

## 13 CO<sub>2</sub> Enrichment of a Deciduous Forest: The Oak Ridge FACE Experiment

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### 13.1 Introduction

The free-air CO<sub>2</sub> enrichment (FACE) experiment on the Oak Ridge National Environmental Research Park (Tenn., USA) is part of a long-standing effort to understand how the eastern North American deciduous forest will be affected by CO<sub>2</sub> enrichment of the atmosphere and what the feedbacks are from the forest to the atmosphere and the global carbon cycle budget. This is a goal we have been working toward for many years by studying *components* of the deciduous forest system (e.g., individual small trees, isolated processes), but the size and complexity of the forest have heretofore precluded measurement of the *integration* of those components. FACE technology permits us to take the critical leap to measuring the integrated response of an intact forest ecosystem with a focus on stand-level mechanisms.

The Oak Ridge FACE experiment was established in 1997 in a closed-canopy, monoculture plantation of the deciduous hardwood tree, sweetgum (*Liquidambar styraciflua* L.). This sweetgum plantation offers the opportunity for rigorous tests of hypotheses that address the essential features of a forest stand and how they could influence the responses to CO<sub>2</sub> (Norby et al. 1999). These features include: (a) the closed canopy, which constrains growth responses, (b) full occupancy of the soil by the root system, which constrains the nutrient cycle, (c) the larger scale of the trees compared to saplings in open-top chambers, which changes the functional relationships of carbon cycling and water use, and (d) the longer time-scale that can be addressed, permitting studies of soil carbon changes.

## 13.2 Site Description

### 13.2.1 Physical

The experiment is located on the Oak Ridge National Environmental Research Park in Roane County, Tenn. ( $35^{\circ} 54' \text{ N}$ ,  $84^{\circ} 20' \text{ W}$ ) in southeastern United States (Fig. 13.1). The 1.7-ha plantation was established in 1988 on an old terrace of the Clinch River (elevation 230 m). Six 25-m diameter plots were laid out in 1996 and construction of the FACE facility began thereafter, following the design employed at the loblolly pine FACE experiment in North Carolina (Hendrey et al. 1999). Subsequently, one plot was removed from the experiment because of substantial differences in soil characteristics from the other five plots (Norby et al. 2001). Two plots receive air with an elevated concentration of  $\text{CO}_2$  (e[ $\text{CO}_2$ ]) and three receive air with close to the current  $\text{CO}_2$  concentration (c[ $\text{CO}_2$ ]). Two of the c[ $\text{CO}_2$ ] plots have towers, vent pipes, and blowers identical to the e[ $\text{CO}_2$ ] plots; the other c[ $\text{CO}_2$ ] plot does not have any FACE apparatus. After accounting for a buffer zone adjacent to the vent pipes, the effective plot size is 20 m diameter ( $314 \text{ m}^2$ ). The experimental unit is considered to be the whole plot; there is no blocking.

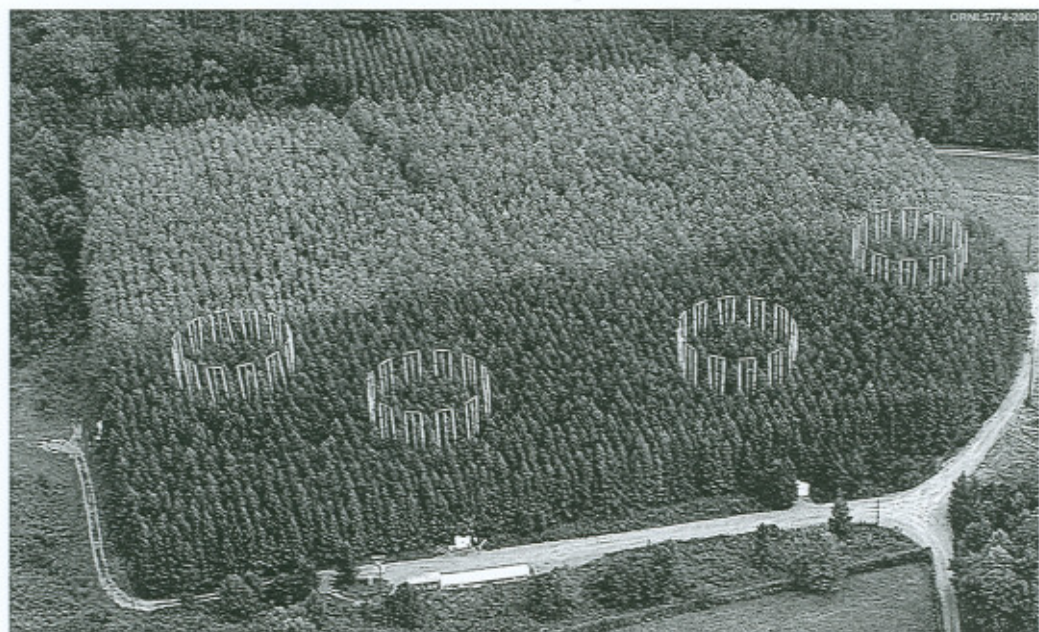


Fig. 13.1 The Oak Ridge FACE experiment is located in a sweetgum (*Liquidambar styraciflua*) plantation on the Oak Ridge National Environmental Research Park in Tennessee, USA



### 13.2.2 Soil Types

The soil at the site, which is classified as an Aquic Hapludult, developed in alluvium washed from upland soils derived from a variety of rocks including dolomite, sandstone, and shale. It has a silty clay loam texture and is moderately well drained (Van Miegroet et al. 1994). The soil is slightly acid (water pH approximately 5.5–6.0) with high base saturation largely dominated by exchangeable Ca. Bulk density is 1.5 g cm<sup>-3</sup>, C content is 74 Mg ha<sup>-1</sup>, and N content is 11 Mg ha<sup>-1</sup>. When the plantation was established in 1988, the soil was disked; and herbicide was used in 1989 and 1990 to control competition from weeds. No fertilizer has been added and there has been no additional soil disturbance, except that associated with sample collection.

### 13.2.3 Meteorological Description

The climate is typical of the humid southern Appalachian region. Mean annual temperature (1962–1993) is 13.9 °C and mean annual precipitation is 1371 mm, with a generally even distribution of precipitation throughout the year, although droughts do occur during the growing season (Gunderson et al. 2002). Weather records during the experiment are reported by Riggs et al. (2003a).

### 13.2.4 Stand Description

When the plantation was established in 1988, one-year-old, bare-rooted sweetgum seedlings from a commercial nursery were planted at a spacing of 2.3 × 1.2 m. Based on analysis of tree rings measured on trees removed during the construction of FACE apparatus, tree growth was in an exponential growth phase until approximately 1993, when it became linear (i.e., basal area increment approximately equal each year.) When pretreatment baseline measurements were initiated in 1997, stand basal area was 29.0 m<sup>2</sup> ha<sup>-1</sup> with an average tree height of 12.4 m and stem diameter of 11.3 cm. The canopy was closed and LAI was 5.5. By 2003, stand basal area had increased to 42.1 m<sup>2</sup> ha<sup>-1</sup>, average tree height was 16.7 m, and stem diameter was 14.4 cm. Leaf area index did not change, but as the top of the canopy moved upward, lower branches were cast off and canopy depth remained constant. Initially there were about 90 trees per plot, but an average of one suppressed tree per plot died each year. As of 2004, the trees had not produced fruit.

