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A multiyear synthesis of soil respiration responses to elevated atmospheric CO_2 from four forest FACE experiments

JOHN S. KING*, PAUL J. HANSON†, EMILY BERNHARDT‡, PAOLO DEANGELIS§, RICHARD J. NORBY† and KURT S. PREGITZER*¶

*School of Forest Resources and Environmental Science, Michigan Technological University, Houghton, MI 49931, USA, †Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, TN 37831, USA, ‡Department of Biology, Duke University, Durham, NC 27708, USA, §Department of Forest Environment and Resources, University of Tuscia, via S. Camillo de Lellis, 01100 Viterbo, Italy, ¶North Central Research Station, USDA Forest Service, Houghton, MI 49931, USA

Abstract

The rapidly rising concentration of atmospheric CO_2 has the potential to alter forest and global carbon cycles by altering important processes that occur in soil. Forest soils contain the largest and longest lived carbon pools in terrestrial ecosystems and are therefore extremely important to the land–atmosphere exchange of carbon and future climate. Soil respiration is a sensitive integrator of many soil processes that control carbon storage in soil, and is therefore a good metric of changes to soil carbon cycling. Here, we summarize soil respiration data from four forest free-air carbon dioxide enrichment (FACE) experiments in developing and established forests that have been exposed to elevated atmospheric [CO_2] (168 μL L^{-1} average enrichment) for 2–6 years. The sites have similar experimental design and use similar methodology (closed-path infrared gas analyzers) to measure soil respiration, but differ in species composition of the respective forest communities. We found that elevated atmospheric [CO_2] stimulated soil respiration at all sites, and this response persisted for up to 6 years. Young developing stands experienced greater stimulation than did more established stands, increasing 39% and 16%, respectively, averaged over all years and communities. Further, at sites that had more than one community, we found that species composition of the dominant trees was a major controller of the absolute soil CO_2 efflux and the degree of stimulation from CO_2 enrichment. Interestingly, we found that the temperature sensitivity of bulk soil respiration appeared to be unaffected by elevated atmospheric CO_2. These findings suggest that stage of stand development and species composition should be explicitly accounted for when extrapolating results from elevated CO_2 experiments or modeling forest and global carbon cycles.

Keywords: Betula, global change, liquidambar, *Pinus*, *Populus*, soil CO_2 efflux

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Introduction

Globally, terrestrial plant communities contain almost as much carbon (C) as the atmosphere, 560 vs. 750 Pg, with forests comprising by far the largest fraction (Schlesinger, 1997). Soil contains the largest pools of C in terrestrial ecosystems, with the longest mean residence times (Dixon *et al.*, 1994; Schlesinger, 1977, 1997). Therefore, increments or decrements of soil C are most relevant to global biogeochemical processes that influence the land–atmosphere exchange of C. Soil respiration is an integrated signal of the complex biotic and abiotic processes that occur in soil, and therefore is a sensitive indicator of alterations in soil C cycling that may result from human-caused environmental change. Of particular concern is the rapid rise in the concentration of atmospheric CO_2 because of its potential to directly affect the production and chemistry of plant detritus that drives the belowground C cycle.

Soil respiration, comprising both autotrophic (root) and heterotrophic respiration, is one of the largest

Correspondence: John S. King, tel. +1 906 482 6303, fax +1 906 482 2915, e-mail: jsking@mtu.edu

fluxes of C in terrestrial ecosystems (Mahli *et al*., 1999; Curtis *et al*., 2002; Norby *et al*., 2002; Law *et al*., 2003). Forests allocate a large proportion, often the majority, of net primary production to the root systems of both overstory and understory plants (Grier *et al*., 1981). Respiration to support the growth, maintenance, and nutrient uptake of the root systems results in large fluxes of CO_2 into the soil (Edwards & Harris, 1977). Heterotrophic soil organisms contribute to soil C losses through respiration associated with root herbivory, predation, consumption of root exudates, and the decomposition of root and leaf litter. Partitioning total soil respiration into components of roots, soil fauna, and soil microbial respiration is, however, still a major challenge of current research (Hanson *et al*., 2000; Epron *et al*., 2001; Högberg *et al*., 2001). Elevated atmospheric CO_2 concentration has been shown to affect root production (Pregitzer *et al*., 1995; King *et al*., 1996, 2001), root morphology and chemistry (King *et al*., 1997; Runion *et al*., 1999), soil fauna communities (Klironmos *et al*., 1996; Lussenhop *et al*., 1998), and microbial community composition and function (Zak *et al*., 1993, 2000). The net effect on land–atmosphere exchange of C from these changes in the components of the soil C cycle under elevated [CO_2] is currently a very active field of research.

Experimental evidence from a wide variety of ecosystems shows that growth in elevated atmospheric [CO_2] usually stimulates soil respiration (Janssens & Ceulemans, 2000; Zak *et al*., 2000), indicating that the mechanisms being altered in the soil C cycle may be universal, or at least very common. Data reported in a recent summary of the agricultural literature (Kimball *et al*., 2002), show an average 24% stimulation in soil respiration for a variety of crops grown in elevated [CO_2] using mostly open-top chambers, but also free-air carbon dioxide enrichment (FACE). Using small growth chambers in natural Mediterranean grasslands, Luo *et al*. (1996) observed a 42% stimulation of soil respiration under elevated [CO_2]; similarly, in natural marsh vegetation Ball & Drake (1998) reported 15% stimulation. In experiments using tree species, soil respiration has been shown to be consistently greater under elevated [CO_2] (Zak *et al*., 2000). Norby *et al*. (1992) provided data showing a 22–24% increase in soil CO_2 efflux under elevated [CO_2] treatments of yellow-poplar growing in the ground within open-top chambers. Körner & Arnone (1992) reported that soil respiration doubled in artificial tropical ecosystems developing in mesocosms in CO_2-enriched environments. Longer term exposures using open-top chambers have shown stimulation in *Pinus ponderosa* (Johnson *et al*., 1994; Vose *et al*., 1997), *Acer rubrum* and *Acer saccharum* (Edwards & Norby, 1999), and *Pinus sylvestris* (Janssens *et al*., 1998). Finally, using FACE technology to expose intact forest ecosystems on natural soils, Andrews & Schlesinger (2001) showed increased soil respiration beneath *Pinus taeda* in elevated [CO_2] (+ 27%), and King *et al*. (2001) showed similar results for *Populus tremuloides* and *Betula papyrifera* (+ 39%).

Ecosystem responses to a CO_2-enriched atmosphere do not always include increased soil respiration. *Lolium perenne* showed a 10% *decrease* in soil respiration under elevated [CO_2] compared with control plots (Ineson *et al*., 1998). Oberbauer *et al*. (1986) found that exposure of tussock tundra to elevated [CO_2] for 2.5 growing seasons resulted in no stimulation of soil respiration. Oechel *et al*. (1994) reported that complete homeostasis of ecosystem CO_2 flux was reestablished within 3 years in undisturbed tussock tundra exposed to elevated [CO_2]. They argued that CO_2 fertilization effects must be considered in the context of genetic limitations, resource availability, etc. As with many ecosystem properties, inter-annual variation in weather and resource availability may alter the magnitude, and possibly the direction, of soil respiration responses to elevated [CO_2] from year to year. Further, we need to consider how soil respiration responses may change over time as ecosystems proceed from rapidly aggrading young stages of development to more slowly growing, older ecosystems.

