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Soil pCO_2, soil respiration, and root activity in CO_2-fumigated and nitrogen-fertilized ponderosa pine

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Abstract

The purpose of this paper is to describe the effects of CO_2 and N treatments on soil pCO_2, calculated CO_2 efflux, root biomass and soil carbon in open-top chambers planted with *Pinus ponderosa* seedlings. Based upon the literature, it was hypothesized that both elevated CO_2 and N would cause increased root biomass which would in turn cause increases in both total soil CO_2 efflux and microbial respiration. This hypothesis was only supported in part: both CO_2 and N treatments caused significant increases in root biomass, soil pCO_2, and calculated CO_2 efflux, but there were no differences in soil microbial respiration measured in the laboratory. Both correlative and quantitative comparisons of CO_2 efflux rates indicated that microbial respiration contributes little to total soil CO_2 efflux in the field. Measurements of soil pCO_2 and calculated CO_2 efflux provided inexpensive, non-invasive, and relatively sensitive indices of belowground response to CO_2 and N treatments.

Introduction

There is increasing evidence that belowground processes can be strongly affected by increases in atmospheric CO_2. Several studies have shown that root growth responds disproportionately to increases in atmospheric CO_2 (Norby et al., 1986, 1987, 1992; Rogers et al., 1992; Walker et al., 1994). Norby et al. (1987) found increased root exudation from *Pinus echinata* under elevated atmospheric CO_2, and suggested that this may provide a mechanism for enhancing rhizosphere nutrient availability. Körner and Arnone (1992) noted increases in fine root biomass and soil respiration with elevated CO_2 in an artificial tropical ecosystem. The authors also found a reduction in soil C, which they attributed to stimulation of decomposition in the rhizosphere though root exudation. Zak et al. (1993) found that elevated CO_2 caused increases in labile C and N in soil from *Populus grandidentata* seedlings grown under elevated CO_2. The authors suggested that elevated CO_2 may create a positive feedback on soil C and N dynamics and tree growth because of increased N availability in the rhizosphere caused by root exudation.

It is obvious from the literature cited above that belowground effects of elevated atmospheric CO_2 are important and must be monitored in experiments involving CO_2 treatments. There are some significant methodological problems in monitoring belowground activity, however. Destructive methods such as soil coring and root harvesting give the best quantitative estimates of belowground response, but cannot be conducted on a routine basis in small plots. Non-destructive measurements such as soil respiration and nutrient leaching provide sensitive indices of overall belowground activity, but generally do not provide information on the responses of individual belowground components (i.e., roots vs microbes).

The Forest Response to CO_2 project (Ball et al., 1992) is studying the responses of ponderosa and loblolly pine (*Pinus ponderosa* and *P. taeda*) to CO_2 and N treatments in open top chamber facilities. A major goal of this research is to gain a comprehensive picture of belowground response to treatments by combining a variety of non-destructive belowground moni-

toring techniques (video imaging with mini-rhizotrons, soil solution sampling, soil atmosphere CO_2 concentration [pCO_2] and CO_2 efflux) — with periodic destructive sampling of soils and vegetation. Previous papers have reported the initial results of soil respiration measurements using dynamic chambers (Vose et al., 1994) and root phenology using mini-rhizotrons (Johnson et al., 1994) in the ponderosa pine site. This paper will focus upon responses of soil pCO_2 and calculated CO_2 efflux to treatments, comparing these responses to changes in root biomass and soil carbon content. Of all of the methods listed, measurements of soil pCO_2 and calculation of CO_2 efflux are the least invasive, require the least equipment and are most easily made on an extensive, routine basis (de Jong and Schappert, 1972). Based upon the literature, we hypothesized that elevated CO_2 and N treatments would cause increased root biomass which would in turn cause increased total soil CO_2 efflux, root and microbial respiration.

Site and methods

Site

The open-top chamber site was located at the Institute of Forest Genetics in Placerville, California. The soil is Aiken clay loam, a Xeric Haplohumult derived from andesite. Soils were intensively sampled prior to chamber establishment, and were found to be very uniform. Some average chemical and physical properties of the soils from the site are shown in Table 1.

