FOREST FLOOR CO_2 FLUX FROM TWO CONTRASTING ECOSYSTEMS IN THE SOUTHERN APPALACHIANS

James M. Vose[1], Barton D. Clinton[1], and Verl Emrick[2]

Abstract: We measured forest floor CO_2 flux in two contrasting ecosystems (white pine plantation and northern hardwood ecosystems at low and high elevations, respectively) in May and September 1993 to quantify differences and determine factors regulating CO_2 fluxes. An automated, IRGA based, flow through system was used with chambers inserted into the soil. This approach allowed quantification of diurnal flux patterns which were subsequently averaged to estimate daily mean flux rates (μmol m^{-2} s^{-1}). Mean flux rates were 60 percent greater in the white pine ecosystem (8.9 μmole m^{-2} s^{-1}) than in the northern hardwood ecosystem (5.6 μmole m^{-2} s^{-1}). Across ecosystems and sample dates, the most important regulating factor was soil temperature ($r^2 = 0.70$; $p < 0.0001$). Mean (24-hr) soil temperature (at 5 cm depth) was 2.5 °C lower in the northern hardwood stand relative to the white pine stand. All other parameters considered (i.e., soil C:N, root mass, root C:N, litter C:N, litter mass) did not explain the differences in flux rates between sites, but variation in fine root mass and litter C:N did explain spatial and temporal variation within the northern hardwood site. These results indicated that at large spatial scales, variation in soil temperature was more important in regulating forest floor CO_2 flux than factors more closely associated with the species composition and productivity of the sites (e.g., litter and root mass and quality).

INTRODUCTION

Carbon dioxide (CO_2) evolution from the forest floor is due to the metabolic activity of roots, mycorrhizae, and soil micro- and macro-organisms. Although precise estimates of carbon (C) recycled to the atmosphere from belowground sources are unavailable, Raich and Schlesinger (1992) propose that the belowground contribution exceeds 70 Pg $year^{-1}$ globally. This represents a major component of C flux in the global C cycle. Belowground C cycling processes and subsequent forest floor CO_2 fluxes are equally important at ecosystem scales; however, we have limited knowledge of the magnitude of fluxes within and across ecosystems. Increased knowledge of the magnitude of C fluxes, as well as the factors which regulate these fluxes is critical for understanding ecosystem C cycling and potential effects of forest management or other factors such as climatic change. In this study, we quantified forest floor CO_2 flux in two contrasting ecosystems: a low elevation 36-yr-old white pine plantation and a high elevation mature northern hardwood stand.

Separating the contributing sources (i.e., roots vs. microbes) of forest floor CO_2 flux has proven difficult. The relative contribution of roots versus other soil components has been estimated to vary between 35 to 65% of the total CO_2 evolved (Edwards and Harris 1977, Ewel and others 1987, Bowden and others 1993). Factors influencing the rate of CO_2 evolution include soil temperature and moisture (through their influence on metabolic activity of both roots and microbes) (Edwards 1975, Schlentner and Van Cleve 1985, Weber 1985), soil organic matter (Ewel and others 1987), soil and root nitrogen (N) levels (Söderstrõm and others 1983, Ryan 1991), and root biomass (Behera and others 1990).

Several techniques are available for measuring CO_2 evolution from the forest floor. Static chamber methods include soda lime or bases (KOH or NaOH) which measure CO_2 "trapped" over the measurement interval (see Cropper and others 1985). Static measures of CO_2 evolution may also be made by gas chromatograph analysis of air samples collected from sealed chambers on the soil surface (Raich and others 1990). de Jong and Schappert (1972) describe a

[1]Research Ecologists and [2]Biological Technician, Southeastern Forest Experiment Station, USDA Forest Service, Coweeta Hydrologic Laboratory, 999 Coweeta Lab Rd., Otto, NC 28763.

variation of the static method by using a chamberless technique based on CO_2 profiles (pCO_2) in the soil. Dynamic chamber methods quantify CO_2 evolution by continuously monitoring CO_2 levels in chambers with either a closed or flow-through system and an infrared gas analyzer (IRGA). Studies comparing measurement techniques have found wide disparity between static chamber, static chamberless, and dynamic chamber methods (Edwards and Sollins 1973, Cropper and others 1985, Raich and others 1990, Rochette and others 1992, Norman and others 1992). In general, static chamber techniques provide lower estimates of CO_2 evolution than dynamic chamber techniques, while pCO_2 techniques provide higher CO_2 evolution estimates than dynamic chamber techniques (de Jong and others 1979). Although more difficult and expensive to conduct, dynamic, IRGA based techniques are considered more reliable (Ewel and others 1987) and they can be configured to quantify diurnal patterns.

