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Soil respiration response to three years of elevated CO_2 and N fertilization in ponderosa pine (*Pinus ponderosa* Doug. ex Laws.)

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Abstract

We measured growing season soil CO_2 evolution under elevated atmospheric [CO_2] and soil nitrogen (N) additions. Our objectives were to determine treatment effects, quantify seasonal variation, and compare two measurement techniques. Elevated [CO_2] treatments were applied in open-top chambers containing ponderosa pine (*Pinus ponderosa* L.) seedlings. N applications were made annually in early spring. The experimental design was a replicated factorial combination of CO_2 (ambient, + 175, and +350 $\mu L\ L^{-1}$ CO_2) and N (0, 10, and 20 g m^{-2} N as ammonium sulphate). Soils were irrigated to maintain soil moisture at > 25 percent. Soil CO_2 evolution was measured over diurnal periods (20–22 hours) in October 1992, and April, June, and October 1993 and 1994 using a flow-through, infrared gas analyzer measurement system and corresponding pCO_2 measurements were made with gas wells. Significantly higher soil CO_2 evolution was observed in the elevated CO_2 treatments; N effects were not significant. Averaged across all measurement periods, fluxes, were 4.8, 8.0, and 6.5 for ambient + 175 CO_2, and +350 CO_2 respectively).

Treatment variation was linearly related to fungal occurrence as observed in minirhizotron tubes. Seasonal variation in soil CO_2 evolution was non-linearly related to soil temperature; i.e., fluxes increased up to approximately soil temperature (10cm soil depth) and decreased dramatically at temperatures > 18°C. These patterns indicate exceeding optimal temperatures for biological activity. The dynamic, flow-through measurement system was weakly correlated ($r = 0.57$; $p < 0.0001$; $n = 56$) with the pCO_2 measurement method.

Introduction

Pools and fluxes of soil carbon (C) are major components of the terrestrial C cycle (Raich and Schlesinger, 1992). There have been numerous recent studies examining soil CO_2 evolution, due in part, to predictions that [CO_2]-induced global change will lead to substantial increases in soil CO_2 evolution in temperate and boreal ecosystems (Ryan, 1991). Hence, understanding the effects of altered environmental conditions on the soil C cycle is critical for assessing ecosystem responses to factors such as elevated [CO_2], climatic change, or atmospheric deposition. A more complete understanding of the role of soil C pools and fluxes in regulating the terrestrial C cycle will require soil C budgets from many different ecosystems and different successional stages.

The flux of CO_2 from soils is due to the combined metabolic activity of roots and free living and symbiotic heterotrophs (i.e. fungi, mycorrhizae, and soil

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micro- and macro-organisms). Previous research has documented that soil CO_2 flux is a function of root biomass (Behera et al., 1990), soil temperature and moisture (Edwards, 1975; Hanson et al., 1993; Peterjohn et al., 1994), soil N content (Söderström et al., 1983), and fungal populations (Rygiewicz and Anderson, 1994; Vose et al., 1995). Hence, changes in these driving variables as a result of an altered atmospheric environment could have a direct impact on soil C cycling.

For example, elevated atmospheric [CO_2] has been shown to increase root biomass (Norby et al., 1987; Rogers et al., 1992) and fungal populations (Vose et al., 1995). Increased soil N availability could alter soil CO_2 flux by changing root (Ryan, 1991) and microbial activity and/or biomass (Söderström et al., 1983). Abiotic driving variables vary seasonally and annually; thus, biotic responses to altered environmental conditions may change after long term exposure. Hence, understanding the effects of an altered environmental condition on the soil C cycle requires a long-term study which also accounts for intra-annual variation. Several techniques are available for measuring soil CO_2 evolution from soils. Static methods include soda lime or bases (KOH or NaOH) which measure CO_2 trapped in a collection chamber over the measurement interval (e.g. Cropper et al., 1985). Static measures may also be made by gas chromatography or infrared gas analysis of air samples collected from sealed chambers on the soil surface over time (e.g. Raich et al., 1990). de Jong and Schappert (1972) describe a variation of the static method by using a chamberless technique based on CO_2 concentration 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 (Hanson et al., 1993) or flow-through system (Edwards and Sollins, 1973 ; Vose et al., 1995). Previous comparisons of these measurement techniques have found a wide disparity in soil CO_2 evolution estimates (Cropper et al., 1985; Edwards and Sollins, 1973; Norman et al., 1992; Raich et al., 1990; Rochette et al., 1992). This disparity is particularly problematic when trying to accurately assess the role of soil C cycling in overall system C budgets.

