Global Change Biology (2003) **9,** 849–861

Reduction of forest floor respiration by fertilization on both carbon dioxide-enriched and reference 17-year-old loblolly pine stands

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Abstract

Elevated atmospheric carbon dioxide (CO_2^e) increases soil respiration rates in forest, grassland, agricultural and wetland systems as a result of increased growth, root biomass and enhanced biological activity of soil microorganisms. Less is known about how forest floor fluxes respond to the combined effects of elevated CO_2 and nutrient amendments; until now no experiments have been in place with large forest trees to allow even preliminary investigations. We investigated changes in forest floor respiration (S_{ff}) in a *Pinus taeda* L. plantation fumigated with CO_2 by using free-air CO_2 enrichment (FACE) technology and given nutrient amendments. The prototype FACE apparatus (FACEp; 707 m^2) was constructed in 1993, 10 years after planting, on a moderate fertility site in Duke Forest, North Carolina, USA, enriching the stand to 55 Pa (CO_2^e). A nearby ambient CO_2 (CO_2^a) plot (117 m^2) was designated at the inception of the study as a reference (Ref). Both FACEp and Ref plot were divided in half and urea fertilizer was applied to one half at an annual rate of 11.2 g N m^{-2} in the spring of 1998, 1999 and 2000. Forest floor respiration was monitored continuously for 220 days – March through November 2000 – by using two Automated Carbon Efflux Systems. Thirty locations (491 cm^2 each) were sampled in both FACEp and Ref, about half in each fertility treatment. Forest floor respiration was strongly correlated with soil temperature at 5 cm. Rates of S_{ff} were greater in CO_2^e relative to CO_2^a (an enhancement of ~178 g C m^{-2}) during the measurement period. Application of fertilizer resulted in a statistically significant depression of respiration rates in both the CO_2^a and CO_2^e plots (a reduction of ~186 g C m^{-2}). The results suggest that closed canopy forests on moderate fertility sites cycle back to the atmosphere more assimilated carbon (C) than similar forests on sites of high fertility. We recognize the limitations of this non-replicated study, but its clear results offer strong testable hypotheses for future research in this important area.

Keywords: elevated atmospheric CO_2, FACE, forest floor respiration, *Pinus taeda*, soil fertility, soil respiration

Received 17 May 2002; revised version received 13 January 2003 and accepted 16 January 2003

Introduction

The role played by forests in mitigating rising carbon dioxide (CO_2) levels in the atmosphere is currently the subject of interest and debate. Forests in the northern hemisphere are considered to be a large sink for atmospheric CO_2 (Ciais *et al*., 1995; Schimel, 1995; Tans & White, 1998). Considering the positive effect that elevated CO_2 has on carbon (C) assimilation via photosynthesis in trees and forests systems (Ceulemans *et al*., 1999), it may seem logical that this C sink would at the very least remain if not increase. New research indicates that soil fertility limits the ability of forests to sequester and store C in a CO_2-enriched environment (Oren *et al*., 2001). In the absence of adequate soil fertility, trees may be unable to sequester carbohydrates into woody tissues. Forest floor respiration (S_{ff}) or soil respiration is the major

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avenue for C loss from the terrestrial pool and is considered the main determinant of C balance in forests in the northern hemisphere (Valentini *et al*., 2000). Microbial and soil respiration rates have been almost universally found to increase when exposed to elevated CO_2 (Zak *et al*., 2000), whereas the effect of fertilization on S_{ff} is much more complex and variable. No studies using mature trees have been reported to investigate CO_2–soil fertility interactions in S_{ff}.

Forest floor respiration is the net result of both autotrophic and heterotrophic below-ground C processes, which include root respiration and respiration associated with decomposition and soil organisms. These components can be very difficult to separate, so many studies use S_{ff} to balance C budgets and quantify how much C is released from the below-ground 'black box' to the atmosphere. When assessing the literature to elucidate the impact of elevated CO_2 and fertilization on S_{ff} it is helpful to separate or identify the reported responses as tree (autotroph) response, microbial response (heterotroph), the age of the stand (seedling vs mature) and measurement technique/experimental design (field, growth chamber, soil incubation measures) for judging the applicability of the results.

Elevated atmospheric CO_2 (CO_2^e) commonly enhances both net photosynthesis and growth in forest seedlings (Jach *et al*., 2000; King *et al*., 2001) and in trees (Ceulemans *et al*., 1999; DeLucia *et al*., 1999; Ellsworth, 1999; Oren *et al*., 2001). Such responses have been consistently demonstrated in *Pinus taeda* L. (loblolly pine) (Groninger *et al*., 1999). Although long-term increases in above-ground net primary productivity (NPP) under CO_2^e may be limited by nutrient availability (Ceulemans *et al*., 1999; Oren *et al*., 2001), a significant enhancement in photosynthesis persists, suggesting enhanced C allocation below-ground. Indeed, production of fine roots has been shown to increase with CO_2^e in seedlings (Jach *et al*., 2000) and in intact forests (Matamala & Schlesinger, 2000). Consequently, this enhanced investment of C below-ground results in greater soil C inputs (Janssens *et al*., 1998; Cheng, 1999), providing additional substrate for microbial activity (Ceulemans *et al*., 1999; Zak *et al*., 2000) or more recalcitrant C forms for storage in the soil. Considering the C budget of an ecosystem, net ecosystem productivity (NEP) reflects C incorporated into biomass minus CO_2 produced in respiration of all ecosystem components, including S_{ff}.

Although CO_2^e often increases NPP, it can also result in greater losses of C (relative to CO_2^a) via soil respiration. Such responses have been observed in forest, agricultural, grassland and wetland systems (Vose *et al*., 1995, 1997; Ball & Drake, 1998; Verburg *et al*., 1998; Lin *et al*., 1999; Mikan *et al*., 2000; Sowerby *et al*., 2000; Zak *et al*., 2000; Andrews & Schlesinger, 2001; King *et al*., 2001; Pendall *et al*., 2001). The majority of studies relating CO_2^e to forest systems utilize individual tree seedlings, or artificial stands planted in open top chambers or growth chambers where CO_2^e can be readily controlled. Elevated atmospheric CO_2 has been demonstrated to increase allocation of fixed C to fine roots and enhance root exudation to soil microbes, thereby increasing S_{ff} in tree seedling studies (e.g. Norby *et al*., 1992; Johnson *et al*., 1994, 2000; Vose *et al*., 1995, 1997; Mikan *et al*., 2000) and early results from the Aspen FACE study in Wisconsin (King *et al*., 2001). Others have noted stimulation of S_{ff} under CO_2^e when working with seedlings planted in fertile soils, but no effect on nutrient poor sites (Spinnler *et al*., 2002). Elevated atmospheric CO_2 has also been found to increase the life span of fine roots in *P. ponderosa* seedlings (Johnson *et al*., 2000), allowing them to function/respire for a longer period of time. Using 4-year-old *Pseudotsuga menziesii* seedlings, planted in reconstructed forest soils, Lin *et al*. (1999) found that the loss of newly fixed C via root respiration was the soil respiration component most responsive to CO_2^e. The authors found that litter decomposition increased with the CO_2^e, but they were at a loss to explain the cause as only a small fraction of the litter was formed under CO_2^e. This could be an artifact of their experimental and sampling methodology that assessed C isotope discrimination.

