This funding from DOE-PER (DE-FG02-95ER62124) was for the systematic examination of potential homeostatic adjustments in the canopy loblolly pine trees in the Brookhaven/Duke Free Air CO₂ Enrichment (FACE) experiment. The Duke Forest FACE study which began in August 1997 is located in a Piedmont forest dominated by loblolly pine trees (*Pinus taeda* L.) with sweetgum trees (*Liquidambar styraciflua* L.) and yellow poplar trees (*Liriodendron tulipifera* L.) as secondary associates. We found that exposure of an intact pine forest (Duke FACTS1 experiment) to an increase in atmospheric CO₂ of 200 ul⁻¹, operating through a sustained stimulation of photosynthesis (Myers et al. 1999), caused a 27% stimulation in net primary production (NPP; DeLucia et al. 1999) and a 41% stimulation in net ecosystem production (NEP; Hamilton unpublished). A stimulation of global forest NEP of this magnitude would store only ~10% of the fossil fuel CO₂ in the atmosphere by the year 2050.

Terrestrial ecosystems, particularly forest ecosystems, are important in regulating atmospheric CO₂ through the balanced effects of photosynthesis and respiration. Many experiments indicate that increased CO₂ will stimulate plant growth and suggest that this increase in growth will sequester CO₂ thereby slowing its rate of increase. While some studies show an enduring growth stimulation by elevated CO₂, others indicate that the growth enhancement decreases with time, and under nutrient-limited conditions typical of most forests there may be no growth stimulation. A central question in "climate change" research remains whether the initial photosynthetic and growth enhancement observed for tree seedlings and saplings with a doubling of CO₂ will be sustained for large trees, and hence forested ecosystems, growing within the full suite of forest ecosystem processes. The objective of our proposed research was to determine if a time-dependent decline in growth occurs in an intact forest ecosystem.

We examined three broad mechanisms operating at the tree level that are homeostatic in that they may serve to maintain a proper balance of tissue carbohydrate and nutrient status but at a potentially lower growth rate. The mechanisms are: 1) down-regulation of photosynthesis resulting from source/sink constraints; 2) increased allocation to support structure and roots with concomitant increases in maintenance respiration; and 3) plant nutrient imbalance as growth exceeds the delivery of limiting nutrients. We studied these processes by estimating a) changes in leaf-level photosynthetic capacity and photosynthetic enzymes, b) changes in the allocation of biomass to above- and below-ground structures c) alterations in respiration rates, d) changes in foliage dynamics and nutrient levels, and e) carbon budgets of individuals and loblolly pine stands. These mechanisms are interdependent and represent homeostatic adjustment of trees to altered resource states that directly influence carbon cycling and storage in a forest ecosystem.

The coordinated series of physiological measurements we conducted provided new insight into processes regulating the forest C cycle under elevated CO₂. Combined with ongoing measurements of tree growth, data from this research will contribute to a dynamic forest carbon budget that will provide a benchmark for other modeling and empirical studies.

An annotated bibliography of publications from this project is presented.
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We compared size-dependent allometries of canopy dominant and suppressed loblolly pine trees from stands of different ages to determine if patterns of biomass allocation were different. This study developed the allometric relationships of loblolly pine trees that we use to estimate biomass production from tree diameter at breast height in the Duke FACE experiment.


This study showed that trees in elevated CO2 rings grew 25% faster than trees in the ambient CO2 rings after two years of CO2 enrichment. The findings provided the first real data that allowed for global extrapolation on the ability of forests to sequester increasing human-caused carbon dioxide emissions. These results suggested that if all forests worldwide were to grow 25% faster in 50 years than they do now, forest trees could absorb about half the expected CO2 emissions from fossil-fuel combustion. Obviously, loblolly pines are fast growing species and don't represent forest species globally so the 25% stimulation in growth is more likely an upper limit for what the world's vegetation can do.


This special issue of Tree Physiology was a collection of peer-reviewed papers presented at a workshop entitled Critical Assessment of the Response of Forest Ecosystems to Elevated Atmospheric Carbon Dioxide, partially supported by U.S. Department of Energy.