This study is part of a long-term project assessing the impacts of elevated CO_2 and soil N on a variety of above- and belowground processes (Ball and Johnson, 1993). In a previous paper, we reported the first-year responses of soil CO_2 evolution to elevated atmospheric [CO_2] (Vose et al., 1995). However, we must also understand longer-term responses before considering the potential impacts of elevated atmospheric CO_2 on C cycling and other ecosystem processes. In this paper, we report on > 2 years of soil CO_2 flux measurements. Our specific objectives were : (1) to examine the impacts of elevated atmospheric CO_2 and N fertilization on soil CO_2 evolution, (2) to quantify seasonal patterns in soil CO_2 evolution, (3) to examine changes in soil CO_2 evolution over two measurement years, and (4) to compare estimates using an IRGA based dynamic system with pCO_2 measurements.

Materials and methods

Site description

The study was conducted at the USDA Forest Service Institute of Forest Genetics in Placerville, CA. Site elevation is 843 m, receives an average of 1000 mm of annual precipitation, and has a mean annual temperature of 18°C. The soil is Aiken clay loam (Xeric Haplomumult) derived from andesite. Extensive sampling prior to study establishment indicated uniform soil chemical and textural characteristics across the study area. Bulk density of the soil averaged 1.14 g cm^{-3}, porosity was 54%, reaction was moderately acid (pH_{CaCl} = 5.1 in upper 18 cm), and base saturation (1 *M* NH_4Cl extraction) was 50 to 60%. Soil N content in unfertilized soil was 900 $\mu g\ g^{-1}$.

Experimental design and treatments

The experiment used open-top chambers (8.4 m^2; hexagonal shape) to elevate atmospheric CO_2 concentration (Ball and Johnson, 1993). Air was delivered to the chambers using a 45 cm diameter plastic plenum at three air changes per minute. The experimental design consisted of three levels of N (0, 10, and 20 $g\ m^{-2}\ yr^{-1}$ as ammonium sulfate, applied to the soil surface in the spring), and four CO_2 treatments (ambient, no chamber; ambient, chamber; ambient + 175 $\mu L\ L^{-1}$; and ambient + 350 $\mu L\ L^{-1}$). Each of the chambered treatments was replicated three times, and the unchambered treatment was replicated twice. Due to cost limitations the 10 $g\ m^{-2}\ N\ yr^{-1}$ with + 175 $\mu L\ L^{-1}$ CO_2 treatment was omitted from the experiment. Hence, there were a total of 11 treatments which began in 1990. Each chamber contained ponderosa pine seedlings (grown from seed) equally spaced in the ground at about 0.3 m in all directions. Density in each chamber was 24 in 1992, 21 in 1993, and 21 in 1994. The decrease in seedling

density through time occurred as seedlings were sampled for root biomass determination (no seedlings were sampled in 1994). Choice of seedlings for destructive harvest was based on minimizing crowding within the chambers. Soils were irrigated weekly with sufficient water to maintain soil water potential at > -0.07 MPa, corresponding to a moisture content of > 25%.

Gas wells were established at 15 cm and 30 cm depths within each open top chamber. During the same weeks as the dynamic IRGA sampling, gas wells were sampled during daytime hours with a syringe, and CO_2 concentration was determined with a LICOR 6262 analyzer. Soil CO_2 flux was estimated using a procedure based on the concentration gradient (pCO_2 between two depths) and a CO_2 diffusion coefficient. This is described in the following formula:

$$q = -D(dc/dz)$$

where q = flux (mg CO_2 m^{-2} min^{-1}), D = diffusion coefficient (m^2 mm^{-1}), c = concentration (mg CO_2 m^{-3}), and z = depth (m) (from de Jong and Schappert 1972). The diffusion coefficient, D, was calculated using the equation (Rolston, 1986):

$$D = (P_{eff}{}^{10/3}/E^{2})$$

where D = diffusion coefficient of CO_2 in soil (m^2 min^{-1}), P_{eff} = effective porosity (air-filled soil pores, a function of soil porosity and water content), and E = total porosity. Soil moisture release curves were constructed to determine the relationship between soil water tension and water content. The relationship between soil water tension and P_{eff} was determined by subtracting soil water content from total porosity across a range of soil water tensions. Hence, for each sample period soil water content was determined gravimetrically and corresponding soil water tension was determined from soil moisture release curves. Effective soil porosity at a given soil water content was then determined from the relationship between soil water tension and P_{eff}.