The objectives of our study were: (1) to quantify and contrast forest floor CO_2 evolution in two ecosystems in late spring and summer using a dynamic, IRGA based measurement system, and (2) to qualitatively assess the importance of regulating factors such as, fine and coarse root biomass and C:N, soil temperature, litter mass and C:N, and soil C:N.

METHODS

Site Description

The study was conducted at the Coweeta Hydrologic Laboratory in the southern Appalachians of western North Carolina, USA. Two sites were selected for the present study (Table 1). Watershed one (WS1) is a 16.1 ha, 36-year-old white pine plantation (*Pinus strobus* L.). The watershed has a southerly aspect and spans an elevation range of 705 to 988 m. The site selected for study was located in the lower portion (≈715 m) of the watershed. Watershed 27 (WS27) is a 39 ha, ≈85-year-old mixed hardwood watershed. The watershed has a northeast aspect and spans an elevation range of 1061 to 1454 m. The site selected for study is in the upper portion (≈1375 m) of the watershed and contains a northern hardwood forest type.

The range in elevation and aspect between the two watersheds results in differences in climatology. At lower elevations, mean annual precipitation averages ≈1800 mm, while at higher elevations mean annual precipitation averages ≈2200 mm (Swift et al. 1988). Air temperature is also substantially lower (10-15%) at higher elevation sites (Swift et al. 1988).

Table 1. Summary of stand and site characteristics for the white pine and northern hardwood study sites.

Variable	White Pine	Northern Hardwood
elevation (m)	715	1375
stand age (years)	36	≈85
aspect	S	NE
trees ha^{-1}	1015	405
basal area (m^2 ha^{-1})	53.2	32.1
major species	*Pinus strobus* L.	*Quercus rubra* L. *Quercus prinus* L. *Acer rubrum* L.

Forest Floor CO_2 Flux Measurements

Sampling was conducted on four consecutive days in May and September 1993. In the southern Appalachians, May is a period where biological activity is beginning to occur and September is a period of active biological activity. Soil CO_2 flux was measured for 20-22 hrs (i.e., a diurnal cycle) using an automated, flow-through, IRGA based measurement system. Data were averaged to provide an average flux rate (μmol m^{-2} s^{-1}) over the entire sampling interval. The system measured flux sequentially from five soil chambers (10 cm diameter, 10 cm height, 785 cm^3 volume) constructed of PVC pipe. Soil chamber edges were sharpened on the open end and driven approximately 2 cm into the soil surface (at random locations) with a rubber mallet. All tubing was 5 mm (i.d.) flexible PVC. Air was passed through the chambers via inlet and outlet fittings attached to the upper sides of the chamber. Air flow through the chambers was regulated with a dual-sided air pump (Spec-Trex Corp.) which balanced flow into and out of the chambers. Actual flow rate (ml min^{-1}) was controlled by varying voltage (0-12 VDC) supplied to the pump and was measured and logged electronically with a flow meter and data logger (Campbell 21X). An air flow rate of 800 to 1000 ml min^{-1} provided stable readings within 7 to 8 minutes. Chamber sampling was controlled with a multiplexer, data logger, and solenoids which opened sequentially (chambers 1 - 5) at ten minute intervals. Carbon dioxide concentrations of air entering and exiting the chambers was measured and logged electronically with an IRGA (ADC LCA3) operating in differential mode and a data logger (Campbell 21X), respectively. Forest floor CO_2 flux (μmole CO_2 m^{-2} s^{-1}) was calculated based on the difference in CO_2 entering and exiting the chamber, the soil area sampled beneath the chamber, and the flow rate. Only data from the last minute of sampling were used in flux calculations.