The understory was very sparse when the experiment was started in 1997 but gradually increased. Important species include an invasive C<sub>4</sub> annual grass (*Microstegium vimineum*), non-native, invasive woody plants (*Lonicera*

*japonica*, *Ligustrum sinense*), and other taxa. Tree seedlings, including *Acer negundo*, *A. rubra*, *Liriodendron tulipifera*, and *Quercus alba*, are sparse (Belote et al. 2004).

### 13.3 Experimental Treatments

Exposure to  $e[\text{CO}_2]$  commenced in two plots in April 1998 and has continued during the growing season (April–November) since then. The  $\text{CO}_2$  is a byproduct of the natural gas used in ammonia production and has a  $\delta^{13}\text{C}$  signature of approximately  $-50\text{‰}$ . The  $[\text{CO}_2]$  set-point in 1998 was a constant 565 ppm. In 1999 and 2000, a dual set-point (565 ppm day and 645 ppm night, with the beginning of day and night defined by a solar angle of  $0^\circ$ ) was used to better represent the diurnal variation in  $c[\text{CO}_2]$ . Nighttime fumigation was discontinued in 2001 because it interfered with soil respiration measurements. The average daytime  $[\text{CO}_2]$  during the 1998–2003 growing seasons was 544 ppm in the two  $\text{CO}_2$ -enriched plots, including periods when the exposure system was not functioning, and 391 ppm in  $c[\text{CO}_2]$  plots. The “current” concentration is higher than the global average because of high values in early morning hours when the wind is low. Contamination of  $c[\text{CO}_2]$  plots by adjacent  $e[\text{CO}_2]$  plots was approximately 10 ppm, based on comparison with  $[\text{CO}_2]$  measured distant from the FACE array (Norby et al. 2001). Hourly records of  $[\text{CO}_2]$  are given by Riggs et al. (2003b). There are no other treatments applied to the plots.

### 13.4 Resource Acquisition

#### 13.4.1 $\text{CO}_2$ Effects on Physiological Functions and Metabolites

##### 13.4.1.1 Carbon

Photosynthetic and stomatal responses to  $e[\text{CO}_2]$  were measured over six growing seasons in upper and mid-crown foliage to evaluate the impacts of environmental variation, exposure duration, and changes in foliar biochemistry. Measurements were taken at saturating irradiance, encompassing the full range of variability in temperature, vapor pressure deficit (VPD), and soil water potential occurring within and across seasons. Photosynthetic  $\text{CO}_2$  assimilation ( $A$ ) averaged 46 % higher in  $e[\text{CO}_2]$  (Fig. 13.2), in both mid- and upper canopy foliage (Gunderson et al. 2002); this response was sustained over the 6-year period. The stimulation of  $A$  by  $\text{CO}_2$  enrichment was greatest



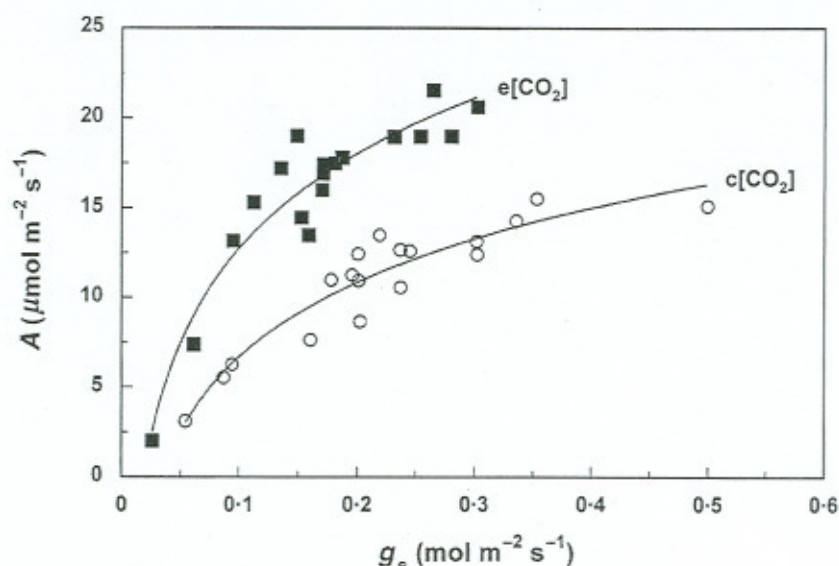


Fig. 13.2 Upper canopy photosynthesis as a function of stomatal conductance to water vapor ( $g_s$ ) on 23 dates over six summers. Modified from Gunderson et al. (2002), with permission of New Phytologist Trust

at sample times when  $g_s$  was least responsive to  $[\text{CO}_2]$ . Late-season droughts in 1998 and 1999 led to dry soils and high VPD, reducing  $A$  in both treatments, through both stomatal and non-stomatal limitations (Gunderson et al. 2002). Absolute treatment differences were noticeably diminished whenever  $g_s$  was below  $0.15 \text{ mol m}^{-2} \text{ s}^{-1}$ , although relative effects (elevated:current) varied greatly under those conditions. In all cases,  $\text{CO}_2$  responses returned when atmospheric and soil moisture conditions improved. The ratio of intercellular  $[\text{CO}_2]$  to ambient  $[\text{CO}_2]$  ( $C_i/C_a$ ) in the upper canopy was 0.67 in  $c[\text{CO}_2]$  and 0.64 in  $e[\text{CO}_2]$ . Measurement of  $A$  as a function of  $C_i$  revealed no significant  $\text{CO}_2$  treatment effects on photosynthetic or biochemical capacity (i.e., no change in  $A_{\text{max}}$ ,  $V_{\text{cmax}}$  or  $J_{\text{max}}$ ), although starch concentration was increased (+16%) and N concentration was reduced (-10%; Sholtis et al. 2004). In contrast, soluble sugar concentrations (mass basis) were not affected by  $\text{CO}_2$  (Sholtis et al. 2004; Tschaplinski, unpublished data), despite the consistently higher  $A$ . These results suggest that established sweetgum trees in closed-canopy forests would sustain a long-term positive response to  $e[\text{CO}_2]$  without reductions in photosynthetic capacity, subject only to seasonal variability and constraints associated with environmental conditions.

Nighttime respiration ( $R_N$ ) was measured on leaves in the upper and lower canopy in 1999 and 2000; and leaf respiration in the light ( $R_L$ ) was estimated in the upper canopy in 2000 (Tissue et al. 2002). There were no significant short-term effects of  $e[\text{CO}_2]$  on  $R_N$  or long-term effects on  $R_N$  or  $R_L$ , when expressed on an area, mass or nitrogen basis. Upper-canopy leaves had 54%



higher  $R_N$  (area basis) than lower-canopy leaves.  $\text{CO}_2$  enrichment significantly increased the number of leaf mitochondria by 62%. Growth in  $e[\text{CO}_2]$  did not affect the relationships between  $R_N$  and any measured leaf structural or chemical characteristic.

