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

Final Report 1984-1995

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Submitted by

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1. Summary

Supervision of the project was transferred to two new postdoctoral fellows (Kelly McConnaughay and Shili Miao) in the spring of 1990. In March 1990, we upgraded two glasshouse modules for CO₂ control. That spring, we initiated the multi-year project examining the response of temperate deciduous trees to CO₂ in variable light and nutrient environments. These efforts were supported in part through funds from other grants. By the end of the summer of 1990, the last of our previous cohort of postdoctoral fellows had left for faculty positions. At that time, a third postdoctoral fellow who had previously worked in our lab on DOE grant research (Eric Fajer) was hired on a part time basis in order to facilitate DOE research during the time of personnel turn over. Additionally, two graduate students and three research associates were assigned to specific projects in addition to our postdoctoral fellows: David Ackerly (Population Dynamics); Glenn Berntson (Growth Under Elevated CO₂: The Shape as Well as the Size of Pots is Important); Adrienne Nicotra (The Impact of Soil Volume on the Physiological Acclimation of Temperate Deciduous Trees in Elevated CO₂); Line Rochefort (A Survey of Closely Related Birch Species, Population Dynamics, Heat Shock in Elevated CO₂: Is There a Change in Temperature Sensitivity?); and Peter Wayne (Elevated CO₂ Differentially Alters the Responses of Birch and Maple Seedlings to a Moisture Gradient).

Over the past fiscal year, we have made excellent progress. We have seen the completion of several major projects from previous grants, culminating in seven published and four submitted papers. In addition, we have completed an extensive invited review paper summarizing our own and other research on responses of terrestrial life to elevated CO₂ atmospheres for *Scientific American*. During the past year, our collaboration with Jim Reynold's group has continued to be productive. In March 1990, I had extensive discussions with Jim and members of his research group. A manuscript born of these interactions is currently in preparation. We have been strengthening our interactions among other global change researchers, particularly Jerry Melillo (Ecosystem Center at Wood's Hole) and Steve Wofsy (Harvard University, Division of Applied Sciences). Our lab continues to play a vital role in shaping the direction of global change research through attending key scientific meetings. In addition to myself, David Ackerly ("The Response of Vegetation to Elevated Atmospheric CO₂ Concentration", Washington, D.C.) and Kelly

McConnaughay ("Responses of Vegetation to Elevated Atmospheric Concentrations of Carbon Dioxide", Canberra, Australia) have represented our research program in national and international conferences.

All of the research goals for the current fiscal have been met (Soil Volume, A Survey of Growth Responses of Temperate Deciduous Trees to Elevated CO₂, The Response of Temperate Deciduous Trees to CO₂ In Variable Light and Nutrients Conditions, Population Dynamics) and we have initiated investigations into additional areas (Elevated CO₂ Differentially Alters the Responses of Birch and Maple Seedlings to a Moisture Gradient, Heat Shock in Elevated CO₂: Is There a Change in Temperature Sensitivity?). We have already prepared eight manuscripts (four are currently in review) reporting the results of these studies. We anticipate continued productivity for the upcoming fiscal year. The following is a more detailed description of our experimental findings and future research plans.

2. Individual Experiments

2.1. Soil Volume

2.1.1. The Impact of Soil Volume on the Physiological Acclimation of Temperate Deciduous Trees in Elevated CO₂

Methods: To determine the effect of soil volume and soil nutrient concentration on the growth responses of Harvard Forest tree seedlings, four species of tree seedlings (red maple, yellow birch, gray birch, and red oak) were grown in one of four soil volumes (0.3 L, 0.7 L, 1.2 L, and 3.0 L), at either of two nutrient levels (1.27 and 0.127 g N/L soil/wk) and two CO₂ levels ("ambient" -- 350 $\mu\text{L L}^{-1}$, and "elevated" -- 700 $\mu\text{L L}^{-1}$). Nutrients were added in proportion to soil volume; thus, soil nutrient concentration was equivalent for all treatments, because individual treatments received different total nutrient amounts. The experimental phase of this project has not been completed yet. The trees will be harvested during the last week in September, 1991. At that time performance characters, including stem, leaf, and root dry weight, leaf number and area and specific leaf weight will be measured. In addition, a subset of species and treatments were selected to investigate whether photosynthetic acclimation occurs in tree seedlings grown at elevated CO₂ levels. Red maple and yellow birch seedlings, grown at either nutrient concentrations, in either 0.3 L and 3.0 L soil volumes, and at ambient or elevated CO₂ levels were chosen for these measurements. On three occasions during the course of the experiment, light saturated photosynthesis was measured at both CO₂ levels for three replicates of each treatment. One more set of physiological measurements will be conducted before harvest.

Results: Plants grown at elevated CO₂ levels had consistently lower light saturated photosynthetic rates than ambient CO₂-grown plants, when measured at either 350 or 700 $\mu\text{L L}^{-1}$ CO₂. When light saturated photosynthetic rates, measured at "growth" CO₂ concentrations, were compared over the course of the experiment, we found that the photosynthetic rates of both ambient and elevated CO₂-grown plants converged, and that the rates of the elevated CO₂-grown plants declined over time. These phenomena were most apparent in plants grown in high nutrients (N2) and with 3.0 L soil volume (V2). The photosynthetic rates of the ambient CO₂-grown plants remained relatively constant. High nutrient (N2), 0.3 L volume (V1) plants and the low nutrient (N1), 3.0 L volume (V2) plants of both species had similar photosynthetic responses to CO₂ levels over time. These treatments received identical absolute nutrient additions, but had a tenfold difference in soil volume. These results indicate that soil volume was probably not critical to the decline of photosynthetic rates in these treatments. Future results should show whether photosynthetic acclimation to elevated CO₂ atmospheres is present in seedlings of these species, and whether the availability of below-ground resources, particularly soil volume and nutrients, affects this response. Further, these data will be applicable to results of previous and future glasshouse projects.

