses. Equation 1 was used to describe the relationship between Fs and temperature:

$$\ln(\mathrm{Fs}) = a + b*\ln\ \mathrm{Ts} \qquad (1)$$

where ln Fs and ln Ts are log transformed Fs and Ts. Analysis of covariance was used to test for site and site x location effects on the regression parameters. Regression lines were first analyzed by testing the entire line (i.e. intercepts and slopes simultaneously) with full and reduced models (Zarnoch 2009). If significant site or site x location effects were detected, separate analyses were performed for slope or intercepts effects. Linear contrasts were used to test for differences between regressions and for making pairwise comparisons. When making multiple comparisons, Type I experimentwise error was minimized by using the Bonferroni correction to derive the appropriate significance level (α). For example, with a full model comparing four regression lines, there would be six contrasts and the appropriate significance level would be: $\alpha=(0.05/6)=0.008$ (Zarnoch 2009).

RESULTS

Temporal and Spatial Variation in Fs and Site Characteristics

Average daily Ts varied seasonally from around 5 °C in the winter to greater than 30 °C in the summer (fig. 1). Sites were measured on different days within each period, and day to day variation in temperature resulted in a significant site and site x period interaction (table 2). Within a site, Ts was similar among chamber locations on beds and inter-rows (site x location, p=0.78). Averaged θ over the study was 47.5, 30.1, 23.4, and 12.9 $m^3\ m^{-3}$ for sites A, C, O, and W, respectively. There was a significant site x location x period interaction; where θ was significantly higher in the inter-rows than beds for at least part of the year on all of the sites (fig.1).

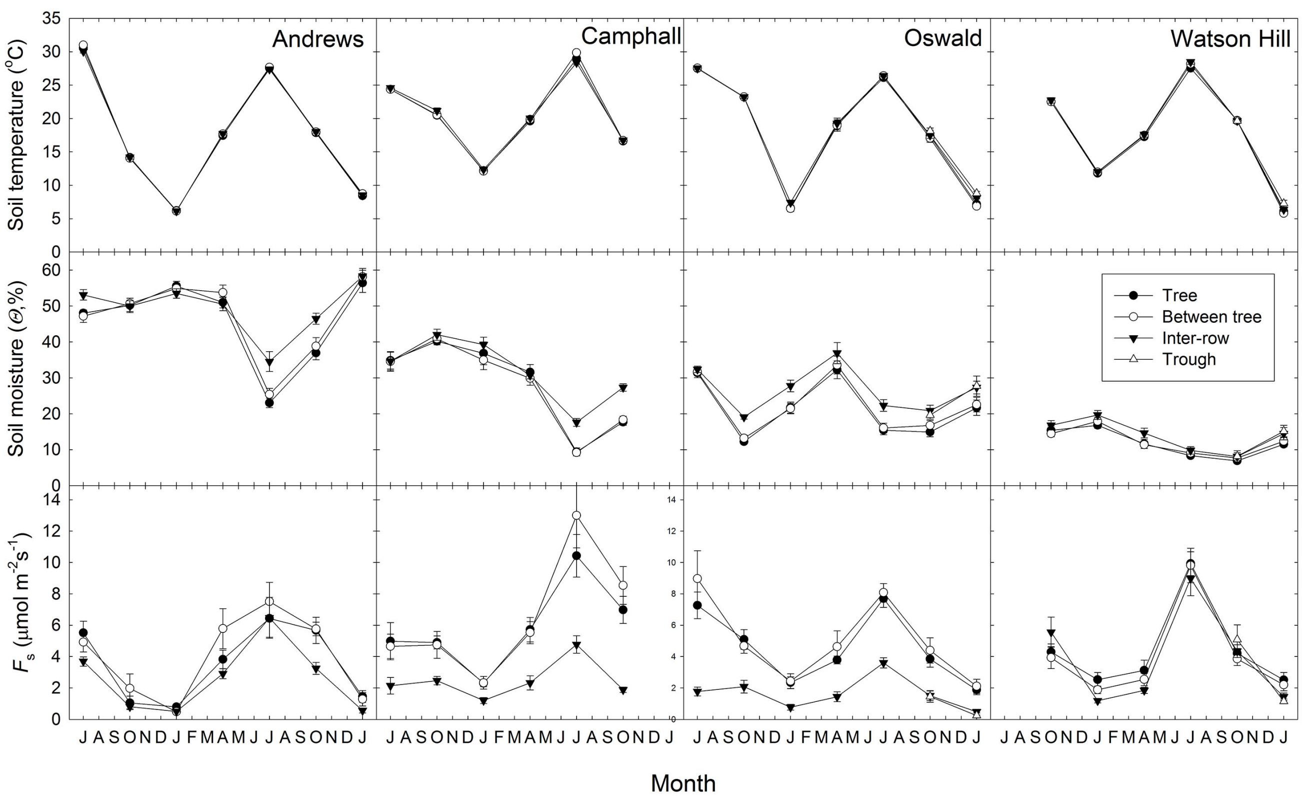

Figure 1—Temporal and spatial patterns of daily average soil temperature (Ts) measured at 10 cm, volumetric soil moisture (θ), and soil CO_2 efflux (Fs) measured on the beds adjacent to and half-way between planted seedlings and between the beds in the inter-row, and trough. Data are least square means (LSMEAN) and standard error.