Dynamic system soil CO_2 evolution sampling

We measured diurnal patterns of soil CO_2 flux using an automated, flow-through, Infrared Gas Analyzer (IRGA) measurement system. The system has been described previously (Vose et al., 1995) so only a brief description is presented here. The system measured flux from ten soil chambers which were constructed of PVC pipe (10 cm diameter, 10 cm height, 785 cm volume), sharpened on one end, and driven approximately 2 cm into the ground with a rubber mallet. An airflow unit, solenoids, and data logger were used to deliver and monitor flow to and from each chamber. Carbon dioxide concentration of air entering and exiting the chambers was measured and logged electronically with an IRGA (ADC LCA3, Hoddeson, UK) and data logger, respectively. Soil evolution rate (g CO_2 m^2 min^{-1}) was calculated based on the difference in [CO_2] entering and exiting the chamber, the ground area sampled, and flow rate. To allow for equilibrium between chambers, only data from the last minute of sampling were used in the flux calculations.

Measurements began in October 1992 and were repeated in April, June, and October of 1993 and 1994. Sampling was conducted over consecutive six day periods during each sample month. On each day, two soil chambers were randomly placed in each of five treatment replication combinations, with the restriction that chambers could be no closer than 2.5 cm from the stem of a seedling. This restriction was imposed so that seedlings were not damaged when chambers were installed. Soil CO_2 evolution was measured for 22–24 hrs (i.e. a diurnal cycle) on each day. Sampling was initiated in the early morning (approximately 09:00) and concluded between 08:00 to 09:00 the following day. On each successive day, the chambers were moved to a new set of treatment-replication combinations and the diurnal measurements repeated until all treatments and replications were sampled. On each day, treatment replication combinations selected for sampling were chosen to span the factorial combinations of CO_2 and N treatments. Using this sampling approach, we assumed that there would be minimal day to day variation in soil CO_2 evolution and/or if day to day variation did occur, the selection of representative treatment combinations would minimize any potential bias.

Soil temperature

With the exception of October 1992, soil temperature at 10 cm depth was measured for complete diurnal cycles at each soil respiration chamber location. In October 1992, temperature was measured in five randomly located open-top chambers and hence, were not co located with soil respiration chambers. These data were used only as an index of overall diurnal and measurement period variation in soil temperature. Measurements were made with Type-T thermocouples

connected to a data logger (Campbell 21X) and multiplexer.

Fine root, fungi, and mycorrhizae

Fine root (< 2 mm), fungi, and mycorrhizae occurrence were quantified using minirhizotron technology. Detailed descriptions of the methods have been described elsewhere (Brown and Upchurch, 1987; Vose et al., 1995), so only a brief description is provided here. During the week of 17 August 1992, three 1 m long minirhizotron tubes were installed at a 45° angle into the Bt horizon in each of the open-top chambers. Minirhizotron images were recorded with a video camera which recorded images (1.8 cm^2 field of view) on the upper sides of the tubes at regularly spaced intervals. Forty-five frames were recorded in each tube, for a total of 135 frames per open-top chamber per sampling event. Root data were extracted from the video tapes using ROOTS software (Hendrick and Pregitzer, 1992). Data were summarized based on occurrence of fine roots (percent roots), fungal hyphae (percent fungi), and mycorrhizae (percent mycorrhizae) as measured by the percentage of the total minirhizotron frames in which they occurred. Data from the three tubes in each open-top chamber were averaged to provide a chamber-level estimate. Between October 1992 and 1994, 14 measurements were conducted. In this study, only measurements from April, June, and October of 1993 and 1994 (± 1 week of the soil CO_2 measurements) were used. October 1992 measurements were excluded because insufficient time had elapsed to allow for re-growth of roots after tube installation.