2.1.2. Growth Under Elevated CO₂: The Shape as Well as the Size of Pots is Important

Methods: We examined how both total soil volume and the dimensions of a given soil volume (i.e., amount and shape of space available for root foraging) affect the growth patterns of two annual species under elevated CO₂ conditions. *Abutilon theophrasti* Medic. and *Setaria faberii* Herm. were selected as experimental plants because of their contrasting physiology and root architecture. *Abutilon* is a C₃ dicot with a deep tap root and *Setaria* is a C₄ monocot with a shallow diffuse root system. We grew plants in specially constructed growth containers which allowed us to monitor non-destructively the temporal and spatial dynamics of individual root development. There were three types of growth containers:

Container	Height (cm)	Diameter (cm)	Volume (mL)
Small-Tall	18	8	640
Small-Short	9	10.5	640
Large	18	10.5	1280

To differentiate effects resulting from either the physical space of each pot, or the total amount of nutrients available to each plant, we scaled the rate of nutrient addition so that plants grown in containers of different sizes received the same total amount of nutrients. The experiment lasted ten weeks.

Results: By the end of the experiment, CO₂ treatment had no significant effect on the total biomass of either species. There was a significant CO₂ * species interaction for final fruit biomass; *Abutilon* plants had significantly more fruit biomass at elevated than ambient CO₂ levels, whereas *Setaria* plants had a similar fruit biomass regardless of CO₂ levels. For both species, plants grown in larger growth containers, independent of nutrient availability, had a greater final size and more fruit biomass. However, the shape of the growth container had little influence on the final total or fruit biomass. The production rate of new leaves for *Setaria* was influenced by both CO₂ treatment and pot shape: leaf production decreased in elevated versus ambient CO₂ conditions, and in plants grown in shallower versus deeper pots. Pot volume, though, did not significantly influence *Setaria* leaf production rates. For *Abutilon* plants, CO₂ treatment only slightly affected rate of node (leaf) production; however, the rate of leaf senescence was accelerated for plants grown under elevated CO₂ conditions and in the small-tall pots. The rate of flower head production for *Setaria* was unaffected by CO₂ conditions, but accelerated in the larger growth containers. Similarly, fruit production rates for *Abutilon* plants were accelerated in the larger pots, and especially under elevated CO₂ conditions. These results clearly demonstrate that the shape, as well as the size, of growth containers exerts a strong influence on the growth of plants and that these treatments differentially affect different species. Studies of the impact of elevated CO₂ on plant growth that grow plants in growth containers need to be designed with a knowledge of this phenomena in order to ameliorate the production of spurious results.

2.2. A Survey of Growth Responses of Temperate Deciduous Trees to Elevated CO₂

2.2.1. A Community Level Survey

Methods: We examined how an elevated CO₂ environment affected the growth of seven co-occurring tree species: American beech (*Fagus grandifolia* Ehrh.), paper birch (*Betula papyrifera* Marsh.), black cherry (*Prunus serotina* Ehrh.), white pine (*Pinus strobus* L.), red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh.), and eastern hemlock (*Tsuga canadensis* (L.) Carr). We also tested whether degree of shade tolerance per species and age of seedlings affect plant responses to enhanced CO₂ levels. Seedlings that were at least 1 year old, for all species except beech, were removed while dormant from Harvard Forest, Petersham, Massachusetts. Seeds of red maple and paper birch were obtained from parent trees at Harvard Forest, and seeds of American beech were obtained from a population of beeches in Nova Scotia. Seedlings and transplants were grown in one of four plant growth chambers for 60 d (beech, paper birch, red maple, black cherry) or

100 d (white pine, hemlock, sugar maple) under CO₂ levels of either 400 or 700 $\mu\text{L L}^{-1}$. Plants were then harvested for biomass and growth determinations.

Results: The results showed that the biomass of beech, paper birch, black cherry, sugar maple and hemlock significantly increased in an elevated CO₂ environment, but that the biomass of red maple and white pine only marginally increased in these conditions. Furthermore, there were large inter-species differences in the magnitude of growth enhancement induced by increased levels of CO₂. Thus, it seems reasonable to predict that one consequence of rising levels of atmospheric CO₂ may be to increase the competitive ability of some tree species relative to others. Additionally, the three species exhibiting the largest increase in growth under elevated CO₂ concentrations were the shade-tolerant species (i.e. beech, sugar maple, and hemlock). Elevated CO₂ levels, then, may enhance the growth of relatively shade-tolerant forest trees to a greater extent than growth of shade-intolerant trees, at least under the light and nutrient conditions of this experiment. We found no evidence to suggest that the age of tree seedlings greatly affected their response to elevated CO₂ concentrations.

