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# Long-term effects of free air $CO_2$ enrichment (FACE) on soil respiration

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**Abstract.** Emissions of $CO_2$ from soils make up one of the largest fluxes in the global C cycle, thus small changes in soil respiration may have large impacts on global C cycling. Anthropogenic additions of $CO_2$ to the atmosphere are expected to alter soil carbon cycling, an important component of the global carbon budget. As part of the Duke Forest Free-Air $CO_2$ Enrichment (FACE) experiment, we examined how forest growth at elevated (+200 ppmv) atmospheric $CO_2$ concentration affects soil $CO_2$ dynamics over 7 years of continuous enrichment. Soil respiration, soil $CO_2$ concentrations, and the isotopic signature of soil $CO_2$ were measured monthly throughout the 7 years of treatment. Estimated annual rates of soil $CO_2$ efflux have been significantly higher in the elevated plots in every year of the study, but over the last 5 years the magnitude of the $CO_2$ enrichment effect on soil $CO_2$ efflux has declined. Gas well samples indicate that over 7 years fumigation has led to sustained increases in soil $CO_2$ concentrations and depletion in the $\delta^{13}C$ of soil $CO_2$ at all but the shallowest soil depths.

## Introduction

Soil carbon efflux is one of the largest fluxes in the global carbon cycle ($\sim 75 \times 10^{15}$ g C/year), with close to 10% of the atmosphere's $CO_2$ passing through soils each year (Schlesinger 1977; Raich and Potter 1995; Schlesinger and Andrews 2000). Thus even small changes in this large flux have the potential to impact atmospheric $CO_2$ accumulation and the global carbon budget. Because soil $CO_2$ efflux also includes autotrophic root respiration, soil respiration exceeds global estimates of net primary production (NPP; $50–60 \times 10^{15}$ g C/year). Several recent analyses of the global carbon cycle suggest that terrestrial uptake and storage of C can be an important buffer of rising atmospheric $CO_2$ (Schimel 1995; Fan et al. 1998; Houghton et al. 1999; Rayner and Law 1999; Schimel et al. 2000). However, if soil respiration increases at the same rate as terrestrial C fixation under rising atmospheric $CO_2$, it is unlikely that increased C storage in soils or biomass will offset increasing

global emissions of $CO_2$. More critically, if soil respiration increases at a faster rate than carbon fixation, these increases in soil $CO_2$ emissions could exacerbate rising atmospheric $CO_2$ levels and provide a positive feedback to global warming (Raich and Schlesinger 1992; Raich and Tufekcioglu 2000). Thus, describing what controls variation in soil C efflux and understanding how these factors will change as a result of increasing $CO_2$ concentrations in the atmosphere are critical to refining our predictions about changes in C sequestration under scenarios of rising $CO_2$.

Soil respiration consists of autotrophic root respiration, as well as heterotrophic respiration associated with the decomposition of litter, roots and soil organic matter (SOM). Across biomes soil respiration is highly correlated with plant litter production (Raich and Nadelhoffer 1989) and with NPP (Raich and Schlesinger 1992), both of which may be stimulated by rising levels of atmospheric $CO_2$. Plant production of belowground biomass increases when plants are grown under elevated $CO_2$ (e.g. Matamala and Schlesinger 2000, King et al. 2001, Maberly et al. 2002), and that increase is often accompanied by increased $CO_2$ loss from the soil proportionate to greater root biomass (Luo 1996; Edwards and Norby 1998). Increased soil C inputs due to greater above- and belowground NPP under elevated $CO_2$ (e.g. Gunderson and Wullschleger 1994, Allen et al. 2000) will provide additional carbon supplies to decomposers (Zak et al. 2000), also leading to higher rates of soil respiration. During the first four years of fumigation in the Duke Forest free air carbon dioxide enrichment (FACE) experiment (1997–2000), NPP increased by 27% in the high $CO_2$ plots (DeLucia et al. 1999; Hamilton et al. 2002). During the first 2 years of treatment, soil respiration rates were also reported to be 27% higher in elevated $CO_2$ plots relative to ambient plots (Andrews and Schlesinger 2001). Maximum daily rates of soil respiration increased by 131% in elevated plots during the first two years of fumigation (Andrews and Schlesinger 2001). Andrews and Schlesinger (2001) attributed this increase in soil respiration to increased root and rhizosphere respiration under elevated $CO_2$. This hypothesis was supported by the significant increase in live fine root biomass (86%) as a result of $CO_2$ enrichment during the same time period (Matamala and Schlesinger 2000).

Soil respiration rates are largely dependent upon soil temperature and moisture, thus seasonal changes and climatic differences generate differences in respiration rates across time and between sites (Raich and Potter 1995). In addition to stimulating the production of new photosynthetic biomass and litter, rising $CO_2$ can have indirect effects on soil microclimate that may influence respiration rates. Although Ellsworth (1999) reported no significant treatment effects of elevated $CO_2$ on stomatal conductance at the Duke Forest FACE site, reduced stomatal conductance of plants growing under elevated $CO_2$ can enhance plant water use efficiency (Morison 1993; Drake et al. 1997) potentially resulting in conserved soil moisture (e.g., Field et al. 1995). Increased litter production can also lead to greater soil moisture content under elevated $CO_2$ due to its insulating effect, reducing the evaporation of soil water

(e.g., Schäfer et al. 2002). Schlesinger and Lichter (2001) showed that forest floor litter is indeed accumulating faster in the elevated $CO_2$ plots in the Duke forest experiment. The resulting higher soil moisture could reduce diffusivity, leading to higher soil $CO_2$ concentrations at the same level of $CO_2$ production. Conserved soil moisture has been suggested to be a mechanism for enhanced biomass production under elevated $CO_2$, and has been shown to influence the response of soil respiration to high atmospheric $CO_2$ concentrations (Davidson et al. 1998, Pendall et al. 2003, Suwa et al. 2004).

The majority of studies using either open-top chamber or FACE experiments suggest that soil respiration rates increase under elevated $CO_2$ (Janssens and Ceulemans 2000; Zak et al. 2000; Andrews and Schlesinger 2001; King et al. 2001, 2004); however, no previous study has exceeded 5 years in duration. If increases in photosynthetic carbon gain at elevated $CO_2$ are not matched by increases in nutrient supply and/or increases in plant nutrient-use efficiency, then the effect of $CO_2$ enrichment may decline over time (Comins and McMurtrie 1993; Diaz et al. 1993; Finzi et al. 2002). Modeling efforts suggest that an instantaneous experimental increase in atmospheric $CO_2$ concentrations may cause dramatic, but transient, changes in ecosystem processes (Comins and McMurtrie 1993; Luo 2001).

Here we extend the analysis of $CO_2$ fumigation effects on soil $CO_2$ efflux in the Duke Forest FACE experiment to include the first 7 years of the experiment (1997–2003). We examine: (I) Whether the stimulatory effect of $CO_2$ fumigation on soil C efflux has been maintained throughout 7 years of treatment; and (II) What mechanisms may account for temporal changes in the treatment effect on soil C efflux. We discuss the implications of these results in the context of predicting changes in forest C sequestration and cycling under elevated $CO_2$.

