Ecological Lessons from Free-Air CO_2 Enrichment (FACE) Experiments

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Abstract

Free-air CO_2 enrichment (FACE) experiments have provided novel insights into the ecological mechanisms controlling the cycling and storage of carbon in terrestrial ecosystems and contribute to our ability to project how ecosystems respond to increasing CO_2 in the Earth's atmosphere. Important lessons emerge by evaluating a set of hypotheses that initially guided the design and longevity of forested FACE experiments. Net primary productivity is increased by elevated CO_2, but the response can diminish over time. Carbon accumulation is driven by the distribution of carbon among plant and soil components with differing turnover rates and by interactions between the carbon and nitrogen cycles. Plant community structure may change, but elevated CO_2 has only minor effects on microbial community structure. FACE results provide a strong foundation for next-generation experiments in unexplored ecosystems and inform coupled climate-biogeochemical models of the ecological mechanisms controlling ecosystem response to the rising atmospheric CO_2 concentration.

INTRODUCTION

eCO_2: elevated concentration of CO_2 in atmosphere

FACE: free-air CO_2 enrichment

During the past two centuries—a tiny sliver of time since life first appeared on Earth—human activity has released vast amounts of carbon (C) into the atmosphere as carbon dioxide (CO_2). Before the industrial revolution, this C had been sequestered for millennia in fossilized deposits of organic matter. From the perspective of geologic time, the transfer of C from these deposits to the atmosphere is like an explosion. From the human perspective, it is a consequence of modern life that, if unabated, will continue to alter the radiation balance of Earth and warm our planet.

Early efforts to evaluate the potential for human-induced climate change included simple analyses of the terrestrial biosphere and the global C budget (Bacastow & Keeling 1973). Fluxes of C into and out of the terrestrial biosphere are roughly in balance, i.e., the annual uptake of C in photosynthesis approximates C released during respiration. Imbalances between uptake and release that occur over very long time frames [e.g., in relation to orbital oscillations (Prentice et al. 2011)] or over much shorter time frames [e.g., global response to volcanic eruptions (Gu et al. 2003) or El Niño events (Zeng et al. 2005)] are reflected in the atmospheric CO_2 concentration, but the sustained and very rapid rise in atmospheric CO_2 over the past two centuries is unprecedented. After accounting for increases in atmospheric C content, the net uptake of C into oceans, and C losses attributable to land-use change, the amount of C from fossil fuel releases that is not accounted for—the "missing sink"—is assumed to result from uptake (i.e., photosynthesis) by the terrestrial biosphere in excess of terrestrial respiration (Field 2001, Canadell et al. 2007). What, then, is the basis for a sustained imbalance between photosynthesis and respiration? A prominent hypothesis is that, as the atmospheric CO_2 concentration increases, the CO_2 acts as a fertilizer for plant growth, which in turn leads to additional storage of organic matter in plant biomass and detritus. Increased C storage in the terrestrial biosphere creates a negative feedback on the rate of CO_2 accumulation in the atmosphere (Cramer et al. 2001, Bonan 2008). Will this CO_2 fertilization effect persist into the future as atmospheric CO_2 reaches much higher concentrations? If so, the trajectory of climate change will be moderated (Matthews 2007).

There is strong, physiological evidence that CO_2 enrichment increases plant growth. Crop and horticultural plants were the focus of early experiments investigating plant growth under elevated CO_2 (eCO_2), often with the goal of informing management of commercial greenhouses to maximize plant growth and development (Wittwer & Robb 1964). Recognizing the emerging importance of eCO_2 in the context of the global C cycle, Kramer (1981) questioned whether trees, which are most often limited by water or nutrient supply, would benefit from eCO_2 in the same way as crop plants. In so doing, he shifted the focus of research from the fields of agronomy and plant physiology to ecology and global C cycling. Trees, and the forest ecosystems in which they live, dominate the annual C fluxes of the terrestrial biosphere (Melillo et al. 1993, Bonan 2008), but the interaction of eCO_2 with the long-term processes that define tree growth and forest ecology are not revealed in short-term experiments with annual crop plants in fertilized soil. For relevance to the global C cycle, longer-term experiments with trees under conditions relevant to forest ecosystems were needed. Unfortunately, years of study have struggled against two immutable facts: Trees are big, and they live a long time.

The size and longevity of trees means that manipulative experiments with future atmospheric CO_2 concentrations cannot be conducted for a full life cycle. A number of trade-offs in experimental design and measurement protocol are inevitably required to accommodate processes that occur at the spatial scale of trees and forests. The physiological potential for responses to eCO_2 were revealed in experiments with tree seedlings and saplings in growth chambers, greenhouses, or outdoor field chambers, but many questions about the projected responses of intact forest ecosystems over several decades were left unanswered. The advent of free-air CO_2 enrichment (FACE) technology, and its application to forest ecosystems (Hendrey et al. 1999), significantly extended the spatial and temporal scales that could be investigated and revealed long-term, ecosystem-level responses. Many FACE experiments have now reached their end, as agencies invest in other high-priority questions of global importance (Luo et al. 2011). It is appropriate, then, to explore what lessons we learned from FACE experiments. We do so with a focus on the ecological mechanisms in forests that are most important for informing C cycling models that are coupled to climate models.

OTC: open-top chamber

HYPOTHESES TO GUIDE FACE RESEARCH

Ecosystem experiments are best done in intact ecosystems that capture the (*a*) integration of physiological processes of plants and soil microorganisms to eCO_2; (*b*) complexities of plant-soil interactions and feedbacks; and (*c*) varying influences of multiple, fluctuating, and interacting climatic conditions. Open-top chambers (OTCs) and other open or closed field chambers were adequate for whole-ecosystem experiments in relatively small-statured ecosystems, and they afforded the opportunity to grow tree seedlings and saplings in unconstrained soil for several growing seasons. However, whole-ecosystem studies were precluded for most forest ecosystems. Nevertheless, field-chamber experiments with tree species were valuable for determining whether short-term physiological responses to eCO_2 would persist under field conditions (Norby et al. 1999). Many of the responses observed in OTC experiments with young trees could be considered ecologically relevant; however, the experiments also highlighted our inability to extrapolate the response of small trees growing in small chambers to that of mature forest ecosystems distributed across the planet. The critical questions that needed to be addressed concerned how responses to eCO_2 would change during stand development as tree ontogeny changed, biogeochemical cycles adjusted, and plant and microbial communities responded. Those critical questions, coupled with the strong foundation of the physiological responses of plants to eCO_2 that were revealed in OTC experiments, gave rise to hypotheses designed to guide the FACE experiments that followed.

