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Progress Report of Research: **EFFECTS OF ELEVATED CO_2 ON CHESAPEAKE BAY WETLANDS. V. Ecosystem and Whole Plant Responses. April - November 1989.**

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Chapter 1. Executive Summary

B.G. Drake.

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 factors controlling this process would be those most important for the long-term ecosystem responses. Thus our emphasis shifted from determining the growth responses to exploring photosynthesis in greater detail. This does not mean that we made no measurements of biomass accumulation, only that we shifted manpower resources where possible to emphasize aspects of photosynthesis which we could best address.

The main questions were: does acclimation to high CO2 involve reduction of some aspect of photosynthesis either at the single leaf level or in canopy structure? How much more carbon will be accumulated in a high CO2 than under present CO2 concentration? Our results give us partial answers to these questions but since the long term aspect of CO2 stimulation remains the most important one, it is unlikely that we can do more than add some pieces of data to a continuing debate in the ecological community regarding the eventual effect of CO2 on ecosystems.

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. This work was supported jointly through Smithsonian Institution Post Doctoral Research Fellowships to Ziska and Hogan and by the DOE grant. 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. His work was supported by a short term visitor fellowship from the Smithsonian Institution as well as by the DOE grant for the work on effects of elevated CO2 on ecosystem processes. 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.

The main findings of our research continue to support the conclusion that rising CO2 will increase carbon accumulation in natural ecosystems. In the wetland system this is promoted mainly by increased photosynthesis delayed senescence, increased numbers of green shoots, reduced respiration and decomposition.

I. Research findings.

A. Photosynthesis

1. Tropical species

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 od CO2 assimilation efficiency.
This work is reported in two publications listed below but is not included in the Greenbook as this is a summary of work on the effects of CO2 on the salt marsh ecosystem.

2. Quantum yield and fluorescence

Some have suggested that the effects of rising CO2 may be light dependent. It was therefore important to determine whether acclimation of photosynthesis to elevated CO2 occurs in low light. Quantum yield is the efficiency of CO2 assimilation per unit of light absorbed.is difficult to determine. 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. 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 is often 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 is 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 at different levels within the plant canopy.

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. The consequences of this observation for modeling the responses to elevated CO2 are significant.

B. Respiration

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. We do not understand what the mechanism of this response is and thus it's relationship to elevated CO2 is unclear.

C. Growth

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

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 probably do much better than C4 species even in communities dominated by perennials and may eventually dominate.

E. Methane production (John Dacey and Michael 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 by 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. Moreover, the inclusion of other greenhouse gasses should be included in any further attempts to determine the role of elevated CO2 in the carbon budget of ecosystems.

F. Carbon budget

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

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

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 since the start of the grant.

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.T. 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.T. 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.T. 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.T. 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.T. 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 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

Chapter 2. Plant growth and Decomposition

After extensive sampling during the first two years of exposure, in the 1989 season the vegetation in each community was sampled only once in August/September. The data from this harvest serve as a point of comparison with the data from the previous two years. The methods used for this harvest were somewhat different from those used in 1987 and 1989 (greenbooks 044 and 051 respectively) and included several new procedures. These methods are described below.

Aboveground biomass.

W.J. Arp, R. Cousimano, D. D'Abundo, W.T. Pockman, P. Utley, A.C. Villegas.

Methods.

The Scirpus community was sampled during the period September 5 - 13, 1989. All Scirpus stems at each site were counted and their total length, green length and width at 40 cm. determined. Additionally, all shoots of other species were counted and their height and number of leaves/branches determined. During the measurements at each site, every thirtieth stem was harvested and its top and bottom widths, total length, green length, total dry weight and green dry weight determined.

The relationship between total dry weight and stem length and senescent stem length and stem weight were established using a quadratic regression forced through the origin (see greenbook #051). The total and senescent dry weight in each chamber at the time of the harvest was calculated by summing the estimated dry weights of each shoot. The green dry weight was calculated as the total dry weight less the total senescent dry weight in the chamber.

The Spartina community was sampled during the period August 15-22, 1989. All living shoots within each of ten, 5 X 5 cm plots were harvested from the site and the tissue analyzed in the laboratory. The location of plots to be sampled was determined

by a computer generated diagram of each chamber with numbers 1 - 20 randomly positioned on the diagram. Plots were harvested in ascending order until ten samples were obtained. A plot was rejected only if it contained an obstacle (i.e. a PVC salinity well, a regrowth core or other impediment). The total length and number of leaves were measured for each stem before it was separated into leaf, stem and senescent categories. After drying, the dry weights and tissue nitrogen and carbon content were determined.

The Mixed community was sampled during the period August 24 - September 1, 1989. Sampling combined the procedures used in the Scirpus and Spartina communities. Scirpus stems were measured and harvested as in the Scirpus community while Spartina and Distichlis were harvested as in the Spartina community and separated in the laboratory.

Results.

Figure 2.1 shows a three year comparison of August biomass by chamber for the Scirpus and Spartina communities. Using data from all stems harvested in a given year linear regressions (forced through the origin) were determined for total weight to total length and senescent weight to senescent length. Total, green and senescent biomass were then estimated using the measured total and green lengths of each stem in each chamber. Biomass in the Scirpus chambers shows a decreasing trend , especially in the last two blocks (chambers 10 - 15) while biomass in the Spartina community tends to remain stable or increase during the three year period.

Scirpus community

Figure 2.2 shows a comparison of August biomass in the Scirpus community by treatment over the three years with CO2 treatment (1987-1989). Biomass in the control chambers appears to be decreasing steadily though this may be attributed to the substantial encroachment of other species during 1988 and especially during 1989. The biomass data for Scirpus in August 1989 include a correction for stems removed during the early part of the season for use in single leaf respiration measurements and water potential measurements. This correction was made by multiplying the mean stem

biomass in August by the number of stems removed and adding the product to the estimated biomass number obtained directly from the harvest data.

Figure 2.3 shows the Scirpus biomass (total, green, senescent) by chamber at the time of the harvest in August/September, 1989. Biomass decreases with each successive block. This trend represents the relative location of each block to the densest Scirpus stands. The final block, with the lowest Scirpus biomass is located in the beginning of a transition to Mixed and Spartina vegetation. Figure 2.4 (A,B,C) shows percent reproduction, percent senescence, and shoot width by height class and treatment in the Scirpus community. The percentage of stems that are reproductive (A) shows a chamber effect but the elevated and ambient treatments are indistinguishable. Senescence (B) also shows a chamber effect however percent senescence is reduced in the elevated treatment above the 80cm. height class. There appears to be no treatment or chamber effect on shoot width (D) in the Scirpus community. Figure 2.5 shows the number of shoots in each 10cm height class by treatment in the Scirpus community (A) and in the Mixed community (B). Growth in elevated CO2 and the block in which a site is located appears to determine the height class containing the greatest number of shoots (significant?). The height with the maximum number of stems tended to decrease with the presence of a chamber and with increasing block number. The modal height class was the same for both ambient and elevated CO2 treatment however the elevated chambers contained substantially more stems.

Scirpus in the Mixed community

Figure 2.6 shows the total, green and senescent biomass for Scirpus growing in the Mixed community. In each block the elevated chamber has substantially more green biomass than the ambient or control sites. Figure 2.7 (A,B,C) shows the percent reproductive stems, percent senescent tissue and the shoot width by treatment for Scirpus growing in the Mixed community.

Spartina and Mixed community

The following section describes the results for Spartina growing in the Spartina community and in the Mixed community, Distichlis growing in the Mixed community, and for Scirpus growing in the Mixed community.

Figure 2.8 shows the total biomass, broken down by leaves, stems and senescent tissue, of Spartina in the Spartina and Mixed communities and Distichlis in the Mixed community. Differences among Spartina treatments are minimal in the Spartina community however total biomass of the elevated treatment was less than ambient or control in the Mixed community. Distichlis exhibits a trend that suggests a chamber effect and a treatment effect.

Figure 2.9 (A,B,C,D) shows the shoot density, stem dry weight, leaf dry weight and senescent dry weight for C_4 species in Spartina and Mixed communities by treatment. Senescent dry weight in the control sites was substantially higher in Spartina and Distichlis.

Figure 2.10 (A,B,C,D) shows the mean shoot weight, percent senescent leaves, percent senescent biomass and percent stems for Spartina in both the Spartina and Mixed communities and Distichlis in the Mixed community. As in fig 2.9, the percent senescent leaves and percent senescent biomass was almost double in the control sites compared to the ambient and elevated chambers. Percent stems and mean shoot weight were not significantly different among treatments in the same community.

Figures 2.11, 2.12, and 2.13 show the number of shoots, mean shoot weight and the number of shoots by treatment and height class for Spartina in the Spartina community (2.11), Spartina in the Mixed community (2.12), and for Distichlis in the Mixed community (2.13).

Spartina in the Spartina community

In the middle height classes the ambient treatment contained more shoots than either elevated or control suggesting a chamber effect and a decrease with elevated CO2. The presence of a chamber and treatment with elevated CO2 both appear to increase the modal height class and decrease the number of shoots in that class. Mean shoot weight appeared unaffected by either the presence of a chamber or treatment with elevated CO2.

Spartina in the Mixed community

The number of leaves showed no response to treatment or chamber within height class. Like Spartina in the Spartina community, the modal height increased while the number of shoots at the mode decreased. The mean shoot weight showed no response

to chamber or treatment.

Distichlis in the Mixed community

The number of leaves showed no clear response to chamber or treatment within height class. Like Spartina in both the Spartina and the Mixed communities, the modal height of Distichlis increased with chamber and treatment and the number of shoot at the mode decreased. Mean shoot weight was higher in the control chambers between the 50 and 90 cm height classes but there was no difference between ambient and elevated.

Belowground biomass.

Regrowth cores placed in the chambers at the end of the 1988 season were left intact for the 1989 field season and will be harvested at the end of 1990 (after two full years in the ground). No data for belowground biomass are reported here.

Decomposition

D. Whigham.

Methods

Decomposition studies were conducted in the Scirpus and Spartina communities during the 1988/89 season. Samples of standing senescent Scirpus olneyi and Spartina patens were collected from each chamber in December, 1988. Scirpus stems were divided into top and bottom tissues while Spartina shoots were cut into leaf and stem components. The resulting samples were dried, weighed and placed in decomposition bags. Each tissue type from each chamber was contained in a seperate compartment of the same bag.

The bags consisted of a frame of narrow nylon mesh covered with larger nylon net to contain the plant tissue inside. The design permitted living shoots to grow through the bag without allowing the loss of tissue sections from inside the bag. Each decomposition bag was placed at ground level in the chamber from which the plant material in the bag was originally collected. Identical samples of tissue from each

chamber were prepared, dried, ground and sent to the University of Maryland's Horn Point Laboratories for carbon and nitrogen assays.

Bags were left in position for one year (December, 1988 - December, 1989). Over the course of the year some bags were lifted slightly above the surface of the marsh by the shoots growing through them. In December, 1989 the bags were collected and, like the time zero samples, dried, weighed, ground and sent out for carbon and nitrogen analysis.

Results

Preliminary text (7/13/90): No differences were observed in either leaf or stem tissue of Spartina patens. Significant differences were observed only in Scirpus tops.

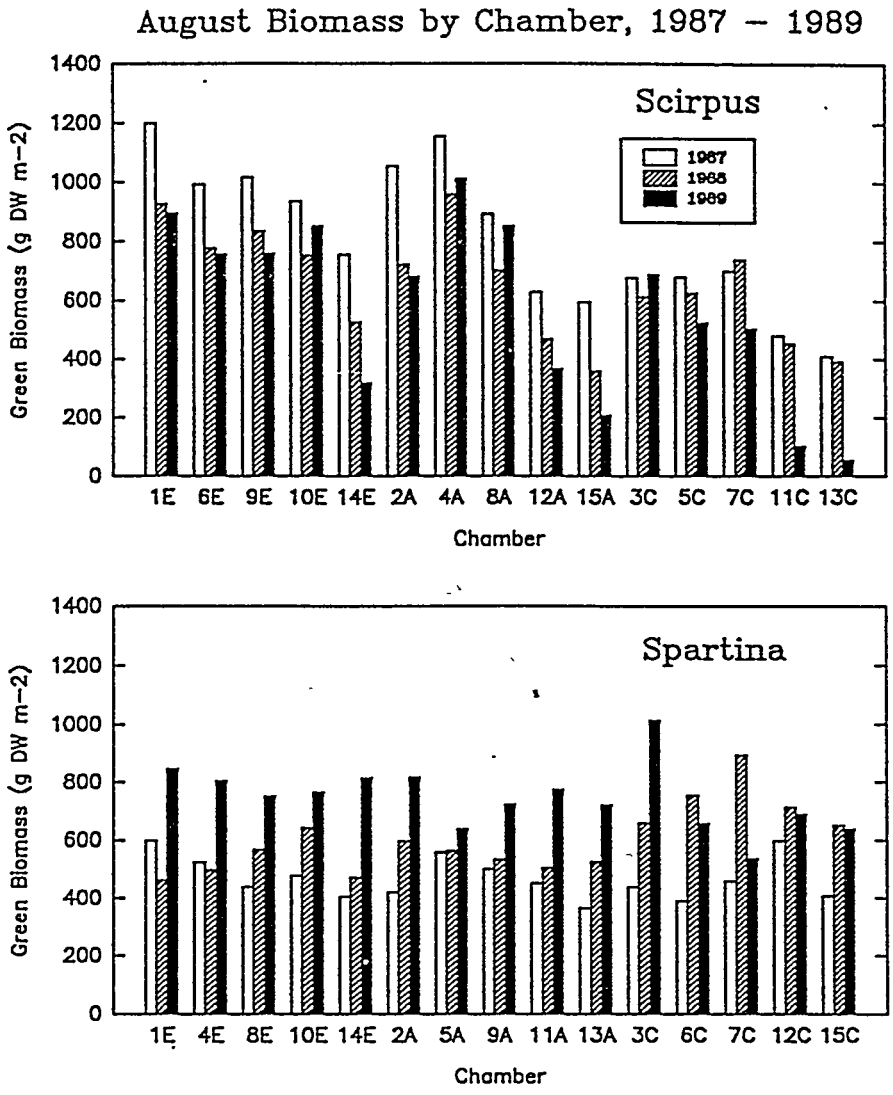

Figure 2.1

August biomass of Scirpus and Spartina by chamber, 1987-1989. Green biomass of Scirpus in the Scirpus community and Spartina in the Spartina community are expressed on a dry weight basis at the time of the August/September census. An explanation of the biomass calculations may be found in the text. Scirpus biomass remains stable in some chambers over three years but decreases in two blocks (chambers 9-11, 12-15). Spartina biomass increases over the three year period in every site.

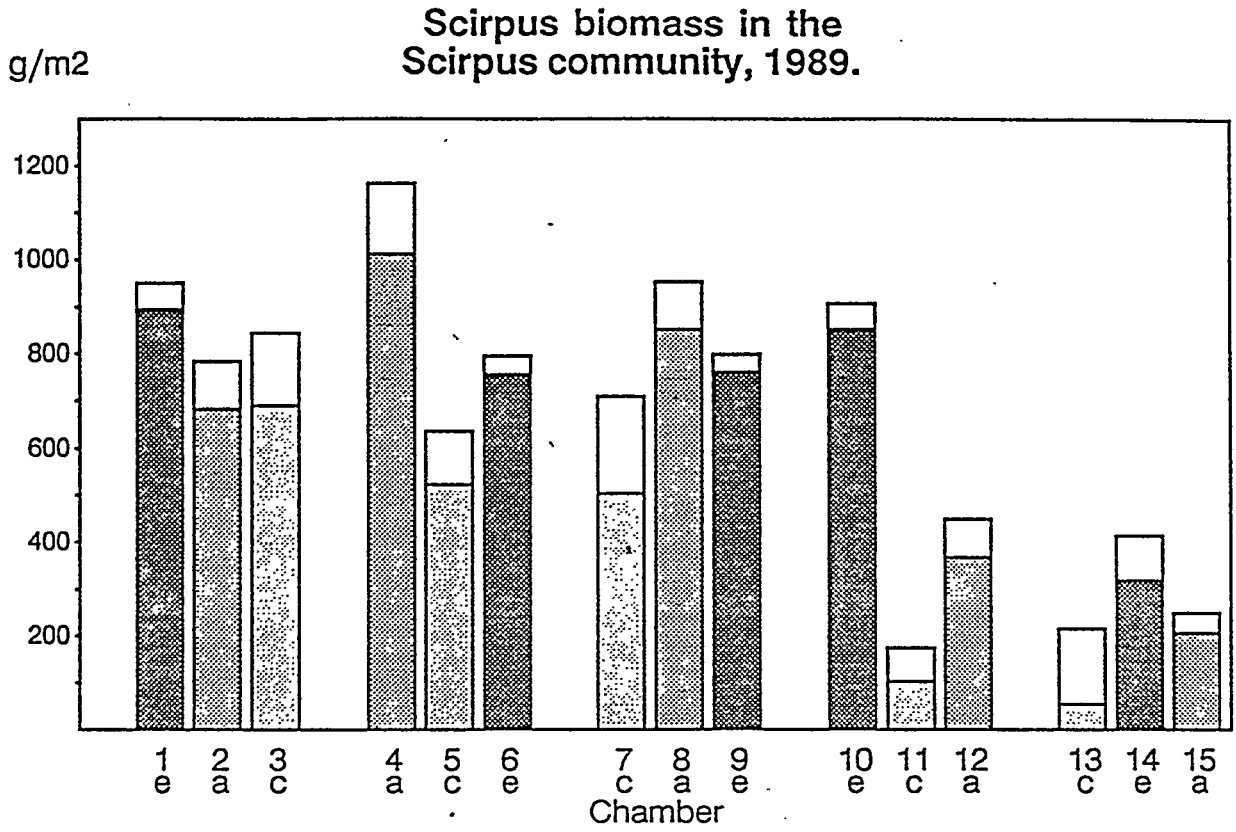

Figure 2.2

Scirpus biomass by chamber in the Scirpus community, 1989 Scirpus biomass in each chamber of the Scirpus community is shown by treatment and block. Within each block the green and senescent biomass are shown. The shaded portion of each bar (dark, elevated; gray, ambient; lightest, control) while the unshaded portion denotes the senescent biomass. Variation among blocks is demonstrated by the low biomass in chambers 11-15.

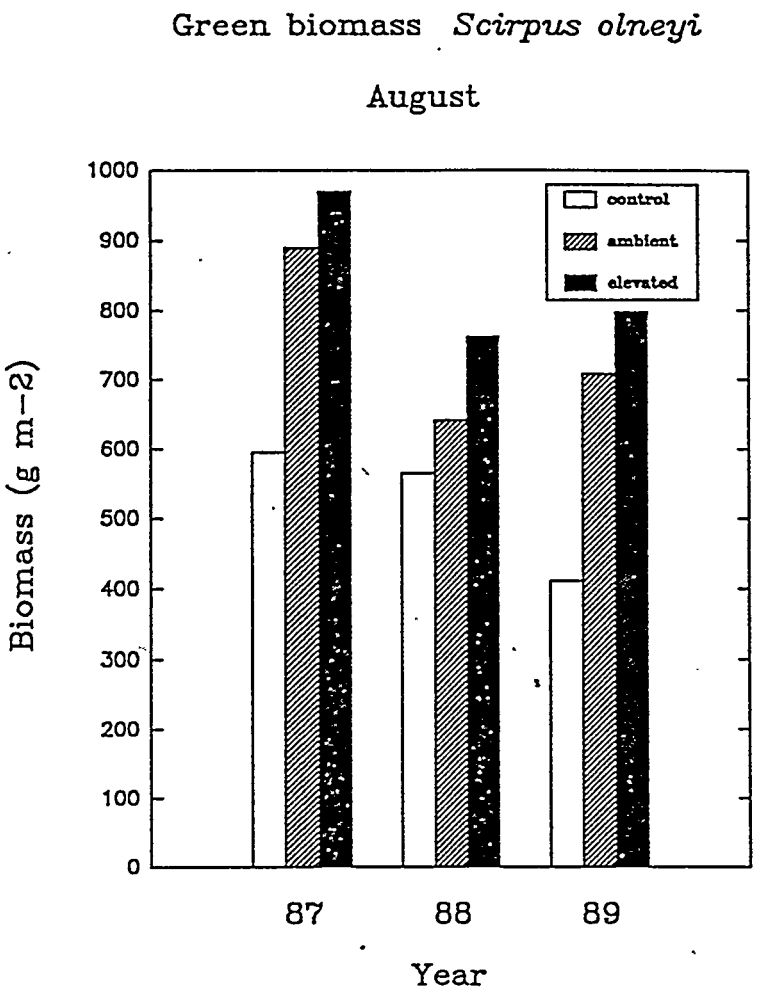

Figure 2.3

Scirpus green biomass in the Scirpus community by treatment, 1987-1989. Green biomass is expressed on a dry weight basis by treatment for Scirpus growing in the Scirpus community.

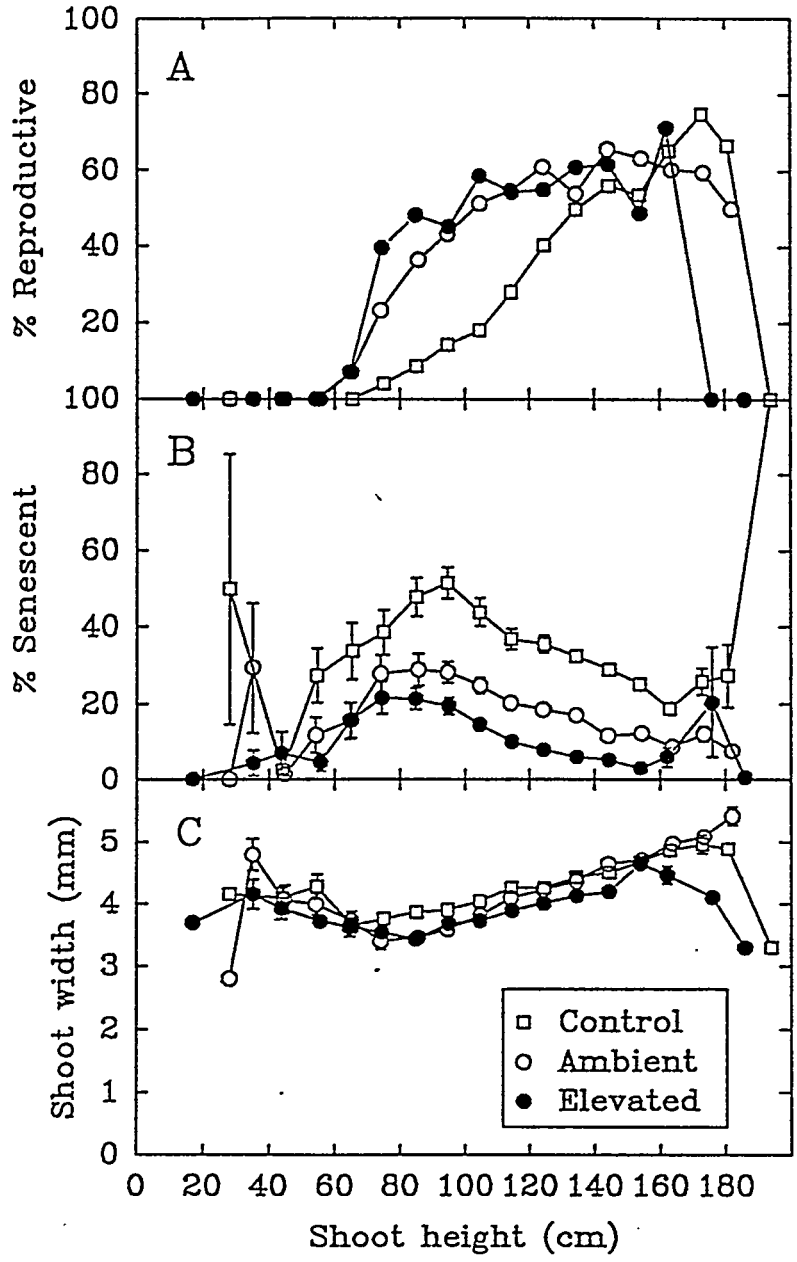

Figure 2.4

Analysis of Scirpus growing in the Scirpus community by height class, 1989. (A) percent reproductive tissue, (B) percent senescent tissue and (C) mean shoot width are shown for Scirpus growing in the Scirpus community. Percent reproduction in the middle height classes increases with the presence of a chamber however it does not show a treatment effect. Percent senescence shows both a chamber and a treatment effect in all except the extreme height classes. Shoot width is indistinguishable among the treatments.

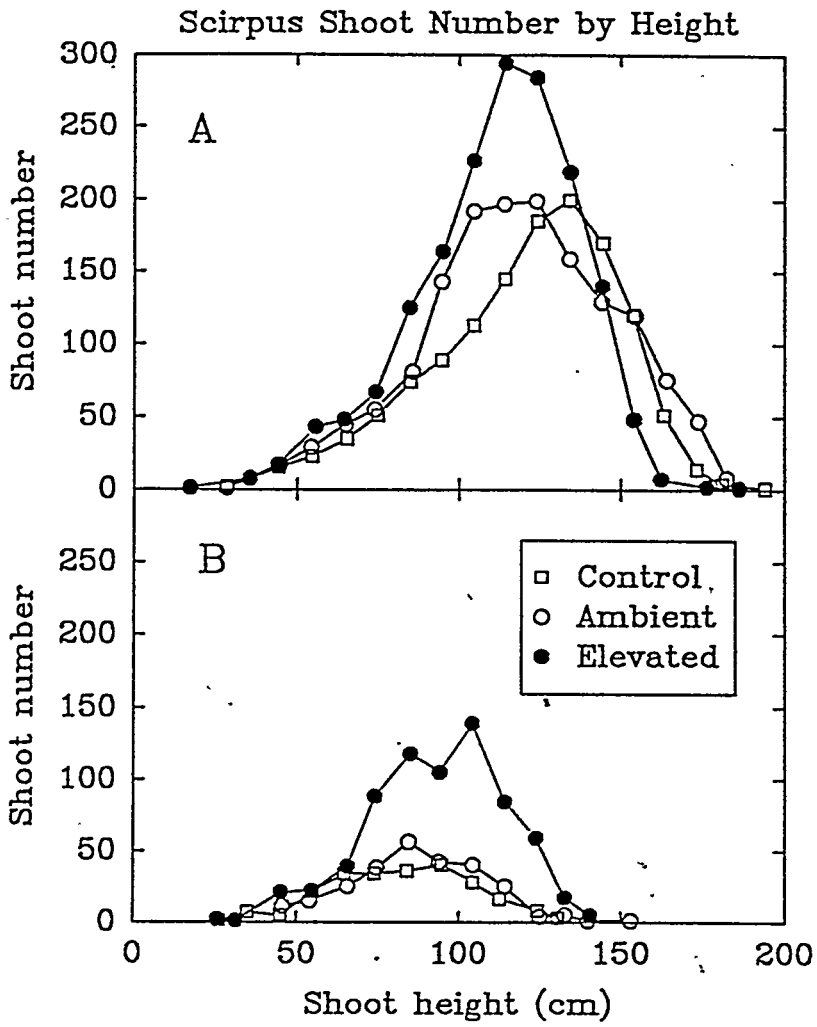

Figure 2.5

Scirpus shoot number by height class and treatment in the Scirpus and Mixed communities. The number of shoots in each 10cm. height class is shown by treatment for Scirpus grown in the Scirpus community (A) and the Mixed community (B). In the Scirpus community, the modal height class shows a chamber effect while the number of shoots in the modal height class shows a treatment effect. In the Mixed community the ambient and control data are indistinguishable while the elevated treatment had significantly more shoots in each height class above 70cm.

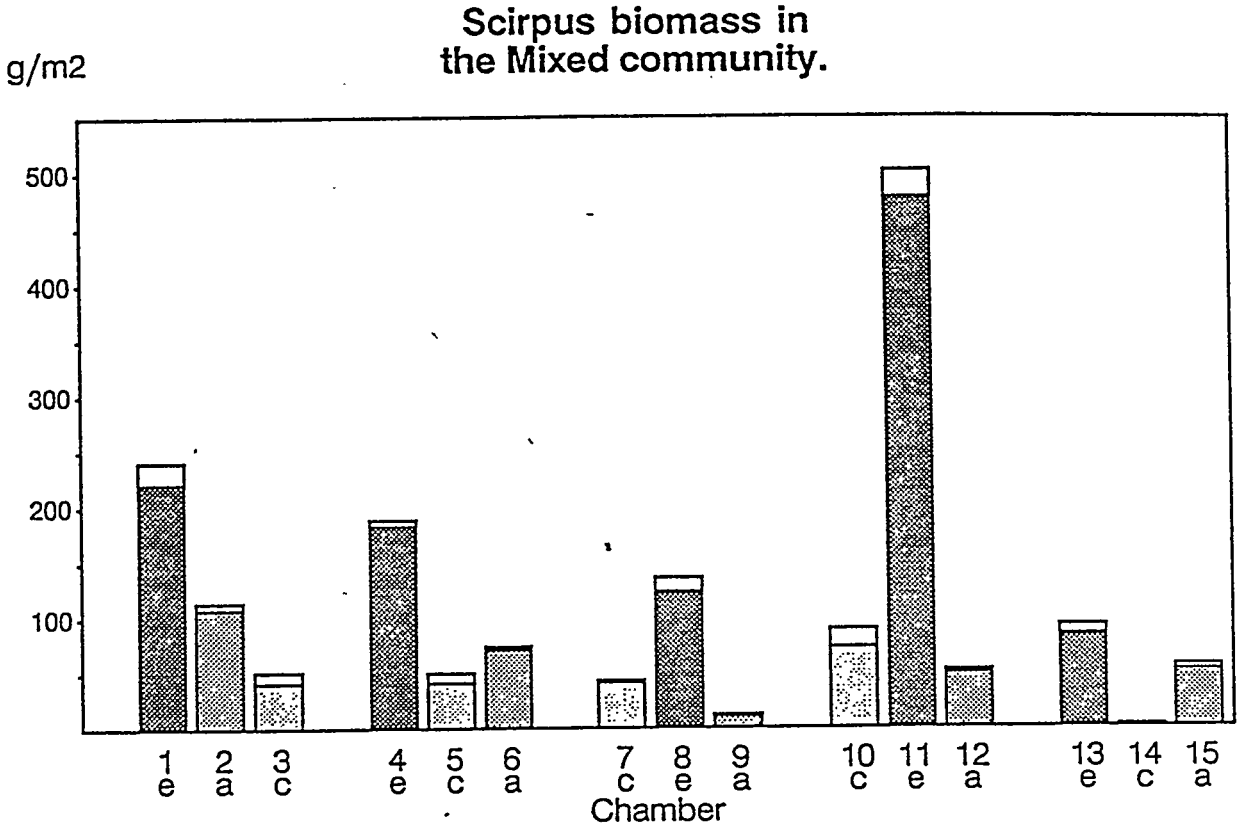

Figure 2.6

Scirpus biomass by block and treatment in the Mixed community, 1989. Scirpus green biomass in the Mixed community is shown by block and treatment (dark, elevated; gray, ambient; lightest, control) the unshaded portion of each bar represents the senescent biomass in that chamber. In each block the elevated treatment contained more biomass than either the ambient or control. Biomass values are expressed on a dry weight basis.

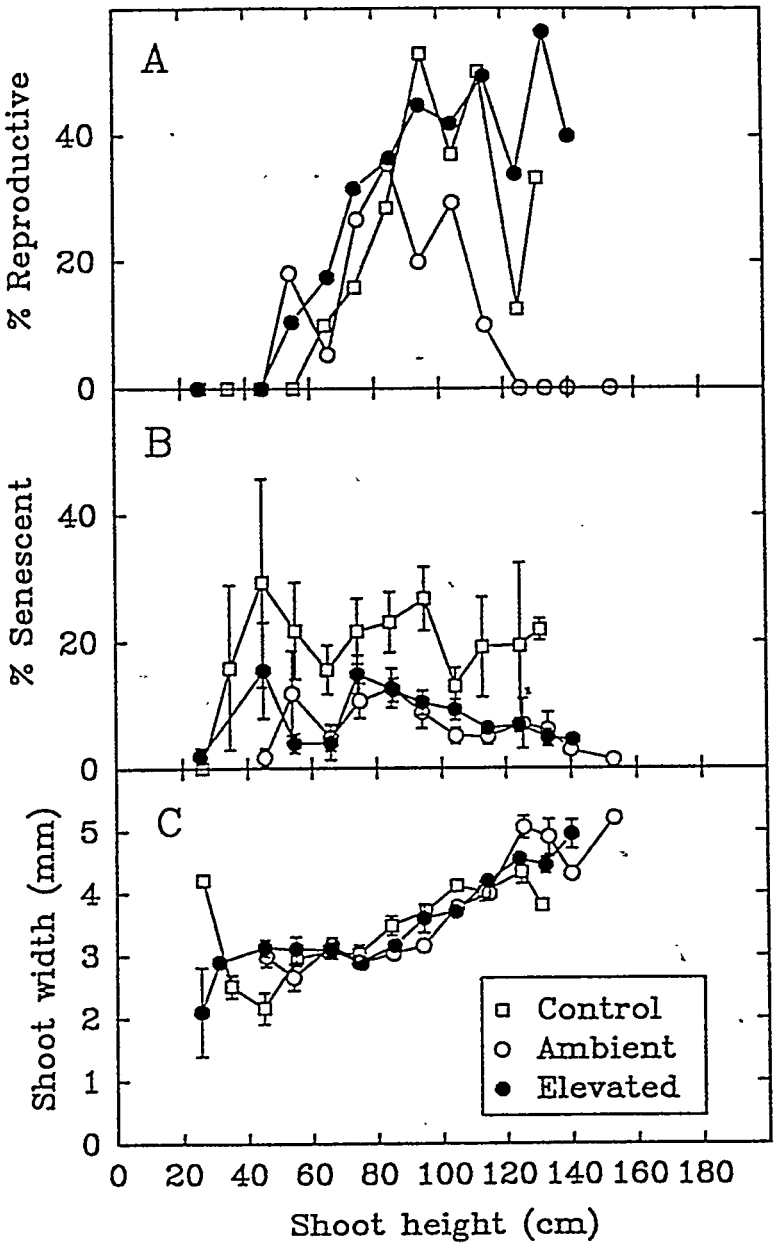

Figure 2.7

Analysis of Scirpus growing in the Mixed community by height class, 1989. (A) percent reproductive tissue, (B) percent senescent tissue and (C) mean shoot width are shown for Scirpus growing in the Mixed community. Percent reproduction was higher in the ambient and elevated treatments in the upper height classes. Percent senescence was lower in the ambient and elevated treatments however the difference was found only in specific height classes. Shoot width showed no chamber or treatment response.

