Final report: ***Mechanisms of Carbon Accumulation in Florida Scrub Oak: Ecosystem Gas Exchange, Biomass accumulation, and Soil Carbon.***

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Since May of 1996, we have conducted an experiment in Florida Scrub Oak to determine the impact of elevated atmospheric CO_2 and climate change on carbon, water, and nutrient cycling in this important terrestrial ecosystem. Florida scrub oak is the name for a collective of species occupying much of the Florida peninsula. The dominant tree species are oaks and the dwarf structure of this community makes it an excellent system in which to test hypotheses regarding the potential capacity of woody ecosystems to assimilate and sequester anthropogenic carbon. Scrub oak is fire dependent with a return cycle of 10-15 years, a time which would permit an experiment to follow the entire cycle. Our site is located on Cape Canaveral at the Kennedy Space Center, Florida. After burning in 1995, we built 16 open top chambers, half of which have been fumigated with pure CO_2 sufficient to raise the concentration around the plants to 350 ppm above ambient. In the intervening 10 years we have non destructively measured biomass of shoots and roots, ecosystem gas exchange using chambers and eddy flux, leaf photosynthesis and respiration, soil respiration, and relevant environmental factors such as soil water availability, temperature, light, etc.

The overwhelming result from analysis of our extensive data base is that elevated CO_2 has had a profound impact on this ecosystem that, overall, has resulted in increased carbon accumulation in plant shoots, roots and litter. Our measurements of net ecosystem gas exchange also indicate that the ecosystem has accumulated carbon much in excess of the increased biomass or soil carbon suggesting a substantial export of carbon through the porous, sandy soil into the water table several meters below the surface. A major discovery is the powerful interaction between the stimulation of growth, photosynthesis, and respiration by elevated CO_2 and other environmental factors particularly precipitation and nitrogen.

Our measurements focused attention on: stimulation of ecosystem gas exchange by elevated atmospheric CO_2; the architecture and distribution of coarse roots using the novel approach of ground penetrating radar; mechanisms for the disturbance of soil carbon pools via the “priming” effect; and how interannual and seasonal variation in precipitation alters the physiological response of key species to elevated CO_2.

This project was a collaboration between research groups at the Smithsonian Institution, NASA, the Dynamac Corporation, Northern Arizona University, and Old Dominion University in Norfolk, Virginia.

Relevance Statement: How the work addressed specific DOE goals including long-term metrics.

(1) The processes by which elevated CO_2 influences carbon cycle dynamics.

Our experiments in Florida scrub oak since 1996 have identified the following physiological mechanisms for the stimulation of carbon assimilation in native plants by elevated atmospheric CO_2:

Photosynthesis: In several papers, we have documented the stimulation of photosynthesis in the dominant oak species, Q. myrtifolia, Q. geminate, and Q. chapmanii (Ainsworth, et al. 2002; Hymus et al., 2002; Li et al. 1999; Powell et al. 2006). A key finding is that there are large differences in the response of photosynthesis and growth in different species to the elevated CO_2 treatment.

Water use efficiency: Elevated CO_2 reduced transpiration in all species tested.(Lodge, et al. 2001; Li et al., 2003; Li et al. 2009). Reduction in transpiration resulted in more soil water available for plant growth (Hungate et al., 2002). This is an important and powerful factor in ecosystem carbon accumulation.

Growth of leaves: We have shown that there is a seasonally variable stimulation of leaf area index in the dominant species and the ecosystem (Hymus et al. 2003). During summer, the combined effect of growth of additional new leaves and increased stimulation of photosynthesis for each leaf caused by the elevated CO_2 are both amplified by higher temperature resulting in a stimulation of ecosystem carbon assimilation that sometimes exceeds 100%.

Growth of shoots: Dijkstra et al. (2002) documented the high stimulation of shoot growth in elevated CO_2. Subsequent measurements (Seiler et al. 2009) indicate that the stimulation of soot growth has been sustained throughout the study.

Growth of fine and coarse roots: Frank Day, using minirhizotrons, has shown a transient effect of elevated CO_2 on fine root growth (Dilustro et al. 2002, Day et al. 2006), and recently, using ground penetrating radar, his group has documented a substantial increase in coarse roots in elevated CO_2(Stover et al. 2007, 2010).

