

# 11 The Duke Forest FACE Experiment: CO<sub>2</sub> Enrichment of a Loblolly Pine Forest

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## 11.1 Introduction

The free-air CO<sub>2</sub> enrichment (FACE) experiment in the Duke Forest tests how a forest will respond to future, higher levels of CO<sub>2</sub> in Earth's atmosphere. The experiment is focused on changes in tree growth, water use, and the sequestration of carbon in wood and soils. CO<sub>2</sub> fumigation began in a prototype plot in 1994 and in three additional experimental plots in 1996 in a 16-year-old stand of loblolly pine (*Pinus taeda*). Loblolly pine is a widespread early successional tree in the southeastern United States (Oosting 1942), where it is also a major commercial species dominating  $>10 \times 10^6$  ha (Burns and Honkala 1990; Harlow et al. 1991). Growth of pine plantations on abandoned agricultural land is thought to yield a substantial carbon sink in the southeast (Delcourt and Harris 1980; Caspersen et al. 2000). This reforestation may account for part of the large putative carbon sink in North America (Tans et al. 1990; Fan et al. 1998). Some investigators believe that an enhanced C sink due to CO<sub>2</sub> fertilization of forests might ultimately slow the rise of CO<sub>2</sub> in Earth's atmosphere (Idso et al. 1991), but that hypothesis remains untested in nature (but see Schimel et al. 2000).

Prior work in open-top chambers and glass-house experiments had shown large increases in the biomass of loblolly pine in response to growth at elevated CO<sub>2</sub> concentrations (e[CO<sub>2</sub>]) with ample soil nutrients (Thomas et al. 1994; Tissue et al. 1996, 1997). An initial motivation for the FACE experiment in Duke Forest was to examine this growth response in natural conditions, where trees experience competition, drought, nutrient limitations, pests, and pathogens. The Duke FACE experiment seeks to answer a critical question for

foresters and policy makers: Can we expect more growth and carbon sequestration in these forests in the future? FACE technology allows us to answer that question today, by applying  $e[\text{CO}_2]$  to experimental plots with unaltered, natural levels of other growth parameters (see Chapter 1).

## 11.2 Site Description

Located in Orange County, North Carolina, USA ( $35^{\circ}97'$  N,  $79^{\circ}09'$  W), the experimental site was clear-cut in 1982, to remove a 40- to 60-year-old mixed pine forest. The site was drum-chopped and burned prior to tree planting in 1983. The 32-ha experimental forest of loblolly pine is derived from 3-year-old, half-sibling seedlings planted in  $2.4 \times 2.4$  m spacing. In 1994, when  $\text{CO}_2$  enrichment commenced in the prototype plot, the pine trees had grown to 12 m height, reaching 14 m height in 1996 at the start of the formal experiment. In 1998, the leaf area index of pine was  $3.7 \text{ m}^2 \text{ m}^{-2}$  (Schäfer et al. 2002) and the stand was just beginning to enter a stage of competitive self-thinning (Peet and Christensen 1980; Christensen and Peet 1981). Pine composed 98% of the canopy. Deciduous tree species, which dominate the understory, include sweetgum (*Liquidambar styraciflua*), red maple (*Acer rubrum*), winged elm (*Ulmus alata*), red bud (*Cercis canadensis*), and dogwood (*Cornus florida*) that have sprouted from stumps or dispersed from the surrounding vegetation. A few of these individuals, most often sweetgum and tulip polar (*Liriodendron tulipifera*), reach the canopy.

The soils are clay loams, classified as low-fertility Ustic Hapludalfs of the Enon series, which are typical of many upland areas in the southeastern United States. Throughout this region, these soils supported many decades of cotton and tobacco agriculture before abandonment to silviculture in the early 1900s (J. Edeburn, personal communication). The soils are relatively homogeneous, derive from mafic bedrock, and exhibit acidic (pH 5.75), well developed profiles of mixed clay mineralogy. Boreholes show up to 1 m of topsoil underlain by 5 m of saprolite, above a highly fractured granodiorite or diorite bedrock. Variation in elevation ranges up to 15 m across the site, but topographic relief is generally less than  $1^{\circ}$ . The static water table lies at 6 m depth, but the site drains poorly and surface soils often become saturated in the spring. The mean annual temperature is  $15.5^{\circ}\text{C}$  and the mean annual precipitation is 1140 mm.

