

Report of progress for 1989-1990

I. Research

Research during 1988-89 focused on several new aspects of the response of the salt marsh ecosystem to elevated CO₂. In previous years we gave highest priority to studies of the effect of CO₂ on biomass production into above and belowground tissues, nitrogen content, light response of photosynthesis of single leaves, leaf water potential and carbon dioxide and water vapor exchange between the plant canopy and the ambient air. Result from the work in 87 and 88 had shown that the C₃ plant, *Scirpus olneyi*, responded vigorously to elevated CO₂ but the two C₄ species, *Spartina patens* and *Distichlis spicata* did not. The responses of photosynthesis were also reflected in the canopy and ecosystem processes: carbon accumulated in the C₃ community into belowground tissues but not in the C₄ community suggesting that the main factor in the ecosystem responses would be photosynthesis and that the environmental controls on this process would determine the long-term ecosystem responses to rising CO₂. Thus our emphasis shifted from determining the growth responses to exploring photosynthesis in greater detail while continuing to measure biomass accumulation, but with less frequent harvests.

Several collaborators joined the CO₂ study during the past year. In December 1988, L. Ziska, K. Hogan and A. Smith conducted a three month pilot study on Barro Colorado Island, Republic of Panama to determine the possible effects of elevated CO₂ on endemic tropical species grown in their native environment. During June and July, 1989, Dr. Steve P. Long of the Biology Department, University of Essex spent three months with us working on measurement of quantum yield and photoinhibition. Dr. Kevin Hogan of the Smithsonian Tropical Research Institute also participated in this work. In October, 1989, J. Dacey of the Woods Hole Oceanographic Institution and M. Klug of the Kellogg Biological Station, attempted to determine whether elevated CO₂ causes increased methane production. Although their experiment are preliminary, the results encourage us that we should be following these effects by studies in greater detail. These projects were supported jointly through Smithsonian Institution Post Doctoral Research Fellowships to Long, Ziska and Hogan and by the DOE grant.

The main question at the outset of this project was: How much more carbon will be accumulated in the salt marsh ecosystem in a high CO₂ atmosphere than is being accumulated under present CO₂ concentration? This experiment has raised the possibility that rising CO₂ will make the salt marsh ecosystem a bigger sink for carbon than we have previously thought it to be. By extrapolation, this finding suggests that other, terrestrial ecosystems may also become larger sinks for carbon. The data produced in the short time that this work has been in progress has added another dimension to

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the continuing debate in the ecological community regarding the eventual effect of CO₂ on ecosystems.

The findings of our research continue to support the conclusion that rising CO₂ will increase carbon accumulation in terrestrial ecosystems. In the wetland system this is promoted through a complex interdependence of processes beginning with increased photosynthesis and including reduced respiration of both green tissues and decomposition of dead stems, storage of carbon into belowground parts, delayed senescence of green stems and improved water and nitrogen use efficiency.

A. Photosynthesis

1. Tropical species (Ziska, Hogan and Smith)

Studies of the effects of elevated CO₂ on tropical species showed that photosynthesis increased in elevated CO₂ and that there was an increased efficiency of utilization of CO₂ after growth in elevated CO₂. This is contrary to the finding of other studies, including the Arctic study, that growth in elevated CO₂ results in down regulation of CO₂ assimilation efficiency. This work is reported in two publications listed below, Ziska et al., In Review; and Hogan et al., In review.

2. Quantum yield and photoinhibition (S. Long)

This study attempted to determine whether the efficiency of light harvesting in the C₃ plant, *Scirpus olneyi*, acclimated to elevated CO₂. Quantum yield is the efficiency of CO₂ assimilation per unit of light absorbed. The assimilation of CO₂ is relatively easy to determine but the absorption of photosynthetically active photons is not. Dr. Long used an integrating sphere which was modified to allow simultaneous measurement of net CO₂ exchange and absorption of photosynthetically active photon flux. It was determined that elevated CO₂ increased quantum yield in plants grown in elevated CO₂ and that this increase does not diminish even after three years of exposure to elevated CO₂. This finding was confirmed by two separate methods for measuring quantum yield and it suggests that photosynthesis of plants operating at low light levels within the canopy of wild species will be increased irrespective of whether or not increased CO₂ stimulates photosynthesis of plants exposed to high light.