2.2.2. A Survey of Closely Related Birch Species

Methods: Four birch species, black birch (*Betula lenta*), white birch (*B. papyrifera*), gray birch (*B. populifolia*) and yellow birch (*B. alleghaniensis*) are important co-occurring trees in the forests of New England. We anticipated that birch species would differ in the magnitude and pattern of their growth responses to an elevated CO₂ environment due to their individual shade tolerances and successional niche preferences. For example, gray birch, found in large forest clearings and very shade intolerant, is likely to differ in its elevated CO₂-induced growth response compared to yellow birch, the most shade tolerant of the four birch species.

To test whether these closely related and co-occurring birch species differed in their response to an elevated CO₂ atmosphere, we grew 10 seedlings from each species individually in either a near ambient (380 $\mu\text{L L}^{-1}$) or an elevated (690 $\mu\text{L L}^{-1}$) CO₂ environment for 90 days. After 30 and 45 days of growth, plant height, leaf number and length of the longest leaf was measured for each plant to evaluate their performance non-destructively. At day 90, plants were harvested, branches were counted and leaf area was determined. Then, plants were dried, roots were washed, and the shoots, leaves and roots were weighed. Tissue nitrogen concentrations was also determined from dried leaves. To examine whether the CO₂-induced growth response is modified when the plants are grown in competition, plants were grown in competitive arrays such that an individual of either

gray, black or yellow birch grew with a neighbor of either the same or a different birch species. Each combination (black X gray; black X yellow; yellow X gray; plus conspecific pairs) was replicated 10 in each CO₂ treatment. Measurements were identical with those taken from plants grown in individual pots (described above).

Results: The key findings of this study were:

- (1) The survival of yellow birch seedlings was significantly higher in an elevated CO₂ environment (ambient CO₂: 25/40 survived; elevated CO₂: 33/40 survived), whereas the survival of the other birch species was not significantly affected by CO₂ treatment. Further, the survival of birch species was not affected by the presence of neighbors, regardless of CO₂ treatment.
- (2) All individually grown birch species responded to an elevated CO₂ environment in fundamentally the same way: seedling performance, in terms of leaf number, length of longest leaf, and plant height, all increased dramatically in an elevated CO₂ atmosphere, and root, leaf, stem and total biomass and leaf area nearly doubled for all plant species grown under an elevated CO₂ atmosphere. Furthermore, allocation to roots versus shoots increased for all species in an elevated CO₂ atmosphere, and leaf nitrogen concentrations were lower for all birch species grown in an elevated CO₂ environment.
- (3) The effect of an elevated CO₂ environment on birch growth was not altered when they were grown with either a conspecific or heterospecific birch neighbor. Generally, all birch seedlings approximately doubled their growth in an elevated CO₂ environment, regardless of the presence of a neighbor.

In summary, all birch species responded in a similar positive way to a doubling of atmospheric CO₂ concentration, whether grown individually in competition. Only the survival of yellow birch seedlings improved in an elevated CO₂ environment.

2.3. The Response of Temperate Deciduous Trees to CO₂ In Variable Light and Nutrients Conditions

2.3.1. The Biomass Component

Methods: This project examines the long-term effects of elevated CO₂ levels on carbon gain, growth, biomass allocation and physiological functions of temperate tree seedlings. We studied how an enriched CO₂ environment, in concert with a fully crossed design of light and nutrients, influenced first year seedling growth in six New England forest species. The species, in the order of increasing shade-tolerance, were gray birch (*Betula*

populifolia), ash (*Fraxinus americana* L.), red maple (*Acer rubrum* L.), red oak (*Quercus rubra* L.), yellow birch (*Betula alleghaniensis* Britton), and striped maple (*Acer pensylvanicum*). Seedlings of all six species were transplanted into 6 inch diameter of standard plastic pots with a 1:1:1 mixture of sand:perlite:peat. The transplants were placed in glasshouse modules having 350 or 700 $\mu\text{L L}^{-1}$ CO_2 . In each module, there were three benches (blocks). Each of the three benches was divided in half and the two halves were randomly assigned to high and low light. Within each plot (i.e., light treatment), two replicate seedlings were randomly assigned to one of two nutrient treatments. This resulted in 2 CO_2 x 2 light x 2 nutrient x 6 species x 3 block x 2 replicates, a total of 288 plants. The elevated CO_2 (700 $\mu\text{L L}^{-1}$) treatment represented the predicted values for atmospheric CO_2 concentration 50 (+) years hence, whereas the low value (350 $\mu\text{L L}^{-1}$) was the estimated ambient CO_2 level for the present decade. The high light treatment (natural light) represents the light condition of a large gap at Harvard Forest (300 m^2), whereas the low light treatment (37% of high light) represents approximately equivalent to the light condition of understory. The two nutrient treatments (high and low) simulated high nutrient deposition and organic matter mineralization rates (equivalent to 400 $\text{Kg N ha}^{-1} \text{yr}^{-1}$) and nutrient-poor forest soil at Harvard Forest (equivalent to 40 $\text{Kg N ha}^{-1} \text{yr}^{-1}$), respectively. Once transplanted and assigned to the high or low nutrient treatment, the plants received either 1.8 or 0.18 g of Osmocote (a slow-release fertilizer, 15: 10: 10 N-P-K plus micronutrients, 5 - 6 month formulation) per pot, respectively. This design allows us to explore how the level of resource heterogeneity found in natural ecosystems affects the ability of temperate deciduous forests to take up and use carbon.

