Predicting the Response of a Temperate Forest Ecosystem to Atmospheric CO₂ Increase

DOE/ER/60257--7

DE93 010081

Annual Report 1992-1993
Request for Funds 1993-1994

Department of Energy grant DE-FGO2-84-ER60257

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1. The responses of temperate forest tree to 3 years of exposure to elevated CO₂, and high and low nutrient and light levels

In this study, six species were grown for three years under different CO₂, light, and nutrient conditions. The species used were ash (*Fraxinus americana* L.), gray birch (*Betula populifolia*), red maple (*Acer rubrum*), yellow birch (*Betula alleghaniensis*), striped maple (*Acer pensylvanicum*), and red oak (*Quercus rubra* L.), important tree species of temperate forests in New England, USA. The plants were grown in controlled environments either at 350 or 700 (ambient or elevated) $\mu\text{l l}^{-1}$ CO₂. The high light treatment (natural light) represented the light condition of a large gap at Harvard Forest (300 m²), whereas the low light treatment (37% of high light) approximately represented the light condition of the understory. The two nutrient treatments (high and low) simulated high nutrient deposition and organic matter mineralization rates (equivalent to 400 Kg N ha⁻¹ yr⁻¹) and nutrient-poor forest soil at Harvard Forest (equivalent to 40 Kg N ha⁻¹ yr⁻¹), respectively.

Plants growing in elevated CO₂ environments were larger than those growing at ambient CO₂ after three years (Fig. 4). Two-way analysis of variance (CO₂ and species) showed that there was a significant CO₂ main effect in all three years (in the 1st year $P < 0.0006$, in the 2nd year $P < 0.0009$, and in the 3rd year $P < 0.0069$). Weight ratios (the weight of plants grown in high CO₂ divided by that of plants grown in ambient CO₂) declined for four of the six species after the 1st year (Fig. 5). Only one species (striped maple) showed reduction in weight ratio after two years of increase. The enhancement of plant growth in response to high CO₂ levels was highly resource-dependent. Species identity determined whether weight ratio was stable or decreased or increased in the other three resource treatments.

Figure 1. Total plant mass of six temperate tree species grown under various levels of CO₂, nutrients and light for three years by pooling various light and nutrient treatments together. Error bars refer to one standard error.

Figure 2. Total weight of plants grown in $700\mu\text{l l}^{-1}$ CO_2 divided by that of plants grown in $350\mu\text{l l}^{-1}$ CO_2 for three years for five temperate tree species grown in four combinations of light and nutrient levels. "L" and "N" represent light and nutrient levels.

Photosynthesis of fully-developed leaves was measured on plants in each treatment. For each leaf, five measurements were taken at various CO_2 levels (900, 700, 500, 300, and $100 \pm 20\mu\text{mol}$). A/C_i curves were fit to the nonlinear model $A = A_{\infty}[1 - e^{-k(C_i - X_0)}]$, where the asymptotic level is the predicted saturated rate of CO_2 uptake, k is the rate of increase in photosynthesis with increase in CO_2 , and X_0 is the CO_2 compensation point. Relative stomatal limitation of photosynthesis (L) was calculated from this data using the formula $L = (1 - (A / A_0)) * 100$, where A is the actual P_s value at the ambient concentration of CO_2 and A_0 is the P_s value if the conductance to diffusion of CO_2 is infinite (no stomatal limitation). The CO_2 response of photosynthesis to intercellular CO_2 concentration (C_i) are shown in Fig. 6 for gray birch and red maple plants grown in ambient and elevated CO_2 , in conjunction with different light and nutrient treatments for three years. Symbols represent the measured data points and lines show the curves fitted to the data for each plant. The R_2 value for all curves was above 0.98 for gray birch and 0.95 for red maple. In general, in gray birch long-term exposure to elevated CO_2 affected the CO_2 response of photosynthesis in one of three ways: (a) the initial slope of the CO_2 response decreased, but the predicted CO_2 -saturated rate of photosynthesis (A_{∞}) increased (plants grown in the low nutrient); (b) the initial slope decreased, but the A_{∞} was unaffected (plants grown in high nutrient and high light); (c) the initial slope was unaffected, but the A_{∞} decreased (plants grown in high nutrient and low light). In contrast, in red maple long-term exposure to elevated CO_2 affected the CO_2 response of photosynthesis in one of three additional ways: (a) the initial slope increased, but A_{∞} decreased (plants grown in the high light); (b) the initial slope increased, but A_{∞} was unaffected (plants grown in the low nutrient and low light); (c) the initial slope was unaffected but A_{∞} slightly increased. The transition C_i