Table 2—Probability values for effects of site (S), sampling location (L, bed or inter-row), and sampling period (P) on coarse organic (COF, kg m^{-2}) and fine (FOF, kg m^{-2}) organic fragments, mineral soil carbon (Cs, mg g^{-1}) and nitrogen (Ns, mg g^{-2}), total root biomass (Rb, kg m^{-2}), soil CO_2 efflux (Fs, µmol m^{-2} s^{-1}), soil temperature (Ts, °C), and volumetric soil moisture (θ) (n = number of observations)

Effect	COM	FOM	Cs	Ns	Rb	Fs[1]	Ts	**θ**
S	0.0139	0.0053	0.2436	0.0007	0.1195	0.0447	0.0032	<0.0001
L	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.1425	<0.0001
S x L	<0.0001	<0.0001	<0.0001	<0.0069	0.3834	<0.0001	0.7890	0.0861
P	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
S x P	0.0992	<0.0001	0.0122	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
L x P	0.2245	0.6225	0.1102	0.1993	<0.0001	0.0082	0.5723	0.0015
S x L x P	0.1515	0.4950	0.7932	0.9159	0.1098	0.1465	0.9233	0.0072
n	1209	1209	1209	1209	1209	853	853	853

[1] Analysis is for sampling periods when all sites were measured.

Soil CO_2 efflux averaged across all measurement periods, was 3.74, 5.41, 3.76, and 4.57 µmol m^{-2} s^{-1} (se=0.33) for sites A, C, O, and W, respectively, and site C was significantly greater than sites A (p=0.034) and O (p=0.034) (table 2). Fs varied from <0.5 mmol m^{-2} s^{-1} in January to >12 mmol m^{-2} s^{-1} in July and closely followed the seasonal trend in Ts (fig. 1). Within a site, there was no significant difference in Fs measured on beds next to a tree or between trees (figs.1 and 2); however, Fs was significantly higher on beds than inter-rows at sites C and O (p<0.0001) and marginally greater at site A (p=0.1067). Measurement location had no effect on Fs at site W (p=0.998). Fs measured in troughs were similar to inter-rows (sites O and W).

There were significant period and site x period interactions for COF, FOF, Cs, and Ns (table 2); however, there were no discernible trends over time for any of the parameters (data not shown). Site A had greater COF than site W (p=0.036), while site C had greater FOF than site A (p=0.049) and O (p=0.0007) (fig.2). There was a significant site x location interaction where beds had greater COF at sites A and O and greater FOF at sites A, C, and O than inter-rows. In contrast, there were no location effects on COF or FOF at site W. There was no site effect on Cs (table 2); however, there was a significant site x location effect where Cs was greater in the beds than inter-row (p<0.05) for sites A, C, and O, but not W (p=0.99). Site A had significantly greater Ns than the other sites (table 2, fig.2) and Ns was greater in beds than in the inter-row at A, C, and O, but not at W. There were no site differences in Rb (table 2) and there was no site x location interaction; although beds tended to have more Rb than the inter-rows (fig.2).

Fs Response to Site and Environmental Variables

Soil CO_2 efflux was best correlated with Ts at all the sites (table 3). There was a significant (p<0.001) site* Ts effect (i.e. slope) on the relationship between Fs and Ts (equation 1) (data not shown), indicating the need for site specific regressions. Within site, Ts explained 26 to 55 percent of the variance in Fs and inter-row locations had better fits with Ts than beds (fig. 3). The temperature sensitivity (slope) of Fs was similar for bed and inter-row locations at sites A (p=0.457) and C (p=0.377); however, beds had a greater intercept indicating that at a given temperature; beds had higher Fs than inter-rows. In contrast, Fs was more sensitive to Ts in the inter-rows than beds at sites O (p=0.011) and W (p=0.019).

Fs was negatively correlated with θ at sites A, C, and W, but not site O, while Fs was positively correlated with Rb at sites C, O, and W, but not site A (table 3). There was a positive correlation between Fs and FOF at all sites and positive correlation with COF, Cs, and Ns at some sites, but not others. There was also significant covariation among environmental and site variables. For example, θ was higher during the winter when Ts was low (fig.1) resulting in a negative correlation between θ and Ts at sites A, C, and W. Rb was positively correlated with Ts, but negatively correlated with θ at sites C, O, and W, and FOF was positively correlated with Ts at all of the sites.

