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Elevated CO_2 increases belowground respiration in California grasslands

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Abstract This study was designed to identify potential effects of elevated CO_2 on belowground respiration (the sum of root and heterotrophic respiration) in field and microcosm ecosystems and on the annual carbon budget. We made three sets of respiration measurements in two CO_2 treatments, i.e., (1) monthly in the sandstone grassland and in microcosms from November 1993 to June 1994; (2) at the annual peak of live biomass (March and April) in the serpentine and sandstone grasslands in 1993 and 1994; and (3) at peak biomass in the microcosms with monocultures of seven species in 1993. To help understand ecosystem carbon cycling, we also made supplementary measurements of belowground respiration monthly in sandstone and serpentine grasslands located within 500 m of the CO_2 experiment site. The seasonal average respiration rate in the sandstone grassland was 2.12 μmol m^{-2} s^{-1} in elevated CO_2, which was 42% higher than the 1.49 μmol m^{-2} s^{-1} measured in ambient CO_2 (P = 0.007). Studies of seven individual species in the microcosms indicated that respiration was positively correlated with plant biomass and increased, on average, by 70% with CO_2. Monthly measurements revealed a strong seasonality in belowground respiration, being low (0–0.5 μmol CO_2 m^{-2} s^{-1} in the two grasslands adjacent to the CO_2 site) in the summer dry season and high (2–4 μmol CO_2 m^{-2} s^{-1} in the sandstone grassland and 2–7 μmol CO_2 m^{-2} s^{-1} in the microcosms) during the growing season from the onset of fall rains in November to early spring in April and May. Estimated annual carbon effluxes from the soil were 323 and 440 g C m^{-2} $year^{-1}$ for the sandstone grasslands in ambient and elevated CO_2. That CO_2-stimulated increase in annual soil carbon efflux is more than twice as big as the increase in aboveground net primary productivity (NPP_a) and approximately 60% of NPP_a in this grassland in the current CO_2 environment. The results of this study suggest that below-ground respiration can dissipate most of the increase in photosynthesis stimulated by elevated CO_2.

Key words Carbon cycle · Ecosystem · Global change · Respiration

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Introduction

Belowground respiration is one of the primary pathways through which terrestrial ecosystems exchange carbon with the atmosphere. Studying belowground respiration as influenced by elevated CO_2 is essential for understanding carbon balance in terrestrial ecosystems in the future CO_2-enriched environment. In the past 15 years, experimental studies have indicated that photosynthetic carbon uptake is generally increased for plants grown in elevated CO_2 (Strain and Cure 1985; Luo et al. 1994). For example, photosynthesis averaged 44% higher for 39 tree species grown in elevated than in ambient CO_2 (Gunderson and Wullschleger 1994). Additional carbon uptake in elevated CO_2 can stimulate carbon allocation to soil compartments through increased root biomass and exudation (Norby et al. 1987), accelerated root turnover rates (Rogers et al. 1994), and greater litterfall (N.R. Chiariello, unpublished data). Increased root biomass growth may respire more carbon, and increased availability of soil carbon may stimulate microbial activity in decomposing litter, all potentially leading to increased belowground respiration.

CO_2 effects on belowground respiration have been found to vary among ecosystems. Belowground respira-

tion in the Alaskan tundra was not significantly affected by either long- or short-term CO_2 enrichment (Oberbauer et al. 1986). Belowground respiration at 525 ppm CO_2 was 50% higher than at 350 ppm in a ponderosa pine forest near Placerville, California, whereas 700 ppm CO_2 resulted in little change in belowground respiration for all three levels of nitrogen fertilization (Johnson et al. 1994; Vose et al. 1995). In a free-air CO_2 enrichment (FACE) experiment with cotton at the Maricopa Agricultural Center, Arizona, CO_2 enrichment at approximately 550 ppm significantly increased belowground respiration (Nakayama et al. 1994). Variation in CO_2 effects on belowground respiration may be related to other ecosystem attributes and processes. Long-term CO_2 enrichment in the Alaskan tundra, for example, did not stimulate ecosystem photosynthetic carbon fixation (Tissue and Oechel 1987; Grulke et al. 1990), whereas the FACE experiment with cotton led to changes in photosynthetic carbon uptake, soil carbon content (Wood et al. 1994), and root growth (Rogers et al. 1993; Prior et al. 1994).

Soil carbon dioxide is released to the atmosphere by respiration of living roots and microbial decomposition of litter added to soil from aboveground and belowground sources, including root exudates (Singh and Gupta 1977; Bowden et al. 1993). Annual belowground respiration rates correlate positively with aboveground litter production in forest ecosystems (Raich and Nadelhoffer 1989) and with mean productivity in different vegetation biomes on a global scale (Raich and Schlesinger 1992). Studies in specific ecosystems indicate that belowground respiration is also influenced by soil water content, temperature, and plant phenology (Singh and Gupta 1977). Seasonal patterns of belowground respiration, for example, are strongly associated with variations in soil water content in a tall prairie grassland (Grahammer et al. 1991) and with soil temperature and root activity in a Tennessee upland oak forest (Hanson et al. 1993).

