

# Final Technical Report

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by

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Project Title: Forest Response to CO<sub>2</sub> Enrichment: Physiology and Ecology of Loblolly Pine

Objective:

To examine the direct physiological effects of CO<sub>2</sub> on plants with emphasis on the long-term effects on loblolly pine.

Abstract:

This report covers the results of a long-term project with the primary objective of developing and testing hypotheses on the environmental and physiological controls of loblolly pine response to atmospheric CO<sub>2</sub> enrichment. Earlier research under DOE funding had provided information from loblolly pine and other plant species which allowed the development of specific hypotheses. Phase 1 of this research was a two year pot study of loblolly seedlings to determine the interaction of CO<sub>2</sub> enrichment with soil nutrition. Phase 2 began with the enrichment of loblolly seedlings being grown in the ground, rather than pots, and continued through December 1995. Phase 3 began in April 1994 with the enrichment of undisturbed Piedmont North Carolina old field undergoing succession, including herbaceous annual plants, perennial grasses, and loblolly pine tree seedlings. Phase 3 was designed to gather preliminary information on a regenerating loblolly forest to be used for the development of hypotheses and measurement techniques for a long-term Free Air CO<sub>2</sub> Enrichment (FACE) study of regenerating forest in Duke Forest.

Summary Research Results

Our hypothesis was that elevated atmospheric CO<sub>2</sub> concentrations would act to enhance the growth, productivity and carbon sequestration of loblolly pine trees when soil nutrients and other environmental factors are in non-limiting ranges. When the environment is severely limiting, the enhancement response of loblolly to CO<sub>2</sub> would not be sustained.

Measurements of total growth of two-year old loblolly pine seedlings showed that well fertilized trees produced more dry mass at elevated  $\text{CO}_2$  levels. A doubling of  $\text{CO}_2$  at high levels of N and P resulted in a 60% increase at the end of year 1 but only a 9% increase in final total biomass at the end of two years treatment. Stringent reduction in available soil phosphorus or nitrogen greatly reduced overall plant growth and eliminated any  $\text{CO}_2$  response. Long-term effects of elevated  $\text{CO}_2$  and nutrient supply on photosynthesis and the photosynthetic enzyme, ribulose biphosphate carboxylase, demonstrated that photosynthetic rates were higher for plants grown at elevated  $\text{CO}_2$  only when they received supplemental N in the soil. Stomatal conductance was reduced at high  $\text{CO}_2$  reducing instantaneous water loss in transpiration under conditions of atmospheric  $\text{CO}_2$  enrichment independent of soil N or P fertility.

A second two year experiment confirmed that  $\text{CO}_2$  enrichment of 150 ppm and 300 ppm above ambient with fertile soil would produce 2-year old loblolly pine seedlings with 20% and 50% greater total biomass respectively. Plants grown at elevated  $\text{CO}_2$  were also taller, had greater photosynthetic leaf area, and more frequent flushes of growth. Net photosynthesis was higher for plants grown in elevated  $\text{CO}_2$ , but this difference was much greater in spring and summer. Rubisco content, activity, and activation state were unaffected by growth at elevated  $\text{CO}_2$ . Results from both Phase 1 and 2 indicate the importance of soil fertility in determining the magnitude of the  $\text{CO}_2$  response in terms of total carbon sequestration.

Although field studies have not shown a  $\text{CO}_2$  enhancement of growth when soil N or P are stringently limited, we examined several possible mechanisms whereby long-term  $\text{CO}_2$  enrichment might alleviate moderate nutrient limitations to growth, leading to greater carbon storage than predicted from existing information and models. We found that:

1. Root growth is stimulated by  $\text{CO}_2$  enrichment more than shoot growth. In addition to greater root surface area, greater allocation to root biomass increased the potential of loblolly pine to obtain nutrients. Increased organic matter also feeds back on the mineral substrate thereby increasing soil fertility by increasing mineralization rates.

2. Reallocation of nutrients within the plant or increased efficiency of metabolic processes occasionally occurs lowering nutrient stress.

3. Symbiotic root associations with mycorrhizal fungi were also stimulated by CO<sub>2</sub> enrichment and resulted in increased nutrient supply to the plant.