The covariation between Ts and other variables made it difficult to discern independent relationships with Fs. To minimize the confounding temperature effect, Fs was normalized to 20 °C (Fs(20)) by using equation 1 and the parameter estimates in figure 3. Relationships between Fs(20) and other variables were examined with stepwise regression. Soil moisture, Cs, COF, FOF, and Rb together accounted for 6 to 32 percent of the variance in Fs(20); however, the effect of any individual parameter was relatively weak and the relative importance differed with site (table 4). Soil moisture and Cs were significant

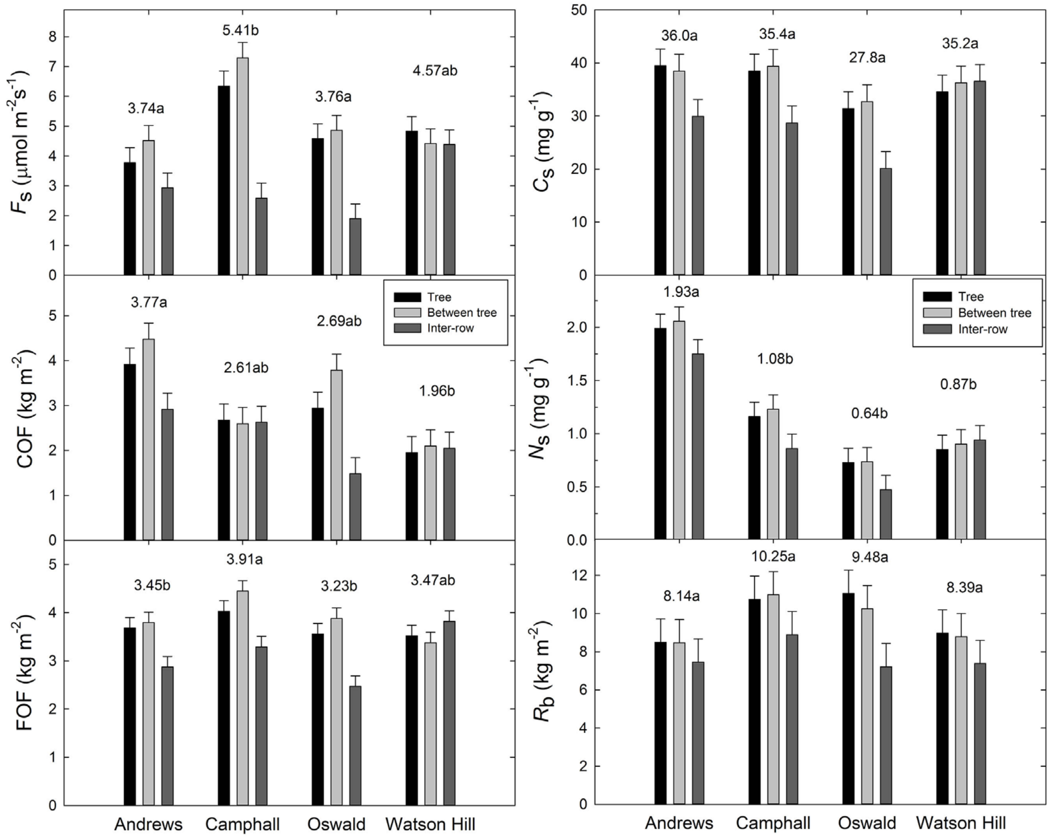

Figure 2—Means and standard errors for soil CO_2 efflux (Fs), coarse (COF) and fine (FOF) organic fragments, mineral soil carbon (Cs) and nitrogen (Ns) and live root biomass (Rb) measured on the beds adjacent to and half-way between planted seedlings and between the beds in the inter-row, and trough. Each bar is the average and standard error across all measurement periods (n=6 or 7). Values above bars are the site average across measurement locations and the letter denotes a significant difference between sites at p=0.05. Data are least square means (LSMEAN) and standard error.

at all of the sites, while COF, FOF, and Rb were important variables at site O. Root biomass was the single most important variable at the dry site (W). When all site were considered together, Cs θ, Rb, and COF explained 18 percent of the variance in Fs(20).

Annual Estimates

Annual soil carbon efflux was computed by using the site-specific temperature equations (fig. 3) and average daily Ts measured at on-site weather stations. Carbon efflux from the beds was more than twice that in inter-rows at sites C and O (fig. 4), and was 42 and 6 percent greater at sites A and W, respectively. Accounting for the spatial coverage of beds, troughs, and inter-rows and assuming troughs had similar Ts and Fs to inter-rows, the annual carbon efflux was 12.7, 18.7, 11.7, and 15.9 Mg C ha^{-1} at sites A, C, O, and W, respectively.

DISCUSSION

The range of average daily Fs (0.5 – 12 µmol m^{-2} s^{-1}) were similar to those observed in nearby one to three year-old plantations that received the same site preparation (Gough and others 2005, Tyree and others 2014). These values are much higher than that measured in 1 to 2 year-old stands located in the Virginia piedmont (< 2 µmol m^{-2} s^{-1}) (Pangle and Seiler 2002, Wiseman and Seiler 2004). These large regional differences are likely due to increased heterotrophic respiration caused by bedding on the South Carolina sites (Gough and others 2005). However, the effect of bedding on Fs is site specific. On the wetter sites (A, C, and O), Fs was 42 to193 percent greater on beds than inter-rows, while bedding had no effect on Fs on the well-drained site (site W). Annual soil C loss ranged from 11.7 to 18.7 Mg C ha^{-1}, greater than measured in other loblolly pine stands (Butnor and others 2003, Gough and others 2005, Maier and Kress 2000, Palmroth and others 2005), but lower than that reported for a recently clearcut *Pinus eliottii* plantation (22.7 Mg C ha^{-1}, Ewel and others 1987a). The high rates of annual carbon flux are likely to persist. Gough and others (2005) measured Fs over a loblolly pine chronosequence (0 to 22 years) on sites close to our study sites and found that Fs rates were stable over time decreasing only slightly with stand age. They attributed this response to offsetting effects of root and heterotrophic respiration as stands age. These stands may take 5-8 years to become annual net carbon sinks (+NEP) depending on soil type, severity