FACE experiments have been implemented in a wide variety of ecosystems including agroecosystems; a desert; grasslands; bogs; and deciduous, evergreen, and alpine forests (**http://public.ornl.gov/face**). Here, we focus on the responses of forest ecosystems but recognize that responses of other ecosystem types can provide useful information for interpreting the forest experiments. The plots in many FACE experiments are as large as 30 m in diameter and can accommodate trees up to 25-m tall—much larger than a typical OTC of 3-m diameter and 3-m tall. Pure CO_2, or air enriched with CO_2, is released into the wind from vent pipes surrounding the plots. The flow rate of CO_2 into the plots is continuously adjusted by a computer-controlled system to regulate the CO_2 concentration at the center of the plot to the desired set point, typically 550–580 ppm. Important advantages afforded by the FACE approach are the larger size that permitted longer-duration experiments with forest stands and the avoidance of artifacts associated with chamber walls (Hendrey et al. 1999). Most of the forested FACE experiments were conducted in young, planted tree stands rather than in mature, complex, native forests: *Pinus taeda* (loblolly pine) plantation in North Carolina (Duke-FACE) (Hendrey et al. 1999), *Populus tremuloides* (trembling aspen) and aspen mixed with maple (*Acer saccharum*) or birch (*Betula papyrifera*) in Wisconsin (Rhinelander-FACE) (Karnosky et al. 2003), *Populus* clones in Italy (POPEuro-FACE) (Liberloo et al. 2009), and *Liquidambar styraciflua* (sweetgum) in Tennessee (ORNL-FACE) (Norby et al. 2002), but an exception to this generalization was an experiment in a mixed-deciduous forest in Switzerland (Web-FACE) (Körner et al. 2005), in which the crowns of individual tall, mature trees were exposed to eCO_2. This experiment illustrates the trade-offs that are necessary in all experiments: It provided valuable data on responses of mature forest trees that were otherwise

LAI: leaf area index

unobtainable from plantation-based FACE experiments, but the focus of the measurements was necessarily the tree rather than the forest ecosystem. Other experiments with smaller-scale woody systems in an alpine environment (Handa et al. 2006) and in oak scrublands (Hymus et al. 2003) also provide useful ecological insights.

Now, with the conclusion of many of the FACE experiments, it is timely to look back at the hypotheses that were formulated before the experiments began and evaluate them using the knowledge gained over the past decade from FACE experiments. Six of these hypotheses were originally proposed (Norby et al. 1999) to highlight ecosystem-scale questions that limited our ability to project forest responses from the results of experiments with young trees in OTC experiments—questions that required larger-scale experiments such as FACE to address. In the sections of this review that follow, we repeat the hypotheses verbatim, while recognizing that we would most certainly revise them if newly written today. In so doing, it should become clear that the scientific method works: Observations lead to hypotheses, which are tested in new experiments, and a richer understanding emerges. We expect this process to continue: FACE experiments should facilitate the testing of new, specific, and well-defined hypotheses that guide the development of ecosystem models of the long-term forest response to changing environmental conditions.

HYPOTHESIS 1: LEAF AREA INDEX

Leaves are the primary point of interaction among atmospheric CO_2, energy (light), and plant physiology. The amount of leaf area, and how that leaf area is displayed in space and time, is a primary determinant of productivity. Increased leaf area production in eCO_2 was frequently observed in OTC experiments (Norby et al. 1995), but these observations on young trees that were in an exponential growth phase and not yet competing with neighbors were not informative about the potential responses that would occur in a forest stand where stand-level leaf area index (LAI) is constrained by resource availability, e.g., water, nutrients, or light. Hence, the response of forest LAI to eCO_2 was a first-order uncertainty remaining at the end of the OTC experiments. From what was known in 1999, reasonable hypotheses could have been proposed projecting increased, decreased, or no change in LAI in CO_2-enriched forests. Our hypothesis was based on observations on seedlings that showed the light compensation point for photosynthesis to increase in eCO_2 (Hättenschwiler 2001), suggesting that trees in eCO_2 may be able to retain leaves deeper in the canopy.

Hypothesis 1 Defined

"Maximum LAI will increase in elevated CO_2 because shaded leaves deep in the canopy will be retained longer" (Norby et al. 1999). FACE experiments provided the first opportunity to assess critically whether LAI of closed-canopy forest stands would increase in eCO_2. In six tree stands that had reached canopy closure (i.e., had attained a quasi-stable LAI), the response to eCO_2 varied from a 43% increase to an 8% decrease. The variation is not random: Stands with low LAI (<3.5) had a larger response than did stands with high LAI (>5) (**Figure 1**). Given that the global mean of LAI in temperate broadleaf forests is 5.1 (Asner et al. 2003), stands approaching or exceeding this value apparently do not have a capacity for increasing LAI. However, even in ORNL-FACE with high LAI, eCO_2 caused modest increases in peak LAI in some years. LAI was 8–9% greater in eCO_2 in years without a midseason drought, but in drought years, leaf abscission was accelerated in eCO_2 such that late-season LAI was reduced, with carry-on effects the following year (Warren et al. 2011a).

Hypothesis 1 suggests that eCO_2 could alleviate a constraint on LAI by altering crown architecture, but assessments of crown architecture were difficult in intact forest stands until trees were

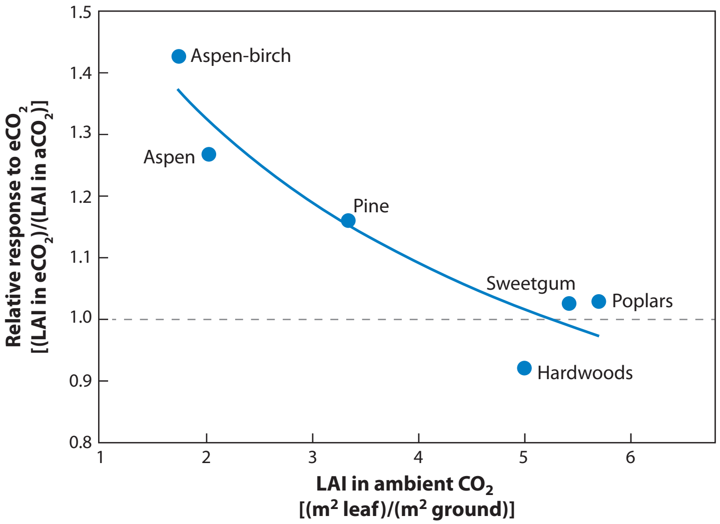

Figure 1

The response of leaf area index (LAI) to elevated CO$_2$ (eCO$_2$) in five free-air CO$_2$ enrichment (FACE) experiments varied with LAI in ambient plots. Aspen and aspen-birch: Rhinelander-FACE, plots from year 2000 for ambient ozone treatments only (Karnosky et al. 2003). Pine: Duke-FACE, total pine plus hardwood LAI, average over 1999–2004 (McCarthy et al. 2007). Sweetgum: ORNL-FACE, average over 1998–2008, data online at **http://public.ornl.gov/face/ORNL/ornl_data_plantresponse.shtml**. Hardwoods: Web-FACE, average of all species over 2002–2004, LAI in ambient CO$_2$ (aCO$_2$) is approximate (Körner et al. 2005). Poplars: PopEuro-FACE, average of three species over 2002–2004 (Liberloo et al. 2006). Regression line: $y = 1.56–0.34 \ln(x)$; $R^2 = 0.89$.

