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Fine root respiration in mature eastern white pine (*Pinus strobus*) *in situ*: the importance of CO_2 in controlled environments

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Summary We measured seasonal fine root respiration rate *in situ* while controlling chamber temperature and $[CO_2]$. Atmospheric $[CO_2]$ ($[CO_2]_a$) and measured soil $[CO_2]$ ($[CO_2]_s$) were alternately delivered to a cuvette containing intact fine roots of eastern white pine (*Pinus strobus* L.). Respiration rates were consistently higher in $[CO_2]_a$ than in $[CO_2]_s$ and were almost three times higher during midsummer. Respiration rates were immediately reversed after returning to the alternate $[CO_2]$ (i.e., $[CO_2]_a \rightarrow [CO_2]_s \rightarrow [CO_2]_a$, and *vice versa*) suggesting a direct effect of elevated $[CO_2]$ on apparent respiration. Soil-$[CO_2]$-based respiration rates decreased with increasing $[CO_2]$ on a dry mass and tissue [N] basis. We conclude that estimates of soil CO_2 flux and soil carbon budgets may be improved by more completely accounting for the rhizosphere microclimate (i.e., soil temperature and $[CO_2]_s$) during measurement of fine root respiration.

Keywords: atmospheric carbon dioxide, carbon dioxide inhibition, rhizosphere microclimate, soil carbon dioxide, soil temperature.

Introduction

Respiration losses account for a large fraction of fixed carbon in plants and may affect yield more than photosynthetic rates (Pearcy et al. 1987). Because of typically high rates of respiration and growth (Ryan et al. 1999), fine roots comprise a potentially large component of overall ecosystem respiration (Bowden et al. 1993, Haynes and Gower 1995, Ryan et al. 1996). Hence, precise estimates of the fine root component of ecosystem carbon (C) cycling are required to develop accurate C budgets. Although there is some information on root respiration rates based on laboratory observations of excised tissue from seedlings (e.g., Barnard and Jorgensen 1977, Drew and Ledig 1981, Lawrence and Oechel 1983) and *in situ* measurements (e.g., Cropper and Gholz 1991, Bowden et al. 1993, Cheng et al. 1993, Ryan et al. 1996), few studies have measured root respiration under conditions comparable to the environment in which roots grow. Only recently have researchers begun to investigate the effects of the rhizosphere environment on fine root respiration (e.g., Qi et al. 1994, Bouma et al. 1997, Burton et al. 1997). The lack of information on *in situ* fine root respiration may be attributed in large part to the methodological difficulties associated with separating roots from the soil while measuring respiration under ambient soil conditions.

Studies determining regulatory controls on fine root (i.e., < 2 mm diameter) respiration have shown that temperature (Cropper and Gholz 1991, Conlin and Lieffers 1993) and tissue nitrogen (N) are major regulatory factors (Amthor 1989, Ryan 1991). In most root respiration studies, respiration rates have been determined over a range of temperatures and tissue N concentrations but not under controlled CO_2 concentration ($[CO_2]$) (except Ryan et al. 1999). Hence, it is not certain how rhizosphere $[CO_2]$ affects root metabolism and the release of fixed carbon from roots. Because rhizosphere $[CO_2]$ can exceed 19,000 ppm (Brook et al. 1983, Kiefer and Amey 1992, Mattson 1994, Yavitt et al. 1995) and varies seasonally and diurnally, the potential interaction between root metabolism and rhizosphere $[CO_2]$ could affect passive as well as active release of CO_2 (Amthor 1991). Recent studies (Qi et al. 1994, Burton et al. 1997) have demonstrated that short-term exposure to elevated $[CO_2]$ results in reduced root respiration; however, the magnitude of the response appears to vary greatly among species. Several mechanisms have been proposed to explain this response, including direct effects (i.e., immediately reversible), indirect effects (e.g., mediated by changes in growth or phytomass composition), and alteration of the CO_2 concentration gradient between rhizosphere and root interior with no actual change in the basal respiration rate (Amthor 1991).