Table 3—Correlation coefficients for soil CO_2 efflux (Fs), soil temperature (Ts), volumetric soil moisture (Θ), live root biomass (Rb), coarse (COM) and fine (FOM) organic fragments, and mineral soil carbon (Cs) and nitrogen (Ns)

	Fs	Ts	Θ	Rb	COM	FOM	Cs
				Andrews			
Ts	0.55						
Θ	-0.50	-0.52					
Rb	0.05	0.05	-0.26				
COM	0.07	-0.01	0.02	-0.05			
FOM	0.15	0.21	-0.09	-0.00	0.44		
Cs	0.11	-0.18	0.05	-0.09	0.28	0.33	
Ns	-0.05	-0.28	0.17	0.00	0.12	0.16	0.71
				Camphall			
Ts	0.51						
Θ	-0.51	-0.40					
Rb	0.47	0.43	-0.55				
COM	0.23	0.13	0.09	-0.01			
FOM	0.30	0.49	-0.23	0.35	0.22		
Cs	0.24	0.02	-0.01	-0.05	0.14	0.37	
Ns	0.10	-0.03	0.20	-0.02	0.03	0.15	0.55
				Oswald			
Ts	0.44						
Θ	-0.19	-0.07					
Rb	0.39	0.24	-0.29				
COM	0.42	0.10	-0.00	-0.11			
FOM	0.38	0.19	-0.42	0.48	0.08		
Cs	0.32	0.03	-0.03	0.03	0.30	0.29	
Ns	0.12	0.05	-0.10	-0.05	0.12	0.05	0.56
				Watson Hill			
Ts	0.69						
Θ	-0.32	-0.30					
Rb	0.68	0.46	-0.25				
COM	-0.08	-0.12	0.25	-0.09			
FOM	0.50	0.45	-0.06	0.59	0.28		
Cs	0.13	-0.02	0.25	0.12	0.34	0.31	
Ns	-0.00	-0.04	0.14	-0.01	0.14	0.05	0.58