To fully assess the effects of the rising concentration of atmospheric CO_2 on soil C cycling, experiments that allow long-term monitoring of soil respiration in forest ecosystems developing under realistic soil conditions and climate are needed. FACE systems (Hendrey *et al*., 1999; Karnosky *et al*., 2001; Miglietta *et al*., 2001) ideally fill this role because there are no confining walls to create micrometeorological artifacts or impede the natural movements of insects, small animals, seeds, and spores. FACE systems allow imposition of well-controlled, replicated atmospheric treatments over large areas (30 m diameter plots) for long periods of time. Because climatic and hydrologic features of the landscape are preserved, the cycling of carbon and nutrients is representative of natural systems. FACE systems are excellent for studying responses of ecosystem-level processes such as net primary production, nutrient cycling, soil C formation, and CO_2 exchange in response to the changing atmosphere.

Here we present several years of data on soil respiration from four forest FACE experiments in six distinct forest communities. We explicitly compared forests at early and mid-stages of stand development to explore commonalities in responses across sites, and possibly determine, which site characteristics explain differences that might exist. The 'developing' forests

were planted as small seedlings or clones in open fields after the FACE hardware had been installed at the beginning of the experiments. The FACE hardware was installed in the 'established' forests when they were 10 (ORNL) and 13 (FACTS-I) years old, in the linear phase of growth, and had closed canopies and greater root development. We hypothesized that cumulative soil C efflux in the young stands would increase monotonically from year to year since they are rapidly aggrading and exploiting the soil volume. Conversely, the more established forests with more fully occupied soil and canopy space would exhibit more consistent soil C efflux from year to year. We hypothesized that soil respiration would increase under elevated atmospheric [CO_2] consistent with increases in forest biomass. Our expectation was that the young aggrading forests would exhibit a greater degree of stimulation in response to elevated [CO_2] compared with the older forests. Finally, we characterized the year-to-year variability in soil respiration, and examined whether responses to elevated atmospheric [CO_2] persist over time.

Materials and methods

Study sites

This study is a synthesis of several years of soil respiration data from four FACE experiments in forest ecosystems (Table 1). Two of the sites, ORNL and FACTS-I, represent established plantation forests of a deciduous, broadleaf tree, *Liquidambar styraciflua*, and an evergreen conifer, *P. taeda*. The other two sites, POPFACE and FACTS-II, represent developing, mixed plantations of *Populus* sp. aggrading on old agricultural fields. Mean annual temperature of the sites ranged from 4.9 °C to 15.5 °C, and mean annual precipitation ranged from 810 to 1390 mm. The POPFACE experiment used irrigation to avoid drought, so inferences related to precipitation should be avoided for this site. Soils are loams of varying texture, from clayey to sandy. Experimental plots ranged in size from 22 to 30 m in diameter, and were replicated two or three times. One site, FACTS-I, provides continuous fumigation, 24 h day^{-1}, 365 days yr^{-1} when weather conditions permit. The other sites fumigate during the growing season, ranging from 139 to 228 days yr^{-1} (Table 1). Averaged over all sites, mean daytime atmospheric CO_2 concentration in control rings was 376 μL L^{-1}, while in the elevated CO_2 treatment it was 544 μL L^{-1}, for an average enrichment of 168 μL L^{-1}.

Soil respiration measurement

Soil respiration was measured biweekly or monthly at all sites during the fumigation periods. Measurements were made manually at mid-day with infrared gas analyzers (IRGA) operated in the closed-path mode. Three of the projects used the PP Systems EGM-2 environmental gas monitor equipped with the SRC-1 soil respiration cuvette (Haverhill, MA, USA), while the ORNL project used the Li-Cor 6200 with the standard vented chamber (Lincoln, NE, USA). In a short-term, comparative study it was shown that the PP Systems method yielded higher fluxes than the Li-Cor, eddy covariance, and soda lime methods (Janssens *et al.*, 2000), although other studies have found close agreement between the PP Systems and Li-Cor instruments (Giardina & Ryan, 2002; Litton *et al.*, 2003). Because differences in soil texture and moisture content could also influence instrument performance between sites (Howard & Howard, 1993), this synthesis does not attempt strict comparisons of absolute values of soil CO_2 efflux, but rather focuses on the relative stimulation of soil respiration due to elevated atmospheric [CO_2].

Three projects installed semi-permanent plastic collars into the soil surface to engage the soil respiration cuvette, ensuring repeated sampling of the same soil over time and reducing disturbance. Early tests indicated that use of the collars did not affect measurements. The ORNL project did not use fixed collars, but instead placed the soil respiration cuvette directly on the soil to avoid unnatural accumulation of water on the litter in collars after precipitation events. Soil respiration units were adjusted for changes in atmospheric pressure and calibrated with certified gas traceable to National Institute of Standards and Technology (NIST) each day of sampling. Individual soil respiration measurements were made until the rate of soil CO_2 efflux became consistent, usually within 2 min. At the time of measurement, soil temperature was recorded using manual digital thermometers to a depth of 3–10 cm.

Statistical analysis

Absolute values for soil respiration at each site are provided to show temporal patterns and treatment effects within sites. Cross-site comparisons of the long-term effects of [CO_2], however, were expressed as the relative change over time (e.g. increasing or decreasing trends). Responses to elevated CO_2 treatments are expressed relative to the control (% change).

Soil respiration data (S_r) for a given site and year were fit to the following exponential relationship relating S_r to seasonal changes in site temperature using nonlinear regression approaches (SPSS Regression Models (Version 11.0.1), SPSS Inc., Chicago, IL, USA):

$$S_r = B_{20}Q^{((T-20)/10)},$$

Table 1 Characteristics of the four free-air carbon dioxide enrichment experiments comprising the multiyear synthesis of forest soil respiration responses to elevated atmospheric CO_2

Name	FACTS-I	FACTS-II	ORNL	POPFACE
Location	Durham, NC, USA	Rhinelander, WI, USA	Oak Ridge, TN, USA	Tuscania (Viterbo), Italy
Latitude, longitude	35°58′N, 79°05′W	45°40′N, 89°37′W	35°54′N, 84°20′W	42°22′N, 11°48′E
Elevation (m)	163	490	230	150
Mean annual precipitation (mm)	1140	810	1390	818*
Mean annual temperature (°C)	15.5	4.9	14.2	14.1
Land use	Pine plantation	Old agricultural field	Sweetgum plantation	Old agricultural field
Size (ha)	90	32	1.7	9
Soil classification (US)	Acidic Hapludalf	Alfic Haplorthod	Aquic Hapludult	
Soil texture	Clay loam	Sandy loam	Silty clay loam	Heavy clay loam
Overstory vegetation	*Pinus taeda*	*Populus tremuloides*, *Acer saccharum*, *Betula papyrifera*	*Liquidambar styraciflua*	*Populus alba* *P. nigra* *Populus* × *euramericana*
Date planted	1983	1997	1988	1999
Planting density (m)	2 × 2.4	1 × 1	1.2 × 2.3	1 × 1
Statistical design	Randomized block with three replicates (six plots)	Randomized complete block with three replicates (six plots†), species mix is split-plot effect	Distributed (nonrandom) with two replicates (five plots)	Randomized complete block with three replicates (six plots), genotype and nitrogen treatment are split-plot effects
Fumigation system	BNL design‡ Diluted CO_2 released from rigid vertical vent pipes, 30 m diameter plots	BNL design Diluted CO_2 released from rigid vertical vent pipes, 30 m diameter plots	BNL design Diluted CO_2 released from rigid vertical vent pipes, 25 m diameter plots	IATA-CNR design§ Pure CO_2 released from flexible pipes, 22 m diameter plots
Exposure period¶				
1996 (Begin, end, days)	Continuous fumigation since 1996, except when temperature < 5 °C or wind speed > 5 m s^{-1}**			
1997		Pretreatment tests	Pretreatment tests	
1998		01 May, 13 Oct, 165	05 Jun, 05 Nov, 153	
1999		10 May, 01 Oct, 144	06 Apr, 03 Nov, 211	1 Apr, 15 Nov, 228
2000		14 May, 30 Sep, 139	03 Apr, 29 Oct, 209	1 Apr, 15 Nov, 228
2001		10 May, 30 Sep, 143	09 Apr, 26 Oct, 200	1 Apr, 15 Nov, 228

continued

Table 1. (Contd.)

