

## Review article

# Oaks in a high-CO<sub>2</sub> world

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**Summary** — The concentration of carbon dioxide in the atmosphere is one environmental factor that is certain to influence the physiology and productivity of oak trees everywhere. Direct assessment of the impact of increasing CO<sub>2</sub> is very difficult, however, because of the long-term nature of CO<sub>2</sub> effects and the myriad potential interactions between CO<sub>2</sub> and other environmental factors that can influence the physiological and ecological relationships of oaks. The CO<sub>2</sub> responses of at least 11 *Quercus* species have been investigated, primarily in experiments with seedlings. The growth response varies considerably among these experiments, and there appears to be no basis for differentiating the response of oaks as a group from those of other woody plants. The more important challenge is to find a basis for addressing questions about the responses of oak forest ecosystems from experimental data on individual seedlings and saplings. A series of experiments with white oak (*Quercus alba* L.) seedlings and saplings was focused toward larger-scale questions, such as whether N limitations would preclude growth responses to elevated CO<sub>2</sub> and whether short-term physiological responses could be sustained over longer time scales. These experiments suggested three issues that are particularly important for addressing forest responses: leaf area dynamics, fine root production, and biotic interactions. By focusing seedling and sapling experiments toward these issues, we gain insight into the important processes that will influence ecosystem response and, at least in a qualitative sense, the sensitivity of those processes to elevated CO<sub>2</sub>.

### atmospheric carbon dioxide / global change / *Quercus*

**Résumé** — Les chênes dans une atmosphère enrichie en CO<sub>2</sub>. La concentration en dioxyde de carbone dans l'atmosphère est un facteur de l'environnement qui influencera certainement la physiologie et la productivité des chênes partout à travers le monde. Une évaluation directe de l'impact d'un accroissement des concentrations en CO<sub>2</sub> est cependant difficile, du fait de la durée de ces effets et de la myriade d'autres facteurs de l'environnement susceptibles d'interagir avec le CO<sub>2</sub> pour influencer les caractéristiques physiologiques et écologiques de ces espèces. Les réponses à l'augmentation de CO<sub>2</sub> d'au moins 11 espèces de chênes ont été analysées, le plus souvent au travers d'expériences portant sur des jeunes plants. La croissance a été très diversement affectée au cours de ces expérimentations, et aucune différenciation des chênes en tant que taxon n'a pu être établie en comparaison avec d'autres espèces ligneuses sur la base de ces réponses. Cependant, la nécessité d'extrapoler les réponses obtenues à l'échelle de semis et de jeunes plants à celle des écosystèmes à base de chênes

constitue un redoutable défi. Une série d'expériences avec des semis et de jeunes plants de chêne blanc (*Quercus alba*) a été menée dans le but de répondre à deux questions sur la réaction de chênaies adultes : i) les limitations de croissance imposées par la disponibilité en azote pourront-elles contrebalancer l'effet positif potentiel de l'accroissement de  $CO_2$  ? ii) Les réponses physiologiques observées à court terme seront-elles maintenues à plus long terme ? Les expériences présentées suggèrent que trois phénomènes revêtent une importance particulière à l'échelle des écosystèmes forestiers : les dynamiques d'installation de la surface foliaire, la production de racines fines et les interactions biotiques. En orientant les expérimentations futures menées sur des jeunes plants de manière à répondre à ces questions, nous pourrions obtenir des informations intéressantes sur des processus importants pour la réponse des écosystèmes, et, au moins de manière qualitative, la sensibilité de ces processus à des augmentations de  $CO_2$ .

### **dioxyde de carbone atmosphérique / changements globaux**

#### **THE PROBLEM OF SCALE**

Among the many environmental factors that will be influencing the physiology and productivity of oak trees in the coming decades, one factor – the concentration of carbon dioxide in the atmosphere – is certain to increase in importance wherever oaks grow. From a preindustrial concentration of about  $280 \mu\text{mol mol}^{-1}$  and the current value of about  $360 \mu\text{mol mol}^{-1}$ , the  $CO_2$  concentration is increasing about 0.5% per year, and it could reach as high as twice the preindustrial concentration during the next century, even if anthropogenic emissions of  $CO_2$  were kept constant at present day rates (Watson et al, 1990). Because  $CO_2$  is a radiatively active gas in the atmosphere, the increased concentration is expected to cause an alteration in earth's climate system, leading to a general warming of the planet and disruption of precipitation patterns.

These global changes in the atmospheric and climatic system are expected to have an important impact on the terrestrial biosphere, and the potential impact on forests is especially important given their prominent role in the global carbon cycle (Post et al, 1990). Climate change – specifically, increased temperature and altered water balance – could lead to changes in the productivity of trees and the composition of forests. While oak species generally are well

adapted to growth on drought-prone sites (Abrams, 1990), they nevertheless respond physiologically to water deficits, and drought may alter their resistance to other stresses, pests, or pathogens. While such responses to climate change could be profound, they are very difficult to predict because of the large uncertainty in relating global climate change to the environment affecting an individual tree. This paper, then, focuses on the *direct* effects of increasing  $CO_2$  concentration on trees and forests, and not on the indirect effects via climate change.

As the primary substrate for photosynthesis, and hence tree growth and biomass accumulation,  $CO_2$  plays a fundamental role in tree physiology, and increased  $CO_2$  concentrations can be presumed in the first analysis to lead to a stimulation of tree growth and forest productivity. If increased forest productivity also means increased sequestration of carbon by forests, then the rate of increase in atmospheric  $CO_2$  could be slowed. Hence, an understanding of the response of trees to elevated concentrations of atmospheric  $CO_2$  will improve not only our ability to predict the productivity of oak trees in the future, but it will also contribute to the analysis of the complex issue of global change.