Interactions between CO_2 stimulated growth and other factors: we have shown the interaction between key environmental factors, rainfall and mineral nutrient availability and the effects of elevated CO_2 on ecosystem carbon balance (Hungate et al. 2005a,b; Powell et al. 2006, Seiler, et al. 2009).

(2) Measure ecosystem level carbon cycle responses to elevated CO_2.

We have proven that we can measure ecosystem gas exchange using the open top chambers as cuvettes by validation experiments with eddy flux (Dore, et al. 2003; Hymus et al. 2003; Powell et al. 2006). Our results indicate that much more carbon is assimilated than we can account for the in the stimulation of carbon accumulation by elevated CO_2 in the standing stocks of carbon in shoots, roots, and soil. We have summarized all productivity measurements (for above and belowground carbon pools (Hungate et al. In Review)

(3) Understand feedbacks among carbon nutrient and water cycles in the context of elevated CO_2

Bruce Hungate's group has identified a potential limitation on the elevated CO_2 stimulation of carbon accumulation acting through leaching of molybdenum, which reduced nitrogen fixation by a major N fixer, *Galactia eliotta*.(Hungate et al. 2006).

We have seen a very large, interannual effect of rainfall on the stimulation of growth and photosynthesis by elevated CO_2 (Powell et al. 2006; Seiler et al. 2009).

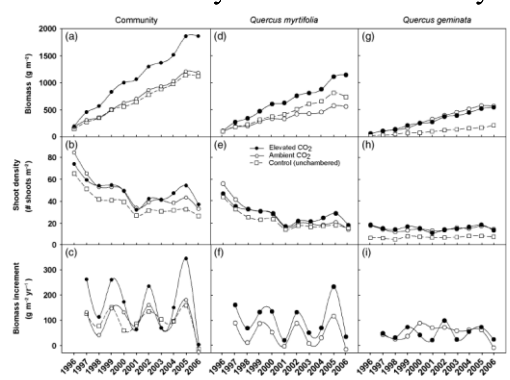
(4) Provide validation data and understanding of mechanisms for models.

Our long-term data sets on ecosystem gas exchange, biomass pools, nutrients, and plant/insect interactions will be made available to modelers who wish to collaborate with us in our effort to understand carbon cycling in the scrub oak ecosystem. We have contributed our eddy flux data to the Ameriflux data sets. These data have been used by several other groups in projects to evaluate ecosystem carbon dynamics.

Conceptual Framework

What is the capacity for land ecosystems to sequester carbon and partially mitigate climatic change? How can we best assess this question now, when the answers – and there will be more than one – presume some certainty about a future decades to centuries away? Thousands of experiments unequivocally demonstrate that photosynthesis increases with increasing CO_2 concentrations, and that this response has been sustained in studies of up to 19 years (e.g. Rasse et al, 2005; Erickson et al. 2006).

The Florida scrub-oak ecosystem was a good model ecosystem for determining the long-term impacts of elevated CO_2 on carbon cycling in terrestrial ecosystems dominated by woody vegetation. The CO_2 responses were followed during canopy development (when there was no light limitation) completely through to fully closed canopy with leaf area index of 1.5-2.5. Among unmanaged ecosystems, the Florida scrub-oak exhibited the highest ever growth response to elevated CO_2 (Seiler et al. 2009). During the first four years of the experiment, elevated CO_2 dramatically increased aboveground NPP, by 40% the first year increasing to 100% the fourth year (Dijkstra et al. 2002; Seiler et al. 2009). Initial root responses were also dramatic: fine root length increased by 184% two years after fumigation began (Dilustro et al. 2002)



Our estimates of NEE from open top chambers at ambient CO_2 agree very well with eddy flux measurements at the same site, which give us confidence that we have accurately estimated the elevated CO_2 stimulation of carbon uptake from the atmosphere (Dore et al. 2003, Powell et al. 2006).

Summary of final results and publications.

Plant growth and biomass pools

Aboveground. The most direct measurement of the effects of elevated atmospheric CO_2 on carbon pools in the Florida scrub oak ecosystem is the annual census and biomass estimate conducted each January. Stem diameters are recorded for each species and using allometric relationships developed previously, biomass of shoots is estimated (Dijkstra, et al. GCB 2002; Seiler et al. 2009).) The data in Figure 1 show that the shoot biomass response to elevated CO_2 has been sustained throughout the study. **Figure 1**. Total biomass of all species in the scrub oak ecosystem for nine years.