Treatments

During February–April 1991, 24 hexagonal open-top chambers (3.6 m in diameter) were established on the site. The basic experimental design consisted of three levels of nitrogen (0, 10, and 20 g m^{-2} yr^{-1} of N as ammonium sulfate, applied in early spring), and four CO_2 treatments (ambient, no chamber; ambient, chambered; 525 μL L^{-1} CO_2; and 700 μL L^{-1} CO_2). Water was delivered to each plot via a timed stand pipe to a looped one inch diameter manifold, and low pressure spray heads. Each of the chambered treatments was replicated three times, and each of the unchambered treatments was replicated twice. Only the results from the chambered measurements will be reported here. Due to cost limitations, the 10 g m^{-2} yr^{-1} N, 525 μL L^{-1} CO_2 treatment was excluded. Treatments were begun in May, 1991. A full description of chamber operation is given by Ball et al. (1992). In May of 1991, Ponderosa pine (*Pinus ponderosa*) was planted in each chamber. Seedlings were grown from seed (21 planting locations per chamber) and seedlings (21 per chamber), the latter being a backup in the event of excessive mortality. Seed-grown seedling survival was very good, and the seedling-grown stock was removed in October 1991. Weeds were controlled by laying weedcloth around seedlings in each chamber. Weedcloth was found to have no effect on CO_2 retention in the soil: CO_2 concentrations beneath the weedcloth and above the soil surface were at ambient levels for the chamber being sampled, and there were no discernible effects of weedcloth presence or absence upon pCO_2.

Biomass harvesting

In October 1991, three trees from each chamber were harvested, including complete root systems. In 1992, three trees from each chamber were harvested again, but only one complete root system per chamber was obtained because of the increased size of the seedlings and concern for excessive plot disturbance. Root biomass by size class and mycorrhizal infection were analyzed in each case and will be reported in later papers (R.F. Walker, unpubl. data). Only total root biomass will be reported here.

Soil pCO_2, temperature and moisture monitoring

Gas wells were established at 15 and 30 cm depths in each chamber. The gas wells consisted of 4 mm tubing inserted to the proper depths in the soil and fitted with a stoppered, female end of a plastic union at the surface. During gas collections, stoppers were removed and 15 mL of gas was withdrawn from the well (enough to completely evacuate the tubing and obtain soil gas) using a 50 mL syringe fitted with tygon tubing and the male half of the union. Samples for CO_2 analyses were obtained with Hamilton gas syringes from the section of tygon tubing between the large syringe and the union. CO_2 analyses were performed on a LiCOR 6250 CO_2 analyzer using peak heights compared to a standard gas of 0.877% CO_2. Soil moisture was measured by various methods during the early part of the study. From July–August 1992 portable tensiometers (Soil Moisture Corp.) were used. In that soil moisture tension was normally kept well below 50 kPa by irrigation, there was little concern that tensiometers would become inoperable. The portable tensiometers provided adequate estimates of soil moisture content, as evidenced by comparisons with gravimetric analyses, but they were abandoned in October 1992 in

Table 1. Some chemical and physical properties of the Placerville site soils (Aiken clay loam, Xeric Haplohumult derived from andesite)

Horizon and depth (cm)	Db ($g\ cm^{-3}$)	%>2mm (%)	C[a] ($mg\ g^{-1}$)	N[b] ($mg\ g^{-1}$)	C/N	Bray P[b] ($mg\ kg^{-1}$)	pH[c]	CEC[d]	Exchangeable cations ($cmol_c\ kg^{-1}$)					%BS[e] (%)
									Ca	Mg	K	Na	Al	
Ap (0–18)	1.14	1	22.0	0.9	24	12.1	5.1	11.24	4.37	0.62	0.74	0.04	0.68	51
Bw (18–30)	1.24	1	18.0	0.9	21	10.9	5.1	9.39	4.26	0.62	0.74	0.03	0.78	65
Bt (30+)			7.1	0.4	16	1.6	5.5	14.89	6.11	1.18	0.90	0.04	0.02	57

[a] Perkin-Elmer 2400 CHN Analyzer.
[b] 0.5 *M* HCl + 1 *M* NH_4F (Olson and Sommers, 1982).
[c] 0.1 *M* $CaCl_2$.
[d] Cation exchange capacity and exchangeable cations by 1 *M* NH_4Cl extraction followed by 1 *M* KCl.
[e] Percent base saturation.

favor of gravimetric samples because the time necessary to obtain tensiometer measurements was greater than that needed to take soil samples for gravimetric analyses. Between October 1992 and May 1993 gravimetric analyses were used for estimation of soil water content. After that time, gypsum blocks were calibrated and used for estimations of water content, because of concern over the repeated effects of destructive soil sampling.

Measurement and calculation of soil CO_2 efflux

Respiration by the chamber method was measured with a continuous flow infrared gas analyzer (IRGA) system. Soil CO_2 flux was measured from soil chambers (10 cm diameter, 10 cm high, 785 cm^3 volume) inserted 1.25 cm into the ground. During measurement, caps with inlet and outlet ports were placed on each core to measure CO_2 evolution. Flow rate was 800 to 1200 mL min^{-1} to minimize turbulence within the sample core and to ensure measurable levels of CO_2 evolution. In addition, inlet and outlet flow were carefully monitored to ensure that no suction was created in the outlet sample. Carbon dioxide concentrations of air entering and leaving the chambers were measured and logged electronically with an ADC LCA3 IRGA and a Campbell 21 X data logger. Continuous measurements were taken across treatments (i.e., all factorial combinations) within a randomly selected replication (chamber) at each sample period (October 1992, April 1993, and June 1993.)