## Methods

### *Site description*

The site characteristics of the Duke Forest FACE Experiment have been extensively documented elsewhere (e.g., Matamala and Schlesinger 2000; Andrews and Schlesinger 2001; Finzi et al. 2001); we provide only a brief description here. The experiment consists of six 30-m diameter plots established in a 15-year-old (in 1996) loblolly pine (*Pinus taeda* L.) plantation in the Duke Forest, Orange County, North Carolina. Three treatment plots (referred to as "elevated") are fumigated with $CO_2$ to increase atmospheric concentrations by 200 ppmv above ambient concentrations (e.g., 565 ppmv in 1996); the three control plots are fumigated with ambient air only (referred to as "control" or "ambient"). For statistical analysis, plots are grouped into three blocks, each including one ambient and one fumigated plot. Fumigation of all plots began on August 27, 1996, and was continuous (24 h $d^{-1}$; 365 d $year^{-1}$)

except in extreme weather until 2003 when fumigation was reduced to only daylight hours. The $CO_2$ used for fumigation is derived from natural gas and is strongly depleted in $^{13}C$ ($\delta^{13}C = -43.1 \pm 0.6‰$ (mean ± SE)) relative to PeeDee belemnite (PDB). Adding this $CO_2$ to elevate atmospheric concentration by 200 ppmv changes the $^{13}C$ of atmospheric $CO_2$ in the FACE plots from $-8‰$ to $-20‰$. As a result of photosynthetic fractionation by loblolly pine, needles grown under FACE have $\delta^{13}C = -39.3 \pm 1.4‰$ (Ellsworth 1999), and fine roots (< 1 mm diameter) had $\delta^{13}C = -39.3 \pm 0.5‰$ (Matamala and Schlesinger 2000). Further details are available in (Hendrey et al. 1999).

*Maximum daily rates of soil respiration*

Soil respiration rates were measured at approximately monthly intervals using a field-portable infrared gas analyzer (IRGA) from August 1996 to December 2003. Twelve PVC couplings (10-cm diameter) were permanently installed in each of the six plots; each collar was inserted 3-cm into the mineral soil. All of the FACTS-1 plots are divided into four equal quadrants, each of which is further subdivided into two subquadrants designated for soil or vegetation sampling. Three soil respiration collars were placed at random within each of the four soil sampling subquadrants in each plot. The chambers were open to litterfall and rainfall except during monthly measurements. Litter that fell partially into the open chamber was cut where it met the chamber rim so that aerial litterfall rates were not artificially increased or reduced. Once a month, measurements were taken during a 1–2 min interval between 1200 and 1600 h (measurements during this period shown to be within 6% of the daily maximum rate 1400 h) (Andrews 1999). During each respiration measurement soil temperature was measured simultaneously using permanently installed Type K thermocouples associated with each soil collar at a depth of 3 cm. These thermocouples were not equipped with dataloggers and thus provided only instantaneous temperature measurements. We used statistical modeling approaches to look for treatment effects (see below). For comparison with previous work (Andrews and Schlesinger 2001), we also used paired *t*-tests to compare treatment average values for each date ($n = 1$ per treatment, 88 dates) as one measure of treatment effects. We also looked for significant treatment effects for each sampling date using paired t tests with plot averages ($n = 3$ per treatment).

*Soil temperature and soil moisture*

In addition to the concurrent soil temperature measurements taken with soil efflux measurements, continuous soil temperatures were measured with Siemens Type M 841/S1 thermistors (one per FACE plot) at a depth of 10–12 cm.

Continuous soil moisture content was measured with Campbell Scientific (Logan, Utah, USA) Model CS615 probes consisting of two 30 cm long metal rods, where the soil moisture content is integrated, thus encompassing >90% (or whatever the appropriate number here is) of the fine root zone. Temperatures and moisture contents were measured every 5 or 30 s, averaged over 30-minute intervals and automatically logged by Campbell 21X or 23X dataloggers. The resulting 30-minute temperature averages were then used to calculate daily mean temperatures for our statistical models (see below).

*Estimating annual soil $CO_2$ efflux using a statistical model*

An understanding of the underlying rationale of any modeling approach is important to provide credence in conclusions that are based on the modeling results. Our approach uses methodology which, by now, has been embraced by the statistical community but remains relatively unfamiliar to ecologists. For this reason, we take this opportunity to provide exposition which would not typically be included as when using, say, a paired *t*-test or analysis of variance (ANOVA).

Estimating annual soil $CO_2$ efflux from monthly afternoon measurements is problematic in several ways. First, estimating annual soil respiration by integrating under the values of maximum daily rates of soil efflux generates extremely high annual efflux rates for the FACTS-1 site (see King et al. 2004) that are 3–4× higher than measurements derived from 2 years of continuous soil $CO_2$ efflux measured in the FACTS-1 prototype and reference plots (Palmroth et al. 2005). Second, statistical analyses such as paired *t*-tests and repeated measures ANOVA are inadequate for analyzing this dataset since they: (1) treat plot averages as the unit of replication and thus ignore within plot variability, and (2) are poorly suited to detecting treatment effects in such a temporally variable process.

In order to generate estimates of annual soil respiration rates that more accurately reflect the variability in the entire data set, we fit a statistical model relating soil temperature and soil respiration from instantaneous measurements, and then used this statistical model along with the continuous temperature measurements to generate daily estimates of mean (rather than maximum) rates of soil respiration.

We begin with the familiar Q10 function as the mean of a stochastic model which relates respiration to temperature,

$$y = B_{25} Q_{10}^{\left(\frac{T-25}{10}\right)} + \varepsilon \tag{1}$$

where $y$ is soil respiration rate (g $m^{-2}$ $d^{-1}$), $T$ is temperature (°C), $B_{25}$ is the soil respiration rate at 25 °C, $Q_{10}$ is the (multiplicative) increase in respiration per 10 °C increase in temperature and ε is random error. We caution the reader

that we refer to the mean of Equation 1 as the Q10 *function* (no subscript) and to $Q_{10}$ as the $Q_{10}$ *parameter* (subscript). The parameters $B_{25}$ and $Q_{10}$ are typically considered as fixed parameters to be estimated using, say, a non-linear least-squares procedure. We extend this basic model to allow the parameters to vary with covariates. Thus, our extended model may be viewed hierarchically: Equation 1 is now viewed conditionally on the values of the parameters, then, at the second stage, we model these parameters as functions of fixed and/or random effects as explained below. This approach allows a rich and otherwise complex model to be created with relatively simple components at each stage. As a result, hierarchical models are becoming popular for analyzing complex environmental phenomenon from either a Bayesian (e.g., Clark 2005) or frequentist (e.g., Peek et al. 2002) perspective. Studies showing the temperature dependence of the $Q_{10}$ *parameter* (Winkler et al. 1996; Tjoelker et al. 2001) provide us with a biologically realistic basis for the second-stage modeling of the parameter as a function of temperature. Our model not only incorporates this dependence but, more generally, allows for both the base rate, $B_{25}$, and $Q_{10}$ parameters to vary with other covariates (e.g., N mineralization), thus helping to explain the variability in soil respiration that cannot be captured by the simpler, single-stage specification (Equation 1) alone.

The Q10 function has been used to describe the phenomenon of respiration across a range of biological scales, and its parameters retain some level of biological interpretation. In this sense, its use as a starting point – the first stage – in our modeling efforts results in a more phenomenological and less empirical model that helps to explain variability that might otherwise be attributed to more biologically meaningful mechanisms. Ideally, our model would attribute all variability to biologically meaningful parameters, leaving only the residual uncertainty of measurement error. But, because we currently have a poor understanding of such biological mechanisms, efforts to develop more mechanistic and explanatory models must be left to future research. Thus, we view our model as a reasonable first step towards the development of a more realistic model. The hierarchical approach can only become more useful as we strive to increase our understanding of complex biological phenomena in the future.

Much of the above discussion about hierarchical models as a framework for developing models to explain complex biological phenomenon would be irrelevant to the task of inferring the effect of $CO_2$ fertilization if it were not for the fact that the entire framework is statistical; inference is relatively easy once we arrive at a model. We chose to use non-linear mixed effects methodology (Davidian and Giltinan 1995; Vonesh and Chinchilli 1997; Pinheiro and Bates 2000), which may be viewed as part of the more general enterprise of hierarchical statistical modeling. We now give more modeling details.