This study is part of the Jasper Ridge CO_2 project designed to exlore ecosystem-scale responses to elevated CO_2 (Field et al. 1996). The objective of this work was to identify the effect of increased CO_2 on belowground respiration in natural grasslands. We made three sets of measurements of belowground respiration: (1) seasonal time courses throughout one growing season in a sandstone grassland and in microcosms with mixed species from November 1993 to June 1994; (2) at peak biomass in both the serpentine and sandstone grassland in 1993 and 1994; and (3) at peak biomass in microcosms tubes with seven individual species in 1993. To help interpret and understand CO_2 effects on ecosystem carbon cycling, we made supplementary measurements to characterize seasonal patterns of belowground respiration, soil temperature, water content, and organic matter in the sandstone and serpentine grasslands adjacent to the CO_2 site. Based on the seasonal patterns and a simple model we developed, we estimate annual carbon fluxes and the ratio of annual belowground respiration to ecosystem productivity for the two CO_2 treatments and in the two natural grasslands.

Materials and methods

Site description

The CO_2 experiments, including microcosms and the two natural grasslands, are located at the Jasper Ridge Biological Preserve of Stanford University, California, (37° 24′ N, 122° 14′ W; elevation 150 m). The site has a mediterranean-type climate, wet in winter and dry in summer. During the last 20 years, annual precipitation varied from 200 mm (in 1975–1976) to 1200 mm (in 1982–1983), with an average of 595 mm from 1975 to 1990. The rainy season starts in fall, usually October or November, and lasts approximately until April (Chiariello 1989).

Soil properties of the two grasslands are listed in Table 1. The serpentine grassland at Jasper Ridge occupies serpentine-derived soils (Montara Series: loamy, serpentinitic, thermic, lithic haploxerolls) and sandstone grassland occupies sandstone-derived soil (Dibble Series, Millsholm variant: loamy, mixed, thermic, lithic xerochrepts; Kashiwagi 1985). Soil of the serpentine grassland has higher pH, cation exchange, soil nitrogen, and organic matter than the sandstone grassland soil but lower soil potassium (Table 1). The sandstone grassland is dominated by *Avena barbata* Link and *Bromus hordeacus* L. in spring and *Hemizonia congesta* DC. ssp. *luzulifolia* (DC.) Babc. & H.M. Hall (Hickman 1993) in summer and early fall. Common species in the serpentine grassland include *Bromus hordeacus*, *Calycadenia multiglandulosa* DC., *Lasthenia californica* Lindley, and *Plantago erecta* E. Morris (McNaughton 1968; Hobbs and Mooney 1985; Hickman 1993).

CO_2 experiments

The CO_2 experiments in the field used 30 plots of 0.33 m^2 soil area (0.65 m in diameter) randomly selected in each of the sandstone and serpentine grasslands for three treatments: ten replicates of no-chamber controls, open-top chambers with ambient CO_2, and open-top chambers with elevated CO_2 (ambient +350 ppm, a seasonal average of 723 ppm). Each cylindral open-top chamber was 1 m tall and CO_2 fumigation started in January 1991. We focused on the two chamber treatments to examine CO_2 effects on belowground respiration.

For the microcosm experiments, 20 open-top chambers at either ambient or ambient+350 ppm CO_2 each contained an array of approximately 30 tubes which were 0.2 m in diameter and 1 m deep. The tubes were filled with an upper 0.15 m of shredded serpentine topsoil and 0.80 m of crushed rock from a serpentine quarry in 1992 and half of the tubes were filled with sandstone soil in 1993. We added one 38-mm watering in November of 1992 to ini-

Table 1 Soil Properties [pH, cation exchange (*CE*), Phosphorus (*P*), Potassium (*K*), nitrogen (*N*), soil organic matter (*SOM*), and texture (mean ± Se)] of the sandstone and serpentine grasslands. Kjeldahl nitrogen was analyzed as in Bremner and Mulvaney (1982), and P and K were extracted with 0.5 M sodium bicarbonate. SOM was measured by combusting dried soil samples at 500°C for 5 h. The data were averages from 0–3 cm surface soil for SOM and from 0–20 cm soil for the other attributes. Sample size was 3 for pH, CE, P, K, and N and 39 for SOM. *P* is a value of probability for the comparative *t* test from the sandstone and serpentine grasslands

Soil Properties	Sandstone	Serpentine	*P*
pH	5.5 ± 0.08	6.6 ± 0.03	0.002
CE (mmhos cm^{-1})	0.1 ± 0.00	0.7 ± 0.14	0.001
P (mg kg^{-1})	1.8 ± 0.09	1.8 ± 0.11	0.952
K (mg kg^{-1})	71 ± 2.2	44 ± 5.1	0.005
N (%)	0.10 ± 0.00	0.14 ± 0.01	0.004
SOM (%)	5.2 ± 0.1	7.5 ± 0.4	0.001
Texture	Loam	Clay loam	

tiate germination and did not add any supplemental water during the experiment. Monocultures of seven annual species common to Jasper Ridge grasslands were grown in the 1992–1993 season. The seven species included four C_3 grasses, *Avena barbata*, *Bromus hordeacus*, *Lolium multiflorum* L., and *Vulpia microstachys* (Nutt.) Benth var. *pauciflora* (Beal) Lonard & Gould and three C_3 forbs, *Hemizonia congesta*, *Calycadenia multiglandulosa*, and *Plantago erecta* (Hickman 1993). In the 1993–1994 season, we grew two communities, a serpentine mixture [including *Vulpia microstachys*, *Lasthenia californica*, *Plantago erecta*, *Calycadinia multiglandulosa*, and *Lotus wrangelianus* Fischer & C. Meyer (Hickman 1993)] and a sandstone mixture (including *Avena barbata*, *Bromus hordeacus*, *Hemizonia congesta*, and *Lotus wrangelianus*). The density for all treatments was 100–200 plants per tube, depending on species.

