

# U.S. Department of Energy Free-Air CO<sub>2</sub> Enrichment Experiments

*FACE Results, Lessons, and Legacy*



U.S. DEPARTMENT OF  
**ENERGY**

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Duke FACE



Oak Ridge National Laboratory FACE



Nevada Desert FACE



Rhineland FACE

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June 2020



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# Preface and Acknowledgements

Starting in the 1970s and continuing to today, the U.S. Department of Energy (DOE) has explored critical scientific questions and uncertainties surrounding the long-term consequences of increasing carbon dioxide (CO<sub>2</sub>) concentrations from fossil fuel emissions in the atmosphere. Early studies on the role of vegetation in carbon sequestration were limited to greenhouses or small-growth chambers, and the results were difficult to scale to entire ecosystems or biomes. Considerable credit is given to DOE program manager Roger Dahlman, who helped launch efforts in the early 1980s to study the carbon cycle and vegetation at larger scales and in natural environments using open-top chambers (OTCs). In the mid 1980s, DOE engineered new approaches for manipulating CO<sub>2</sub> levels at larger scales that avoided potential biases (e.g., warming) often seen with OTC studies. The Free-Air CO<sub>2</sub> Enrichment (FACE) approach, which consisted of large-scale plots ringed by towers, allowed for the manipulation of CO<sub>2</sub> levels inside the plots. From 1995 to 2007, DOE's Terrestrial Carbon Program (managed by Roger Dahlman) and Program in Ecosystem Research (managed by Jeff Amthor) supported the operations and scientific studies at four FACE and two OTC sites that represented diverse vegetation types and biomes across the United States.

A key challenge with such experiments is knowing when to end them. In 2005, DOE's Biological and Environmental Research Advisory Committee (BERAC) raised concerns about the FACE studies with respect to their value as single-factor experiments, environmental impacts from a decade of plant and soil sampling, and support for data management and data synthesis (BERAC 2005). The following year, the committee recommended that DOE should complete, harvest, conduct within- and cross-site syntheses, and close out the FACE studies, as well as begin planning for the next generation of ecosystem experiments that would build on the FACE program's legacy (BERAC 2006). Although this recommendation was generally unpopular among the ecological community, there were compelling scientific reasons to evolve DOE's carbon cycle, vegetation, and climate research efforts. These reasons included the need to target the high-priority climatically and environmentally sensitive ecosystems that represent significant uncertainties in global models. Also, new studies needed to be co-designed by the experimental and modeling communities to ensure that experimental research objectives are cooperatively designed to address key model deficiencies, and that modeling efforts are designed to inform the experimental and empirical research. This approach was intended to maximize the return on scientific investments by reducing duplication of efforts, encouraging collaboration, and accelerating the adoption of scientific findings into more robust model projections. Although the strong scientific value of the FACE studies was widely recognized, there was a corresponding recognition of the need for a next generation of ecosystem experiments focusing on an iterative dialogue between the modeling and experimental components. This resulted in competing research priorities compounded with the realities of budget limitations.



As the experiments were brought to an end, the research enabled by FACE continued. In the late 2000s and early 2010s, a series of FACE Model-Data Synthesis (MDS) meetings and associated activities were launched that brought researchers and the modeling community together to apply FACE findings to advance carbon modeling. This grass-roots effort addressed an opportunity and need highlighted by the community and the BERAC reports. In parallel, DOE's Terrestrial Ecosystem Science (TES) program (managed by Daniel Stover and Michael Kuperberg) supported efforts to continue gathering and curating critical datasets from the community and archive them in DOE's public data repositories. Over the past decade, Oak Ridge National Laboratory's (ORNL) Richard Norby and Anthony Walker championed the FACE-MDS effort, which has dramatically enhanced the impacts of the FACE studies. The resulting model-data integration and synthesis publications have enabled this community to address and answer questions posed in the early years of DOE's carbon cycle research programs.

DOE is honored to have the distinction among many federal agencies of bringing together the scientific and engineering communities to design, build, and operate experiments on the unprecedented scales of FACE. The methodology was, and to some degree still is, the gold standard for ecological manipulation experiments. While DOE invested more than \$100 million into the FACE program, the scientific return on that investment has been priceless. In the end, FACE was more than just a collection of experiments; it created a community of dedicated scientists who collaborated to tackle some of the most challenging questions in global carbon cycling, including plant physiology, allocation, root ecology, plant-soil feedbacks, biogeochemistry, and nutrient and water limitations.

This report was developed through support from the TES program to the FACE-MDS effort to highlight the legacy and results of the FACE studies. The report's overarching goal is threefold. First, it provides a historical perspective on DOE's carbon-climate-vegetation research that has evolved significantly over the past 40 years to address some of the nation's most pressing energy and scientific challenges. Second, it provides insight to the experimental design logic and challenges associated with experimental manipulation studies. Third, it serves as a guide for lessons learned operating first-of-a-kind ecosystem manipulation experiments, including what should have been incorporated at the start of the study (e.g., strong data management plans, model-data integration, sampling strategies, community engagement, and project lifecycle and closure). As FACE's successor, the Next-Generation Ecosystem Experiments (NGEE)-Arctic project, enters the final phase of its decadal effort, DOE is challenged again to envision future ecosystem studies that are needed to address the nation's critically important energy-relevant environmental challenges. Learning from and building on the legacy of past research programs such as FACE (and NGEE-Arctic) allow DOE and the nation to grasp opportunities, identify challenges, and accelerate understanding of the Earth system.

DOE would like to thank Richard Norby and Anthony Walker (ORNL) for their leadership in maximizing the value of the FACE investments through the FACE-MDS activities to advance knowledge of the relationship between terrestrial ecosystem communities to atmospheric CO<sub>2</sub>. Richard Norby in particular has selflessly advocated for the importance of the FACE manipulations and tirelessly worked with the community

to develop deeper understanding of vegetation responses to novel environmental conditions. In so doing, he has enabled and advanced countless scientific careers within the FACE community. His effort and dedication to leading and assembling this report and providing a unique perspective on the FACE legacy will empower and enable the design of future ecosystem manipulation studies.

We also would like to acknowledge report contributions from Martin De Kauwe, Bert Drake, Dave Evans, Lynn Fenstermaker, George Hendrey, Bruce Kimball, Patrick Megonigal, Clenton Owensby, Elise Pendall, Stan Smith, Anthony Walker, and Donald Zak. Staff from ORNL's Biological and Environmental Research Information System also contributed their expertise in editing and preparing this report for publication.





# Executive Summary

In the 1970s, growing concern about potential long-range consequences of carbon dioxide (CO<sub>2</sub>) emissions from the combustion of fossil fuels prompted the U.S. Department of Energy (DOE) to begin developing a CO<sub>2</sub> research program. The goal was to obtain the scientific information needed to reduce uncertainty and develop a knowledgebase for decision-making. At its start in 1980, this program had three components: the global carbon cycle, climate effects, and vegetation effects. The vegetation effects component recognized that increased atmospheric CO<sub>2</sub> could be a potential benefit to vegetation and crops because CO<sub>2</sub> is an essential resource for plant growth. In addition to increasing crop yield, program developers and researchers recognized that this fertilizer effect could also result in greater storage of fossil fuel CO<sub>2</sub> by forests.

Initial experiments were small in scale and scope and focused on the photosynthesis, physiology, and water use of crop plants, but the focus shifted toward responses of plants in natural systems, as needed for connections to the global carbon cycle. Program research investigated CO<sub>2</sub> interactions with other environmental variables, emphasizing field research whenever possible and recognizing that exposure to elevated CO<sub>2</sub> concentrations under realistic field conditions should lead to better predictions of plant response.

Whole-ecosystem field experiments were instituted in low-stature ecosystems, but experiments to address forest responses necessarily relied on tree seedlings or saplings in open-top chambers (OTCs) and not within intact forest ecosystems. The need for larger-scale, longer-duration experiments in each of the world's six major biomes (tundra, boreal forest, temperate forest, tropical forest, grassland, and desert) became clear, and for these experiments, free-air CO<sub>2</sub> exposure facilities were necessary. This report summarizes the objectives and main results of DOE-sponsored experiments employing such facilities, along with the outcomes from research on ecosystem responses using field chambers (see Fig. ES.1, p. x). Additionally, this report highlights the many successes of DOE CO<sub>2</sub> enrichment studies and considers the lessons learned that can be used to guide future initiatives.

## FACE Experiments

The Free-Air CO<sub>2</sub> Enrichment (FACE) technology was first developed by Brookhaven National Laboratory (BNL) for use in an agricultural setting. Elevated CO<sub>2</sub> experiments, combined with manipulations of water and nitrogen supply, were conducted from 1989 to 1999 in Maricopa, Ariz., with cotton, wheat, and sorghum. Cotton was shown to be highly responsive to CO<sub>2</sub> enrichment, but the C<sub>4</sub> sorghum was not. Interactions with water and nitrogen varied across species.

The BNL FACE system was scaled up for use with tall vegetation, and a prototype forest FACE system was tested in the Duke University Forest in 1994 and 1995, leading to a fully replicated FACE experiment in the loblolly pine forest in 1996. Other FACE experiments with forest stands and native vegetation began in 1997 at Oak Ridge National

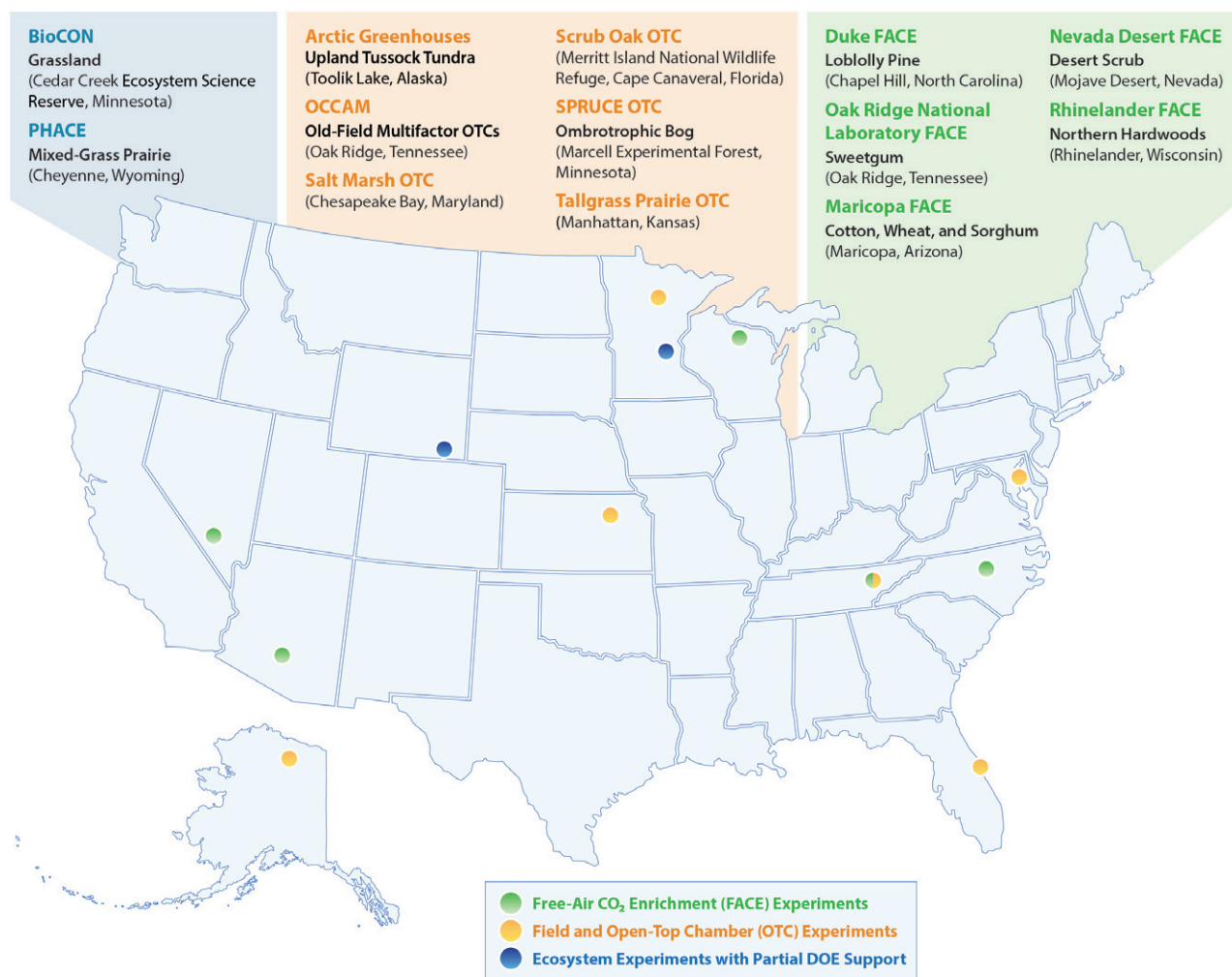


Fig. ES.1. Elevated Carbon Dioxide Experiments.

Laboratory (ORNL) in Tennessee (ORNL FACE in a sweetgum plantation), at the Nevada National Security Site (Nevada Desert FACE), and on U.S. Forest Service land in Wisconsin (Rhineland FACE with trembling aspen mixed with sugar maple and paper birch). Over 10 to 12 years, these experiments exposed the vegetation in replicated, 25-m to 30-m diameter plots to ambient or elevated CO<sub>2</sub> (about 550 to 565 parts per million). In the Rhineland FACE experiment, the CO<sub>2</sub> treatments were combined with ambient or elevated ozone, and the Duke FACE experiment added a nitrogen fertilization treatment toward the end. Some key results from these experiments include:

- Increased net primary production (NPP) in elevated CO<sub>2</sub> was sustained throughout the Duke FACE experiment and resulted in greater woody biomass

accumulation. The increased production was supported by an increased flux of carbon below ground, which stimulated tree uptake of nitrogen bound in soil organic matter and created a positive feedback through increased canopy nitrogen and greater photosynthesis. Slow adjustments in canopy structure meant that short-term leaf-scale responses of stomatal conductance to elevated CO<sub>2</sub> were not translated directly to canopy water-use responses, emphasizing the importance of long-term experiments whose durations are sufficient for slow responses to manifest.

- An initial stimulation of aboveground growth by elevated CO<sub>2</sub> in the ORNL FACE experiment was quickly dissipated, but NPP was enhanced with the additional productivity accounted for by enhanced production of fine roots, especially deeper in the soil, which sustained increased nitrogen uptake needed to support increased NPP. However, nitrogen availability steadily declined, leading to a loss of photosynthetic enhancement and the NPP response. This decline occurred faster in elevated CO<sub>2</sub>, supporting the premise of progressive nitrogen limitation.
- The Nevada Desert FACE Facility was the only DOE FACE experiment that examined the impact of elevated atmospheric CO<sub>2</sub> on an arid ecosystem and took place in an undisturbed, natural ecosystem. Responses of the desert vegetation to elevated CO<sub>2</sub> were highly dependent on precipitation patterns. Photosynthesis was stimulated by elevated CO<sub>2</sub>, increasing leaf-level carbon gain, with larger effects in wet years than during extended drought years. This response supported increased aboveground growth only in the wet years. After 10 years, there was no detectable effect of elevated CO<sub>2</sub> on aboveground biomass or community structure of the perennial plant community.
- The Rhinelander FACE experiment was initiated in a seedling stand and, therefore, was an expanding system through most or all of the experimental duration. Many of the responses reported early in the experiment were not sustained, emphasizing the importance of projecting the responses of seedlings and young trees to mature forests, as well as the value in maintaining experiments for as long as is feasible. Ozone was found to counteract some of the effects of elevated CO<sub>2</sub>, suggesting that projections of CO<sub>2</sub> responses will be overstated if the co-occurrence of ozone is not considered. However, the negative effects of ozone on growth dissipated by the end of the experiment.

## OTC Experiments

OTCs have been widely used to investigate responses to elevated CO<sub>2</sub> of individual plants, small groups of young trees, and small-statured and constructed plant assemblages. DOE supported many such experiments, whose results were important for establishing hypotheses to test in subsequent FACE experiments. In addition, DOE has supported several completed and ongoing OTC experiments in intact ecosystems addressing questions and using approaches similar to those of FACE studies.

An ongoing Maryland salt marsh OTC study is one of the first and longest-running elevated CO<sub>2</sub> experiments in an intact ecosystem. Three plant communities in a brackish



high marsh—a C3 grass, a C4 grass, and a C3-C4 mixed community—have been exposed to elevated CO<sub>2</sub> since 1985. The greatest effects of rising atmospheric CO<sub>2</sub> on carbon assimilation, plant growth, and microbial processes in this study result from interactions with environmental stress, primarily caused by interannual variation in rainfall and salinity. Important ecosystem functions have been altered by long-term exposure to elevated atmospheric CO<sub>2</sub>, including species composition, nitrogen fixation, and palatability of foliage for herbivores.

In an OTC experiment in a naturally occurring scrub oak ecosystem in Florida, photosynthesis and aboveground plant growth exhibited strong responses to chronic exposure to elevated atmospheric CO<sub>2</sub>, leading to increases in aboveground carbon content and in coarse roots that were related to the site's fire history. CO<sub>2</sub> altered the carbon and nitrogen cycles in this ecosystem but not in ways that promoted large or even detectable increments in total ecosystem carbon mass.

An 8-year OTC experiment in a C4-dominated tallgrass prairie in Kansas documented increased photosynthesis and biomass production in dry years. Significant reductions in stomatal conductance resulted in reduced water use by the plant canopy under elevated CO<sub>2</sub>, which extended the photosynthetically active period when water became limiting in the ecosystem. The result was an increase in above- and belowground biomass production during years when water stress was frequent.

Results from an ecosystem-scale field chamber experiment conducted in an Alaskan tussock tundra showed complete homeostasis of CO<sub>2</sub> flux after 3 years of CO<sub>2</sub> enrichment, and plants exposed to elevated CO<sub>2</sub> switched from being net sinks of CO<sub>2</sub> for the first 2 years to a net source in the third year. However, when elevated CO<sub>2</sub> was combined with elevated temperature, the plots remained net carbon sinks.

To address interactions between elevated CO<sub>2</sub> and other environmental factors, a constructed old-field community was exposed to all combinations of ambient or elevated CO<sub>2</sub>, ambient or elevated air temperature, and two levels of soil moisture in OTCs in Oak Ridge, Tenn. Plant community biomass increased with elevated atmospheric CO<sub>2</sub> and warming, but results indicated that induced shifts in plant community composition likely will modify or counteract the direct atmospheric and climate change effects on soil ecosystem functioning.

In an ongoing study in an ombrotrophic bog ecosystem in northern Minnesota, the Spruce and Peatland Responses Under Changing Environments (SPRUCE) experiment uses large, open-top enclosures to expose the ecosystem to a range of air and soil warming in combination with ambient or elevated CO<sub>2</sub>. Preliminary analysis has shown few effects of elevated CO<sub>2</sub> in this system.

### Studies with Partial DOE Support

In addition to the primary FACE experiments and OTC ecosystem experiments supported by DOE, two other experiments received partial DOE support in addition to their primary support from the National Science Foundation, U.S. Department of Agriculture, and other sources.

Biodiversity, CO<sub>2</sub>, and Nitrogen (BioCON) is an ongoing ecological experiment in Minnesota using FACE to explore the ways in which plant communities will respond to three environmental changes known to be occurring on a global scale: increasing nitrogen deposition, increasing atmospheric CO<sub>2</sub>, and decreasing biodiversity. The experiment also considers the interactive effects of warming, water, CO<sub>2</sub>, and nitrogen. Data from this long-term experiment suggest that current trait-based functional classifications might be useful, but not sufficient, for understanding plant and ecosystem responses to elevated CO<sub>2</sub> and nitrogen availability. Furthermore, short-term drivers of plant response to global change might not predict long-term results.

The Prairie Heating and CO<sub>2</sub> Enrichment (PHACE) experiment in Wyoming tested model-based hypotheses derived from the results of a previous OTC experiment to determine how future environmental conditions will influence mixed-grass prairie. Intact ecosystems were exposed to a factorial combination of two levels of CO<sub>2</sub> (using FACE) and two temperature regimes. The effect of elevated CO<sub>2</sub> on soil moisture was the dominant driver of plant biomass responses in this semiarid grassland. Carbon dioxide increased plant productivity most when plants were actively growing but water limited.

### FACE Experiments as Community Science Resources

All the DOE-supported FACE and OTC experiments provided superb research platforms for many university researchers, whose collaborative research benefitted the core projects and enhanced DOE's research investment. Numerous independent researchers took advantage of multiple sites to conduct new measurements or synthesize existing data across different ecosystems. Collaborative studies included cross-site surveys of responses to elevated CO<sub>2</sub> of photosynthesis, stomata, isoprene emission, and nitrate reductase; isotopic studies of water-use efficiency and nitrogen use; measurements and data syntheses of root production, rooting depth, and root respiration; and studies of soil carbon accrual, litter palatability and decomposition, and soil mercury concentration.

### Data Synthesis and Model-Data Synthesis

A concerted effort was made to consider DOE's FACE and OTC experiments as a network of sites. Collectively, they have provided a valuable trove of data and insight, and data synthesis thus has been an important activity of this research program. Following the conclusion of the FACE studies, the research community decided to implement some of the recommended data management activities and model-data synthesis efforts. While DOE was not able to enact these changes during the closeout of the FACE experiments, the research community supported a follow-up effort to ensure data were properly curated and available for the experimental and modeling communities. Later, with DOE support, a FACE data management system was established to support open access to FACE data for many independent synthesis studies and meta-analyses. Data from the forest FACE experiments on responses of soil CO<sub>2</sub> efflux, nitrogen mineralization, nitrogen uptake, and NPP were synthesized to help inform ecosystem models. The NPP

synthesis, which indicated a median 23% enhancement of NPP across a wide range of productivity, has been used as a benchmark for ecosystem models.

As the FACE experiments reached their conclusion, a unique opportunity became apparent for initiating a multimodel intercomparison activity. Initially focusing on the Duke and ORNL FACE experiments, the objectives of this Phase 1 Model-Data Synthesis activity were to evaluate model performance in predicting the measured responses and the models' ability to explain observed variability in responses. An important goal was to provide guidance for improving all the models and gain increased confidence in their predictive capacity. A series of publications explored modeling approaches to water-use efficiency, nitrogen dynamics, carbon allocation, and long-term projections of responses to elevated CO<sub>2</sub> and how well those approaches matched experimental observations. An "assumption-centered" approach was employed, whereby the underlying reasons for model representations of key ecological processes were diagnosed and then evaluated against experimental data. The assumption-centered approach produced a clear roadmap for reducing model uncertainty, improving model capacity to predict effects of elevated CO<sub>2</sub> on forests, and identifying key research tasks for both modelers and experimentalists.

DOE initiated Phase 2 of the FACE Model-Data Synthesis activity with an expanded scope that included more experiments—Nevada Desert FACE, Florida scrub oak OTC, Rhinelander FACE, and the PHACE project. The diversity of these ecosystems created new challenges in data synthesis and modeling. Model comparisons with data from the PHACE experiment highlighted model failures at simulating grasslands, particularly with respect to carbon allocation, phenology, and the impact of water stress on phenology. Data from the Duke, ORNL, and Rhinelander FACE experiments, as well as the scrub oak OTC experiment, were used to analyze whether a decade of CO<sub>2</sub> enrichment in woody ecosystems leads to an increase in the vegetation biomass increment and whether models accurately captured the mechanisms behind the response. These four experiments represent the most direct evidence for decadal biomass responses to CO<sub>2</sub> enrichment in early–secondary succession, temperate woody ecosystems.

## Lessons and Legacy

By many measures, the DOE program supporting research on the effects of elevated atmospheric CO<sub>2</sub> on plant growth was a resounding success. The program evolved from small, narrowly focused laboratory studies to multiyear studies under field conditions and then to larger-scale, decade-long FACE experiments in intact ecosystems. At each step, science questions were addressed and resolved, leading to new questions at a higher level of complexity. An important and general finding from the FACE activities is that ecosystems are exceedingly complicated, making it difficult to tease out a single "answer" for carbon sequestration and feedbacks that scales to every biome. FACE research produced hundreds of papers; trained dozens of students; advanced the careers of many scientists within the national laboratories and at universities; and, through the popular press, videos, and tours, introduced the general public to the important science questions being addressed and the methods used to answer them. Another important legacy of this DOE program is that coordination among models and experiments and open sharing of data are now part of the initial planning of a research project. As

with many long-term field studies, there were missed opportunities and challenges associated with the need to balance current research needs with evolving priorities and initiation of next-generation large-scale studies. Numerous lessons were learned during the closing of FACE sites, including how to determine the lifecycle of long-term research investments. Overall, the operational and scientific lessons gained during FACE research have inspired and are informing current DOE research projects including the Next-Generation Ecosystem Experiments (NGEE) in the Arctic and Tropics, DOE national laboratory scientific focus areas, and other research initiatives. DOE's leading science example of the power of manipulative field studies and model-data integration also continues to influence new and proposed FACE experiments in the United Kingdom, Australia, and Brazil. Important questions about ecosystem responses to atmospheric and climatic change remain, and some critical biomes have yet to be tested. The mandate to continue manipulation studies is compelling, as FACE experiments have demonstrated the value of experimental studies at a scale that can encompass the feedbacks between biotic systems and the atmosphere and soil. The DOE CO<sub>2</sub> research program provided a sharper definition to the outstanding questions and the approaches to address them, and as the international science community takes these questions on, DOE's important contribution to ecosystem science will continue for many years.





# Understanding Ecosystem Responses to Elevated Carbon Dioxide

**G**lobally, atmospheric carbon dioxide (CO<sub>2</sub>) has risen more than 40%, from a pre-industrial level of about 280 parts per million (ppm) to the current concentration of more than 400 ppm. Terrestrial ecosystems act as a “sink” for a significant portion of this carbon, removing and sequestering it from the atmosphere. Understanding the future response of these ecosystems to increasingly higher concentrations of CO<sub>2</sub> under a changing climate has important implications for the global carbon cycle.

For nearly 4 decades, the U.S. Department of Energy (DOE) has been the world leader in research on vegetation responses to elevated atmospheric CO<sub>2</sub>. Beginning in 1980, the DOE Office of Basic Energy Sciences established the Carbon Dioxide Research Division to coordinate the federal government’s research on atmospheric CO<sub>2</sub> and to obtain the scientific information needed to reduce uncertainty in the biosphere’s response to rising levels of CO<sub>2</sub>. Vegetation response was a core component of the division, which included research on the global carbon cycle and the effects of climate change. This new line of research was consistent with DOE’s mandate to consider the environmental consequences of energy technologies. Today, the Terrestrial Ecosystem Science program within DOE’s Office of Biological and Environmental Research manages the research portfolio that arose from these first studies on vegetation response and CO<sub>2</sub> feedbacks.

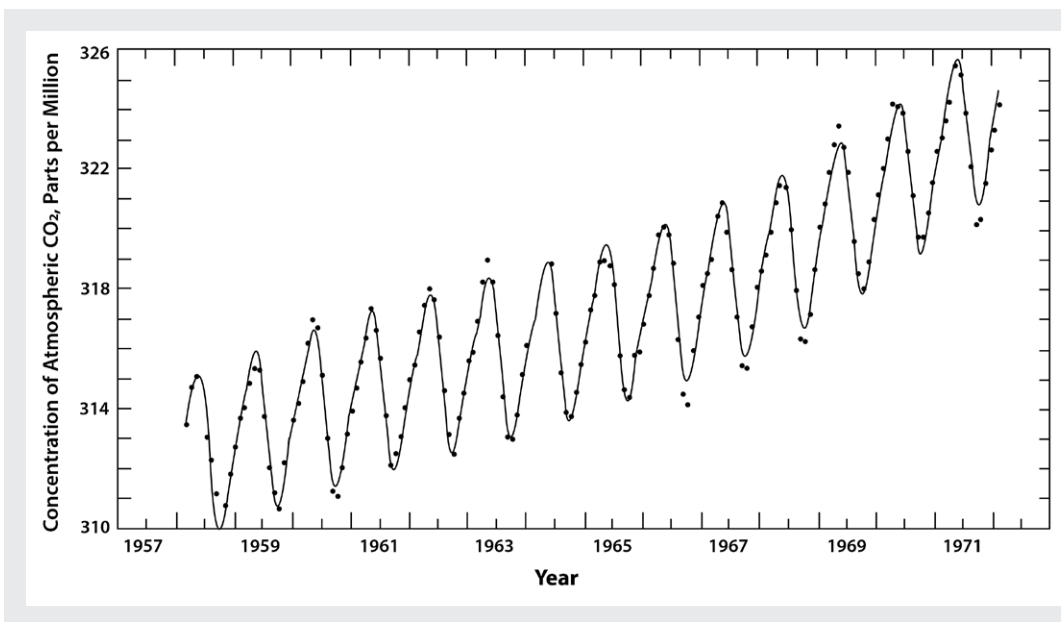
Initial experiments were small in scale and scope, but they identified key research questions involving intact ecosystems. To answer these questions, DOE supported engineering studies on CO<sub>2</sub> exposure methods that led to the development and testing of Free-Air CO<sub>2</sub> Enrichment (FACE) experiments, first in low-statured systems and then in areas with tall trees. FACE technology was deployed in long-term experiments in agricultural, forested, and desert ecosystems. The objectives and major results of those experiments are summarized in this report, along with outcomes from DOE-sponsored research on ecosystem responses using field chambers and from two FACE experiments partially supported by DOE.

The FACE experiments have been very successful, resulting in hundreds of research papers, many of which are highly cited and have been influential in global change analyses. The research clarified numerous critical questions concerning the biosphere’s response to rising CO<sub>2</sub> concentrations while also highlighting areas of continued uncertainty. The modeling activity that followed completion of the experiments set a new standard for model-data interaction that is guiding new research programs within DOE and around the world. This report highlights and celebrates the many successes of DOE FACE research and also considers the lessons gleaned from FACE experiments that will guide future initiatives.



## Historical Development of DOE's CO<sub>2</sub> Research Program

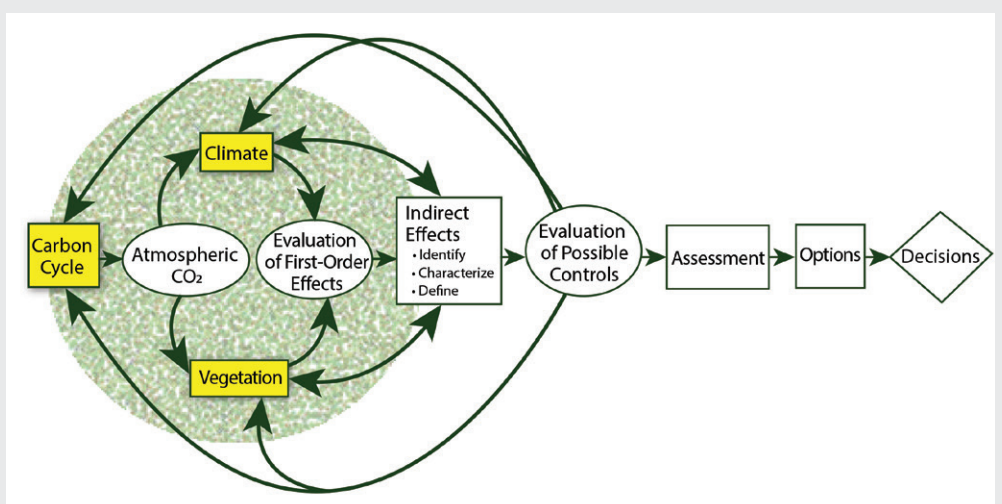
The initiation of atmospheric carbon dioxide (CO<sub>2</sub>) monitoring at the Mauna Loa Observatory in 1958 was a momentous event in the history of global environmental science. After just 2 years of observation, the seasonal cycle in CO<sub>2</sub> concentration was clear, and this signal was immediately recognized to be related to the biology of the terrestrial biosphere (Keeling 1960). A decade later, observational data clearly indicated that atmospheric CO<sub>2</sub> was steadily increasing (see Fig. 2.1, this page; Ekdahl and Keeling 1973). Moreover, this increase was most likely attributable to human activity, and the consequences for the climate could be severe (Baes et al. 1977). Growing concern about long-range effects of CO<sub>2</sub> emissions from fossil fuel combustion prompted the U.S. Department of Energy (DOE) to begin planning development of a CO<sub>2</sub> research program. Carbon cycle research was justified by the need to understand the sources and sinks of CO<sub>2</sub>—where does the CO<sub>2</sub> come from and what components of the biogeochemical system absorb it? The program's goal would be to obtain the scientific information



**Fig. 2.1. Concentrations of Atmospheric Carbon Dioxide (CO<sub>2</sub>) Measured from the Mauna Loa Observatory, Hawaii, 1958–72.** [Redrawn from Ekdahl, C. A., and C. D. Keeling. 1973. "Atmospheric Carbon Dioxide and Radiocarbon in the Natural Carbon Cycle. I. Quantitative Deductions from Records at Mauna Loa Observatory and at the South Pole." In *Carbon and the Biosphere: Proceedings of the 24th Brookhaven Symposium in Biology*, Upton, New York, May 16–18, 1972, pp. 51–85. Eds. Woodwell, G. M., and E. V. Pecan.]

**Fig. 2.2. Structure of the Early U.S. Department of Energy Carbon Dioxide Research Program.**

Primary topics of emphasis are indicated by the shaded area. [Modified and republished with permission of Copyright Clearance Center from Dahlman, R., et al. 1985. "Research on the Response of Vegetation to Elevated Atmospheric Carbon Dioxide," *Journal of Environmental Quality* **14**(1), 1–8 and from Riches and Koomanoff 1985.]



needed to reduce uncertainty and develop a knowledgebase for decision-making. Program development—beginning in 1976—was guided by a series of workshops. The first one was held in 1977 in Miami Beach, Fla., to “discuss the current knowledge of the CO<sub>2</sub> cycle and the consequences of increases in CO<sub>2</sub> content” (Elliott and Machta 1979).

Established by DOE within the Carbon Dioxide Research Division of the Office of Basic Energy Sciences, the program had three components: the global carbon cycle, climate effects, and vegetation effects (see Fig. 2.2, this page; Dahlman et al. 1985; Riches and Koomanoff 1985). The initial climate change component aimed to verify atmospheric models by observing the effects on climate and assessing model predictions of those effects. The vegetation effects component recognized that increased atmospheric CO<sub>2</sub> could be a potential benefit to vegetation and crops because CO<sub>2</sub> is an essential resource for plant growth. In addition to increasing crop yield, program developers and researchers recognized that this fertilizer effect could result in greater storage of fossil fuel CO<sub>2</sub> by forests. In the early 1980s, program research was focused on photosynthesis, physiology, and water use (Dahlman et al. 1985).

## 2.1 Initiating Research on Plant Responses to Elevated CO<sub>2</sub>

Early discussions leading to the vegetation component of DOE’s CO<sub>2</sub> research program, which previously had focused primarily on projected climate change, began at a workshop at Duke University in 1978. This so-called Quail Roost study reviewed for DOE “what is known and not known about the response of plants to CO<sub>2</sub> enrichment” (Dahlman 1993). The review determined that there were essentially no field data on this question and that new techniques were needed for field experiments in representative ecosystems. In 1979, a workshop was held in Annapolis, Md., that focused on the “Environmental and Societal Consequences of a Rising Level of Atmospheric CO<sub>2</sub>.” The workshop was supported by DOE, organized by the American Association for the Advancement of Science, and chaired by Roger Revelle. Two of the six workshop panels considered the managed and unmanaged biosphere. Recommendations from this workshop led to an international

conference that focused specifically on plant responses to elevated CO<sub>2</sub>. Convened in Athens, Ga., in 1982 as “Rising Atmospheric Carbon Dioxide and Plant Productivity: An International Conference,” the workshop aimed to review current understanding about plant responses to twice-ambient CO<sub>2</sub> levels and to identify needed research. The book that emerged from the conference (Lemon 1983) presents many prescient and perceptive research perspectives, describes critical uncertainties, and sets forth a research agenda that has guided research on elevated CO<sub>2</sub> for 35 years (see timeline, pp. 6–7).

## 2.2 Connecting Vegetation Effects Studies to Global Carbon Cycle

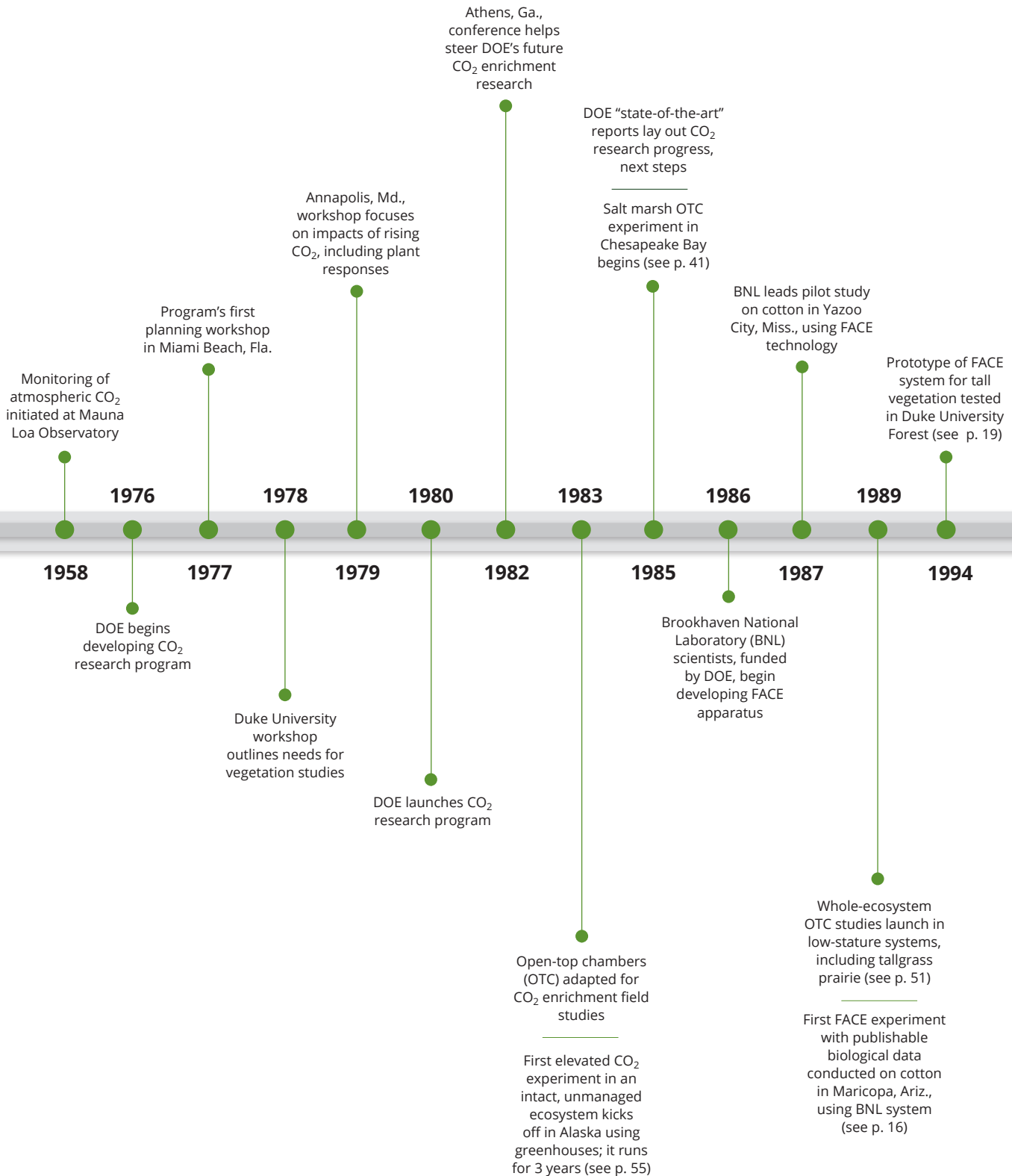
Although Free-Air CO<sub>2</sub> Enrichment (FACE) experiments grew out of this original vegetation component, the research focus of elevated CO<sub>2</sub> studies initially was not well integrated with carbon cycle studies. Note that in the schematic of the program components (see Fig. 2.2, p. 4), there is no arrow from vegetation to carbon cycle. Nevertheless, the science community recognized the potential for a feedback from vegetation response to atmospheric CO<sub>2</sub> through the global carbon cycle, dating back at least to 1970 (Woodwell et al. 1978). Bacastow and Keeling (1973) suggested that the increase in carbon fixation by photosynthesis was large enough to slow down the increase in atmospheric CO<sub>2</sub> concentration caused by fossil fuel burning. Bolin (1977) generally discounted this effect because of nutrient limitation. In their analysis that the biosphere was a net source of CO<sub>2</sub> to the atmosphere, Woodwell et al. (1978) concluded that the potential increase in net primary production (NPP) due to increasing CO<sub>2</sub> was too small to compensate for the release of CO<sub>2</sub> from fossil fuels and forest clearing. In one of the earliest reports and papers that led to the development of DOE's research program, Baes et al. (1977) recognized the importance of land-use change (i.e., conversion of more land to forests or, conversely, deforestation), which could significantly impact the global carbon cycle. Regarding the effect of enhanced photosynthesis in response to increasing atmospheric CO<sub>2</sub> concentration, they concluded that “its importance in the carbon cycle is presently unclear.” Siegenthaler and Oeschger (1978) stated: “Some plants probably react to a higher CO<sub>2</sub> level by enhanced photosynthetic activity, so the biosphere might act as a sink for additional CO<sub>2</sub>.” Their model predicting future atmospheric CO<sub>2</sub> levels, driven primarily by fossil fuel emissions and ocean uptake, included a simple biosphere growth factor that included both deforestation and CO<sub>2</sub> fertilization, with the assumption that the two processes compensate each other to some unknown extent.

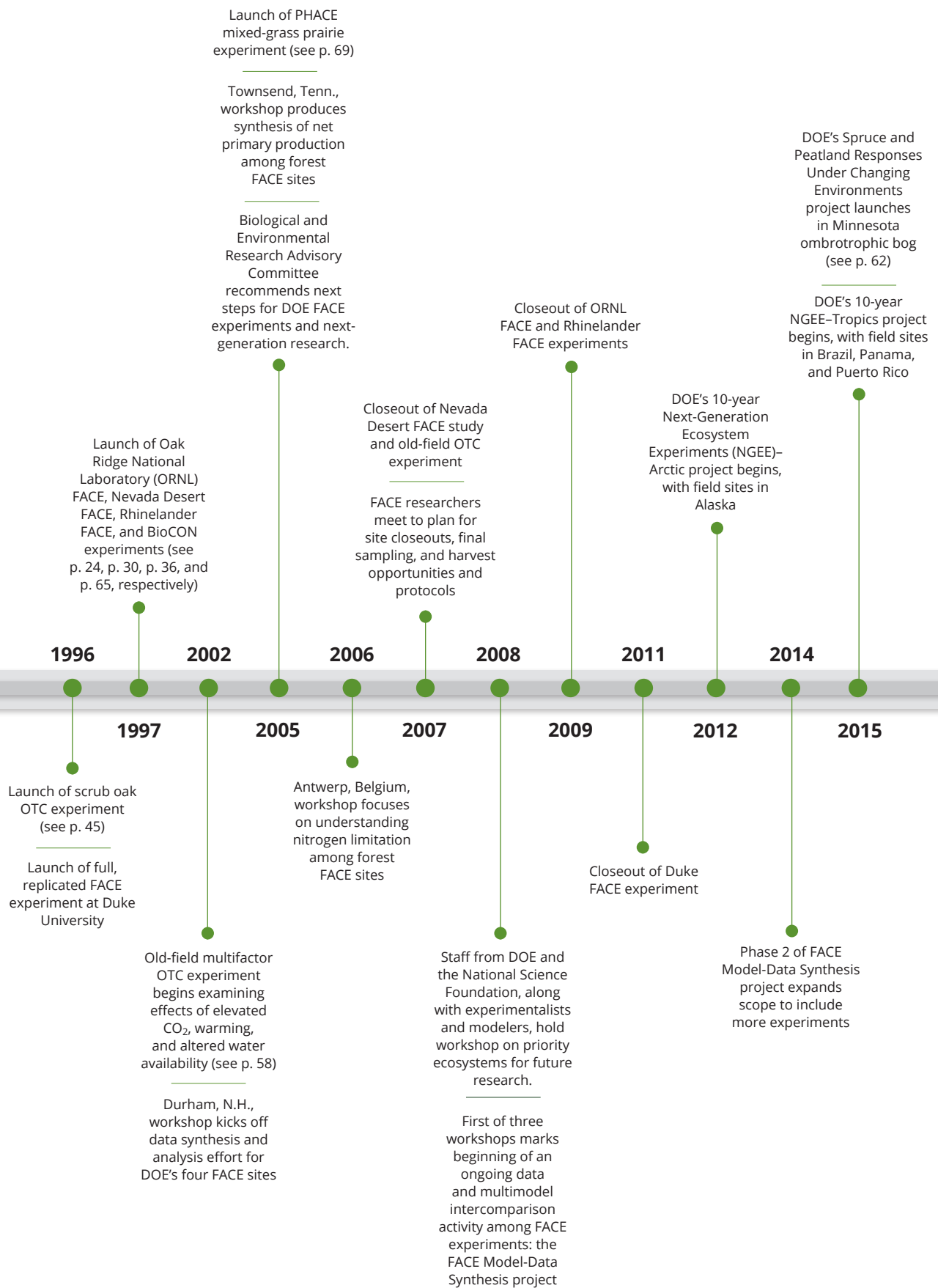
As estimation of the deforestation flux improved, researchers recognized that the flux to oceans and the observed increase of CO<sub>2</sub> in the atmosphere could not account for the total anthropogenic release of CO<sub>2</sub>—there must be a “missing sink” (Field 2001). Carbon dioxide fertilization of the biosphere was a strong candidate for the missing sink, but testing this hypothesis required analyses that were more sophisticated than simple proportional increases in photosystems. To address the important uncertainty as to whether the physiological response of plants (e.g., photosynthetic enhancement) will necessarily increase net carbon storage in the biosphere, the 1977 Miami Beach workshop report stated that “Research will be required on the role of nutrient availability, water availability, and sunlight on the effect of CO<sub>2</sub> increases on plant productivity, particularly on trees.” The workshop also called for much improved simulation models on all geographical scales, noting: “Modeling teams must be closely coupled with field researchers.”



# Understanding Ecosystem Responses to Rising CO<sub>2</sub>

## A Timeline of Select DOE Milestones



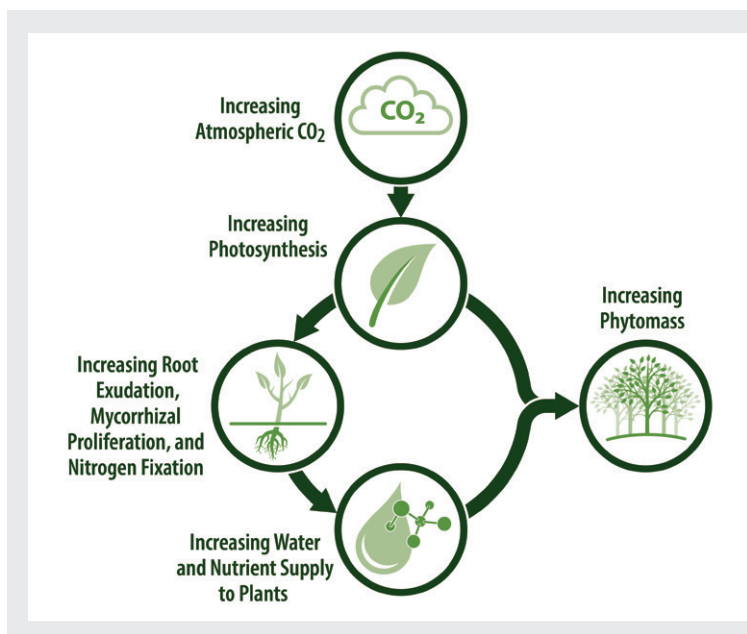


Much of the earliest work on plant responses to elevated CO<sub>2</sub> focused on crop and horticultural plants, but an important paper by Kramer (1981) shifted the focus toward responses of plants in natural systems, as needed for connections to the global carbon cycle. Kramer summarized the extensive literature on photosynthesis and dry matter production of crop plants in elevated CO<sub>2</sub>. Then he challenged whether these results would pertain in nature, where photosynthesis and biomass production probably are limited more often by water and nitrogen deficiency than by low CO<sub>2</sub> concentration, noting: “Increasing the CO<sub>2</sub> concentration will have little effect if the stomata are closed, the cell enlargement is inhibited by water stress, or the use of photosynthate is limited by lack of nitrogen.” Hence, elevated CO<sub>2</sub> was projected to have the least effect on plant growth in closed stands where other resources are limiting. However, knowledge at that time was based chiefly on short-term laboratory experiments and greenhouse studies that used crop plants or tree seedlings in setups where other resources are rarely limiting. Kramer concluded that the projections of vegetation responses to a doubling of atmospheric CO<sub>2</sub> concentration were likely overestimated; moreover, reliable predictions of the global effects of increasing CO<sub>2</sub> concentration required long-term measurements of plant growth from experiments in which elevated CO<sub>2</sub> is combined with water and nitrogen stress.

The themes enunciated by Kramer (1981) were further explored and defined by Strain and Bazzaz (1983). They noted that the initial effect of elevated CO<sub>2</sub> in most plant communities will be to increase NPP, but “a critical question is the extent to which the increase in NPP will lead to a substantial increase in plant biomass. Alternatively, increased NPP could simply increase the rate of turnover of leaves or roots without changing plant biomass.” This statement clearly makes the connection between physiological responses and ecosystem responses that are relevant to the global carbon cycle (although, curiously, soil carbon is left out of this equation). Strain and Bazzaz (1983) recommended the initiation of long-term studies of CO<sub>2</sub> effects in representative ecosystems. They posited three primary justifications for an ecological approach to the analysis and prediction of direct effects of elevated CO<sub>2</sub>: (1) resolving uncertainty in the responses of agroecosystems; (2) alerting the scientific community to possible long-term disequilibria in semi-natural ecosystems; and (3) determining the role of CO<sub>2</sub> fertilization in the global carbon cycle (e.g., will elevated CO<sub>2</sub> make terrestrial ecosystems a net carbon sink?). Strain and Bazzaz also noted: “Energy policy and scientific decisions are at stake.”