The Duke forest FACE experiment is a nested design with repeated observations over time. Data used for the model fitting was collected on each date $d$ from collar $c$ located within plot $r$ randomly assigned to receive treatment $t$, where $c = 1,\ldots,12$ for each plot, $r = 1,2,3$ for each treatment, $t = 1$ (ambient) or $t = 2$ (elevated), and $d = 1,\ldots,89$ with $d = 1$ corresponding to 8/27/1996,

$d = 89$ corresponding to 12/19/2003, and interim collection dates occurred at approximately monthly intervals. On each collection date, soil respiration rate and temperature were measured at each collar/plot/treatment combination as described above; we denote these as $y_{trcd}$ and $T_{trcd}$, respectively.

Nitrogen mineralization rates for each plot, $N_{tr}$, were obtained from Finzi et al. (in review). We use $J_d$ to denote the time between date $d$ and 8/27/1996 in terms of days/365 ($J_1 = 0$).

Each of the parameters, $B_{25}$ and $Q_{10}$, may be modeled as functions of various fixed and/or random effects. The fixed effects structure arises from consideration of which covariates may be related to and, thus, explain variation in these parameters and, consequently, in soil respiration. The random effects structure follows from the experimental design; more specifically, the plot/collar nesting structure suggests variance components for plots and for collars within plots. We also consider a date random effect which may be justified as a proxy for the collective effect of unmeasured factors that influence soil respiration over time. The measurements over time also suggest consideration of temporal autocorrelation in our model. We argue that the resulting model gives a better characterization of the variability in soil respiration and improves our ability to infer about the effects of $CO_2$ treatment when compared to, for example, the more simplistic model underlying the paired $t$-test.

The modeling procedure began by specifying a ''full'' model with respect to both fixed and random effects as well as to the error variance–covariance structure, with subsequent comparison to and selection of more parsimonious models using likelihood ratio tests, AIC (Akaike Information Criterion) and BIC (Bayesian Information Criterion) as selection criteria. Modeling was performed in SAS (SAS Institute 2001). The model selection procedure was performed using maximum likelihood (ML) with final model parameter estimates obtained via restricted maximum likelihood (REML). See, for example, (Pinheiro and Bates 2000) for practical suggestions about the modeling procedure. The final model is discussed below.

The final model for the base respiration parameter in Equation 1 is given by

$$B_{25} = b_d + b_{rc} + \beta_{t0} + \beta_{t1} J_d + \beta_{t2} J_d^2, \tag{2}$$

where $b_d \sim N(0, \sigma^2_{b(d)})$ are independent date random effects and $b_{rc} \sim N(0, \sigma^2_{b(rc)})$ are independent collar-within-plot random effects. The betas are treatment specific parameters of a quadratic relationship with time (Table 1). The model for the $Q_{10}$ parameter is

$$Q_{10} = g_{rc} + \gamma_0 + \gamma_1 T_{trcd} + \gamma_2 N_{tr} + \gamma_3 T_{trcd} N_{tr}, \tag{3}$$

where $g_{rc} \sim N(0, \sigma^2_{g(rc)})$ are independent collar-within-plot random effects (intra-plot variability), and the gammas describe the relationship of temperature and plot-specific nitrogen mineralization rates (inter-plot variability) (Table 1). Note that plot random effects were removed according to the results

*Table 1.* Parameter estimates for the Q10 function model.

| Parameter | Description | Estimate | Standard error |
|---|---|---|---|
| *Fixed effects parameters* | | | |
| $\beta_{10}$ | $B_{25}$ on 8/27/1996 (ambient) | 1.4373 | 0.1513 |
| $\beta_{20}$ | $B_{25}$ on 8/27/1996 (treatment) | 1.6053 | 0.1569 |
| $\beta_{11}$ | $B_{25}$ linear time effect (ambient) | 0.0222 | 0.0673 |
| $\beta_{21}$ | $B_{25}$ linear time effect (treatment) | 0.0861 | 0.0685 |
| $\beta_{12}$ | $B_{25}$ quadratic time effect (ambient) | −0.0087 | 0.0091 |
| $\beta_{22}$ | $B_{25}$ quadratic time effect (ambient) | −0.0191 | 0.0092 |
| $\gamma_0$ | Q10 at zero temp and zero N min. rate | 3.3702 | 0.2035 |
| $\gamma_1$ | Q10 linear temp. effect | −0.0711 | 0.0189 |
| $\gamma_2$ | Q10 linear *N* min. rate effect | −0.0196 | 0.0044 |
| $\gamma_3$ | Q10 *N* min.* temp interaction effect | 0.0009 | 0.0004 |
| *Covariance parameters* | | | |
| $\sigma^2_{b(d)}$ | $B_{25}$date variance component | 0.1103 | 0.0181 |
| $\sigma^2_{b(rc)}$ | $B_{25}$collar within plot variance component | 0.0698 | 0.0143 |
| $\sigma^2_{g(rc)}$ | Q10 collar within plot variance component | 0.0262 | 0.0128 |
| $\rho$ | monthly auto corelation | 0.1907 | 0.0132 |
| $\sigma^2$ | Error variance component | 0.1746 | 0.0035 |

of (non-significant) likelihood ratio tests and by way of comparing model information criteria. Moreover, none of the final model parameters may be removed without a statistically significant reduction in the explained variability of soil respiration.

Residuals from the fitted respiration rates indicated that the error variance increases with increasing respiration rate. We define $\varepsilon_{trcd}$ as a normally distributed error effect and $\widehat{y}_{trcd}$ as the fitted respiration rate, with subscripts analogous to the previously established notation. We modeled the error variance as a power of the fitted value, the resulting variance being $\sigma^2 \widehat{y}^{1.7}_{trcd}$, where $\sigma > 0$ is a scale parameter. Although we did not restrict $\widehat{y}_{trcd}$ to be positive, there were no negative fitted values. Unlike the remaining parameters in the model, the exponent of the variance function was fixed at 1.7 after a grid search of values using AIC and BIC selection criteria. In addition to this non-homogenous variability, the residuals within each collar exhibited temporal autocorrelation which we modeled by the exponential correlation function $\rho^{|s|}$ (sometimes referred to as the continuous time AR(1) correlation function or as the power correlation function) where $s$ is time in days/30 and $\rho$ describes the degree of (positive) temporal correlation between errors at 30 days separation (i.e., $\rho$ is the monthly autocorrelation parameter).

### *Using the fitted model to estimate daily respiration rates*

We use the final fitted model, to estimate respiration rates for dates within the data collection period. The estimated respiration rates are based on the

estimates of the fixed effects parameters with random effects set to zero. These so-called ''population level'' estimates are most relevant since we wish to infer about respiration rates beyond the particular collars, plots and dates observed here. Thus, to estimate soil respiration rates we require the nitrogen mineralization rate, $N_{tr}$, daily soil temperature, $T_{trcd}$, and (scaled) days since 8/27/1996, $J_d$. We also use summaries of soil temperature to obtain temperature adjusted respiration rates. For example, to compare respiration rates between the ambient and elevated treatments, it may be desired that this comparison be done at a common temperature. Indeed, such ''adjusted'' comparison may be argued to be the most sensible way to compare elevated versus ambient treatments in the same sense that we would not normally assess treatment effects by comparing respiration on elevated plots during the summer to respiration of the ambient plots during the winter. The nitrogen mineralization rates used to fit the model are also used for estimating respiration rates, and we note that, similar to the case for soil temperature, we also obtain estimates using a common (i.e., mean) N mineralization rate. We integrate daily respiration rates over time to obtain yearly and study-period summaries.

We obtain approximate 95% confidence intervals based on the estimated variance-covariance matrix of the asymptotically normal REML estimators of fixed parameter effects and on the first order Taylor approximation to the (population level) model. The approximation gives a linear combination of fixed effect estimators, thus allowing use of standard results for computing variances and covariances of linear combinations of random variables and, hence, for constructing approximate normal-based intervals (Casella and Berger 2002).