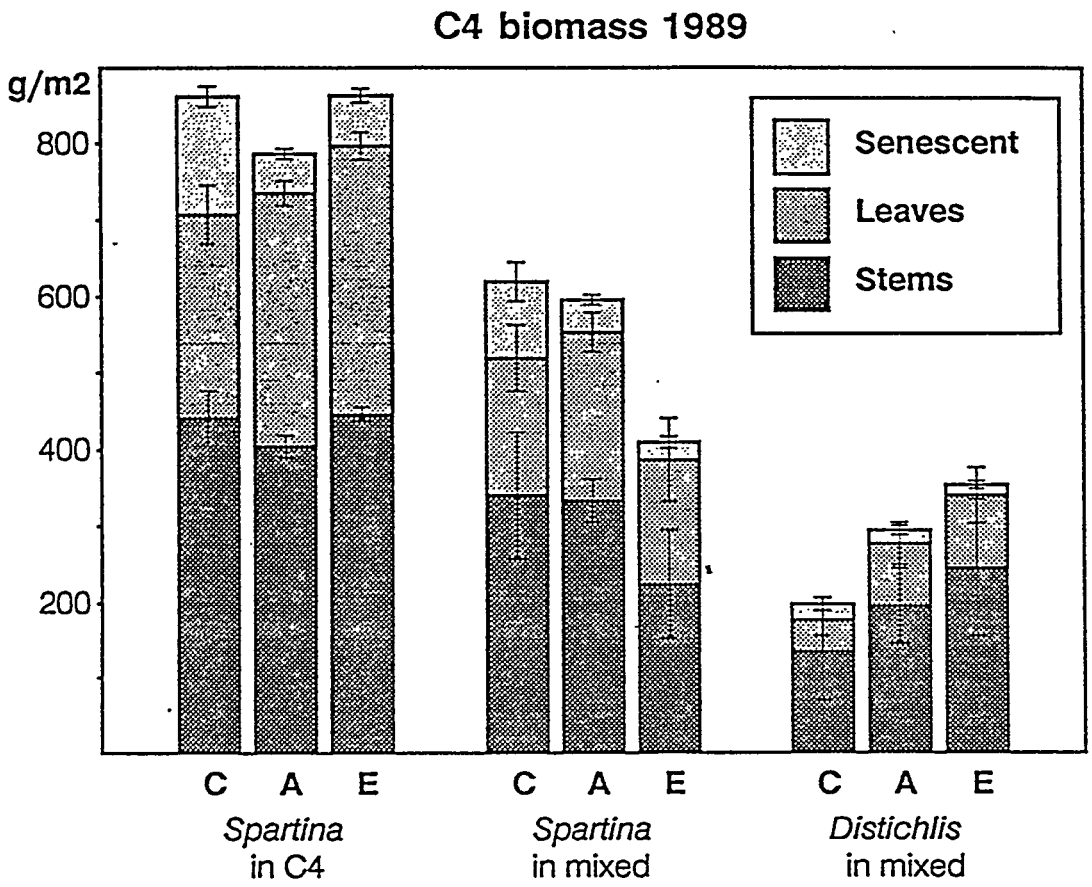

Figure 2.8

Spartina and Distichlis biomass by treatment, 1989. Total biomass, divided into senescent, leaf and stem dry weights, is shown by treatment for Spartina in the Spartina and Mixed communities and Distichlis in the Mixed community.

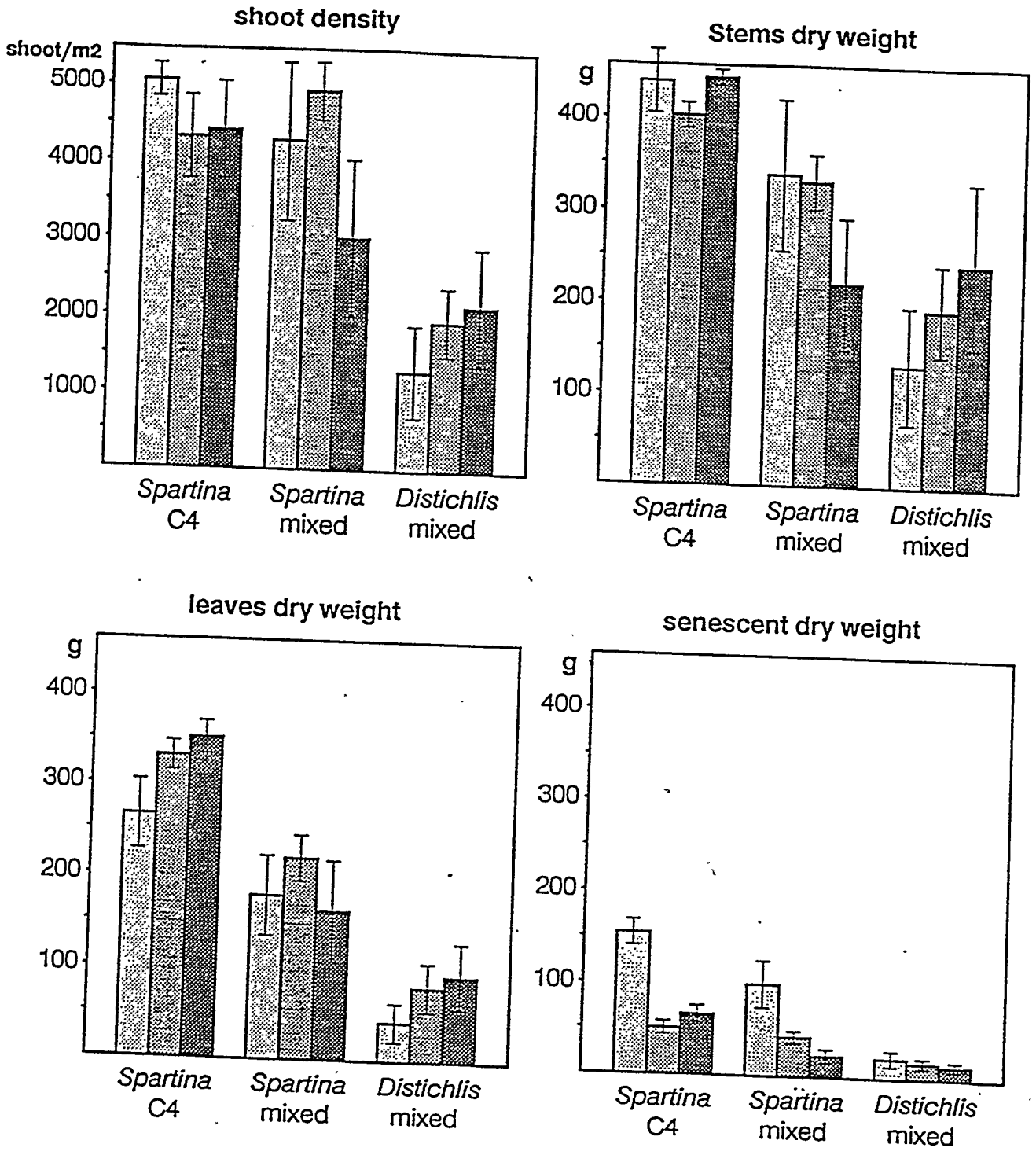

Figure 2.9

Analysis of Spartina and Distichlis biomass, 1989. Shoot density (A), stem dry weight (B), leaf dry weight (C), and senescent dry weight (D) are shown by treatment for Spartina in the Spartina and Mixed communities and Distichlis in the Mixed community. (Control, lightest shade; ambient, gray; elevated, darkest shade).

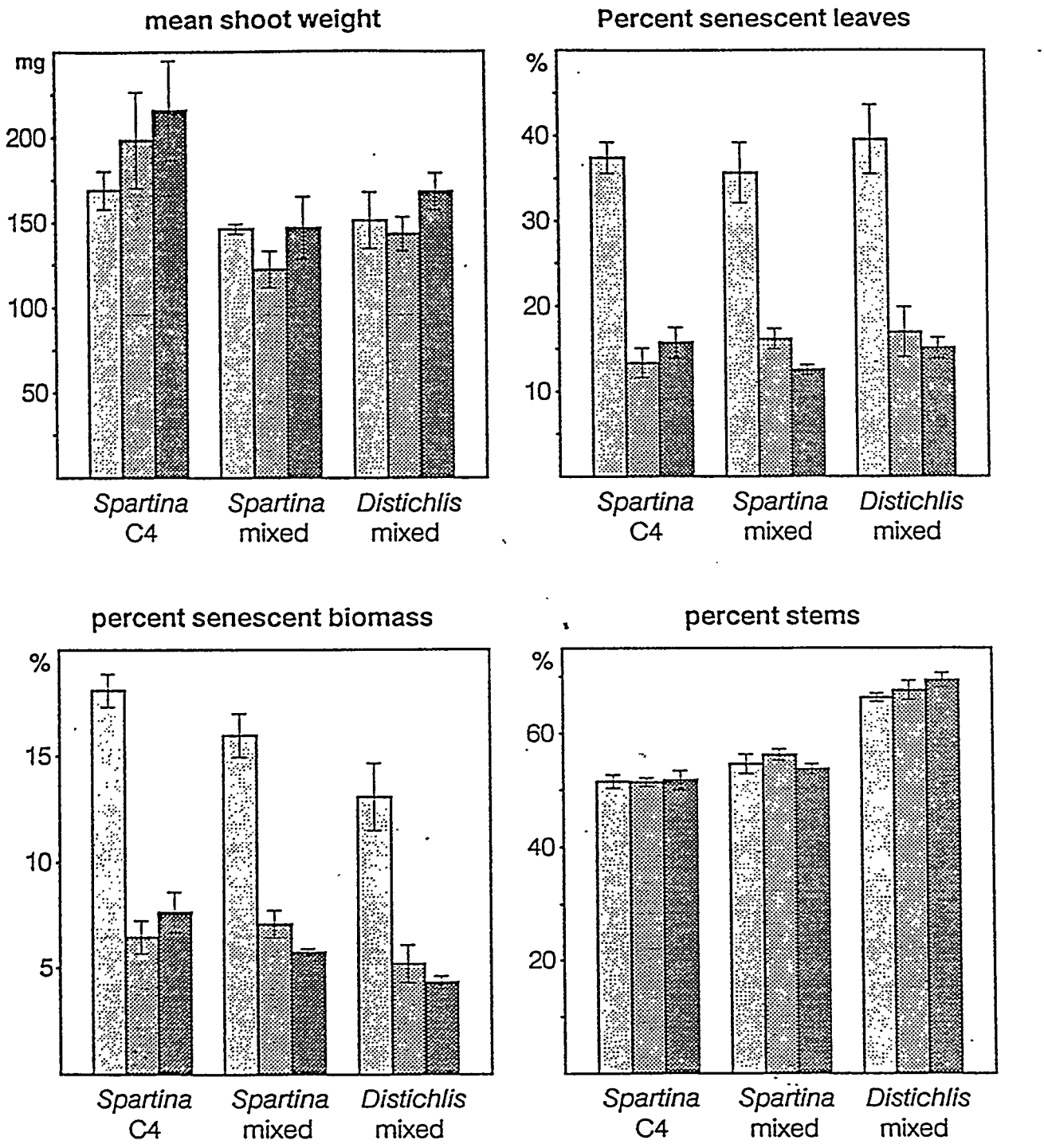

Figure 2.10

Analysis of Spartina and Distichlis biomass, 1989. Mean shoot weight (A), percent senescent leaves (B), percent senescent biomass (C), and percent stem tissue (D) are shown by treatment for Spartina in the Spartina and Mixed communities and Distichlis in the Mixed community. Percent senescent leaves and biomass are higher in the control sites than in the ambient or elevated chambers.

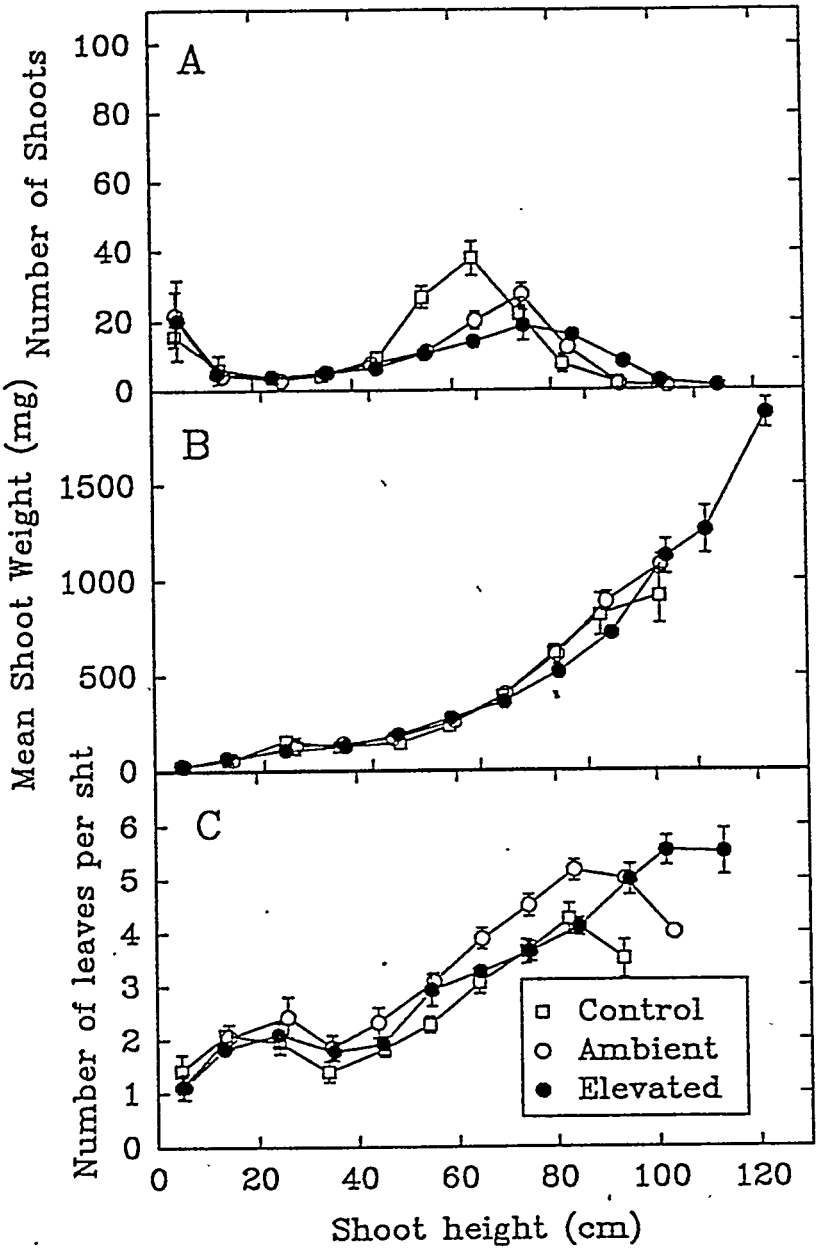

Figure 2.11

Analysis of Spartina vegetation in the Spartina community, 1989. Number of shoots (A), mean shoot weight (B), and number of leaves per shoot (C) are shown by height class and treatment.

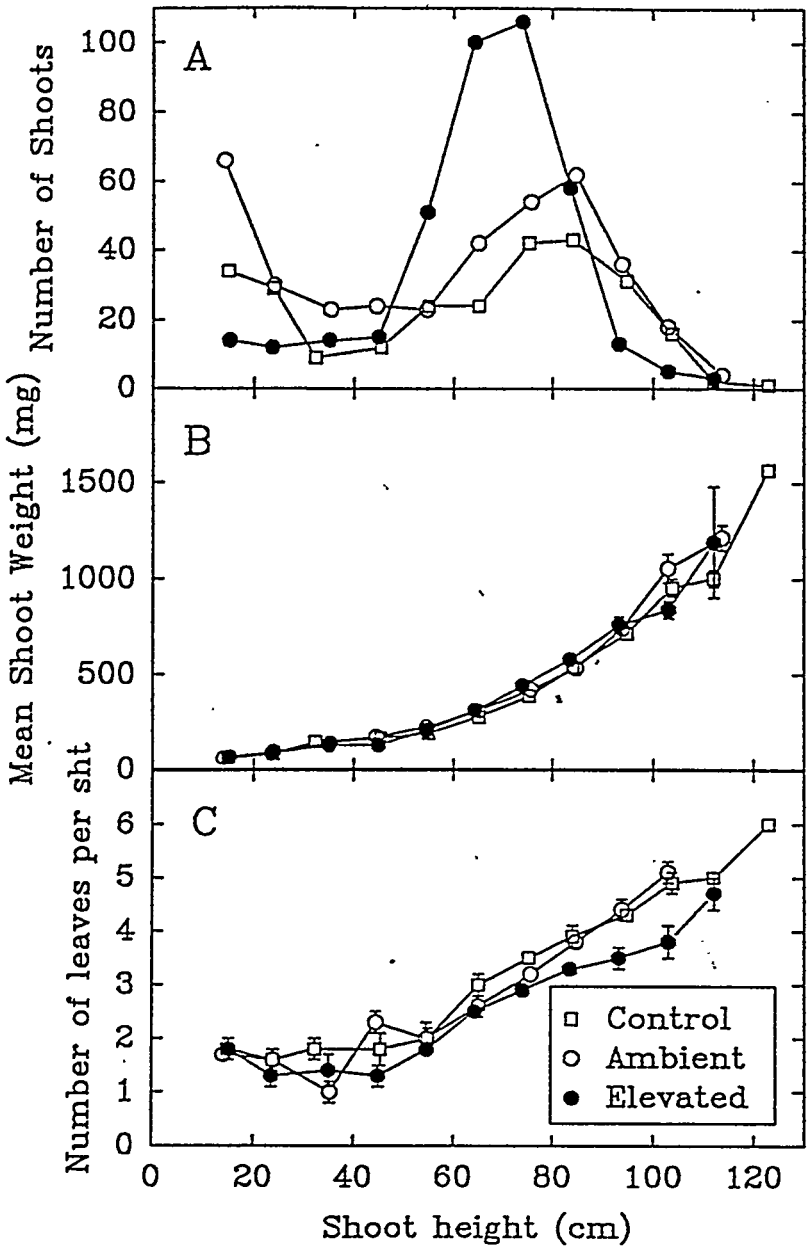

Figure 2.12

Analysis of Spartina vegetation in the Mixed community, 1989. Number of shoots (A), mean shoot weight (B), and number of leaves per shoot (C) are shown by height class and treatment.

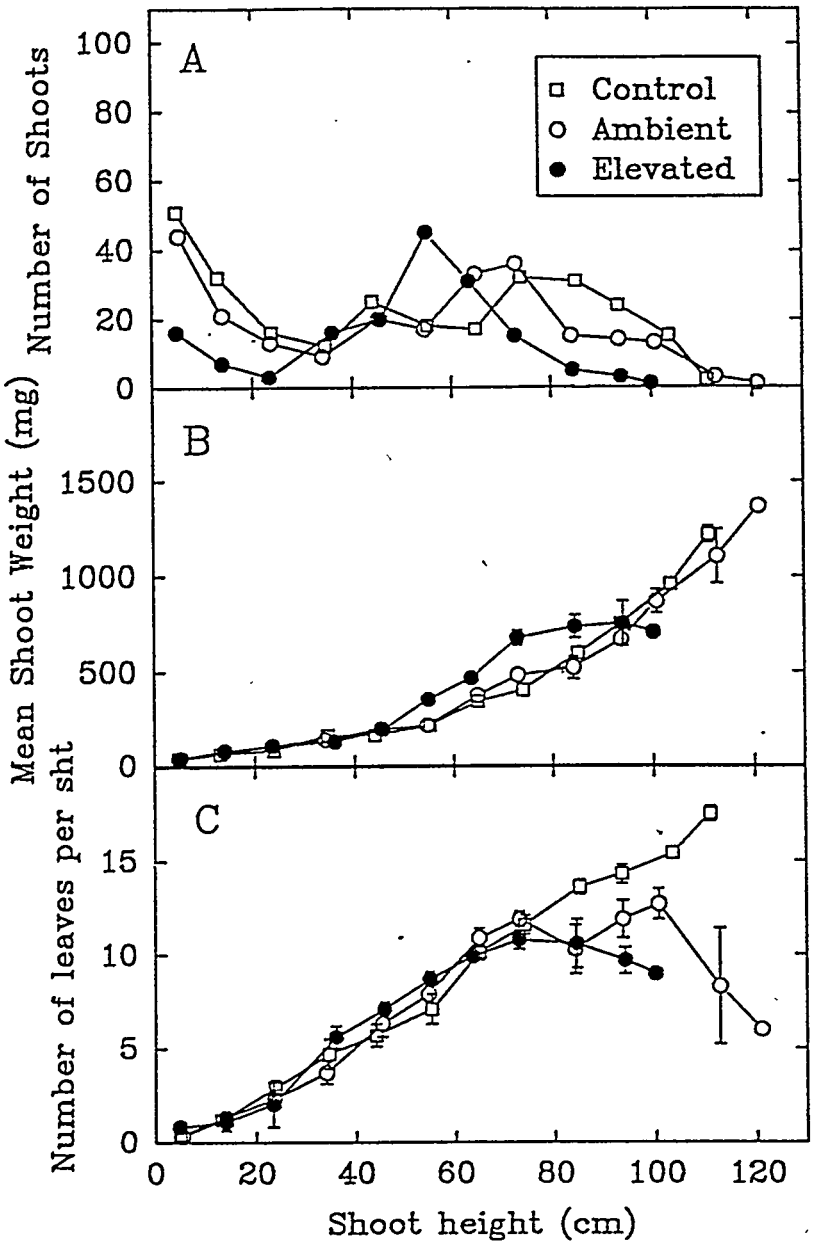

Figure 2.13

Analysis of Distichlis vegetation in the Mixed community, 1989. Number of shoots (A), mean shoot weight (B), and number of leaves per shoot (C) are shown by height class and treatment.

Chapter 3. Nitrogen.

Aboveground

Methods

Plant material collected during the 1989 sampling procedures described in chapter 2 was analyzed for carbon and nitrogen content using a Carbon-Hydrogen-Nitrogen analyzer (Control Equipment Corp.) at the Horn Point Laboratory of the University of Maryland. The percent nitrogen and carbon on a weight basis, the C/N ratio and total nitrogen aboveground were calculated.

Results

Figure 3.1 shows the results of the nitrogen analysis of plant tissue collected during the August, 1989 harvest. In both Scirpus and Spartina the percent carbon decreased significantly in senescent tissue. The percent carbon of flowers in the elevated and ambient treatments in Scirpus was also lower than in the control sites. Percent nitrogen decreased in Scirpus flowers and green tissue and Spartina leaves and stems while it remained the same in senescent tissue.

Belowground

No data for belowground nitrogen content were obtained during the 1989 season.

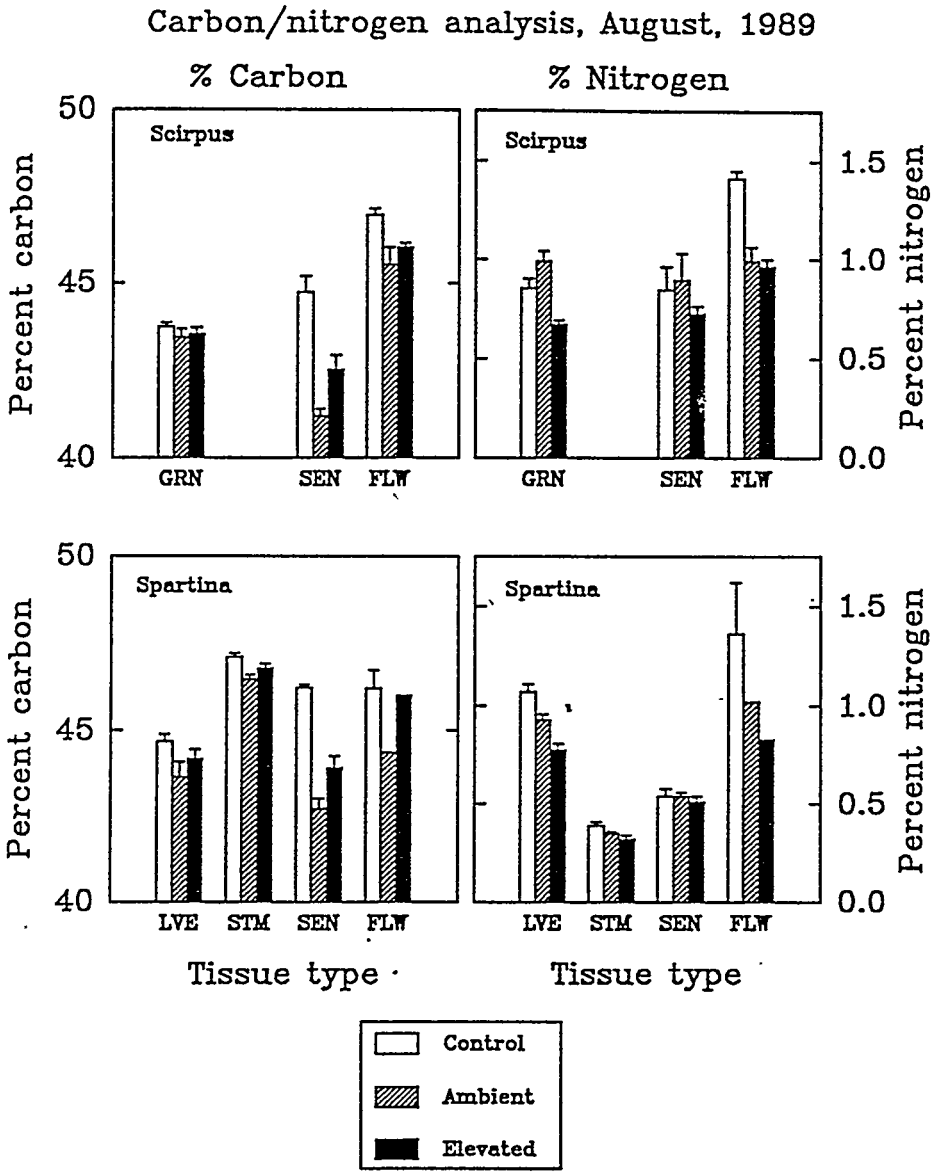

Figure 3.1

Carbon/Nitrogen analysis of tissue harvested August/September, 1989. Percent carbon and percent nitrogen are expressed on a weight basis for green stem tissue (GRN), senescent stem tissue (SEN), and flowers (FLW) in *Scirpus olneyi* and green leaf tissue (LVE), green stem tissue (STM), senescent leaf and stem tissue (SEN), and flowers (FLW) in *Spartina patens*.

Chapter 4. Single Leaf Gas Exchange.

This chapter contains data from single leaf gas exchange and flourescence work in the field. Additionally, the results of quantum yield and single leaf respiration experiments conducted in the laboratory using field collected tissue are reported.

Gas Exchange of High and Low Canopy Scirpus Stems in the Field.

A.C. Villegas.

INTRODUCTION

It has been observed consistently that Scirpus olneyi responds to elevated carbon dioxide concentrations with an increased rate of CO2 fixation. The resolution of these measurements however is at the community level and therefore they are unable to distinguish between the different components of the system enclosed by the chamber. While other components (soil respiration, gas exchange of other plant species) probably represent a small portion of the total gas exchange in the system, it is also impossible to differentiate the relative contributions of different parts of the Scirpus olneyi canopy.

To attempt to understand the variability of gas exchange rates in different parts of the canopy single leaf measurements of gas exchange were made at two heights in the Scirpus canopy (referred to hereafter as tops and bottoms). The results reported here are for gas exchange measurements made periodically throughout the day on 25 July and 4 August, 1989.

METHODS

Photosynthesis was measured in single shoots of Scirpus olneyi growing in ambient and elevated chambers of the Scirpus community using an ADC portable gas analyzer (Analytical Development Corp., U.K.; open system configuration). The leaf chamber used (Parkinson) included a quantum sensor and thermocouple allowing simultaneous measurement of light, temperature and gas exchange. The air flowing through the the cuvette during the measurements came from tanks of the same approximate CO2 concentration as the air in the chambers where the measurements were

taken. Dry air from the tanks was passed first through a humidifier and then through a water bath to set the relative humidity at 60 percent. The leaf chamber was held vertical and directed toward the sun to duplicate the normal pattern of exposure Scirpus, determined by its characteristic three sided stem. There was no temperature control during these measurements.

At the beginning of each day ten shoots were labelled, five in an elevated chamber and five in the ambient chamber of the same block. Each shoot was marked at points 30-40 cm. and 60 cm. above the soil surface. The same ten shoots were measured at both heights every two hours over a twelve hour period from 7 a.m. to 7 p.m.. The experiment was repeated twice during the summer, 25 July and 4 August, 1989. The general linear models procedure in the Statistical Analysis System (SAS) was used to test significance.

RESULTS AND DISCUSSION

There were no significant differences in temperature between the chambers or the tops and bottoms (Figure 4.1). While the light environments were not different between chambers, light levels in the upper part of the canopy were substantially higher than in the lower canopy (Figure 4.1). Data for one day's photosynthesis measurements (4 August, 1989) are shown in Figure 4.2. Plants grown under both ambient (340 ul/l) and elevated (680 ul/l) exhibited higher photosynthetic rates in top part of the canopy than in the lower part. Because the meristem in Scirpus olneyi is at the bottom of the stem, these results indicate that the oldest tissue on the stem also exhibits the greatest rates of carbon uptake. While photosynthetic rates in tops grown under elevated CO2 were significantly higher than tops grown in ambient air, there was no difference between the bottoms in the two treatments. The absence of any response to elevated CO2 in the low canopy suggests that the photosynthetic rate is limited by light. To fully answer this question will require the construction of light response curves for bottoms and tops of both treatments.

Flourscence of Scirpus in the Mixed Community.

S.P. Long.

INTRODUCTION

Several studies have shown that light levels beyond those normally experienced in a plant's natural environment will produce an irreversible or slowly reversible inhibition of photosynthesis. However, under sub-optimal conditions, e.g. during chilling or drought, such damage is also apparent at light levels within the range experienced in the field. This light dependent damage to the photosynthetic apparatus is termed photoinhibition (reviewed Powles, 1983). More recently it has been observed that a short-lived inhibition of photosynthetic capacity can also occur in leaves exposed during periods of high natural irradiation even when other environmental conditions are near-optimal. Such reductions in photosynthetic capacity have been observed in stands of Salix in summer in N. Sweden (Ågren & Öquist, 1988), in Arbutus unedo in the Mediterranean (Demmig & Winter, 1989) and in a variety of field crops in Central Europe (Bolhar-Nordenkampf & Lechner, 1989). This loss of efficiency is apparent as decreases in the quantum yield of photosynthetic O2 evolution and CO2 uptake, and in a decrease in the photochemical efficiency of photosystem II (PSII), as estimated from the ratio of variable to maximal chlorophyll fluorescence (Fv/Fm) from photosystem II. Recovery of this form of inhibition is relatively rapid, occurring within 1 - 2 hours, or less, and is considered to result from a protective mechanism quenching excitation energy within the photosynthetic membrane and preventing a potentially damaging build-up of excitation energy which might otherwise lead to oxidative damage to the photosynthetic apparatus (Demmig & Winter, 1989). Whilst a protective reaction, it respresents an inhibition of photosynthetic capacity. It is characterised by a decrease in the photochemical efficiency of PSII, indicated by a decline in Fv/Fm, and a parallel decline in the quantum yield of photosynthesis. Thus, there is a loss of potential CO2 assimilation.

How might rising atmospheric CO_2 concentrations influence this high light inhibition of

photosynthesis? Increased supply of CO_2 could have conflicting effects on PÇ3 light inhibition of photosynthesis. Increased photosynthesis due to an improved supply of CO_2 could decrease the probability of inhibition, by diverting more of the trapped light energy into photosynthesis itself and decreasing the potential for a build-up of excitation energy within the chloroplast membrane. Such a protective effect of increased CO_2 concentration has been demonstrated in crop plants during exposure to high light whilst being chilled (Rowley & Taylor, 1972). By contrast, Sharkey et al (1990) suggested that increased CO_2 concentrations could increase the probability of light inhibition, through a build-up of carbohydrate end-product in the leaf and "end-product" inhibition of photosynthesis.

Chlorophyll fluorescence provides a particularly useful tool for investigating this form of light inhibition for two reasons. First, it is rapid requiring only a few seconds. By contrast gas exchange measurements of quantum yield require ca. >15 minutes, during which time recovery may occur (e.g. Demmig and Winter, 1989). Secondly, the marked heterogeneity of photon fluxes within a plant canopy mean that different surfaces will receive very different amounts of light, producing marked variation in the degree of inhibition. The rapidity of chlorophyll fluorescence measurements allows a statistically valid sample to be taken.

The objectives of this study were threefold. 1. To determine whether high photon fluxes in the field produced a similar depression of F_v/F_m in S. olneyi, indicating light inhibition of quantum yield. 2. To determine if the occurrence of light inhibition was modified by the CO_2 concentration in which the plants developed and are growing. 3. How CO_2 concentration, light and position within the canopy may influence inhibition.

METHODS

Plant Material

As part of a long-term investigation of the effects of elevated CO_2 on vegetation of a tidal marsh, 30 open-top chambers have been placed within the boundary of three

mesohaline marsh community types of the Rhode River, a sub-estuary of the Chesapeake Bay in eastern Maryland (Curtis et al., 1989). Via a computer controlled system c_a in half of these chambers has been maintained at 700 μmol mol-1 for the complete growing seasons of the past 3 years (Drake et al., 1989). The remaining chambers were maintained at c_a = 350 μmol mol-1 to provide controls for the modification of plant microclimate produced by the presence of the chamber. Twenty of these chambers included plants of the C_3 sedge S. olneyi and were used in the current investigation. The only photosynthetic organ of this species is its triangular stem. For the measurement of chlorophyll fluorescence mature stems were selected at random from within the open-top chambers, or in the initial experiments form adjacent areas of the marsh. Measurements were made in situ at about 15 cm below the top of the stem, unless stated otherwise.

Measurement of chlorophyll fluorescence

The quantum yield of photochemistry at photosystem II is proportional to the ratio of the variable (Fv) to maximal fluorescence (Fm) emission from chlorophyll (Butler & Kitijima, 1975). This interpretation assumes that PSII is fully oxidised at the point of addition of saturating light to induce the rise in fluorescence to Fv. Measurement of Fv/Fm therefore requires material that has been "dark-adapted", i.e. it has been in darkness for sufficient time for the primary acceptor molecules of photosystem II to become fully oxidised. Tubes black on the inside and reflective on the outside, made light tight at the ends with closed cell black foam were slid onto the S. olneyi stems in situ. PÇ3 Chlorophyll fluorescence at 695 nm was measured in the field with a portable fluorimeter using an excitation photon flux of 400 μmol m-2 s-1 (Type PSM, BioMonitor S.C.I. AB, Malmö, Sweden). After a fixed period of dark-adaptation, the "adaptation sleeve" was slid away and replaced by a light-tight clamp into which the fibre optic for illuminating the leaf had been sealed. The clamp was placed below and immediately adjacent to the sleeve. As the black closed cell foam of the clamp and sleeve overlapped no light should reach the stem during this operation. To ensure no leakage of light onto the specimen, a black bag was placed over the stem for this operation. Once in position the dark-adapted portion

of stem was excited, the induction of chlorophyll fluorescence recorded into the solid-state memory of the fluorimeter and then later dumped to microcomputer (Vectra, Hewlett-Packard) for subsequent analysis.

The conditions used for the measurement of F_v/F_m were determined by a set of preliminary measurements. Populations of stems were examined at 20:30 hours, i.e. after dusk, when light inhibition would be minimal and at 15:00 hours when the potential for light inhibition would be close to maximal. Using a range of dark-adaptation periods and excitation light levels, no significant increase in F_v/F_m was found after 10 minutes of placing the tissue in complete darkness (Fig. 1). Similarly, increase in the photon flux density of the actinic excitation beam above 400 μmol m-2 s-1, determined by placing a quantum sensor (Li-190, Li-Cor, Lincoln, Nebraska, USA) in the position normally occupied by the stem, produced no further increase in F_v/F_m ratio (

Fig. 2). As a further check on the validity of the F_v/F_m estimates, a sample of 20 stems were removed from the field and Fv/Fm was measured with both the PSM portable fluorimeter and a modulated fluorimeter (PAM 101 & PAM 103, H. Walz, Effeltrich, FRG) and excitation light of 7 000 μmol m-2 s-1 (KL10, Schott GmbH, Mainz, FRG) which should ensure full trap closure in the determination of F_m. Half of the stems were measured with the PSM fluorimeter, and then allowed a further 10 minutes dark adaptation before measurement with the PAM fluorimeter. For the other half the order PÇ3 was reversed. To ensure that measurements were made by both fluorimeters on the same point of the stem, both were connected to the same sample holder (MFMS holder, Hansatech Ltd., Kings Lynn, U.K.). This comparison showed that despite the very different modes of measurement of Fv/Fm in the two instruments (Bolhar-Nordenkampf et al., 1989), the ratio of Fv/Fm(PAM fluorimeter) to Fv/Fm(PSM fluorimeter) was 1.02 $\pm$ 0.02, i.e. there was no significant difference in the value of F_v/F_m (Fig. 3). For all subsequent measurements an excitation photon flux of 400 μmol m-2 s-1 following 10 min dark adaptation was used to determine F_v/F_m.