Belowground

The study of fine root biomass indicated a different pattern. During the first few years, there was a rapid and sustained increment in fine roots in elevated CO_2 but by the fourth year of the study, there was essentially no difference between treatments (Dilustro et al. 2002). The results suggest that ambient and elevated chambers may have reached closure of the root systems within a few years following the burn, but the CO_2 fertilized chambers reached closure first (Day et al. 2006). Recently, ground penetrating radar has been used to estimate coarse root biomass and these data indicate a 40% stimulation of coarse root biomass (ambient biomass = 5740; elevated = 8060 gdw/m^2) (Pagel et alo. 2007; Stover et al. 2007, 2010.)

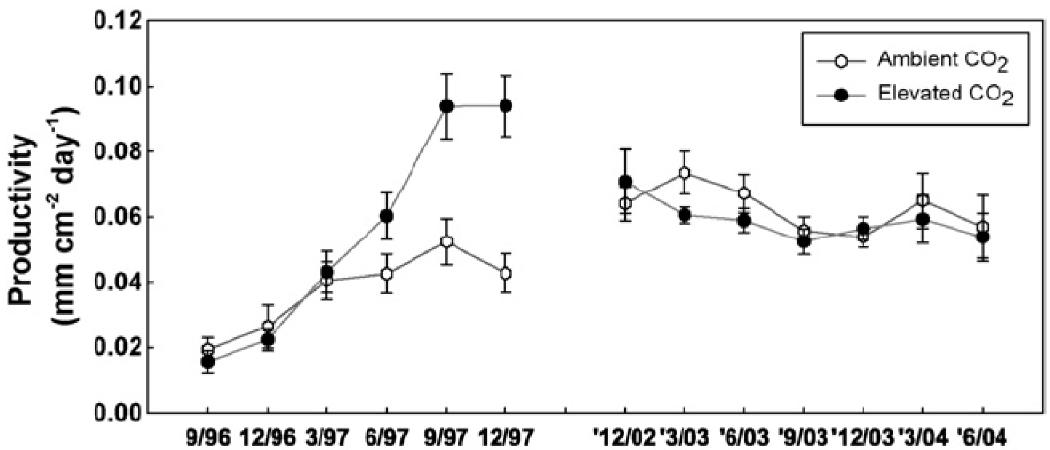


Figure 2. Growth of fine roots in elevated and ambient CO_2(Stover et al. 2010).

Ecosystem gas exchange

We have used the open top chambers for measuring net ecosystem CO_2 exchange (NEE) and compared the results with NEE measured by eddy covariance. Sabina Dore showed that ecosystem gas exchange can be measured by either approach.

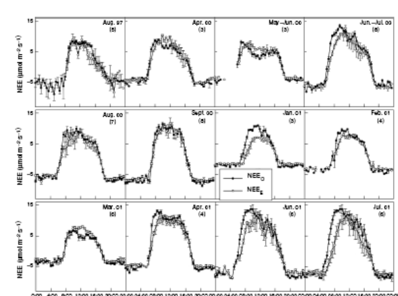


Figure 3. Comparison of net ecosystem gas exchange data measured using the open top chamber (NEE_o) with data collected simultaneously in the same ecosystem using the method of eddy covariance (NEE_e).(Dore, et al. 2003, Global Change Biology 9:84-95).

However, only the chamber can be used to measure NEE at elevated CO_2. We now have 9 years of data on NEE in Florida scrub oak which clearly shows that NEE at elevated CO2 is more than 50% greater than at normal ambient. An example of the relationship between NEE determined at normal ambient and after growth in elevated CO2 is given in Figure 3.

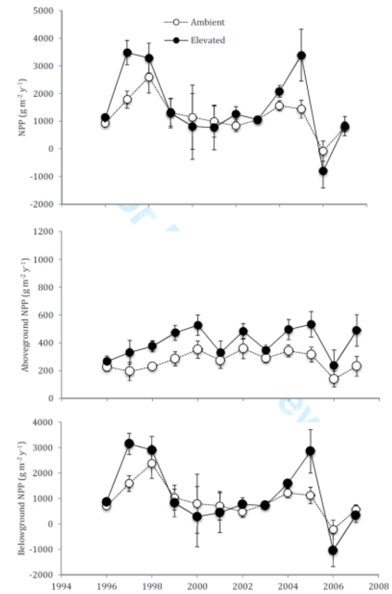


Figure 4. A comparison of the monthly NEE ($gCm^{-2}month^{-1}$) measured at normal ambient and elevated CO_2.