The important questions about oak trees and global change are easier to ask than they are to answer. The large size and long

life of trees preclude experiments in which the future atmospheric environment is simulated for a significant portion of a tree's life span. Realistic experimental approaches to forest ecosystem responses are even more difficult. Nevertheless, the questions are too important to ignore, and indirect experimental approaches must be used. In particular, it is important to interpret data from experiments with seedlings and young trees in a manner consistent with the critical processes controlling longer-term and larger-scale responses. The objectives of this paper are first, to consider whether the existing data on tree seedling responses to elevated CO<sub>2</sub> allow us to draw any conclusions specific to the genus *Quercus*, and second, to consider how seedling data on carbon and nutrient interactions might be used to address questions pertaining to larger trees and forest ecosystems in the CO<sub>2</sub>-enriched world of the future.

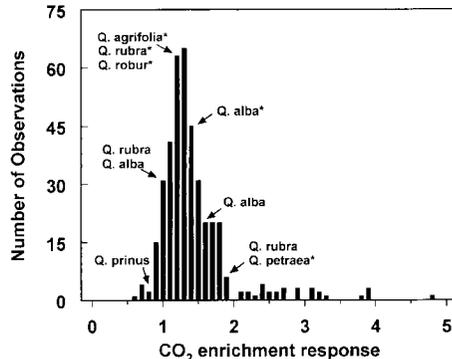
## RESPONSES OF OAK SPECIES TO ELEVATED CO<sub>2</sub>

### Growth responses

A wide variety of woody plants have been used in CO<sub>2</sub> enrichment experiments ranging from short-term (days or weeks) characterization of biochemical and photosynthetic responses to longer-term studies (months or several years) of interactions with herbivores and soil microbes. Growth responses are a common feature of most of these studies (Eamus and Jarvis, 1989; Ceulemans and Mousseau, 1994). There have probably been more species of *Quercus* investigated in these studies than for any other angiosperm tree genus (table I). Are there any common features of their response to elevated CO<sub>2</sub> that differentiates them from other species?

The growth response of 73 tree species to elevated CO<sub>2</sub> concentrations in controlled-environment experiments was compiled from the literature by Wullschlegel et al (1995b). The average response was a 32% increase in plant mass, but the response varied over a wide range (fig 1). The oak species included in this data base (and other observations not in the original data base) appear throughout the frequency distribution, and there is no indication of clumping. There is as much variation within the genus as within the woody plant population as a whole. This variation is more likely to be associated with differences in experimental protocol and other environmental variables than with inherent differences between the species. From this analysis there is no basis for statements about growth response to CO<sub>2</sub> enrichment that are particular to the genus *Quercus*.

The various investigations of oaks in elevated CO<sub>2</sub> have considered many other



**Fig 1.** Frequency distribution of the response of woody plants to elevated CO<sub>2</sub> in controlled-environment experiments. The figure was adapted from Wullschlegel et al (1995b). The CO<sub>2</sub> enrichment response is the ratio of plant dry mass in elevated CO<sub>2</sub> to dry mass in ambient CO<sub>2</sub>, as reported in 58 studies with 73 species. The geometric mean response was 1.32, or a 32% increase in mass in elevated CO<sub>2</sub>. The occurrence of several *Quercus* species in this data base is indicated; additional *Quercus* species that were not part of this analysis are also included (indicated by \*).

**Table I.** *Quercus* species used in elevated CO<sub>2</sub> experiments.

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<i>North American species</i>	
Deciduous	
<i>Q. alba</i>	Norby et al, 1986a,b; O'Neill et al, 1987; Norby and O'Neill, 1989; Wullschlegler and Norby, 1992; Wullschlegler et al, 1992; Gunderson et al, 1993; Cooper and Norby, 1994; Norby et al, 1995; Wullschlegler et al, 1995a
<i>Q. prinus</i>	Bunce, 1992
<i>Q. rubra</i>	Williams et al, 1986; Sharkey et al, 1991; Bazzaz and Miao, 1993; Bazzaz et al, 1993; Lindroth et al, 1993; Dixon et al, 1995
Evergreen	
<i>Q. agrifolia</i>	Oechel and Gluckman, 1992
<i>Q. geminata</i>	Vieglais et al, 1994
<i>Q. myrtifolia</i>	Vieglais et al, 1994
<i>European species</i>	
Deciduous	
<i>Q. petraea</i>	Guehl et al, 1994; Epron et al, 1994; Seegmüller and Rennenberg, 1994; Picon et al, 1996a,b
<i>Q. pubescens</i>	Miglietta and Raschi, 1993
<i>Q. robur</i>	Bunce, 1992; Beerling and Chaloner, 1993; Vivin et al, 1995, 1996
Evergreen	
<i>Q. ilex</i>	Paoletti and Gellini, 1994; De Angelis and Scarascia-Mugnozza, 1994
<i>Q. suber</i>	Pereira et al, 1994

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\* Only full papers are referred to unless only reports or abstracts are available for the species.

measures of response besides growth. Generally, the responses to CO<sub>2</sub> enrichment in oaks, as in other tree species, usually include increased photosynthesis rate, water-use efficiency, and leaf mass per unit area, and decreased respiration and foliar N concentration. The studies discussed below represent a wide range of objectives and approaches. However, there seems to be no common thread differentiating the responses of oaks from those of other woody species.