Occurrence of light inhibition of F_v/F_m and the effects of CO_2 elevation

To determine the occurrence of light inhibition of PSII efficiency. A series of measurements were conducted. 1) F_v/F_m was determined at hourly intervals throughout a day with clear skies to establish the occurrence of light dependent inhibition in S. olneyi. As a check on the light dependence of inhibition a reflective aluminium screen was placed in front of a population of stems to provide a shaded control. 2) F_v/F_m was determined on stems selected at random within control and elevated CO_2 open top chambers, to examine variation in F_v/F_m with both time of day and position in canopy. Differences in mean F_v/F_m with time of day and between the CO_2 concentration of the growth environment were examined by two-way analysis of variance. Differences between mean F_v/F_m in the two growth environments at single times in the day were tested by Student's t-test (Sokal & Rohlf, 1981).

RESULTS

Fig. 4 shows that the mean F_v/F_m of S. olneyi stems declines in an anti-parallel manner to the mean incident photon flux (Fig. 4). Dawn values of F_v/F_m were 0.86 and dusk values 0.83, close to the maximum values suggested for C_3 species (Björkman & Demmig, 1987) indicating the absence of any long-term impairment of photochemical efficiency of PSII in these stems. By 14:00 hours F_v/F_m was depressed by 14% relative to dawn values, a highly significant difference (t, $p<0.01$). Shading of stems at 15:00 hours allowed complete recovery of F_v/F_m within 2 hours (Fig. 4a).

F_v/F_m had decreased by 22% at 15:30 for stems in full sunlight growing in a control open-top chamber, supplied with 350 μmol mol-1 of CO_2 in air. By comparison similar stems which were growing in an adjacent chamber elevated CO_2 chamber, with 700 μmol mol-1 of CO_2 in air, showed a decline in F_v/F_m of only 13% by 15:30 hours (Fig. 5a). Decreases are relative to the post-dusk values of F_v/F_m measured at 20:30 hours (Fig 5a)/ This greater decrease in F_v/F_m in the control chamber was highly significant (t, $p<0,01$). F_v/F_m was measured in the same chambers on three successive days (Fig. 5). The pattern observed on June 27 was repeated on June 29 (Fig. 5c), both days with clear

skies with high photon fluxes of >2 000 μmol m-2 s-1 at solar noon. June 28 was overcast with low photon fluxes, and here only small decreases in F_v/F_m of 6% in the control and 3% in the elevated CO_2 chamber were observed. Examination of decline in F_v/F_m with canopy height appears to confirm the implied interaction with photon flux. Relative to stems growing in the elevated CO_2 chamber the reduction in F_v/F_m in the control chambers were 7%, 7% and 0% greater for portions of stem in the upper, middle and lower canopy, respectively (Fig. 6). Differences in F_v/F_m between the two chambers at each position within the canopy were significantly different (F, $p<0.05$). Fig. 7 shows that F_v/F_m is similar for stems in both elevated and control chambers at dawn and dusk. PÇ3 However, as the day progresses, F_v/F_m becomes increasingly lower in the stems of the control chambers relative to those of the elevated chambers, the greatest difference being apparent in the late afternoon (Fig. 7). By dusk, F_v/F_m had recovered in both elevated and control chambers to the dawn values.

DISCUSSION

The results infer that photosynthetic capacity in S. olneyi is inhibited by exposure to direct sunlight in the field and that this inhibition is alleviated when plants are grown in an atmosphere in which the CO_2 concentration is elevated above the present mean atmospheric level. This inference is made from observed changes in F_v/F_m. Variation in F_v/F_m has been experimentally shown to be linearly and positively linked to the maximum quantum yields of O_2 evolution and CO_2 uptake (Björkman & Demmig, 1987; Genty et al., 1989). The rapid recovery of F_v/F_m over 1 - 2h which occurs in low light, suggests that the light inhibition of photosynthesis observed here is not photoinhibitory damage of the type observed, for example during chilling stress (e.g. Baker et al., 1989), but most probably the development of an additional slowly reversible non-photochemical quenching mechanism of the type described by Winter & Demmig (1989) for Arbutus unedo.

As noted by Bolhar et al. (1989), changes in F_v/F_m may also be artifacts of the method of measurement, and care was taken to check for these. Decrease in F_v/F_m could result, if the time required for re-oxidation of the initial electron acceptors of PSII was altered,

since this would change the period required for dark adaptation. Fig. 1 however, shows that for stems sampled at 15:30 when depression of F_v/F_m was maximal and at dusk when F_v/F_m values were maximal no significant increase in F_v/F_m occurs after 10 minutes, indicating that the dark-adaptation period was adequate. Changes in the rate PÇ3 constants for transfer of excitation energy from PSII could alter the minimum photon flux required to approach saturation of PSII during the induction of fluorescence emission. If the photon flux is too low reduction of PSII during the rise to F_m may be incomplete before photochemical and slow non-photochemical quenching processes commence, leading to an underestimation of F_v and therefore F_v/F_m. Fig. 2 & 3 however shows that F_v/F_m was maximal when an excitation photon flux of 400 μmol m-2 s-1 was used and that similar values were found regardless of whether measurements were made with a photon flux of 400 μmol m-2 s-1 or 7 000 μmol m-2 s-1, which would almost certainly saturate PSII.

Given the linear relationship of F_v/F_m with the quantum yield of CO_2 assimilation, these fluorescence studies suggest that light inhibition could lead to significant decreases in canopy photosynthesis. However, the results obtained here suggest that rising atmospheric CO_2 concentrations may alleviate this loss of photochemical capacity. Plants grown and measured in an atmosphere with 700 μmol mol-1 CO_2 showed roughly half the decrease in F_v/F_m of adjacent plants grown and measured in 350 μmol mol-1 CO_2 in air. Of particular note is the increasing difference in F_v/F_m which develops over the course of the day, so that the decrease in F_v/F_m of plants growing in the control chambers is greatest relative to those growing in the elevated CO_2 chambers in the late afternoon (Fig. 7). This pattern parallells the changes in canopy CO_2 assimilation (A_c) observed for these plants. At the beginning of the day A_c in the elevated CO_2 chambers is greater, as would be expected due to decreased photorespiratory losses (Tolbert & Zelitch, 1983). However, as the day progresses the difference between elevated and control chambers increases to a maximum in the late afternoon, even in the absence of significant temperature changes (Bert, can you add a reference to those chamber CO_2 fluxes that you showed to me??). The results obtained here suggest alleviation of light

inhibition of photosynthesis by elevated CO_2 as a possible cause of this pattern of change.

No evidence of the basis of alleviation of light inhibition in elevated CO_2 was obtained in this study. One possible cause could be increased photochemical quenching of PSII as a result of increased supply of CO_2 for photosynthesis. CO_2 has been observed to alleviate the development of photoinhibition during chilling and water stress (Rowley & Taylor, 1972; Powles et al. 1981). Another possible cause is decreased water stress, which may interact with light in the development of inhibition of PSII (Powles et al., 1983; Ludlow and Powles, 1988). Water use efficiency is substantially increased in the elevated CO_2 chambers (Bert, reference), and thus depression of stem water potential could be expected to be less in these chambers with differences becoming greatest in the late afternoon.

In conclusion this study shows that rising CO_2 levels alleviate light inhibition of photosynthesis for plants in the field. Thus, this may be a factor in addition to decreased photorespiration, that would lead to increased photosynthetic productivity of C_3 plants in the predicted future atmosphere with increased CO_2 concentrations.

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Quantum yield of Scirpus.

S.P. Long.

Abbreviations: A, rate of CO2 uptake per unit projected area of stem (μmol m-2 s-1); Asat, A at light saturation (μmol m-2 s-1); ca, the concentration of CO2 in the ambient air (μmol mol-1); Fm, maximum emission of photosystem II chlorophyll fluorescence (arbitrary units); Fo, the initial fluorescence level, practically determined as the prompt (<ms) fluorescence emission level; Fv, variable component of Fm; LCP, the light compensation point of photosynthesis (μmol m-2 s-1); Q, photosynthetically active photon flux (μmol m-2 s-1); Qabs, Q absorbed per unit of projected stem area; Qwall, Q on the wall of the Ulbricht sphere; RubP, Ribulose 1,5 bisphosphate; RubisCO, Ribulose 1,5 bisphosphate carboxylase/oxygenase; t0.5, the half rise time of photosystem II chlorophyll fluorescence from the initial O level to the peak level at Fm (ms); α, the absorptance of the stem surface; ϕabs, the maximum quantum yield, i.e. the ratio of CO2 molecules absorbed per photon absorbed (dimensionless).

ABSTRACT

CO2 concentration has been elevated over three years around stands of the C3 sedge Scirpus olneyi on a tidal marsh of the Chesapeake Bay. The hypothesis that tissues developed in an elevated CO2 atmosphere will show an acclimatory decrease in photosynthetic capacity under light limiting conditions was examined. The absorbed light quantum yield of CO2 uptake (ϕabs) and the efficiency of photosystem II (PSII) photochemistry were determined for plants which had developed in open top chambers with CO2 concentrations in air of 700 μmol mol-1 and of 350 μmol mol-1, as controls. An Ulbricht sphere leaf chamber incorporated into an open gas exchange system was used to determine ϕabs and a portable chlorophyll fluorimeter was used to estimate the photochemical efficiency of PSII. When measured in an atmosphere with 1% O2 to eliminate photorespiration, shoots showed a ϕabs of 0.095±0.003, with no statistically significant difference between shoots grown in elevated or control CO2 concentrations. Efficiency of PSII photochemistry was also unchanged by development in an elevated

CO_2 atmosphere. In 21% O_2 and 350 μmol mol-1 CO_2, ϕabs of shoots which had developed in 700 μmol mol-1 CO_2 were 6% lower than for shoots which had developed in 350 μmol mol-1 CO_2, this difference was not statistically significant. However, shoots grown and measured in 700 μmol mol-1 of CO_2 in air showed a ϕabs of 0.078±0.003 compared to a ϕabs of 0.065±0.003 for leaves grown and measured in 350 μmol mol-1 CO_2 in air; a statistically highly significant difference. In accordance with the change in ϕabs, the light compensation point of photosynthesis was found to decrease. Light compensation occurred at photon fluxes of 51±3 μmol m-2 s-1 and 31±3 μmol m-2 s-1 for stems grown and measured in the control and in the elevated CO_2 chambers, respectively. The results suggest that even after three years of growth in elevated CO_2, there is no evidence of acclimation in capacity for photosynthesis under light limited conditions to counteract the stimulation of photosynthetic CO_2 uptake that would otherwise be expected through decrease photorespiration. The implications of this PÇ3 increase in ϕabs for canopy photosynthesis in an atmosphere with a doubled CO_2 concentration are discussed.

Temporary elevation of the CO_2 concentration in the air (ca) around the leaf of a C3 plant is well known to increase the photosynthetic rate of CO_2 uptake (A), through partial inhibition of photorespiration (reviewed: Pearcy & Björkman, 1983; Tolbert & Zelitch, 1983). Such observations suggest that the doubling of global CO_2 concentration projected to occur during the next century (Bolin, 1986) would result in an increased photosynthetic potential in C3 plant communities. However, a number of studies have now shown that growth at a ca elevated above the current atmospheric concentration of 350 μmol mol-1 to 600 - 700 μmol mol-1 can depress photosynthetic capacity. Leaf photosynthetic rates of plants grown and measured in elevated CO_2 concentrations may be lower than those of plants grown in current concentrations of CO_2 (350 μmol mol-1) but measured in elevated concentrations (Oechel & Strain, 1985; Sage et al., 1989). Thus, development of photosynthetic organs in elevated CO_2 may result in acclimation, partially or wholly offsetting the increase that results from decreased photorespiration.

The net result is that for many species, photosynthetic rates of plants measured and grown in elevated CO2 concentrations are similar to rates for plants measured and grown in current ambient CO2 concentrations. Possible mechanisms of this acclimation of photosynthesis to elevated CO2 include decreases: in amounts of ribulose bisphosphate carboxylase/oxygenase (Schmitt & Edwards, 1981), in the activation state of this enzyme, and in capacity for regeneration of the substrate RubP (Sage et al., 1989). Other possible changes that could account for acclimation include changes in stomatal limitations (Woodward, 1987).

Most studies of the effects of growth at elevated ca on photosynthetic CO2 uptake have concerned effects on rates at or close to light saturation (Asat). Within a closed PÇ3 canopy many leaves will be shaded for most of the day and even exposed leaves will experience low light on dull days and around dawn and dusk. In these situations, light limited rather than light saturated rates of CO2 uptake will be critical to the rate of photosynthetic carbon gain by plant canopies (Beadle et al., 1985; Baker et al., 1989). The initial phase of the response curve of A to increase in the rate of photon absorption by photosynthetic tissue (Qabs) is both linear and the slope maximal.This initial linear region represents the maximum efficiency of utilisation of absorbed light in CO2 fixation, i.e. the maximum quantum yield of photosynthesis (ϕabs), and provides a measure of photosynthetic capacity when light flux is limiting. Measurement of ϕabs is complicated by the need to ensure that calculations of slope are based on the initial linear portion of the response of A to Qabs avoiding any subtle changes in linearity (Sharp et al., 1984). In addition changes in surface absorptance will alter the quantum yield on an incident photon flux basis, thus to separate absorptance changes from changes in the efficiency of photosynthesis photon flux is calculated on an absorbed light basis (Qabs) yielding the quantum yield on an absorbed light basis (ϕabs). A solution is the use of a leaf chamber incorporated into an integrating sphere, enabling simultaneous measurement of a A and Qabs (Ireland et al., 1989).

Quantum yield (ϕabs) is a function of 1) the efficiency of energy transduction into NADPH and ATP on the photosynthetic membrane and 2) the metabolic pathways in which this

reducing and phosphorylating potential is utilised. Both of these characters show remarkable consistency within C3 plants, a factor possibly reflected in the low interspecific variability in quantum yield within a photosynthetic type (Ehleringer & Björkman, 1977; Pearcy & Ehleringer, 1984; Björkman & Demmig, 1987). At current atmospheric CO2 concentrations healthy C3 plants show a ϕabs of ca. 0.055 at 30°C. In an atmosphere of 1% O2 ϕabs rises to 0.08-0.09 due to the inhibition of photorespiratory metabolism which would otherwise consume some of the ATP and NADPH generated PÇ3 on the photosynthetic membrane. In an atmosphere with an elevated CO2 concentration, quantum yield would be expected to rise in proportion to the stochiometric increase in the ratio of carboxylations of RubP to oxygenations. This will be determined by the ratio of substrate concentrations (CO2/O2) and the ratios of the maximum velocities (V) and Michaelis constants (k) for oxygenation and carboxylation. Since a change in the ratios of these kinetic constants would require a change within the structure of the enzyme, any adaptation to elevated ca would seem unlikely. However, whilst ϕa is remarkably constant among healthy leaves of different species grown in controlled environments, leaves in sub-optimal conditions in the field can show lower values of ϕa (Baker et al., 1988). Baker et al. (1988) enumerate several potential causes of decrease in ϕabs through changes in the composition of the photosynthetic membrane induced by environmental perturbation. Marked heterogeneity of stomatal opening, induced by environmental treatments, can also produce apparent decreases in ϕabs (Terashima et al., 1988). Further, CO2 concentration has been shown to modulate protein biosynthesis in photosynthetic cells (Bailly & Coleman, 1988). Thus, the possibility of change in photosynthetic capacity and ϕabs under light limiting conditions, induced by development in elevated CO2 atmospheres, cannot be dismissed.

The objective of this study was to determine whether development over three years in an atmosphere in which the CO2 concentration has been elevated to 700 μmol mol-1 has resulted in acclimation of the capacity for photosynthesis under light limiting conditions. Both the quantum yields of CO2 assimilation and efficiency of PSII photochemistry were determined for plants from natural stands of the C3 sedge, Scirpus

olneyi Gray (De Jong et al., 1981). .pa

MATERIALS AND METHODS

Plant Material

As part of a long-term investigation of the effects of elevated CO_2 on vegetation of a tidal marsh, 30 open-top chambers have been placed within the boundary of three mesohaline marsh community types of the Rhode River, a sub-estuary of the Chesapeake Bay in eastern Maryland (Curtis et al., 1989). Via a computer controlled system c_a in half of these chambers has been maintained at 700 μmol mol^{-1} for the complete growing seasons of the past 3 years (Drake et al., 1989). The remaining chambers were maintained at c_a = 350 μmol mol^{-1} to provide controls for the modification of plant microclimate produced by the presence of the chamber. Ten of these chambers are within a large monotypic stand of the C_3 sedge S. olneyi. Plants in these chambers were used in the current investigation. The only photosynthetic organ of this species is its triangular stem. For the determination of ϕ_{abs}, mature stems were selected at random from within the open-top chambers, cut close to their base under distilled water, and immediately transferred to the assimilation chamber in a field laboratory adjacent to the site. Measurements of chlorophyll fluorescence were made in situ.

Quantum yield of CO2 assimilation

The unusual shape of the photosynthetic organ of S. olneyi presents a particular problem when trying to determine the quantum yield of photosynthesis using direct illumination of conventional chambers. First, direct illumination of one surface will place the other surfaces in a very much lower photon flux, thus photosynthesis on one surface may be light saturated while photosynthesis on the other surfaces is light limited. Secondly, determination of the area for expression of photosynthetic rate and light interception is complicated by the triangular cross-section. Use of an Ulbricht sphere leaf cuvette, eliminates these problems. Since the light is fully diffused, all surfaces will receive the same photon flux. Further, absorption of light is measured simultaneously PÇ3 with absorption of CO2, eliminating the need to determine leaf area in the measurement of

quantum yield. In these experiments a leaf chamber developed from the design of Ireland et al. (1989) was incorporated into an open gas exchange system. The chamber was as described previously, except in the following aspects. 1. The sphere was constructed from aluminium, to allow improved temperature control. 2. Glass windows faced the inner gas exchange cuvette. 3. A 7.4 cm diameter and 4 mm thick white teflon disc was placed below the light pipe to improve scattering of radiation on entry into the sphere. 4. A paddle fan bridging the gas inlet and outlet was used to recirculate air within the chamber and raise the boundary layer conductance. The efficiency of diffusion of light within the sphere and the absorptance of the sphere was determined with a black absorber of 10 cm by 5 mm, simulating a grass leaf or stem. The absorber was made by spraying a strip of paper with three coats of non-reflective black paint (Ultra Flat Black Lacquer, 32N282, Newark Electronics, Chicago, U.S.A.). The absorptance of the coated paper was determined at 0.952 using a Taylor integrating sphere (LI-1800-12, Li-Cor inc., Lincoln, NE., U.S.A.) following the procedure of Rackham & Wilson (1967). When the absorber was turned through 360° in 15° steps, the measured decrease in photon flux within the chamber varied by 4%, indicating a largely homogeneous distribution of light. The mean absorptance of the sphere surfaces was determined at 0.124 by the method of Idle and Proctor (1983).

The quantum yield of each stem, ten from each of the two growth treatments, was determined in three different gas mixtures: 1) air containing 350 μmol mol^{-1} of CO_2 and 21 mmol mol^{-1} O_2, to represent current atmospheric conditions and the control CO_2 growth environment; 2) 700 μmol mol^{-1} CO_2 and 21 mmol mol^{-1} of O_2 in air to simulate the predicted "doubled CO_2" atmosphere and used in the elevated CO_2 growth environment; and 3) 350 μmol mol^{-1} CO_2 and 1 mmol mol^{-1} O_2 in air to provide an atmosphere in which photorespiration would be almost fully suppressed. Nitrogen provided the balance of these mixtures supplied as compressed gases (Air Products Inc., Tamaqua, PA., U.S.A.). The flow of dry gas from the cylinders to the leaf chamber was monitored with a mass flowmeter (Type H-1K, Matheson Gas Products, East Rutherford, NJ., U.S.A.), previously calibrated against a bubble flow-meter (Long and Ireland, 1985). Prior to entry into the

chamber the air was humidified over distilled water at ca. 25°C. Air leaving the chamber was dried over anhydrous magnesium perchlorate (Long & Hällgren, 1985) before entering the infra-red gas analyser. The change in CO2 concentration across the chamber and the absolute CO2 concentration was measured with a two channel infra red gas analyser (Binos 2, Leybold-Heräus), calibrated against mixtures of CO_2 in air retained in aluminium cylinders which had been previously cross- calibrated against a gravimetrically prepared CO_2 standard, traceable to a N.B.S. standard (Matheson Gas Products). The photosynthetically active photon flux (Q) within the sphere was measured with a miniature quantum sensor (QS 1, Delta-T Devices, Burwell, U.K.) which was cross-calibrated against a solarimeter (Precision Spectral Pyranometer, Eppley Lab. Inc., Newport, RI, U.S.A.) in diffuse daylight using the conversion factors of Anderson (1971). The quantum sensor was also cross-checked in day-light against a second quantum sensor (Li-191, Li-Cor) which had just been recalibrated by the manufacturer. The two were found to agree over a range of light levels within $\pm$ 1.0%. Light fluxes within the sphere (Q_{wall}) in the range of 0 - 250 umol m-2 s-1 were obtained within the sphere by interposing neutral density filters between the quartz iodide source and light pipe entering the sphere. The quantity of light absorbed by the portion of stem within the chamber was determined by the method of Idle & Proctor (1983). Stem surface temperature was 28°C $\pm$ 1.5°C for all measurements of ϕ_{abs}. The stem surface area is not required for calculation of ϕ_{abs} (Ireland et al., 1989) but was determined to allow expression of photosynthetic rates and light absorption in conventional dimensions of mass per unit area per unit time. The projected area was determined with an area meter (LI-3100, Li-Cor). To determine ϕ_{abs} PÇ3 for any one stem in any one measuring gas composition, A was determined at 10 values of Q_{abs} from 5 - 200 μmol m^{-2} s^{-1}, within this range dA/dQ_{abs} was constant, but above it began to decline. An averaged ϕ_{abs} for each replicate was determined as the slope of the line (e.g. Fig. 1) fitted by least squares linear regression analysis of A to Q_{abs} between 0 and 200 μmol m^{-2} s^{-1} (Sokal & Rohlf, 1982). Linearity over this range was indicated by the high correlation coefficients (r^2) which exceeded 0.98 in all cases. Differences between the mean ϕ_{abs} for stems from the two growth environments and for the three measuring gas compositions were analysed by

two-way anova (Sokal & Rohlf, 1981).

Photochemical efficiency of PSII

The quantum yield of photochemistry at photosystem II is proportional to the ratio of the variable (F_v) and maximal fluorescence (F_m) emission from chlorophyll (Butler & Kitijima, 1975). This interpretation assumes that PSII is fully oxidised at the point of addition of saturating light to induce the rise in fluorescence to F_v. Measurement of F_v/F_m therefore requires material that has been "dark-adapted", i.e. it has been in darkness for sufficient time for the primary acceptor molecules of photosystem II to become fully oxidised. F_v/F_m has been shown to be linearly related with the quantum yield of O_2 evolution and CO_2 assimilation (e.g. Björkman & Demmig, 1987; Baker et al., 1989). Induction of fluorescence emission was measured in situ on 20 stems from five control and 20 stems from five elevated CO_2 open-top chambers, using a portable fluorimeter (Type PSM, BioMonitor S.C.I. AB, Malmö, Sweden). Measurements were made between 30 min. and 1 hour after sunset, to ensure that any short-term reductions in F_v/F_m that might result from exposure to high light during the day (e.g. Demmig & Winter, 1989) would be removed. After 10 minutes of dark adaptation, the stem was excited with light of 400 umol m^{-2} s^{-1} and the kinetics of chlorophyll fluorescence monitored over the subsequent 10 s. Differences in mean F_v/F_m and $t_{0.5}$ between the two growth treatments were tested by Student's t-test (Sokal & Rohlf, 1981).

The conditions used for the measurement of F_v/F_m were determined by a set of preliminary measurements. Using a range of dark-adaptation periods and excitation light levels, no significant increase in F_v/F_m was found after 10 minutes of placing the tissue in complete darkness. Similarly, increase in the photon flux density of the actinic excitation beam above 400 umol m^{-2} s^{-1} produced no further increase in F_v/F_m ratio. Two potential limitations of the portable fluorimeter (PSM, Biomonitor), as supplied here, in determining F_v/F_m accurately are the relatively low photon flux of the excitation beam and the time required for shutter opening in resolving the prompt fluorescence level (Bolhàr-Nordenkampf et al., 1989). To examine the significance of any possible errors

in determining F_v/F_m with this instrument, a sample of 20 stems removed from the field and F_v/F_m was measured with both the PSM portable fluorimeter and a second modulated fluorimeter (PAM 101 & PAM 103, H. Walz, Effeltrich, FRG). The PAM system uses a distinct approach to resolving F_o and was also used with an excitation photon flux of 7 000 umol m^{-2} s^{-1}, which should ensure full trap closure in the determination of F_m. Half of the stems were measured with the PSM fluorimeter, and then allowed a further 10 minutes dark adaptation before measurement with the PAM fluorimeter. For the other half the order was reversed. To ensure that measurements were made by both fluorimeters on the same point of the stem, both were connected to the same sample holder (MFMS holder, Hansatech Ltd., Kings Lynn, U.K.). This comparison showed that despite the very different modes of measurement of F_v/F_m in the two instruments (Bolhàr-Nordenkampf et al., 1989), the ratio of F_v/F_m (PAM fluorimeter) to F_v/F_m (PSM fluorimeter) was 1.02 $\pm$ 0.02, i.e. there was no significant difference in the value of F_v/F_m determined for these stems by the two contrasting methods.

RESULTS

The response of CO_2 uptake to absorbed photon flux (Q_{abs}) was linear up to ca. 200 μmol m^{-2} s^{-1} for all measuring gas compositions (Fig. 1). Although no attempt was made to select stems of uniform age or developmental stage, ϕ_{abs} was remarkably uniform between replicates. Fig. 1 suggests that for individual stems, there is a marked difference between the three measurement gas concentrations, but that for any single measuring gas composition there is no apparent difference in ϕ_{abs} between the stem developed in 350 μmol mol^{-1} CO_2 and that developed in 700 μmol mol^{-1} CO_2. This lack of difference in ϕ_{abs} is confirmed when the samples as a whole are considered. Fig. 2 illustrates the mean ϕ_{abs} for all 10 stems from each growth treatment. The mean ϕ_{abs} of all of the stems measured at in an atmosphere of 21% O_2 and 350 μmol mol^{-1} CO_2 was 0.063. Increase in CO_2 concentration to 700 μmol mol^{-1} increased ϕ_{abs} to 0.080 whilst decrease in O_2 concentration to 1% to eliminate photorespiration increased ϕ_{abs} to 0.095. Difference in mean ϕ_{abs} between the three measurement gas mixtures was highly significant ($F = 26.26^{***}$). Although mean ϕ_{abs} for plants grown in 700 μmol mol^{-1} CO_2 were slightly lower

than those for plants grown in 350 μmol mol^{-1} CO_2 levels, when both were measured in the same gas mixture, these differences were not statistically significant ($F=1.18^{n.s.}$) nor was there any significant interaction between the CO_2 concentration of the growth environment ($F=1.75^{n.s.}$). The key comparison is between stems that had developed in and were measured in 350 μmol mol^{-1} CO_2 with stems that had developed in and were measured in 700 μmol mol^{-1} CO_2. Here elevated CO_2 is seen to lead to a statistically significant increase in ϕ_{abs} of 20%, from 0.065 ± 0.003 to 0.078 ± 0.003. In the field such an increase in ϕ_{abs} could be offset if the absorptance (α) of the photosynthetic tissue was decreased, since quantum yield on an incident light basis will be the product of ϕ_{abs} and α. However, no difference in α was found between stems developed in 350 μmol mol^{-1} and in 700 μmol mol^{-1} (Table 1), indicating that quantum yield on an incident light basis would be increased in proportion with ϕ_{abs}.

Table 4.1. The mean (+/- 1 s.e.) light absorbance, ratio of variable to maximum photosystem II chlorphyll flourescence (F_v/F_m), and the half rise time ($t_{0.5}$) of variable flourescence for stems of *S. olneyi* which have developed in open top chambers either with ambient CO_2 concentrations (350 umol mol^{-1}) or elevated concentrations (680 umol mol^{-1}). The significance of the differences in means from the two growth treatments has been examined at the 0.05 significance level of Student's t distribution.

CO_2 concentration during growth	Leaf absorbtance (a)	F_v/F_m	$t_{0.5}$
350 umol mol^{-1}	.85 +/- .02 (n=10)	.846 +/- .004 (n=20)	10.7 +/- .8 (n=20)
700 umol mol^{-1}	.84 +/- .02 (n=10)	.851 +/- .005 (n=20)	11.0 +/- .5 (n=20)
Significance of difference between means (p<0.05)	*n.s*	*n.s*	*n.s*

It follows that if ϕ_{abs} is increased for plants grown and measured in c_a = 700 μmol mol^{-1} CO_2, but respiration is unchanged, then the light compensation point of photosynthesis should rise, as indicated in Fig. 1. Fig. 3 shows that this expectation is fulfilled when mean values for all stems are considered. LCP for stems grown and measured at c_a = 700 μmol mol^{-1} CO_2 is 31 ± 3 μmol m^{-2} s^{-1} compared to 51 ± 3 μmol m^{-2} s^{-1} for stems grown and measured at c_a = 350 μmol mol^{-1} CO_2. As in the case of ϕ_{abs}, LCP showed a highly significant difference between the measuring gas mixtures ($F=55.5^{***}$), but no significant difference between the CO_2 concentration during growth ($F=0.85^{n.s.}$).

When ϕ_{abs} is determined in a lowered O_2 concentration (1 mmol mol^{-1}, as opposed to 21 mmol mol^{-1} in normal air), ϕ_{abs} is almost identical regardless of whether the stems were grown at c_a = 350 μmol mol^{-1} and c_a = 700 μmol mol^{-1} (Figs. 1 & 2). This suggests that under conditions in which photorespiration is virtually eliminated, there is no difference in the maximum efficiency with which these stems utilise absorbed photons in CO_2 fixation. This lack of difference in ϕ_{abs} is parallelled by the observation that neither F_v/F_m nor the half time of the rise to F_m ($t_{0.5}$) differ significantly between stems from the two growth environments. These results suggest that the maximum quantum yield of PSII photochemistry is unchanged. The $t_{0.5}$ is suggested to be proportional to the area over the fluorescence induction curve, which in turn is related to the size of the PSII acceptor pool (Bolhar-Nordenkampf et al., 1989). Lack of change in $t_{0.5}$ may infer that the size of the acceptor pool is unchanged by the CO_2 concentration of the growth environment. This interpretation however assumes that the shape of fluorescence induction curve is unchanged. Examination of individual curves revealed no difference in the shape of this curve for the two growth treatments.

DISCUSSION

Björkman & Demmig (1987) in a survey of a wide range of vascular plants showed a mean absorbed light quantum yield for O_2 evolution $\phi_{abs,O}$ of 0.105 in ca. 10 mmol mol^{-1} CO_2. Given the fact that some of the products of non-cyclic electron transport will be

used in processes other than CO_2 fixation, ϕ_{abs} for CO_2 uptake may be expected to be lower. ϕ_{abs} obtained here when the O_2 concentration was lowered to 1 mmol mol^{-1} to inhibit photorespiration was 0.095. Although ca. 10% less than the value for O_2 evolution obtained by Björkman & Demmig (1987), it is among the highest values of ϕ_{abs} that have been determined (Pearcy & Ehleringer, 1984; Sharp et al., 1984; Björkman & Demmig, 1987). These values suggest that the factors in the organisation and composition of the photosynthetic apparatus which are critical to the efficiency of photosynthesis under light-limiting conditions are unaffected by development in an elevated CO_2 atmosphere in the field.

A number of studies have suggested that growth in elevated CO_2 can lead to an acclimatory decrease in photosynthetic capacity (reviewed: Long & Hutchings, 1990). The results show that despite three years of growth in elevated CO_2 there is no evidence of acclimation with respect to either the maximum quantum yield of CO_2 assimilation or the quantum yield of photochemistry at photosystem II inferred from chlorophyll fluorescence. In the absence of any significant acclimation, ϕ_{abs} would be expected to benefit fully from the potential decrease in photorespiration with elevation of c_a. This is clearly evident when plants grown and measured at c_a = 350 μmol mol^{-1} are compared to those grown and measured at c_a = 700 μmol mol^{-1} (Fig. 2). What significance might these increases in ϕ_{abs} have to plants in the doubled CO_2 environment predicted for the next century? Charles-Edwards (1982) suggests a simple equation for examining the consequences of change in leaf photosynthetic parameters to gross canopy CO_2 uptake. This is adapted here for use with photon flux and ϕ_{abs} (Eqn. 1). This equation assumes a rectangular hyperbolic response of the rate of CO_2 uptake to photon flux over the full range of light levels, an exponential decline in light with depth into the canopy, and that a diurnal course of incident photon flux described by a sine function:

$$A_{c,tot} = \alpha.\phi_{abs}.Q_{tot}.h.A_{sat}.(1-e^{-kL})/(k.\alpha.\phi_{abs}.Q_{tot} + h.A_{sat})$$

Where

$TTA_{c,tot}$ is the daily integral of gross photosynthetic CO_2 uptake (mol m^{-2} d^{-1})

TTA_{sat} is the light saturated rate of CO_2 uptake (mol m^{-2} s^{-1})

TTh is the time between sunrise and sunset in seconds (s d^{-1})

TTk is the foliar extinction coefficient (dimensionless)

TTL is the foliar area ratio (dimensionless)

TTQ_{tot} the accumulated photon flux for the day (mol m^{-2} d^{-1})

TTα surface absorptance

Considering a canopy with a stem area index (L) of 5 and a foliar extinction coefficient of 0.5, which would be typical for an erectophile canopy such as that of S. olneyi, and an A_{sat} of 20 μmol m^{-2} s^{-1}, what effect will the increase of ϕ from 0.065 for plants growing in c_a = 350 μmol mol^{-1} to a ϕ of 0.078 for plants growing in c_a = 700 μmol mol^{-1}(Fig. 2) have on $A_{c,tot}$? For a mid-summer's day with clear skies with a total incident photon flux (Q_{tot}) of 40 mol m^{-2} d^{-1} over a 14h photoperiod eqn. 1 predicts an increase in $A_{c,tot}$ from 1.03 to 1.12 mol m^{-2} s^{-1} (+8.6%). For a cloudy day with a Q_{tot} of 10 mol m^{-2} d^{-1} the increase would be +15.8%. Thus, even in the absence of any net change in light saturated rates of CO_2 uptake for plants in a doubled CO_2 atmosphere, increased ϕ_{abs} alone will produce a marked increase in canopy rates of carbon gain. The increase in PÇ3 canopy photosynthesis arising from increased ϕ_{abs} is likely to be greater with increased c_a than predicted here. Firstly, the prediction assumes a constant L, however observations of S. olneyi show that the L increases with prolonged growth in elevated CO_2 (Bert to add reference?), increasing shading within the canopy and so increasing the significance of any change in ϕ_{abs} and LCP to canopy rates of CO_2 uptake. Secondly, temperatures are widely predicted to increase with rising atmospheric CO_2 concentration (Idso, 1989). Since increase in temperature favours the oxygenation of RubP relative to carboxylation, the difference observed here between plants growing in atmospheres of 350 μmol mol^{-1} and 700 μmol mol^{-1} (Fig. 2) would be accentuated by increased temperatures.