### *Soil $CO_2$ concentrations*

The concentration of soil atmosphere $CO_2$ was measured using infrared gas analysis of samples drawn from four gas wells each at 15-, 30-, and 70-cm depths per plot and two wells each at 100- and 200-cm depths per plot. Each gas well consisted of a PVC pipe (5-cm diameter × 20-cm length (12 cm for the 15 cm wells)) situated vertically in the soil. Gas wells were placed at random locations within each soil sampling quadrant. Pipes were placed in a 10-cm diameter augered hole so that pipe bottoms rested at the depth of interest. Soil was replaced around each pipe in reverse order of removal. The top of each pipe was closed with a two-holed rubber stopper which was connected directly to the soil surface with two 0.6-cm diameter Kynar® plastic tubes. Gas samples were drawn directly from each well through a magnesium perchlorate ($Mg(ClO)_4$) or calcium sulfate ($CaSO_4$) water trap and into a field portable IRGA (EGM-1; PPSystems, Inc., Haverhill, Massachussets). Soil temperature was measured at each depth at the time of gas analysis using permanently installed Type K thermocouples. We used a General Linear Model (SYSTAT 11.0) to ascertain statistically significant treatment effects (unit of replication

set as plot average values for each sampling date, with date, treatment × date, and plot as other factors in the analysis).

### *$\delta^{13}C$ of soil $CO_2$*

Gas samples were collected for stable carbon isotope analysis from 2 soil gas wells and a single respiration chamber (see description below) within each ring every 1–2 months. Samples were collected in 75-$cm^3$ Whitey® stainless steel gas cylinders that were sealed with Nupro® bellows valves equipped with Kel-F® stem tips. The cylinders were pre-evacuated in the laboratory to $10^{-5}$ Pa. Samples from the gas wells were pulled through a portable stainless steel vacuum manifold that was evacuated with two equivalent volumes of sample gas using a hand vacuum pump. Samples from respiration chambers were collected for $\delta^{13}C$ of $CO_2$ determination in one of two ways. (1) Prior to March 1998, each 10 cm respiration chamber was sealed with a reflective Plexiglas lid sealed against an O-ring with Apezion® grease. The lid contained a sampling port and a 2.5×2.5-cm fan to mix the air within the chamber. The chambers remained closed for 1–3 h to allow $CO_2$ to accumulate; the sample was then taken directly into the pre-evacuated sampling cylinder. (2) Beginning in April 1998, a null-balance flux chamber system (details in Andrews and Schlesinger 2001) was used in order to reduce atmospheric $CO_2$ contamination and alterations to the $CO_2$ flux gradient inside the chamber. We used Repeated Measures ANOVA (SYSTAT 11.0) to examine statistically significant treatment effects (unit of replication set as plot average values for each year, with $CO_2$ treatment and plot as factors in the analysis).

## Results

### *Maximum daily rates of soil respiration*

Midday soil respiration rates were typically higher in elevated plots, with the greatest magnitude of difference occurring during the growing season of each year (Figure 1). When all observations are considered, midday soil respiration rates were 23.9 ± 2.7% higher in elevated plots (based on the mean ± SE for the percent difference between average ambient ($n$ = 3) and average elevated ($n$ = 3) measured soil efflux for all 88 observation dates). A $t$-test comparing treatment averaged ($n$ = 1 per treatment) soil respiration rates (paired by date) indicated that soil respiration rates were significantly higher in the elevated rings ($t$ = 8.502, df = 88, $p < 0.001$). Paired $t$-tests for plot average respiration rates for each of the 88 individual dates also indicated that elevated plots had significantly higher rates of soil $CO_2$ efflux on seven dates (comparison-wise $p$ value $< 0.05$) (Figure 1) while control plots were not significantly higher than elevated plots on any individual date. This

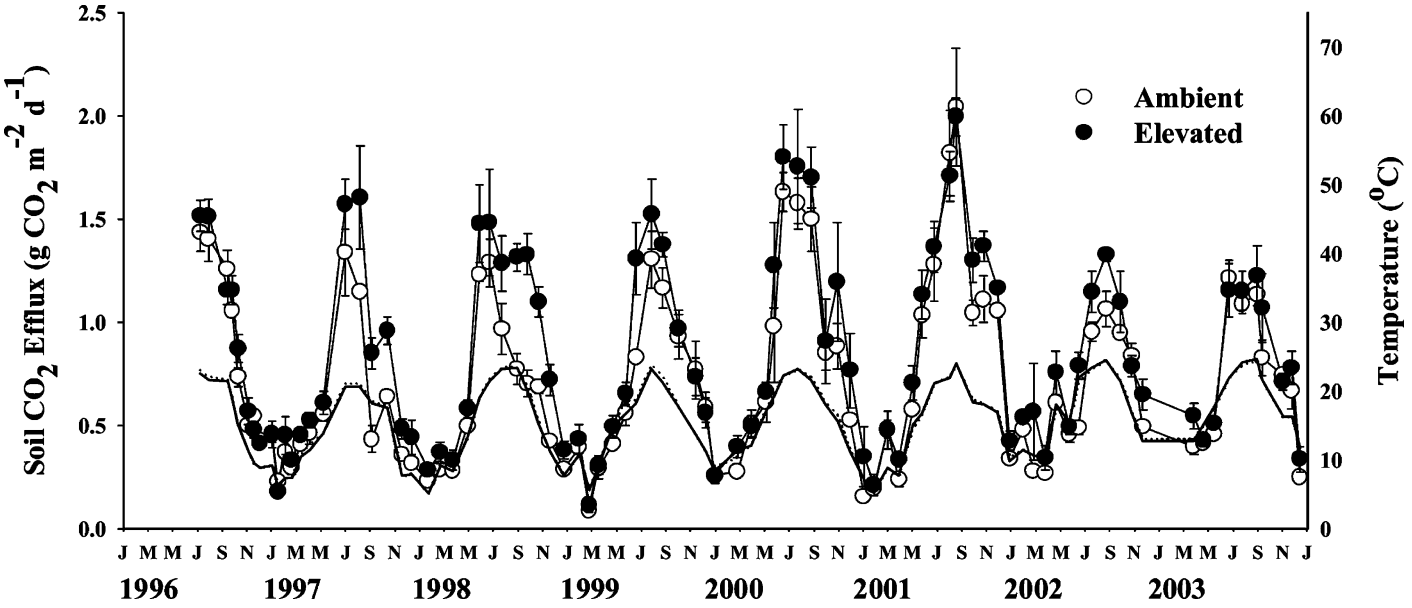


*Figure 1.* Monthly measurements of maximum daily rates of soil respiration from one month prior to initiating the fumigation in July 1996 to December 2003. Rates are shown as the average ± 1 standard error values for plots within each treatment (with plot average values as the unit of replication, $n = 3$ per treatment). The average soil temperature (measured simultaneously with efflux measurements in each soil respiration collar and averaged by plot and then by treatment) are shown as solid (elevated) and dotted (ambient) lines.

treatment response was most marked in year 2 (1998) during which the average daily maximum rate of $CO_2$ efflux was $39.9 \pm 7.3\%$ higher under elevated $CO_2$. In contrast, there was no difference in soil respiration rates between elevated and control plots before the start of the experiment (paired $t$ test, $p = 0.4$ as reported in Andrews and Schlesinger 2001). Note that these statistics are provided only for comparison with the previous study (Andrews and Schlesinger 2001), and do not take into account the autocorrelation between repeated measures, or the large amounts of intra and inter plot variability. Both are considered in our statistical model.

*Fitted respiration model*

Parameter estimates for the final model are given in Table 1. According to the model, differences in soil respiration between treatments depend entirely on the treatment-specific quadratic model for the $B_{25}$ parameter (Figure 2a). Base respiration rate $B_{25}$ on 8/27/1996 ($J_1 = 0$) may be expected to be the same between treatments. Results are not entirely inconsistent with this expectation since the (approximate) 95% confidence intervals for the treatment-specific intercept terms do contain each other's estimate. However, a likelihood ratio test indicates that treatment-specific intercepts are highly significant ($p < 0.0001$). We attribute this result as much to the somewhat restrictive "global" nature of the polynomial model for $B_{25}$ than to a real difference in base respiration at the beginning of fumigation, yet we must acknowledge that insufficient pre-treatment data make it impossible to rule out preexisting differences between the ambient and elevated plots.