Soil CO_2 efflux was calculated according to the CO_2 profile method outlined by de Jong and Schappert (1972). This method is based upon the assumption that CO_2 efflux is dominated by diffusion and therefore controlled by the partial pressure of CO_2 in the soil atmosphere (pCO_2) and the diffusivity of CO_2 in the soil (de Jong and Schappert, 1972; Rolston, 1986). At steady-state,

$$q = D\frac{dC}{dz} \qquad (1)$$

where q= CO_2 efflux (g CO_2 -C m^{-2} day^{-1}) = root and microbial respiration at steady-state, C = soil CO_2 -C concentration (g m^{-3}), z = depth (m), D = diffusion coefficient (m^2 day^{-1}).

Because CO_2 diffusion through water is much lower than in air, D is strongly affected by soil water content. There are several formulations for D (Collin and Rasmuson, 1988), all of which take soil moisture content into account. In this paper, we used a modification of the equation given by Millington (1959) (as quoted by Rolston, 1986):

$$D = (\partial)(D_a)(P_{eff}^{10/3})/E^2 \qquad (2)$$

where D = diffusion coefficient of CO_2 in air (cm^2 sec^{-1}), (E = voids ratio, or total soil porosity, P_{eff} = effective porosity = total porosity (E) minus volumetric water content (V_w), and ∂ = a coefficient to account for non-ideal pore shape and dead-end pores (Collin and Rasmuson, 1988). For the Placerville soil, the value of

∂ was determined to be 0.1 based upon comparisons with measured CO_2 efflux using dynamic chambers (Vose et al., 1994).

Soil sampling and analysis

In March of 1991 and 1993, three replicate soil samples were taken in each chamber from the Ap (0–18 cm) and Bw (18–30 cm) horizons for bulk density, percent gravel, and chemical analyses. Samples were dried, sieved (< 2 mm), bulked by chamber, and analyzed for total C and total N on a Perkin-Elmer 2400 CHN analyzer.

On July 8, 1993, additional samples were taken as above from the Ap horizon for laboratory incubation. The samples were sieved and bulked by chamber in a field-moist condition, taking great care to remove root fragments. 100 g of field-moist soil was placed in 255 mL fruit jars fitted with septa for gas sampling and incubated at 25°C for 21 days. Gas samples from the headspace were taken at the initiation and on a daily basis and analyzed for CO_2 as described above. When headspace pCO_2 levels exceeded 1.5% (the maximum levels found at 15 cm in the field), the chambers were flushed with ambient air, resampled to establish baseline values again, and allowed to incubate further. Flushings took place on days 6 and 14.

Statistical analyses

Statistical analyses included two-way analysis of variance, with treatment effects considered significant only at $p \leq 0.05$ (SYSTAT software). Treatment means were compared using Tukey's HSD procedure, $p \leq 0.05$.

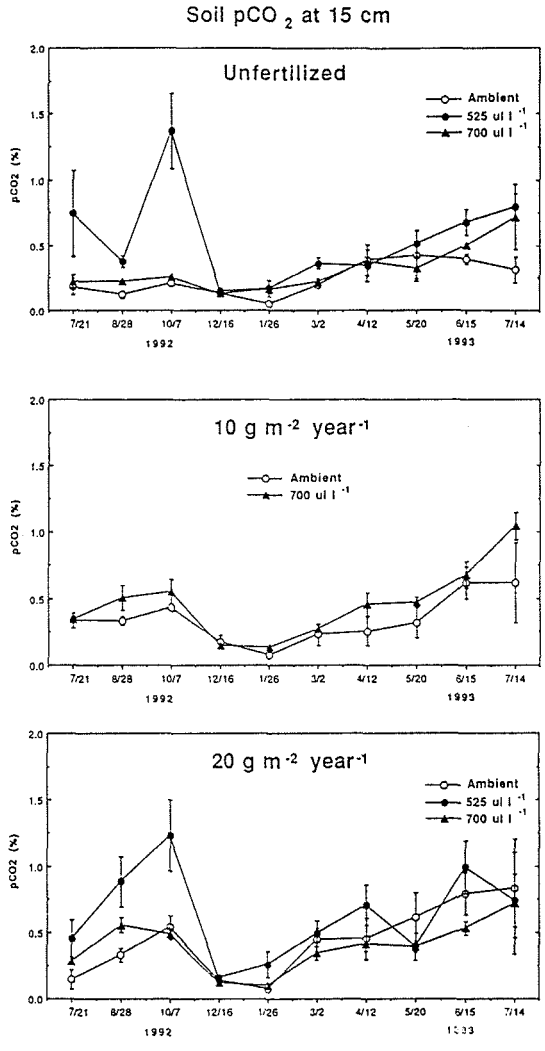

Fig. 1. Seasonal trends in soil pCO_2 at the 15 cm depth at the Placerville field site.