Although no significant decrease in ϕ_{abs} is seen in plants grown in elevated CO_2, examination of mean values for stems measured at both 350 μmol mol^{-1} and 700 μmol mol^{-1} CO_2, indicates a small decline (6%) in ϕ_{abs} (Fig. 2). Further replication would be necessary to establish whether this small indicated difference reflects a real effect of growth environment or is simply the result of random variation. If the difference is upheld by further replication, what cause could underlie the decrease? Previous studies suggest two possible explanations of this slight depression of ϕ_{abs}. 1. An increased diversion of intercepted light energy into non-photochemical processes, as can occur as a result of low temperature stress (Baker et al., 1989). 2. The closure of patches of stomata, such that some areas of the leaf are unable to assimilate any CO_2, with the effect that ϕ_{abs} is zero in these patches, so lowering the mean ϕ_{abs} of the leaf as a whole, as has been shown for sunflower leaves in response to abscissic acid applications (Terashima et al., 1988). The first cause could not account for the decrease seen here since F_v/F_m is unaffected and ϕ_{abs} measured in 1 mmol mol^{-1} O_2 is maximal (Table 1, Fig. 2). Increased stomatal restriction is a possible explanation. This would be consistent with the disappearance of the difference between growth treatments when measurements are made in lowered O_2 concentrations to eliminate photorespiration (Fig. 2). At normal PÇ3 O_2 concentrations, increased stomatal limitation in patches would result in local decreases in the intercellular CO_2 concentration (c_i), causing increase in the intercellular O_2:CO_2 mol. ratio, producing increased diversion of absorbed light energy into photorespiration and thus a decreased ϕ_{abs}. This effect would be eliminated by lowering O_2 concentration to prevent photorespiration and hence any effect of lowered c_i.

In conclusion, long-term growth in elevated CO_2 has not produced significant acclimation in photosynthetic capacity under light limiting conditions. These results therefore suggest that rising CO_2 levels will result in an increase in the photosynthetic efficiency of Scirpus olneyi at low light levels, irrespective of any acclimation of photosynthetic response in saturating light.

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Single leaf respiration.

R. Cousimano, D. D'Abundo, B.G. Drake, W.T. Pockman.

In addition to the canopy measurements, respiration was measured in excised tissue of Scirpus and Spartina beginning in June, 1989.

Methods

Tissue collected at various times of the day was placed in plastic cuvettes and measured using an ADC LCA-2 IRGA. Tissues were measured first in the CO2 concentration in which the were grown and later in CO2-free air to try to distinguish tissue-level differences from feedback inhibition of respiration by the background CO2 concentration during measurement. Later experiments were conducted using only CO2-free air because background CO_2 concentration had no effect in early experiments.

Results

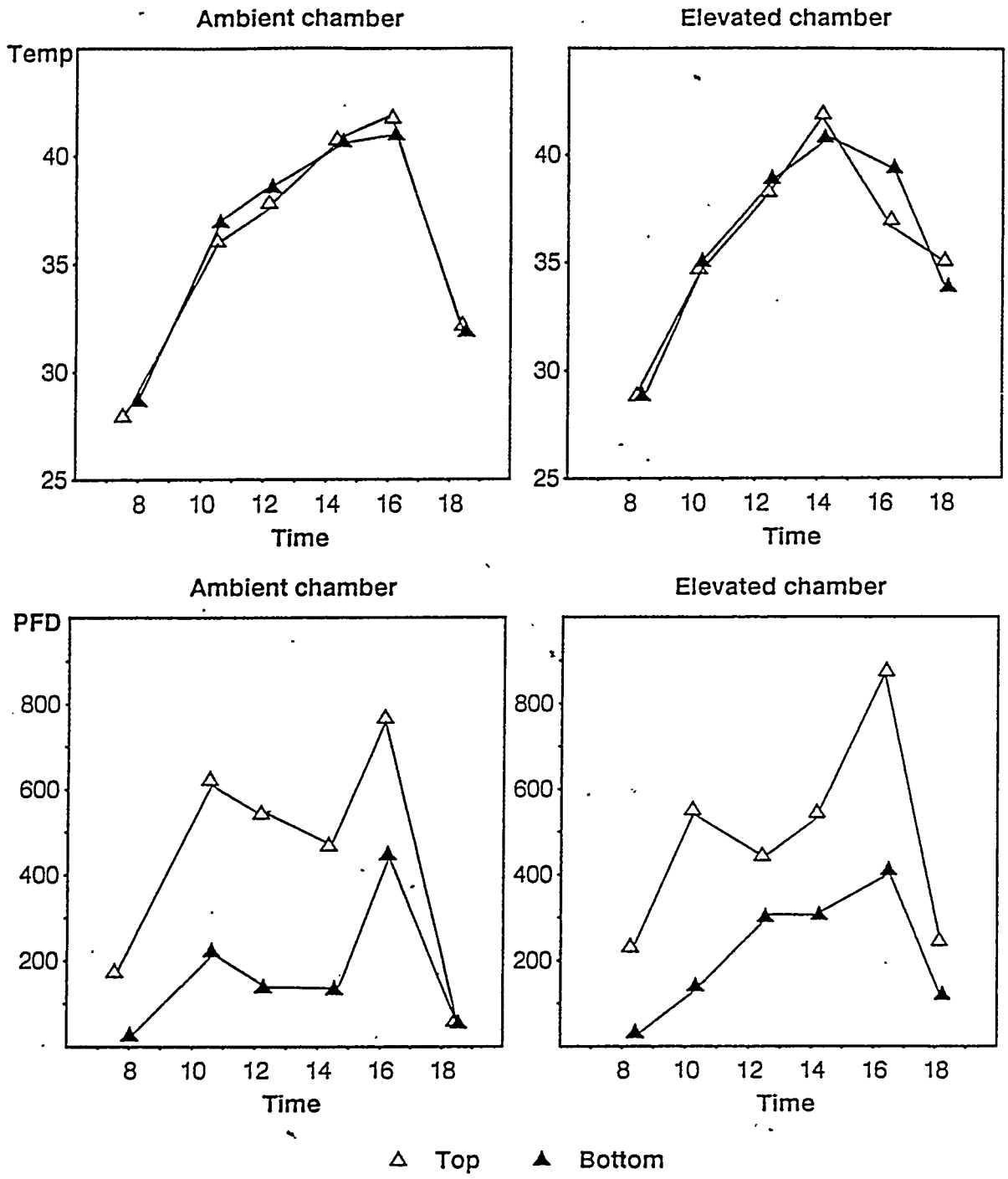

Figure 4.1

Temperature and Light Data from High and Low canopy in Scirpus chambers, 4 August, 1989. A) Temperature data for high and low canopy in one elevated and one ambient chamber. Temperatures between treatments and between height levels were not significantly different. B) Light data from high and low canopy for the same chambers as in (A). Light levels were not significantly different between treatments however differences between high and low canopy were significant.

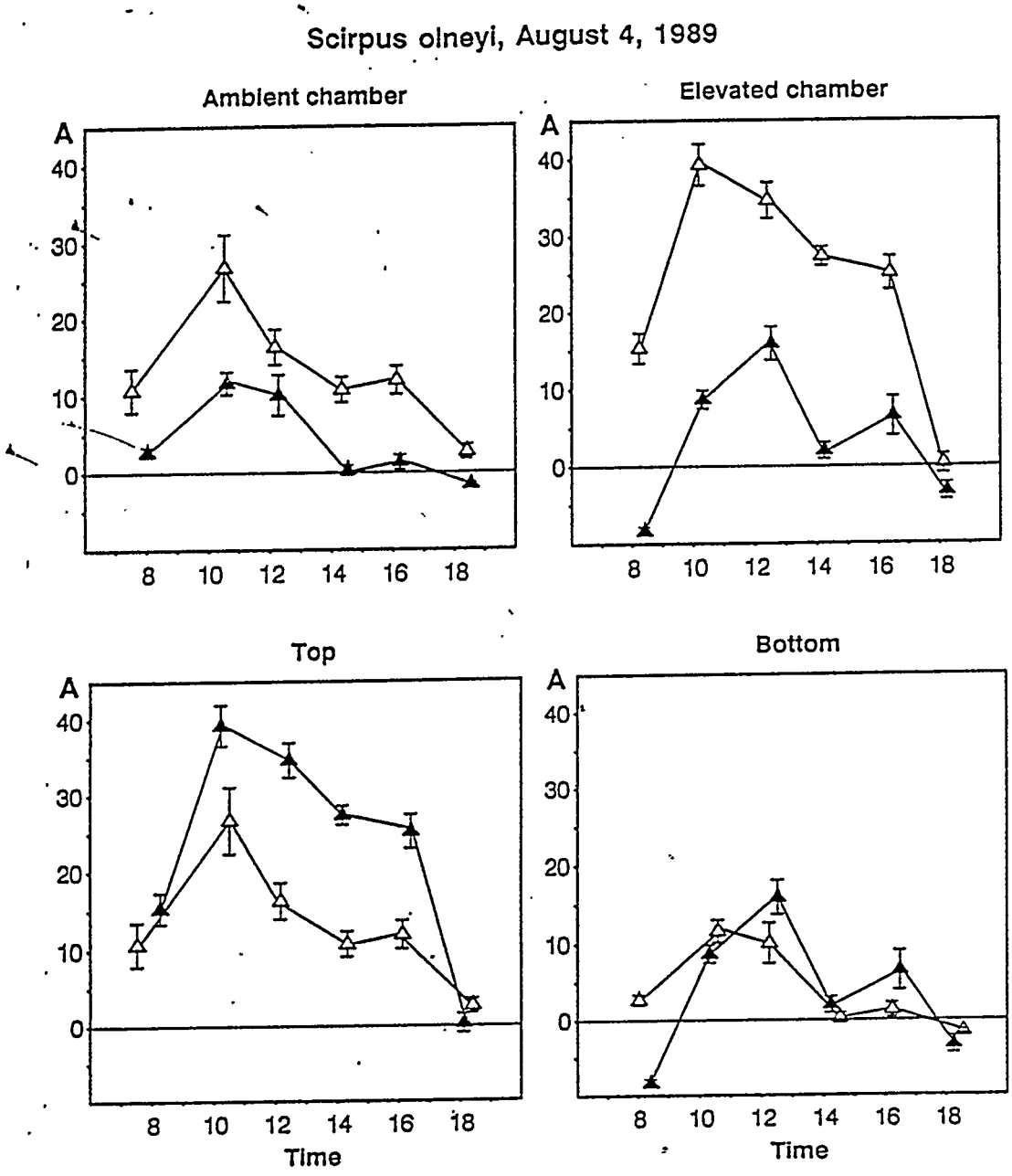

Figure 4.2

High and low canopy photosynthesis of Scirpus olneyi in an ambient and an elevated chamber. Data are arranged by treatment (top two graphs) and by canopy level (bottom two graphs). In the treatment graphs (top row) the symbols are tops (open triangles) and bottoms (solid triangles) while in the canopy level graphs the symbols are ambient (open triangles) and elevated (closed triangles). Each point in all four graphs is the mean of five measurements. Differences were significant between tops and bottoms within treatments and between tops across ambient and elevated. Differences between bottoms were not significant.

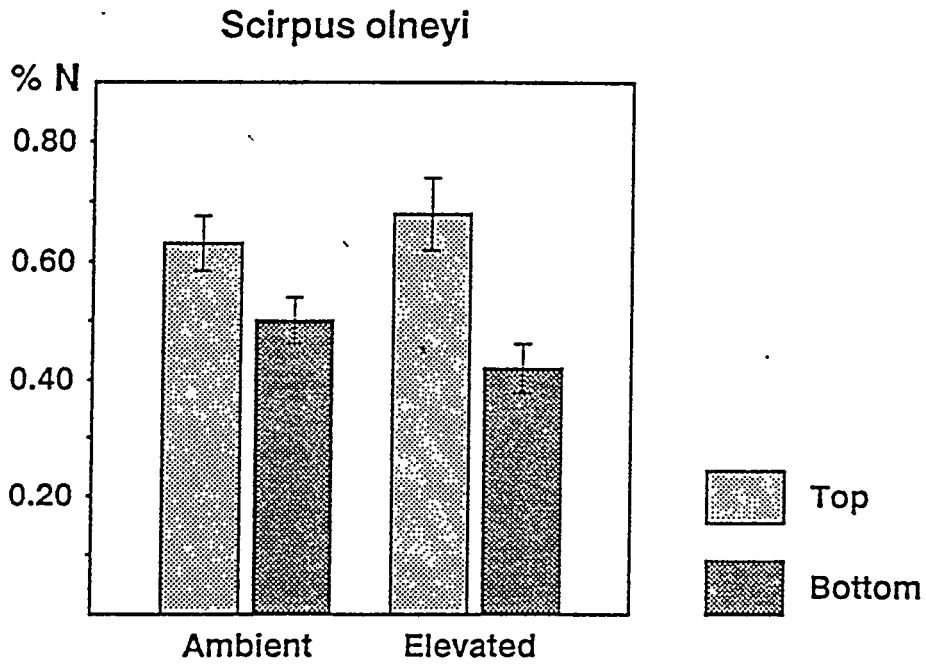

Figure 4.3

Percent nitrogen by weight in tops and bottoms of Scirpus olneyi grown under ambient and elevated CO2 concentrations. Tissue was collected during winter 87/88. Differences between canopy levels are significant for both treatments. Differences between the same canopy levels in the two treatments are not significantly different. (see also discussion in chapter 3).

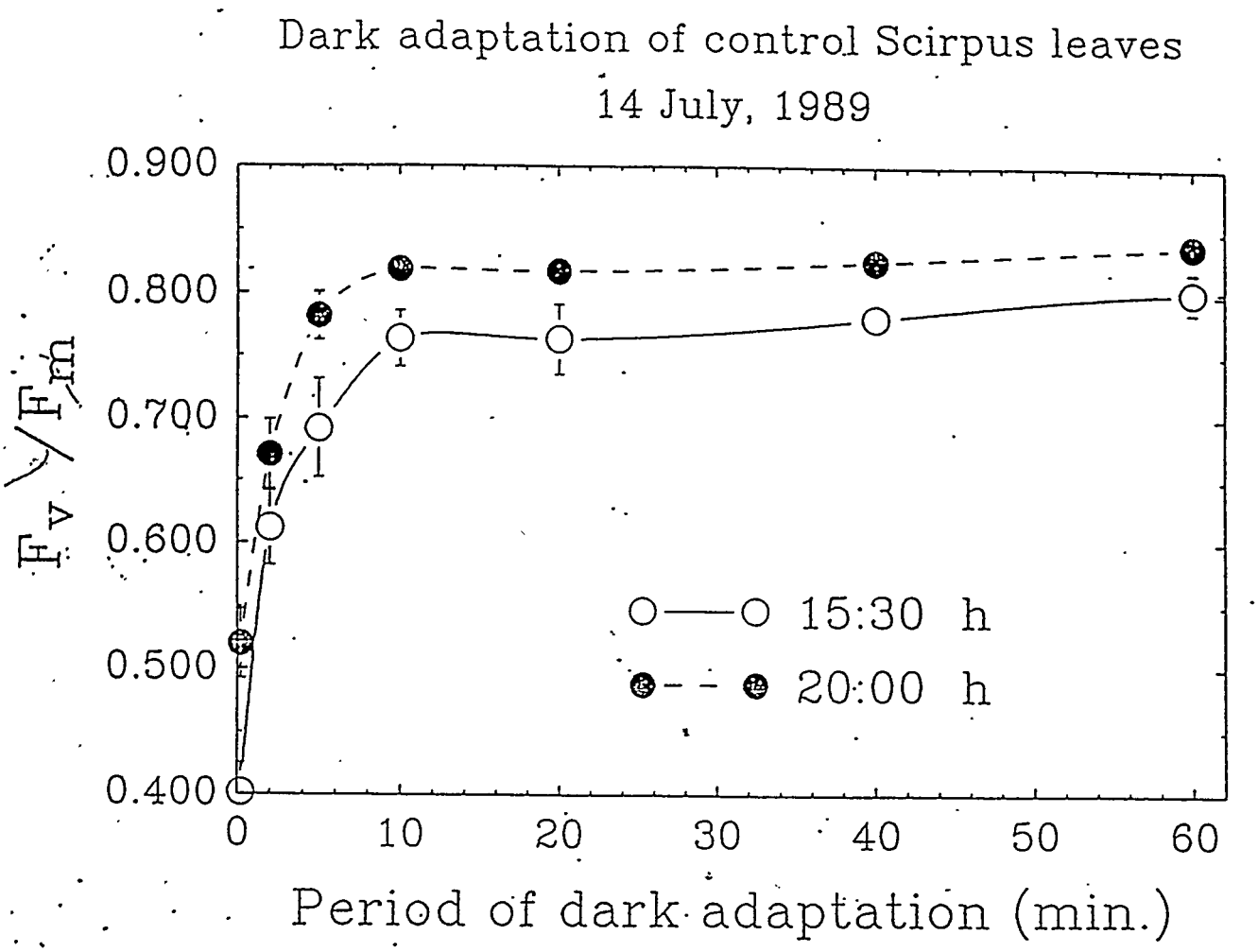

Figure 4.4

The mean F_v/F_m (±s.e.) for samples of ten stems of S. olneyi, at each of seven dark adaptation intervals. One set of samples were taken at ca. 15:30 hours ( ) on a clear July day, the other set at 20:00 hours ( ), i.e. at dusk on the same day.

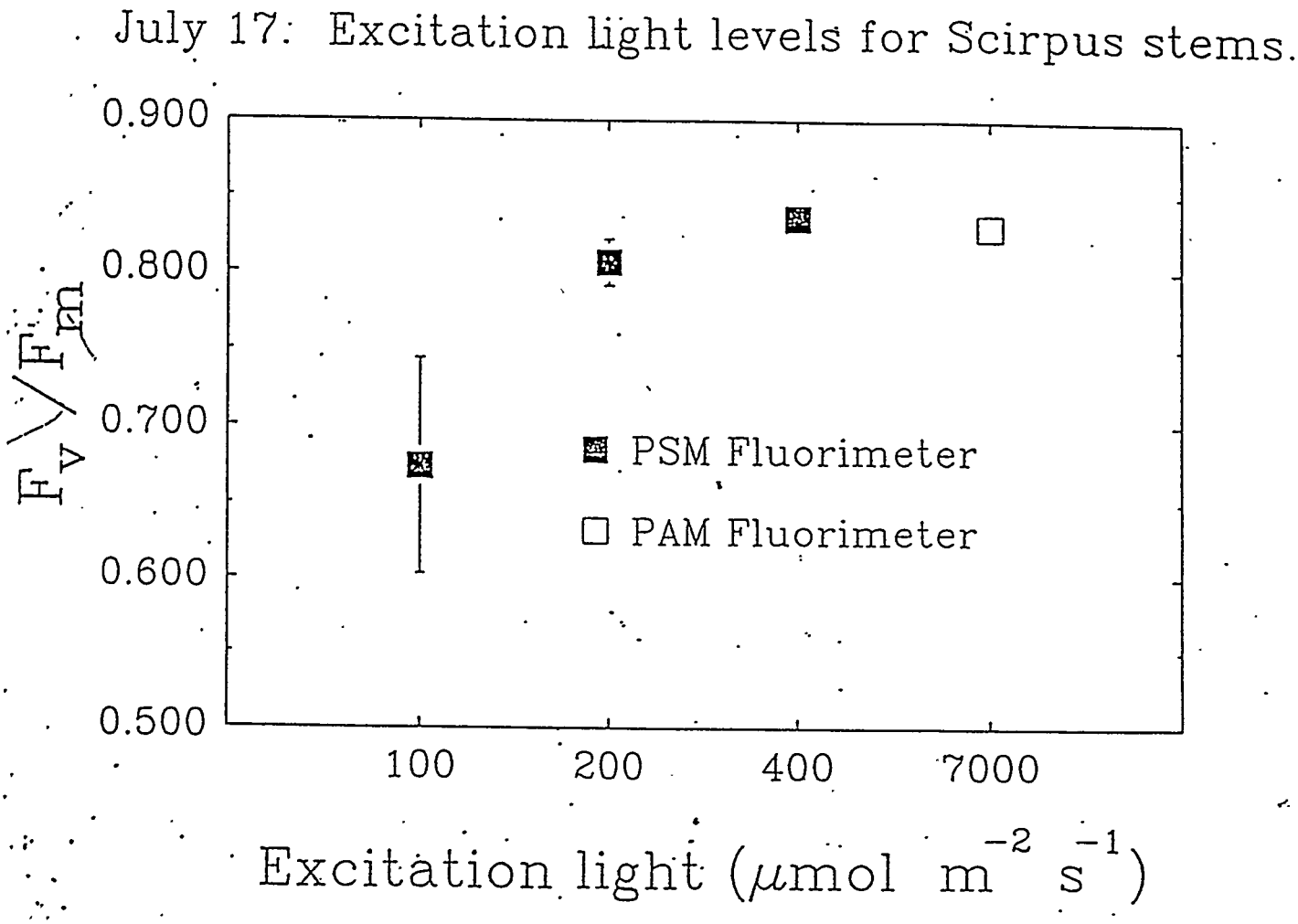

Figure 4.5

The mean F_v/F_m (±s.e.) for samples of ten stems of S. olneyi, at each of four excitation photon fluxes. Measurements at 100 - 400 μmol m-2 s-1 were made with a portable PSM fluorimeter. The measurement at 7 000 μmol m-2 s-1 was made with modulated PAM fluorimeter.

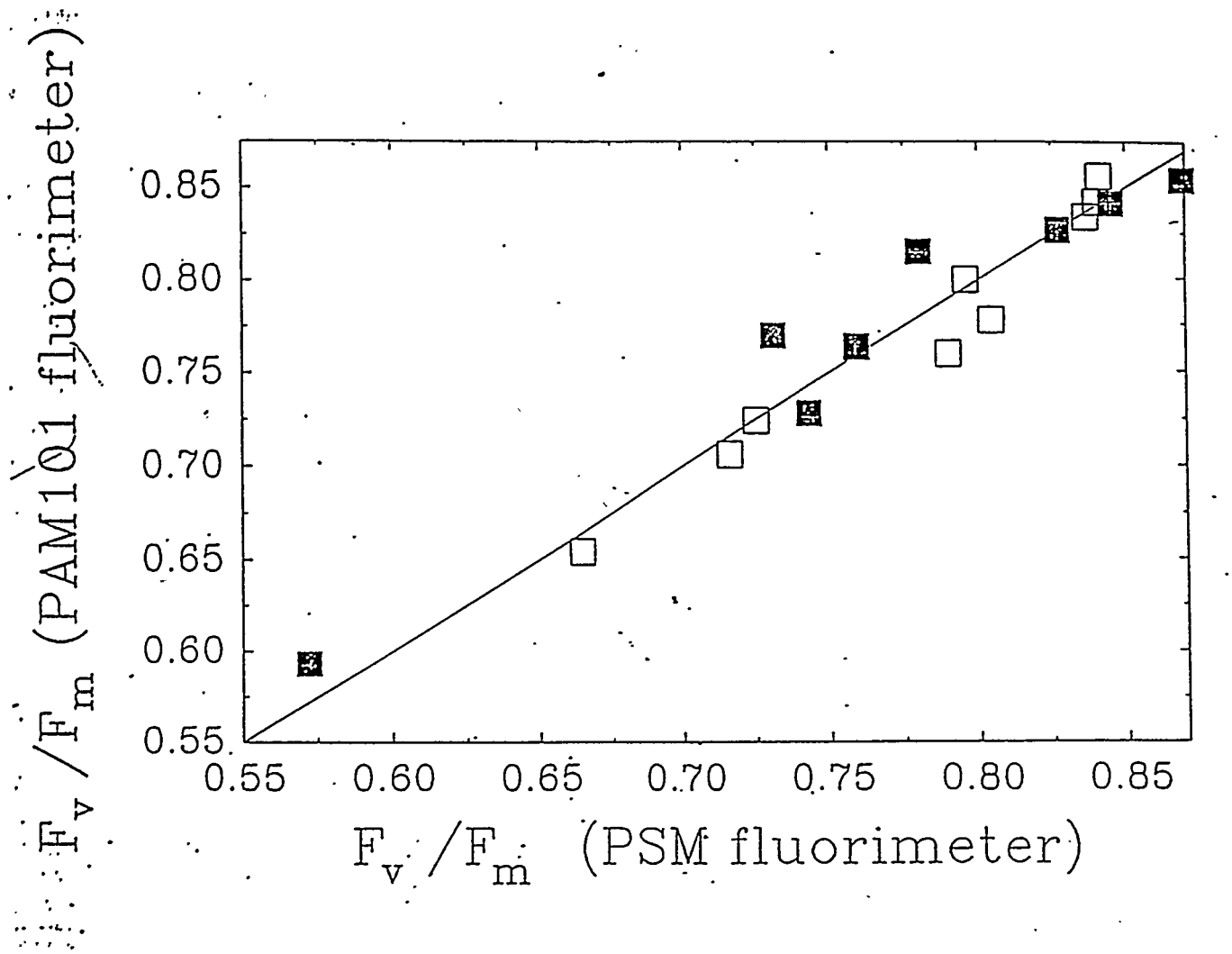

Figure 4.6

F_v/F_m determined for individual stems of S. olneyi stems removed from the field at different times throughout a clear sky July day with a mean mid-day temperature of 32•C. For one half of the samples F_v/F_m was measured first with the PSM fluorimeter and then, following a further 10 min dark adaptation F_v/F_m, was measured with the PAM modulated fluorimeter system ( ). For the other half of the samples the order of measurements was reversed ( ). The line illustrates the theoretical 1:1 relationship.

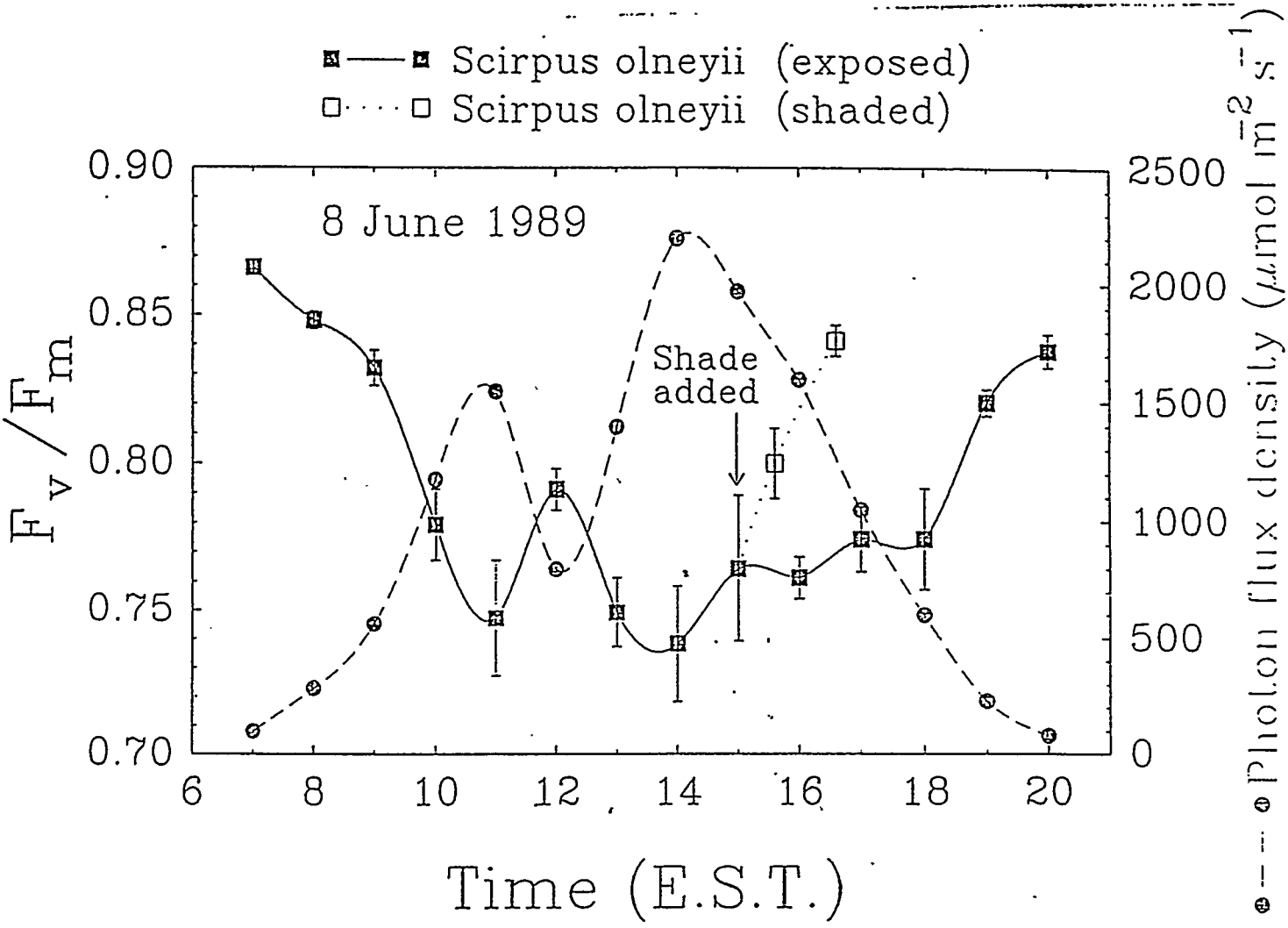

Figure 4.7

(a) The variability of mean F_v/F_m (±s.e.) of stems of S. olneyi in a 2 m2 area of the site measured at hourly intervals through the course of June 8 1989. At 15:00 a reflective aluminium shade was erected to exclude direct sunlight from one half of the area, the mean photon flux in this shaded area was ca. 20% of the adjacent unshaded area between 15:00 and 17:00 hours. Change in F_v/F_m in this shaded population of stems was monitored over the next two hours ( ). Each point is the mean of 12 stems. (b) Concurrent changes in photon flux density and air temperature at the study site.

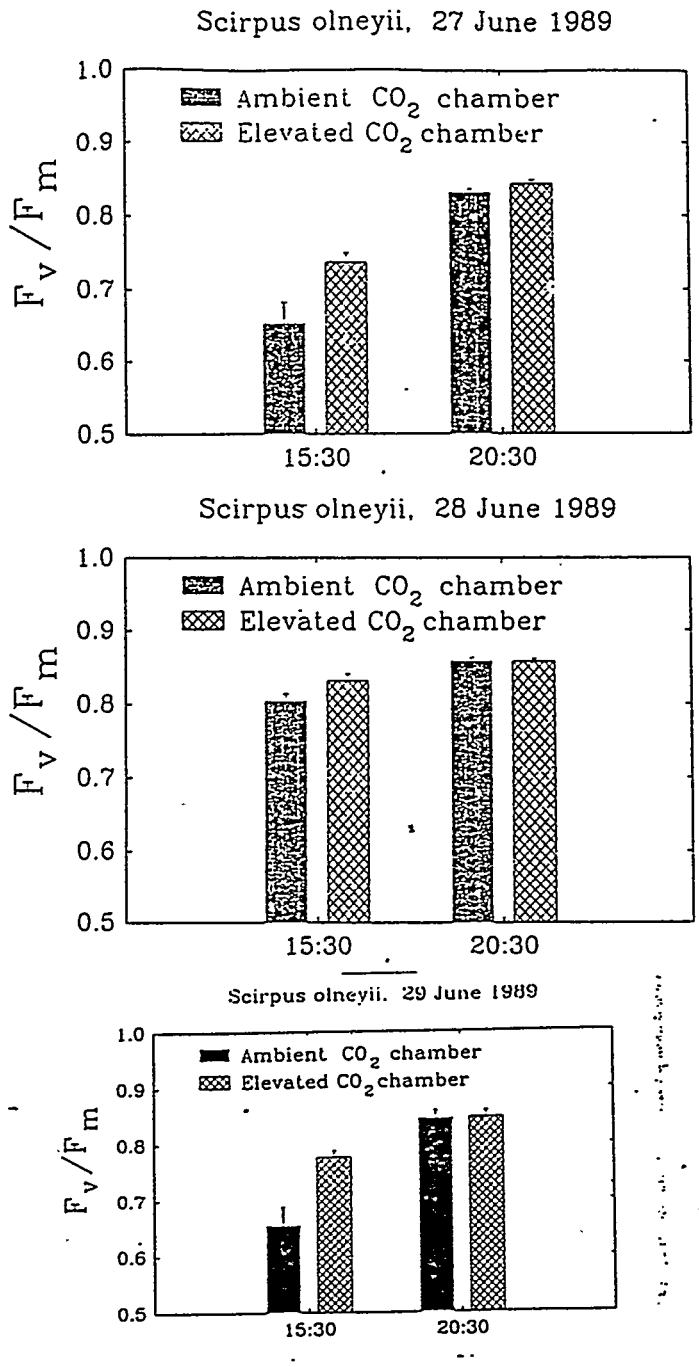

Figure 4.8

The mean F_v/F_m (±s.e.) of stems of S. olneyi in adjacent open top chambers, one with a mean CO_2 concentration in air of 350 μmol mol-1 (solid bars) the other with PP700 μmol mol-1 (cross-hatched bars). Each bar is the mean of 16 stems. Measurements were made at 15:30 and 20:30 hours on three consecutive days: a) June 27, b) June 28, and c) June 29. June 27 and 29 were days with clear skies and mean photon fluxes of 2 100 and 2 200 μmol m-2 s-1 at 13:00 hours, June 28 was an overcast day with a mean photon flux density of 450 μmol m-2 s-1 at 13:00 hours. Mean air temperatures within the open-top chambers at 13:00 were 38•C, 32•C and 32•C on the 27, 28, and 29 June, respectively.