CO_2 fluxes measurements

Soil surface respiration was measured with a modified Li-Cor LI 6200 closed gas-exchange system (Li-Cor, Lincoln, Neb., USA) similar to that of Norman et al. (1992). The system provides belowground respiration values comparable to those measured by eddy correlation apparatus and potassium hydroxide traps (Norman et al. 1992; Dugas 1993). An open-ended cylinder was fitted with a Li-Cor sensor housing (Part No. 9960–035) with gas inlet and outlet ports. The belowground respiration chamber was 20.25 cm high and 4.10 cm in diameter, with a measurement surface area of 13.20 cm^2 and a chamber volume of 267.3 cm^3. A leakage port in the upper part of the chamber maintained pressure equilibrium between the air inside and outside the chamber. The chamber was pressed slightly into the soil to ensure a good seal at the chamber-soil interface.

We avoided measurements within 5 days after rain because Norman et al. (1992) reported, and our preliminary data indicated, that soil degassing immediately after rain may result in overestimation of belowground respiration at the water-saturated soil surface. We did not make measurements under other atypical weather conditions (e.g., cloudy days), either, to avoid bias estimation of annual carbon flux from soil. We measured soil temperature at a depth of 3 cm below the soil surface with Type-T thermocouples connected to a data logger (Campbell 21 ×) and multiplexer. Soil samples in the surface 3-cm soil were taken for moisture measurement in the two grassland ecosystems. Soil water content was determined gravimetrically at 80°C.

Four to ten measurements were taken for each of the CO_2 treatments and in each of the two grassland ecosystems on each sampling date. For the supplementary measurements adjacent to the CO_2 site, individual measurement sites were randomly distributed throughout each system to incorporate natural spatial heterogeneity. All measurements were taken between 1100 and 1400 hours PST to minimize diurnal variability. The sampling time interval for these experiments to characterize time-courses of belowground respiration was approximately 1 month.

Estimation of the annual carbon flux from soil

Our estimates of annual total carbon efflux from the soil assume that our monthly measurements captured the broad seasonal patterns in below-ground respiration and that our midday measurements were approximate daily maxima. The latter were adjusted by soil temperature and a Q_{10} relationship to estimate daily efflux, which is used to estimate annual carbon efflux by multiplying the number of days (about 30 days) between measurement intervals.

Belowground respiration is generally predicted by both soil temperature and soil water content (Kim and Verma 1992). Due to little diurnal variation in soil water content, our estimates of daily carbon efflux were based on soil temperature. Belowground respiration at time h [$R(h)$] is estimated by

$$R(h) = \frac{R_{max}}{Q_{10}^{[T_{max}-T(h)]/10}}$$

where Q_{10} is a quotient indicating the increase in belowground respiration caused by a temperature increase of 10°C, R_{max} is the daily maxima of belowground respiration, equaling our measured midday values, T_{max} is the daily maximum temperature (°C) and $T(h)$ is the temperature at time h (°C), estimated by a general diurnal temperature oscillation equation (Monteith and Unsworth 1990). That is

$$T(h) = \frac{T_{max} - T_{min}}{2} \mathrm{Sin}\left(2\pi \frac{h-6}{24}\right) + \frac{T_{max} + T_{min}}{2}$$

where T_{min} is the daily minimum temperature (°C). Our measured values of midday soil temperature at the depth of 3 cm are used as T_{max} and T_{min} was the minimum soil temperature obtained from the weather station about 500 m away from the experimental sites.

Q_{10} values compiled by Raich and Schlesinger (1992) range from 1.3 to 3.3. We also performed a brief experiment to estimate a Q_{10} value in the sandstone grassland as a check on the model assumptions. Our measurements of belowground respiration, temperature, and water content started at 0900 hours on 6 March and ended at 0100 hours on 7 March 1993, with values taken every 2 h. Both belowground respiration and temperature in the two ecosystems were highest at midday and lowest at night while soil water varied little (data not presented). Belowground respiration increased as soil temperature increased with a Q_{10} value of 1.5, indicating that belowground respiration increased approximately 50% when soil temperature increased by 10°C. The measured Q_{10} value suggests that the relationship of belowground respiration with temperature in these grasslands may be close to the lower end of Raich and Schlesinger's (1992) Q_{10} range. In order to account for possibly different Q_{10} relationships in other seasons, we bracket our estimated daily and annual carbon fluxes for a range of Q_{10} between 1.5 and 2.5. Effects of seasonal variation in soil water content and temperature on belowground respiration were assumed to be reflected in our monthly measurements. Note that this simple model does not account for temperature gradient in the soil profile. Sensitivity analysis with Q_{10} ranging from 1.5 to 2.5, however, may bound variation in the annual carbon flux caused by the temperature gradient.