Because most published estimates of fine root respiration have not accounted for the effects of high $[CO_2]$ in the rhizosphere and responses appear to be species specific, additional studies are required to quantify the effects of high $[CO_2]$ and to provide species-level corrections to adjust fine root respiration estimates for the effects of $[CO_2]$. Our objective was to quantify the effects of variation in $[CO_2]$ on respiration rates of fine roots of *Pinus strobus* L. We measured root respiration *in situ* and compared respiration rates (after normalizing for the effects of temperature and N) measured at soil $[CO_2]$ ($[CO_2]_s$) with those measured at atmospheric $[CO_2]$ ($[CO_2]_a$).

Materials and methods

Study site

The study was conducted in a 39-year-old white pine planta-

tion (WS1) at the Coweeta Hydrologic Laboratory in the southern Appalachian Mountains of western North Carolina, USA. The watershed is 16.1 ha, has a southerly aspect, and ranges in elevation from 715 to 990 m. There is little or no understory vegetation because of intensive site preparation and heavy shade. Soils are mesic Typic Hapaludults of the Fannin soil series. Mean (1935–1996) annual rainfall at a nearby climatic station (at 675 m elev.) is 1790 mm. Mean annual air temperature is 12.6 °C and ranges from a mean of 6.7 °C in the dormant season to 18.5 °C in the growing season.

Instrumentation

To maintain and control root temperature comparable to rhizosphere values over the entire $[CO_2]$ exposure period, we enclosed the roots in a custom built, temperature-controlled cuvette (TCC; Hubbard et al. 1995) that maintains temperature within ± 0.5 °C of a set point. The TCC comprised a 460-cm^3 chamber, stirring fan, thermocouples for monitoring chamber and plant tissue temperatures, and a Peltier plate for heating and cooling. Cooling or heating was controlled by a Campbell 21X data logger (Campbell Scientific, Inc., Logan, UT). Soil temperature was monitored in the upper 5 cm of soil with a digital temperature probe (Reotemp Instrument Corp., San Diego, CA), and root temperature in the TCC was adjusted to match rhizosphere conditions. The inlet and outlet sides of the TCC were connected with hoses to a portable infrared gas analyzer (IRGA, ADC LCA-3, Analytical Development Corporation, Hoddeson, England).

Sampling

Sampling was conducted in a 0.10-ha plot located in the lower portion of WS1. Within the plot, 6–12 fine root (< 2 mm diameter) samples were taken from random locations during each measurement period. Sample size was variable because rain forced us to terminate measurements on some sample dates. Loose soil and organic matter were carefully removed by hand from fine roots (located at about 5 cm depth) to ensure that fine roots were not damaged and remained attached to larger root segments. Before placement in the chamber, roots were washed with deionized H_2O to remove tightly held soil and organic matter that would affect dry weights and could be potential sources of CO_2. Roots were patted dry with paper towels before measurement. Approximately 0.2 to 1.5 g dry mass (g_{dm}) of fine roots was placed in the chamber for each measurement.

Soil $[CO_2]$ was determined by measuring $[CO_2]$ at 5 cm beneath the forest floor at several locations with the IRGA's reference sample line and internal pump. Mean $[CO_2]_s$ was calculated and used as the reference concentration for soil in the TCC. This procedure was repeated several times at different locations on each sampling date to account for spatial and temporal variations in $[CO_2]_s$. A low sampling rate (120 ml min^{-1}) was used to measure $[CO_2]_s$ to minimize dilution of $[CO_2]_s$ with $[CO_2]_a$. Although the suction created using our approach is comparable to sampling with a syringe (i.e., 25-ml syringe for 10 s = 2.5 ml s^{-1} with an IRGA sampling line), it is possible that our $[CO_2]_s$ values were lower than actual $[CO_2]_s$ values because of dilution with $[CO_2]_a$. Reference concentrations for atmospheric CO_2 were derived from continuous sampling at 1 m above the forest floor.