The FACE experiment consists of seven circular plots, 30 m in diameter (Fig. 11.1). Four of the seven plots are fumigated with  $\text{CO}_2$  to maintain an atmospheric concentration 200 ppm above current  $\text{CO}_2$  levels ( $c[\text{CO}_2]$ ), to simulate the Earth's atmosphere in the year 2050 (Hendrey et al. 1999; Chapter 2). The three remaining, control plots are identical to the  $e[\text{CO}_2]$  plots, except that they are fumigated with ambient air (i.e.,  $c[\text{CO}_2]$ ). The formal



**Fig. 11.1** The Duke Forest free-air CO<sub>2</sub> enrichment (FACE) project, shown looking south, with the six experimental plots in the foreground and the prototype plot in the distance. Photo by Will Owens

experiment was begun on 27 August 1996; and the  $e[\text{CO}_2]$  was maintained continuously when the air temperature was  $>5^\circ\text{C}$  during the first 6 years, except for brief periods during Hurricane Fran in 1996 and Hurricane Floyd in 1999. Beginning in 2003, the fumigation has been maintained only during daylight hours and when the ambient air temperature is  $>5^\circ\text{C}$ , similar to the fumigation protocol at the FACE prototype plot.

The CO<sub>2</sub> used for fumigation is derived from natural gas and consequently is strongly depleted in <sup>13</sup>C relative to <sup>12</sup>C (the  $d^{13}\text{C}$  value is  $-43.0 \pm 0.6$ ). Raising the atmospheric CO<sub>2</sub> concentration by 200 ppm with this source of CO<sub>2</sub> reduces the  $d^{13}\text{C}$  ratio of the atmosphere in the fumigated plots from  $-8\text{‰}$  to  $-20\text{‰}$ . One would expect that new photosynthate produced from this atmos-

phere would carry a  $\delta^{13}\text{C}$  ratio of approximately  $-40\text{‰}$  (Farquhar et al. 1982). In fact, we have measured values of  $-39\text{‰}$  to  $-42\text{‰}$  in new pine needles and fine roots grown in FACE conditions (Ellsworth 1999; Finzi et al. 2001; Matala et al. 2003). We track the incorporation of this isotopic signature into soil organic matter to estimate the turnover of soil organic fractions (Schlesinger and Lichter 2001; Lichter et al. 2005).

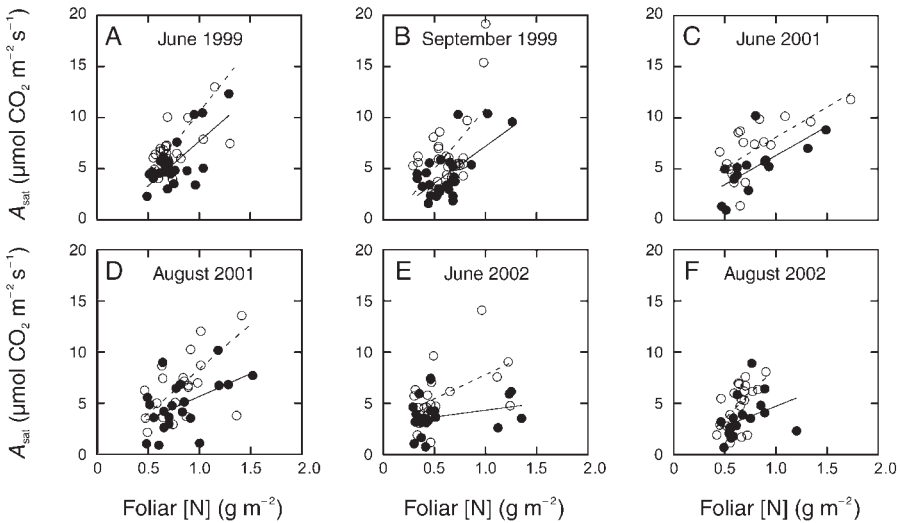
Prior to the experiment, samples of the upper mineral soil at 0–12 cm depth were collected from 119 locations spanning the 32-ha research site. These samples were analyzed for C, N, P, Ca, Mg, and K; and the results were tested for spatial autocorrelation. This analysis indicated that the spatial dependence of each soil parameter was less than the shortest distance between any two experimental plots (i.e., 85 m), implying that the plots were independent replicate samples of this pine forest. At the start of the experiment, the plots were paired, based on subjective criteria of similarity, and one member of each pair was assigned to control or fumigated status. As the experiment has unfolded, we have realized the importance of subtle variations in forest and soil conditions across the site, requiring the use of pretreatment conditions as a covariate in analysis of variance, with  $n=3$  in each category, analyzing the prototype data separately. Some values cited here differ from those published earlier as a result of this reanalysis of data.

