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Biotic and abiotic factors regulating forest floor CO_2 flux across a range of forest age classes in the southern Appalachians

James M. Vose[a,*], Paul V. Bolstad[b]

[a]USDA Forest Service Coweeta Hydrologic Laboratory, 3160 Coweeta Lab Rd, Otto, NC 28763, USA
[b]Department of Forest Resources, College of Natural Resources, 115 Green Hall, University of Minnesota, St. Paul, MN 55108-1027, USA

Summary

We measured forest floor CO_2 flux in three age classes of forest in the southern Appalachians: 20-year-old, 85-year-old, and old-growth. Our objectives were to quantify differences in forest floor CO_2 flux among age classes, and determine the relative importance of abiotic and biotic driving variables. Forest floor CO_2 flux was measured using an openflow infrared gas analyzer measurement system for 24 h periods and samples were taken every 2 months over a 2-year period. Litter/soil interface, soil temperature (5 cm depth), soil moisture (%), forest floor moisture (%), forest floor mass, fine root ($\leqslant 2$ mm) mass, coarse root mass (> 2 mm), forest floor C and N (%), fine root C and N, coarse root C and N, and soil N and C were co-measured during each sample period. Results showed significant nonlinear relationships ($r^2 = 0.68$ to 0.81) between litter/soil interface temperature and forest floor CO_2 flux for all three forest age classes, but no differences in temperature response parameters. These results indicated no differences in forest floor CO_2 flux among age classes. Considerable temporal variation in abiotic and biotic variables was observed within and among forests. Biotic variables correlated with forest floor CO_2 flux included indices of litter and root quality. Differences in biotic variables correlated with forest floor CO_2 flux among forests may have been related to shifts in the relative importance of heterotrophic and autotrophic respiration components to overall forest floor CO_2 flux.
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*Corresponding author. Tel.: +1 11 828 524 2128.
E-mail address: jvose@fs.fed.us (J.M. Vose).

Introduction

Terrestrial forest ecosystems are major components of the global C cycle. Estimates of forest respiration contributions to the atmosphere are substantial (e.g. $>100\,\mathrm{Gt\,y^{-1}}$), but there is considerable uncertainty in these estimates. Carbon dioxide evolution from the forest floor (soil and litter combined) is a major component of C cycling in terrestrial forest ecosystems. Because a significant portion of total ecosystem C is below ground (approximately 50%, Raich and Nadelhoffer, 1989), knowledge of below ground C dynamics is critical for understanding ecosystem C cycling. However, despite numerous studies of forest floor respiration, the magnitude and variation in forest floor CO_2 flux among and within both disturbed and undisturbed forest ecosystems are still largely unknown.

There are several sources of forest floor CO_2: root-derived CO_2, plant-derived CO_2, soil organic matter derived CO_2, rhizosphere respiration, heterotrophic respiration, and respiration by autotrophs (Kuzyakov, 2006). Determining the relative importance of each of these contributing sources has proven problematic (Singh and Gupta, 1977; Hanson et al., 2000; Kuzyakov, 2006); however, studies indicate that the root contribution varies between one-third and two-thirds of the total (e.g., Edwards and Sollins, 1973; Ewel et al., 1987; Raich and Nadelhoffer, 1989; Behera et al., 1990; Bowden et al., 1993b; Borken and Beese, 2005). Variation in root contribution implies substantial variation in root biomass and activity, variation in the population size and activities of soil/litter microbes and fauna, and variation in the quantity and quality of soil and litter C pools.

Forest floor CO_2 evolution varies seasonally, diurnally, and spatially. This is due in part to temperature-, moisture-, and nutrient-driven changes in microbial and microfaunal populations and metabolic activity, and in part to variation in root biomass and respiration associated with forest type, structure, and disturbance (Anderson, 1973; Edwards and Sollins, 1973; Edwards and Harris, 1977; Garrett et al., 1978; Schlentner and Van Cleve, 1985; Weber, 1985; Gordon et al., 1987; Weber, 1990; Hanson et al., 1993; Murthy et al., 2003; Gough and Seiler, 2004). Forest floor CO_2 evolution is also influenced by organic matter quantity and quality, as demonstrated by the positive correlation between litter fall type and respiration at global scales (Raich and Nadelhoffer, 1989).