Results and discussion

Effects of treatments on root biomass, soil pCO_2, soil CO_2 efflux, and soil C pools

In the summer and autumn of 1992, there was a significant positive effect of CO_2 treatment on soil pCO_2 and calculated CO_2 efflux, especially in the 525 μL L^{-1} CO_2-treated chambers (Figs. 1–3). There was also a smaller but significant N fertilizer effect upon soil pCO_2 and calculated CO_2 efflux during the spring and summer of 1992. Soil pCO_2 in all treatments decreased substantially during the winter of 1992–1993, probably in response to the precipitous decrease in soil temperature (Fig. 4). The removal of 20% of the biomass in late October 1992 may also have caused some reduction in soil pCO_2 and calculated CO_2 efflux. Both soil pCO_2 and temperature rose again in the spring and summer of 1993, and by June of 1993, there were significant effects of both CO_2 and N treatments. However, the predominance of the 525 μL L^{-1} CO_2 treatments did not re-emerge after the winter of 1992.

Between October 1991 and October 1992, root biomass increased by approximately 2 orders of magnitude, and CO_2 treatment effects began to predominate over the initial N treatment effects (Fig. 5). In October 1991, there was a significant N treatment effect upon root biomass but no significant CO_2 treatment effect. In October 1992, there was a significant N treatment

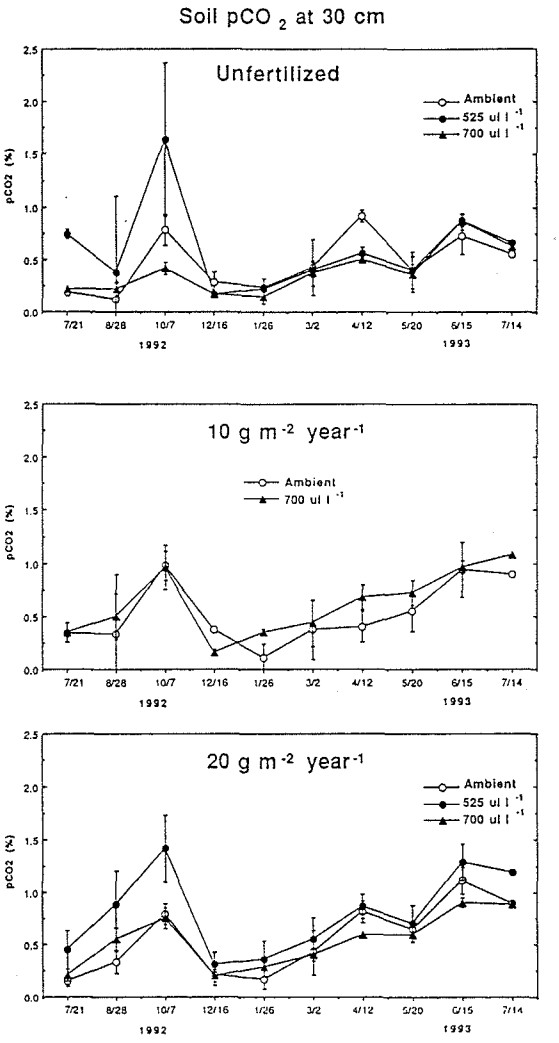

Fig. 2. Seasonal trends in soil pCO_2 at the 30 cm depth at the Placerville field site.