### 2.3 Developing Open-Top Chamber CO<sub>2</sub> Studies

An important milestone in DOE’s CO<sub>2</sub> research program was a series of interim research assessments in 1985 called state-of-the-art (SOA) reports (Riches and Koomanoff 1985). The SOA report on vegetation response, “Direct Effects of Increasing Carbon Dioxide on Vegetation” (Strain and Cure 1985), focused on current research progress and needs in acquiring laboratory and field data on CO<sub>2</sub> effects on plant physiology and growth, with simultaneous development of models for predicting direct responses to CO<sub>2</sub>. Program research also investigated CO<sub>2</sub> interactions with other environmental variables (Dahlman et al. 1985), emphasizing field research whenever possible and recognizing that exposure to elevated CO<sub>2</sub> concentrations under realistic field conditions should lead to better predictions of plant response. The development of open-top chamber (OTC) systems for elevated CO<sub>2</sub> studies (Rogers et al. 1983) was an important component of this new research. Experimental studies were conducted



**Fig. 2.3. Elucidating Interactions Among Roots, Nutrients, Water, and Plant Growth Under Elevated Carbon Dioxide (CO<sub>2</sub>).** Luxmoore (1981) proposed this hypothetical scheme whereby increased allocation of carbon to belowground processes could alleviate resource limitations and create a positive feedback to plant growth in elevated CO<sub>2</sub>. [Adapted by permission of Oxford University Press from Luxmoore, R. J. 1981. "CO<sub>2</sub> and Phytomass," *BioScience* **31**(9), 626.]

with soybeans and other crop plants, as well as with several tree species (Dahlman et al. 1985). While providing valuable data and insights into the fundamental responses of plants to CO<sub>2</sub>, these early studies could not address uncertainties about the role of CO<sub>2</sub> fertilization in the global carbon cycle or the feedbacks between the biosphere and atmospheric CO<sub>2</sub>. The critical uncertainties regarding interactions between CO<sub>2</sub> response and nutrient or water stress were more difficult and expensive to approach in field experiments, especially in plant communities (particularly forests) that significantly influence the global carbon cycle. Consequently, experimental studies to inform plant-atmosphere feedbacks began on a small scale—tree seedlings in controlled environment chambers at the Duke University Phytotron (e.g., Tolley and Strain 1985) and at Oak Ridge National Laboratory (e.g., Norby et al. 1986a). The research program at Duke focused on physiological responses and moved from the Phytotron studies to field experiments using OTCs. The research program at Oak Ridge National Laboratory developed from a hypothesis put forth by Luxmoore (1981; see Fig. 2.3, this page) in response to the paper by Kramer (1981). The hypothesis stated that elevated CO<sub>2</sub> would stimulate carbon allocation to root systems. In turn, this stimulation would support increased root exudation, mycorrhizal proliferation, and microbial growth, thereby promoting increased nutrient availability and creating a positive feedback to photosynthesis and plant growth. This hypothesis was explicitly tied to globally relevant questions concerning elevated CO<sub>2</sub> and the plant-atmosphere feedback.

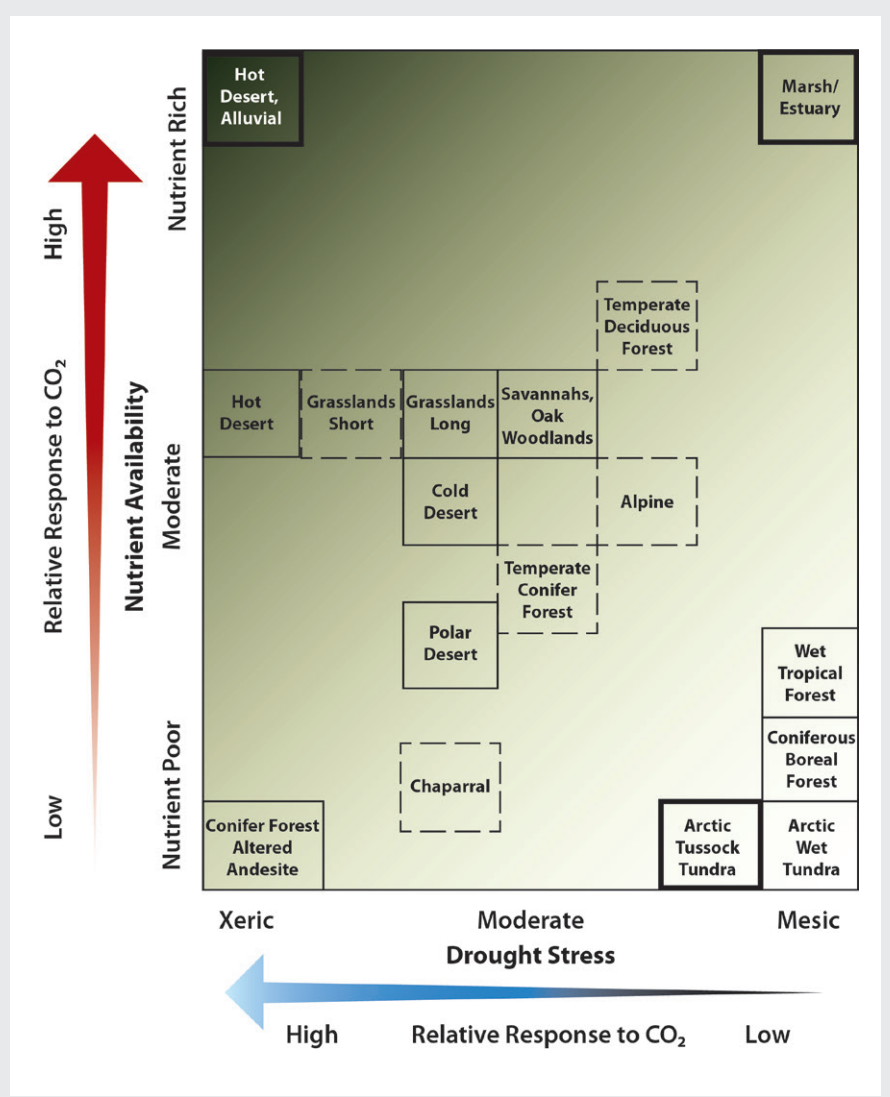
## 2.4 Expanding Elevated CO<sub>2</sub> Field Experiments to Whole Ecosystems

The first two field experiments investigating elevated CO<sub>2</sub> effects on plant communities in intact ecosystems were in the Alaskan tussock tundra (Tissue and Oechel 1987) and the Chesapeake Bay salt marsh (Curtis et al. 1989). The low stature of these two

ecosystems permitted sustained exposure to elevated CO<sub>2</sub> in chambers with minimal alteration to the environment. The low responsiveness of the Arctic system contrasted with the high responsiveness of the salt marsh system, leading to many spirited discussions as to which response was “correct” or most representative of ecosystems in general. Mooney et al. (1991) discussed these two experiments and emphasized the obvious conclusion that “ecosystems are likely to vary in their response to elevated CO<sub>2</sub>. Studies over a range of ecosystem types are required before credible generalizations and predictions can be made.” To provide context for the disparate responses, as well as to set a future research agenda, Mooney et al. (1991) presented a hypothetical scheme (see Fig. 2.4, this page), modified from one previously presented by Strain and Bazzaz (1983), that placed the world’s ecosystems on axes representing drought stress and nutrient availability. The hypothesis of Mooney et al. (1991) was that the relative

**Fig. 2.4. Hypothesized Ecosystem Responses to Elevated Carbon Dioxide (CO<sub>2</sub>) Relative to Nutrient and Water Availability.**

The heavy outlines indicate those ecosystems that had been studied in the field in 1991. Dashed outlines indicate those where aspects of the system had been studied under controlled environmental conditions. The remaining ecosystems were largely unstudied in 1991. Since then, field studies, including Free-Air CO<sub>2</sub> Enrichment (FACE) experiments, have been conducted in deserts, grasslands, chaparral and alpine systems, and temperate deciduous forests but not in tropical forests or coniferous boreal forests. Increasingly darker green indicates greater relative response to CO<sub>2</sub>, based on the assumptions that response increases with drought stress and with nutrient availability. [Reprinted with permission from Norby, R. J., et al. 2016 (originally adapted from Mooney et al. 1991 and modified from Strain and Bazzaz 1983).]





response to CO<sub>2</sub> should increase with drought stress and with nutrient availability, putting the marsh and tundra systems at opposite ends of the response spectrum.

When the Mooney et al. (1991) scheme was put forward, other ecosystems—including temperate deciduous and coniferous forests, shortgrass prairie, and alpine and chaparral ecosystems—had been studied only in experiments where certain aspects of the system response were examined in controlled environment chambers. While such experiments can be informative about ecosystem-scale processes (e.g., Norby et al. 1986b), field experiments were needed to test whether the relatively short-term responses observed in growth chamber experiments would be sustained over several growing seasons and under the influence of multiple, variable, and fluctuating environmental conditions and resources (Norby et al. 1992). New, whole-ecosystem field experiments were instituted in other low-stature ecosystems (i.e., tallgrass prairie; Owensby et al. 1993), but experiments to address forest responses necessarily relied on tree seedlings or saplings in OTCs and not within intact forest ecosystems. As these experiments neared completion, both in the United States with DOE support and in Europe, their results were summarized and synthesized (Norby et al. 1999). The rationale for most of these studies was the need to assess the role of forests in the global carbon cycle and how that role might change in the face of increasing atmospheric CO<sub>2</sub> concentration. The analysis indicated that most of what was learned from previous seedling studies was qualitatively correct, but some previous conclusions were challenged by the field experiments, and there remained important obstacles to using the experimental results to predict forest responses to elevated CO<sub>2</sub>. Furthermore, researchers recognized that the walls of OTCs shaded the plants inside, drastically changed wind flow, increased temperatures and humidities inside, and produced other effects as well (e.g., Kimball et al. 1997). New, larger-scale CO<sub>2</sub> experiments were called for, and the OTC experiments provided testable hypotheses and a research framework for guiding new experiments (Norby et al. 1999). This recognition echoed the call by Mooney et al. (1991) for larger-scale, longer-duration experiments in each of the world's six major biomes (tundra, boreal forest, temperate forest, tropical forest, grassland, and desert). They suggested that free-air fumigation facilities would be necessary, as previously discussed by Drake et al. (1985) in a DOE SOA report.

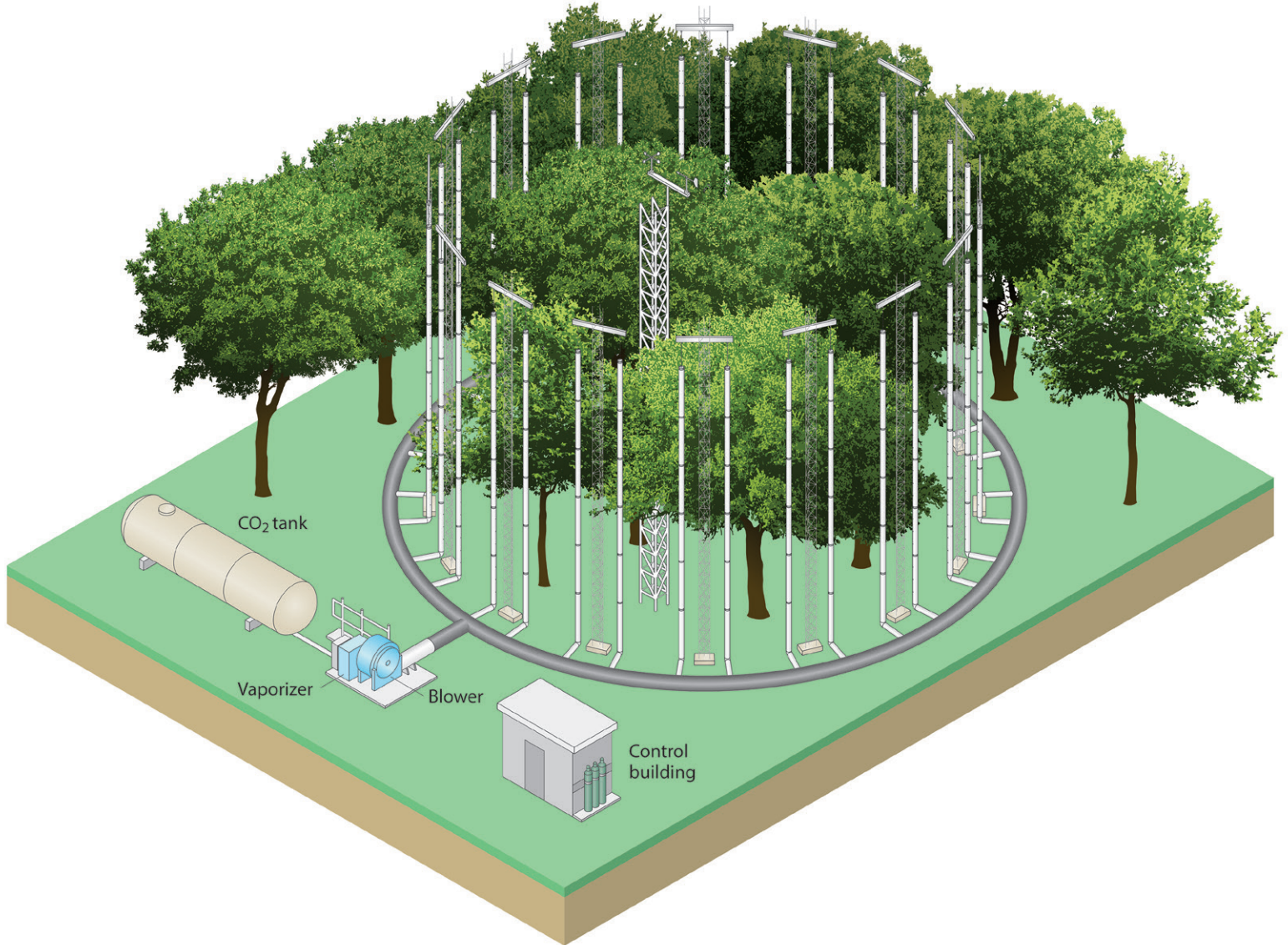


## DOE's FACE Experiments

The stage was set for the next generation of elevated carbon dioxide (CO<sub>2</sub>) studies using Free-Air CO<sub>2</sub> Enrichment (FACE) technology. Fortunately, while open-top chamber (OTC) and other experiments were developing the scientific foundation for this next generation of experiments, the U.S. Department of Energy (DOE) was investing in the development of FACE technology and engineering (see Allen 1992 for a history of FACE technology development). Discussions at the 1982 conference in Athens, Ga., led to proposals submitted to Roger Dahlman at DOE for feasibility studies for field-scale CO<sub>2</sub> enrichment research. These studies were subsequently conducted through a partnership between DOE (Joseph Shinn at Lawrence Livermore National Laboratory) and the U.S. Department of Agriculture's Agricultural Research Service (USDA ARS; Hartwell Allen). This analysis built on the experience with open-air fumigation systems for air pollutants, especially that of McLeod et al. (1985), whose approach researchers at Brookhaven National Laboratory (BNL) thought could be adapted to CO<sub>2</sub>. In March 1986, a pivotal meeting occurred during a workshop at Mississippi State University. USDA ARS scientist Jackson Mauney, a CO<sub>2</sub> cotton researcher funded by DOE to do OTC studies in Phoenix, Ariz., learned about a nearby cheap source of CO<sub>2</sub>. This discovery—along with the availability of a nexus of researchers experienced with OTCs and BNL researchers' fresh approach for designing FACE apparatus—led the community and DOE's Dahlman to optimistically view FACE as feasible. George Hendrey of BNL subsequently led a proposed 1987 pilot study in a cotton field near a fertilizer factory in Yazoo City, Miss. In 1989, the FACE feasibility study on cotton was moved to the Maricopa Agricultural Center of the University of Arizona, where Bruce Kimball, Mauney, and colleagues were already doing DOE-funded CO<sub>2</sub> cotton research in nearby Phoenix.

The construction and operation of the FACE facility at Maricopa were described by Hendrey et al. (1993) and Lewin et al. (1994). Following the successful demonstration of FACE technology for short-stature agricultural crops, the system (see Fig. 3.1, p. 14) was scaled up for use with tall vegetation (e.g., in forests). A prototype of the forest FACE system was tested in the Duke University Forest in 1994 and 1995 (Hendrey et al. 1999).

The BNL system was used in all DOE-supported FACE experiments, with some modifications as needed for different sites or experimental objectives. Another FACE system, using pure CO<sub>2</sub> emitted at high velocity through small-diameter tubes (Miglietta et al. 2001), has also been employed, especially in Europe. A similar system designed by



**Fig. 3.1. FACE Experimental Setup.** This simplified version of the Brookhaven National Laboratory FACE system was modified for use in different ecosystems and for combined ozone fumigation. The system consisted of a high-volume blower, a plenum encircling a 30-m diameter experimental plot, and 32 evenly spaced vertical standing vent pipes. Food-grade liquified carbon dioxide (CO<sub>2</sub>) was stored in a refrigerated tank. The CO<sub>2</sub> was vaporized via electrical or solar heating units and metered into the plenum where it was mixed with air from the blower. The prediluted CO<sub>2</sub> was emitted through holes in the vent pipes and distributed by wind throughout the experimental plot; only those vent pipes upwind of the plot were open, requiring constant adjustment as wind direction changes. Monitoring of wind speed and CO<sub>2</sub> concentration at the center of the plot provided a computer-controlled feedback to the metering of pure CO<sub>2</sub> into the plenum to maintain the desired CO<sub>2</sub> set point, generally 150 to 200 parts per million greater than the CO<sub>2</sub> concentration in ambient air.

Okada et al. (2001)—also using pure CO<sub>2</sub> with varying pressure dispersed through porous pipes—has been used on rice and wheat in Asia.

In 1994, after the successful demonstration of FACE technology in the agricultural crop studies at Maricopa, DOE FACE began to focus on forests and native vegetation in FACE experiments geared toward carbon cycle feedbacks and community ecology. In addition to four primary experiment locations—Duke University (North Carolina), Oak Ridge National Laboratory (Tennessee), the Nevada National Security Site, and the USDA Rhinelander Forest Service Station (Wisconsin)—DOE provided partial support for the Biodiversity, CO<sub>2</sub>, and Nitrogen (BioCON) experiment at Cedar Creek (Minnesota) and the Prairie Heating and Carbon Dioxide Enrichment (PHACE) experiment (Wyoming), both summarized in Ch. 5: Studies with Partial DOE Support, p. 65. DOE-supported ecosystem-scale experiments using OTCs rather than FACE are described in Ch. 4: Field Chamber Experiments, p. 41. In addition, BNL engineers funded by DOE also helped initiate agricultural FACE experiments in Switzerland, Germany, and New Zealand, as well as forest experiments in Australia and England.

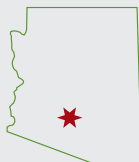
In the sections that follow, this chapter provides some details of the Maricopa and four primary DOE FACE sites and describes experimental results of each.



## Maricopa FACE

*Cotton, Wheat, and Sorghum*

*Maricopa, Arizona*



1989–1999

### Lead Institution

Agricultural Research Service, U.S. Department of Agriculture

### Key Reference

Kimball, B. A. 2006. "The Effects of Free-Air [CO<sub>2</sub>] Enrichment of Cotton, Wheat, and Sorghum." In *Managed Ecosystems and CO<sub>2</sub>: Case Studies, Processes, and Perspectives*, 47–70. Eds. Nösberger, J., et al. Springer, Berlin.



## 3.1 Maricopa FACE

### 3.1.1 Objectives

Objectives were to (1) determine the responses of important agricultural crops (i.e., cotton, wheat, and sorghum) to elevated CO<sub>2</sub> under open-field conditions at ample and limiting levels of water and nitrogen and (2) obtain data suitable for validating crop-growth simulation models that can predict the likely effects of increasing atmospheric CO<sub>2</sub> concentration and climatic warming on future crop productivity around the world.

### 3.1.2 Description of Experiment

#### Site

The experimental site at the University of Arizona Maricopa Agricultural Center was in Maricopa, Ariz. (33°05'N, 111°59'W), which is about 50 km south of Phoenix. It was within an irrigated agricultural area extending several kilometers in every direction, which in turn is surrounded by desert. The land has been leveled, and flooding is the typical irrigation method. Average annual temperature is 22.4°C, with an average summer high temperature exceeding 41°C; annual precipitation is 200 mm. The soil is classified as a reclaimed Trix clay loam (Kimball 2006).

#### Experimental Design

Four experiments were conducted. In 1989, cotton (*Gossypium hirsutum*) was exposed to ambient or elevated CO<sub>2</sub>. In 1990 and 1991, experiments with cotton were in a split-plot design, with one-half of each plot receiving ample irrigation water and the other half with

limiting water supply. This design was repeated with wheat (*Triticum aestivum*) in 1992–1993 and 1993–1994. In the 1995–1996 and 1996–1997 periods, experiments with wheat split the main CO<sub>2</sub> plots into ample- or low-nitrogen treatments. The CO<sub>2</sub> × water supply design was repeated with sorghum (*Sorghum bicolor*) in 1998 and 1999. The target CO<sub>2</sub> concentration was 550 parts per million (ppm) in the cotton and first wheat experiments and ambient +200 ppm in subsequent experiments. There were four replicates of each treatment.

### Measurements

In each experiment, primary measurements included above- and belowground biomass, seed yield, soil carbon, water use, tissue nitrogen concentrations, and nitrogen yield. The experiments with cotton also measured the fraction of absorbed photosynthetically active radiation (PAR) and light-use efficiency. These experiments were among the first to apply stable isotope tracers to quantify the effects of elevated CO<sub>2</sub> on shifts in soil carbon storage and carbon loss via decomposition (see Fig. 3.2, this page; Leavitt et al. 2001; Pendall et al. 2001).

### 3.1.3 Results

Kimball (2006) summarizes the outcomes of the four Maricopa experiments examining the response of cotton, wheat, and sorghum to elevated CO<sub>2</sub> under the different nutrient and water conditions.

- Under ample water and nutrient supplies, cotton (a C<sub>3</sub> woody plant grown in the summer) was highly responsive to elevated CO<sub>2</sub>, showing increases in

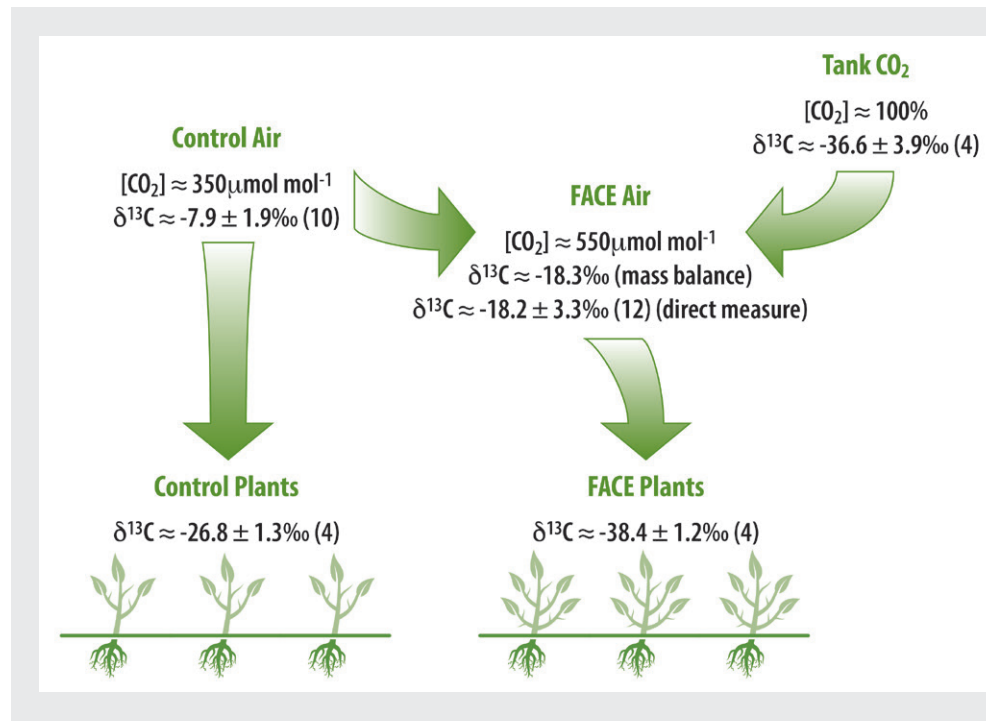
### Websites

#### Project

[www.ltrr.arizona.edu/~sleavitt/MaricopaFACE.htm](http://www.ltrr.arizona.edu/~sleavitt/MaricopaFACE.htm)

#### Data

[library.wur.nl/ojs/index.php/ODJAR/article/view/15826](http://library.wur.nl/ojs/index.php/ODJAR/article/view/15826)



**Fig. 3.2. Stable Carbon Isotope Compositions (δ<sup>13</sup>C) of Air and Cotton Plants in the Maricopa FACE Experiment During the 1991 Growing Season.** [Reprinted by permission from Springer Nature from Leavitt, S. W., et al. 1996. "Carbon Isotopes and Carbon Turnover in Cotton and Wheat FACE Experiments," *Plant and Soil* **187**, 147–55. Copyright 1996.]

aboveground biomass and boll yields of about 40%. However, in sorghum (a C4 herbaceous plant also grown in the summer), there was little photosynthetic response to CO<sub>2</sub> enrichment and negligible biomass and yield response. Wheat (a C3 herbaceous plant grown in the winter) had increases in aboveground biomass (~9%) and grain yield (~13%).

- When water was limiting, the growth and yield stimulations of cotton were about the same as under ample water (~40%), whereas those for wheat increased to about 15% aboveground biomass and 22% for grain yield. In contrast to the negligible response at ample water, increases were seen in sorghum's aboveground biomass (~16%) and grain yield (~26%) with elevated CO<sub>2</sub> under limited water. This response was attributed to water conservation from reduced stomatal conductance. When nitrogen was limiting, the increases in aboveground biomass and yield of wheat due to elevated CO<sub>2</sub> were only ~5% and ~9%, respectively.
- Root growth responses of cotton and wheat due to elevated CO<sub>2</sub> were larger than those of aboveground biomass. Cotton root biomass increased 29% to 157%, and wheat root biomass increased 14% to 28%.
- Soil carbon concentrations tended to increase (by an average of ~11%), but variability was too high for statistical significance in individual studies.
- Under ample supplies of both soil nitrogen and water, leaf nitrogen concentrations were reduced for cotton (~7%) and for wheat (~4%). When soil nitrogen was limited, wheat leaf nitrogen concentrations decreased (~21%).





## Duke FACE

*Loblolly Pine*

*Chapel Hill,  
North Carolina*



**1994–2011**

### Lead Institutions

- Duke University
- Brookhaven National Laboratory

### Key Reference

McCarthy, H. R., et al. 2010. "Re-Assessment of Plant Carbon Dynamics at the Duke Free-Air CO<sub>2</sub> Enrichment Site: Interactions of Atmospheric CO<sub>2</sub> with Nitrogen and Water Availability over Stand Development," *New Phytologist* **185**, 514–28.

## 3.2 Duke FACE

### 3.2.1 Objectives

The Duke FACE experiment tested forest response to future, higher levels of atmospheric CO<sub>2</sub> and sought to answer a critical question for foresters and policymakers: Can more growth and carbon sequestration be expected in these forests in the future? The experiment in Duke Forest examined changes in tree growth, water use, and carbon sequestration in wood and soils. Common species of pine within this forest are loblolly, shortleaf, and Virginia pine, which typically grow in drier areas. In the U.S. Southeast, pine plantations on abandoned agricultural land are believed to represent a considerable carbon sink partially accounting for the large putative sink in North America. An enhanced carbon sink resulting from CO<sub>2</sub> fertilization of forests might ultimately slow the rise of atmospheric CO<sub>2</sub>, and prior work in OTCs and glass-house experiments showed large increases in the biomass of loblolly pine in response to elevated CO<sub>2</sub> concentrations in soils with ample nutrients (Tissue et al. 1996, 1997). An initial motivation for the FACE experiment in Duke Forest was to examine this growth response in natural conditions, where trees experience competition, drought, nutrient limitations, pests, and pathogens.

### 3.2.2 Description of Experiment

#### *Site*

The Duke FACE experiment, also known as Forest Atmosphere Carbon Transfer and Storage (FACTS-I), was located in the Blackwood Division of the Duke University

## Websites

### Project

web.archive.org/  
web/201208191  
60517/http://face.  
env.duke.edu/main.  
cfm (archived)

### Publications

web.archive.org/web  
/20120708011212/  
http://face.env.duke.  
edu/publications.cfm  
(archived)

### Data

- facedata.ornl.gov
- facedata.ornl.gov/  
facemds/

Forest near Chapel Hill, N.C. (35°59'N, 79°06'W; elevation 163 m). Mean annual precipitation is 1,140 mm, and mean annual temperature is 15.5°C. Soils are low-fertility acidic Hapludalf in the Enon Series, which are typical of uplands in the southeastern United States, with a clayey loam in the upper 0.3 m and clay below down to the bedrock at 0.7 m. Maximum soil moisture is 0.54 m<sup>3</sup> per m<sup>3</sup>; soil pH is ~6.0. Local topographic variations are small (<5% slopes; Schlesinger et al. 2006).

## Plant Community

The FACE experiment was conducted in a loblolly pine (*Pinus taeda*) forest established in 1983 as a plantation. The forest contains more than 40 woody species, mostly in the subcanopy dominated by sweetgum (*Liquidambar styraciflua*), elm (*Ulmus alata*), red maple (*Acer rubrum*), dogwood (*Cornus florida*), and oak-hickory. The 90-hectare (ha) block of the stand was established from seedlings following clearcutting and burning. Loblolly pine trees from a Piedmont provenance were planted at a spacing of 2 m × 2.4 m, and natural regeneration added numerous other species. Density of co-dominant pines at the experimental site is about 1,600 trees per ha, and total tree density of dominant and subcanopy hardwood trees is 3,700 trees per ha. Concentrations of nitrogen (~1.1%) and phosphorus (~0.3%) in the pine foliage tend to be at the middle range for mid-rotation loblolly pine in the region. The site index is between 21 m and 22 m at age 25.

## Experimental Design

Four FACE plots at the experimental site provided elevated atmospheric CO<sub>2</sub> concentrations, and three provided ambient CO<sub>2</sub> control. The system began operation in June 1994 with a prototype plot designed to test the forest FACE fumigation approach. Six additional plots were established, with three of them receiving elevated CO<sub>2</sub> beginning in August 1996. At the start of the experiment, the plots were paired, based on subjective criteria of similarity, and one member of each pair was assigned to the control or fumigated status. As the experiment unfolded, the importance of subtle variations in forest and soil conditions across the site was recognized, requiring the use of pretreatment conditions as a covariate in analysis of variance, with  $n = 3$  in each category, analyzing the prototype data separately.

The prototype plot and its reference plot were halved with a barrier inserted in the soil in 1998 to conduct, together with five additional plot pairs, a CO<sub>2</sub> × soil nutrient enrichment experiment. The rest of the plots were partitioned and incorporated into this experiment in early 2005. Ammonium nitrate pellets were applied annually to one-half of each plot. The CO<sub>2</sub> enrichment ended October 31, 2010, and a final harvest began.

The target CO<sub>2</sub> concentration was 200 ppm above current ambient CO<sub>2</sub>. The CO<sub>2</sub> fumigation was maintained continuously until 2003, whenever air temperature was greater than 5°C. After 2003, CO<sub>2</sub> fumigation occurred only during daylight hours. The CO<sub>2</sub> used for fumigation was derived from natural gas and had a stable carbon isotope ( $\delta^{13}\text{C}$ ) signature of -43.0 per mil.

## Measurements

Throughout the duration of the experiment, a comprehensive set of measurements was conducted, including leaf gas exchange; leaf, stem, and fine-root growth; water relations; nutrient relations; and soil carbon and nitrogen cycling. When the experiment ended

after 14 years of treatment, the trees were harvested. Half of each plot was harvested initially, while monitoring continued in the other half. The general timeline of sampling was as follows:

- Fall 2010 — Pine branches for determination of allometry, leaf sampling of hardwood trees, biomass determination of hardwood trees <2 cm and 2 to 8 cm in diameter at breast height, collection of standing dead biomass.
- February–March 2011 — Harvest of hardwoods >8 cm in diameter at breast height and all pines.
- April–May 2011 — Taproot harvest.

### 3.2.3 Results

#### *Photosynthesis and Respiration*

Photosynthesis rates in pine needles were directly related to nitrogen content. Although nitrogen content was reduced slightly under elevated CO<sub>2</sub>, the slope of the relationship between light-saturated net photosynthesis ( $A_{\text{sat}}$ ) and nitrogen was 81% greater in elevated CO<sub>2</sub>. There was no indication that the responses of photosynthesis to long-term CO<sub>2</sub> enrichment were different from responses to a short-term increase (Springer et al. 2005).

Net photosynthesis of current-year needles in the upper crown was enhanced 67% under elevated CO<sub>2</sub> over 10 years. Enhancement increased twofold from driest to wettest years. Previous-year needles showed less enhancement (30%). Photosynthesis of co-dominant and subcanopy sweetgums was increased 62% (Ellsworth et al. 2012).

Specific root respiration was greater under elevated CO<sub>2</sub> in September 1997 and May 1998 but not at other times during the year (Matamala and Schlesinger 2000).

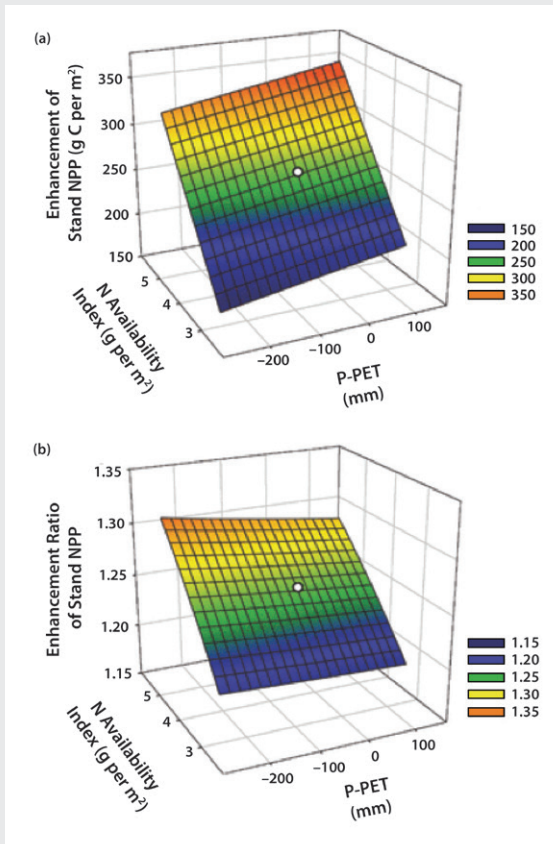
#### *Growth*

One measure of tree growth is the annual increase in the cross-sectional area of the bole at 1.3 m in height, called the basal area increment (BAI). BAI was 13% to 27% greater in elevated CO<sub>2</sub> over 8 years. In most years, elevated CO<sub>2</sub> increased the growth rate but not the duration of the active growth period. BAI was usually positively correlated with precipitation amount during the active growing season. Interannual variation in the relative enhancement of BAI was strongly related to temperature and precipitation and was greatest in years with a high vapor pressure deficit (Moore et al. 2006).

Net primary production (NPP) was enhanced 22% to 30% in different plots and years. Spatial variation was controlled mainly by nitrogen availability, and interannual variability was explained primarily by the difference between precipitation and potential evapotranspiration (see Fig. 3.3, p. 22). There was no effect of elevated CO<sub>2</sub> on carbon partitioning among plant biomass pools (McCarthy et al. 2010).

Elevated CO<sub>2</sub> enhanced pine leaf area index (LAI) 16% and hardwood LAI 14% after canopy closure. LAI and its response to elevated CO<sub>2</sub> were spatially correlated with nitrogen availability. Pine LAI reached the maximum for the site under elevated CO<sub>2</sub>, where native nitrogen was highest. This result implies that closed-canopy pine forests





**Fig. 3.3. Duke FACE Net Primary Production (NPP).** Models accounting for the combined effects of nitrogen (N) and water availabilities on NPP were used to generate a continuous surface of absolute (a) and relative (b) NPP enhancement induced by elevated concentrations of carbon dioxide ( $\text{CO}_2$ ). This demonstrated the dependence of  $\text{CO}_2$ -induced enhancement of stand NPP on available N and precipitation minus growing season potential evapotranspiration (P-PET). Open circles in both panels indicate the enhancement at the average N availability index and the P-PET value observed in the study. [Reprinted by permission from Wiley from McCarthy H. R., et al. 2010. "Re-assessment of Plant Carbon Dynamics at the Duke Free-Air  $\text{CO}_2$  Enrichment Site: Interactions of Atmospheric  $[\text{CO}_2]$  with Nitrogen and Water Availability over Stand Development," *New Phytologist* **185**, 514–28. Copyright 2009 The Authors.]

may be able to increase LAI under elevated  $\text{CO}_2$  at sites with moderate fertility but not at those that are infertile or highly fertile (McCarthy et al. 2007).

Elevated  $\text{CO}_2$  resulted in greater LAI and thus greater NPP. After canopy closure, elevated  $\text{CO}_2$  did not enhance NPP at a given LAI regardless of soil water availability. Aboveground NPP responded to  $\text{CO}_2$  only through enhancement of leaf area duration (McCarthy et al. 2006a).

Elevated  $\text{CO}_2$  also increased average fine-root standing crop by 23%, annual root length production by 25%, and annual root length mortality by 36%; average life span decreased from 574 to 500 days. Effects of elevated  $\text{CO}_2$  shifted from shallow to deeper soil during the study. Averaged over 6 years, annual fine-root production was 163 g per  $\text{m}^2$  in elevated  $\text{CO}_2$  versus 130 g per  $\text{m}^2$  in ambient (Pritchard et al. 2008a).

### Nutrient Interactions

During the first 4 years of the experiment, nitrogen-use efficiency (NUE) increased under elevated  $\text{CO}_2$  for 2 years. In the other 2 years, the nitrogen requirement rose by 27% to 33%; this increase was met by increased uptake. There was no evidence for increased nitrogen mineralization. NPP was co-limited by carbon availability and nitrogen availability from soil (Finzi et al. 2002).

In the first 6 years, more nitrogen was immobilized in tree biomass and in the oxygen horizon in elevated  $\text{CO}_2$ , but microbial nitrogen immobilization did not increase. The nitrogen mineralization rate declined through time, but the decline was not affected by elevated  $\text{CO}_2$ . The ecosystem carbon:nitrogen ratio (C:N) widened more rapidly in elevated  $\text{CO}_2$  (Finzi et al. 2006).

### Water Use

Stomatal conductance was reduced 21%—an indirect effect of decreased hydraulic conductance and increased leaf shading rather than a direct effect of elevated  $\text{CO}_2$ . Canopy transpiration was not affected by elevated  $\text{CO}_2$  because 19% greater LAI nullified reduced stomatal conductance (Tor-ngern et al. 2015).

### Soil

Forest floor carbon and nitrogen pools increased during the first 6 years of the experiment with greater

accumulations under elevated CO<sub>2</sub>. After that, however, organic matter pools stabilized, with 30 g of carbon per m<sup>2</sup> per year sequestered in elevated CO<sub>2</sub>, related to enhanced litterfall inputs. There were no detections of elevated CO<sub>2</sub> effects on carbon and nitrogen pools of surface and deep mineral soil horizons, but the C:N ratio of soil organic matter (SOM) widened, indicating nitrogen was being transferred from soil to plants and at a higher rate under elevated CO<sub>2</sub> (Lichter et al. 2008).

Annual soil CO<sub>2</sub> efflux increased 17% under elevated CO<sub>2</sub> and decreased 21% with nitrogen fertilization. Base respiration rates increased with leaf productivity but declined after leaf production saturated. Effects of elevated CO<sub>2</sub> were sustained beyond the early stages of stand development and through stabilization of annual leaf production.

The rate of root exudation of soluble carbon was enhanced 55%. The increase in root-derived carbon was correlated with an accelerated rate of organic matter turnover and the microbial release of extracellular enzymes involved in the breakdown of organic nitrogen (Phillips et al. 2011).

Mycorrhizal root tip production increased in elevated CO<sub>2</sub> by 194% in deep soil, but there was no effect in shallow soil. Production of rhizomorph length was 27% greater (Pritchard et al. 2008b). Responses are thought to contribute to sustained NPP stimulation.

### **Plant Community Dynamics**

The number of mature, viable seeds per unit basal area doubled under elevated CO<sub>2</sub> from 1997 to 2008, and there was no effect on mean seed mass, viability, or nutrient content (Way et al. 2010).

An ice storm in December 2002 severely affected the forest, breaking off tops and side branches of many trees. Elevated CO<sub>2</sub> reduced ice-storm carbon transfer from living to detrital pools to one-third. With less leaf area reduction, biomass production in elevated CO<sub>2</sub> the following year was reduced less (McCarthy et al. 2006b).

Aboveground biomass and density of the understory decreased in all plots with increasing overstory LAI, but there was no effect of elevated CO<sub>2</sub> on aboveground biomass, tree density, community composition, or the fraction of shade-tolerant species (Kim et al. 2016).

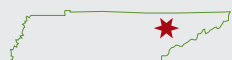
### **3.2.4 Summary**

Increased NPP in elevated CO<sub>2</sub> was sustained throughout the experiment and resulted in greater woody biomass accumulation. The increased production was supported by an increased flux of carbon below ground, which stimulated tree uptake of nitrogen bound in SOM and created a positive feedback through increased canopy nitrogen and greater photosynthesis. This mining of organic nitrogen precluded a large carbon sink in soil and presumably could not be sustained indefinitely (Drake et al. 2011). Slow adjustments in canopy structure meant that short-term leaf-scale responses of stomatal conductance to elevated CO<sub>2</sub> were not translated directly to canopy water-use responses, emphasizing the importance of long-term experiments whose durations are sufficient for slow responses to manifest (Torgner et al. 2015).

## Oak Ridge National Laboratory FACE

*Sweetgum*

Oak Ridge, Tennessee



1997–2009

### Lead Institution

Oak Ridge National Laboratory

### Key Reference

Norby, R. J., et al. 2010. "CO<sub>2</sub> Enhancement of Forest Productivity Constrained by Limited Nitrogen Availability," *Proceedings of the National Academy of Sciences USA* **107**(45), 19368–373.



## 3.3 Oak Ridge National Laboratory FACE

### 3.3.1 Objectives

Previous efforts to understand how eastern deciduous forests will be affected by CO<sub>2</sub> enrichment of the atmosphere focused on experiments examining only components of the forest system. Initiated in 1997, the Oak Ridge National Laboratory (ORNL) FACE experiment took a critical leap by measuring the integrated response of an intact forest with a focus on stand-level mechanisms. The primary objective was to understand (1) the effects on the eastern deciduous forest by CO<sub>2</sub> enrichment of the atmosphere and (2) the feedbacks from the forest to the atmosphere (Norby et al. 2016).

### 3.3.2 Description of Experiment

#### Site

The research site was located in the ORNL Environmental Research Park (35°54'N, 84°20'W) in eastern Tennessee. The soil at the site is classified as Wolftever, an Aquic Hapludult. With a silty clay loam texture, the soil is moderately well drained, slightly acidic (i.e., water pH, approximately 5.5 to 6.0), and has a high base saturation largely dominated by exchangeable calcium. The climate is typical of the humid southern Appalachian region. Mean annual temperature is 14.2°C, and mean annual precipitation is 1,390 mm. Precipitation generally is evenly distributed throughout the year (Norby et al. 2001).

#### Plant Community

The experiment was conducted in a sweetgum (*Liquidambar styraciflua*) monoculture plantation on an old terrace of the Clinch River (elevation 230 m). The plantation was established in 1988 with the planting of 1-year-old, bare-rooted sweetgum seedlings at

a spacing of 2.3 m × 1.2 m. A total of 1.7 ha was planted with sweetgum in two areas—a 185 m × 70 m area and a smaller 85 m × 50 m area, separated by a stand of sycamore (*Platanus occidentalis*). When the FACE experiment launched, stand basal area was 29 m<sup>2</sup> per ha with an average tree height of 12.4 m, a stem diameter of 11.3 cm, and an LAI of 5. The understory was very sparse when the experiment began but became more aggressive. Important species include an invasive C4 annual grass (*Microstegium vimineum*), non-native invasive woody plants (*Lonicera japonica* and *Ligustrum sinense*), and other taxa. Tree seedlings, including *Acer negundo*, *Acer rubra*, *Liriodendron tulipifera*, and *Quercus alba*, were sparse (Norby et al. 2001, 2006).

### Experimental Design

Six 25-m diameter plots were initially laid out in 1997, but one had significantly different soil characteristics and thus was removed from the experiment. The subsequent experimental design and construction comprised two plots with elevated CO<sub>2</sub> and three plots with ambient CO<sub>2</sub>. The CO<sub>2</sub> came from a natural gas source and had a δ<sup>13</sup>C signature of −51‰.

Carbon dioxide treatment was initiated in April 1998, prior to leafout. The CO<sub>2</sub> setpoint was a constant 565 ppm. From 1998 to 2008, the daytime average CO<sub>2</sub> concentration was 395 ppm in ambient plots and 547 ppm in elevated CO<sub>2</sub> plots (Riggs et al. 2009).

A nitrogen fertilizer trial was initiated in an 85 m × 50 m section of the sweetgum plantation separate from the FACE experiments. Nitrogen as urea was distributed in early spring at 200 kg N per ha in replicate plots in 2004 and 2005.

### Measurements

The ORNL FACE experiment consisted of an interrelated set of measurements designed to determine the integrated response of an intact forest ecosystem, with a focus on stand-level mechanisms. An overarching goal of these tasks was to determine how forest carbon, nutrient, and water cycles respond to elevated CO<sub>2</sub>. There was a special emphasis on exploring the implications of the dramatic fine-root response to elevated CO<sub>2</sub> for soil carbon and nitrogen dynamics.

Carbon dioxide treatments lasted 12 years, concluding in 2009. Research tasks related to the shutdown of the experiment included (1) digging two soil pits, each measuring 80 cm × 80 cm × 90 cm, to quantify root mass and length as a function of depth and provide access for detailed analysis of the root-soil interface; (2) harvesting trees in July (with leaves) and November (leafless) to update allometric relationships and canopy structure; and (3) archiving soil and plant samples for subsequent analyses.

## 3.3.3 Results

### Photosynthesis and Respiration

Early in the experiment, photosynthetic CO<sub>2</sub> assimilation (A) averaged 46% higher in elevated CO<sub>2</sub> in mid- and upper-canopy foliage. Stomatal conductance (g<sub>s</sub>) was reduced 14% in the mid-canopy and 24% in the upper canopy by elevated CO<sub>2</sub> (Gunderson et al. 2002). There were no significant CO<sub>2</sub> treatment effects on (1) photosynthetic

### Websites

#### Project

[face.ornl.gov](http://face.ornl.gov)

#### Publications

[face.ornl.gov/pubs.html](http://face.ornl.gov/pubs.html)

#### Data

- [facedata.ornl.gov](http://facedata.ornl.gov)
- [facedata.ornl.gov/facemds/](http://facedata.ornl.gov/facemds/)



or (2) biochemical capacity [i.e., no change in (1) photosynthetic capacity ( $A_{\max}$ ) or (2) maximum rate of carboxylation ( $V_{\text{cmax}}$ ) or maximum rate of electron transport ( $J_{\max}$ )] despite increased area-based leaf sugar (10%) and starch content (27%) and reduced mass-based leaf nitrogen concentration (10%; Sholtis et al. 2004).

In year 11, photosynthesis was less than in previous years in both treatments, and there was no longer a significant stimulation by elevated  $\text{CO}_2$ . Reductions in leaf photosynthesis through time and with  $\text{CO}_2$  treatment reflect differences in the parameters of photosynthetic biochemistry,  $V_{\text{cmax}}$  and  $J_{\max}$ . Foliar nitrogen per unit leaf area ( $N_{\text{area}}$ ) in the upper 2 m of the canopy decreased from 1999 to 2008 and was less in elevated  $\text{CO}_2$  than in ambient  $\text{CO}_2$ ; hence,  $V_{\text{cmax}}$  and  $J_{\max}$  were reduced concomitantly. There was no change in the relationships between  $V_{\text{cmax}}$  or  $J_{\max}$  and  $N_{\text{area}}$  with time or with  $\text{CO}_2$  enrichment (Warren et al. 2015).

Elevated  $\text{CO}_2$  concentration had no direct effect on leaf respiration (Tissue et al. 2002). However,  $\text{CO}_2$  enrichment caused a 23% increase in annual stem growth respiration and a 48% increase in stem maintenance respiration (Edwards et al. 2002).

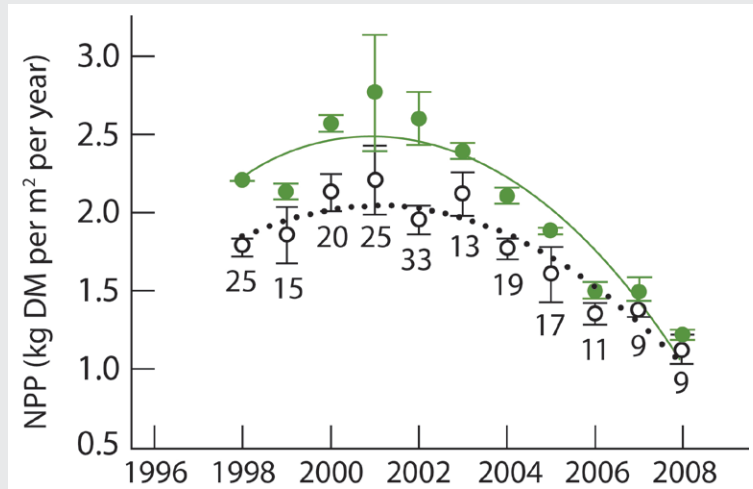
### Growth

Elevated  $\text{CO}_2$  caused a significant increase in wood increment in the first year after treatment initiation (1998), but the response diminished in subsequent years and in later years was not statistically different from FACE controls (Norby et al. 2010).

During the first 6 years of the experiment, NPP was significantly enhanced in forest plots under elevated  $\text{CO}_2$  compared with those under ambient  $\text{CO}_2$ , a response that was consistent and sustained (see Fig. 3.4, p. 27). However, this enhancement declined from 24% in the 2001–2003 time frame to 9% in 2008, and there was no significant enhancement after 2004. From 2003 to 2008, NPP in ambient  $\text{CO}_2$  was diminished by 47%. The decline in NPP and the loss in NPP response to elevated  $\text{CO}_2$  was entirely accounted for by changes in fine-root production (Norby et al. 2010).

In the first 6 years of the experiment, annual production of fine roots more than doubled in elevated  $\text{CO}_2$  compared with plots in ambient air. This response was the primary component of the sustained increase in NPP (Norby et al. 2004). Though fine-root turnover declined under elevated  $\text{CO}_2$  concentrations, fine-root mortality also nearly doubled under  $\text{CO}_2$  enrichment. Over 9 years, root mortality resulted in 681 g per  $\text{m}^2$  of extra carbon and 9 g per  $\text{m}^2$  of extra nitrogen input to the soil system under elevated  $\text{CO}_2$  concentrations. At least half these inputs were below a 30-cm soil depth (Iversen et al. 2008).

During the first 4 years of the experiment, LAI remained relatively constant and comparable to pretreatment values and was similar in ambient and elevated  $\text{CO}_2$  (Norby et al. 2003). During an extreme drought in 2007, premature leaf senescence and abscission increased rapidly and was 30% greater for elevated  $\text{CO}_2$  (Warren et al. 2011a). Leaf area duration (LAD) varied year to year with no clear trend over time and with no effect of  $\text{CO}_2$  concentration. NPP increased with LAD in ambient  $\text{CO}_2$ , but there was no significant relationship between NPP and LAD in elevated  $\text{CO}_2$  (Norby et al. 2010). At final harvest there was no change in canopy structure.