harvested at the end of experiments. In ORNL-FACE, 12 years of growth in eCO$_2$ did not affect crown structure. Although the crown had advanced in height above the ground, crown depth and the vertical distribution of leaf area within the crown had not changed through time or with eCO$_2$ (R.J. Norby, unpublished data). eCO$_2$ also had no effect on the vertical distribution of leaf area in PopEuro-FACE (Gielen et al. 2003). In Duke-FACE, eCO$_2$ had a modest effect: Pine leaf area tended to move upward in eCO$_2$ with a ∼6% increase in crown length (McCarthy et al. 2007).

Conclusion from FACE

Hypothesis 1 is not supported as stated. Nevertheless, there is evidence that eCO$_2$ can increase LAI after canopy closure in stands with relatively low LAI. However, there is no evidence that eCO$_2$ can substantially increase the ultimate leaf-area carrying capacity of a site.

HYPOTHESIS 2: TREE GROWTH

Although tree growth response to eCO$_2$ is fundamental to the overarching questions about CO$_2$ fertilization and feedbacks to the atmosphere, a relevant evaluation of this response in the OTC experiments with young trees was difficult. Trees undergoing an expanding canopy and exponential growth often exhibited very large growth responses to eCO$_2$ (Idso & Kimball 1993, Norby et al. 1995), but such responses cannot (or should not) be extrapolated to the global C cycle. Normalizing growth data to a constant LAI provided an expression more relevant to the growth of forest stands in which leaf area is constrained (Norby 1996). The relevance of this growth index to C cycle analyses rested on the assumption that growth per unit leaf area was a robust response that would persist after canopy closure. This assumption could not be tested until FACE experiments produced data on growth responses following canopy closure.

DMI: dry matter increment

NPP: net primary productivity

Hypothesis 2 Defined

"Annual tree growth per unit LAI will continue to be enhanced by CO_2 after canopy closure" (Norby et al. 1999). Continuous estimates of tree growth, expressed as dry matter increment (DMI), were obtained through application of site-specific allometric equations (McCarthy et al. 2010, Norby et al. 2001) to nondestructive measures of aboveground stem growth, including basal cross-sectional area, height, and taper. In ORNL-FACE, DMI was significantly greater in eCO_2 during the first year of treatment. However, this response did not persist (Norby et al. 2002), and by the end of the experiment, there was no treatment effect (Norby et al. 2010). Similarly, some trees in Web-FACE apparently had a very large response to the first-year exposure to eCO_2, but the response was not sustained (Körner et al. 2005). However, DMI of *Pinus taeda* trees was increased by eCO_2 throughout 10 years in Duke-FACE (McCarthy et al. 2010). Species differences in stem growth response were indicated in the Swiss tree line study: The indeterminate growth strategy of early successional *Larix decidua* trees was associated with a 41% increase in radial stem growth over 4 years in eCO_2, whereas the later successional *Pinus uncinata* trees showed no change in ring width (Handa et al. 2006).

Although conceptually simple and economically important, DMI is not the best metric for analyzing FACE results in an ecological context. A better measure is net primary productivity (NPP), or the total amount of organic C entering the ecosystem. NPP comprises fluxes into C pools with very different turnover rates (e.g., wood versus ephemeral leaves and fine roots). Although NPP does not represent ecosystem C storage (Körner 2006), it provides a better linkage to calculations and modeling of whole-ecosystem C storage than does aboveground stem growth alone. NPP increased 23% in eCO_2 in four experiments in forest ecosystems with relatively constant LAI, and the response was robust across a broad range of productivity (Norby et al. 2005). Although all four experiments were located in tree plantations in the temperate zone, their range in productivity was similar to the range in forest productivity across all Earth (Field et al. 1998). Where LAI was high, most of the stimulation in NPP was attributable to an increase in NPP per unit leaf area. At lower LAI, increases in absorbed photosynthetically active radiation were more important. This synthetic analysis provided a useful benchmark for ecosystem and global models used in coupled carbon cycle–climate modeling (Friedlingstein et al. 2006, Hickler et al. 2008, Matthews 2007). However, the analysis concealed important sources of variation. For example, in Duke-FACE, there was plot-to-plot variation in NPP response, which was closely related to differences in nitrogen (N) availability among plots (Finzi et al. 2002). Interannual variation in NPP response to eCO_2 was apparent in ORNL-FACE, but much of that variation collapsed when NPP was expressed per unit leaf area.

The physiological basis for an increase in NPP per unit leaf area is the increase in leaf-level photosynthesis. FACE experiments confirmed that photosynthetic C uptake increases in response to eCO_2 under field conditions, and the enhancement is sustained over time (Ainsworth & Long 2004). Enhancement of photosynthesis in eCO_2 with no sign of photosynthetic downregulation was observed in the 35-m tall, 100-year-old deciduous trees in the Web-FACE experiment after 8 years of CO_2 enrichment (Bader et al. 2010). The maintenance of this primary physiological response in older and larger forest-grown trees provides a measure of confidence that the responses measured in the younger plantation trees of other FACE experiments are relevant for addressing questions of longer-term forest response to eCO_2. It remains to be determined whether the responses observed in these FACE experiments apply as well to tropical forests and high-latitude ecosystems (Hickler et al. 2008, Luo et al. 2011).

Conclusion from FACE

Net primary production per unit LAI can be enhanced by eCO_2 after canopy closure. Other environmental factors, however, may constrain this response over time (see Hypothesis 4).

HYPOTHESIS 3: FINE-ROOT PRODUCTION

The importance of root growth and root-soil interactions to integrated analyses of plant responses to eCO_2 has long been known (Rogers et al. 1994), but as with leaf area, fine-root growth responses must be separated from ontogenetic effects to be relevant to a fully developed forest ecosystem. On the basis of observations of trees in OTCs with expanding root systems, it was reasonable to suggest that C allocation to root systems, and therefore root production, should increase in eCO_2. However, it also was reasonable to predict that, in a closed-canopy forest, the root system has attained its maximum size and does not have the capacity to increase the standing crop with eCO_2. Hence, the turnover rate of the root population (production divided by standing crop) would necessarily increase if root production is stimulated by eCO_2. The distinction between responses of root standing crop and root turnover is important for higher-order responses: Root standing crop constrains nutrient uptake, whereas root turnover directly impacts C cycling.