Litter and Humus Measurements

Litter and humus were removed from beneath the chambers after flux measurements, dried, weighed, ground, and analyzed for N and C concentration (Perkin-Elmer 2400 CHN Analyzer).

Root Biomass Measurements

Root biomass, separated into fine (< 2 mm) and coarse (>2 mm) fractions, was determined using coring. After flux measurements, a 10 cm diameter metal pipe was placed in the exact chamber location and driven to a 30 cm depth with a mallet. The core was removed and the contents were placed in paper bags, transported to the laboratory, and washed over a fine mesh screen where live and dead roots were visually separated. Roots were dried, weighed, ground, and analyzed for N and C concentration (Perkin-Elmer 2400 CHN Analyzer).

Soil Measurements

Soil N and C (Perkin-Elmer 2400 CHN Analyzer) were determined on a sub-sample of soil from the cores. Soil temperature (5 cm depth) was measured with Type-T thermocouples and a datalogger (Campbell 21X). Soil moisture was not measured.

Statistical Analyses

Differences in temporal and spatial site means of average flux rates were determined with analysis of variance (SAS 1987). Stepwise regression analyses were used to relate between and within site variation (spatial and temporal) in average flux rates to soil temperature, litter mass, fine and coarse root mass, and the quality (i.e., C:N ratio) of soil, roots, and litter (SAS 1987). In all cases, $\alpha = 0.05$ was used for statistical significance and selection of significant parameters in multiple regression analyses.

RESULTS AND DISCUSSION

Forest Floor CO_2 Flux

The magnitude of forest floor CO_2 flux varied considerably between ecosystems and sample dates (Table 2). For example, averaged across sample dates, the flux rate for the white pine stand was 8.9 *u*mole m^{-2} s^{-1} versus 5.6 *u*mole m^{-2} s^{-1} for the northern hardwood stand (differences significant at $p<0.05$). Averaged across sites, May flux rates were also significantly ($p < 0.01$) lower than September flux rates (Table 2). Variation in flux rates within and between ecosystems has been observed in other studies (Garrett and Cox 1973, Hanson and others 1993). For example, Hanson and others (1993) found a maximum 2-fold variation in forest floor flux rates between ridge and valley locations within the same watershed. The values obtained in our study are in the upper range of those observed for many ecosystems (e.g., Weber 1985, Hanson and others 1993); however, comparison of rates with studies using other measurement techniques should be done with caution. Where measurement techniques were similar, our rates are in the range of values obtained by others (e.g., Edwards and Sollins 1973, Ewel and others 1987).

Table 2. Forest floor CO_2 flux by site and date (n = 5 for each sample date and site; † indicates significant [$p < 0.05$] difference between sites for mean flux rate; ‡ indicates significant [$p < 0.05$] difference between sample dates within a site).

Site	Date	Forest Floor CO_2 Flux (standard error)
White Pine	May	5.20(1.28)
	September	11.80(1.59)‡
	Mean =	8.87(1.52)
Northern Hardwood	May	3.22(0.12)
	September	7.46(1.61)‡
	Mean =	5.57(1.13)†

Regulating Abiotic and Biotic Factors

There was substantial variation in most abiotic and biotic factors between and within sites (Table 3). Coefficients of variation ranged from 12 to 118% for the northern hardwood ecosystem and from 19 to 87% for the white pine ecosystem. Based on the results from previous studies, higher forest floor CO_2 flux rates should occur in conjunction with warmer soils, lower C:N ratios in soil and litter, higher root biomass (especially fine roots). Regression analyses using data from both sites and sample periods indicated that temperature was the primary factor regulating spatial and temporal variation in forest floor CO_2 flux across ecosystems (Table 4). This emphasizes the importance of temperature in regulating heterotrophic and autotrophic activity in these ecosystems and indicates that temperature regulation may override variation in biotic factors at large spatial scales (i.e., between ecosystem types occurring at different climatic regimes). In our study, this was true even when the variation in ecosystem type (i.e., pine vs. hardwood ecosystems) and corresponding biotic components was quite large (Table 3). Other studies have also demonstrated the importance of temperature in determining forest floor CO_2 flux (Hanson and others 1993, Peterjohn others 1993). Soil and litter moisture has been shown to influence CO_2 flux in some studies (e.g., Hanson and others

Table 3. Means (n = 10), standard errors (SE), and coefficients of variation for ecosystem parameters used in regression analyses relating forest floor CO_2 flux to abiotic and biotic parameters across and within ecosystem types.