### **Environmental Interactions**

Many of the CO<sub>2</sub> enrichment studies conducted with oak species have emphasized

the interactions with other environmental resources. Seedling growth of *Q. rubra* and other late successional species was stimulated by elevated CO<sub>2</sub> more in low light than in high light, and large-seeded species, such as oak, were more responsive to CO<sub>2</sub> than small-seeded species (Bazzaz and Miao, 1993). Elevated CO<sub>2</sub> for one growing season increased growth of *Q. petraea* by 138% under well-watered conditions, but only 47% under drought conditions (Guehl et al, 1994). Increases in leaf area were proportionately less: 112% in well-watered plants and 21% in droughted plants. Whole-plant water-use efficiency was 80% higher in elevated CO<sub>2</sub>. Although the growth responses of *Q. robur* to elevated CO<sub>2</sub> were less than those of *Q. petraea*, a similar rela-

tionship with drought was reported (Picon et al, 1996a). CO<sub>2</sub> enrichment increased dry mass by 39% in optimally watered seedlings, and there was no significant effect in droughted seedlings. Whole-plant water-use efficiency increased by 47 and 18%, respectively. Osmotic adjustment occurred only in CO<sub>2</sub>-enriched plants, but this was insufficient to alleviate drought stress (Vivin et al, 1996).

### **Leaf-level responses**

Responses to CO<sub>2</sub> are also measured at the leaf level. Stomatal density of herbarium specimens of *Q robur* (Beerling and Chaloner, 1993) and *Q ilex* (Paoletti and Gellini, 1993) showed significant reductions in stomatal density over the past 150–200 years, which the authors associated with the increasing CO<sub>2</sub> concentration over that time. Similar effects were observed on *Q pubescens* leaves growing in a natural CO<sub>2</sub> spring in Italy (Miglietta and Raschi, 1993). Stomatal density was not affected by CO<sub>2</sub> concentration in *Q petraea* (Guehl et al, 1994) or *Q rubra* (Dixon et al, 1995).

Increased whole-plant water-use efficiency in elevated CO<sub>2</sub> (Norby and O'Neill, 1989; Guehl et al, 1994; Picon et al, 1996a) can occur because of increased photosynthesis, decreased stomatal conductance, or decreased respiration. While decreased stomatal conductance is a common response to elevated CO<sub>2</sub> (Eamus and Jarvis, 1989), and lower conductance (or leaf transpiration rate) in elevated CO<sub>2</sub> has been reported for *Q robur* (Picon et al, 1996a), *Q petraea* (Picon et al, 1995b), and *Q alba* (Norby and O'Neill, 1989), in other studies there was no effect of CO<sub>2</sub> on stomatal conductance of *Q prinus*, *Q robur* (Bunce, 1992), or *Q rubra* (Dixon et al, 1995). Photosynthetic CO<sub>2</sub> assimilation was increased by elevated CO<sub>2</sub> in *Q alba* (Norby and O'Neill, 1989), and this response, along

with a lower transpiration rate, contributed to an increase in water-use efficiency measured both at the leaf level and at the whole-plant level. Leaf-level water-use efficiency increased in *Q petraea* without a significant increase in photosynthesis (Picon et al, 1996b). The initial increase in photosynthetic rate in *Q robur* was not sustained, but *Q prinus* seedlings always had higher photosynthesis in elevated CO<sub>2</sub> (Bunce, 1992). Both species had lower whole-plant respiration rates in elevated CO<sub>2</sub>. There also was no down-regulation of photosynthetic capacity in response to long-term CO<sub>2</sub> enrichment of *Q petraea* seedlings and no effect on the quantum yield of photosynthesis (Epron et al, 1994). The occurrence of down-regulation of photosynthesis during exposure to high CO<sub>2</sub> may be related to sink strength. Vivin et al (1995) showed that the effect of elevated CO<sub>2</sub> on photosynthesis and growth of *Q robur* seedlings was larger when sink strength, particularly of root tips, also was stimulated by CO<sub>2</sub>. The aforementioned increase in whole-plant water-use efficiency of *Q petraea* in elevated CO<sub>2</sub> (Guehl et al, 1994) was associated with a decrease in the proportion of daytime carbon fixation lost in respiration. Water-use efficiency of a native Florida scrub oak-palmetto community containing two dominant oak species (*Q myrtifolia* and *Q geminata*) was increased 34% in elevated CO<sub>2</sub>, and leaf respiration was reduced by 20% (Vieglais et al, 1994).

### **Secondary responses**

In addition to these primary effects of CO<sub>2</sub> enrichment, various secondary effects have been investigated in oaks, such as the influence of CO<sub>2</sub> on secondary metabolites. Isoprene is a hydrocarbon that is emitted by tree leaves and subsequently affects air quality. *Q rubra* leaves in high CO<sub>2</sub> (650 μmol mol<sup>-1</sup>) had twice the rate of isoprene emission as leaves grown at 400 μmol

mol<sup>-1</sup> CO<sub>2</sub> (Sharkey et al, 1991). At high temperature this stimulation in isoprene emission consumed over 15% of the photosynthetically fixed carbon. While the mechanism of this response was not known, the results were consistent with metabolic control of isoprene release. Foliar metabolites that can influence insect herbivory were measured in *Q rubra* grown in ambient and elevated CO<sub>2</sub> (Lindroth et al, 1993). Hydrolyzable and condensed tannins, which increased significantly in CO<sub>2</sub>-enriched *Acer saccharum* leaves, either declined or showed no change in *Q rubra* leaves, but starch concentration more than double in elevated CO<sub>2</sub>. Nitrogen concentration in these leaves was not affected by CO<sub>2</sub> concentration. This is not the typical response of most plants to elevated CO<sub>2</sub> (Conroy and Hocking 1993), and in other studies foliar N concentration declined with increasing CO<sub>2</sub> in *Q alba* (Norby et al, 1986a; O'Neill et al, 1987) and *Q petraea* (Guehl et al, 1994).