Results indicate that the $Q_{10}$ parameter depends on soil temperature, N mineralization rate and their interaction (Table 1 and Figure 2b). The $Q_{10}$ parameter decreases with temperature over the range of N mineralization rates observed here (12 to 43 kg N $ha^{-1}$ $y^{-1}$ from A. Finzi, *in review*). The rate of change of $Q_{10}$ with temperature ranges from $-0.88$ at the minimum observed N mineralization rate to $-0.30$ at the maximum N mineralization rate. At the average observed N mineralization rate (30.97 kg N $ha^{-1}$ $y^{-1}$), the rate of change of $Q_{10}$ with temperature is $-0.65$. Thus, the magnitude of the temperature dependence of the $Q_{10}$ parameter decreases with an increasing N mineralization rate. These values are consistent with the temperature dependence of the $Q_{10}$ parameter reported by (Winkler 1996; Tjoelker et al. 2001). The value of the $Q_{10}$ parameter ranges from 2.95 at the lowest observed soil temperature (3 °C) to 1.52 at the highest observed soil temperature (26.9 °C) (both estimates at the low observed N mineralization rate). Thus, soil respiration ($y$) increases with temperature as in a typical Q10 function, but the increase is diminishing with increasing temperature. Loosely speaking, the multiplicative increase in respiration per 10 °C increase in temperature decreases with increasing temperature. Note that the direction of the N mineralization dependence of the $Q_{10}$ parameter changes

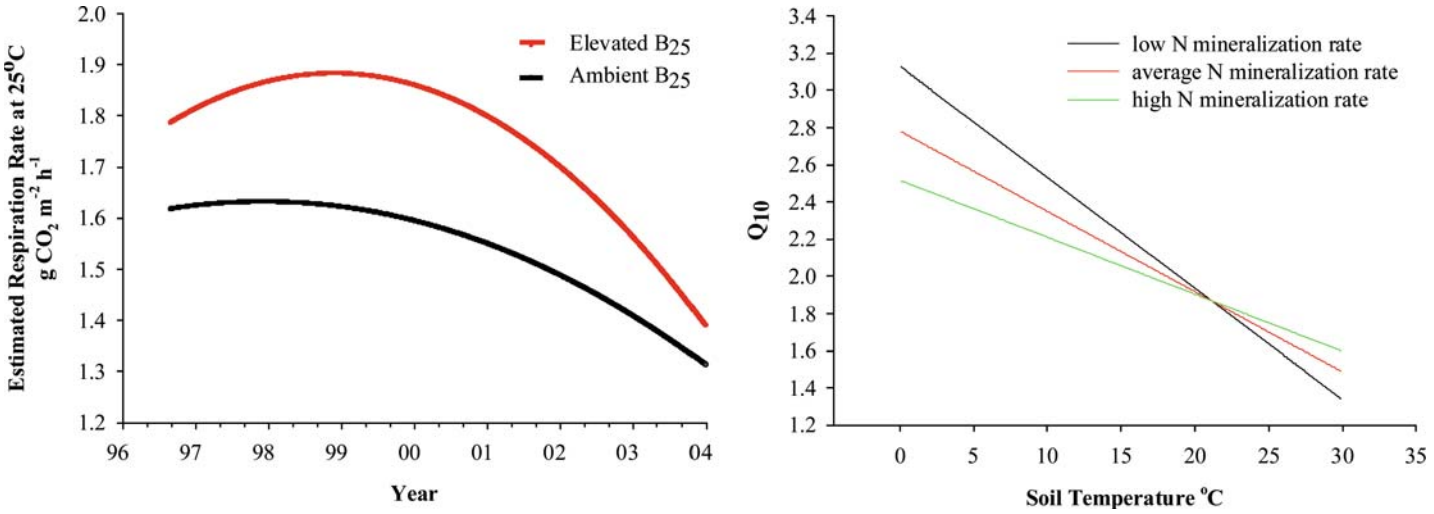


*Figure 2*. (a) Demonstrates the model predictions of $B_{25}$ for ambient and elevated plots; (b) demonstrates the interaction between soil temperature (°C) and N mineralization rate in predicting Q10.

at 21.8 °C: $Q_{10}$ decreases with an increasing N mineralization rate at fixed temperatures below 21.8 and increases with an increasing N mineralization rate above 21.8.

*Estimating annual soil respiration*

Model estimates of mean daily soil respiration require soil temperature and N mineralization rates as covariates. We use daily average plot soil temperatures, available from 5/1/97 to 12/31/03, to obtain estimates of daily average soil respiration that are used to obtain integrated total or average values on a yearly and study-period basis. We used the average plot N mineralization rate (30.97 kg N $ha^{-1}$ $y^{-1}$) for all daily estimates. Using a common temperature (for each day) and common N mineralization rate effectively adjusts for these effects between treatments and facilitates comparison of treatment effects on soil respiration rates over time. The 95% confidence bands for the mean respiration rates in elevated plots do not overlap with ambient plot estimates until 12/24/02 and thereafter.

Annual respiration rates were obtained by integrating (i.e., summing) the daily estimates (based on daily average soil temperature) and, hence, are also adjusted for differential temperature and N mineralization rate between treatments. The 95% confidence intervals for ambient and elevated contain each others estimate only for 2003 (Table 2). However, the question of differences between treatments is more appropriately answered by inspecting directly the estimates and confidence intervals for the difference between ambient and elevated plots, which do not contain zero for any year (Figure 3). As an ''overall summary'' of the treatment effect on soil respiration we calculated the integrated difference for the six-year period 1998–2003: plots under elevated $CO_2$ respired an additional $0.25 \pm 0.07$ kg C $m^{-2}$ $y^{-1}$ relative to the ambient plots. Data from 1997 are not included in this calculation, since the daily soil temperature covariate was first measured on 5/1/97.

*Table 2.* 95% confidence intervals for the model estimated annual soil C efflux from FACE plots (in kg C $m^{-2}$ $y^{-1}$, $n = 3$) are shown for each year of the experiment.

| Year | Ambient $CO_2$ | Elevated $CO_2$ | % increase |
|---|---|---|---|
| 1997 | $1.23 \pm 0.14$ | $1.42 \pm 0.14$ | 15.15 |
| 1998 | $1.67 \pm 0.16$ | $1.96 \pm 0.16$ | 17.35 |
| 1999 | $1.65 \pm 0.16$ | $1.95 \pm 0.16$ | 18.56 |
| 2000 | $1.59 \pm 0.15$ | $1.89 \pm 0.16$ | 18.57 |
| 2001 | $1.53 \pm 0.13$ | $1.80 \pm 0.14$ | 17.24 |
| 2002 | $1.47 \pm 0.13$ | $1.69 \pm 0.14$ | 14.45 |
| 2003 | $1.39 \pm 0.19$ | $1.52 \pm 0.21$ | 9.57 |

The proportional increase in average annual C efflux is also reported. *Note that daily temperature data were available beginning May 1997, thus the 1997 estimate is for a partial year.*

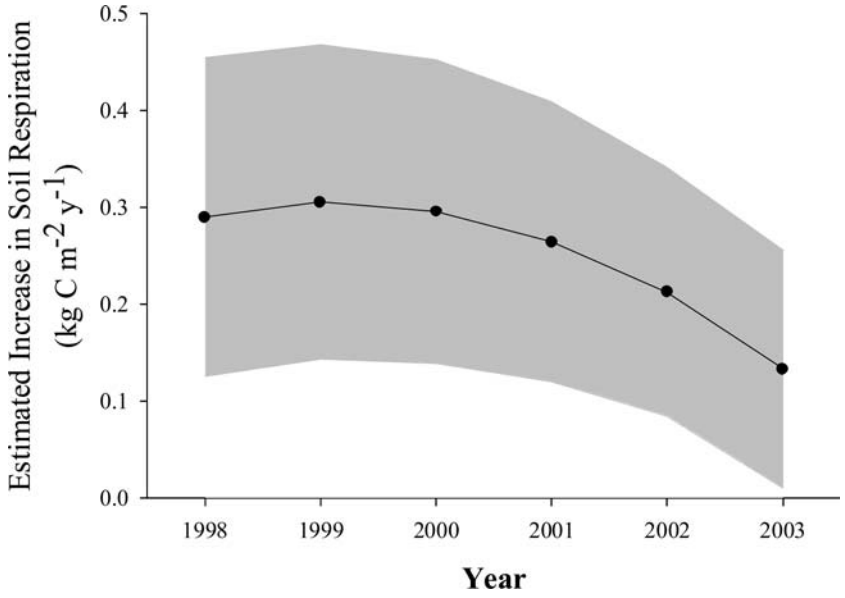


*Figure 3*. Model estimates of the average annual increase in soil respiration (in kg C $m^{-2}$ $year^{-1}$) due to $CO_2$ fumigation are shown as ●. The shaded area represents the 95% confidence interval around these estimates.