Name	FACTS-I	FACTS-II	ORNL	POPFACE
Mean‖ *(SD) atmospheric CO_2 concentration ($\mu L\,L^{-1}$)*				
1996 (control, elevated CO_2)	379** (20), 574 (24)			
1997	375 (20), 568 (37)			
1998	378 (20), 572 (34)	No data, 523 (76)	389 (42), 528 (55)	
1999	375 (21), 569 (33)	346 (22), 548 (71)	393 (43), 538 (55)	No data, 544 (48)
2000	373 (20), 568 (39)	359 (22), 549 (46)	394 (44), 545 (58)	No data, 532 (83)
2001	375 (21), 567 (42)	354 (13), 529 (91)	394 (45), 548 (44)	No data, 554 (95)
Soil respiration methods	Monthly, PP Systems EGM-2 closed-mode IRGA, cuvette placed on fixed PVC collars, 12 measurements	Biweekly, PP Systems EGM-2 closed-mode IRGA, cuvette placed on fixed PVC collars, calibrated on-site daily, 10 measurements	Biweekly, Li-Cor 6200 closed-mode IRGA, cuvette placed directly on soil, 6 measurements	Bi-weekly, PP Systems EGM-2 closed-mode IRGA, cuvette place on fixed PVC collars, 5 measurements
Soil temperature depth (cm)	3	10	10	5
References	Delucia *et al*. (1999) Hamilton *et al*. (2002)	Dickson *et al*. (2000) Karnosky *et al*. (2001)	Norby *et al*. (2001) Norby *et al*. (2002)	Scarascia Mugnozza *et al*., 2000 Miglietta *et al*., 2001
Web site	http://www.env.duke.edu/forest/FACTSI.htm	http://aspenface.mtu.edu/	http://face.ornl.gov	http://www.unitus.it/euroface/

*The POPFACE experiment used irrigation to avoid drought, so inferences regarding precipitation should be avoided for this site.

†The FACTS-II experiment has a total of 12 rings, six of which have an elevated tropospheric ozone treatment. Data from the three control and three elevated CO_2 plots only are included in the current analysis.

‡BNL denotes 'Brookhaven National Laboratory'; see Hendrey *et al*. (1999) for details of the forest fumigation system. This design uses a circular plenum on which vertical vents pipes are mounted around the ring. Pure CO_2 is introduced into a blower box attached to the plenum and mixed with ambient air before release. Computer algorithms monitor CO_2 concentration, wind speed and direction at ring center, and control the direction and volume of fumigation in proportion to the difference between target and measured CO_2 concentrations.

§See Miglietta *et al*. (2001) for details of the POPFACE fumigation system. This system also uses computer algorithms connected to centrally located sensors to monitor and control fumigation. However, pure CO_2 is released slowly from flexible, perforated vent pipes connected to a central manifold. There is no blower system, and mixing of fumigation CO_2 with ambient air is passive.

¶Fumigation was 24 h day^{-1} at FACTS-I and ORNL (1998–2000), and only during daylight hours at FACTS-II, POPFACE, and ORNL (2001).‖ Calculated from daytime data only.

**Treatment summaries for FACTS-I do not include periods of nonfumigation due to low temperature, since the plants are inactive. However, periods of nonfumigation due to high wind conditions are included in the calculations.

where B_{20} is the base rate of soil respiration at 20 °C, Q is the seasonal Q_{10}, or the rate of change in bulk soil respiration for a 10° rise in soil temperature, and T is the soil temperature at 3–10 cm depth. Seasonal Q_{10} does not follow the strict definition of Q_{10} because of differential contributions of roots and heterotrophic organisms, and because other environmental factors (soil water content, nutrient availability, light, etc.) vary along with soil temperature throughout the growing season. However, it still allows an analysis of the temperature sensitivity of bulk soil processes (Widén & Majdi, 2001). Although soil moisture can also be an important factor controlling rates of soil CO_2 efflux (Dörr & Münnich, 1987; Howard & Howard, 1993), its use as a predictor is complicated by direct effects on CO_2 diffusion, and root and microbial respiration. Unless the soil is extremely wet or extremely dry, soil moisture has been shown to have little predictive power, and soil temperature is the best overall predictor of soil respiration, usually in some form of the Arrhenius equation (Edwards, 1975; Hanson *et al*., 1993; Fang & Moncrieff, 2001). In addition, not all sites had a continuous soil moisture record. Our analytical approach integrates the soil respiration record over the growing season for all sites and years, allows analysis of the seasonal Q_{10} sensitivity, and is more straightforward than trying to adapt various univariate statistical models between sites.

The influence of $[CO_2]$ on S_r–temperature relationships was evaluated for each site and year using an F-test appropriate for nonlinear situations (Hanson *et al*., 1988). The analysis tests the hypothesis that the two sets of model parameter estimates for the S_r–temperature relationships (i.e., ambient vs. elevated CO_2) are not significantly different. Lack of significant differences (i.e., P-value >0.05) implies no differences in the S_r–temperature relationship between treatments. *Post hoc* evaluation of individual parameter estimates for the S_r–temperature relationship is needed to attribute significant treatment differences to the size of the combined root and heterotrophic respiratory pool (a change in B_{20}), or a change in the curvature of the seasonal temperature response (a change in Q). When the seasonal temperature response surfaces are not significantly different between treatments, it is still possible for significant effects of $[CO_2]$ to occur on individual dates. However, day-by-day evaluation of the $[CO_2]$–S_r responses is beyond the scope of this synthesis study, and may be discussed in publications containing the primary data from the individual sites.

Soil respiration rates for each site were integrated over time to evaluate the effects of elevated $[CO_2]$ on cumulative soil C efflux at seasonal or annual scales. For FACTS-I and FACTS-II, this was done by linear interpolation of soil respiration rates between sample dates and integration of the area under the curve. For the ORNL site, the fitted temperature relationship was used to interpolate soil C efflux using a continuous soil temperature record. As a check, both methods were used for the POPFACE site and produced similar results.