(C_i where a RuBP- saturated to a RuBP-limited state occurs) in the CO_2 response of photosynthesis curves was also affected by long-term exposure to elevated CO_2 . For plants grown at high CO_2 , the A/C_i curves did not bend off until much higher C_i levels compared with plants grown in ambient CO_2 in gray birch, but there was change in maple.

Figure 3. Photosynthesis as a function of intercellular CO_2 concentrations for gray birch and red maple plants grown in various levels of CO_2 , nutrients and light for three years. Each curve was fitted to the nonlinear model: $A = A_{\max}(1 - e^{-k(C_i - X_0)})$ from five measurements (open circle for 350 ppm plants and closed circle for 700 ppm plants) for one leaf per plant.

2. Pot-size limitations in CO_2 studies

A second area our research has focused on assessing the extent to which pot size and nutrient availability may influence the degree of CO_2 enhancement in our, and other CO_2 research. To investigate the relative importance of limited physical rooting space separate from and in conjunction with soil nutrients, we grew plants at ambient and double-ambient CO_2 levels in growth containers of varied volumes, shape, nutrient concentration, and total nutrient content. Two species (*Abutilon theophrasti*, a C_3 dicot with a deep tap root and *Setaria faberii*, a C_4 monocot with a shallow diffuse root system) were selected for their contrasting physiology and root architecture. Shoot demography was determined weekly and biomass was determined after eight and ten weeks of growth. Increasing total nutrients, either by increasing nutrient concentration or by increasing pot size, increased

plant growth. Further, increasing pot size while maintaining equal nutrients per pot, resulted in increasing total biomass for both species. But growth and reproductive yield enhancement under elevated CO_2 was either unaffected by pot size or was greater in smaller pots (Figure 2). CO_2 -induced growth enhancement was greatest in pots with high nutrient concentrations, regardless of total nutrient content or pot size, and was also mediated by the shape of the pot.

Figure 4. Reproductive and total biomass ($\text{g} \pm \text{SE}$) of 8 and 10 week old *Abutilon theophrasti* seedlings as a function of growth container nutrient content and volume, and CO_2 environment [$400 \mu\text{L L}^{-1}$ (solid bars) or $700 \mu\text{L L}^{-1}$ (shaded bars)], and enhancement of biomass production due to CO_2 enrichment. The three contrasts displayed represent the effects of 1) doubling total nutrient content per pot by a) doubling nutrient concentration within a constant soil volume ([N]) versus b) doubling soil volume at the same nutrient concentration (V) and of 2) doubling growth container (and soil) volume while maintaining the same total nutrient content per pot (V_p).

To gain better insight into how elevated CO_2 atmospheres affect how plant specifically utilize available below ground space, we also measured patterns of deployment of roots within pots through time. Contrary to aboveground responses, patterns of belowground deployment were most strongly influenced by elevated CO_2 in pots of different volume and shape (Fig 3). Further, elevated CO_2 conditions interacted differently with limited belowground space for the two species we studied. For *Setaria*, elevated CO_2 increased the size of the largest region of low root density at the pot surface in larger rooting volumes independent of nutrient content, thereby decreasing their efficiency of deployment. For *Abutilon*, plants responded to elevated CO_2 concentrations by equalizing the pattern of

deployment in all pots. Nutrient concentrations, and not pot size or shape, greatly influenced the density of root growth. Root densities for *Abutilon* and *Setaria* were similar to those observed in field conditions, for annual dicots and monocots respectively, suggesting that studies using pots may successfully mimic natural conditions.