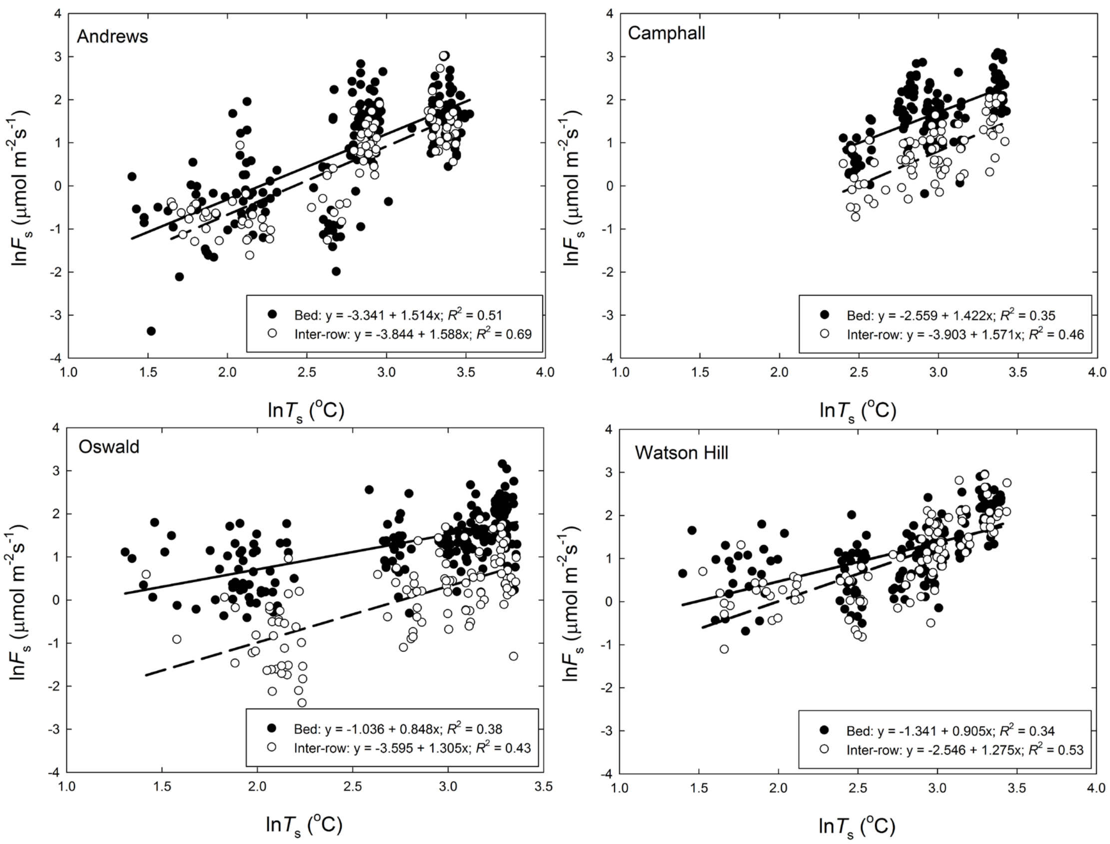

Figure 3—The relationship between log transformed soil CO_2 efflux (Fs) and soil temperature (Ts). Data are individual chamber measurements across all sampling periods. The line is the least square fit for beds (solid) and inter-row (dashed) locations (equation 1).

of soil disturbance, and management (e.g. fertilization, weed control) (Sampson and others 2008). Fertilization can reduce the time for stands to gain positive NEP. For example, four years of fertilization of an infertile sandy site shifted NEP of a 12 year-old loblolly pine stands from carbon neutral (0.28 Mg C ha^{-1}yr^{-1}, non-fertilized) to strong carbon sinks (6.4 Mg C ha^{-1}yr^{-1}, fertilized) (Maier et al 2004). The increase in NEP was primarily a function of NPP. However, fertilization may also increase NEP by decreasing Fs (Butnor and others 2003, Haynes and Gower 1995, Samuelson and others 2004) primarily through decreased soil organic matter decomposition (Janssens and others 2010).

Soil temperature was the primary driver of Fs explaining 26-55 percent of the variation, comparable to that reported in other studies for young loblolly pine (Gough and others 2005, Maier and Kress 2000, Pangle and Seiler 2002, Samuelson and others 2009). There were significant site differences in the temperature response indicating that site-specific equation were needed to model Fs. Furthermore, on the drier sites (O and W), the sensitivity of Fs to Ts was greater in the inter-rows than beds. The cause of this site specific effect is unknown, but may be due to the dissimilar sensitivities of root and heterotrophic respiration to changes temperature, moisture, and substrate supply (Boone and others 1998, Davidson and others 2006, Johnsen and others 2007).

Spatial variation in Fs was correlated to differences in θ, COF, FOF, Cs, Ns, and Rb associated with bedding (fig. 2, table 3); however, individual relationships with Fs were generally weak. After accounting for temperature effects, Cs explained a significant but small amount of variation (3to13 percent) in Fs at all of the sites, while COF and FOF explained an additional 10 percent of the variation at site O. Root biomass had little influence on Fs except at the dry site (site W) where it was the single most important variable explaining 17 percent of the variance in Fs(20). It makes sense that due to low root biomass, heterotrophic processes are the dominant source of Fs in young developing stands (Ewel and others 1987b). Several studies have found a correlation between Fs and Cs, and coarse organic debris or fragments (Gough and Seiler 2004, Hanson and others 1993, Mallik and Hu 1997, Pangle and Seiler 2002,); however, relationships are generally weak. Tyree and others (2014) found that soils augmented with logging residues increased heterotrophic respiration, but had no effect on Fs. These studies indicate that static estimates of carbon pool size in Cs, COF, FOF, or Rb are not particularly useful for predicting instantaneous

Table 4—Summary of stepwise multiple regression of factors that influence soil CO_2 efflux normalized to 20°C (Fs(20)). Factors are volumetric soil moisture (θ), coarse organic fragments (COF), fine organic fragments (FOF), live root biomass (Rb), and mineral soil carbon (Cs). Only parameters significant at p=0.05 were included in the analysis (n=number of observations)

Variable	Partial R^2	Model R^2	C(p)	F-value	P>F	n
			Andrews			
θ	0.0310	0.0310	15.64	9.10	0.0028	286
Cs	0.0297	0.0607	8.52	8.94	0.0030	
			Camphall			
Cs	0.1028	0.1028	29.66	22.23	<0.0001	196
θ	0.1186	0.2214	2.37	29.39	<0.0001	
			Oswald			
Cs	0.1329	0.1329	82.30	46.13	<0.0001	303
FOF	0.0683	0.2012	54.26	25.66	<0.0001	
θ	0.0508	0.2520	33.93	20.29	<0.0001	
COF	0.0437	0.2957	16.70	18.51	<0.0001	
Rb	0.0289	0.3246	6.00	12.7	0.0004	
			Watson Hill			
Rb	0.1674	0.1674	27.12	53.48	<0.0001	268
Cs	0.0460	0.2134	13.04	15.49	<0.0001	
θ	0.0295	0.2429	4.71	10.3	0.0015	
			All Sites			
Cs	0.0809	0.0809	123.27	92.46	<0.0001	1053
θ	0.0557	0.1366	54.22	67.74	<0.0001	
Rb	0.0301	0.1667	17.79	37.93	<0.0001	
COF	0.0124	0.1791	4.03	15.77	<0.0001	