Results

Seasonality and inter-annual variability

All sites exhibited strong seasonality in soil respiration that was highly correlated to the seasonal progression of soil temperature (Fig. 1). The 6-year continuous record from the FACTS-I site indicates that the average rate of soil respiration increased approximately fivefold during the year, from 2 $\mu mol\, m^{-2} s^{-1}$ in winter to 10 $\mu mol\, m^{-2} s^{-1}$ in summer. Soil temperature at the FACTS-I site ranged from an average of 5 °C in winter to 24 °C in summer. From early spring to mid-summer, soil respiration at ORNL increased approximately fourfold, from 1 to 4 $\mu mol\, m^{-2} s^{-1}$, respectively, over a soil temperature range of 7–23 °C. At POPFACE, the increase was about fivefold, rising from 1 to 5 $\mu mol\, m^{-2} s^{-1}$, over a soil temperature range of 4–23 °C. At FACTS-II, rates of soil respiration increased fivefold from approximately 2 $\mu mol\, m^{-2} s^{-1}$ in early spring to 10 $\mu mol\, m^{-2} s^{-1}$ in summer, over a soil temperature range of 7–15 °C. Interestingly, the four- to fivefold seasonal increase of soil respiration did not differ between the developing (FACTS-II, POPFACE) and established (FACTS-I, ORNL) systems. It should be kept in mind that for the seasonally measured sites, the start dates reported here are arbitrary, and therefore the corresponding soil temperatures have no specific biological significance, although efforts are made at each site to time the beginning and end of fumigation with bud break and leaf fall, respectively.

Additionally, the pattern and absolute magnitude of soil respiration rates varied from year to year. Inter-annual variation in weather determined the rate and extent to which soils warmed, thereby influencing biological activity, including plant (root) growth (Fig. 1). Examination of base rates of soil respiration from the nonlinear regression analysis further illustrates this point (Table 2). In general, base rates of soil respiration increased over time, and this pattern was more consistent at the developing sites (POPFACE, FACTS-II).

Effects of elevated $[CO_2]$ on B_{20} and the seasonal Q_{10} relationship

Elevated atmospheric $[CO_2]$ significantly stimulated the base rate (B_{20}) of soil respiration at all sites, in most years, as indicated by nonoverlapping 95% confidence

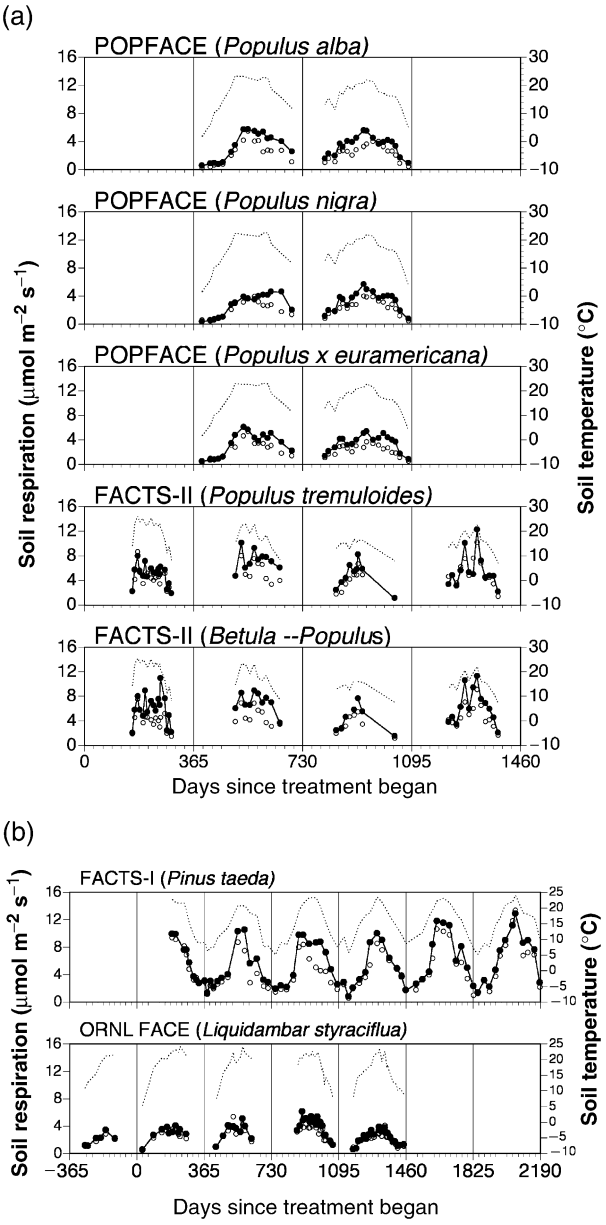

Fig. 1 Mean instantaneous soil respiration rates for forest ecosystems in early development (a) and established (b) from four forest free-air carbon dioxide enrichment (FACE) experiments. Dashed lines are soil temperature at 3–10 cm depth, and open and closed symbols are ambient and elevated CO_2 plots, respectively.

intervals for B_{20} (Table 2). However, the degree of stimulation varied from year to year. At FACTS-I, B_{20} in CO_2-enriched plots exhibited 36% stimulation by the third year of exposure, but the stimulation declined to only 5% by the fifth year (Table 2). Stimulation of B_{20} for FACTS-I ranged from 2.1% to 36.2%, and averaged 15.8% over all years. For the ORNL site, the degree of stimulation ranged from 8.9% to 18.0%, and averaged 12.0%, but like the FACTS-I site the degree of stimulation declined after several years. After 4–5 years of exposure to elevated [CO_2] the established stands exhibited 5–10% stimulation of B_{20}.

The developing stands showed a contrasting pattern. At POPFACE, for all genotypes and all years, the degree of stimulation in B_{20} due to elevated [CO_2] was much greater, ranging from 31.0% to 49.6%, and averaging 38.7%. Finally, in the *Populus* community at FACTS-II, the degree of stimulation due to CO_2 enrichment ranged from 12.6% to 40.8%, and averaged 23.7%. In the *Populus–Betula* community, the degree of stimulation ranged from 43.1% to 76.9%, and averaged 53.9%. In general, the developing forests had greater stimulation of B_{20} in response to elevated [CO_2] (24–54%) than did the established forests. Although we averaged over a longer soil respiration record for the established forests, the sustained high degree of stimulation at FACTS-II, especially in the *Populus–Betula* community, suggests the higher degree of stimulation persists in the developing forests.

The temperature sensitivity of soil respiration as characterized by the seasonal Q_{10} relationship ranged from 2.06 to 3.37 at FACTS-I, 1.89 to 2.60 at ORNL, 1.98 to 2.54 at POPFACE, and 1.20 to 4.79 at FACTS-II (Table 2). It exhibited no consistent trends over time and was not significantly or consistently affected by elevated atmospheric [CO_2] at any of the sites, as indicated by the overlapping 95% confidence intervals. The 95% confidence intervals for Q_{10} were on average much wider for FACTS-II than for FACTS-I or ORNL, and the nonlinear model generally fits the data better for these latter sites.