Figure 5. Thin root mass and thin root density for *Abutilon* and *Setaria* as a function of pot volume, shape, and nutrient concentration. The three different types of pots are indicated by schematic drawings. The unshaded bars represent the low nutrient concentration (0.5 g L⁻¹) and the shaded bars represent the high nutrient concentration (1.0 g L⁻¹).

3. Interactive effects of Carbon Dioxide and Soil Moisture Availability on Tree Seedling's Tissue Water Relations, Growth, Niche Characteristics.

Our studies of the effects of increasing atmospheric CO₂ concentrations and a range soil moisture availabilities on the tissue water relations, growth, and niche characteristics of gray birch (*Betula populifolia*) and red maple (*Acer rubrum*) seedlings were brought to near completion this year. Components of tissue water relations were estimated from pressure volume curves of trees grown under mesic and xeric water regimes, and either ambient (350 μ L L⁻¹) or elevated CO₂ (700 μ L L⁻¹).

1). Both CO₂ and water treatment had small but significant effects on osmotic potential at full hydration, apoplastic fractions, and tissue elastic moduli. Under ambient CO₂ concentrations, plants showed a decrease in osmotic potentials of 0.15 MPa and an increase in tissue elastic moduli at full hydration of 1.5 MPa when grown under xeric conditions. The decrease in elasticity may enable plants to improve the soil-plant water potential gradient for a small change in water content while lower osmotic potentials shift the zero turgor loss point to lower water potentials. Under elevated CO₂, plants in xeric conditions also had reduced osmotic potentials (0.2 MPa) lower than the mesic plants and decreased elastic moduli at full hydration (1.5 MPa). Together these changes at elevated CO₂ enabled the xeric plants to maintain positive turgor pressures to lower water potentials and water contents. Surprisingly, the elevated CO₂ plants under mesic conditions had the most inelastic tissues. We propose that this inelasticity may enable plants to generate an adequate water potential gradient from the soil to the plant with the low conductances observed under elevated CO₂ conditions.

Table 1. Tissue osmotic potential at full hydration (π_i), tissue elastic modulus at full hydration (E_i), and apoplastic fraction (R_a) for *Betula populifolia* grown under either mesic or xeric conditions, and either ambient or elevated CO₂. Means and standard deviations for three branches.

Treatment	π_i (MPa)	E_i (MPa)	R_a
350 $\mu\text{L L}^{-1}$			
mesic	-0.92 (0.01)	4.87 (0.57)	0.67 (0.02)
xeric	-1.06 (0.01)	6.26 (0.77)	0.54 (0.02)
700 $\mu\text{L L}^{-1}$			
mesic	-1.03 (0.07)	6.81 (0.22)	0.61 (0.03)
xeric	-1.23 (0.02)	4.97 (0.37)	0.49 (0.03)

The second half of this study was designed to determine the effects of elevated CO₂ and soil moisture status on growth and niche characteristics of birch and maple seedlings, gray birch (*Betula populifolia*) and red maple (*Acer rubrum*) were experimentally raised along a soil moisture gradient ranging from extreme drought to flooded conditions at both ambient and elevated atmospheric CO₂ levels. Our results have shown that the magnitude of growth enhancement due to CO₂ was largely contingent on soil moisture conditions, but differently so for maple than for birch seedlings. Red maple showed greatest CO₂ enhancements under moderately moist soil conditions, whereas gray birch showed greatest enhancements under moderately dry soil conditions (Fig 1). Additionally, CO₂ had a relatively greater ameliorating effect in flooded conditions for red maple than for gray birch, whereas the reverse pattern was true for these species under extreme drought conditions. For both species, elevated CO₂ resulted in a reduction in niche breadths on the moisture gradient; 5% for gray birch and 23% for red maple. Species niche overlap (proportional overall) was also lower at elevated CO₂ (.98 to .88: 11%). This study highlights the utility

of experiments crossing CO₂ levels with gradients of other resources as effective tools for elucidating the potential consequences of elevated CO₂ on species distributions and potential interactions in natural communities.

Figure 6. Total biomass of gray birch and red maple grown under various levels of CO₂ and moisture. "B" refers to niche breadth (Levins 1968). Numbers on the top of lighter columns represent percent increase in total biomass of plants grown in 700 ppm CO₂ relative to plants grown in 350 ppm CO₂. Error bars refer to one standard error.