Stem respiration rates (per unit stem volume) of individual trees in August 2002 ranged over 33–66  $\mu\text{mol CO}_2 \text{ m}^{-3} \text{ s}^{-1}$  in control plots and 40–94  $\mu\text{mol CO}_2 \text{ m}^{-3} \text{ s}^{-1}$  in  $\text{CO}_2$ -enriched plots (Edwards et al. 2002). Respiration rates were consistently higher under  $\text{CO}_2$  enrichment than at  $c[\text{CO}_2]$  throughout both the growing season and the dormant season. Averaged over an entire year, stem respiration was increased 33% by  $\text{CO}_2$  enrichment because of a 23% increase in growth respiration and a 48% increase in maintenance respiration. Respiration rates of the upper stem and small branches were  $4 \times$  to  $6 \times$  higher than that of the lower bole, which is an important consideration in scaling these volume-specific rates to whole-tree and whole-plot respiration (Edwards et al. 2002). The  $\text{CO}_2$ -induced increase in stem respiration rates occurred concomitantly with elevated (28%) sucrose concentrations in stems, whereas the concentrations of other soluble carbohydrates were not different between treatments (Edwards et al. 2002). Furthermore, the treatment difference in stem sucrose concentration was eliminated within 4 days of turning off the  $\text{CO}_2$  fumigation temporarily in June 2001. There were, however, no treatment differences in stem soluble carbohydrate concentrations in the dormant season when differences in respiration were still evident, suggesting that substrates other than sucrose may drive the higher respiration rate.

Fine-root respiration ( $R_T$ ) was partitioned between maintenance ( $R_M$ ), growth ( $R_G$ ), and N uptake respiration ( $R_N$ ; George et al. 2003). Maintenance respiration was the majority (86%) of  $R_T$ . There was no significant effect of  $\text{CO}_2$  enrichment on instantaneous  $R_M$ , whether expressed on a mass or nitrogen basis, and no effect on tissue construction cost. Specific rates were scaled to annual, whole-plot rates using data on fine-root production, fine-root standing crop, and the temperature-sensitivity of the response (George et al. 2003).

#### 13.4.1.2 Water

Mid-day measurements of stomatal conductance for leaves sampled in plots with  $e[\text{CO}_2]$  were as much as 44% lower at elevated than at  $c[\text{CO}_2]$  (Wullschlegel et al. 2002). Leaves in the upper canopy showed the strongest response to  $\text{CO}_2$  enrichment, with no significant differences observed for leaves located in the middle and lower portions of the canopy. Estimates of canopy conductance averaged over the growing season were 14% lower in stands exposed to  $\text{CO}_2$  enrichment, although the magnitude of this response was dependent on vapor pressure deficit, radiation, and soil water potential (Wullschlegel et al. 2002). The compensated heat-pulse technique was used to



measure rates of sap velocity in 1999 (Wullschlegel and Norby 2001). Sap velocity averaged 13 % less for trees in e[CO<sub>2</sub>] compared with c[CO<sub>2</sub>].

### 13.4.1.3 Nitrogen

Whole-canopy nitrogen concentration ( $N_M$ ) was 16.8 mg g<sup>-1</sup> in c[CO<sub>2</sub>] and 11 % lower (14.9 mg g<sup>-1</sup>) in e[CO<sub>2</sub>] (Norby and Iversen 2006). Except in the first year of treatment (1998), the difference in canopy  $N_M$  was also observed in leaf litter.  $N_M$  was lower in e[CO<sub>2</sub>] than in c[CO<sub>2</sub>] plots at every depth of the canopy, but the CO<sub>2</sub> effect was greater toward the top because of a dilution effect. Leaf mass per unit area ( $LM_A$ ) was higher in e[CO<sub>2</sub>] only at the top of the canopy because of increased leaf density, which was related in part to a higher content of nonstructural carbohydrates (Sholtis et al. 2004). However, N expressed on a leaf area basis ( $N_A$ ) was lower in e[CO<sub>2</sub>] in the middle layers of the canopy, indicating a real effect on N content (Norby and Iversen 2006). Fine root  $N_M$  was more variable than leaf  $N_M$  and there was no significant effect of [CO<sub>2</sub>] (Norby and Iversen 2006).

## 13.4.2 CO<sub>2</sub> Effects on Tree and Stand Structure

### 13.4.2.1 Leaf Area Index

Leaf area index (LAI) and its seasonal dynamics are key determinants of terrestrial productivity and, therefore, of the response of ecosystems to a rising atmospheric [CO<sub>2</sub>]. Despite the central importance of LAI, there is very little evidence from which to assess how forest LAI will respond to increasing [CO<sub>2</sub>]. LAI throughout the 1999–2002 growing seasons was assessed using a combination of data on transmittance of photosynthetically active radiation (PAR), mass of litter collected in traps, and  $LM_A$  (Norby et al. 2003). There was no effect of [CO<sub>2</sub>] on any expression of leaf area, including peak LAI, average LAI, or leaf area duration. Peak canopy mass was increased 8 % by CO<sub>2</sub> enrichment, reflecting a similar increase in  $LM_A$ .

### 13.4.2.2 Root System Structure

The root system of the sweetgum trees comprises a woody heart root, woody lateral roots that extend several meters from the trunk, and smaller and fine roots. Excavation of some trees revealed that most (90 %) of the root biomass was in the heart root and woody lateral roots, and based on allometric analysis, woody root biomass was not affected by CO<sub>2</sub> enrichment. Minirhizotron



analysis indicated that approximately 80% of fine-root length was in roots <0.5 mm diameter and less than 5% was in roots >1 mm diameter (Norby et al. 2004). The fine-root standing crop was usually at a maximum in mid-July in  $c[\text{CO}_2]$  and in August–September in  $e[\text{CO}_2]$ . Beginning in 2000, the peak standing fine-root mass in  $\text{CO}_2$ -enriched plots was more than doubled that in  $c[\text{CO}_2]$  plots. In 1998, most of the root length was in the upper soil: 40% in the top 15 cm and 79% in the top 30 cm. Five years later, 63% of the root length was still at 0–30 cm depth in  $c[\text{CO}_2]$ , but the root distribution was distinctly different in  $e[\text{CO}_2]$  plots.  $\text{CO}_2$  enrichment increased root length in the upper profile, but the largest increases occurred in deeper soil: 3-fold more length at 30–45 cm and 4-fold more at 45–60 cm.

### 13.4.3 Structure–Function Integration

#### 13.4.3.1 Carbon Uptake

Gross primary productivity (GPP) is a function of leaf-level photosynthesis and LAI. Since leaf-level photosynthesis increased in  $e[\text{CO}_2]$  and there was no change in LAI, an increase in GPP is implied. Based on calculations from canopy conductance (Wullschleger et al. 2002), GPP in 1999 was 27% higher in  $e[\text{CO}_2]$  (Norby et al. 2002). A similar estimate (22%) of the response of GPP to  $\text{CO}_2$  enrichment was generated by adding net primary productivity (NPP, see Section 13.5.1.3) to annual whole-tree (autotrophic) respiration (DeLucia et al. 2005). Autotrophic respiration in 2000 was calculated by summing leaf, wood, and fine-root respiration across the whole plot and for the whole year (DeLucia et al. 2005). Respiration was 28% higher in  $e[\text{CO}_2]$  and consumed 48% of GPP in  $c[\text{CO}_2]$  and 51% of GPP in  $e[\text{CO}_2]$ . Consistent with the lack of effect of  $[\text{CO}_2]$  on LAI, there also was no effect on absorbed photosynthetically active radiation (APAR). Hence, the observed increase in C uptake (GPP and NPP) was attributed to an increase in light-use efficiency (LUE; Norby et al. 2003) and reflected the sustained response of leaf-level photosynthesis to  $\text{CO}_2$  enrichment. The current evidence from this and other experiments seems convincing that LAI of non-expanding forest stands will not be different in a future  $\text{CO}_2$ -enriched atmosphere (Körner et al. 2005, 2006) and that increases in LUE and productivity in  $e[\text{CO}_2]$  are driven primarily by functional responses (e.g., increased photosynthesis) rather than by structural changes.