Statistical analysis

We used integrated values of diurnal measurements to estimate daily soil CO_2 flux (g CO_2 m^2 day^{-1}) for each open-top chamber treatment combination. Integrated values were calculated by determining the area under each segment of two consecutive sample points and then summing the segments for a total daily flux rate. When the sampling interval was < 24 hrs, the values were extrapolated to 24 hrs by connecting the last sample point to the first sample point of the sampling period. These values were used in the analyses of variance (ANOVA) to test for treatment effects (PROC GLM, SAS Institute, 1987). A reduced error term (chamber(treatment)), which accounted for the subsample of two soil CO_2 evolution chambers per open-top chamber, was used in the ANOVAs to test for treatment

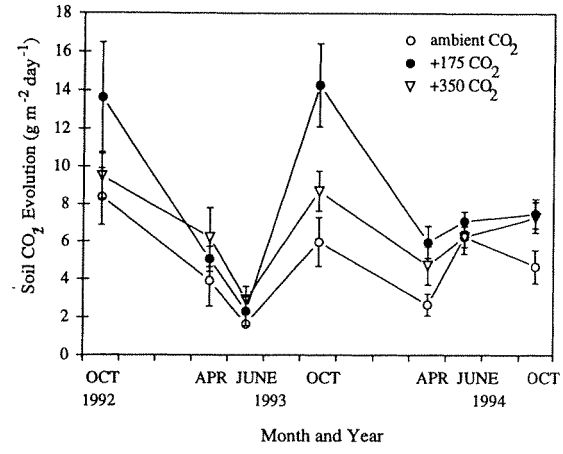

Figure 1. Mean soil CO_2 evolution (g m^{-2} day^{-1}) for all measurement periods. Data were averaged across N levels because effects were not significant. Bars represent one standard error.

effects. Because we had an unbalanced experimental design, contrast statements (Snedecor and Cochran, 1980) were constructed to determine the effects of CO_2, N, and CO_2 × N interaction on soil CO_2 evolution. Repeated measures ANOVAs were used to test for seasonal (monthly for years 1993 and 1994;) and annual (October 1992, 1993, and 1994) effects on soil CO_2 evolution (PROC GLM, SAS Institute Inc., 1987). We performed a separate analyses for each CO_2 treatment averaging across N additions for seasonal and annual comparisons. If an overall significant F-value was found, tests for significant differences among seasonal (April, June, and October 1993 and 1994) and annual (October 1992,1993, and 1994) rates of soil CO_2 evolution were made using the appropriate orthogonal contrasts. To determine relationships among soil CO_2 evolution and driving variables, we used simple and multiple regression analyses (PROC REG, SAS Institute Inc., 1987).

Results

Soil CO_2 evolution varied considerably across CO_2 treatments and the relative magnitude of fluxes varied across measurement years (Figure 1). N effects were never significant (Table 1) so the data plotted in Figure 1 were averaged across N levels. In general, soil CO_2 evolution was greatest in the elevated CO_2 treatments (particularly the + 175 μL L^{-1} CO_2); however, statistically significant ($p < 0.05$) differences were observed

Table 1. *p*-values for statistical tests comparing treatment effects[a] (elevated CO_2 and N) on integrated soil CO_2 flux measurements

	1992	1993			1994			
Effects	October	April	June	October	April	June	October	Overall
N	0.716	0.511	0.174	0.117	0.667	0.949	0.270	0.429
CO_2	0.155	0.031	0.664	0.001	0.909	0.217	0.084	0.001

[a]Because there was no significant difference between ambient CO_2 in chambers and chamberless treatment, CO_2 effects were tested using the average of the chamberless and ambient chambered treatments vs. the average of the + 175 CO_2 and ambient +350 CO_2 across nitrogen levels. N effects were tested using the + 0 N vs. the average of the + 10 N and + 20 N treatments across CO_2.

only in April and October 1993 (Table 1). In October 1994, CO_2 effects were significant at the $p < 0.10$ level. Averaged across all measurement periods and years, soil CO_2 evolution was 4. 8, 8. 0. and 6. 5 g m^{-2} day^{-1} for the ambient, + 175 CO_2, and +300 CO_2 treatments, respectively. Overall CO_2 effects were significant, but N effects were not (Table 1).