**Fig. 3.4. Oak Ridge National Laboratory FACE Experiment's Net Primary Production (NPP) Under Elevated (green) and Ambient (black) Carbon Dioxide (CO<sub>2</sub>).** The number at each point is the percentage increase under elevated CO<sub>2</sub>. [Reprinted from Norby, R. J., et al. 2010. "CO<sub>2</sub> Enhancement of Forest Productivity Constrained by Limited Nitrogen Availability," *Proceedings of the National Academy of Sciences USA* **107**(45), 19368–373.]

### Nutrient Interactions

In sweetgum plots separate from the FACE experiment, annual nitrogen fertilization caused an immediate and sustained increase in wood increment compared with unfertilized plots. Addition of nitrogen increased NPP as well as nitrogen availability, uptake, and requirement, confirming that the stand was nitrogen limited (Iversen and Norby 2008).

Elevated CO<sub>2</sub> resulted in increased uptake of and requirement for nitrogen, primarily because of greater root turnover. Elevated CO<sub>2</sub> had no significant effects on tissue concentrations of phosphorus, potassium, calcium, or magnesium but caused a significant increase in the uptake and requirement of all of these but phosphorus. There also were no significant treatment effects on the rate of fine-root decomposition (Johnson et al. 2004).

Canopy-averaged foliar nitrogen concentration [N] declined over time in both ambient and elevated CO<sub>2</sub>. Although it did not differ among plots before the onset of CO<sub>2</sub> exposure, foliar [N] was consistently lower in elevated CO<sub>2</sub> after treatments began in 1998. There was a linear relationship between NPP and foliar [N] beginning in the third year of treatment. The slope of the NPP-[N] relationship was significantly steeper in elevated CO<sub>2</sub> than in ambient CO<sub>2</sub>. Foliar [N] was the only significant predictor of NPP in elevated CO<sub>2</sub>, accounting for 73% of the variation (Norby et al. 2010).

Greater carbon inputs from fine-root detritus under elevated CO<sub>2</sub> concentrations did not result in increased net nitrogen immobilization or carbon mineralization rates in long-term laboratory incubations, possibly because microbial biomass was lower in the CO<sub>2</sub>-enriched plots (Iversen et al. 2012).

Stable nitrogen isotope ( $\delta^{15}\text{N}$ ) content of leaf litter declined from 1998 to 2005, and the rate of decline was significantly faster in elevated CO<sub>2</sub>. Declining leaf litterfall  $\delta^{15}\text{N}$  is



indicative of a tighter ecosystem nitrogen cycle and more limited soil nitrogen availability (Garten et al. 2011).

### **Water Use**

Stand transpiration was reduced as much as 22% by elevated CO<sub>2</sub>, but differences only occurred under conditions of higher daily radiation and vapor pressure deficit (Wullschlegel and Norby 2001).

Elevated CO<sub>2</sub> reduced sap flow by 28% during the early summer of 2007 and by up to 45% during an extreme drought with record-setting temperatures. Modeled canopy conductance declined more rapidly in elevated CO<sub>2</sub> plots during this period, thereby directly reducing carbon gain at a greater rate than in ambient CO<sub>2</sub> plots (Warren et al. 2011a).

Average soil moisture (at 0 to 20 cm in depth) during the summer growing season varied year to year and tended to be greater in elevated versus ambient CO<sub>2</sub> but was only weakly associated with NPP. Progressively drier summers from 2004 to 2007 may have been partially responsible for declining NPP, but NPP continued to decline in 2008 despite more mesic conditions (Norby et al. 2010).

### **Soil**

Organic carbon in the top 5 cm of forest soil increased linearly in elevated CO<sub>2</sub> plots during the first 5 years of the experiment, while carbon in the ambient plots remained relatively constant; there was no difference in deeper soil. Elevated CO<sub>2</sub> increased carbon stocks in the forest soil at an average rate of 44.9 g C per m<sup>2</sup> per year. The proportion of whole-soil carbon found in microaggregated soil averaged 58% in both elevated and ambient CO<sub>2</sub> plots 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 ambient soil, with little apparent saturation of this protection mechanism, even after 5 years (Jastrow et al. 2005).

At the conclusion of the experiment, soil carbon and nitrogen contents were greater throughout the soil profile under elevated CO<sub>2</sub> concentrations. Greater inputs of fine roots over the course of the experiment resulted in the incorporation of new carbon into root-derived particulate organic matter pools to a 90-cm depth. Analysis of the  $\delta^{13}\text{C}$  of the carbon mineralized from SOM suggested that carbon inputs from relatively deep roots under elevated CO<sub>2</sub> may increase the potential for long-term soil carbon storage (Iversen et al. 2012).

Elevated CO<sub>2</sub> had no effect on soil bacterial substrate utilization, extracellular enzyme activity, microbial community structure, or microbial activity (Austin et al. 2009; Sinsabaugh et al. 2003).

### **Plant Community Dynamics**

Aboveground biomass of the understory community was on average 25% greater in elevated CO<sub>2</sub> than in ambient CO<sub>2</sub>. From 2001 to 2003, little of the understory biomass was in woody species; herbaceous species made up 94% of the total understory biomass across all plots. Through time, woody species increased in importance, mostly in elevated CO<sub>2</sub>. In 2008, the contribution of herbaceous species to total understory biomass was 61% in ambient CO<sub>2</sub> and only 33% in elevated CO<sub>2</sub> treatments (Souza et al. 2010).

### 3.3.4 Summary

The trajectory of the NPP response was the most important single product from the ORNL FACE experiment. The dynamics of the sweetgum stand and its response to elevated CO<sub>2</sub> were dominated by interactions with nitrogen. The initial stimulation of aboveground growth by elevated CO<sub>2</sub> was quickly dissipated, but NPP was enhanced with the additional productivity accounted for by enhanced production of fine roots, especially deeper in the soil, which sustained increased nitrogen uptake to support increased NPP. However, nitrogen availability steadily declined, leading to a loss of photosynthetic enhancement and the NPP response. This decline occurred faster in elevated CO<sub>2</sub>, supporting the premise of progressive nitrogen limitation.

## Nevada Desert FACE

*Desert Scrub*

*Mojave Desert, Nevada*



1997–2007

### Lead Institutions

- Desert Research Institute
- University of Nevada–Las Vegas
- Brookhaven National Laboratory

### Key Reference

Evans, R. D., et al. 2014. "Greater Ecosystem Carbon in the Mojave Desert After 10 Years Exposure to Elevated CO<sub>2</sub>," *Nature Climate Change* 4(5), 394–97.



## 3.4 Nevada Desert FACE

### 3.4.1 Objectives

The Nevada Desert FACE Facility was the only DOE FACE experiment that (1) examined the impact of elevated atmospheric CO<sub>2</sub> on arid ecosystems and (2) took place in an undisturbed, natural ecosystem. It serves as the model for desert ecosystems around the world and is especially relevant to desertification, which is a major land-use problem in North America as well as globally. As summarized in the following sections, Nevada Desert FACE research included comprehensive measurements of (1) physiological responses and growth of the area's dominant species and (2) ecosystem-level responses including carbon fluxes, water use, plant community dynamics, and soil microbial responses.

### 3.4.2 Description of Experiment

#### Site

The experiment was located in southern Nevada on the Nevada National Security Site (formerly Nevada Test Site; 36°49'N, 115°55'W; elevation 970 m), which is near the northern ecotone of the Mojave Desert. This fairly homogeneous area is on a broad, gently sloping bajada (alluvial fan; Jordan et al. 1999). The soil is an Aridosol derived from calcareous alluvium with textures of the <2-mm fraction ranging from loamy sands in the shallow A1 horizon (0 to 0.16 m) to coarse sands in the subsoil horizons. With the exception of the surface soil horizon, the <2-mm fraction is structureless. The rock content is variable but often quite high. Hotter than the Great Basin Desert on its northern boundary, the Mojave Desert is the driest region in the United States. Mean annual precipitation is about 140 mm, with most precipitation occurring as winter rainfall and

episodic summer monsoonal rains. Temperatures range from 48°C in summer to –19°C in winter.

### Plant Community

The plant community is Mojave Desert scrub with <20% perennial cover dominated by bursage (*Ambrosia dumosa*; a small drought-deciduous shrub) and creosote bush (*Larrea tridentate*; an evergreen shrub that reaches over 1 m in height). Other predominant shrubs include the drought-deciduous Anderson's wolfberry (*Lycium andersonii*), pale wolfberry (*Lycium pallidum*), desert ratany (*Krameria erecta*), and the evergreen Mormon tea (*Ephedra nevadensis*). Abundant perennial grasses are Indian ricegrass (*Achnatherum hymenoides*; a C3 bunchgrass), big galleta (*Pleuraphis rigida*; a C4 bunchgrass), and fluffgrass (*Dasyochloa*, formerly *Erioneuron pulchella*). Up to 75 annual species may occur, depending on timing and amount of rainfall, including the exotic annual grass red brome (*Bromus madritensis* ssp. *rubens*; Jordan et al. 1999). Due to a lack of historical disturbance, biological soil crusts (i.e., cyanobacteria, lichens, and moss) cover 30% to 60% of the ground surface (Smith et al. 2014).

### Experimental Design

The Nevada Desert FACE Facility began operating in April 1997 and continued to provide elevated atmospheric CO<sub>2</sub> to undisturbed Mojave Desert plots for 10 years, through June 2007. Consisting of nine study plots, each 23 m in diameter, the experiment comprised (1) three FACE rings at elevated CO<sub>2</sub> concentration (550 ppm); (2) three FACE rings at ambient CO<sub>2</sub> concentration (i.e., blower control rings at ambient CO<sub>2</sub> concentration, naturally increasing from 360 to 380 ppm throughout the 10-year period); and (3) three nonblower control plots. The Nevada FACE site maintained continuous CO<sub>2</sub> enrichment during >95% of daylight hours, except when the 5-minute wind speed average exceeded 6.0 m per second (7.0 m per second in the growing season) or when air temperature was below 3°C. Throughout the experiment, mean CO<sub>2</sub> concentrations were 550 ppm in elevated CO<sub>2</sub> plots and 375 ppm in ambient plots. Plants were accessed from an overhead moveable walkway system and an attached sampling platform that prevented surface disturbance of the plots.

The split-plot experimental design was identical for all dependent variables, and all data were analyzed using mixed-effects analysis of variance. The CO<sub>2</sub> treatment was applied to entire plots. Each variable was sampled at two time points within each plot (initial and final). Therefore, all models contained CO<sub>2</sub> treatment as a fixed effect (i.e., tested over plot within CO<sub>2</sub> treatment), time as a fixed effect, and an interaction between CO<sub>2</sub> treatment and time (i.e., both tested over the interaction between time and plot). Also estimated were the differences between final and initial values for each CO<sub>2</sub> treatment as *a priori* contrasts.

### Measurements

A variety of physiological measurements were made throughout the experiment, including for photosynthesis, stomatal conductance, transpiration, and nutrient concentrations. Aerial photographs helped researchers determine the cover of the dominant plant species, and aboveground growth of perennial species was measured using nondestructive methods. Production of annual plants was assessed by quantifying plant

### Websites

#### Project

[www.dri.edu/nevada-desert-research-center/nevada-desert-face-facility](http://www.dri.edu/nevada-desert-research-center/nevada-desert-face-facility)

#### Publications

[www.dri.edu/component/content/article/359-nevada-desert-face-facility/5321-nevada-desert-research-center-publications](http://www.dri.edu/component/content/article/359-nevada-desert-face-facility/5321-nevada-desert-research-center-publications)

#### Data

- [facedata.ornl.gov](http://facedata.ornl.gov)
- [facedata.ornl.gov/facemds/](http://facedata.ornl.gov/facemds/)



density across transects and destructive harvests. Fine-root data were obtained from minirhizotrons installed beneath *Larrea* and *Ambrosia* shrubs and in intershrub spaces. Prior to CO<sub>2</sub> cutoff in 2007, about two-thirds of each plot was extensively surveyed and sampled for biological soil crust cover, soil microbial DNA analysis, and aboveground cover biomass. After CO<sub>2</sub> treatment ended, extensive fine- and coarse-root samples and soil samples to 1 m in depth were acquired from the same area for analysis.

### 3.4.3 Results

#### *Photosynthesis and Respiration*

Early in the experiment, during an El Niño year in 1998, well-watered *Larrea tridentata* downregulated photosynthesis in elevated CO<sub>2</sub> so significantly that photosynthetic rates were similar in ambient and elevated CO<sub>2</sub>. Drought diminished downregulation, resulting in seasonally transient patterns of enhanced carbon gain (Huxman et al. 1998), and net photosynthesis was enhanced during both moist and dry periods of the potential growing season (Hamerlynck et al. 2000). During an anomalously wet year (1998), integrated photosynthesis was enhanced 26% in *Larrea*, 102% in *Ambrosia*, and 42% in *Krameria*. In a dry year (2001), all photosynthesis rates were reduced, but the relative effect of elevated CO<sub>2</sub> was similar to or greater than that in the dry year (Housman et al. 2006). After 8 years, both the evergreen *Larrea* and the drought-deciduous *Ambrosia* maintained their photosynthetic capacities under elevated CO<sub>2</sub> (Aranjuelo et al. 2011).

*Larrea* stomatal conductance decreased by 25% to 50% in elevated CO<sub>2</sub> but only at the onset of the summer dry season and after late summer precipitation. Two other species showed no stomatal response (Naumburg et al. 2003). The degree of photosynthetic enhancement under elevated CO<sub>2</sub> was directly proportional to the response of stomatal conductance (Naumburg et al. 2004).

During the El Niño year (1998) when resource availability was relatively greater compared to that in dry years, an invasive annual grass *B. madritensis* ssp. *rubens* showed consistently greater photosynthesis rates throughout most of its lifecycle and no consistent response of stomatal conductance. The native herbaceous perennial *Erigeron inflatum*, however, showed significant photosynthetic downregulation in elevated CO<sub>2</sub> late in the season and reduced stomatal conductance throughout much of the season (Huxman and Smith 2001).

#### *Growth*

Elevated CO<sub>2</sub> increased aboveground production in *Larrea*, *Ambrosia*, and winter-deciduous *Krameria* during an anomalous wet year (the 1998 El Niño year), with relative enhancements ranging from 59% in *Krameria* to 131% in *Larrea*. In below-average rainfall years, growth was much reduced and only *Ambrosia* had greater growth in elevated CO<sub>2</sub> (Housman et al. 2006).

Early in the experiment, there were no effects of elevated CO<sub>2</sub> on fine-root standing crop, production, or mortality, except for reduced root length in the interspaces between shrubs (Phillips et al. 2006). During the last 4.5 years of the experiment, treatment effects occurred sporadically for some fine-root measurements, but differences were transitory and often in opposite directions in different time periods (Ferguson and

Nowak 2011). There was no effect of elevated CO<sub>2</sub> on root respiration or specific root length (Clark et al. 2010).

Despite the increases in photosynthesis and growth in elevated CO<sub>2</sub> during occasionally favorable conditions, the final harvest after 10 years revealed no effect of elevated CO<sub>2</sub> on standing biomass, biomass allocation, canopy cover, or C:N ratios of above- or belowground components. Importantly, however, precipitation was uncharacteristically low for several years prior to the final harvest. This high frequency of low-precipitation years apparently constrained the cumulative biomass responses to elevated CO<sub>2</sub> (Newingham et al. 2013).

### Nutrient Interactions

Leaves of *Larrea* and *Lycium pallidum* had significantly lower nitrogen concentration in elevated CO<sub>2</sub> in 1 of the 3 years measured; two other shrubs showed no difference. There was no effect of elevated CO<sub>2</sub> on the leaf litter C:N ratio or on lignin or cellulose concentrations (Billings et al. 2003). In another study, the litter C:N ratio was greater in elevated CO<sub>2</sub>, but there was no difference in litter decomposition (Weatherly et al. 2003).

In laboratory assays, net ammonification increased under shrubs exposed to elevated CO<sub>2</sub>, while net nitrification decreased (Schaeffer et al. 2007). Extracellular enzyme activity involved in cellulose and orthophosphate degradation decreased during the growing season in ambient CO<sub>2</sub> but increased under elevated CO<sub>2</sub>. Microbial carbon-use and substrate-use diversity were positively affected by elevated CO<sub>2</sub>. However, microbial biomass nitrogen was lower in elevated CO<sub>2</sub> soil (Jin and Evans 2007).

Organic nitrogen in soil increased under elevated CO<sub>2</sub>, a result that could be attributed only partially to increased rates of heterotrophic nitrogen fixation (Jin and Evans 2010). There was no evidence for progressive nitrogen limitation (Evans et al. 2014).

### Water Use

*Ephedra nevadensis* responded to elevated CO<sub>2</sub> in the FACE plots with a 33% reduction in the ratio of transpirational surface area to sapwood area, thereby increasing leaf-specific hydraulic conductivity; stomatal conductance remained constant or was increased under elevated CO<sub>2</sub>. *Larrea tridentata* did not show a reduced ratio in the field; stomatal conductance was reduced in elevated CO<sub>2</sub> but only under conditions of high soil moisture (Pataki et al. 2000). However, reduced stomatal conductance in elevated CO<sub>2</sub> did not result in greater soil water content (Nowak et al. 2004).

The biocrust cover was very responsive to precipitation: drought reduced the moss and lichen cover to near zero in both ambient and elevated CO<sub>2</sub> plots. Elevated CO<sub>2</sub> did not alleviate water stress to mitigate the drought-induced reduction in cover (Wertin et al. 2012).

### Soil

Significant carbon accumulation was caused by CO<sub>2</sub> enhancement over the 10 years of the experiment, and the gain in carbon was due solely to soil organic carbon (SOC). Aboveground sources were the origins of 70% of the accrued SOC. The increase in soil carbon was attributed to belowground allocation of the gain in leaf-level carbon through



photosynthetic enhancement that occurred when moisture was readily available (Evans et al. 2014).

Root exudation and microbial necromass from stabilization of labile carbon and nitrogen were probably more important than carbon input from fine-root turnover. Plant-derived compounds were the main constituents of stabilized SOM (Evans et al. 2014; Tfaily et al. 2018).

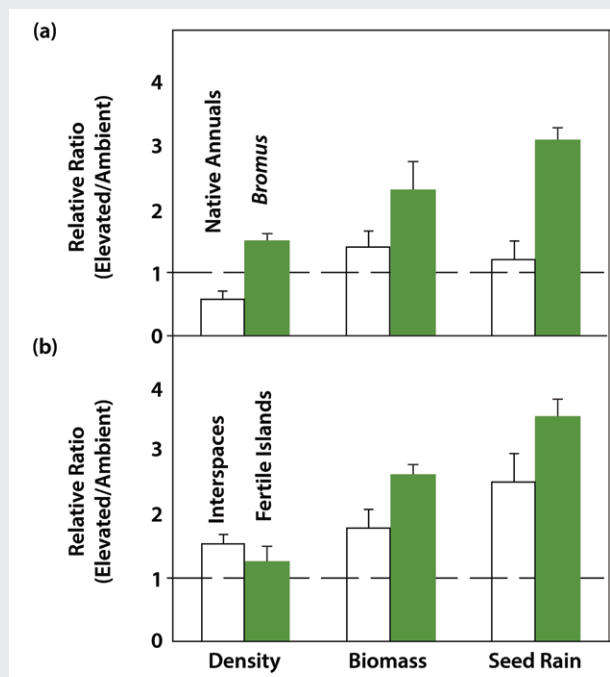
The biocrust in elevated CO<sub>2</sub> plots had less cyanobacterial biomass than in ambient plots (Steven et al. 2012). The structure and representation of microorganisms associated with roots were altered by elevated CO<sub>2</sub> (Nguyen et al. 2011), but there were no effects on any measured traits of arbuscular mycorrhizal fungi (Clark et al. 2009).

### Plant Community Dynamics

Community structure of the perennial plant community was not affected by elevated CO<sub>2</sub>. There were no changes in total cover, species richness, or diversity over the course of the experiment. There also were no elevated CO<sub>2</sub> effects on changes in *Larrea* cover, but decreases in cover of a C4 bunchgrass were alleviated and the cover of C3 drought-deciduous shrubs was slightly reduced. The lack of strong shifts in the plant community after 10 years of elevated CO<sub>2</sub> can be explained by the extended drought, slow plant growth rates, and highly episodic germination and recruitment of new individuals (Newingham et al. 2013).

The invasive annual grass *B. rubens* dramatically responded to elevated CO<sub>2</sub> during a high-rainfall El Niño year—a 2.3-fold increase in aboveground biomass in elevated CO<sub>2</sub> and threefold higher seed rain (see Fig. 3.5, this page). The shift in species composition

**Fig. 3.5. Productivity of Invasive Grasses in Nevada Desert FACE Experiment.** The relative effect of elevated carbon dioxide on plant density, aboveground biomass, and seed rain of (a) native annuals and the invasive *Bromus madritensis* spp. *rubens* and (b) the *Bromus* species in open interspaces and fertile islands. [Reprinted with permission from Springer Nature from Smith, S. D., et al. 2000. "Elevated CO<sub>2</sub> Increases Productivity and Invasive Species Success in an Arid Ecosystem," *Nature* **408**, 79–82. Copyright 2000.]



in favor of exotic annual grasses has the potential to accelerate the fire cycle, reduce biodiversity, and alter ecosystem function in this ecosystem (Smith et al. 2000). However, the multiyear dry cycle that followed the wet year resulted in no increases in productivity or reproductive allocation of *B. madritensis* ssp. *rubens*. Hence, relative stimulation of invasive grasses to elevated CO<sub>2</sub> will depend on future precipitation patterns, both the timing (late fall through early winter) and amount (about 10 mm cumulatively; Smith et al. 2014).

### 3.4.4 Summary

The Mojave Desert ecosystem of the Nevada Desert FACE Facility is strongly dominated by water, and responses to elevated CO<sub>2</sub> were highly dependent on precipitation patterns. Photosynthesis was stimulated by elevated CO<sub>2</sub>, increasing leaf-level carbon gain, with larger effects in wet years (e.g., an El Niño year) than during extended drought years, but this response supported increased aboveground growth only in the wet years. After 10 years, there was no detectable effect of elevated CO<sub>2</sub> on aboveground biomass or community structure of the perennial plant community. However, there was a significant accumulation of organic carbon in soil that, if extended over other arid and semiarid ecosystems, could account for 4% to 8% of global CO<sub>2</sub> emissions and 15% to 28% of terrestrial carbon uptake at that time (in 2014; Evans et al. 2014).

## Rhineland FACE

Northern  
Hardwoods

Rhineland,  
Wisconsin



1997–2009

### Lead Institutions

- Michigan Technological University
- Forest Service, U.S. Department of Agriculture
- Brookhaven National Laboratory

### Key Reference

Burton, A. J., et al. 2014. *Impacts of Interacting Elevated Atmospheric CO<sub>2</sub> and O<sub>3</sub> on the Structure and Functioning of a Northern Forest Ecosystem: Operating and Decommissioning the Aspen FACE Project.*



## 3.5 Rhineland FACE

### 3.5.1 Objectives

The Rhineland FACE experiment was a multidisciplinary study to assess the effects of increasing tropospheric ozone (O<sub>3</sub>) and CO<sub>2</sub> levels on the structure and function of a regenerating, northern hardwood ecosystem over its early life history. Specific scientific objectives included examining (1) the interacting effects of elevated CO<sub>2</sub> and O<sub>3</sub>, alone and in combination, on the resultant productivity, sustainability, competitive interactions among species and genotypes, and carbon and nitrogen fluxes; (2) foliar defense compounds related to stress tolerance; (3) responses to insects, diseases, and other stresses; and (4) ecosystem processes such as litter decomposition, mineral weathering, and carbon and nutrient cycling. An additional objective was to parameterize and validate an ecophysiological process model of growth and development to scale individual tree responses to the ecosystem level.

### 3.5.2 Description of Experiment

#### Site

The Rhineland FACE experiment was in northern Wisconsin near Rhineland (45°41'N, 89°38'W) on the Harshaw Experimental Farm of the USDA Forest Service. The 32-ha site is old agricultural land that was farmed for potatoes and small grains for more than 50 years. From 1976 to 1990, about 80% of the Rhineland FACE site was planted with different hybrid poplar clones and some larch for short-rotation intensive culture and mixed-genetics forest research (Dickson et al. 2000). The remaining area

reverted to old-field vegetation. Soil at the site is characterized as level to gently rolling Pandus sandy loam (i.e., mixed, frigid, and coarse loamy Alfic Haplorthod). The sandy loam topsoil (about 15 cm thick) grades into a plow layer, clay loam accumulation layer (about 30 cm thick) and then grades back into a sandy loam, stratified sand, and gravel substratum. Occasional clay layers at 30 to 60 cm are found throughout the field (Dickson et al. 2000). The site has a continental climate with a frost-free growing season of approximately 120 days, with summer temperatures averaging 16.1°C and reaching highs of about 32°C; winter temperatures average -6.7°C, reaching as low as -20°C. Average annual precipitation is 800 mm.

### Plant Community

All poplar and larch plantings were cleared from the site in 1996 and 1997, all stumps in the ring areas were pulled, and the rings were disked and planted in rye cover crop in the summer of 1996 (Dickson et al. 2000). In June 1997 each experimental plot was planted with three model communities of trembling aspen (*Populus tremuloides*): trembling aspen monoculture, trembling aspen and paper birch (*Betula papyrifera*), and trembling aspen and sugar maple (*Acer saccharum*). The aspen monoculture consisted of the five clones that had been studied previously for responses to elevated CO<sub>2</sub> and O<sub>3</sub>. Rooted greenwood cuttings of aspen clones were planted as pairs of individuals of each clone, with the pairs randomly distributed throughout the 1 × 1 m grid. Seedlings of maple and birch were grown from local seed. The aspen-birch and aspen-maple mixed communities were planted in an alternating pattern throughout the 1 × 1 m grid (Dickson et al. 2000).

### Experimental Design

Three replicate FACE rings were established in 1997 for a factorial combination of four treatments (CO<sub>2</sub>, O<sub>3</sub>, CO<sub>2</sub> + O<sub>3</sub>, and control) in a randomized block design (Dickson et al. 2000). The three plant communities were treated as split-plots, with the aspen monoculture in one-half of the plot and the aspen-maple and aspen-birch each in one-quarter. Fumigations with elevated CO<sub>2</sub> (target concentration of 560 ppm during daylight hours) and O<sub>3</sub> (about 1.5 × ambient) were conducted over growing seasons of 165, 144, 145, 150, 137, 143, 154, 143, 140, 125, and 140 days from 1998 to 2008, respectively, and in 2009 through to the harvest date. Actual CO<sub>2</sub> concentrations measured during the experiment were 347 to 362 ppm in ambient CO<sub>2</sub> plots and 530 to 548 ppm in elevated CO<sub>2</sub> plots. Ozone concentration averaged 39 to 41 parts per billion (ppb) in ambient plots and 49 to 54 ppb in elevated O<sub>3</sub> plots. Soil properties differed little among the 12 plots, and there were no significant differences among replications or gradients across the field.

### Measurements

Response variables quantified during the experiment included growth (i.e., height, diameter, biomass, leaf area, root production, and fine root mortality). Researchers also assessed competitive interactions and stand dynamics, physiological processes (i.e., photosynthesis, respiration, stomatal conductance, and chlorophyll content), plant nutrient status and uptake (nitrogen), tissue biochemistry (i.e., carbohydrates, phenolic glycosides, and antioxidants), litter quality and decomposition rates, hydrology, soil respiration, microbial community composition and respiration, volatile organic compound

#### Websites

##### Project

[aspenface.mtu.edu](http://aspenface.mtu.edu)

##### Publications

[aspenface.mtu.edu/publications.htm](http://aspenface.mtu.edu/publications.htm)

##### Data

- [facedata.ornl.gov](http://facedata.ornl.gov)
- [facedata.ornl.gov/facemds/](http://facedata.ornl.gov/facemds/)

(VOC) production, treatment-pest interactions, and treatment-phenology interactions. From mid-June to mid-August, the plots were harvested, which entailed detailed sampling of a subset of trees by component (i.e., leaves and buds, fine branches, coarse branches and stems, coarse roots, and fine roots) as well as soil excavation to a depth of 1 m. An excavator and commercial soil sieve were used to recover coarse roots, with additional cores from pit faces used to capture fine-root biomass (Burton et al. 2014).

### 3.5.3 Results

#### *Photosynthesis and Respiration*

Throughout the experiment, photosynthesis increased with elevated CO<sub>2</sub> and tended to decrease with elevated O<sub>3</sub>, compared to that of the control. Elevated CO<sub>2</sub> enhanced photosynthesis of the early successional species by 20% to 30% in aspen and by 50% to 70% in birch, but there was no effect on maple photosynthesis (Karnosky and Pregitzer 2006). There also was no evidence for photosynthetic acclimation in the two aspen clones that were examined (Darbah et al. 2010). Stimulation of photosynthesis in elevated CO<sub>2</sub> was more pronounced on days with environmental stress (i.e., drought and high temperature; Kets et al. 2010). There was little effect on nighttime foliar respiration (Davey et al. 2004).

#### *Growth*

Elevated CO<sub>2</sub> stimulated both aboveground and belowground growth. Responses were species and genotype dependent, with birch and aspen being most responsive and maple being least responsive. The positive effects of elevated CO<sub>2</sub> on NPP were sustained through the end of the experiment, but negative effects of elevated O<sub>3</sub> on NPP had dissipated during the final 3 years of treatments (2006–2008). During the last 3 years of the experiment, elevated CO<sub>2</sub> enhanced NPP by 40%, 14%, and 25%, respectively, and there were no effects of O<sub>3</sub> or CO<sub>2</sub> × O<sub>3</sub> interaction (Burton et al. 2014). Cumulative NPP over the course of the experiment was 39% greater in elevated CO<sub>2</sub> and 10% less in elevated O<sub>3</sub> (see Fig. 3.6, p. 39; Talhelm et al. 2014). Treatment effects of elevated CO<sub>2</sub> on NPP were attributed both to stimulation of photosynthesis and increases in leaf area. Leaf mass was 36% greater in elevated CO<sub>2</sub> (Talhelm et al. 2012). There were no CO<sub>2</sub> effects on the proportional distribution of wood, leaf, and root production (King et al. 2005). Initially, fine-root production was stimulated by elevated CO<sub>2</sub> (King et al. 2001), but the response was not sustained.

#### *Water Use*

Changes in stand-level leaf area tended to offset the leaf-level effects of the treatments on stomatal conductance and thus potential stand water use. Stand-level canopy conductance was significantly increased by elevated CO<sub>2</sub> but not significantly affected by elevated O<sub>3</sub>, demonstrating that short-term primary stomatal closure responses to elevated CO<sub>2</sub> and O<sub>3</sub> were completely offset by long-term cumulative effects of these trace gases on tree and stand structure in determining canopy- and leaf-level conductance in pure aspen and mixed aspen-birch forest (Uddling et al. 2010). Leaves from trees grown in elevated CO<sub>2</sub> or O<sub>3</sub> exhibited weaker short-term responses of stomatal conductance to both an increase and a decrease in CO<sub>2</sub> concentration from the current ambient level



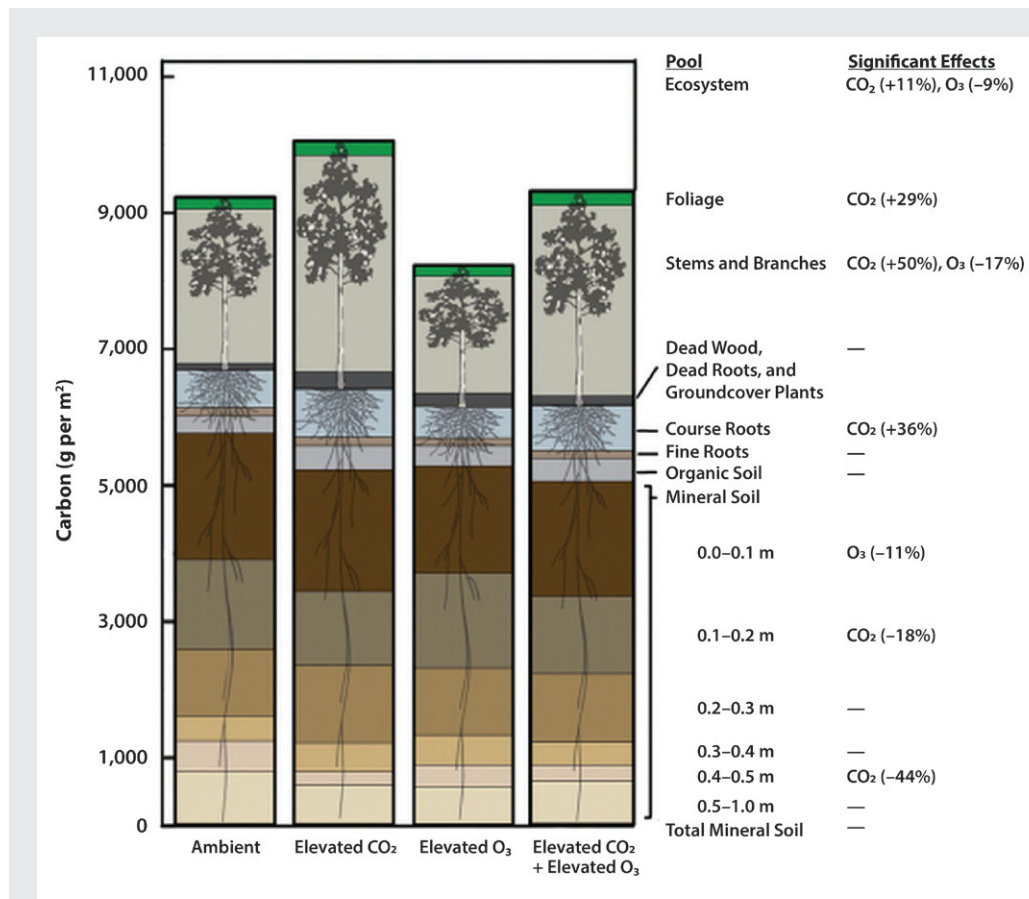
(Onandia et al. 2011). Thus, model assumptions of large reductions in stomatal conductance under rising atmospheric CO<sub>2</sub> are very uncertain for forests.

**Nutrient Interactions**

Effects of elevated CO<sub>2</sub> on foliar nitrogen concentration [N] were inconsistent, with decreases in [N] reported early in the experiment (Ellsworth et al. 2004) and minimal effects reported later (Couture et al. 2017). Total nitrogen mass in leaves, however, was increased 30% by elevated CO<sub>2</sub>, reflecting accelerated nitrogen cycling (Talhelm et al. 2012). Enhanced NPP under elevated CO<sub>2</sub> was sustained by greater root exploration of soil for growth-limiting nitrogen, as well as more rapid rates of litter decomposition and microbial nitrogen release during decay (Zak et al. 2011, 2012). There was no indication of progressive nitrogen limitation.

**Soil**

Increased carbon inputs to soil under elevated CO<sub>2</sub> resulted in a significant increase in soil respiration (King et al. 2004). The treatment responses in soil respiration were correlated with fine-root biomass. SOM accumulated at a slower pace under elevated CO<sub>2</sub>, despite the fact that both above- and belowground litter production significantly



**Fig. 3.6. Carbon Content of a Northern Hardwood Ecosystem After 11 Years of Exposure to Elevated Carbon Dioxide and Ozone During the Rhinelander FACE Experiment.** [Reprinted under a Creative Commons License (CC BY-NC-ND 2.0) from Talhelm, A. F., et al. 2014. "Elevated Carbon Dioxide and Ozone Alter Productivity and Ecosystem Carbon Content in Northern Temperate Forests," *Global Change Biology* 20(8), 2492–504.]



increased under elevated CO<sub>2</sub> (Talhelm et al. 2009). SOM decay apparently occurred more rapidly under elevated CO<sub>2</sub>, in parallel with the increased rate of forest floor nitrogen cycling. After 11 years, there were no significant main effects of CO<sub>2</sub> or O<sub>3</sub> on surface soil (0 to 20 cm) carbon content across all three communities. However, within the aspen community, elevated CO<sub>2</sub> caused a significant decrease in soil carbon content (Talhelm et al. 2009).

### ***Biotic Interactions***

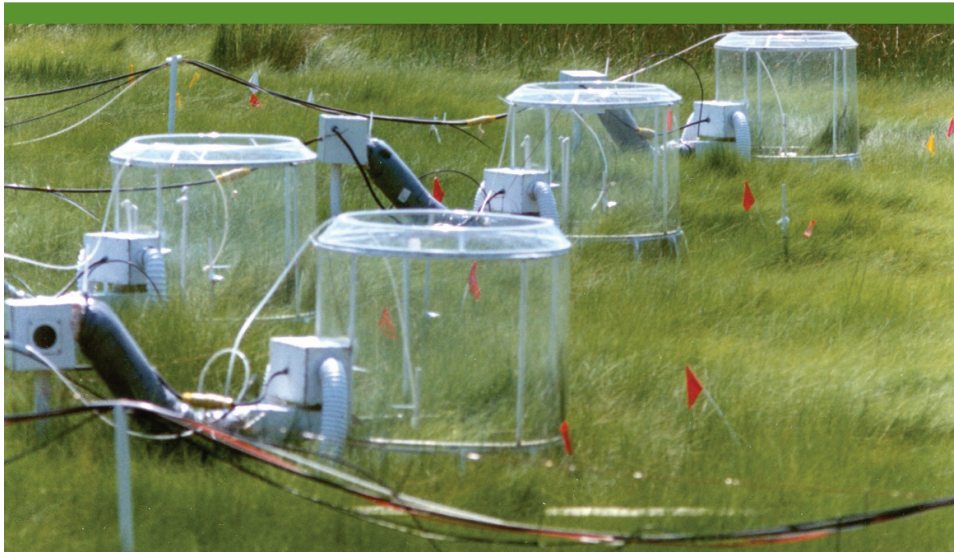
Canopy damage from herbivorous insects was markedly greater in elevated CO<sub>2</sub> plots (Couture et al. 2015). Treatment effects on arthropods were weak and idiosyncratic. The insect community composition on birch trees was occasionally affected by CO<sub>2</sub> or ozone, but there were no effects on arthropod abundance or species richness on aspen.

### **3.5.4 Summary**

The Rhinelander FACE experiment differed from the other FACE experiments supported by DOE in two important ways. First, it was initiated in a seedling stand and, therefore, was an expanding system through most or all of the experimental duration. Many of the responses reported early in the experiment were not sustained, emphasizing the importance of projecting the responses of seedlings and young trees to mature forests, as well as the value in maintaining experiments for as long as is feasible. Second, the Rhinelander FACE study also included an O<sub>3</sub> treatment in a factorial combination with CO<sub>2</sub>. Ozone was found to counteract some of the effects of elevated CO<sub>2</sub>, suggesting that projections of CO<sub>2</sub> responses will be overstated if the co-occurrence of O<sub>3</sub> is not considered. However, the negative effects of O<sub>3</sub> on growth dissipated by the end of the experiment, and global projections of ozone effects should consider the possibility of ozone-tolerant plants replacing ozone-sensitive plants. If similar forests growing throughout northeastern North America respond in the same manner, then enhanced forest NPP under elevated CO<sub>2</sub> may be sustained for a longer duration than previously thought. In addition, the negative effect of elevated O<sub>3</sub> may be diminished by compensatory growth of O<sub>3</sub>-tolerant plants as they begin to dominate forest communities (Burton et al. 2014).

## Field Chamber Experiments

Open-top chambers (OTCs) have been widely used to investigate responses to elevated carbon dioxide ( $\text{CO}_2$ ) of individual plants, small groups of young trees, and small-statured and constructed plant assemblages. The U.S. Department of Energy (DOE) supported many such experiments, whose results were important for establishing hypotheses to test in subsequent Free-Air  $\text{CO}_2$  Enrichment (FACE) experiments (Norby et al. 1999). In addition, DOE has supported several completed and ongoing OTC experiments in intact ecosystems addressing questions and using approaches similar to those of FACE studies. This chapter describes six ecosystem-scale experiments that use OTCs or greenhouses to manipulate atmospheric  $\text{CO}_2$  concentration.



### 4.1 Salt Marsh OTC

#### 4.1.1 Objective

As one of the first and longest-running elevated  $\text{CO}_2$  experiments in an intact ecosystem, the ongoing Maryland salt marsh study seeks to determine the response of plants to elevated  $\text{CO}_2$  *in situ* and to discover the response of an entire wetland to this single

#### Salt Marsh OTC

#### Chesapeake Bay, Maryland



1985–present

#### Lead Institution

Smithsonian Environmental Research Center

#### Key Reference

Drake, B. G. 2014. "Rising Sea Level, Temperature, and Precipitation Impact Plant and Ecosystem Responses to Elevated  $\text{CO}_2$  on a Chesapeake Bay Wetland: Review of a 28-Year Study," *Global Change Biology* **20**(11), 3329–43.

**Websites****Project**

serc.si.edu/gcrew

**Publications**research.serc.si.edu/  
researchdata/  
publication\_data\_  
cfm/drake\_pub.cfm**Data**serc.si.edu/gcrew/  
CO2data

but crucial component of climate change. The central objective is to determine the impact of elevated atmospheric CO<sub>2</sub> on the mechanisms that regulate CO<sub>2</sub> assimilation, biomass allocation, organic matter decomposition, plant and ecosystem respiration, nutrient mineralization, and carbon storage and export. Research considers whether the effect of elevated CO<sub>2</sub> on photosynthesis and growth will persist over the long term and how elevated CO<sub>2</sub> might shift the species makeup of a wetland.

## 4.1.2 Description of Experiment

### Site

The experimental site is a brackish high marsh on the Rhode River, a subestuary of the Chesapeake Bay (38°53'N, 76°33'W). Average temperature is 15°C, with an average summer high temperature of 31.9°C and a wintertime low of -1.6°C. Average annual precipitation is 1,202 mm. Soils are Histosols with 79% organic matter and a bulk density of 0.12 g per m<sup>3</sup> to a depth of 5 to 6 m (Morris et al. 2016). The site is flooded infrequently.

### Plant Community

The marsh is a mosaic of plant associations primarily dominated by *Spartina patens*, *Schoenoplectus americanus* (previously called *Scirpus olneyi*), *Distichlis spicata*, *Typha angustifolia*, or *Iva frutescens*. Three communities on the marsh were selected for this study. One community is dominated by the C4 grass *S. patens*, one by the C3 sedge *S. americanus*, and one that is a mixed C3-C4 community (Curtis et al. 1989).

### Experimental Design

Within each of the three plant communities, 15 permanent circular plots, 0.8 m in diameter, were established along transect lines. Treatments are assigned to plots according to a randomized block design, with three treatments per block and five blocks per community (Curtis et al. 1990). Within each community, five plots have exposure chambers with CO<sub>2</sub> concentrations 336 parts per million (ppm) above ambient levels, five plots have chambers receiving no additional CO<sub>2</sub>, and five plots have no chambers but are treated identically to chambered plots (i.e., control treatment; Curtis et al. 1989). Each year treatments begin in late April and end in mid- to late November.

### Measurements

Researchers have surveyed the plant communities each year since 1987 at the peak of the growing season (last week in July and first week in August), recording numbers of shoots and lengths and widths of stems in each of the study plots. Shoot density, leaf area index (LAI), and biomass are calculated. In addition to leaf-level photosynthesis measurements, whole-ecosystem gas exchange is determined using the OTC as a cuvette. Soil cores are collected to determine carbon and nitrogen pools and processes.

## 4.1.3 Results

### Photosynthesis and Respiration

In shoots of the *Schoenoplectus* C3, elevated CO<sub>2</sub> stimulated photosynthesis, increased quantum yield, and decreased the light compensation point, but not in *Spartina* C4. However, in both species, elevated CO<sub>2</sub> reduced ecosystem respiration associated with reduced nitrogen in plants (Drake 2014). Photosynthetic acclimation occurred in the

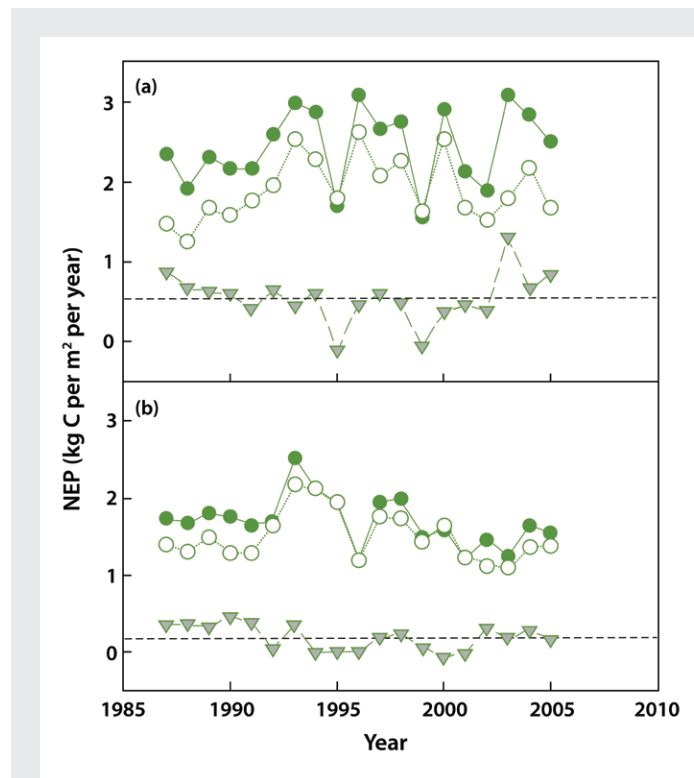
dominant sedge but did not obviate a strong response of photosynthesis at the leaf level. Acclimation caused a 50% reduction in total protein concentration and in Rubisco. A correlation between acclimation and rainfall showed that acclimation reduced photosynthetic capacity *less* during high rainfall than during drought (Jacob et al. 1995).

### Plant Growth and Net Ecosystem Production

Elevated CO<sub>2</sub> increased shoot density and biomass in *Schoenoplectus* C3 but decreased density and biomass in *Spartina* C4. Net ecosystem production (NEP), measured by ecosystem gas exchange, increased 35% in *Schoenoplectus* C3 and 15% in *Spartina* C4 as a result of elevated CO<sub>2</sub> (see Fig. 4.1, this page). Increased ecosystem CO<sub>2</sub> assimilation occurred in part by reduced dark respiration. The effects of elevated CO<sub>2</sub> on tissue nitrogen concentration, total canopy nitrogen, and ecosystem respiration in both *Schoenoplectus* C3 and *Spartina* C4 were related through reduced evapotranspiration. Increasing temperature reduced NEP 6% to 8% per degree Celsius (Drake 2014).

### Water Use

Elevated CO<sub>2</sub> reduced stomatal density, stomatal conductance, and transpiration of leaves and stems of both *Schoenoplectus* C3 and *Spartina* C4. Evapotranspiration was reduced in both species, but about twice as much in *Spartina* as in *Schoenoplectus* (Drake 2014). Water-use efficiency (WUE) increased 80% in both the C3 and C4 communities (Li et al. 2010).



**Fig. 4.1. Net Ecosystem Production (NEP) of (a) the *Schoenoplectus* C3 community and (b) *Spartina* C4 community.** Responses to elevated carbon dioxide (CO<sub>2</sub>; solid circles) and ambient CO<sub>2</sub> (open circles) are shown, along with the difference between them (triangles). [Redrawn by permission from Wiley from Drake, B. G., 2014. "Rising Sea Level, Temperature, and Precipitation Impact Plant and Ecosystem Responses to Elevated CO<sub>2</sub> on a Chesapeake Bay Wetland: Review of a 28-Year Study," *Global Change Biology* **20**(11), 3329–43. Copyright 2014.]

### Nutrient Interactions

Elevated CO<sub>2</sub> reduced nitrogen concentration in both *Schoenoplectus* C3 and *Spartina* C4 at a rate proportional to precipitation (Drake 2014), and a decrease in exchangeable soil nitrogen was consistently observed for both plant communities. Nitrogen uptake did not increase; hence, nitrogen-use efficiency (NUE) was greater in elevated CO<sub>2</sub>. There also was no evidence that nitrogen was limiting in this system (Matamala and Drake 1999).

### Soil

Responses to elevated CO<sub>2</sub> across all levels of the ecosystem (i.e., photosynthesis, respiration, growth of shoots and roots, and increased biogeochemical activity) suggest there is a substantial amount of carbon sequestered or cycled through this ecosystem. A negligible fraction of the additional soil carbon is exported from the site as methane (CH<sub>4</sub>) or in shallow groundwater (Marsh et al. 2005). Some of the excess carbon produced in response to elevated CO<sub>2</sub> was feeding heterotrophic processes such as nitrogen fixation (Dakora and Drake 2000), CH<sub>4</sub> production (Dacey et al. 1994), and microbial respiration (Ball 1997). An analysis of the balance of gaseous and hydrologic fluxes did not reveal the fate of the extra carbon taken up at elevated CO<sub>2</sub> (Marsh et al. 2005). This uncertainty inspired a separate experiment to test the hypothesis that carbon was accumulating in soil as an increase in elevation rather than an increase in soil organic matter (SOM) concentration. The results of the new experiment suggest that elevated CO<sub>2</sub> increased soil carbon sequestration (Langley et al. 2009).

### Plant Community

Rising sea level shifted the *Schoenoplectus* C3 community to higher elevations on the marsh and led to increased *Schoenoplectus* C3 shoot biomass in the mixed community and decreased *Spartina* C4 biomass in both the mixed and pure *Spartina* C4 communities (Drake 2014).

### 4.1.4 Summary

These long-term studies indicate that rising atmospheric CO<sub>2</sub> will increase carbon cycling in native plant communities through various mechanisms that all depend on the responses of photosynthesis and transpiration. The greatest effects of rising atmospheric CO<sub>2</sub> on carbon assimilation and plant growth and on microbial processes result from interactions with environmental stress, primarily caused by interannual variation in rainfall and salinity. Results suggest that an accumulation of the products of CO<sub>2</sub> stimulation of photosynthesis and growth in the litter and soil raises the surface of the marsh. This accumulation of carbon in the form of undecomposed litter is the most likely sink for the additional carbon.

The importance of rainfall in the responses to elevated CO<sub>2</sub> was unexpected, as was the shift from relatively labile or short-lived carbon to more recalcitrant (long-lasting) soil carbon. More stable carbon compounds may mean a long-term shift in the rate of decomposition. Expansive growth, represented as shoot density, had a relatively large stimulation during periods of high salinity, which accompanies low rainfall. Important ecosystem functions have been altered by long-term exposure to elevated atmospheric CO<sub>2</sub>, including species composition (i.e., a change in the relative dominance of the C4 plants in the mixed community), nitrogen fixation, and palatability of foliage for herbivores (Drake 2014).





## Scrub Oak OTC

*Merritt Island National Wildlife Refuge, Cape Canaveral, Florida*



**1996–2007**

### Lead Institution

Smithsonian Environmental Research Center

### Key Reference

Hungate, B. A., et al. 2013. "Cumulative Response of Ecosystem Carbon and Nitrogen Stocks to Chronic CO<sub>2</sub> Exposure in a Subtropical Oak Woodland," *New Phytologist* **200**(3), 753–66.