The strong linkages between forest floor CO_2 flux and the physical environment, species composition, and litter production implies that surface CO_2 evolution should vary with disturbances that alter these driving variables. Therefore, we require an understanding of both (1) the causes, magnitude, and duration of forest floor CO_2 evolution responses to disturbance, and (2) the significance and temporal/spatial variation of abiotic and biotic driving variables. The purpose of our study was to understand and predict variation in forest floor CO_2 flux over broad environmental and biological gradients driven by differences in topography and disturbance history. More specifically, our objectives were: (1) to quantify forest floor CO_2 flux in three forest age classes (20-year-old, 85-year-old, and old-growth (>150-year-old)), and (2) to identify and contrast functional relationships between forest floor CO_2 flux and relevant abiotic and biotic factors among forest age classes.

Materials and methods

Site descriptions

The study was conducted at the Coweeta Hydrologic Laboratory, a 2100 ha forested basin, located in Macon County, North Carolina and at the Joyce Kilmer-Slickrock Wilderness, a 6805 ha basin located in Graham County, North Carolina and Monroe County, Tennessee. Both study locations are situated in the Blue Ridge Province of the southern Appalachians, which is characterized by abundant rainfall (mean annual precipitation is $\sim$1800 mm) and moderate temperatures (mean annual temperature is $\sim$12.6 °C) (Swift et al., 1988; Newell et al., 1997).

Within the Coweeta basin, two paired watersheds (WS2 and WS7) were selected for study. Watershed 2 is 12 ha, has a south-southeast aspect, and spans an elevation range of 709–1004 m. Watershed 2 was selectively logged in the mid-1920s and represents an 85-year-old aggrading second-growth forest. Watershed 7 is 59 ha, has a south aspect, and spans an elevation range of 722–1077 m. Watershed 7 was also selectively logged in the 1920s, and then commercially clear-cut and cable logged in 1977, representing a 20-year-old third-growth forest. Within the Joyce Kilmer-Slickrock basin, we selected the Little Santeelah Creek Watershed because it contained an $\sim$200 ha area which has never been logged; i.e., the Joyce Kilmer Memorial Forest. The Little Santeelah watershed is $\sim$600 ha, has a northeast aspect, and spans an elevation of 762–1318 m. Soil series on WS7 and WS2 include the Chandler

Table 1. Summary of stand characteristics (stems >10 cm) for the three watersheds

Watershed	Basal area ($m^2 ha^{-1}$)	Density (stems ha^{-1})	Aboveground biomass ($t ha^{-1}$)	Belowground mass ($kg ha^{-1}$)	Forest floor mass ($t ha^{-1}$)
~20-year-old	8.6(0.2)	368(57)	75.2(2.0)	10.6(1.2)	22.2(3.1)
~85-year-old	26.9(3.3)	390(27)	224.7(37.7)	24.2(2.8)	26.0(2.7)
Old-growth	76.8(7.4)	276(24)	451.0(47.6)	14.3(1.9)	26.7(2.4)

Data are plot means ($n = 3$) and standard errors.

(WS7 only) and Fannin Series (slopes and ridges) and the Cullasaja-Tuckasegee complex (coves). Soil series at Joyce-Kilmer include the Cheoah and Jeffrey (slopes and ridges) and the White Oak and Spivey (coves).

Study plots

Three 0.15 ha circular plots were located in each watershed in cove, mid-slope, and ridge topographic positions. On each plot, overstory (trees >10 cm at dbh) trees were measured for dbh (by species) at the beginning of the sample period (Table 1). Biomass was estimated using equations from Clark and Schroeder (1986). Substantial differences in basal area and aboveground biomass existed among the sites, which is reflective of the vast differences in stand ages and disturbance history. Species composition also varied among the sites (Table 2), with the 85-year-old stand composed primarily of a mixture of *Quercus* spp. *Quercus* species were present in the 20-year-old and old-growth stands as well; however, both age classes had a higher proportion of *Liriodendron tulipifera* relative the 85-year-old-stand.