#### 13.4.3.2 Stand Water Use

There is widespread belief that  $\text{CO}_2$ -induced reductions in stomatal conductance will have important consequences for forest water use, and in turn,



ecosystem-scale processes that depend on water availability. Simple measurements of water use by seedlings or saplings growing in isolation, however, are insufficient to capture the complex temporal and spatial control of transpiration that inevitably takes place in closed-canopy stands. Whole-stand transpiration in the FACE experiment was estimated as a function of measured sap velocity, total stand sapwood area, and the fraction of sapwood functional in water transport (Wullschleger and Norby 2001). Maximum daily rates of stand transpiration during the 1999 growing season were 5.6 mm day<sup>-1</sup> in c[CO<sub>2</sub>] and 4.4 mm day<sup>-1</sup> in e[CO<sub>2</sub>], a 21 % reduction. Averaged across the entire growing season, the relative effect of [CO<sub>2</sub>] was only a 10 % reduction: 3.1 mm day<sup>-1</sup> and 2.8 mm day<sup>-1</sup> in c[CO<sub>2</sub>] and e[CO<sub>2</sub>], respectively. Similar patterns were observed again in 2004 (Wullschleger, unpublished data; Fig. 13.3). The largest differences in 1999 occurred during May when stand water use was 104 mm in c[CO<sub>2</sub>], but only 84 mm in e[CO<sub>2</sub>], a 19 % reduction (Wullschleger and Norby 2001). In 2004 e[CO<sub>2</sub>] reduced transpiration 20 % in both June and July (Fig. 3).

When transpiration of the trees was combined with calculations of evaporation from soil, estimates of annual evapotranspiration showed relatively small reductions due to atmospheric CO<sub>2</sub> enrichment (Wullschleger et al. 2002). The attenuation of CO<sub>2</sub> response from the scale of the leaf to tree to stand to ecosystem illustrates that the hydrological response of a closed-canopy plantation to e[CO<sub>2</sub>] depends on the temporal and spatial scale of observation. These observations emphasize the importance of interacting variables (e.g., soil moisture, VPD) and confirm that integration of measurements over space and time reduce what, at the leaf level, might otherwise appear to be a large and significant response.

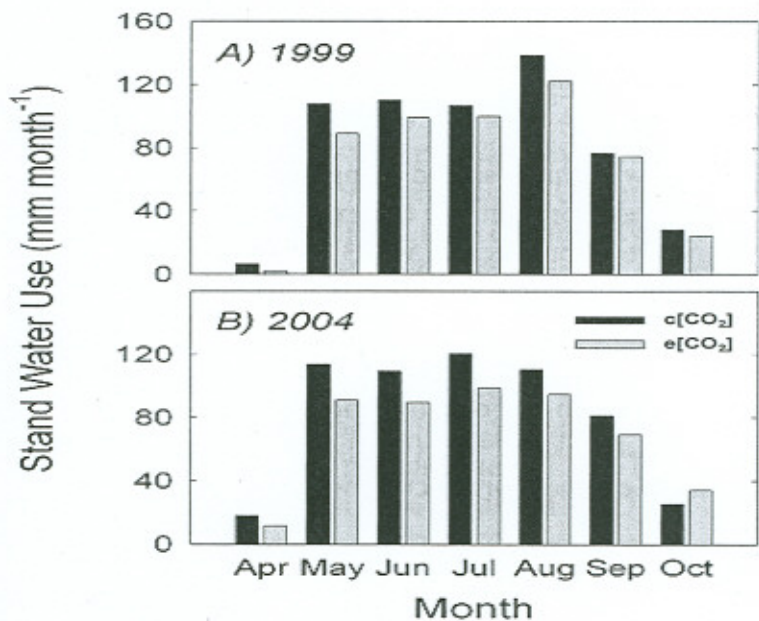


Fig. 13.3 Seasonal pattern of monthly stand water use for trees grown in current or elevated CO<sub>2</sub> concentrations. Measurements were made in the second year of treatment (1999) and in the seventh year (2004)



### 13.4.3.3 Nitrogen Cycling

Nitrogen cycling in mature forests is characterized by tight internal cycles that are not replicated in CO<sub>2</sub> enrichment experiments with tree seedlings or saplings in chambers (Johnson et al. 2004). In the FACE experiment, increased leaf mass production (Section 13.4.2.1) in CO<sub>2</sub>-enriched canopies was offset by the reduced concentration of N, such that there was no effect on peak canopy N mass (Norby and Iversen 2006). The total amount of N used in fine-root production varied with year and increased significantly with CO<sub>2</sub> enrichment, reflecting an increase in root production (Section 13.5.1.2) with no effect on N concentration in roots (Section 13.4.1.3). Annual N uptake, which comprises the N content of leaf litter, wood increment, fine-root production, and throughfall minus deposition (Johnson et al. 2004), was significantly higher in e[CO<sub>2</sub>], with an average increase over the period 1998–2003 of 29%. Most of the difference was in the fine-root component. Uptake accounted for 74% of annual N requirement in c[CO<sub>2</sub>] and a significantly higher fraction (79%) in e[CO<sub>2</sub>], with retranslocation accounting for the remaining fraction of requirement (Norby and Iversen 2006). Annual N uptake increased linearly with fine-root length duration (the integration of root length over the growing season), suggesting that the greater investment in fine-root production in e[CO<sub>2</sub>] increased the access to available soil N and thereby precluded the development of N limitations (Norby et al. 2004).

## 13.5 Resource Transformation

### 13.5.1 Productivity

#### 13.5.1.1 Aboveground Production

Stem growth was assessed using allometric relationships developed on harvested trees from outside the experimental plots (Norby et al. 2001). Aboveground wood production was 35% greater in CO<sub>2</sub>-enriched plots during the first year of exposure (1998). In the second year, however, the difference in growth was reduced to 15% and was no longer statistically significant, with further reductions in the third and subsequent years. The total dry matter increment of aboveground woody tissue from 1998 to 2003 was 7.2 kg m<sup>-2</sup> in c[CO<sub>2</sub>] and 7.7 kg m<sup>-2</sup> in e[CO<sub>2</sub>]; this difference of 6.9% is not statistically significant. Leaf mass production was 7.4% higher in e[CO<sub>2</sub>] (Norby et al. 2003).



### 13.5.1.2 Belowground Production

Fine-root production and mortality were measured through analysis of minirhizotron images, which were collected biweekly from 1998 through 2003 (Norby et al. 2004). Annual production of fine roots more than doubled in response to CO<sub>2</sub> enrichment; and the nearly continuous 6-year record revealed the highly dynamic responses of the root system and its changing distribution in the soil profile. Although the seasonal pattern of fine-root production varied year to year, root productivity generally was higher in March through June than in July through October. The effect of [CO<sub>2</sub>] on annual production, which was first observed during the third year, was highly significant, with production 2.2-fold higher in CO<sub>2</sub>-enriched plots from 2000 to 2003. Mortality was highest in late summer and fall. Annually, mortality matched production in both c[CO<sub>2</sub>] and e[CO<sub>2</sub>]; hence, net production was close to zero. Root turnover, which is the fraction of the root population that is replaced during a year, was calculated as annual production divided by the maximum standing crop. Averaged over the 6 years of observation, root turnover was 1.7 year<sup>-1</sup>, corresponding to mean residence time (MRT) of 0.62 year. Root turnover rate was not affected by [CO<sub>2</sub>]. Cohort analysis also was used to estimate fine-root longevity (Norby et al. 2004), yielding an MRT ranging from 0.81 year to 1.4 year, with no effect of [CO<sub>2</sub>] and in agreement with an analysis based on the replacement of pre-treatment roots with new roots with the distinct <sup>13</sup>C signature of the added CO<sub>2</sub> (Matamala et al. 2003). The absence of an effect of [CO<sub>2</sub>] on turnover rate indicates that the increase in root mortality and concomitant input of root C into the soil was a direct result of increased root production and not an alteration of root physiology.