Exposure to full sunlight often leads to photoinhibition which can be measured as a reduction of the photosynthetic capacity. If elevated CO₂ provides a sink for the additional photons absorbed in full sunlight, it might be expected that it would also relieve possible photoinhibition resulting from high light and other

stresses. The approach was to measure the potential capacity for photon capture by comparing the variable fluorescence (Fv) in leaves of plants grown in normal ambient CO₂ concentration with Fv in plants growing elevated CO₂. Steve Long used a recently developed instrument for determining fluorescence yield on leaves in the field. Fv was normalized on the maximum possible fluorescence (Fm) for each leaf used. The ratio Fv/Fm has been found to correlate with quantum yield and is thus a useful measure of the effect of environmental factors on fundamental aspects of photosynthesis. It was found that elevated CO₂ reduces the normal diurnal trend in photoinhibition (as determined by Fv/Fm). This is another indication that rising CO₂ will reduce the effects of environmental stress on higher plants.

3. The effect of elevated CO₂ on photosynthesis at different levels within the plant canopy. (A. Villegas)

Experiments were conducted to determine where the added CO₂ is most effective in increasing carbon assimilation within the plant canopy of the C₃ sedge, *Scirpus olneyi*. Measurements were made throughout several days at two levels within the plant canopy suggest that most of the effects of CO₂ on photosynthesis occurs mainly within the upper 1/3 of the plant canopy.

B. Respiration (W. Pockman)

Studies of dark respiration were continued. Elevated CO₂ caused a reduction in dark respiration of *Scirpus olneyi* but not in *Distichlis spicata* and *Spartina patens*. This response seems to be time dependent in that it appears later in the growing season but not early. We do not know what the mechanism of this response is and thus it's relationship to elevated CO₂ is unclear.

C. Growth (W. Arp, W. Pockman, and P. Utley)

A comparison was made of the growth of aboveground biomass for three years in the C₃ plant *Scirpus olneyi*. The effect of elevated CO₂ on aboveground biomass production is of the order of 10-15% and the year to year variations in growth exceed the effects of elevated CO₂ on above-ground biomass production during any one year. There is no apparent reduction in the relative effect of elevated CO₂ on aboveground biomass production during the three years of the study.

D. Competition (W. Arp)

A comparison of growth of the C₃ plant *Scirpus olneyi* and the two C₄ species, *Spartina patens* and *Distichlis spicata* in the mixed community, showed that the C₃ sedge increased biomass production by 265% between the start of the project in 1986 and the

summer of 1989. This did not occur evenly in all sites and was highly dependent on the species mixture which is probably a reflection of the effects of the edaphic environment on the relative responses of each species to the stress of anoxia, salt, water stress, etc. The effects of CO₂ on competition show that C₃ species will do much better than C₄ species even in communities dominated by perennials.

E. Methane production (J. Dacey and M. Klug)

An attempt was made to determine whether there is an effect of elevated CO₂ on methane production by salt marsh communities. Methane originates in anaerobic systems, such as the salt marsh, and it was hypothesized that increased CO₂ would stimulate greater methane flux where the supply of belowground carbon was increased. It was found that elevated CO₂ stimulated an increase in methane flux in the C₄ *Spartina patens* community and that the effect was highly significant in two of the five sites studied. However, this study occurred in October and data were intensively collected only during three days. Thus the results cannot be taken to be definitive of the effects of CO₂ on the methane budget. Dacey and Klug believe that this study should be attempted in a more rigorous way with greater attention to the geochemistry of methane production than was possible in this brief exercise.