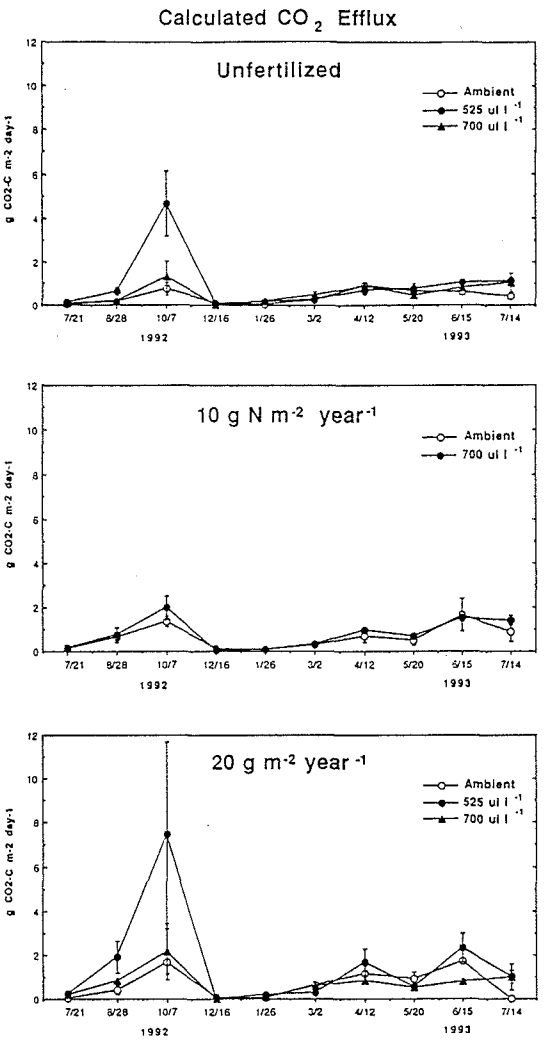

Fig. 3. Seasonal trends in calculated CO_2 efflux at the Placerville field site.

effect in the ambient and 700 μL L^{-1} CO_2 chambers, but CO_2 effects were larger and statistically significant at all fertilization levels. There was a tendency for greater root biomass in the 525 μL L^{-1} than in the 700 μL L^{-1} CO_2 treatments, but the differences were statistically significant only in the unfertilized chambers.

There were statistically significant correlations among root biomass, measured and calculated soil CO_2 efflux, pCO_2 at 15 and 30 cm in October 1992 (Table 2). These correlations suggest that roots make a major contribution to total soil respiration. The literature suggests that from 1/3 to 2/3 of total soil respiration can be attributed to roots in mature forest ecosystems with well-developed litter layers (Edwards and Harris, 1977; Johnson et al., 1975; Ewell et al., 1987b; Raich and Nadelhoffer, 1989). Given the fact that no litter layer was present in this study, it is probable that the role of roots in total soil respiration was even more significant than in mature forests.

Results from laboratory incubations suggest that microbial respiration from bulk soils contributed relatively little to total soil respiration. There were no significant treatment effects on CO_2 efflux from laboratory-incubated soils samples, whereas there were statistically significant effects of both CO_2 and N treatment upon soil pCO_2 and calculated CO_2 efflux in the field on the sampling date (Fig. 6). Furthermore, the rates of CO_2 efflux in the laboratory, when

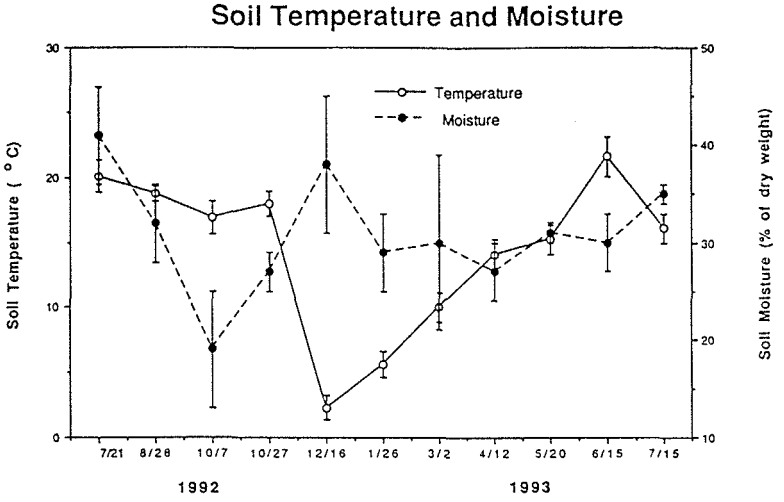

Fig. 4. Seasonal trends in soil temperature and moisture at the Placerville field site.

Table 2. Correlation coefficients (r^2) among root biomass, pCO_2, and CO_2 flux in the Placerville field site in October 1992

Variable	Root Biomass (g tree^{-1})	pCO_2 at 15 cm (%)	pCO_2 at 30 cm (%)	Measured CO_2 flux (g m^{-2}day^{-1})
pCO_2 at 15 cm (%)	0.71	-	-	-
pCO_2 at 30 cm (%)	0.50	0.83	-	-
Measured CO_2 flux (g m^{-2} day^{-1})	0.45	0.69	0.70	-
Calculated CO_2 flux (g m^{-2} day^{-1})	0.58	0.83	0.54	0.50

scaled up to a g m^{-2} day^{-1} level (using Ap horizon soil weights) equalled about 10% of calculated CO_2 efflux in the field for the sampling date (Fig. 6). Actual microbial CO_2 efflux rates in the field were probably considerably less than those determined in the laboratory under ideal temperature and moisture conditions after substantial soil disturbance due to sampling and processing.