### 13.5.1.3 Ecosystem Productivity

Aboveground productivity of the forest understory was estimated in 2001 and 2002. The productivity of *Lonicera japonica* was consistently greater under e[CO<sub>2</sub>], whereas the response of *Microstegium vimineum* to CO<sub>2</sub> enrichment differed between wet and dry years and mediated total community response (Belote et al. 2004). The understory accounted for less than 5% of ecosystem NPP (Norby et al. 2002).

NPP of the forest plots was strongly dominated by the sweetgum trees. In c[CO<sub>2</sub>], sweetgum NPP ranged over 852–1062 g C m<sup>-2</sup> year<sup>-1</sup> (1.85–2.33 kg dry matter m<sup>-2</sup> year<sup>-1</sup>), with wood production (bole, branches, and woody root) accounting for 65%, leaf litter 21%, and fine-root production 14% (Fig. 13.4). Averaged over 6 years (1998–2003), NPP was 22% higher in e[CO<sub>2</sub>] (24% if expressed in dry matter units). The response of NPP to CO<sub>2</sub> enrichment varied from 16% to 38% in different years, but showed no trend through time. The



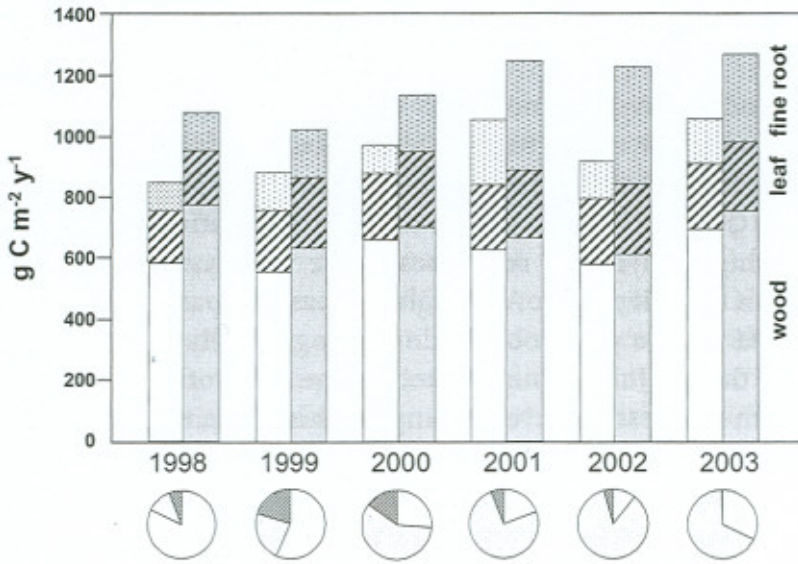


Fig. 13.4 Net primary productivity of sweetgum trees and the relative allocation of the additional C taken up in response to CO<sub>2</sub> enrichment. For each set of bars, unshaded bars on the left are for plots in c[CO<sub>2</sub>] and shaded bars on the right are e[CO<sub>2</sub>]; lowest section is wood, middle section (striped) is leaf, and upper section (stippled) is fine roots. Pie charts show the relative distribution between wood (clear), leaves (striped), and fine roots (stippled) of the additional C taken up in CO<sub>2</sub>-enriched plots

additional C taken up and converted to organic matter by trees in CO<sub>2</sub>-enriched plots was allocated primarily to fine-root production. Excluding the first year of treatment (to exclude pre-treatment influences), 65% of the pool of additional C was allocated to fine roots, 28% to wood, and 7% to leaves (Fig. 13.4). The additional allocation to wood did not produce a significant increase in wood increment.

Annual NEP was estimated from NPP and soil respiration (Norby et al. 2002). Elevated atmospheric [CO<sub>2</sub>] stimulated soil respiration (King et al. 2004). From early spring to mid-summer, soil respiration increased approximately four-fold, from 1 μmol m<sup>-2</sup> s<sup>-1</sup> to 4 μmol m<sup>-2</sup> s<sup>-1</sup>, respectively, over a soil temperature range of 7–23 °C, and stimulation of CO<sub>2</sub> efflux at 20 °C averaged 12.0%. Most of the stimulation occurred mid growing season when fine-root activity was greatest. The seasonal Q<sub>10</sub> relationship ranged from 1.89 to 2.60. Total soil C efflux in c[CO<sub>2</sub>] plots increased from 600 g C m<sup>-2</sup> year<sup>-1</sup> in 1997 to 996 g C m<sup>-2</sup> year<sup>-1</sup> in 2000, but then dropped to 698 g C m<sup>-2</sup> year<sup>-1</sup> in 2001. Stimulation of cumulative soil C efflux by eCO<sub>2</sub> ranged from 8.3% to 17.1% and averaged only 12.0% for all years. The temperature sensitivity of bulk soil respiration appeared to be unaffected by [CO<sub>2</sub>].

The heterotrophic component of soil respiration was estimated based on analysis of the <sup>13</sup>C content of soil CO<sub>2</sub> efflux in relation to seasonal variation in fine-root standing crop (Norby et al. 2002). R<sub>H</sub> was higher in e[CO<sub>2</sub>], offsetting



some of the gain in NPP, but total NEP for the years 1998–2001 was 679 g C m<sup>-2</sup> higher in CO<sub>2</sub>-enriched plots (170 g C m<sup>-2</sup> year<sup>-1</sup>). Half of this gain in ecosystem C was in wood, but this fraction was declining steeply (Fig. 13.4), and the overall contribution of wood to C sequestration was becoming progressively smaller as the experiment continued. Over the longer term, if present trends continue, an increase in NEP in e[CO<sub>2</sub>] in this forest will be associated with changes in soil C.

### 13.5.2 Soil C

#### 13.5.2.1 Carbon Input and Decomposition

The preferential allocation of additional C to fine roots rather than to woody biomass has significant implications for the potential of this forest to sequester C. Fine roots in this sweetgum stand have a mean residence time of approximately 1 year (Matamala et al. 2003, Norby et al. 2004), so the C that is allocated to them is not sequestered in plant biomass as is the C allocated to wood. Annually, 131 g C m<sup>-2</sup> are added to soil through fine-root mortality in c[CO<sub>2</sub>], and almost twice that amount in e[CO<sub>2</sub>] (average over 1998–2003). After fine-root C is transferred to soil pools, it might be returned rapidly to the atmosphere through microbial respiration or stored as longer-lived organic compounds. Hence, it is important to understand the fate of the C in dead fine roots. In both laboratory and field incubations, fine roots lost 35–42% of their dry mass over 360 days; and there was no effect of the CO<sub>2</sub> concentration in which they had been produced (Johnson et al. 2004).