## 4.2 Scrub Oak OTC

### 4.2.1 Objectives

This long-term experiment, which ran from May 1996 to June 2007, was organized around five questions investigating the primary responses of a subtropical scrub oak ecosystem to rising atmospheric CO<sub>2</sub> and climate change:

1. How important is acclimation of photosynthesis to CO<sub>2</sub> fertilization of ecosystem carbon assimilation?

**Website****Publications**

research.serc.  
si.edu/researchdata/  
publication\_data\_  
cfm/drake\_pub.cfm

**Data**

data.ess-dive.  
lbl.gov/view/  
doi:10.15485/1480325

2. What are the mechanisms by which nutrient limitations mitigate growth response to elevated atmospheric CO<sub>2</sub>?
3. What are the mechanisms for improved water balance of plants to increase ecosystem CO<sub>2</sub> fertilization? Does stimulation of growth by elevated CO<sub>2</sub> deplete soil water?
4. Will elevated CO<sub>2</sub> alter carbon partitioning among foliage, wood, and roots?
5. Will elevated CO<sub>2</sub> increase ecosystem carbon?

## 4.2.2 Description of Experiment

### Site

The scrub oak experiment was conducted at the Merritt Island National Wildlife Refuge on the east coast of Florida (28°38'N, 80°42'W). Soils at the site, classified as Arenic Haplahumods and Spodic Quartzipsamments, are sandy with a low pH of about 4. The 100-year average annual precipitation is 1,310 mm, a total that masks high year-to-year variability. The climate is warm and humid, where 100-year average mean maximum and minimum temperatures in July (the hottest month) are 33.3°C and 21.8°C, respectively, and in January (the coldest month) are 22.3°C and 9.5°C (Johnson et al. 2001).

### Plant Community

The experimental site is representative of a fire-maintained, scrub oak–palmetto community. The shrub layer comprised rhizomatous sclerophyllous evergreen oaks, which resprouted from below ground after fire. Three oak species—myrtle oak (*Quercus myrtifolia*), sand live oak (*Q. geminata*), and Chapman oak (*Q. chapmanii*)—accounted for 96% of aboveground biomass. Also present is the saw palmetto (*Serenoa repens*), which generally contains considerable biomass in its rhizomes (Johnson et al. 2001; Dijkstra et al. 2002).

### Experimental Design

After controlled burning, 16 OTCs were established over the regrowing vegetation, each covering 9.42 m<sup>2</sup>. Eight chambers received ambient air, and eight received ambient air + 350 ppm CO<sub>2</sub>. A large blower circulated air through each chamber at a rate of 24 to 30 m<sup>3</sup> per minute, replacing the chamber air volume 1.3 to 1.6 times per minute. The chambers increased the air temperature and vapor pressure deficit while decreasing light microenvironmental effects that did not significantly alter growth or species composition (Hungate et al. 2013).

### Measurements

Leaf gas exchange (i.e., photosynthesis and stomatal conductance) was measured throughout the experiment. Constant-power sap flow gauges were used to measure transpiration of *Q. myrtifolia*. Fine-root production, turnover, and biomass were measured using minirhizotrons; coarse-root biomass was measured using ground-penetrating radar (GPR); and total root biomass was measured in soil cores.

During June to July 2007, all aboveground material was harvested from the chambers, and roots and soils were collected using multiple cores in each chamber. Belowground

biomass was also sampled indirectly using GPR (Stover et al. 2007; Day et al. 2013). Total soil carbon, nitrogen,  $^{15}\text{N}$ , and  $^{13}\text{C}$  were measured in bulk soil from the cores. A combination of density and biological fractionations was used to estimate soil carbon pools of varying turnover rates. Labile and active soil carbon pools were estimated from incubations, and microbial biomass was measured using the chloroform-fumigation extraction method in mineral soil (0 to 15 cm) sampled in July 1997; June, July, September, and December 1998; September 1999; and May 2004 (Hungate et al. 2013).

### 4.2.3 Results

#### *Photosynthesis and Respiration*

Within the scrub oak system, elevated  $\text{CO}_2$  stimulated net ecosystem exchange (NEE) of  $\text{CO}_2$  by 50% per unit ground area in winter to 180% in summer (Hymus et al. 2003). Increased NEE was related to sustained increase of photosynthetic capacity (72% in *Q. myrtifolia*; Ainsworth et al. 2002) and to the combination of high temperature and increased growth of leaves (Hymus et al. 2003). Acclimation of photosynthesis occurred only in *Q. geminata* (Hymus et al. 2002a).

Carbon dioxide effluxes from the ecosystem at night were on average 39% higher in elevated  $\text{CO}_2$  and varied between 6% and 64%. Increased leaf biomass, high temperature, and wetter soil produced greater ecosystem respiration during summer (Dore et al. 2003).  $\text{CO}_2$  stimulation of nighttime NEE resulted largely from stimulation of belowground respiration, although shoot respiration also was stimulated by elevated  $\text{CO}_2$ . There was no detectable direct effect of elevated  $\text{CO}_2$  on leaf respiration (Hymus et al. 2002a).

#### *Growth*

Shoot growth was stimulated 44% during 1996, and total biomass stimulation increased subsequently to about 60% (Dijkstra et al. 2002), leveling off at 65% but with high interannual variations in the amount of carbon added annually. Most of the additional growth each year (70%) was added by the largest shoots (>2 cm in diameter), which constitute only a small fraction (<10%) of the total number of shoots. Extensive defoliation caused by hurricanes in September 2004 was followed by a strong increase in shoot density in 2005 that may have resulted from reopening the canopy and relocating nitrogen from leaves to the nutrient-poor soil. Biomass response to elevated  $\text{CO}_2$  was driven primarily by stimulation of growth of the dominant species, *Q. myrtifolia*, while *Q. geminata*, the other co-dominant oak, displayed no significant response (Seiler et al. 2009). Leaf area was stimulated by elevated  $\text{CO}_2$  by 40% to 60% during the summer growing season but only 20% to 30% during the fall and winter (Hymus et al. 2002b).

Elevated  $\text{CO}_2$  initially stimulated fine-root growth, mortality, and turnover during the first 2 years of exposure (Dilustro et al. 2002), but these responses were absent after several years (Stover et al. 2010; Day et al. 2013). A greater proportion of fine roots was deeper in the soil profile, but there was no effect of elevated  $\text{CO}_2$  on distribution with depth (Stover et al. 2010). Fine-root biomass fluctuated by more than a factor of two, with no unidirectional temporal trend, whereas leaf biomass accumulated monotonically. Strong increases in fine-root biomass with elevated  $\text{CO}_2$  occurred after fire and hurricane disturbances (Day et al. 2013). The mass of carbon in fine roots was

not significantly affected by the elevated CO<sub>2</sub> treatment at the final harvest (Hungate et al. 2013). Coarse-root biomass was significantly greater in plots receiving elevated CO<sub>2</sub> (Stover et al. 2007; Day et al. 2013).

Plant carbon accumulation by the end of the experiment was 71.5 g C per m<sup>2</sup> per year greater in elevated CO<sub>2</sub> compared to ambient CO<sub>2</sub>. This carbon was roughly equally distributed above ground (37.5 g per m<sup>2</sup> per year) and below ground (33.5 g per m<sup>2</sup> per year; Hungate et al. 2013).

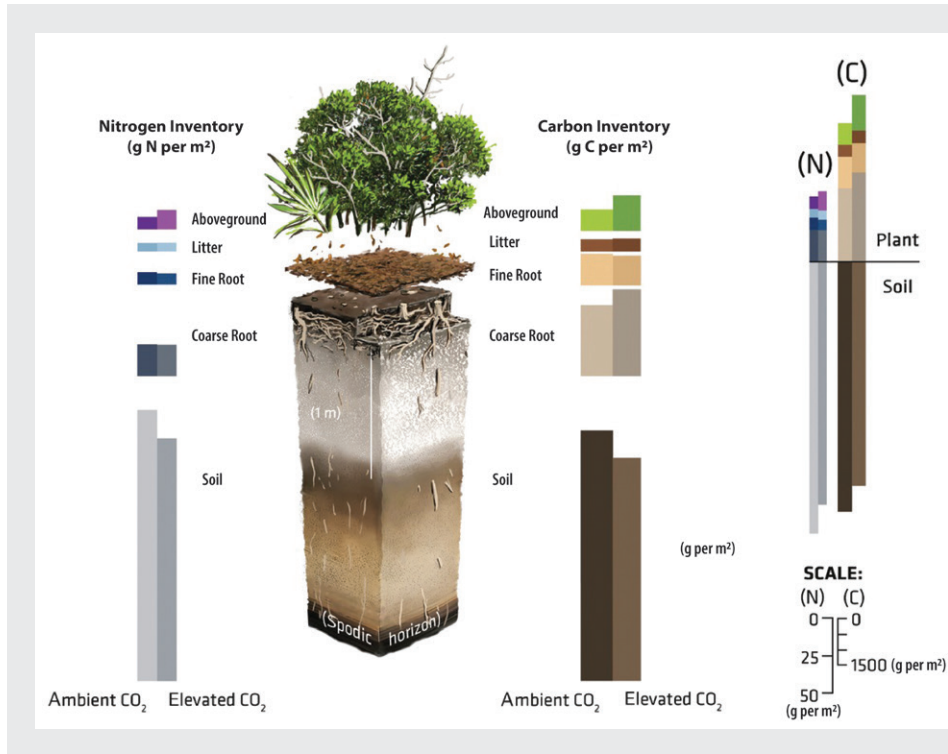
### **Water Use**

Elevated CO<sub>2</sub> reduced average transpiration per unit leaf area by 37% to 49% in the fourth year of the experiment. This reduction was the result of an immediate, reversible response to elevated CO<sub>2</sub> due to changes in stomatal conductance and an apparent indirect effect on transpiration caused mainly by greater self-shading arising from enhanced LAI, not from stomatal acclimation (Li et al. 2003). Increased LAI eliminated and, in some cases, reversed the effect of elevated CO<sub>2</sub> on ecosystem evapotranspiration. When LAI was below about 2.0, elevated CO<sub>2</sub> reduced evapotranspiration and increased soil water. However, when elevated CO<sub>2</sub> stimulated LAI, it also stimulated water loss. Earlier interpretations (Hungate et al. 2002) suggested that there might be a “mulch” effect of leaf litter on evapotranspiration, possibly explaining the long-term effect of elevated CO<sub>2</sub> on soil water balance. Hymus et al. (2003) showed that daily maximum NEE is positively dependent on soil water content, suggesting an additional layer of complexity in the interaction between the effect of elevated CO<sub>2</sub> on carbon cycling and environmental factors.

### **Nutrient Interactions**

Nitrogen uptake by the dominant oaks initially increased in response to elevated CO<sub>2</sub>, but the stimulation declined after 3 years, a pattern mirrored but even more pronounced in the uptake of tracer <sup>15</sup>N. Greater accumulation of nitrogen in biomass and in the surface organic layer of soil may have caused progressive nitrogen limitation at this site, possibly contributing to the low growth response to elevated CO<sub>2</sub> observed in 2001. However, subsequent stimulation of carbon assimilation in 2002 runs counter to the progressive nitrogen limitation explanation (Hungate et al. 2006). At the end of the experiment, elevated CO<sub>2</sub> increased the nitrogen content in aboveground plants but not in coarse and fine roots, yielding no effect on total plant nitrogen. Increased carbon in plant pools with only small changes in nitrogen means higher carbon:nitrogen ratios (C:N). Indeed, higher C:N ratios under elevated CO<sub>2</sub> were observed for leaves, coarse roots, and the sum of all plant parts (see Fig. 4.2, p. 49; Hungate et al. 2013). Elevated CO<sub>2</sub> increased root pools of most other elements, except zinc. Carbon dioxide stimulation of plant calcium was larger than the decline in the extractable calcium pool in soils, whereas, for other elements, increased plant uptake matched the decline in the extractable pool in soil. Elevated CO<sub>2</sub> also caused net transfer of a subset of nutrients from soils to plants, suggesting that ecosystems with a positive plant growth response under high CO<sub>2</sub> will likely cause mobilization of elements from soil pools to plant biomass (Duval et al. 2013).





**Fig. 4.2. Scrub Oak Ecosystem Carbon (C) and Nitrogen (N) Inventories After 11 Years of Exposure to Elevated Carbon Dioxide (CO<sub>2</sub>).** [Reprinted under a Creative Commons License (CC BY 2.0) from Hungate, B. A., et al. 2013. "Cumulative Response of Ecosystem Carbon and Nitrogen Stocks to Chronic CO<sub>2</sub> Exposure in a Subtropical Oak Woodland," *New Phytologist* **200**(3), 753–66.]

Elevated CO<sub>2</sub> increased the C:N ratio of the litter layer but not of any soil pool. The only soil pool to respond—the heavy-density fraction—actually declined in the C:N ratio. Changes in plant and soil C:N ratios were compensatory, so that elevated CO<sub>2</sub> had no effect on the C:N ratio of the plant-soil system to a 1-m depth (Hungate et al. 2013).

### Soil

The carbon content of the litter layer, coarse particulate organic matter (POM), total mineral soil carbon, and the light- and medium-density fractions did not respond significantly to the CO<sub>2</sub> treatment, but the heavy-density soil carbon pool declined substantially. Elevated CO<sub>2</sub> had no effect on soil carbon in the spodic horizon, with no significant impact on total mineral soil carbon or on light-, medium-, and heavy-density fractions. Thus, carbon in the deep soil was also insensitive to the CO<sub>2</sub> treatment. In general, increased mass of plant carbon caused by elevated CO<sub>2</sub> did not translate to increased carbon storage in other ecosystem reservoirs (Hungate et al. 2013). The incorporation of the depleted  $\delta^{13}\text{C}$  signature into organic matter pools revealed rates and patterns of the flow of “new” carbon into the system (i.e., the carbon that had been fixed since CO<sub>2</sub> fumigation began in May 1996).

### Biotic Interactions

All insect species indigenous to scrub oak were present in both ambient and elevated atmospheric CO<sub>2</sub> treatments. There were fewer insects in the elevated CO<sub>2</sub> chambers, perhaps because the lower nitrogen concentration of leaves in elevated CO<sub>2</sub> are less palatable for insects, and mortality increased for those that remained in the elevated CO<sub>2</sub>



chambers (Stiling et al. 2002). Although damage by herbivore populations declined under elevated CO<sub>2</sub> (because there were fewer insects), total herbivore damage per capita of insects increased (because each insect consumes more leaves). Damaged leaves did not senesce prior to being dropped by the plant, and these leaves could have altered nitrogen cycling.

#### 4.2.4 Summary

In this experiment, spanning more than a decade in a naturally occurring ecosystem, photosynthesis and aboveground plant growth exhibited strong responses to chronic exposure to elevated atmospheric CO<sub>2</sub> (see Fig. 4.2, p. 49). These responses led to increases in aboveground carbon content and in coarse roots that were related to the site's fire history. The elevated CO<sub>2</sub> treatment did not affect carbon in fine roots at the final harvest, although such roots responded sporadically in this experiment, with particularly strong responses following the initial fire disturbance and after a hurricane in year 8. Elevated CO<sub>2</sub> did not increase soil carbon and, in fact, tended to decrease it, which is probably a consequence of increased microbial activity. Elevated CO<sub>2</sub> also increased plant nitrogen uptake, possibly driven by higher microbial activity and increased soil nitrogen availability. However, these responses also were associated with reduced recovery of a long-term <sup>15</sup>N tracer, likely indicating enhanced ecosystem nitrogen losses. Thus, CO<sub>2</sub> altered the carbon and nitrogen cycles in this ecosystem but not in ways that promoted large or even detectable increments in total ecosystem carbon mass. The effect of elevated CO<sub>2</sub> on soil carbon turnover via the "priming effect" was large enough to modulate net carbon balance. The response of soil carbon to labile substrate inputs suggests a previously unrecognized sensitivity of what was thought to be a long-term, stable carbon sink in the biosphere (Hungate et al. 2013).



## Tallgrass Prairie OTC

Manhattan,  
Kansas



1989–1996

### Lead Institution

Kansas State  
University

### Key Reference

Owensby, C. E., et al. 1999. "Biomass Production and Species Composition Change in a Tallgrass Prairie Ecosystem After Long-Term Exposure to Elevated Atmospheric CO<sub>2</sub>," *Global Change Biology* 5(5), 497–506.

## 4.3 Tallgrass Prairie OTC

### 4.3.1 Objective

The Tallgrass Prairie OTC study aimed to determine the long-term consequences of elevated CO<sub>2</sub>, including potential changes in biogeochemical cycling, on biomass production and community composition in tallgrass prairie.

### 4.3.2 Description of Experiment

#### Site

The study was conducted in pristine tallgrass prairie north of Manhattan, Kan. (39°7'N, 96°21'W). Soils in the area are transitional from Ustolls to Udolls (i.e., Tully series: fine, mixed, mesic, montmorillonitic, and Pachic Argiustolls). The prairie was burned two to three times in the 10 years prior to the study. Past history included primarily winter grazing by cow-calf pairs. The 30-year average annual precipitation is 840 mm, with 520 mm occurring during the growing season (Owensby et al. 1999).

#### Plant Community

Vegetation on the site was a mixture of C3 and C4 species, dominated by the C4 warm-season grasses, *Andropogon gerardii* and *Sorghastrum nutans*. Subdominants included the C3 cool-season grass *Poa pratensis* and two other C4 warm-season grasses: *Bouteloua curtipendula* and *Sporobolus asper* var. *asper*. Members of the Cyperaceae (C3 cool-season monocot) made up 5% to 10% of the plant community. Principal forbs (i.e.,

all C3 warm-season) included *Vernonia baldwinii* var. *interior*, *Ambrosia psilostachya*, *Artemisia ludoviciana*, and *Psoralea tenuiflora* var. *floribunda* (Owensby et al. 1999).

### Experimental Design

Open-top fumigation chambers (4.5 m in diameter by 4 m in height) were installed over the natural vegetation in late March 1989 and remained in place for 8 years. Treatments, which were replicated three times, consisted of ambient CO<sub>2</sub> with no chamber, ambient CO<sub>2</sub> with chamber, and twice-ambient CO<sub>2</sub>-enriched with chamber (Owensby et al. 1999). In 1991 and 1992, a nitrogen-fertilized treatment (56 kg per hectare) was added and compared to the other treatments. Annually, the CO<sub>2</sub> enrichment began on April 1 and, along with environmental data acquisition, was continuous each year until late October. Measured CO<sub>2</sub> concentrations in the elevated treatment averaged 709 ppm during the day and 811 ppm at night (Jastrow et al. 2005).

### Measurements

In 1989 and 1990, aboveground biomass sampling began in mid-May and continued at 2-week intervals until mid-July and then at 4-week intervals until mid-October. Samples were clipped to ground level from two subplots (0.2 m × 0.5 m) randomly located in each plot. From 1991 to 1996, peak live biomass was estimated by clipping two 50 cm × 100 cm subplots randomly located in each plot in early August. Peak biomass in tallgrass prairie normally occurs in early August. Leaf area and dry mass were measured. Basal cover and species composition were determined in late June 1989 and 1996 using a 1-m rod placed along 10 permanently fixed, 1-m lines in each plot and recording plants that touched the rod (Owensby et al. 1999).

Relative belowground biomass production was estimated from 1990 to 1995 using buried root ingrowth bags. In late March of each year, eight soil cores, 5 cm in diameter, were removed to a depth of 15 cm along the center line of each plot. Fine-mesh nylon bags, filled with a mixture of fine and coarse sand to a volume equal to the soil core, were placed in the core holes. Root ingrowth bags were removed from the soil in early November of each year, and roots that had grown into the bags were removed, dried, and weighed (Owensby et al. 1999).

Soil was sampled at the end of the experiment with a 4.8-cm diameter corer after removal of surface litter. Four cores were taken down to 30 cm and two additional cores were taken to 5 cm per plot. Cores were divided into depth increments of 0 to 5, 5 to 15, and 15 to 30 cm and pooled within plots.

Forage quality for ruminants was determined by monthly collection of forage samples using esophageally fistulated sheep in all chambers and in the unchambered plots. Samples were analyzed for nutrient concentrations, detergent extractions, and digestibility. The effect of elevated CO<sub>2</sub> on livestock gain was modeled.

## 4.3.3 Results

### Photosynthesis and Respiration

During a wet year, no significant differences were found in midday rates of photosynthesis or in daily carbon accumulation as a result of CO<sub>2</sub> enrichment. In the dry year, midday

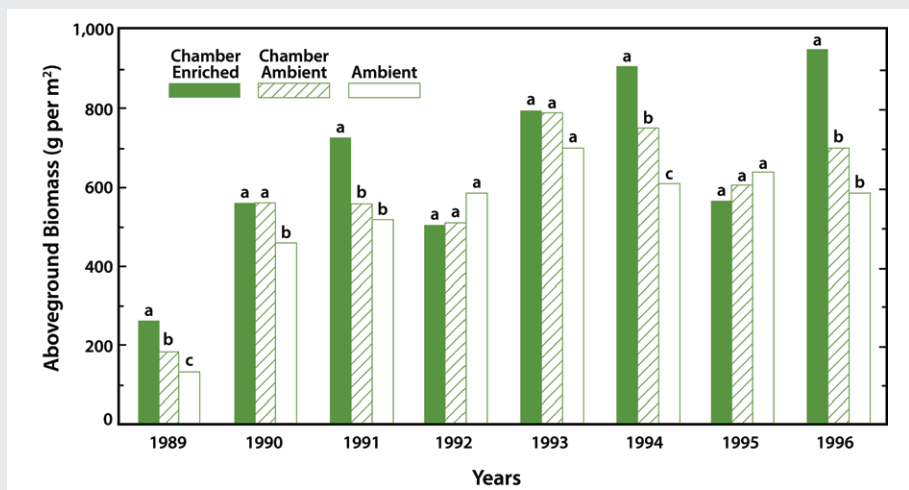
rates of photosynthesis were significantly higher in elevated  $\text{CO}_2$  throughout the season. Estimates of daily carbon accumulation also indicated that  $\text{CO}_2$  enrichment allowed plants to maximize carbon acquisition on a diurnal basis. The increased carbon accumulation was accounted for by greater rates of photosynthesis in elevated  $\text{CO}_2$  during midday. During the wet year,  $\text{CO}_2$  enrichment decreased stomatal conductance, allowing plants to decrease transpiration while still photosynthesizing at rates similar to plants in ambient conditions. During the dry year,  $\text{CO}_2$  enrichment allowed plants to maintain photosynthetic rates even though stomatal conductance and transpiration had been reduced in all treatments due to stress. Estimates of instantaneous WUE were reduced under  $\text{CO}_2$  enrichment for both years (Adam et al. 2000).

### Growth

Peak aboveground biomass was greater on elevated  $\text{CO}_2$  plots than on ambient  $\text{CO}_2$  plots with chambers during significantly dry years (see Fig. 4.3, this page). Aboveground regrowth biomass was greater under elevated versus ambient  $\text{CO}_2$  in a year with late-season water stress but did not differ in a wetter year. Root ingrowth biomass also was greater in elevated  $\text{CO}_2$  plots when water stress occurred during the growing season. The basal cover and relative amount of warm-season perennial grasses (C4) in the stand changed little during the 8-year period, but basal cover and relative amount of cool-season perennial grasses (C3) in the stand declined in both the elevated  $\text{CO}_2$  plots and in ambient  $\text{CO}_2$  plots with chambers. Forbs (C3) and members of the Cyperaceae (C3) increased in basal cover and relative amount in the stand at elevated compared to ambient  $\text{CO}_2$  (Owensby et al. 1999).

### Water Use

Stomatal conductance was reduced by as much as 50% under elevated  $\text{CO}_2$ . The result was an improved water status for plants exposed to elevated  $\text{CO}_2$ , an outcome reflected by a less negative xylem pressure potential compared to plants exposed to ambient  $\text{CO}_2$ . Sap flow rates were 20% to 30% less in plants exposed to elevated  $\text{CO}_2$ . At the canopy



**Fig. 4.3. Peak Aboveground Biomass of Native Tallgrass Prairie Exposed to Ambient and Twice Ambient Carbon Dioxide Concentrations.** [Redrawn by permission from Wiley from Owensby, C. E., et al. 1999. "Biomass Production and Species Composition Change in a Tallgrass Prairie Ecosystem After Long-Term Exposure to Elevated Atmospheric  $\text{CO}_2$ ," *Global Change Biology* 5(5), 497–506. Copyright 1999 Blackwell Science Ltd.]

level, evapotranspiration was reduced by 22% under elevated CO<sub>2</sub>. Reduced water use by the plant canopy under elevated CO<sub>2</sub> extended the photosynthetically active period when water became limiting in the ecosystem. The result was an increase in above- and belowground biomass production during years when water stress was frequent (Owensby et al. 1997).

### **Nutrient Interactions**

Above- and belowground biomass production and leaf area of nitrogen-fertilized plots were greater under elevated CO<sub>2</sub> during both the wet and dry years. The increase in biomass at high CO<sub>2</sub> occurred mainly above ground in 1991, a dry year, and below ground in 1990, a wet year. Nitrogen concentration was lower in plants exposed to CO<sub>2</sub>, but total standing crop nitrogen was greater at high CO<sub>2</sub>. Increased root biomass under elevated CO<sub>2</sub> apparently increased nitrogen uptake. Biomass production response to elevated CO<sub>2</sub> was (1) much greater on nitrogen-fertilized than unfertilized prairie, particularly in the dry year and (2) suppressed by nitrogen limitation in years with below-normal precipitation. Reduced nitrogen concentration in above- and belowground biomass could slow microbial degradation of SOM and surface litter, thereby exacerbating nitrogen limitation in the long term (Owensby et al. 1994).

After 8 years of elevated CO<sub>2</sub>, total soil nitrogen content had increased, suggesting that rates of ecosystem nitrogen flux into or out of tallgrass prairie had been altered. Measurements of surface soil <sup>15</sup>N indicate that a change in nitrogen inputs and outputs occurred as a result of elevated atmospheric CO<sub>2</sub>. In addition to possible changes in denitrification and N<sub>2</sub> fixation, other sources of nitrogen, such as the nitrogen re-translocated to the surface from deeper soil layers, need to be quantified to explain how nitrogen accrues in surface soils as a consequence of elevated CO<sub>2</sub>. Overall, these results support the notion that carbon accrual may promote nitrogen accrual, possibly driven by high plant and microbial nitrogen demand amplified by soil nitrogen limitation (Williams et al. 2006).

### **Soil**

Under elevated CO<sub>2</sub>, soil carbon increased significantly throughout the top 30 cm of surface. The incremental increase in carbon stocks corresponded to an average accrual rate of 59 ± 19 g C per m<sup>2</sup> per year. A portion of the accumulated carbon was associated with soil minerals in stable aggregates. Of the accrued carbon, 55% was incorporated into microaggregates, but the extent of protection varied with depth. In the top 5 cm of the surface, where native SOM was greatest, the capacity of microaggregates to protect additional carbon appeared saturated, and carbon accumulated in less-protected nonmicroaggregated pools—mostly as POM. Below 5 cm, however, most of the accrued carbon was incorporated into microaggregates. Soil carbon accrual was accompanied by significant increases in soil nitrogen at average rates of 3.4 ± 1.3 g N per m<sup>2</sup> per year (Jastrow et al. 2005).

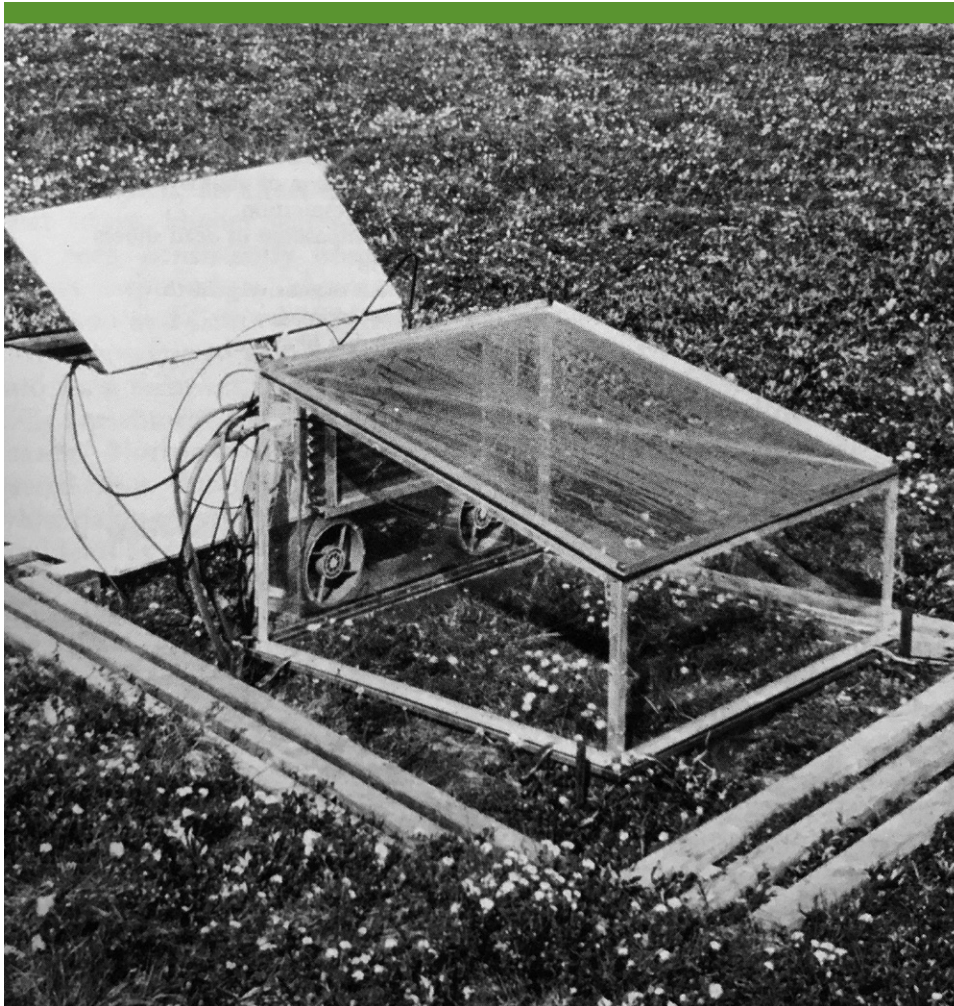
### **Forage Quality**

Reduced nitrogen concentration and increased fiber components under elevated CO<sub>2</sub> reduced ruminant forage intake and productivity (Owensby et al. 1996).

## **4.3.4 Summary**

Greater biomass production under elevated CO<sub>2</sub> in C4-dominated grasslands may lead to greater carbon sequestration by those ecosystems and reduce peak atmospheric CO<sub>2</sub> concentrations in the future (Owensby et al. 1999).

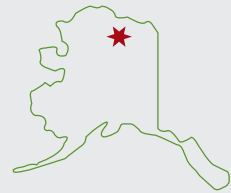




## Arctic Greenhouses

*Upland Tussock Tundra*

*Toolik Lake, Alaska*



1983–1985

### Lead Institution

San Diego State University

### Key Reference

Oechel, W. C., et al. 1994. "Transient Nature of CO<sub>2</sub> Fertilization in Arctic Tundra," *Nature* 371, 500–503.

## 4.4 Arctic Greenhouses

### 4.4.1 Objective

This 3-year study was the first elevated CO<sub>2</sub> experiment in an intact, unmanaged ecosystem. Given measurements in the 1980s indicating that tussock and wet sedge tundra had become net sources of CO<sub>2</sub> to the atmosphere, the experiment was designed to test whether elevated CO<sub>2</sub> would facilitate Arctic ecosystems becoming a net carbon sink and provide a negative feedback on atmospheric CO<sub>2</sub>.

### 4.4.2 Description of Experiment

#### Site

The experiment was conducted in upland tussock tundra in the northern foothills of the Brooks Range at Toolik Lake, Alaska (68°2'N, 149°2'W; elevation 760 m), 225 km south of Prudhoe Bay.

### Plant Community

The study site's plant community is similar to tussock tundra in other parts of Alaska, Canada, and Russia, with a maximum vegetation height of about 40 cm. Within the treatment chambers, vascular plants dominated (55% cover), specifically, *Eriophorum vaginatum* (14%), *Betula nana* (13%), *Ledum palustre* ssp. *decumhens* (12%), *Vaccinium vitis-idaea* (8%), *Carex bigelowii* (3%), *Salix pulchra* (2%), and *Empetrum nigrum* ssp. *hermaphroditum* (1%). Moss cover was high (35%), and lichen cover was low (3%; Grulke et al. 1990).

### Experimental Design

Twelve small greenhouses were placed on a gentle west-facing slope dominated by tussock tundra. Randomly assigned to the greenhouses were different CO<sub>2</sub> treatments: (1) ambient (340 ppm), (2) intermediate (510 ppm), and (3) doubled CO<sub>2</sub> (680 ppm). A fourth treatment of doubled CO<sub>2</sub> (680 μL per L) with a temperature rise of 4°C above ambient was used to represent predicted CO<sub>2</sub> and summer temperature conditions. Otherwise, the chamber temperatures tracked current ambient air temperature. Each of the treatments and a control (an untreated plot without a greenhouse) were replicated three times. Each greenhouse had a basal area of 1.49 m<sup>2</sup> and a volume of 1,015 L. The acrylic plastic chambers transmitted 90% to 92% of the photosynthetically active radiation but attenuated all of the ultraviolet radiation (Tissue and Oechel 1987).

### Measurements

Photosynthetic and transpiration rates were measured on leaves at four CO<sub>2</sub> concentrations (170, 340, 510, and 680 ppm) in each of the four treatments and the untreated control during four periods. Growth measurements were taken on 60 marked tillers in each treatment. Green leaf area and the number of leaves per tiller were measured, and whole-system carbon balance was determined by flux analysis (Tissue and Oechel 1987).

## 4.4.3 Results

### Photosynthesis and Respiration

Tussock tundra exposed to elevated CO<sub>2</sub> and ambient temperatures exhibited a loss of photosynthetic capacity, whereas plots exposed to both elevated CO<sub>2</sub> and elevated temperature retained the enhanced photosynthetic capacity during the 3-year experiment (Oechel et al. 1994). In the first year of treatment, photosynthetic rates appeared to be nearly a linear function of CO<sub>2</sub> concentration up to 680 ppm, whether the plant was grown at 340 or 680 ppm. However, at each measurement CO<sub>2</sub> concentration, plants grown at 340 ppm had a much higher photosynthetic rate than the plants grown at 680 ppm. Adjustments in the photosynthetic capacity of the plants resulted in similar photosynthetic rates at the two growth CO<sub>2</sub> concentrations. This result indicates a high degree of homeostasis in photosynthetic rate. The reduction in photosynthetic capacity for plants grown at elevated CO<sub>2</sub> levels did not appear to be due to stomatal closure or end-product inhibition (Tissue and Oechel 1987).

Plots exposed to elevated CO<sub>2</sub> were net CO<sub>2</sub> sinks during the first 2 years of exposure; however, during the third year of the experiment, such plots were net sources of CO<sub>2</sub> of 1 g C per m<sup>2</sup> per day. Plots exposed to both elevated CO<sub>2</sub> and elevated temperature were net sinks for atmospheric CO<sub>2</sub> throughout the 3 years of continuous growing-season experimental manipulation (Oechel et al. 1994).

### Growth

Growth of existing plant tillers did not significantly change in response to the CO<sub>2</sub> or temperature treatments, neither did leaf area per tiller or relative leaf growth rates. However, elevated CO<sub>2</sub> concentration did lead to a dramatic increase in the production of new tillers. The tillering rate of plants grown at a CO<sub>2</sub> concentration of 680 ppm was almost six times as great as that of plants grown at 340 ppm, although other growth parameters were relatively unaffected (Tissue and Oechel 1987).

### Water Use

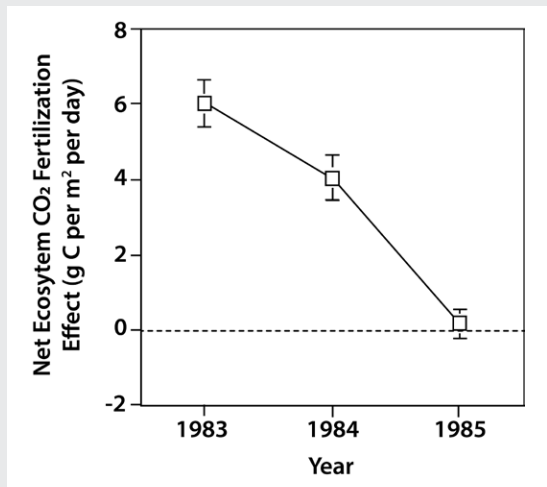
Transpiration rates and WUE did not differ among treatments in the generally wet environment of tussock tundra (Tissue and Oechel 1987).

### Nutrient Interactions

Evidence suggested that elevated temperatures coupled with absolute air humidities and soil water tables enhanced rates of mineralization and nutrient supply and increased potential sink activity, thereby resulting in prolonged stimulation of photosynthesis (Oechel et al. 1994).

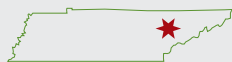
## 4.4.4 Summary

For the doubled CO<sub>2</sub> level alone, complete homeostasis of the CO<sub>2</sub> flux was re-established within 3 years. However, in the regions exposed to a combination of both higher temperatures and doubled CO<sub>2</sub>, the fertilization effect on net ecosystem carbon sequestration persisted over this time (see Fig. 4.4, this page). This difference may result from enhanced sink activity associated with (1) the direct effects of higher temperatures on growth and (2) the indirect effects from enhanced nutrient supply caused by increased mineralization. These results indicate that the responses of native ecosystems to elevated CO<sub>2</sub> may not always be positive and are unlikely to be straightforward. Clearly, CO<sub>2</sub> fertilization effects must always be considered in the context of genetic limitation, resource availability, and other such factors (Oechel et al. 1994).



**Fig. 4.4. Carbon Dioxide (CO<sub>2</sub>) Fertilization Effect in Tussock Tundra over Three Growing Seasons.** Data show the stimulation of net ecosystem CO<sub>2</sub> flux by a doubling of atmospheric CO<sub>2</sub> concentration from 340 to 680 parts per million. The CO<sub>2</sub> fertilization effect is calculated as the difference between the flux measured at double and ambient CO<sub>2</sub> levels. [Reprinted by permission from Springer Nature from Oechel, W. C., et al. 1994. "Transient Nature of CO<sub>2</sub> Fertilization in Arctic Tundra," *Nature* **371**, 500–503. Copyright 1994.]



**OCCAM***Old-Field  
Multifactor OTCs**Oak Ridge,  
Tennessee***2002–2007****Lead  
Institutions**

- Oak Ridge National Laboratory
- University of Tennessee–Knoxville

**Key Reference**

Kardol, P., et al. 2010. "Climate Change Effects on Plant Biomass Alter Dominance Patterns and Community Evenness in an Experimental Old-Field Ecosystem," *Global Change Biology* **16**(10), 2676–87.



## 4.5 Old-Field Community, Climate, and Atmospheric Manipulation (OCCAM)

### 4.5.1 Objective

The OCCAM study investigated interactive effects of elevated CO<sub>2</sub>, warming, and altered water availability in a constructed ecosystem with plants typical of an old-field system (including C3 and C4 grasses, forbs, and legumes). The hypotheses and research approach were built around three general predictions:

1. The response of an old-field community to elevated CO<sub>2</sub> and increased air temperature will be mediated by the availability of soil water.
2. Community composition and production will be driven by interactions between the component taxa and their individual and combined responses.
3. Ecosystem-level responses will depend on the interactions between above- and belowground processes.

### 4.5.2 Description of Experiment

#### *Site*

The experiment was conducted at the Global Change Field Research Facility on the Oak Ridge National Laboratory Environmental Research Park in Oak Ridge, Tenn. (35°54'N, 84°20'W). The site was abandoned from agricultural use in 1943 and left fallow until 1964 when a managed fescue field was established. The soil, which is derived

from floodplain alluvium deposited by the nearby Clinch River, is classified as Captina silt loam—fine-silty, siliceous, mesic Typic Fragiudult, well drained, and slightly acidic (Wan et al. 2007). Precipitation generally is evenly distributed throughout the year, with an annual mean of 1,322 mm. The mean July maximum temperature is 31.2°C, and the mean January minimum temperature is -2.7°C (Kardol et al. 2010).

### Plant Community

Fifteen plots were laid out in a randomized complete block design in 2002. A Ditch Witch was used to trench around each 4-m diameter plot and through the center of the plot on a north-south axis. Foam insulation and plastic sheeting were buried to 0.75 m to provide a thermal and moisture barrier. In July 2002 and April 2003, the plots were planted with seedlings of seven species grown from seed: (1) ribgrass (*Plantago lanceolata*, an herbaceous annual C3 dicot); (2) broomsedge (*Andropogon virginicus*, a caespitose C4 bunchgrass); (3) meadow fescue (*Festuca pratense* syn *F. elatior*, a C3 bunchgrass); (4) orchardgrass (*Dactylis glomerata*, a C3 bunchgrass); (5) red clover (*Trifolium pratense*); (6) goldenrod (*Solidago canadensis*, a perennial forb); and (7) *Lespedeza* (*Lespedeza cuneata*, a perennial nitrogen-fixing shrub (Kardol et al. 2010).

### Experimental Design

Beginning in May 2003, this multifactor experiment employed OTCs to administer treatments of elevated CO<sub>2</sub>, air warming, and altered soil moisture in a randomized complete block, split-plot design. The old-field ecosystems were constructed within 12 OTCs (4 m in diameter) and three open plots. The whole plots, which were replicated three times, were exposed to ambient or elevated CO<sub>2</sub> concentrations combined with ambient or elevated temperature. Two levels of soil moisture were maintained as split-plots within the chambers. Air temperature was maintained at ambient or ambient +3.5°C. The CO<sub>2</sub> concentration was maintained at ambient or ambient +300 ppm. Rain shelters excluded ambient precipitation, and water was added manually to maintain two levels of soil water moisture. Two permanent (0.49 m<sup>2</sup>) subplots were established in each split-plot to enable the collection of plant response data throughout the experiment. Each subplot contained one to three individuals of each of the seven planted species and had identical initial species composition and layout in different chambers (Wan et al. 2007).

### Measurements

In autumn of 2005, 2006, and 2007, aboveground biomass was harvested by clipping plant shoots 5 cm above the soil surface (Kardol et al. 2010). Foliar cover for each species was measured, and community richness, evenness, and diversity from 2003 to 2005 were calculated. Soil respiration was measured biweekly from two polyvinyl chloride (PVC) soil collars. Root production was measured with minirhizotrons.

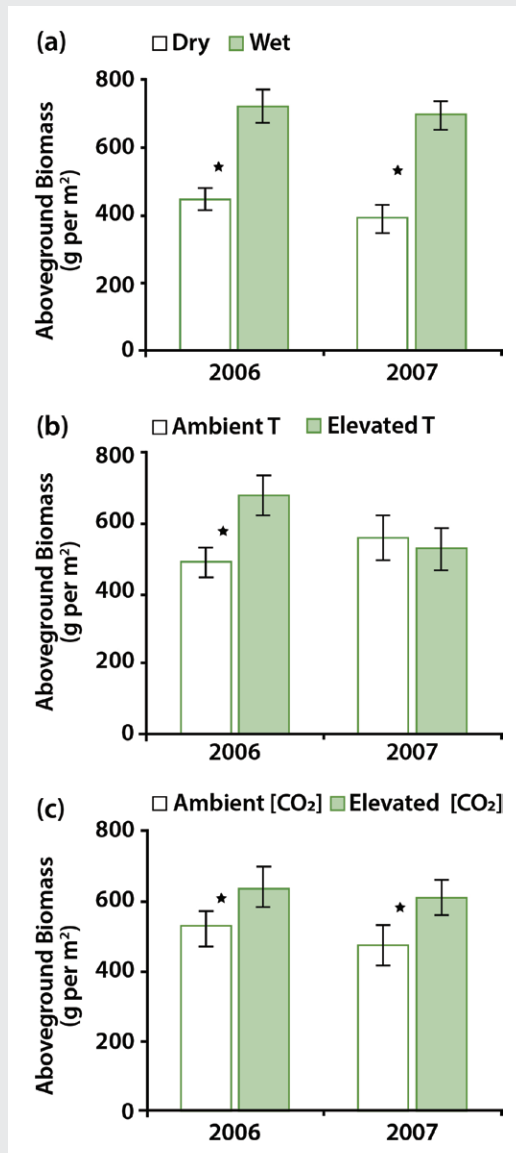
## 4.5.3 Results

Although many of the most prominent results of this experiment were the primary responses to warming, water regime, and changes in community composition, this report focuses on responses to elevated CO<sub>2</sub>.

### Website

web.archive.org  
web/20161115092115/  
http://warming.ornl.  
gov/OCCAM/index.html  
(archived)





**Fig. 4.5. Aboveground Plant Community Biomass in Response to Warming, Soil Moisture, and Carbon Dioxide Treatments in an Old-Field Ecosystem.** [Redrawn by permission from Wiley from Kardol, P., et al. 2010. "Climate Change Effects on Plant Biomass Alter Dominance Patterns and Community Evenness in an Experimental Old-Field Ecosystem," *Global Change Biology* **16**(10), 2676–87.]

### Growth

All treatments—elevated CO<sub>2</sub>, warming, and increased precipitation—increased plant community biomass, and the effects were additive rather than interactive (see Fig. 4.5, this page). Plant species differed in their response to the treatments, shifting the proportional biomass of individual species and, in turn, altering plant community composition. However, the plant community response was largely driven by the positive precipitation response of *Lespedeza*, and precipitation explained most of the variation in plant community composition among treatments (Kardol et al. 2010).

### Water Use

Warming consistently reduced soil moisture content, an effect exacerbated by reduced irrigation. However, elevated CO<sub>2</sub> concentration mitigated the effects of warming and drying on soil moisture. Leaf area duration and canopy size were increased by irrigation and elevated CO<sub>2</sub>. Changes in LAI were closely linked to soil moisture status (Dermody et al. 2007).

### Nutrient Interactions

Foliar nitrogen concentrations declined significantly under elevated CO<sub>2</sub>. High rates of symbiotic nitrogen fixation annually contributed 44% to 51% to the aboveground nitrogen stock in the old-field community. This fixation was an important process driving changes in species composition during 3 years of measurements (2003–2005), but symbiotic N<sub>2</sub> fixation rates were largely independent of manipulations of CO<sub>2</sub>, temperature, and water (Garten et al. 2008).

### Soil

From June 2003 to December 2004, greater CO<sub>2</sub> concentration and soil water availability significantly increased mean soil respiration by 35.8% and 15.7%, respectively. On the wet side of the elevated CO<sub>2</sub> chambers, air warming consistently caused increases in soil respiration, whereas in the other three combinations of CO<sub>2</sub> and water treatments, warming tended to decrease soil respiration over the growing season but increase it over the winter (Wan et al. 2007).

After four growing seasons, elevated CO<sub>2</sub> had no measurable effect on carbon and nitrogen concentrations

in whole soil, POM, and mineral-associated organic matter. Analysis of stable carbon isotopes, under elevated CO<sub>2</sub>, indicated between 14% and 19% new soil carbon under two different watering treatments with as much as 48% new carbon in POM. Despite significant belowground inputs of new organic matter, soil carbon concentrations and stocks in POM declined over 4 years under soil moisture conditions that corresponded to prevailing precipitation inputs (1,300 mm per year). In this experiment, soil moisture (produced by different watering treatments) was more important than elevated CO<sub>2</sub> and temperature as a control on soil carbon dynamics (Garten et al. 2009).

### **Biotic Interactions**

There were no treatment effects on microarthropod abundance, but microarthropod richness was less in dry treatments than in wet. In ambient temperature treatments, richness was greater under elevated CO<sub>2</sub> concentrations than under ambient CO<sub>2</sub>. Differential responses of individual taxa to the climate change treatments resulted in shifts in community composition (Kardol et al. 2011).

Endophyte infection frequency of tall fescue was greater under elevated CO<sub>2</sub> (91% infected) than under ambient CO<sub>2</sub> (81%) but was not affected by warming or precipitation treatments. Within infected tillers, elevated CO<sub>2</sub> decreased alkaloid concentrations by about 30%. Results suggest that elevated CO<sub>2</sub> may promote this grass-fungal symbiosis, leading to higher endophyte infection frequency in tall fescue in old-field communities (Brosi et al. 2011).

### **4.5.4 Summary**

Results indicate that accurate assessments of climate change impacts on soil ecosystem functioning require incorporating the concurrent changes in plant function and plant community composition. Climate change–induced shifts in plant community composition likely will modify or counteract the direct atmospheric and climate change effects on soil ecosystem functioning. Hence, these indirect effects should be taken into account when predicting the manner in which global change will alter ecosystem functioning. Understanding and predicting how multiple climate change factors interact to shape plant community biomass are challenging because of the large number of indirect effects and feedbacks involved. In this constructed old-field ecosystem in the southeastern United States, plant community biomass increased with elevated atmospheric CO<sub>2</sub> and warming, but these increases could be diminished by changes in the precipitation regime, such as dry summer conditions. The relative importance and potential interactions of simultaneously occurring climate change factors that affect plant community biomass are likely to vary geographically and among ecosystems and be driven by a single species (*Lespedeza* in this experiment). Community-level biomass responses to climate changes may thus obscure any primary responses to elevated CO<sub>2</sub> (Kardol et al. 2010).

## SPRUCE

*Ombrotrophic  
Bog*

*Marcell  
Experimental  
Forest,  
Minnesota*



**2015–present**  
*(expected  
completion 2025)*

### Lead Institutions

- Oak Ridge National Laboratory
- Forest Service, U.S. Department of Agriculture

### Key Reference

Hanson, P. J., et al. 2017. "Attaining Whole-Ecosystem Warming Using Air and Deep-Soil Heating Methods with an Elevated CO<sub>2</sub> Atmosphere," *Biogeosciences* **14**(4), 861–83.



## 4.6 Spruce and Peatland Responses Under Changing Environments (SPRUCE)

### 4.6.1 Objectives

The ongoing SPRUCE project is addressing how air and soil warming, in combination with elevated CO<sub>2</sub>, will affect ecosystem productivity and carbon balance, hydrological and nutrient cycling responses, microbial responses, and plant community ecology of a peatland bog in northern Minnesota. The primary emphasis is on the response to warming, with secondary questions regarding how elevated CO<sub>2</sub> alters the responses to increased temperature of different ecosystem processes and components.

### 4.6.2 Description of Experiment

#### *Site*

The SPRUCE experiment is located in the Marcell Experimental Forest in northern Minnesota (47°30'N, 93°29'W) at the southern edge of the boreal zone. Mean annual temperature (1961 to 2009) is 3.4°C, and the average July temperature is 18.9°C, increasing 0.3°C per decade during summer months; average annual precipitation is 780 mm. The soil is a Typic Haplohemist, with average peat depths of 2 to 3 m. The bog is ombrotrophic (i.e., it receives all water and nutrients from direct precipitation) and has a developing hummock and hollow microtopography. The perched water table,

which has little regional groundwater influence, is typically 10 to 20 cm above the hollows after snowmelt, receding deeper later in the growing season.