Hypothesis 3 Defined

"Fine-root [standing crop] will not change in elevated CO_2 but fine-root turnover will increase" (Norby et al. 1999). FACE experiments have displayed a wide range of fine-root responses to eCO_2, from large increases (Iversen et al. 2008) to no response (Handa et al. 2008), and one suggestion of a negative response (Bader et al. 2009). Identifying the ecological attributes that predict fine-root responses remains challenging. In ORNL-FACE, fine-root production displayed little response to eCO_2 for the first 2 years of enrichment, but root-length production in eCO_2 doubled after 3 years (Norby et al. 2004) and remained significantly enhanced for 5 more years before declining to values similar to those in ambient CO_2 (Ledford et al. 2008). Across all years, eCO_2 increased fine-root biomass production, mortality, and peak standing crop approximately twofold, whereas root population turnover decreased (Iversen et al. 2008). Therefore, Hypothesis 3 was not supported in ORNL-FACE. Other analysis suggested that turnover should decrease in eCO_2 if root N concentration, and therefore respiration, were reduced (Eissenstat et al. 2000). However, decreased root turnover in ORNL-FACE was associated not with lower root [N] but with slower turnover of roots produced deeper in the soil (Iversen et al. 2008). Fine-root production, mortality, and standing crop also increased in eCO_2 in Duke-FACE, but in contrast with ORNL-FACE, root turnover rate was not altered (Pritchard et al. 2008). Fine-root responses to eCO_2 were much smaller than at ORNL, reflecting slower root turnover in the pine stand (Matamala et al. 2003). Fine-root production and standing crop also increased with eCO_2 in Rhinelander-FACE with no change in turnover rate (Pregitzer et al. 2008), although here the eCO_2-specific responses may be confounded with an expanding root system. Fine-root growth may be less responsive to eCO_2 in late-successional ecosystems, such as in an ericaceous dwarf shrub community at the tree line in the Swiss Alps (Handa et al. 2008). After 4 years of CO_2 enrichment at this site, only 30% of new fine-root biomass had been formed with newly fixed C, indicating slow root turnover. Although some species showed significant aboveground responses to eCO_2, there was no stimulation of root growth.

PNL: progressive nitrogen limitation

SOM: soil organic matter

It is often assumed that the majority of fine roots resides in the upper 10 to 30 cm of soil, and data will support this assumption if one looks no deeper. An unexpected observation from many FACE experiments was an increase in fine-root production at deeper soil depths under eCO_2. In ORNL-FACE, more than half of the increases in root production and peak standing crop under eCO_2 occurred at soil depths of 30 to 60 cm (Iversen et al. 2008, Norby et al. 2004). Deeper rooting distributions under eCO_2 appear to be a general phenomenon in forests: Three-quarters of FACE and OTC experiments with woody plants that examined rooting depth reported deeper distributions in eCO_2 (Iversen 2010). Rooting distribution should have consequences for both C and N cycling throughout the soil profile. For example, by producing more roots deeper in the soil, trees in eCO_2 may have access to more N (Iversen et al. 2011, McKinley et al. 2009).

Conclusion from FACE

The hypothesis as written is rejected. However, the premise behind the hypothesis was valid: In most FACE experiments, the root population was not expanding in ambient CO_2 and appeared to have attained its maximum standing crop for the site. Furthermore, fine-root production and throughput of root biomass into the soil increased in eCO_2 in most experiments, as suggested in the hypothesis. However, fine-root standing crop also increased with eCO_2 in some experiments, so population turnover rate was not greater.

HYPOTHESIS 4: NITROGEN CYCLING

Kramer (1981) speculated that "increasing the CO_2 concentration will have little effect [on photosynthesis and biomass production] if. . . the use of photosynthate is limited by lack of nitrogen." There are strong linkages between C and N cycles in all terrestrial ecosystems, and N availability is well documented to limit the productivity of many forests. However, conclusions based on a simplistic invocation of Liebig's Law of the Minimum do not hold: Controlled environment experiments demonstrated that N deficiency does not preclude a growth response to eCO_2 (Norby et al. 1986). Nevertheless, many model analyses assumed that CO_2 responses will not persist because of N limitation (e.g., Comins & McMurtrie 1993, Rastetter et al. 1992).

Hypothesis 4 Defined

"Down-regulation of tree growth responses will occur through long-term changes in the N cycle" (Norby et al. 1999). As FACE experiments proceeded, a new hypothesis was developed to describe the interaction between eCO_2 and the N cycle in forests. The progressive nitrogen limitation (PNL) hypothesis proposes that plant growth in eCO_2 sequesters N in wood or soil organic matter (SOM), leading to reduced N availability and negative feedback on growth (Luo et al. 2004). FACE experiments provided an opportunity to test this hypothesis, which requires observations over multiple years. Evidence supporting PNL emerged from FACE studies in grasslands (Hovenden et al. 2008, Reich et al. 2006). Initial analyses of forest FACE experiments, however, failed to show evidence for PNL. Although the forests were N limited, NPP remained enhanced in eCO_2, and there was no indication of diminished N availability or uptake (Norby & Iversen 2006, Zak et al. 2007a). Finzi et al. (2007) concluded that forests in eCO_2 compensated for limited N availability through various mechanisms that led to increased N uptake and continued response of NPP to eCO_2. These mechanisms could include increased soil exploration by fine roots and stimulation of N mineralization by fungal activity. Ecosystem models were not representing C-N interactions well enough to simulate the observed responses of N uptake (Finzi et al. 2007).

After initial analysis rejecting the occurrence of PNL in ORNL-FACE, the forest response changed. NPP in ambient CO_2 began to decline as a consequence of N deficiency occurring during stand development. As NPP declined and the N deficiency increased, forest response to eCO_2 also declined (Norby et al. 2010). The experiment no longer supported the premise that the CO_2 fertilization effect would be sustained. In support of the PNL hypothesis, ^{15}N analysis of leaf litter indicated that N availability in soil was declining, and it was declining faster in eCO_2 (Garten et al. 2011). An unanswered question has been why the negative feedback through the N cycle developed in ORNL-FACE and not in other forested FACE experiments. There may be a fundamental difference in the biology of the various systems, such as a reliance on ectomycorrhizae as opposed to arbuscular mycorrhizae (Drake et al. 2011). Another possibility is that downregulation of forest growth response would have occurred across all experiments given enough time. Tissue turnover times are faster in the ORNL sweetgum stand than in the Duke-FACE pine stand, which may have accelerated the development of N limitation. Although these questions cannot currently be answered, results from ORNL-FACE highlight the important need for models to represent the N cycle better if we are to have confidence in their predictions about the C cycle.

