

The response of soil CO₂ flux to changes in atmospheric CO₂, nitrogen supply and plant diversity

JOSEPH M. CRAINE*, DAVID A. WEDIN† and PETER B. REICH‡

*Department of Integrative Biology, University of California, Berkeley, CA 94720, USA, †School of Natural Resource Sciences, University of Nebraska, Lincoln, NE 68583, USA, ‡Department of Forest Resources, University of Minnesota, St. Paul, MN 55108 USA

Abstract

We measured soil CO₂ flux over 19 sampling periods that spanned two growing seasons in a grassland Free Air Carbon dioxide Enrichment (FACE) experiment that factorially manipulated three major anthropogenic global changes: atmospheric carbon dioxide (CO₂) concentration, nitrogen (N) supply, and plant species richness. On average, over two growing seasons, elevated atmospheric CO₂ and N fertilization increased soil CO₂ flux by 0.57 μmol m⁻² s⁻¹ (13% increase) and 0.37 μmol m⁻² s⁻¹ (8% increase) above average control soil CO₂ flux, respectively. Decreases in planted diversity from 16 to 9, 4 and 1 species decreased soil CO₂ flux by 0.23, 0.41 and 1.09 μmol m⁻² s⁻¹ (5%, 8% and 21% decreases), respectively. There were no statistically significant pairwise interactions among the three treatments. During 19 sampling periods that spanned two growing seasons, elevated atmospheric CO₂ increased soil CO₂ flux most when soil moisture was low and soils were warm. Effects on soil CO₂ flux due to fertilization with N and decreases in diversity were greatest at the times of the year when soils were warm, although there were no significant correlations between these effects and soil moisture. Of the treatments, only the N and diversity treatments were correlated over time; neither were correlated with the CO₂ effect. Models of soil CO₂ flux will need to incorporate ecosystem CO₂ and N availability, as well as ecosystem plant diversity, and incorporate different environmental factors when determining the magnitude of the CO₂, N and diversity effects on soil CO₂ flux.

Keywords: Nitrogen fertilization, CO₂, biodiversity, soil CO₂ flux, carbon cycle

Received 28 February; revised version received and accepted 3 July 2001

Introduction

Increasing atmospheric carbon dioxide (CO₂) concentrations, increasing rates of nitrogen (N) deposition, and declining plant diversity are three major global changes caused by human activities (Vitousek 1994; Sala *et al.* 2000). Soil CO₂ flux represents an integrated measure of root and microbial activity (Raich & Nadelhoffer 1989; Schlesinger & Andrews 2000) and is an important source of atmospheric CO₂ with annual global flux equivalent to approximately 10% of the atmospheric CO₂ pool (Schlesinger & Andrews 2000). Soil CO₂ flux is an important component of below-ground ecosystem car-

bon (C) cycling and storage and is likely to be altered by increases in resource availability and decreases in diversity (Knapp *et al.* 1998).

Soil CO₂ flux generally increases with elevated CO₂ in forest and grassland systems (Allen *et al.* 2000), with a wide variety of responses of soil CO₂ flux to elevated CO₂ (-10% to +162%) (Zak *et al.* 2000). Nitrogen fertilization often does not alter or decreases soil CO₂ flux (Raich & Tufekcioglu 2000). Little is known about the relationship between diversity and soil CO₂ flux, or about potential interactions between elevated CO₂, N supply and plant diversity in their effects on soil CO₂ flux.

Temporal patterns of soil CO₂ flux are important to models of ecosystem carbon balance (Raich & Potter

Correspondence: Joseph M. Craine, Landcare Research, Private Bag 1930, Dunedin, NZ, tel +64 3477 4050, fax +64 3477 5232, jcraine@socrates.berkeley.edu

1995) and soil CO₂ flux is highly responsive to short-term variation in carbon inputs (Fitter *et al.* 1997; Craine *et al.* 1998; Allen *et al.* 2000). Quantifying whether the effects of elevated CO₂, N fertilization or plant diversity on soil CO₂ flux covary over a growing season can help to simplify models of ecosystem function and will help clarify the mechanisms underlying changes in soil CO₂ flux. For example, if there are similar temporal patterns to the effects of two treatments on soil CO₂ flux, these two treatments may alter soil CO₂ flux through the same mechanism and share similar interactions with other factors such as soil temperature or soil moisture.