Results: Elevated CO_2 environments significantly stimulated the biomass of all six species. The greatest stimulation was found under low light and high nutrients; however, individual species responded differently to elevated CO_2 . Among the three early-successional species (gray birch, ash, and red maple), a significant increase in plant growth under elevated CO_2 condition was found only with high nutrients. The three late-successional species grown under elevated CO_2 condition (red oak, yellow birch, and striped maple) showed a greater percent increase in growth in low light than in high light. Thus, for the early-successional species, the degree of growth enhancement by elevated CO_2 was greatly influenced by nutrient levels, whereas for the late-successional species this enhancement was greatly influenced by light levels. Moreover, species with large seeds (e.g. red oak) exhibited a greater response to elevated CO_2 under low light than species with smaller seeds (e.g. gray birch). Considering the light and nutrient environment observed in forest gaps of various

sizes, the results in the present experiment suggest seedling regeneration in New England deciduous forests may be altered by a future high CO₂ world.

2.3.2. The Demographic and Architectural Components

Methods: Plants used in the present experiment were the same plants described above. Shoot growth was investigated by repeated non-destructive measurements. Shoot height (from the soil-stem interface to the tip of the tallest apical bud), the numbers of live and dead leaves on the main shoot, and the number of branches were determined at two-week intervals for 112 days. A new leaf was recognized once it had developed to the stage at which it began to lean away from the apical bud, and it possessed leaf shape. Basal diameter was measured before plants were harvested. Relative elongation rates of shoots (RER) were determined using the formula $RER = (\ln(\text{shoot height}_2) - \ln(\text{shoot height}_1)) / (t_2 - t_1)$. The relationship between final biomass and RER over time was examined by stepwise regression. Plant allometric relationships between height, basal diameter, leaf number and plant weight were studied with a linear regression model.

Results: The enhancement of RER (mm per mm per day) by elevated CO₂ was more pronounced at the early stage of plant life span (during 20 and 48 days after transplanting). Stepwise regression of final plant weight on RERs over time showed that final plant weight was significantly positively correlated with RER on day 48 ($R^2=21.9\%$, $P<0.001$, $df=265$), indicating that plants which exhibited higher RER on day 48 had greater plant weight at the final stage. For percent increases (the ratio of 700 plants to 350 plants) in final plant weight and RER on day 48, a significant linear relationship between these two characteristics among species was observed, in which approximately 45% percent of the variation in final plant weight was accounted for by the variation of RER on day 48. Elevated CO₂ differentially altered the allometric relationships between height, basal diameter, leaf number and plant height within species. In most cases, a species exhibited changes in only one or two of these allometric relationships and these changes were different for each species studied. The results show that growth enhancement during early life stages greatly influence the total accumulation of plant biomass by the late stage. When grown in an elevated CO₂ environment, plants not only altered their physiological functions, growth rates and biomass, but also changed their allometric growth patterns. These changes are likely to influence individual survivorship and plant-plant interactions within populations and communities.

2.3.3. The Physiological Component

Methods: Seedlings of four New England tree species (gray birch, red maple, yellow birch, and striped maple) grown in a high nutrient environment and in either an ambient or elevated CO₂ atmosphere (see above) were used for this analysis. We measured leaf level gas exchange from days 67–74 after transplanting, incorporating two to three replicates per treatment. Plants grown in either ambient or elevated CO₂ conditions had their photosynthetic measurements taken at either 350 $\mu\text{L L}^{-1}$ or 700 $\mu\text{L L}^{-1}$ CO₂ levels. Using the youngest fully developed leaf on each plant, leaf photosynthetic rate (Ps) as a function of intercellular CO₂ level were measured with a Li-COR 6250. After the measurements of Ps, we used the same leaves to obtain diurnal stomatal conductances, under plant growth conditions, using a Li-COR 1600 porometer at two-hour intervals from 800 hr to 1600 hr. Then, the following night (from 2100 to 2300 hr), we examined dark respiration rates at a temperature of 15° C. We also determined leaf chlorophyll content by spectrophotometry, measuring the absorbance spectrum at 647 and 664.5 nm of 1 ml of N, N-Dimethylformamide (DMF) from the crude leaf extract. Specific leaf area (dm^2/mg , SLA) was determined using a parallel set of leaf discs with the leaves used for chlorophyll analysis, and stomatal density (stomata/ mm^2) was obtained from a stomatal peel using clear nail polish applied to the underside of the same leaf that was used for physiological measurements.

Results: We found that both ambient CO₂-grown or elevated CO₂-grown plants exposed to an elevated CO₂ atmosphere during their physiological measurements had significantly higher leaf-level photosynthetic rates (Ps), regardless of light treatments. In contrast, the CO₂ environment under which plants grew differentially affected the Ps of species also exposed to different light conditions. For example, at high light, plants of all species exhibited a significant reduction in photosynthetic capacity after long-term exposure to elevated CO₂, i.e., a downward adjustment of Ps to elevated CO₂ levels. However, at low light, while red and striped maple exhibited downward adjustment of Ps, yellow birch showed upward adjustment and gray birch did not show either an up- or downward adjustment. Stepwise regression illustrated that among eight physiological characteristics studied, only two variables, CO₂-saturated Ps and specific leaf area (SLA), were significantly correlated with Ps. CO₂-saturated Ps was negatively correlated with Ps, whereas SLA was positively correlated with Ps. Thus, an upward or downward adjustment of Ps to elevated CO₂ levels may result from either an increase or decrease in RuBP, and /or the regeneration capacity of phosphorus (Pi) in the chloroplasts, and not to increases in accumulated foliar starch content. This suggests that the changes in plant Ps in

response to elevated CO₂ levels may involve alterations in a number of physiological characteristics.