Conclusion from FACE

The hypothesis is supported by ORNL-FACE but not by other forest FACE experiments.

HYPOTHESIS 5: WATER USE

A primary effect of eCO_2 is to reduce stomatal conductance to water vapor through partial stomatal closure (Morison 1985). This response has been observed in short-term studies, and it persists over time under field conditions. Stomatal conductance decreased 21% in eCO_2 across all OTC experiments with trees, with a smaller response in needle-leaf species and no evidence of acclimation (Medlyn et al. 2001). For changes in stomatal conductance under eCO_2 to be ecologically relevant, however, responses must scale to altered tree water use and whole-stand hydrology. In many experiments, reductions in stomatal conductance in eCO_2 were associated with increased leaf area such that total water use was not altered (Wullschleger et al. 2002b). In plant canopies with large LAI, leaf boundary layer and aerodynamic conductance were more important to water use than were CO_2 effects on stomatal conductance (Wullschleger et al. 2002b). Hence, instantaneous leaf-level responses are often attenuated at the whole-plant level (Morison 1985), i.e., tree water use is decoupled from eCO_2 effects on stomatal conductance.

Hypothesis 5 Defined

"Tree water use will be decoupled from any persistent [elevated] CO_2 effects on stomatal conductance" (Norby et al. 1999). FACE experiments have confirmed the persistence of stomatal closure as a primary physiological response to eCO_2 in some experiments, but the magnitude of the response varied widely (4–44%) (Warren et al. 2011a). The reduction in stomatal conductance initially observed in Rhinelander-FACE disappeared in the later years in the experiment (Uddling et al. 2009), and in Duke-FACE, stomatal conductance in pine was not reduced initially (Schäfer et al. 2002). Mature forest trees in Web-FACE exhibited reduced stomatal conductance in eCO_2 (~10%), but responses were species specific and were sometimes obscured by feedbacks through soil moisture (Keel et al. 2007).

At the scale of the forest stand, a reduction in canopy conductance in Duke-FACE was not a direct CO_2 effect at the leaf level but rather an indirect effect of shading due to slightly increased LAI and adjustments in the hydraulic pathway (Domec et al. 2009, 2010). Despite transient effects of eCO_2 on LAI in ORNL-FACE, the relative effect on transpiration remained fairly constant, probably reflecting the plasticity of the stomatal response (Warren et al. 2011b). Responses diminished as the scale of observation increased from leaf to canopy to whole-stand evapotranspiration; nevertheless, tree water use was not decoupled from effects on stomatal conductance (Wullschleger et al. 2002a).

Responses of stomatal conductance and stand-level transpiration to eCO_2 may be small and subtle, but water has such a fundamental role in shaping ecological processes that the follow-up effects could be large. FACE experiments indicated that reductions in canopy transpiration in eCO_2 will be reflected in increased soil water content in temperate deciduous forests, barring any compensating effects on LAI (Warren et al. 2011b). Models support the premise that potential water yield would increase in eCO_2 (Warren et al. 2011b), but experimental results suggest that increases in runoff due to the direct effect of eCO_2 on stomatal conductance are small relative to the influence of rainfall pattern (Leuzinger & Körner 2010). Increased soil moisture in eCO_2 altered N dynamics in the Jasper Ridge multifactor FACE experiment in a grassland ecosystem (Hungate et al. 1997). In contrast to the normal water-saving aspect of reduced conductance in eCO_2, stomatal closure can also increase susceptibility to severe drought, as evidenced by premature leaf fall in eCO_2 during an extraordinarily hot, dry year in ORNL-FACE (Warren et al. 2011a).

Conclusion from FACE

Hypothesis 5 has been rejected. Effects of eCO_2 on stomatal conductance are generally reflected in stand-level transpiration, although the relationship is moderated by internal feedbacks and stand structure.

HYPOTHESIS 6: STAND COMPOSITION

In describing responses of young trees to eCO_2 over several growing seasons under field conditions, OTC experiments addressed many of the physiological and biogeochemical responses that will determine long-term forest response to CO_2 enrichment. However, two critical elements of forest response remained highly uncertain: forest-stand establishment and responses after canopy closure. Tree establishment is a multistep process including flowering, seed production, seed dissemination, germination, and early growth. The outcome depends on stochastic processes and on many environmental filters and is highly variable (Dickie et al. 2007). Hence, tree establishment has not been widely studied in FACE or other manipulative experiments, but the hypothesis conceived at the conclusion of the OTC experiments is nevertheless relevant.

Hypothesis 6 Defined

"Differential effects of [elevated] CO_2 on competing species during establishment phase will alter long-term stand composition and productivity" (Norby et al. 1999). With the exception of Rhinelander-FACE, which was uniquely designed to understand how eCO_2 influences competitive interactions among tree species and aspen genotypes that differ in growth response to eCO_2, most of the evidence that exists to evaluate Hypothesis 6 comes from observations of separate phases of establishment, coupled with speculation about the possible long-term implications.

Several FACE experiments have been of long enough duration to reveal effects of eCO_2 on flowering and seed production. Pine trees in Duke-FACE matured earlier in eCO_2 and produced more seeds per unit basal area compared with trees in ambient CO_2 (Ladeau & Clark 2006); the doubling of seed production in eCO_2 was not accompanied by any effect on seed mass, viability, or nutrient content, which contrasts with observations that had been made on herbaceous species (Way et al. 2010). In Rhinelander-FACE, eCO_2 increased the flowering, seed mass, germination rate, and seedling vigor of birch trees (Darbah et al. 2008).

Given the importance of forest regrowth following agricultural abandonment to the global C cycle (Albani et al. 2006), the processes that control encroachment of woody plants into grasslands have been a prominent issue, especially because increasing CO_2 concentration may have accelerated woody thickening in the past (Prentice et al. 2011) and could continue to do so in the future (Bond & Midgley 2000). eCO_2 increased survival and growth of *Quercus ellipsoidalis* seedlings under hot and dry conditions in a bare and unshaded area of their old-field assemblages within FACE rings in Minnesota, thereby expanding the establishment windows for trees encroaching into a grassland (Davis et al. 2007). Although eCO_2 had no direct effects on tree seedling emergence or establishment in old-field assemblages in a multifactor OTC experiment, eCO_2 indirectly moderated the deleterious effects of warming on seedling establishment through its effects on soil moisture (Classen et al. 2010). In contrast, eCO_2 had no effect on seedling survivorship of annuals or perennials in a grassland FACE study in Tasmania, and it did not make the seedlings more resistant to dry soils resulting from the warming treatment (Hovenden et al. 2008).