We addressed the response of soil CO₂ flux to increases in atmospheric CO₂, increases in N supply and decreases in plant diversity in the second and third years of a well-replicated experimental grassland study (the BioCON experiment). Each factor was directly manipulated with a full factorial combination of treatment levels. We test for differences in soil CO₂ flux among CO₂, N and plant diversity treatments as well as whether these treatments interact in their effects on soil CO₂ flux. By conducting multiple samplings throughout the two growing seasons, we examine (i) temporal patterns in treatment effects, (ii) the timing and magnitude of treatment effects over the course of the two growing seasons, and (iii) the seasonal relationships among soil CO₂ flux, treatment effects on soil CO₂ flux, soil temperature and soil moisture.

Materials and methods

BioCON design and sampling

The BioCON experiment (Reich *et al.* 2001a) is located at Cedar Creek Natural History Area, in central Minnesota, USA (Tilman 1988). The portion of the BioCON experiment that we sampled is composed of 296 plots, 2 × 2 m each. Prior to planting, the experimental area was tilled to a depth of 25 cm, fumigated with methyl bromide to eliminate seeds of undesired plant species, and the soil reinoculated with unfumigated soil suspended in water. These plots were planted to various combinations of 1, 4, 9 or 16 prairie plant species randomly chosen from 16 species in four plant functional groups (C₃ grass, C₄ grass, forb and legume). Plots were seeded in June, 1997 at a rate of 12 g m⁻² plot⁻¹, with seed mass evenly divided among the species in a plot.

Half of all of the plots were fertilized at 4 g N m⁻² y⁻¹ applied as NH₄NO₃ over three dates during each growing season whereas the other half of the plots are not fertilized. Work in this and other upland ecosystems at Cedar Creek has shown that N is the major limiting soil resource (Tilman 1987; Reich *et al.* 1997). Plots are evenly partitioned among six 14-m diameter circular

experimental areas (rings), three of which are exposed to ambient CO₂ and three to elevated CO₂ during daylight hours (560 μmol mol⁻¹) using Free Air Carbon dioxide Enrichment (FACE) technology (Lewin *et al.* 1994). For the main experiment, the 296 plots were randomly assigned to 32, 15, 15 and 12 replicates of the 4 levels of plant diversity (16, 9, 4 and 1 species, respectively) at each unique CO₂ and N level. CO₂ treatment began in April 1998 and the first N treatment began in May 1998. Plots were irrigated during the 1997 growing season to ensure good plant establishment, but were not irrigated in subsequent years. Plots were weeded at least twice a year during 1998 and 1999 to remove undesired species. Species richness of clipped above-ground biomass in plots planted with 16, 9, 4 and 1 species averaged 13.6, 8.0, 3.8 and 1.0 for four harvests over the 2 years (Reich *et al.* 2001a).

Soil CO₂ flux was measured approximately every 3 weeks between 26 May and 30 September 1998 (seven sampling dates) and approximately every 2 weeks between 13 April and 13 October 1999 (12 sampling dates). Measurements of soil CO₂ flux were performed with the LI-COR 6200 gas exchange system (LI-COR, Lincoln, NE, USA) fitted with the LI-COR 6400-09 soil respiration chamber (Craine *et al.* 1998). Briefly, soil CO₂ flux was measured at a permanent location in a plot, where on 30 April 1998, approximately one month before the first measurement of soil CO₂ flux, all above-ground vegetation was clipped from a 10 × 10 cm location in the plot. In the recently clipped area, a plastic collar, 10 cm across and 5 cm high was inserted approximately 2.5 cm into the soil. Any subsequent above-ground biomass was removed at each sampling. Any moss that had accumulated was scraped from the surface each year, mid-season. A measurement of soil CO₂ flux consisted of placing the chamber on the collar, scrubbing the CO₂ to sub-ambient levels, and determining soil CO₂ flux over 6 five-second periods that spanned 60 seconds. For each plot, soil CO₂ flux was calculated at ambient atmospheric CO₂ concentrations. With each measurement of soil CO₂ flux, we also measured the temperature of the soil at 10 cm. All measurements in a given sampling period were made over the course of 2 days between the hours of 8:30 and 18:00. At each sampling period, the order that the rings were sampled was randomized with the restriction that control- and elevated-CO₂ rings alternated in their order.