In this study using the dominant hardwood tree in the forest, we determined whether photosynthetic behavior of leaves from the top of the tree differed from that of leaves from the bottom of the tree. We found that they did differ and the differences were based on differing leaf morphology and physiology in the sun and the shade. Sun leaves of sweetgum trees had greater thickness, N and chlorophyll per unit leaf area than shade leaves, as well as higher light-saturated net photosynthetic rates. As a result, the CO2-stimulation of photosynthesis of sun leaves was almost twice as great as the CO2-stimulation of shade leaves. Since shade leaves make up a higher percentage of the total
foliage than sun leaves, this is an important consideration in determining the net effect of elevated CO₂ on photosynthesis in the forest.


We examined changes in photosynthetic capacity of loblolly pine trees after experimentally manipulating sink demand by excising the emerging terminal cohort during a period of rapid needle expansion. Reduced sink demand resulted in an imbalance between photosynthate production and export and produced physiological characteristics indicative of down-regulation of photosynthetic capacity.


We examined the environmental and biochemical basis for CO₂ stimulation of photosynthesis in the dominant tree species, loblolly pine. We found that the CO₂ enhancement varied greatly with season primarily due to changes in temperature. The greatest enhancement was at the highest seasonal temperature because elevated CO₂ stimulated the carboxylase activity of Rubisco, the CO₂-fixing enzyme of photosynthesis, the greatest at warm temperatures. The least enhancement of photosynthesis by elevated CO₂ was during the cold winter months because as growth ceased, the carboxylase activity of Rubisco in the needles declined. The study provided a linear relationship between photosynthetic stimulation by CO₂ versus temperature that can be used to predict seasonal CO₂ enhancement.


We found a large amount of variation in the response of understory tree species to elevated CO₂. This is one of the few published CO₂ studies that shows that elevated CO₂ can induce a reallocation of resources between the light reactions and carbon reduction reactions. This suggests that CO₂ enrichment may increase the efficiency that sunflecks can be used by the shaded understory species.


A feature of many CO₂ studies is a time dependent decline in the photosynthetic enhancement by elevated CO₂ and this is a very important complexity that arises in estimating carbon uptake of the forest. This decline in photosynthetic enhancement is often called “photosynthetic down-regulation” and is characterized by a decline in leaf N and CO₂-fixing enzyme, Rubisco, and leads to a reduction of photosynthetic capacity. This study found no evidence of photosynthetic down regulation in the dominant hardwood tree. We did find a strong relationship between the components of photosynthetic capacity, Rubisco activity and electron transport, and leaf N indicating the
probability that as N becomes more limiting in the Duke Forest, photosynthetic capacity will be negatively affected.


After correcting for measurement artifacts, a short-term increase in elevated CO2 reduced leaf respiration by 7-14% for sweetgum and had no effect on loblolly pine. Growth under elevated CO2 had no 'indirect' effect on leaf maintenance respiration or on the response of respiration to variation in air temperature. We concluded that elevated CO2 had little effect on the tissue-specific rates of leaf respiration.


Evidence suggests that photosynthesis, growth rates, and NPP of young forests will increase as the level of CO2 in the atmosphere continues to rise. The magnitude and duration of these increases are, however, highly uncertain. In addition to being modulated by the availability of other resources, the growth response to CO2 may abate sharply as trees age, suggesting that carbon storage in biomass of living trees will be smaller than expected from the initial responses of NPP.


The objective of this study was to determine whether elevated CO2 affected leaf senescence of sweetgum trees at the Duke/Brookhaven FACE experiment. A change in late season leaf phenology due to CO2 enrichment, either accelerating or retarding senescence, could substantially affect seasonal carbon gain by these trees. Elevated CO2 enhanced net photosynthesis at growth CO2 concentration by 74% in the sun leaves and 35% in the shade leaves through the senescent period but the timing of decline of photosynthesis was not affected by CO2 enrichment.