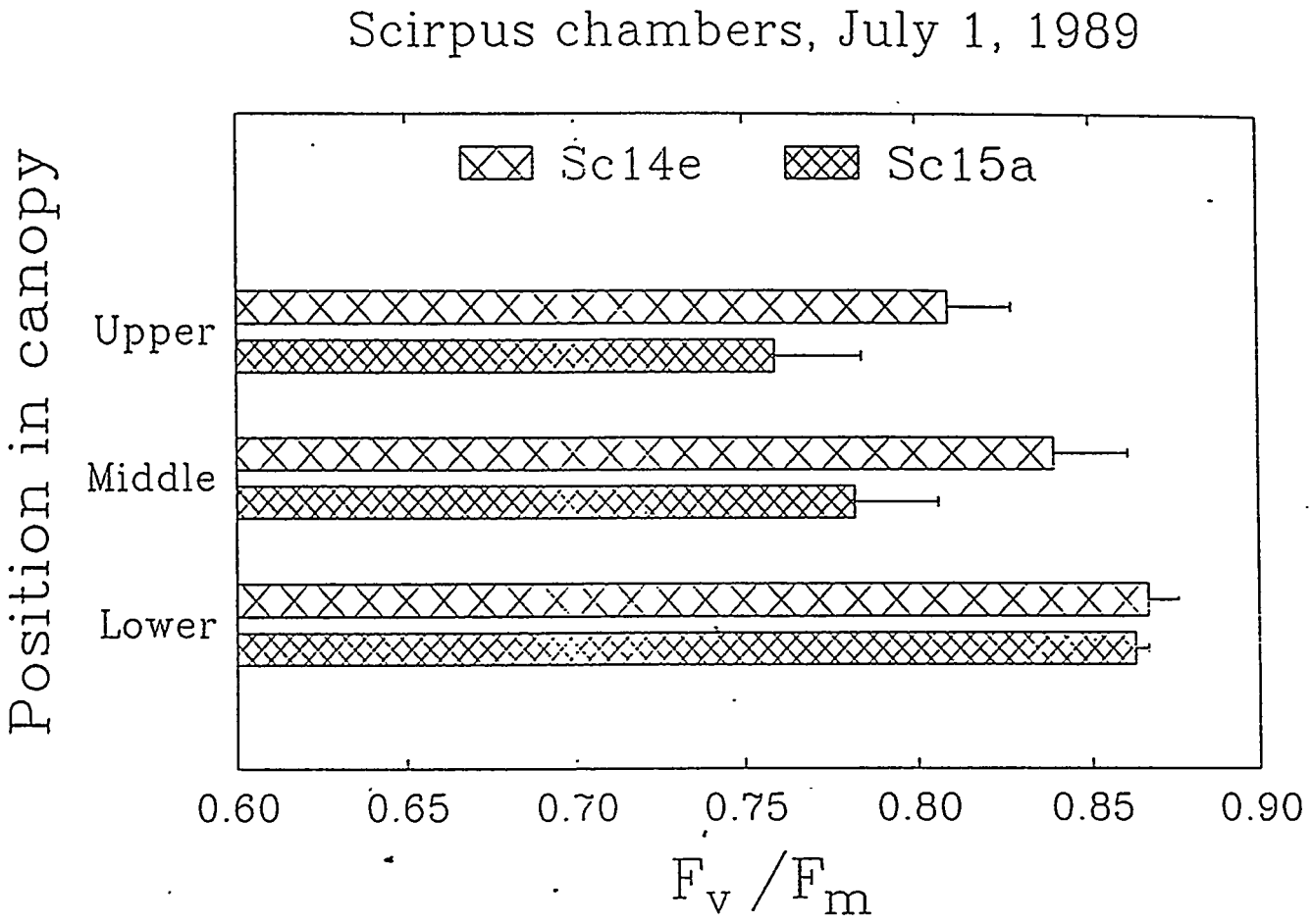

Figure 4.9

The mean F_v/F_m (±s.e.) of stems of S. olneyi in adjacent open top chambers, one with a mean CO_2 concentration in air of 350 μmol mol-1 (solid bars) the other with 700 μmol mol-1 (cross-hatched bars). Each bar is the mean of 10 stems. Measurements were made in the upper, middle and lower portions of the canopy, i.e. approximately 15 cm, 40 cm, and 65 cm from the top of the canopy formed by the S. olneyi stems. Measurements were made between 14:30 and 16:30 hours on July ?? which was a day with clear skies, a photon flux of 1 950 μmol m-2 s-1 at 13:00 hours and a mean temperature within the open-top chambers of 35•C.

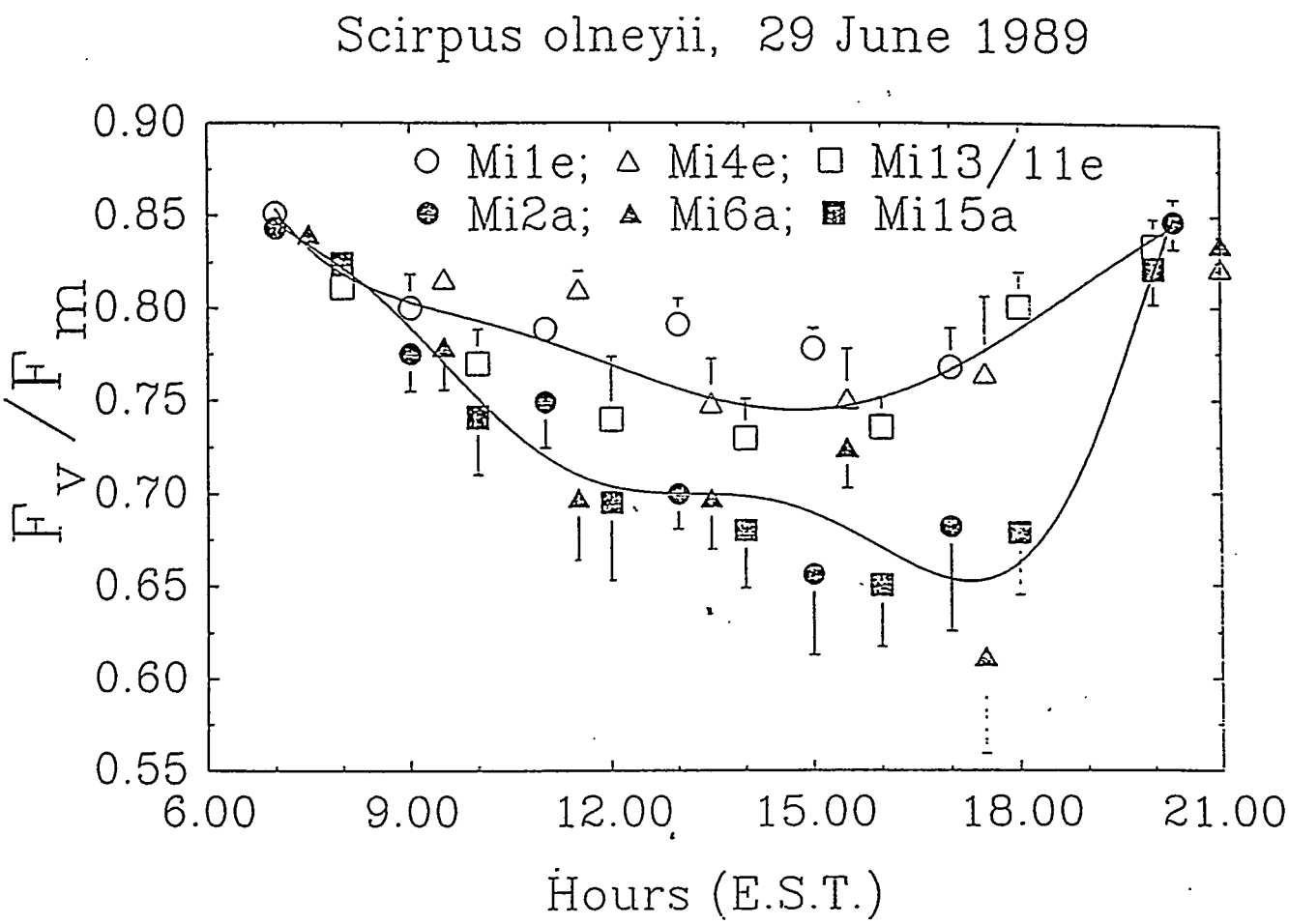

Figure 4.10

The variability of mean F_v/F_m (±s.e.) for stems of S. olneyi from three open top chambers in which the mean CO_2 concentration in air was maintained at 350 μmol mol-1 ( ) and three chambers in which the mean CO_2 concentration was maintained at 700 μmol mol-1 ( ). Ambient and elevated CO_2 chambers were paired so that the same symbol type, e.g. triangle, indicates two chambers with matched edaphic conditions. Lines indicate the best-fitting curves determined by splined regression. Each point is the mean of 8 stems2 from each chamber measured at 1.5 hourly intervals through the course of June 29 1989. July 29 was a day with clear skies and a mean photon flux of 2 200 μmol m-2 s-1 at 13:00 with a mean air temperature in the chambers of 32•C.

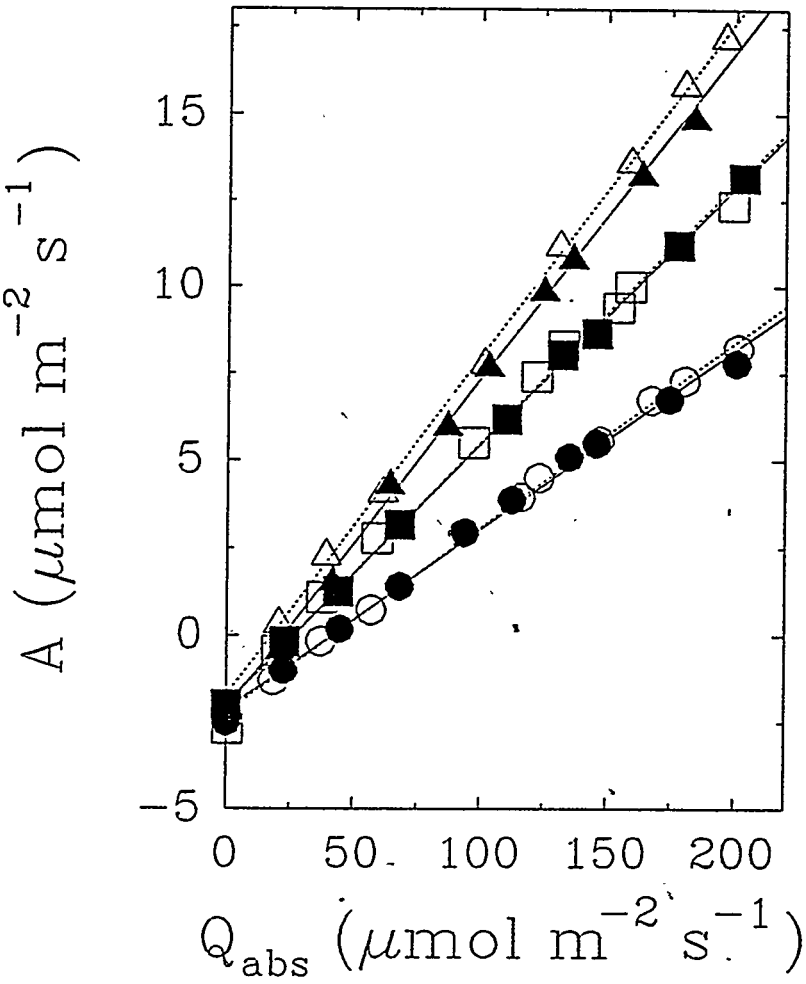

Figure 4.11

The initial slope of the response of CO_2 uptake per unit projected area (A) to the absorbed photon flux per unit projected area (Q_{abs}) for a stem of S. olneyi grown in 350 μmol mol^{-1} CO_2 in air (open symbols and broken lines) and a stem grown in 700 μmol m^{-2} s^{-1} CO_2 in air (closed symbols and solid lines). For both stems, the response of A to Q_{abs} was determined in three gas mixtures: 1 mmol mol^{-1} O_2 and PP350 μmol m^{-2} s^{-1} CO_2 in air (,); 21 mmol mol^{-1} and 350 μmol m^{-2} s^{-1} (,); and 21 mmol mol^{-1} and 700 μmol m^{-2} s^{-1} (,), in each case the balance of the mixture was N_2. Lines illustrate the best-fit relationship determined by the least-squares method for the displayed data points. Solid lines represent 3 leaves of each treatment in the three gas mixtures.

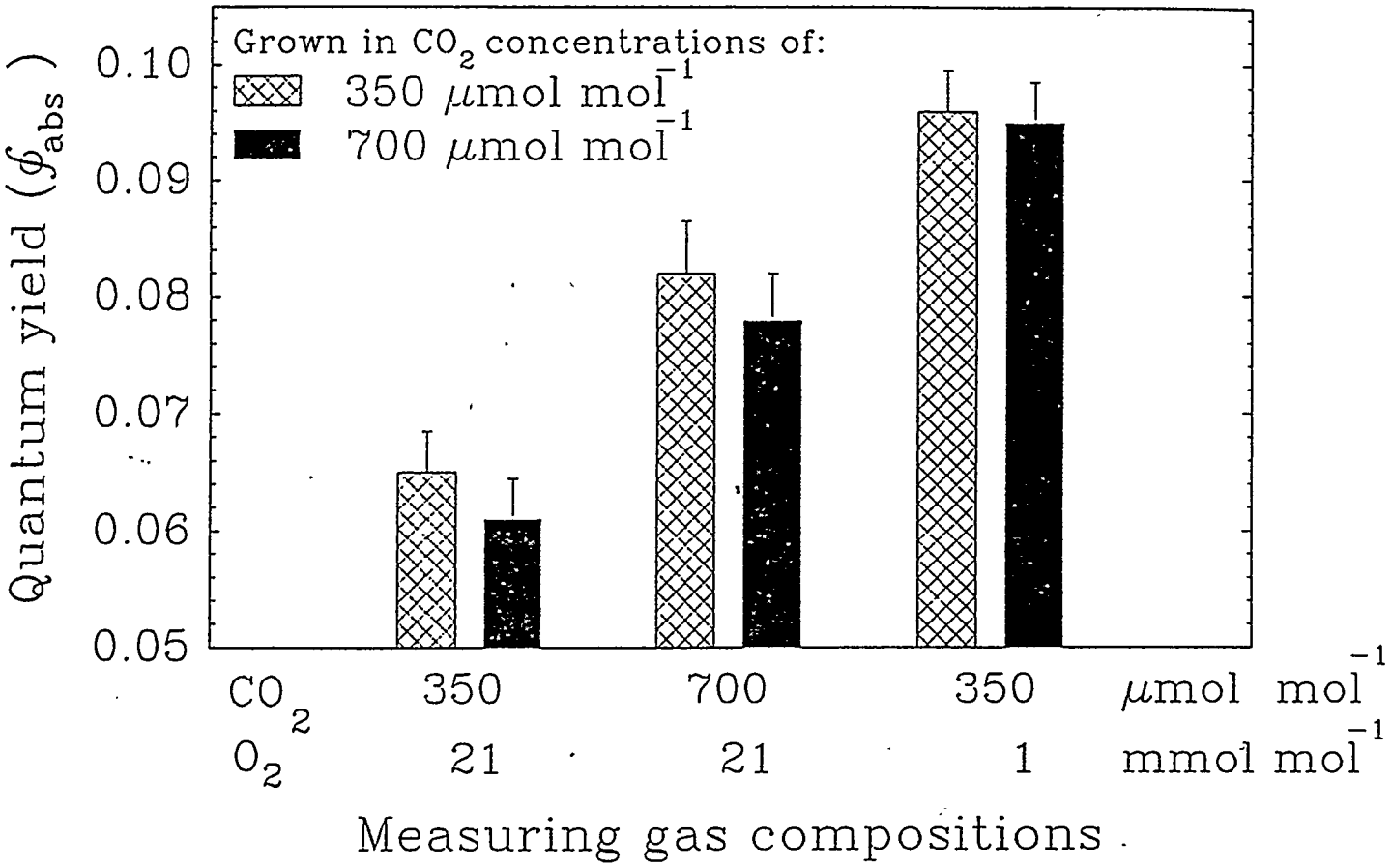

Figure 4.12

The mean quantum yields on an absorbed light basis (ϕ_{abs}) of 10 stems of S. olneyi PPgrown in 700 μmol m^{-2} s^{-1} and 10 stems grown in 350 μmol m^{-2} s^{-1}. Vertical bars indicate +1 s.e. ϕ_{abs} was determined for each stem in three measuring gas mixtures, as detailed in Fig. 1.

Fig. 3. The mean light compensation point of photosynthesis (LCP) for 10 stems of S. olneyi grown in 700 μmol m^{-2} s^{-1} and 10 stems grown in 350 μmol m^{-2} s^{-1}. Vertical bars indicate +1 s.e. ϕ_{abs} was determined for each stem in three measuring gas mixtures, as detailed in Fig. 1.

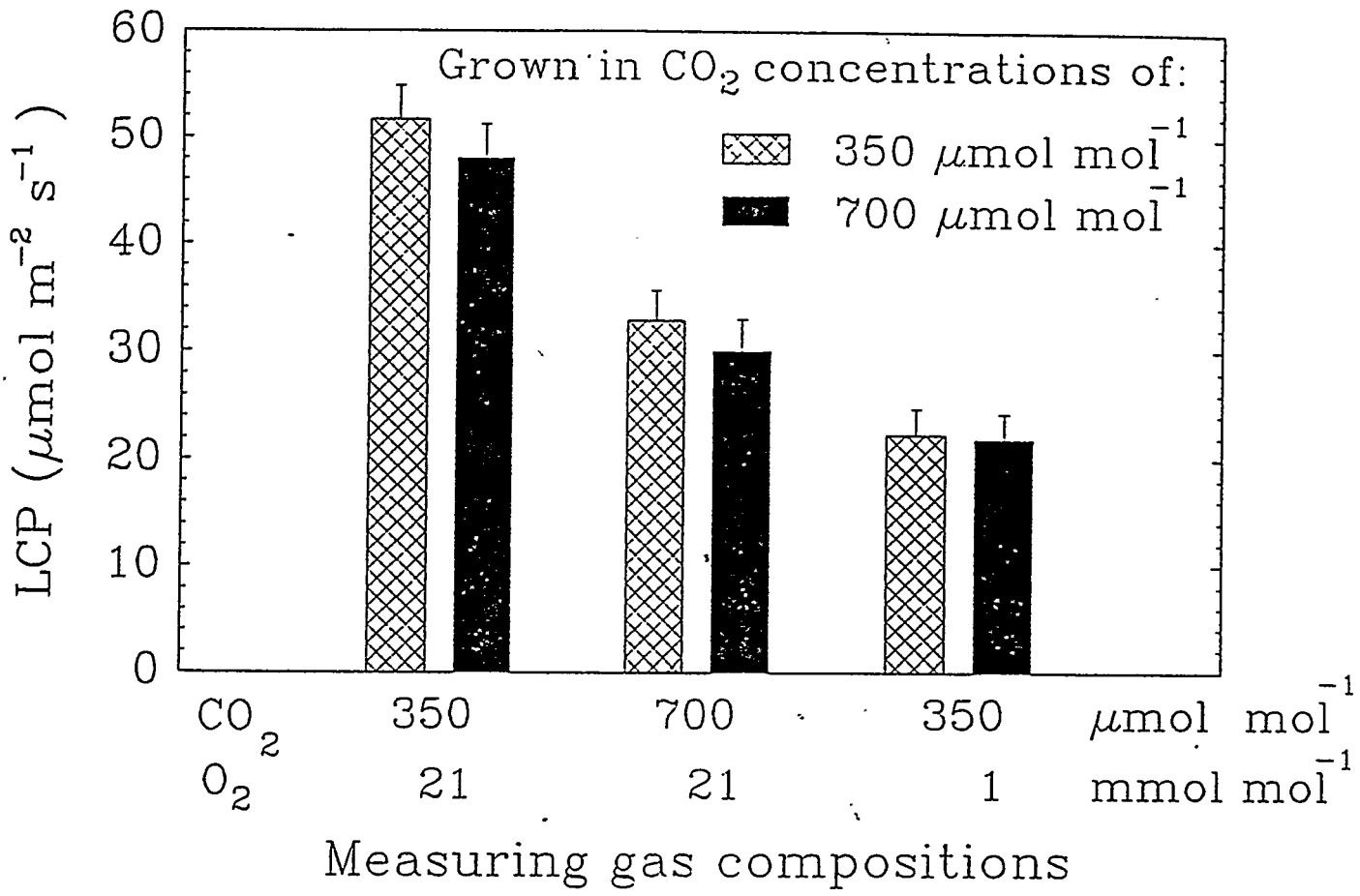

Figure 4.13

The mean light compensation point of photosynthesis (LCP) for 10 stems of *S. Olneyi* grown in 700 umol m^{-2} s^{-1} and 10 stems grown in 350 m^{-2} s^{-1}. Vertical bars indicate +1 s.e. ϕ_{abs} was determined for each stem in three measuring gas mixtures, as detailed in Fig. 1.

Chapter 5. Canopy Gas Exchange

Photosynthesis

L. Balduman, W.T. Pockman, P. Utley.

Methods

The normally open top chambers can be set up to measure exchange of carbon dioxide and water vapor through the addition of tops with restricted openings. Gas exchange is calculated by measuring the difference between the concentration of CO2 or water vapor in the air entering the chamber and the air leaving the chamber. Gas exchange was measured in one community at a time for three or four days approximately every two weeks from May through November. Each chamber was measured every eight to ten minutes during the period of gas exchange measurements. The gas circuit, chamber design and the complete description of gas exchange measurements can be found in greenbooks #038 and #044 and in Drake et al. (1989).

Results

Figures 5.1 - 5.3 show sample gas exchange measurements from the Scirpus, Spartina and Mixed communities over a twenty four hour period at the beginning, middle and end of the season. Figure 5.4 shows total daily carbon uptake in each of the three communities over the course of the season. The Scirpus community showed a strong response to exposure to elevated CO2 while the Spartina and Mixed community exhibited little or no difference. Figure 5.5 shows photosynthesis at maximum light (Pmax) for each of the three communities over the course of the season. Consistent with the data for total daily carbon uptake, the Scirpus community responded to elevated CO2 while the Spartina and Mixed communities did not. Figure 5.6 shows enhancement (E-A/A) of Pmax in the elevated chambers in each community. Figures 5.7 and 5.8 show the effect of temperature on Pmax and total daily carbon gain respectively.

Dark respiration.

W.T. Pockman and P. Utley.

The effects of elevated CO2 on dark respiration are unclear. Increases and decreases in dark respiration have been reported in the literature (citations). Changes in respiration are difficult to understand because they can be attributed to changes in tissue composition (starch accumulation, altered specific nitrogen content, reduced demand for enzyme/protein turnover) and to the direct effects of elevated CO2 during the measurements themselves (i.e. feedback inhibition). Field measurements are further complicated by the difficulty of measuring small differentials (0-5 ppm) in a chamber with a background CO2 concentration twice that of the surrounding air.

Canopy respiration.

Canopy dark respiration rates (Figure 5.x) are presented for each community during the period 0-0600 over the course of the season. These data are more highly variable than the daytime gas exchange data due to frequent fluctuations in the ambient CO2 concentration on the marsh at night. A system correction equivalent to -4.31 umol m-2 s-1 has been included in the data from the elevated chambers to account for slight dilution of the air in the chambers by ambient air. Figure 5.x shows the effect of temperatute on morning respiration rates.

Methane Fluxes.

J. Dacey.

Methane is an important greenhouse gas because of its efficient absorbance of infrared radiation. Even at its relatively low concentration (<2ppmv), it is the third major IR absorber in the atmosphere after water vapor and carbon dioxide. The concentration of methane in the atmosphere has also been rising at about 1.5% per year in recent years, and the reasons for this rise are not understood. In a summary of methane sources, Ehhalt (1987) concluded that wetlands and rice paddies are major sources in the methane: together these systems constitute 35-50% of the global methane emission. Any systematic change in the rate of emission from these systems could have a dramatic effect on the global budget of methane.

Vegetation is central in structuring these wetland systems, and changes in vegetation will certainly change the pattern of trace gas emission. Rooted vascular plants have several impacts on the behavior of trace gases. In the case of methane, which is produced by anaerobic bacteria in the sediment, there are a number of relevant processes with positive and negative impacts on emission:

1) **Supply of organic carbon to the sediment:** Vegetation provides the fixed carbon which fuels most of the microbial activity of the soil. A change in the quantity and composition of that organic carbon will certainly influence the nature of microbial processes. Seiler et al. (1984) and Huang and Klug (1987) demonstrated that the presence of vegetation greatly increased the production and emission of methane from flooded soils. Plants contribute organic carbon to the sediment in a couple of ways: by adding litter to the bulk sediment (by leaf litter, for example) and by losing organic material lost from living roots.

2) **Plant-mediated emission:** Rooted aquatic plants typically have large internal gas spaces which serve to deliver O_2 to belowground tissues. These lacunae also accelerate the emission of soil-derived trace gases to the atmosphere. Since the significance of this process was first documented by Dacey and Klug (1979), plant-mediated transport has been shown to dominate the emission of methane from a variety of wetland systems, including rice paddies. Most methane leaving the saltmarsh system probably passes through the lacunae in higher plants.

3) **Rhizosphere oxidation:** Vegetation provides a mechanism for oxidizing the soil by delivering O_2 deep belowground via internal gas spaces. Holzapfel-Pschorn et al. (1985) and Huang and Klug (1987) found substantially more methane formation than emission in rice systems - rhizosphere oxidation is the most likely methane sink. This process is important because not only does it reduce overall flux, but it may also change the isotopic signature of the emitted methane which has important implications for atmospheric budget calculations.

4) **Plant-mediated sediment desaturation:** Vegetation plays a dominant role in the hydrology of the saltmarsh sediment by taking up water at its roots, and transpiring it to the atmosphere (Dacey & Howes 1984). Sediment desaturation will increase the supply of oxygen to the surface sediment. Dacey & Howes (1984) found, for example, that sulfide levels were lower in areas of saltmarsh fertilized with nitrogen, presumably because increased biomass results in increased transpiration and accelerated entry of air into the sediment. Desaturation may also have the obverse effect of accelerating the flux of sediment gases to the atmosphere across the sediment surface.

Which processes dominate, whether increasing atmospheric CO_2 increases or decreases CH_4 emission from wetlands, requires a long term study of the sort coordinated by Bert Drake. The CO_2 enrichment experiment at S.E.R.C. represents a unique opportunity to evaluate the possibilities of feedback between the two major greenhouse gases, CO_2 and CH_4. The increase in belowground biomass that accompanies CO_2 enrichment must certainly have an important effect on the nature of belowground decomposition processes. Simply adding more organic carbon to the sediment suggests that a new steady state will be reached with a higher throughput of carbon. The overwhelming importance of anaerobic decomposition in these systems means that unless delivery of O_2 or other electron acceptors is somehow accelerated, the magnitude of methanogenesis to the turnover of carbon will increase. The increased belowground biomass will also have two counteracting effects, one accelerating the efflux of methane from the sediment, and the other accelerating the influx of O_2 into the sediment through root aerenchyma, thereby increasing the potential for *in situ* CH_4 oxidation.

Dacey and Klug visited S.E.R.C. during October 1989 to conduct an initial study of the effects of the longterm CO_2 addition on methane emission. The primary goal was to test our hypothesis that increased carbon fixation would lead to increased methane emission. We brought a system designed to operate in conjunction with the extant CO_2 sampling system: a Varian 3700 GC system with a flame ionization detector in a system was controlled by a PC which selected samples from any of 20 input streams (10 chambers,

influx and efflux air) and a reference stream from a tank of compressed air. Detector output was integrated by HP3390 and output from the integrator was stored in PC files. The system sampled automatically roughly every 3 minutes, analyzing and storing the data.

Air in the field experiment chambers turns over about 3 times per minute in order to minimize the enclosure effects on the vegetation. This is an essential aspect of the experimental design of the CO_2 study, and it represents an analytical challenge for studying CH_4 emission. For a methane flux of 1 mmol m^{-2} d^{-1} we needed to able to resolve differences in the input stream and output stream of about 10 ppbv. The analytical system can resolve differences of that magnitude, but the system was vulnerable to fluctuations of ambient methane. These fluctuations were most severe when wind velocity was low. During nighttime, when winds drop, the background variability in methane concentration becomes very high (Figure 5.11). Methane over the marsh varies by several 10's ppb (up to 1ppm in one 24-hour period); these variations exceed the increment in the flushing chambers due to emission. Synchronization of air sampling led to a situation where comparisons of inlet and efflux air were made on air "separated" by several turnovers of chamber air. As a result, variations in background CH_4 swamped out the emission signal when emission was low, as in the Scirpus and Mixed communities (Figure 5.12,B).

Even with these unanticipated problems, we can make some conclusions about methane emission from the Edgewater marsh. There were differences in rates of methane emission across the marsh surface, and within communities (Figure 5.12,A). The highest rates (3-16 mmol/m^2/d), which are comparable to many freshwater sites, were observed in the Spartina patens zone - the highest elevation plant community. Fluxes in the lower, more sulfate-rich sites were one-quarter or less in rate. The rates of emission are consistent with the observed concentrations in sediment cores (Figure 5.13). Methane was substantially higher in the Spartina sediment, lower in Mixed, and lowest in Scirpus.

There is also substantial variability in emission within plant communities, both between chambers, and from hour to hour. The sources of variability must be understood in order to develop predictive models. Short-term, side-by-side measurements of gas emission are therefore insufficient because of changes in plant life history. During the growing season the rate of decomposition changes, generally peaking sometime during fall, which is when we would expect the maximum rate of emission for methane. The fact that CO2 enrichment delays the senescence of vegetation suggests that decomposition processes in the sediment may also be delayed. We need an integrated annual methane flux to understand the effect of CO2 enrichment on methane emission.

In an effort to gain some insight into the CO_2 treatment effect on CH_4 from Scirpus and Mixed communities, we also conducted some closed chamber flux experiments by stopping flow through the chambers, and measuring methane accumulation in the chambers. These experiments could only be performed at night because the chambers would become too hot during daylight. The data showed a strong tendency for methane concentration to increase, but its rate of increase slows within 15-30 minutes. We have not observed this in flooded wetland systems, and conclude that methane is being lost from the system in a yet undetermined fashion. The most obvious possibility is that it leaks out of the chamber, although laboratory experiments suggest that Mellinex is relatively impermeable to methane. The other possibility is that methane is being oxidized at the sediment surface. If bacterial oxidation is responsible for the observed loss of methane, microbial processes will have to be considered seriously in any attempt to evaluate methane emission from this system. We are currently investigating this effect by using inert tracers to measure air movement in the chambers. Although we believe that closed chambers are not the approach to use in studying gas emission in this system, we are pursuing this question because of its possible implications. If methane is being consumed biologically within the chambers at the rates required to stop CH_4 accumulation, this is an extremely important process in methane cycling.

In conclusion, in our week-long visit to S.E.R.C. we were unable to answer our primary

question about feedbacks between CO_2 enrichment and CH_4 emission. We had hypothesized that CH_4 emission would be increased in CO_2-enriched Scirpus and Mixed communities where C3 plants are present. The rates of methane emission from these communities were too low, however, to be measured against the fluctuating background methane concentration by the sampling technique we used. We must work with the existing chambers, since they have been carefully designed to minimize disturbance of the plant community. Closing the chambers, or slowing their flowthrough can only be used at limited times, and our attempts at this have exposed other problems in measurement of CH_4 emission. This problem has two practical solutions: synchronize sampling of influx and efflux air to reflect the turnover time of air in the chamber; increase the rate of sampling to improve the power of statistical tests.

Methane emission was highest from the Spartina community, as expected. Methane concentrations are highest in the porewater of this community because of the lower sulfate concentrations in the high marsh. Surprisingly, it appears that there may be an augmentation of CH_4 emission from this system. We had not expected this because Spartina does not show increased carbon assimilation at elevated CO_2 levels. The explanation may lie in water turnover. The most dramatic effect observed in the Spartina community is the decrease in water use (transpiration) in CO_2-enriched community. As we described above, lowered rates of water turnover lead to decreased supply of electron acceptors for respiration in the sediment. This observation underscores the point made at the outset. The behavior of trace gases in the wetland system is subject to a variety of conflicting processes dominated by the vegetation. The processes we described are not limited to methane. The emission of other gases, such as N_2O, NO_x, and sulfur gases are also intimately linked to plant processes, either directly, or mediated through the effects of vegetation on sediment biogeochemistry.

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Chapter 5 Appendix. Chamber Performance

Empty Chamber Gas Exchange

During measurement of ecosystem gas exchange we observed anomolies in the zero for measurement of photosynthesis and respiration. These data suggested that the field system might be diluting the air in the elevated chambers slightly giving an offset in our signal the effect of which was to decrease respiration and increase photosynthesis. In October, 1989, experiments were performed to investigate the observed zero shift.

Methods

A chamber with the bottom sealed shut with the same Melinex material used to cover the sides of the chambers was placed in the Mixed community and set up to measure gas exchange in the same fashion as the experimental chambers. During the period 10/23/89 - 10/31/89, the gas exchange characteristics of the chamber were measured over a range of CO_2 concentrations and with and without the use of the mixing circuit. In the absence of any substantial quantity of living material in the chamber that might absorb or release CO_2, these gas exchange measurements should provide a 'blank' reflecting the ability of the chamber to measure zero gas exchange at different background levels of CO_2.

Results

Figure P5.1 shows gas exchange data collected from the empty chamber during the period 23 October - 25 October, 1989 and Table P5.1 shows the regression data from Fig. P5.1. The slopes of the lines through data collected in the morning (0000-0759) and evening (1800-2400) are greater than that for the data collected during the day (0800-1759; Fig. P5.1,A). Differences were greater for data collected with and without the use of the mixing circuit (Figure P5.1,B).

The slope of the response (Fig P5.1,B) decreased 30% when the mixing circuit

was off suggesting that the air inside the chamber was diluted slightly with ambient air. That the slope did not decrease more however suggests that the mixing circuit is not solely responsible for the zero shift observed in the experimental chambers. Other factors that could produce this effect include the wind and CO_2 gradient producing dilution through the seal of the closed top used for photosynthesis measurements or the restricted opening where air exits the chamber during gas exchange measurements. The role of such dilution has yet to be evaluated using the empty chamber apparatus.

After the empty chamber data were collected it was found that leakage might have occurred at the power cord attachment on the mixing blower. Such a leak could offer an explanation for the reduced dilution with the mixing circuit turned off.

Mixing Circuit in Use	Time	Slope	Y Int	R^2	Differential Zero		
					ppm	350 ppm	750 ppm
Yes	AM	.0166	-7.47	.9262	450	-1.66	4.15
Yes	MID	.0137	-5.44	.8931	396	-0.64	4.15
Yes	PM	.0180	-9.05	.9428	503	-2.75	3.54
No	24 Hr	.0113	-6.21	.7197	549	-2.52	1.70
Yes	24 Hr	.0155	-6.54	.8577	421	-1.11	4.31

Table P5.1. **Regression data for empty chamber gas exchange.** Regression data are shown for empty chamber gas exchange data collected 23 -25 October, 1989. Data are broken down by time of day and condition of mixing circuit. Slope, intercept, R^2, CO_2 concentration where differential is zero, and differential zeros at 350 and 700 ppm background CO_2.

Adjustment of Canopy Gas Exchange Data

Based on the data reported above, all gas exchange measurements from all elevated chambers in each community were adjusted for a 4.31 umol m-2 s-1 rate of CO_2 uptake. The adjustment represents the apparent rate of CO_2 uptake from the empty chamber over the course of the entire day at a background CO_2 concentration of 700 umol mol-1. In light of the possible leak discovered after the data were

collected this adjustment is probably a conservative one. No attempt was made to include any correction for differences created by the time of day during which the measurements were made. Respiration rates, the most dramatically changed by the adjustment, were no longer above zero and were in fact greater than in the ambient chambers. Photosynthesis measurements, because of the higher rates, and thus larger differentials across the chamber, did not exhibit as dramatic a change in the direction of response but instead a small change in magnitude. While the actual rate of dilution undoubtedly varies between chambers, this adjustment represents the best approximation of the zero shift available in the absence of more extensive data. Measurements of the empty chamber will occur throughout the 1990 field season to describe the zero shift in greater detail.