Results

CO_2 effects in field plots

Elevated CO_2 increased belowground respiration in the sandstone grassland from December to April, the active growing season for these plants (1993–1994, Fig. 1, $P = 0.007$). Belowground respiration was similar for the two CO_2 levels at the beginning or the end of the growing season, when the soil was dry and plant and microbial activity were minimal. In comparison to that in ambient CO_2, belowground respiration in elevated CO_2 increased 35% in December, about 60% in January and February, and 130% in March, when biomass approached its seasonal peak. The seasonal average of belowground respiration was 2.12 μmol m^{-2} s^{-1} in elevated CO_2, which is significantly higher than 1.49 μmol m^{-2} s^{-1} in ambient CO_2 ($P = 0.007$ by repeated measures analysis).

Relative effects of elevated CO_2 on belowground respiration were higher in 1994 than in 1993 in both sandstone and serpentine grasslands. In the sandstone grassland, where peak plant biomass occurs from March to May, belowground respiration was 43% ($P = 0.193$) higher in elevated CO_2 than that in ambient CO_2 in 1993 (Fig. 2A), 134% higher in March but much less stimulated in April and May in 1994 (Fig. 1). In the serpentine

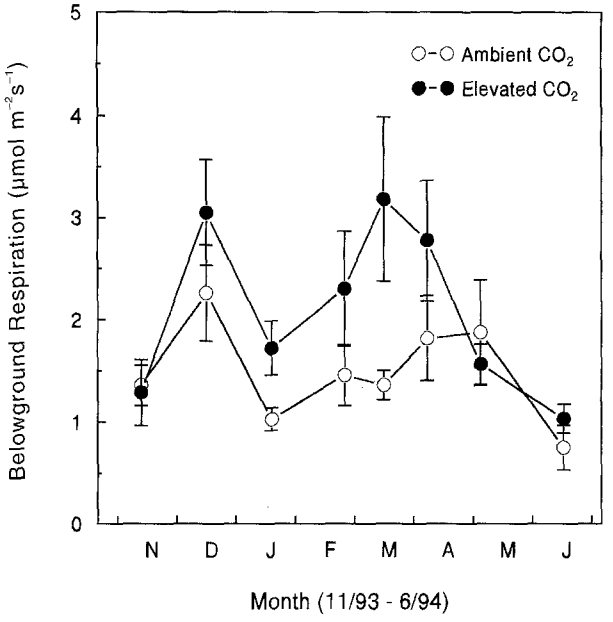

Fig. 1 Seasonal courses of belowground respiration in the sandstone grassland in ambient (*open circles*) and elevated CO_2 (*solid circles*; mean ± SE, n = 6–10) from November 1993 to June 1994. Measurements were initiated in mid-November, a few days after the first major precipitation in fall, and continued though plant senescence in mid-June. Measurements were taken on bare spots underneath canopy in each field plot (10 plots per treatment)

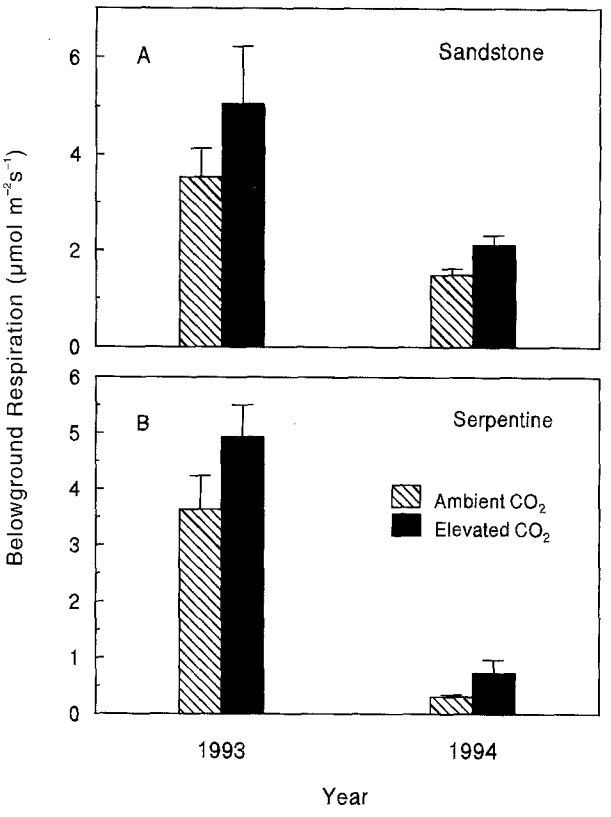

Fig. 2 Belowground respiration in the sandstone (**A**) and serpentine (**B**) grasslands in the ambient CO_2 (*hatched bars*) and elevated CO_2 (*solid bars*; mean + SE, n = 4–10) in 1993 and 1994. Measurements of belowground respiration were taken on the harvest rings immediately after cutting on 1 May 1993 in the sandstone grassland, on 5 April 1993 and 6 April 1994 in the serpentine grassland when plant biomass reached approximately the maximum. Data for the sandstone grassland in 1994 were the seasonal average from Fig. 1

grassland when peak biomass generally occurs in March and April, belowground respiration in elevated CO_2 was 36% higher (P = 0.151) in 1993 and 139% higher (P = 0.062) in 1994 than in ambient CO_2 (Fig. 2B). Differences between 1993 and 1994 were due primarily to a much drier growing season in 1994.