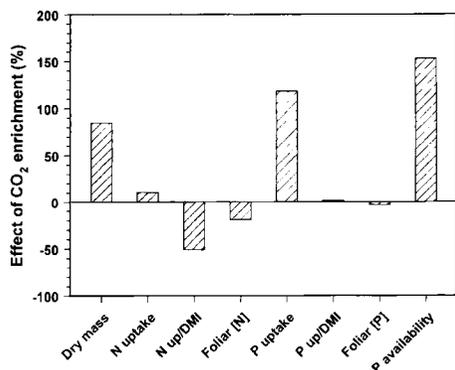
### **CAN ECOSYSTEM QUESTIONS BE ADDRESSED WITH SEEDLING STUDIES?**

While an important goal in global change research is to identify CO<sub>2</sub> responses across genera or functional types of plants (Poorter, 1993), an even more critical need is to examine the implications of seedling responses to the responses that can be expected in larger trees and forests. The primary rationale for conducting CO<sub>2</sub> enrichment experiments is the hope that such studies will provide insights to help predict larger-scale responses that have implications for the global carbon cycle or environmental quality. Rarely is the response of a seedling in a growth chamber, greenhouse, or open-top chamber of interest by itself. To examine the problems and possibilities of using results of experiments with seedlings to address ecosystem questions,

I will focus on the research program at the Oak Ridge National Laboratory, where we have examined the responses of *Q alba* L (white oak) to elevated CO<sub>2</sub> both in controlled environment chambers with potted seedlings and in open-top field chambers containing saplings rooted in the ground.

In our first experiment, white oak seedlings were grown in pots containing nutrient-poor forest soil and maintained in growth chambers for several months in ambient or elevated CO<sub>2</sub> (Norby et al, 1986a). The primary rationale for the experiment was that forest trees typically grow in nutrient-poor habitats, and it was essential to determine whether tree growth can be stimulated by elevated CO<sub>2</sub> when it is also limited by nutrient deficiency (Kramer, 1981). After 40 weeks in elevated CO<sub>2</sub>, whole-plant dry mass of the white oak seedlings was 85% greater than that of seedlings in ambient CO<sub>2</sub> (Norby et al, 1986a). This growth response was associated with increased retention of leaves (higher leaf area duration) in the CO<sub>2</sub>-enriched plants. Despite the increase in growth, N uptake from the unamended soil did not increase, and N concentration in the plant was significantly lower in elevated CO<sub>2</sub> (fig 2). Phosphorus uptake, on the other hand, did increase in elevated CO<sub>2</sub>, apparently because of an indirect effect of CO<sub>2</sub> on P availability (fig 2). This study demonstrated that a growth response to CO<sub>2</sub> enrichment is possible in nutrient-limited systems, and that the mechanism of response may include either increased nutrient supply or decreased physiological demand.

While some of the initial questions – which were derived from an ecosystem perspective – were answered in this study, it was also clear that the responses of seedlings over a 40-week period could not easily be extended to the scale of a forest. Some of the critical uncertainties that limited the extent to which the data could be extrapolated were canopy dynamics, the



**Fig 2.** The effect of elevated CO<sub>2</sub> (690  $\mu\text{mol mol}^{-1}$ ) on N and P relations in *Q. alba* seedlings during a 40 week experiment (Norby et al, 1986a), relative to seedlings in ambient (362  $\mu\text{mol mol}^{-1}$ ) CO<sub>2</sub>. DMI is dry matter increment. Total P availability was assumed to be equal to the sum of soil extractable P, plant uptake, and the small amount lost in leachate.

ersistence of increased N-use efficiency, litter quality and N cycling (Norby et al, 1986b). In order to begin addressing such questions, a deeper understanding of the physiological underpinnings of the response of white oak to elevated CO<sub>2</sub> was necessary. Therefore, a subsequent growth chamber study was designed to define the relative importance of photosynthetic enhancement versus leaf area adjustment as the basis for the growth response (Norby and O'Neill, 1989). The growth enhancement in this experiment was smaller than in the first experiment: a 29% increase at the highest CO<sub>2</sub> concentration. The response of leaf area production to CO<sub>2</sub> enrichment was the key factor explaining the difference in responsiveness between the two experiments. In this second experiment there was no difference in leaf area ratio (leaf area divided by plant mass) because leaf retention was not altered as in the first experiment. The growth response, then, was directly associated with the CO<sub>2</sub> stimulation at the leaf level rather than increased leaf production, a result that was observed

through mathematical growth analysis and direct measurement of photosynthetic CO<sub>2</sub> assimilation. This contrast between the two experiments was an early warning of the importance of separating leaf area dynamics, which may be especially sensitive to specific aspects of experimental design and protocol, from a more fundamental response in leaf-level physiology.

A central hypothesis of these and related experiments with other species was that elevated CO<sub>2</sub> would stimulate below-ground activity such that nutrient availability would increase. In the first experiment (Norby et al, 1986a), fine roots were the most responsive plant component to CO<sub>2</sub> enrichment – a potentially important response that we would have missed if fine roots had been lumped with woody roots. An increased proliferation of fine roots in the nutrient-poor soil was assumed to provide an increase in the total numbers of rhizosphere bacteria and mycorrhizal root tips in the system since these populations per unit fine root did not change significantly. Consistent with this reasoning was the apparent increase in P availability (fig 2). More detailed observations of mycorrhization on white oaks showed that CO<sub>2</sub> enrichment immediately stimulated the establishment of mycorrhizae, and the effect persisted through time (O'Neill et al, 1987). It was recognized that longer-term experiments would be necessary to determine whether the enhancement of mycorrhization would persist for multiple-growing seasons.