4. We also found that there is a relationship between atmospheric CO<sub>2</sub> concentration, plant growth stage, and carbon acquisition, allocation and storage. Reduced growth and net photosynthesis in plants grown in long-term elevated CO<sub>2</sub> is apparently related to inadequate sink strength in the growing points of the plant. We also found that there is a seasonal component to the response of loblolly pine to CO<sub>2</sub> due to seasonal pulses of nutrients into the system, as well as seasonal changes in light and temperature. Seasonal pulses of nitrogen (a warm week in January, for example) will induce short-term enhancement of the response to CO<sub>2</sub>. Because growth rates and carbon allocation patterns of loblolly change seasonally, the degree of CO<sub>2</sub> response will change seasonally. Shoots of loblolly, for example, grow mostly in the early spring and summer, but roots continue to grow for most of the winter. In addition, loblolly maintains its needles for two growing seasons and depending on site quality and latitude, it may produce from one to seven distinct flushes of growth during a growing season. For this reason, we conducted long-term experiments and analyzed seasonal events and responses. By the time the experimental work was terminated following the 1995 growing season, we had 4-year old loblolly pine trees that were continuously exposed to high CO<sub>2</sub> and soil nutrient fertility.

In the 4-year study we found that:

1. Total plant biomass increased in response to elevated CO<sub>2</sub>. The absolute difference in tree mass between ambient and elevated CO<sub>2</sub> grown trees was 0.024 kg, 0.63 kg, 4.37 kg, 11.39 kg after one, two, three, and four growing seasons respectively.

2. After four growing season elevated CO<sub>2</sub> trees were 10% taller, had 39% more leaf area and had 90% more biomass than ambient CO<sub>2</sub> trees.

3. Growth related analyses of biomass allocation patterns demonstrated size dependent shifts in carbon allocation.

4. No direct effects of CO<sub>2</sub> concentration on partitioning of biomass.

5. Leaf photosynthetic rates were always higher in trees grown in elevated CO<sub>2</sub>, but these differences were greater in the summer months (60-130% increase) than in the winter months (14-44% increase) reflecting a strong temperature effect on photosynthesis.

6. Seasonal photoperiodic changes in daylength, interacting with temperature controlled leaf photosynthesis rates will induce seasonal variation in tree biomass and size growth.

7. Measurements of total nonstructural carbohydrates (sugars and starch) demonstrated that seasonal differences in growth were not always explained by sugars and starch concentrations as originally hypothesized.

8. Reductions in leaf stomatal conductance of water vapor were sufficient to induce decreases in transpirational water loss per leaf. Increasing leaf area on trees grown for four years under enhanced CO<sub>2</sub> levels, however, indicate that whole tree water use will be higher in future loblolly pine forests.

9. Although some photosynthetic down-regulation (acclimation) occurred, net photosynthetic increase was still sufficient to support enhanced tree growth during the four years of this study.

10. The overall conclusion of this ten-year study is that loblolly pine stands and forests will be significant temporary sinks for atmospheric CO<sub>2</sub> in the future. Permanent sequestration of the carbon will, of course, require that pine products be permanently used or stored.

Our study of the effects of increased CO<sub>2</sub> on the early stages of old field succession (Phase 3) is incomplete. Analyses are underway that will provide information on a successional loblolly ecosystem. We are still in the process of measuring a fairly detailed carbon balance of this system which will provide valuable information on whether regenerating pine

forests of the southeastern United States represent a major carbon sink for sequestering excess atmospheric CO<sub>2</sub>.

#### Transition to whole ecosystem studies utilizing FACE technology

This ten-year study in open-top chambers provided essential background information and hypotheses for the important work currently underway at the Duke University free air CO<sub>2</sub> experiment (FACE). Further studies at the FACE research site are focusing on changes in species composition in this diverse system, changes in soil properties such as nitrogen mineralization and soil carbon sequestration, and changes in insect composition. The importance of the contribution of this study to the establishment of the FACE research facility at Duke University was underscored in November 18, 1996 when the Duke FACE research facility was formally dedicated to Boyd R. Strain.

#### Publications

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Additional important loblolly pine papers published from DOE research funding that preceded this grant (DE-AS05-83ER60177).

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Strain, B.R. 1987. Direct effects of increasing atmospheric CO<sub>2</sub> on plants and ecosystems. Trends Ecology Evolution. 2: 18-21.

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Graduate students trained during the duration of this grant

DUKE UNIVERSITY  
GRADUATE TRAINING IN GLOBAL CHANGE  
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1985-1997

Physiological Ecology Laboratory of Boyd R. Strain  
DOE Grants (DEA101-81ER60012, DE-AS05-83ER60177,  
DE-FG05-87ER60575)

Name: Susan Marks Wray  
Year: 1985  
Title: "Comparative physiological ecology of two old field  
perennials, *Aster pilosus* and *Andropogon virginicus*,  
under CO<sub>2</sub> enrichment and drought stress"  
Degree: MS.  
Univ.: Duke University  
No pp: 52  
Maj. Prof: Boyd R. Strain  
Maj. Dept: Botany  
PI: Boyd R. Strain  
Grant #: DE-AS05-83ER60177

