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The influence of environmental, soil carbon, root, and stand characteristics on soil CO_2 efflux in loblolly pine (*Pinus taeda* L.) plantations located on the South Carolina Coastal Plain

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Abstract

While the effect of soil temperature and moisture on soil CO_2 efflux (E_c) has been widely investigated, the relationship between E_c and soil carbon (C), root, and stand parameters has not been comprehensively examined or quantified across extensive spatial and temporal scales. We measured E_c in loblolly pine (*Pinus taeda* L.) stands located on the South Carolina Coastal Plain across sites, seasons, and ages. Concurrent with E_c measurements, we monitored soil temperature (top 10 cm) and soil moisture (top 10 cm) along with mineral soil C concentration [C], coarse woody debris (CWD), root surface area, and root volume in the top 20 cm of the mineral soil below the measurement chamber. We also examined the effects of stand age, stand volume, and site quality on E_c. Using linear regression analysis, we determined that E_c was most highly correlated with soil temperature alone ($R^2 = 0.263$). Mineral soil [C] alone explained a small, but significant amount of E_c variance ($R^2 = 0.026$). When all variables were considered simultaneously, only soil temperature ($R^2 = 0.249$), mineral soil C ($R^2 = 0.0378$), and root surface area ($R^2 = 0.0149$) explained a significant amount of variance in E_c. Other variables tested were not significantly correlated with E_c. Mineral soil C concentration was greater in samples taken directly adjacent to trees (on beds) compared with samples between rows (interbeds), which partially explained why we observed greater E_c rates next to trees. With increasing stand age, CWD decreased and root surface area increased suggesting that opposite shifts in total root and microbial respiration over time are responsible for the lack of correlation between E_c and stand age.
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1. Introduction

Soil CO_2 efflux (E_c), which includes respiration from roots (autotrophic) and soil organisms (heterotrophic), is a key source of CO_2 from terrestrial ecosystems and an important component of the global carbon cycle (Raich and Schlesinger, 1992; Raich and Tufekcioglu, 2000; Rustad et al., 2000; Schlesinger and Andrews, 2000). Several factors affect E_c and the return of stored soil carbon (C) to the atmosphere including soil temperature, soil moisture, vegetation type, substrate quality (e.g. type of organic matter), net ecosystem productivity, allocation of assimilate to above- and belowground biomass, population and community

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interactions, and land use disturbances (Rustad et al., 2000). While the influence of major E_c drivers including soil temperature and moisture have been extensively quantified, the effect soil C and root parameters have on E_c measurements from small chamber studies has not been adequately studied (Rustad et al., 2000). Quantifying the influence of factors driving E_c may assist in resolving uncertainties regarding spatial and temporal variability in soil CO_2 efflux across small and large scales (Raich and Potter, 1995). Further, enhancing current knowledge of spatial and temporal E_c patterns will allow for results from small chamber studies to be scaled-up to the landscape level with greater certainty (Rustad et al., 2000). Environmental, soil C, and root measurements paired with E_c measurements may assist in explaining variability in soil CO_2 efflux since small chamber measurements are influenced by the immediate soil environment (Maier and Kress, 2000; Pangle and Seiler, 2002).

E_c is affected by environmental factors and soil characteristics that are both inherent to a location and also influenced by practices common to intensive forest management. To a large extent, temporal (i.e. daily and seasonal) and spatial (i.e. latitudinal and intrasite) variation in E_c and its components is driven by differences in soil temperature and moisture (Kowalenko et al., 1978; Howard and Howard, 1993; Pajari, 1995; Bouma et al., 1997; Maier and Kress, 2000; Pangle and Seiler, 2002). However, studies are lacking that simultaneously examine the influence of soil temperature and moisture on E_c along with other factors including root and soil C characteristics across spatial and temporal scales. Although the relative influence of roots and soil C on E_c is sparsely quantified in the literature, previous investigators have shown that spatial variation in E_c on a given site is partly related to the proximity of roots to the measurement chamber in loblolly pine stands (*Pinus taeda* L.). E_c rates observed at the base of seedlings in Virginia Piedmont stands were consistently higher than those observed between planting rows (Popescu, 2001; Pangle and Seiler, 2002). These results indicate that small-scale spatial variation and the contribution of roots to total E_c (near the plant) may be fairly significant, even during the seedling stage. Other evidence suggests that factors including soil C concentration [C] and coarse woody debris (CWD) content of the mineral soil influence E_c rates (Trumbore et al., 1996; Progar et al., 2000; Wang et al., 2002).