CO_2 effects in the microcosms

Time-course measurements in the microcosm experiment suggested little difference in belowground respiration between the two CO_2 levels before March 1994 (Fig. 3A, B). From March to May, belowground respiration in elevated CO_2 was 75% higher (P = 0.046) in the tubes filled with the sandstone soil and 60% higher (P = 0.009) with the serpentine soil than that in ambient CO_2. The seasonal average was not significantly different between the two CO_2 levels for the sandstone soil (P = 0.788), but approached significance for the serpentine (P = 0.052).

Studies of individual species in the microcosms indicated that below-ground resiration and its response to elevated CO_2 greatly varied with species (Fig. 4A). It was 1.5–2.5 μmol m^{-2} ground area s^{-1} for *Plantago*, *Bromus*, *Hemizonia*, and *Calycadenia* and reached as high as 4–6 μmol m^{-2} ground area s^{-1} for *Lolium*, *Avena*, and *Vulpia*. Elevated CO_2 had a significant effect on belowground respiration in the tubes with *Plantago*, *Bromus*, *Hemizonia*, and *Lolium* but not for the other three species. The average of belowground respiration across species was 3.52 μmol m^{-2} s^{-1} at elevated CO_2, nearly 70% greater than 2.10 μmol m^{-2} s^{-1} at ambient CO_2 (P = 0.001). Belowground respiration in the tubes with monoculture of seven species was highly correlated with shoot biomass (R^2 = 0.73; data not shown) and total biomass (R^2 = 0.65) in the final harvest at the end of April and the beginning of May 1993 (Fig. 4B).

Annual carbon fluxes

In order to estimate annual carbon fluxes, we made monthly measurements of belowground respiration for 1 year in sandstone and serpentine grasslands located within 500 m of the CO_2 experiment site. Belowground respiration in the two natural grasslands increased from nearly zero in October to about 3 μmol m^{-2} s^{-1} in November with the onset of fall rains (Fig. 5A, B). Respiration was maintained around 3 μmol m^{-2} s^{-1} through the growing season from November to April. Summer belowground respiration was very close to zero (0–0.5 μmol m^{-2} s^{-1}; Fig 5A, B), as most of the plants had senesced and little carbon was translocated below ground. Seasonal patterns of belowground respiration mirrored soil water availabil-

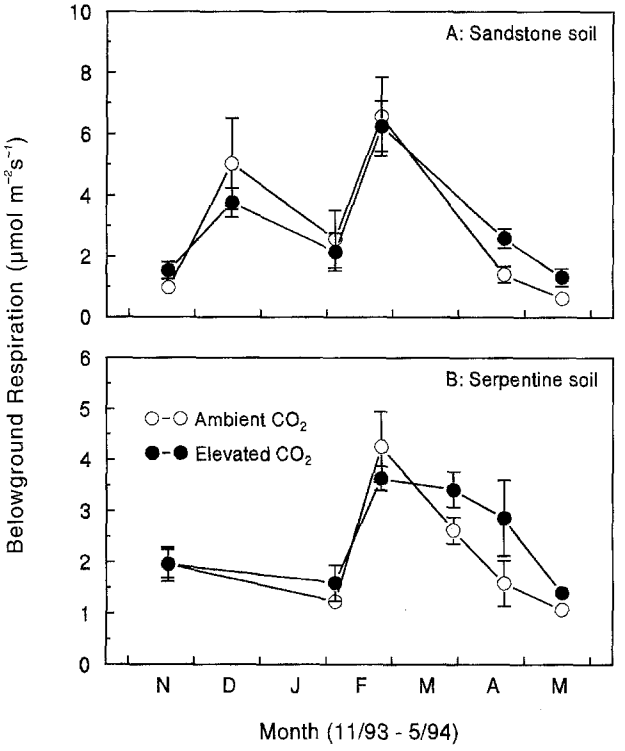

Fig. 3 Seasonal courses of belowground respiration in microcosms tubes with sandstone (**A**) and serpentine (**B**) soils in ambient (*open circles*) and elevated CO_2 (*solid circles*; mean ± SE, n = 4–6) from November 1993 to May 1994. Measurements were initiated in mid-November and continued though peak biomass harvests in mid-May. Measurements were taken on bare spots between plants. Each microcosms tube was filled with well-mixed soils of either sandstone or serpentine at the beginning of growing season. Initial carbon contents in either sandstone or serpentine soils were presumably similar