## 11.3 Results

### 11.3.1 Resource Acquisition

Photosynthetic rates of canopy leaves (i.e., pine needles) are directly related to leaf nitrogen content (Fig. 11.2). Growth in  $e[\text{CO}_2]$  slightly reduces the concentration of N in canopy leaves (Oren et al. 2001; Finzi et al. 2004), but throughout the experiment, the canopy loblolly pine have shown a 40–50 % increase in photosynthesis (Ellsworth 1999; Myers et al. 1999; Schäfer et al. 2003; Springer et al. 2005; Ellsworth and Klimas 2005). The increase in photosynthesis is not accompanied by a reduction in the amount of water used by canopy pine trees (Ellsworth et al. 1995; Ellsworth 1999; Schäfer et al. 2002).

Understory species show a variable response to growth at  $e[\text{CO}_2]$  (DeLucia and Thomas 2000), but no understory species contributes a significant amount to forest production or carbon storage. There is some evidence for a reduction in water use by sweetgum (*Liquidambar styraciflua*; Schäfer et al. 2002; Herrick et al. 2004).



**Fig. 11.2** Photosynthetic rate ( $A$ ) of loblolly pine and other canopy species in full sunlight, shown as a function of foliage N content ( $\text{g N m}^{-2}$  leaf area) in the Duke Forest CO<sub>2</sub> enrichment (FACE) experiment. *Open circles* are from  $c[\text{CO}_2]$  plots, *closed circles* are from  $e[\text{CO}_2]$  (Springer et al. 2005)

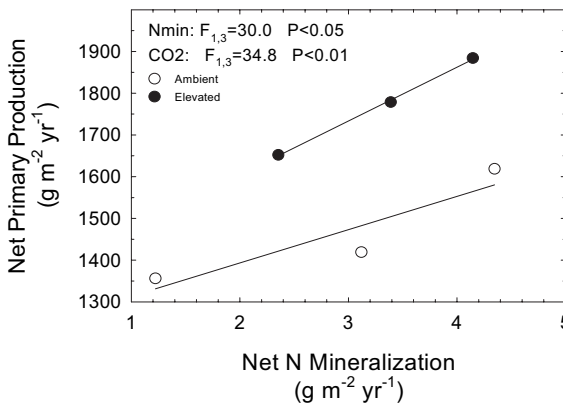
### 11.3.2 Resource Transformation

We made repeated measures of tree diameter growth and litterfall and used these to estimate the effect of growth at  $e[\text{CO}_2]$  on net primary production (NPP) in the loblolly pine plantation (DeLucia et al. 1999; Hamilton et al. 2002; Moore et al. 2005). Elevated CO<sub>2</sub> increased the annual basal area increment (BAI) of individual canopy pine trees by 13–27% during the first 8 years of the experiment (Moore et al. 2005). BAI in ambient and fumigated plots was positively correlated with growing season temperature and the amount of rainfall. Exposure to  $e[\text{CO}_2]$  increased the rate but not the duration of growth in most years. The stimulation was largely confined to emergent and dominant individuals and was not evident in sub-canopy trees. However, an understory vine, poison ivy (*Toxicodendron radicans*), showed a 77% increase in growth over the same interval (Mohan et al. 2005). Exposure to  $e[\text{CO}_2]$  caused an increase in the biomass increment of  $108 \text{ g C m}^{-2} \text{ year}^{-1}$  (27%) in the pine trees, contributing nearly half of the  $185 \text{ g C m}^{-2} \text{ year}^{-1}$  (35%) increase in net carbon storage in this forest.