Seasonal patterns

There was variation in seasonal patterns of soil CO_2 evolution in 1993, but much less so in 1994 (Figure 1). In 1993, the lowest fluxes were observed in June (2 to 3 g m^{-2} day^{-1}) and the highest in October (6 to 14 g m^{-2} day^{-1}). In 1994, the lowest fluxes were generally observed in April (3 to 6 g m^{-2} day^{-1}) and the highest in October (4 to 7 g m^{-2} day^{-1}). In June of 1993 and 1994 there were no differences (qualitative or statistical) between treatments, while in April and October there were at least trends (statistically significant in April 1993 and October 1993 and 1994) of higher soil CO_2 evolution in the elevated atmospheric CO_2 treatments. Statistical contrasts revealed that many of the seasonal patterns observed within elevated CO_2 treatments were significant (Table 2).

Annual patterns

Comparing October measurements, soil CO_2 evolution for the + 175 CO_2 treatment was essentially the same (i.e. 14 g m^{-2} day^{-1}) in 1992 and 1993, but declined almost two-fold in 1994 (i.e. 7 g m^{-2} day^{-1}) (Figure 1). Both the +350 CO_2 and the ambient CO_2 treatment showed a slight, but statistically non-significant decrease in October over the three measurement years. For April measurements, differences were small and the patterns were inconsistent between measurement

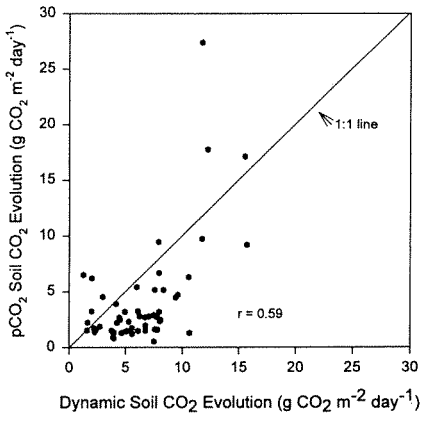

Figure 2. Correlation between pCO_2 and dynamic IRGA soil CO_2 evolution measurement techniques. Data are averaged across replicates and represent data from all measurement periods.

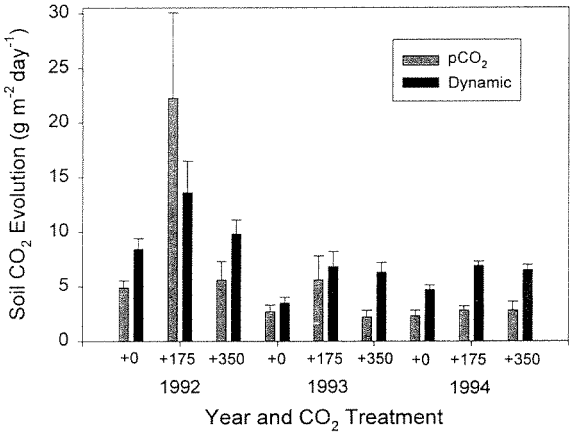

Figure 3. Qualitative comparison of soil CO_2 evolution estimates using the pCO_2 and dynamic IRGA measurement techniques. Data are averaged across N levels, months, and. replicates. Bars represent one standard error.

Table 2. p-values for test of seasonal variation in soil CO_2 flux within a treatment. Because N effects were not significant, data were averaged across N levels

Treatment	Time effects	Contrasts		
		April vs. June	April vs. October	June vs. October
1992				
Ambient CO_2	0.0009	0.0454	0.0003	0.0008
+175 CO_2	0.0001	0.0475	0.0012	0.0001
+350 CO_2	0.0116	0.1825	0.1049	0.0017
1993				
Ambient CO_2	0.0002	0.0001	0.0035	0.0363
+175 CO_2	0.1620	0.1970	0.0642	0.6306
+350 CO_2	0.0482	0.0518	0.0437	0.2607