Cumulative efflux of soil C

Trends in cumulative soil C efflux varied from year to year at all sites except FACTS-I, which showed a monotonic increase in ambient plots over time, from 1457 g C m^{-2} yr^{-1} in 1997 to 2194 g C m^{-2} yr^{-1} in 2001 (Table 3). At ORNL, ambient total soil C efflux increased from 600 g C m^{-2} yr^{-1} in 1997 to 996 g C m^{-2} yr^{-1} in 2000, but then dropped to 698 g C m^{-2} yr^{-1} in 2001. At POPFACE and FACTS-II, the mixed communities of *Populus* clones and *Betula*/*Populus* species in ambient plots exhibited alternating increases and decreases in total soil C efflux over time, ranging from as low as 707 g C m^{-2} yr^{-1} to as high as 1033 g C m^{-2} yr^{-1}. Consistent with B_{20}, the effect of elevated [CO_2] on cumulative soil C efflux varied with community composition. At FACTS-II, averaged over all years, soil C efflux increased 38% in communities dominated by *Populus–Betula* compared with an increase of 22% in communities dominated only by *Populus*. Similarly, at

Table 2 Nonlinear regression analysis of soil respiration and soil temperature data from four forest free-air carbon dioxide enrichment (FACE) experiments

Genus/species	Site	Treatment	Year	B_{20}	(+/−)	95% confidence interval of base respiration	% increase	Q_{10}	(+/−)	95% confidence interval Q_{10}	R^2
Liquidambar	ORNL	Ambient	1997	2.4	0.1	2.2–2.5	5.5	2.2	0.3	1.9–2.5	0.52
Liquidambar	ORNL	Pre-elevated	1997	2.5	0.2	2.3–2.7		2.6	0.9	1.7–3.5	0.42
Liquidambar	ORNL	Ambient	1998	2.6	0.1	2.4–2.7	8.9	1.9	0.3	1.6–2.2	0.36
Liquidambar	ORNL	Elevated	1998	2.8	0.1	2.6–3.0		1.9	0.4	1.6–2.3	0.4
Liquidambar	ORNL	Ambient	1999	3.1	0.1	3.0–3.3	10.2	2.0	0.3	1.7–2.3	0.35
Liquidambar	ORNL	Elevated	1999	3.5	0.2	3.2–3.7		1.9	0.5	1.5–2.4	0.29
Liquidambar	ORNL	Ambient	2000	3.5	0.1	3.4–3.6	18.0	2.1	0.2	1.9–2.3	0.47
Liquidambar	ORNL	Elevated	2000	4.2	0.2	4.0–4.3		2.2	0.3	1.9–2.5	0.43
Liquidambar	ORNL	Ambient	2001	2.6	0.1	2.5–2.7	11.1	2.2	0.2	2.0–2.5	0.42
Liquidambar	ORNL	Elevated	2001	2.9	0.2	2.7–3.1		2.3	0.3	2.0–2.6	0.41
Pinus	FACTS-I	Ambient	1996	7.2	0.3	6.9–7.5	2.1	2.3	0.3	2.1–2.6	0.54
Pinus	FACTS-I	Elevated	1996	7.4	0.4	7.0–7.7		2.3	0.3	2.0–2.6	0.47
Pinus	FACTS-I	Ambient	1997	6.4	0.3	6.0–6.7	28.1	2.7	0.3	2.4–3.0	0.5
Pinus	FACTS-I	Elevated	1997	8.1	0.4	7.7–8.6		2.9	0.3	2.5–3.2	0.47
Pinus	FACTS-I	Ambient	1998	5.4	0.2	5.2–5.7	36.2	2.1	0.2	1.9–2.3	0.45
Pinus	FACTS-I	Elevated	1998	7.4	0.4	7.0–7.8		2.1	0.2	1.8–2.3	0.39
Pinus	FACTS-I	Ambient	1999	6.2	0.3	5.6–5.9	9.5	2.6	0.3	2.3–2.9	0.46
Pinus	FACTS-I	Elevated	1999	6.8	0.4	6.5–7.2		2.7	0.3	2.4–3.0	0.46
Pinus	FACTS-I	Ambient	2000	7.2	0.3	6.9–7.5	14.0	3.4	0.5	2.9–3.8	0.53
Pinus	FACTS-I	Elevated	2000	8.2	0.4	7.8–8.7		2.8	0.4	2.4–3.3	0.39
Pinus	FACTS-I	Ambient	2001	8.2	0.3	7.9–8.6	5.2	3.2	0.3	2.8–3.5	0.64
Pinus	FACTS-I	Elevated	2001	8.7	0.4	8.3–9.0		2.6	0.3	2.4–2.9	0.57
Populus	FACTS-II	Ambient	1998	4.02	0.2	3.8–4.2	17.4	1.7	0.1	1.5–1.8	0.24
Populus	FACTS-II	Elevated	1998	4.72	0.2	4.5–4.9		1.5	0.1	1.4–1.7	0.24
Populus	FACTS-II	Ambient	1999	5.97	0.4	5.6–6.3	24.0	1.5	0.2	1.3–1.7	0.12
Populus	FACTS-II	Elevated	1999	7.4	0.6	6.8–8.0		1.2	0.2	1.0–1.4	0.02
Populus	FACTS-II	Ambient	2000	6.84	1.2	5.7–8.0	40.8	3.2	1.3	2.0–4.5	0.24
Populus	FACTS-II	Elevated	2000	9.63	1.8	7.8–11.5		4.1	1.7	2.4–5.8	0.35
Populus	FACTS-II	Ambient	2001	7.4	0.4	7.0–7.8	12.6	2.6	0.3	2.3–3.0	0.41
Populus	FACTS-II	Elevated	2001	8.33	0.6	7.7–9.0		2.8	0.5	2.3–3.4	0.31
Betula/Populus	FACTS-II	Ambient	1998	3.8	0.2	3.6–4.0	49.7	1.7	0.1	1.5–1.8	0.3
Betula/Populus	FACTS-II	Elevated	1998	5.69	0.3	5.3–6.0		1.5	0.2	1.3–1.7	0.15
Betula/Populus	FACTS-II	Ambient	1999	5.1	0.3	4.8–5.4	43.1	1.5	0.2	1.3–1.7	0.15
Betula/Populus	FACTS-II	Elevated	1999	7.3	0.5	6.8–7.8		1.3	0.2	1.1–1.5	0.06
Betula/Populus	FACTS-II	Ambient	2000	5.77	0.9	4.8–6.7	76.9	2.6	0.9	1.8–3.5	0.23
Betula/Populus	FACTS-II	Elevated	2000	10.21	2.3	7.9–12.5		4.8	2.1	2.6–6.9	0.37
Betula/Populus	FACTS-II	Ambient	2001	6.53	0.5	6.0–7.0	45.9	2.5	0.4	2.1–2.9	0.3
Betula/Populus	FACTS-II	Elevated	2001	9.53	0.8	8.7–10.3		2.6	0.5	2.3–3.4	0.31
P. alba	POPFACE	Ambient	2000	2.6	0.2	2.4–2.8	42.7	2.2	0.5	1.9–2.8	0.3
P. alba	POPFACE	Elevated	2000	3.71	0.3	3.4–4.0		2.0	0.3	1.7–2.4	0.33
P. alba	POPFACE	Ambient	2001	3.04	0.2	2.8–3.3	34.5	2.4	0.6	1.8–3.0	0.2
P. alba	POPFACE	Elevated	2001	4.09	0.2	3.8–4.3		2.2	0.4	1.8–2.7	0.3
P. nigra	POPFACE	Ambient	2000	2.48	0.2	2.3–2.7	34.3	2.3	0.5	1.7–2.8	0.33
P. nigra	POPFACE	Elevated	2000	3.33	0.2	3.1–3.6		2.1	0.4	1.7–2.5	0.36
P. nigra	POPFACE	Ambient	2001	3.19	0.2	3.0–3.4	31.0	2.5	0.6	2.0–3.1	0.26
P. nigra	POPFACE	Elevated	2001	4.18	0.3	3.9–4.5		2.4	0.5	1.9–3.0	0.26
P. × *eur.*	POPFACE	Ambient	2000	2.69	0.2	2.5–2.9	40.1	2.0	0.2	1.7–2.4	0.39
P. × *eur.*	POPFACE	Elevated	2000	3.77	0.3	3.5–4.0		2.4	0.5	1.9–2.9	0.39
P. × *eur.*	POPFACE	Ambient	2001	2.7	0.2	2.5–2.9	49.6	2.0	0.4	1.6–2.3	0.24
P. × *eur.*	POPFACE	Elevated	2001	4.04	0.3	3.7–4.3		2.0	0.4	1.6–2.4	0.19

See Methods for details of the modeling. Estimates are based on nonlinear regression analysis with SPSS, with initial values for B_{20} started at 3 and Q_{10} started at 2.