Each year, a substantial portion of the forest NPP returned to the soil as litterfall, which was 21% greater in fumigated plots during 1998–2000 (Finzi et al. 2002). Early studies indicated that the leaf area index is similar in control and fumigated plots (DeLucia et al. 2002; Schäfer et al. 2002), but more recent

work suggests an increase in LAI in  $e[\text{CO}_2]$  plots (McCarthy et al., personal communication). Although pine cones and seeds account for only a small fraction of all litterfall (<1%; Finzi et al. 2002), these tissues showed a surprising, disproportionate increase (200%) in response to tree growth at  $e[\text{CO}_2]$  (LaDeau 2005). Production of fine roots also accounted for only a small fraction (5–7%) of NPP, but fine root growth was consistently greater, as much as 86%, during the summer in plots maintained at  $e[\text{CO}_2]$  (Matamala and Schlesinger 2000; Pritchard et al. 2001). There were no long-term changes in the winter-time biomass of fine roots, so the higher rate of fine root growth was accompanied by greater root death, resulting in a greater absolute turnover, but no change in percentage turnover, of root tissues as a result of growth at  $e[\text{CO}_2]$  (Matamala et al. 2003). The mean residence time for carbon in fine roots was 4.2 years – much longer than traditionally thought but consistent with recent measurements of the radiocarbon content of roots in various eastern forests (Gaudinski et al. 2001).

Across the six experimental plots, NPP was directly related to soil nitrogen mineralization, but the rate of production at a given level of nitrogen availability was substantially higher in  $e[\text{CO}_2]$  plots (Fig. 11.3). Greater growth of perennial tissue (i.e., wood) and greater turnover of foliage, roots, and reproductive tissues is necessarily associated with a greater nutrient demand by the forest (Table 11.1). For instance, as a consequence of the significant increase in foliage biomass, there were significant increases in canopy N and P content at  $e[\text{CO}_2]$  (Finzi et al. 2002, 2004). Some of the nutrient demand can be met through increases in nutrient-use efficiency, such as by the resorption of nutrients from senescent foliage before it drops. The remainder of the nutrient demand must be met by greater uptake from the soil. As each cohort of pine needles age over their 19-month lifetime (Zhang and Allen 1996), the content of N and P declines, suggesting that the demand set by rapid forest growth under  $e[\text{CO}_2]$  is not matched by nutrient uptake



**Fig. 11.3** The relationship between NPP and annual rate of net nitrogen mineralization during the second year of the experiment. *Open circles* are from  $c[\text{CO}_2]$  plots, *closed circles* are from  $e[\text{CO}_2]$  (from Finzi et al. 2002)

**Table 11.1** Nutrient budget of control (ambient) and fumigated (elevated CO<sub>2</sub>) plots of the Duke Forest FACE experiment, average of 1998–2000 (from Finzi et al. 2002)

Component	Control plot (kg ha <sup>-1</sup> year <sup>-1</sup> )	Fumigated plot (kg ha <sup>-1</sup> year <sup>-1</sup> )	Change (%)
Plant requirement	51.9	61.5	18.5
Retranslocation	28.6	31.5	10.2
Uptake from soil	23.3	30.0	28.9
Nitrogen-use efficiency (NPP/requirement)	292	311	6.6

from the soil (Finzi et al. 2004). We also measured slightly greater retranslocation of nitrogen and phosphorus from foliage before abscission, conferring greater nutrient-use efficiency in production (i.e., NPP per unit nitrogen uptake from the soil).