We applied the data from the gas exchange in chambers to the eddy covariance data. Figure 5 shows what the effect of elevated CO2 would have been had the un-chambered ecosystem behaved as did the plants within the open top chambers.

Figure 5. Time series plot of annual net ecosystem production (NEP) determined by direct eddy covariance measurements (NEP_a) and the estimated effect of C_e on NEP (NEP_e). NEP_e was scaled-up each year by the slopes in Figure 4.

We applied the data from the gas exchange in chambers to the eddy covariance data. Figure 4 shows what the effect of elevated CO2 would have been had the un-chambered ecosystem behaved as did the plants within the open top chambers.

Our work is unique in applying the gas exchange approach to measure ecosystem carbon balance. The elevated CO_2 effect on NEE of Florida Scrub Oak varies seasonally because the leaf area is also affected by the elevated CO_2. During the summer, the stimulation of leaf area by elevated CO_2 increases and so does NEE but the stimulation of photosynthesis per unit leaf area varies much less (Hymus et al. 2003). Maximum NEE is correlated strongly with soil water content (Hymus et al. 2003).

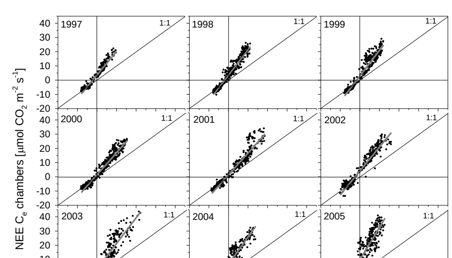
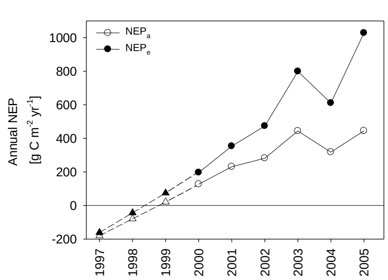


Figure 6 NPP above and below ground. Hungate et al. submitted.

Net Primary Production

NPP varied throughout the study dependent on disturbance, rainfall, etc. Net production was about 5% for the period of the study. Belowground production was as much as 7 times aboveground production. Loss of soil carbon belowground dominated and NPP was greatest following disturbance.



Soil carbon decomposition

Surface soil carbon loss: the priming effect Our findings that elevated CO_2 increases plant growth are in agreement with most CO_2 enrichment studies and they support the case that plant tissues are likely to constitute an expanded carbon sink in a future, CO_2-rich world.

Elevated CO_2 has caused a steady reduction of the active soil carbon pool in the surface soils of the Florida scrub-oak experiment, tending to reduce the surface soil carbon reservoir (Figure 7, Carney et al. 2007).

We have evidence that this response is related to a shift in the soil microbial community structure .

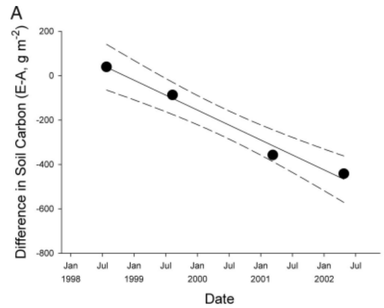


Figure 7. CO2 effect on loss of soil carbon in the Florida scrub oak(Carney et al. 2007).

While losses of soil carbon are not the expected in response to elevated CO_2, such responses are not unique to the Florida experiment. Elevated CO_2 simultaneously increased inputs of new carbon and losses of old carbon in soil in a FACE experiment with poplar plantations; as in Florida, this effect was explained as CO_2 enhancement of the priming effect. Non-significant declines in total soil C have also been observed in ponderosa pine, Mediterranean woodland, cold perennial grasslands, and in a shortgrass prairie. Therefore, this effect may be more widespread than expected, so understanding the mechanisms through which it occurs will be critical to predicting soil carbon stocks in a future, CO_2-rich world.

Subsurface soil carbon gain: a new carbon sink?