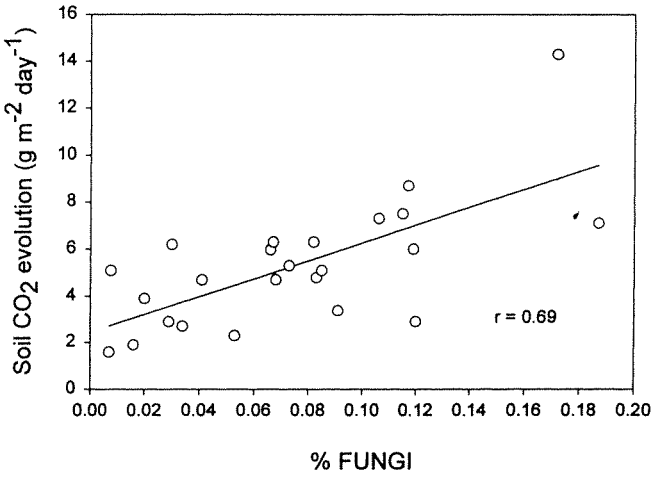

Figure 4. Correlation between fungi observed in minirhizotron tubes and measured soil CO_2 evolution (dynamic IRGA). Data are averaged across replicates and N levels.

years. In June, values were two to three-fold higher in 1994 than in 1993.

pCO_2 vs. dynamic IRGA

Using data from all individual chambers and sample periods, there was a statistically significant, but weak correlation ($r = 0.27$; $p < 0.0001$; $n = 170$) between pCO_2 and the dynamic IRGA soil CO_2 evolution estimates. When averaged across replicates (Figure 2), the correlation improved ($r = 0.57$; $p < 0.0001$; $n = 56$), but there was still considerable variation between the two techniques. In general, pCO_2 estimates tended to be lower than IRGA estimates, particularly at the lower range of soil CO_2 evolution. While quantitative analyses indicated disparity between techniques, qualitative patterns among years and $[CO_2]$ treatments were in general agreement (Figure 3). For example, the highest values for both techniques were observed in 1992 (October sample only) for the +175 $\mu L\ L^{-1}$ $[CO_2]$ treatment. Similarly, the lowest values were typically observed for the controls across all measurement years.

Discussion

Treatment effects

The trend of greater soil CO_2 evolution (e.g. almost two-fold differences between average ambient and + 175 CO_2) under elevated atmospheric CO_2 could be caused by several factors. First, changes in the mass or activity of roots could directly increase soil CO_2 evolution by increased root respiration and indirectly,

by increased heterotrophic respiration in response to a larger rhizosphere. Increased root biomass is a common response to elevated CO_2 (Nakayama et al., 1994; Norby et al., 1987; Rogers et al., 1992; and increased microbial activity has also been shown (Nakayama et al., 1994). In a previous study, we demonstrated qualitative relationships between root biomass and soil CO_2 evolution (Vose et al., 1995) so increased root biomass may be an important factor influencing the patterns observed over the measurement periods. However, fine root biomass was not determined in 1994 so we can not assess it's role in regulating the patterns of soil CO_2 evolution we observed in 1994. Variation in decomposer populations due to elevated atmospheric CO_2, could also influence soil CO_2 evolution. For example, in 1993, we found that 63% of the variation in soil CO_2 evolution could be explained by fungal occurrence and fungal occurrence was greatest in elevated CO_2 treatments (Vose et al., 1995). Re-analysis after including fungal occurrence data from 1994 (averaged across N treatments) indicated that these patterns held in the second year as well; i.e. percent fungi was positively related to soil CO_2 flux and percent fungi was greater under elevated CO_2 ($r = 0.69$; $p < 0.0001$; $n = 24$) (Figures 4 and 5). Like the 1993 analyses, fine root and mycorrhizae occurrence were not correlated with soil CO_2 evolution. Fungi have been shown to contribute as much as 19% to total soil CO_2 evolution (Rygiewicz and Anderson, 1994). Hence, the greater soil CO_2 evolution in the elevated CO_2 treatments is most likely due to greater root respiration relative to controls and higher respiration from decomposing organisms (e.g. fungi) feeding on these roots as they turnover.

The lack of N effect could be due to counteracting autotrophic and heterotrophic response patterns. It is well documented that plant respiration rate increases with increased tissue N (e.g. Field and Mooney, 1986; Ryan, 1991). Based on that information alone, we would predict increased soil CO_2 evolution from N fertilized chambers due to a positive autotrophic response. However, N fertilization has also been shown to decrease heterotrophic respiration via decreased microbial activity and biomass (Söderström et al., 1983). The lack of soil CO_2 evolution response to N fertilization does not necessarily imply that the components of the belowground system did not respond to N fertilization. Rather, we postulate that they responded in counteracting directions and the net effect was no measurable difference in soil CO_2 evolution among N treatments.

