# *Commentary*

## Rising $CO_2$ – future ecosystems

> *'Every beginning biology student knows that photosynthesis will increase if you give a plant a 'squirt' of $CO_2$ – given enough light, nutrients, and water, and a suitable temperature. Logic tells us that if this is so, then more $CO_2$ 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'* (Lemon, 1983).

This *Special Issue* of *New Phytologist* focuses on the responses of ecosystems to increased $CO_2$ concentration. The responses of plants are central to this focus, but the questions being asked have changed, and nature's complexities become paramount. Our concern is the human effect on the composition of the atmosphere and how it could have profound effects on our economic and social systems, options for energy production and use, and our capacity to grow food and fiber for an expanding population. The primary interaction between plants and atmospheric $CO_2$ is just the starting point for our analysis.

### Research context

Lemon (1983), and the contributors to the international conference on which he was reporting, laid out a research agenda for investigating the responses of plants to future atmospheric $CO_2$ concentrations. The mostly short-term experiments that were appropriate for understanding the fundamental physiology of plants or the commercial aspects of $CO_2$ enrichment of glasshouse atmospheres (Witter & Robb, 1964) were seen as insufficient for understanding the more complex issues of plant productivity in a future, $CO_2$-enriched atmosphere. The conference participants urged experimental work with $CO_2$ enrichment at all levels to elucidate biochemical, physiological and microbial responses, as well as community-scale responses and species interactions in complex environments.

Now, almost 20 years later, a great deal of that research agenda has been taken on. Not only do we know much more about the response of photosynthesis to a 'squirt' of $CO_2$ (Cousins *et al.* – see pp. 275–284 in this issue; Rodriguez *et al.* – pp. 337–346; Williams *et al.* – pp. 285–293), we have also studied everything from the effect of $CO_2$ concentration on the genetic control of stomatal density (Gray *et al.*, 2000) to the quality of bread and wine made from $CO_2$-enriched plants (Kimball *et al.* – pp. 295–303; Bindi *et al.*, 2001). Hundreds of plant species have been exposed to experimental manipulations of $CO_2$ concentration, and the unit of reference has progressed from small, potted plants in growth cabinets, to groups of plants in glasshouses or field chambers, to intact ecosystems and forest stands (Box 1). The $CO_2$ treatments have been combined with simultaneous manipulations of temperature, water, nitrogen, ozone, light, and competition. Research programs have increasingly been focused on describing how the primary responses to $CO_2$ concentration will be manifested in future ecosystems, understanding the feedbacks between those primary responses and the atmospheric and climatic systems, and developing plant and ecosystem models to make the predictions of plant responses to a future atmosphere.

These trends – larger-scale experiments, a focus on future ecosystems, and modeling – are reflected in the papers presented in this volume. A wide range of ecosystems is considered (Fig. 1): agricultural systems in Japan, Germany, and Arizona (USA); grasslands and pastures in Switzerland, Australia, New Zealand, and Minnesota (USA); bogs throughout Europe; a desert in Nevada (USA); and forests in Italy and Tennessee (USA).

### Scale

In 1982, H. Z. Enoch spoke of the need for the scientific community to participate in a multinational effort to study the effects of elevated atmospheric $CO_2$ concentration on managed and unmanaged ecosystems, an admittedly expensive and difficult endeavor (Lemon, 1983). At the time, most of the information on $CO_2$ responses of plants came from short-term experiments (days or weeks) of potted plants in controlled-environment chambers (Kimball, 1983). It was recognized, however, that the short-term responses might not prevail over longer time periods, and that interactions between a plant and its environment (both biotic and abiotic)

**Box 1** FACE technology

Exposure of ecosystems to controlled levels of elevated $CO_2$ under open-field conditions requires sophisticated free-air $CO_2$ enrichment (FACE) technology.