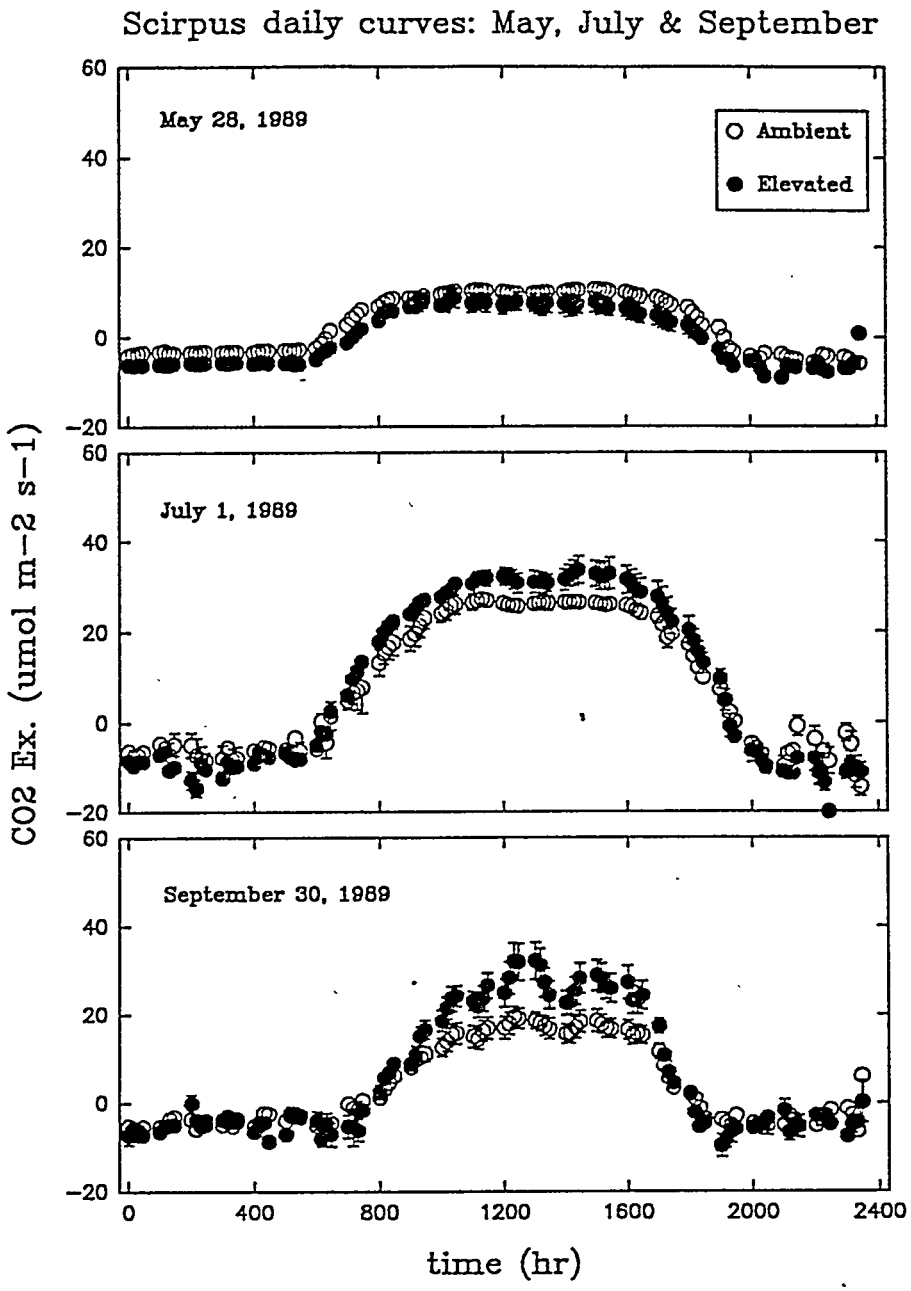

Figure 5.1

Photosynthesis in Scirpus community at early, middle and late season. Mean gas exchange and standard error are shown for the five chambers in each treatment. Open circles represent ambient treatment while closed circles represent the elevated treatment.

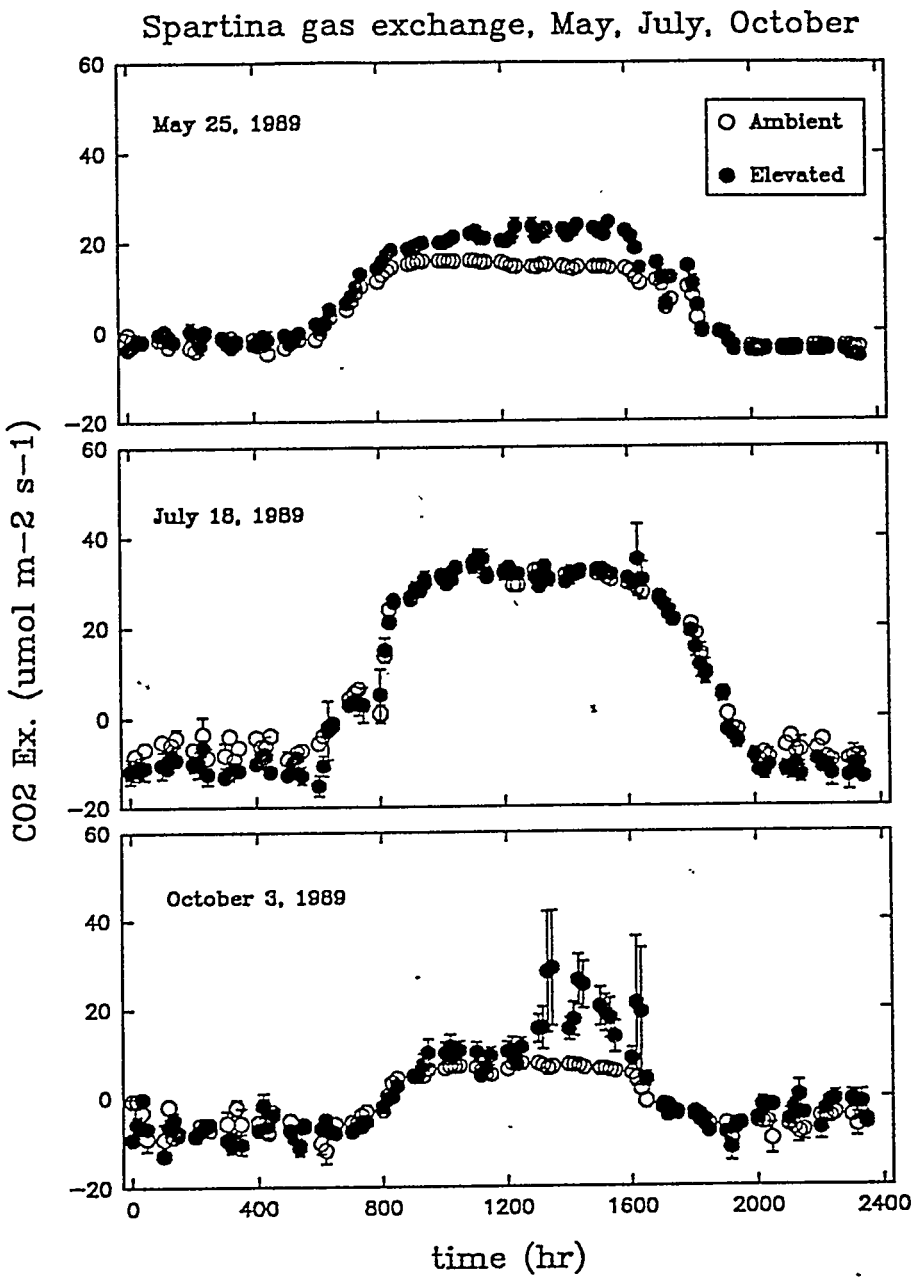

Figure 5.2

Photosynthesis in Spartina community at early, middle and late season. Mean gas exchange and standard error are shown for the five chambers in each treatment. Open circles represent ambient treatment while closed circles represent the elevated treatment.

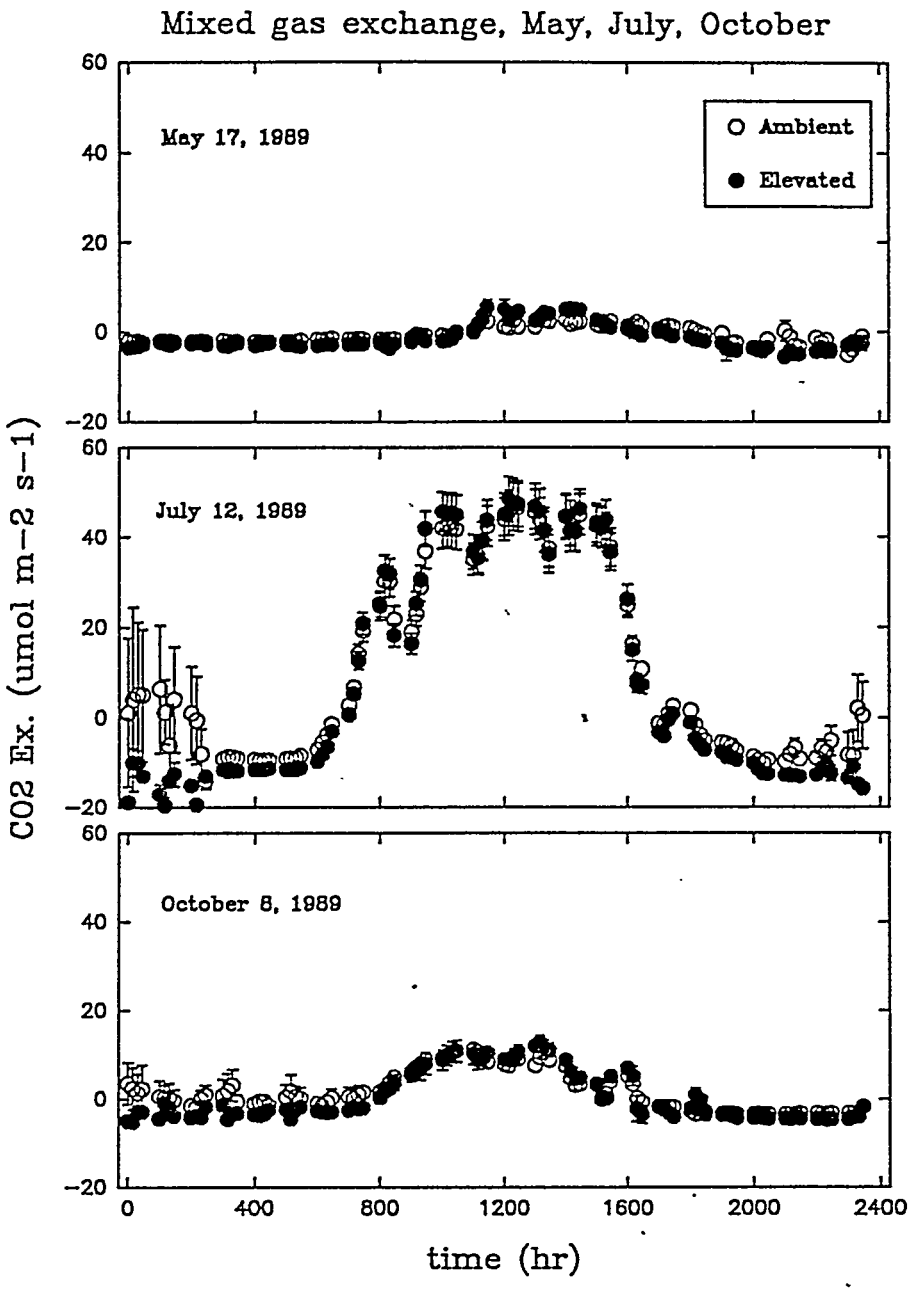

Figure 5.3

Photosynthesis in Mixed community at early, middle and late season. Mean gas exchange and standard error are shown for the five chambers in each treatment. Open circles represent ambient treatment while closed circles represent the elevated treatment.

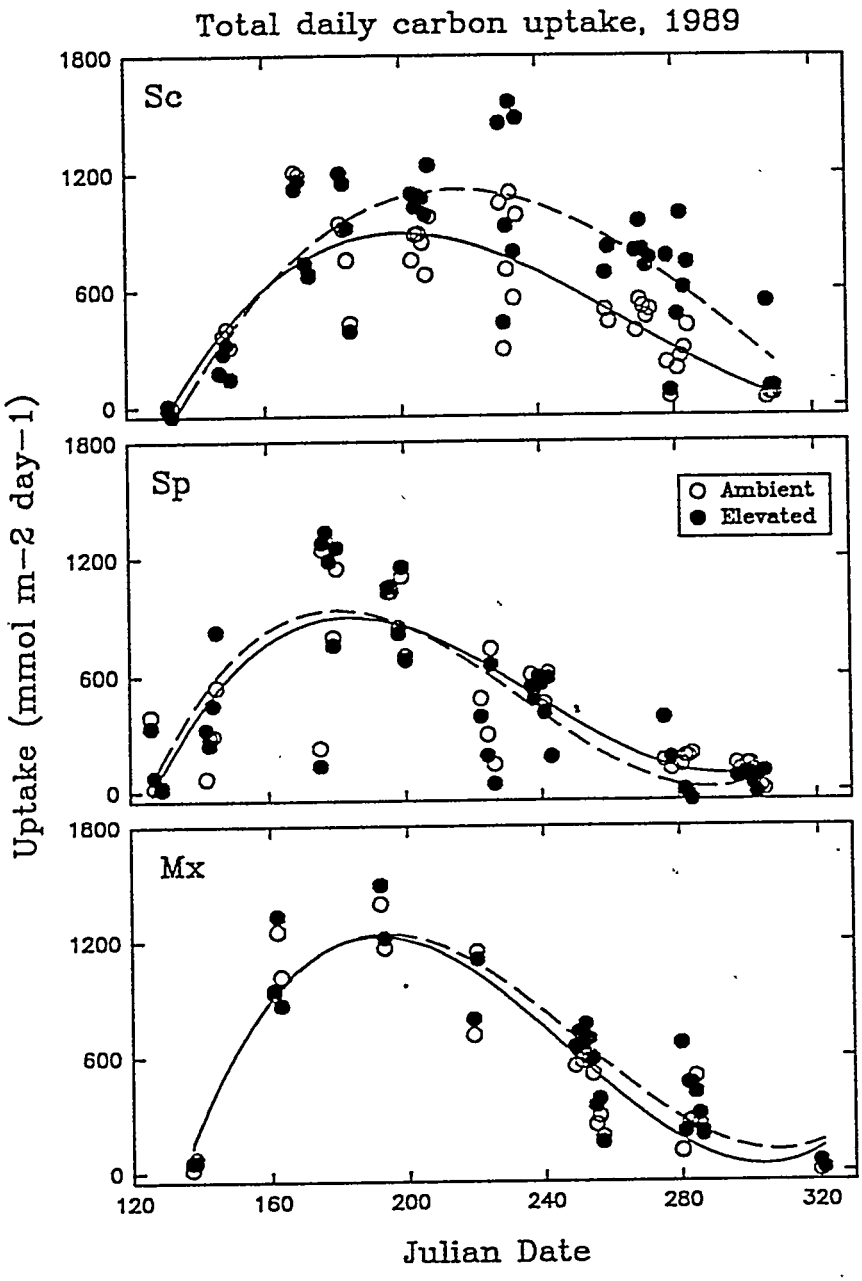

Figure 5.4

Total daily carbon uptake in the Scirpus, Spartina and Mixed communities, 1989. The sum of all gas exchange measurements during a period when PPF exceeded 50 umol m-2 s-1 are shown for each day during the season when data were collected. Elevated chambers include a correction for dilution with ambient air.

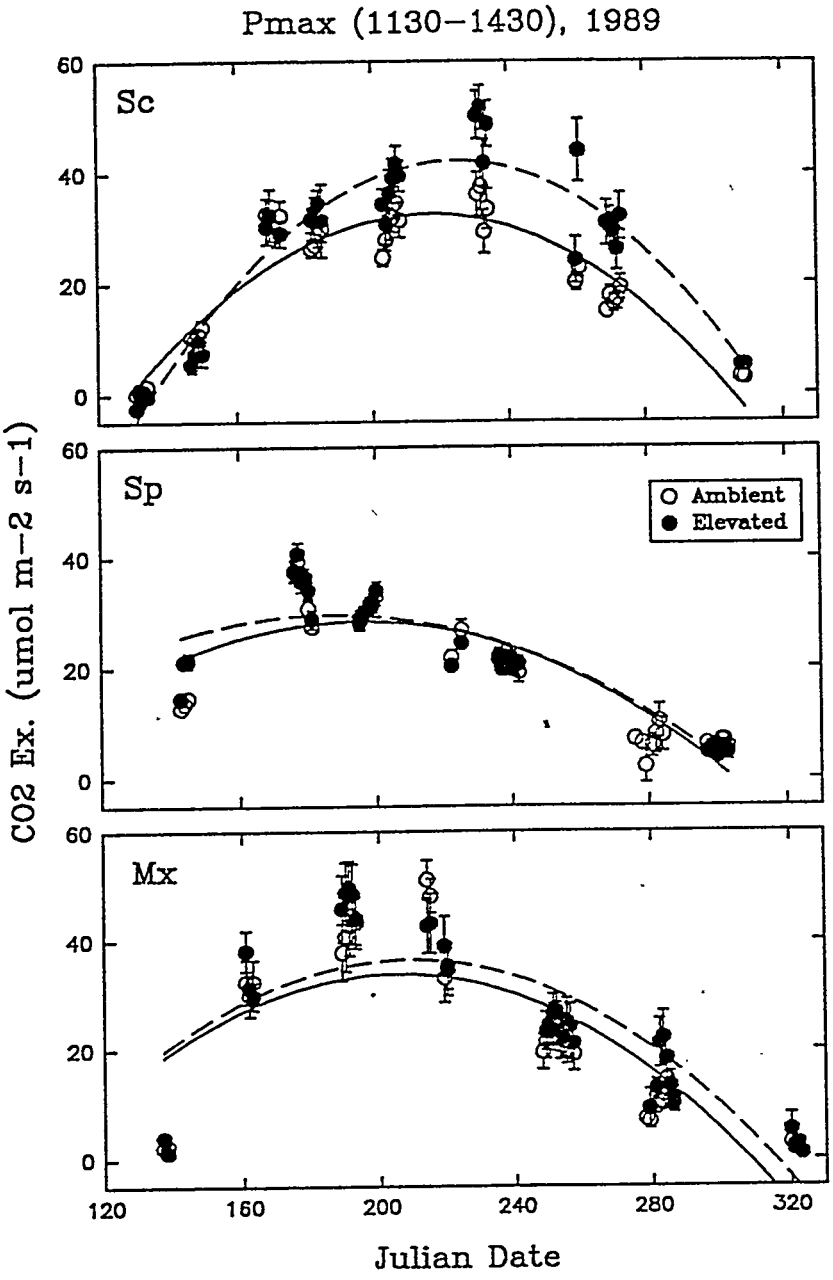

Figure 5.5

Photosynthesis at maximum light (P_{max}) in the Scirpus, Spartina, and Mixed communities, 1989. P_{max} was calculated as the rate of photosynthesis occurring during the period 1130-1430 and during light conditions where PPF exceeded 1000 umol m-2 s-1. Data shown are means and standard errors of the five chambers of ambient and elevated treatment. Open circles represent ambient chambers while closed circles represent elevated chambers. Elevated chambers are corrected for the dilution effect of the chamber mixing system.

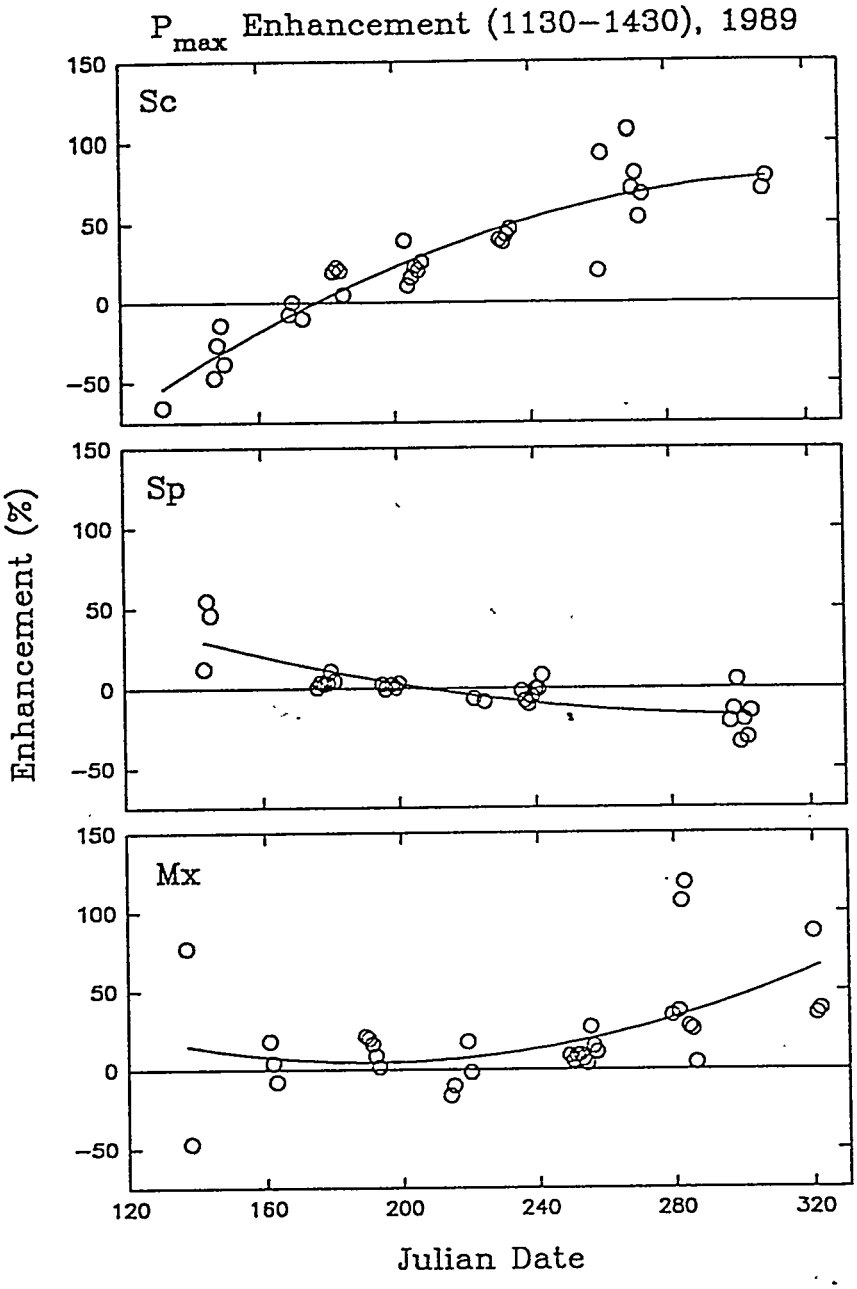

Figure 5.6

Enhancement of P_{max} by growth in elevated CO_2 in the Scirpus, Spartina and Mixed communities, 1989. Enhancement ($E\text{-}A*A^{-1}*100$) is shown for all three communities throughout the season. A second order polynomial regression has been fitted to each data set.

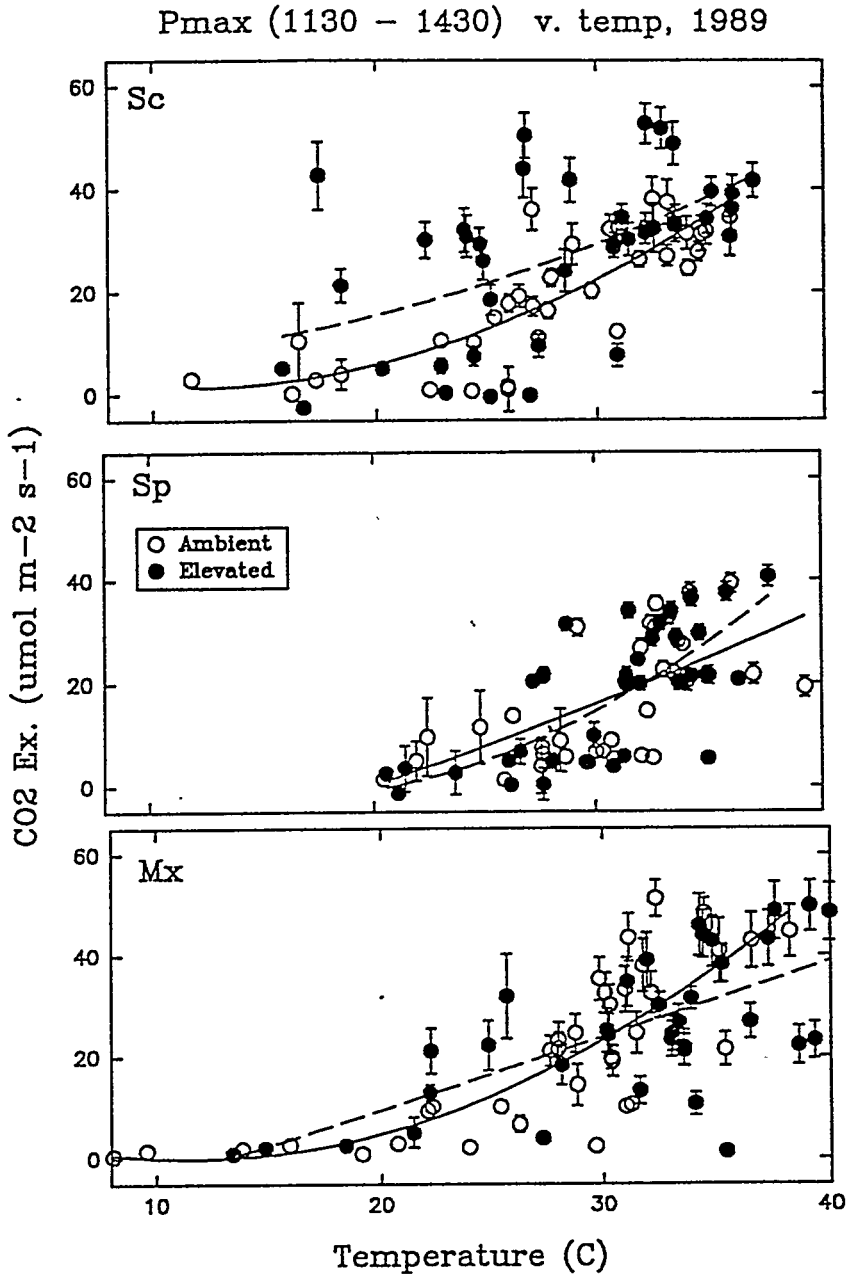

Figure 5.7

Effect of temperature on P_{max} in the Scirpus, Spartina and Mixed communities, 1989. Mean P_{max} values and standard errors are plotted against the mean temperature in the chambers during the measurement period. Open circles denote ambient chambers while closed circles represent elevated chambers. Data are shown with a second order polynomial regression (ambient=solid line, elevated=broken line).

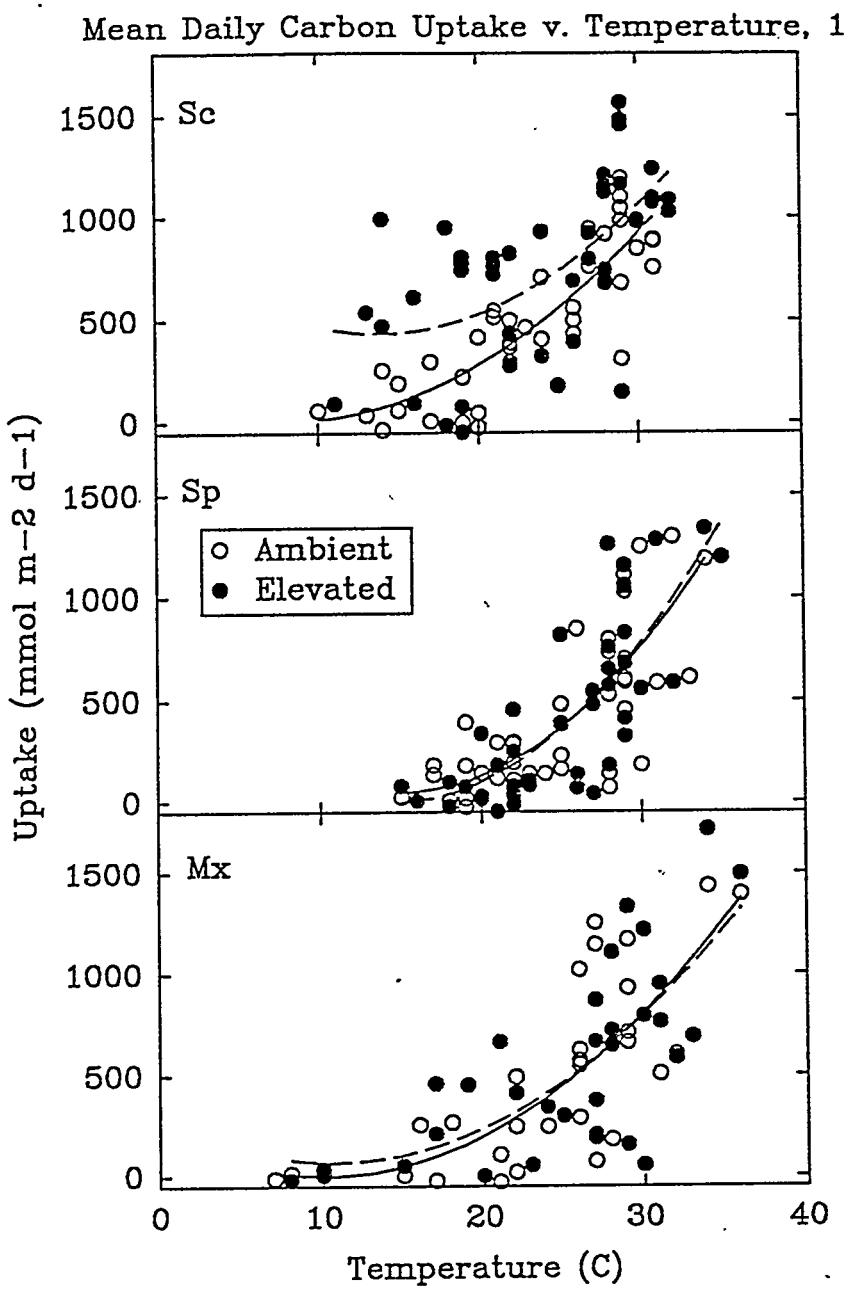

Figure 5.8

Effect of temperature on total daily carbon uptake in the Scirpus, Spartina and Mixed communities, 1989. Mean total daily carbon uptake (determined as above) in the ambient and elevated chambers is shown with standard error bars against mean temperature during the measurement period. Open circles denote ambient chambers while closed circles represent the elevated chambers.

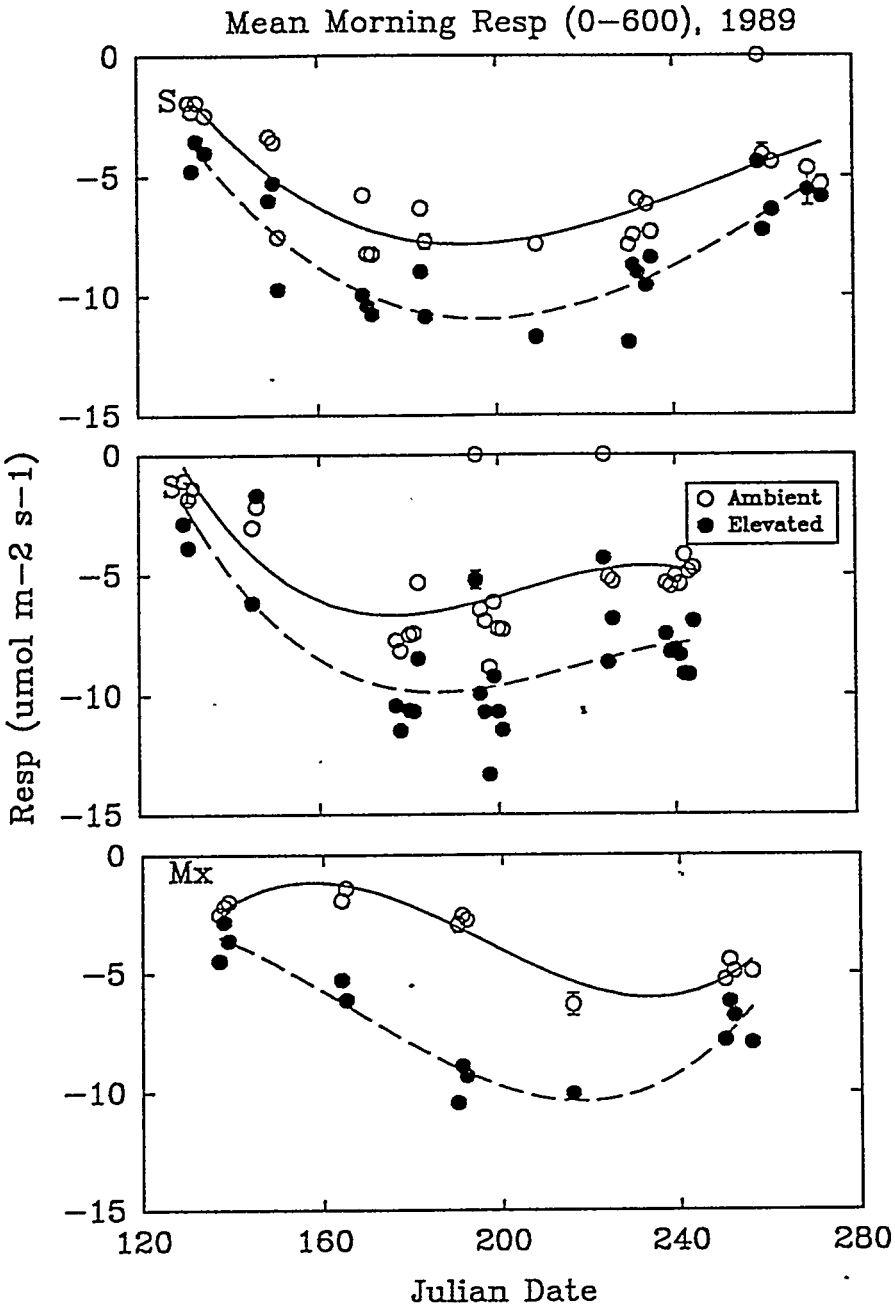

Figure 5.9

Mean morning respiration rates in the Scirpus, Spartina and Mixed communities, 1989. Mean morning respiration of all five chambers of each treatment was calculated during the period 0000 - 0600. The data for elevated treatment include a correction for the slight dilution that occurs in the mixing circuit of the elevated chambers.

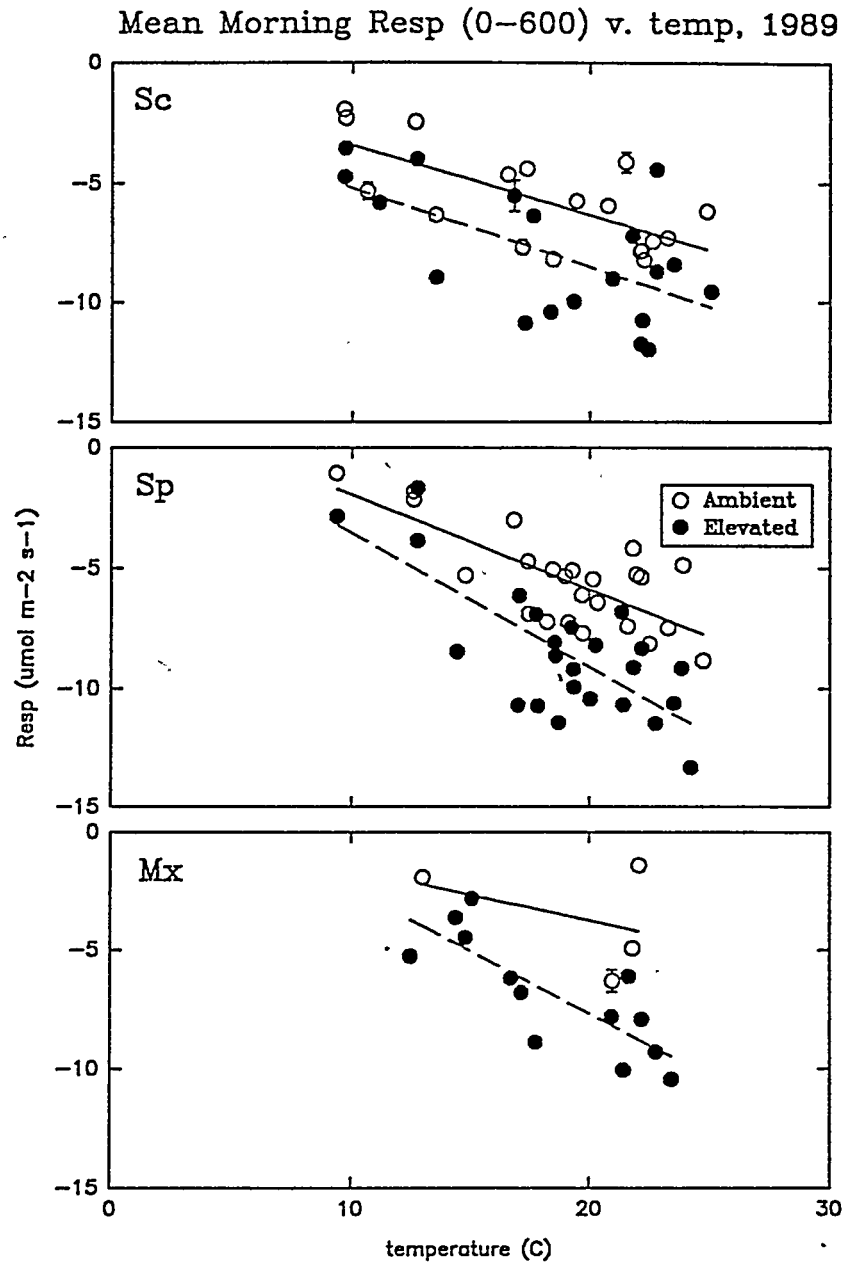

Figure 5.10

Effect of temperature on mean morning respiration in both treatments of the Scirpus, Spartina and Mixed communities, 1989. Mean morning respiration (calculated as above during the period 0000 - 0600) is shown against the mean temperature during the measurement period. Open circles denote the ambient treatment while the closed represent the elevated treatment.