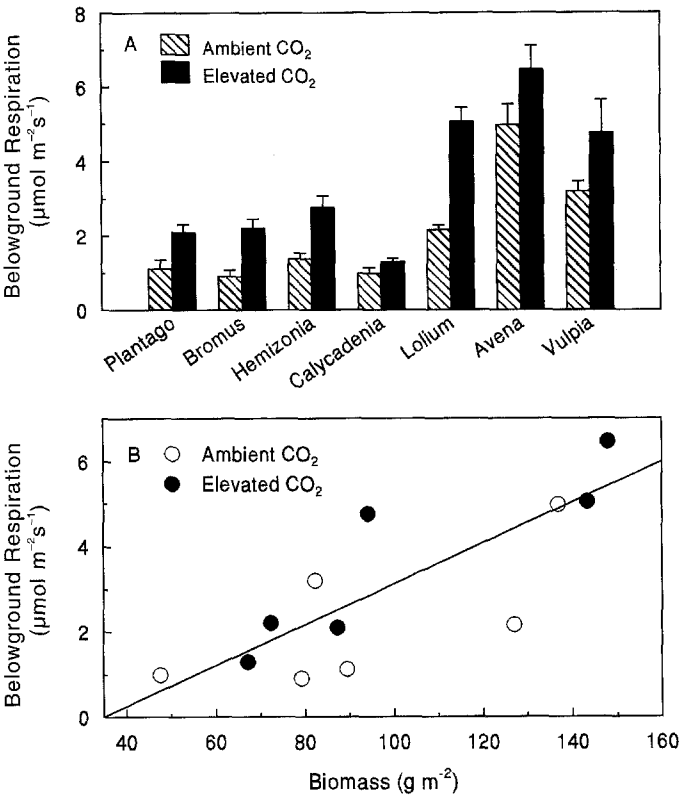

Fig. 4 **A** Belowground respiration in monoculture of seven species in microcosms tubes with ambient (*hatched bars*) and elevated CO_2 (*solid bars*; mean + SE, n = 4–7). Each tube was filled with well-mixed serpentine soils at the beginning of growing season. Measurements were taken in March and April 1993 when plant biomass reached the maximum. (**B**) The correlation between belowground respiration and total plant biomass (shoots plus roots) in the final harvest at the end of April and the beginning of May 1993 (R^2 = 0.65). No biomass data were available for *Calycadenia*

ity quite closely (Fig. 5C, D). Belowground respiration was correlated positively with soil water content but negatively with soil temperature.

Using our model and the monthly measurements, we estimated that annual total carbon efflux from the soil of the sandstone grassland was 323 and 440 g C m^{-2} $year^{-1}$, respectively, for the field plots with the ambient and elevated CO_2, differing by 36%, (Table 2, Q_{10} = 2). Total carbon released from the sandstone and serpentine grasslands adjacent to the CO_2 site was 485 and 346 g C m^{-2} $year^{-1}$. Annual carbon efflux from the CO_2 plots was less than that in the natural ecosystems partly because open-top chambers may alter microclimate (Drake and Peresta 1993; Lee and Barton 1993). Sensitivity analysis indicated that estimated annual carbon release decreases as Q_{10} increases (this relationship occurs in our case because we estimate daily total carbon flux from a maximal respiration value at midday). When Q_{10} varies from 1.5 to 2.5, estimated soil carbon was reduced by about 23%.

Based on the Raich and Nadelhoffer's (1989) approach, we also estimated the ratio of annual soil carbon efflux to aboveground net primary productivity which ranged from 2.07 to 7.69 for the two natural grasslands and with the two CO_2 treatments (Table 2). The ratio was

Table 2 Annual carbon release from soils to the atmosphere (R_{an}; Q_{10} = 2), aboveground net primary productivity (NPP_a), and the R_{an}/NPP_a ratio with the two CO_2 treatments in the sandstone grassland and in the sandstone and serpentine ecosystems outside the CO_2 site. R_{an} was estimated with our model and monthly measurements. Carbon efflux during the dry season from July to October in the plots with CO_2 treatments was assumed to be the same as in the natural ecosystem adjacent to the CO_2 site and was very close to zero. Values of NPP_a for the CO_2 treatments were estimated from data of live and dead biomass harvested in January and May 1994 (Field et al. 1996). Estimates of NPP_a for the sandstone and serpentine grassland ecosystems are from McNaughton (1968) and data of live and dead biomass on the no-chamber control plots in the CO_2 experiment (Chiariello et al., unpublished data). For all estimates, plant biomass is assumed to contain 45% carbon

Treatment	R_{an} g C m^{-2} $year^{-1}$	NPP_a g C m^{-2} $year^{-1}$	R_{an}/NPP_a
CO_2 concentrations in plots on the sandstone grassland			
Ambient	323	104	3.11
Elevated	440	153	2.88
Ecosystems outside of the CO_2 site			
Sandstone	485	135–234	2.07–3.59
Serpentine	346	45–90	3.84–7.69