### *Soil $CO_2$ concentrations*

In all plots both soil $CO_2$ concentrations and the amplitude of seasonal variation in soil $CO_2$ concentrations increased with soil depth. Greater soil $CO_2$ efflux in the elevated plots corresponds to higher $CO_2$ concentrations in soil pore space. Soil $pCO_2$ concentrations were not significantly different between the elevated and ambient plots prior to fumigation (reported in Andrews and Schlesinger 2001), but tended to be higher at all but the shallowest (15 cm) measured depths within the first two full years of fumigation (Figure 4). Despite these trends, treatment, or treatment by date effects are statistically significant only at 100 cm ($t_{trt}\times$date = 1.968, $p$ = 0.05) and 200 cm ($t_{CO_2}$ = −3.085, $p$ = 0.002; $t_{CO_2}\times$date = 3.128, $p$ = 0.002). A repeated measures ANOVA of annual average soil $CO_2$ concentrations at each depth showed no statistically significant treatment effects at any depth, this likely reflects that seasonal variation in $CO_2$ concentrations far exceeds variation due to the fumigation. Soil $CO_2$ concentrations have continued to rise in the fumigated plots below 70 cm, but these increases are not statistically significant (Table 3). Although there is significant seasonal variation in soil $CO_2$ concentrations, the fumigation effect is aseasonal (Figure 5).

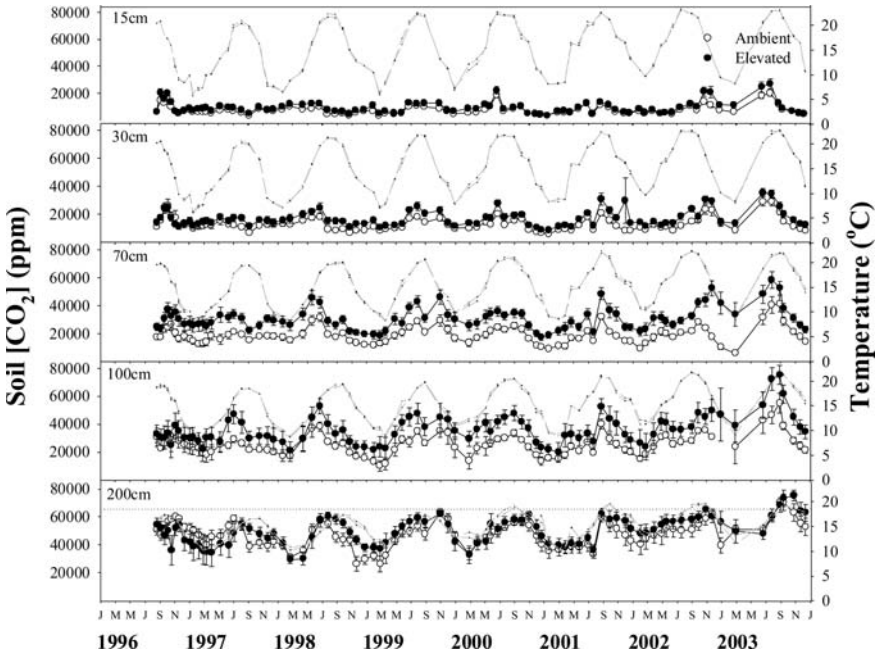


*Figure 4.* $CO_2$ concentrations throughout the soil profile. Closed (elevated) and open (ambient) circles represent the average ± one standard error (with plot average values as the unit of replication, $n = 3$ per treatment). The reference line shown for the 200 cm graph represents the upper detection limit for our PP System. Concentration differences between elevated and ambient plots are likely underestimated due to instrument limitations, as evidenced by the higher concentrations (and treatment effects) observed in 2003 after the PP System was retrofitted to increase its high detection limit.

*Table 3*. Average annual soil $CO_2$ concentrations at each soil depth. The values shown are the average of plot ($n = 3$) estimates for each year ± one standard error.

| Year | $CO_2$ concentrations (ppm) | | % Increase |
|---|---|---|---|
| | Ambient | Elevated | |
| *15 cm* | | | |
| 1996 | 9968 ± 1665 | 11582 ± 1690 | 16 |
| 1997 | 6640 ± 1092 | 8200 ± 1678 | 24 |
| 1998 | 6850 ± 650 | 8820 ± 2130 | 29 |
| 1999 | 6989 ± 756 | 8757 ± 1895 | 25 |
| 2000 | 8054 ± 763 | 9228 ± 1211 | 15 |
| 2001 | 7113 ± 447 | 7675 ± 1046 | 8 |
| 2002 | 7684 ± 810 | 10101 ± 1061 | 31 |
| 2003 | 10239 ± 1375 | 12539 ± 1061 | 22 |
| *30 cm* | | | |
| 1996 | 17234 ± 4048 | 17211 ± 3568 | 0 |
| 1997 | 12051 ± 2763 | 15023 ± 3528 | 25 |
| 1998 | 11561 ± 1814 | 16669 ± 4176 | 44 |
| 1999 | 12596 ± 2313 | 16483 ± 2810 | 31 |
| 2000 | 12365 ± 2496 | 16377 ± 2689 | 32 |
| 2001 | 11372 ± 1575 | 17187 ± 4715 | 51 |
| 2002 | 13748 ± 3203 | 18094 ± 3059 | 32 |
| 2003 | 16691 ± 3884 | 21527 ± 4130 | 29 |
| *70 cm* | | | |
| 1996 | 20184 ± 3449 | 29346 ± 6037 | 45 |
| 1997 | 16625 ± 3486 | 27703 ± 5826 | 67 |
| 1998 | 19095 ± 2583 | 28832 ± 4998 | 51 |
| 1999 | 20144 ± 4153 | 29977 ± 5931 | 49 |
| 2000 | 18667 ± 3276 | 28342 ± 4760 | 52 |
| 2001 | 13748 ± 792 | 27875 ± 5412 | 66 |
| 2002 | 18826 ± 2442 | 31638 ± 5567 | 68 |
| 2003 | 27377 ± 8244 | 37858 ± 5112 | 38 |
| *100 cm* | | | |
| 1996 | 28321 ± 4476 | 32381 ± 10589 | 14 |
| 1997 | 22321 ± 3850 | 31448 ± 6948 | 41 |
| 1998 | 24197 ± 2732 | 31303 ± 9243 | 29 |
| 1999 | 24290 ± 3990 | 34569 ± 9138 | 42 |
| 2000 | 24222 ± 2675 | 35477 ± 6468 | 46 |
| 2001 | 23150 ± 2103 | 31849 ± 8757 | 38 |
| 2002 | 27298 ± 518 | 37019 ± 9782 | 36 |
| 2003 | 35675 ± 6524 | 51277 ± 8705 | 44 |