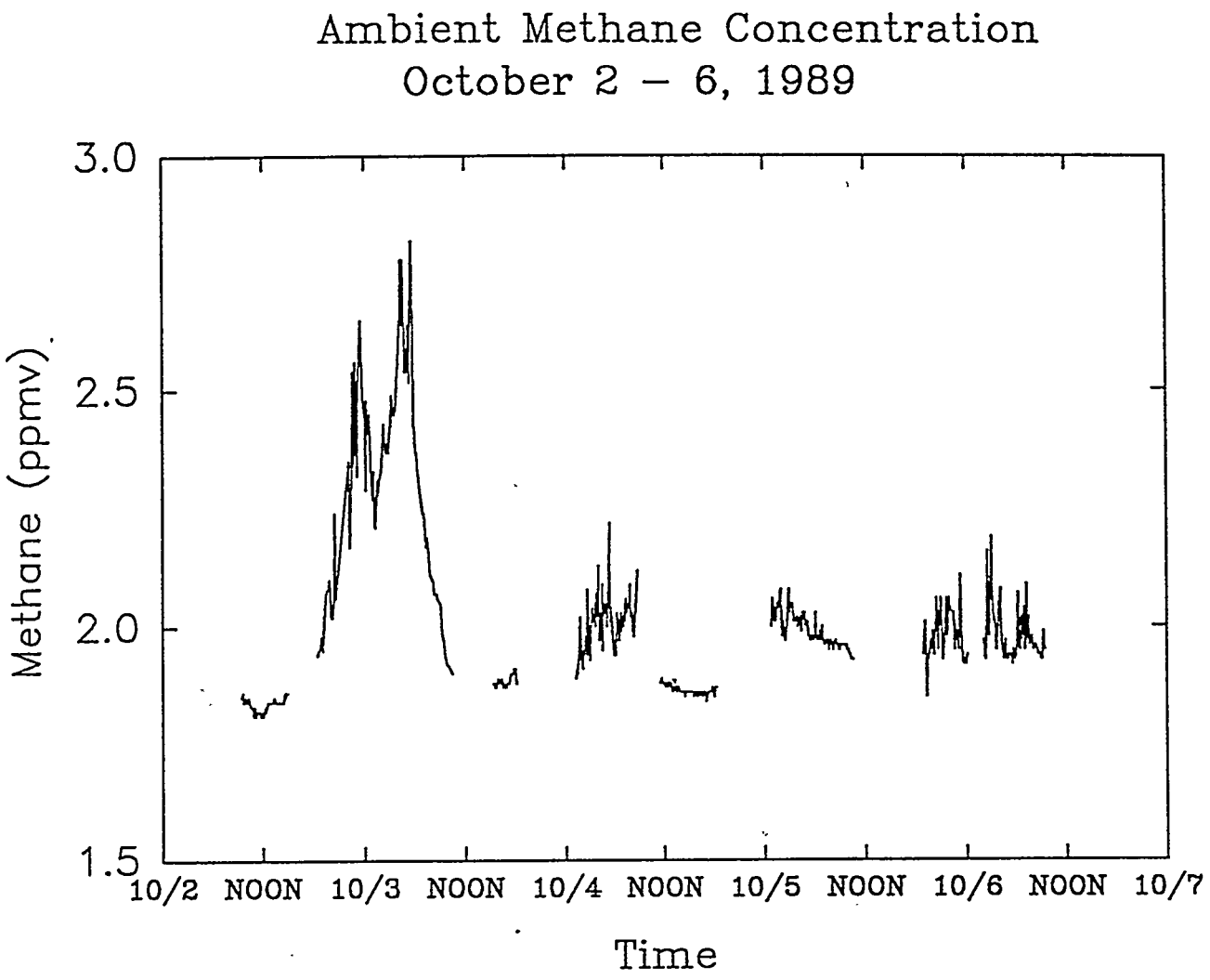

Figure 5.11

Time-course of methane concentration in ambient air over the marsh. The increases in CH_4 concentration and variability in that concentration correspond to times of low wind speed.

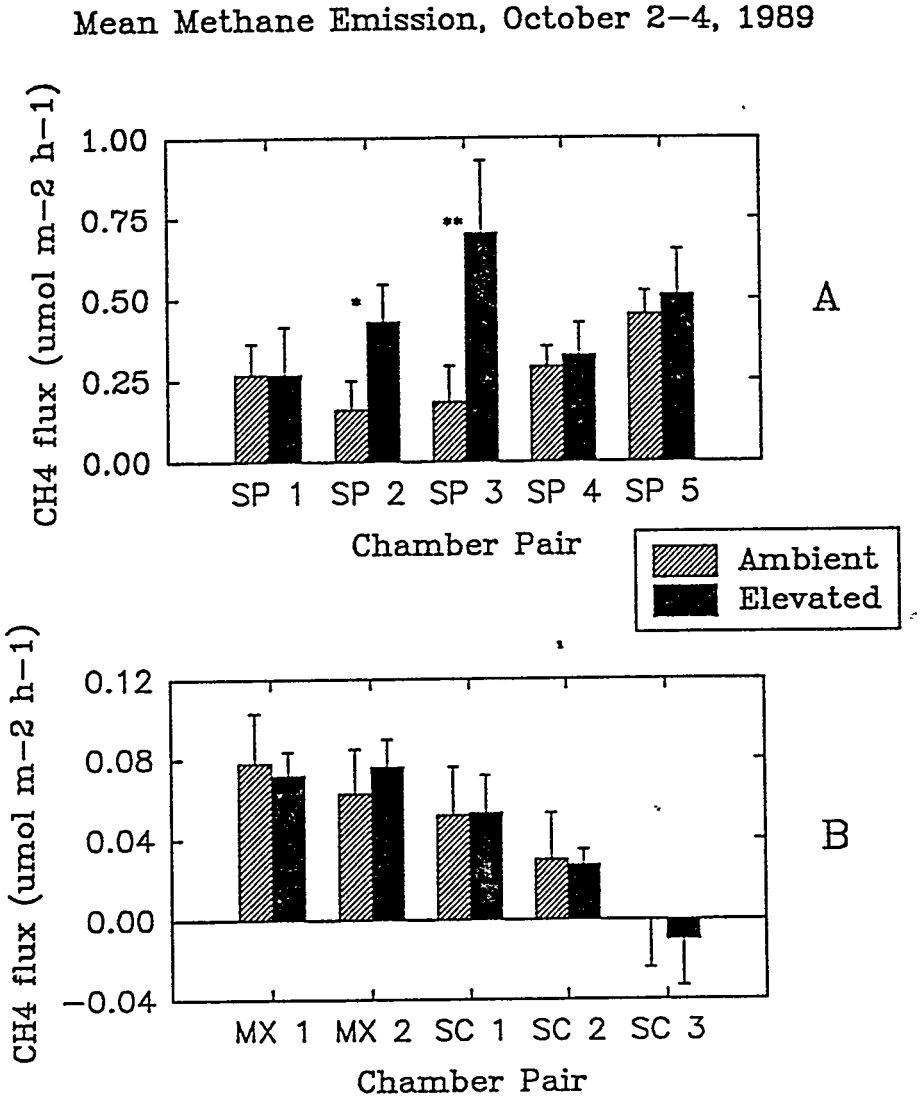

Figure 5.12

Mean methane emission from paired chambers in the Scirpus, Spartina and Mixed communities. (A) Mean methane emission in the Spartina community (10/02/89 & 10/03/89) and (B) Mean methane emission in the Mixed and Scirpus communities (10/4/89) . Generally methane emission from Scirpus was lowest. Estimates at these low flux rates are susceptible to relatively large errors due to variability in ambient methane concentration. (paired t-test, * $p < 0.06$, ** $p < 0.0005$).

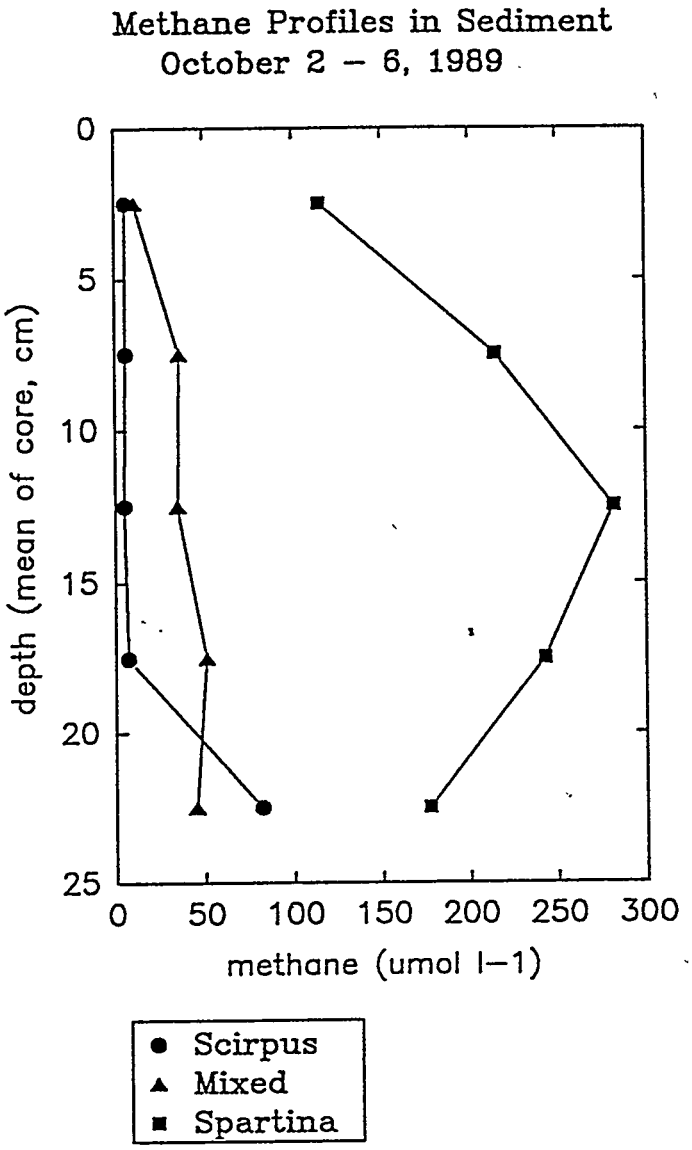

Figure 5.13

Profiles of methane concentration in sediment porewater in the Scirpus, Spartina and Mixed communities. Data represent means for two cores in each of Scirpus and Mixed communities, means for three cores in Spartina community.

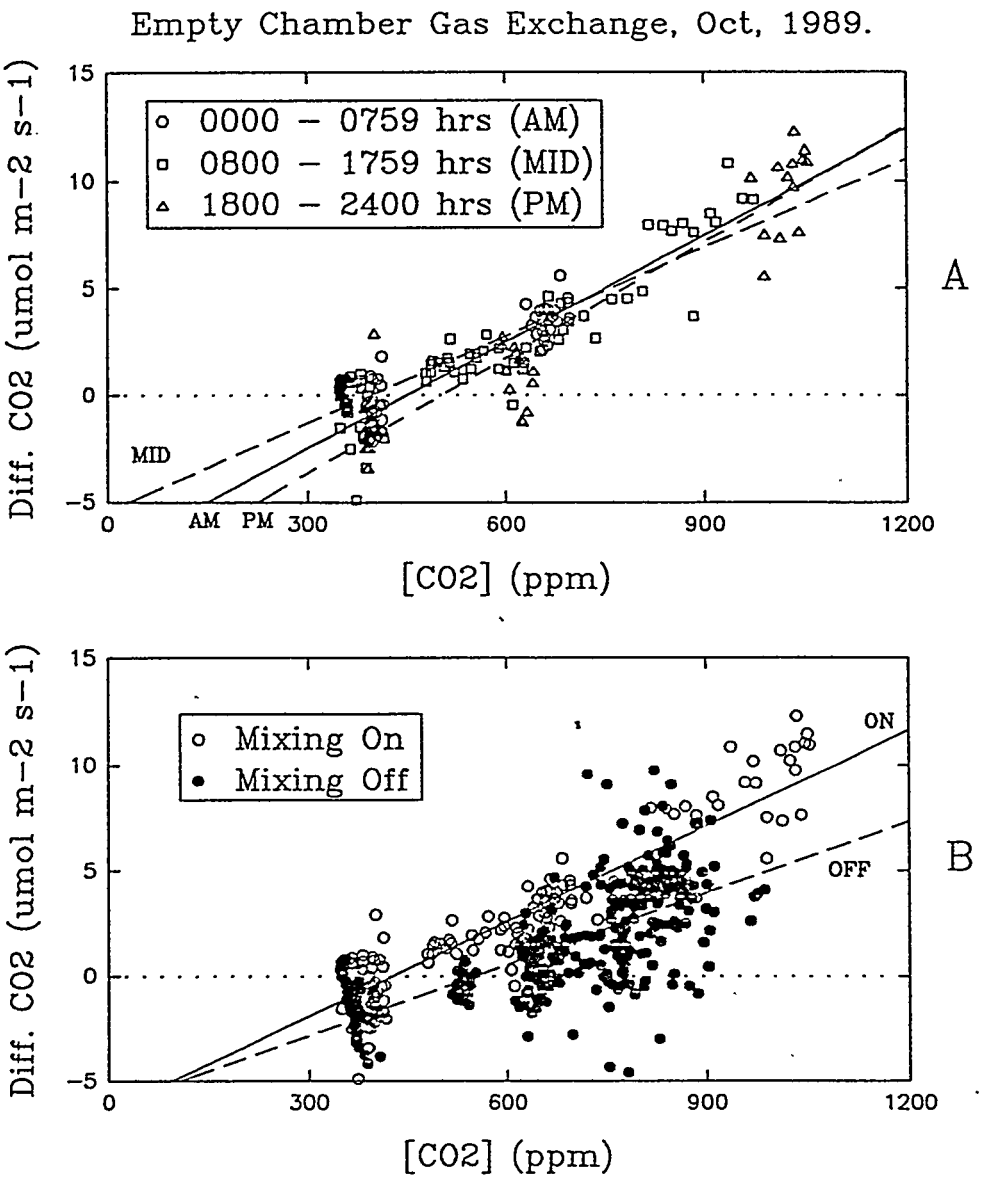

Figure P5.1

Empty chamber gas exchange data, 23-25 October, 1989. Gas exchange data are shown by time of collection (A) and with and without the use of the mixing circuit(B). Linear regressions are shown for each set (regression parameters shown in Table P5.1).

Chapter 6. Carbon Budget.

W.T. Pockman.

A carbon budget represents a seasonal accounting for gross carbon uptake and carbon losses and allows the calculation of net carbon gain during an entire growing season. Figures 6.1 and 6.2 show the calculation of total daily carbon gain and total daily carbon loss via respiration respectively. Third order polynomial regressions were fitted to the ambient and elevated data sets from each community and the parameters from these regresssions (Table 6.1) used to generate estimated carbon gain and carbon loss for each day during the growing season (Figure 6.3). The difference of the sum totals of the daily carbon gain and carbon loss represents an estimate for the net carbon gain of the community during the 1989 season (Figure 6.4). Due to the photosynthetic contribution of other plant species in the chambers and the respiratory activity of these species and the microbial community in the chambers, the carbon budget can only be said to represent the community defined by the chamber (as opposed to Scirpus or Spartina plants specifically). The starting and ending dates of the season did not correspond exactly to the dates produced by the regressions however the total contribution during the period not included by the regressions probably represents only a small fraction of the total carbon budget.

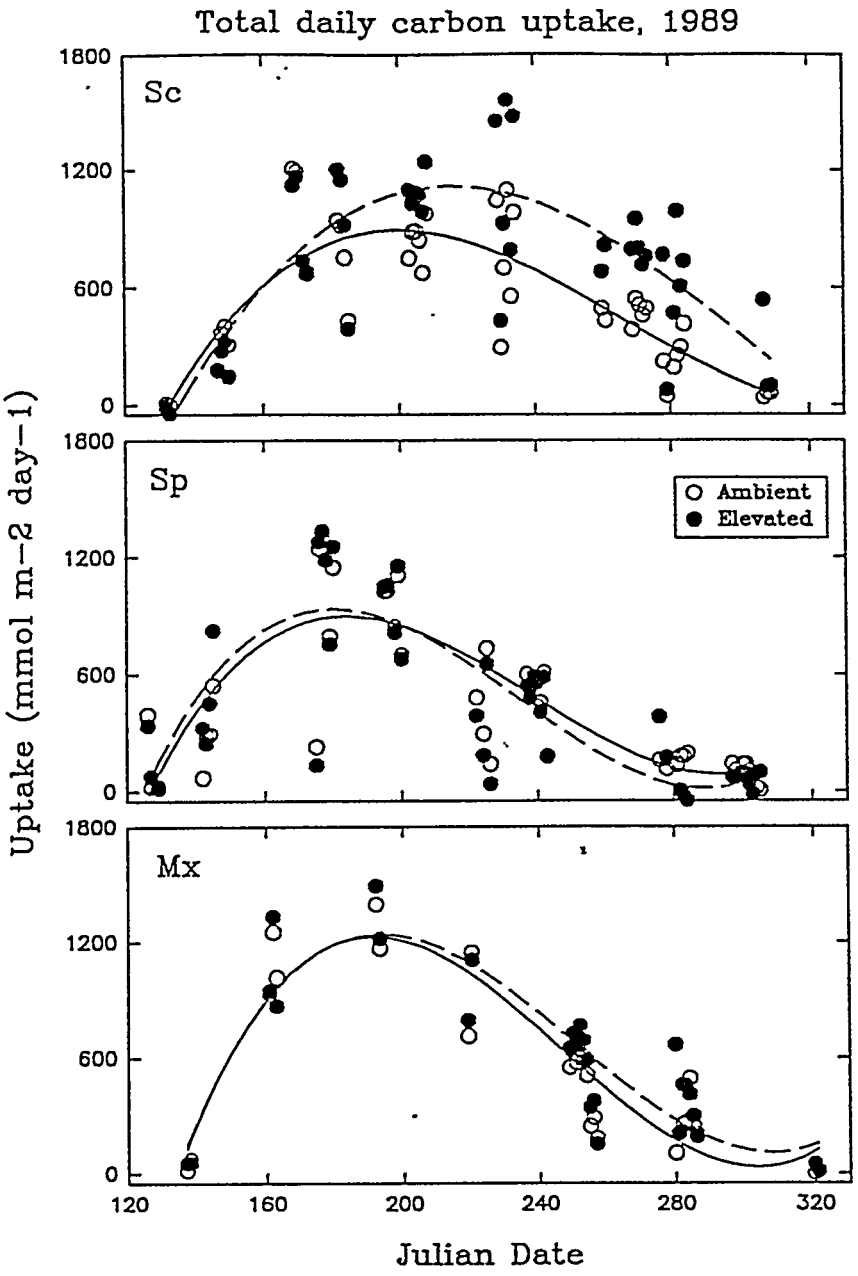

Figure 6.1

Mean total daily carbon uptake in the Scirpus, Spartina and Mixed communities, 1989. Mean total daily carbon uptake of all five chambers in each treatment is plotted for all days with data. Open circles are ambient chambers while closed circles are elevated treatment. A third order polynomial was fit to the data as shown. Solid line is the regression for ambient treatment and broken line is the regression for the elevated treatment.

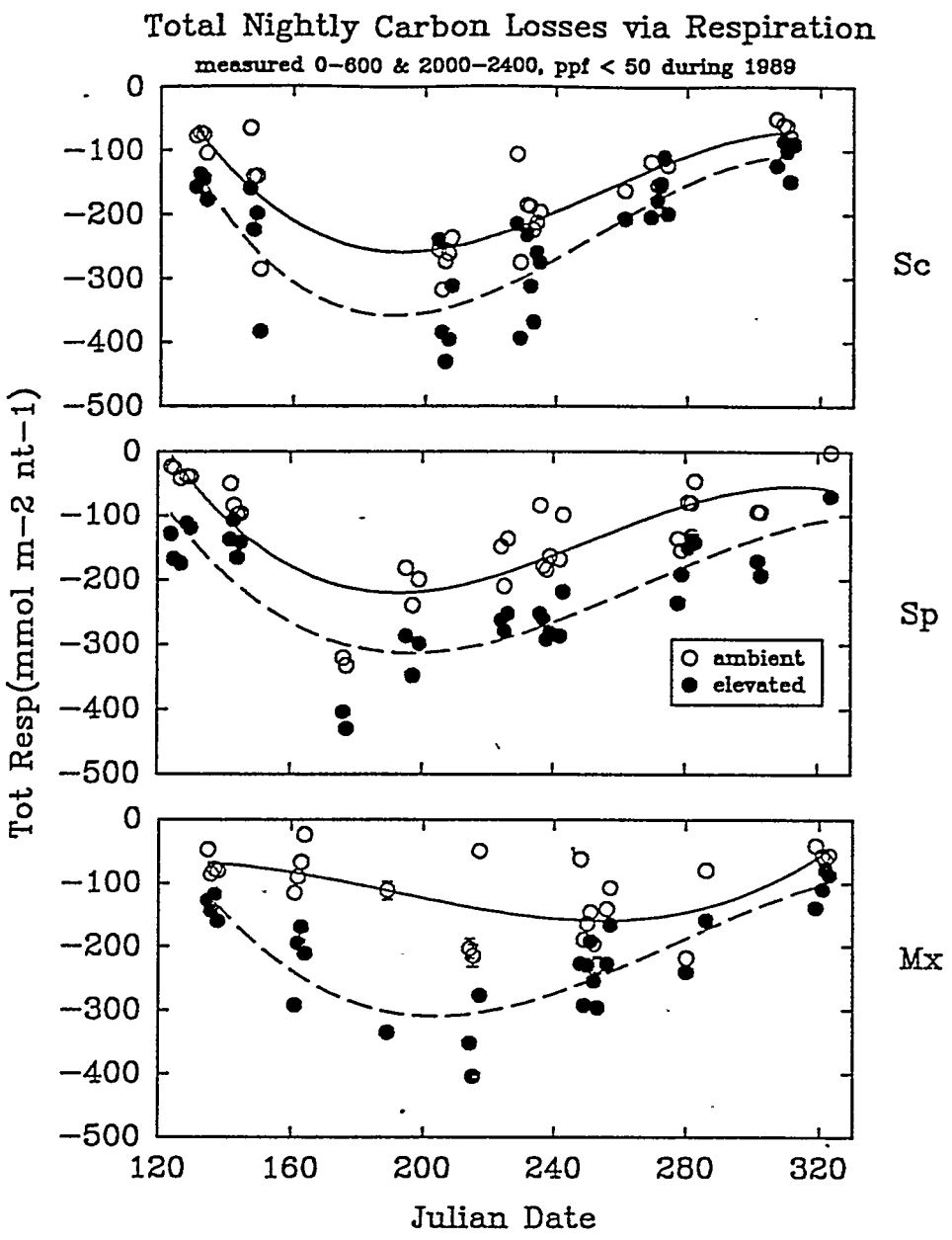

Figure 6.2

Mean total daily carbon loss in the Scirpus, Spartina and Mixed communities, 1989. The mean total daily carbon loss for each treatment was calculated as the sum of all gas exchange measurements during the period 0000 - 0600 hrs and 2000 - 2400 hrs. These data were plotted against the day of the year and a third order polynomial curve was fit to the data for each treatment of each community.

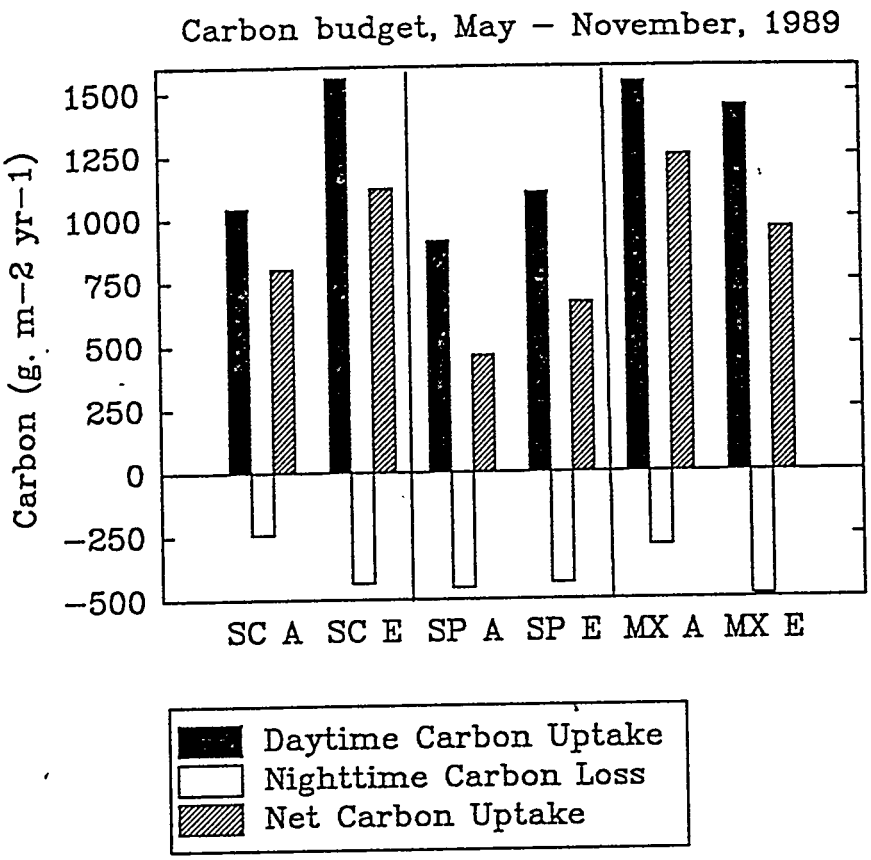

Figure 6.3

Carbon budget for Scirpus, Spartina and Mixed community, 1989. Using the mean total daily carbon uptake and loss regressions calculated above, estimated total uptake and carbon loss were calculated for each day of the growing season. The carbon budget expressed above consists of the sum of each days estimated uptake and loss and the difference of these two sums, the net seasonal carbon uptake.

Chapter 7. Ecosystem water balance.

W.J. Arp, W.T. Pockman, and P. Utley

Differential water vapor measurements are made at the same time as CO2 exchange measurements using two dew point hygrometers (Bingham 5E). Reliable evapotranspiration data can usually only be obtained between 1000 and 1800 hrs while the relative humidity is low enough to eliminate condensation in the gas lines.

Results

Figure 7.1 - 7.3 shows sample data from each community on one day of the 1989 season. In each community evapotranspiration was decreased and water use efficiency was increased in the chambers exposed to elevated CO_2. Figure 7.4 shows the mean rate of evapotranspiration in the elevated and ambient treatments of each community during the entire field season. While the Spartina and Mixed community show only a limited photosynthetic response to elevated CO2 (see Chap. 5), all three communities, as in previous years, show a 20 - 40% decrease in evapotranspiration. Similarly, Figure 7.5 shows the mean water use efficiency of elevated and ambient treatments in each community over the course of the season. The Scirpus and Spartina communities showed a 60-70% increase in water use efficiency throughout the season while WUE was as large but more variable in the Mixed community. Figure 7.6 shows the soil salinity data measured at 15, 30, 50, and 100 cm. over the course of the season in the three communities. The salinity profiles, while variable, were the same among treatments. Salinity was highest at the 30 and 50 cm. points and lower at the extremes. While salinity might be expected to be lower in the elevated chambers due to reduced water use, the chamber size in this work may be too small for differences to develop inside the chamber. Figures 7.7 and 7.8 shows the midday and pre-dawn tissue water potential data over the course of the season. Because tissue water potential is influenced by a number of environmental parameters (i.e. temperature, precipitation, etc.), these data are somewhat difficult to interpret. While water potentials in all three treatments are sometimes indistinguishable, more often the elevated and control treatments exhibited the same

tissue water potentials while the ambient treatment was more negative. These data suggest that the introduction of the chamber stresses the plants (by elevating the ambient temperature) and the addition of CO_2 relieves that stress. While this pattern is not uniform, it was observed in both pre-dawn and midday measurements in the Scirpus and Spartina communities.

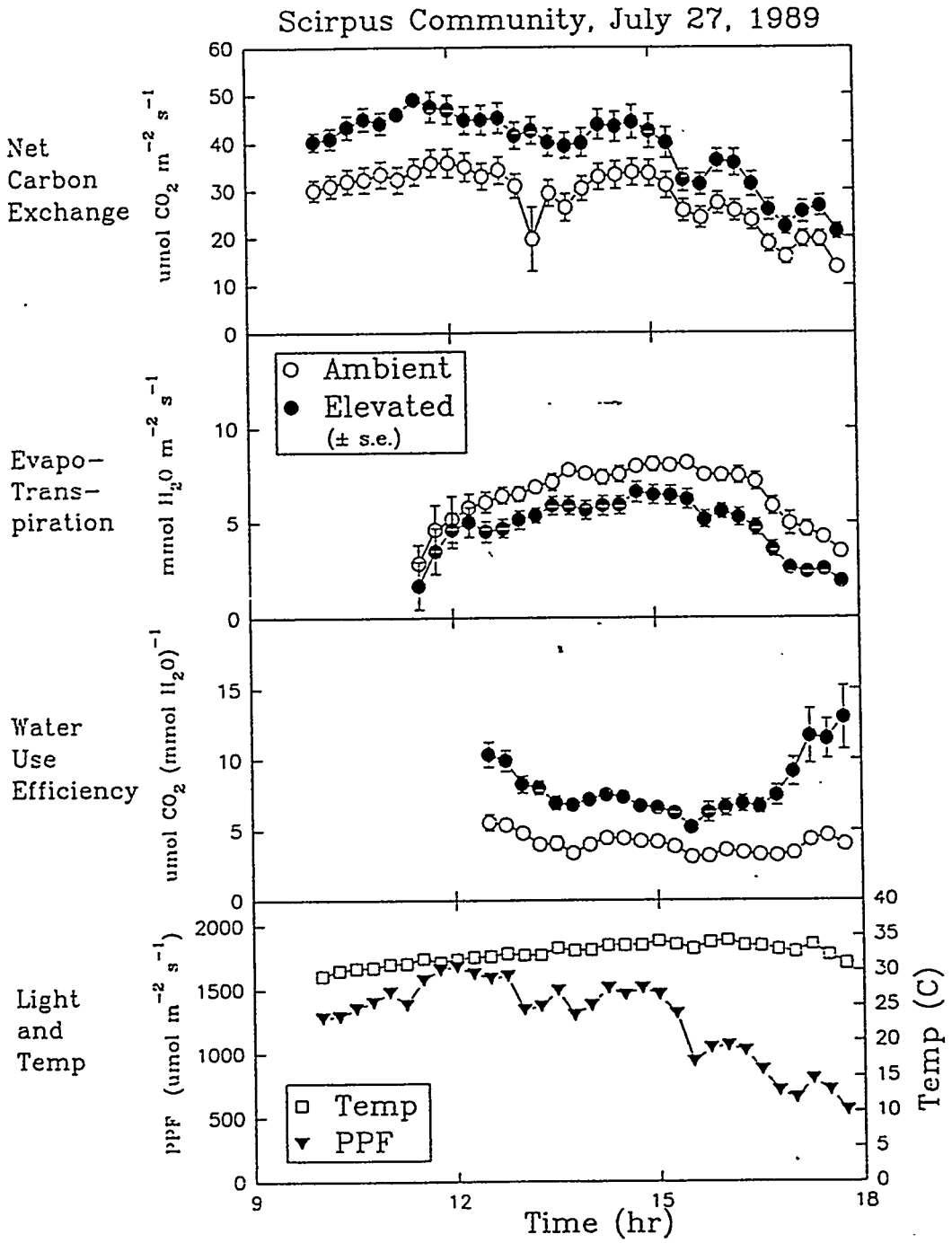

Figure 7.1

Sample daily evapo-transpiration measurements in the Scirpus community, 1989. Net carbon exchange (NCE), evapo-transpiration (ET), water use efficiency (WUE), and light and temperature conditions are shown for the Scirpus community between 1000 and 1800 hrs. on July 27, 1989. Data for NCE, ET, and WUE are the mean of five chambers and standard error.

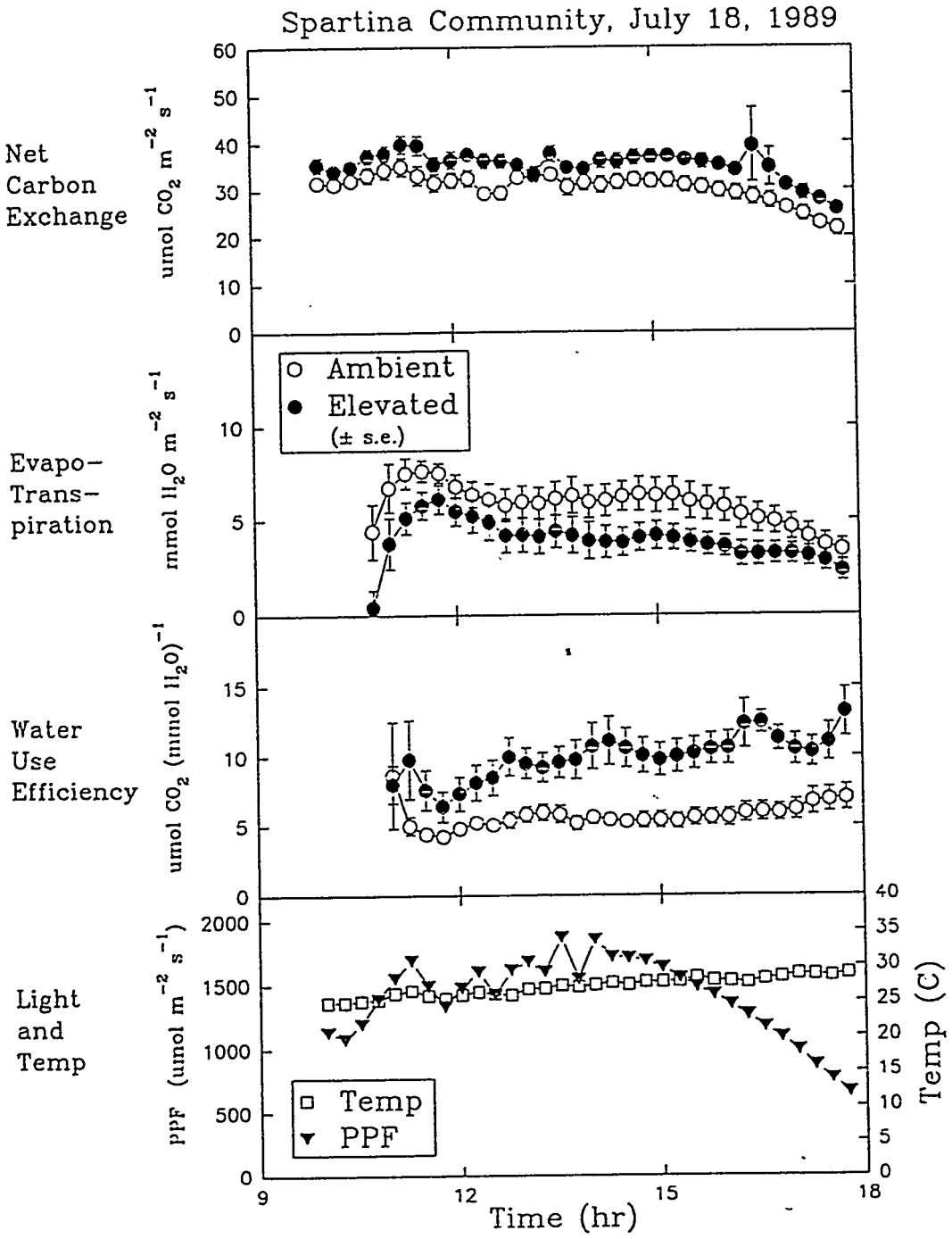

Figure 7.2

Sample daily evapo-transpiration measurements in the Spartina community, 1989. Net carbon exchange (NCE), evapo-transpiration (ET), water use efficiency (WUE), and light and temperature conditions are shown for the Spartina community between 1000 and 1800 hrs. on July 18, 1989. Data for NCE, ET, and WUE are the mean of five chambers and standard error.