Duke University's replicated FACE experiment (Hendrey *et al*., 1999) in the Duke Forest, North Carolina, USA, is a unique site where an intact *Pinus taeda* stand has been exposed to CO_2^e without chambers or root disturbance and provides an excellent model system in order to study the effects of CO_2^e. In this mid-rotation *P. taeda* plantation, CO_2^e increased S_{ff} by 27% relative to ambient CO_2 (CO_2^a) (Andrews & Schlesinger, 2001). This was observed in conjunction with large increases (86%) in fine root mass after 2 years of CO_2^e (Matamala & Schlesinger, 2000). The quantity of litterfall increased under CO_2^e, but the litter quality and the rate of decomposition were unchanged (Finzi *et al*., 2001; Finzi & Schlesinger, 2002). Loblolly pine litter is quite recalcitrant and decomposes slowly under a closed canopy and often increases mass under positive growing conditions; pine litter has even been found to restrict S_{ff} by limiting CO_2 diffusion (Maier & Kress, 2000).

Southern pine forests are often nutrient limited. Nitrogen and phosphorus (P) limitations are widespread throughout the managed range of *P. taeda* and potassium (K) is limiting on particular soils of the coastal plain (Allen *et al*., 1990, 2001). Operational applications of nitrogen (N) fertilizer have been shown to consistently increase *P. taeda* productivity throughout its range in the southern US (Allen, 1987; Allen *et al*., 1990; Schultz, 1997). Fertilization can affect C allocation in seedlings (Tingey *et al*., 1996; Lu *et al*., 1998) and in forest trees (Axelsson &

Axelsson, 1986; Haynes & Gower, 1995; Albaugh *et al*., 1998). Changes in C allocation can affect S_{ff}, C storage in plant tissues and storage in recalcitrant forms. However, it is not realistic to make generalized statements regarding the impact of fertilizer application on S_{ff}. The effect of fertilizer can depend on C allocation in the trees, age of the stand, tree species, form of fertilizer, application rate, frequency and timing, and effects on microbial population dynamics and activity.

The effect of fertilization (primarily N with micronutrients) on a seedling generally results in increased photosynthesis, leaf area and biomass accumulation (Tingey *et al*., 1996, 1997; Pangle & Seiler, 2002). Reduction in below-ground allocation has been observed (Lu *et al*., 1998), but it is more common to see a reduction in fine roots and a shift to coarse root production (Tingey *et al*., 1996, 1997; Maier & Kress, 2000). Fertilization increases root mortality and stimulates root turnover in seedlings (Pregitzer *et al*., 1995, Tingey *et al*., 1997). The effect of fertilization on S_{ff} is mixed; reductions in S_{ff} at high levels of N (Lu *et al*., 1998), no effect on S_{ff} (Vose *et al*., 1995, 1997; Pangle & Seiler, 2002) and increases in S_{ff} (Griffin *et al*., 1997; Mikan *et al*., 2000) have been observed. Lu *et al*. (1998) have indicated that the response to N in *P. ponderosa* seedlings is non-linear, increasing with root mass until an optimal level is reached, beyond which excess N seems to induce toxicity. The difference may depend on whether an absolute reduction in total root biomass has occurred (Lu *et al*., 1998) and whether any change in root-specific respiration is observed (Lu *et al*., 1998; Maier & Kress, 2000; Pangle & Seiler, 2002).

Fertilizer application of mid-rotation mature stands impacts photosynthesis to a lesser degree or duration than in seedlings, although leaf area and biomass accumulation are typically increased (Axelsson & Axelsson, 1986; Lai *et al*., 2002; Maier *et al*., 2002). Changes in C allocation shift from below-ground to above-ground accretion (Haynes & Gower, 1995; Albaugh *et al*., 1998) and coarse root production is favored at the expense of fine root production (Axelsson & Axelsson, 1986; Haynes & Gower, 1995; Maier & Kress, 2000; Retzlaff *et al*., 2001). As with seedlings, root mortality has been found to be higher with N fertilization (Aber *et al*., 1985). Fertilization has been found to decrease S_{ff} in forest stands (Haynes & Gower, 1995; Maier & Kress, 2000), but application of N in the form of urea typically increases S_{ff} temporarily followed by a long-term reduction in S_{ff} (Martikainen *et al*., 1989; Nohrstedt *et al*., 1989; Aarnio & Martikainen, 1994, 1996). Use of nitroform fertilizers to supply N does not cause any ephemeral spike in S_{ff} and simply results in a marked decrease in S_{ff} (Aarnio & Martikainen, 1996). Other workers have reported no significant difference in S_{ff} with N-based fertilizer amendments (Castro *et al*., 1994; Lai *et al*., 2002). The 7-year-old loblolly pine forest used by Lai *et al*. (2002) had been fertilized since planting and the plots receiving fertilizer had vastly greater above- and below-ground biomass accumulation, although they exhibited little difference in S_{ff}. Nitrogen fertilization has the greatest influence on S_{ff} in nutrient poor soils, where it has the greatest effect on growth (Arnebrandt *et al*., 1996), while depression of S_{ff} can be limited on nutritionally rich sites (Martikainen *et al*., 1989; Arnebrant *et al*., 1996).

Depression of S_{ff} by N fertilization may be related to reduced microbial activity as a result of modified soil pH, reduced C allocation to roots as above-ground sink strength increases and changes in fine root dynamics (Haynes & Gower, 1995; Arnebrant *et al*., 1996; Matamala & Schlesinger, 2000; Thirukkumaran & Parkinson, 2000). Fertilizer can also directly suppress microbial respiration independently from any plant responses to fertilization (Kowalenko *et al*., 1978; Foster *et al*., 1980, Thirukkumaran & Parkinson, 2000). The chemical effects of specific fertilizers and rates of application can either stimulate or suppress S_{ff} depending on the response and the composition of native microbial populations (Thirukkumaran & Parkinson, 2000).