Due to the nature of the CO₂ fumigation system, it was necessary to cease CO₂ enrichment during the c. 1 hour that it took to measure all the plots in a ring. Similar to calculations made by Allen *et al.* (2000), this is unlikely to increase flux by more than c. 1%. In separate test measurements, turning off the CO₂ for this length of

time did not affect soil CO₂ flux (J. M. Craine, unpublished data).

A total of 10 individual data points (< 0.2% of all measurements) were lost and replaced by a period's average soil CO₂ flux. Soil CO₂ flux is reported in units of $\mu\text{mol m}^{-2} \text{s}^{-1}$. For reference, $1 \mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$ is equivalent to $1.04 \text{ g C m}^{-2} \text{d}^{-1}$.

For each plot, percentage soil moisture in the 0–20 cm depth interval was measured for 9 of the sampling periods over the two growing seasons using time-domain reflectometry (TDR) (Topp & Davis 1985). These values for TDR have not been calibrated for the BioCON soils at the time of manuscript preparation, but are generally well-correlated ($r = 0.8\text{--}0.9$) with gravimetric soil moisture on similar soils at Cedar Creek (Wrage, unpublished data). Measurements of soil moisture in a plot were generally made within a few hours of the soil CO₂ flux measurement. We report the average soil moisture for all 16-species plots.

Data analysis

All statistical analyses were performed in JMP 3.2.2. For the 19 samplings, the effects of elevated CO₂, elevated N and decreases in plant diversity on soil CO₂ flux were determined with a repeated measures multivariate model. The regression model included CO₂ treatment, identity of the ring nested within CO₂ treatment (random effects), N treatment and planted diversity (categorical) and all pairwise interactions of these factors.

If CO₂, N or diversity affects soil CO₂ flux on average across all dates, these parameters would be significant in the between-subjects portion of the model. The within-subjects portion of the model tests for differences between the pattern of effects of treatments and the pattern of soil CO₂ flux over the 19 periods, equivalent to an interaction between sampling period and the treatment. The coefficients for the interactions between sampling period and treatments were used to determine the treatment effect at each sampling period.

	Estimate	F	P > F
Between Subjects			
CO ₂		47.0	< 0.001
Elevated	4.93		
Ambient	4.36		
Ring [CO ₂]		9.3	< 0.01
Ring 1 [Elev]	4.57		
Ring 2 [Amb]	4.23		
Ring 3 [Elev]	5.15		
Ring 4 [Amb]	4.66		
Ring 5 [Elev]	5.06		
Ring 6 [Amb]	4.20		
N		20.0	< 0.001
Elevated	4.83		
Ambient	4.46		
Diversity		45.0	< 0.001
16	5.08		
9	4.85		
4	4.67		
1	3.99		
CO ₂ × N		1.3	NS
CO ₂ × Diversity		1.0	NS
Nitrogen × Diversity		0.7	NS
Within subject			
Period		472.6	< 0.001
CO ₂ × Period		11.0	< 0.001
Ring[CO ₂] × Period		14.8	< 0.001
N × Period		5.1	< 0.001
Diversity × Period		3.4	< 0.001
CO ₂ × N × Period		1.4	NS
CO ₂ × Diversity × Period		1.2	NS
Nitrogen × Diversity × Period		1.2	NS

Table 1 Results of a repeated measures linear regression model of soil CO₂ flux with data from 19 sampling periods during the 1998 and 1999 growing seasons. Predictors include CO₂ treatment, identity of the experimental ring nested within CO₂ (Ring[CO₂]), N treatment (N), planted diversity (Diversity) and all pairwise interactions. For CO₂, Ring[CO₂], N and Diversity, we include the least square means of the categories. $r^2 = 0.70$. $n = 5605$

Table 2 Matrix of pairwise correlation coefficients for treatment effects on soil CO₂ flux. Treatment effects for CO₂ and nitrogen are based on the differences between the least square means of soil CO₂ flux in elevated and ambient plots. Treatment effects for diversity treatments are based on the difference between the least square means of soil CO₂ flux for a given diversity treatment relative to the least square means of 16-species plots. Soil CO₂ flux (SCF), soil temperature at 10 cm (Tsoil₁₀) and soil moisture at 0–20 cm (Moisture) were averaged among all plots for a sampling period. **P* < 0.05; ***P* < 0.01; ****P* < 0.001. *n* = 19 for all measures except soil moisture (*n* = 9)