In contrast to the results of Körner and Arnone (1992) we found no reduction in soil C with CO_2 treatments. With one exception, there were no statistically significant differences in soil C content between 1991 and 1993 (Table 3). The exception was in the Bw horizon of the 700 μL L^{-1}, 20 g N m^{-2} year^{-1} treatment, where 1993 soil C was significantly greater than 1991 soil C. However, the 1991 soil C in this particular case was unusually low, suggesting the possibility of a Type II statistical error.

One of the probable reasons for the differences in our results and those of Körner and Arnone (1992) is that we used a natural soil with relatively large, stable soil C pools (approximately 6,000 to 8,000 g C m^{-2}), whereas the artificial soil used by Körner and Arnone (1992) (a mineral mixture of silicate sand and vermiculite) contained only 15 to 20% as much total C (1280 g C mm^{-2}) which was derived from overlying compost material. Also, soil C losses of the magnitude reported by Körner and Arnone (1992) (75 to 300 g C m^{-2}) could have gone undetected in the Placerville soil. The differences in soil C between 1991 and 1993 at Placerville (from -725 to +1239 g C m^{-2}), while mostly non-significant, were much greater than those measured by Körner and Arnone (1992) (Table 3).

The absolute values of soil C change calculated as a daily loss can be compared to soil CO_2 efflux rates determined in the laboratory and in the field in order to gain additional insight into the relative roles of roots and microbes in affecting total soil respiration. These daily values were similar in magnitude to soil CO_2 efflux rates measured in the laboratory (Table 3 and

Table 3. Changes in soil C at Placerville, 1991–1993

Treatment		Horizon	Soil C content ($g\ m^{-2}$)			Percent change	Daily soil C loss	Average annual CO_2-C Efflux
CO_2	N		1991	1993	1993-1991	(%)		($g\ m^{-2}\ day^{-1}$)
Ambient	Unfertilized	Ap	4557±604	4205±264	-352	-8	0.48	
Ambient	Unfertilized	Bw	2857±434	2484±295	-373	-13	0.51	
Ambient	Unfertilized	Total	7415±695	6689±296	-725	-10	0.99	1.4±0.5
Ambient	10 $g\ m^{-2}\ yr^{-1}$	Ap	4150±470	3832±416	-318	-8	0.44	
Ambient	10 $g\ m^{-2}\ yr^{-1}$	Bw	2651±230	2779±374	128	5	-0.17	
Ambient	10 $g\ m^{-2}\ yr^{-1}$	Total	6802±524	6612±560	-191	-3	0.26	3.4±1.4
Ambient	20 $g\ m^{-2}\ yr^{-1}$	Ap	4448±669	4069±411	-379	-9	0.52	
Ambient	20 $g\ m^{-2}\ yr^{-1}$	Bw	2636±269	2469±123	-167	-6	0.23	
Ambient	20 $g\ m^{-2}\ yr^{-1}$	Total	7085±749	6539±429	-546	-8	0.75	1.8±0.8
525 $\mu L\ L^{-1}$	Unfertilized	Ap	4564±328	5105±520	542	12	-0.74	
525 $\mu L\ L^{-1}$	Unfertilized	Bw	2970±537	2627±806	-344	-12	0.47	
525 $\mu L\ L^{-1}$	Unfertilized	Total	7534±630	7732±959	198	3	-0.27	2.2±0.7
525 $\mu L\ L^{-1}$	20 $g\ m^{-2}\ yr^{-1}$	Ap	5329±981	4780±692	-548	-10	0.75	
525 $\mu L\ L^{-1}$	20 $g\ m^{-2}\ yr^{-1}$	Bw	2789±245	2563±317	-226	-8	0.31	
525 $\mu L\ L^{-1}$	20 $g\ m^{-2}\ yr^{-1}$	Total	8118±1011	7343±761	-774	-10	1.06	2.6+0.7
700 $\mu L\ L^{-1}$	Unfertilized	Ap	4543±809	4015±96	-528	-12	0.72	
700 $\mu L\ L^{-1}$	Unfertilized	Bw	2484±274	2622±549	137	6	-0.19	
700 $\mu L\ L^{-1}$	Unfertilized	Total	7028±854	6637±557	-391	-6	0.54	2.7±0.8
700 $\mu L\ L^{-1}$	10 $g\ m^{-2}\ yr^{-1}$	Ap	3974±438	4631±1002	657	17	-0.90	
700 $\mu L\ L^{-1}$	10 $g\ m^{-2}\ yr^{-1}$	Bw	2877±450	2293±264	-584	-20	0.80	
700 $\mu L\ L^{-1}$	10 $g\ m^{-2}\ yr^{-1}$	Total	6852±628	6924±1036	73	1	-0.10	6.0±4.1
0.00								
700 $\mu L\ L^{-1}$	20 $g\ m^{-2}\ yr^{-1}$	Ap	4225±583	4536±393	311	7	0.43	
700 $\mu L\ L^{-1}$	20 $g\ m^{-2}\ yr^{-1}$	Bw	1934±356	2872±362***	938	48	-1.28	
700 $\mu L\ L^{-1}$	20 $g\ m^{-2}\ yr^{-1}$	Total	6160±683	7409±534*	1249	20	-1.71	2.4±1.1