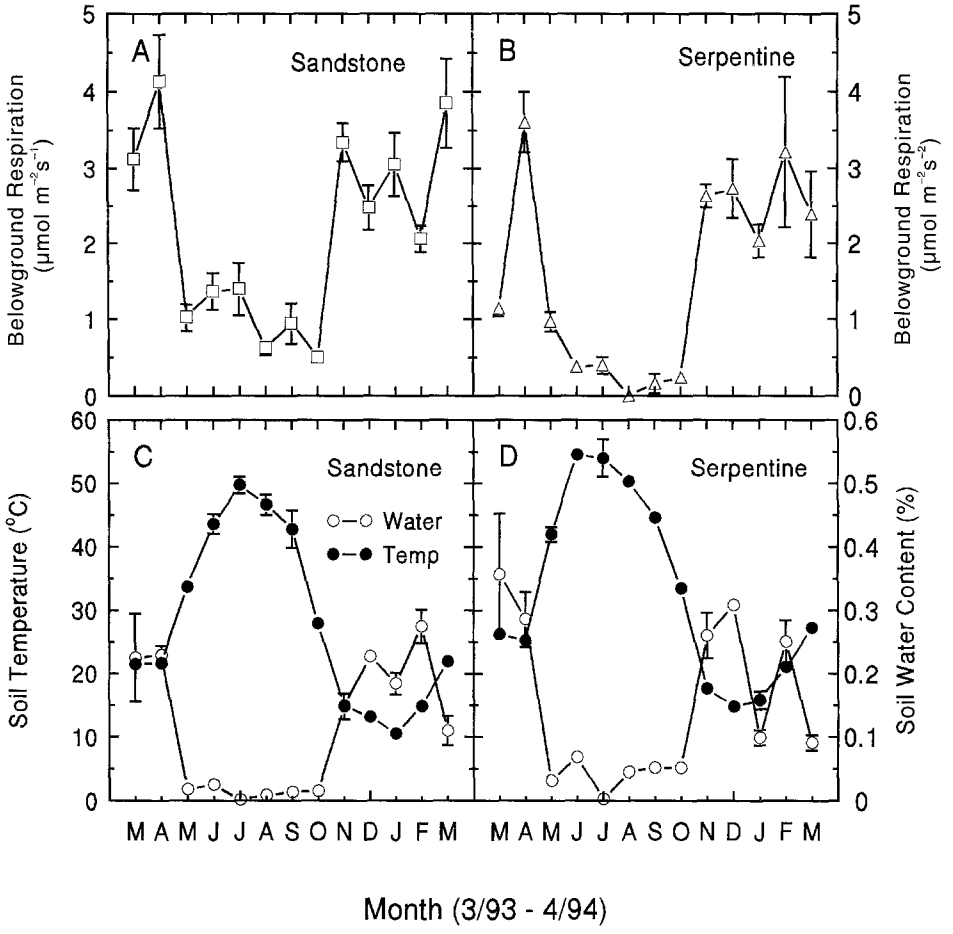

Fig. 5A, B Belowground respiration (μmol m^{-2} s^{-1}; mean ± SE, n = 5–7), **C, D** soil temperature (°C) at a depth of 3 cm (*solid circles*; mean ± SE, n = 3–6), and gravitational water content (%) (*open circles*; mean ± SE, n = 3) in the sandstone and serpentine grasslands located within 500 m of the CO_2 experiment site from March 1993 to March 1994. All measurements were made at noon between 1100 to 1400 hours PST once a month. Monthly summary of precipitation at the Jasper Ridge was 61.25, 22.10, 15.24, 0.00, 0.00, 0.00, 1.02, 15.74, 42.17, 96.27, 69.09, 163.58, and 7.62 mm, from March 1993 to March 1994, totaling 494.08 mm. The onset of fall rains occurred after our monthly respiration measurement in October. Belowground respiration (y) was positively correlated with soil water content (x) as $y = 1.14 + 8.87x$ ($R^2 = 0.54$; $P = 0.004$, where R^2 is determinant coefficient and P is a value of probability) for sandstone grassland and $y = 0.47 + 7.25x$ ($R^2 = 0.50$; $P = 0.007$) for serpentine grassland. Belowground respiration (y) is negatively correlated with soil temperature (x) as $y = 3.91–0.06x$ ($R^2 = 0.48$; $P = 0.009$) for sandstone grassland and $y = 3.86–0.07x$ ($R^2 = 0.66$; $P = 0.001$) for serpentine grassland

similar for the two CO_2 levels, indicating that elevated CO_2 altered aboveground productivity and belowground respiration proportionally. The ratio in the natural sandstone grassland ranged from 2.1 to 3.6, similar to values reported for other ecosystems. Values were much higher in the serpentine (3.8–7.7), possibly reflecting increased respiratory costs for growth and maintenance in stressful serpentine soils. Using different Q_{10} values between 1.5 and 2.5, the ratio varies only by about 20%.

Discussion

Our three sets of data all indicate that belowground respiration was higher in elevated than in ambient CO_2. Elevated CO_2 increased the seasonal average of belowground respiration in the sandstone grassland by 42% in comparison to that in ambient CO_2. Belowground respiration averaged across seven monoculture species in microcosm tubes was nearly 70% higher in elevated CO_2 than in ambient CO_2. Although the seasonal average was not significantly different between the two CO_2 treatments in the microcosm tubes filled with either sandstone or serpentine soils, belowground respiration in the late growing season was significantly higher in elevated CO_2 than in ambient CO_2. Elevated CO_2 increased belowground respiration at the peak biomass by 30–40% in 1993 and by about 130% in 1994 in both serpentine and sandstone grasslands. The yearly variation in CO_2 effects resulted from many factors, including a large difference in precipitation (905 mm in 1993 vs 433 mm in 1994) and consequent differences in plant growth and phenology (Jackson et al. 1995; Field et al. 1996).