	N	9 species	4 species	1 species	Tsoil ₁₀	SCF	Moisture
CO ₂	0.08	– 0.10	0.14	0.22	0.38	0.18	– 0.60
N		0.29	0.62**	0.70**	0.54*	0.84***	– 0.03
9 species			0.82***	0.73***	0.58**	0.44**	– 0.36
4 species				0.81***	0.64**	0.64**	– 0.31
1 species					0.75***	0.81***	– 0.29
Tsoil ₁₀						0.82***	– 0.18
SCF							– 0.05

Soil temperature was not included in the model of soil CO₂ flux. Although soil CO₂ flux and soil temperature are correlated at annual time-scales (see Table 2), there is a negative relationship between soil temperature and soil CO₂ flux within a sampling period (see Table 1). This more than likely reflected differences in leaf area between plots, because plots that have less leaf area also have less carbon allocation below-ground and higher soil temperatures, causing a negative relationship between the two factors. This does not reflect the standard *Q*₁₀ response that is normally associated with soil temperature. Including this factor in the model of soil CO₂ flux would help ‘standardize’ plots within a sampling period to a common soil temperature, but due to the potential relationship among treatments and leaf area, this would most likely decrease our ability to understand the treatment effects, which also alter soil temperature.

Including the time of day that plots were measured in the regression model showed that soil CO₂ flux increased as the day progressed, but did not change the interpretation of the results. Because treatments were sampled randomly with regard to time of day, and because including the time of day in the repeated measures multivariate model makes the model more complex, we did not include it in the regression model.

We ran pairwise correlations for each possible pairing of the following factors to determine their relationships across sampling periods: CO₂ effects, N effects, three sets of diversity effects, soil temperature at 10 cm, soil moisture 0–20 cm and soil CO₂ flux. Treatment effects for diversity treatments represent the effect of decreasing diversity from 16 species to 9, 4 and 1 species and are based on the difference between the least squares means of soil CO₂ flux for a given diversity treatment and the least squares mean of 16-species plots. Correlations between effects are interpreted such that, for example,

if the CO₂ and N effects were positively correlated, conditions that lead to greater soil CO₂ flux under elevated CO₂ at a sampling period would lead to greater soil CO₂ flux under elevated N. Correlations between a treatment effect and soil CO₂ flux, soil temperature or soil moisture were interpreted as the treatment effect being more likely when soil temperatures, soil moistures or soil CO₂ flux were higher or lower.

Results

Over the 1998 and 1999 growing seasons, elevated CO₂ and N both led to greater soil CO₂ flux, while decreased plant diversity led to decreases in soil CO₂ flux (Table 1). On average, soil CO₂ flux was 0.57 μmol m^{–2} s^{–1} greater under elevated CO₂ (13% increase), 0.37 μmol m^{–2} s^{–1} greater under elevated N (8% increase), and 0.23, 0.41 and 1.09 μmol m^{–2} s^{–1} lower with diversity from 16 to 9, 4 and 1 species, respectively (5%, 8% and 21% decreases) (Table 1). The identity of the ring was significant, yet this variance was effectively separated from the CO₂ effect by including it in the model (Table 1). There were no significant interactions among CO₂, N and diversity (Table 1).

CO₂ effects ranged from –0.04 to +1.56 μmol m^{–2} s^{–1} across sampling periods (Fig. 1a) with no simple temporal patterns to the CO₂ effect in 1998 and 1999. N effects ranged from –0.13 to 1.10 μmol m^{–2} s^{–1} (Fig. 1b) and were positively correlated with soil temperature (*P* < 0.05; Table 2). The diversity effects varied over the sampling periods, with the magnitude and ranking of the effects varying among and between diversity levels and time (Fig. 1c). Diversity effects were also correlated with soil temperature.