- **Origins** L. Hartwell Allen (1992), who coined the acronym FACE, attributes the first attempts to H. Lundegårdh in the 1920s. Lundegårdh devised a ground-level tube distribution system using $CO_2$ from decomposing manure. In the 1960s, D. W. Kretchman studied the effects of $CO_2$ on many field-grown crops, attempting (unsuccessfully) to get a yield benefit economically – as was becoming standard in glasshouse horticultural production – using ground-level release systems in combination with windbreaks. Additional ground-level releases were made later to use $CO_2$ as a tracer of atmospheric dispersion, and by the early 1970s Allen and colleagues had FACE-type research as a goal.
- **Air pollution** Allen (1992) describes attempts to simulate the effects of $CO_2$ releases on plant responses. One conclusion from these and from the prior ground-level releases was that the $CO_2$ concentration at the upper canopy level, where the greatest effect of $CO_2$ on photosynthesis would be expected, was much lower than that at ground level. Fortunately, air pollution scientists had also been attempting to control the concentration of gases over field plots, and had begun to experiment with releasing the gases near the top of the canopy. The circular system designed by McLeod *et al.* (1985) probably came closest to providing the dispersal needed for large-area $CO_2$-enrichment plots.
- **Brookhaven National Laboratory** In 1986, Lance Evans, from Manhattan College, together with Keith Lewin and George Hendrey from Brookhaven National Laboratory (BNL) proposed a consortial attempt to develop a FACE system using concepts from McLeod and other air pollution scientists. Also, Jackson Mauney from the USDA-ARS Western Cotton Research Laboratory identified geological $CO_2$ wells and a fertilizer factory at Yazoo City, Mississippi, that might be potential sources of cheap $CO_2$ for research – and publicised these to US researchers. Enthusiasm was high, and the upshot was that the DOE funded BNL to develop FACE apparatus and, subsequently, to conduct a FACE experiment on cotton.
- **Apparatus for diverse ecosystems** The BNL team designed a FACE release system for 1-m-tall agricultural crops that featured a circular array of vertical vent pipes with each pipe having its own computer controlled valve (Hendrey, 1993). $CO_2$ was released only upwind of the plots, with the decision as to which pipes to release from, and the release rate, continually updated (in seconds). With firmer data on $CO_2$ requirements in hand – and with the realization that scientific labor dominates research budgets in spite of the high cost of commercially available $CO_2$ (Kimball, 1992) – the decision was made to move the system to Maricopa, Arizona, near where a team of $CO_2$ researchers led by Bruce Kimball and Jackson Mauney had been using open-top chambers to study the effects of elevated $CO_2$ on cotton. The first FACE experiment with publishable biological data was conducted there in 1989 (Hendrey, 1993). Following their success, the BNL apparatus were adapted to enable enrichment of forest ecosystems (e.g. DeLucia *et al.*, 1999) and to accommodate release of ozone in interactive experiments (e.g. Karnosky *et al.*, 2001) – opening up the technology for use on diverse ecosystems during the past decade. Most of the FACE projects listed in the the following websites, and many of the papers in this volume, utilize BNL-designed apparatus:

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| BNL FACE Group | http://www.face.bnl.gov/ |
| Carbon Dioxide Information and Analysis Center | http://cdiac.esd.ornl.gov/programs/FACE/face.html |
| GCTE Elevated $CO_2$ Network | http://gcte-focus1.org/co2.html |