## SAPLING STUDIES AND THEIR IMPLICATIONS FOR ECOSYSTEMS

The experiments with seedlings were successful in answering many of our initial questions. They demonstrated that nutrient limitations do not necessarily preclude growth responses to elevated CO<sub>2</sub>. They also emphasized the importance of leaf area

dynamics and fine root production to the overall growth response. Furthermore, it became clear that the critical questions concerning longer-term forest response to elevated  $\text{CO}_2$  would depend on how  $\text{CO}_2$  affected the interaction of trees with other environmental resources. For example, would the enhancement of photosynthesis be sustained or would carbon or nutrient feedbacks dampen the response over time? What are the implications of increased leaf-level water-use efficiency for a tree's drought resistance? Does increased wood production imply that more N is sequestered in wood and not available for cycling? If so, increased growth in an N-limited system could only be sustained if N availability increased (eg, increased mineralization or N deposition). While the experiments with potted seedlings enabled us to ask these questions more clearly, longer-term experiments (ie, more than one growing season) under conditions more closely resembling the forest environment were needed even to begin to answer them. Hence, an open-top chamber experiment was initiated in 1989 (fig 3). Three primary objectives of this field experiment were to: i) determine whether the short-term responses of tree seedlings to elevated  $\text{CO}_2$  are sustained over several growing seasons under field conditions; ii) compare the responses of white oak to elevated  $\text{CO}_2$  with those of yellow-poplar (*Liri-*



**Fig 3.** Open-top field chambers with *Q alba* saplings in Oak Ridge, TN, USA.

*odendron tulipifera* L) (Norby et al, 1992; and iii) provide data and insights relevant for predicting forest ecosystem responses to elevated  $\text{CO}_2$ .

Many of the responses of the oaks in this experiment during the 4 years of exposure to elevated  $\text{CO}_2$  have been discussed elsewhere (Wullschleger and Norby, 1992; Gunderson et al, 1993; Wullschleger et al, 1995a; Norby et al, 1995). Here, I will consider three themes suggested from our seedling studies that are particularly important for addressing forest responses: leaf area dynamics, fine root production, and biotic interactions. Additional considerations of  $\text{CO}_2$  effects on water relations and drought resistance have not been adequately addressed in our experiment beyond the seedling level.

### **Leaf area dynamics**

After four full growing seasons in elevated  $\text{CO}_2$  ( $650 \mu\text{mol mol}^{-1}$ ), the white oaks in this experiment had 130% more dry mass than the oaks grown in open-top chambers with ambient  $\text{CO}_2$  ( $350 \mu\text{mol mol}^{-1}$ ). If this large growth response were to be sustained for many years, there would be a substantial increase in the amount of carbon sequestered by oak forests, with a beneficial negative feedback on the accumulation of carbon in the atmosphere. Analysis of the leaf area dynamics of the oaks in this system, however, clearly indicate that the large difference in tree mass could not be sustained. The effect of  $\text{CO}_2$  on growth was established very early in the experiment when the seedlings were being raised from acorns in  $\text{CO}_2$ -controlled growth chambers and for the first several months after they were planted in the field chambers. This initial stimulation of growth in elevated  $\text{CO}_2$  was associated with increased leaf area, and increased leaf area provides greater growth potential and subsequent leaf area

production, and so on with compound interest (Blackman, 1919). Hence, the absolute difference between CO<sub>2</sub> treatments increased with time, even without a sustained CO<sub>2</sub> effect on growth rate. This compounding interest effect, however, would be sustainable only so long as the potential to produce leaf area is not constrained. In a developing forest, leaf area eventually reaches a maximum determined primarily by the availability of light, water, nutrients, and other resources (Waring and Schlesinger, 1985). Hence, the longer-term implication of this data set – which is what we are really interested in – is not that white oak trees will be 130% larger in the future, but perhaps that the time required for an oak stand to reach canopy closure is shortened by about 1 year (Norby et al, 1995).

Whole tree dry mass is seemingly the measure most relevant to questions about effects of CO<sub>2</sub> concentration on carbon storage in forests, and the absence of a sustained effect on growth rate in this experiment seems to imply that tree mass will not increase over the long term. However, further analysis suggests that there is potential for elevated CO<sub>2</sub> to have lasting effects in an oak forest. Photosynthesis per unit leaf area remained higher in the CO<sub>2</sub>-enriched oaks (Gunderson et al, 1993), and leaf respiration was lower (Wullschlegel and Norby, 1992). The annual increment in stem biomass per unit leaf area (growth efficiency; Waring and Schlesinger, 1985) was 37% higher in elevated CO<sub>2</sub> (Norby et al, 1995), quite similar to the 35% increase observed in yellow-poplar (Norby et al, 1992). Unlike the response of biomass production, which could not continue to the same degree after leaf area reaches a maximum, there is no obvious reason to assume that the relative effect of CO<sub>2</sub> on growth efficiency would decline after canopy closure. The ultimate effect of rising CO<sub>2</sub> on net primary productivity of forests stands might best be considered by separating the response into two

principal components: i) the primary effect of CO<sub>2</sub> on the efficiency of leaves to produce woody biomass; and ii) secondary responses to CO<sub>2</sub> that alter the effect of various environmental influences on leaf area index. Awareness of the importance of leaf area dynamics will increase the value of data from seedling and sapling studies for addressing larger-scale forest response issues.

### **Root growth**

The focus of our seedling studies was on below-ground responses to elevated CO<sub>2</sub>, but in designing a field study in which an important feature was providing an unconstrained rooting environment to support several years' of tree growth, we precluded extensive observation and measurement of below-ground responses. However, the importance of root growth, carbon flux to soil, and microbial activity to the integrated response of ecosystems to elevated CO<sub>2</sub> is becoming increasingly clear (Curtis et al, 1994). Hence, despite the experimental difficulties, and the incomplete and fragmentary data sets that resulted, some measurements of below-ground responses were essential.