Soil CO₂ flux appears to be enhanced most by elevated CO₂ when plants are active and there is at least mild water stress, with little effect of elevated CO₂ when soil

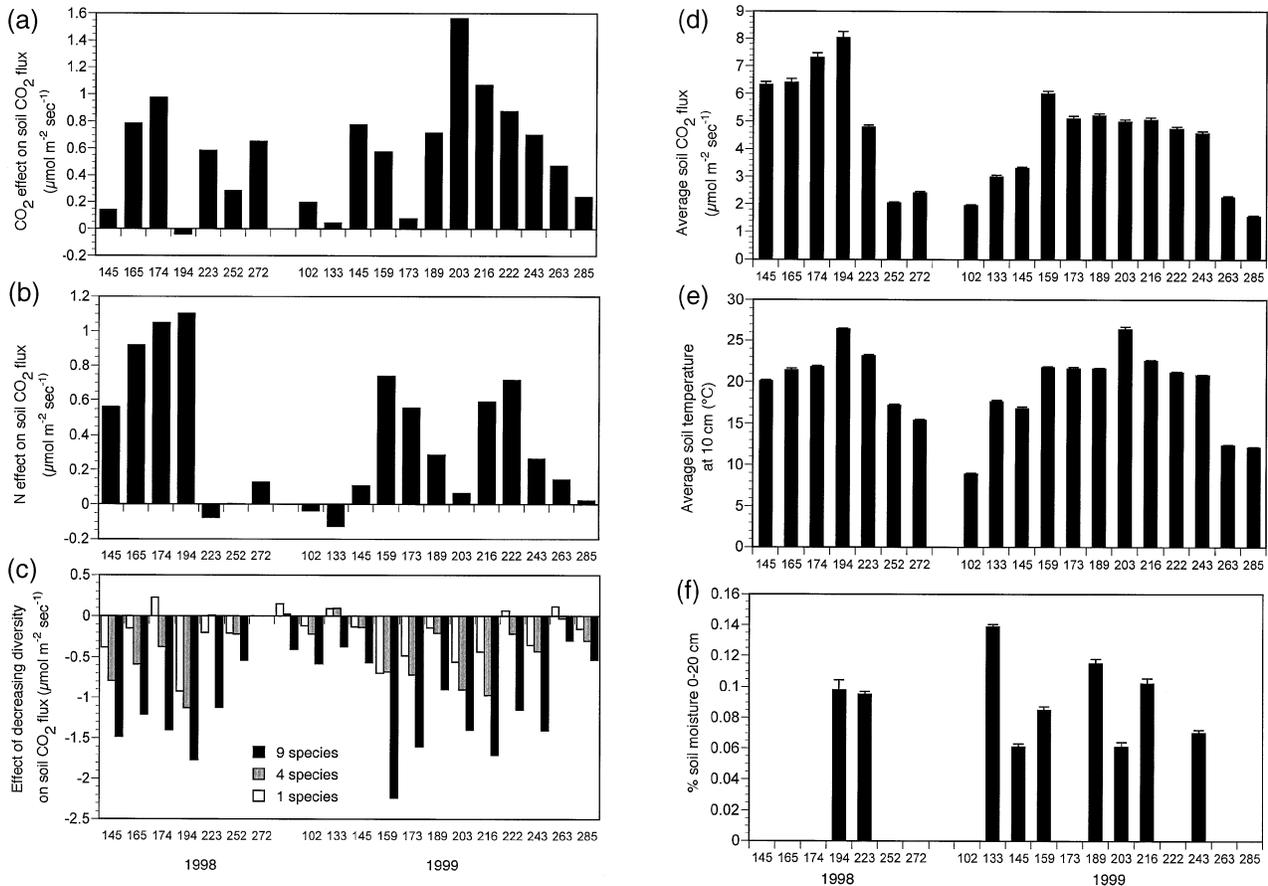


Fig. 1 (a) Effects on soil CO₂ flux of elevated CO₂, (b) N fertilization, and (c) decreases in plant diversity from 16 to 9, 4 and 1 species for each sampling period. (d) Average soil CO₂ flux, (e) soil temperature at 10 cm, and (f) soil moisture 0–20 cm for all plots for each sampling period in 1998 and 1999. These effects are derived from the multiple regression and represent the difference between the least squares means of the treatment and the control.

moisture is high. In general, there was a negative correlation between soil moisture and the absolute CO₂ effect ($r = -0.60$, $P = 0.09$, Table 2). The correlation is stronger when the CO₂ effect is expressed relative to soil CO₂ flux ($r = -0.69$, $P = 0.04$). For example, the CO₂ effect on soil CO₂ flux on Julian day 194 in 1998 was conspicuously low (Fig. 1a) and on this date soil CO₂ flux, soil temperature and soil moisture were all high (Fig. 1d–f). In contrast, the CO₂ effect on soil CO₂ flux on Julian day 203 in 1999 was conspicuously high (Fig. 1a) and on this date, soil CO₂ flux and soil temperature were both high, but soil moisture was low (Fig. 1d–f). There was no correlation between the CO₂ effect and any other factor (Table 2).