2.4. Elevated CO₂ Differentially Alters the Responses of Birch and Maple Seedlings to a Moisture Gradient

Methods: To determine the effects of an elevated CO₂ atmosphere and soil moisture status on the growth and niche characteristics of birch and maple seedlings, seedlings of gray birch (*Betula populifolia*) and red maple (*Acer rubrum*) were raised along a soil moisture gradient ranging from extreme drought to flooded conditions at either ambient and elevated atmospheric CO₂ levels. Seedlings were harvested after two months of growth. Total biomass, biomass allocation, and shoot architectural characteristics were recorded, and niche breadth (Levin's B) and proportional similarity along the moisture gradient were recorded (based on biomass data), for both species, in both CO₂ levels.

Results: The magnitude of growth enhancement due to an elevated CO₂ atmosphere was largely contingent on soil moisture conditions, but differently so for maple than for birch seedlings. Red maple showed the largest CO₂-induced growth enhancement under moderately moist soil conditions, whereas gray birch showed it under moderately dry soil conditions. Additionally, an elevated CO₂ environment better ameliorated the adverse effects of flooding for red maple than for gray birch, whereas, for these species, the reverse pattern was observed under extreme drought conditions. For both species, plants grown in an elevated CO₂ atmosphere experienced a reduction in niche breadths along the moisture gradient; by 5% for gray birch and by 23% for red maple. Species niche overlap (proportional overall) was also lower at elevated CO₂ levels (.98 to .88: an 11% reduction). This study highlights how experiments which cross atmospheric CO₂ levels with gradients of other resources, such as soil moisture, serve as effective tools for elucidating the potential consequences of future elevated CO₂ conditions on both species distributions and plant-plant interactions within natural communities.

2.5 Population dynamics

Methods: To explore how an elevated CO₂ environment may effect plant population dynamics, artificial populations of *Abutilon theophrasti* were grown at four densities and either of two atmospheric CO₂ concentrations, 350 and 700 $\mu\text{L L}^{-1}$. The numbers of plants surviving, flowering and fruiting, and the number and weight of seeds produced by each population were monitored periodically throughout the experiment. The seeds produced by these plants were then used in germination experiments to determine how the effects of parental density, seed density in the soil, and exposure to different CO₂ concentrations at

either the parental or germination stage, impacts germination percentage. The data from this experiment were then used to construct a simple model of population dynamics based on density-dependent difference equations. The effects of ambient versus elevated CO₂ levels, various germination behaviors, and the inclusion of a persistent seed bank on the dynamics of the population were examined through model simulations.

Results: Survivorship, the proportion of plants flowering and fruiting, and the number of seeds produced per individual all declined monotonically with density, and, as a consequence, the total seed production per population also declined with density. Plants grown in an elevated CO₂ environment experienced a decrease in survivorship and an increase in the proportion flowering at the high densities. Moreover, there was a non-significant trend towards increased total population fecundity under elevated CO₂ conditions. The number of seeds per individual and mean seed weight were not influenced by the CO₂ concentration in which the adult plants grew, and both parental and seed density, but not the CO₂ concentration at either the parental or germination stage, influenced germination success. Due to the strong density-dependence of population level fecundity, the model displayed a wide variety of dynamic behaviors, depending on germination behavior. Given the observed response of fecundity and germination to both CO₂ level and plant or seed density, the simulated ambient CO₂ population reached a stable density while the elevated CO₂ population rose to a very high density and then went extinct. Under a variety of other germination behaviors the populations either reached stable points, oscillated in periodic or non-periodic cycles, or went extinct. In general, however, the elevated CO₂ population exhibited similar or less stable behavior than the ambient population under equivalent conditions. These effects resulted from the higher fecundity of the elevated CO₂ population at low density combined with the strong decline in fecundity at higher densities, leading to strong oscillations. These results highlight the importance of considering how an elevated CO₂ atmosphere might affect different levels of biological organization, since, in this instance, effects on fecundity of individual plants can lead to unexpected results for the dynamics of populations.

2.6. Heat Shock in Elevated CO₂: Is There a Change in Temperature Sensitivity?

Methods: It is anticipated that future elevated atmospheric CO₂ levels will likely induce changes in global climatic patterns. Among these changes may be an increase in the number of unseasonably warm days found during the growing season of plants. Despite the fact that many plant species, especially those possessing the C₃ carbon-fixation pathway, often grow larger under elevated CO₂ conditions, we expected that elevated CO₂-

grown plants would be more adversely affected by an exposure to acute temperature stress ("heat shock") than would plants grown under ambient CO₂ conditions. The thermotolerance of plants (as well as many other organisms) is determined, in part, by their ability to produce appropriate levels of heat shock proteins during times of temperature stress. Because plants predominantly respond to elevated CO₂ conditions by lowering the nitrogen concentrations of their leaves, we suspected that this would render them less able to augment heat shock protein production, and thus less able to grow and reproduce normally, under conditions of thermal stress than plants grown in ambient CO₂ levels which had been exposed to a heat shock.

