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"Effects of long term elevated CO₂ exposure on a Chesapeake Bay wetland."

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A. Site and facility

Since 1987, a field project to determine the effects of elevated CO₂ on a ecosystem processes has been in progress on a Chesapeake Bay wetland. Open top chambers are used to create a test atmosphere of present ambient CO₂ and twice ambient (Drake, et al., 1989). Chambers were placed on the marsh from April as shoots emerge until late November. There were 45 sites in three plant communities. In each community, one third of the sites were exposed to normal ambient CO₂, one third to elevated CO₂ and the remaining sites have no chambers. CO₂ was provided to increase the midday CO₂ concentration 350 ppm above normal ambient and was continuously provided each growing season beginning in April, 1987. There were three plant communities: a monoculture of the C4 grass, *Spartina patens*, a monoculture of the C3 sedge, *Scirpus olneyi*, and the third a mixture of the other two with a third species, the C4 grass, *Distichlis spicata*. The site included a building to house monitoring equipment and personnel as well as a large screened porch where field experiments are assembled and other work is carried out. The goals of this project were to determine the impact of elevated CO₂ on ecosystem processes. To do this, we studied biomass production, nutrient and water balance, net ecosystem CO₂ and H₂O exchange (measured by converting open top chambers to open gas exchange chambers with addition of a top and stack and monitoring change in CO₂ and H₂O concentrations of air passing through chamber), single leaf gas exchange, dark respiration, and competition among the three perennial species.

B. Major findings

1. Biomass production, nitrogen, water balance, competition.

Elevated CO₂ stimulated growth of above and belowground biomass (by 15% and 85% respectively) in the community dominated by the C3 sedge, *Scirpus olneyi*, in all three years of elevated CO₂ treatment but did not significantly increase them in the C4 community (Curtis, et al. 1989a; Curtis et al. In press). Thus the major sink for additional carbon in the perennial C3 community is belowground. Elevated CO₂ extends the growing season in all three communities (Curtis et al., 1989a). Nitrogen content of shoots and roots decreased in the C3 sedge but not in the two C4 species (Curtis, et al., 1989b; Curtis et al., In press) and this increased C:N. Total nitrogen in aboveground plant material has remained constant between the treatments but there was a net increase in nitrogen in roots and rhizomes because the increase in belowground biomass

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accumulation exceeds the reduction in tissue nitrogen concentration.

Dark respiration of leaves and stems of two of the three species being studied is actually reduced (dry wt basis) and the other was not affected by growth in elevated CO₂ (Drake, et al. In review). We have extended this observation to 9 more species (Figure 3). This was an unexpected finding with implications for ecosystem carbon accumulation. Similar results are reported by Bunce, (In press).

Evapotranspiration was measured simultaneously with net CO₂ exchange and water use efficiency was computed. Elevated CO₂ decreased evapotranspiration uniformly in all three communities, but water use efficiency increased more in the C3 than the C4 dominated community (139% compared to 70-80%, respectively). Shoot water potential was increased about equally in all three species by about 0.5 MPa. Elevated CO₂ may result in a net water savings in some natural communities.

In the mixed community, standing crop of the C3 plant has gradually increased from 65 to 230 g/m² with elevated CO₂ between 1986 and 1989 while the C4 grass, *Distichlis spicata* has remained unchanged. The standing crop of the C3 plant in ambient CO₂ and the control sites was essentially unchanged. This is consistent with the hypothesis that elevated CO₂ would result in changes in the composition of plant communities.

2. Photosynthesis of single leaves.

a. Light response of net CO₂ assimilation.

Net CO₂ assimilation of single leaves of the three species was determined in the field during 1987 and 1988. Elevated CO₂ increased photosynthesis in stems of the C3 sedge, *Scirpus olneyi* but not in the C4 grass, *Spartina patens* (Ziska, et al., In press). **Light saturated photosynthesis rates of *Scirpus olneyi* increased an average of 68% in elevated CO₂ (= 700 ppm) and the level of stimulation did not differ between plants grown in 350 or 700 ppm, Figure 1A.**

b. Quantum yield

Using the method of Ireland et al., (1989) no differences were found in the ϕ of *Scirpus olneyi* in stands grown in elevated CO₂ for three years compared to control stands, when measured under the same conditions (Figure 1B) implying there was no acclimation of ϕ . **The ϕ of plants grown and measured in 700 ppm CO₂ was ca. 20% higher than in plants grown and measured in concentrations of 350 ppm.** Given these changes in ϕ and assuming no increase in respiration the light compensation point of photosynthesis would be lowered for plants grown and measured in elevated CO₂. Figure 1C shows that the light compensation point was decreased by ca. 40%. **Light limited photosynthesis**

should be markedly increased by higher atmospheric CO₂ concentrations, which would increase the overall rates of canopy carbon accumulation. However, it is unclear if these results are representative of *Scirpus* stands throughout the year or indeed of C3 plants generally.

3. Photoinhibition.

Using a portable fluorimeter (PSM, Biomonitor AS, Sweden) and a larger laboratory modulated PSII fluorimeter (PAM101, Walz, W. Germany) F_v/F_m was shown to decrease on sunny days during July; the decline was far less for plants in elevated CO₂ (Figure 1D). Differences were greatest in late afternoon correlating with differences in canopy photosynthesis. Assuming that the linear relationship between F_v/F_m capacity for CO₂ assimilation observed in other species also applies in *Scirpus*, then ϕ of CO₂ uptake may be lowered by ca. 25% in plants grown in 350 ppm, but by only 12% in plants in elevated CO₂ which may also be less susceptible to high irradiance. In both treatments, F_v/F_m was fully recovered within 2 hours of the plants being placed in the shade.