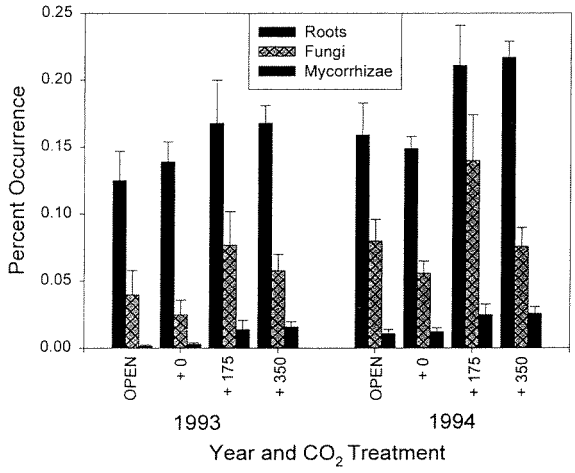

Figure 5. Root, fungi, and mycorrhizae occurrence (%) in minirhizotron tubes by year and CO_2 treatment. Data are averaged across months, replicates, and N levels. Bars represent one standard error.

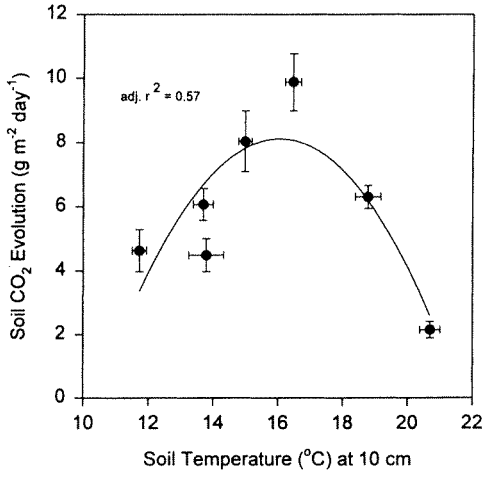

Figure 6. Soil temperature and soil CO_2 evolution relationship. The line was fit with a second order quadratic regression model. Data are sample period means (averaged across treatments) and bars represent one standard error.

Seasonal and annual patterns

Several factors have been suggested to regulate seasonal variation in soil CO_2 evolution such as, soil moisture (e.g. Gorden et al., 1987; Schlentner and Van Cleve, 1985) soil temperature (e.g. Hanson et al., 1993; Peterjohn et al., 1993), root biomass (Behera et al., 1990), and decomposer populations (Rygiewicz and Anderson, 1994; Vose et al., 1995). Soil moisture is unlikely to be a significant factor because of irrigation which maintained soil moisture at > 25%. In a

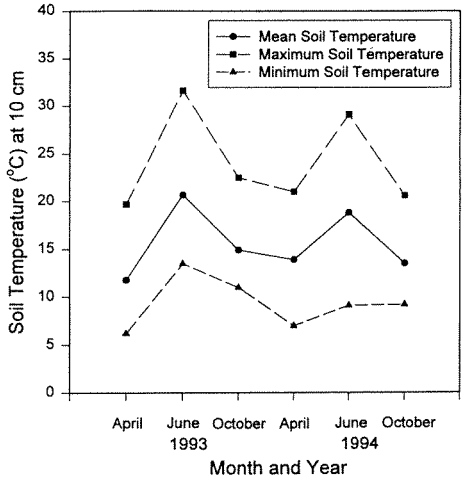

Figure 7. Mean, minimum, and maximum soil temperature measured with thermocouples at 10 cm soil depth.

