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

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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 (Söderström 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

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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.

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

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).

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