In this study, we examined the soil environment, sources of soil C, roots, and stand characteristics concurrently with E_c in loblolly pine stands in an effort to determine the extent to which these factors influence E_c. Specifically, through regression, we addressed the relative influence of soil temperature, soil moisture, root volume, root surface area, CWD, mineral soil [C], stand age, stand volume, and site productivity in explaining variance in E_c in South Carolina Coastal Plain stands. Quantifying the influence of less commonly addressed soil factors including soil C, CWD, and root volume on E_c will assist researchers in defining the utility of such measurements since they are often time consuming and expensive procedures.

2. Materials and methods

2.1. Study sites

Sites were located approximately 40 km northwest of Charleston, SC, USA in Berkeley County (33.18°N, 79.95°W) on MeadWestvaco Corporation land located on upper Coastal Plain flats. The average annual temperature in Berkeley County is 17.7 °C, with an average maximum of 28.2 °C and an average minimum of 9.89 °C. Average annual rainfall is 125 cm. Flooding due to ponding is relatively common; however, severe drought frequently occurs during the summer and fall seasons as well (SCSCO, 2000). Precipitation for the months coinciding with measurements was on average 15.5% lower than the 30-year mean (SRCC, 2003). Elevation ranges from 1.5 to 4.6 m a.s.l. with mild slopes of less than 2%. Soil parent material is generally Wicomico or Penholoway backberrier flats, former shoreline, or offshore deposits. Soils are generally acidic and low in phosphorus.

Sixteen plots were chosen for the study, representing a range of ages, soils, and stand characteristics common to managed loblolly pine stands located on the southeastern US Coastal Plain (Table 1). Soil CO_2 efflux was investigated on four soil types in efforts to capture spatial variability across the landscape and to examine the relationship between E_c and environmental, soil C, root, and stand characteristics that are likely

Table 1

Soils and stand characteristics of intensively managed loblolly pine plots located on the South Carolina Coastal Plain. Means are presented with one standard error in parenthesis unless value given is not a mean. Means are given for 16 observations. See text for details concerning how each parameter was calculated

Soils series and taxonomy	Age (years)	Site $index_{25}$ (m)	Volume ($m^3\ ha^{-1}$)	Soil temperature (°C)	Volumetric moisture (%)	Root surface area density (m^2 roots m^{-3} soil)	Root volume density (m^3 roots m^{-3} soil)	CWD density (kg CWD m^{-3} soil)	Soil [C] (%)
Coxville series: fine, kaolinitic,	1	23.5	5.2	21.7 (1.83)	14.4 (1.80)	2.86 (1.01)	0.000454 (0.00195)	32.1 (8.30)	5.5 (1.6)
thermic Typic Paleaquults	5	22.3	94.1	18.8 (1.25)	12.5 (4.17)	8.99 (1.27)	0.00212 (0.00374)	11.2 (4.74)	4.7 (0.78)
	9	22.3	191	19.4 (1.35)	6.96 (1.06)	11.8 (1.25)	0.00323 (0.00608)	1.71 (0.671)	2.0 (0.61)
	24	19.8	392	19.1 (1.11)	10.1 (1.63)	12.4 (3.57)	0.00309 (0.00131)	1.17 (0.307)	2.9 (0.35)
Rains series: fine-loamy,	1	23.2	8.3	21.3 (1.80)	14.4 (1.94)	3.15 (1.06)	0.000541 (0.000250)	6.46 (1.71)	5.9 (0.52)
siliceous, semiactive,	7	22.3	74.9	19.2 (1.41)	9.02 (0.819)	11.0 (1.34)	0.00309 (0.000541)	1.44 (0.628)	2.7 (0.33)
thermic Typic Paleaquults	11	21.3	257	18.5 (1.24)	8.79 (1.01)	6.32 (1.22)	0.00210 (0.00707)	2.12 (0.564)	2.9 (0.37)
	20	20.4	329	18.9 (1.12)	8.68 (0.813)	10.5 (3.57)	0.00325 (0.00130)	2.24 (0.488)	3.6 (0.39)
Bonneau series: loamy, siliceous,	1	18.3	2.5	21.7 (1.47)	9.31 (1.46)	4.26 (0.647)	0.000864 (0.000192)	14.2 (4.16)	2.5 (0.43)
thermic Arenic Paleudults	6	20.7	66.2	19.3 (1.26)	7.63 (1.40)	12.3 (1.59)	0.00315 (0.000595)	2.93 (1.54)	1.9 (0.32)
	13	24.4	151	19.4 (1.23)	9.25 (1.93)	12.3 (1.57)	0.00304 (0.000491)	1.09 (0.367)	1.1 (0.15)
	19	20.1	254	19.4 (1.02)	6.26 (0.620)	19.1 (2.39)	0.0208 (0.0160)	1.89 (0.522)	1.9 (0.38)
Lynchburg series: fine-loam,	1	21.0	8.9	21.4 (1.80)	13.0 (1.88)	4.27 (1.59)	0.000809 (0.000328)	7.36 (1.63)	3.4 (0.69)
siliceous, semiactive,	5	21.3	75.3	19.2 (1.52)	8.19 (0.794)	15.8 (1.40)	0.00411 (0.000660)	3.72 (1.15)	3.8 (0.68)
thermic Aeric Paleaquults	11	21.3	78.9	19.0 (1.33)	7.64 (0.438)	13.3 (1.68)	0.00840 (0.005139)	1.74 (0.628)	1.3 (0.14)
	20	19.8	294	19.4 (1.22)	8.20 (0.921)	11.4 (1.34)	0.00268 (0.000536)	2.34 (0.678)	3.2 (0.41)