Forest floor CO₂ flux measurements

Forest floor CO_2 flux was measured with a custom built, automated, flow-through system (FTS). The FTS uses a combination of solenoids, a multiplexor, push and pull pumps, a datalogger, and flow meters to deliver, control, and monitor airflow to and from the measurement chambers (Bolstad and Vose, 2005). Chambers were constructed of PVC pipe (7.62 cm diameter) with inlet and outlet fittings in the top of the chambers. Chambers were sharpened on the open end to facilitate placement. Within the chambers, perforated tubing was used to mix the air. The system is designed to measure up to ten chambers sequentially for 24-h periods. Carbon dioxide concentration [CO_2] entering and exiting the chambers was measured and logged with a battery powered infrared gas analyzer (IRGA, ADC-LCA4). Air delivered to the chambers was drawn

Table 2. Overstory species composition for each site. Species listed comprise >70% of the biomass at each site

Site	Species (% total biomass)
20-year-old-stand	*Liriodendron tulipifera* (15%) *Acer rubrum* (15%) *Quercus prinus* (9%) *Betula lenta* (9%) *Robinia pseudoacacia* (8%) *Carya* spp. (6%) *Tsuga canadensis* (5%) *Quercus rubra* (3%)
85-year-old-stand	*Quercus prinus* (33%) *Quercus alba* (10%) *Acer rubrum* (10%) *Oxydendrum arboreum* (8%) *Quercus velutina* (7%) *Quercus coccinea* (7%)
Old-growth-stand	*Liriodendron tulipifera* (21%) *Quercus rubra* (15%) *Acer rubrum* (12%) *Tsuga canadensis* (9%) *Quercus prinus* (9%) *Betula lenta* (6%)

from a 20 l ballast from the inlet side of pump #1 and delivered to the chamber from the outlet side of the pump #1. A sample line was also connected to the ballast from the reference side of the IRGA to measure [CO_2] of the inlet air. Outlet air was sampled from the chamber using pump #2, which sampled at a rate equal to or within ±5% of the inlet air flow rate, and delivered outlet air to the IRGA, where outlet [CO_2] was measured. Typical air flow rates ranged from 1000 to 1500 ml min⁻¹. The higher flow rates (i.e., 1500 ml min⁻¹) are used in the summer to ensure steady-state conditions during the measurement period. Chambers were measured for 10-min intervals, with inlet and outlet flow rate and inlet and outlet [CO_2] measured and logged at 1-min intervals. At the end of a 10 min measurement period, the solenoids for the next chamber were opened and the measurement cycled repeated. Prior to calculating a flux rate, data were examined to ensure that

steady-state conditions were obtained within the measurement period (defined as a constant difference between inlet and outlet $[CO_2]$ for the last 4–5 min of the sample). If steady-state conditions were obtained and inlet and outlet flow rates were balanced (or within $\pm 5\%$), then flux ($\mu mol\,m^{-2}\,s^{-1}$) was calculated based on inlet flow rate, the difference in inlet and outlet $[CO_2]$, and chamber surface area.

Plots were sampled approximately 9–10 times each over a 2-year period during 1995 through 1996. Sampling was conducted nearly bimonthly, although cold temperatures in the winter (which fell below the operating temperature of the IRGA) and limited plot access from treefall caused by hurricane Opal in the Fall 1996 limited sampling on some plots. Despite the weather and access limitations, sample periods were generally equally distributed among seasons. Plots were subdivided into pie-shaped quadrats, and during each sampling period, the quadrat to be sampled was randomly selected. Ten soil chambers were randomly located within each quadrat. One-half of the chambers measured soil CO_2 flux from both the soil and litter (the sharpened end of the chamber was pushed through the litter layer and approximately 1 cm into the soil surface). The other one-half of the soil chambers measured soil CO_2 flux from the soil surface only. For this half the forest floor material was removed, replaced with Styrofoam peanuts approximately 2.5 depth, and the soil chambers placed 1 cm into the soil surface.

Biotic variables

Forest floor mass, moisture content, and N and C concentrations were determined beneath the chambers which measured the combined contributions of soil and forest floor to overall flux. After CO_2 measurements, the forest floor within the dimension of the soil chamber was removed down to the mineral soil, placed in paper bags, and transported to the laboratory where it was weighed, dried at 60 °C for 48 h, and re-weighed. Dried forest floor material was composited across cores, ground, and analyzed for N and C with a Perkin-Elmer CHN Analyzer. Hence, forest floor N and C data were available at the plot level for each measurement period.

Fine ($\leqslant 2$ mm) and coarse root (> 2 mm) mass beneath each soil chamber (with and without litter) was determined by sampling soil and roots with a 7.6 cm diameter and 50 cm depth steel cylinder. The cylinder was sharpened on one

end and driven into the ground with a hammer to 30 cm depth. Soil and roots were extracted from the cylinder and returned to the laboratory, where they were stored in a refrigerator at 5 °C until processed. In the first processing step, soil and root samples were thoroughly mixed in a five-gallon bucket, and a 50 g composite soil sample was taken. The remaining soil/root mixture was washed over a 1 mm sieve and live roots (separated by fine and coarse size classes) and dead roots were separated from the soil. Dead roots were determined by visual inspection and texture. Root material was dried at 60 °C for 48 h, weighed, and ground. Dried fine roots, coarse roots, dead roots, and soil samples were composited (separately) across cores, root tissue was ground, and N and C determined using a Perkin-Elmer CHN Analyzer. Hence, root N and C data were available at the plot level for each measurement period.