	White Pine		Northern Hardwood	
Parameter	Mean (SE)	Coefficient of Variation %	Mean (SE)	Coefficient of Variation %
Fine Root Mass ($g\ m^{-2}$)	432.4(72.3)	50.2	517.4(102.5)	59.4
Coarse Root Mass ($g\ m^{-2}$)	491.7(151.2)	87.0	762.0(299.9)	118.1
Fine Root C:N	63.9(4.1)	19.1	55.1(2.6)	14.3
Coarse Root C:N	110.6(10.7)	27.3	92.6(9.7)	31.4
Litter Mass ($g\ m^{-2}$)	1018.7(201.8)	59.4	938.0(114.8)	36.7
Litter C:N	40.1(2.5)	18.7	37.4(2.5)	20.0
Soil C:N	23.6(2.9)	36.3	21.2(0.9)	12.4
Soil Temperature (°C)	17.4(1.1)	18.8	15.6(0.7)	13.9

Table 4. Regression equations relating forest floor CO_2 flux to abiotic and biotic driving variables. All variables are significant at $P < 0.05$.

Model Type	Model	r^2	F	P>F
Across Ecosystems	Flux = -14.211 + 1.321 (soil temperature)	0.70	34.6	0.0001
w/in Northern Hardwood	Flux = 13.884 + 0.0099 (fine root biomass) -0.3604 (litter C:N ratio)	0.90	26.7	0.0010
w/in White Pine	Flux = -13.381 + 1.325 (soil temperature)	0.84	32.3	0.0013

1993). While we did not measure soil moisture, litter moisture in our study was always greater than 50%. In addition, we explained from 70 to 90% (see below) of the variation in forests floor CO_2 flux without accounting for variation in soil moisture. This suggests that soil moisture was not a dominant factor regulating spatial and temporal variation in forest floor CO_2 flux in our study.

Within the northern hardwood ecosystem, spatial and temporal variation in fine root mass and litter C:N ratio were important regulators of forest floor CO_2 flux (Table 4). Roots can contribute as much as 60% to forest floor CO_2 flux so it is not surprising that fine root mass is significantly and positively related to forest floor CO_2 flux. Litter quality (i.e., C:N ratio) is an important parameter regulating decomposition rate and the negative regression coefficient indicates less forest floor CO_2 flux (i.e., decomposition) as litter quality decreases. These results contrast with those found across ecosystems, where only soil temperature was related to spatial and temporal variation in forest floor CO_2 flux. Hence, during late spring and summer, within site variation in forest floor CO_2 flux was driven primarily by variation in biological components (i.e., root mass and litter quality) rather than soil temperature. We are reasonably certain, however, that temporal variation in soil temperature within the northern hardwood ecosystem would be an important variable if measurements in winter months were also included.

In the pine ecosystem, soil temperature was the only statistically significant factor regulating temporal and spatial variation in forest floor CO_2 flux (Table 4). It is noteworthy that some of the other parameters (i.e., soil C:N, coarse root C:N, and coarse root mass) were marginally significant ($p < 0.10$) when included in multivariable regressions. This indicates that while temperature is the most important factor, other factors may also be important and larger sample sizes are required to detect statistical significance.

SUMMARY AND CONCLUSIONS

Based on measurements in early spring and summer, forest floor CO_2 flux rates varied considerably (60 percent) between the white pine and northern hardwood ecosystems. Flux rates are a function of multiple and complex abiotic and biotic factors which vary in time and space. Between ecosystems, temperature was the most important driving variable; however, within the hardwood ecosystem, variation in fine root mass and litter quality were important. Hence, the relative importance of driving variables depends on the scale of study and the magnitude of variation in climatic, edaphic, and biological parameters within and between ecosystems. The short-term study presented here provides some interesting preliminary insights, however a more complete understanding of these relationships will require a much more intensive and extensive study. Our current research is focusing on including more ecosystem types and more intensive measurements (i.e., monthly sampling intervals).