Elevated $[CO_2]$ supplied from an external tank of 2000 ppm CO_2 was scrubbed with soda lime as it passed through the IRGA to reduce the $[CO_2]$ delivered to the TCC to match $[CO_2]_s$. Flow rate through the chamber was 200 ml min^{-1}. Roots were first exposed to $[CO_2]_a$ and respiration measured; roots were then exposed to $[CO_2]_s$ and respiration remeasured. The chamber $[CO_2]$ was then returned to the initial concentration, and the process was repeated on a new sample of fine roots. Stable respiration rates were obtained within 15 min of exposure to either $[CO_2]$ treatment. Previous studies (Qi et al. 1994, Burton et al. 1997) have shown that effects of elevated $[CO_2]$ are similar regardless of the order of $[CO_2]$ treatments (e.g., elevated $[CO_2]$ then atmospheric $[CO_2]$ versus atmospheric $[CO_2]$ then elevated $[CO_2]$). Most of the sampling occurred between May and September with additional sampling in November of the same year and February of the following year. During the February measurement period, atmospheric and soil $[CO_2]$ were similar, so no elevated $[CO_2]_s$ measurements were conducted. To test for the reversibility of $[CO_2]$ effects, we measured root respiration on two sampling dates (July and September) at $[CO_2]_a$, followed by measurement at $[CO_2]_s$ generated from the external tank, and remeasurement at $[CO_2]_a$.

After sampling, roots were excised, removed from the chamber, and stored in a cooler until all sampling on that day was complete. Roots were dried at 55 °C for 48 h and weighed. Samples were ground and analyzed for %N with a Perkin-Elmer (Norwall, CT) 20400 CHN elemental analyzer. Respiration rate was expressed on both a dry mass (nmol CO_2 g_{dm}^{-1} s^{-1}) and N (nmol g^{-1} N s^{-1}) basis.

In October, we used the TCC to develop temperature response curves at atmospheric (~370 ppm) and at the mean soil $[CO_2]$ calculated from all sample dates (~800 ppm). Approximately 0.40 to 1.20 g dry mass of root material was placed in the TCC (n = 4 and 5 for atmospheric and soil $[CO_2]$, respectively, and fine root respiration was determined across a range of temperatures from 5 to 30 °C in 5 °C increments). Temperature response curves were fit with an exponential model (i.e., fine root respiration = $(\beta_0 e^{(\beta 1 * T)}$; PROC NLIN, SAS software package; SAS Institute, Cary, NC), yielding β_1 values of 0.027 and 0.048 for atmospheric and soil $[CO_2]$, respectively. Although the β_1 parameters for $[CO_2]_a$ and $[CO_2]_s$ were not significantly different (i.e., 95% confidence intervals overlapped), we used these coefficients to adjust fine root respiration rates for all measurement periods to 15 °C.

We tested for the effects of residence time of roots within the chamber by monitoring fine root respiration rates for 45 min at ambient $[CO_2]_a$ (370 ppm) and at the peak $[CO_2]_s$ (~1200 ppm). We chose to test for the effects of residence time at peak $[CO_2]_s$ based on the assumption that responses at lower $[CO_2]_s$ would be similar or lower than those observed at maximum $[CO_2]_s$. In September, we randomly sampled roots from the plot and prepared them by the same procedures described above. Approximately 0.4 to 0.7 g dry weight of material was placed in the cuvette (n = 3). Stable respiration rates were

obtained after 15 min. There were slight decreases in respiration rates of 9.7 and 8.0% for $[CO_2]_s$ and $[CO_2]_a$, respectively, during the 25–35 min exposure period used in our study, and a 20–22% reduction at 45 min. Hence, our estimates of fine root respiration rates may be slightly lower (8–10%) than actual field values. This reduction is likely a result of root desiccation caused by removing the roots from the moist soil environment and placing them in a stirred chamber. Comparable results for $[CO_2]_s$ and $[CO_2]_a$ indicate that the dry air used to obtain $[CO_2]_s$ did not have a disproportionate effect on root drying, and hence did not influence response patterns.

Statistical analysis

Analysis of variance (PROC ANOVA; SAS software package) was used to test for differences between atmospheric and soil $[CO_2]$ and to test for differences in root respiration rate between $[CO_2]$ treatments by measurement date. The ANOVA and Duncan's Multiple Range Tests were used to determine significant differences in root N among measurement dates. Significant linear relationships between root respiration, root N, and $[CO_2]$ were identified with Pearson correlation analysis and linear regression (PROC CORR and PROC REG, SAS software package). Significant differences for all statistical tests were evaluated at $\alpha = 0.05$.