4. Individual versus population responses to elevated CO₂ levels in two species of annual weeds.

In nature, plants generally grow in the presence of other neighboring plants. While many experiments on the effects of elevated CO₂ levels on the growth of individual plants have been conducted, there is little information on the responses of plants grown in dense populations. It may or may not be the case that the growth responses of individual plants are the same as that of the population as a whole. To examine these issues we grew plants of two species of annual weeds (Velvetleaf [*Abutilon theophrasti*], and Common Dandelion

[*Taraxacum officinale*] as individual plants grown in well-spaced pots, and as dense populations grown in flats.

The overall biomass responses to elevated CO₂ levels were greater for individual plants than for plants grown at high population densities: for *Taraxacum* there was even a slight (non-significant) decrease in total biomass at high CO₂ for dense populations. These preliminary results strongly suggest that biomass responses predicted on the basis of individual plant responses may not be good a predictor of species responses at the stand level.

Species	Density	Proportional increase in biomass with 2 x CO ₂
<i>Abutilon theophrasti</i>	High	+ 0.013 %
	Low	+0.237 %
<i>Taraxacum officinale</i>	High	-0.025 %
	Low	+0.449 %

We also observed consistent differences in population size structure in response to elevated CO₂ levels. Size variability, as measured by the coefficient of variation of total plant biomass, was higher at high CO₂ levels than at ambient CO₂ levels, this increase being greater for high density populations than individually-grown plants (see fig.7). This results is of particular interest, since size variability is closely associated with variability in reproductive output within plant populations, this being the basis for genetic change through natural selection and drift. We speculate that sieve selection processes may operate more strongly in dense populations in nature, and that as global CO₂ levels increase, this process will be of particular importance in leading to rapid evolutionary change in plant responses to CO₂.

Figure 7. Interactive effects of elevated CO_2 and population density on population size structure in the common dandelion (*Taraxacum officinale*). The increase in size variability with increasing CO_2 may lead to rapid evolutionary responses of annual plants to rising CO_2 levels (Thomas and Bazzaz, unpublished data).

5. The development of gypsy moth larvae raised on gray and yellow birch foliage grown in ambient and elevated CO_2 environments

This study addresses insect-host plant interactions in an elevated CO_2 atmosphere. Previous studies we have conducted with herbs have demonstrated that larval performance of Lepidoptera decreases when they are fed leaves of plants grown in elevated CO_2 atmospheres. However, little work has been conducted with woody species. It is not known whether closely related host species are affected differently by elevated CO_2 in their suitability to insect herbivores. In this study, gypsy moth larvae (*Lymantria dispar*) were obtained from the USDA facility at Otis Air Force Base and raised on two of their natural host species of New England's temperate forest, yellow and gray birch (*Betula alleghaniensis* and *B. populifolia*). Birch seedlings were germinated and grown at either ambient (350 ppm) or elevated (700 ppm) CO_2 in light and temperature controlled chambers. After four months of growth, we placed first instar gypsy moth larvae on these plants. Twenty-four mesh cages, each containing one caterpillar and one plant, were set up for each treatment (2 host species x 2 CO_2 levels). Over the next two months, larval weights and behavioral measurements were recorded for each of the 96 larvae. We destructively measured a sub sample of plants at the beginning and the end to quantify characteristics that might affect larval performance and to see how they change with time. Meanwhile, other groups of second and third instar larvae were offered choices of leaves.

Three different preference tests were performed in petri dishes: two different (1) species (same CO₂, leaf age), (2) CO₂ levels (same species, leaf age), or (3) leaf ages (same CO₂, species). The data examined so far suggest that larval preference of gypsy moth does change with elevated CO₂. Furthermore, larvae grow significantly smaller and reach maturity slower at 700 ppm CO₂ and on yellow birch (see Graph 1). Preference data is still being processed, but early results suggest that low CO₂ leaves are preferred over high CO₂, and yellow birch over gray birch.

Figure 8. Gypsy moth larval growth as a function of species and CO₂ levels.

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