Abiotic variables

During CO_2 sampling, soil temperature under a chamber was measured at 5 randomly selected chamber locations using thermocouples located at the litter soil interface and 5 cm soil depth. Soil moisture was measured using Time Domain Reflectometry (TDR) to a 15 cm depth. TDR rods were inserted in the center locations of the soil beneath each soil chamber and pre- and post-measurement soil moisture determined, and subsequently averaged to determine soil moisture over the measurement period.

Statistical analyses

Differences in forest floor CO_2 flux from chambers with litter vs. chambers without litter were determined with analyses of variance (PROC ANOVA; SAS, 1987). Analyses were conducted separately for each watershed using plot level means for all measurements ("annual") and for data separated by growing season (April–September = 'growing season'; October–March = 'dormant season'). Temperature and moisture response functions of the form:

$$\text{forest floor } CO_2 \text{ flux} = \beta_0\, e(\beta_1\, T),$$

where forest floor CO_2 flux = mean daily (24 h) flux from chambers with litter, β_0 and β_1 are parameters of the regression, and T = mean daily (24 h) litter/soil interface temperature, was fit using nonlinear regression (PROC NLIN; SAS, 1987). Significance of the regressions was determined by examining the asymptotic 95% confidence intervals of the

parameter estimates (i.e., if the 95% CI encompassed zero, then the parameter was not significant). The importance of soil moisture was tested using the model form reported in Bolstad and Vose (2005); however, soil moisture was never significant in the models. The importance of biotic variables in explaining variation in forest floor CO_2 flux was determined by correlation analyses both within and among sites. A significance level of $\alpha = 0.05$ was used for all statistical tests.

Results

Variation in abiotic and biotic variables

There was substantial variation in abiotic and biotic driving variables both within a watershed and among watersheds (Table 3). For example, across measurement periods, litter/soil interface temperature varied by ~20 °C, soil moisture varied by ~20%, and forest floor moisture varied by ~40–60%. Substantial within/among watershed variation was also observed for biotic variables. Most biotic variables varied three to fourfold (e.g., forest floor N, soil C, coarse root N, fine root N, and some varied as much as 25-fold (e.g., soil N)). There was very little difference in forest floor mass among the three forest age classes. Coarse root and fine root mass were considerably greater (two- to threefold) in the 85-year-old forest relative to either the 20-year-old forest or old-growth forest, whose values were comparable. Soil C and N were twofold greater in the old-growth forest than the 20- and 85-year-old forest. Soil temperature was slightly lower and soil moisture higher at the old-growth site.

Measured flux rates

Annual forest floor CO_2 flux rates ranged from 5.19 $\mu mol\,m^{-2}\,s^{-1}$ in the 20-year-old stand to 7.34 $\mu mol\,m^{-2}\,s^{-1}$ in the 85-year-old stand (Table 4). Growing season values were approximately 30% higher than the annual averages, and ranged from 7.34 $\mu mol\,m^{-2}\,s^{-1}$ in the 20-year-old-stand to 9.10 $\mu mol\,m^{-2}\,s^{-1}$ in the 85-year-old stand. Non-growing values were approximately 50% lower than the annual averages, and ranged from 2.74 $\mu mol\,m^{-2}\,s^{-1}$ for the 20-year-old stand to 4.29 $\mu mol\,m^{-2}\,s^{-1}$ for the 85-year-old stand.