### Plant Community

The bog is dominated by *Picea mariana* and *Larix laricina*, with an understory of ericaceous shrubs, including Labrador tea (*Rhododendron groenlandicum*) and leatherleaf (*Chamaedaphne calyculata*), along with a limited number of herbaceous plants. Typical of other bogs in northern Minnesota with an open tree cover, there is a nearly continuous cover of mosses, primarily *Sphagnum angustifolium*, *S. fallax*, and *S. magellanicum*.

### Experimental Design

Climate change manipulations were established in 10 large, open-top enclosures described by Hanson et al. (2017). The octagonal enclosures (12.8 m in diameter × 7 m tall) sheathed with double-walled transparent greenhouse panels enable regulation of air and soil temperature and elevation of CO<sub>2</sub> concentration. A subsurface corral constructed of interlocking vinyl sheet-pile walls surrounds each plot to effect hydrological isolation of the interior of the plot from its surrounds. Air warming is achieved with propane-fired heat exchangers and a system of blowers and conduits. The air-warming treatments were initiated in August 2015. Target values are +0, +2.25, +4.5, +6.75, and +9°C; the +0°C enclosures generally are 1 to 2°C warmer than outside ambient air. Soil (peat) warming is achieved with a belowground heating array of 3-m vertical low-wattage heating elements installed within plastic-coated iron pipe. One of the two enclosures at each temperature began to receive elevated CO<sub>2</sub> on June 15, 2016, to provide an air concentration of 500 ppm greater than ambient, or about 900 ppm.

### Measurements

Measurements of ecosystem response have focused on the carbon budget (Hanson et al. 2020). Assessment of net primary production includes annual nondestructive measurements of aboveground tree and shrub growth coupled with allometric relationships, *Sphagnum* growth measurements coupled with measurements of community cover, and root production measurement from ingrowth cores. Efflux of CO<sub>2</sub> and CH<sub>4</sub> is measured monthly from 1.2-m diameter chambers, and losses of total organic carbon and dissolved inorganic carbon are measured via a subsurface corral and outflow system (Hanson et al. 2020). Phenology is tracked by automated cameras as a part of the PhenoCam network (Richardson et al. 2018).

## 4.6.3 Results

The warming treatments during the project's first 3 years caused a net loss of carbon from the ecosystem, with the loss increasing linearly with increasing temperature. However, elevated CO<sub>2</sub> has not altered the response to warming (Hanson et al. 2020). Elevated CO<sub>2</sub> increased nonstructural carbohydrates in leaves of the woody plants, and there is evidence that the unique isotopic label of the elevated CO<sub>2</sub> is showing up in the heterotrophic soil community (Hopple et al. 2020). *Sphagnum* productivity was reduced in elevated CO<sub>2</sub>, with a significant CO<sub>2</sub> × temperature interaction attributed to an indirect effect of CO<sub>2</sub> stimulation of shrubs (Norby et al. 2019).

### Website

[mnspruce.ornl.gov](https://mnspruce.ornl.gov)





## Studies with Partial DOE Support

In addition to the primary Free-Air CO<sub>2</sub> Enrichment (FACE) experiments and open-top chamber (OTC) ecosystem experiments supported by the U.S. Department of Energy (DOE), two other experiments received partial support from DOE in addition to their primary support from the National Science Foundation (NSF), U.S. Department of Agriculture (USDA), and other sources.



### BioCON

*Grassland*

*Cedar Creek  
Ecosystem  
Science Reserve,  
Minnesota*



*1997–present*

### Lead Institution

University of  
Minnesota

### Key Reference

Reich, P. B., et al. 2006.  
“Nitrogen Limitation  
Constrains Sustain-  
ability of Ecosystem  
Response to CO<sub>2</sub>,”  
*Nature* **440**, 922–25.

## 5.1 Biodiversity, CO<sub>2</sub>, and Nitrogen (BioCON)

### 5.1.1 Objectives

BioCON is an ongoing ecological experiment whose initial goal was to explore the ways in which plant communities will respond to three environmental changes known to be occurring on a global scale: increasing nitrogen deposition, increasing atmospheric carbon dioxide (CO<sub>2</sub>), and decreasing biodiversity. The experiment was extended to consider interactive effects of warming, water, CO<sub>2</sub>, and nitrogen. The overarching hypothesis is that low-water and low-nitrogen supply fundamentally constrain the

**Websites****Project**

[biocon.umn.edu](http://biocon.umn.edu)

**Publications**

[biocon.umn.edu/publications](http://biocon.umn.edu/publications)

**Data**

[cedarcreek.umn.edu/research/data/](http://cedarcreek.umn.edu/research/data/)

response of net primary production (NPP) to elevated CO<sub>2</sub> such that NPP shows little response to elevated CO<sub>2</sub> under low-water or -nitrogen availability (BioCON 2019).

## 5.1.2 Description of Experiment

### Site

BioCON is located at the Cedar Creek Ecosystem Science Reserve in east central Minnesota, about 50 km north of Minneapolis-St. Paul (45°24'N, 93°12'W). The site is located on a glacial outwash sandplain, and biomass production is nitrogen limited. The experiment was set up in a secondary successional old field after the existing vegetation was cleared.

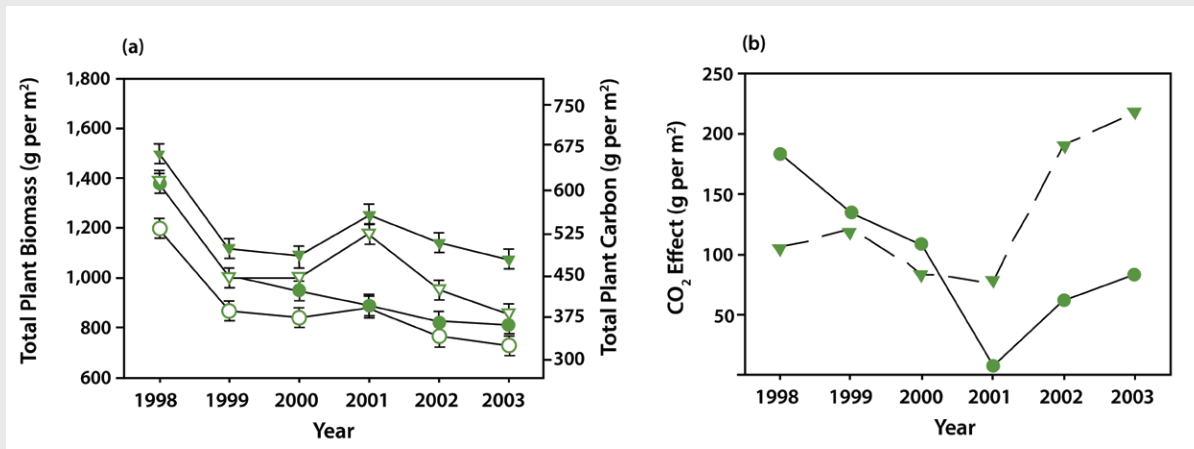
### Plant Community

BioCON consists of 371 plots (2 m × 2 m) planted in 1997 and arranged into six circular areas or “rings” (20 m in diameter), each containing 61, 62, or 63 plots. Each plot was seeded with 12 g per m<sup>2</sup> of seed, split equally among the planted species, with 0, 1, 4, 9, or 16 species randomly selected (without replication) from a 16-species pool equally divided among four functional groups. A species had to (1) be native or naturalized to the area; (2) have a proven record of establishment in previous experiments at Cedar Creek; and (3) belong to one of four functional groups: leguminous forbs, nonleguminous forbs, C3 grasses, and C4 grasses (BioCON 2019). The planted species were *Andropogon gerardi*, *Asclepias tuberosa*, *Amorpha canescens*, *Bouteloua gracilis*, *Schizachyrium scoparium*, *Sorghastrum nutans*, *Solidago rigida*, *Anemone cylindrica*, *Koeleria cristata*, *Lespedeza capitata*, *Lupinus perennis*, *Petalostemum villosum*, *Achillea millefolium*, *Agropyron repens*, *Bromus inermis*, and *Poa pratensis*. In 1997 the plots were watered regularly to ensure germination and establishment but were not watered thereafter. Species composition is controlled by hand weeding the experiment two to four times per growing season.

### Experimental Design

BioCON is a split-plot arrangement of treatments in a completely randomized design. The CO<sub>2</sub> treatment is the whole-plot factor and is replicated three times among the six rings. The subplot factors of species number and nitrogen treatment were assigned randomly and replicated in individual plots among the six rings. For each of the four combinations of CO<sub>2</sub> and nitrogen levels, pooled across all rings, there were 32 randomly assigned replicates, depending on the number of species per plot. This arrangement applies to the “main” experiment that uses 296 plots. There also is a subexperiment within BioCON’s framework in which functional group and species assignments were not completely random; functional group diversity was controlled, thereby limiting the choices for species composition. The spatial distribution of plots within the rings was still randomly chosen (BioCON 2019).

Half the plots receive a nitrogen addition of 4 g per m<sup>2</sup> per year (this amount approximately doubles current rates of nitrogen deposition at the site). This treatment is applied as 34% ammonium nitrate pellets (i.e., regular lawn or agricultural fertilizer) three times per growing season: mid-May, mid-June, and mid-July. Air enriched with CO<sub>2</sub> at 560 parts per million (ppm) is applied to three of the six rings. The vegetation is exposed to elevated CO<sub>2</sub> 7 days per week during daylight hours for the full growing season, which is roughly May 1 to October 15 (BioCON 2019).



**Fig. 5.1. BioCON Plant Growth and Nitrogen Effects.** (a) Total plant biomass and carbon from 1998 to 2003. Open circles represent ambient carbon dioxide (CO<sub>2</sub>) and ambient nitrogen; filled circles: elevated CO<sub>2</sub> and ambient nitrogen; open triangles: ambient CO<sub>2</sub> and enriched nitrogen; filled triangles: elevated CO<sub>2</sub> and enriched nitrogen. (b) CO<sub>2</sub> effect on total biomass under ambient (circles) and enriched (triangles) nitrogen supply. [Redrawn with permission from Springer Nature from Reich, P. B., et al. 2006. "Nitrogen Limitation Constrains Sustainability of Ecosystem Response to CO<sub>2</sub>," *Nature* **440**, 922–25. Copyright 2006.]

An NSF-funded project extended the BioCON experiment, focusing largely on a multifactor subexperiment that uses 48 of the original 2 m × 2 m BioCON plots planted with nine species in 1997. Warming treatments began in spring 2012 using soil rod and infrared lamp technology. The treatment was deployed by continuously elevating growing-season plant and soil temperatures by about 1.8°C. The water treatments are ambient and represent a 45% reduction in precipitation.

### Measurements

Variables measured include net photosynthesis, leaf nitrogen concentration, stomatal conductance, specific leaf area, above- and belowground biomass, above- and belowground plant nitrogen, root growth and mortality, percentage of cover, light interception, soil pH, soil CO<sub>2</sub> flux, nitrogen fixation in legume species, net nitrogen mineralization, and others.

## 5.1.3 Results

### Growth and Nutrient Interactions

Low availability of nitrogen progressively suppressed the positive response of plant biomass to elevated CO<sub>2</sub> (see Fig. 5.1, this page). Initially, the stimulation of total plant biomass by elevated CO<sub>2</sub> was no greater at enriched nitrogen supply than at ambient. After 4 to 6 years, however, elevated CO<sub>2</sub> stimulated plant biomass much less under ambient than enriched nitrogen supply. Given that limitations to productivity resulting from the insufficient availability of nitrogen are widespread in both unmanaged and managed vegetation, soil nitrogen supply is probably an important constraint on global terrestrial responses to elevated CO<sub>2</sub> (Reich et al. 2006). Enhanced biomass accumulation

in response to elevated levels of CO<sub>2</sub> or nitrogen, or their combination, was less in species-poor than in species-rich assemblages (Reich et al. 2001a).

Functional groups responded differently to CO<sub>2</sub> and nitrogen in terms of biomass, tissue nitrogen concentration, and soil solution nitrogen. Initially, under elevated CO<sub>2</sub>, forbs, legumes, and C3 grasses increased in total biomass by 31%, 18%, and 9%, respectively, whereas biomass was reduced in C4-grass monocultures (Reich et al. 2001a). However, the pattern reversed after 12 years: biomass was markedly enhanced in elevated CO<sub>2</sub> relative to ambient CO<sub>2</sub> in C4 but not C3 plots, partially explained by a shift in nitrogen availability (Reich et al. 2018). Two of the four legume species showed increased biomass and total plant nitrogen pools under elevated CO<sub>2</sub>, probably due to stimulated nitrogen fixation. Only one species markedly shifted the proportional distribution of below- versus aboveground biomass in response to CO<sub>2</sub> or nitrogen. Although functional groups varied in responses to CO<sub>2</sub> and nitrogen, there also was substantial variation in responses among species within groups (Reich et al. 2001b).

### 5.1.4 Summary

In the BioCON experiment, manipulation of biodiversity, nitrogen, CO<sub>2</sub>, and water provides the opportunity to examine how each of these factors affects ecosystem processes independently and in combination. The experiment also is helping determine whether the effects of one of these environmental changes enhance or dampen the impacts of the others, and to what degree. The fact that BioCON is being done under field conditions rather than in growth chambers or greenhouses also enables interpretation of the results in the context of global change issues. Data from this long-term experiment suggest that current trait-based functional classifications might be useful, but not sufficient, for understanding plant and ecosystem responses to elevated CO<sub>2</sub> and nitrogen availability (Reich et al. 2001b). Furthermore, short-term drivers of plant response to global change might not predict long-term results (Reich et al. 2018).





## PHACE

*Mixed-Grass  
Prairie*

*Cheyenne,  
Wyoming*



**2005–2013**

### Lead Institutions

- University of Wyoming
- Agricultural Research Service, U.S. Department of Agriculture

### Key Reference

Morgan, J. A., et al. 2011. "C4 Grasses Prosper as Carbon Dioxide Eliminates Desiccation in Warmed Semi-Arid Grassland," *Nature* **476**, 202–205.

## 5.2 Prairie Heating and Carbon Dioxide Enrichment (PHACE)

### 5.2.1 Objective

The PHACE experiment sought to determine how future environmental conditions will influence mixed-grass prairie. As the largest remaining grassland ecosystem in North America, mixed-grass prairie is integral to both agricultural productivity and conservation of biological diversity in the western United States. PHACE tested model-based hypotheses that were derived from the results of a previous OTC experiment (Parton et al. 2007).

### 5.2.2 Description of Experiment

#### Site

The experiment was conducted at the USDA Agricultural Research Service (ARS) High Plains Grasslands Research Station, west of Cheyenne, Wyo. (41°11'N, 104°54'W; elevation 1,930 m). Annual precipitation is 384 mm, and mean air temperatures are 17.5°C in summer and –2.5°C in winter. The average annual wind speed is 6 m per second, with a growing-season wind speed of 4.1 m per second. A 2.4-hectare site, which had been grazed by cattle at least since 1974, was fenced to prevent cattle entering in 2005. Soils are an Ascalon variant loam (i.e., fine loamy, mixed mesic) at the north end of the study site and an Altvan loam (i.e., fine loamy over sandy, mixed mesic) at the south end (Morgan et al. 2011).



**Websites****Project**[bit.ly/2UOwkIF](http://bit.ly/2UOwkIF)**Publications**[bit.ly/3ajf5Pu](http://bit.ly/3ajf5Pu)**Data**

- [datadryad.org/stash/dataset/doi:10.5061/dryad.3mf71/](https://datadryad.org/stash/dataset/doi:10.5061/dryad.3mf71/)
- [www.nature.com/articles/sdata201688/tables/2](http://www.nature.com/articles/sdata201688/tables/2)

**Plant Community**

The ecosystem is a northern mixed-grass prairie, with a plant community of about 55% cool-season C3 grasses (mostly *Pascopyrum smithii* and *Hesperostipa comata*, both perennials); 25% warm-season C4 grasses (almost exclusively the perennial *Bouteloua gracilis*); and 20% sedges, forbs, and small shrubs (Morgan et al. 2011).

**Experimental Design**

The experiment had a factorial combination of two levels of CO<sub>2</sub>—present ambient (385 ppm) and elevated (600 ppm)—and two temperature regimes—present ambient and elevated (1.5/3°C warmer day/night), with five replications, making 20 experimental plots. Treatments were randomly assigned to 20 plots in two soil types (northern and southern blocks). Experimental plots were circular with a diameter of 3.3 m (area of 8.6 m<sup>2</sup>). Before instrumentation was installed, hexagonal trenches 60 cm deep were dug around the circumference of each plot and a plastic barrier was installed to isolate treated plots hydraulically from outside nontreated soils. This hydraulic separation helped maintain any water-relation effects of the treatments (Morgan et al. 2011). The CO<sub>2</sub> fumigation system used the mini-FACE approach of Miglietta et al. (2001), whereby pure CO<sub>2</sub> is released into the rings at high velocity through small gas jets. Warming was achieved with infrared heaters (Kimball et al. 2008), which were set 1.5 m above the soil surface in a hexagonal arrangement with two heaters per side at an angle of 45° to horizontal and pointed toward the center of the plot. Control (reference) plots had the same infrastructure as warmed plots except with unwarmed “dummy” heaters to ensure similar patterns of shading and rain influence. Elevated and reference plot temperatures were monitored using infrared radiometers (LeCain et al. 2015).

**Measurements**

During mid-July, aboveground biomass was measured by species in 2005, 2006 (the first year of CO<sub>2</sub> treatments), and from 2007 to 2009 (the years of combined elevated CO<sub>2</sub> and warming treatments). Mid-July is the approximate time of peak seasonal aboveground biomass and provides a good estimate of aboveground NPP. Beginning in 2007, near the time of the peak standing aboveground biomass harvest, three soil cores (30 cm deep, 5 cm in diameter) were collected from each plot, divided into depths of 0 to 5, 5 to 15, and 15 to 30 cm, and composited into one sample per depth. Fine roots (less than 1 mm) were handpicked from the composited samples, and root fragments were washed, weighed, and ash-corrected (Morgan et al. 2011). Photosynthesis, soil CO<sub>2</sub> efflux, net ecosystem CO<sub>2</sub> exchange and evapotranspiration, and canopy phenology were all measured routinely, along with soil carbon, nutrient responses, and microbial responses.

**5.2.3 Results****Water Use and Growth**

In this semiarid grassland, elevated CO<sub>2</sub> effects on soil water content counteract the desiccating effect of warmer temperatures. Warming induced soil drying, but elevated CO<sub>2</sub> increased soil water content by increasing plant water-use efficiency (WUE), and the combination of elevated CO<sub>2</sub> and elevated temperature resulted in no difference in soil water content relative to control plots. These soil water effects influenced plant biomass

responses ; soil matric potential explained 76% of the variation in the biomass enhancement ratio (see Fig. 5.2, this page). Elevated CO<sub>2</sub> increased plant biomass, especially in dry years when water savings were most important to growth (2006 to 2008). Warming alone did not significantly affect total aboveground biomass, likely because potential increases in plant growth were limited by lower soil water. There were no net decreases in plant growth between current and future conditions (i.e., elevated CO<sub>2</sub> and temperature; Morgan et al. 2011).

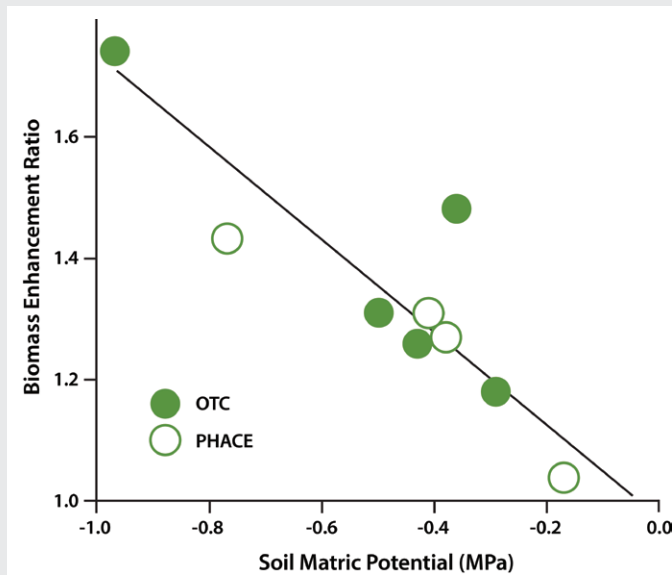
### Nutrient Interactions

Elevated CO<sub>2</sub> and warming had contrasting effects on nitrogen availability as well as moisture and productivity. Under elevated CO<sub>2</sub>, soil inorganic nitrogen decreased, likely a result of increased microbial nitrogen immobilization. The CO<sub>2</sub>-induced increase in soil moisture facilitated greater nitrogen uptake by microbes but did not affect plant nitrogen pool sizes. In contrast, warming increased soil inorganic nitrogen and plant nitrogen. Direct effects of warming on net nitrogen mineralization appeared to be more important than a warming-induced decrease in soil moisture (Dijkstra et al. 2010).

Wetter soil conditions under elevated CO<sub>2</sub> increased phosphorus availability to plants and microbes relative to that of nitrogen, while drier conditions with warming reduced phosphorus availability relative to nitrogen. Soil moisture exerts an important control on inorganic phosphorus supply from desorption and dissolution reactions. This means that despite the fact that warming may alleviate nitrogen limitation under elevated CO<sub>2</sub>, warming and drought can exacerbate phosphorus limitation on growth and microbial activity (Dijkstra et al. 2012).

### Plant Community

Over the 7 years of the PHACE experiment, elevated CO<sub>2</sub> and warming together increasingly favored cool-season (C3) graminoids, reversing an initial shift toward



**Fig. 5.2. Response of Biomass to Elevated Carbon Dioxide (CO<sub>2</sub>) in a Semiarid Mixed-Grass Prairie.** The biomass enhancement ratio increased in dry soil and reversed the effects of warming on desiccation. Data are from the PHACE experiment (4 years of measurements) and a previous open-top chamber (OTC) CO<sub>2</sub> enrichment experiment conducted on a Colorado shortgrass steppe. [Redrawn by permission from Springer Nature from Morgan, J. A., et al. 2011. "C4 Grasses Prosper as Carbon Dioxide Eliminates Desiccation in Warmed Semi-Arid Grassland," *Nature* **476**, 202–205. Copyright 2011.]

warm-season (C4) grasses (i.e., primarily, blue grama *B. gracilis*). Forbs declined in response to warming alone. Plant community composition changed progressively from the study's beginning to its end, while plant biomass was regulated year to year by differences in precipitation.

Throughout the experiment, total plant biomass was consistently enhanced by the combination of elevated CO<sub>2</sub> and warming, owing to strong stimulation of root biomass (Mueller et al. 2016). Evidence suggests that invasive plants are poised to take advantage of the changes in the amount and timing of resources brought about by rising CO<sub>2</sub> and warmer temperatures (Blumenthal et al. 2013, 2016).

### 5.2.4 Summary

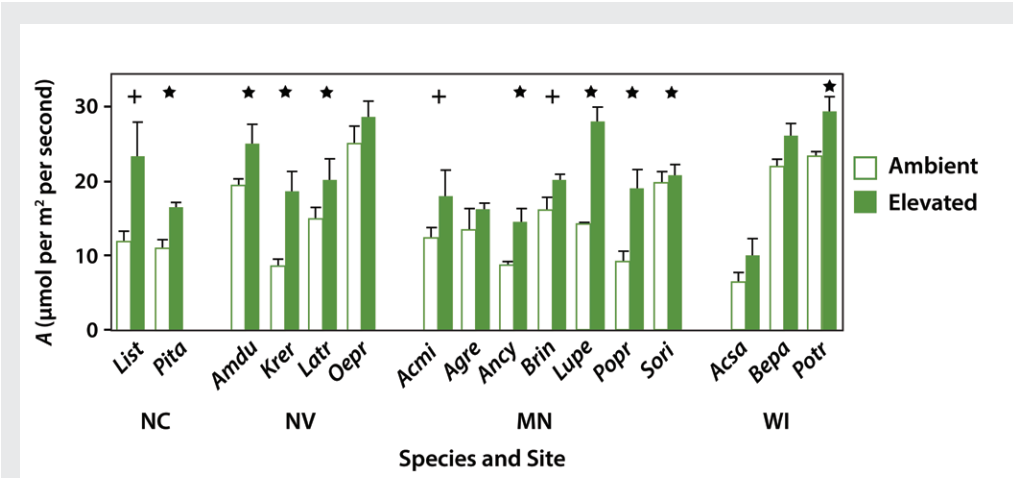
The effect of elevated CO<sub>2</sub> on soil water appears to be the dominant driver of plant biomass responses in semiarid grasslands. Relative to plots at ambient CO<sub>2</sub>, the increase in aboveground biomass at elevated CO<sub>2</sub> was stronger at a more negative early-season soil matric potential. Carbon dioxide will increase plant productivity most when plants are actively growing but water limited.

# FACE Experiments as Community Science Resources

All of the U.S. Department of Energy’s (DOE) Free-Air CO<sub>2</sub> Enrichment (FACE) and open-top chamber (OTC) experiments operated as science resources for the research community, providing a superb research platform for many university scientists, as well as benefitting the core projects and DOE’s research investment. Many independent researchers took advantage of multiple sites to conduct new measurements or synthesize existing data across different ecosystems.

## 6.1 Physiology

Ellsworth et al. (2004) analyzed gas exchange data from Duke FACE; Nevada Desert FACE; Rhinelander FACE; and Biodiversity, CO<sub>2</sub>, and Nitrogen (BioCON). Among species and across herbs, trees, and shrubs there were significant enhancements in photosynthesis by 40% ± 5% in elevated carbon dioxide (CO<sub>2</sub>; see Fig. 6.1, this page). The effects of elevated CO<sub>2</sub> on leaf carbon assimilation and carboxylation capacity occurred largely through changes in leaf nitrogen, rather than through elevated CO<sub>2</sub> effects on the relationships themselves.



**Fig. 6.1. Maximum Photosynthesis Rate (A) of 16 Species in Ambient and Elevated Carbon Dioxide at Four Experimental Sites.** Duke FACE (NC), Nevada Desert FACE (NV), BioCON (MN), and Rhinelander FACE (WI). [Redrawn by permission of Wiley from Ellsworth, D. S., et al. 2004. “Photosynthesis, Carboxylation and Leaf Nitrogen Responses of 16 Species to Elevated pCO<sub>2</sub> Across Four Free-Air CO<sub>2</sub> Enrichment Experiments in Forest, Grassland and Desert,” *Global Change Biology* 10(12), 2121–38. Copyright 2004 Blackwell Publishing Ltd.]

Reid et al. (2003) examined the effect of rising atmospheric CO<sub>2</sub> on the phenotypic responses of stomatal index (SI), stomatal density (SD), and aperture in 15 species at three FACE sites and found no significant changes. They concluded that without evolutionary changes, SI and SD are unlikely to decrease in a future high-CO<sub>2</sub> world.

Monson et al. (2007) measured isoprene emissions at Oak Ridge National Laboratory (ORNL) FACE, Rhinelander FACE, and a temperature and precipitation manipulation experiment in Texas. Results showed that growth in elevated CO<sub>2</sub> inhibited the emission of isoprene at levels that completely compensated for possible emission increases due to increases in aboveground net primary production (NPP). These data suggest that the current generation of models intended to predict the response of isoprene emission to future global change probably contain large errors.

Battipaglia et al. (2012) combined tree ring analysis with isotope measurements at forest FACE sites covering the entire life of the trees. Carbon isotope discrimination and changes in water-use efficiency (WUE) were assessed with  $\delta^{13}\text{C}$ , while direct CO<sub>2</sub> effects on stomatal conductance were explored using  $\delta^{18}\text{O}$  as a proxy. Across all the sites, elevated CO<sub>2</sub> increased  $\delta^{13}\text{C}$ -derived WUE on average by 73% for *Liquidambar styraciflua*, 77% for *Pinus taeda*, and 75% for *Populus* sp., but the response occurred through different ecophysiological mechanisms.

Natali et al. (2009) found that elevated CO<sub>2</sub> decreased foliar nitrate reductase activity in *P. taeda* at Duke FACE, but there were no effects on *L. styraciflua* at ORNL FACE or Duke FACE. The *P. taeda* nitrate reductase activity was negatively correlated with bioavailable molybdenum concentrations in soils, suggesting that CO<sub>2</sub>- and nitrogen-mediated changes in soil nutrient status may be altering soil-plant nitrogen dynamics. The researchers suggested that variation in response among species may reflect different strategies for acquiring nitrogen and proposed that elevated CO<sub>2</sub> may alter plant nitrogen dynamics through changes in nitrate reductase.

BassiriRad et al. (2003) measured the  $\delta^{15}\text{N}$  of foliage of 27 field-grown plant species from six FACE experiments representing desert, temperate forest, Mediterranean-type, grassland prairie, and agricultural ecosystems. Within species, the  $\delta^{15}\text{N}$  of foliage produced under elevated CO<sub>2</sub> was significantly lower compared with that of foliage grown under ambient conditions, and this response was consistent across all functional groups tested.

## 6.2 Roots

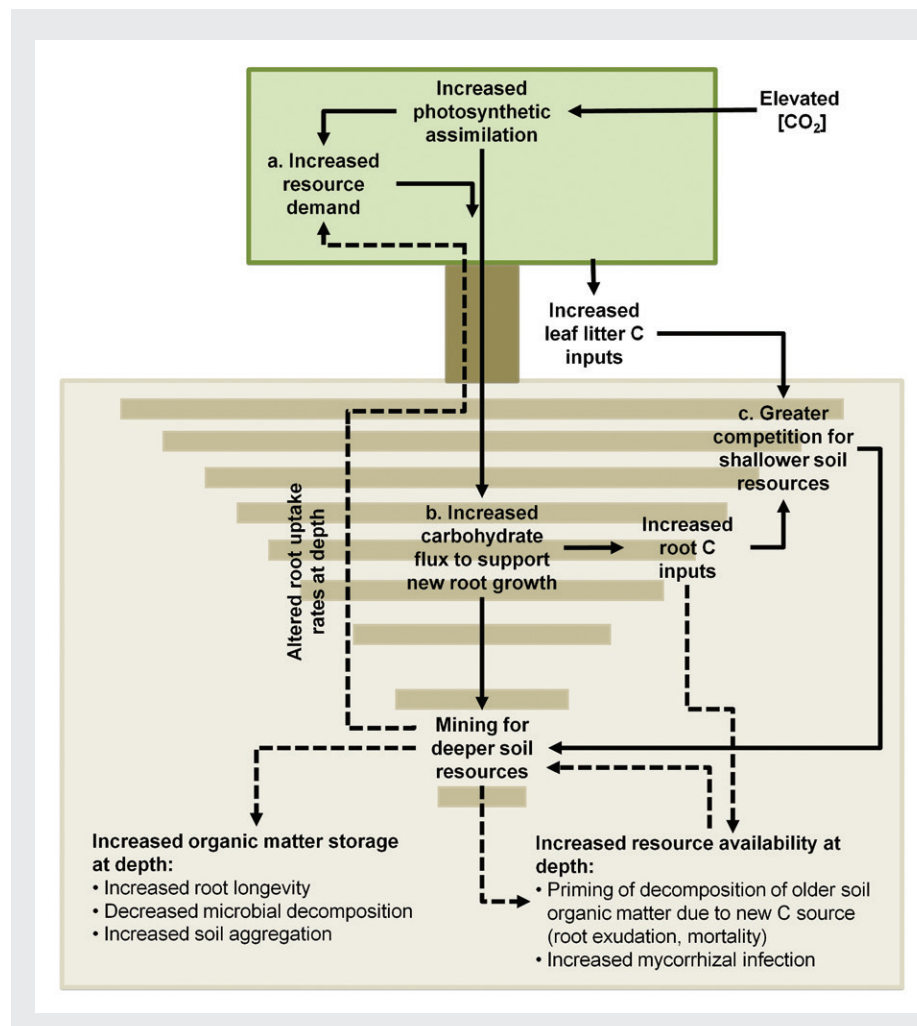
Matamala et al. (2003) assessed root turnover with the use of an isotope tracer at the Duke and ORNL FACE sites. Growth at elevated CO<sub>2</sub> did not accelerate root turnover at either site. Turnover of fine-root carbon, which varied from 1.2 to 9 years, depended on root diameter and dominant tree species. This finding suggests that root production and turnover in forests may have been overestimated and that sequestration of anthropogenic atmospheric carbon in forest soils may be lower than currently estimated. Subsequent analysis suggested that there may be a sampling bias with isotopic approaches to root turnover. For example, first- and second-order roots, which have the smallest diameter and fastest turnover times, may be missed in sampling, and minirhizotrons may



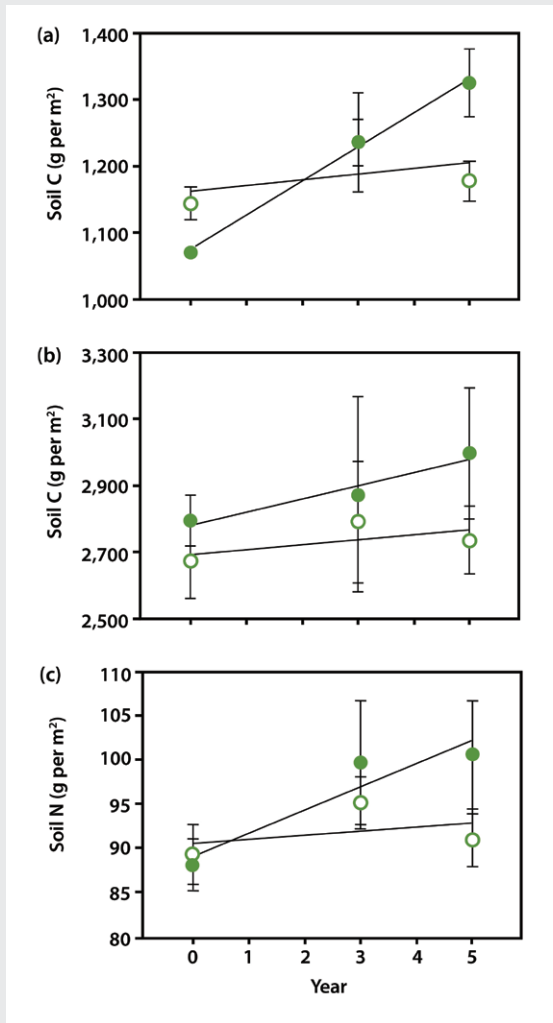
miss larger-diameter, higher-order fine roots that turn over more slowly (Pritchard and Strand 2008).

Iversen (2010) analyzed data on the depth distribution of fine roots in elevated  $\text{CO}_2$  experiments in forests, including the FACE and OTC experiments in this report, and reported that in 73% of the experiments, elevated  $\text{CO}_2$  led to deeper root distributions. This finding has implications for root chemistry, physiological function, mycorrhizal infection, nitrogen uptake rates, turnover, microbial decomposition, and soil carbon (see Fig. 6.2, this page). These cross-site observations supported modeling studies of the implications of root distribution on root foraging for nitrogen (McMurtrie et al. 2012).

George et al. (2003) tested the hypothesis that a reduction in nitrogen concentration in tree fine roots grown under elevated  $\text{CO}_2$  would reduce maintenance respiration and that more energy would be used for root growth and nitrogen uptake. They partitioned total fine-root respiration between maintenance, growth, and nitrogen uptake respiration for loblolly pine and sweetgum for the Duke and ORNL FACE experiments. The team



**Fig. 6.2. Conceptual Model of Processes Leading to Deeper Rooting Distributions Under Elevated Carbon Dioxide (solid lines) and Feedbacks from Production of Deeper Roots (dashed lines).** [Reprinted by permission of Wiley from Iversen, C. M. 2010. "Digging Deeper: Fine-Root Responses to Rising Atmospheric  $\text{CO}_2$  Concentration in Forested Ecosystems," *New Phytologist* **186**(2), 346–57. Copyright 2009 New Phytologist Trust.]



**Fig. 6.3. Soil Carbon and Nitrogen Stocks for the Oak Ridge National Laboratory FACE Experiment in Ambient (open circles) and Elevated Carbon Dioxide (solid circles).** Carbon at a depth of (a) 0 to 5 cm and (b) 0 to 15 cm, along with (c) nitrogen at 0 to 5 cm in depth. [Redrawn by permission of Wiley from Jastrow, J., et al. 2005. "Elevated Atmospheric Carbon Dioxide Increases Soil Carbon," *Global Change Biology* 11, 2057–64. Copyright 2005 Blackwell Publishing Ltd.]

found that the majority of fine-root respiration was used for maintenance and was not reduced by changes in root nitrogen concentration under elevated CO<sub>2</sub>.

### 6.3 Soil

Jastrow et al. (2005) measured carbon accrual in the soil of a deciduous forest (ORNL FACE) and a grassland (tallgrass prairie OTC) at rates exceeding 40 g C per m<sup>2</sup> per year for 5 to 8 years. Over half of the accrued carbon at both sites was incorporated into microaggregates, which protect carbon and increase its longevity. These observations in two ecosystems in which elevated CO<sub>2</sub> increased root production demonstrated the potential for mineral soils to store additional carbon in response to CO<sub>2</sub> enrichment (see Fig. 6.3, this page).

Cotrufo et al. (2005) obtained hardwood leaf litter from the Duke FACE, ORNL FACE, and scrub oak OTC experiments. The litter from trees grown in ambient and elevated CO<sub>2</sub> had distinct δ<sup>13</sup>C signatures, which were exploited in isopod feeding trials. The <sup>13</sup>C label was clearly carried from the litter source to the isopods' bodies and feces. With the exception of *Quercus myrtifolia* leaf litter, elevated CO<sub>2</sub> did not affect litter palatability to isopods nor the microbial degradation of any of the litters, possibly as a result of unaltered litter nitrogen concentration. However, significant differences in litter palatability and decay rates were observed among the different species.

Natali et al. (2008) reported that soil mercury concentrations were almost 30% greater under elevated atmospheric CO<sub>2</sub> in the Duke and ORNL FACE experiments, but there were no direct effects of CO<sub>2</sub> on litterfall, throughfall, or stemflow mercury inputs. Rather, the increased soil mercury was attributed to CO<sub>2</sub>-mediated changes in soil organic matter.

## Data Synthesis

The carbon dioxide (CO<sub>2</sub>) research community has always recognized that no one experiment could represent the responses to elevated CO<sub>2</sub> of all plants in diverse ecosystems. Collectively, however, the Free-Air CO<sub>2</sub> Enrichment (FACE) studies and ecosystem-scale open-top chamber (OTC) experiments summarized in this report have supported a multitude of reviews, meta-analyses, and conceptual syntheses, often in combination with data from international CO<sub>2</sub> experiments. These results and analyses are far too numerous to list or describe here, other than several particularly prominent syntheses. For example, Ainsworth and Long (2005) conducted a meta-analysis of data from 120 primary, peer-reviewed publications from 12 large-scale FACE experiments, focusing on physiology and production. Ainsworth and Rogers (2007) similarly focused on photosynthesis and stomatal conductance. Other meta-analyses of FACE data were summarized by Haworth et al. (2016), who argue that these meta-analyses have likely exaggerated the magnitude of the effect size of elevated CO<sub>2</sub>. Other reviews have taken a more conceptual approach, such as an analysis of soil processes (Kuzyakov et al. 2019) or carbon metabolism (Dusenge et al. 2019). Nowak et al. (2004), Leakey et al. (2009), and Norby and Zak (2011) considered how responses from FACE experiments matched previous expectations and the lessons that could be learned from the experiments.

In addition to these many synthesis activities across the broad, international scientific community, there was a concerted effort within the U.S. Department of Energy (DOE) to consider the FACE experiments as a network of sites. Although objectives and approaches varied among the different experiments, collectively they provided a valuable trove of data and insight. Hence, data synthesis has been an important activity of this research program.

### 7.1. Forest FACE Synthesis

Models of forest response to future atmospheric and climatic conditions are sensitive to assumptions about the primary and secondary responses of trees to elevated CO<sub>2</sub> concentrations. Prior to the FACE experiments, these assumptions were necessarily based on the short-term responses of tree seedlings and young saplings grown in isolation from a forest ecosystem. The FACE experiments in four forest systems—Duke FACE (Section 3.2, p. 19), Oak Ridge National Laboratory (ORNL) FACE (Section 3.3, p. 24), Rhinelander FACE (Section 3.5, p. 36), and POP-EUROFACE in Italy—provided data on longer-term responses at the forest stand-level. In 2001, however, modelers wanting to benchmark their model simulations of forest productivity

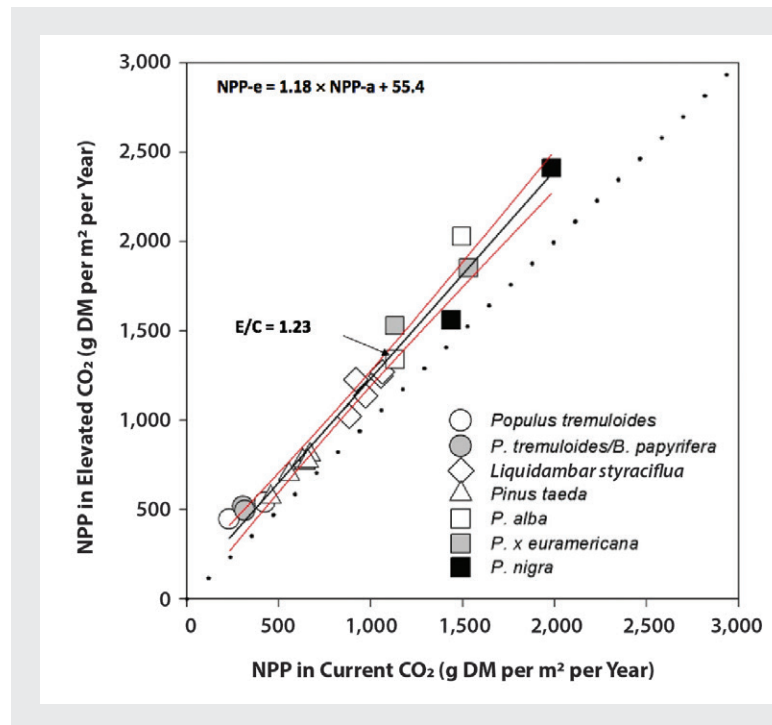
responses had to pick and choose which data to reference. Early results from Duke FACE suggested that there would not be a long-term increase in net primary production (NPP) under elevated CO<sub>2</sub> (Oren et al. 2001), but results from ORNL suggested a sustained response (Norby et al. 2002). Given the confusion and disagreement as to what the “correct” response should be, the experimental community decided it should synthesize the data from forest FACE experiments in a way that could be of best use as model benchmarks.

The first step in the process of analysis, hypothesis testing, and synthesis was to combine common datasets from the different experiments. To bring together experimentalists from the four sites to work out challenges in data comparability and format, a May 2002 workshop in Durham, N.H., was funded by DOE, the Northern and Southern Global Change Research Programs of the U.S. Department of Agriculture Forest Service, and the National Council of Air and Stream Improvement. The workshop objective was to begin the process of synthesizing the datasets from ongoing forest FACE experiments and make them available for modeling, assessment, and a generalized understanding of forest metabolism in the future. Motivating this objective was the idea that data from a single experiment, no matter how well documented, would be anecdotal and provide no basis for drawing conclusions beyond the specific attributes of the particular experimental system. However, four relatively similar experiments—with different site factors (e.g., climate and soil), different species, different stand structures, and a wide range in NPP—would allow experimentalists to look for commonalities in responses and response mechanisms, as well as to search for explanations for differences among sites. While these four experimental systems clearly did not represent the diversity of the world’s forests—they all were young, planted stands in the temperate zone—they undoubtedly offered more value together than would one site alone.

Synthesizing the data from these experiments is a difficult, multiphasic, multidimensional process involving many researchers from different disciplines. The workshop approach was to focus initially on a horizontal (i.e., cross-site) synthesis of several critical data streams that all sites had in common. The basic premise was that there is an essential commonality in the primary responses to elevated CO<sub>2</sub> across the four sites, and cross-site differences in the outcome of those responses can be attributed to species, environmental interactions (e.g., soil and weather), or stand developmental history (i.e., closed versus developing canopy and linear versus exponential growth). Representatives from each of the four forest FACE experiments formed working groups to discuss photosynthesis, plant respiration, aboveground growth and leaf area, root production and turnover, water relations, nitrogen cycling, soil respiration, and plant biochemistry. Two of these groups produced publications as a direct product of the workshop. The nitrogen cycling group had the benefit of having used common field and laboratory methods at the three U.S. sites. They reported no effect of atmospheric CO<sub>2</sub> concentration on any microbial nitrogen cycling pool or process, indicating that greater litter production had not initially altered the microbial supply of nitrogen for plant growth (Zak et al. 2003). Thus, there was no evidence that changes in plant litter production under elevated CO<sub>2</sub> will initially slow soil nitrogen availability and produce a negative feedback on NPP. The soil respiration group reported that elevated atmospheric CO<sub>2</sub> stimulated soil

respiration at all sites, and this response persisted for up to 6 years. Young, developing stands experienced greater stimulation than did more established stands, increasing 39% and 16%, respectively, averaged over all years and communities (King et al. 2004). Species composition of the dominant trees was a major controller of the absolute soil CO<sub>2</sub> efflux and the degree of stimulation from CO<sub>2</sub> enrichment.

Other working groups realized that the available data were insufficient to support a synthesis, or that more work would be needed to integrate several different data streams. A follow-up workshop in Townsend, Tenn., in May 2005 was organized to assemble and analyze the data contributing to an assessment of NPP. Objectives were to (1) describe NPP response to CO<sub>2</sub> in four contrasting forest stands; (2) explain variability in response among sites based on stand development, site characteristics, and climate; and (3) present results in a manner useful for regional and global carbon cycle models. The resulting workshop report showed that the response of forest NPP to elevated CO<sub>2</sub> concentrations is highly conserved across a broad range of productivity, with a stimulation at the median of 23% ± 2% (Norby et al. 2005; see Fig. 7.1, this page). At low leaf area index (LAI), a large portion of the response was attributable to increased light absorption, but as LAI increased, the response to elevated CO<sub>2</sub> was wholly caused by increased light-use efficiency. This NPP report firmly established for the broad scientific community the positive effect of CO<sub>2</sub> fertilization on forest NPP, at least for young stands in the temperate zone. However, the concurrence across sites in the NPP response did not resolve all issues attending CO<sub>2</sub> fertilization. The mean response, while a useful benchmark for global analyses, masks several sources of



**Fig. 7.1. Response of Net Primary Production (NPP) to Elevated Carbon Dioxide (CO<sub>2</sub>) in Four Forest FACE Experiments.**

Dotted line represents a 1:1 relationship between NPP [in grams dry matter (DM) per m<sup>2</sup> per year] in elevated CO<sub>2</sub> and NPP in ambient CO<sub>2</sub>. The regression line has a slope significantly different from 1, with a median response indicating a 23% enhancement of NPP in elevated CO<sub>2</sub>. [Modified from figure in Norby, R. J., et al. 2005. "Forest Response to Elevated CO<sub>2</sub> is Conserved Across a Broad Range of Productivity," *Proceedings of the National Academy of Sciences USA* **102**(50), 18052–56.]

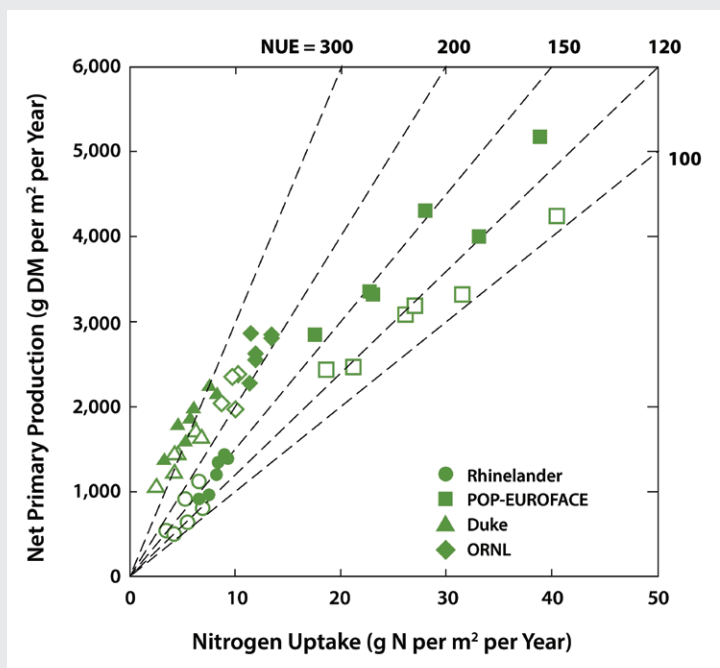


significant variation that could be especially important in determining how a specific site will respond to rising atmospheric CO<sub>2</sub>. Nevertheless, the surprising consistency of response across diverse sites provided a benchmark to evaluate predictions of ecosystem and global models, and the effort's success is seen in the use of its results in modeling papers (Matthews 2007; Hickler et al. 2008).

The NPP analysis also stimulated a focus on unresolved questions about carbon partitioning, carbon retention, and spatial variation in NPP response caused by availability of other growth-limiting resources. With a particular focus on potential nitrogen limitation, and the hypothesis that elevated CO<sub>2</sub> would accelerate progressive nitrogen limitation (Comins and McMurtrie 1993; Luo et al. 2004), a workshop was held in Antwerp, Belgium, in April 2006. The workshop objectives were to determine the relative importance of increases in (1) nitrogen uptake from the soil and (2) nitrogen-use efficiency (NUE) as processes supporting higher rates of NPP under elevated CO<sub>2</sub> (Finzi et al. 2007; see Fig. 7.2, this page). Although fertilization studies at the Duke and ORNL FACE sites showed that tree growth and forest NPP were strongly limited by nitrogen availability, the analysis at the workshop demonstrated that plant uptake of nitrogen increased under elevated CO<sub>2</sub>, a response also observed at Rhinelander FACE. By contrast, NUE increased under elevated CO<sub>2</sub> at the agroforestry POP-EUROFACE site, where nitrogen was not limiting to tree growth. The study concluded that regardless of the specific mechanism, the larger quantities of carbon entering the belowground system under elevated CO<sub>2</sub> resulted in greater nitrogen uptake in nitrogen-limited

**Fig. 7.2. Relationship Between Net Primary Production (NPP) and Nitrogen Uptake at Four FACE Sites.**

Points represent the means for different years in ambient carbon dioxide (CO<sub>2</sub>, open symbols) and elevated CO<sub>2</sub> (solid symbols). In the POP-EUROFACE experiment in Italy, NPP was higher in elevated CO<sub>2</sub>, but nitrogen uptake was not, indicating increased nitrogen-use efficiency (NUE). In the three U.S. Department of Energy FACE experiments, the alignment of points in ambient and elevated CO<sub>2</sub> suggest a constant NUE and increased nitrogen uptake in elevated CO<sub>2</sub>. [Redrawn from Finzi, A. C., et al. 2007. "Increases in Nitrogen Uptake Rather than Nitrogen-Use Efficiency Support Higher Rates of Temperate Forest Productivity Under Elevated CO<sub>2</sub>," *Proceedings of the National Academy of Sciences USA* **104**(35), 14014–19. Copyright 2007 National Academy of Sciences.]



ecosystems. This conclusion has important implications for the formulation of biogeochemical models being used to address elevated CO<sub>2</sub> responses.