## *$\delta^{13}C$ of soil $CO_2$*

Within the first two years of fumigation, the $\delta^{13}C$ of soil $CO_2$ at all depths in the elevated plots was depleted below $-28‰$ (signature of new photosynthate in the ambient plots), indicating the respiration of newly fixed C from the isotopically depleted fumigation gas (Figure 6). Throughout the study, the $\delta^{13}C$ of soil $CO_2$ at all soil depths in the fumigated plots has been significantly

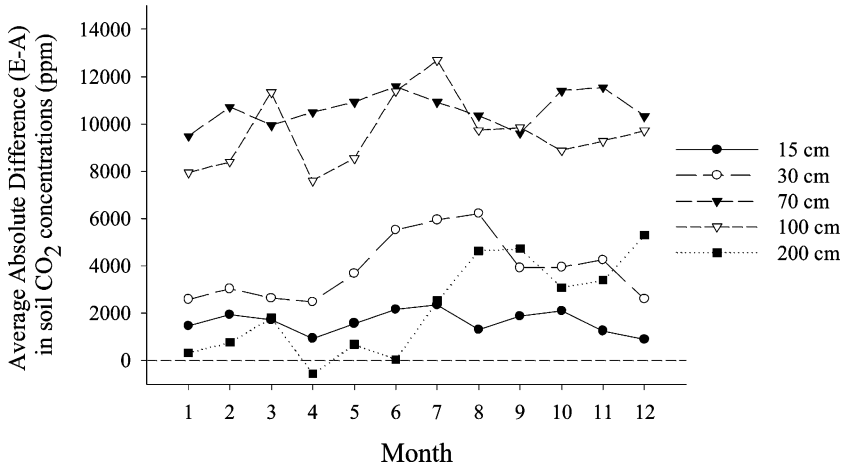


*Figure 5.* Treatment effects on average monthly soil $CO_2$ concentrations throughout the soil profile are shown as the average difference between monthly mean $CO_2$ concentrations between blocked pairs of elevated and ambient plots. For the sake of clarity, error bars are not included in this graph, but standard errors for these estimates do overlap 0 for some months of the year at each depth except 70 cm.

depleted relative to the ambient plots (repeated measures ANOVA, $F_{CO_2} > 100$, $p < 0.001$ for all depths), and this difference has increased since the first year of fumigation ($F_{Year} > 10$, $p < 0.001$ for all depths). The $\delta^{13}C$ of soil $CO_2$ appears to be continuing to decline in the deepest (200 cm) wells, while the isotopic signature in shallower gas wells (15, 30, and 70 cm) has remained relatively stable since 1999, suggesting a new level of steady-state exchange with atmospheric $\delta^{13}C$ of $CO_2 = -20‰$ in shallow soils within the fumigated plots (Table 4). There is little seasonal variation in the isotopic signature of $CO_2$ at any soil depth, while the $\delta^{13}C$ of respired $CO_2$ does vary interannually with the most depleted values seen during the late growing season in the elevated plots (Figure 6). More in-depth discussion of the $^{13}C$ isotope data can be found in Taneva et al. (in press).

## Discussion

Loblolly pine forest grown under FACE continues to have higher soil $CO_2$ efflux and soil $CO_2$ concentrations after 7 years of continuous fumigation, but the magnitude of this stimulatory effect has declined since 1999 (the third full year of treatment). The sustained treatment effect on soil respiration agrees with sustained increases in NPP (Finzi et al., in review; Moore et al. in review), litter production (Finzi et al. 2002, and A. Finzi, unpublished data), and fine root biomass (Matamala and Schlesinger 2000 and R.B. Jackson, unpublished data) in fumigated plots. However, the declining magnitude of the treatment

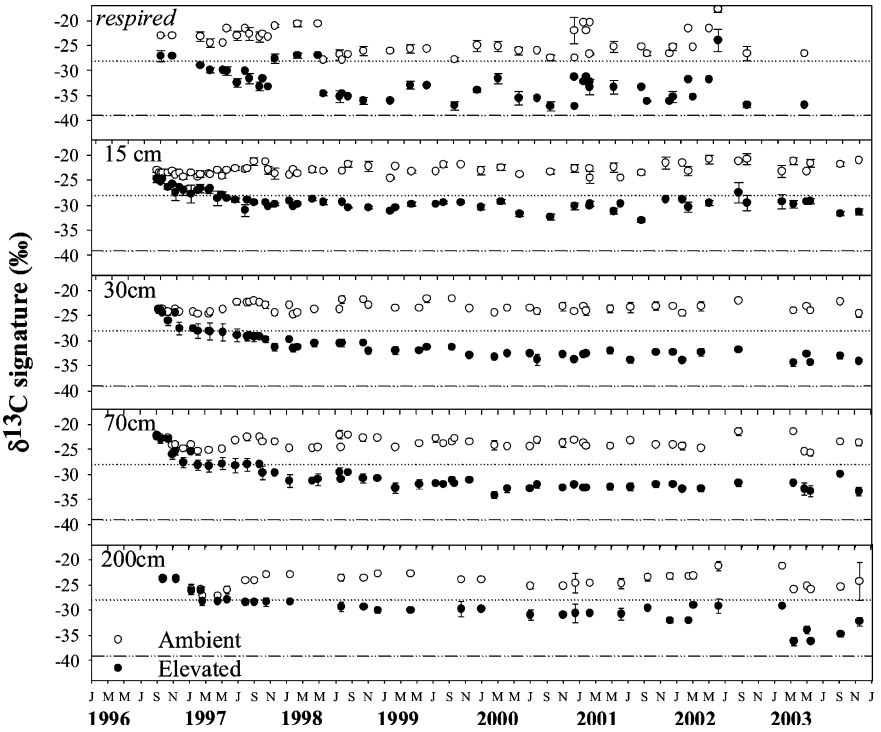


*Figure 6*. The $\delta^{13}C$ signature of soil $CO_2$ throughout the soil profile. Closed (elevated) and open (ambient) circles represent the average ± one standard error (with plot average values as the unit of replication, $n = 3$ per treatment). The dotted line at $-28‰$ indicates the isotopic signature for new photosynthate in the ambient plots, while the dashed line at $-39‰$ indicates the signature for new photosynthate in the fumigated plots. The atmospheric $\delta^{13}C$ is $\sim -8‰$ in ambient plots and $\sim -20‰$ in the elevated plots.

*Table 4*. Average annual $\delta^{13}C$ of $CO_2$ at at each measured soil depth.

| Year | Ambient | | | | | Elevated | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Respired | 15 cm | 30 cm | 70 cm | 200 cm | Respired | 15 cm | 30 cm | 70 cm | 200 cm |
| 1996 | −23.08 | −23.63 | −23.99 | −23.67 | −23.71 | −27.17 | −25.85 | −25.51 | −24.88 | −23.88 |
| 1997 | −22.80 | −23.20 | −23.40 | −24.14 | −25.05 | −30.58 | −28.77 | −29.18 | −28.36 | −27.76 |
| 1998 | −25.38 | −22.85 | −23.35 | −23.56 | −23.04 | −33.85 | −29.67 | −31.20 | −30.66 | −29.83 |
| 1999 | −26.18 | −23.18 | −22.92 | −23.71 | −23.96 | −34.65 | −30.07 | −32.10 | −31.90 | −29.78 |
| 2000 | −25.63 | −23.13 | −23.86 | −23.88 | −24.51 | −34.31 | −30.92 | −33.14 | −32.91 | −30.72 |
| 2001 | −25.68 | −23.06 | −23.90 | −24.18 | −23.71 | −34.43 | −31.73 | −32.60 | −32.31 | −31.24 |
| 2002 | −26.09 | −22.02 | −23.30 | −23.51 | −23.22 | −35.92 | −30.01 | −32.44 | −32.49 | −29.00 |
| 2003 | −24.64 | −22.19 | −23.52 | −24.44 | −25.03 | −32.96 | −30.18 | −33.59 | −32.59 | −34.08 |

The average values are calculated as the average of plot means ($n = 3$ per treatment).

effect on soil respiration since 1999 contrasts with the six years (1997–2002) of sustained increases in annual net primary production (NPP) between the fumigated and ambient plots (Finzi et al. in review). Each year of the experiment, NPP has been 18–40% higher in the elevated plots than in the control plots (DeLucia et al. 1999, Finzi et al. in press). This difference in response may suggest that a higher proportion of production may be stored in the elevated plots. This storage is most likely to be as plant tissue and/or forest floor biomass (Schlesinger 2000; Schlesinger and Lichter 2001; Luo et al. 2003).