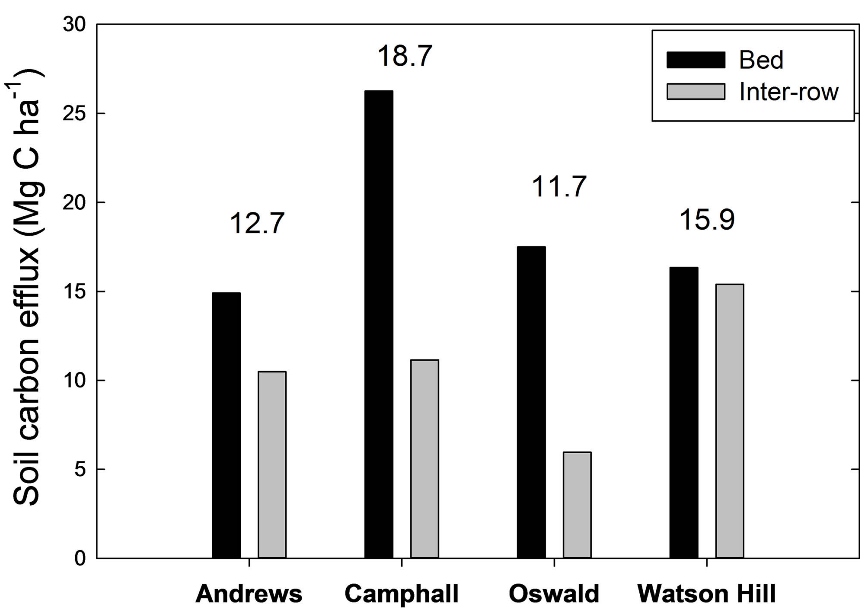

Figure 4—Annual soil carbon efflux from the bed and inter-row locations for each site. The value above the bar is the annual carbon efflux for the site accounting for spatial coverage of the bed, inter-row, and trough.

measures of Fs (Gough and Seiler 2004, Reichstein and others 2003).

Soil CO_2 efflux was weakly (<12 percent) negatively related to θ. A strong soil moisture effect on Fs has not been observed in loblolly pine plantations even when measured across a wide range of θ (Gough and Seiler 2004, Pangle and Seiler 2002, Selig and others 2008, Samuelson and others 2009). The shape of the response of Fs to θ is variable, and depends on soil physical characteristics, organic matter content, and to the differential effects of moisture on root and heterotrophic respiration (Hanson and others 2000). Extreme wet or dry soil can inhibit Fs and between the extremes, θ may have no obvious effect (Fang and Moncrieff 2001, Lavigne and others 2004). For example, on well drained sandy soils, irrigation treatments increased Fs in loblolly pine but only when the soil was dry (Maier and Kress 2000, Samuelson and others 2009). In mixed pine stands, Fs was positively correlated to θ on sandy soils but not on fine textured clays (Dilustro and others 2005) and on a clay piedmont soil, Fs increased with θ, but only when $θ < 0.2$ $m^3 m^{-3}$ (Palmroth and others 2005).

These studies suggest that loblolly pine plantations may rarely experience critical levels of θ that inhibit Fs. However, infrequent (e.g. weekly or monthly) measurements of Fs may miss or may not be able to discern subtle moisture effects on Fs such as short-term changes that occurs after rainfall. For example, Ford and others (2012) estimated annual soil carbon efflux in irrigated and non-irrigated longleaf pine stands using continuous (i.e. hourly) and biweekly measurements of Fs. Irrigated stands had 37 percent greater carbon flux than non-irrigated stands when estimated using continuous measurements of Fs; however, there was no significant irrigation effect on carbon efflux when estimated from biweekly measurements. They concluded that biweekly measurements missed short-term increases of Fs that occurred after irrigation treatments. Clinton and others (2011) made hourly measurements of Fs in a mid-rotation longleaf pine stand, found that Fs increased sharply following a 13 mm rainfall event, and then steadily fell over the next two weeks as θ declined. Others have also reported short-term increases in Fs after rainfall events (Jarvis and others 2007, Xu and Qi 2001). These short-term pulses in Fs can account for 5 to 37 percent of annual carbon flux (Daly and others 2008, Lee and others 2002, Lee and others 2004, Palmroth and others 2005). Short-term changes in θ following rainfall can also increase the temperature sensitivity of Fs (Palmroth and others 2005). These studies indicate that infrequent chamber-based measurements of Fs probably do not have the resolution for capturing soil moisture effects on Fs and potential interactions between soil moisture and temperature.

CONCLUSION

Annual soil carbon efflux rates ranged between 11 and 18 Mg C ha^{-1} yr^{-1} and are some of the highest reported for young loblolly pine. Bedding had site specific effects on the spatial variation in Fs, θ, and soil carbon pools. Bedding increased Fs, soil carbon stocks, and decreased θ on sites with poor to moderately poor drainage, but not on a well-drained site. Wet sites will likely experience accelerated carbon loss because of bedding. Conversely, bedding should increase site carbon uptake through increased tree survival and growth and may quickly offset high Fs. The site-specific spatial variation in Fs and associated drivers should be considered when modeling Fs in young pine stands.