Comparison of the seasonal course of CO_2 effects on belowground respiration in the sandstone grassland (Fig. 1) with those on the microcosm tubes (Fig. 3) suggests that elevated CO_2 may have altered soil carbon processes after the 2-year field CO_2 fumigation. The microcosm tubes were filled with well-mixed soils at the be-

ginning of the experiments, presumably having similar heterotrophic respiration for both CO_2 treatments. As a result, belowground respiration was not much different between the elevated and ambient CO_2 in the early growing season (Fig. 3A, B). Later in the growing season (March to May), plants grew larger and the contribution of root respiration to soil carbon fluxes may have been substantial as suggested by the correlation between biomass and respiration (Fig. 4B; Vose et al. 1995). Plant roots may respire some portion of increased carbon newly fixed in photosynthesis at elevated CO_2 (Bowden et al. 1993; Cheng et al. 1994), resulting in higher belowground respiration than at ambient CO_2 in the late growing season.

For plots with open-top chambers in the sandstone grassland, root respiration during the early growing season was unlikely to contribute much to belowground respiration because the plants were very small. Increased belowground respiration at elevated CO_2 may be attributable to litter feedback effects. Aboveground litter was increased by 44% in January 1993 and 30% in May 1994 in elevated CO_2 compared to ambient CO_2 (Field et al. 1996). Root biomass growth was increased by 26% (Hungate et al. 1996), leading to increased belowground litter in elevated CO_2. In addition, the lignin content of roots was reduced in elevated compared to ambient CO_2 (Chu et al. 1996), suggesting higher decomposability of soil organic matter. Increased carbon availability in soil and reduced lignin content may stimulate microbial population and activities. Indeed, soil microbial biomass increased by 55% in April 1992, 15% in January and 40% in May 1994 in elevated CO_2 (Hungate et al. 1996). Overall, elevated CO_2 in the sandstone grassland may have increased litterfall with less lignin which stimulated microbial population and heterotrophic respiration, resulting in higher belowground respiration in elevated than in ambient CO_2, even in the early growing season.

In the late growing season in the sandstone grassland, belowground respired carbon came partly from litter and partly from current photosynthesis (Bowden et al. 1993; Cheng et al. 1994). Photosynthetic carbon uptake of *Avena barbata*, the dominant species, was stimulated by up to 70% in comparison to that in ambient CO_2 in 1992–93 and 1993–94 growth season (Jackson et al. 1994, 1995). Modeling studies indicate that such an increase in leaf photosynthetic carbon uptake in elevated CO_2 may lead to a 30–110% increase in seasonal carbon influx into the system, depending on physiological adjustments in leaf death, allocation, and nonstructural carbon storage (Luo et al. 1996). In addition, increased soil water availability in elevated CO_2 (Field et al. 1995) may possibly amplify CO_2 effects on belowground respiration in the late growing season through enhanced plant growth (Field et al. 1996) and microbial decomposition (Hungate et al. 1996).

Annual soil carbon efflux in the sandstone grassland was estimated to increase by about 120 g m^{-2} $year^{-1}$ in elevated CO_2 (Table 2). This CO_2-stimulated increase in soil carbon efflux is more than twice as large as the increase in aboveground net primary productivity (NPP_a) and approximately 60% of NPP_a in this grassland in the current CO_2 environment. The increase in respiration indicates that a considerable amount of carbon was translocated below ground for root respiration, root turnover rate, and root exudation. Based on the general relationship between belowground respiration and NPP_a by Raich and Schlesinger (1989), Hungate et al. (1996) estimated that a combination of root respiration, turnover rate, and exudation was increased by 56% in the sandstone grassland in elevated CO_2 in comparison to that in ambient CO_2. In addition, that increase in belowground respiration may signify changes in carbon residence time in elevated CO_2. Total soil carbon content is estimated to be 8000 g C m^{-2} in the sandstone grassland (Hungate et al. 1996). Carbon residence time is estimated to be nearly 25 years in ambient CO_2 with annual carbon efflux being 323 g m^{-2} $year^{-1}$. Elevated CO_2 increased carbon fluxes to 440 g m^{-2} $year^{-1}$ but did not significantly change soil carbon content (Hungate et al. 1996). Carbon residence time is consequently decreased to about 18 years in elevated CO_2, potentially reducing carbon sequestration capacity in the grassland ecosystem.

Overall, elevated CO_2 increased belowground respiration in comparison to that in ambient CO_2, consistently across different CO_2 experiments. Belowground respiration and its response to elevated CO_2 varied with plant biomass in the microcosms, exhibited a strong seasonality and were subjected to year-to-year variation. Comparative analysis on these sets of data from the microcosms and field CO_2 plots may suggest litter feedback effects on belowground respiration in the sandstone grassland after the 2-year CO_2 fumigation. Estimated annual carbon effluxes from the soil were increased by nearly 120 g C m^{-2} $year^{-1}$, implying that belowground respiration was sufficiently large to dissipate most of the increase in photosynthetic carbon fixation stimulated by elevated CO_2.

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