Effects of litter

Averaged across all measured periods, CO_2 flux from chambers with the forest floor layer ranged from 5% (old-growth) to 16% (85-year-old forest) greater than from chambers without the forest floor layer (Table 4); however, due to substantial seasonal and spatial variation within watersheds, these differences were not statistically significant. To account for some of the seasonal variation in biological activity (temperature and non-temperature dependent) we also performed ANOVA's on soil CO_2 flux data separated by growing season (April to September = 'growing season' and October to March = 'non-growing season') (Table 4). Patterns of differences between intact forest vs. no forest

Table 3. Summary of abiotic and biotic driving variables

Variable	~20-year-old		~85-year-old		Old-growth	
	Mean	Range	Mean	Range	Mean	Range
Litter T (°C)	9.6(1.3)	−2.5–19.8	11.0(1.2)	−2.6–21.3	8.8(1.0)	0.2–17.9
Soil T (°C @5 cm)	10.2(1.1)	2.3–19.6	11.7(1.1)	3.3–19.5	8.6(0.9)	−0.3–16.9
Soil moisture (%)	21.0(0.01)	13.0–30.0	26.0(0.01)	13.0–34.0	28.0(0.01)	20.0–39.0
Forest floor mass (g m^{-2})	2224(178)	1214–5210	2600(179)	1214–4938	2667(143)	1708–4419
Coarse root mass (g m^{-2})	720(81)	269–2022	1468(204)	695–4273	978(99)	331–2150
Fine root mass (g m^{-2})	340(24)	170–720	947(279)	287–7773	453(36)	210–812
Forest floor N (%)	1.34(0.06)	0.52–1.80	1.04(0.05)	0.71–1.74	1.37(0.05)	0.91–1.93
Forest floor C (%)	41.2(1.3)	19.8–49.4	43.2(2.0)	22.7–62.8	44.0(1.3)	28.7–50.7
Coarse root N (%)	0.88(0.07)	0.35–1.87	0.47(0.04)	0.20–0.90	0.66(0.03)	0.28–0.97
Coarse root C (%)	47.8(0.9)	44.3–69.2	47.3(0.4)	41.7–51.8	47.4(0.4)	40.8–50.0
Fine root N (%)	1.11(0.06)	0.55–1.87	0.68(0.02)	0.52–0.92	1.06(0.03)	0.74—1.39
Fine root C (%)	43.9(1.1)	31.3–51.4	47.9(0.5)	43.3–52.4	45.8(0.7)	39.1–50.5
Soil N (%)	0.19(0.03)	0.05–0.65	0.21(0.04)	0.04–1.02	0.39(0.03)	0.18–0.62
Soil C (%)	3.0(0.2)	1.3–6.5	2.9(0.2)	1.8–5.2	6.9(0.6)	2.9–12.0

Data are sample period means, standard errors, and range.

Table 4. Mean measured forest floor CO_2 flux ($\mu mol\,m^{-2}\,s^{-1}$) for annual, growing season, and non-growing season measurement periods

Stand age	Period	With litter	Without litter
~20-year-old	Annual	5.19(1.01)	4.77(0.79)
	Growing season	7.34(1.65)	6.32(1.14)
	Non-growing season	2.74(0.66)	3.01(0.89)
~85-year-old	Annual	7.34(1.19)	6.31(1.02)
	Growing season	9.10(1.67)	8.15(1.39)
	Non-growing season	4.29(0.97)	3.44(0.78)
Old-growth	Annual	5.41(0.98)	5.16(1.05)
	Growing season	7.99(1.39)	7.53(1.73)
	Non-growing season	4.20(1.20)	4.04(1.26)

No statistically significant differences were detected when comparing litter vs. without litter flux rates. Data are means and standard errors.

Table 5. Parameters for non-linear regression of mean daily (24 h) litter/soil interface temperature vs. mean daily (24 h) forest floor CO_2 flux ($\mu mol\,m^{-2}\,s^{-1}$)

Stand age	Parameter (SE)	95% confidence interval	Q_{10}	$\sim r^2$
20-year-old	β_0 1.85(0.89)	0.02–3.68	2.64	0.68
	β_1 0.10(0.03)	0.04–0.16		
85-year-old	β_0 1.31(0.63)	0.01–2.61	3.56	0.81
	β_1 0.13(0.03)	0.07–0.18		
Old-growth	β_0 2.09(0.91)	0.22–3.97	2.64	0.70
	β_1 0.10(0.03)	0.03–0.16		
All stands	β_0 2.34(0.63)	1.08–3.59	2.14	0.65
	β_1 0.08(0.02)	0.04–0.11		

Approximate r^2 calculated as 1−(sum of squares residual/uncorrected total sum of squares).

floor were generally comparable to annual values and no statistically significant differences were observed.