influenced by these soils. Specific soil series and taxonomic classifications for each soil grouping include: (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; (4) Lynchburg series: fine-loam, siliceous, semiactive, thermic Aeric Paleaquults. Within each soil series, four stand age groups were investigated. Across soil types, these age groups averaged 1, 6, 11, and 21 years-old at the beginning of the study.

All sites were bedded prior to hand planting. Interbeds were frequently submerged during the cooler, wetter winter months. Site indices range from 20.0 to 22.3 m at 25 years for loblolly pine (MeadWestvaco, unpublished data). The native forest cover type is a loblolly pine-hardwood mix.

2.2. Study design

All stands were in close proximity to each other (<5 km). Stands were accessed by road and all measurements were taken beyond three planting rows to minimize edge effects. Within each study plot, measurements described below were taken directly adjacent to the base of the tree and between rows (two measurement positions) in order to account for spatial variability described by Pangle and Seiler (2002). Measurements began in August 2001 and continued bimonthly through the following August. An additional 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 32 measurements (on each parameter described below) were collected on a sampling date (four soil series × four age groups × two measurement positions). The resulting dataset contained 256 measurements on each variable over the course of the study.

2.3. Soil CO_2 efflux measurements

Soil CO_2 efflux was measured using the LiCor 6200 infrared gas analyzer (IRGA) (LiCor Inc., Lincoln, NB) and a dynamic closed cuvette chamber system (Janssens et al., 2000). Measurements were taken on the surface of the forest floor where living plant material was not present. This was an effort to eliminate CO_2 efflux detection from aboveground plant tissues and respiring senescent tissue in the cuvette. The chamber was constructed from a 20.3 cm internal diameter PVC end cap assembled with a foam gasket around the base to provide a seal with the ground. The chamber height at the center was approximately 10 cm. A gas sampling line and a return port (from the LiCor) was attached to the chamber in order to provide both a gas input and output from the chamber to the IRGA. The internal volume of the chamber was 4105 cm^3 and the LiCor was calibrated accordingly. 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:

$$E_c = \frac{(\Delta C/\Delta t)(PV_t/RT)}{\text{soil surface area covered by chamber}}$$

where $C = [CO_2]$, t is the time, P the atmospheric pressure, V_t the system volume, R the universal gas constant, and T the temperature.

2.4. Soil temperature and moisture measurements

Soil temperature and moisture were determined at each soil CO_2 efflux measurement location. Soil temperature at 10 cm was measured at each location using a Digi-sense temperature gauge (model no. 8528-20, Cole-Parmer Instrument Co., Niles, IL). Volumetric soil moisture was determined to a depth of 10 cm using time domain reflectometry (Soil Moisture Equipment Corporation, 6050X1, Golena, CA).

2.5. Soil excavation

After soil CO_2 efflux, temperature, and moisture measurements were completed at a location, a cylindrical corer with a 10 cm diameter by 20 cm depth was used to extract a 0.0157 m^3 soil sample from beneath the measurement location in order to evaluate soil parameters. The O horizon (L, F, H layers) was removed prior to the excavation of the mineral soil and associated roots.