Studies assessing the effects of CO_2^e and fertilization (primarily N) on S_{ff} have been limited to experimentation with seedlings. Both CO_2^e and fertilization have been shown to increase S_{ff} in tree seedlings (Griffin *et al*., 1997; Mikan *et al*., 2000). Long-term seedling studies (3 years) by Vose *et al*. (1995, 1997) showed evidence of CO_2^e stimulating S_{ff}; N fertilization had no effect. These results with seedlings can be best applied to aggrading forest systems where soil resources have not been fully exploited (Mikan *et al*., 2000). Owing to experimental constraints – that is, having a FACE system with a mid rotation forest available for fertilizer treatments manipulations – research of this type has not been performed in forest stands. Data from forest stands are needed in order to parameterize models and scale treatment effects temporally, because these forests have already captured much of the available rooting volume and have progressed beyond the initial disturbance of site preparation as well as the exponential growth phase.

While, the singular impacts of CO_2^e and N fertilization on S_{ff} are often contradictory, the potential effects of N addition on S_{ff} and NEP in the future with CO_2-enriched atmosphere have yet to be quantified. Consideration of these interactions is important with respect to managed forests, forests receiving increased atmospheric N additions and natural forests growing on nutrient-limited sites. This study examines the impact of fertilization and atmospheric CO_2^e concentration on S_{ff} by using the Duke Forest FACE Prototype and its Reference plot that were both split into fertilized and non-fertilized

halves (Oren *et al*., 2001). At the time we took our measurements, the stands were 17-year-old.

Methods

Site

The FACE Prototype experiment is located at the Blackwood Division of the Duke Forest, Orange County, North Carolina (35°58′N, 79°08′W). The soil in this lower Piedmont Plateau site is acidic clay-loam of moderately low fertility. Rooting depth is usually less than 30 cm (Oren *et al*., 1998). The region is typified by warm summers and moderate winters and receives an average of 1100–1200 mm of precipitation annually, distributed evenly throughout the year. Free-air CO_2-enrichment (FACE) technology was used in order to enrich plots 30 m in diameter within an intact *P. taeda* plantation with CO_2 without enclosure (Hendrey *et al*., 1999). The FACE prototype (FACEp; 707 m^2) was constructed in 1993 in a 10-year-old loblolly pine plantation as an engineering prototype for the development of FACE systems in forests and has been used for enriching atmospheric CO_2 concentrations (to 550 p.p.m.) since 1994, so represents the longest running FACE plot of large forest trees in the world. A nearby plot (117 m^2) was delineated at the inception of the study in order to serve as reference (Ref.) Ref. was not significantly different in growth rate or foliar N content from FACEp at the start of study (Oren *et al*., 2001).

In 1998, both FACEp and Ref were divided into two sections containing approximately the same aboveground biomass per unit area. A trench was dug to a depth of 1 m and backfilled after a polyethylene-sheeting material was inserted in the trench in order to prevent root intrusion (Oren *et al*., 2001). Fertilizer amendments were applied to both the FACEp and the reference plot using 'optimum' application rates (Table 1) (Allen, 1987; Albaugh *et al*., 1998). The plots are referred to as CO_2^a-NF (ambient CO_2, no fertilizer), CO_2^a-F (ambient CO_2, fertilizer applied), CO_2^e-NF (elevated CO_2, no fertilizer) and CO_2^e-F (elevated CO_2, fertilizer applied).

Soil respiration measures

Forest floor respiration was measured with the Automated Carbon Efflux System (ACES) (patent pending) developed at USDA Forest Service, Southern Research Station Laboratory, Research Triangle Park, North Carolina. Automated Carbon Efflux System is a chamber-based, multiport respiration measurement system that is similar in concept to that used by Maier & Kress (2000). Automated Carbon Efflux System uses open system, dynamic soil respiration chambers measuring 25 cm in diameter (491 cm^2) equipped with air and soil thermocouples (inserted to depth of 5 cm). Chambers were designed with pressure equilibration ports to ensure minute differences in chamber pressure do not compromise the quality of the respiration measurement (Fang & Moncrieff, 1996). Fifteen sample chambers and one null calibration chamber were measured sequentially for 10 min each allowing a complete run every 2 h and 40 min or nine complete runs per day. When not being actively sampled, the other 15 chambers were refreshed with reference air to prevent any buildup of CO_2 in the chambers. One ACES unit was installed in each of the two plots. Within each CO_2 treatment plot soil respiration chambers were placed randomly, eight in control (no fertilizer amendments) and the other seven chambers in the fertilized portion of the plot. In order to minimize the effect of precipitation and litterfall exclusion on the soil substrate within the chambers, the chambers were exchanged every 3–4 days between two adjacent sample points. The ACES units collected data continuously from March 2000 through November 2000 (day 83 through 303), with the exception of periods for system maintenance or gaps from system or power failures.

In Ref, a 135-L ballast tank was used to provide reference air for the ACES, which was buffered against minor fluctuations in atmospheric CO_2 concentration. In FACEp, fluctuations of CO_2 at ground level were too great to be buffered by the standard ballast tank. An air compressor, acting as a gas mixer, was added in order to provide consistent reference air for the ACES. While the compressor was running, it collected air of fluctuating CO_2 concentration and stored it in the reserve tank. Outgoing air was de-pressurized to ambient conditions and its CO_2 concentration was stable ($\pm$ 2 p.p.m. per compressor cycle).

Table 1 Fertilizer amendments applied to both the FACEp and Ref, using optimum application rates (Allen, 1987; Albaugh *et al*., 1998)

Year of application	Element sources	Element	Rate $g\,m^{-2}\,yr^{-1}$
1998	urea* and diammonium phosphate	N	11.200
		P	2.800
1999	urea* and potassium chloride	N	11.200
		K	5.600
2000	urea*, diammonium phosphate and boron	N	11.200
		P	1.120
		B	0.112

*Application of urea $(NH_2)_2CO$ results in a 4.8 $g\,m^{-2}\,yr^{-1}$ amendment of C.