## 7.2 Synthesis of Agricultural Studies

The agricultural sector also has made efforts to synthesize its results and make the data available for further analyses. Several meta-analyses have been performed to determine overall effects of elevated CO<sub>2</sub> on various crops. The most recent compilation of agricultural FACE studies, conducted by Kimball (2016), includes data for 18 crops. DOE-funded research contributed to the data acquisition for eight of these (cotton, wheat, sorghum, ryegrass, clover, barley, sugar beet, and maize), either directly or via Brookhaven National Laboratory assistance in constructing the FACE apparatus for the experiments.

The results showed that, for a forage crop like perennial ryegrass, the yield stimulation was about 10% with CO<sub>2</sub> enrichment to about 550 parts per million (ppm) under ample nitrogen and water. Under limited nitrogen, the average ryegrass stimulation to elevated CO<sub>2</sub> was close to zero. The average increase in grain yield due to elevated CO<sub>2</sub> of C3 grasses (e.g., wheat, rice, and barley) was about 19% under ample nitrogen and water. Under limited nitrogen, it was slightly less (16%). When water was limited, the average yield response was somewhat higher (about 22%). The average grain yield of C3 grain legumes (e.g., soybean, pea, peanut, and common bean) increased about 16% in elevated CO<sub>2</sub>. For the C4 grass grain crops (e.g., sorghum and maize), the average response to elevated CO<sub>2</sub> was slightly negative at ample nitrogen and water, consistent with the lack of photosynthetic responses to elevated CO<sub>2</sub>. However, when water was limited, there was a substantial increase (about 30%) in grain yield due to CO<sub>2</sub> enrichment. Such an increase with limited water undoubtedly was due to a reduction in evapotranspiration following rain or irrigation that enabled the plants to conserve water and to grow longer into a drying cycle than did the control plants at ambient CO<sub>2</sub>. Potato tuber yields were stimulated about 27% at elevated CO<sub>2</sub>. Sugar beet, a root crop, was somewhat less responsive to elevated CO<sub>2</sub> than was potato, with average increases of about 9% and 15% at ample and low supplies of nitrogen, respectively. The reason for a larger response at low nitrogen is puzzling, but the soil nitrogen levels probably were not very low. For clover, a legume forage crop, the yield stimulation was about 24% at both ample and low levels of soil nitrogen. Cotton boll yield was highly responsive to elevated CO<sub>2</sub> (an increase of about 38%) at ample nitrogen and water. When water was limiting, the yield response tended to be slightly larger. Although the variability was quite large, the yield increase of lint (i.e., separate from the seeds) tended to be even higher (about 55%). The yield increase of the berries of grape, another woody crop like cotton, was also fairly large (about 28%). Conversely, coffee (also a woody crop) was less responsive, with a yield increase of only about 13% (Kimball 2016).

Almost all the data from the FACE wheat experiments have been published in an “open” journal, and they are available for download by any user (Kimball et al. 2017). These data have been used in about 20 papers featuring validation of the CO<sub>2</sub> response aspects of wheat growth models.

### 7.3 Data and Sample Archives

DOE FACE researchers embraced the mandate to make experimental data publicly available to facilitate effective collaboration, which depends on data being readily available and documented on operational aspects (e.g., meteorological data and CO<sub>2</sub> concentrations) and ecosystem responses. The Carbon Dioxide Information Analysis Center (CDIAC) at ORNL established the FACE Data Management System for data from the Rhinelander, Duke, Nevada Desert, and ORNL FACE experiments. In addition to brief descriptions of the experiments and site characteristics, data were provided on hourly and daily weather and CO<sub>2</sub> concentrations for each plot. The amount of plant and soil response data (e.g., LAI, basal area, and soil moisture) varies for the different experiments. The datasets developed for cross-site syntheses on NPP and nitrogen uptake (see Section 7.1, p. 77) also are posted. All these datasets are fully documented and citable. The original FACE data website ([facedata.ornl.gov](http://facedata.ornl.gov)) has moved to the DOE Environmental Systems Science Data Infrastructure for a Virtual Ecosystem (ESS-DIVE) data archive ([cdiac.ess-dive.lbl.gov/vegetation.html](http://cdiac.ess-dive.lbl.gov/vegetation.html)).

The FACE model-data synthesis activity described in Ch. 8, p. 83, set a higher standard for submitting experimental data because a common and consistent format was required for model input and comparison between model output and measured responses. Measured ecosystem data from the four sites in the original FACE data archive are supplemented with data from the Prairie Heating and Carbon Dioxide Enrichment (PHACE) experiment and the Florida scrub oak OTC experiment. These six sites were the study sites of the FACE Model-Data Synthesis (FACE-MDS) project phase 2. The file-naming convention and information about variable-naming conventions were provided to project participants. The ALMA version 3 convention for meteorological variables was followed, and a hierarchical naming scheme was developed for ecosystem variables.

The FACE experiments maintained a sample archive that proved valuable to numerous researchers. Oven-dried and ground leaf, root, and wood samples permitted retrospective analyses as new questions developed. For example, Garten et al. (2011) analyzed the <sup>15</sup>N content of archived leaf litter samples from ORNL FACE, which provided strong evidence of an increasingly tighter nitrogen cycle and acceleration of progressive nitrogen limitation in elevated CO<sub>2</sub>. Archived plant and soil samples were analyzed for changes in their carbon oxidation state as a proxy for oxidative ratio, or the stoichiometric ratio (O<sub>2</sub>:CO<sub>2</sub> of ecosystem gas exchange; Hockaday et al. 2015). The distinct  $\delta^{13}\text{C}$  signature in plant samples from the elevated CO<sub>2</sub> plots has been useful in several decomposition studies.

# Model-Data Synthesis

## 8.1 Initiating the Data and Model-Intercomparison Activity

One initial objective of all the Free-Air CO<sub>2</sub> Enrichment (FACE) experiments was providing data for ecosystem and global models being used to assess the impact of atmospheric and climatic change on terrestrial ecosystems and the feedbacks that ecosystem responses provide to the climate system. Model predictions of feedbacks between the terrestrial biosphere and atmosphere are critical components of coupled carbon-climate models; having confidence in their predictions requires the models be benchmarked against relevant experimental data. During the course of the FACE experiments, models were employed at individual sites (e.g., Luo et al. 2003) or across sites to address a particular response such as water relations (Warren et al. 2011b) or carbon allocation (Palmroth et al. 2006). As the experiments reached their conclusion, a unique opportunity became apparent to initiate a multimodel intercomparison activity similar to the successful model intercomparison with the Throughfall Displacement Experiment (Hanson et al. 2005). With support from the National Center for Ecological Analysis and Synthesis (NCEAS), representatives from 11 ecosystem and land surface models and from the Duke and Oak Ridge National Laboratory (ORNL) FACE experiments met in three workshops at NCEAS from 2008 to 2010 to develop a modeling protocol and harmonize experimental data. This activity, “Benchmarking Ecosystem Response Models with Experimental Data from Long-Term CO<sub>2</sub> Enrichment Experiments,” comprised four objectives:

1. Evaluate the ability of models to reproduce the measured processes of the carbon, water, and nitrogen cycles of the experimental forest stands and their responses to elevated atmospheric carbon dioxide (CO<sub>2</sub>) concentration.
2. Ask whether the models explain observed variability in responses within and differences between the two experiments in forest stands.
3. Use the similarities and differences among the models and between models and experimental data to provide guidance for improving all the models and gain increased confidence in their predictive capacity.
4. Demonstrate the utility of models to produce decadal predictions of forest growth and carbon sequestration under scenarios of gradually rising atmospheric CO<sub>2</sub> concentrations and associated climate variables.

These objectives were consistent with a specific recommendation of the 2006 Biological and Environmental Research Advisory Committee (BERAC) review of the U.S.

Department of Energy's (DOE) FACE and open-top chamber (OTC) projects: "A synthesis of results to date combined with modeling should be used to come up with explicit and testable hypotheses for the next generation of experiments; one major result would be to test our ability to predict what will happen based on extrapolations from existing knowledge, or specifically address the factors associated with the largest uncertainties in model predictions of response" (BERAC 2006).

The FACE Model-Data Synthesis (FACE-MDS) activity became a national and international collaboration of scientists at 20 institutions across six nations led by principal investigators at ORNL, with key partners at Hawkesbury Institute for Environment and Macquarie University in Australia and at the Max Planck Institute for Biogeochemistry in Germany. The initial focus was on data from the Duke and ORNL FACE experiments because they offered some of the longest and most comprehensive experimental datasets on ecosystem responses to elevated CO<sub>2</sub>. Additionally, the two experiments and the forests they investigated were similar in many respects, while also having contrasting responses to elevated CO<sub>2</sub>. In 2008, the modeling protocol was established, and site data were put into a standard format. This process proved to be difficult and time consuming, and clearly the model-data connection would have been much more efficient if it had been established before the data were collected. After initial model runs, problems with datasets or model parameterization were identified and resolved (2009). In September 2010, model runs were completed, and a set of papers to describe the model output were tentatively outlined. Progress on the papers, however, was slow as investigators completed their modeling efforts with minimal support while working on other funded commitments. DOE began supporting FACE-MDS in 2011, enabling the completion of the initiated activity. The significant conclusions from the resulting series of papers are summarized in the next sections.

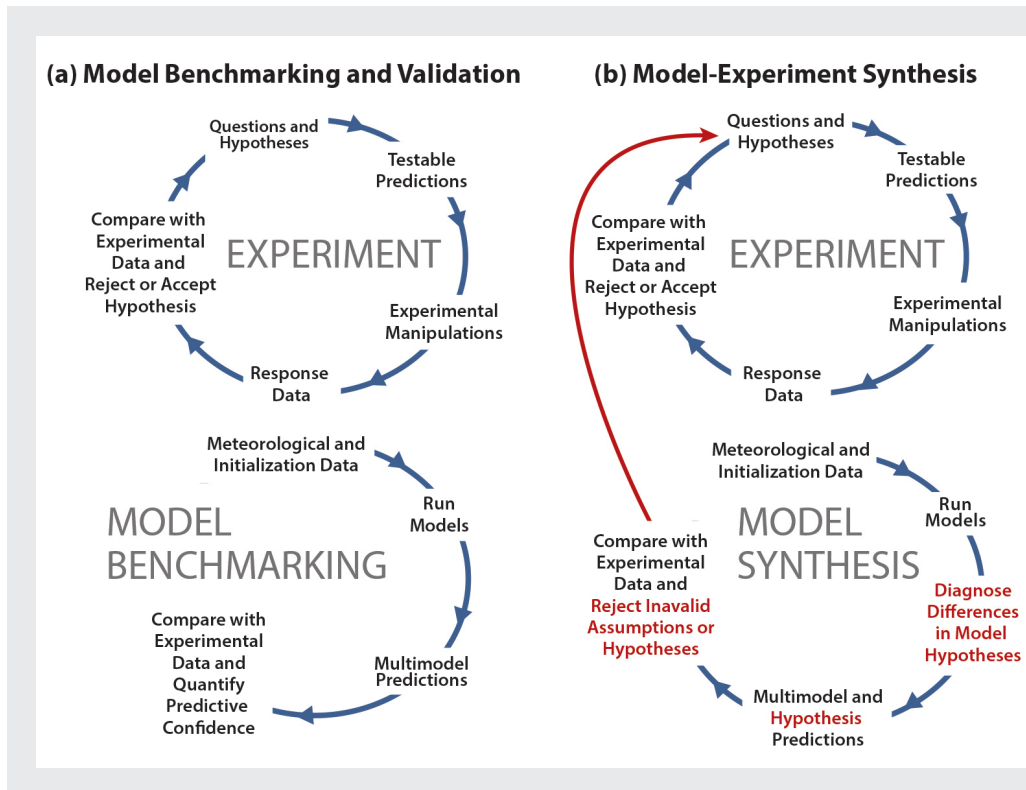
## 8.2 Results from Phase 1 of the Synthesis

Walker et al. (2014) described the approach of the FACE-MDS (see Fig. 8.1, p. 85) and evaluated the ability of 11 terrestrial ecosystem models to reproduce observed net primary production (NPP), transpiration, and leaf area index (LAI) in the ambient CO<sub>2</sub> plots. Many of the models simulated annual NPP and transpiration within observed uncertainty, but high goodness-of-fit values did not necessarily indicate a successful model because simulation accuracy was sometimes achieved through compensating biases in component variables. For example, transpiration accuracy was sometimes accomplished with compensating biases in LAI and transpiration per unit leaf area. Hence, the approach to model-data synthesis used here and in other papers from the project went beyond goodness of fit to investigate the success of alternative representations of component processes.

### *Water Use and Water-Use Efficiency*

De Kauwe et al. (2013) explored the models' representation of water use and water-use efficiency (WUE) at the two experimental sites. Key assumptions in model structures regarding the coupling between CO<sub>2</sub> assimilation, stomatal conductance, and transpiration caused differences in model predictions of transpiration and WUE and how well they agreed with observations of the response to elevated CO<sub>2</sub>. For example, some





**Fig. 8.1. Schematic Showing (a) Traditional Model Benchmarking Approach Compared with (b) the Model-Experiment Synthesis Approach Used in the FACE Model-Data Synthesis Project.** [Redrawn by permission of Wiley from Walker, A. P., et al. 2014. "Comprehensive Ecosystem Model-Data Synthesis Using Multiple Data Sets at Two Temperate Forest Free-Air CO<sub>2</sub> Enrichment Experiments: Model Performance at Ambient CO<sub>2</sub> Concentration," *Journal of Geophysical Research: Biogeosciences* **119**, 937–64. Copyright 2014 American Geophysical Union.]

models correctly captured the leaf-scale coupling between assimilation and stomatal conductance. However, at the canopy scale, an additional assumption in relation to how leaves interact with the surrounding airstream (i.e., leaf boundary layer) meant that models such as the Community Atmosphere-Biosphere-Land Exchange (CABLE) land surface model underestimated the CO<sub>2</sub> effect on transpiration. Similarly, Community Land Model version 4 (CLM4) captured leaf-scale coupling between assimilation and stomatal conductance, but, as nitrogen became progressively limiting, CLM4 assumed that assimilation was reduced but not so with stomatal conductance; this assumption was unsupported by the observations.

### **Nitrogen and Forest Growth**

Zaehle et al. (2014) concluded that models of FACE experiments did not reproduce nitrogen constraints on forest productivity that develop under elevated CO<sub>2</sub> (see Fig. 8.2, p. 86). Many models reproduced the initial enhancement of NPP in elevated CO<sub>2</sub>, but this response resulted from compensating errors in underlying process responses related to nitrogen uptake and nitrogen-use efficiency (NUE). As described by the nitrogen synthesis (Finzi et al. 2007), NPP responses were supported by nitrogen uptake at Duke and ORNL, but models predicted little change in nitrogen uptake and instead predicted that NPP responses were supported by increased NUE. Models captured the observed decline in NPP response at ORNL but also predicted a decline at Duke, a trend that was not observed. The analysis highlighted the need for better

understanding and model formulation of stoichiometric flexibility, root allocation, and regulation of nitrogen uptake in response to increased nitrogen demand to accurately capture the nitrogen constraint on the carbon cycle response to elevated  $\text{CO}_2$ .

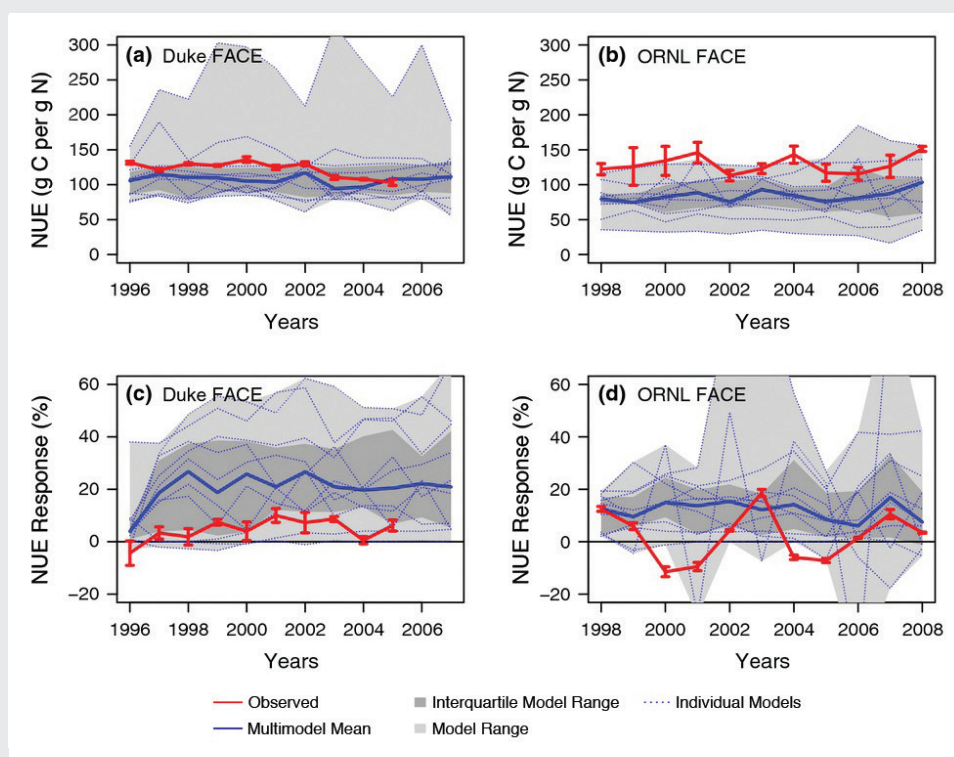
### Carbon Allocation

Allocation has long been recognized as a critical process to represent correctly in models, and differences in allocation patterns between the Duke and ORNL experiments were thought to be an important challenge to the models. De Kauwe et al. (2014) found that allocation schemes based on functional relationships among biomass fractions that vary with resource availability were best able to capture the general features of the experimental observations. Allocation schemes based on constant fractions or unconstrained resource limitations performed less well, with some models having unintended outcomes. Few models represent turnover processes mechanistically, and there was wide variation in predictions of tissue lifespan. Consequently, models did not perform well at predicting  $\text{CO}_2$  effects on vegetation carbon storage. The analyses led to recommendations for reducing uncertainty, including the use of allocation schemes constrained by biomass fractions, careful testing of allocation schemes, and synthesis of allocation and turnover data in terms of model parameters.

### Decadal and Century Projections

In line with the objective of interpreting FACE results in the context of gradual increases in atmospheric  $\text{CO}_2$  over decades to centuries, Walker et al. (2015) used a

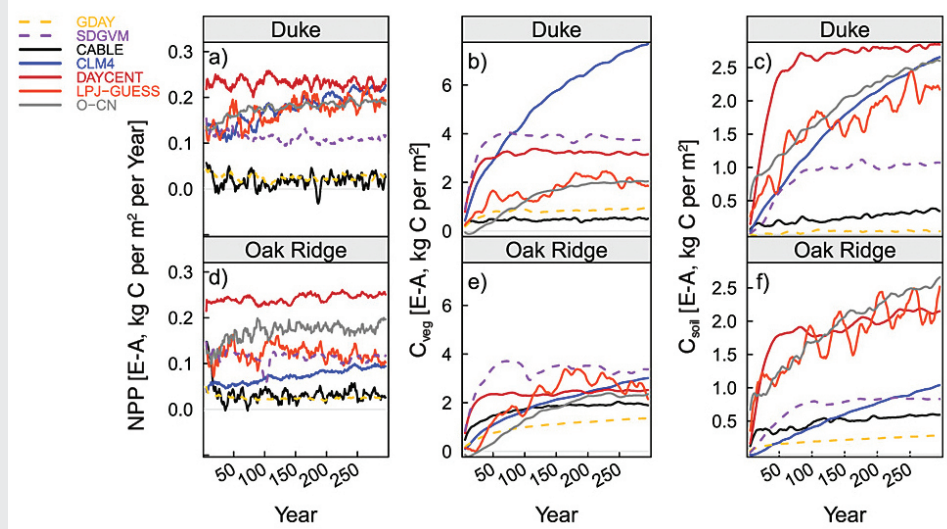
**Fig. 8.2. Comparison of Measured and Modeled Nitrogen-Use Efficiency (NUE) at Duke and Oak Ridge National Laboratory (ORNL) FACE Sites. (a-b)** NUE in ambient carbon dioxide ( $\text{CO}_2$ ). **(c-d)** NUE response to elevated  $\text{CO}_2$ . [Reprinted under a Creative Commons License (CC BY 3.0) from Zaehle, S., et al. 2014. "Evaluation of 11 Terrestrial Carbon-Nitrogen Cycle Models Against Observations from Two Temperate Free-Air  $\text{CO}_2$  Enrichment Studies," *New Phytologist* **202**(3) 803–22.]



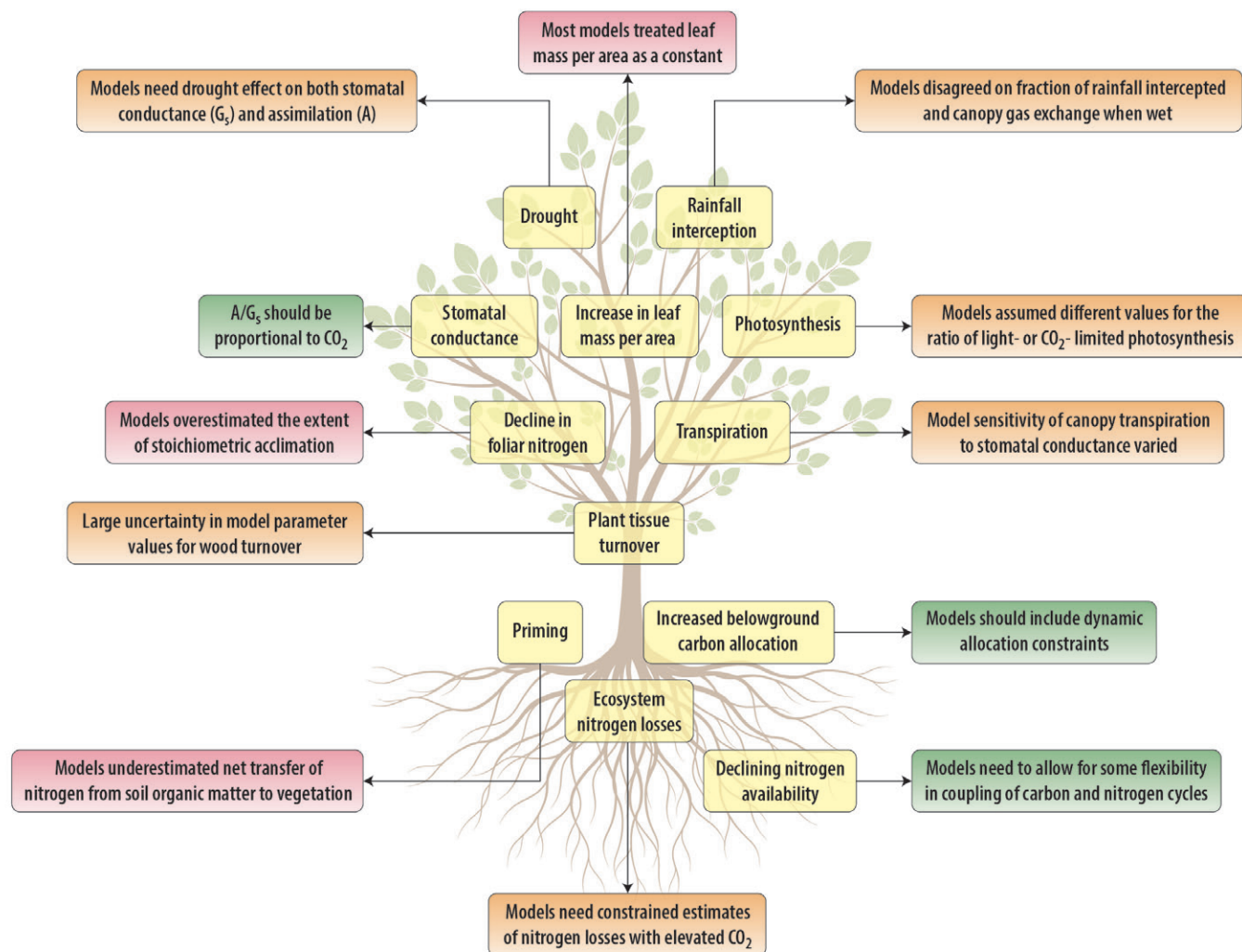
suite of seven models to simulate the Duke and ORNL FACE experiments extended for 300 years of CO<sub>2</sub> enrichment (see Fig. 8.3, this page). All models simulated increased terrestrial carbon pools resulting from CO<sub>2</sub> enrichment but with substantial variability in quasi-equilibrium carbon sequestration and rates of change. In two models that assume that plant nitrogen uptake is solely a function of soil nitrogen supply, the NPP response to elevated CO<sub>2</sub> became progressively nitrogen limited. In four of five models that assume that nitrogen uptake is a function of both soil nitrogen supply and plant nitrogen demand, elevated CO<sub>2</sub> led to reduced ecosystem nitrogen losses and thus an accumulation of nitrogen in the ecosystem over time that supported higher rates of productivity. Many allocation assumptions resulted in increased wood allocation relative to leaves and roots, reducing the vegetation turnover rate and increasing carbon sequestration. Increased wood allocation also interacted with self-thinning assumptions in several models, leading to either increases or decreases in tree mortality, depending on the exact assumptions made by the model. This analysis showed that accurate representation of nitrogen process dynamics (in particular, nitrogen uptake), allocation, and forest self-thinning is key to minimizing uncertainty in projections of future carbon sequestration in response to elevated atmospheric CO<sub>2</sub>.

### “Assumption-Centered” Approach for Understanding Model Differences

At the conclusion of this first phase of the FACE-MDS, Medlyn et al. (2015) presented a summary and synthesis of the approach and key results. Medlyn described the “assumption-centered” approach, whereby the underlying reasons for model behavior were diagnosed and then evaluated against experimental data based on the ways



**Fig. 8.3. Modeled Long-Term Response of Net Primary Production (NPP), Vegetation Carbon Content ( $C_{veg}$ ), and Soil Carbon Content ( $C_{soil}$ ) to a Step Change in Carbon Dioxide Concentration at the Duke and Oak Ridge National Laboratory FACE Sites.** Solid lines denote models that assume nitrogen uptake is a function of soil nitrogen supply and plant nitrogen demand. Dashed lines denote models that assume nitrogen uptake is a function of soil nitrogen supply. [Reprinted by permission of Wiley from Walker, A. P., et al. 2015. “Predicting Long-Term Carbon Sequestration in Response to CO<sub>2</sub> Enrichment: How and Why Do Current Ecosystem Models Differ?” *Global Biogeochemical Cycles* **29**, 476–95. Copyright 2015 American Geophysical Union.]



**Fig. 8.4. Summary of Findings from the FACE Model-Data Synthesis (FACE-MDS) Project.** **Green:** Processes for which FACE datasets allowed discrimination among alternative model assumptions. **Red:** Processes for which FACE datasets identified missing or wrong model assumptions. **Orange:** Processes for which additional data are needed to discriminate among model assumptions. [Reprinted by permission from Springer Nature from Medlyn, B. E., et al. 2015. "Using Ecosystem Experiments to Improve Vegetation Models," *Nature Climate Change* 5, 528–34. Copyright 2015.]

in which the models represent key ecological processes. The assumption-centered approach evolved beyond the original project goals of benchmarking and beyond many of the previous model intercomparisons by delving deeper into model results and rigorously explaining the causes of model differences in the context of ecological process. Evaluation of the differences resulted in grouping the key ecological processes into three categories: (1) processes for which FACE data allowed discrimination among model assumptions, (2) those for which FACE data identified missing or wrong assumptions in the models, and (3) processes for which additional data are needed to discriminate among model assumptions (see Fig. 8.4, this page). The assumption-centered approach produced a clear roadmap for reducing model uncertainty, improving model capacity



to predict effects of elevated CO<sub>2</sub> on forests, and identifying key research tasks for both modelers and experimentalists.

### 8.3 Results from Phase 2 of the Synthesis

#### *Expanding Models to Include More Sites, More Variables*

Researchers from ORNL with support from DOE initiated phase 2 of the FACE-MDS with an expanded scope that included more experiments—Nevada Desert FACE, Florida scrub oak OTC, Rhinelander FACE, and the Prairie Heating and Carbon Dioxide Enrichment (PHACE) project. The diversity of these ecosystems created new challenges in data synthesis and modeling. For example, the ecosystem models did not work well with the early-growth phase in the Rhinelander FACE experiment. The combination of warming and irrigation in the PHACE experiment created both opportunities and challenges for the models, partly due to the frequent water limitation in this semiarid grassland. Ryan et al. (2017) used 6 years of gross primary production (GPP) data from PHACE to calibrate a light-response model. Antecedent air and vapor pressure deficit effects on photosynthetic capacity, or  $A_{\max}$ , (over the past 3 to 4 days and 1 to 3 days, respectively) were the most significant predictors of temporal variability in GPP among most treatments. De Kauwe et al. (2017) noted that terrestrial biosphere models have been tested primarily against single-factor experiments despite the frequent call for multifactor experiments. Applying the assumption-centered approach to the PHACE experiment, they found that models performed poorly in ambient conditions; there was a wide spread in simulated aboveground NPP, ranging from 31 to 390 g C per m<sup>2</sup> per year. Model comparisons with data highlighted model failures at simulating grasslands, particularly with respect to carbon allocation, phenology, and the impact of water stress on phenology. Observed interactive (CO<sub>2</sub> × warming) treatment effects were subtle and contingent on water stress, phenology, and species composition. As the models did not correctly represent these processes under ambient and single-factor conditions at PHACE, little extra information was gained by comparing model predictions against interactive responses.

#### *Predicting Biomass Response*

Walker et al. (2019) analyzed data from the Duke, ORNL, and Rhinelander FACE experiments, as well as the scrub oak OTC experiment, to determine whether a decade of CO<sub>2</sub> enrichment in woody ecosystems leads to an increase in the vegetation biomass increment (see Fig. 8.5, p. 90). Additional objectives were to interpret any observed biomass response through the effects of CO<sub>2</sub> enrichment on NPP and carbon allocation and evaluate the ability of an ensemble of terrestrial ecosystem models to reproduce the observed responses. Carbon dioxide enrichment increased the biomass increment by  $1.05 \pm 0.26$  kg C per m<sup>2</sup> over a full decade, a  $29.1\% \pm 11.7\%$  stimulation of biomass gain in these early–secondary succession temperate ecosystems. This response was predictable by combining the CO<sub>2</sub> response of NPP and the CO<sub>2</sub>-independent, linear slope between biomass increment and cumulative NPP. An ensemble of terrestrial ecosystem models failed to predict both terms correctly. Carbon allocation to wood was a driver of across-site, and across-model, response variability. Together with CO<sub>2</sub> independence of biomass retention, this analysis highlights the value of understanding



drivers of wood allocation under ambient conditions to correctly interpret and predict CO<sub>2</sub> responses.

### **New Questions on Impacts of Soil Carbon Dynamics, Nutrient Limitation, Succession**

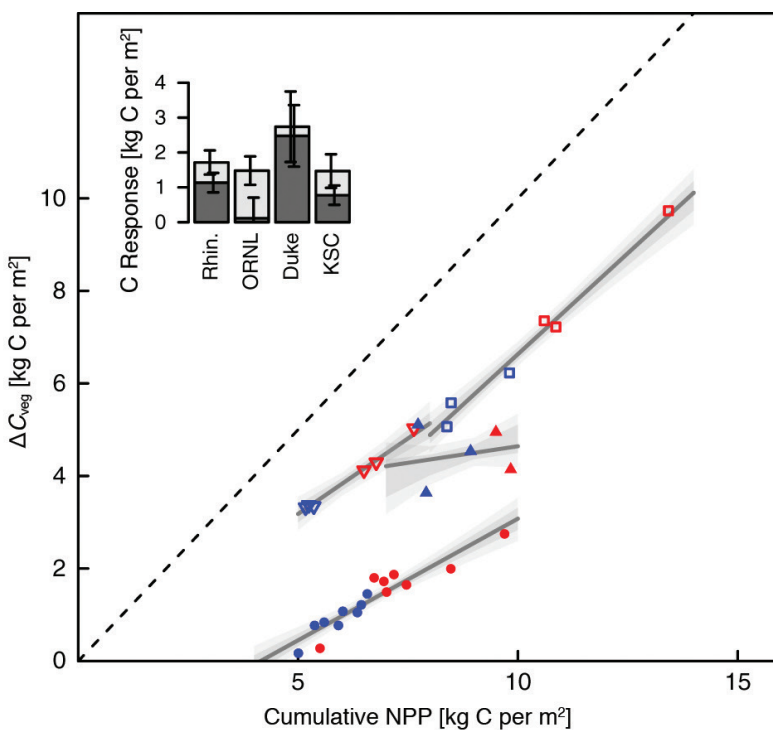
These four experiments represent the most direct evidence for decadal biomass responses to CO<sub>2</sub> enrichment in early–secondary succession, temperate woody ecosystems. The experimental data, and the analysis by Walker et al. (2019), directly address the fundamental question posed 36 years earlier:

“... the initial effect of elevated CO<sub>2</sub> will be to increase NPP in most plant communities. This increase in NPP could be limited or reversed by nutrient availability, herbivory, or successional dynamics [...]. However, even without such effects, a critical question is the extent to which the increase in NPP will lead to a substantial increase in plant biomass. Alternatively, increased NPP could simply increase the rate of turnover of leaves or roots without changing plant biomass” (Strain and Bazzaz 1983).

Hence, this analysis could be interpreted as the culmination of the FACE research program. However, critical questions remain unanswered. The dichotomy put forward by Strain and Bazzaz (1983) did not consider the possibility of increased turnover of leaves or roots adding carbon to protected soil pools and enhancing *ecosystem* carbon

**Fig. 8.5. Relationship Between Forest Biomass Increment ( $\Delta C_{veg}$ ) and Cumulative Net Primary Production (NPP) for Three FACE Experiments and One Open-Top Chamber (OTC) Study.** Rhineland FACE (open triangles), Oak Ridge National Laboratory (ORNL) FACE (filled triangles), Duke FACE (open squares), and scrub oak OTC experiment near Kennedy Space Center (KSC, filled circles). Each point represents an individual sample plot; ambient carbon dioxide (CO<sub>2</sub>) plots are shown in blue and elevated CO<sub>2</sub> plots in red. Inset shows the CO<sub>2</sub> stimulation of cumulative NPP  $\pm$  the standard error of the mean (SEM; light grey bars), along with the forest biomass increment  $\pm$  SEM (dark grey bars), over the duration of the experiments.

At the three sites with a biomass response to CO<sub>2</sub> enrichment, the negative intercept of the relationship indicates that the fraction of cumulative NPP retained as  $\Delta C_{veg}$  (the biomass retention ratio) increased as cumulative NPP increased. [Reprinted under a Creative Commons License (CC BY 4.0) from Walker, A. P., et al. 2019. “Decadal Biomass Increment in Early Secondary Succession Woody Ecosystems Is Increased by CO<sub>2</sub> Enrichment,” *Nature Communications* **10**, 454.]



sequestration, even if carbon storage in plant biomass were not enhanced. Outstanding critical issues include:

- FACE experiments revealed soil processes to be a potentially important mechanism (Jastrow et al. 2005; Iversen et al. 2008), but effects of elevated CO<sub>2</sub> on soil carbon fluxes are much larger than effects on pool sizes (Kuzyakov et al. 2019), and the data on soil organic matter inventories are insufficient to constrain models (Zaehle et al. 2014). New sampling and measurement approaches are needed to detect small changes in the very large pool of soil carbon, or experiments need to be much longer in duration.
- The possibility of nutrient availability limiting the response of NPP was recognized by Strain and Bazzaz (1983), and experimental data on nitrogen limitations have confirmed this (e.g., Norby et al. 2010). However, models still struggle to capture the mechanisms correctly (Zaehle et al. 2014).
- Experiments and modeling of phosphorus limitation of CO<sub>2</sub> responses are just beginning (Ellsworth et al. 2017; Norby et al. 2017; Jiang et al. 2019), although CO<sub>2</sub>-phosphorus interactions are likely to be critical determinants of tropical forest responses (Yang et al. 2014, 2019; Fleischer et al. 2019).
- Strain and Bazzaz (1983) also suggested successional dynamics as an important consideration. Walker et al. (2019) agreed: “Thus post-disturbance stands and early successional forests are likely to be a major component of the climate-relevant, temperate forest responses to increasing CO<sub>2</sub>.” But they note that the full range of secondary succession has not been sampled in FACE experiments and implementing secondary succession in models as a means for scaling predictions of terrestrial ecosystem responses to increasing CO<sub>2</sub> will require further development and synthesis of mechanistic theory.

As is true across all science, answering questions will inevitably lead to compelling new questions. Phase 3 of FACE-MDS will leverage DOE’s substantial investment in the largest and longest-running CO<sub>2</sub> manipulation experiments and Earth system models to investigate how forest structure, demographic processes, and soil processes interact to shape terrestrial ecosystem CO<sub>2</sub> responses at decadal timescales. This work will transform the understanding of key processes driving CO<sub>2</sub> fertilization, placing DOE’s Functionally Assembled Terrestrial Ecosystem Simulator (FATES) land surface model at the forefront of that understanding for application within the DOE Energy Exascale Earth System Model (E3SM).



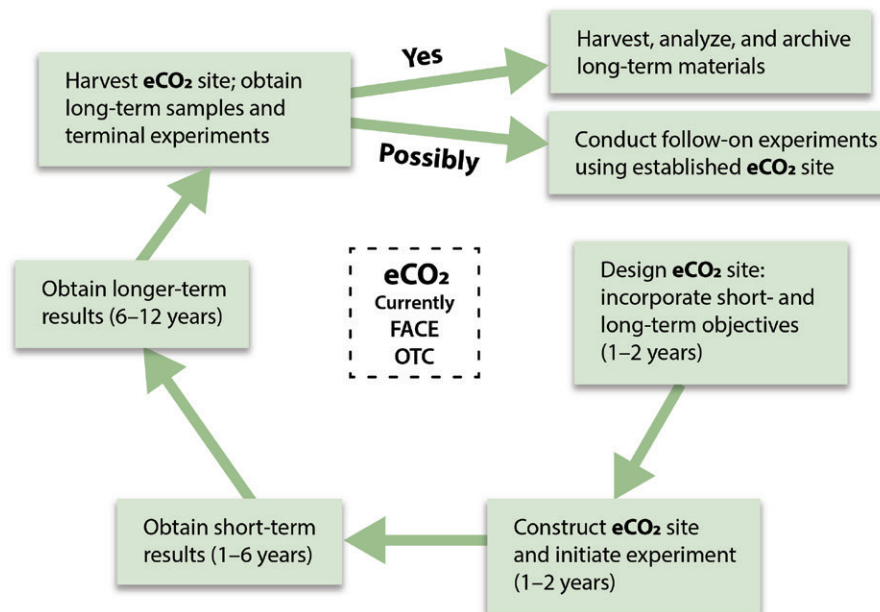
# Conclusion and Closeout of FACE Experiments

## 9.1 BERAC Evaluations of FACE

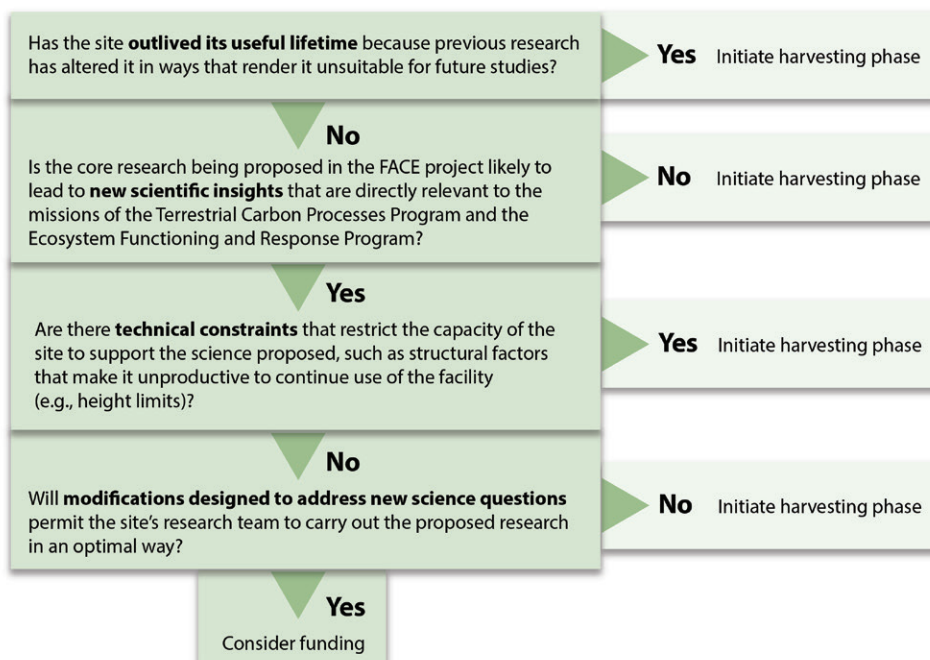
In December 2005, members of the Biological and Environmental Research Advisory Committee (BERAC) reported on their review of the U.S. Department of Energy's (DOE) Terrestrial Carbon Cycle Research Program, including the Free-Air CO<sub>2</sub> Enrichment (FACE) activities. (BERAC is organized under the Federal Advisory Committee Act and provides official advice to federal agencies.) The subcommittee's report (BERAC 2005) observed that DOE FACE research did not have a scientific steering committee (SSC) to set strategic directions for the collective FACE experiments, which were 7 to 9 years old at the time. Instead, each site appeared to have its own set of objectives and operational approaches. The subcommittee discussed the lifecycle of a typical FACE or open-top chamber (OTC) experiment and developed a decision framework to guide experiment transitions and closeouts (see Fig. 9.1, p. 94). Two major questions were raised: (1) how long should a current site remain operational and (2) where might new sites be established? While recognizing the need for long-term continuity of some FACE experiments, committee members recommended periodic evaluation of the sites to determine when an experiment had reached a point of diminishing scientific returns. Although it did not make specific recommendations as to which experiments should be terminated, the subcommittee noted that in some cases, tree height created logistical difficulties in continuing the experiment. At other sites, interannual variation was small and additional measurements might not yield enough new information to justify the continued investment. "The substantial DOE FACE investment might then yield more valuable information if moved to a site where no information now exists and uncertainty about potential ecological responses is high" (BERAC 2005; see box, BERAC's 2005 Recommendations, p. 95).

Some of these recommendations were subsequently implemented; others were not. For example, as called for, there was a BERAC review of the FACE and OTC projects in 2006 that led to the phase-out and decommissioning of most of the sites (BERAC 2006). New research priorities, including ones highlighted in community workshops, led DOE to reinvest former FACE support into the Next-Generation Ecosystem Experiments (NGEE). In addition, the Carbon Dioxide Information Analysis Center (CDIAC) independently established a FACE data web portal, and DOE began to support the FACE Model–Data Synthesis activity and some associated data management. Unfortunately, an SSC was never established for the FACE sites.

**(a) Lifecycle of an Elevated CO<sub>2</sub> (eCO<sub>2</sub>) Ecosystem Experiment**



**(b) Decision Chart to Guide FACE Experiments' Next Steps**



**Fig. 9.1 Approach for Assessing FACE Experiments.** The Biological and Environmental Research Advisory Committee's (BERAC) view of **(a)** the lifecycle of a FACE or open-top chamber (OTC) experiment. **(b)** BERAC schematic of a decision-based flowchart to guide the transitioning of a project from the experimental phase, in which an ecosystem is exposed to eCO<sub>2</sub> levels, to the harvesting phase, during which CO<sub>2</sub> is turned off and below- and aboveground biomass is fully harvested and analyzed. [Redrawn from BERAC. 2006. *Report of the BERAC Subcommittee Reviewing the FACE and OTC Elevated CO<sub>2</sub> Projects in DOE. Subcommittee of the Biological and Environmental Research Advisory Committee.*]



### BERAC's 2005 Recommendations

- Initiate a review of existing scientific information and the potential for new findings at each experimental installation.
- Potentially phase out some sites following the review and transfer the investment to new areas not currently sampled (e.g., drought-prone forests, peat bogs, nitrogen-deficient locations, or areas with highly variable climate).
- Schedule periodic self-evaluations of the sites and use the results to set priorities for locating future FACE sites and decommissioning existing sites.
- Provide funding to establish and maintain a database for data collected at all DOE FACE sites.
- Establish a science steering committee (SSC) comprising a FACE scientific director and representatives from each site, the modeling and data management communities, and scientific fields related to major crosscutting topics. The SSC should meet regularly and organize annual meetings.

Following the recommendation in the 2005 BERAC report, a 2006 BERAC subcommittee was charged with reviewing FACE and OTC projects, including the Duke, Oak Ridge National Laboratory, Nevada Desert, and Rhinelander FACE experiments, along with the Smithsonian salt marsh and scrub oak OTC experiments. Their review did not include other experiments partially supported by DOE. The subcommittee was instructed to:

- Review and assess information from existing DOE experiments (i.e., determine what has been learned).
- Assess the potential of existing experiments to yield new findings, if continued.
- Provide recommendations on whether existing experiments have reached or are reaching the point of diminishing scientific return.
- Provide recommendations on which experiments should be maintained or discontinued and on locations for potential new experiments required to address programmatic goals.
- Consider how the escalating costs of FACE experiments might be reduced.
- Evaluate the scientific need and technical feasibility of modifying FACE experimental approaches to consider other greenhouse gases or climatic influences on carbon cycle processes and on the functioning and response of terrestrial ecosystems.
- Propose alternative approaches for conducting FACE-type experiments that offer significant cost advantages.

The subcommittee's report (BERAC 2006) celebrated DOE's leading role in pioneering long-term climate change research, noting that it stood alone as the lead agency in funding such research with experiments like FACE. Ecosystem research requires long-term support, and the panel applauded DOE's long-term commitment to experimental climate change research. The panel also concluded that FACE studies had achieved the most realistic elevated carbon dioxide (CO<sub>2</sub>) environment for ecosystem studies and that properly

### BERAC's 2006 Recommendations

- Transition several elevated carbon dioxide (CO<sub>2</sub>) projects into the harvesting phase during fiscal year (FY) 2007.
- Harvest the rest of the existing elevated CO<sub>2</sub> projects by FY 2010 at the latest.
- Immediately convene one or more workshops to plan the next generation of elevated CO<sub>2</sub> experiments.
- Do not initiate new elevated CO<sub>2</sub> projects until after workshop decisions on the future design of such experiments to address multiple interacting factors.
- Consider funding for any new or renewal research proposals for FACE and OTC projects in the context of the schedule for harvesting a site.
- As soon as harvesting is determined, convene workshops for FACE and OTC projects to plan for their harvesting phases.
- Provide funding after “turning off the elevated CO<sub>2</sub>” to allow publishing of original research, within-site syntheses, and cross-site syntheses.

implemented OTCs were useful for small plot studies. FACE experiments were found to have been quite productive by any metric, having produced fundamental new insights into carbon dynamics and supporting progress in the development of multiscale predictive models. Important results that emerged from FACE research included the significance of belowground processes and factor interactions. Additional findings emphasized the importance of increased interaction with DOE programs in microbial processes and genomics and strongly endorsed the previous BERAC report calling for coordinated data archiving (BERAC 2005). Subcommittee members also stated in their evaluation that the FACE design imposes sampling constraints that lead to a useful experimental life expectancy of 10 to 12 years. They noted that harvesting at the conclusion of the experiments would be a critical, productive research phase yielding some of the most useful samples for future research, analyses, and insights (see box, BERAC's 2006 Recommendations, this page).

## 9.2 Planning and Follow-Up of Site Harvests

After careful consideration of the 2006 BERAC subcommittee report, DOE implemented many of the recommendations, including the scheduling of experimental harvests and shutdowns. Similar to the shutdown of many long-term studies or research sites, there was considerable disappointment and some controversy within the community, since many research questions were still not completely answered. In June 2007, FACE researchers and other interested scientists assembled in a workshop with the objectives of (1) informing potential collaborators and the wider scientific community of the opportunities presented by the end of FACE and OTC experiments, (2) eliciting community advice on how FACE and OTC investigators might best manage the shutdown, and (3) ensuring uniformity in sampling and measurement protocols across sites. Representatives from each experiment shared with the group their current experimental design and research focus, the anticipated termination date, and tentative harvesting protocols. The group also considered cross-site issues including connections with modelers, data format, and uniformity of sampling and measurements protocols. The considerable expertise at the workshop informed discussions on how best to proceed with tree harvesting, soil sampling, metagenomics, and other topics. There was

enthusiasm for sample and data archiving, model-data collaborations, and cross-site measurements to take advantage of the harvesting. Unfortunately, some of the enthusiasm for addressing a number of these closeout strategies and plans was not realized due to limitations in funding and other research priorities.

The opportunity for destructive belowground harvests was especially important and produced data that could not have been obtained without compromising an ongoing experiment (e.g., Iversen et al. 2012; Hungate et al. 2013; Evans et al. 2014). Cross-site explorations of microbial community structure were implemented (Deng et al. 2016; Yu et al. 2018). Other post-harvest studies leveraged the residual carbon isotope signature in the soil (e.g., Lynch et al. 2013), and project researchers shared the harvested and archived plant tissue and soil samples with other scientists (e.g., Kim et al. 2015). Ultimately, there were a number of critically important scientific discoveries from the site closures and harvests, despite limitations in program funding.

### 9.3 Post-FACE Planning Workshops

Over the next several years after the 2006 BERAC report, a series of workshops was convened on topics recommended by the subcommittee. In April 2008, 50 experimentalists and modelers (about one-quarter of whom had been closely associated with FACE or OTC experiments) assembled along with agency representatives from DOE and the National Science Foundation at a workshop on “Ecosystem Experiments: Understanding Climate Change Impacts on Ecosystems and Feedbacks to the Physical Climate” (U.S. DOE 2008). The group considered two general questions: (1) What are the key scientific uncertainties surrounding the combined impacts and feedbacks of warming and changes in moisture status, in combination with elevated CO<sub>2</sub> concentration, on the functioning, structure, and composition of terrestrial ecosystems? and (2) What existing or new facilities and methods are needed to conduct long-term ecosystem-scale warming, precipitation, elevated CO<sub>2</sub>, or multifactor-manipulation experiments in the field?