2.6. Laboratory analyses

Soil samples were seived through a 6.4 mm screen to separate soil from live roots and CWD. No attempt was made to separate pine from non-pine roots. A subsample of soil was collected from each soil sample after manual homogenization. Soil subsamples were oven-dried at 65 °C for 48 h and seived through a 2 mm sieve to remove coarser organic matter. Samples were analyzed for [C] using a Carlo-Erba elemental analyzer (Model NA 1500, Fison Instruments, Danvers, MA). Live root surface area and root volume were determined using the WinRhizo 5.0A software (Regent Instruments Inc., Que., Canada). CWD was oven-dried at 65 °C for 48 h, weighed in the laboratory, 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 in order to correct for mineral content.

2.7. Aboveground biomass estimates

When CO_2 efflux measurements were completed (January 2003), standing stem volumes of the three oldest age classes were estimated in each plot based on a 1/50 ha sampling of tree diameter breast height (DBH) and height using the following volume equation for loblolly pine:

$$\text{stem volume (ft}^3) = 0.21949 + 0.00238D^2H$$

where D is the DBH in inches and H the total tree height in feet (Tasissa et al., 1997). All volume estimates were converted to metric units. Seedling volume in 1-year-old stands was determined by multiplying ground-line diameter squared by seedling height.

2.8. Statistical analyses

Simple linear regression analysis was used to examine the relationship between E_c and individual parameters collected across the landscape and over time and to assess spatial and temporal trends in soil and root parameters. Explanatory variables examined for their relationship with E_c include soil temperature, soil moisture, root surface area density, root volume density, CWD density, mineral soil [C], stand age, stand volume, site index, and measurement location in the stand (i.e. adjacent to seedling on bed and on the interbed). Spatial trends within stands were also compared via regression by examining the relationship between measurement position and CWD density, soil [C], and root parameters. Similarly, trends in CWD density and root parameters across stand ages were investigated using simple linear regression. Simple linear regression served two specific purposes including the identification of trends (i.e. the response surface) between explanatory and response variables, and the evaluation of the strength (R^2) and significance (P-value) of the correlation between explanatory and response variables.

Variables were transformed when necessary to allow for the best fit of the trend line with the data. Initially, a regression line was fit to data (i.e. response variable versus individual explanatory variable) without transformation. Standardized residuals and normality plots from simple linear regression analyses were then examined to determine whether the best fit had been accomplished and to assess the need for transformation of the data in order to eliminate bias. Based on observations of the residuals, soil temperature data were natural log transformed to better define the relationship between E_c and soil temperature. Stand age data were also log transformed to better describe the trend between stand age and both CWD density and root area density. No other variables were transformed either because data transformation did not improve the fit of the regression line or because no significant relationship existed between non-transformed explanatory and response variables.

Multiple linear regression analysis was performed using the SAS stepwise procedure in order to determine the primary explanatory variables driving soil CO_2 efflux in the context of all possible variables. For the analysis, natural log transformed soil temperature data were used since this provided the best fit with E_c in the simple linear regression analysis. No other variables were transformed prior to the analysis. The purpose of the multiple linear regression analysis was to determine whether the simultaneous partitioning of variation in E_c to multiple sources changes the relationship between E_c and certain parameters. The inclusion of multiple variables in a model can increase the likelihood of detecting a significant relationship between explanatory and response variables since the error term is minimized when all parameters accountable for variability in the response variable are included in the model. The stepwise model selection procedure in SAS was chosen because the procedure simultaneously minimizes multicollinearity among explanatory variables and maximizes explanation of the variance in the response variable (Montgomery et al., 2001). All statistical analyses were performed using PROC REG in SAS (SAS Institute, Cary, NC).

3. Results

3.1. Soil microclimate and soil CO_2 efflux

Simple linear regression indicated a relatively strong positive relationship between E_c and soil temperature ($R^2 = 0.262, P < 0.0001$), while no significant relationship existed between E_c and the range of soil moistures observed on our sites ($R^2 = 0.009, P = 0.1512$; Fig. 1A and B).