Data analysis

The plots used for this work presented a unique opportunity for examining fertilization effects on intact stands receiving ambient or elevated atmospheric CO_2. As fertilization plots were replicated, statistical tests of significance of fertilization effects are presented. However, only one FACE and one control plot were used, so descriptive statistics will only be provided for atmospheric CO_2 effects and interactions between fertilization and CO_2 treatment across these plots. These descriptive statistics allow comparison to responses reported in the literature and provide clues as to the importance of interaction effects.

The soil respiration data were analyzed for component or power failures; any obvious systematic errors were parsed from the data set. Ground-level fluctuations of CO_2 concentration in FACEp were the largest source of unusable data points until the situation was improved by the replacement of the ballast tank with an air compressor. Any time the CO_2 concentration of the reference gas (ballast or compressor) fluctuated more than 30 p.p.m. in 10 min, the measurement was discarded. Data points were also discarded if they exceeded the period (160 min) mean by more than three standard deviations. A total of 41 172 measurements, 65% of potential number of measurements in the 220-day experiment, were deemed acceptable for analysis.

Forest floor respiration data collected over the entire study period were analyzed with non-linear regression (Proc NLIN, SAS Institute) in order to determine the response to soil temperature measured at a depth of 5 cm (Ts_5) for each location. Exponential S_{ff}–temperature response curves were fitted for each location using non-linear regression in the form:

$$S_{ff} = a \cdot e^{(T_{s5} \cdot b)} \quad (1)$$

An alternate model that incorporates soil moisture and temperature was tested with linear models (Proc GLM, SAS Institute). A fertilizer impact analysis consisting of normalizing fertilized S_{ff} by its split-plot control was performed in order to determine whether any time-dependent (number of days since fertilization) factors other than temperature were influencing S_{ff}. Results of the temperature only model were compared with the model which integrates fertilizer impact analysis in order to determine which best describes S_{ff} in year 2002. In order to verify the model results, it was necessary to have observed data that were spatially and temporally representative, especially as 35% of the potential measurements were missing or discarded. Mean S_{ff} and Ts_5 were calculated for each unique soil position per day and a mean value for each treatment was determined for each day. In order to reduce the effects of missing days or time lags in autotrophic feedback, monthly means (March through October 2000) were compared to model estimates. It is recognized that replication exists to test fertilizer effects, but not CO_2[e]. Treatment differences between S_{ff} modelled by month and cumulative efflux over the measurement period were analyzed with analysis of variance (Proc ANOVA, SAS Institute).

Results

Mean soil temperatures within the respiration chambers ranged from 9 to 23 °C (Fig. 1a) and were not significantly different between FACEp and the Ref plot ($P = 0.14$). Daily S_{ff} varied from 1 to 10.5 μmol $m^2 s^{-1}$ during the measurement period (Day 83 to 303; (Fig. 1b). Mid-year rates were the highest and had the greatest variability both within and among treatments, yet treatment effects were discernible. During the early spring, when soil temperatures were low, the differences between treatments were small. Modelling daily rates with Ts_5 (Eqn (1)) were highly effective and explained much of the variation in observed daily S_{ff} (maximum $P < 0.0001$; R^2 ranged

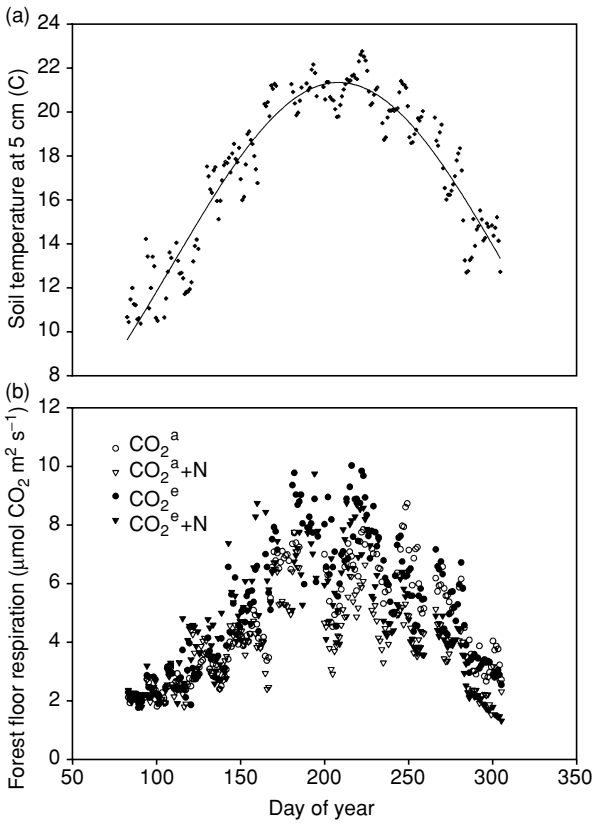

Fig. 1 Daily mean soil temperature at 5 cm (a) and daily mean S_{ff} (μmol CO_2 $m^2 s^{-1}$) (b), across all treatments for the 220-day measurement period.

among treatments from 0.67 to 0.84). The mean values of the coefficients and Q_{10} values for each treatment are presented in Table 2.

Fertilizer application (Day 118) initiated an immediate increase in S_{ff} in both CO_2^a and CO_2^e that was followed by a substantial suppression of S_{ff} for the rest of the experiment. Analysis of F plot results that have been normalized by NF (within the same CO_2 treatment) reveals changes in S_{ff} as a result of fertilizer application that are separate from impacts of soil temperature and seasonal variation (Fig. 2). The fertilizer impact was very similar between CO_2 treatments, though the stimulation of S_{ff} after fertilization was slightly shorter in CO_2^a. A second S_{ff} model was developed combining the Ts_5 response model with the results of the fertilizer impact analysis ($Ts_5{}^*F$ model) in order to describe this phenomenon. The $Ts_5{}^*F$ response model shows that S_{ff} was more responsive to soil temperature in CO_2^e than in CO_2^a and within CO_2 treatments the addition of fertilizer initiated a temporary stimulation followed by suppression in S_{ff} (Fig. 3, Eqn (2)). The $Ts_5{}^*F$ response model follows the form:

$$S_{ff} = a \cdot e^{(T_{s5} \cdot b)^*} FR \qquad (2)$$

where NF plots and F plots prior to annual fertilizer application have an FR (fertilizer response) value of 1 until fertilizer is applied. For the rest of the year the fertilizer response equation (multiplier) was calculated using the number of days since fertilization:

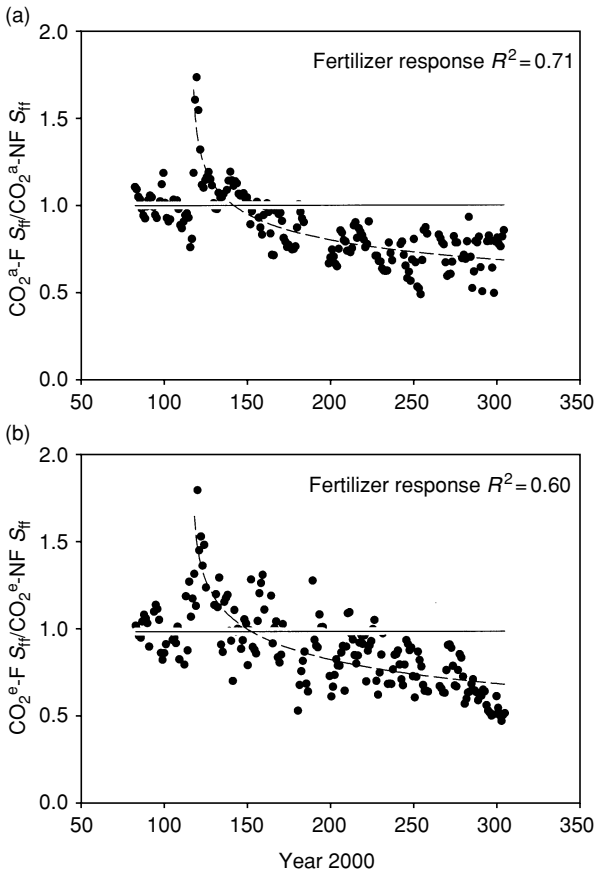

Fig. 2 Values of S_{ff} in fertilized plots normalized by their unfertilized split-plot control for both CO_2^a(a) and CO_2^e(b). Prior to fertilizer application on day 118, there was no significant deviation from 1. The post-fertilization response was fitted with Eqns (2) and (3) using coefficients in Table 3.

Table 2 Mean values (± SE) of the temperature response model coefficients (Eqn (1)) and the parameters of the fertilizer response equation (Eqn (3)). The temperature response (Ts_5) model (Eqn (1)) predicts S_{ff} with the coefficients listed under $S_{ff} = f(Ts_5)$. The combined soil temperature and fertilizer response ($Ts_5{}^*F$) model (Eqn (2)) uses Ts_5 coefficients from CO_2^a-NF and CO_2^e-NF, while the parameters of $FR = f$ (days since F application) are derived from the analysis of F plot results that have been normalized by NF (within the same CO_2 treatment); Q_{10} values are presented for each plot

$S_{ff} = f(Ts_5)$	a	b	Q_{10}*
CO_2^a-NF†	0.8689 (0.0834)	0.0943 (0.0060)	2.57 (0.16)
CO_2^a-F	0.8586 (0.0593)	0.0876 (0.0040)	2.40 (0.10)
CO_2^e-NF†	0.6749 (0.0554)	0.1152 (0.0049)	3.16 (0.16)
CO_2^e-F	0.5974 (0.0527)	0.1130 (0.0052)	3.09 (0.17)
$FR = f$ (days since F application)	c	d	e
CO_2^a-F	0.2473	0.3528	0.2359
CO_2^e-F	0.4332	0.1690	0.3405

*$Q_{10} = e^{(b^*10)}$ for Ts_5 from 9 to 23 °C.
†Ts_5 component of $Ts_5{}^*F$ model.

$$FR = \frac{1}{c + d \cdot (\text{days})^e} \qquad (3)$$

The coefficients for Eqns (2) and (3) are presented in Table 2.

Both models adequately describe soil respiration during the measurement period and there is little difference between them when compared with observed monthly mean S_{ff}: Ts_5 model (mean 4.66 μmol m^{-2} s^{-1}, MSE = 0.44, $R^2 = 0.93$, $P < 0.0001$), $Ts_5{}^*F$ model (mean 4.65 μmol m^{-2} s^{-1}, MSE = 39, $R^2 = 0.94$, $P < 0.0001$). The $Ts_5{}^*F$ model more directly tracks the process-level effects of fertilizer application and allows this model to closely follow observed soil respiration over time (Fig. 4a–d). Despite similarities in total variation explained by each model, the temporal response of the $Ts_5{}^*F$ model effectively models time lags noted in observed S_{ff} (Fig. 4e); F plots achieved peak S_{ff} earlier than NF plots. The $Ts_5{}^*F$ model shows fertilizer effects remained near the

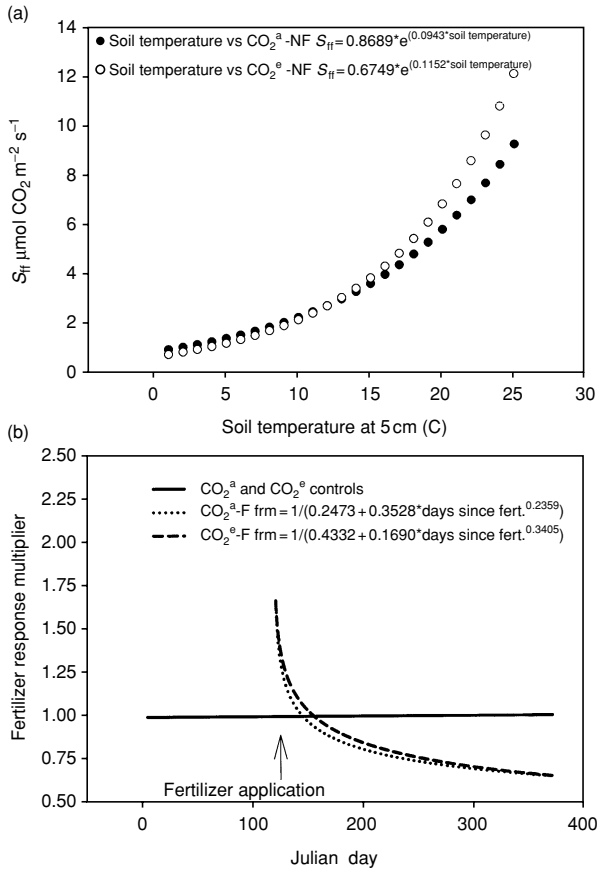

Fig. 3 Components of combined soil temperature and fertilizer response model ($Ts_5{}^*F$) which predicts S_{ff} using soil temperature (Ts_5) and number of days since fertilization. Non-fertilized plots use the exponential model (a) to predict S_{ff}. Fertilized treatments use the same exponential model prior to fertilization (a), after fertilization, the base exponential equation is multiplied by the fertilizer response equation (b).

end of the measurement period, while differences in CO_2 were not evident Fig. 4(e), matching observed data in Fig. 4(a–d). The temperature model is simple and is able to elucidate major trends across treatments, but cannot account for fine scale temporal response; hence, modeling of cumulative C loss with the $Ts_5{}^*F$ model is preferred. Direct comparisons with observed soil respiration were made with linear regression to verify the $Ts_5{}^*$F model results (Fig. 4a–d).