As expected, Ts explained the largest amount of variation in Fs. Soil moisture, soil carbon, and root biomass explained only a small amount of spatial variation in Fs. These variables are not likely to be useful for predicting instantaneous measures of Fs. Furthermore, infrequent chamber-based measurements of Fs probably do not have the resolution for capturing transient θ effects on Fs.

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LITERATURE CITED

Allen, H.; Campbell, R.; Hook, D. 1988. Wet site pine management in the southeastern United States. In: Hook, D.D.; McKee, W.H.; Smith, H.K. [and others], eds. The ecology and management of wetlands. Vol. 2: Management, use and value of wetlands. Kent, UK: Croom Helm Ltd.: 173-184.

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

Butnor, J.R.; Johnsen, K.H.; Maier, C.A. 2005. Soil properties differently influence estimates of soil CO2 efflux from three chamber-based measurement systems. Biogeochemistry. 73: 283-301.

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

Chapin, F.S., III; Matson, P.A.; Mooney, H.A., eds. 2002. Principles of Terrestrial Ecosystem Ecology. New York: Springer-Verlag. 436 pp.

Clinton, B.D.; Maier, C.A.; Ford, C.R.; Mitchell, R.J. 2011. Transient changes in transpiration, and stem and soil CO2 efflux in longleaf pine (*Pinus palustris* Mill.) following fire-induced leaf area reduction. Trees. 25: 997-1007.

Daly, E.; Oishi, A.C.; Porporato, A.; Katul, G.G. 2008. A stochastic model for daily subsurface CO_2 concentration and related soil respiration. Advances in Water Resources. 31: 987-994.

Davidson, E.A.; Janssens, I.A. 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature. 440: 165-173.

Dilustro, J.J.; Collins, B.; Duncan, L.; Crawford, C. 2005. Moisture and soil texture effects on soil CO_2 efflux components in southeastern mixed pine forests. Forest Ecology and Management. 204: 87-97.

Ewel, K.; W.P. Cropper, W.P.; Gholz, H.L. 1987a. Soil CO_2 evolution in Florida slash pine plantations II. Importance of root respiration. Canadian Journal of Forest Research. 17: 330-333.

Ewel, K.; W.P. Cropper, W.P.; Gholz, H.L. 1987b. Soil CO_2 evolution in Florida slash pine plantations. I. Changes through time. Canadian Journal of Forest Research. 17: 325-329.

Fang, C.; Moncrieff, J.B. 2001. The dependence of soil CO_2 efflux on temperature. Soil Biology and Biochemistry. 33: 155-165.

Ford, C.R.; McGee, J.; Scandellari, F. [and others]. 2012. Long- and short-term precipitation effects on soil CO_2 efflux and total belowground carbon allocation. Agricultural and Forest Meteorology. 156: 54-64.

Gough, C.M.; Seiler, J.R. 2004. The influence of environmental, soil carbon, root, and stand characteristics on soil CO_2 efflux in loblolly pine (*Pinus taeda* L.) plantations located in the South Carolina coastal plain. Forest Ecology and Management. 191: 353-363.

Gough, C.M.; Seiler, J.R.; Wiseman, P.E.; Maier, C.A. 2005. Soil CO_2 efflux in loblolly pine (*Pinus taeda* L.) plantations on the Virginia Piedmont and South Carolina Coastal Plain over a rotation-length chronosequence. Biogeochemistry. 73: 127-147.

Haines, L.; Maki, T.; Sanderford, S. 1975. The effect of mechanical site preparation treatments on soil productivity and tree (*Pinus taeda* L. and *P. elliottii* Engelm. var. *elliottii*) growth. Forest soils and forest land management. Quebec, Canada: University of Laval Press: 379-395.

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

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

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

Henderson, G.S.; McFee, W.; Kelly, J. 1995. Soil organic matter: a link between forest management and productivity. In: Carbon forms and functions in forest soils. Soil Science Society of America Inc.: 419-435.

Janssens, I.A.; Dieleman, W.; Luyssaert, S. [and others]. 2010. Reduction of forest soil respiration in response to nitrogen deposition. Nature Geoscience. 3: 315-322.

Janssens, I.A.; Lankreijer, H.; Mattaucci, G. [and others]. 2001. Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. Global Change Biology. 7: 269-278.

Jarvis, P.; Rey, A.; Petsikos, C. [and others]. 2007. Drying and wetting of Mediterranean soils stimulates decomposition and carbon dioxide emission: the “Birch effect”. Tree Physiology. 27: 929-940.

Johnsen, K.; Maier, C. ;Sanchez, F. [and others]. 2007. Physiological girdling of pine trees via phloem chilling: proof of concept. Plant, Cell and Environment. 30: 128-134.

Lavigne, M.B., Foster, R.J., Goodine, G. 2004. Seasonal and annual changes in soil respiration in relation to soil temperature, water potential and trenching. Tree Physiology. 24: 415-424.