**Statistically significant, 95% level.
***Statistically significant, 99% level.

Fig. 6), but were 30–90% lower than average annual calculated CO_2 efflux (Table 3).

It seems clear from these comparisons and the correlations among root biomass, soil pCO_2, and CO_2 efflux that microbial respiration contributes little to total CO_2 efflux. This does not necessarily imply that autotrophic root respiration completely dominates total soil CO_2 efflux, however: there is the distinct possibility that rhizosphere microbial activity is also a significant CO_2 source (Zak et al., 1993). The possibility of treatment effects on rhizosphere soil C and microbial communities is currently under investigation.

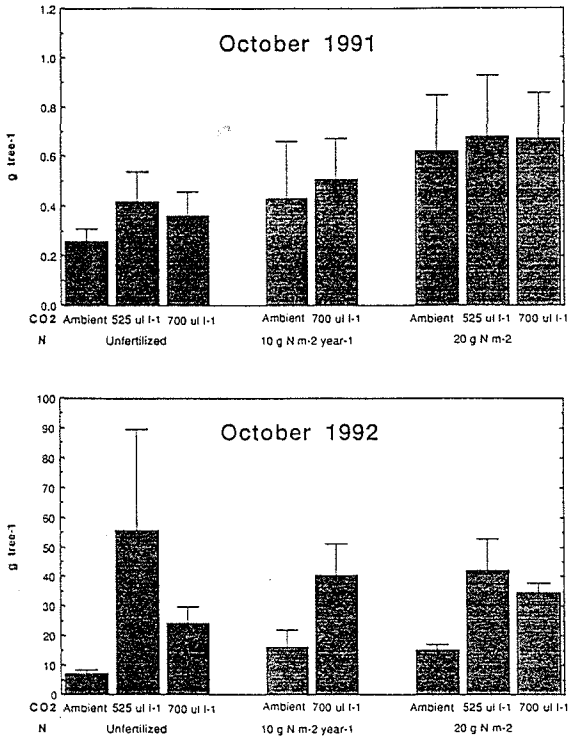

Fig. 5. Root biomass in October 1991 and October 1992.

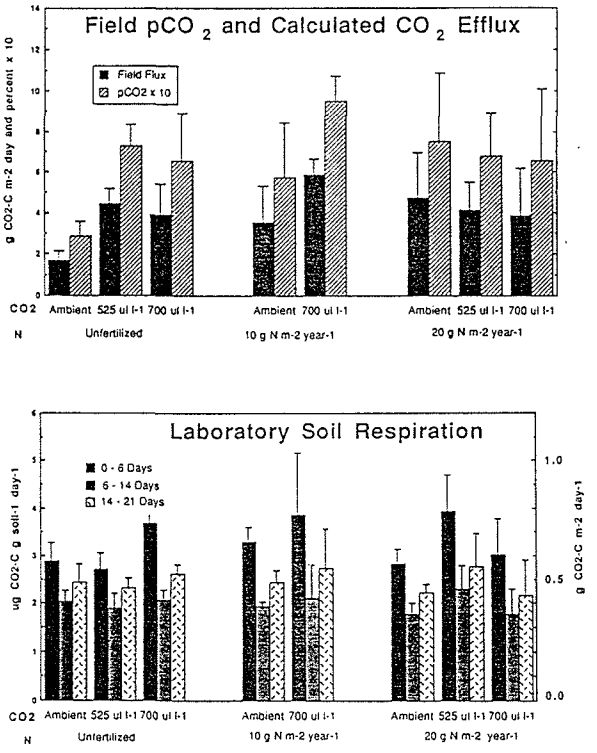

Fig. 6. Soil pCO_2 and calculated CO_2 efflux in the field (top) and soil CO_2 efflux during laboratory incubations of samples taken in July 1993.