Soil moisture is typically considered one of the key variables controlling S_{ff}. During the measurement period in year 2000 there were seldom periods of water stress; mean volumetric soil water content was 24% (range 18–38%). Linear models were applied to examine the influence of soil moisture on daily S_{ff} by treatment. The effect of soil moisture was only significant in $CO_2{}^a$-F ($P = 0.0086$), resulting in a slight increase in S_{ff} with increasing soil moisture, though the contribution toward describing the overall variation in S_{ff} was very small (improvement in $R^2 = 0.01$). At no time was soil moisture found to be limiting S_{ff}.

The $Ts_5{}^*F$ model was used to estimate monthly averages and these values were subjected to ANOVA in order to test the effect of fertilizer on S_{ff}, by month (Fig. 4f). The FACEp and REF plots were used as blocks providing replication of fertilizer treatments. Forest floor respiration response to fertilization displayed three distinct phases (Fig. 4f). Prior to fertilization there was no effect of previous fertilizer applications. Immediately after fertilization there was a small but significant increase in S_{ff}. After June there was a significant decrease that persisted through the end of the measurement period. For the entire measurement period, cumulative C loss via S_{ff} was 15% lower in the fertilized plots and this difference was statistically significant (Table 3). While unable to test significance of the CO_2 effects on S_{ff} or any interaction with fertilizer treatment, model-estimated cumulative C losses are presented in Table 3. Model-estimated cumulative S_{ff} under $CO_2{}^a$ was 14% lower than under $CO_2{}^e$ (Table 3). Comparing $CO_2{}^a$-F to $CO_2{}^e$-NF yields a 28% difference indicating that the fertilizer and CO_2 effects are additive.

Discussion

Forest floor respiration rates were successfully predicted by both models, one based Ts_5 and the other combining soil temperatue and fertilizer impact ($Ts_5{}^*F$ model). Along with soil temperature, soil moisture often exerts a strong influence on S_{ff} in terrestrial systems (Singh & Gupta, 1977; Lomander *et al*., 1998; Davidson *et al*., 2000), but including soil moisture did not appreciably improve model fits with these data. Rainfall in year 2000 was close to the annual average in the region and evenly distributed throughout the year. Subsequently, the high soil moisture and its minor variability elicited negligible influences on S_{ff}.

In the absence of soil moisture effects, the most dynamic and direct environmental variable to correlate with S_{ff} is soil temperature (Singh & Gupta, 1977). The Ts_5 model presented in this work effectively summarized treatment effects; however, these modeled impacts of fertilization are dispersed over the course of the entire experiment deviating from observed phenomenon (Fig. 2). The model cannot predict the effects of non-thermal events, such as timing of fertilization on S_{ff}. The $Ts_5{}^*$F model utilizes the fundamental difference in S_{ff} sensitivity to temperature in $CO_2{}^a$ and in $CO_2{}^e$ (Fig. 3a), then overlays fertilization response. This procedure helps separate temperature and fertilizer effects on soil respiration. This model does not elucidate the process by which