Table 3 Annual integrated soil respiration carbon for ambient and elevated CO_2 in several forest free-air carbon dioxide enrichment (FACE) experiments

Genus/species	Year	Ambient ($g C m^{-2} yr^{-1}$)	Elevated ($g C m^{-2} yr^{-1}$)	Increase (%)	Significance (F, P) df = 2, >120
FACTS-I					
Pinus	1997	1457	1885	29.4	24.0, <0.005
	1998	1503	2092	39.2	35.0, <0.005
	1999	1591	1840	15.6	3.2, <0.05
	2000	2000	2340	16.9	7.0, <0.005
	2001	2194	2414	10.0	4.5, <0.025
ORNL					
Liquidambar	1997-pretreat	600	598	−0.3	1.0, ns
	1998	784	849	8.3	2.9, ns
	1999	898	999	11.2	2.8, ns
	2000	996	1166	17.1	25.0, <0.005
	2001	698	772	10.6	5.2, <0.01
FACTS-II					
P. tremuloides	1998	707	797	12.6	11.0, <0.005
	1999	997	1489	49.4	15.0, <0.005
	2000	710	865	21.8	12.0, <0.005
	2001	1033	1060	2.7	3.1, <0.05
Betula/Populus	1998	657	936	42.5	59.0, <0.005
	1999	860	1373	59.5	32.0, <0.005
	2000	606	737	21.7	16.0, <0.005
	2001	924	1093	29.2	26.0, <0.005
POPFACE					
P. eur	2000	808	1096	35.6	26.0, <0.005
	2001	724	1062	46.7	33.0, <0.005
P. alba	2000	747	1117	49.5	18.0, <0.005
	2001	751	1069	42.3	21.0, <0.005
P. nigra	2000	707	960	35.7	14.0, <0.005
	2001	753	1011	34.2	17.0, <0.005

Annual estimates for the FACTS-I and FACTS-II sites were calculated by multiplying the days between measurement dates by the average of the consecutive estimates. The annual estimate for ORNL was derived from the fitted temperature relationship and a complete annual soil temperature database. Estimates for POPFACE were attempted with both approaches and produced similar results. The F-value and probability provided in the last column represent a test of the influence of elevated CO_2 exposures on the S_r–temperature response surfaces used to generate the annually integrated soil respiration values in this table. ns, nonsignificant.

POPFACE the degree of stimulation in total soil C efflux in communities dominated by *P. alba*, *P. euramericana*, and *P. nigra* were 48%, 37%, and 32%, respectively.

Consistent with results from the nonlinear modeling analysis of soil respiration rates, elevated atmospheric [CO_2] produced variable stimulation of cumulative soil C efflux for all sites and all years. The stimulation of soil respiration by elevated [CO_2] was significant in all years at all sites, except ORNL. At this site, the stimulation was marginally significant the first 2 years of fumigation, and became significant during the third and fourth years. During the first two full years of fumigation at FACTS-I the relative stimulation due to CO_2 enrichment was 29.0–39.0%, which dropped to 10.0% by the fifth year in 2001 (Table 3). The average stimulation for all years was 22.0%. At ORNL, stimulation of cumulative soil C efflux ranged from 8.3% to 17.1% and averaged only 12.0% for all years. At POPFACE, the stimulation in soil C efflux ranged from 34.2% to 49.5%, and averaged 40.6% overall. Finally, the stimulation in cumulative soil C efflux at FACTS-II ranged from a low of 2.7% to a high of 59.5%, and averaged 30.0% over all years. As with B_{20}, stimulation of cumulative soil C efflux due to CO_2 enrichment was higher for developing compared with established forest stands, and the FACTS-II data indicate this response persisted for up to 4 years.

Discussion

Soil respiration was consistently stimulated by growth under elevated atmospheric [CO_2] at four separate

experiments representing six distinct forest communities, and this response persisted for up to 6 years. However, the degree of stimulation was greatly influenced by inter-annual variation in weather, community composition, and was highly dependent on the stage of stand development. Along with atmospheric [CO_2], these factors were important in determining cumulative soil C efflux from year to year.

Soil temperature relationships

Data from the different sites were compared by fitting soil respiration to soil temperature using a common nonlinear regression model (Table 2). In this application, the seasonal Q_{10} values are often much higher than expected (i.e. $>>2$) if root growth is high. Boone *et al*. (1998) reported a seasonal Q_{10} of 3.5 for hardwood forests in the Northeast USA, while Kicklighter *et al*. (1994) reported a value of 3.1 for hardwood forests globally. Cost of growing roots is a substantial and short-lived phenomenon coupled with temperature response, and often leads to higher than expected Q_{10} values (Hanson *et al*., 1993, 2003; Boone *et al*., 1998; Widén & Majdi 2001). Even though we did not attribute differences across sites to defined soil processes, the fitted values provide an efficient and unbiased integration of the annual soil respiration record at each site. The fit of the model was better for the established sites (FACTS-I, ORNL) than the developing sites (FACTS-II, POPFACE), which may be a function of the more uniform micrometeorological conditions under the intact canopies of the established stands. If this were the case, we would expect the fit to improve over time as the forest canopy closes, which is indeed indicated by the increasing R^2 in later years of the experiment (Table 1).

Annual and inter-annual patterns of soil respiration in developing and established forests

Clearly, patterns of soil respiration were highly dependent on the seasonal progression of weather through the year at all sites (Fig. 1). Soil respiration increased approximately four- to fivefold from the seasonal low in winter or early spring to the seasonal high in mid-summer in developing and established forest stands. This is consistent with results from an 11-year-old loblolly pine plantation that reported a fivefold increase in rates of soil respiration from winter to summer (Maier & Kress, 2000), and a 30-year-old beech forest that experienced a fourfold increase (Epron *et al*., 2001). Luo *et al*. (1996) reported strong seasonality in soil respiration of California grassland ecosystems, as did Hanson *et al*. (1993) in an upland oak forest. In temperate climates, root growth activity may be correlated to the seasonal progression of soil temperature (King *et al*., 2001, 2002). Therefore, seasonal peaks in soil respiration often attributed to increased heterotrophic activity in response to warming may be confounded with root growth (Hanson *et al*., 2000). Although, instantaneous rates of mid-season soil respiration generally increased through time (Table 2), the seasonal progression of soil temperature (and soil respiration) at all sites differed in each year, which ultimately controlled the cumulative soil C efflux (Table 3).

We expected the younger forest stands at POPFACE and FACTS-II to exhibit a clear trend of increasing cumulative soil C efflux over time, as root systems progressively colonized the soil volume. We thought the greater root occupancy of the soil volume in the more established forests (FACTS-I, ORNL) might cause these forests to exhibit less of an increase in soil respiration from year to year. Contrary to this expectation, we found that the older forests exhibited a clear pattern of increasing cumulative soil C efflux in ambient plots over time, except for a decrease at ORNL in 2001 (Table 3). This suggests that root systems of the more established forests may not have fully occupied the respective sites, and are still increasing in total root biomass (coarse and fine roots). Minirhizotron data from ORNL show variable net fine root production (standing crop) during the period 1998–2001. However, there is evidence that root biomass is increasing under elevated CO_2 by going deeper into the soil (Norby *et al*., in preparation). However, there are substantial differences between the two developed stands in their fine root dynamics that create differences in the flux of C into the soil. Sweetgum root production was 45–50% greater than that of the pine trees at FACTS-I, and coupled with the higher annual turnover of these roots, annual C input into the soil at ORNL could be two times greater than at FACTS-I (Matamala *et al*., 2003).