Results and discussion

Mean root [N] varied considerably across sample dates, with values ranging from 0.70 to 1.38% (Table 1). There was a weak but statistically significant correlation ($r = 0.30$; $P < 0.05$) between root [N] and fine root respiration (nmol g^{-1} s^{-1}, normalized to 15 °C) when measured at $[CO_2]_s$, but not when respiration was measured at $[CO_2]_a$. A positive relationship between tissue [N] and maintenance respiration has been reported previously (Ryan 1991, Ryan et al. 1996) and is related to protein (most N in plant cells is associated with Rubisco protein; Lexander et al. 1970) repair and replacement (Ryan 1995). The lack of a relationship between atmospheric $[CO_2]$ and N may be a result of the $[CO_2]$ to which the roots have been exposed during development (i.e., the CO_2-history of the roots), because growth rate and protein content are, in part, functions of the conditions under which the tissue developed or has been exposed to for an extended period (Amthor 1991). Hence, exposure of fine roots to $[CO_2]_a$ may represent a significant enough departure from $[CO_2]_s$ conditions that respiration responses attributable to tissue [N] are confounded. Because root [N] varies seasonally and affects respiration rate, our analysis of the effects of seasonal variation in $[CO_2]_s$ on respiration rates was potentially confounded by the effects of seasonal variation in [N]. To correct for the effects of [N] on root respiration, we also report analyses on a per unit N basis (i.e., nmol CO_2 g^{-1} N s^{-1}) (Figures 1 and 2).

Soil $[CO_2]$ at 5 cm soil depth varied considerably during the measurement period (Table 1), with values ranging from 345 to 1122 ppm. Differences between $[CO_2]_a$ and $[CO_2]_s$ were significant for all but the February measurement period. Seasonal patterns of root and heterotrophic respiration rates are sources of most of the observed variability in $[CO_2]_s$, which occurs in response to seasonal variation in soil water, soil temperature, root tissue [N] (Barnard and Jorgensen 1977, Cropper and Gholz 1991, Conlin and Lieffers 1993), and root extension or thickening (Head 1968). Agreement between soil and atmospheric $[CO_2]$ during February when soil temperatures were low (4.5 °C) (Table 1) may have resulted from dilution of soil air with atmospheric air, although other studies have also found that $[CO_2]_s$ is close to $[CO_2]_a$ in winter months (Yavitt et al. 1995). Cold soils undoubtedly reduced heterotrophic and root respiration rates such that $[CO_2]_s$ in February was considerably lower than later in the season when soils were warmer. If dilution of soil air did occur, then any subtle differences between $[CO_2]_s$ and $[CO_2]_a$ that might have been difficult to detect in cold soils should be larger and more easily detected in warm soil, because differences between $[CO_2]_s$ and $[CO_2]_a$ increase with increasing soil temperature.

Differences in root respiration rates between soil and atmospheric $[CO_2]$ were greatest during midsummer when the difference between $[CO_2]_s$ and $[CO_2]_a$ was greatest (Figures 1a and 1b). During the dormant season and mid-spring, root respiration rates measured in soil or atmospheric $[CO_2]$ were not significantly different. However, averaged across the measurement periods, fine root respiration estimates made at $[CO_2]_a$ were 2.5-times greater than those made at ambient $[CO_2]_s$.

There was a significant, negative linear relationship between root respiration (at 15 °C) and $[CO_2]_s$ (Figures 2a and 2b). Although we did not determine causal mechanisms, others

Table 1. Reference $[CO_2]$ (ppm; at 5 cm depth for $[CO_2]_s$), soil temperature (°C at 5 cm soil depth), and N concentrations by sample month. Values in parentheses are standard errors. Significant differences ($\alpha = 0.05$) in $[CO_2]$ between atmosphere and soil are indicated by an asterisk. Mean values for %N with the same superscript are not significantly different ($\alpha = 0.05$) across sample dates.