Observations of the naturally occurring understory in FACE experiments also provide insights into the possible effects of eCO_2 on forest successional trajectories. In Rhinelander-FACE, eCO_2 increased the growth and acquisition of soil N by both aspen and paper birch, although the latter responded to a much greater extent (Zak et al. 2007b). There also were differential effects on the growth and acquisition of soil N among aspen genotypes. Hence, eCO_2 has the potential to modify inter- and intraspecific competition for soil resources and could alter population genetic structure. Species composition and biomass of the understory herbaceous community in Rhinelander-FACE were driven by the structure of the overstory community and only indirectly affected by the eCO_2 treatment (Bandeff et al. 2006). The hardwood tree understory in Duke-FACE, which accounted for ~10% of the stand's NPP and biomass, was unaffected by time or eCO_2 (McCarthy et al. 2010). The understory in ORNL-FACE increased in importance during the experiment, and total understory biomass was 25% greater in eCO_2 after 10 years. Woody species increased in importance relative to herbaceous species, and this change was especially prominent in eCO_2, suggesting that rising atmospheric $[CO_2]$ could accelerate successional development and have a longer-term impact on forest dynamics (Souza et al. 2010). The N-fixing woody plant *Elaeagnus umbellata* was increasing in dominance in the final years of the experiment and contributing exogenous N to the ecosystem, suggesting longer-term adjustments in the N cycle (L. Souza & R.J. Norby, unpublished results). Legumes increased in abundance in response to eCO_2 in a grassland FACE study in New Zealand, thereby partially offsetting a decline in soil N availability (Newton et al. 2010).

Conclusion from FACE

Elevated CO_2 can affect the growth of forest trees through alterations of both intra- and interspecific competition for soil resources. The observations support the premise that eCO_2 effects on tree establishment and subsequent forest composition could be important. Hypothesis 6 cannot be broadly evaluated because most forest FACE experiments were not designed to test competition or other phases of tree establishment. Understanding how eCO_2 could alter forest composition, and hence growth and C storage, remains an important challenge (Luo et al. 2011).

HYPOTHESIS 7: SOIL MICROBIAL RESPONSES

Biotic communities composed of plants and animals are structured by the availability of limiting resources and competitive interactions, but it remains uncertain whether these same ecological forces shape the composition and function of saprotrophic microbial communities in soil. These organisms compete with one another to harvest energy in plant detritus enzymatically, which results in the return of CO_2 to the atmosphere, the transformation of detritus into SOM, and the release of N into soil for plant uptake. In combination, these processes control the amount of anthropogenic C stored in soil as well as constrain plant growth responses to eCO_2 (Reich et al. 2006, Zak et al. 2000a). The physiological activity of soil microorganisms is largely constrained by the input of organic substrates (Zak et al. 2000b), and OTC experiments showed that eCO_2 effects on leaf litter production, fine roots, and mycorrhizae could change substrate input. If eCO_2 increases resource availability to saprotrophic bacteria and fungi, changes in the structure and function of the soil microbial community could be expected.

Hypothesis 7 Defined

Changes in availability (amount and biochemistry) of organic substrates from plant production will alter the function and composition of the soil microbial community (revised from Zak et al. 2000b). FACE experiments provided a unique and direct manipulation of resource availability (i.e., plant detritus) to saprotrophic microbial communities in relatively intact plant-soil systems and thereby dramatically advanced our understanding of plant-microbe feedbacks that shape microbial community composition and control the cycling and storage of C and N in soil. However, despite the wealth of observations documenting greater detrital production under eCO_2, the change in resource availability appears to have had only a subtle influence on the composition of soil bacteria and fungi, relative to other ecological factors. Molecular surveys of bacteria and fungi growing beneath forest trees exposed to eCO_2 demonstrate significant increases in some bacterial (e.g., *Arthrobacter* spp., *Lechevalieria* spp.), saprotrophic fungal (e.g., *Sistotrema* spp.), and mycorrhizal taxa (*Tylospora* spp., *Russula* spp.) as well as declines in others. However, the vast majority of soil fungi and bacteria did not respond to increased resource availability under eCO_2 (Austin et al. 2009, Chung et al. 2006, Edwards & Zak 2011, Feng et al. 2010, Lesaulnier et al. 2008). Hence, increased detritus production in eCO_2 was insufficient to alter dramatically the overall composition of saprotrophic bacteria and fungi in soil. Other factors exert a greater influence on microbial community composition, including spatial variability in soil properties, temporal changes in environmental conditions, and plant community composition (i.e., differences in litter biochemistry) (Edwards & Zak 2011, Parrent & Vilgalys 2007).

In many experiments, eCO_2 was more likely to accelerate the physiological activity of the extant community rather than alter the microbial community composition. Saprotrophic microorganisms produce extracellular enzymes to forage for energy contained in carbohydrate polymers composing plant cell wall, and because their synthesis can be induced by available substrate, greater rates of extracellular enzyme activity under eCO_2 indicate that greater detrital production (i.e., greater substrate availability) has enhanced saprotrophic activity. Greater rates of cellulolytic (β-glucosidase and cellobiohydrolase) enzyme activity characterize the response of microbial communities in Duke-FACE and Rhinelander-FACE, whereas the response of ligninolytic (phenol oxidase, peroxidases) extracellular enzymes has been inconsistent (Chung et al. 2006, Finzi et al. 2006, Larson et al. 2002). In contrast, microbial enzyme activity and microbial respiration rates were not enhanced in the early (Sinsabaugh et al. 2003) or later stages of ORNL-FACE (Austin et al. 2009). In all these studies, spatial variability in soil properties and temporal variability in environmental conditions (temperature and water potential) appear to exert substantial influences on extracellular enzyme activity. Although the response of extracellular enzymes involved with plant litter decay can be variable, other observations (discussed in Hypothesis 8) support the idea that microbial activity, organic matter decay, and soil N availability can increase under eCO_2 (Drake et al. 2011, Phillips et al. 2011, Talhelm et al. 2009).

Conclusion from FACE

There is only weak support for the hypothesis that increased detrital inputs under eCO_2 will alter microbial community composition. Physiological activity of the microbial community is often accelerated by eCO_2, but the magnitude of response to increased substrate availability is much less than the impacts of other ecological and environmental factors. Given the importance of soil N availability to the ecosystem-level response to eCO_2, resolving the ecological and environmental factors shaping the response of soil microbial communities remains an important challenge.

HYPOTHESIS 8: CARBON CYCLING

Starting from the assumption that the initial effect of eCO_2 would be to increase NPP in most plant communities, Strain & Bazzaz (1983) posed a critical question: Would the increase in NPP lead to a substantial increase in plant biomass, or would the rate of turnover of leaves or roots simply increase without changing plant biomass? If we extend the question to consider total ecosystem C storage and not just plant biomass, we find that the question they elucidated 30 years ago has been fundamentally driving most eCO_2 experiments in unmanaged ecosystems, including FACE experiments. It is a reasonable expectation that we should now be able to answer that question. Unfortunately, whether most of the additional C is stored or cycles faster depends on a host of additional factors and conditions, and the question is not easily answered.