The respiration model explained significantly more variability in soil respiration when N mineralization and its interaction with temperature was included (likelihood ratio $p$-value $< 0.0001$). This indicates that preexisting characteristics (e.g., soil fertility) that vary from site to site within a seemingly homogeneous pine forest may affect forest response to rising $CO_2$. Because of the interaction effect $\gamma_3$, the effect of N mineralization rate on soil respiration (via the $Q_{10}$ parameter) depends on soil temperature (and vice-versa) (Table 1, Figure 2b). Our results showed that the $Q_{10}$ parameter decreases with an increasing N mineralization rate for a given temperature below 21.8 °C and increases with an increasing N mineralization rate above 21.8 °C. Thus, increasing N mineralization rates above this temperature would result in increased soil respiration and vice-versa.

This result may help to explain contrasting results from two previous FACE studies. Additions of N to FACE soil cores incubated at 22 °C led to increased forest floor respiration and mineral soil microbial biomass (Allen and Schlesinger 2004). However, experimental results in the FACE prototype plot (Oren et al. 2001) showed that adding nitrogen fertilizer led to reduced soil respiration response to elevated $CO_2$ (Butnor et al. 2003) similar to findings in other fertilization studies (Bowden et al. 2004; Compton et al. 2004). Our model results suggest these differences in responses between the lab and field experiments could be explained in part by differences in conditions between the two studies. The soil core incubations were all done at warm temperatures and measured only heterotrophic respiration while the field sampling was done across all seasons and included both autotrophic and heterotrophic respiration (Allen and Schlesinger 2004, Oren et al. 2001). A new experimental fertilization of the FACE plots will allow future tests of whether soil respiration depends on N availability. We note that this resulting impetus to explore an heretofore unposed question illustrates a virtue of our modeling approach that is not likely shared by a more simplistic approach.

As our model demonstrates, nitrogen mineralization is likely to be a useful additional factor in predicting soil respiration rates. Nitrogen often limits primary production and is likely to be a good predictor of root respiration and litter production, two major contributors to soil respiration. Since N is believed to constrain the ability of forests to respond to elevated $CO_2$ it is not surprising that incorporating the large differences in N mineralization between FACTS-1 plots into our model (Finzi et al. in review) helped elucidate treatment effects. In the simplest sense, N mineralization can provide a useful measure of soil

fertility. What is more interesting is that our modeling results suggest that N supply may either exacerbate or dampen the soil respiration response to elevated $CO_2$ depending on climate. This is an interesting outcome of our model, and suggests that the interacting effects of global warming and increasing atmospheric $CO_2$ may generate surprising effects and deserve further study (as argued by Norby and Luo 2004 and Pendall et al. 2004).

Indirect effects of $CO_2$ fumigation could be responsible for the declining magnitude of the treatment effect. During the first 2 years of the FACE experiment, there were no differences in temperature or soil volumetric moisture content between the treatments; thus, the soil respiration response could be directly linked to the $CO_2$ manipulation. Soil temperatures have not been affected by the $CO_2$ treatment, but, since 1998, soil moisture has been consistently higher in the elevated $CO_2$ plots (Schafer et al. 2002). In later years of the experiment higher volumetric moisture content in the fumigated plots may be as important in stimulating $CO_2$ efflux as is the plant biomass response to elevated $CO_2$. Soil moisture is often not considered a major factor in controlling rates of soil respiration except during periods of moisture extremes (Schlesinger 1977), yet a number of recent papers suggest that soil moisture may be as important as temperature in controlling respiration rates (Hanson et al. 2003, Palmroth et al. 2005). Incorporating available field soil moisture measurements from the FACTS-1 plots into alternative statistical models did not improve model fit; thus we are unable to support the hypothesis that soil moisture differences directly control respiration rates. However, the soil moisture data available to us would have required extensive gap filling to provide information comparable to the continuous temperature monitoring data, thus we were unable to adequately represent this term in our model. Future efforts to incorporate soil moisture data will likely improve model fits (see Palmroth et al. 2005 for a more in-depth study of the relationship between soil moisture and soil respiration in FACTS-1 soils).

The magnitude of the stimulation of $CO_2$ efflux by elevated $CO_2$ seen in the initial years of FACTS-1 remains significantly different from 0, but is declining. However, concentrations of $CO_2$ in the soil increased in all plots during 2001–2003, and the magnitude of the treatment effect has remained at all depths, with a more than 7000 ppm increase in annual average soil $CO_2$ concentrations at 100 cm depth in all seven full years of fumigation (Table 3). The isotopic signature of soil $CO_2$ has grown increasingly depleted in $\delta^{13}C$ at all depths, also indicating that an increasingly large fraction of soil respiration is from root respiration or the decomposition of C assimilated during the fumigation period (Davidson and Trumbore 1995) . This pattern may be exacerbated by the indirect $CO_2$ effect on soil moisture as higher soil moisture in the fumigated plots may reduce soil diffusivity (Suwa et al. 2004). The magnitude of the fumigation effect on soil $CO_2$ concentration has remained relatively constant while its effect on $CO_2$ efflux has declined, this suggests that both production of soil $CO_2$ and soil diffusivity may have declined. If the treatment effects on belowground respiration had remained at the levels seen in the initial years of

the experiment, the stimulation of soil $CO_2$ efflux and/or soil $CO_2$ concentrations would have to increase. Taneva et al. (in press) found that about 70% of soil respiration in the treatment plots at FACTS-1 originates from soil carbon pools with fairly rapid turnover time (~1 month), while the remainder originates in slow turnover C pools. In contrast, the contribution of soil C pools with decadal turnover times can be up to 50% of total soil $CO_2$ concentrations with depth, suggesting that soil respiration has possibly reached a new steady state, but not enough time has passed for deep soil $CO_2$ concentrations to reach this new equilibrium (Taneva et al. in press).

During the first 2 years of FACE, higher concentrations of soil $CO_2$ were linked to increased weathering rates under elevated $CO_2$ treatments (Andrews and Schlesinger 2001). It has been suggested that rising $CO_2$ may reduce soil solution pH and speed the loss of soil nutrients from the rooting zone (Andrews and Schlesinger 2001; Williams et al. 2003; Oh and Richter 2004). Measurement of soil $CO_2$ concentrations from the subsequent 5 years of treatment suggests that while the effect of elevated $CO_2$ on soil respiration has declined through time, the potential for increased weathering in fumigated soils persists.

## Conclusions

Over the course of 7 years, $CO_2$ fumigation has led to significantly higher rates of soil respiration. However, the magnitude of the treatment effect appears to be declining through time (Figure 3). Our modeling analyses of soil respiration trends suggest that N mineralization rates (probably as a proxy for soil fertility) help explain between plot differences in soil respiration responses to elevated $CO_2$, and further supports the hypothesis of progressive nutrient limitation limiting ecosystem responses to rising $CO_2$ (Oren et al. 2001; Luo et al. 2004; Finzi et al. in review). While the effect of experimentally elevated atmospheric $CO_2$ concentrations on soil respiration rates appears to be dampening, soil $CO_2$ concentrations and the isotopic signature of soil $CO_2$ from gas wells indicate persistently higher rates of respiration at depth in the fumigated plots. These trends may suggest that the continued stimulation of aboveground biomass under elevated $CO_2$ requires exploitation of deep soil resources.

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