We have independent evidence from several experiments that microbial activity in the soil is limited by the supply of organic carbon, such that one might expect an increase in microbial activity with the greater inputs of dead plant materials in plots maintained at e[CO<sub>2</sub>] (Gallardo and Schlesinger 1994; Allen and Schlesinger 2004). Nevertheless, in comparisons of control and fumigated plots at the FACE experiment, there is no evidence of substantial changes in soil microbial activity that allow an easy identification of the source of additional nutrients for plant uptake. There are no significant changes in soil microbial biomass, gross nitrogen mineralization, and absolute or specific nitrogen immobilization by soil microbes, at this and other FACE sites (Finzi and Schlesinger 2003; Zak et al. 2003). Decomposition of foliage is similar between control and fumigated plots (Finzi et al. 2001). Rates of asymbiotic nitrogen fixation in the soil are low and not significantly different among plots (Hofmockel and Schlesinger 2005); and we have not been able to establish nitrogenase activity in *Cercis canadensis*, despite observations of nitrogen fixation by other members of this genus in Europe (Bryan et al. 1996). Thus, increased nitrogen demand must be satisfied by greater root growth and exploration of the soil.

Evidence for a greater activity of roots is seen in higher root respiration (George et al. 2003), higher accumulations of CO<sub>2</sub> in the soil pore space, and greater CO<sub>2</sub> efflux from the soil surface (Andrews and Schlesinger 2001; Bernhardt et al. 2005). Root activity is estimated to account for 55 % of the respiration at the soil surface (Andrews et al. 1999). Greater CO<sub>2</sub> in the soil pore space is associated with greater faster rates of chemical weathering of soil minerals via the formation of carbonic acid. We have measured higher concentrations of weathering products in the soil solution collected at 200 cm depth, with proportional increases of cations and bicarbonate much greater than for Cl,

which increases with depth as a result of the plant uptake of water (Table 11.2). Some of the greater flux of cations may derive from the pool held on the cation exchange capacity in these soils, but the greater flux of silicon indicates direct chemical weathering of soil minerals. The greater flux of bicarbonate in seepage waters results in a small, incremental net sink for carbon ( $5 \text{ g m}^{-2} \text{ year}^{-1}$ ) in the forest maintained at  $e[\text{CO}_2]$ . This flux is consistent with the increasing content of alkalinity in North American riverwaters and a small global sink for carbon via this pathway during the past century (Raymond and Cole 2003).

In control plots, carbon in undecomposed plant debris on the forest floor accumulated at a rate of  $78 \text{ g m}^{-2} \text{ year}^{-1}$ , similar to forest floor accumulations in other aggrading loblolly pine plantations in this region (Richter et al. 1999; Johnson et al. 2003). Observation of a significant increase in the mass of the forest floor in  $e[\text{CO}_2]$  plots is consistent with our observations that there have been few significant changes in soil microbial activity as a result of plant growth at  $e[\text{CO}_2]$ . During the first 6 years of the Duke Forest FACE experiment, organic C accumulated in the forest floor of the  $e[\text{CO}_2]$  plots at a rate which was  $52 \pm 16 \text{ g C m}^{-2} \text{ year}^{-1}$  faster than in  $c[\text{CO}_2]$  plots (Lichter et al. 2005).

In contrast to the forest floor, we detected no statistically significant incremental storage of carbon in the soil organic matter of the  $e[\text{CO}_2]$  plots relative to  $c[\text{CO}_2]$  plots (Lichter et al. 2005). Carbon sequestration in the soil (0–30 cm depth) was  $89 \pm 44 \text{ g C m}^{-2} \text{ year}^{-1}$ , averaged across  $e[\text{CO}_2]$  and  $c[\text{CO}_2]$  plots during the first 6 years of the experiment. The accumulation of soil organic carbon in the Duke forest plots is greater than average rates reported for other loblolly pine forests in the Southeast, including values of  $28 \text{ g C m}^{-2} \text{ year}^{-1}$  in Virginia (Schiffman and Johnson 1989),  $4 \text{ g C m}^{-2} \text{ year}^{-1}$  in South Carolina (Richter et al. 1999), and virtually no change in the content of soil organic matter in a forest in Tennessee (Johnson et al. 2003). We found substantial changes in the  $\delta^{13}\text{C}$  of labile fractions of soil organic matter in the fumigated