White oak has a large tap root, and it invests a considerable amount of carbon to root growth, especially early in its life (Abrams, 1990). Previous studies with seedlings indicated that much of the response to CO<sub>2</sub> would be observed in the root (Norby et al, 1986a). We excavated the woody root system of the white oaks in the open-top chambers at the end of the experiment. The tap root, which extended as deep as 1.2 m, was pulled from the ground after lateral roots had been severed. The mass of the lateral roots, which extended in a radius of 1–2 m from the trunk, was estimated from their diameter at the point of attachment to the tap root, using a regression relationship established with 46 lateral root systems that

had been completely excavated. Woody root mass increased with increasing CO<sub>2</sub> concentration in similar proportion to the increases observed in stem mass. However, analysis of the allometric relationship between root mass and stem mass suggested that ontogenetic shifts may have concealed an increased allocation of carbon to root systems in CO<sub>2</sub>-enriched plants (Norby, 1994).

Ontogenetic relationships are especially critical with regard to fine root production (Norby, 1994). In seedlings, fine roots may comprise a significant percentage of the total root mass; hence, a CO<sub>2</sub> effect on fine root production translates into an increase in root mass. In saplings and larger trees, however, fine root mass is a much smaller percentage of the root system, and significant increases with CO<sub>2</sub> enrichment will not necessarily be associated with increased whole-plant dry mass or carbon storage (Norby et al, 1992). Nevertheless, fine roots are important physiologically (water and nutrient uptake), as a platform for rhizosphere microbial activity, and over decadal time frames as a source of carbon sequestered as soil organic matter (Norby, 1994). The importance of fine roots compared to woody roots

depends on the question or issue being addressed. Failure to separate these two components of the root system, whether in seedling or field studies, will limit the value of the data in addressing larger-scale issues of forest ecosystem response to CO<sub>2</sub>. Root-to-shoot mass ratio of seedlings in response to CO<sub>2</sub>, for example, will probably have limited utility beyond the outlines of the specific experiment because it ignores ontogenetic changes in root structure.

Fine root density (mass of fine roots per unit soil surface area) was measured in soil cores in the open-top chambers with the white oak trees. There was a greater fine root density in the CO<sub>2</sub>-enriched chambers, and this increase was associated with increased efflux of CO<sub>2</sub> from the soil, even though specific respiration rate of the fine roots was lower in elevated CO<sub>2</sub> (table II). While these observations are useful for formulating hypotheses about below-ground processes, they are inadequate for actually answering the important long-term questions. One of the critical uncertainties is whether higher fine root density in high CO<sub>2</sub> indicates increased fine root production and root turnover. Continuous observations of fine root production and mortality in a CO<sub>2</sub>

**Table II.** Root respiration and CO<sub>2</sub> efflux from soil around white oaks grown for 4 years in ambient or elevated CO<sub>2</sub>.

<i>CO<sub>2</sub> enrichment</i> ( $\mu\text{mol mol}^{-1}$ )	<i>Specific root respiration</i> ( $\text{nmol g}^{-1} \text{s}^{-1}$ )	<i>Root mass density</i> ( $\text{g m}^{-2}$ )	<i>Total fine root respiration</i> ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	<i>CO<sub>2</sub> efflux from soil</i> ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )
Ambient (+0)	100	100	100	100
+150	90	124	111	122
+300	65	242	157	137

Specific respiration of fine (< 1 mm diameter) roots was measured with a LiCor 6200 immediately after removal from a 10 cm diameter soil core. The cores were taken for quantification of fine root density from the positions where steady-state CO<sub>2</sub> efflux had previously been measured with a modified LiCor 6200 system (Hanson et al, 1993). Because of the many potential errors in calculation of total root respiration, the data are expressed here in relative terms. Values are expressed as percentages of ambient values.

experiment with *Populus* showed that CO<sub>2</sub> stimulated both production and mortality, and turnover could not be predicted from static measures (Pregitzer et al, 1995). Another uncertainty is the extent to which fine root density continues to increase in a developing forest stand; that is, can the response to CO<sub>2</sub> be sustained over time? CO<sub>2</sub> effects on fine root production may be irrelevant once a site has reached a maximum fine root density. In that case, only changes in activity per unit root tissue would be useful for scaling up. The importance of this scaling consideration is apparent in our measurements of white oak root respiration: specific fine root respiration decreased with increasing CO<sub>2</sub>, but the calculated total fine root respiration increased (table II).

### **Biotic interactions**

The differences in time and space scales between an oak forest and an oak seedling in a pot, or several oak saplings in an open-top chamber, are obvious, but another important scaling issue is the increasing complexity of biotic interactions. While it is clear that biotic interactions should be an important part of our analysis of how elevated CO<sub>2</sub> will affect forests in the future, smaller-scale studies can investigate only isolated components of the complex system. Three areas of interest have been identified in studies with white oak: rhizosphere (including mycorrhizal) responses, litter decomposition, and herbivory.

Mycorrhization of the white oak root system was assessed when the saplings were harvested. The response was quite similar to that previously reported for oak seedlings: with increasing CO<sub>2</sub> concentration, there was a significant increase in percentage of roots that were mycorrhizal (O'Neill, 1994). Hence, it appears that this is not simply a short-term response but is one that could persist and shape the overall response of

an ecosystem to elevated CO<sub>2</sub> (O'Neill et al, 1991). Consideration of mycorrhizal responses at higher scales must focus on the importance of increased mycorrhization on nutrient availability and the carbon economy of the ecosystem. Other microbial populations in the rhizosphere were not as responsive as mycorrhizal fungi. Ringelberg and White (1994) assessed white oak rhizosphere populations and community structure through the signature lipid biomarker technique (Vestal and White, 1989). There were no CO<sub>2</sub> effects on these measures when expressed relative to fine root mass, which suggests that responses controlled by the rhizosphere might scale simply with fine root density.