Hypothesis 8 Defined

"The predicted increase in net primary productivity of individual plants and crops may not necessarily mean increased net ecosystem productivity in lightly or unmanaged ecosystems" (Strain & Bazzaz 1983). FACE experiments have provided estimates of all (or most) of the terms necessary for constructing an ecosystem C budget, but combining them into a robust, balanced C budget has proved more difficult. For example, eCO_2 led to a sustained increase in leaf photosynthesis without any compensatory decrease in leaf area in Web-FACE. However, the C gained via photosynthetic stimulation could not be accounted for in other components of the forest stand's C budget, and its fate remains uncertain (Bader et al. 2010, Bader & Körner 2010). Despite uncertainties in C budget estimation, comparison of the C budgets of Duke-FACE and ORNL-FACE highlighted the critical role of C allocation in determining C cycling. The experiments were located in tree plantations of similar stature, stage of development, and climatic zone, and they displayed similar NPP responses to eCO_2 for much of the experiment's duration (Norby et al. 2005). However, the dominant trees displayed different patterns of C allocation, and this trait altered the fate of C and the projections of C storage into the future (DeLucia et al. 2005). The pine forest added C primarily to long-lived woody tissues, whereas the sweetgum forest primarily increased production of short-lived fine roots. Though the pine forest response would seem more favorable for C storage, wood is not a permanent C pool. The residence time of wood in the Duke-FACE ecosystem is only 19 to 27 years (DeLucia et al. 2005), and wood is susceptible to fire, harvesting, and, eventually, decomposition. In contrast to wood, fine roots die and decompose relatively quickly; however, some proportion of root necromass is incorporated into SOM and can be the predominant source of stable C in SOM (Crow et al. 2009). The comparison of C cycling in these two experiments illustrates a key point: The distribution of C among pools of differing residence times depends on physiological differences in plant C partitioning, which ultimately control the capacity of an ecosystem to sequester C (Luo et al. 2003).

Soil processes are an important determinant of the relative partitioning of extra C under eCO_2 between long-term storage versus faster C cycling. However, C flux to belowground pools is especially difficult to evaluate. Increased CO_2 efflux from soil would indicate faster C cycling. FACE studies have generally shown modest increases in CO_2 efflux with eCO_2 (Jackson et al. 2009, King et al. 2004, Lukac et al. 2009). Young, developing forest stands experienced greater stimulation of CO_2 efflux (39% increase in eCO_2) than did the more established stands (16% stimulation) (King et al. 2004). Stimulation of soil CO_2 efflux by eCO_2 increased over time in Duke-FACE (Jackson et al. 2009), but there was no stimulation in cumulative efflux over the growing season in the older, mature forest stand in Web-FACE (Bader & Körner 2010). Greater C inputs to the soil under eCO_2 without a concomitant increase in CO_2 efflux or other losses from soil would imply an increase in SOM. Quantifying change in soil C in eCO_2 was a primary rationale for maintaining FACE experiments for more than a decade because of the inherent difficulty in detecting changes in such a large and variable pool (Billings et al. 2010). FACE experiments have provided a valuable template for many basic studies of soil C cycling processes, but the final evaluation of whether eCO_2 increases SOM remains elusive. After 6 years of CO_2 enrichment in ORNL-FACE, C stocks were significantly greater in the top 5 cm of soil, where inputs from leaf and root litter were greatest (Jastrow et al. 2005). After 12 years, soil C was, on average, 20% greater in eCO_2 throughout the soil column to 90-cm depth (C.M. Iversen, personal communication). There was no effect of eCO_2 on C pools in surface or deep mineral soil horizons in Duke-FACE after 9 years, although there was an increased C sink in the forest floor, which was attributed to increased litterfall in eCO_2 rather than to changes in litter decomposition or chemistry (Lichter et al. 2008). In contrast, SOM accumulated more slowly under eCO_2 beneath the aspen community in Rhinelander-FACE, despite the fact that eCO_2 substantially increased above- and belowground litter production (Talhelm et al. 2009), suggesting that eCO_2 accelerated decomposition. Meta-analyses (de Graaff et al. 2006, Jastrow et al. 2005, Luo et al. 2006, van Groenigen et al. 2006) have come to different conclusions regarding the effect of eCO_2 on soil C. Hungate et al. (2009) concluded from a synthesis of these meta-analyses that the effect of eCO_2 on soil C accumulation was not significant when N inputs were low but increased with addition of N fertilizers. Contrary results were found in a long-term CO_2-enrichment experiment in an agroecosystem (Moran & Jastrow 2010) and in a more recent meta-analysis (Dieleman et al. 2010).

Even our longest FACE experiments may be inadequate for detecting small increases in soil C that are meaningful to ecosystem biogeochemistry and feedbacks to the atmosphere (Luo et al. 2011). Hence, it may be more important to understand the processes involved in soil C dynamics. The soil C pool comprises a wide array of material with vastly different turnover rates, and any assessment of eCO_2 effects on C sequestration must include consideration of the stability of the C pools. Analysis of the ^{13}C content of soil CO_2 efflux in Duke-FACE indicated that 71% came from soil pools with turnover time of $\sim$35 days; the rest came from pools that turn over at decadal time frames (Taneva et al. 2006). Fast oxidation of labile C substrates may limit additional C accumulation in eCO_2 and result in shorter ecosystem C residence times (Taneva et al. 2006). However, unlike the C accumulated in the litter layer in Duke-FACE (Lichter et al. 2008), which is stabilized only through biochemical resistance to decomposition, C accrual in mineral soil resulting from fine-root input can be protected from oxidation by the formation of microaggregates, which provide physical protection of relatively labile SOM from rapid decomposition and facilitate the stabilization into long-lived organomineral complexes (Jastrow et al. 2005, Six et al. 2002). More than half of the C accrued in ORNL-FACE was incorporated into microaggregates, and there was little saturation of this protection mechanism after 5 years (Jastrow et al. 2005). In addition, carbon retained in chaparral soil in response to eCO_2 was more durable in deeper soils than in surface soils (Trueman et al. 2009). Bioturbation, or the mixing of surface litter into deeper soil horizons by soil fauna, may be an important determinant of the capacity of an ecosystem to accumulate soil C (Hoosbeek & Scarascia-Mugnozza 2009).