Name: Catherine Jeanne Potvin  
Year: 1985  
Title: "Responses of two C<sub>4</sub> grasses to CO<sub>2</sub> enrichment and  
temperature: Implication on biogeographical distribution  
of C<sub>4</sub> plants"  
Degree: Ph. D.  
Univ.: Duke University  
No pp: 156  
Maj. Prof: Boyd R. Strain  
Maj. Dept: Botany  
PI: Boyd R. Strain  
Grant #: DEA101-81ER60012, DE-AS05-83ER60177

Name: Thomas William Sasek  
Year: 1985  
Title: "The implications of atmospheric carbon dioxide enrichment for the physiological ecology and distribution of two introduced woody vines, *Pueraria lobata* Ohwi (Kudzu) and *Lonicera japonica* Thunb. (Japanese honeysuckle)"

Degree: Ph. D.  
Univ.: Duke University  
No pp: 203  
Maj. Prof: Boyd R. Strain  
Maj. Dept: Botany  
PI: Boyd R. Strain  
Grant #: DEA101-81ER60012, DE-AS05-83ER60177

Name: Susan Marks Wray  
Year: 1987  
Title: "Competitive interactions of two old-field perennials, *Aster pilosus* and *Andropogon virginicus* under CO<sub>2</sub> enrichment".

Degree: Ph. D.  
Univ.: Duke University  
No pp: 167  
Maj. Prof: Boyd R. Strain  
Maj. Dept: Botany  
PI: Boyd R. Strain  
Grant #: DE-AS05-83ER60177, DE-FG05-87ER60575

Name: YaoHua Luo  
Year: 1989  
Title: "Responses of well-watered and water-stressed *Abutilon theophrasti* (C3) and *Amaranthus hybridus* (C4) to long-term differences to CO<sub>2</sub> and humidity"

Degree: Ph. D.  
Univ.: Duke University  
No pp: 192  
Maj. Prof: Boyd R. Strain  
Maj. Dept: Botany  
PI: Boyd R. Strain  
Grant #: DE-AS05-83ER60177, DE-FG05-87ER60575

Name: Chantal Danielle Reid  
Year: 1990  
Title: "The carbon balance of shade-tolerant seedlings of *Fagus grandifolia* and *Acer saccharum* under low irradiance and CO<sub>2</sub> enrichment"  
Degree: Ph. D.  
Univ.: Duke University  
No pp: 180  
Maj. Prof: Boyd R. Strain  
Maj. Dept: Botany  
PI: Boyd R. Strain  
Grant #: DE-AS05-83ER60177, DE-FG05-87ER60575

Name: Joy Kirsten Dippery  
Year: 1993  
Title: "Effects of reduced and elevated CO<sub>2</sub> partial pressure on C3 and C4 plant growth"  
Degree: MS.  
Univ.: Duke University  
No pp: 52  
Maj. Prof: Boyd R. Strain  
Maj. Dept: Botany  
PI: Boyd R. Strain  
Grant #: DE-FG05-87ER60575

Name: Kevin Lee Griffin  
Year: 1994  
Title: "Effects of resource availability on carbon utilization in *Pinus taeda* L. and *Pinus ponderosa* Dougl. ex Laws. seedlings"  
Degree: Ph. D.  
Univ.: Duke University  
No pp: 169  
Maj. Prof: Boyd R. Strain  
Maj. Dept: Botany  
PI: Boyd R. Strain  
Grant #: DE-AS05-83ER60177, DE-FG05-87ER60575

Name: James D. Lewis  
Year: 1994  
Title: "Effects of mycorrhizae and phosphorus supply on  
response of *Pinus taeda* L. seedlings to elevated CO<sub>2</sub>"  
Degree: Ph. D.  
Univ.: Duke University  
No pp: 180  
Maj. Prof: Boyd R. Strain  
Maj. Dept: Botany  
PI: Boyd R. Strain  
Grant #: DE-AS05-83ER60177, DE-FG05-87ER60575

Name: Joy Kirsten Dippery  
Year: 1997  
Title: "The evolution of *Arabidopsis thaliana* in response to low  
and elevated CO<sub>2</sub> partial pressure /  
Degree: Ph.D.  
Univ.: Duke University  
No pp: 155  
Maj. Prof: Boyd R. Strain  
Maj. Dept: Botany  
PI: Boyd R. Strain  
Grant #: DE-FG05-87ER60575

Name: John Stephen King  
Year: 1997  
Title: "Carbon and nutrient cycling in *Pinus taeda* L. and *Pinus  
ponderosa* Dougl. ex Laws. as affected by the belowground  
response to altered environmental conditions"  
Degree: Ph.D.  
Univ.: Duke University  
No pp: 189  
Maj. Prof: Boyd R. Strain  
Maj. Dept: Botany  
PI: Boyd R. Strain  
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