Sample month	CO_2 concentration		Soil temperature	%N
	Atmospheric	Soil		
May	382 (0.5)	504 (1.3)*	14.1 (0.10)	1.38 (0.09)[a]
June	359 (4.9)	569 (2.0)*	17.0 (0)	0.70 (0.05)[b]
July	360 (2.7)	760 (8.5)*	18.0 (0)	0.91 (0.07)[c]
August	397 (8.4)	675 (81.3)*	18.0 (0)	0.88 (0.04)[bc]
September	381 (3.0)	1122 (4.0)*	18.3 (0.10)	0.87 (0.04)[bc]
November	355 (8.4)	600 (9.7)*	6.7 (0.24)	0.93 (0.04)[c]
February	345 (4.0)	345 (4.0)	4.5 (0.16)	1.03 (0.05)[c]

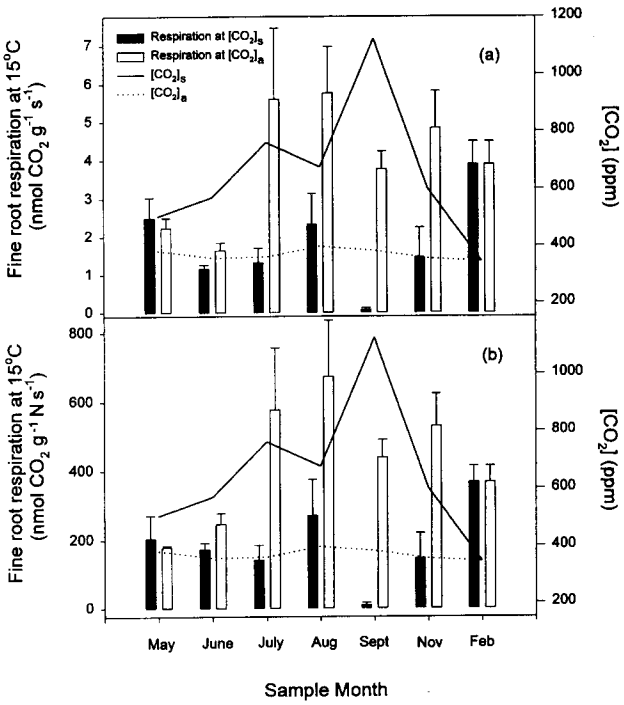

Figure 1. Mean seasonal fine root flux rates (a) nmol CO_2 g_{dw}^{-1} s^{-1}; and (b) nmol CO_2 g^{-1} N s^{-1} measured *in situ* on mature eastern white pine using $[CO_2]_a$ versus $[CO_2]_s$ across seven sample dates. Vertical lines represent +1 SE.

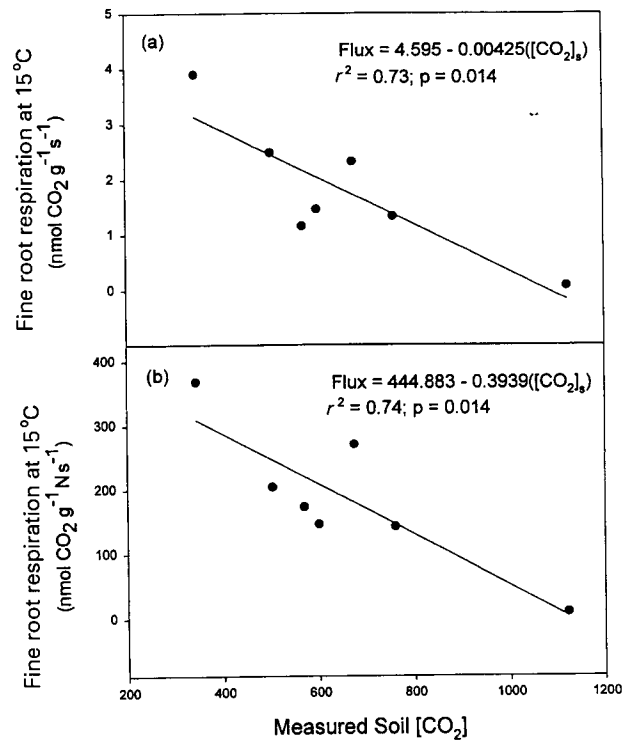

Figure 2. Relationship between $[CO_2]_s$-based fine root respiration rates and measured $[CO_2]_s$. Symbols represent means for each sampling date.