To test this hypothesis, and to test whether, in general, a reduced foliar nutrient status affected the thermotolerance of plants, we grew a C₃ annual herb (*Abutilon theophrasti*), a C₃ crop (*Sinapis alba*), and a C₄ annual herb (*Amaranthus retroflexus*) under either an ambient (400 $\mu\text{L L}^{-1}$) or an elevated (700 $\mu\text{L L}^{-1}$) atmospheric CO₂ concentration and with either a low or high nutrient regime. Heat shocks of up to 20°C above normal daily temperature were applied for 4 hours to some of the plants, while others not exposed to heat shocks served as controls. Heat shocks were applied once for individual plants at one particular stage of their development (i.e., vegetative (day 24) and reproductive (day 56) for *Abutilon* and *Amaranthus*; and seedling (day 10), vegetative (day 18) and reproductive (day 26) for *Sinapis*) because the effects of elevated CO₂ environments on plants differs for plants at different phenological stages.

At day 87 for *Abutilon* and *Amaranthus*, and at day 40 for *Sinapis*, plants were harvested because over 50% of the fruits had ripened. Subsequently, plants were separated into vegetative (shoots, roots, leaves) and reproductive structures, dried, and weighed to compare the effects of CO₂ concentration, nutrient regime, and heat shock exposure at different times in a plant's life cycle on plant growth and reproductive output. Further, leaves from other vegetative plants which did not experience a heat shock were analyzed for their nitrogen content to compare the effects of CO₂ concentration and nutrient regime on foliar nitrogen concentration. The latter analysis was performed to see if a link existed between leaf nitrogen status and heat shock tolerance in plants.

Results: We found that, in contrast to our expectations, the CO₂ environment in which plants grew did not affect their response to heat shock. Plants of all species experienced similar reductions in both total plant biomass and reproductive biomass in response to heat shock, despite growing in different CO₂ treatments. Plants exhibited these responses to heat shock despite reductions in foliar nitrogen concentrations induced by either an elevated

CO₂ or low nutrient environment. In fact, for *Sinapis*, "heat shocked" plants grown in the high nutrient treatment (i.e., those which had leaves with higher percent nitrogen) actually had a greater reduction in reproductive biomass compared to controls than those grown in the low nutrient treatment. These results clearly suggest that (1) elevated CO₂-grown herbaceous plants are not more adversely affected by heat shocks than ambient CO₂-grown plants; and (2) the link between reduced foliar nitrogen status and lower plant thermotolerance is weak, at best, and potentially nonexistent.

Other important findings were evident from our work, much of which supports notions about how plants respond to changing environmental resources and modifiers. First, the growth of the C₃ herb, *Abutilon*, increased its total biomass by approximately 25% in an elevated versus an ambient CO₂ environment, whereas the growth of *Amaranthus*, the C₄ herb, appeared unaffected. Second, the idea that the fertilizing effect of an elevated CO₂ environment is dependent on the nutrient status of the environment was also supported: the C₃ crop, *Sinapis*, only increased its growth in elevated CO₂ conditions when it also received the high nutrient treatment. Third, nutrient availability was the most important factor determining plant biomass, reproductive biomass, and leaf nitrogen concentration, accounting for as much as 40% of the variance in ANOVA models used to analyze the data. For example, *Sinapis* plants grown with high nutrients were 250% larger than those grown with low nutrients. And finally, the timing of heat shock dramatically impacted the final vegetative and reproductive weights of all plant species: plants exposed to acute temperature stress during their vegetative phases suffered greater losses in vegetative and reproductive weight than those heat shocked during their reproductive phases.

3. Response of Temperate Deciduous Trees to CO₂ in Variable Light and Nutrient Conditions: A Continuation

The work we have completed to date clearly demonstrates that it is critical to understand the interactive effects of elevated CO₂ and other environmental conditions. From the work we have completed to date we would predict that the heterogeneity of resources within natural forest communities will lead to extremely complex patterns of regeneration of trees of different successional statuses. The work we have completed is, however, preliminary. It is our goal to continue this work so we can monitor the long term response of tree seedlings. If we can ascertain the extent to which the fertilizing effect of CO₂ is maintained over longer periods of time for different species of trees, we will have a much better idea about how to extend our findings and make predictions about the future responses of temperate deciduous forest ecosystems.

4. Changes in Tree Community Composition, and Their Consequences to Ecosystem Productivity

Since the responses of the different species to CO₂, light and nitrogen gradients differ, it follows that the relative performance and representation of the different tree species in a birch-maple community will change as a function of the specific CO₂, nitrogen and light environment. These changes may have profound effects on ecosystem productivity because these species differ in their inherent rates of carbon acquisition and growth, and rates of decomposition and effects on litter quality and soil microflora. These differences, by altering the patterns of energy flow and nutrient cycling in a forest, may affect long-term forest productivity. Thus we propose to investigate potential patterns of community change in response to these three resource variables by addressing changes in the abundance and performance of individual species within multiple species artificial communities through time.