F. Carbon budget (W. Pockman and P. Utley)

Net ecosystem photosynthesis was compared for the three years 87, 88, and 89, showed that the effects of elevated CO₂ continue to cause increased CO₂ assimilation. For 1989, more carbon accumulated in the community dominated by the C₃ sedge, *Scirpus olneyi*, than in either the C₄ dominated or mixed community.

G. Ecosystem water balance (W. Arp, W. Pockman and P. Utley)

Elevated CO₂ reduced water loss in all three communities studied. The range of reduction in evapotranspiration was 20-40% of the rate in normal ambient CO₂. This resulted in an increase in water use efficiency of between 60 and 90%, the results varying somewhat between communities and at different times during the season. Midday and dawn tissue water potential was increased in elevated CO₂ for all species by an amount which varied between species and at different times of the season but which was approximately 0.2-0.5 Mpa at midday.

H. Decomposition (D. Whigham)

An experiment to determine the rate of decomposition of dead material was conducted. Shoots with leaves and stems were enclosed in mesh bags and returned to the sites where the material had been collected. At the end of the season, material remaining

was determined. Shoots of C3 *Scirpus olneyi* plants grown in elevated CO₂ were the slowest to decay while there were no differences between treatments in plant material from the other two species. This conclusion is consistent with the earlier measurements of the effects of elevated CO₂ on the respiration rate of the microbial community on dead stems.

II. Publications.

Drake, B. G., P. W. Leadley, W. J. Arp, D. Nassiry, and P. Curtis. 1989. An open top chamber for controlling CO₂ concentration and measuring net ecosystem gas exchange. *Functional Ecology*, 3:363-371.

Curtis, P. S., B. G. Drake, P. W. Leadley, W. J. Arp, and D. F. Whigham. 1989. Growth and senescence in plant communities exposed to elevated CO₂ concentration on an estuarine marsh. *Oecologia* 78:20-26.

Curtis, P. S., B. G. Drake, and D. F. Whigham. 1989. Nitrogen and carbon dynamics in C₃ and C₄ estuarine marsh plants grown under elevated CO₂ in situ. *Oecologia* 78:297-301.

Curtis, P.S., Balduman, L.M., Drake, B.G., and D.F. Whigham. The effect of elevated atmospheric CO₂ on belowground processes in C₃ and C₄ estuarine marsh communities. In press. *Ecology*.

Mooney, H.A., Drake, B.G., Luxmore, R.J., Oechel, W.C., and L.F. Pitelka. Predicting ecosystem responses to elevated CO₂ concentrations. In press *BioScience*.

Ziska, L.H., Chamberlain, S., and B.G. Drake. Long term photosynthetic response in single leaves of a C₃ and C₄ salt marsh species grown in elevated atmospheric CO₂ in situ. In press. *Oecologia*.

Drake, B.G., Leadley, P.W., Arp, W.J., Curtis, P., and D.F. Whigham. The effect of elevated atmospheric CO₂ on C₃ and C₄ vegetation on Chesapeake Bay. In: (Arnsen, A. and T. Madsen, ed's; *The Physiological Ecology of Aquatic Plants, Symposium Proceedings*, Aarhus, Denmark, September, 1988) In Press.

Publications in review.

Drake, B.G., Ziska, L.H., Bunce, J.A., Arp, W.J., Hogan, K. and Smith A.P. Dark respiration in plants grown in elevated CO₂. *Nature*.

Ziska, L.H., K.P. Hogan, A.P. Smith, and B.G. Drake. Growth and Photosynthetic response of nine tropical species with long-term exposure to elevated carbon dioxide. *Oecologia*.

Hogan, K.P., L.H. Ziska, A.P. Smith, and B.G. Drake. Changes in photosynthetic capacity, quantum yield, and fluorescence characteristics of three tropical species due to long term exposure to elevated CO₂. *Oecologia*.

Long, S.P. and B.G. Drake. The effect of the long-term CO₂ fertilization in the field on the quantum yield of photosynthesis in the C₃ sedge, *Scirpus olneyi*. Plant Physiology.