The correlations among the N effect, the diversity effects, soil CO₂ flux and soil temperature reveal that in general, when plants and microbes are most active below-ground (high soil temperature and high soil CO₂ flux), increases in N supply and decreases in diversity

have their largest effects on soil CO₂ flux (Table 2). There was no relationship between soil moisture and the N effect ($P > 0.9$, Table 2), and correlations between the diversity effects and soil moisture were negative, although not significant (Table 2).

Discussion

On average, elevating atmospheric CO₂ concentrations to 560 μmol mol⁻¹ caused a 13% increase in soil CO₂ flux. The magnitude of this increase was within the very broad reported range of changes in soil CO₂ flux with elevated CO₂ (–10% to +162%; Zak *et al.* 2000), but much less than the average CO₂ response seen across studies (45%; Zak *et al.* 2000).

In BioCON, elevated CO₂ increased the rate of photosynthesis (Lee *et al.*, 2001), leaf area index and above-ground biomass (Reich *et al.* 2001a), which creates a higher potential for carbon allocation below-ground.

Elevated CO₂ increased below-ground biomass by 14% (Reich *et al.* 2001a), and fine root respiration rates per unit mass were 13% greater under elevated CO₂ in June 1998 (J. M. Craine unpublished data), indicating that multiple components of the below-ground carbon cycle are affected by elevated CO₂.

Elevated CO₂ increased soil CO₂ flux most when soils were dry, potentially indicative of the increased photosynthetic water use efficiency due to elevated CO₂ (Lee *et al.* 2001) that led to increased residual soil moisture (Reich *et al.* 2001a; Reich *et al.* 2001b). Greater soil moisture decreases water stress and also creates a more favourable environment for respiration by plant roots and heterotrophs, both of which may have contributed to the increased soil CO₂ flux.

With N fertilization in BioCON, total carbon acquisition increases due to increases in leaf area index (LAI) and photosynthetic rates (Lee *et al.* 2001; Reich *et al.* 2001a). Generally, fertilization decreases the relative allocation of C below-ground, which often leads to absolute decreases in soil CO₂ flux. Although we could not calculate relative carbon partitioning above-ground and below-ground, soil CO₂ flux increased by 8% with fertilization, similar to the increase in fine root biomass (8%) in fertilized plots (Reich *et al.* 2001a).

Over the two growing seasons, there was no correlation between the CO₂ and N effects at the individual sampling dates, suggesting different mechanisms underlying the effects of N and CO₂ on soil CO₂ flux. Although elevated CO₂ increased fine root production, fine root biomass, and fine root respiration rates, N fertilization did not significantly change the specific respiration rates of fine roots (J. M. Craine, unpublished). Fine root production increased more than fine root biomass (28% vs. 8%) in fertilized vs. control plots (Reich *et al.* 2001a). This may indicate that greater soil CO₂ flux with N fertilization is due to greater root production and turnover of the root system, though more work is necessary to determine the effects of N fertilization on transfers to the microbial community and decomposition.

The lack of an interaction between CO₂ and N may be due to the relative young age of the plots. Although established grasslands at Cedar Creek are strongly N-limited (Tilman 1987), N limitation is probably not as strong in these recently established plots. N availability and mineralization in this system were high compared to other grasslands at Cedar Creek and both were about 50% of their 1998 values in 1999 (P. B. Reich, unpublished).

Just as fertilization with N affected soil CO₂ flux by increasing productivity and associated measures, decreasing diversity in BioCON lowered all components of productivity, such as above-ground biomass, below-

ground biomass and fine root production (Reich *et al.* 2001a). With decreases in above-ground biomass, there is less total carbon acquisition and therefore less carbon allocated below-ground. This decrease in allocation below-ground due to decreases in diversity is greatest when plants are most active (e.g. warm soils). Although there were interactions between diversity and either CO₂ or N for many plant and ecosystem properties such as total biomass, fine root production and total plant N content (Reich *et al.* 2001a), there were no interactions between species diversity and either CO₂ or N for soil CO₂ flux.