Leaf litter accounts for an annual addition to soil of 214 g C m<sup>-2</sup> in c[CO<sub>2</sub>] and 230 g C m<sup>-2</sup> in e[CO<sub>2</sub>]. Leaf litter does not accumulate in this ecosystem due to the activity of earthworms: usually one year's cohort of leaf litter has disappeared by the time the next year's cohort falls (Johnson et al. 2004). Although the lower N concentration of litter in e[CO<sub>2</sub>] would suggest a slower decomposition rate, the rapid disappearance renders moot any difference with respect to C storage or N availability.

#### 13.5.2.2 Carbon Pools

Mineral soil was sampled in depth increments of 0–5, 5–15, and 15–30 cm after removing surface litter. Soils were fractionated into stable microaggregates (53–250 μm diam.) and non-microaggregated soil by using a microaggregate isolator (Six et al. 2000) and analyzed for organic C and C isotopic composition (Jastrow et al. 2005). Soil C in the surface 5 cm increased linearly during the first 5 years of exposure to e[CO<sub>2</sub>], but remained constant in the



c[CO<sub>2</sub>] plots. No significant changes in soil C were found for either e[CO<sub>2</sub>] or c[CO<sub>2</sub>] at deeper depths. Isotopic data confirmed that net C inputs in the surface 5 cm were more than double those at 5–15 cm and over four times the inputs at 15–30 cm. Soil C stocks increased by 220±45 g C m<sup>-2</sup> during the initial 5 years of exposure to e[CO<sub>2</sub>]. Hence, the average accrual rate of 44±9 g C m<sup>-2</sup> year<sup>-1</sup> corresponded to more than half of the estimated annual NEP not accounted for by woody increment. (The remaining fraction might be in deeper soil, which was not sampled or lost in the error terms.) A portion of accrued soil C was stabilized by association with soil minerals. The proportion of C in microaggregated soil averaged 58% under both e[CO<sub>2</sub>] and c[CO<sub>2</sub>] and was unchanged over time, suggesting that additional inputs derived from CO<sub>2</sub> enrichment were processed and protected in much the same manner as in soil in c[CO<sub>2</sub>] plots with little apparent saturation of this protection mechanism (Jastrow et al. 2005). The formation and cycling of microaggregates is a key factor in physically protecting detrital inputs from rapid decomposition and helps to create conditions wherein microbial residues and breakdown products can become stabilized in organomineral complexes (Christensen 2001).

### 13.5.2.3 Microbial Activity and Nutrient Cycling

The indirect responses of soil microbiota to e[CO<sub>2</sub>] have the potential to alter nutrient availability and soil carbon storage. However, despite the substantial increase in C deposition to soil in CO<sub>2</sub>-enriched plots, there have been no detectable changes in microbial activity. Substrate utilization by soil bacteria and extracellular enzyme activities associated with bulk soil and fine-root rhizoplanes were measured over 1999–2001 (Sinsabaugh et al. 2003). Rhizoplane enzyme activity was similar to that of bulk soil; and there was no response to e[CO<sub>2</sub>] in any of the measured variables. Johnson et al. (2004) noted a weak trend of increased soil microbial activity in e[CO<sub>2</sub>] (5–23%) and possibly increased microbial immobilization of some mineral nutrients, including N. The additional amount immobilized into microbial biomass in e[CO<sub>2</sub>] represented approximately 4–22 kg N ha<sup>-1</sup> in the 0–20 cm top soil layer, which is similar in magnitude to the amount of N needed for net woody tissue increment. However, no effect of [CO<sub>2</sub>] on microbial N, gross N mineralization, microbial N immobilization, or specific microbial N immobilization was observed by Zak et al. (2003). Overall, there is little evidence that changes in plant litter production under e[CO<sub>2</sub>] will initially slow soil N availability and produce a negative feedback on NPP; but our ability to predict long-term changes in soil N availability and hence whether greater NPP will be sustained in a CO<sub>2</sub>-enriched atmosphere depends on an understanding of the time-scale over which greater plant production modifies microbial N demand (Zak et al. 2003).



### 13.5.3 Products

Although this sweetgum plantation was initially established to evaluate the species' potential as a biofuel (Van Miegroet et al. 1994), it has not been managed in that way; and questions about the effect of  $e[\text{CO}_2]$  on the production of biofuel feedstock or other forest products are not relevant to the objectives of the FACE experiment. Wood density was measured on a subset of trees as part of the allometric estimation of dry matter increment (Norby et al. 2001); and there has been no indication of a CO<sub>2</sub> effect on wood density. The trees in the FACE plots have not flowered or produced fruit as of 2004.

### 13.5.4 Biotic Interactions

Based on sweepnet and pitfall techniques, Sanders et al. (2004) determined that total arthropod abundance and richness across all trophic groups did not differ between  $c[\text{CO}_2]$  and  $e[\text{CO}_2]$  plots. However, particular trophic groups, especially the predators, were more abundant and had higher levels of species richness in  $c[\text{CO}_2]$  than in  $e[\text{CO}_2]$  plots. There were no distinct treatment effects on arthropod community composition, but there were strong temporal effects on community composition.

Neher et al (2004) extracted and enumerated nematodes in soil cores collected in 1999 and 2000. CO<sub>2</sub> enrichment decreased the total abundance of nematodes and decreased the respiration and biomass of the nematode community. Composition of the community changed, with a higher relative abundance of fungivores in  $e[\text{CO}_2]$  and a lower abundance of herbivores, bacterivores, and predators. Estimated annual productivity of soil nematode communities ranged from 0.6 g C m<sup>-2</sup> year<sup>-1</sup> to 4.7 g C m<sup>-2</sup> year<sup>-1</sup>, representing ca. 1 % of ecosystem NPP.

## 13.6 Consequences and Implications

### 13.6.1 Forest Management

Carbon sequestration in forests could be an important strategy for managing the global carbon cycle and slowing the inexorable increase in atmospheric [CO<sub>2</sub>]. An increased rate of sequestration in response to  $e[\text{CO}_2]$ , as observed in this experiment, would appear to be an important factor to incorporate into the design or evaluation of forest C sequestration projects; and forest FACE experiments are sometimes justified on this basis. However, extrapolations from perturbation experiments such as these are difficult because ecosystem



C sequestration rates are projected to respond differently to gradual versus step increases in atmospheric  $\text{CO}_2$ ; and transient responses are expected (Luo et al. 2003). Furthermore, the relatively small increment in C storage in the sweetgum forest in response to the atmospheric  $\text{CO}_2$  concentration that will be attained in about 2050 suggests a much smaller increment within the period that a C sequestration project might be implemented.

Converting unproductive land to forests or improving the silviculture of existing forests is likely to yield far greater rates of C sequestration that render the  $\text{CO}_2$  fertilization effect trivial. Nevertheless, the intensive and integrated evaluation of C metabolism and cycling in the FACE experiment should help to inform forest C management. For example, the large response of fine roots to  $\text{CO}_2$  enrichment in this experiment and the resulting deposition of increased C to deeper soil profiles suggests that forests may have more potential for C sequestration than may be apparent from aboveground analysis (e.g., Casperson et al. 2000), but this observation must be tempered with the formidable difficulty in measuring belowground processes (Norby et al. 2004).