Much of the discussion revolved around consideration of priority ecosystems for future experimental research. Workshop criteria for ranking ecosystems included their inherent sensitivity to global change factors, areal extent, ability to serve as model systems for testing cumulative interactions, and the potential loss of critical ecosystem services. Participants highlighted northern high-latitude ecosystems and wet tropical forest systems as the highest priorities. DOE’s NGEE–Arctic and NGEE–Tropics research programs emerged from these discussions and embraced the new coupled model-experimental (ModEx) approach. Building off FACE successes, DOE supported the multifactor Spruce and Peatland Responses Under Changing Environments (SPRUCE) experiment, which is the only CO<sub>2</sub> manipulation field study the agency currently supports.

A second workshop was convened in August 2009 to identify key long-term issues and uncertainties in global change research, develop effective approaches for addressing them, review the results of extant long-term research efforts, and examine the effectiveness of maintaining long-term experiments (Luo et al. 2011). The analysis recognized the critical need for experiments on decadal timescales to address ecological responses to global change that are regulated by slow processes. However, many such processes

have characteristic timescales much longer than experiments can be maintained. Hence, workshop participants recommended a coordinated approach combining long-term, large-scale global change experiments with process studies and modeling, which is the approach used in NGEF and is the foundation of DOE's Terrestrial Ecosystem Science program. The group considered the question "How long is long enough?" but was unable to develop a clear, definitive answer or recommendation. The general consensus was that the lifetime of an experiment should be determined primarily by the core questions to be addressed and the impacts on the study sites. Experiments should last long enough to enable identification of important but unexpected responses; however, by definition, the ideal duration to accomplish this task is unknowable (Luo et al. 2011). Nevertheless, experiments cannot last forever, and, given finite budgets, decisions about closeouts and the necessary trade-offs between continuation and the opportunity for new experiments and approaches will often be difficult (Ledford 2008). This was true for FACE closeouts even though the experiments were supported by DOE much longer than most ecosystem studies. Ultimately, the scientific value of the site harvesting and the success of the NGEF projects that followed are part of FACE's positive legacy (see Ch. 10, p. 99).

## Lessons and Legacy of DOE's Elevated CO<sub>2</sub> Research Program

**B**y many measures, the U.S. Department of Energy (DOE) programs supporting research on the effects of elevated atmospheric carbon dioxide (CO<sub>2</sub>) on plant growth were a resounding success. The programs evolved from small, narrowly focused laboratory studies to multiyear studies under field conditions and then to larger-scale, decade-long Free-Air CO<sub>2</sub> Enrichment (FACE) experiments in intact ecosystems. At each step, science questions were investigated and resolved, leading to new questions at a higher level of complexity. The FACE experiments produced many hundreds of papers; trained dozens of students; advanced the careers of many scientists within the national laboratories and universities; and, through the popular press, videos, and tours, introduced the general public to the important science questions being addressed and the methods used to answer them.

Compelling evidence from FACE and other experiments has dispelled all previous doubts about whether effects of elevated CO<sub>2</sub> on plants need consideration in global change analyses. Publications resulting from FACE research are highly cited and have been used in U.S. national assessments and Intergovernmental Panel on Climate Change (IPCC) evaluations. Operational and scientific lessons gained during the FACE experiments have inspired and are informing current DOE research, including Next-Generation Ecosystem Experiments (NGEE) in the Arctic and Tropics, DOE national laboratory scientific focus areas, and other research projects. DOE's leading science example demonstrating the power of manipulative field studies and model-data integration also continues to influence new and proposed FACE experiments in the United Kingdom, Australia, and Brazil, an impact that will continue for many years.

What was learned from these experiments? If there is a single scientific conclusion from the many years of investigation and more than \$100 million invested, it might simply be that most of the C3 plants and terrestrial ecosystems studied do respond positively to increased concentrations of atmospheric CO<sub>2</sub>. This response is due to the primary effects of CO<sub>2</sub> on photosynthesis and stomatal aperture, but many other environmental factors tend to lessen the effects of CO<sub>2</sub> on plant growth and ecosystem carbon cycling. The numerous responses described in this report clearly indicate that a single, simple conclusion to the entire DOE CO<sub>2</sub> research program will never be sufficient. As Lemon (1983) observed, "Logic tells us that ... more CO<sub>2</sub> in the atmosphere should mean



more photosynthesis. This, in turn, should mean more yield or accumulated carbon in plants. This logic is fine for beginning biology; unfortunately, nature is not that simple.”

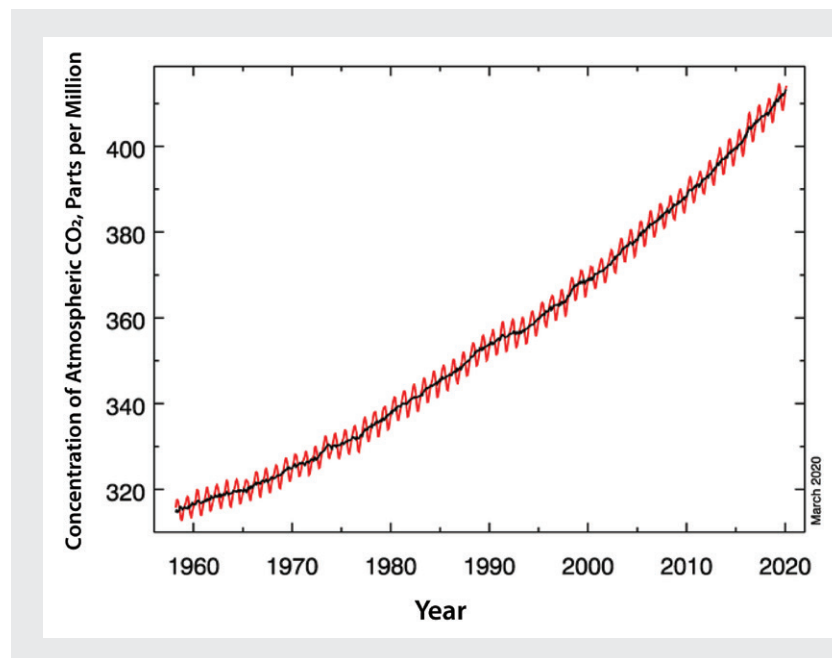
Knowing that responses to elevated CO<sub>2</sub> will vary with environmental conditions, such as soil nutrient status, drought, air pollution, and impact of herbivores, emphasizes the importance of a modeling framework that can capture these critical interactions. A noteworthy finding of DOE’s decadal programs was that environmental interactions with CO<sub>2</sub> response often were revealed without requiring multifactor experiments. Moreover, although the primary responses of a plant occur in the leaf, the experiments emphasized the importance of understanding the controls on how photosynthate is allocated to wood production relative to other plant organs and processes. Belowground responses—root production and distribution, microbial activity, and soil organic matter dynamics—often were revealed as critical to understanding how the resources needed to support a CO<sub>2</sub> response are supplied in unmanaged ecosystems, providing a potential route for increased ecosystem carbon sequestration.

Regardless of the program’s successes, looking back it is evident that many aspects of FACE could have been better implemented, but the lessons learned along the way have led to improved ongoing research projects. DOE recognized the importance of communicating clearer expectations of the outcomes and metrics for evaluating success and project lifecycles. Because the experiments described in this report developed independently, with different institutional research priorities and different funding mandates, critical cross-study measurements were not made to support the most useful comparisons across sites. Nevertheless, synthesis and modeling did become important and productive elements of the FACE studies (see Ch. 8, p. 83). The cross-site data synthesis papers are among the most cited and influential of the FACE publications. The model-data activity not only has improved understanding of terrestrial ecosystem responses to elevated atmospheric CO<sub>2</sub>, it has also identified areas for model improvements and questions for further experimental analysis, advancing a new standard for model intercomparison. A lesson learned by DOE is that long-term research programs should be started with data management, data-model integration, and the broader concepts of open science in mind. Important legacies of FACE are that coordination among models and experiments and open sharing of data are now part of the initial planning of many new research programs. Reliance on a model parameter list developed through the FACE Model-Data Synthesis (FACE-MDS) activity has become common as other experiments are initiated (e.g., Fleischer et al. 2019); the list also has helped to inform experimentalists of the need for setting up model simulations. A model intercomparison employing the FACE-MDS approach successfully generated testable predictions and guided measurements in a new FACE experiment (EucFACE) in a eucalyptus stand in Australia (Medlyn et al. 2016). DOE’s FACE approach also is guiding a FACE experiment in an old oak woodland in Birmingham, United Kingdom, and a proposed experiment in the Amazon forest of Brazil (Norby et al. 2016; Fleischer et al. 2019; Hart et al. 2019).

The plea from Mooney et al. (1991) from almost 3 decades ago for larger-scale, longer-duration manipulative experiments in each of the world’s six major biomes (i.e., tundra, boreal forest, temperate forest, tropical forest, grassland, and desert) remains

highly relevant today. Many aspects of ecosystem response to atmospheric and climatic change have not yet been addressed, and not all the critical biomes have been tested. Given the complexity of potential responses, direct experimentation on intact ecosystems must be at a large enough scale to encompass the feedbacks between biotic systems and the atmosphere and soil, and to support measurements of pools and fluxes without excessive disturbance. Manipulative experiments remain the best way to obtain the knowledge needed “to understand the role and responses of terrestrial ecosystems on our changing planet” (Mooney et al. 1991).

Good science should lead to new questions. Critical questions about ecosystem responses to increasing atmospheric CO<sub>2</sub> concentration remain, including: Are responses to elevated CO<sub>2</sub> substantially different in unstudied biomes? Do responses dissipate in mature forest stands? What are the long-term effects on demographic processes and community composition? Can CO<sub>2</sub> fertilization result in long-term increases in soil organic matter? DOE's FACE experiments provided sharper definition to these outstanding questions. As the international science community takes them on, the important contribution of DOE to ecosystem science will continue. The mandate for continued research through manipulative field studies and model-data integration is compelling: the atmospheric concentration of CO<sub>2</sub> continues to increase from 352 parts per million (ppm) at the time of the first FACE experiment in 1989 to 410 ppm today (see Fig. 10.1, this page).



**Fig. 10.1. Concentrations of Atmospheric Carbon Dioxide (CO<sub>2</sub>) Measured from the Mauna Loa Observatory, Hawaii, 1958–2020.** [Scripps Institution of Oceanography and National Oceanic and Atmospheric Administration Earth System Research Laboratory.]



## Appendix A: Resources

### Books

- Lemon, E. R. (Ed.), 1983. *CO<sub>2</sub> and Plants*. Westview Press, Boulder, Colo.
- Koch, G. W., and H. A. Mooney (Eds.), 1996. *Carbon Dioxide and Terrestrial Ecosystems*. Academic Press, San Diego.
- Karnosky, D. F., et al. (Eds.), 2001. *The Impact of Carbon Dioxide and Other Greenhouse Gases on Forest Ecosystems. International Union of Forest Research Organizations Research Series 8*. CABI Publishing, Wallingford, Conn., and New York.
- Nösberger, J., et al. (Eds.), 2006. *Managed Ecosystems and CO<sub>2</sub>: Case Studies, Processes, and Perspectives*. Ecological Studies, Vol. 187. Springer-Verlag Berlin Heidelberg, Berlin.

### Reports from the U.S. Department of Energy and the Biological and Environmental Research Advisory Committee

- BERAC. 2002. *An Evaluation of the Department of Energy's Free-Air Carbon Dioxide Enrichment (FACE) Experiments as Scientific User Facilities*. Biological and Environmental Research Advisory Committee. [[https://science.osti.gov/-/media/ber/berac/pdf/Face\\_report.pdf](https://science.osti.gov/-/media/ber/berac/pdf/Face_report.pdf)]
- BERAC. 2005. *Recommendations on the DOE Terrestrial Carbon Cycle Research Program. Subcommittee of the Biological and Environmental Research Advisory Committee*. [[https://science.osti.gov/-/media/ber/berac/pdf/Tccrp\\_report.pdf](https://science.osti.gov/-/media/ber/berac/pdf/Tccrp_report.pdf)]
- BERAC. 2006. *Report of the BERAC Subcommittee Reviewing the FACE and OTC Elevated CO<sub>2</sub> Projects in DOE*. Subcommittee of the Biological and Environmental Research Advisory Committee. [[https://science.osti.gov/-/media/ber/berac/pdf/Face\\_2006\\_report.pdf](https://science.osti.gov/-/media/ber/berac/pdf/Face_2006_report.pdf)]
- U.S. DOE. 2008. *Ecosystem Experiments: Understanding Climate Change Impacts on Ecosystems and Feedbacks to the Physical Climate*. U.S. Department of Energy Office of Science. [[https://tes.science.energy.gov/files/Ecosystem\\_experiments.pdf](https://tes.science.energy.gov/files/Ecosystem_experiments.pdf)]

### Project Websites

- FACE Engineering** — [www.bnl.gov/envsci/testgroup/face.php](http://www.bnl.gov/envsci/testgroup/face.php)
- Maricopa FACE** — [www.ltrr.arizona.edu/~sleavitt/MaricopaFACE.htm](http://www.ltrr.arizona.edu/~sleavitt/MaricopaFACE.htm)
- Duke FACE** — [web.archive.org/web/20120819160517/http://face.env.duke.edu/main.cfm](http://web.archive.org/web/20120819160517/http://face.env.duke.edu/main.cfm) (archived)
- Oak Ridge National Laboratory (ORNL) FACE** — [face.ornl.gov](http://face.ornl.gov)
- Nevada Desert FACE** — [www.dri.edu/nevada-desert-research-center/nevada-desert-face-facility](http://www.dri.edu/nevada-desert-research-center/nevada-desert-face-facility)
- Rhineland FACE** — [aspenface.mtu.edu](http://aspenface.mtu.edu)
- Salt Marsh Open-Top Chamber (OTC)** — [serc.si.edu/gcrew](http://serc.si.edu/gcrew)
- Old-Field Community Climate and Atmospheric Manipulation (OCCAM)** — [web.archive.org/web/20161115092115/http://warming.ornl.gov/OCCAM/index.html](http://web.archive.org/web/20161115092115/http://warming.ornl.gov/OCCAM/index.html) (archived)

### Spruce and Peatland Responses Under Changing Environments (SPRUCE)

- [mnspruce.ornl.gov/](http://mnspruce.ornl.gov/)
- Biodiversity, CO<sub>2</sub>, and Nitrogen (BioCON)** — [www.biocon.umn.edu](http://www.biocon.umn.edu)
- Prairie Heating and CO<sub>2</sub> Enrichment (PHACE)** — [bit.ly/2UOwkIF](http://bit.ly/2UOwkIF)
- FACE Model-Data Synthesis** — [facedata.ornl.gov/facemds/](http://facedata.ornl.gov/facemds/)

### Project Publication Lists

- FACE publications prior to 2004** — [cdiac.ess-dive.lbl.gov/programs/FACE/facepubs](http://cdiac.ess-dive.lbl.gov/programs/FACE/facepubs)
- Duke FACE** — [web.archive.org/web/20120708011212/http://face.env.duke.edu/publications.cfm](http://web.archive.org/web/20120708011212/http://face.env.duke.edu/publications.cfm) (archived)
- ORNL FACE** — [face.ornl.gov/pubs.html](http://face.ornl.gov/pubs.html)
- Nevada Desert FACE** — [www.dri.edu/component/content/article/359-nevada-desert-face-facility/5321-nevada-desert-research-center-publications](http://www.dri.edu/component/content/article/359-nevada-desert-face-facility/5321-nevada-desert-research-center-publications)
- Rhineland FACE** — [aspenface.mtu.edu/publications.htm](http://aspenface.mtu.edu/publications.htm)
- Salt Marsh and Scrub Oak OTCs** — [research.serc.si.edu/researchdata/publication\\_data\\_cfm/drake\\_pub.cfm](http://research.serc.si.edu/researchdata/publication_data_cfm/drake_pub.cfm)
- BioCON** — [www.biocon.umn.edu/publications](http://www.biocon.umn.edu/publications)
- PHACE** — [bit.ly/3aJf5Pu](http://bit.ly/3aJf5Pu)
- FACE Model-Data Synthesis** — [facedata.ornl.gov/facemds/](http://facedata.ornl.gov/facemds/)

### Project Data

- Maricopa FACE** — [library.wur.nl/ojs/index.php/ODJAR/article/view/15826](http://library.wur.nl/ojs/index.php/ODJAR/article/view/15826)
- Duke, ORNL, Nevada Desert, and Rhineland FACE**
- [facedata.ornl.gov](http://facedata.ornl.gov)
  - [facedata.ornl.gov/facemds/](http://facedata.ornl.gov/facemds/)
- BioCON**
- [cedarcreek.umn.edu/research/data/](http://cedarcreek.umn.edu/research/data/)
- PHACE**
- [datadryad.org/stash/dataset/doi:10.5061/dryad.3mf71](http://datadryad.org/stash/dataset/doi:10.5061/dryad.3mf71)
  - [www.nature.com/articles/sdata201688/tables/2](http://www.nature.com/articles/sdata201688/tables/2)
- Salt Marsh OTC** — [serc.si.edu/gcrew/CO2data](http://serc.si.edu/gcrew/CO2data)
- Scrub Oak OTC** — [data.ess-dive.lbl.gov/view/doi:10.15485/1480325](http://data.ess-dive.lbl.gov/view/doi:10.15485/1480325)
- FACE Model-Data Synthesis** — [facedata.ornl.gov/facemds/](http://facedata.ornl.gov/facemds/)

## Appendix B: References

- Adam, N. R., et al. 2000. "The Effect of CO<sub>2</sub> Enrichment on Leaf Photosynthetic Rates and Instantaneous Water Use Efficiency of *Andropogon gerardii* in the Tallgrass Prairie," *Photosynthesis Research* **65**(2), 121–29. DOI:10.1023/a:1006489919192.
- Ainsworth, E. A., and A. Rogers. 2007. "The Response of Photosynthesis and Stomatal Conductance to Rising [CO<sub>2</sub>]: Mechanisms and Environmental Interactions," *Plant Cell and Environment* **30**(3), 258–70. DOI:10.1111/j.1365-3040.2007.01641.x.
- Ainsworth, E. A., and S. P. Long. 2005. "What Have We Learned from 15 Years of Free-Air CO<sub>2</sub> Enrichment (FACE)? A Meta-Analytic Review of the Responses of Photosynthesis, Canopy Properties and Plant Production to Rising CO<sub>2</sub>," *New Phytologist* **165**(2), 351–71. DOI:10.1111/j.1469-8137.2004.01224.x.
- Ainsworth, E. A., et al. 2002. "Long-Term Response of Photosynthesis to Elevated Carbon Dioxide in a Florida Scrub-Oak Ecosystem," *Ecological Applications* **12**(5), 1267–75. DOI:10.2307/3099970.
- Allen, L. H., Jr. 1992. "Free-Air CO<sub>2</sub> Enrichment Field Experiments — An Historical Overview," *Critical Reviews in Plant Sciences* **11**(2–3), 121–34. DOI:10.1080/07352689209382334.
- Aranjuelo, I., et al. 2011. "Maintenance of C Sinks Sustains Enhanced C Assimilation During Long-Term Exposure to Elevated [CO<sub>2</sub>] in Mojave Desert Shrubs," *Oecologia* **167**(2), 339–54. DOI:10.1007/s00442-011-1996-y.
- Austin, E. E., et al. 2009. "Assessment of 10 Years of CO<sub>2</sub> Fumigation on Soil Microbial Communities and Function in a Sweetgum Plantation," *Soil Biology and Biochemistry* **41**(3), 514–20. DOI:10.1016/j.soilbio.2008.12.010.
- Bacastow, R., and C. D. Keeling. 1973. "Atmospheric Carbon Dioxide and Radiocarbon in Natural Carbon Cycle: II. Changes from A.D. 1700 to 2070 as Deduced from a Geochemical Model," *Brookhaven Symposia in Biology* **30**, 86–135. PMID: 4807349.
- Baes, C. F., et al. 1977. "Carbon Dioxide and Climate — The Uncontrolled Experiment: Possibly Severe Consequences of Growing CO<sub>2</sub> Release from Fossil Fuels Require a Much Better Understanding of the Carbon Cycle, Climate Change, and the Resulting Impacts on the Atmosphere," *American Scientist* **65**(3), 310–20.
- Ball, A. S. 1997. "Microbial Decomposition at Elevated CO<sub>2</sub> Levels: Effect of Litter Quality," *Global Change Biology* **3**(4) 379–86. DOI:10.1046/j.1365-2486.1997.t01-1-00089.x.
- BassiriRad, H., et al. 2003. "Widespread Foliage δ<sup>15</sup>N Depletion Under Elevated CO<sub>2</sub>: Inferences for the Nitrogen Cycle," *Global Change Biology* **9**(11), 1582–90. DOI:10.1046/j.1365-2486.2003.00679.x.
- Battipaglia, G., et al. 2012. "Elevated CO<sub>2</sub> Increases Tree-Level Intrinsic Water Use Efficiency: Insights from Carbon and Oxygen Isotope Analyses in Tree Rings Across Three Forest FACE Sites," *New Phytologist* **197**(2), 544–54. DOI: 10.1111/nph.12044.
- BERAC. 2006. *Report of the BERAC Subcommittee Reviewing the FACE and OTC Elevated CO<sub>2</sub> Projects in DOE*. Subcommittee of the Biological and Environmental Research Advisory Committee. [https://science.osti.gov/-/media/ber/berac/pdf/Face\_2006\_report.pdf]
- BERAC. 2005. *Recommendations on the DOE Terrestrial Carbon Cycle Research Program*. Subcommittee of the Biological and Environmental Research Advisory Committee. [https://science.osti.gov/-/media/ber/berac/pdf/Tccrp\_report.pdf]
- BERAC. 2002. *An Evaluation of the Department of Energy's Free-Air Carbon Dioxide Enrichment (FACE) Experiments as Scientific User Facilities*. Biological and Environmental Research Advisory Committee. [https://science.osti.gov/-/media/ber/berac/pdf/Face\_report.pdf]
- Billings, S. A., et al. 2003. "Effects of Elevated Carbon Dioxide on Green Leaf Tissue and Leaf Litter Quality in an Intact Mojave Desert Ecosystem," *Global Change Biology* **9**(5), 729–735. DOI:10.1046/j.1365-2486.2003.00608.x.
- BioCON (Biodiversity, CO<sub>2</sub>, and Nitrogen). 2019. The University of Minnesota. [http://www.biocon.umn.edu]
- Blumenthal, D. M., et al. 2016. "Cheatgrass Is Favored by Warming but Not CO<sub>2</sub> Enrichment in a Semi-Arid Grassland," *Global Change Biology* **22**(9), 3026–38. DOI:10.1111/gcb.13278.
- Blumenthal, D. M., et al. 2013. "Invasive Forb Benefits from Water Savings by Native Plants and Carbon Fertilization Under Elevated CO<sub>2</sub> and Warming," *New Phytologist* **200**(4), 1156–65. DOI:10.1111/nph.12459.
- Bolin, B. 1977. "Changes of Land Biota and Their Importance for Carbon Cycle," *Science* **196**(4290), 613–15. DOI:10.1126/science.196.4290.613.
- Brosi, G. B., et al. 2011. "Effects of Multiple Climate Change Factors on the Tall Fescue–Fungal Endophyte Symbiosis: Infection Frequency and Tissue Chemistry," *New Phytologist* **189**(3), 797–805. DOI:10.1111/j.1469-8137.2010.03532.x.
- Burton, A. J., et al. 2014. Impacts of Interacting Elevated Atmospheric CO<sub>2</sub> and O<sub>3</sub> on the Structure and Functioning of a Northern Forest Ecosystem: Operating and Decommissioning the Aspen FACE Project. [https://www.osti.gov/biblio/1135783/]
- Clark, N. M., et al. 2010. "The Effects of Elevated CO<sub>2</sub> on Root Respiration Rates of Two Mojave Desert Shrubs," *Global Change Biology* **16**(5), 1566–75. DOI:10.1111/j.1365-2486.2009.02075.x.
- Clark, N. M., et al. 2009. "Arbuscular Mycorrhizal Fungal Abundance in the Mojave Desert: Seasonal Dynamics and Impacts of Elevated CO<sub>2</sub>," *Journal of Arid Environments* **73**(9), 834–43. DOI:10.1016/j.jaridenv.2009.03.004.



- Comins, H. N., and R. E. McMurtrie. 1993. "Long-Term Response of Nutrient-Limited Forests to CO<sub>2</sub> Enrichment; Equilibrium Behavior of Plant-Soil Models," *Ecological Applications* **3**(4), 666–81. DOI:10.2307/1942099.
- Cotrufo, M. F., et al. 2005. "Palatability Trials on Hardwood Leaf Litter Grown Under Elevated CO<sub>2</sub>: A Stable Carbon Isotope Study," *Soil Biology & Biochemistry* **37**(6), 1105–12. DOI:10.1016/j.soilbio.2004.11.009.
- Couture, J. J., et al. 2017. "Effects of Elevated Atmospheric Carbon Dioxide and Tropospheric Ozone on Phytochemical Composition of Trembling Aspen (*Populus tremuloides*) and Paper Birch (*Betula papyrifera*)," *Journal of Chemical Ecology* **43**(1), 26–38. DOI:10.1007/s10886-016-0798-4.
- Couture, J. J., et al. 2015. "Insect Herbivory Alters Impact of Atmospheric Change on Northern Temperate Forests," *Nature Plants* **1**(3), 15016. DOI:10.1038/nplants.2015.16.
- Curtis, P. S., et al. 1990. "Elevated Atmospheric CO<sub>2</sub> Effects on Belowground Processes in C<sub>3</sub> and C<sub>4</sub> Estuarine Marsh Communities," *Ecology* **71**(5), 2001–2006. DOI:10.2307/1937608.
- Curtis, P. S., et al. 1989. "Growth and Senescence in Plant Communities Exposed to Elevated CO<sub>2</sub> Concentrations on an Estuarine Marsh," *Oecologia* **78**(1), 20–26. DOI:10.1007/bf00377193.
- Dacey, J. W. H., et al. 1994. "Stimulation of Methane Emission by Carbon Dioxide Enrichment of Marsh Vegetation," *Nature* **370**(6484), 47–49. DOI:10.1038/370047a0.
- Dahlman, R. C. 1993. "CO<sub>2</sub> and Plants: Revisited," *Vegetatio* **104**, 339–55. DOI:10.1007/bf00048164.
- Dahlman, R. C., et al. 1985. "Research on the Response of Vegetation to Elevated Atmospheric Carbon Dioxide," *Journal of Environmental Quality* **14**(1), 1–8. DOI:10.2134/jeq1985.00472425001400010001x.
- Dakora, F. D., and B. G. Drake. 2000. "Elevated CO<sub>2</sub> Stimulates Associative N<sub>2</sub> Fixation in a C<sub>3</sub> Plant of the Chesapeake Bay Wetland," *Plant Cell and Environment* **23**(9), 943–53. DOI:10.1046/j.1365-3040.2000.00610.x.
- Darbah, J. N. T., et al. 2010. "Differential Response of Aspen and Birch Trees to Heat Stress Under Elevated Carbon Dioxide," *Environmental Pollution* **158**(4), 1008–14. DOI:10.1016/j.envpol.2009.10.019.
- Davey, P. A., et al. 2004. "Respiratory Oxygen Uptake Is Not Decreased by an Instantaneous Elevation of CO<sub>2</sub>, but Is Increased with Long-Term Growth in the Field at Elevated CO<sub>2</sub>," *Plant Physiology* **134**(1), S20–27. DOI:10.1104/pp.103.030569.
- Day, F. P., et al. 2013. "The Effects of 11 yr of CO<sub>2</sub> Enrichment on Roots in a Florida Scrub-Oak Ecosystem," *New Phytologist* **200**(3), 778–87. DOI:10.1111/nph.12246.
- De Kauwe, M. G., et al. 2017. "Challenging Terrestrial Biosphere Models with Data from the Long-Term Multifactor Prairie Heating and CO<sub>2</sub> Enrichment Experiment," *Global Change Biology* **23**(9), 3623–45. DOI:10.1111/gcb.13643.
- De Kauwe, M. G., et al. 2014. "Where Does the Carbon Go? A Model-Data Intercomparison of Vegetation Carbon Allocation and Turnover Processes at Two Temperate Forest Free-Air CO<sub>2</sub> Enrichment Sites," *New Phytologist* **203**(3), 883–99. DOI: 10.1111/nph.12847.
- De Kauwe, M. G., et al. 2013. "Forest Water Use and Water Use Efficiency at Elevated CO<sub>2</sub>: A Model-Data Intercomparison at Two Contrasting Temperate Forest FACE Sites," *Global Change Biology* **19**(6), 1759–79. DOI:10.1111/gcb.12164.
- Deng, Y., et al. 2016. "Elevated Carbon Dioxide Accelerates the Spatial Turnover of Soil Microbial Communities," *Global Change Biology* **22**(2), 957–64. DOI:10.1111/gcb.13098.
- Dermody, O., et al. 2007. "How Do Elevated CO<sub>2</sub>, Warming, and Reduced Precipitation Interact to Affect Soil Moisture and LAI in an Old Field Ecosystem?" *Plant and Soil* **301**(1–2), 255–66. DOI:10.1007/s11104-007-9443-x.
- Dickson, R. E., et al. 2000. *Forest Atmosphere Carbon Transfer Storage-II (FACTS-II) — The Aspen Free-Air CO<sub>2</sub> and O<sub>3</sub> Enrichment (FACE) Project: An Overview*, General Technical Report NC-214. U.S. Department of Agriculture Forest Service North Central Research Station. St. Paul, Minn. 68 pp.
- Dijkstra, F. A., et al. 2012. "Climate Change Alters Stoichiometry of Phosphorus and Nitrogen in a Semiarid Grassland," *New Phytologist* **196**(3), 807–15. DOI:10.1111/j.1469-8137.2012.04349.x.
- Dijkstra, F. A., et al. 2010. "Contrasting Effects of Elevated CO<sub>2</sub> and Warming on Nitrogen Cycling in a Semiarid Grassland," *New Phytologist* **187**(2), 426–37. DOI:10.1111/j.1469-8137.2010.03293.x.
- Dijkstra, P., et al. 2002. "Elevated Atmospheric CO<sub>2</sub> Stimulates Aboveground Biomass in a Fire-Regenerated Scrub-Oak Ecosystem," *Global Change Biology* **8**(1), 90–103. DOI:10.1046/j.1354-1013.2001.00458.x.
- Dilustro, J. J., et al. 2002. "Abundance, Production, and Mortality of Fine Roots Under Elevated Atmospheric CO<sub>2</sub> in an Oak-Scrub Ecosystem," *Environmental and Experimental Botany* **48**(2), 149–59. DOI:10.1016/S0098-8472(02)00020-5.
- Dore, S., et al. 2003. "Cross Validation of Open-Top Chamber and Eddy Covariance Measurements of Ecosystem CO<sub>2</sub> Exchange in a Florida Scrub-Oak Ecosystem," *Global Change Biology* **9**(1), 84–95. DOI:10.1046/j.1365-2486.2003.00561.x.
- Drake, B. G. 2014. "Rising Sea Level, Temperature, and Precipitation Impact Plant and Ecosystem Responses to Elevated CO<sub>2</sub> on a Chesapeake Bay Wetland: Review of a 28-Year Study," *Global Change Biology* **20**(11), 3329–43. DOI:10.1111/gcb.12631.
- Drake, B. G., et al. 1985. "2. Methods of Exposing Plants to Elevated CO<sub>2</sub>," DOE/ER-0238. In *Direct Effects of Increasing Carbon Dioxide on Vegetation*. Eds. Strain, B. R., and J. D. Cure. U.S. Department of Energy Office of Energy Research. pp. 11–32. [https://www.osti.gov/servlets/purl/6134866#page=38]

- Drake, J. E., et al. 2011. "Increases in the Flux of Carbon Belowground Stimulate Nitrogen Uptake and Sustain the Long-Term Enhancement of Forest Productivity Under Elevated CO<sub>2</sub>," *Ecology Letters* **14**(4), 349–57. DOI:10.1111/j.1461-0248.2011.01593.x.
- Dusenge, M. E., et al. 2019. "Plant Carbon Metabolism and Climate Change: Elevated CO<sub>2</sub> and Temperature Impacts on Photosynthesis, Photorespiration and Respiration," *New Phytologist* **221**(1), 32–49. DOI:10.1111/nph.15283.
- Duval, B. D., et al. 2013. "Element Pool Changes within a Scrub-Oak Ecosystem After 11 Years of Exposure to Elevated CO<sub>2</sub>," *PLOS One* **8**(5), e64386. DOI:10.1371/journal.pone.0064386.
- Edwards, N. T., et al. 2002. "Stem Respiration Increases in CO<sub>2</sub>-Enriched Sweetgum Trees," *New Phytologist* **155**(2), 239–48. DOI:10.1046/j.1469-8137.2002.00458.x.
- Ekdahl, C. A., and Keeling, C. D. 1973. "Atmospheric Carbon Dioxide and Radiocarbon in the Natural Carbon Cycle. I. Quantitative Deductions from Records at Mauna Loa Observatory and at the South Pole," CONF-720510. In *Carbon and the Biosphere*. Eds. Woodwell, G. M., and Pecan, E. V. U.S. Atomic Energy Commission, Springfield, Va. *Brookhaven Symposia in Biology* **30**, 51–85.
- Elliott, W. P., and L. Machta. 1979. *Carbon Dioxide Effects: Research and Assessment Program. Workshop on the Global Effects of Carbon Dioxide from Fossil Fuels*. U.S. Department of Energy. [https://www.osti.gov/biblio/6385084/]
- Ellsworth, D. S., et al. 2017. "Elevated CO<sub>2</sub> Does Not Increase Eucalypt Forest Productivity on a Low-Phosphorus Soil," *Nature Climate Change* **7**(4), 279–82. DOI:10.1038/nclimate3235.
- Ellsworth, D. S., et al. 2012. "Elevated CO<sub>2</sub> Affects Photosynthetic Responses in Canopy Pine and Subcanopy Deciduous Trees over 10 Years: A Synthesis from Duke FACE," *Global Change Biology* **18**(1), 223–42. DOI:10.1111/j.1365-2486.2011.02505.x.
- Ellsworth, D. S., et al. 2004. "Photosynthesis, Carboxylation and Leaf Nitrogen Responses of 16 Species to Elevated pCO<sub>2</sub> Across Four Free-Air CO<sub>2</sub> Enrichment Experiments in Forest, Grassland and Desert," *Global Change Biology* **10**(12), 2121–38. DOI:10.1111/j.1365-2486.2004.00867.x.
- Evans, R. D., et al. 2014. "Greater Ecosystem Carbon in the Mojave Desert After 10 Years Exposure to Elevated CO<sub>2</sub>," *Nature Climate Change* **4**(5), 394–97. DOI:10.1038/nclimate2184.
- Ferguson, S. D., and R. S. Nowak. 2011. "Transitory Effects of Elevated Atmospheric CO<sub>2</sub> on Fine Root Dynamics in an Arid Ecosystem do not Increase Long-Term Soil Carbon Input from Fine Root Litter," *New Phytologist* **190**(4), 953–67. DOI:10.1111/j.1469-8137.2011.03654.x.
- Field, C. B. 2001. "Plant Physiology of the 'Missing' Carbon Sink," *Plant Physiology* **125**(1), 25–28. DOI:10.1104/pp.125.1.25.
- Finzi, A. C., et al. 2007. "Increases in Nitrogen Uptake Rather Than Nitrogen-Use Efficiency Support Higher Rates of Temperate Forest Productivity Under Elevated CO<sub>2</sub>," *Proceedings of the National Academy of Sciences USA* **104**(35), 14014–19. DOI:10.1073/pnas.0706518104.
- Finzi, A. C., et al. 2006. "Progressive Nitrogen Limitation of Ecosystem Processes Under Elevated CO<sub>2</sub> in a Warm-Temperate Forest," *Ecology* **87**(1), 15–25. DOI:10.1890/04-1748.
- Finzi, A. C., et al. 2002. "The Nitrogen Budget of a Pine Forest Under Free Air CO<sub>2</sub> Enrichment," *Oecologia* **132**(4), 567–78. DOI:10.1007/s00442-002-0996-3.
- Fleischer, K., et al. 2019. "Amazon Forest Response to CO<sub>2</sub> Fertilization Dependent on Plant Phosphorus Acquisition," *Nature Geoscience* **12**(9), 736–41. DOI:10.1038/s41561-019-0404-9.
- Garten, C. T., Jr., et al. 2011. "Litterfall <sup>15</sup>N Abundance Indicates Declining Soil Nitrogen Availability in a Free-Air CO<sub>2</sub> Enrichment Experiment," *Ecology* **92**(1), 133–39. DOI:10.1890/10-0293.1.
- Garten, C. T., Jr., et al. 2009. "Soil Moisture Surpasses Elevated CO<sub>2</sub> and Temperature as a Control on Soil Carbon Dynamics in a Multi-Factor Climate Change Experiment," *Plant and Soil* **319**(1–2), 85–94. DOI:10.1007/s11104-008-9851-6.
- Garten, C. T., Jr., et al. 2008. "Role of N<sub>2</sub>-Fixation in Constructed Old-Field Communities Under Different Regimes of CO<sub>2</sub>, Temperature, and Water Availability," *Ecosystems* **11**(1), 125–37. DOI:10.1007/s10021-007-9112-1.
- George, K., et al. 2003. "Fine-Root Respiration in a Loblolly Pine and Sweetgum Forest Growing in Elevated CO<sub>2</sub>," *New Phytologist* **160**(3), 511–22. DOI:10.1046/j.1469-8137.2003.00911.x.
- Gulke, N. E., et al. 1990. "Carbon Balance in Tussock Tundra Under Ambient and Elevated Atmospheric CO<sub>2</sub>," *Oecologia* **83**, 484–94. DOI:10.1007/BF00317199.
- Gunderson, C. A., et al. 2002. "Environmental and Stomatal Control of Photosynthetic Enhancement in the Canopy of a Sweetgum (*Liquidambar styraciflua* L.) Plantation During 3 Years of CO<sub>2</sub> Enrichment," *Plant Cell and Environment* **25**(3), 379–93. DOI:10.1046/j.0016-8025.2001.00816.x.
- Hamerlynck, E. P., et al. 2000. "Photosynthetic Responses of *Larrea tridentata* to a Step-Increase in Atmospheric CO<sub>2</sub> at the Nevada Desert FACE Facility," *Journal of Arid Environments* **44**(4), 425–36. DOI:10.1006/jare.1999.0615.
- Hanson, P. J., et al. 2020. "Rapid Net Carbon Loss from a Whole-Ecosystem Warmed Peatland," *AGU Advances*. Submitted.
- Hanson, P. J., et al. 2017. "Attaining Whole-Ecosystem Warming Using Air and Deep-Soil Heating Methods with an Elevated CO<sub>2</sub> Atmosphere," *Biogeosciences* **14**(4), 861–83. DOI:10.5194/bg-14-861-2017.
- Hanson P. J., et al. 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 Biology* **11**(9), 1402–23. DOI:10.1111/j.1365-2486.2005.00991.x
- Hart, K. M., et al. 2019. "Characteristics of Free Air Carbon Dioxide Enrichment of a Northern Temperate Mature Forest," *Global Change Biology* **26**(3), 1023–37. DOI: 10.1111/gcb.14786.

- Haworth, M., et al. 2016. “Has the Impact of Rising CO<sub>2</sub> on Plants Been Exaggerated by Meta-Analysis of Free Air CO<sub>2</sub> Enrichment Studies?” *Frontiers in Plant Science* **7**, 1153. DOI:10.3389/fpls.2016.01153.
- Hendrey, G. R., et al. 1999. “A Free-Air Enrichment System for Exposing Tall Forest Vegetation to Elevated Atmospheric CO<sub>2</sub>,” *Global Change Biology* **5**(3), 293–309. DOI:10.1046/j.1365-2486.1999.00228.x.
- Hendrey, G. R., et al. 1993. “Free Air Carbon-Dioxide Enrichment: Development, Progress, Results,” *Vegetatio* **104**, 17–31. DOI:10.1007/bf00048142.
- Hickler, T., et al. 2008. “CO<sub>2</sub> Fertilization in Temperate FACE Experiments not Representative of Boreal and Tropical Forests,” *Global Change Biology* **14**(7), 1531–42. DOI: 10.1111/j.1365-2486.2008.01598.x.
- Hockaday, W. C., et al. 2015. “Forest Soil Carbon Oxidation State and Oxidative Ratio Responses to Elevated CO<sub>2</sub>,” *Journal of Geophysical Research—Biogeosciences* **120**(9), 1797–1811. DOI:10.1002/2015jg003010.
- Hopple, A. M., et al. 2020. “Massive Peatland Carbon Banks Vulnerable to Rising Temperatures,” *Nature Communications*. Accepted.
- Housman, D. C., et al. 2006. “Increases in Desert Shrub Productivity Under Elevated Carbon Dioxide Vary with Water Availability,” *Ecosystems* **9**(3), 374–85. DOI:10.1007/s10021-005-0124-4.
- Hungate, B. A., et al. 2013. “Cumulative Response of Ecosystem Carbon and Nitrogen Stocks to Chronic CO<sub>2</sub> Exposure in a Subtropical Oak Woodland,” *New Phytologist* **200**(3), 753–66. DOI:10.1111/nph.12333.
- Hungate, B. A., et al. 2006. “Nitrogen Cycling During Seven Years of Atmospheric CO<sub>2</sub> Enrichment in a Scrub Oak Woodland,” *Ecology* **87**(1), 26–40. DOI:10.1890/04-1732.
- Hungate, B. A., et al. 2002. “Evapotranspiration and Soil Water Content in a Scrub-Oak Woodland Under Carbon Dioxide Enrichment,” *Global Change Biology* **8**(3), 289–98. DOI:10.1046/j.1365-2486.2002.00468.x.
- Huxman, T. E., and S. D. Smith. 2001. “Photosynthesis in an Invasive Grass and Native Forb at Elevated CO<sub>2</sub> During an El Niño Year in the Mojave Desert,” *Oecologia* **128**(2), 193–201. DOI:10.1007/s004420100658.
- Huxman, T. E., et al. 1998. “Photosynthetic Down-Regulation in *Larrea tridentata* Exposed to Elevated Atmospheric CO<sub>2</sub>: Interaction with Drought Under Glasshouse and Field (FACE) Exposure,” *Plant Cell and Environment* **21**(11), 1153–61. DOI:10.1046/j.1365-3040.1998.00379.x.
- Hymus, G. J., et al. 2003. “Effects of Elevated Atmospheric CO<sub>2</sub> on Net Ecosystem CO<sub>2</sub> Exchange of a Scrub-Oak Ecosystem,” *Global Change Biology* **9**(12), 1802–12. DOI:10.1111/j.1365-2486.2003.00675.x.
- Hymus, G. J., et al. 2002a. “Acclimation of Photosynthesis and Respiration to Elevated Atmospheric CO<sub>2</sub> in Two Scrub Oaks,” *Global Change Biology* **8**(4), 317–28. DOI:10.1046/j.1354-1013.2001.00472.x.
- Hymus, G. J., et al. 2002b. “Seasonal Variability in the Effect of Elevated CO<sub>2</sub> on Ecosystem Leaf Area Index in a Scrub-Oak Ecosystem,” *Global Change Biology* **8**(10), 931–40. DOI:10.1046/j.1365-2486.2002.00526.x.
- Iversen, C. M. 2010. “Digging Deeper: Fine-Root Responses to Rising Atmospheric CO<sub>2</sub> Concentration in Forested Ecosystems,” *New Phytologist* **186**(2), 346–57. DOI:10.1111/j.1469-8137.2009.03122.x.
- Iversen, C. M., and R. J. Norby. 2008. “Nitrogen Limitation in a Sweetgum Plantation: Implications for Carbon Allocation and Storage,” *Canadian Journal of Forest Research* **38**(5), 1021–32. DOI:10.1139/x07-213.
- Iversen, C. M., et al. 2012. “Soil Carbon and Nitrogen Cycling and Storage Throughout the Soil Profile in a Sweetgum Plantation After 11 Years of CO<sub>2</sub>-Enrichment,” *Global Change Biology* **18**(5), 1684–97. DOI:10.1111/j.1365-2486.2012.02643.x.
- Iversen, C. M., et al. 2008. “CO<sub>2</sub> Enrichment Increases Carbon and Nitrogen Input from Fine Roots in a Deciduous Forest,” *New Phytologist* **179**(3), 837–47. DOI:10.1111/j.1469-8137.2008.02516.x.
- Jacob, J., et al. 1995. “Acclimation of Photosynthesis in Relation to Rubisco and Non-Structural Carbohydrate Contents and *In Situ* Carboxylase Activity in *Scirpus olneyi* Grown at Elevated CO<sub>2</sub> in the Field,” *Plant, Cell, & Environment* **18**(8), 875–84. DOI:10.1111/j.1365-3040.1995.tb00596.x.
- Jastrow, J. D., et al. 2005. “Elevated Atmospheric Carbon Dioxide Increases Soil Carbon,” *Global Change Biology* **11**(12), 2057–64. DOI:10.1111/j.1365-2486.2005.01077.x.
- Jiang, M. K., et al. 2019. “Towards a More Physiological Representation of Vegetation Phosphorus Processes in Land Surface Models,” *New Phytologist* **222**(3), 1223–29. DOI:10.1111/nph.15688.
- Jin, V. L., and R. D. Evans. 2010. “Elevated CO<sub>2</sub> Increases Plant Uptake of Organic and Inorganic N in the Desert Shrub *Larrea tridentata*,” *Oecologia* **163**(1), 257–66. DOI:10.1007/s00442-010-1562-z.
- Jin, V. L., and R. D. Evans. 2007. “Elevated CO<sub>2</sub> Increases Microbial Carbon Substrate Use and Nitrogen Cycling in Mojave Desert Soils,” *Global Change Biology* **13**(2), 452–65. DOI:10.1111/j.1365-2486.2006.01308.x.
- Johnson, D. W., et al. 2004. “Effects of Elevated CO<sub>2</sub> on Nutrient Cycling in a Sweetgum Plantation,” *Biogeochemistry* **69**(3), 379–403. DOI:10.1023/B:BI0G.0000031054.19158.7c.
- Johnson, D. W., et al. 2001. “Effects of Elevated Carbon Dioxide on Soils in a Florida Scrub Oak Ecosystem,” *Journal of Environmental Quality* **30**(2), 501–507. DOI:10.2134/jeq2001.302501x.
- Jordan, D. N., et al. 1999. “Biotic, Abiotic and Performance Aspects of the Nevada Desert Free-Air CO<sub>2</sub> Enrichment (FACE) Facility,” *Global Change Biology* **5**(6), 659–68. DOI:10.1046/j.1365-2486.1999.00255.x.



- Kardol, P., et al. 2011. "Climate Change Effects on Soil Microarthropod Abundance and Community Structure," *Applied Soil Ecology* **47**(1), 37–44. DOI:10.1016/j.apsoil.2010.11.001.
- Kardol, P., et al. 2010. "Climate Change Effects on Plant Biomass Alter Dominance Patterns and Community Evenness in an Experimental Old-Field Ecosystem," *Global Change Biology* **16**(10), 2676–87. DOI:10.1111/j.1365-2486.2010.02162.x.
- Karnosky, D. F., and K. S. Pregitzer. 2006. "Impacts of Elevated Atmospheric CO<sub>2</sub> and O<sub>3</sub> on Northern Temperate Forest Ecosystems: Results from the Aspen FACE Experiment." In *Ecological Studies, Vol. 187: Managed Ecosystems and CO<sub>2</sub>: Case Studies, Processes, and Perspectives*, pp. 213–29. Eds. Nösberger, J., et al. Springer-Verlag, Berlin and Heidelberg.
- Keeling, C. D. 1960. "The Concentration and Isotopic Abundances of Carbon Dioxide in the Atmosphere," *Tellus* **12**(2), 200–203. DOI:10.3402/tellusa.v12i2.9366.
- Kets, K., et al. 2010. "Diurnal Changes in Photosynthetic Parameters of *Populus tremuloides*, Modulated by Elevated Concentrations of CO<sub>2</sub> and/or O<sub>3</sub> and Daily Climatic Variation," *Environmental Pollution* **158**(4), 1000–1007. DOI:10.1016/j.envpol.2009.09.001.
- Kim, D., et al. 2016. "Response to CO<sub>2</sub> Enrichment of Understory Vegetation in the Shade of Forests," *Global Change Biology* **22**(2), 944–56. DOI:10.1111/gcb.13126.
- Kim, K., et al. 2015. "Chemical and Anatomical Changes in *Liquidambar styraciflua* L. Xylem After Long Term Exposure to Elevated CO<sub>2</sub>," *Environmental Pollution* **198**, 179–85. DOI:10.1016/j.envpol.2015.01.006.
- Kimball, B. A. 2016. "Crop Responses to Elevated CO<sub>2</sub> and Interactions with H<sub>2</sub>O, N, and Temperature," *Current Opinion in Plant Biology* **31**, 36–43. DOI:10.1016/j.pbi.2016.03.006.
- Kimball, B. A. 2006. "3. The Effects of Free-Air [CO<sub>2</sub>] Enrichment of Cotton, Wheat, and Sorghum." In *Ecological Studies, Vol 187: Managed Ecosystems and CO<sub>2</sub>: Case Studies, Processes, and Perspectives*, pp. 47–70. Eds. Nösberger, J., et al. Springer-Verlag, Berlin and Heidelberg.
- Kimball, B. A., et al. 2017. "Data from the Arizona FACE (Free-Air CO<sub>2</sub> Enrichment) Experiments on Wheat at Ample and Limiting Levels of Water and Nitrogen," *Open Data Journal for Agricultural Research* **3**, 29–38.
- Kimball, B. A., et al. 2008. "Infrared Heater Arrays for Warming Ecosystem Field Plots," *Global Change Biology* **14**(2), 309–20. DOI:10.1111/j.1365-2486.2007.01486.x.
- Kimball, B. A., et al. 1997. "Comparisons of Responses of Vegetation to Elevated CO<sub>2</sub> in Free-Air and Open-Top Chamber Facilities." In *Advances in Carbon Dioxide Effects Research. American Society of Agronomy (ASA) Special Publication 61*. Eds. Allen, L. H., Jr., et al. ASA; Crop Science Society of America; Soil Science Society of America, Madison, Wis. pp. 113–30. DOI:10.2134/asapecpub61.c5.
- King, J. S., et al. 2005. "Tropospheric O<sub>3</sub> Compromises Net Primary Production in Young Stands of Trembling Aspen, Paper Birch and Sugar Maple in Response to Elevated Atmospheric CO<sub>2</sub>," *New Phytologist* **168**(3), 623–36. DOI:10.1111/j.1469-8137.2005.01557.x.
- King, J. S., et al. 2004. "A Multiyear Synthesis of Soil Respiration Responses to Elevated Atmospheric CO<sub>2</sub> from Four Forest FACE Experiments," *Global Change Biology* **10**(6), 1027–42. DOI:10.1111/j.1529-8817.2003.00789.x.
- King, J. S., et al. 2001. "Fine-Root Biomass and Fluxes of Soil Carbon in Young Stands of Paper Birch and Trembling Aspen as Affected by Elevated Atmospheric CO<sub>2</sub> and Tropospheric O<sub>3</sub>," *Oecologia* **128**(2), 237–50. DOI:10.1007/s004420100656.
- Kramer, P. J. 1981. "Carbon Dioxide Concentration, Photosynthesis, and Dry-Matter Production," *Bioscience* **31**(1), 29–33. DOI:10.2307/1308175.
- Kuzyakov, Y., et al. 2019. "Review and Synthesis of the Effects of Elevated Atmospheric CO<sub>2</sub> on Soil Processes: No Changes in Pools, but Increased Fluxes and Accelerated Cycles," *Soil Biology & Biochemistry* **128**, 66–78. DOI:10.1016/j.soilbio.2018.10.005.
- Langley, J. A., et al. 2009. "Priming Depletes Soil Carbon and Releases Nitrogen in a Scrub-Oak Ecosystem Exposed to Elevated CO<sub>2</sub>," *Soil Biology & Biochemistry* **41**(1), 54–60. DOI:10.1016/j.soilbio.2008.09.016.
- Leakey, A. D. B., et al. 2009. "Elevated CO<sub>2</sub> Effects on Plant Carbon, Nitrogen, and Water Relations: Six Important Lessons from FACE," *Journal of Experimental Botany* **60**(10), 2859–76. DOI:10.1093/jxb/erp096.
- Leavitt, S. W., et al. 2001. "Stable-Carbon Isotopes and Soil Organic Carbon in Wheat Under CO<sub>2</sub> Enrichment," *New Phytologist* **150**(2), 305–14. DOI:10.1046/j.1469-8137.2001.00113.x.
- LeCain, D., et al. 2015. "Microclimatic Performance of a Free-Air Warming and CO<sub>2</sub> Enrichment Experiment in Windy Wyoming, USA," *PLOS ONE* **10**(2), e0116834. DOI:10.1371/journal.pone.0116834.
- Ledford, H. 2008. "Forestry Carbon Dioxide Projects to Close Down," *Nature* **456**(7220), 289. DOI: 10.1038/456289a.
- Lemon, E. R. Ed. 1983. *CO<sub>2</sub> and Plants: The Response of Plants to Rising Levels of Atmospheric Carbon Dioxide. AAAS Selected Symposium 84*. Westview Press, Boulder, Colo. 280 pp.
- Lewin, K. F., et al. 1994. "Design and Application of a Free-Air Carbon Dioxide Enrichment Facility," *Agricultural and Forest Meteorology* **70**(1–4), 15–29. DOI:10.1016/0168-1923(94)90045-0.
- Li, J. H., et al. 2010. "Evapotranspiration and Water Use Efficiency in a Chesapeake Bay Wetland Under Carbon Dioxide Enrichment," *Global Change Biology* **16**(1), 234–45. DOI:10.1111/j.1365-2486.2009.01941.x.