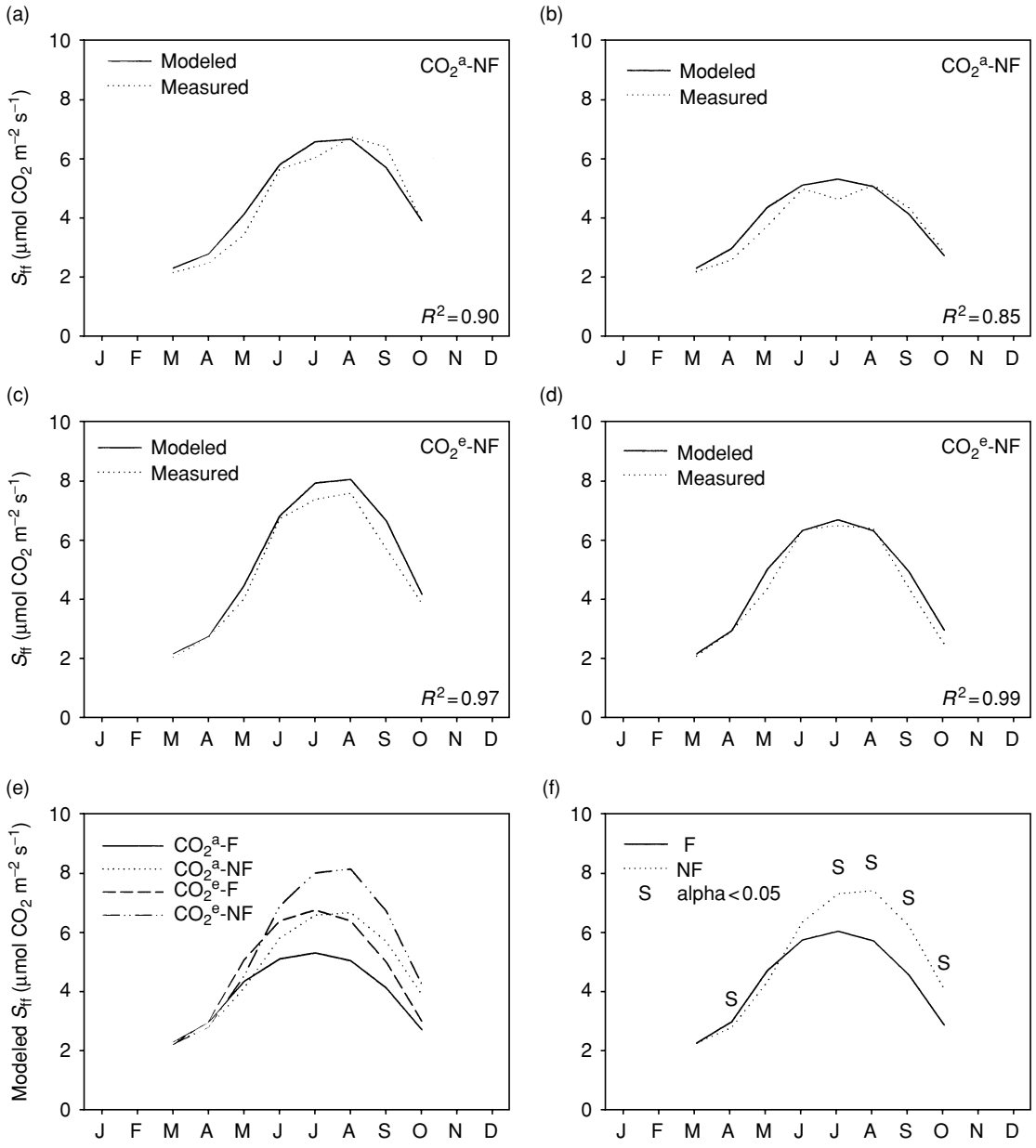

Fig. 4 Mean monthly S_{ff} measured in each plot compared with model results calculated using the $Ts_5{}^*F$ model (a–d), modelled S_{ff} data presented on one graph illustrating temporal variation among the plots (e), and comparison of F and NF plots (using CO_2 treatment for replication) using analysis of variance in order to identify months where F and NF were significantly different (f).

fertilizer briefly stimulates, then suppresses soil respiration, but clearly defines the response. The $Ts_5{}^*$F predicts several phenomenon in observed soil respiration that the Ts_5 model does not: (i) the small but significant increase in soil respiration immediately after fertilization, (ii) fertilized plots achieve peak soil respiration approximately 1 month earlier than non-fertilized plots, (iii) late in the growing season, significant differences exist between fertilized and non-fertilized plots (Fig. 4f). For this study, the $Ts_5{}^*$F model best approximates the observed data and is the most appropriate for modeling year 2000 responses. The Ts_5 model would be most useful to modelers when the exact timing of fertilizer application was unknown. The $Ts_5{}^*F$ model does not directly utilize the Q_{10} function, though Q_{10} can be a useful parameter to compare temperature sensitivity across ecosystems; Q_{10} values of $CO_2{}^a$, regardless of fertilizer treatment, were similar to values reported for an 11-year-old *P. taeda* plantation (Maier & Kress, 2000), but were 20% higher in $CO_2{}^e$ (Table 2).

Table 3 Total carbon (C) loss via soil respiration ($g C m^2$) modeled for each treatment using the combined Ts_5 and fertilizer response model for the 220-day measurement period. Means with the same letter are not statistically different at the $\alpha = 0.05$ level

CO_2 enhancement*		$g C m^2$
CO_2^e		1233
CO_2^a		1047
Fertilization		
NF	*a*	1229
F	*b*	1051
Combined*		
CO_2^e-NF		1320
CO_2^e-F		1146
CO_2^a-NF		1138
CO_2^a-F		956

*Not testable because of lack of replication.

Our results indicate that CO_2^e increased S_{ff}, but this response was not based on replicated plots (Table 3). However, the response is consistent with results from the near-by replicated FACE study (Allen *et al*., 2001; Andrews & Schlesinger, 2001) and agrees with the comprehensive review of CO_2^e, fine roots and response of soil microorganisms by Zak *et al*. (2000). Thus, these results provide reassurance that our soil respiration measurement system was detecting biologically meaningful responses. Soil respiration provides the total C loss to the atmosphere from the soil surface and is extremely useful in summarizing a variety of complex autotrophic and heterotrophic processes and relationships that can be very difficult or impractical to separate. As CO_2^e typically results in increased allocation of C to roots and stimulates root activity (Rogers *et al*., 1994), changes in S_{ff} are expected. The bulk of the response is as a result of increased root biomass (Pregitzer *et al*., 2000) and proliferation of fine roots (Matamala & Schlesinger, 2000), while evidence suggests that there is little change in specific root respiration in mid-rotation loblolly pine plantations because of CO_2^e (Matamala & Schlesinger, 2000). Microbial respiration is controlled by temperature and the quantity of available C, and will be directly impacted by the deposition of autotrophic detritus (Raisch & Nadelhoffer, 1989) as well as the rate that trees shunt photosynthate below-ground. At the nearby replicated FACE study, the rate of loblolly pine leaf litter decomposition has been unaffected by CO_2, but litter mass is significantly higher (Finzi *et al*., 2001) providing greater overall decomposition. Photosynthesis rates under elevated CO_2 are substantially higher in *P. taeda* and (Ellsworth, 2000; Maier *et al*., 2002) depending on nutrient availability, carbohydrates unable to be fixed into woody tissue may be lost via root exudation, providing substrate for microbial respiration. More work needs to be done to determine how trees allocate photosynthate in nutrient-poor environments. Studies for addressing forest fertilization and carbohydrate loss/use efficiency are ongoing at Ref and FACEp by using techniques that capture root exudates lost to the soil.

Over the measurement period, fertilized plot cumulative S_{ff} was 15% less than in control plots. Although the 220-day measurement period prevented a full annual cycle to be revealed, fertilizer-induced suppression of S_{ff} did not occur in the spring, peaked in August and began to diminish in early autumn. This trend is similar to that described by Maier & Kress (2000), studying an extremely well-drained site in a warmer climate, where *P. taeda* plots fertilized in the spring had significantly lower S_{ff} September through November, after which treatment differences were not evident throughout the rest of the winter.

There are examples of residual suppression of S_{ff} many years after fertilization (Martikainen *et al*., 1989; Aarnio & Martikainen, 1996); however, this was not the case on our site. This is further supported because annual fertilizer applications have continued at FACEp and at Ref. in years 2001 and 2002, and no residual differences in S_{ff} from fertilization have yet been observed in the spring prior to fertilization (Palmroth and McCarthy unpublished data). Martikainen *et al*. (1989) observed that low fertility pine sites in southern Finland exhibited reduced soil respiration 7–14 years after fertilization (urea or ammonium nitrate) while soil respiration at high productivity pine sites actually increased. The research site within the Duke Forest where FACEp and Ref are located is best described as a shallow rooting (< 30 cm), medium fertility site (Oren *et al*., 2001). Considering mean soil temperatures and decomposition rates – which are substantially greater – FACEp and Ref, where suppression of S_{ff} lasts for less than 1 year, seem to fall between the boundaries of soil nutrition studied by Martikainen *et al*. (1989).