Consideration of oak seedling responses suggested that increased N-use efficiency in elevated CO<sub>2</sub> could not be sustained indefinitely, and for a continued growth response of forest trees to CO<sub>2</sub> enrichment there must be an increase in N availability (Norby et al, 1986b). Nitrogen availability in forests is largely regulated by the soil microbial community, which mineralizes soil organic matter, and by the quality of the substrate (eg, leaf litter) introduced into the soil system. While the biotic interactions between soil microorganisms and leaf litter from trees grown in elevated CO<sub>2</sub> are difficult to quantify, it is possible to quantify CO<sub>2</sub> effects on leaf litter quality. The chemical composition of white oak leaves from each of the four growing seasons of the open-top chamber experiment is shown in table III. Nitrogen concentration tended to be slightly lower in the elevated CO<sub>2</sub> treatments, and lignin-to-N ratio tended to be higher, but the differences were small, not statistically significant, and translated into small differences in predicted decomposition rates. The concentration of phenolics tended to be higher in elevated CO<sub>2</sub>, as we had previously observed in white oak litter from growth chamber experiments (Norby and Pastor, unpublished data). As would be predicted

**Table III.** Litter quality of white oak leaves grown in open-top chambers and collected after they had senesced and abscised naturally at the end of each of the four growing seasons.

Year	CO <sub>2</sub> enrichment (μmol mol <sup>-1</sup> )	Nitrogen <sup>a</sup> (mg g <sup>-1</sup> )	Extractives <sup>a</sup> (mg g <sup>-1</sup> )	Lignin <sup>a</sup> (mg g <sup>-1</sup> )	Cellulose <sup>a</sup> (mg g <sup>-1</sup> )	Phenolics <sup>b</sup> (mg g <sup>-1</sup> )	Lignin to N ratio	k <sup>c</sup>
1989	+0	10.0 ± 1.2	489 ± 6	136 ± 10	375 ± 4	134 ± 10	13.7 ± 2.7	0.95 ± 0.07
	+150	8.7 ± 0.5	473 ± 9	139 ± 1	388 ± 11	167 ± 12	16.2 ± 1.2	0.88 ± 0.03
	+300	9.2 ± 3.2	481 ± 17	140 ± 2	379 ± 16	163 ± 22	16.8 ± 6.0	0.88 ± 0.15
1990	+0	10.3 ± 0.5	409 ± 9	150 ± 3	442 ± 6	136 ± 3	14.6 ± 1.1	0.92 ± 0.03
	+150	9.0 ± 0.1	408 ± 3	152 ± 3	440 ± 1	139 ± 20	16.8 ± 0.4	0.87 ± 0.01
	+300	9.8 ± 0.3	409 ± 3	152 ± 2	440 ± 2	136 ± 11	15.6 ± 0.3	0.90 ± 0.01
1991	+0	10.3	385	152	463	148	10.7	0.92
	+150	9.5	377	159	464	167	11.1	0.87
	+300	10.1	371	161	468	159	12.5	0.89
1992	+0	11.0 ± 1.3	373 ± 30	162 ± 11	464 ± 24	74 ± 29	14.9 ± 2.1	0.92 ± 0.05
	+150	10.2 ± 2.0	377 ± 38	156 ± 20	464 ± 24	98 ± 45	15.8 ± 3.8	0.90 ± 0.10
	+300	10.0 ± 2.0	390 ± 40	155 ± 17	456 ± 27	97 ± 36	16.1 ± 4.2	0.89 ± 0.10

Data from 1989 and 1990 are the means (± SD) of composited samples from two open-top chambers per treatment. Litter samples from 1991 were composited prior to analysis. Data from 1992 were collected from each of five plants per chamber and analyzed by plant. No differences are statistically significant.

<sup>a</sup>The concentrations of N, lignin, and cellulose were measured by near-infrared reflectance spectroscopy (Wessman et al., 1988), using prediction equations established from forage fiber analysis (Goering and Van Soest, 1970; Ryan et al., 1990) conducted at A & L Laboratories (Memphis, TN, USA) on a subset of the 1989 white oak litter samples and yellow-poplar (*Liriodendron tulipifera*) litter samples from another experiment. The regression equations developed by Ryan et al. (1990) were used to adjust the cellulose and lignin values to those corresponding to wood chemistry analysis. The extractives fraction was calculated by difference. <sup>b</sup>The concentration of phenolics was also measured by near-infrared reflectance spectroscopy using a prediction equation based on an analysis of the water-soluble compounds in white oak litter by the Folin-Denis method (Swain and Hillis, 1959), with the data reported as tannic acid equivalents. This analysis was conducted by John Pastor and Brad Dewey, University of Minnesota-Duluth. <sup>c</sup>The exponential decay coefficient (*k*), which describes the mass loss of litter over time, was predicted from the lignin-to-N ratio of the litter using the equation of Pastor and Post (1986), adjusted for the actual evapotranspiration in Oak Ridge, TN (797 mm year<sup>-1</sup>).

from these observations, there was no effect of the growth CO<sub>2</sub> concentration on the subsequent rate of decomposition (mass loss) of white oak leaf litter maintained for 2 years in mesh bags in the litter layer of an oak forest (O'Neill, personal communication). Leaf litter chemistry is an excellent example of how a response to CO<sub>2</sub> enrichment at the level of physiology can provide information relevant to the longer-term responses of a forest ecosystem.

The basic concepts of how CO<sub>2</sub> effects on leaf litter quality could interact with soil biota also apply to an above-ground biotic interaction (herbivory). The performance of phytophagous insects is influenced by the availability of carbon and N in leaf tissue (Lindroth et al., 1993). To test whether CO<sub>2</sub> effects on leaf chemistry influenced the performance of the gypsy moth (*Limantria dispar*), second instar larvae were fed young, expanding white oak leaves from the open-top chambers, while fifth instar larvae received older, mature foliage (Williams and Lincoln, 1994). Growth of the early instar larvae was significantly reduced on CO<sub>2</sub>-enriched leaves because of a lower concentration of N in these leaves. The performance of older larvae was not affected by the lower N concentration in CO<sub>2</sub>-enriched litter because of a compensatory increase in N utilization efficiency of the larvae. The conclusion from this study was that there were some negative effects of elevated CO<sub>2</sub> on the gypsy moth, but compensatory mechanisms over both the short and long term resulted in no significant alteration in this important biotic interaction (Williams and Lincoln, 1994).