- Li, J. H., et al. 2003. "Direct and Indirect Effects of Elevated CO<sub>2</sub> on Transpiration from *Quercus myrtifolia* in a Scrub-Oak Ecosystem," *Global Change Biology* **9**(1), 96–105. DOI:10.1046/j.1365-2486.2003.00557.x.
- Lichter, J., et al. 2008. "Soil Carbon Sequestration in a Pine Forest After 9 Years of Atmospheric CO<sub>2</sub> Enrichment," *Global Change Biology* **14**(12), 2910–22. DOI:10.1111/j.1365-2486.2008.01701.x.
- Luo, Y., et al. 2011. "Coordinated Approaches to Quantify Long-Term Ecosystem Dynamics in Response to Global Change," *Global Change Biology* **17**(2), 843–54. DOI:10.1111/j.1365-2486.2010.02265.x.
- Luo, Y., et al. 2004. "Progressive Nitrogen Limitation of Ecosystem Responses to Rising Atmospheric Carbon Dioxide," *Bioscience* **54**(8), 731–39. DOI:10.1641/0006-3568(2004)054[0731:pnloer]2.0.co;2.
- Luo, Y., et al. 2003. "Sustainability of Terrestrial Carbon Sequestration: A Case Study in Duke Forest with Inversion Approach," *Global Biogeochemical Cycles* **17**(1), 1021. DOI:10.1029/2002gb001923.
- Luxmoore, R. J. 1981. "CO<sub>2</sub> and Phytomass," *Bioscience* **31**(9), 626. DOI:10.2307/1308630.
- Lynch, D. J., et al. 2013. "Stored Carbon Partly Fuels Fine-Root Respiration but Is Not Used for Production of New Fine Roots," *New Phytologist* **199**(2), 420–30. DOI:10.1111/nph.12290.
- Marsh, A. S., et al. 2005. "Effect of Elevated CO<sub>2</sub> on Carbon Pools and Fluxes in a Brackish Marsh," *Estuaries* **28**(5), 694–704. DOI:10.1007/bf02732908.
- Matamala, R., and W. H. Schlesinger. 2000. "Effects of Elevated Atmospheric CO<sub>2</sub> on Fine Root Production and Activity in an Intact Temperate Forest Ecosystem," *Global Change Biology* **6**(8), 967–79. DOI:10.1046/j.1365-2486.2000.00374.x.
- Matamala, R., and B. G. Drake. 1999. "The Influence of Atmospheric CO<sub>2</sub> Enrichment on Plant-Soil Nitrogen Interactions in a Wetland Plant Community on the Chesapeake Bay," *Plant and Soil* **210**(1), 93–101. DOI:10.1023/a:1004690220705.
- Matamala, R., et al. 2003. "Impacts of Fine Root Turnover on Forest NPP and Soil C Sequestration Potential," *Science* **302**(5649), 1385–87. DOI:10.1126/science.1089543.
- Matthews, H. D. 2007. "Implications of CO<sub>2</sub> Fertilization for Future Climate Change in a Coupled Climate-Carbon Model," *Global Change Biology* **13**(5), 1068–78. DOI:10.1111/j.1365-2486.2007.01343.x.
- McCarthy, H. R., et al. 2010. "Re-Assessment of Plant Carbon Dynamics at the Duke Free-Air CO<sub>2</sub> Enrichment Site: Interactions of Atmospheric CO<sub>2</sub> with Nitrogen and Water Availability over Stand Development," *New Phytologist* **185**(2), 514–28. DOI:10.1111/j.1469-8137.2009.03078.x.
- McCarthy, H. R., et al. 2007. "Temporal Dynamics and Spatial Variability in the Enhancement of Canopy Leaf Area Under Elevated Atmospheric CO<sub>2</sub>," *Global Change Biology* **13**(12), 2479–97. DOI:10.1111/j.1365-2486.2007.01455.x.
- McCarthy, H. R., et al. 2006a. "Canopy Leaf Area Constrains CO<sub>2</sub>-Induced Enhancement of Productivity and Partitioning Among Aboveground Carbon Pools," *Proceedings of the National Academy of Sciences USA* **103**(51), 19356–61. DOI:10.1073/pnas.0609448103.
- McCarthy, H. R., et al. 2006b. "Interaction of Ice Storms and Management Practices on Current Carbon Sequestration in Forests with Potential Mitigation Under Future CO<sub>2</sub> Atmosphere," *Journal of Geophysical Research—Atmospheres* **111**(D15), D15103. DOI:10.1029/2005jd006428.
- McLeod, A. R., et al. 1985. "Open-Air Fumigation of Field Crops: Criteria and Design for a New Experimental System," *Atmospheric Environment* **19**(10), 1639–49. DOI:10.1016/0004-6981(85)90216-1.
- McMurtrie, R. E., et al. 2012. "Plant Root Distributions and Nitrogen Uptake Predicted by a Hypothesis of Optimal Root Foraging," *Ecology and Evolution* **2**(6), 1235–50. DOI:10.1002/ece3.266.
- Medlyn, B. E., et al. 2016. "Using Models to Guide Field Experiments: A Priori Predictions for the CO<sub>2</sub> Response of a Nutrient- and Water-Limited Native Eucalypt Woodland," *Global Change Biology* **22**(8), 2834–51. DOI:10.1111/gcb.13268.
- Medlyn, B. E., et al. 2015. "Using Ecosystem Experiments to Improve Vegetation Models," *Nature Climate Change* **5**(6), 528–34. DOI:10.1038/nclimate2621.
- Miglietta, F., et al. 2001. "Free-Air CO<sub>2</sub> Enrichment (FACE) of a Poplar Plantation: The POPFACE Fumigation System," *New Phytologist* **150**(2), 465–76. DOI:10.1046/j.1469-8137.2001.00115.x.
- Monson, R. K., et al. 2007. "Isoprene Emission from Terrestrial Ecosystems in Response to Global Change: Minding the Gap Between Models and Observations," *Philosophical Transactions of the Royal Society A—Mathematical Physical and Engineering Sciences* **365**(1856), 1677–95. DOI:10.1098/rsta.2007.2038.
- Mooney, H. A., et al. 1991. "Predicting Ecosystem Responses to Elevated CO<sub>2</sub> Concentrations: What Has Been Learned from Laboratory Experiments on Plant Physiology and Field Observations?" *Bioscience* **41**(2), 96–104. DOI:10.2307/1311562.
- Moore, D. J. P., et al. 2006. "Annual Basal Area Increment and Growth Duration of *Pinus taeda* in Response to Eight Years of Free-Air Carbon Dioxide Enrichment," *Global Change Biology* **12**(8), 1367–77. DOI:10.1111/j.1365-2486.2006.01189.x.
- Morgan, J. A., et al. 2011. "C4 Grasses Prosper as Carbon Dioxide Eliminates Desiccation in Warmed Semi-Arid Grassland," *Nature* **476**(7359), 202–205. DOI:10.1038/nature10274.
- Morris, J. T., et al. 2016. "Contributions of Organic and Inorganic Matter to Sediment Volume and Accretion in Tidal Wetlands at Steady State," *Earths Future* **4**(4), 110–21. DOI:10.1002/2015ef000334.
- Mueller, K. E., et al. 2016. "Impacts of Warming and Elevated CO<sub>2</sub> on a Semi-Arid Grassland Are Non-Additive, Shift with Precipitation, and Reverse over Time," *Ecology Letters* **19**(8), 956–66. DOI:10.1111/ele.12634.



- Natali, S. M., et al. 2009. "Effects of Elevated Carbon Dioxide and Nitrogen Fertilization on Nitrate Reductase Activity in Sweetgum and Loblolly Pine Trees in Two Temperate Forests," *Plant and Soil* **314**(1–2), 197–210. DOI:10.1007/s11104-008-9718-x.
- Natali, S. M., et al. 2008. "Increased Mercury in Forest Soils Under Elevated Carbon Dioxide," *Oecologia* **158**(2), 343–54. DOI:10.1007/s00442-008-1135-6.
- Naumburg, E., et al. 2004. "Photosynthetic Responses of *Larrea tridentata* to Seasonal Temperature Extremes Under Elevated CO<sub>2</sub>," *New Phytologist* **162**(2), 323–30. DOI:10.1111/j.1469-8137.2004.01023.x.
- Naumburg, E., et al. 2003. "Photosynthetic Responses of Mojave Desert Shrubs to Free Air CO<sub>2</sub> Enrichment Are Greatest During Wet Years," *Global Change Biology* **9**(2), 276–85. DOI:10.1046/j.1365-2486.2003.00580.x.
- Newingham, B. A., et al. 2013. "No Cumulative Effect of 10 Years of Elevated CO<sub>2</sub> on Perennial Plant Biomass Components in the Mojave Desert," *Global Change Biology* **19**(7), 2168–81. DOI:10.1111/gcb.12177.
- Nguyen, L. M., et al. 2011. "Effects of Elevated Atmospheric CO<sub>2</sub> on Rhizosphere Soil Microbial Communities in a Mojave Desert Ecosystem," *Journal of Arid Environments* **75**(10), 917–25. DOI:10.1016/j.jaridenv.2011.04.028.
- Norby, R. J., and D. R. Zak. 2011. "Ecological Lessons from Free-Air CO<sub>2</sub> Enrichment (FACE) Experiments." *Annual Review of Ecology, Evolution, and Systematics* **42**(1), 181–203. Eds. Futuyma, D. J. et al.
- Norby, R. J., et al. 2019. "Rapid Loss of an Ecosystem Engineer: *Sphagnum* Decline in an Experimentally Warmed Bog," *Ecology and Evolution* **9**(22), 12571–85. DOI:10.1002/ece3.5722.
- Norby, R. J., et al. 2017. "Informing Models Through Empirical Relationships Between Foliar Phosphorus, Nitrogen and Photosynthesis Across Diverse Woody Species in Tropical Forests of Panama," *New Phytologist* **214**(4), 1425–37. DOI:10.1111/nph.14319.
- Norby, R. J., et al. 2016. "Model-Data Synthesis for the Next Generation of Forest Free-Air CO<sub>2</sub> Enrichment (FACE) Experiments," *New Phytologist* **209**(1), 17–28. DOI:10.1111/nph.13593.
- Norby, R. J., et al. 2010. "CO<sub>2</sub> Enhancement of Forest Productivity Constrained by Limited Nitrogen Availability," *Proceedings of the National Academy of Sciences USA* **107**(45), 19368–73. DOI:10.1073/pnas.1006463107.
- Norby, R. J., et al. 2006. "CO<sub>2</sub> Enrichment of a Deciduous Forest: The Oak Ridge FACE Experiment." In *Ecological Studies, Vol. 187: Managed Ecosystems and CO<sub>2</sub>: Case Studies, Processes, and Perspectives*, pp. 231–51. Eds. Nösberger, J., et al. Springer-Verlag, Berlin and Heidelberg.
- Norby, R. J., et al. 2005. "Forest Response to Elevated CO<sub>2</sub> Is Conserved Across a Broad Range of Productivity," *Proceedings of the National Academy of Sciences USA* **102**(50), 18052–56. DOI:10.1073/pnas.0509478102.
- Norby, R. J., et al. 2004. "Fine-Root Production Dominates Response of a Deciduous Forest to Atmospheric CO<sub>2</sub> Enrichment," *Proceedings of the National Academy of Sciences USA* **101**(26), 9689–93. DOI:10.1073/pnas.0403491101.
- Norby, R. J., et al. 2003. "Leaf Dynamics of a Deciduous Forest Canopy: No Response to Elevated CO<sub>2</sub>," *Oecologia* **136**(4), 574–84. DOI:10.1007/s00442-003-1296-2.
- Norby, R. J., et al. 2002. "Net Primary Productivity of a CO<sub>2</sub>-Enriched Deciduous Forest and the Implications for Carbon Storage," *Ecological Applications* **12**(5), 1261–66. DOI:10.1890/1051-0761(2002)012[1261:nppoac]2.0.co;2.
- Norby, R. J., et al. 2001. "Allometric Determination of Tree Growth in a CO<sub>2</sub>-Enriched Sweetgum Stand," *New Phytologist* **150**(2), 477–87. DOI:10.1046/j.1469-8137.2001.00099.x.
- Norby, R. J., et al. 1999. "Tree Responses to Rising CO<sub>2</sub> in Field Experiments: Implications for the Future Forest," *Plant Cell and Environment* **22**(6), 683–714. DOI:10.1046/j.1365-3040.1999.00391.x.
- Norby, R. J., et al. 1992. "Productivity and Compensatory Responses of Yellow-Poplar Trees in Elevated CO<sub>2</sub>," *Nature* **357**(6376), 322–24. DOI:10.1038/357322a0.
- Norby, R. J., et al. 1986a. "Effects of Atmospheric CO<sub>2</sub> Enrichment on the Growth and Mineral-Nutrition of *Quercus alba* Seedlings in Nutrient-Poor Soil," *Plant Physiology* **82**(1), 83–89. DOI:10.1104/pp.82.1.83.
- Norby, R. J., et al. 1986b. "Carbon-Nitrogen Interactions in CO<sub>2</sub>-Enriched White Oak: Physiological and Long-Term Perspectives," *Tree Physiology* **2**(1–3), 233–41. DOI:10.1093/treephys/2.1-2-3.233.
- Nowak, R. S., et al. 2004. "Elevated Atmospheric CO<sub>2</sub> Does Not Conserve Soil Water in the Mojave Desert," *Ecology* **85**(1), 93–99. DOI:10.1890/03-3054.
- Oechel, W. C., et al. 1994. "Transient Nature of CO<sub>2</sub> Fertilization in Arctic Tundra," *Nature* **371**(6497), 500–503. DOI:10.1038/371500a0.
- Okada, M., et al. 2001. "Free-Air CO<sub>2</sub> Enrichment (FACE) Using Pure CO<sub>2</sub> Injection: System Description," *New Phytologist* **150**(2), 251–60. DOI:10.1046/j.1469-8137.2001.00097.x.
- Onandia, G., et al. 2011. "Exposure to Moderate Concentrations of Tropospheric Ozone Impairs Tree Stomatal Response to Carbon Dioxide," *Environmental Pollution* **159**(10), 2350–54. DOI:10.1016/j.envpol.2011.06.001.
- Oren, R., et al. 2001. "Soil Fertility Limits Carbon Sequestration by Forest Ecosystems in a CO<sub>2</sub>-Enriched Atmosphere," *Nature* **411**(6836), 469–72. DOI:10.1038/35078064.
- Owensby, C. E., et al. 1999. "Biomass Production and Species Composition Change in a Tallgrass Prairie Ecosystem After Long-Term Exposure to Elevated Atmospheric CO<sub>2</sub>," *Global Change Biology* **5**(5), 497–506. DOI:10.1046/j.1365-2486.1999.00245.x.

- Owensby, C. E., et al. 1997. "Water Vapour Fluxes and Their Impact Under Elevated CO<sub>2</sub> in a C<sub>4</sub>-Tallgrass Prairie," *Global Change Biology* **3**(3), 189–95. DOI:10.1046/j.1365-2486.1997.00084.x.
- Owensby, C. E., et al. 1996. "Effects of Elevated Carbon Dioxide on Forage Quality for Ruminants." In *Carbon Dioxide, Populations, and Communities. Physiologic Ecology Series*. Eds. Koerner, C., and F. Bazzaz. Academic Press, San Diego, Calif. pp. 363–71.
- Owensby, C. E., et al. 1994. "Biomass Production in a Nitrogen-Fertilized, Tallgrass Prairie Ecosystem Exposed to Ambient and Elevated Levels of CO<sub>2</sub>," *Plant and Soil* **165**(1), 105–13. DOI:10.1007/BF00009967.
- Owensby, C. E., et al. 1993. "Biomass Production in a Tallgrass Prairie Ecosystem Exposed to Ambient and Elevated CO<sub>2</sub>," *Ecological Applications* **3**(4), 644–53. DOI:10.2307/1942097.
- Palmroth, S., et al. 2006. "Aboveground Sink Strength in Forests Controls the Allocation of Carbon Below Ground and Its CO<sub>2</sub>-Induced Enhancement," *Proceedings of the National Academy of Sciences USA* **103**(51), 19362–67. DOI:10.1073/pnas.0609492103.
- Parton, W. J., et al. 2007. "Projected Ecosystem Impact of the Prairie Heating and CO<sub>2</sub> Enrichment Experiment," *New Phytologist* **174**(4), 823–34. DOI:10.1111/j.1469-8137.2007.02052.x.
- Pataki, D. E., et al. 2000. "Water Use of Two Mojave Desert Shrubs Under Elevated CO<sub>2</sub>," *Global Change Biology* **6**(8), 889–97. DOI:10.1046/j.1365-2486.2000.00360.x.
- Pendall, E., et al. 2001. "Elevated CO<sub>2</sub> Stimulates Soil Respiration in a FACE Wheat Field," *Basic and Applied Ecology* **2**(3), 193–201. DOI:10.1078/1439-1791-00053.
- Phillips, D. L., et al. 2006. "Effects of Elevated CO<sub>2</sub> on Fine Root Dynamics in a Mojave Desert Community: A FACE Study," *Global Change Biology* **12**(1), 61–73. DOI:10.1111/j.1365-2486.2005.01085.x.
- Phillips, R. P., et al. 2011. "Enhanced Root Exudation Induces Microbial Feedbacks to N Cycling in a Pine Forest Under Long-Term CO<sub>2</sub> Fumigation," *Ecology Letters* **14**(2), 187–94. DOI:10.1111/j.1461-0248.2010.01570.x.
- Pritchard, S. G., and A. E. Strand. 2008. "Can You Believe What You See? Reconciling Minirhizotron and Isotopically Derived Estimates of Fine Root Longevity," *New Phytologist* **177**(2), 287–91.
- Pritchard, S. G., et al. 2008a. "Fine Root Dynamics in a Loblolly Pine Forest are Influenced by Free-Air-CO<sub>2</sub>-Enrichment: A 6-Year-Minirhizotron Study," *Global Change Biology* **14**(3), 588–602. DOI:10.1111/j.1365-2486.2007.01523.x.
- Pritchard, S. G., et al. 2008b. "Mycorrhizal and Rhizomorph Dynamics in a Loblolly Pine Forest During 5 Years of Free-Air-CO<sub>2</sub>-Enrichment," *Global Change Biology* **14**(6), 1252–64. DOI:10.1111/j.1365-2486.2008.01567.x.
- Reich, P. B., et al. 2018. "Unexpected Reversal of C<sub>3</sub> Versus C<sub>4</sub> Grass Response to Elevated CO<sub>2</sub> During a 20-Year Field Experiment," *Science* **360**(6386), 317–20. DOI:10.1126/science.aas9313.
- Reich, P. B., et al. 2006. "Nitrogen Limitation Constrains Sustainability of Ecosystem Response to CO<sub>2</sub>," *Nature* **440**(7086), 922–25. DOI:10.1038/nature04486.
- Reich, P. B., et al. 2001a. "Do Species and Functional Groups Differ in Acquisition and Use of C, N and Water Under Varying Atmospheric CO<sub>2</sub> and N Availability Regimes? A Field Test with 16 Grassland Species," *New Phytologist* **150**(2), 435–48. DOI:10.1046/j.1469-8137.2001.00114.x.
- Reich, P. B., et al. 2001b. "Plant Diversity Enhances Ecosystem Responses to Elevated CO<sub>2</sub> and Nitrogen Deposition," *Nature* **410**(6830), 809–12. DOI:10.1038/35071062.
- Reid, C. D., et al. 2003. "On the Relationship Between Stomatal Characters and Atmospheric CO<sub>2</sub>," *Geophysical Research Letters* **30**(19), 1983. DOI:10.1029/2003gl017775.
- Richardson, A. D., et al. 2018. "Ecosystem Warming Extends Vegetation Activity but Heightens Cold Temperature Vulnerability," *Nature* **560**, 368–71. DOI:10.1038/s41586-018-0399-1.
- Riches, M. R., and F. A. Koomanoff. 1985. "Overview of the Department of Energy Carbon Dioxide Research Program," *Bulletin of the American Meteorological Society* **66**(2), 152–58. DOI:10.1175/1520-0477(1985)066<0152:ootdoe>2.0.co;2.
- Riggs, J. S., et al. 2009. ORNL FACE CO<sub>2</sub> Data. Carbon Dioxide Information Analysis Center (<http://CDIAC.ornl.gov>), U.S. Department of Energy, Oak Ridge National Laboratory, Oak Ridge, Tenn. [[https://facedata.ornl.gov/ornl/ornl\\_data\\_co2weather.html](https://facedata.ornl.gov/ornl/ornl_data_co2weather.html)]
- Rogers, H. H., et al. 1983. "A Field Technique for the Study of Plant Responses to Elevated Carbon Dioxide Concentrations," *Journal of the Air Pollution Control Association* **33**(1), 42–44. DOI:10.1080/0022470.1983.10465546.
- Ryan, E. M., et al. 2017. "Gross Primary Production Responses to Warming, Elevated CO<sub>2</sub>, and Irrigation: Quantifying the Drivers of Ecosystem Physiology in a Semiarid Grassland," *Global Change Biology* **23**(8), 3092–3106. DOI:10.1111/gcb.13602.
- Schaeffer, S. M., et al. 2007. "Laboratory Incubations Reveal Potential Responses of Soil Nitrogen Cycling to Changes in Soil C and N Availability in Mojave Desert Soils Exposed to Elevated Atmospheric CO<sub>2</sub>," *Global Change Biology* **13**(4), 854–65. DOI:10.1111/j.1365-2486.2007.01324.x.
- Schlesinger, W. H., et al. 2006. "The Duke Forest FACE Experiment: CO<sub>2</sub> Enrichment of a Loblolly Pine Forest." In *Ecological Studies, Vol. 187: Managed Ecosystems and CO<sub>2</sub>: Case Studies, Processes, and Perspectives*, pp. 197–212. Eds. Nösberger, J., et al. Springer-Verlag, Berlin and Heidelberg.
- Seiler, T. J., et al. 2009. "Disturbance, Rainfall, and Contrasting Species Responses Mediated Aboveground Biomass Response to 11 Years of CO<sub>2</sub> Enrichment in a Florida Scrub-Oak Ecosystem," *Global Change Biology* **15**(2), 356–67. DOI:10.1111/j.1365-2486.2008.01740.x.

- Sholtis, J. D., et al. 2004. "Persistent Stimulation of Photosynthesis by Elevated CO<sub>2</sub> in a Sweetgum (*Liquidambar styraciflua*) Forest Stand," *New Phytologist* **162**(2), 343–54. DOI:10.1111/j.1469-8137.2004.01028.x.
- Siegenthaler, U., and H. Oeschger. 1978. "Predicting Future Atmospheric Carbon Dioxide Levels," *Science* **199**(4327), 388–95. DOI:10.1126/science.199.4327.388.
- Sinsabaugh, R. L., et al. 2003. "Soil Microbial Activity in a *Liquidambar* Plantation Unresponsive to CO<sub>2</sub>-Driven Increases in Primary Production," *Applied Soil Ecology* **24**(3), 263–71. DOI:10.1016/s0929-1393(03)00002-7.
- Smith, S. D., et al. 2014. "Long-Term Response of a Mojave Desert Winter Annual Plant Community to a Whole-Ecosystem Atmospheric CO<sub>2</sub> Manipulation (FACE)," *Global Change Biology* **20**(3), 879–92. DOI:10.1111/gcb.12411.
- Smith, S. D., et al. 2000. "Elevated CO<sub>2</sub> Increases Productivity and Invasive Species Success in an Arid Ecosystem," *Nature* **408**(6808), 79–82. DOI:10.1038/35040544.
- Souza, L., et al. 2010. "CO<sub>2</sub> Enrichment Accelerates Successional Development of an Understory Plant Community," *Journal of Plant Ecology* **3**(1), 33–39. DOI:10.1093/jpe/rtp032.
- Springer, C. J., et al. 2005. "Relationships Between Net Photosynthesis and Foliar Nitrogen Concentrations in a Loblolly Pine Forest Ecosystem Grown in Elevated Atmospheric Carbon Dioxide," *Tree Physiology* **25**(4), 385–94. DOI:10.1093/treephys/25.4.385.
- Steven, B., et al. 2012. "Dryland Biological Soil Crust Cyanobacteria Show Unexpected Decreases in Abundance Under Long-Term Elevated CO<sub>2</sub>," *Environmental Microbiology* **14**(12), 3247–58. DOI:10.1111/1462-2920.12011.
- Stiling, P., et al. 2002. "Elevated Atmospheric CO<sub>2</sub> Lowers Herbivore Abundance but Increases Leaf Abscission Rates," *Global Change Biology* **8**(7), 658–67. DOI:10.1046/j.1365-2486.2002.00501.x.
- Stover, D. B., et al. 2010. "The Long-Term Effects of CO<sub>2</sub> Enrichment on Fine Root Productivity, Mortality, and Survivorship in a Scrub-Oak Ecosystem at Kennedy Space Center, Florida, USA," *Environmental and Experimental Botany* **69**(2), 214–22. DOI:10.1016/j.envexpbot.2010.03.003.
- Stover, D. B., et al. 2007. "Effect of Elevated CO<sub>2</sub> on Coarse-Root Biomass in Florida Scrub Detected by Ground-Penetrating Radar," *Ecology* **88**(5), 1328–34. DOI:10.1890/06-0989.
- Strain, B. R., and J. D. Cure, Eds. 1985. *Direct Effects of Increasing Carbon Dioxide on Vegetation*, DOE/ER-0238. U.S. Department of Energy Office of Energy Research. DOI:10.2172/6134866.
- Strain, B. R., and F. A. Bazzaz. 1983. "Terrestrial Plant Communities." In *CO<sub>2</sub> and Plants*, pp. 177–222. Ed. Lemon, E. R. Westview Press, Boulder, Colo.
- Talhelm, A. F., et al. 2014. "Elevated Carbon Dioxide and Ozone Alter Productivity and Ecosystem Carbon Content in Northern Temperate Forests," *Global Change Biology* **20**(8), 2492–2504. DOI:10.1111/gcb.12564.
- Talhelm, A. F., et al. 2012. "Long-Term Leaf Production Response to Elevated Atmospheric Carbon Dioxide and Tropospheric Ozone," *Ecosystems* **15**(1), 71–82. DOI:10.1007/s10021-011-9493-z.
- Talhelm, A. F., et al. 2009. "Species-Specific Responses to Atmospheric Carbon Dioxide and Tropospheric Ozone Mediate Changes in Soil Carbon," *Ecology Letters* **12**(11), 1219–28. DOI:10.1111/j.1461-0248.2009.01380.x.
- Tfaily, M. M., et al. 2018. "Elevated CO<sub>2</sub> Changes Soil Organic Matter Composition and Substrate Diversity in an Arid Ecosystem," *Geoderma* **330**, 1–8. DOI:10.1016/j.geoderma.2018.05.025.
- Tissue, D. T., and W. C. Oechel. 1987. "Response of *Eriophorum vaginatum* to Elevated CO<sub>2</sub> and Temperature in the Alaskan Tussock Tundra," *Ecology* **68**(2), 401–10. DOI:10.2307/1939271.
- Tissue, D. T., et al. 2002. "Leaf Respiration at Different Canopy Positions in Sweetgum (*Liquidambar styraciflua*) Grown in Ambient and Elevated Concentrations of Carbon Dioxide in the Field," *Tree Physiology* **22**(15–16), 1157–66. DOI:10.1093/treephys/22.15-16.1157.
- Tissue, D. T., et al. 1997. "Atmospheric CO<sub>2</sub> Enrichment Increases Growth and Photosynthesis of *Pinus taeda*: A 4 Year Experiment in the Field," *Plant Cell and Environment* **20**(9), 1123–34. DOI:10.1046/j.1365-3040.1997.d01-140.x.
- Tissue, D. T., et al. 1996. "Growth and Photosynthesis of Loblolly Pine (*Pinus taeda*) After Exposure to Elevated CO<sub>2</sub> for 19 Months in the Field," *Tree Physiology* **16**(1–2), 49–59. DOI:10.1093/treephys/16.1-2.49.
- Tolley, L. C., and B. R. Strain. 1985. "Effects of CO<sub>2</sub> Enrichment and Water-Stress on Gas-Exchange of *Liquidambar styraciflua* and *Pinus taeda* Seedlings Grown Under Different Irradiance Levels," *Oecologia* **65**(2), 166–72. DOI:10.1007/bf00379214.
- Tor-ngern, P., et al. 2015. "Increases in Atmospheric CO<sub>2</sub> Have Little Influence on Transpiration of a Temperate Forest Canopy," *New Phytologist* **205**(2), 518–25. DOI:10.1111/nph.13148.
- Uddling, J., et al. 2010. "Stomatal Uptake of O<sub>3</sub> in Aspen and Aspen-Birch Forests Under Free-Air CO<sub>2</sub> and O<sub>3</sub> Enrichment," *Environmental Pollution* **158**(6), 2023–31. DOI:10.1016/j.envpol.2009.12.001.
- U.S. DOE. 2008. *Ecosystem Experiments: Understanding Climate Change Impacts on Ecosystems and Feedbacks to the Physical Climate*. U.S. Department of Energy Office of Science. [[https://tes.science.energy.gov/files/Ecosystem\\_experiments.pdf](https://tes.science.energy.gov/files/Ecosystem_experiments.pdf)]
- Walker, A. P., et al. 2019. "Decadal Biomass Increment in Early Secondary Succession Woody Ecosystems Is Increased by CO<sub>2</sub> Enrichment," *Nature Communications* **10**(1), 454. DOI:10.1038/s41467-019-08348-1.
- Walker, A. P., et al. 2015. "Predicting Long-Term Carbon Sequestration in Response to CO<sub>2</sub> Enrichment: How and Why Do Current Ecosystem Models Differ?," *Global Biogeochemical Cycles* **29**(4), 476–95. DOI:10.1002/2014gb004995.



- Walker, A. P., et al. 2014. "Comprehensive Ecosystem Model-Data Synthesis Using Multiple Data Sets at Two Temperate Forest Free-Air CO<sub>2</sub> Enrichment Experiments: Model Performance at Ambient CO<sub>2</sub> Concentration," *Journal of Geophysical Research—Biogeosciences* **119**(5), 937–64. DOI:10.1002/2013jg002553.
- Wan, S., et al. 2007. "Responses of Soil Respiration to Elevated CO<sub>2</sub>, Air Warming, and Changing Soil Water Availability in a Model Old-Field Grassland," *Global Change Biology* **13**(11), 2411–24. DOI:10.1111/j.1365-2486.2007.01433.x.
- Warren, J. M., et al. 2015. "Carbon Dioxide Stimulation of Photosynthesis in *Liquidambar styraciflua* Is Not Sustained During a 12-Year Field Experiment," *AoB Plants* **7**, plu074. DOI:10.1093/aobpla/plu074.
- Warren, J. M., et al. 2011a. "Elevated CO<sub>2</sub> Enhances Leaf Senescence During Extreme Drought in a Temperate Forest," *Tree Physiology* **31**(2), 117–30. DOI:10.1093/treephys/tpr002.
- Warren, J. M., et al. 2011b. "Ecohydrologic Impact of Reduced Stomatal Conductance in Forests Exposed to Elevated CO<sub>2</sub>," *Ecohydrology* **4**(2), 196–210. DOI:10.1002/eco.173.
- Way, D. A., et al. 2010. "Greater Seed Production in Elevated CO<sub>2</sub> Is Not Accompanied by Reduced Seed Quality in *Pinus taeda* L.," *Global Change Biology* **16**(3), 1046–56. DOI:10.1111/j.1365-2486.2009.02007.x.
- Weatherly, H. E., et al. 2003. "In Situ Litter Decomposition and Litter Quality in a Mojave Desert Ecosystem: Effects of Elevated Atmospheric CO<sub>2</sub> and Interannual Climate Variability," *Global Change Biology* **9**(8), 1223–33 DOI:10.1046/j.1365-2486.2003.00653.x.
- Wertin, T. M., et al. 2012. "Elevated CO<sub>2</sub> Did Not Mitigate the Effect of a Short-Term Drought on Biological Soil Crusts," *Biology and Fertility of Soils* **48**(7), 797–805. DOI:10.1007/s00374-012-0673-6.
- Williams, M. A., et al. 2006. "Natural <sup>15</sup>N Abundances in a Tall-grass Prairie Ecosystem Exposed to 8-Y of Elevated Atmospheric CO<sub>2</sub>," *Soil Biology & Biochemistry* **38**(2), 409–12. DOI:10.1016/j.soilbio.2005.06.009.
- Woodwell, G. M., et al. 1978. "The Biota and World Carbon Budget," *Science* **199**(4325), 141–46. DOI:10.1126/science.199.4325.141.
- Wullschlegel, S. D., and R. J. Norby. 2001. "Sap Velocity and Canopy Transpiration in a Sweetgum Stand Exposed to Free-Air CO<sub>2</sub> Enrichment (FACE)," *New Phytologist* **150**(2), 489–98. DOI:10.1046/j.1469-8137.2001.00094.x.
- Yang, X., et al. 2019. "The Effects of Phosphorus Cycle Dynamics on Carbon Sources and Sinks in the Amazon Region: A Modeling Study Using ELM v1," *Journal of Geophysical Research: Biogeosciences* **124**(12), 3686–98. DOI:10.1029/2019JG005082.
- Yang, X., et al. 2014. "The Role of Phosphorus Dynamics in Tropical Forests — A Modeling Study Using CLM-CNP," *Biogeosciences* **11**(6), 1667–81. DOI:10.5194/bg-11-1667-2014.
- Yu, H., et al. 2018. "Divergent Responses of Forest Soil Microbial Communities under Elevated CO<sub>2</sub> in Different Depths of Upper Soil Layers," *Applied and Environmental Microbiology* **84**(1). DOI:10.1128/AEM.01694-17.
- Zaehle, S., et al. 2014. "Evaluation of 11 Terrestrial Carbon-Nitrogen Cycle Models Against Observations from Two Temperate Free-Air CO<sub>2</sub> Enrichment Studies," *New Phytologist* **202**(3), 803–22. DOI:10.1111/nph.12697.
- Zak, D. R., et al. 2012. "Atmospheric CO<sub>2</sub> and O<sub>3</sub> Alter Competition for Soil Nitrogen in Developing Forests," *Global Change Biology* **18**(4), 1480–88. DOI:10.1111/j.1365-2486.2011.02596.x.
- Zak, D. R., et al. 2011. "Forest Productivity Under Elevated CO<sub>2</sub> and O<sub>3</sub>: Positive Feedbacks to Soil N Cycling Sustain Decade-Long Net Primary Productivity Enhancement by CO<sub>2</sub>," *Ecology Letters* **14**(12), 1220–26. DOI:10.1111/j.1461-0248.2011.01692.x.
- Zak, D. R., et al. 2003. "Soil Nitrogen Cycling Under Elevated CO<sub>2</sub>: A Synthesis of Forest Face Experiments," *Ecological Applications* **13**(6), 1508–14. DOI:10.1890/03-5055.

## Appendix C: Image Credits

### Inside Front Cover



**Duke FACE.** A high carbon dioxide (CO<sub>2</sub>)-ambient air mix is blown into the large, black corrugated pipe on the ground that surrounds the entire plot at the Duke Free-Air CO<sub>2</sub> Enrichment (FACE) site. Based on wind direction, computer-controlled on/off valves regulate which eight of the 32 vertical vent pipes are turned on at any given moment. [Courtesy Jeffrey S. Phippen, Duke University.]



**ORNL FACE.** Aerial view shows the FACE site at Oak Ridge National Laboratory (ORNL) in Tennessee. [Reprinted by permission from Springer Nature from Medlyn, B. E., et al. 2015. "Using Ecosystem Experiments to Improve Vegetation Models," *Nature Climate Change* 5, 528–34. Copyright 2015.]



**Nevada Desert FACE.** The Nevada Desert FACE site was the only U.S. Department of Energy (DOE) FACE experiment that examined the impact of elevated atmospheric CO<sub>2</sub> on arid ecosystems in an otherwise natural environment. [Courtesy DOE.]



**Rhinelander FACE.** A single experiment is shown from above at the Rhinelander FACE site in Wisconsin. [Reprinted under a Creative Commons License (CC-BY-NC-ND 4.0) from McSweeney, R. 2015. "Leaf-Eating Insects May Limit How Much Carbon Forests Absorb, Study Says," *Carbon Brief*. Copyright 2015.]

### Inside Pages



**Section 3.1. Maricopa FACE.** The effects of elevated concentrations of atmospheric CO<sub>2</sub> have been investigated in a wide range of ecosystem types using FACE technology, including initial studies of crop systems at the University of Arizona Maricopa Agricultural Center. [Reprinted by permission of Wiley from Norby, R. J., et al. 2001. "Rising CO<sub>2</sub> – Future Ecosystems," *New Phytologist* 150(2), 215–21.]



**Section 3.2. Duke FACE.** View shows experimental plots emerging from the loblolly pine canopy at the FACE site near Duke University. [Courtesy Jeffrey S. Phippen, Duke University.]



**Section 3.3. ORNL FACE.** Aluminum towers in the middle of sweetgum trees along the Clinch River in Tennessee were part of the ORNL FACE experimental setup designed to determine how forests and ecosystems react to elevated atmospheric CO<sub>2</sub>. [Courtesy Tom Cerniglio, ORNL.]



**Section 3.4. Nevada Desert FACE.** Aerial view shows one research plot within the Nevada Desert FACE Facility that received elevated atmospheric CO<sub>2</sub>. A scientist is seen on the rotating sampling platform used to conduct research throughout the plot. The platform prevented disturbance of the surface soil and the biological soil crust. [Courtesy Stephen Zitzer, formerly Desert Research Institute.]



**Section 3.5. Rhinelander FACE.** Aerial view shows the FACE site in Rhinelander, Wisconsin. After harvesting of original trees during 2009, this new forest sprouted under FACE treatments in 2010. [Courtesy David Karnosky, formerly Michigan Technological University, and Donald Zak, University of Michigan.]



**Section 4.1. Salt Marsh OTC.** Open-top chambers (OTCs) are used in an ongoing 30-year study of the effects of elevated CO<sub>2</sub> on a Chesapeake Bay wetland. This is the longest-running study of CO<sub>2</sub> effects on native vegetation. [Courtesy Bert G. Drake, Smithsonian Environmental Research Center, from Rasse, D. P., et al. 2005. "Seventeen Years of Elevated CO<sub>2</sub> Exposure in a Chesapeake Bay Wetland: Sustained but Contrasting Responses of Plant Growth and CO<sub>2</sub> Uptake," *Global Change Biology* 11, 369–77.]



**Section 4.2. Scrub Oak OTC.** Researchers work among OTCs in a study of the effects of elevated atmospheric CO<sub>2</sub> on scrub oak vegetation at the Kennedy Space Center, Merritt Island National Wildlife Refuge, during a space shuttle launch at Cape Canaveral, Fla., in 2002. [Courtesy Bert G. Drake, Smithsonian Environmental Research Center.]



**Section 4.3. Tallgrass Prairie OTC.** OTCs in a tallgrass prairie experiment were used to assess the impact of doubling ambient CO<sub>2</sub> during the growing season. [Courtesy Clenton Owensby, Kansas State University.]



**Section 4.4. Arctic Greenhouses.** A temperature-controlled greenhouse system was used in the Arctic tundra experiment at Toolik Lake, Alaska. This study was the first elevated CO<sub>2</sub> experiment conducted in an intact, unmanaged ecosystem. [Reprinted by permission of Oxford University Press from Mooney, H. A., et al. 1991. "Predicting Ecosystem Responses to Elevated CO<sub>2</sub> Concentrations," *BioScience* 41(2), 96–104.]



**Section 4.5. OCCAM.** A researcher records field data at the Old-field Community, Climate, and Atmospheric Manipulation (OCCAM) experiment in Oak Ridge, Tenn. Old-field communities constructed by ORNL were exposed to elevated CO<sub>2</sub>, warming, and altered water conditions in OTCs. [Courtesy ORNL.]



**Section 4.6. SPRUCE.** Ten enclosures are being used in the Spruce and Peatland Responses Under Changing Environments (SPRUCE) experiment to expose a bog in northern Minnesota to a range of warming treatments in combination with elevated atmospheric CO<sub>2</sub>. The experiment takes place in the U.S. Forest Service's Marcell Experimental Forest. [Courtesy Richard J. Norby, ORNL.]



**Section 5.1. BioCON.** Pictured is Ring 4 of the BioCON (Biodiversity, CO<sub>2</sub>, and Nitrogen) experiment at the Cedar Creek Ecosystem Science Reserve in Minnesota. BioCON's goal is to examine the response of plant communities to three environmental changes known to be occurring on a global scale: increasing nitrogen deposition, increasing atmospheric CO<sub>2</sub>, and decreasing biodiversity. [Reprinted under a Creative Commons License (CC-BY-SA 4.0). Courtesy Jacob Miller.]



**Section 5.2. PHACE.** As the largest remaining grassland ecosystem in North America, mixed-grass prairie is integral to both agricultural productivity and conservation of biological diversity in the western United States. To evaluate how future environmental conditions will influence this ecosystem, the Prairie Heating and CO<sub>2</sub> Enrichment (PHACE) experiment was launched in 2005 near Cheyenne, Wyo. [Courtesy U.S. Department of Agriculture.]

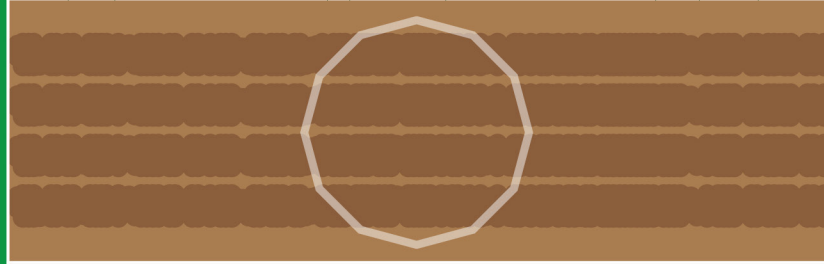
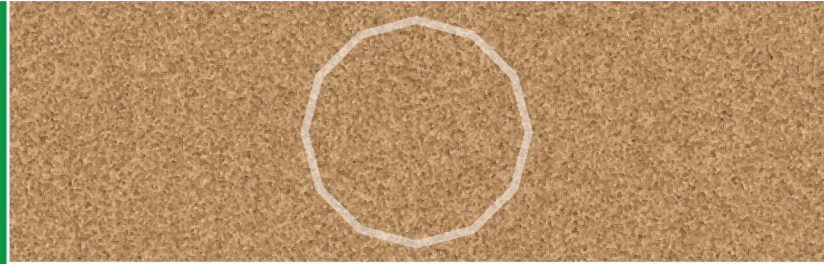
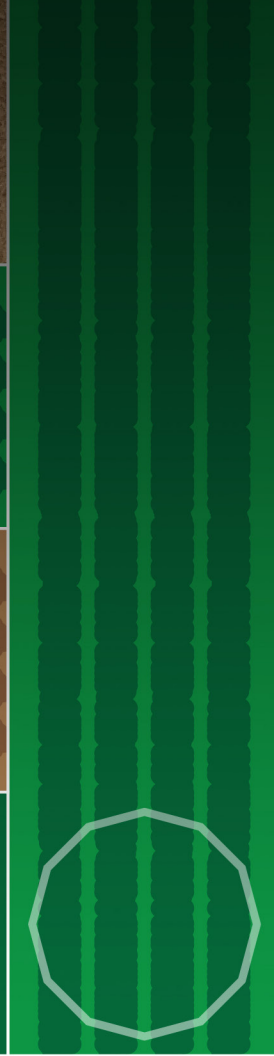
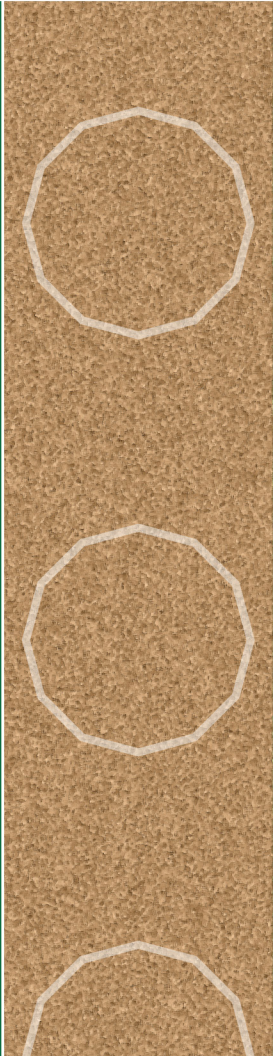
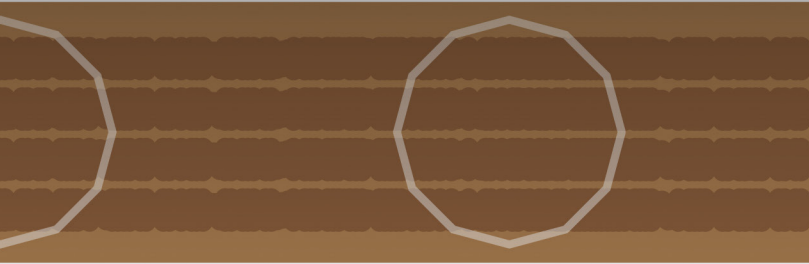
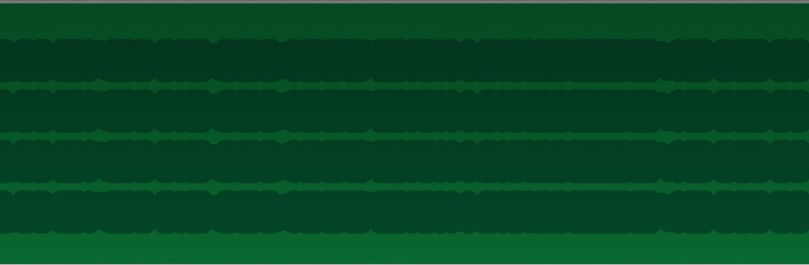


## Appendix D: Acronyms and Abbreviations

<b>ARS</b>	USDA Agricultural Research Service	<b>NEP</b>	net ecosystem production
<b>BAI</b>	basal area increment	<b>NGEE</b>	Next-Generation Ecosystem Experiments
<b>BERAC</b>	Biological and Environmental Research Advisory Committee	<b>NPP</b>	net primary production
<b>BioCON</b>	Biodiversity, CO <sub>2</sub> , and Nitrogen	<b>NSF</b>	National Science Foundation
<b>BNL</b>	Brookhaven National Laboratory	<b>NUE</b>	nitrogen-use efficiency
<b>CO<sub>2</sub></b>	carbon dioxide	<b>O<sub>3</sub></b>	ozone
<b>CDIAC</b>	Carbon Dioxide Information Analysis Center	<b>OCCAM</b>	Old-Field Community, Climate, and Atmospheric Manipulation
<b>δ<sup>13</sup>C</b>	stable carbon isotope	<b>ORNL</b>	Oak Ridge National Laboratory
<b>DOE</b>	U.S. Department of Energy	<b>OTC</b>	open-top chamber
<b>ESS-DIVE</b>	Environmental Systems Science Data Infrastructure for a Virtual Ecosystem	<b>PAR</b>	photosynthetically active radiation
<b>FACE</b>	Free-Air CO <sub>2</sub> Enrichment	<b>PHACE</b>	Prairie Heating and Carbon Dioxide Enrichment
<b>FACE-MDS</b>	FACE Model-Data Synthesis	<b>POM</b>	particulate organic matter
<b>GPP</b>	gross primary production	<b>ppb</b>	parts per billion
<b>GPR</b>	ground-penetrating radar	<b>ppm</b>	parts per million
<b>ha</b>	hectare	<b>SD</b>	stomatal density
<b>J<sub>max</sub></b>	maximum rate of electron transport	<b>SI</b>	stomatal index
<b>LAD</b>	leaf area duration	<b>SOA</b>	state-of-the-art
<b>LAI</b>	leaf area index	<b>SOC</b>	soil organic carbon
<b>ModEx</b>	model-experimental approach	<b>SOM</b>	soil organic matter
<b>δ<sup>15</sup>N</b>	stable nitrogen isotope	<b>SPRUCE</b>	Spruce and Peatland Responses Under Changing Environments
<b>N<sub>area</sub></b>	foliar nitrogen per unit leaf area	<b>SSC</b>	Science Steering Committee
<b>NCEAS</b>	National Center for Ecological Analysis and Synthesis	<b>USDA</b>	U.S. Department of Agriculture
<b>NEE</b>	net ecosystem exchange	<b>V<sub>cmax</sub></b>	maximum rate of carboxylation
		<b>WUE</b>	water-use efficiency







June 2020