Long S.P. and B.G. Drake. Light inhibition of photosynthesis in a doubled CO₂ atmosphere. Planta.

Publications in preparation.

Leadley, P., B.G. Drake, W. Arp, and W. Pockman. A system for exposing wild species to elevated CO₂ and measuring net ecosystem gas exchange.

Drake, B.G., Leadley, P.W., Arp W. and W. Pockman. Net ecosystem carbon dioxide exchange for three salt marsh communities during long term exposure to a doubled CO₂ atmosphere.

Arp. W. A., B.G. Drake, P.W. Leadley, and W. Pockman. Evapotranspiration, water use efficiency and water balance of C₃ and C₄ species exposed in situ to a doubled CO₂ atmosphere.

Drake, B.G., W.A. Arp, P.W. Leadley and W. Pockman. The effect of elevated atmospheric CO₂ concentration on the Carbon budget for three salt marsh communities exposed to a doubled CO₂ atmosphere.

Arp. W. A., B.G. Drake and D. Whigham. Effects of elevated atmospheric CO₂ concentration on competition between perennial C₃ and C₄ species on a Chesapeake Bay wetland.

Drake, B.G and S.P. Long. The effect of elevated atmospheric CO₂ on photosynthesis and crop production. (commissioned review for Advances in Photosynthesis).

III. Other activities

Papers presented at national meetings

Annual Meeting of the American Society of Plant Physiologists, Toronto Canada, 30 July- 3 August, 1989.

B.G. Drake, P.W. Leadley, L. Ziska & W.J. Arp. Elevated atmospheric CO₂ reduces dark respiration in two halophytes.

Ziska, L. Chamberlain, S. and B.G. Drake. The effect of elevated CO₂ during growth in the field on photosynthesis of C₃ and C₄ salt marsh species.

Annual Meeting of the Ecological Society of America. Toronto, Canada, 6-10 August, 1989.

Drake, B.G., P.W. Leadley, W.J. Arp, P.S. Curtis and D.F. Whigham. The effect of two years of elevated CO₂ treatment on a Chesapeake Bay Wetland.

Curtis, P.S., B.G. Drake, D.F. Whigham, L.M. Balduman and M.L. Sutton. Belowground responses of marsh plants to elevated atmospheric CO₂.

Ziska, L. Chamberlain, S. and B.G. Drake. The effect of elevated CO₂ during growth in the field on photosynthesis of C₃ and C₄ salt marsh species.

Arp W.J., B.G. Drake, P.W. Leadley, and W. Pockman. Evapotranspiration, water use efficiency, and water potential in Chesapeake Bay wetlands communities exposed to elevated CO₂.

International Estuarine Research Foundation, Baltimore, Maryland, 8-12 October, 1989

Drake, B.G., W.J. Arp, P.S. Curtis, P.W. Leadley and D.F. Whigham. Global climate change and vegetation: The long-term effect of elevated CO₂ on Chesapeake Bay wetlands.

Invited seminars on the effect of rising CO2 on vegetation and ecosystem processes.

U.S. SCOPE workshop on Large Scale CO2 Enrichment of Ecosystems, National Academy of Sciences, 6 January, 1989,

Michigan Biological Station, Hickory Corners, MI July 12

World Resources Institute, Washington, D.C. August 2

University of Virginia, October 5

Woods Hole Oceanographic Institute, November 9

Rothamsted Experimental Station, Harpenden, England November 22.

U.S. Water Conservation Laboratory, Phoenix, Arizona, 9 January, 1990

U.S. Environmental Protection Agency, Corvallis Oregon, 16 January, 1990

National Council for Air and Stream Improvement, Washington, D.C., 19 March, 1990

U.S. SCOPE Committee on Direct Effects of CO2 on ecosystems, National Academy of Sciences, Washington, D.C. 17 April, 1990

Southern Regional Meeting, NCASI, Nashville, TN June 14

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