**Table 11.2** Chemistry of the soil solution at 15 cm and 200 cm depth in control and fumigated plots of the Duke forest FACE experiment (from Andrews and Schlesinger 2001)

Chemical	Depth (cm)	$c[\text{CO}_2]$	$e[\text{CO}_2]$
Cl	15	0.04	0.05
	200	0.10	0.17
Cations	15	0.36	0.41
	200	0.76	2.82
$\text{HCO}_3^-$ – alkalinity	15	0.13	0.13
	200	0.64	1.68
Dissolved silicon	15	0.07	0.08
	200	0.28	0.35

plots, associated with inputs of new photosynthate under FACE conditions. Similar to Hoosbeck et al. (2004; see Chapter 10), we postulate a priming effect of labile carbon, increasing the decomposition of existing organic matter which is replaced by the new inputs, so there is little increment to storage.

### 11.3.3 Nitrogen Limitation

With the direct relation between forest growth and nitrogen availability (Fig. 11.3) and only indirect evidence that soil nitrogen turnover may have increased, we ask the question: is the CO<sub>2</sub> response that we observe in Duke forest sustainable over many years? Alternatively, one might expect that the higher growth rates at e[CO<sub>2</sub>] would lead to an increasing nutrient deficiency in this forest. Increased rates of fine root growth, such as at the Duke FACE site, are often associated with tree growth in nutrient-deficient soils (Waring and Schlesinger 1985). Norby et al. (2002; see Chapter 13) report a sustained increase in NPP, largely seen in roots, in the deciduous forest FACE experiment at Oak Ridge; and Oren et al. (2001) show that low soil fertility reduced the rate of carbon sequestration in woody biomass in the FACE prototype plot at Duke after 3 years. To date, our evidence on this point is equivocal. Mea-

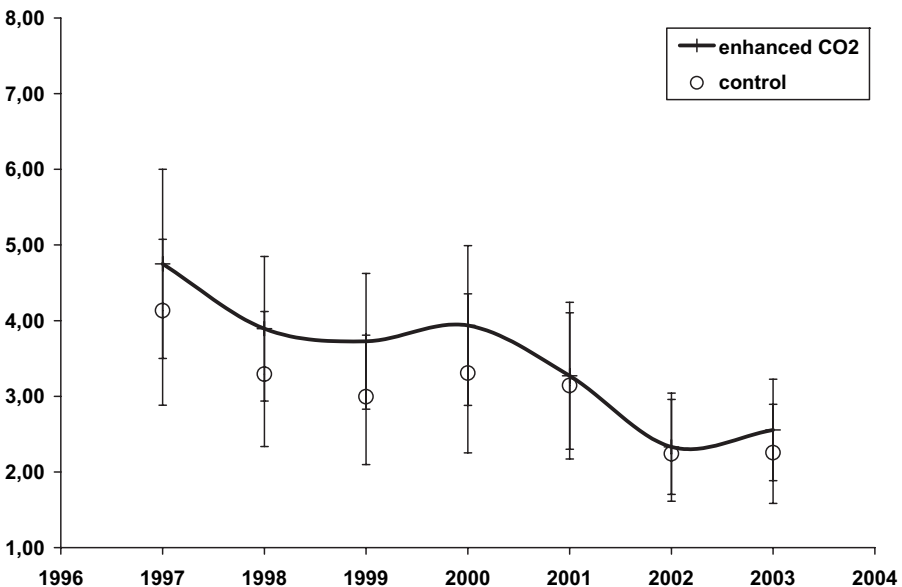


Fig. 11.4 Mean annual wood ring increment in three cores taken from each of five trees in each of the three plots at c[CO<sub>2</sub>] and e[CO<sub>2</sub>]. *Open circles* are from c[CO<sub>2</sub>] plots, *closed circles* are from e[CO<sub>2</sub>]. Unpublished data of J.S. Pippen and A. Ballentyne (Duke University)

