Forest succession at elevated CO₂

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Our research examined impacts of atmospheric carbon dioxide (CO₂) on forest succession, community composition, and ecosystem functioning. Rising CO₂ may change the way temperate forests develop by preferentially benefiting some plant species and groups over others. Forest succession affects biodiversity and carbon cycling as early successional forests tend to have less diverse communities but higher productivity than later successional forests. At the Duke Forest Free-Atmospheric Carbon Dioxide Enrichment (FACE) experiment, we determined fecundity schedules of pines under ambient and elevated CO₂. We found that high CO₂ resulted in a disproportionate allocation to reproduction, with elevated trees reaching maturation at smaller sizes and producing more seed than ambient trees at larger sizes.

We measured biomass and survivorship of naturally-recruited woody understory plants since 1996 (~ 2400 total stems). This work is continuing into the 2001 season. Of the eighteen tree species, several species representing each of the successional groups (early, intermediate, and late successional) show positive effects of elevated CO₂ on growth. The benefit of CO₂ enrichment for early successional species such as *Pinus taeda* and *Quercus phellos* suggests these trees may persist longer in shady forest understories and compete for future canopy dominance, thus lengthening the time forests spend in early successional states. An unexpected finding was that during 1999, a year of severe drought, some species grew more slowly under elevated CO₂ conditions. This diminished growth was particularly important for shade tolerant species such as *Acer rubrum* and *Cercis canadensis*. The southeastern United States is expected to become warmer and drier in the future, perhaps enhancing the benefit of elevated CO₂ for the growth of early successional trees relative to more shade tolerant competitors. Shade tolerant trees, however, exhibit a consistent positive effect of CO₂ on survivorship. We are currently working on population models to understand how future levels of CO₂ will impact the competitive dynamics of understory trees.

In addition to the effects of CO₂, the growth and survivorship of understory plants in the FACE forest are also impacted by deer and rabbit herbivory. We found, for example, that the overall biomass of understory tree populations has not changed from 1996-2000. Instead, mammalian herbivory seems to be impacting tree populations at early life history stages and overwhelming positive effects of atmospheric CO₂ on population sizes. In the autumn of 1998 at FACE we planted 2352 tree seedlings representing 14 species and protected them with herbivore exclosures. The biomass and survivorship of these trees have been monitored since and is continuing into the autumn of 2001. As with the unprotected trees, some species in some years representing each shade tolerance group show increased growth with CO₂ enrichment. However, early successional shade intolerant trees show the largest and most consistent benefit of CO₂ growth enhancement. Interestingly, when protected from herbivores, only intolerant trees

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exhibit no effect of CO₂ on survivorship; tolerant and intermediate trees show decreased survivorship with CO₂ enrichment. Again, these results suggest early successional trees may remain in forest understories for longer time periods and possibly extend the duration of early successional forest productivity.

The impact of herbivores on understory plant populations is particularly notable for poison ivy (*Toxicodendron radicans*). We monitored growth and survivorship of 223 naturally-recruited, unprotected poison ivy plants since 1996. In addition, we placed exclosures around an additional 66 naturally-recruited plants in the autumn of 1998 to protect them from herbivores. Plants growing under elevated CO₂ and available to herbivores exhibit increased growth in only 2 out of 5 years and show no CO₂ effect on survivorship. These plants have a high mortality rate, with only $22 \pm 5\%$ surviving after 5 years. When protected from herbivores, poison ivy tends to grow faster under elevated CO₂, with the elevated-ambient difference being significant in 2 of 3 years. Protected plants also exhibit no CO₂ effects on survivorship. Mortality is low, with $76 \pm 5\%$ surviving after 3 years. While the population biomass of unprotected plants is declining, that of the protected plants is rapidly increasing. The benefit of atmospheric CO₂ for the population growth of understory species depends on the presence of mammalian herbivores.

This project is continuing, with most of the important analyses for this first phase to be completed following the 2001 growing season. The following ms are completed, and we expect several more this year.

Mohan, J. E., J. S. Clark, and W. H. Schlesinger. Intraspecific variation in germination, growth, and survivorship responses of red maple (*Acer rubrum*, L.) to subambient, ambient, and elevated atmospheric CO₂: Evolutionary and ecological implications, in review.

LaDeau, S. and J.S. Clark. 2001. Rising CO₂ and the fecundity of forest trees, *Science* 292:95-98.