Temperature-based models

Litter/soil temperature explained from 68% to 81% of the variation in forest floor CO_2 flux (with litter) among the three watersheds (Table 5; Fig. 1a–c) (soil temperature explained less variation so only litter/soil interface models are presented). All parameters of the nonlinear regressions were statistically significant; however, parameter (β_0 and β_1) values were not significantly different (based on overlapping 95% confidence intervals) among the three forest age classes. Temperature response curves were similar (Fig. 2), except at litter/soil temperatures $>15\,°C$ where the 85-year-old-stand began to rise more sharply than the other stands. Q_{10} values were 2.64 for the 20-year-old and old growth forest, and 3.56 for the 85-year-old forest. The greater Q_{10} value for the 85-year-old forest implies a steeper temperature response for the mid-successional forest relative to early-successional and old-growth forest.

Biotic driving variables

The relationship between biotic variables and forest floor CO_2 flux was determined by correlation analyses with observed forest floor CO_2 flux. Within stands, litter and root N concentration were the primary correlates. In all stands, forest floor CO_2 flux was negatively correlated with litter C/N ratio ($r = -0.32$ in 20-year-old stand; $r = -0.39$ in 85-year-old stand; $r = -0.57$ in old-growth stand; all $P<0.0001$). Litter N was positively correlated with forest floor CO_2 flux in both the 20-year-old stand ($r = 0.26$; $P<0.0001$) and the old-growth stand ($r = 0.59$; $P<0.0001$). Fine root N was positively correlated with forest floor CO_2 flux in the 20-year-old stand ($r = 0.26$; $P<0.0001$) and coarse root N was positively correlated with forest floor CO_2 flux in the 85-year-old stand ($r = 0.34$; $P<0.0001$).
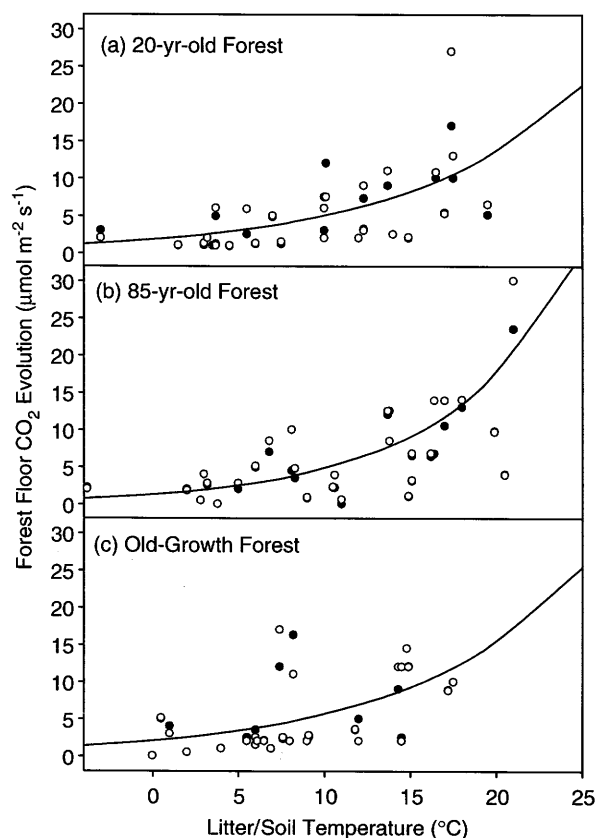
Figure 1. (a–c) Mean daily (24 h) forest floor CO_2 evolution with (open symbols) and without (closed symbols) forest floor vs. mean daily (24 h) litter/soil interface temperature for 20-year-old (a), 85-year-old (b), and old growth (c) forest. Solid lines are predicted values for forest floor CO_2 evolution (with forest floor) using age-specific parameters from Table 5.

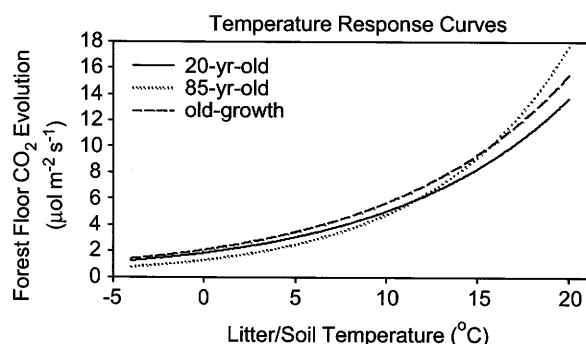Figure 2. Predicted forest floor CO_2 evolution (with litter) for all forest age classes across (parameters from Table 5) across a typical range of litter/soil interface temperatures.