Sequestration of the newly fixed FACE-derived C into stable compounds can be offset by the increases in microbial mineralization of SOM, which may explain the lack of significant increases in soil C in eCO_2 despite increased inputs (Billings et al. 2010, Dieleman et al. 2010). The drivers of SOM decomposition in eCO_2 are not well understood, but several FACE and OTC studies have suggested the importance of priming, whereby new organic inputs promote enhanced microbial activity and accelerated decomposition of both new and old SOM (Fontaine et al. 2004, Fontaine et al. 2007, Kuzyakov et al. 2000, Langley et al. 2009). Although mineralization of old SOM reduces the C sink, it also releases organically bound N, increasing its availability to support plant growth. The widening of the C-to-N ratio of soil in Duke-FACE in response to eCO_2 was attributed to increased root exudation (Phillips et al. 2011), which may have primed SOM decomposition and provided a positive feedback to maintain canopy N content and plant productivity (Drake et al. 2011).

Conclusion from FACE

FACE experiments support Hypothesis 8. Increased NPP in eCO_2 does not necessarily increase ecosystem C storage. There are, however, many indications that C accumulates in either plant biomass or SOM in some ecosystems or under certain conditions. Detecting proportionately small changes in very large and variable C pools remains a formidable challenge (Luo et al. 2011), which emphasizes the importance of incorporating reliable process-level information from experiments into C cycling models.

LESSONS FROM FACE

Having a set of testable hypotheses at the onset of FACE experiments was a valuable approach for extending our knowledge of eCO_2 from plant responses to ecological responses and to the larger spatial and temporal scales necessary for evaluating feedbacks between the biosphere and Earth's atmosphere and climate. That the resolution of these hypotheses usually did not provide clear and simple answers is not surprising, nor should it be discouraging. Although one could conclude from the wide variety of responses that have been observed in FACE and other CO_2-enrichment experiments that tree and forest responses remain largely uncertain and future forest growth cannot be predicted, it should be remembered that plant responses to eCO_2 are actually quite simple. As has been known for many decades, the primary response of any green plant, or an entire ecosystem, is an increase in photosynthesis and decrease in stomatal conductance. All the other responses we measure and compare across sites are a consequence of how energy (i.e., photosynthetically fixed C) flows through the ecosystem, which pools it accumulates in and for how long, and how those fluxes and pools interact with other environmental resources and physical and biological constraints. The highly complex interactions and the feedbacks to the primary responses they create lead to myriad experimental results such that every experiment may seem idiosyncratic and with little predictive power for our future biosphere in a more CO_2-enriched world. The value of FACE experiments, however, is not in providing a definitive answer to the question of how much C will be sequestered by future CO_2-enriched forests and other ecosystems—there is no simple or singular answer to that question. Rather, FACE experiments provide process-level information and understanding for models that can address the longer temporal scale and spatial distribution of forests that are beyond the reach of experiments. The lessons we take from FACE experiments should be those that inform us about the critical processes controlling ecosystem responses to eCO_2 and suggest the way forward for enhancing our understanding of them and incorporating them into global vegetation and C cycle models.

Some of the important, overarching lessons we can take from FACE experiments include the following:

- The element of time is of the highest importance in any consideration of C cycling. A single plant in a pot may respond to, and come to a new equilibrium with, a sudden increase in CO_2 supply very quickly. A mature forest, however, comprises many growth processes, species interactions, organic matter pools, and element cycles that can take decades to come to equilibrium with the new environment. As an experimental system, a fast-growing plantation forest that accelerates the time for self-regulating responses such as PNL to develop is advantageous because it reveals mechanisms of response that may otherwise be beyond the reach of experiments in ecosystems with longer response times (Norby et al. 2010). Forest ecosystems that have slower turnover rates (e.g., longevity of evergreen needles, greater litter recalcitrance) may not fundamentally differ from faster ecosystems, but they will require longer experiments to fully reveal responses. How long is long enough? FACE experiments would have continued to provide valuable data and new insights if maintained for more years, but they were limited by infrastructure constraints and the need to address other compelling research questions with a limited funding base (Luo et al. 2011).
- The controls on C partitioning by plants remain a large source of uncertainty in plant and ecosystem models, yet FACE experiments have emphasized the importance of different partitioning patterns to the fate of the extra C taken up by CO_2-enriched plants. The distribution of the C initially fixed via photosynthesis to leaves, roots, and wood has critical implications for the interactions with other resources and the ultimate fate and persistence of that C in the ecosystem.
- The partitioning of plant-derived C among SOM pools with different biochemical and physical characteristics becomes a primary determinant of the fate of C in the ecosystem. Better understanding and model representation of processes such as exudation, litter fragmentation, bioturbation, priming, microaggregation, and microbial interactions are necessary for reliable predictions of long-term responses of ecosystems to eCO_2.
- The influence of N cycling on plant and ecosystem C cycling continues to be a critical uncertainty and important research topic. FACE experiments have revealed some of the important ecological aspects of C-N interactions: plant species differences, litter biochemistry and decomposition rate, and plant-microbe interactions. The widespread expectation that N limitation will lead to a loss in the capacity of an ecosystem to sequester additional C in eCO_2 was borne out in some experiments but not in others. Regardless of whether a negative N feedback to eCO_2 response occurs in a given ecosystem, it will be difficult to have confidence in ecosystem models unless they include a dynamic N cycle that interacts with the C cycle. As new experiments are initiated in different biomes [e.g., tropical forest and arctic ecosystems (Luo et al. 2011)], it will be especially important to consider interactions with other potentially important elements, notably phosphorus.
- The structure of the plant community can have a dominant influence on C and N cycles and the response of the ecosystem to eCO_2. In the long run, effects of atmospheric and climatic change on plant community composition may be much more important to ecosystem

function than the physiological responses of individual species. An important objective for new experiments should be to incorporate dynamic vegetation into experimental design and models.

- Although the effects of eCO_2 on microbial community composition are subtle, microbial activity can be accelerated. The increased substrate availability associated with greater plant detritus production under eCO_2 can stimulate saprotrophic microbial activity and metabolism of SOM. This mechanism has the potential to sustain greater rates of NPP by increasing soil N availability, but the response may not be sustainable. Spatial variation in soil properties, spatial and temporal patterns of environmental conditions, and differences in plant community composition may be factors more important than eCO_2 in structuring saprotrophic microbial communities.

Perhaps the most important lesson from FACE is the recognition that the responses we have observed in FACE experiments cannot be simply extrapolated to the global forest. The value of FACE experiments has been in defining ecological processes and mechanisms of responses that can inform conceptual and quantitative models of ecosystem responses to eCO_2. FACE experiments provide a benchmark for improving and gaining confidence in the models that we must rely on for evaluating the trajectory of climate change and the impacts of atmospheric and climatic change on terrestrial ecosystems. As with the earlier generation of eCO_2 experiments, FACE experiments provide a strong foundation for the next generation of experiments in unexplored ecosystems and with increasing ecological complexity.

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