Physical factors affecting soil pCO_2 and calculated CO_2 efflux

The data presented above suggest that soil pCO_2 and calculated CO_2 efflux can be used as indices of below-ground activity at the Placerville site. There remains the question as to how soil pCO_2 might respond to changes in the diffusion coefficient (D) caused by changes in soil moisture, however (de Jong and Schappert, 1972; Solomon and Cerling, 1987). The extent to which soil pCO_2 is sensitive to total soil respiration (q, or total soil CO_2 efflux), soil depth (z), and moisture content (Vw) can be seen by combining equations 1 and 2, integrating, and solving for C:

$$C_z = \frac{(q)(z)}{J(Da)[(E - V_w)^{10/3}/E^2]} + C_o \qquad (3)$$

where C_z = pCO_2 at depth z and C_o = pCO_2 in the atmosphere above the soil.

Equation 3 shows that soil pCO_2 (C_z) increases with depth (z) and total respiration (q) for a given (constant) soil moisture content (V_w). Soil pCO_2 at 30 cm was nearly always (89% of the time) greater than pCO_2 at 15 cm, as predicted by equation 3 (as well as by the more sophisticated equations of Wesseling [1962]). Equation 3 also shows that soil pCO_2 at a given depth is more sensitive to changes in soil moisture (V_w) than total respiration (q): C_z is directly proportional to q and inversely proportional to the 10/3 power of the quantity [E-V_w] containing the soil moisture term.

Despite the potential importance of soil moisture on soil pCO_2, there was no correlation between soil pCO_2 and soil moisture over the sampling period ($r^2 = 0.04$) or among chambers on any specific sampling date. There was, however, a weak but statistically significant correlation between soil pCO_2 and soil temperature ($r^2 = 0.29$). In contrast, calculated CO_2 efflux was less correlated with temperature ($r^2 = 0.12$) than with moisture ($r^2 = 0.31$).

The effect of soil moisture on pCO_2 and calculated CO_2 efflux can also be seen clearly from the temporal patterns in these parameters in the spring and summer of 1992. For experimental reasons, the soil was allowed to dry in October 1992 (Fig. 4), causing D to decrease by two orders of magnitude (from 5.4×10^{-8} cm^2 sec^{-1} in July to 1.9×10^{-6} cm^2 sec^{-1}

in October). As the soil dried, calculated CO_2 efflux increased, as would be expected from equation 1, but soil pCO_2 increased as well (Figs. 1–3). Thus, the temporal variations in pCO_2 in this soil appear to be driven primarily by variations in root and soil microbial respiration rather than by variations in soil moisture and D, whereas D is a major factor in calculated CO_2 efflux. This contrasts with the results of de Jong et al. (1974), where wetting and drying cycles had a major effect upon soil respiration in native grasslands and cultivated soils. Solomon and Cerling (1987) found that the presence of a snowpack created a diffusion barrier and produced elevated soil pCO_2 even with low respiration rates in a montane meadow in Utah. Thus, variations in soil moisture may significantly affect soil pCO_2 under other circumstances and will nearly always significantly affect calculated CO_2 efflux.

Conclusions

The hypothesis that elevated CO_2 and N fertilization would cause increased root biomass and total soil CO_2 efflux was supported by the results of these studies: both CO_2 and N treatments had significant, positive effects upon root biomass, soil pCO_2 and calculated CO_2 efflux. The intermediate (525 μL L^{-1}) CO_2 treatment produced the highest soil pCO_2 and root biomass. The hypothesis that treatments would cause increases in microbial respiration were not supported, however: there were no differences in laboratory-determined soil CO_2 efflux. It appears that microbial respiration in bulk soils contributed little to total soil respiration and that the patterns in both pCO_2 and CO_2 efflux are due mainly to differences in root biomass. It remains to be seen as to whether rhizosphere microbial respiration is significant or not, however.

It appears that soil pCO_2 and calculated CO_2 efflux provide sensitive and relatively cheap indices of belowground response to treatments. Treatment effects on soil CO_2 efflux measured by dynamic chambers, although similar in overall pattern and significantly correlated with root biomass, soil pCO_2, and calculated CO_2, were not statistically significant because of high variability (Vose et al., 1994). Soil pCO_2 measurements offer the decided advantage of being easily and, therefore, cheaply obtained, allowing greater flexibility in number of samples and frequency of sampling. The relative times required for soil pCO_2 and chamber CO_2 efflux measurements (four hours as opposed to one week) also give the pCO_2 method the advantage of avoiding temporal variations during the sampling period. Finally, the soil pCO_2 method offers the advantage of observing pCO_2 responses and calculating CO_2 effluxes at different depths. The major disadvantage of the soil pCO_2 method is that CO_2 efflux calculations are highly sensitive to assumptions about the diffusion coefficient (D), a parameter that cannot be directly monitored on a routine basis. Future papers will compare D values calculated from various models in the literature to D values calculated from measurements of CO_2 efflux and soil pCO_2 in the field over a range of soil moisture and temperature conditions.

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