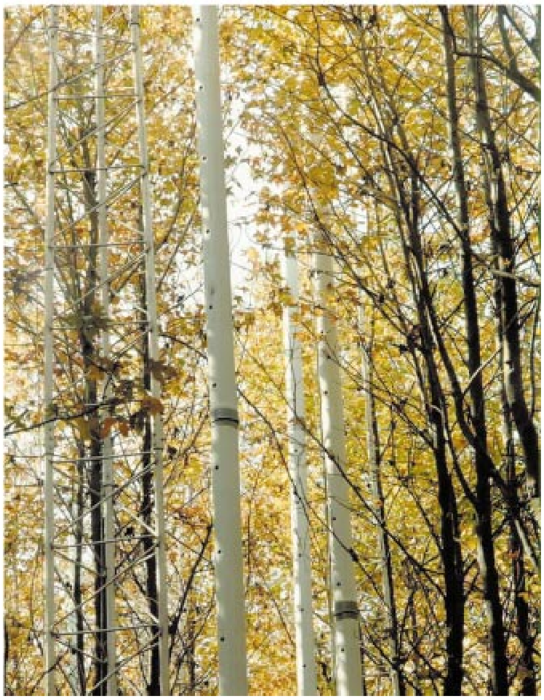
- **Recent advances** The BNL system uses blowers to predilute $CO_2$ with air before release, an aspect of their design which enhances the uniformity and control of the concentration over the plots. However, in 1993, it was realized that the blowers introduce sufficient air turbulence to warm the plant canopy significantly on calm nights (Pinter *et al.*, 2000), emphasizing the need for control plots with identical air flow properties. It also led Okada *et al.* (pp. 251–260 in this issue) and Miglietta *et al.* (pp. 465–476) to devise alternative FACE designs that release pure un-prediluted $CO_2$ over the plots, thus eliminating the blowers. FACE technology continues to evolve.

could alter the system-level response to $CO_2$ (Lemon, 1983). Many of these problems were addressed by new experiments conducted in various field chambers. In short-statured systems such as a salt marsh and tundra, open-top chambers allowed the treatment of intact ecosystems (Mooney *et al.*, 1991). Field chambers also permitted multiyear exposures of tree species without the artifacts associated with confining root systems in pots (Norby *et al.*, 1999).

Although much was learned from field chamber experiments, they fell short of the need expressed by Enoch. Field chambers create artificial environmental conditions, and plants often grow differently inside than outside (Kimball *et al.*, 1997). They can accommodate young trees, but not mature tree stands or forest ecosystems. Hence, the development of free-air $CO_2$ enrichment (FACE) technology for controlling an elevated $CO_2$ concentration in the open air was a critical advancement enabling the study of $CO_2$ effects on ecosystems. The history of FACE technology is described in Box 1.

The importance of the substantial increase in scale afforded by FACE systems is clear in many of the papers in this issue. Edwards *et al.* (pp. 359–369) report that elevated $CO_2$ concentration increased seedling growth of pasture species when grown individually in pots, but not when they were

**Fig. 1** The effects of atmospheric $CO_2$ enrichment have been investigated in a wide range of ecosystem types, including crop systems in Arizona, USA; a bog in Finland; the Mojave desert in Nevada, USA; and a deciduous forest in Tennessee, USA. *Photos courtesy of Bruce Kimball, Topi Ylä-Mononen, Travis Huxman and Steve Eberhardt, respectively*.



grown in a native pasture within their FACE plots. Measurements of the exchange of $CO_2$ between the atmosphere and rice paddy flood water were made in a FACE experiment (Koizumi *et al.*, pp. 231–239), but they would not have been possible in a chamber system with blowers that alter micrometeorological conditions. Physiological responses to elevated $CO_2$ concentration often take on different meaning at a larger scale. Ottman *et al.* (pp. 261–273) suggest that the $CO_2$ effect on stomatal closure might be an advantage under limited water supply but a disadvantage when water supply is ample. Wullschleger & Norby (pp. 489–495) found that the effect of elevated $CO_2$ concentration on stomatal closure, measured on upper canopy leaves under ideal conditions, did not scale to a reduction in season-long, whole-canopy transpiration in a tree stand.

The larger scale of FACE experiments makes possible measurements that otherwise would be unattainable. Norby *et al.* (pp. 477–487) were able to address questions about the growth responses of trees that had reached canopy closure, not heretofore possible in a deciduous forest system. They note that their study trees were in a linear growth phase, but had they been grown in open-top chambers, the experiment would have ended just at the critical transition from exponential growth. Even in those FACE experiments in which the experimental unit is relatively small, the larger exposure unit allowed for a wide range of simultaneous measurements and manipulations (Reich *et al.*, pp. 435–448).