3.2. Soil carbon, coarse woody debris, roots and soil CO_2 efflux

Root surface area ($R^2 = 0.010, P = 0.1650$) and root volume ($R^2 = 0.006, P = 0.3014$) in the top 20 cm of the mineral soil directly below the E_c chamber was not

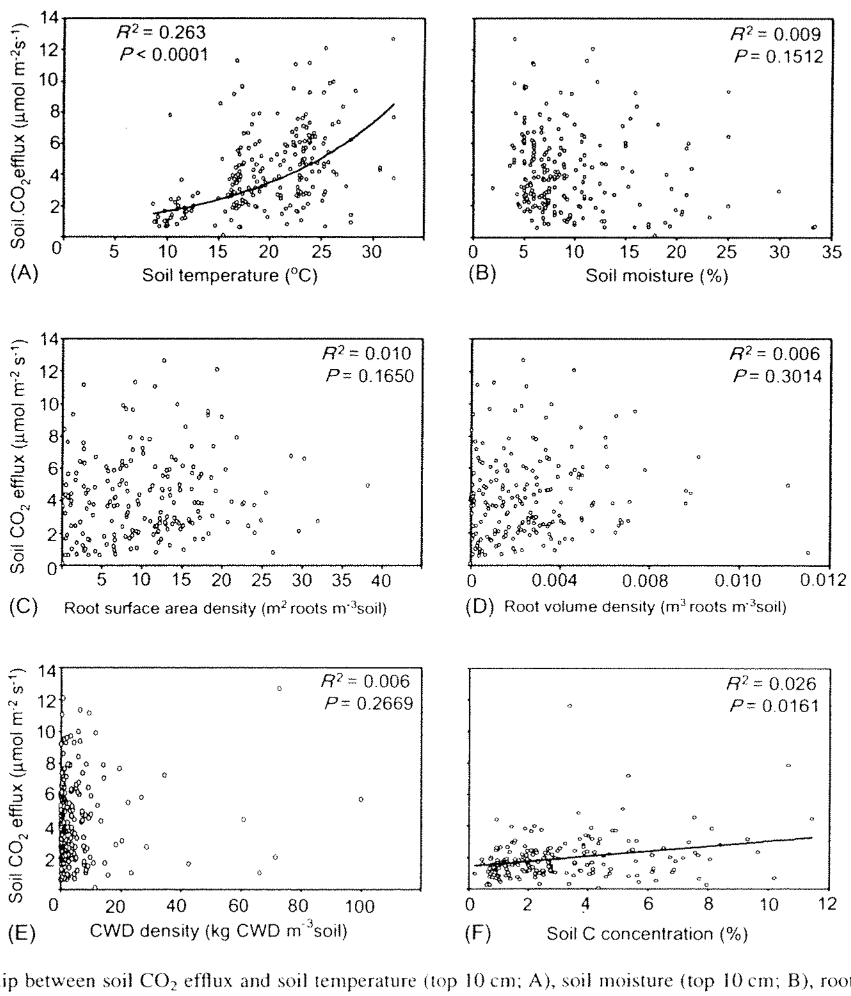

Fig. 1. The relationship between soil CO_2 efflux and soil temperature (top 10 cm; A), soil moisture (top 10 cm; B), root surface area density (top 20 cm; C), root volume density (top 20 cm; D), CWD density (top 20 cm; E) and percent soil carbon (top 20 cm; F) on the South Carolina Coastal Plain. Data were collected concurrently with soil CO_2 efflux measurements. A 10 cm diameter soil core was used to extract the top 20 cm of mineral soil directly below the soil CO_2 measurement chamber. Trend lines are shown only when the relationship is significant ($P < 0.05$).

significantly related to E_c (Fig. 1C and D). There was no relationship between E_c and CWD in the top 20 cm of mineral soil ($R^2 = 0.006, P = 0.2669$; Fig. 1E and F). However, a weak positive relationship existed between E_c and percent soil C in the top 20 cm of the mineral soil on our sites ($R^2 = 0.026$, $P = 0.0161$).

3.3. Stand characteristics and soil CO_2 efflux

Stand age ($R^2 = 0.000, P = 0.9965$), stand volume ($R^2 = 0.006, P = 0.9179$), and site index ($R^2 = 0.004$, $P = 0.3392$) were not significantly correlated with E_c on our sites (Fig. 2).

3.4. Ranking variables simultaneously

Using the stepwise selection process in SAS, we tested all variables in an effort to determine the amount of variance in E_c explained by variables simultaneously. Results acquired from the stepwise procedure were similar to those obtained using simple linear regression. Temperature explained a majority of the variance in E_c and was positively related to E_c (partial $R^2 = 0.249, P < 0.0001$). Soil [C] was weakly positively related to E_c in the context of other variables (partial $R^2 = 0.038, P = 0.0017$). Unlike our simple linear regression results, root surface area was weakly positively related to E_c in the stepwise selection ($R^2 = 0.015, P = 0.0450$). The additional significance of root surface area is probably due to the reduction in error when variance in E_c due to soil temperature and soil C is taken into account. Also, we tested whether accounting for variance in E_c due to temperature would change the significance of other potential explanatory variables by regressing both temperature and each variable individually against E_c. No additional variables became significant when variance in E_c due to soil temperature was removed.