have speculated that decreased respiration at elevated $[CO_2]$ is caused by a combination of direct effects including alterations of intercellular pH, refixation of respired CO_2, suppression of respiratory enzymes, or diversion of electron transport to the cyanide-resistant pathway (Amthor 1991, Amthor et al. 1992, Qi et al. 1994, Burton et al. 1997). On the two sampling dates tested (July and September), the effects of short-term exposure to $[CO_2]$ were reversible (Table 2). However, it is noteworthy that, although differences between respiration rates were not statistically significant, respiration rates were about 20% greater than initial rates when roots were returned to $[CO_2]_a$, indicating that the responses to $[CO_2]$ were not completely reversible perhaps because of the short time frame of our measurements or because of the large difference between $[CO_2]_a$ and $[CO_2]_s$. In studies in which changes in $[CO_2]$ were conducted in a step-wise fashion, complete reversibility was observed for leaves (Amthor et al. 1992) and roots (Nobel and Palta 1989, Burton et al. 1997), indicating a direct effect of elevated $[CO_2]$ (i.e., immediately reversible).

Whatever the causal mechanism, our results are consistent with the pattern of reduced fine root respiration at high soil $[CO_2]$ obtained by Qi et al. (1994) for Douglas-fir (*Pseudotsuga Menziesii* (Mirb.) Franco) and Burton et al. (1997) for sugar maple (*Acer saccharum* Marsh.). However, differences in the magnitude of response among studies suggests that the response is species-specific, perhaps reflecting differences in the relative importance of causal factors contributing to direct effects. For example, across a comparable range of soil $[CO_2]$ (350–1000 ppm), Qi et al. (1994) found a 2.0 to 2.5-times difference in respiration for total and basal respiration, respectively. In contrast, Burton et al. (1997) found only a 1.2-times difference between 350 and 1000 ppm, and we found a 2.5-times difference. Compared with direct effects, indirect effects

Table 2. Fine root respiration rates (normalized to 15 °C) for return samples using $[CO_2]_a$ expressed on a dry weight (nmol CO_2 g_{dw}^{-1} s^{-1} and tissue N basis (nmol CO_2 g^{-1} N s^{-1}); Flux 1 = the initial stable rate based on $[CO_2]_a$ and Flux 2 = the final stable rate based on $[CO_2]_a$ after returning to $[CO_2]_a$ from $[CO_2]_s$. Values in parentheses are standard errors. There were no statistically significant differences in initial and final respiration rates expressed on either a dry weight or N basis for either sample month.

Month	Flux 1		Flux 2	
	Dry weight basis	N basis	Dry weight basis	N basis
July	6.32 (3.83)	618.6 (390.1)	8.09 (5.28)	793.9 (535.4)
September	3.38 (0.29)	392.3 (35.3)	4.17 (0.87)	482.1 (95.3)

include changes in the chemical composition of plant tisue and differences in growth rate (Amthor 1991) resulting from exposure to elevated [CO_2] for extended periods. Although it is unlikely that the short-term [CO_2] exposures used in our experiments and others (Qi et al. 1994, Burton et al. 1997) resulted in any indirect effects, Amthor (1991) speculated that short-term responses to elevated [CO_2] are related to the [CO_2]-history of the plant. Hence, differences in the magnitude of responses among studies may also be related to the experimental approach used. Laboratory studies (e.g., Qi et al. 1994) or studies conducted during only a part of the year (e.g., Burton et al. 1997) may not account for the interaction between [CO_2]-history and short-term responses. This growing body of evidence for reduced root respiration at $[CO_2]_s$ clearly indicates the need to view earlier published estimates of root respiration (measured at lower [CO_2]) with caution. However, differences in the magnitude of the respiration response to [CO_2] among species suggest that there may be no simple correction factor that can be applied universally.

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