The older forests probably are more highly buffered against inter-annual changes in resource availability by well-established root systems and canopies that allow for more continuous growth and carbon assimilation, as indicated by the consistent increase in soil respiration over time. Further, coarse roots make up an increasingly large fraction of total root biomass during stand development and we would expect the dynamic fine root fraction to make up a smaller proportion of the seasonal soil respiration signal as the stands age. As the forest becomes established over time, it is likely that the heterotrophic communities develop in step, as substrates for microbial growth accumulate in the soil (root and leaf litter, abundance of mycorrhizal fine root tips, exudates, etc.). As with root systems, well-established heterotrophic communities could act to stabilize soil respiration rates due to more uniform

nutrient availability from decomposing organic matter and the integrated respiration of the many different functional guilds of soil microbes and fauna.

In contrast to established stands, the physiology and growth of the developing stands are likely more plastic and responsive to variation in weather and resource availability (King *et al*., 1999), and therefore it is not surprising that these young forests display greater inter-annual variation in cumulative soil C efflux (Table 3). Less well-developed heterotrophic communities in developing forests have less buffering capacity of nutrient availability, and soil CO_2 efflux is dominated by young plant root systems. In addition, micrometeorological conditions (namely, soil temperature and moisture) are more variable in the developing stands due to the open canopy, which contributes to variability in root and heterotrophic activity, and therefore soil CO_2 efflux.

Elevated atmospheric CO_2 and instantaneous rates of soil respiration

Our second hypothesis that elevated atmospheric [CO_2] would stimulate soil respiration, was supported in both developing and established forests. As expected, the developing forest stands exhibited a greater relative response than did the established forests across all years of the respective experiments (Table 2). The average stimulation across clones at POPFACE was 39%, while at FACTS-II it was 24% in the *Populus* community and 54% in the *Populus–Betula* community (39% total). Large differences in the degree of stimulation between the split-plots (genotype and species mixes) at POPFACE and FACTS-II indicate that community composition played an important role in determining responses to elevated [CO_2]. All sites reported the greatest stimulation of soil respiration due to elevated [CO_2] at the height of the growing season, lending support to the idea that root growth responses are a main contributor to the observed soil respiration responses.

In contrast to the developing sites, the average stimulation at FACTS-I was 16%, and at ORNL it was only 12%. King *et al*. (2001) reported an average 96% increase in fine root biomass in *Populus* and *Populus–Betula* communities after 2 years of growth under elevated atmospheric CO_2. Matamala & Schlesinger (2000) reported a 14% increase in fine root biomass at FACTS-I after 2 years of exposure to elevated [CO_2]. Due to reduced pools of soil organic C and less well-developed heterotrophic communities, a much larger relative stimulation in soil respiration can be expected from similar stimulation in fine root biomass in the young forests compared with the more established forests. Evidence from ORNL supports this line of reasoning, in that heterotrophic respiration accounted for about 55% of the total soil CO_2 efflux and increased under CO_2 enrichment (Norby *et al*., 2002). Fine root production also increased with CO_2 enrichment at this site, an average 56% over the 1998–2000 period (Norby *et al*., 2002).

After 6 years of fumigation, instantaneous rates of soil respiration (B_{20}) in elevated CO_2 plots at FACTS-I appear to be converging towards ambient rates, suggesting the stimulation of root activity may have been short lived. This could be an indication that stands have fully occupied above- and belowground growing space, which we would expect to occur sooner in the CO_2-enriched plots. To date, all studies reporting stimulation of soil respiration under elevated [CO_2] have been of relatively short duration, less than 3 years (Körner & Arnone, 1992; Luo *et al*., 1996; Vose *et al*., 1997; Ball & Drake, 1998; Janssens *et al*., 1998; Andrews & Schlesinger, 2001; King *et al*., 2001), and much longer observation periods are necessary to determine if initial responses decline, as appears to be happening at FACTS-I. The ORNL data may also be showing a decline in CO_2 response, from 17% to 11% between the third and fourth treatment years (Table 3), but continued observations will be needed to determine if a sustained decline is occurring.

Elevated atmospheric [CO_2] apparently had no consistent effect on the temperature sensitivity of forest soil respiration as estimated by seasonal Q_{10} values (Table 2). In the current study, seasonal Q_{10} ranged from 1.20 to 4.79, showed no consistent effect of elevated CO_2, and was most variable at the FACTS-II site, which was the only site dominated by more than one genus. The cause of the high variation in seasonal Q_{10} at FACTS-II is unknown at present, but may be related to the fact that it is at the highest latitude and experiences the greatest variation in soil temperature across the growing season. Although drought has been shown to reduce root respiration in northern forests (Burton *et al*., 1998), a 4-year record of soil water content at FACTS-II indicates that plant available water has been nonlimiting over the reported measurement period (data not shown). To our knowledge, there are no other reports of the effects of elevated atmospheric [CO_2] on the seasonal Q_{10} of forest soil respiration. Data from the four independent experiments in six distinct forest communities reported here suggests that elevated [CO_2] will have little or no effect on seasonal Q_{10}.

Elevated [CO_2] effects on cumulative soil C efflux

Stimulation of instantaneous rates of soil respiration by elevated atmospheric [CO_2] was cumulative over the

Table 4 Mechanisms for increased rates of soil respiration in forests communities exposed to elevated atmospheric [CO_2] at four forest FACE experiments

		Percent increase under elevated [CO_2]						
				FACTS-II		POPFACE		
Factor	Measurement units	FACTS-I *Pinus*	ORNL *Liquidambar*	*Populus*	*P.-Betula*	*P. alba*	*P. nigra*	*P. × eur.*
Soil respiration[a]	$\mu mol\,m^{-2}\,s^{-1}$	16	12	24	54	38	32	45
Fine root biomass	$g\,m^{-2}$	14[b]	73[k]	113[d]	83[d]	35[e]	84[e]	53[e]
Fine root production	$g\,m^{-2}\,yr^{-1}$	86[b]	56[c]	*	*	42[e]	88[e]	63[e]
Coarse root biomass (+ stump)	$g\,m^{-2}$	*	0 to −5[i]	36[m]	60[m]	38[f]	22[f]	28[f]
Specific root respiration (growth, maintenance, uptake)	$nmol\,CO_2\,g^{-1}\,s^{-1}$	0[b], −22[k]	0[k]	*	*	*	*	*
Root litter inputs	$g\,m^{-2}\,yr^{-1}$	68[b]	12[i]	147[d,†]	112[d,†]	55[e]	27[e]	27[e]
Leaf litter inputs	$g\,m^{-2}\,yr^{-1}$	26[l]	11[c]	54[o]	54[o]	0[f, **]	0[f, **]	0[f, **]
Specific litter decomposition	$g\,m^{-2}\,yr^{-1}$	0[b,l]	*	*	*	*	*	*
Associative microbial biomass	$\mu g\,C$ or $N\,g^{-1}$	0[j,n]	0[n, **]	0[g,n]	0[g,n]	*	*	*
Associative microbial turnover	$g\,m^{-2}\,yr^{-1}$	0[n]	0[n]	0[g,n]	0[g,n]	*	*	*
Specific microbial respiration	$\mu g\,CO_2{-}C\,g^{-1}\,day^{-1}$	0[j], 30[q]	10[c]	0[h], 29[p]	0[h]	*	*	*
VAM colonization	% internal colonization	*	*	*	*	29[e]	36[e]	0[e, **]
Ectomycorrhizal colonization	% root tips colonized	*	NA	*	*	78[e]	0[e, **]	0[e, **]

Values are the percent stimulation of each factor under elevated [CO_2] compared with ambient conditions. Sources (superscripts) of original data are listed below. Original sources may have given small, nonsignificant differences as a percentage change under elevated CO_2, but here they are represented as 0 since effects were not statistically significant (**).