3.5. Root characteristics, carbon and spatial variation

We observed a weak relationship between measurement location and E_c ($R^2 = 0.017, P = 0.0564$). E_c rates were higher near the base of the tree in comparison to those away from the tree. In order to test whether or not roots, CWD, and/or [C] in the top

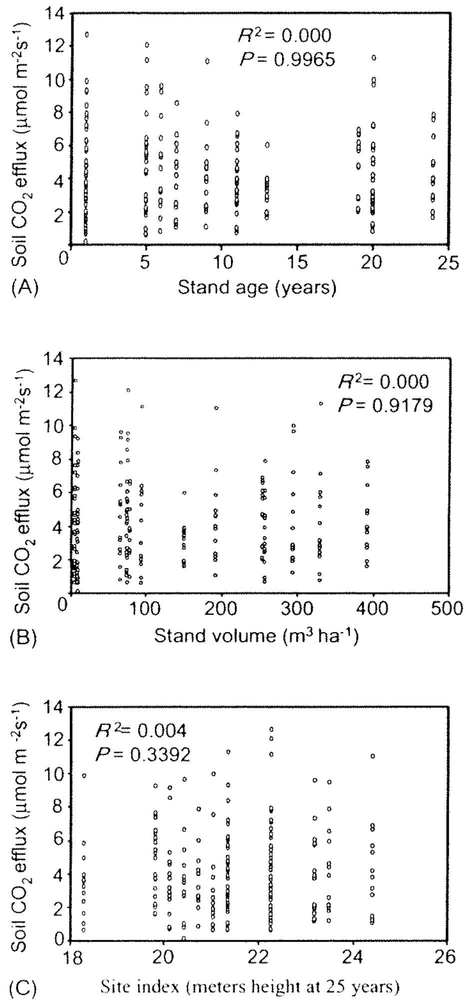

Fig. 2. The relationship between soil CO_2 efflux and stand age (A), stand volume (B), and site index (C) in loblolly pine stands sampled on the South Carolina Coastal Plain.

20 cm below the measurement chamber explains spatial differences in E_c, we used simple linear regression to examine the relationship between measurement location and root volume, root surface area, CWD, and [C]. Root volume, root surface area, and CWD were not significantly correlated with measurement position ($P < 0.05$). In contrast, simple linear regression analysis demonstrated that soil [C] was significantly greater in soil samples taken near the base trees on the beds compared with samples between rows on the interbeds ($R^2 = 0.043, P = 0.0020$).

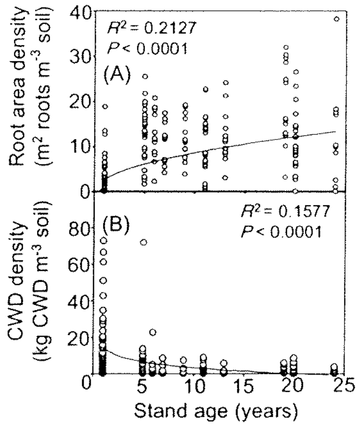

Fig. 3. Relationship between stand age and root area density (A), and stand age and CWD density (B) in South Carolina Coastal Plain loblolly stands. Roots and CWD were sampled concurrently with soil CO_2 efflux measurements in the top 20 cm of the mineral soil.

3.6. *Root characteristics, carbon and stand age*

Since fluctuating relative contributions of autotrophic respiration and heterotrophic respiration over time may partially explain the lack of any trend between E_c and stand age, we investigated changes in the mineral soil components over stand ages that likely parallel trends in autotrophic and heterotrophic respiration. Specifically, we analyzed trends in root surface area and CWD from the upper 20 cm of mineral soil across stand ages (Fig. 3). Root surface area density was positively related ($R^2 = 0.2127, P < 0.0001$) to stand age while CWD was negatively correlated with stand age ($R^2 = 0.1577, P < 0.0001$).