## Ecosystems of the future

The primary rationale for all of the studies reported in this issue concerns prediction of the future behaviour of ecosystems in an atmosphere with a higher concentration of $CO_2$. The most critical issues vary in the different ecosystems. In agricultural systems, the objective might be to predict productivity or quality of the marketable product in response to high $CO_2$ (Kim *et al.*, pp. 223–229; Kimball *et al.*, pp. 295–303; Lilley *et al.* (b), pp. 385–395); this must be done in relation to technological improvements and crop breeding (Amthor, 1998), as well as the overriding influences of environmental stress. In unmanaged systems such as the desert and prairie, effects of $CO_2$ concentration on diversity may be the predominant issue. Smith *et al.* (2000) showed that in a high rainfall year elevated $CO_2$ concentration stimulated the establishment and spread of an invasive annual grass in the Nevada desert FACE experiment; this has the potential to accelerate the fire cycle, reduce biodiversity, and alter ecosystem function in the deserts of western North America. The primary rationale for experiments in forests derives from their very large role in the global carbon budget and the importance of understanding exchanges and feedbacks between forests and a future atmosphere. Forest ecosystems are difficult to manipulate as intact systems because of their size and longevity; hence, forest experiments focus on testing specific hypotheses about forest response (Norby *et al.*, 1999, also pp. 477–487).

Ecosystems provide essential services to humans, and there is increasing concern that those services might be jeopardized by the combined impacts of global change (Daily *et al.*, 1997). The provision of food, fiber, and water is of obvious importance. A less obvious ecosystem service is carbon sequestration, and this has been a particular focus of research because of the possibilities of feedbacks to the climate system. The effects of elevated $CO_2$ concentration on carbon fluxes have been considered at multiple scales: leaf (Tjoelker *et al.*, pp. 419–424), whole-plant (Sakai *et al.*, pp. 241–249), and whole system (Hoosbeek *et al.*, pp. 459–463; Craine *et al.*, pp. 425–434). Nutrient limitations apparently prevented any increases in C storage in bogs (Hoosbeek *et al.*). Stable isotope analysis provides a valuable tool for assessing the mechanisms of sequestration in soil in FACE experiments because the $CO_2$ that is added to the treatment plots is depleted in $^{13}C$ (Leavitt *et al.*, pp. 305–314).

Future ecosystems will be impacted not just by rising $CO_2$ concentration, but by a suite of atmospheric and climatic changes. FACE experiments are usually not as amenable to multifactor manipulations as smaller-scale experiments, but in this issue there are reports about interactions between $CO_2$ and N in rice and wheat (Kim *et al.*; Kimball *et al.*), prairie species (Craine & Reich, pp. 397–403; Lee *et al.*, pp. 405–418), and grasses (Daepp *et al.*, pp. 347–358). Interactions with water supply were studied in wheat (Kimball *et al.*; Williams *et al.*). Air temperature is very difficult to manipulate in open-air systems. Lilley *et al.* (a) (pp. 371–383) grew subterranean clover and phalaris grass in tunnels in which $CO_2$ concentration and temperature were controlled. Previous reports (Newton *et al.*, 1994) had reported that the abundance of clover in pastures increases with rising $CO_2$ concentration. Lilley *et al.* found that elevated temperature caused clover abundance to decrease, although this effect was counteracted by elevated $CO_2$ concentration.

## Modeling

Despite our best efforts to control environmental conditions and avoid artifacts in FACE and other experimental systems, we cannot duplicate future ecosystems or the atmospheric and climatic conditions that will occur at a certain future date. Soils in our experimental systems developed under current conditions, and the plants are today's genotypes. To predict ecosystem responses to future conditions we must rely on models, and we want the response functions in those models (Rodriguez *et al.*) to be informed by the most realistic data possible. FACE experiments are particularly useful for this. In modeling plant responses to elevated $CO_2$ concentration in field chambers, it is necessary to account for the chamber effects, which are in fact plant responses to the altered microclimate due to the chamber enclosure and the plants themselves. Because of their composite nature, the chamber effects are arguably harder to model than the plant responses to elevated $CO_2$ concentration *per se*. Assuming that the effects of elevated $CO_2$ concentration and the chambers on plants are multiplicative, one may compare the relative responses of the plants between the model and observation. The assumption can be disproved, however, by physiological considerations. In FACE experiments, by contrast, the results are almost free from artifacts, and, hence, the modeled plant responses to elevated $CO_2$ concentration can be compared with the observed ones without having to worry about the confounding effects of chambers (Kimball *et al.*, 1997). Grossman-Clarke *et al.* (pp. 315–335) compared model predictions of wheat productivity and water use with results from the Arizona FACE experiment. The model successfully described qualitative and quantitative behavior of the crop under elevated $CO_2$ concentration, making it possible to use the model for predictions about future behavior with greater confidence.