measurements of tree rings in 32 trees from the Duke forest experiment show the expected age-related downtrend in wood increment among trees in the control plots (Fig. 11.4). The wood increment of trees in the fumigated plots was 24 % greater than controls in 1999, declining to an insignificant difference in 2004 (Ballentyne, personal communication). However, among a larger sample of trees instrumented with dendrometer bands, estimates of basal area increment among the canopy pines, which comprise the majority of plant biomass, show no loss of stimulation with time (Moore et al. 2005). Calculated estimates of total stand production and increment (Fig. 11.5) show a decline with time, although a strong percent CO<sub>2</sub> stimulation of growth still persists today. A large stimulation in 2002 is associated with low rates of production, and

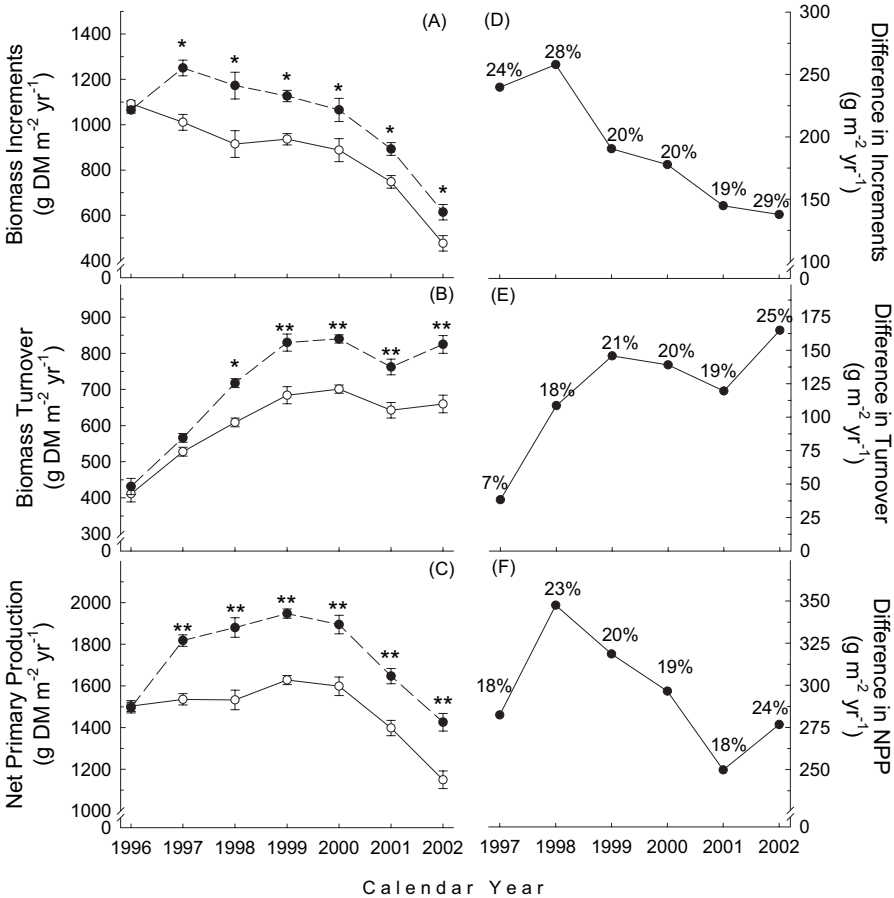


Fig. 11.5 Biomass increment (largely wood), biomass turnover (largely litterfall) and net primary production in the Duke Forest free air CO<sub>2</sub> enrichment (FACE) experiment; and trends in the difference between high CO<sub>2</sub> plots and ambient in each parameter. *Open circles* are from c[CO<sub>2</sub>] plots, *closed circles* are from e[CO<sub>2</sub>] (from Finzi et al. 2005)

presumably low nitrogen demand, during an exceptionally dry year. Various theoretical models suggest that progressive nitrogen limitation should reduce the CO<sub>2</sub> stimulation of plant production (Comins and McMurtrie 1993; Luo et al. 2003). The experimental addition of nitrogen at the prototype plot and in a study of *P. taeda* of similar age growing on sand, indicates that the time-lag for the onset of limitation can vary from zero (i.e., an immediate response to e[CO<sub>2</sub>]) in the nutrient-poor sand to 3 years in the moderately nitrogen-poor FACE prototype (Oren et al. 2001). A direct test of this hypothesis awaits field fertilization trials which are scheduled to begin in the formal, replicated FACE experiment in January 2005.