### 13.6.2 Global C Cycle

The implications of the Oak Ridge FACE experiment reside primarily in the arena of the global carbon cycle and the potential for a negative feedback between increasing atmospheric  $\text{CO}_2$  and forests to alter the rate at which greenhouse warming occurs. The sustained response of NPP to 542 ppm  $\text{CO}_2$  in this experiment (a 24% increase) is consistent with projections from earlier experiments with younger trees (Norby et al. 1999) and ecosystem and global models (e.g., Cramer et al. 2001). The basis for the response of NPP is the sustained stimulation of leaf-level photosynthesis and stand-level LUE. There has been no evidence for acclimation of photosynthesis to  $e[\text{CO}_2]$ , which has sometimes been given as a reason to discount  $\text{CO}_2$  fertilization. There also has been no indication of the development of a progressive N limitation, which has been proposed as a negative feedback on the response of NPP to rising  $[\text{CO}_2]$  (Luo et al. 2004), although we cannot discount the possibility of an N limitation developing in the future. Hence, the Oak Ridge FACE experiment provides support for the inclusion of a  $\text{CO}_2$  fertilization effect in models of the future trajectory of the global C cycle.

The question arises, however, as to whether the responses to  $\text{CO}_2$  enrichment observed in these young, fast-growing plantation trees are predictive of the response of older and larger, mature forest trees. Körner et al. (2005) used a new web-FACE design to expose ten mature, 30-m tall trees in a deciduous forest to 530 ppm for 4 years. The physiological responses of these trees (e.g., photosynthesis, foliar N and non-structural carbohydrate concentrations) were very similar to the responses of the Oak Ridge sweetgum trees, thereby



increasing our confidence that our FACE results are relevant to questions about temperate forests in general. As in the sweetgum experiment, there was no significant increase in basal area increment, although with only ten trees in the web-FACE experiment, the power to detect CO<sub>2</sub> effects on growth was very low. The web-FACE design did not permit analysis of NPP, so there is no basis for comparative analysis of this critical ecosystem-scale response.

The FACE experiment can provide additional guidance for ecosystem models being used to evaluate CO<sub>2</sub> responses. LAI of the sweetgum stand has not increased and there is now strong evidence that LAI of non-expanding forest stands will not be different in a future CO<sub>2</sub>-enriched atmosphere. Model routines that assume increased LAI should be avoided because they alter estimates of N demand and water use. The assumption that CO<sub>2</sub> effects on stomatal conductance result in reductions in forest water use is incorporated into some models, but this has not been supported statistically because of attenuation of the response across scales coupled with the low replication of FACE experiments. Models will be especially challenged to represent C allocation such that the dramatic response of fine-root production observed in this experiment is reproduced. The fine-root response of the sweetgum trees in the FACE experiment has important implications for carbon, water, and nutrient cycles; and understanding how different ecosystems allocate C to fast- or slow-turnover pools may be key to predicting their integrated response to atmospheric CO<sub>2</sub> enrichment. The allocation response is the primary difference between this experiment and the similar FACE experiment in a *Pinus taeda* stand (Chapter 11). NPP and NEP responded similarly to CO<sub>2</sub> enrichment in the two experiments (DeLucia et al. 2005), but in the pines the additional productivity was recovered primarily in wood.

The response of plants to e[CO<sub>2</sub>] should also be considered in the context of other changing environmental variables. Future enhancements of GPP driven by increasing [CO<sub>2</sub>] will be attenuated to varying degrees by increased respiration from warming and by loss of photosynthesis from exposure to drought or air pollutants. Hanson et al. (2005) used the responses to e[CO<sub>2</sub>] in this FACE experiment, combined with other observations of forest responses to increased temperature, ozone, and altered precipitation patterns, in a model-based analysis of an upland-oak forest in 2100. The dominant effects of e[CO<sub>2</sub>] on the simulated forest were reduced when combined with effects of warming, precipitation change, ozone exposure, tissue acclimation, and changes in biomass and element stocks. The analysis of the impact of e[CO<sub>2</sub>] on the global carbon cycle using results from FACE experiments must expand to consider the influence of multiple interacting environmental variables.



### 13.7 Conclusions

Physiological and stand-level responses observed in the closed-canopy *Liquidambar styraciflua* forest in the Oak Ridge FACE experiment are contributing to our understanding of how the eastern North American deciduous forest will be affected by CO<sub>2</sub> enrichment of the atmosphere.

- Photosynthetic CO<sub>2</sub> assimilation averaged 46 % higher in e[CO<sub>2</sub>]. The response was sustained throughout the canopy; and there was no loss of photosynthetic capacity over time.
- Stomatal conductance in upper canopy leaves was reduced as much as 44 % in e[CO<sub>2</sub>], but the responses of canopy conductance and stand transpiration averaged over the growing season were much less (14 % and 10 %, respectively).
- NPP during the first 6 years of treatment averaged 967 g C m<sup>-2</sup> year<sup>-1</sup> in c[CO<sub>2</sub>] and 1164 g C m<sup>-2</sup> year<sup>-1</sup> in e[CO<sub>2</sub>], an increase of 22 %. There was no effect of [CO<sub>2</sub>] on LAI or APAR; hence, the increase in NPP was attributed to greater LUE.
- The increased C uptake in e[CO<sub>2</sub>] was partitioned primarily to fine-root production, which was more than doubled in years 3–6. There was no significant increase in wood production after the first year of treatment.
- Annual N uptake increased linearly with fine-root length duration and was significantly greater in e[CO<sub>2</sub>]. Leaf and litter N concentrations were reduced in e[CO<sub>2</sub>], but there was no indication of a negative feedback of N availability on NPP.
- Increased fine-root mortality added more C to the soil in e[CO<sub>2</sub>]. C efflux from soil also increased; nevertheless, e[CO<sub>2</sub>] caused a significant increase in C accrual in the surface 5 cm of soil. The average accrual rate was 44 g C m<sup>-2</sup> year<sup>-1</sup>.