The work we have completed to date demonstrates that different species have very different responses to elevated CO₂, depending on the light and nutrient conditions experienced. Our previous experiments on competitive interactions among plants show that allocation and architecture can greatly change in competitive situations relative to individually grown plants. In order to gain insight into how competition may change the structure of temperate forest ecosystems we will focus on the following two processes in our future work:

- 1 - The development of size hierarchies in single species stands of young trees.
- 2 - Changes in the abundance and performance of individual species within multiple species artificial communities of young trees through time.

In a follow-up experiment, we studied how an enriched CO₂ atmosphere influences the growth of gray birch (*Betula populifolia*), red maple (*Acer rubrum*), yellow birch (*Betula alleghaniensis*), and striped maple (*Acer pensylvanicum*) in four combinations of light and nutrient levels for two years. These species are important components of the forests of New England. In the first year, plants grown at elevated CO₂ levels were significantly larger than those grown in ambient CO₂. In the second year, however, the relative growth rate of plants grown at high CO₂ declines relative to plants grown in ambient CO₂ in red maple and yellow birch, slightly increased in striped maple, and did not change in gray

birch. although plants grown at high CO₂ were still larger than those grown in ambient CO₂, weight ratios (the weight of plants grown at high CO₂ divided by that of plants grown in ambient CO₂) in the second year declined for all species grown in low light and low nutrients. Species identity determined whether weight ratio increased or decreased in the other three treatments. Therefore, the stimulation of plant growth in a high CO₂ world depends on species identity and the levels of other resources in environments. The stimulation of growth by elevated CO₂ may be of a limited duration.

The species we investigated include gray birch (*Betula populifolia* Marsh.), white ash (*Fraxinus americana* L.), red maple (*Acer rubrum* L.), red oak (*Quercus rubra* L.), yellow birch (*Betula alleghaniensis* Britt.), and striped maple (*Acer pensylvanicum* L.) all major components of deciduous forest ecosystems. After three years of growth, elevated CO₂-grown plants were significantly larger than ambient CO₂-grown plants in only 5 of 24 cases. Additionally, CO₂-induced growth enhancement of the six species declined at different rates during years two and three resulted from increased respiratory cost of larger plants, changed biomass allocation, and shorter growing seasons despite increases in photosynthetic rates. The results suggest that forest productivity enhancements may not be sustained for long periods of time. Thus, it is conceivable that predicted rises in carbon sequestering in terrestrial ecosystems will be less than anticipated. Furthermore, species' differential growth responses to elevated CO₂ could result in compositional changes in forests, resulting in additional feedbacks related to the ability of forest ecosystems to accumulate carbon and thus influence the global carbon cycle.

5. Species Diversity and Ecosystem Response to Carbon Dioxide

Fertilization: Conclusions from a Temperate Forest

In collaboration with S. Pacala of Princeton University, we used our physiological data to model the growth and carbon sequestration in a deciduous forest. We explored how the response of a temperate forest ecosystem to climate change might depend on species diversity and community change. In particular, we looked at the dynamics of a model of temperate forest growth under doubled CO₂. We combined a detailed, field-calibrated model of forest dynamics with greenhouse data on the range of seedling biomass growth response to doubled CO₂ concentrations. Because total ecosystem response to climate change depends delicately on many environmental variables other than CO₂, we isolated the effects of community change by comparing runs of the regular model, allowing dynamic community change, with runs of a reduced model that holds species composition static by using a single tree species with average parameters. Simulations that allow community change instead of holding species composition constant showed a roughly 30% additional increase in total basal area over time scales of 50-150 years. Although the model omits many possible feedbacks and mechanisms associated with climate change. It suggests the large potential effects that species differences and feedback can have in ecosystem models and reinforces the possible importance of diversity to ecosystem function over time scales within the planning horizon for global change policy.

4. Publications from DOE Work (1991-1995)

Bazzaz, F.A. and W.E. Williams 1991. Atmospheric CO₂ concentrations within a mixed forest: Implications for seedling growth. *Ecology* 72:12-16.

Fajer, E.D., M.D. Bowers and F.A. Bazzaz 1991. The effects of enriched CO₂ atmospheres on the Buckeye Butterfly, Junonia coenia. *Ecology* 72:751-754.

Fajer, E.D., Bowers, M.D., and Bazzaz, F.A. 1991. Performance and allocation patterns of the perennial herb, Plantago lanceolata, in response to simulated herbivory and elevated CO₂ environments. *Oecologia* 87: 37-42.

Coleman, J.S., Rockefort, L., Bazzaz, F.A. and Woodward, F.I. 1991. Atmospheric CO₂ enrichment, plant nitrogen status, and the susceptibility of plants to an acute increase in temperature. *Plant, Cell and Environment* 14:667-674.

Bazzaz, F.A. and Fajer, E.D. 1992. Plant life in a CO₂-Rich World. *Scientific American* 266:68-74.

Reekie, E.G., and Bazzaz, F.A. 1992. Phenology and growth in four annual species grown in ambient and elevated CO₂. *Canadian Journal of Botany*, 69:2475-2481.

Miao, S.L., Wayne, P.M., and Bazzaz, F.A. 1992. Elevated CO₂ differentially alters the responses of co-occurring birch and maple seedlings to moisture gradient. *Oecologia* 90:300-304.

Coleman, J.S. and Bazzaz, F.A. 1992. Effects of CO₂ and temperature on growth and resource use of co-occurring C₃ and C₄ annuals. *Ecology* 73:1244-1259.