While elevated CO_2 appears to drive surface soil carbon loss, the full story is more complex: the response varies with depth, and may actually reverse in the soil horizon where the mechanisms promoting carbon stabilization qualitatively shift: in the spodic horizon. Specifically, we found no effect of elevated CO_2 on soil carbon in deeper aerobic soil layers (30-60 cm), but in the soil carbon fraction in the spodic horizon most sensitive to enhanced plant carbon inputs (<1.5 g/cm^3), we found dramatically higher carbon pools: 1256 g C/m^2 in the elevated vs. 558 g C/m^2 in the ambient CO_2 treatment(Carney et al. 2007; McKinley et al. 2009). These results have a number of important implications. First, rapid transport to deep soil carbon reservoirs may constitute a viable carbon storage mechanism in ecosystems with spodic horizons, and these horizons are far more dynamic than previously thought. Second, closing the carbon budget in this scrub-oak ecosystem will require fully characterizing the spodic horizon's response to CO_2 enrichment. And perhaps most important, third: the Florida scrub-oak ecosystem appears to exhibit a strong spatial decoupling of carbon stabilization mechanisms. This decoupling, though unusual, presents a powerful opportunity to disentangle some of the diverse mechanisms of carbon storage in elevated CO_2, in a system where the single well-characterized mechanism – plant inputs via enhanced NPP – is a dominant process (Hungate et al. In review, New Phytologist).

According to biogeochemical theory, increased plant growth and C uptake should immobilize nutrients in plant biomass and soil organic matter, causing nutrient availability to plants to decline, and reducing the long-term CO_2-stimulation of C storage in nutrient limited ecosystems. While many experiments have examined changes in nutrient cycling in response to elevated CO_2, empirical tests of this theoretical prediction are scarce. In the end, our data did not strongly support a case for progressive N limitation. (Hungate et al. In Review New Phytologist)

Interaction between water and CO_2 stimulation of growth

The growth stimulation caused by elevated CO_2 was greatest in wet years (i.e., 1997, 99, 02, 04, 05) but during very dry years (98, 00, 01, 03) elevated CO_2 caused virtually no increase in biomass, clearly indicating a powerful interaction that was counter to the expected response of a relatively greater stimulation of CO_2 during drought(Figure 7). This result was also dependent on the response of the dominant species, *Quercus myrtifolia*, which showed the greatest response to the CO_2 of the three dominant species in the ecosystem. The explanations for either the species difference or the relatively greater response during years of high rainfall are not apparent.

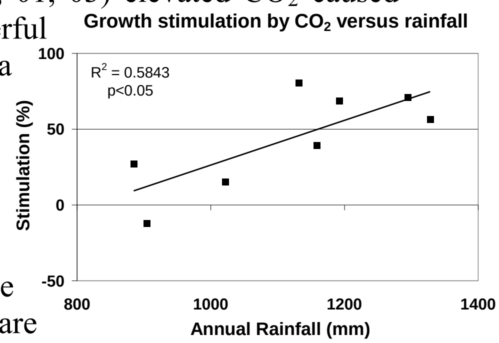


Figure 7. The interaction between the stimulation of growth Scrub Oak to elevated CO_2 and rainfall (Seiler et al. 2009).

Significance of the study

This study is one of the longest running elevated CO_2 studies and the data sets that have been accumulated clearly document the powerful impact of elevated atmospheric CO_2 on ecosystem carbon, water, and nutrient cycles. We have published more than 65 papers in refereed journals on research supported by the DOE and other agencies. This work has had an important impact on our understanding of the impact of rising atmospheric CO_2 and climate change on carbon balance in an important ecosystem. This sub-tropical ecosystem is under represented in both the Ameriflux network and the studies of elevated atmospheric CO_2 impacts and it represents an important contribution to our understanding of global carbon dynamics. The study is unique in several respects including the use of gas exchange to study the impact of elevated atmospheric CO_2 on all scales from leaf to ecosystem. In this respect, the program has been innovative in the application of available methods to study ecosystem processes, including the combination of open top chambers and eddy flux to measure ecosystem gas exchange and the recent addition of ground penetrating radar to study coarse root production is the latest example of this innovation.

The results obtained from this study are now in use by numerous research groups in assessments of the long-term implications of rising atmospheric CO_2 and climate change.

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