Discussion

Measured flux rates

Measured flux rates were comparable to those observed in other studies in the southern Appala-

chian region (Bolstad and Vose, 2005) and those observed in other temperate deciduous forests using a variety of techniques (Hanson et al., 1993; Davidson et al., 1998; Bolstad et al., 2004). The general pattern of increased flux rates in the 20-year-old vs. 85-year-old stand is consistent with Coleman et al. (2002) who re-measured forest floor CO_2 flux in aggrading watersheds using the same measurement technique and found a near doubling of forest floor CO_2 flux in August after 25 years of forest growth. To our knowledge, forest floor CO_2 flux rates for old-growth forests in the southern Appalachians have never been measured prior to our study and very few estimates exists for old-growth ecosystems in general (Sulzman et al., 2005). Despite the more than two-fold difference in aboveground biomass, forest floor CO_2 flux from the old-growth stand was lower than the 85-year-old stand and only slightly greater than the 20-year-old stand. The intermediate forest floor flux rates for the old-growth stand may be due to two factors. First, on average, litter/soil temperature was 1–2 °C lower than either the 20-year-old or 85-year-old stand, respectively. Second, the pattern of response may be related to belowground biomass pools. In the old-growth stands, belowground biomass was about $10\,t\,ha^{-1}$ lower than in the 85-year-old stand and about $4\,t\,ha^{-1}$ greater than in the 20-year-old stand (Table 1). The low belowground root biomass in the old-growth stand was surprising. Net primary production typically declines in older stands and the lower fine root biomass may reflect a decrease in below ground production (Chapin et al., 2002). It may also reflect the difficulty in using coring-based sampling approaches for quantifying roots. For example, we have limited knowledge of the root distribution patterns in old-growth stands and the 30 cm sample depth may not have been sufficient to adequately sample fine roots.

Differences in species composition may also be a factor controlling forest floor flux rates through its influence on litter quality and fine or coarse root respiration rates. The old-growth and 20-year-old stand had generally similar overstory species composition, while the 85-year-old stand had a higher proportion of *Quercus* spp. (Table 2). We did not measure species-specific litter or root respiration rates; however, both litter decomposition studies (White et al., 1988) and studies examining variation in above-ground tissue respiration rates suggest wide variation among species (Mitchell et al., 1999).

Effects of litter

The relative contribution of litter to overall forest floor CO_2 flux is lower than reported for other hardwood forest ecosystems, where estimates range from 21% to 45% (Edwards, 1975; Garrett and Cox, 1973; Bowden et al., 1993b; Borken and Beese, 2005). The lower relative contribution of litter observed in our study may be related to considerably greater rates of forest floor CO_2 flux in our study. For example, Edwards (1975) measured mean annual forest floor respiration rates of $2.6\,\mu mol\,m^{-2}\,s^{-1}$ from litter+soil and $2.2\,\mu mol\,m^{-2}\,s^{-1}$ from soil (litter contribution $= 0.4\,\mu mol\,m^{-2}\,s^{-1}$), and Garrett and Cox (1973) measured $2.7\,\mu mol\,m^{-2}\,s^{-1}$ from litter+soil and estimated that $2.0\,\mu mol\,m^{-2}\,s^{-1}$ of the total was derived from soil (litter contribution $= 0.7\,\mu mol\,m^{-2}\,s^{-1}$). In contrast, our annual forest floor flux rates ranged from 5.2 to $7.3\,\mu mol\,m^{-2}\,s^{-1}$ from litter+soil and from 4.77 to $6.31\,\mu mol\,m^{-2}\,s^{-1}$ from soil. The contribution from litter ranged from 0.25 to $1.03\,\mu mol\,m^{-2}\,s^{-1}$, values comparable to those other studies (Edwards, 1975; Garrett and Cox, 1973). It is difficult, if not impossible, to determine the biological causes for differences in forest floor flux among studies because methodological differences can greatly influence flux estimates (Cropper et al., 1985; Norman et al., 1992; Rochette et al., 1992; Nay et al., 1994; Bekku et al., 1997). However, conditions in the southern Appalachians are warm and wet, quite conducive to high rates of organic matter decomposition and root respiration, and this may be a factor contributing to the high contribution of soil respiration to the overall forest floor CO_2 flux rates we measured.