Acknowledgements

We thank the many individuals who assisted in the creation and sampling of this experiment, especially K. Wrage, J. Goth, W. Bengston and A. Simpson. K. McLauchlan, W. Schlesinger and two anonymous reviewers provided helpful comments. JMC was supported by a NASA Earth Systems Fellowship, a NSF graduate fellowship as well as a NSF dissertation improvement grant. Additional support was provided by NSF grant 9411972 and the U.S. Department of Energy.

References

- Allen AS, Andrews JA, Finzi AC, Matamala R, Richter DD, Schlesinger WH (2000) Effects of free-air CO₂ enrichment (FACE) on belowground processes in a Pinus taeda forest. *Ecological Applications*, **10**, 437–448.
- Craine JM, Wedin DA, Chapin FS (1998) Predominance of ecophysiological controls on soil CO₂ flux in a Minnesota grassland. *Plant and Soil*, **207**, 77–86.
- Fitter AH, Graves JD, Wolfenden J, Self GK, Brown TK, Bogie D, Mansfield TA (1997) Root production and turnover and carbon budgets of two contrasting grasslands under ambient and elevated atmospheric carbon dioxide concentrations. *New Phytologist*, **137**, 247–255.
- Knapp AK, Conard SL, Blair JM (1998) Determinants of soil CO₂ flux from a sub-humid grassland: effect of fire and fire history. *Ecological Applications*, **8**, 760–770.
- Lee T, Tjoelker MG, Ellsworth DS, Reich PB (in press) Leaf gas exchange responses of 13 prairie grassland species to elevated carbon dioxide and increasing nitrogen supply. *New Phytologist*, **150**, 405–418.
- Lewin KF, Hendrey GR, Nagy J, LaMorte R (1994) Design and application of free-air carbon dioxide enrichment facility. *Agricultural and Forest Meteorology*, **70**, 15–29.
- Raich JW, Nadelhoffer KJ (1989) Below-ground carbon allocation in forest ecosystems: Global trends. *Ecology*, **70**, 1346–1354.
- Raich JW, Potter CS (1995) Global patterns of carbon dioxide emissions from soils. *Global Biogeochemical Cycles*, **9**, 23–36.
- Raich JW, Tufekcioglu A (2000) Vegetation and soil respiration: correlations and controls. *Biogeochemistry*, **48**, 71–90.
- Reich PB, Grigal DF, Aber JD, Gower ST (1997) Nitrogen mineralization and productivity in 50 hardwood and conifer stands on diverse soils. *Ecology*, **78**, 335–347.
- Reich PB, Knops JMH, Tilman D, Craine J, Ellsworth D, Tjoelker M, Lee T, Wedin D, Naeem S, Bahaeddin D, Hendrey G, Jose

- S, Wrage K, Goth J, Bengston W (2001a) Plant diversity enhances ecosystem responses to elevated CO₂ and nitrogen deposition. *Nature*, **410**, 809–812.
- Reich PB, Tilman D, Craine J, Ellsworth D, Tjoelker M, Knops J, Wedin D, Naeem S, Bahauddin D, Goth J, Bengston W, Lee T (2001b) Do species and functional groups differ in acquisition and use of C, N and water under varying atmospheric CO₂ and N deposition regimes? A field test with 16 grassland species. *New Phytologist*, **150**, 435–448.
- Sala OE, Chapin FS, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HA, Oesterheld M, Poff NL, Sykes MT, Walker BH, Walker M, Wall DH (2000) Biodiversity: global biodiversity scenarios for the year 2100. *Science*, **287**, 1770–1774.
- Schlesinger WH, Andrews JA (2000) Soil respiration and the global carbon cycle. *Biogeochemistry*, **48**, 7–20.
- Tilman D (1987) Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. *Ecological Monographs*, **57**, 189–214.
- Tilman D (1988) *Plant Strategies and the Dynamics and Function of Plant Communities*. Princeton University Press, Princeton.
- Topp GC, Davis JL (1985) Measurement of soil water content using time-domain reflectometry (TDR): a field evaluation. *Soil Science Society of America*, **49**, 19–24.
- Vitousek PM (1994) Beyond global warming: ecology and global change. *Ecology*, **75**, 1861–1876.
- Zak DR, Pregitzer KS, King JS, Holmes WE (2000) Elevated atmospheric CO₂, fine roots, and the response of soil microorganisms; a review and hypothesis. *New Phytologist*, **147**, 201–222.