*Denotes studies currently underway.

[†]Measured as dead fine root biomass accumulation after 2 years of treatments.

No data are available at this time. NA, not applicable.

[a]Values reported in this study.

[b]Matamala and Schlesinger (2000).

[c]Norby *et al*. (2002).

[d]King *et al*. (2001).

[e]Lukac *et al*. (2003).

[f]Calfapietra *et al*. (2003).

[g]Holmes *et al*. (2003).

[h]Larson *et al*. (2002).

[i]RJ Norby (unpublished).

[j]Allen *et al*. (2000).

[k]George *et al*. (2003).

[l]Finzi *et al*. (2001).

[m]King and Pregitzer (unpublished).

[n]Zak *et al*. (2003).

[o]Parsons, Lindroth, Giardina *et al*. (unpublished).

[p]Phillips *et al*. (2002).

[q]Hamilton *et al*. (2002), See reference regarding uncertainty in this estimate.

course of the growing season, substantially increasing the total amount of soil C emitted to the atmosphere compared with forests under ambient conditions (Table 3). This response was strongly modified by the stage of stand development and community composition. Stimulation of soil C efflux was greater in the developing forest stands compared with established closed-canopy stands. Averaged over all communities and years, total

soil C efflux increased 39% at POPFACE and 30% at FACTS-II, compared with average increases of 22% and 12% for FACTS-I and ORNL, respectively.

Community composition had a major influence on cumulative soil C efflux. Other authors have reported differential responses of root and soil respiration to elevated atmospheric [CO_2] for different species and communities (Luo *et al*., 1996; Ball & Drake, 1998; Edwards & Norby, 1999). In almost all cases, however, elevated [CO_2] increased root or soil respiration, but the extent of stimulation was highly system specific. Together with the data presented here, these findings illustrate that soil respiration responses to elevated atmospheric [CO_2] are highly specific to ecosystems of a particular composition and stage of development.

Mechanisms for increased soil respiration under elevated [CO_2]

Ongoing studies at each of the FACE sites are providing information on specific mechanisms that contribute to the overall increase in soil respiration in response to elevated [CO_2] (Table 4). Chief among these are fine root biomass, fine root production and litter inputs, and coarse root biomass. Correlation was poor between the stimulation in soil respiration (%) due to elevated [CO_2] and fine root biomass ($R^2 = 0.01$, $P = 0.82$) and fine root litter inputs ($R^2 = 0.006$, $P = 0.87$). The percent stimulation of leaf litter inputs was not correlated with soil respiration ($R^2 = 0.006$, $P = 0.86$). However, if the non-responsive POPFACE data are removed, the relationship between soil respiration response and leaf litter production is stronger ($R^2 = 0.56$, $P = 0.24$). The relative response of soil respiration was inversely related to that of fine root production, but the relationship was not significant ($R^2 = 0.06$, $P = 0.68$). Interestingly, the relative CO_2 response of coarse roots was positively correlated to that of soil respiration ($R^2 = 0.68$, $P = 0.04$), suggesting that plant size and productivity (above- and belowground) are primary determinants of soil CO_2 efflux. This analysis is of only a few, highly averaged data points and therefore the inference space is limited. However, our conclusion is supported by work of Janssens *et al*. (2001) who demonstrated that forest productivity overshadows temperature in controlling soil respiration in European forests. Similarly, Litton *et al*. (2003) recently reported that above- and belowground plant biomass was highly correlated to microbial biomass and soil CO_2 efflux in lodgepole pine forests recovering from stand replacing fires. Pregitzer *et al*. (2000) also reported a strong relationship between root biomass and soil respiration in open-top chambers. The strong link between plant size and productivity and soil respiration is due directly to greater plant respiration, and higher availability of labile C to heterotrophic communities through greater litter inputs, consistent with observed ecosystems responses to elevated [CO_2] (Table 4, Zak *et al*. 2003).

At this point in time, there are insufficient data from the FACE experiments to perform correlation analyses for other aspects of the belowground C cycle. Three of the four sites report that changes in associative microbial biomass and specific rates of microbial respiration do not appear highly responsive to elevated [CO_2] (Zak *et al*., 2003). The authors caution that these results should be interpreted as initial responses and cannot be used to characterize long-term patterns of soil nitrogen cycling under elevated [CO_2]. Only the POPFACE site has reported on mycorrhizal colonization, and the response ranged from 0% to 78% stimulation depending on tree species and type of mycorrhizae (Table 4). Effects of elevated [CO_2] on specific rates of root respiration have been well described for the FACTS-I and ORNL experiments (George *et al*., 2003). Maintenance respiration was by far the largest component of total root respiration, and declined 24% in loblolly pine under elevated [CO_2]. The authors concluded this could result in increased C storage in these ecosystems (George *et al*., 2003). Specific rates of leaf litter decomposition were unaltered by elevated [CO_2] at FACTS-I (Finzi *et al*., 2001), consistent with findings of a meta-analysis of the broader elevated CO_2 literature (Norby *et al*., 2001). However, greater litter production under elevated [CO_2] will increase the total amount of substrate available for microbial metabolism, thereby contributing to increased soil CO_2 efflux. Ongoing studies of root and leaf litter production, chemistry, and decomposition at the forest FACE experiments will further elucidate this aspect of terrestrial C cycling. Due to technical challenges, very little work has been done on root exudation and soil priming (enhanced decomposition of 'old' or recalcitrant C due to increased labile C inputs) at any of the sites. Increased rates of C exudation into the rhizosphere under elevated [CO_2] has been reported from smaller scale studies (Rouhier *et al*., 1994; Cheng & Johnson, 1998, 1999), but more research is needed in both areas to determine effects on ecosystem C cycling.

Conclusions

We conclude that the rising atmospheric [CO_2] will increase rates of soil respiration in a wide variety of forest ecosystems. Therefore, some of the increased C assimilated under elevated [CO_2] will rapidly return to the atmosphere. The degree of stimulation in soil respiration under elevated [CO_2] will depend on forest

community composition, with some forest types clearly showing more stimulation than others. In addition, young developing forests are likely to show greater and more variable stimulation than well-established forests, and our evidence suggests that even in established forests responses to elevated [CO_2] will persist over time. We found that elevated atmospheric [CO_2] apparently does not affect the temperature sensitivity of bulk soil respiration, as we observed no consistent changes in seasonal Q_{10}. This should simplify this aspect of ecosystem modeling. In summary, when extrapolating results of elevated CO_2 experiments or modeling forest and global C cycles in a CO_2-enriched atmosphere, explicit consideration must be given to the stage of stand development and species composition.

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