Lee, M.S.; Nakane, K.; Nakatsubo, T. [and others]. 2002. Effects of rainfall events on soil CO_2 flux in a cool temperate deciduous broad-leaved forest. Ecological Research. 17: 401-409.

Lee, X.; Wu, H.-J.; Sigler, J. [and others] 2004. Rapid and transient response of soil respiration to rain. Global Change Biology. 10: 1017-1026.

Maier, C.A.; Albaugh, T.J.; Allen, H.L.; Dougherty, P.M. 2004. Respiratory carbon use and carbon storage in mid-rotation loblolly pine (*Pinus taeda* L.) plantations: the effect of site resources on the stand carbon balance. Global Change Biology. 10: 1335-1350.

Maier, C.A.; Kress, L.W. 2000. Soil CO_2 evolution and root respiration in 11 year-old loblolly pine (*Pinus taeda*) plantations as affected by moisture and nutrient availability. Canadian Journal of Forest Research. 30: 347-359.

Mallik, A.U.; Hu, D. 1997. Soil respiration following site preparation treatments in boreal mixedwood forest. Forest Ecology and Management. 97: 265-275.

McLaughlin, J.W.; Gale, M.R.; Jurgensen, M.F.; Trettin, C.C. 2000. Soil organic matter and nitrogen cycling in response to harvesting, mechanical site preparation, and fertilization in a wetland with a mineral substrate. Forest Ecology and Management. 129: 7-23.

Palmroth, S.; Maier, C.A.; McCarthy, H.R. [and others]. 2005. Contrasting responses to drought of forest floor CO_2 efflux in a loblolly pine plantation and a nearby Oak-Hickory forest. Global Change Biology. 11: 421-434.

Pangle, R.E.; Seiler, J. 2002. Influence of seedling roots, environmental factors and soil characteristics on soil CO_2 efflux rates in a 2-year-old loblolly pine (*Pinus taeda* L.) plantation in the Virginia Piedmont. Environmental Pollution. 116: S85-S96.

Reichstein, M.; Rey, A.; Freibauer, A. [and others]. 2003. Modeling temporal and large-scale spatial variability of soil respiration from soil water availability, temperature and vegetation productivity indices. Global Biogeochemical Cycles. 17: 15-1 – 15-15.

Rustad, L.E.; Huntington, T.G.; Boone, R.D. 2000. Controls on soil respiration: Implications for climate change. Biogeochemistry. 48: 1-6.

Sampson, D.A.; Wynne, R.H.; Seiler, J.R. 2008. Edaphic and climatic effects on forest stand development, net primary production, and net ecosystem productivity simulated for Coastal Plain loblolly pine in Virginia. Journal of Geophysical Research: Biogeosciences. 113: G01003.

Samuelson, L.; Mathew, R.; Stokes, T. [and others]. 2009. Soil and microbial respiration in a loblolly pine plantation in response to seven years of irrigation and fertilization. Forest Ecology and Management. 258: 2431-2438.

Samuelson, L.J.; Johnsen, K.; Stokes, T.; Lu, W. 2004. Intensive management modifies soil CO_2 efflux in 6 year-old Pinus taeda L. stands. Forest Ecology and Management. 200: 335-345.

Selig, M.F.; Seiler, J.R.; Tyree, M.C. 2008. Soil Carbon and CO_2 Efflux as Influenced by the Thinning of Loblolly Pine Plantations on the Piedmont of Virginia. Forest Science. 54: 58-66.

Trettin, C.C.; Davidian; M.; Jurgensen, M.F.; Lea, R. 1996. Organic Matter Decomposition following Harvesting and Site Preparation of a Forested Wetland. Soil Science Society of American Journal. 60: 1994-2003.

Turner, D.P.; Koerper, G.J.; Harmon, M.E.; Lee, J.J. 1995. A carbon budget for forests of the conterminous United States. Ecological Applications. 5: 421-436.

Tyree, M.C.; Seiler, J.R.; Maier, C.A. 2014. Contrasting genotypes, soil amendments, and their interactive effects on short-term total soil CO_2 efflux in a 3-year-old *Pinus taeda* L. plantation. Soil Biology and Biochemistry. 69: 93-100.

Valentini, R.; Matteucci, G.; Dolman, A.J. [and others]. 2000. Respiration as the main determinant of carbon balance in European forests. Nature. 404: 861-865.

Wiseman, P.E.; Seiler, J.R. 2004. Soil CO_2 efflux across four age classes of plantation loblolly pine (Pinus taeda L.) on the Virginia Piedmont. Forest Ecology and Management. 192: 297-311.

Xu, M.; DeBiase, T.A.; Qi, Y. [and others]. 2001. Ecosystem respiration in a young ponderosa pine plantation in the Sierra Nevada Mountains, California. Tree Physiology. 21: 309-318.

Zarnoch, Stanley J. 2009. Testing hypotheses for differences between linear regression lines. e-Res. Note SRS-17. Asheville, NC: U.S. Department of Agriculture Forest Service, Southeastern Forest Experiment Station. 20 p.