Testing models of unmanaged ecosystems in future $CO_2$ concentrations with experimental data is more problematic. In perennial systems in which the FACE experiment is imposed on existing vegetation (e.g. the desert FACE of Nowak *et al.*, pp. 449–458; the bog experiment of Hoosbeek *et al.*; or the deciduous forest FACE of Norby *et al.*), the $CO_2$ treatment is an abrupt increase in $CO_2$ concentration, to which some ecosystem processes could respond in quite a different way from those under gradually increasing $CO_2$ concentration (Cannell & Thornley, 1998). Luo & Reynolds (1999), nonetheless, pointed out that the ecosystem changes in FACE experiments can be analysed to elucidate responses of the individual ecosystem processes to the step change in $CO_2$ concentration, and these individual responses could be incorporated into a model to predict the whole-ecosystem responses to the increasing $CO_2$ concentration.

## Synthesis

A synthesis of the effects of rising $CO_2$ concentration on ecosystems as reported in the papers in this issue and elsewhere in the literature cannot be undertaken lightly. We can safely conclude that in most systems photosynthesis is increased by $CO_2$ enrichment, and this generally results in increased plant growth. It is more difficult to make general statements about whole-system responses, such as carbon storage, water yield, and species composition, that apply across a wide range of ecosystems and the different spatial and temporal scales of their dominant processes. Predictions about the behavior of future ecosystems in an atmosphere with a higher concentration of $CO_2$ require an understanding of how the primary responses to $CO_2$ interact with the attributes of the different systems. As reports in this issue show, we should not expect a bog and a desert, nor a wheat field and a tree plantation, to respond identically to $CO_2$ enrichment – nature is not that simple.

Nevertheless, tremendous progress is being made in providing the data and understanding needed for making – and having confidence in – predictions about the future. Papers in this volume have tackled some of the thorny problems of detecting changes in soil carbon, seeking functional group classifications of plant response, and scaling from leaf to stand. The end-point of experiments in agricultural systems is no longer simply yield, but includes consideration of nutritional quality for grazers or humans. Technological advances in $CO_2$ enrichment technology are allowing ecosystem-scale experiments in a greater diversity of ecosystems. The ongoing research described here is not the culmination of Enoch's call for a multinational effort on $CO_2$ responses of ecosystems, but part of a steady process of hypothesis formulation and testing at ever-increasing scales and levels of complexity. That process needs to continue.

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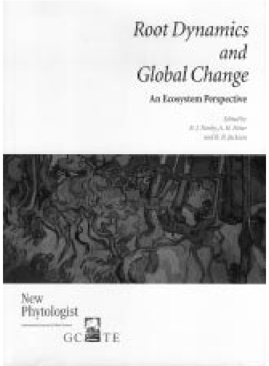
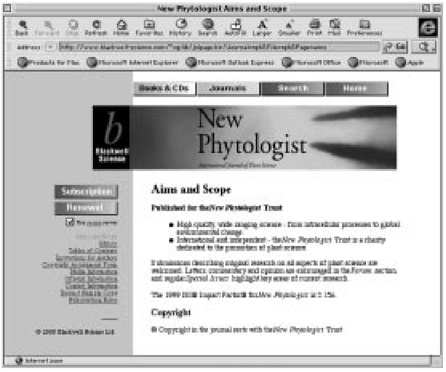
**Key words:** free-air $CO_2$ enrichment (FACE), ecosystems, atmospheric $CO_2$, modeling, scale.





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