The Ts_5*F model may not explain what happens if a fertilizer is applied mid- or late-season, though the timing of fertilizer application in this experiment is commensurate to what is practiced operationally by forest managers in the Piedmont region of North Carolina. It is not clear how S_{ff} will respond in a droughty year; responses will likely be postponed or longer in duration thereby altering the response we present (Fig. 3b). Deficiencies of other nutrients – for example, P and K – and subsequent effects of fertilization on S_{ff} are dependent on how these deficiencies affect the available C pool and impact microbial activity. When N amendments are added to peat soils, increases in S_{ff} have been reported on soils with adequate P, while P-limited soils respond to a

reduction in S_{ff} (Amador & Jones, 1993). Microbial response to P additions is variable and has been reported to have both positive (Van Cleve & Moore, 1978; Amador & Jones, 1993) and negative (Kelly & Henderson, 1978; Flanagan & Van Cleve, 1983) effects on soil respiration. Deficiencies of K have been associated with enhanced root respiration in the vegetable crop *Brassica oleracea* (Singh & Blanke, 2000). In our study we have attempted to alleviate any major nutrient deficiencies in order to allow N to enhance photosynthesis and biomass accumulation.

Our observed response of S_{ff} to urea was similar to results from studies on microbial respiration in an *ex situ* forest soil of *Pinus contorta* (Thirukkumaran & Parkinson, 2000) and *in situ Pinus banksiana* (Foster *et al*., 1980) stands where in both cases respiration was first stimulated and then suppressed following urea fertilization. The temporary stimulation in microbial respiration may have been caused by improved availability of labile C pools as a result of ephemeral increase soil pH (Foster *et al*., 1980, Thirukkumaran & Parkinson, 2000). However, as presented earlier, the stimulation is short-lived and is low in absolute impact relative to the long-term and strong suppression of S_{ff} with improved soil fertility. It is important to note that the urea molecule contains one atom of C (Table 1), which is released when the urea is mineralized. The amount of C released is very small and accounts for approximately 0.5% of the total C loss for the measurement period.

The suppression of S_{ff} with improved fertility is far from being general and is, in part, dependent on the stage of development of the investigated system (Johnsen *et al*., 2001). In studies on seedlings, fertilization often increases the amount of carbohydrates available for the production of roots, resulting in a greater root biomass relative to unfertilized seedlings and thus S_{ff} is not suppressed (Vose *et al*., 1995; Pangle & Seiler, 2002) or even enhanced (Griffin *et al*., 1997). Similar responses have been found in field-planted *P. taeda* seedlings, where foliage mass was increased 48% and root biomass 43% by fertilizer, yet S_{ff} was not significantly different (Pangle & Seiler, 2002). As trees mature, fertilization favors C allocation above-ground at the expense of fine roots and the ratio of fine root-to-above-ground biomass declines (Axelsson & Axelsson, 1986; Haynes & Gower, 1995; Albaugh *et al*., 1998). Two examples clearly illustrate such responses of older but still aggrading *P. taeda* stands to fertilization: an 11-year-old stand exhibited a 30–100% increase in below-ground biomass without an accompanying change in S_{ff} (Maier & Kress, 2000) and a 7-year-old stand had a 260% increase in root biomass (Retzlaff *et al*., 2001) while only incurring an 18% increase in S_{ff} (Lai *et al*., 2002). As long as leaf area index (LAI) is below maximum, the faster increase in LAI with fertilization will be accompanied with an absolute increase in fine roots, establishing a ratio between the two organs that is dependent on soil fertility, physical properties and plant hydraulics (Ewers *et al*., 2000; Hacke *et al*., 2000).

By contrast, the stands studied here were near the maximum LAI and the soil limited the rooting depth to the upper 30 cm (Oren *et al*., 1998). As a result, the primary effect of fertilization was to increase woody biomass production 15% relative to unfertilized stands (Oren *et al*., 2001), likely reducing C allocation below-ground, and thus S_{ff} was reduced to 85% that of native fertility soil in our study (Table 3). Similar to reports from other studies, CO_2^e in the Prototype plot increased S_{ff} 14%. Elevated atmospheric CO_2 is known to increase C assimilation by the foliage in *P. taeda* (Rogers & Ellsworth, 2002), but as woody biomass accumulation attributed to CO_2 enhancement was rather small in 2000 (Oren *et al*., 2001), much of this C was likely allocated below-ground. As under CO_2^a, nutrient addition under CO_2^e increased woody biomass increment while reducing C availability below-ground, accompanied with a decrease in S_{ff} to 87% relative to that with native fertility.

Moreover, the lack of full replication preempts strong conclusions on any fertilization–atmospheric CO_2 interactions. However, the CO_2 response trends were consistent with the literature and our fertilization treatments provided very consistent results on both the FACE and reference plots, plots differing greatly in photosynthetic C gain. Given the scarcity of data such as these, these results are important for guiding future research direction in assessing the impact of elevated CO_2 on C cycles given soil nutrient limitations.

Enhanced plant growth is expected to add more C to soils as the concentration of CO_2 in the atmosphere increases; however, much of it will be lost to respiration (Schlesinger & Andrews, 2000). Our findings, while not statistically testable, support this hypothesis. In conclusion, to the extent that fertilization is permitting an assessment of the effect on S_{ff} of native differences in site fertility, the results suggest that S_{ff} is lower at higher fertility sites, at least once stands approach maximum LAI. This pattern should be incorporated into models estimating C flux at scales that include large heterogeneity in soil fertility. Furthermore, the increase in S_{ff} under CO_2^e may be smaller in fertile sites, while the application of N fertilizer seems to mitigate the effect of elevated atmospheric CO_2 on S_{ff} at infertile sites. Thus, pending consideration of energy costs of producing, transporting and applying fertilizer, the application of fertilizer (primarily N) to forests can potentially augment C sequestration, via increased growth rates and decreased soil respiration and offset increases in S_{ff} anticipated with rising CO_2 concentrations in the atmosphere.

Acknowledgements

We appreciate the assistance of Renee Paddock, who maintained the ACES in the field. Comments and advice of Dr Chris A. Maier, Dr Stan Zarnoch and Dr Sari Palmroth are also appreciated. This study was supported by the Department of Energy through (1) the Office of Biological and Environmental Research supporting the Duke Forest FACE-FACTS I (DE-FG05-95ER62082) and the Terrestrial Carbon Processes Program, (2) National Institute for Global Environmental Change, Southeast Regional Center at the University of Alabama (DE-FC030-90ER61010) and by the US Forest Service through (1) Southern Global Climate Change Program and (2) the Southern Research Station. This work contributes to the Global Change and Terrestrial Ecosystems (GCTE) core project of the International Geosphere–Biosphere Programme (IGBP).

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