## FOREST ECOSYSTEM STUDIES

Seedling and sapling studies can provide valuable insights and even quantitative data about certain components of forest ecosystems and how they might respond to

increased atmospheric CO<sub>2</sub>, but the integration of those component responses is much more difficult. There are, however, new experimental approaches with oaks that will in some way provide true ecosystem-level responses. An open-top chamber experiment in the Florida scrub oak-palmetto community exposes small parts of an intact ecosystem to elevated CO<sub>2</sub> (Vieglais et al., 1994), and in Italy the "macchia" community with evergreen oaks is enclosed intact in chambers (De Angelis and Scarascia-Mugnozza, 1994). These studies are possible because of the slow growth and sparse vegetation of these communities, in contrast to the larger, faster growing, and much more complex temperate deciduous forests with *Q alba*, *Q rubra*, *Q robur* or *Q petraea*. Because of the small size of the exposure chambers relative to the scale of the ecosystem and the necessary use of whole trees or root systems that had developed under current ambient atmospheric conditions, the results from such ecosystem-level experiments must be interpreted cautiously, just as is the case with experiments of saplings planted within CO<sub>2</sub> exposure chambers.

Another promising experimental approach for studying the CO<sub>2</sub> responses of intact oak ecosystems is the use of natural CO<sub>2</sub> springs (Miglietta and Raschi, 1993). Oak trees and the associated community in the vicinity of some of these springs have been exposed to high CO<sub>2</sub> concentrations for centuries, and the systems can be studied without artificial enclosures. There are, of course, problems: no true control, uncertain exposure regime, and possible phytotoxic gases accompanying the CO<sub>2</sub>. Nevertheless, carefully chosen sites could provide valuable measures of the response to CO<sub>2</sub> of an ecosystem that includes oak trees.

Eventually, there may be a controlled, replicated exposure of a complex oak-dominated ecosystem using free air CO<sub>2</sub> expo-

sure (FACE) technology (Hendrey, 1992). This would be a very large and expensive experiment, but it would have important advantages over the current approaches. With a larger and unconfined exposure area, more ecological complexity and diversity could be included in the analysis, while maintaining controlled CO<sub>2</sub> concentrations and rigorous statistical designs. Still, a free air CO<sub>2</sub> exposure will not be a panacea for questions about future forest responses because of the long time constants for so many forest tree and soil processes.

Finally, there is the necessity of process models to address ecosystem questions about global change. Kirschbaum et al (1994) used the G'DAY model of Comins and McMurtrie (1993) to explore whether an instantaneous carbon gain by woody plants would translate into increased growth in the longer term under nutrient-limited conditions. This is the same question that we had asked in our experiments with white oak seedlings and saplings, except the modeling approach allowed addressing the question over a 100-year time period and with the inclusion of many ecosystem properties such as N mineralization and wood decay. The modeling approach also allowed the testing of the importance of various assumptions about the sensitivity of plant production to different processes, using experimental data (such as from white oak experiments) as guidance. The conclusion of this particular exercise was that trees growing under nutrient-limited conditions can respond to increasing atmospheric CO<sub>2</sub> concentrations with considerable (as much as 19%) increases in growth – a conclusion similar to that which emerged from short-term experiments with white oak seedlings (Norby et al, 1986a). While this agreement in conclusions is quite satisfying and increases our confidence in addressing ecosystem questions with physiological data, a more important outcome of the modeling approach is the identification of key assumptions – such as

the effect of CO<sub>2</sub> on the relationship between foliar and wood N – that can be tested in new CO<sub>2</sub> enrichment experiments.

## CONCLUSION

The important questions about how oak forests will be influenced by the increasing concentration of CO<sub>2</sub> in the atmosphere are questions that involve the competitive interactions between trees, nutrient cycling, canopy development, interactions with herbivores, environmental stresses, and myriad other interactions that are part of the complexity of a forest ecosystem. We cannot conduct replicated experiments that incorporate all of this complexity. What we know about how different oak species respond to elevated CO<sub>2</sub> concentrations comes from studies at much smaller and simpler scales. These experiments generally indicate that oaks respond much like other woody species: the 'average' response of the genus (if such a concept is meaningful) and the variation among species in the genus do not support conclusions about qualitative or quantitative differences between *Quercus* and other genera.

The huge gulf between the scale of the data and the scale of the questions might seem to be unbridgeable, but the situation is not so hopeless. By focusing seedling and sapling experiments toward the larger ecosystem questions, we can gain insight into the important processes that will influence ecosystem response and, at least in a qualitative sense, the sensitivity of those processes to elevated CO<sub>2</sub>. In particular, experiments need to address the process involved in carbon sequestration in soil (eg, fine root turnover, microbial respiration), nutrient cycling (eg, retranslocation, litter decomposition, mineralization), and stress resistance (eg, mechanisms of drought stress resistance, herbivore interactions). These all are component processes of the

integrated response an intact ecosystem to global change that can be studied in part in manipulated experimental systems.

The increasing concentration of atmospheric CO<sub>2</sub> is a certainty, and the growth and physiology of oak trees worldwide will in some way be altered. The extent to which elevated CO<sub>2</sub> effects will be evident compared to other influences such as land use changes, insects and disease, or local droughts is impossible to determine. But a globally changing environment cannot be left out of consideration of environmental constraints and oaks.

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