Ackerly, D., Coleman, J.S., Morse, S.R., and Bazzaz, F.A. 1992. CO₂ and temperature effects on leaf area production in two annual plant species. *Ecology* 73:1260-1269.

Fajer, E.D., M.D. Bowers, and F.A. Bazzaz 1992. The effect of nutrients and enriched CO₂ environments on production of carbon-based allelochemicals in *Plantago*: A test of the carbon/nutrient balance hypothesis. *Amer. Nat.* 140:707-723.

Fajer, E.D. and Bazzaz, F.A. 1992. Is carbon dioxide a "Good" greenhouse gas? Effects of increasing carbon dioxide on ecological systems. *Global Environmental Change: Human and Policy Dimensions*. 2:301-310.

Bazzaz, F. A. and McConnaughay, K.D.M. 1992. Plant-plant interactions in elevated CO₂ environments. *Australian Journal of Botany* 40:547-563.

Rockefort, L. and Bazzaz, F.A. 1992. Growth response to elevated CO₂ in seedlings of four co-occurring birch species. *Canadian Journal of Forest Research* 22:1583-1587.

Bazzaz, F.A., Ackerly D.D., Woodward, I. and L. Rockefort 1992. Effects of CO₂ enrichment on the density-dependence of reproduction in an annual plant and a simulation of population dynamics. *Journal of Ecology* 80:643-651.

McConnaughay, K.D.M., Berntson, G.M., and Bazzaz, F.A. 1993. Plant responses to carbon dioxide. *Nature* 361:24.

- Bazzaz, F.A. and Miao, S.L. 1993. Successional status, seed size, and responses of tree seedlings to CO₂, light, and nutrients. *Ecology* 74:104-112.
- Coleman, J.S., McConnaughay, K.D.M. and Bazzaz, F.A. 1993. Elevated CO₂ and plant nitrogen-use: Is reduced tissue nitrogen concentration size-dependent? *Oecologia* 93:195-200.
- Wofsy, S.C., Goulden, M.L., Munger, J.W., Fan, S.-M., Bakwin, P.S., Daube, B.C., Bassow, S.L., Bazzaz, F.A. 1993. Net exchange of CO₂ in midlatitude forest. *Science* 260:1314-1317.
- McConnaughay, K.D.M., Berntson, G.M., and Bazzaz, F.A. 1993. Limitations to CO₂-induced growth enhancement in pot studies. *Oecologia* 94: 550-557.
- Berntson, G.M., McConnaughay, K.D.M., and Bazzaz, F.A. 1993. Elevated CO₂ alters deployment of roots in "small" growth containers. *Oecologia* 94:558-564.
- Morse, S. R. Wayne, P., Miao, S. and Bazzaz, F.A. 1993. Elevated CO₂ and drought alter tissue water relations of birch (*Betula populifolia* Marsh.) Seedlings. *Oecologia* 95:599-602.
- Bazzaz, F. A., Miao, S. and Wayne, P.M. 1993. CO₂-induced growth enhancements of co-occurring tree species decline at different rates. *Oecologia* 96:478-482.
- Bazzaz, F.A. 1993. Use of plant growth analyses in global change studies: Modules, Individuals and Populations. Pages 53-71 in E.D. Schulze and H.A. Mooney eds., Design and Execution of Experiments on CO₂ Enrichment. Commission of the European Communities, Luxembourg.
- Morse, S.R. and Bazzaz, F.A. 1994. Elevated CO₂ and temperature alter recruitment and size hierarchies in C₃ and C₄ annuals. *Ecology* 75:966-975.
- Bassow, S.L., McConnaughay, K.D.M., Bazzaz, F.A. 1994. The response of temperate tree seedlings grown in elevated CO₂ to extreme temperature events. *Ecological Applications* 4:593-603.
- Ackerly, D.D. and F.A. Bazzaz 1995. Leaf dynamics, self-shading and carbon gain in seedlings of a tropical pioneer tree. *Oecologia* 101:289-298.
- Jasienski, M. and Bazzaz, F.A. 1995. Genome size and high CO₂. *Nature* 376:559-560.
- Bazzaz, F.A., Jasienski, M., Thomas, S.C. and Wayne, P. 1995. Microevolutionary responses in experimental populations of plants to CO₂-enriched environments: parallel results from two model systems. *Proceedings of the National Academy of Sciences*. 92:8161-8165.
- Ackerly, D.D. and Bazzaz, F.A. 1995. Plant growth and reproduction along CO₂ gradients: non-linear responses and implications for community change. *Global Change Biology* 1:199-207.
- Wayne, P.M. and Bazzaz, F.A. 1995. Seedling density modifies the growth responses of yellow birch maternal families to elevated carbon dioxide. *Global Change Biology* 1:315-324.

Bolker, B.M., Pacala, S.W., Bazzaz, F.A., Canham, C.D., Levin, S.A. 1995. Species diversity and ecosystem response to carbon dioxide fertilization: Conclusions from a temperate forest model. *Global Change Biology* 1:373-381.

Farnsworth, E.J. and Bazzaz, F.A. 1995. Inter- and intra-generic differences in growth, reproduction, and fitness of nine herbaceous annuals grown in elevated CO₂ environments. *Oecologia* 104:454-466.