4. Canopy gas exchange.

Elevated CO₂ increased seasonal ecosystem photosynthesis in all three communities, but most in the pure C3 community. The duration of carbon accumulation was extended approximately two weeks in the elevated CO₂ treatment in all three communities. Stimulation of ecosystem carbon dioxide assimilation in the C3 dominated *Scirpus olneyi* community was almost constant at about 55% throughout the growing season when normalized on green dry weight. However, because of the increased aboveground biomass production and reduced senescence (see 1 above), the relative stimulation of ecosystem carbon accumulation per unit ground area) increased throughout the season in all communities. **Elevated CO₂ increased net carbon accumulation by approximately 100% for the C3 community in 1988 and results for 1987 and 1989 are essentially the same.**

5. Summary of effect of elevated CO₂ on salt marsh ecosystem.

Elevated CO₂ caused increased growth, mainly of roots and rhizomes, increased photosynthesis in leaves and canopies, and reduced nitrogen content of C3 plants. It is significant that these field results are consistent with and also largely confirm greenhouse and controlled environment studies and it is important to continue the field experiments to determine whether long-term treatment has any substantial impact on these responses. **But many of the effects of long-term growth in elevated CO₂ observed in the marsh study were not anticipated: sustained high photosynthetic responses (i.e., ϕ , A_{max}) of the C3 species, the reduction of apparent photoinhibition, the decrease in respiration, the delay in senescence, the large stimulation of ecosystem carbon assimilation, and the apparent absence of nutrient limitation of the effect of CO₂ on production contributed to the large stimulation of ecosystem carbon accumulation in the C3 dominated community.** These results show the complexity of the response of ecosystems to rising CO₂ and how tightly coupled they are to the effects on photosynthesis.

The sustained high photosynthetic response and growth in the C3 community may be accounted for in terms of the following characteristics of the mesohaline salt marsh:

1. large sink for storage of carbon belowground;
2. relatively high temperature during the growing season;
3. relative abundance of nutrients, particularly phosphate;

The belowground fraction of the total biomass in this community is several times the aboveground standing crop. Temperature of the plant community is typically 25-35C and is often near 40C in midsummer. The stimulation of carbon assimilation by elevated CO₂ is very temperature dependent (Pearcy and Bjorkman, 1983). Availability of phosphate is rather high in the salt marsh soils and this would tend to increase the response of photosynthesis to elevated CO₂. Uniform stimulation of ecosystem assimilation contrasts with the reduction in photosynthesis observed with crop species in controlled environments (see discussion section II. A. above).

The most striking feature of this study was the importance of photosynthesis in determining the impact of CO₂ on the ecosystem. The most important feature of the impact of changed atmospheric composition and climate could be the impact on photosynthesis of different species. Since photosynthesis is tightly coupled to many environmental factors and is central to life cycles it is important to determine how photosynthetic responses of wild species are regulated.

C. Some thoughts on the relationship of these results to potential effects of rising CO₂ on ecosystem processes.

I believe there is a good chance that the effects of rising CO₂ on ecosystem processes, carbon accumulation and the potential feedback on atmospheric CO₂ content may be much greater than has been anticipated to date. The basis for my position is as follows. First, **there is abundant evidence in the literature on CO₂ effects on vegetation to show that elevated CO₂ reduces water loss and increases carbon dioxide assimilation. This conclusion has been confirmed in a wide range of species and under many different conditions (Cure, 1985; Cure and Acock, 1986; Conroy, et al. 1986; Kimball, 1983; Sage, et al., 1989; Ziska, et al., in press).** The exceptions to this generality are interesting more because they may tell us more about the mechanism by which CO₂ has its effect than about whether or not wild species and ecosystems will be effected by rising CO₂ and less because they offer grounds to dismiss the possible stimulation of production by rising CO₂.

Second, in our field study, and to a certain extent in the Arctic study, **the effects of elevated CO₂ on ecosystem level processes are consistent with the effects of CO₂ on molecular and physiological processes.** We found that elevated CO₂ has a small effect on C₄ species but a large effect on C₃ species and the community and ecosystem level processes, such as water balance, carbon balance, nutrient balance, and effects on species composition are all consistent with these results. A very important aspect of these results is that the effects of CO₂ on different ecosystems is best explained by the interaction between elevated CO₂ and temperature. Theory and experimental results both predict that there should be a relatively small effect of elevated CO₂ in cool climates and a large effect in warm climates, and this is the case when the results from the Arctic and Salt Marsh studies are compared (e.g., Pearcy and Bjorkman, 1983; Mooney et al., in press).

There is now evidence to show that the molecular and biochemical aspects of the response of photosynthesis to elevated CO₂ is reflected in ecosystem responses. At Toolik Lake, the response of photosynthesis was very small and acclimation of the photosynthetic apparatus occurred in the one species examined within three weeks. In the salt marsh study, the response of photosynthesis has been large and sustained over the course of three years of field exposure to CO₂. These two field studies are consistent with current understanding of mechanism of the response of photosynthesis to elevated CO₂, especially the interaction with temperature, and with the effects of temperature on partitioning and transport.

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