## 11.4 Estimated Global Carbon Sink in Forests

We can use the data from the Duke Forest FACE experiment to estimate the maximum increment to the carbon sink in forests that might be expected from growth at future, higher levels of atmospheric CO<sub>2</sub>. The incremental sink for carbon in forests grown at e[CO<sub>2</sub>] is 185 g C m<sup>-2</sup> year<sup>-1</sup> (Table 11.3), somewhat less than the estimate of 272 g C m<sup>-2</sup> year<sup>-1</sup> using a variety of coupled models (Schäfer et al. 2003). Houghton (2003) estimates a terrestrial carbon sink of  $2.9 \times 10^{15}$  g C year<sup>-1</sup> in undisturbed forests worldwide during the 1990s. If the world's forests were all to respond similarly to Duke Forest, showing a 32 % increment to the carbon sink (Table 11.3), these forests would accumulate an additional  $0.93 \times 10^{15}$  g C in the year 2050, when atmospheric CO<sub>2</sub> would reach the levels of our experiment. This additional sink for carbon would amount to 6.2 % of the estimated emissions from fossil fuels in 2050 ( $15 \times 10^{15}$  g C year<sup>-1</sup>; IPCC 2001) or 11.6 % of the incremental emissions compared to today. These represent an upper limit for the incremental sink in forests, as we should expect that many forests will be less responsive than young loblolly pine, as will be forests growing on nutrient-poor soils (Oren et

**Table 11.3** Estimated carbon sink in c[CO<sub>2</sub>] and e[CO<sub>2</sub>] plots of the Duke Forest FACE experiment. All data are g C m<sup>-2</sup> year<sup>-1</sup>; from Finzi et al. (2002), Lichter et al. (2005), Andrews and Schlesinger (2001)

Component	c[CO <sub>2</sub> ]	e[CO <sub>2</sub> ]	Difference	%
Stem biomass	397	505	108	27
Forest floor	78	130	52	67
Soil organic matter	89	89	0	
Groundwater flux	16	21	5	31
Total	580	765	185	32

al. 2001). Our work supports the conclusions of Schimel et al. (2000), who suggest that a much greater effect is seen from reforestation than from the direct effects of CO<sub>2</sub> on growing forests. As for the expected sink in agricultural soils, an enhanced sink for carbon in forests seems unlikely to solve the global warming problem; and we must also look hard to cut emissions from fossil fuel combustion (Jackson and Schlesinger 2004).

## 11.5 Conclusions

Free-air CO<sub>2</sub> enrichment (FACE) in the Duke Forest provides a whole-ecosystem arena in which to examine the response of a temperate coniferous forest to high, future levels of atmospheric CO<sub>2</sub>. At the end of 8 years of the experiment, we conclude:

- Photosynthetic rates by canopy foliage have increased up to 50 % over controls.
- Basal area increment has been stimulated 13–27 % versus that in control plots, with interannual variation due to variations in temperature and moisture during the growing season.
- Biomass increment has increased by 108 g C m<sup>-2</sup> year<sup>-1</sup> (27 %) over that in control plots.
- Growth and respiration of roots are higher in CO<sub>2</sub> fumigated plots.
- Litterfall is greater in high CO<sub>2</sub> plots and forest floor accumulation has increased.
- There has been little or no change in the total amount of soil organic matter as a result of CO<sub>2</sub> fumigations.
- While the stimulation of growth by high CO<sub>2</sub> persists after 8 years of fumigation, there is evidence of nitrogen limitation in the fumigated plots.

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