previous study, we documented that soil CO_2 evolution responds to diurnal variation in soil temperature (Vose et al., 1994). Using data from all sample periods (except October 1992 due to different sampling protocol) and chambers, there was a weak, but statistically significant relationship between soil temperature and soil CO_2 evolution (quadratic model adjusted r^2 = 0.11; $p < 0.001$; $n = 151$. One of the potential factors contributing to the low r^2 is spatial variability (within and among chambers due to treatments and inherent site variability) in biotic variables, especially fine roots and associated mycorrhizae and fungi. To minimize the variation associated with non-temperature related factors affecting soil CO_2 evolution, we averaged across replications and treatments to develop a generalized temperature response model. We found a non-linear pattern between soil temperature and soil CO_2 evolution (Figure 6). At temperatures < 18°C, there was a linear increase in soil CO_2 evolution; however, at higher temperatures, soil CO_2 evolution decreased dramatically (quadratic model; adjusted $r^2 = 0.57$; $p < 0.10$; $n = 7$). In addition, treatment variation (expressed by the standard error bars for each soil CO_2 evolution treatment mean) was smaller when temperature was > 18 °C. While not establishing cause and effect, these patterns indicate the potential for exceeding optimal soil temperature (particularly in the surface layers) for organic matter decomposition. This possibility is even more likely when maximum temperatures are plotted (Figure 7), where values exceeding 30 °C at 10 cm are often reached in June. For example, Waide et al. (1988) found reduced microbial activity in response to harsh environmental conditions (e.g. soil/litter maximum temperatures > 40 °C; Swank and Vose, 1988) after clearcutting a south facing watershed. These patterns do not preclude the possibility that other factors, such as changes in root biomass and/or decomposer population size (independently or in response to soil temperature), are also contributing to the patterns observed in Figure 5. For example, multiple regression analyses relating soil CO_2 evolution across treatments, years, and months to both fungal occurrence and soil temperature indicates that both factors explain variation in temporal and treatment response patterns (soil CO_2 flux = -7.57 + 24.37(% fungi) + 1.58 (soil temperature [°C] at 10 cm) - 0.05 (soil temperature at 10 cm × soil temperature at 10 cm); r^2 0.44; $p < 0.0001$; $n = 65$).

Comparison of measurement techniques

Results from our comparisons of the pCO_2 and dynamic IRGA techniques are typical of many other technique comparison studies in that correlations are often weak and biased. One major difficulty with comparative studies is that high spatial and temporal variability requires that measurements be made at the same place and time. In our case, it was physically impossible to place sampling devices in the same location and the effort required to sample pCO_2 over an entire diurnal period was prohibitive; thus, it was not possible to match flux estimates temporally. Agreement between methods improved when averaged across replicates, which indicates that general patterns of response are detectable and consistent with either method. These results agree with our comparison of the two techniques for quantifying responses in the first year of treatment (Johnson et al., 1994). The patterns shown in Figure 3 indicate that while the magnitude of soil CO_2 evolution response to elevated [CO_2] differed between the two methods, the conclusions reached with both techniques would be comparable; i.e. in 1992 and 1993, the greatest response occurred in the + 175 μL L^{-1} treatment, and differences among treatments were declining in 1994. This general agreement between methods is not trivial because cost and sample time requirement varies considerably. For example, the dynamic system costs approximately $15,000 (IRGA plus sampling system) and required six sample days in a measurement period. The pCO_2 method is considerably less expensive (e.g. primarily the cost of an IRGA) and sampling can be conducted in less than one day.

Summary and conclusions

Results from our study indicate that exposure to elevated atmospheric [CO_2] increases soil CO_2 evolution. Averaged over all measurement periods (i.e. October 1992, and April, June, and October of 1993 and 1994), fluxes were 67 and 35% greater than ambient for the + 175 CO_2 and + 350 CO_2 treatments, respectively. Assuming a 180 day growing season, these values equate to average C fluxes of 235, 393, and 319 g C m^{-2} per growing season for ambient, + 175 CO_2 and + 300 CO_2, respectively. Higher losses do not necessarily imply a decrease in the soil C pool, as Johnson et al. (1994) found increased root growth and turnover more than offset the losses from higher soil CO_2 evolution. The applicability of the response patterns we observed to other ecosystems will depend on the magnitude of the belowground response. Our system is rapidly aggrading and exploiting belowground resources. We speculate that mature systems might be less responsive, but results from similar studies in older ecosystems (i.e. FACE experiments) will be required to test that hypothesis. Treatment and temporal variation in soil CO_2 evolution was related to both fungal occurrence and temperature. Soil CO_2 evolution increased up to approximately 18 °C soil temperature (at 10 cm depth), and then decreased dramatically at > 16 °C soil temperature. pCO_2 and dynamic IRGA measurements were weakly correlated, although the strength of the correlation improved when chamber averages were used. Although weakly correlated, the patterns of response were generally comparable.

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