4. Discussion

Our results indicate that soil temperature explains the greatest amount of variance in E_c observed within and across sites and over seasons on the South Carolina Coastal Plain ($R^2 = 0.263, P < 0.0001$). Soil moisture was not a significant E_c driver despite ranging from 2 to nearly 33% volumetric moisture content. Soil [C], CWD, root volume, and root surface area in the top 20 cm of the soil explained little or no significant amount of variance in E_c. Soil [C] alone explained only 2.6% of the variance in E_c within and across plots. When simultaneously considered, soil temperature, soil [C], and root surface area explain 24.9, 3.78, and 1.49% of the variance in E_c on our sites.

Our findings are consistent with previous reports that cite a strong relationship between soil temperature and E_c (Kowalenko et al., 1978; Howard and Howard, 1993; Pajari, 1995; Bouma et al., 1997; Maier and Kress, 2000; Pangle and Seiler, 2002). Soil moisture did not explain a significant amount of variance on our sites, but we may not have observed E_c above and below critical moisture levels. Frequently, soil is saturated on the Coastal Plain, which would prevent aerobic activity from microbes. However, we observed very little water between beds probably because average precipitation was 15.5% less than normal during the measurement months. Therefore, soil moisture on our sites may not have been representative of a typical year. Generally, soil moisture limits E_c at either extremely high or low levels (Kowalenko et al., 1978; Howard and Howard, 1993; Bouma et al., 1997; Pangle and Seiler, 2002).

Respiring roots directly below the measurement chamber should exert a significant influence on E_c since CO_2 efflux from roots comprises 10–90% of the total soil CO_2 efflux in forests (Hanson et al., 2000). However, our results indicate that root surface area and root volume directly below the chamber are weakly or not at all related to E_c. While these results are somewhat surprising, Pangle and Seiler (2002) reported only a minor influence of root biomass on E_c in a young loblolly pine stand. Specifically, they found fine root biomass explained 2.52% of the variance in E_c across a single site on one measurement date, attributing the minor influence of roots to non-vertical movement of CO_2 through the soil profile. CO_2 originating from root respiration will move along the path of least resistance, which may be vertical or lateral. Likewise, roots in the profile that are adjacent to the sampled area beneath the measurement chamber will impact E_c measurements when CO_2 moves laterally in the soil. The degree of lateral movement of CO_2 in soil depends on soil physical properties such as soil texture, strength, pore space, and tortuosity (Weerts et al., 2001; Susfalk et al., 2002).

Similarly, mineral soil C was weakly related to E_c, while CWD was not significantly correlated with E_c. Mineral soil C and CWD represent potential C substrate sources for microbes and should accordingly affect microbial activity (Trumbore et al., 1996; Progar et al., 2000; Wang et al., 2002). However, soil C and CWD in the top 20 cm of the soil below the measurement area may not be good indicators of E_c for two reasons. First, as previously discussed with roots, CO_2 originating from microbial respiration may not move only vertically in the profile. Second, soil C quality (i.e. labile C) may be equally important to quantity when relating C to microbial activity (Giardina and Ryan, 2000). Russell and Voroney (1998) reported that less than 2% of the observed variance in E_c in a boreal aspen forest (*Populus tremuloides*) was explained by soil organic matter (SOM) quantity sampled directly below measurement chambers. They conclude that SOM had little influence on E_c; however, they did not address issues of substrate quality or availability. Pangle and Seiler (2002) found no relationship between E_c and mineral soil C sampled directly below their measurement chamber in a loblolly pine stand on a single day. Our results along with others cited above indicate that uncertainties regarding soil physical and chemical properties limit the value of soil sampling directly below the measurement cuvette using our methodology.

The fact that E_c was not related to stand age, stand volume, or site index implies that the accumulation of respiring root biomass over time that we observed was offset by reductions in microbial respiration on our sites. The effect of stand age on E_c has been shown to be inconsistent (Ewel et al., 1987; Klopatek, 2002; Pypker and Fredeen, 2003). However, E_c generally increases with age and stand volume, presumably due to greater respiring root biomass. Our observations are not typical among other reports in the literature, stressing the need for studies addressing autotrophic and heterotrophic shifts over time. Further, the inconsistent relationship between stand age, stand volume, and E_c reported in the literature may be the result of shifts in autotrophic and heterotrophic components guided by different management regimes. Multiple management activities have been shown to influence both root and microbial biomass and activity (Edwards and Ross-Todd, 1983; Londo et al., 1999; Lee et al., 2002; Mallik and Hu, 1997).