Temperature-based models

The strength of the temperature response relationships is comparable to other studies (Hanson et al., 1993; Bowden et al., 1993a; Toland and Zak, 1994; Bolstad and Vose 2005). Q_{10} values for the 20-year-old stand and the old-growth stand are comparable to values reported elsewhere (Raich and Schlesinger, 1992; Butnor et al., 2003); however, the Q_{10} for the 85-year-old forest is higher than has been previously reported. The greater Q_{10} value for the 85-year-old forest implies a steeper temperature response for the mid-successional forest relative to early-successional and old-growth forest. The impact of the high Q_{10} was especially noticeable at litter/soil temperatures $>15\,^\circ C$ (Fig. 2). Because root biomass was considerably greater in the 85-year-old forest than either the 20-year-old or old growth forest, the higher Q_{10} might be related to greater sensitivity of roots to temperature (Nakane et al., 1983; Toland and Zak, 1994). However, Davidson et al. (2006) suggest that Q_{10} values greater than 2.5 indicate that factors other than temperature (e.g., substrate supply) are confounding the temperature-based model. These results indicate the need for a more mechanistic approach and robust models that go beyond simple temperature-based approaches (Gu et al., 2004; Davidson et al., 2006). Despite these limitations, the comparability of temperature-based response functions among the three forest age classes indicates only minor differences in carbon cycling rates when variation in temperature is accounted for. As these models explain 68–81% of the variation forest floor flux, we conclude that the short (i.e., 20 years) and midterm (i.e., 85 years) effects of harvesting on forest floor CO_2 flux in the southern Appalachians are small. These results are consistent with Jurik et al. (1991) who found little difference in forest floor CO_2 evolution in *Populus tremuloides* stands of different disturbance histories and ages (11–70-year-old) and Weber (1990) who found that forest floor CO_2 evolution returned to precut levels after 3 years. Studies examining more immediate responses (0–5-year post harvest) of forest CO_2 evolution to disturbance such as cutting and burning have shown both increased (e.g., Lyle and Cronan, 1998; Ewel et al., 1987; Gordon et al., 1987), no change (Fernandez et al., 1993; Toland and Zak, 1994), and decreased rates (Hendrickson et al., 1985, Weber, 1990; Mattson and Swank, 1989). Initial changes in forest floor CO_2 evolution are expected since forest removal results in dramatic changes in both abiotic and biotic driving variables (Mattson and Swank, 1989; Lyle and Cronan, 1998). Mattson and Swank (1989) examined forest floor CO_2 flux response 6–8 years after clear cutting in the same early successional watershed (WS7) we studied and found a 33% lower flux rate on the regenerating stand relative to an uncut stand (WS2). Hence, in the southern Appalachian hardwood forests we have studied, it appears that forest removal effects on forest floor CO_2 flux are short-term (i.e., <20 years) and not of sufficient magnitude to decrease soil and forest floor C pools. In fact, the combination of increased inputs from logging slash and root mortality, and decreased flux rates in the early stages of succession (Mattson and Swank, 1989) resulted in higher soil C (relative to an 80-year-old aggrading forest) for as long as 17 years post-harvest (Knoepp and Swank, 1997).

Other driving variables

In addition to temperature, forest floor CO_2 flux was primarily related to variables that regulate heterotrophic respiration (i.e., litter C/N ratio, litter N), and to a lesser extent autotrophic respiration (i.e., fine root N and coarse root N) (Vose and Ryan, 2002). Differences among watersheds in biotic variables correlated with forest floor CO_2 flux may indicate differences in the relative importance of heterotrophic and autotrophic respiration to overall forest floor CO_2 flux. For example, fine root N was correlated with forest floor CO_2 flux in the 20-year-old stand and coarse root N was correlated with forest floor CO_2 flux in the 85-year-old stand. By contrast, in the old-growth-stand, none of the root-related variables correlated with forest floor CO_2 flux. There is a clear linkage between soil N, C, and microbial and fungal pool size and activity levels (Scheu and Parkinson, 1995), although studies have shown considerable differences in microbial respiration and biomass between regenerating and old-growth forests (Chang and Trofymow, 1996).

Conclusions

The importance of the soil C pool to ecosystem C budgets requires a complete understanding of patterns of variation and controlling variables across the landscape. The southern Appalachian region of the southern US is an especially challenging location to quantify soil C cycling processes due to complex terrain (which influences microclimate, soils, and vegetation composition) and disturbance history that creates a mosaic of environmental characteristics, species mixes, and forest age classes. This study examined variation among three age-classes (20-year-old, 85-year-old, and old-growth) and found the highest measured flux rates for the 85-year-old stand, but only minor differences in temperature-based response models. These results indicate that southern Appalachian forest soil C-cycling processes recover rapidly from disturbances such as historical and contemporary logging activities.

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