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## References

- Belote RT, Weltzin JF, Norby RJ (2004) Response of an understory plant community to elevated [CO<sub>2</sub>] depends on differential responses of dominant invasive species and is mediated by soil water availability. *New Phytol* 161:827–835
- Caspersen JP, Pacala SW, Jenkins JC, Hurtt GC, Moorcroft PR, Birdsey RA (2000) Contributions of land-use history to carbon accumulation in US forests. *Science* 290:1148–1151
- Christensen B (2001) Physical fractionation of soil and structural and functional complexity in organic matter turnover. *Eur J Soil Sci* 52:345–353
- Cramer W, Bondeau A, Woodward FI, Prentice IC, Betts RA, Brovkin V, Cox PM, Fisher V, Foley JA, Friend AD, Kucharik C, Lomas MR, Ramankutty N, Sitch S, Smith B, White A, Young-Molling C (2001) Global response of terrestrial ecosystem structure and function to CO<sub>2</sub> and climate change: results from six dynamic global vegetation models. *Global Change Biol* 7:357–373
- DeLucia EH, Moore DJ, Norby RJ (2005) Contrasting responses of forest ecosystems to rising atmospheric CO<sub>2</sub>: implications for the global C cycle. *Global Biogeochem Cycles* 19:GB3006.
- Edwards NT, Tschaplinski TJ, Norby RJ (2002) Stem respiration increases in CO<sub>2</sub>-enriched trees. *New Phytol* 155:239–248
- George K, Norby RJ, Hamilton JG, DeLucia EH (2003) Fine-root respiration in a loblolly pine and sweetgum forest growing in elevated CO<sub>2</sub>. *New Phytol* 160:511–522
- Gunderson CA, Sholtis JD, Wullschlegel SD, Tissue DT, Hanson PJ, Norby RJ (2002) Environmental and stomatal control of photosynthetic enhancement in the canopy of a sweetgum (*Liquidambar styraciflua* L.) plantation during three years of CO<sub>2</sub> enrichment. *Plant Cell Environ* 25:379–393
- Hanson PJ, Wullschlegel SD, Norby RJ, Tschaplinski TJ, Gunderson CA (2005) Importance of changing CO<sub>2</sub>, temperature, precipitation, and ozone on carbon and water cycles of an upland-oak forest: incorporating experimental results into model simulations. *Global Change Biol* 11:1402–1423
- Hendrey GR, Ellsworth DS, Lewin KF, Nagy J (1999) A free-air enrichment system for exposing tall forest vegetation to elevated atmospheric CO<sub>2</sub>. *Global Change Biol* 5:293–309
- Jastrow JD, Miller RM, Matamala R, Norby RJ, Boutton TW, Rice CW, Owensby CE (2005) Elevated atmospheric CO<sub>2</sub> increases soil carbon. *Global Change Biol* 11:2057–2064
- Johnson DW, Cheng W, Joslin JD, Norby RJ, Edwards NT, Todd DE Jr (2004) Effects of elevated CO<sub>2</sub> on nutrient cycling in a sweetgum plantation. *Biogeochemistry* 69:379–403
- King JS, Hanson PJ, Bernhardt E, DeAngelis P, Norby RJ, Pregitzer KS (2004) A multi-year synthesis of soil respiration responses to elevated atmospheric CO<sub>2</sub> from four forest FACE experiments. *Global Change Biol* 10:1027–1042
- Körner C, Asshoff R, Bignucolo O, Hättenschwiler S, Keel SG, Pelaez-Riedl S, Pepin S, Siegwolf RTW, Zotz G (2005) Carbon flux and growth in mature deciduous forest trees exposed to elevated CO<sub>2</sub>. *Science* 309:1360–1362
- Körner C, Morgan J, Norby RJ (2006) CO<sub>2</sub> enrichment: from plot responses to landscape consequences. In: Canadell J, Pataki D, Pitelka L (eds) *Terrestrial ecosystems in a changing world*. Springer, Berlin Heidelberg New York (in press)
- Luo Y, White LW, Canadell JG, DeLucia EH, Ellsworth DS, Finzi A, Lichter J, Schlesinger WH (2003) Sustainability of terrestrial carbon sequestration. A case study in Duke Forest with inversion approach. *Global Biogeochem Cycles* 17:1021



- Luo Y, Su B, Currie WS, Dukes JS, Finzi A, Hartwig U, Hungate B, McMurtrie RE, Oren R, Parton WJ, Pataki DE, Shaw MR, Zak DR, Field CB (2004) Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide. *BioScience* 54:731–739
- Matamala R, González-Meler MA, Jastrow JD, Norby RJ, Schlesinger WH (2003) Impacts of fine root turnover on forest NPP and soil C sequestration potential. *Science* 302:1385–1387
- Neher DA, Weicht TR, Moorhead DL, Sinsabaugh RL (2004) Elevated CO<sub>2</sub> alters functional attributes of nematode communities in forest soils. *Funct Ecol* 18:584–591
- Norby RJ, Iversen CM (2006) Nitrogen uptake, distribution and turnover in a CO<sub>2</sub>-enriched sweetgum forest. *Ecology* 57:5–14
- Norby RJ, Wullschlegel SD, Gunderson CA, Johnson DW, Ceulemans R (1999) Tree responses to rising CO<sub>2</sub>: implications for the future forest. *Plant Cell Environ* 22:683–714
- Norby RJ, Todd DE, Fuels J, Johnson DW (2001) Allometric determination of tree growth in a CO<sub>2</sub>-enriched sweetgum stand. *New Phytol* 150:477–487
- Norby RJ, Hanson PJ, O'Neill EG, Tschaplinski TJ, Weltzin JF, Hansen RT, Cheng W, Wullschlegel SD, Gunderson CA, Edwards NT, Johnson DW (2002) Net primary productivity of a CO<sub>2</sub>-enriched deciduous forest and the implications for carbon storage. *Ecol Appl* 12:1261–1266
- Norby RJ, Sholtis JD, Gunderson CA, Jawdy SS (2003) Leaf dynamics of a deciduous forest canopy: no response to elevated CO<sub>2</sub>. *Oecologia* 136:574–584
- Norby RJ, Ledford J, Reilly CD, Miller NE, O'Neill EG (2004) Fine-root production dominates response of a deciduous forest to atmospheric CO<sub>2</sub> enrichment. *Proc Natl Acad Sci USA* 101:9689–9693
- Riggs JS, Tharp ML, Norby RJ (2003a) ORNL FACE weather data (<http://cdiac.ornl.gov/programs/FACE/ornldata/weatherfiles.html>). Carbon Dioxide Information Analysis Center, Oak Ridge, Tenn.
- Riggs JS, Tharp ML, Norby RJ (2003b) ORNL FACE CO<sub>2</sub> data (<http://cdiac.ornl.gov/programs/FACE/ornldata/CO2files.html>). Carbon Dioxide Information Analysis Center, Oak Ridge, Tenn.
- Sanders NJ, Belote RT, Weltzin JF (2004) Multi-trophic effects of elevated CO<sub>2</sub> on understory plant and arthropod communities. *Environ Entomol* 33:1609–1616
- Sholtis JD, Gunderson CA, Norby RJ, Tissue DT (2004) Persistent stimulation of photosynthesis by elevated CO<sub>2</sub> in a sweetgum (*Liquidambar styraciflua* L.) forest stand. *New Phytol* 162:343–354
- Sinsabaugh RL, Saiya-Cork K, Long T, Osgood MP, Neher DA, Zak DR, Norby RJ (2003) Soil microbial activity in a *Liquidambar* plantation unresponsive to CO<sub>2</sub>-driven increases in primary productivity. *Appl Soil Ecol* 24:263–270
- Six J, Elliott ET, Paustian K (2000) Soil macroaggregate turnover and microaggregate formation mechanism for C sequestration under no-tillage agriculture. *Soil Biol Biochem* 32:2099–2103
- Tissue DT, Lewis JD, Wullschlegel SD, Amthor JS, Griffin KL, Anderson OR (2002) Leaf respiration at different canopy positions in sweetgum (*Liquidambar styraciflua*) grown in ambient and elevated concentrations of carbon dioxide in the field. *Tree Physiol* 22:1157–1166
- Van Mieghroet H, Norby RJ, Tschaplinski TJ (1994) Optimum nitrogen fertilization in a short-rotation sycamore plantation. *For Ecol Manage* 64:25–40
- Wullschlegel SD, Norby RJ (2001) Sap velocity and canopy transpiration for a 12-year-old sweetgum stand exposed to free-air CO<sub>2</sub> enrichment. *New Phytol* 150:489–498



Wullschleger SD, Gunderson CA, Hanson PJ, Wilson KB, Norby RJ (2002) Sensitivity of stomatal and canopy conductance to elevated CO<sub>2</sub> concentration – interacting variables and perspectives of scale. *New Phytol* 153:485–496

Zak DR, Holmes WE, Finzi AC, Norby RJ, Schlesinger WH (2003) Soil nitrogen cycling under elevated CO<sub>2</sub>: a synthesis of forest FACE experiments. *Ecol Appl* 13:1508–1514