LITERATURE CITED

Behera, N., S.K. Joshi, and D. Pati. 1990. Root contribution to total soil metabolism in a tropical soil from Orissa, India. For. Ecol. Manage. 36:125-134.

Bowden, R.D., K.J. Nadelhoffer, R.D. Boone, J.M. Melillo, and J.B. Garrison. 1993. Contributions of aboveground litter, belowground litter, and root respiration to total soil respiration in a temperate mixed hardwood forest. Can J. For. Res. 23:1402-1407.

Cropper, W.P. Jr., K.C. Ewel, and J.W. Raich. 1985. The measurement of soil CO_2 evolution in situ. Pedobio. 28:35-40.

de Jong, E., and H.J.V. Schappert. 1972. Calculation of soil respiration and activity from CO_2 profiles in the soil. Soil Sci. 113:328-333.

de Jong, E., R.E. Redmann, and E.A. Ripley. 1979. A comparison of methods to measure soil respiration. Soil Sci. 127(5): 300-306.

Edwards, N.T., 1975. Effects of temperature and moisture on carbon dioxide evolution in a mixed deciduous forest floor. Soil Sci. Soc. Am. J. 39:361-365.

Edwards, N.T., and W.F. Harris. 1977. Carbon cycling in a mixed deciduous forest floor. Ecology 58:431-437.

Edwards, N.T., and P. Sollins. 1973. Continuous measurement of carbon dioxide from partitioned forest floor components. Ecology 54:406-412.

Ewel, K.C., W.P. Cropper, Jr., and H.L. Gholz. 1987. Soil CO_2 evolution in Florida slash pine plantations. I. Importance of root respiration. Can. J. For. Res. 17:325-329.

Garrett, H.E., and G.S. Cox. 1973. Carbon dioxide evolution from the forest floor of an oak-hickory forest. Soil Sci. Soc. Am. J. 37:641-644.

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

Norman, J.M., R. Garcia, and S.B. Verma. 1992. Soil surface CO_2 fluxes and the carbon budget of a grassland. J. Geophysical Res. 97:18845-18853.

Peterjohn, W.T., J.M., Melillo, F.P. Bowles, and P.A. Steudler. 1993. Soil warming and trace gas fluxes: experimental design and preliminary results. Oecologia 93:18-24.

Raich, J.W., R.D. Bowden, and P.A. Steudler. 1990. Comparison of two static chamber techniques for determining carbon dioxide efflux from forest soils. Soil Sci. Soc. Am. J. 54:1754-1757.

Raich, J.W., and W.S. Schlesinger. 1992. The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. Tellus 44B:81-99.

Rochette, P., E.G. Gregorich, and R.L. Des Jardins. 1992. Comparison of static and dynamic closed chambers for measurement of soil respiration under field conditions. Can. J. Soil Sci. 72:605-609.

Ryan, M.G. 1991. The effect of climate change on plant respiration. Ecol. App. 1:157-167.

SAS Institute. 1987. SAS/STAT guide for personal computers, version 6. SAS Institute Inc., Cary, NC.

Schlentner, R.E., and K. Van Cleve. 1985. Relationships between CO_2 evolution from soil, substrate temperature, and substrate moisture in four mature forest types in interior Alaska. Can. J. For. Res. 15:97-106.

Söderström, B., E. Bååth, and B. Lundgren. 1983. Decrease in soil microbial activity and biomasses owing to nitrogen amendments. Can J. Microbiol. 29:1500-1506.

Swift, L.W., G.B. Cunningham, and J.E. Douglass. 1988. Climate and hydrology. pp. 335-55 In W.T. Swank and D.A. Crossley, Jr. Forest Hydrology and Ecology at Coweeta. Ecological Studies, Vol. 66. Springer-Verlag, New York.

Weber, M.G. 1985. Forest soil respiration in eastern Ontario jack pine ecosystems. Can. J. For. Res. 15:1069-1073.