Root and CWD data from our study support the proposal that changes in autotrophic and heterotrophic respiration over time explain why we did not observe a stand age or stand volume effect on E_c. Root surface area increased over time in our stands, likely resulting in enhanced autotrophic respiration over time (Ewel et al., 1987). At the same time, the declining amount of CWD in the mineral soil with increasing stand age may parallel microbial activity since CWD may serve as a C substrate pool for microbes (Progar et al., 2000; Wang et al., 2002; Davis et al., 2003). Together, these data suggest that autotrophic and heterotrophic contributions to E_c shift inversely over the course of a loblolly pine rotation on our sites, which would explain the weak relationship between E_c and stand age. Other investigators concluded that inverse shifts in autotrophic and heterotrophic respiration prevented them from detecting a change in E_c over time (Edwards and Ross-Todd, 1983; Toland and Zak, 1994).

Spatial differences in E_c may be partly due to variability in the distribution of roots and C across and within sites. Similar to our findings, Pangle and Seiler (2002) reported a relationship between measurement position and E_c, citing higher rates near the base of trees in comparison to rates between rows. While the influence of roots near the base of the tree may partly explain the spatial variability of E_c observed in stands, we found no significant difference between root volume or root surface area and measurement position within a stand. However, as previously discussed, sampling soil directly below the measurement chamber may not adequately capture all roots contributing to the observed soil CO_2 efflux. The fact that we observed an effect due to measurement position may in fact be due to the greater influence of root respiration near the base of a tree; however, our sampling failed to fully capture influential roots if this is the case. For example, the influence of the taproot and major lateral roots were not accounted for in our cores. We also observed no spatial difference in CWD density. The distribution of CWD in the mineral soil, while highly variable across sites, did not vary between locations on the bed and interbeds.

In contrast, we observed a spatial pattern in relation to mineral soil [C] on our sites. Mineral soil C was significantly greater on the beds near trees in comparison to that between rows on the interbeds. The fact that mineral soil C in the top 20 cm below our measurement location is a weak, yet significant E_c driver on our sites and the observation that measurement location affects E_c on our sites suggests that differences in mineral soil C are partly responsible for the spatial variation we observed. Higher mineral soil C near the base of trees may be the combined result of greater root exudates and root turnover near the tree base, which both contribute to the belowground C pool in loblolly pine forests (Andrews et al., 1999; Luan et al., 1999). However, our data do not suggest differences in root-related C additions to the mineral soil are responsible for higher mineral soil C near trees since we did not observe greater root volumes in soil samples taken near the tree base. A more likely explanation is that greater [C] in mineral soil sampled next to trees is due to site preparation utilized on the study sites. All of our sites were bedded, which incorporates residual C and slash (i.e. CWD) closer to the trees. Perhaps CWD incorporated into beds decomposes quickly (i.e. prior to planting), resulting in a greater pool of mineral soil C, which serves as an accessible substrate for microbes. CWD is an important input into the forest soil C pool in some forest systems, and decomposition rates have been shown to vary depending on management and environmental influences (Trumbore et al., 1996; Progar et al., 2000; Wang et al., 2002; Davis et al., 2003).

5. Conclusions

The trends observed on our sites will likely apply to other stands with similar soils and cultural practices. The positive relationship between E_c and soil temperature that we observed is well-documented (e.g. Pangle and Seiler, 2002). Our results further support findings that the relationship between E_c and root and soil characteristics is influenced by loblolly pine forest management (Pangle and Seiler, 2002). Stand age and volume were not correlated with E_c on our sites due to opposite trends over time in belowground autotrophic biomass and C substrate available to heterotrophs, which is likely the result of bedding. However, Wiseman and Seiler (2004) found a positive relationship between E_c and stand age in Virginia Piedmont loblolly pine stands located on well-drained, loamy soils that were chopped and burned prior to planting. Gough et al. (2004) attributed the increase in E_c over time on the same sites to an increase in total respiring root biomass, citing that minimal soil disturbances and fewer soil C inputs on Virginia sites resulted in limited heterotrophic respiration early in the rotation. Therefore, because spatial and temporal trends in soil C and roots vary depending on management and soil properties, the relationships we observed between E_c and some stand parameters, including age and volume, may differ for other less similar stands. Lastly, lateral movement of soil CO_2 in the profile likely limits the value of correlations between E_c and root and soil C parameters directly below the E_c measurement cuvette. Clearly, methodology is an important consideration and challenge when attempting to make correlative comparisons between spot E_c measurements and belowground characteristics.

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