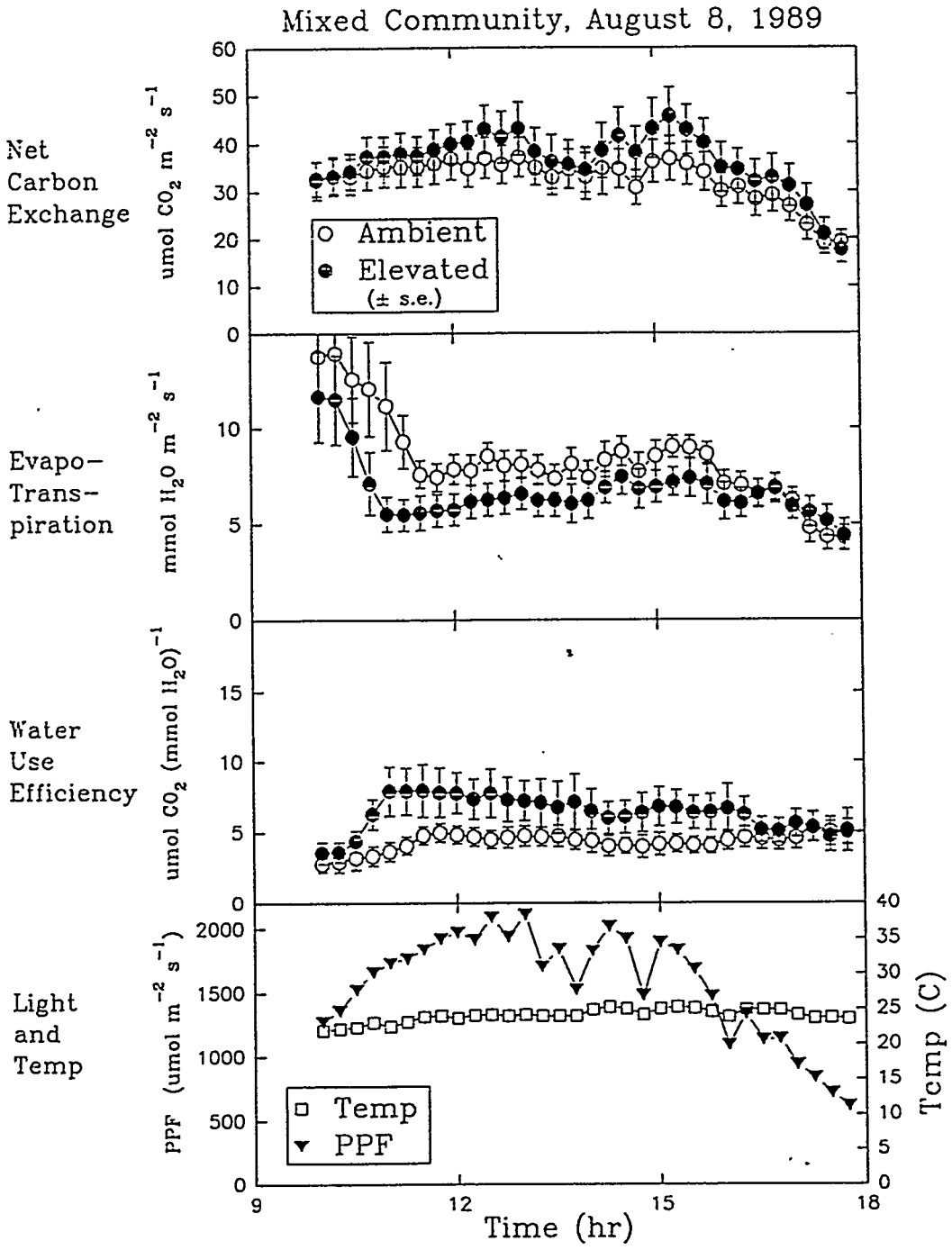

Figure 7.3

Sample daily evapo-transpiration measurements in the Mixed community, 1989. Net carbon exchange (NCE), evapo-transpiration (ET), water use efficiency (WUE), and light and temperature conditions are shown for the Mixed community between 1000 and 1800 hrs. on August 8, 1989. Data for NCE, ET, and WUE are the mean of five chambers and standard error.

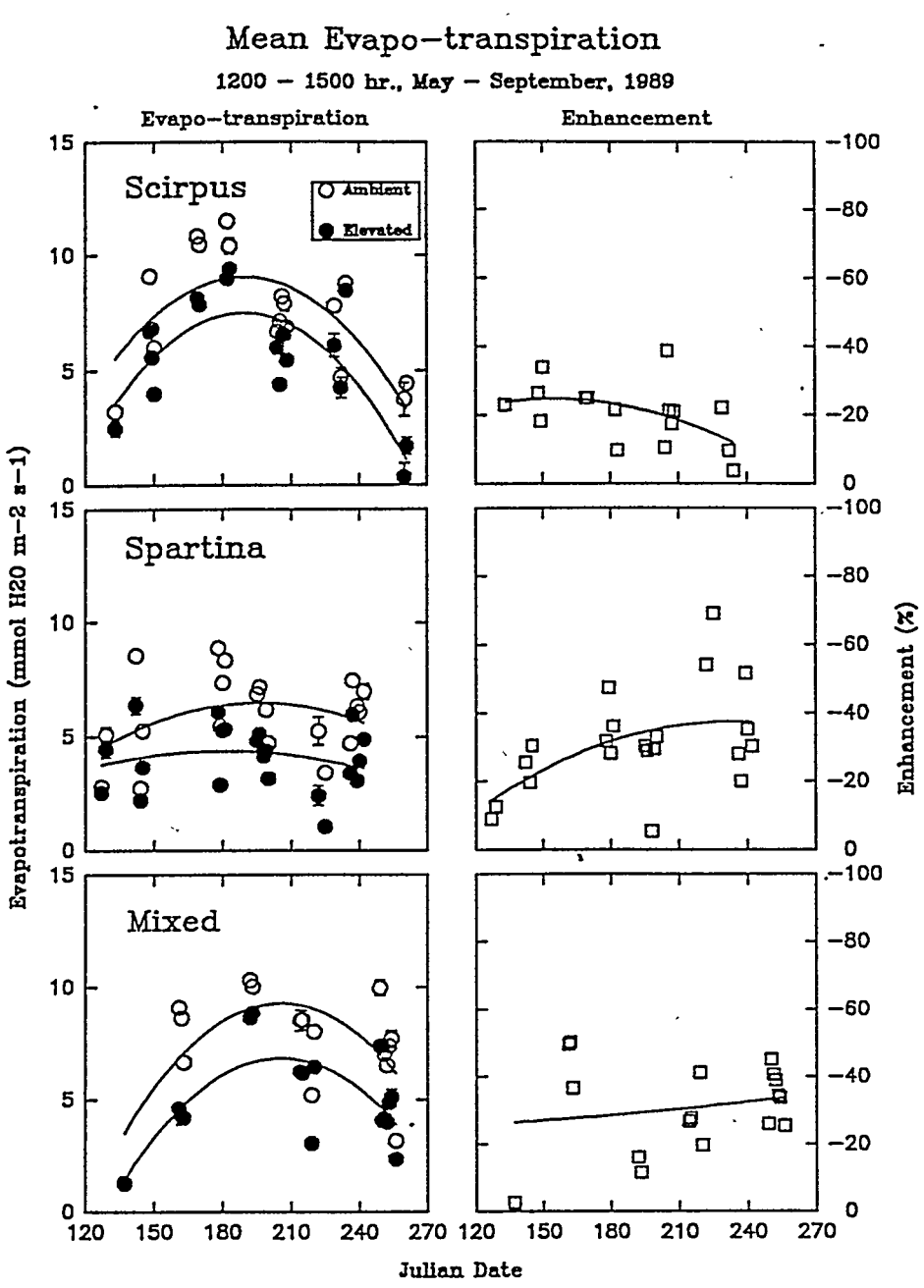

Figure 7.4

Mean evapo-transpiration and enhancement of the Scirpus, Spartina and Mixed community by treatment, 1989. Mean evapo-transpiration is shown for the ambient and elevated treatments of each community during the period 1200 - 1500 hrs.

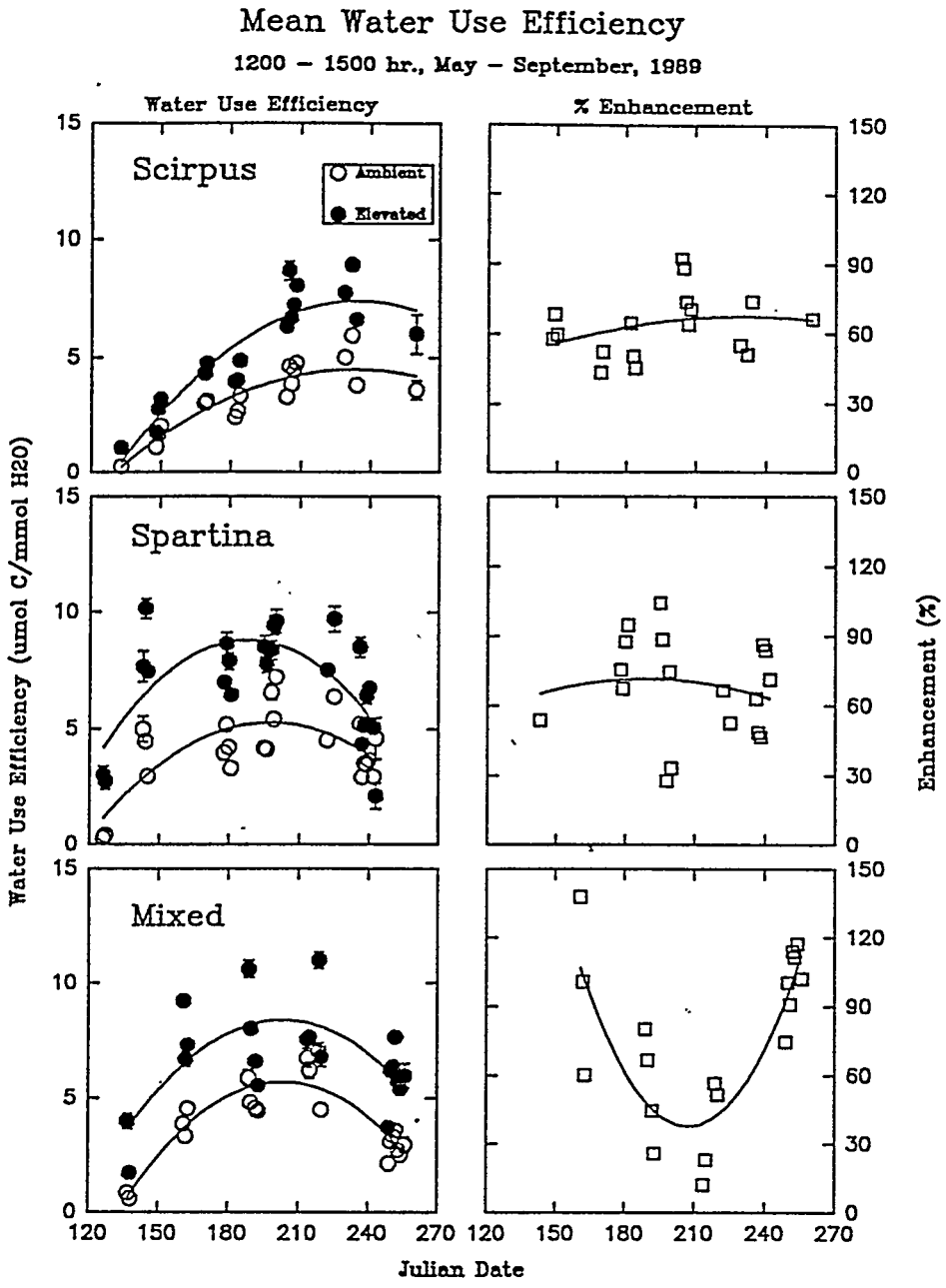

Figure 7.5

Mean water use efficiency and enhancement in the Scirpus, Spartina and Mixed communities by treatment. The mean water use efficiency and its enhancement (E-A/A) were calculated during the period 1200 - 1500 hrs.

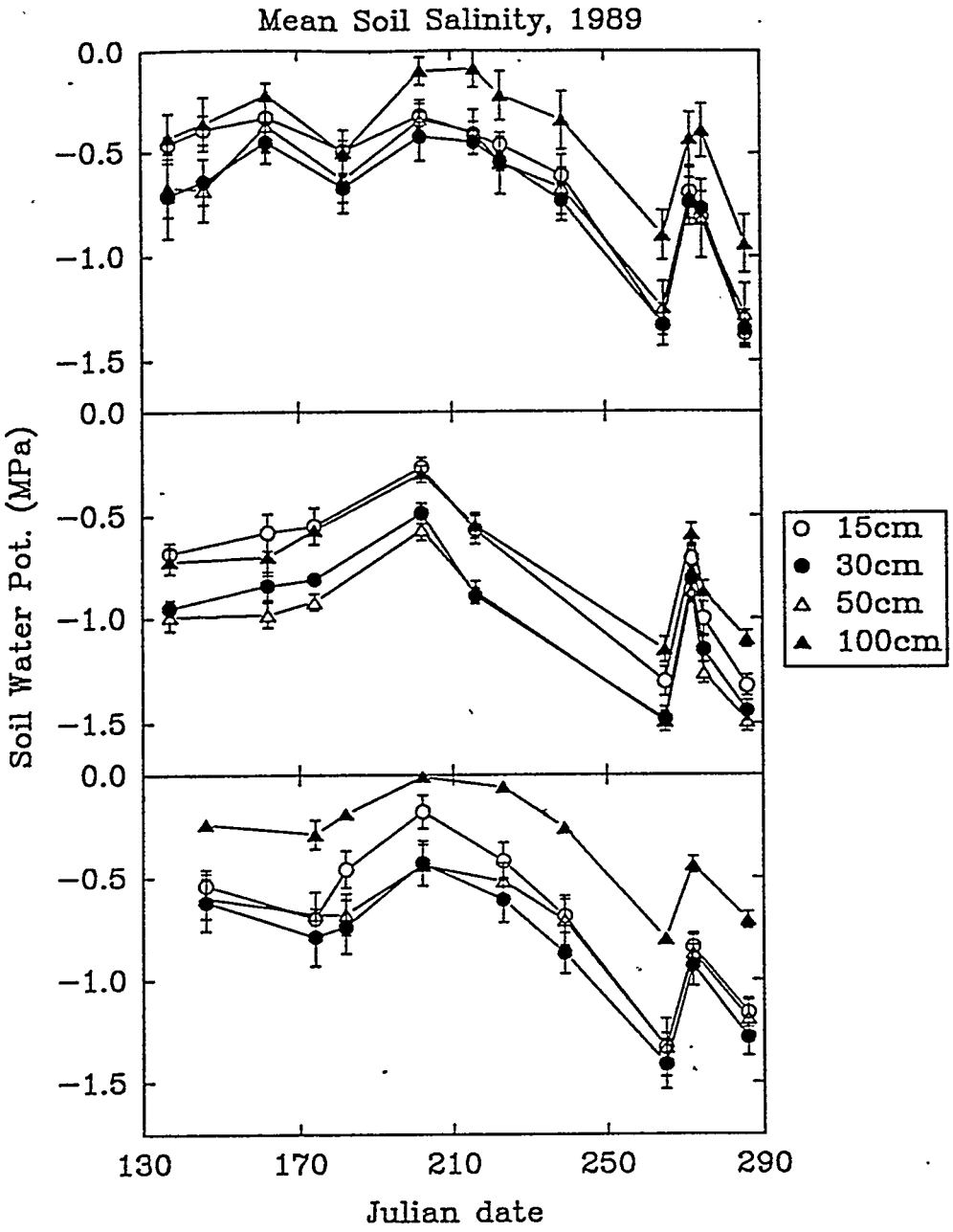

Figure 7.6

Mean soil salinity by depth and community, 1989. Data from periodic measurements of soil salinity are shown by the depth of the sample (15, 30, 50, 100 cm.) and by community.

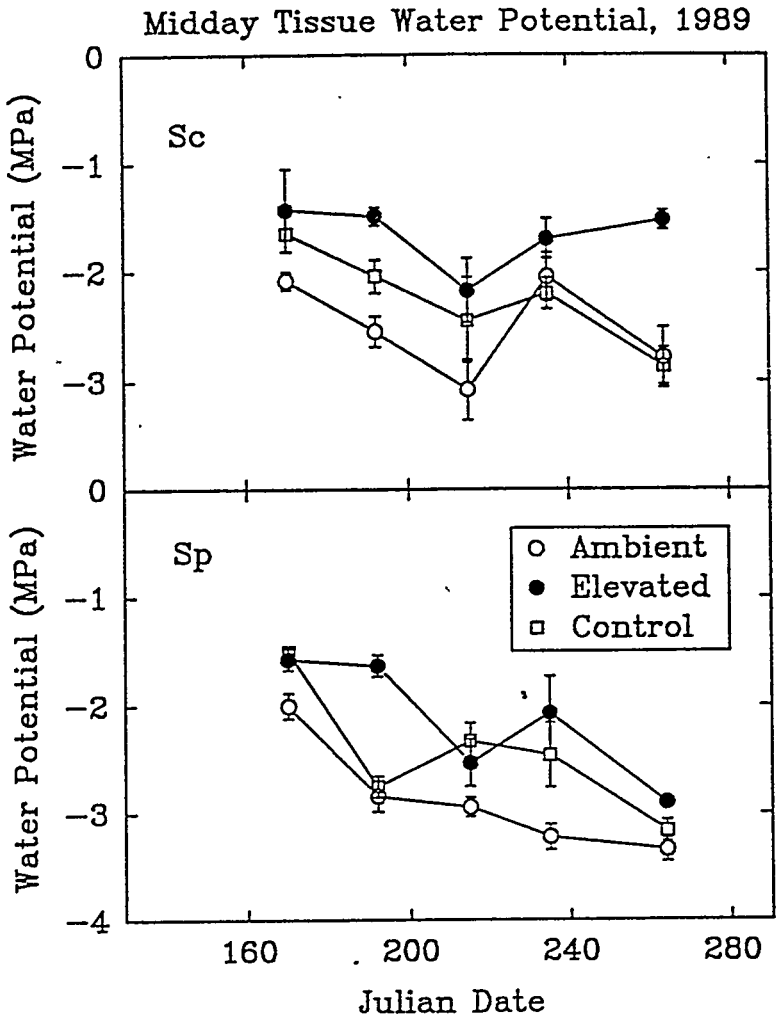

Figure 7.7

Mean midday tissue water potential by community and treatment. Midday (1200 - 1400 hrs.) tissue water potentials measured in the Scirpus and Spartina communities are shown as means by community and treatment.

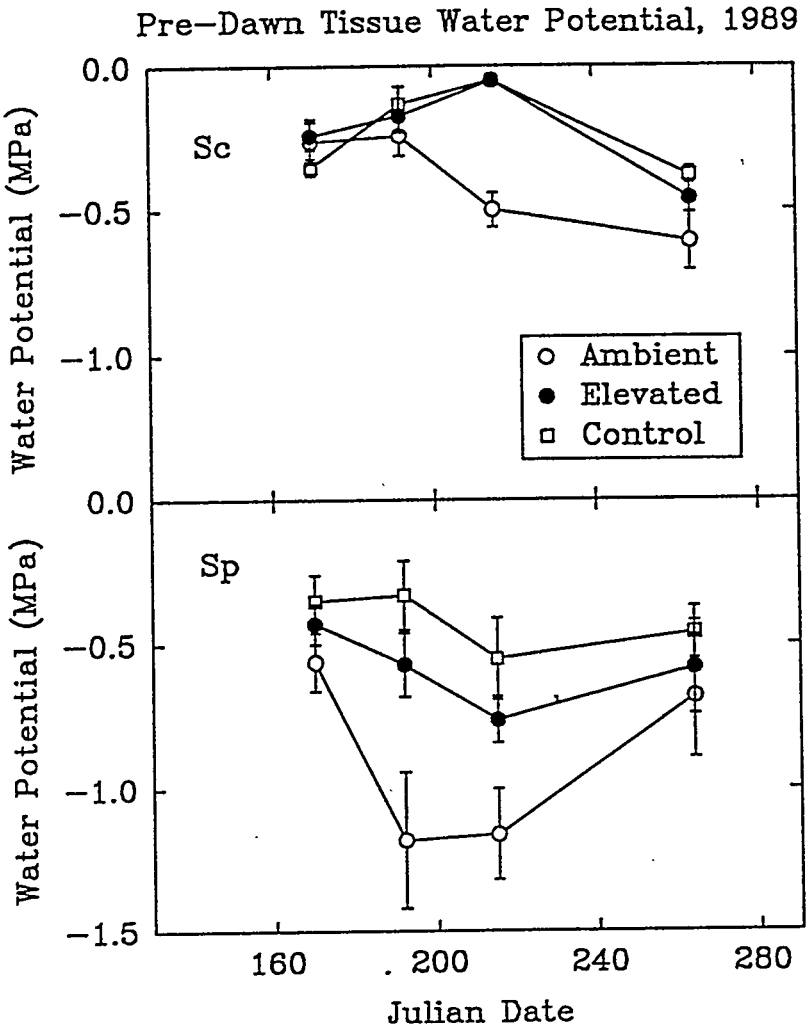

Figure 7.8

Mean pre-dawn tissue water potential by community and treatment, 1989. Pre-dawn (0300 - 0530) tissue water potentials measured in the Scirpus and Spartina communities are shown as means by community and treatment.

Chapter 8. Three Year Comparisons, 1987-1989.

W.T. Pockman.

In this chapter we present comparisons of several key processes that are effected by exposure to elevated CO2. Figure 8.1 shows green dry weight in each treatment of the Scirpus community for each of the last three years. Figure 8.2 shows a comparison of ecosystem assimilation in the Scirpus and Spartina communities during the last three years. Figures 8.3 - 8.5 show a comparison of mean tissue nitrogen content by weight for Scirpus and Spartina, in both pure stands and in the Mixed community and for Distichlis in the Mixed community. Finally, Figures 8.6 and 8.7 show carbon budgets, prepared as in chapter 6, for the Scirpus and spartina communities during the period 1987-1989.

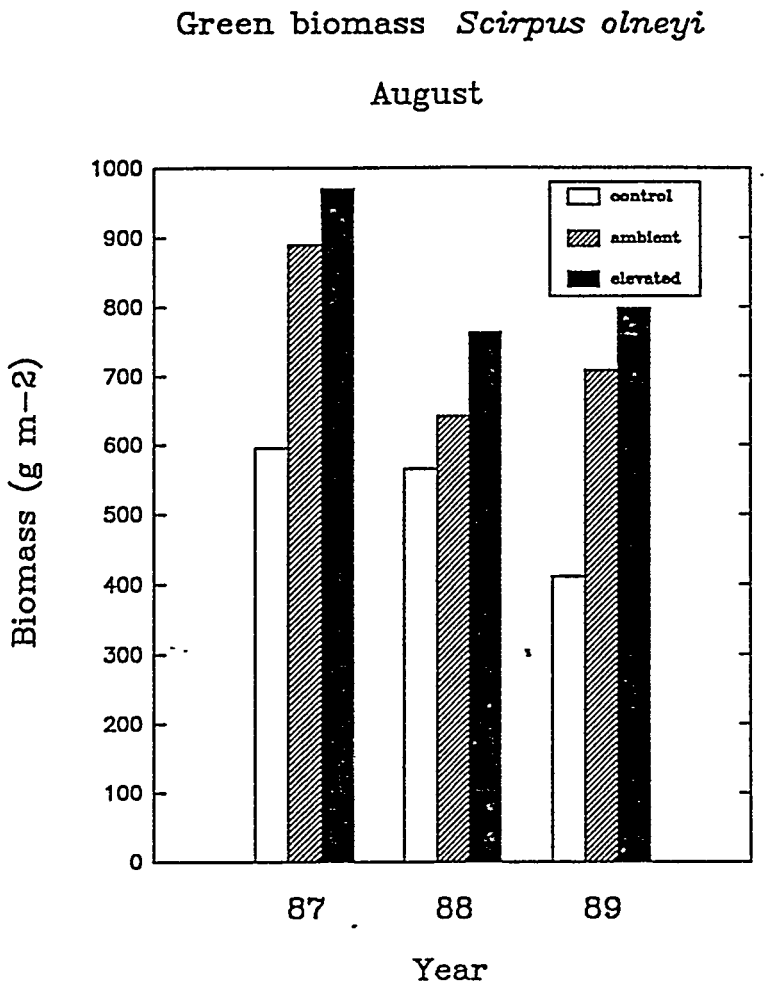

Figure 9.1

Scirpus biomass (green dry weight) by treatment for 1987-1989. At each site in the Scirpus community, each stem was counted and it width at 20cm, green length and total length determined. Every twentieth stem was harvested and used to calculate regressions of total length to total dry weight and senescent length to senescent dry weight. Green dry weight, as shown above, was calculated as the sum of the difference between the estimated total dry weight and the estimated senescent dry weight of each stem in each chamber. The sum of the five chambers in each treatment are shown above for field seasons 1987-1989.

Figure 9.2

Ecosystem assimilation in the Scirpus and Spartina communities, 1987-1989. Total daily carbon uptake by treatment calculated as the sum of all gas exchange measurements during each twenty four hour period when PPF exceeds 50 umol m-2 s-1. Measurements of gas exchange were made periodically from May through Novemeber of each year.

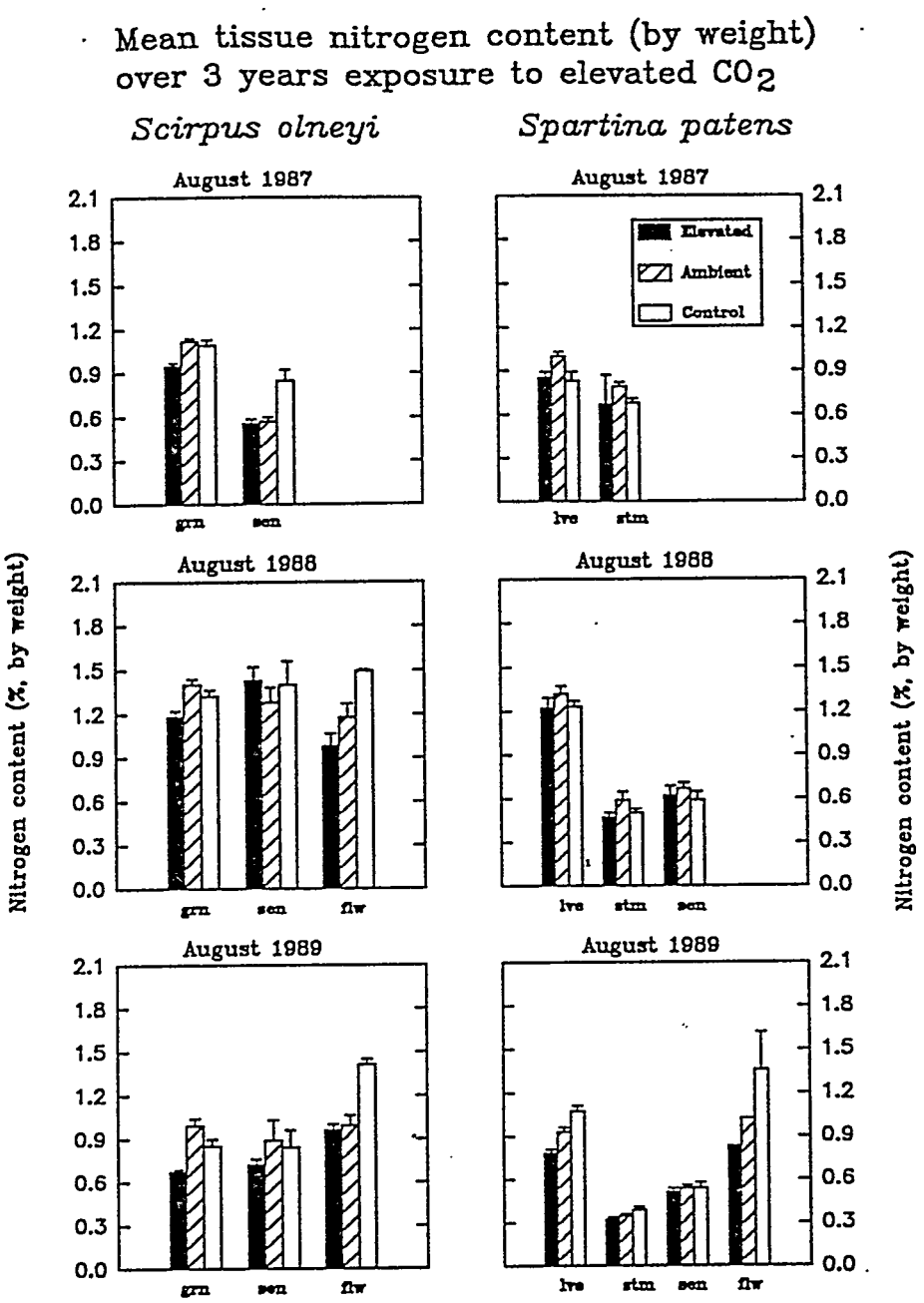

Figure 9.3

Mean tissue nitrogen content of Scirpus and Spartina in pure stands over 3 years exposure to elevated CO_2. Data are expressed as a percentage by weight for Scirpus olneyi grown in the Scirpus community and Spartina patens grown in the Spartina community. Scirpus data are shown for green (grn), senescent (sen) and reproductive structures (flw) while Spartina data are shown for leaves (lve), stems (stm), senescent (sen) and reproductive tissue (flw). All data are from analyses of dried tissue collected during the August/September harvest in 1987-1989.

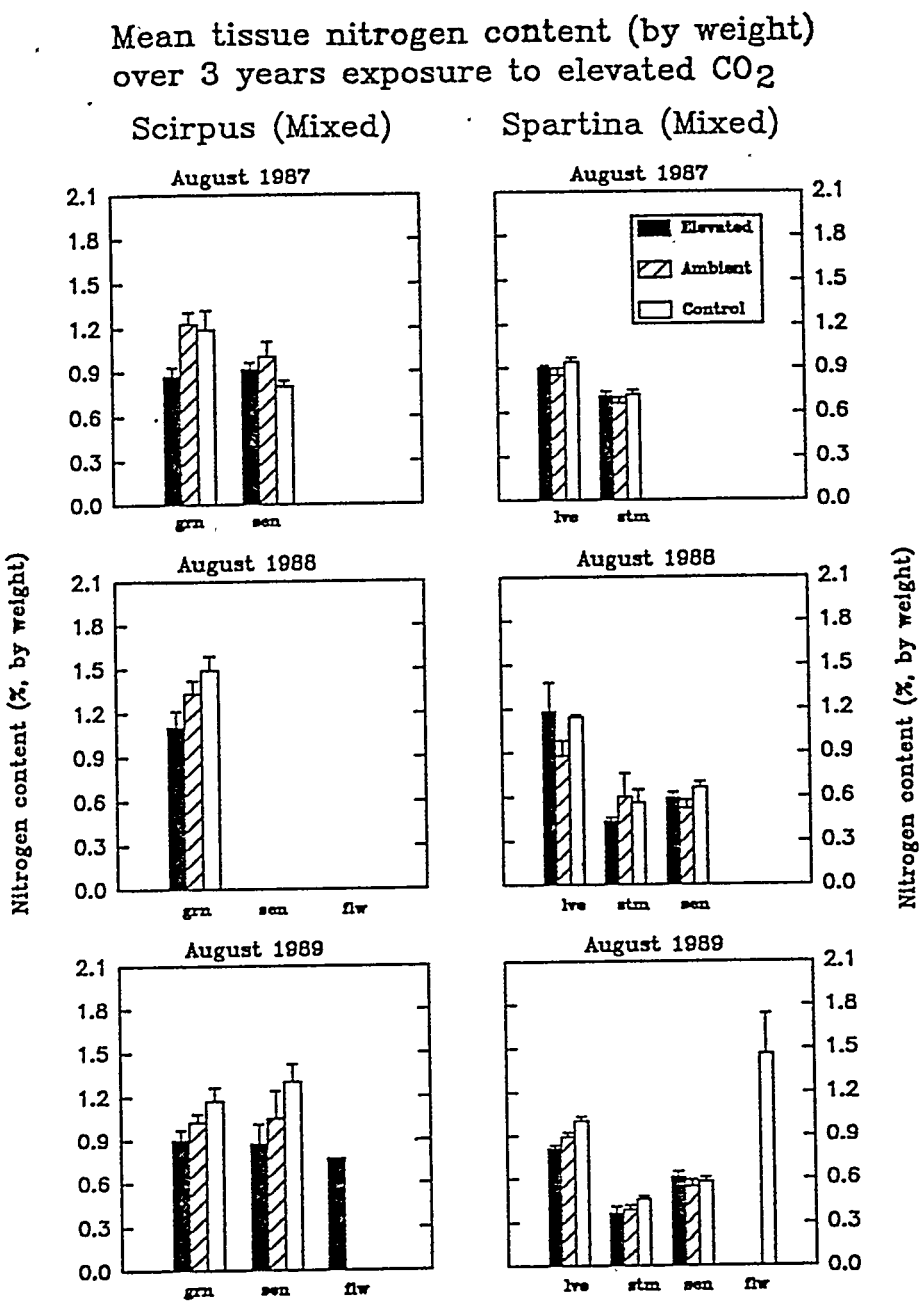

Figure 9.4

Mean tissue nitrogen content of Scirpus and Spartina in the Mixed community over 3 years exposure to elevated CO_2. Data are expressed as a percentage by weight for Scirpus olneyi and Spartina patens grown in the Mixed community. Scirpus data are shown for green (grn), senescent (sen) and reproductive structures (flw) while Spartina data are shown for leaves (lve), stems (stm), senescent (sen) and reproductive tissue (flw). All data are from analyses of dried tissue collected during the August/September harvest in 1987-1989.

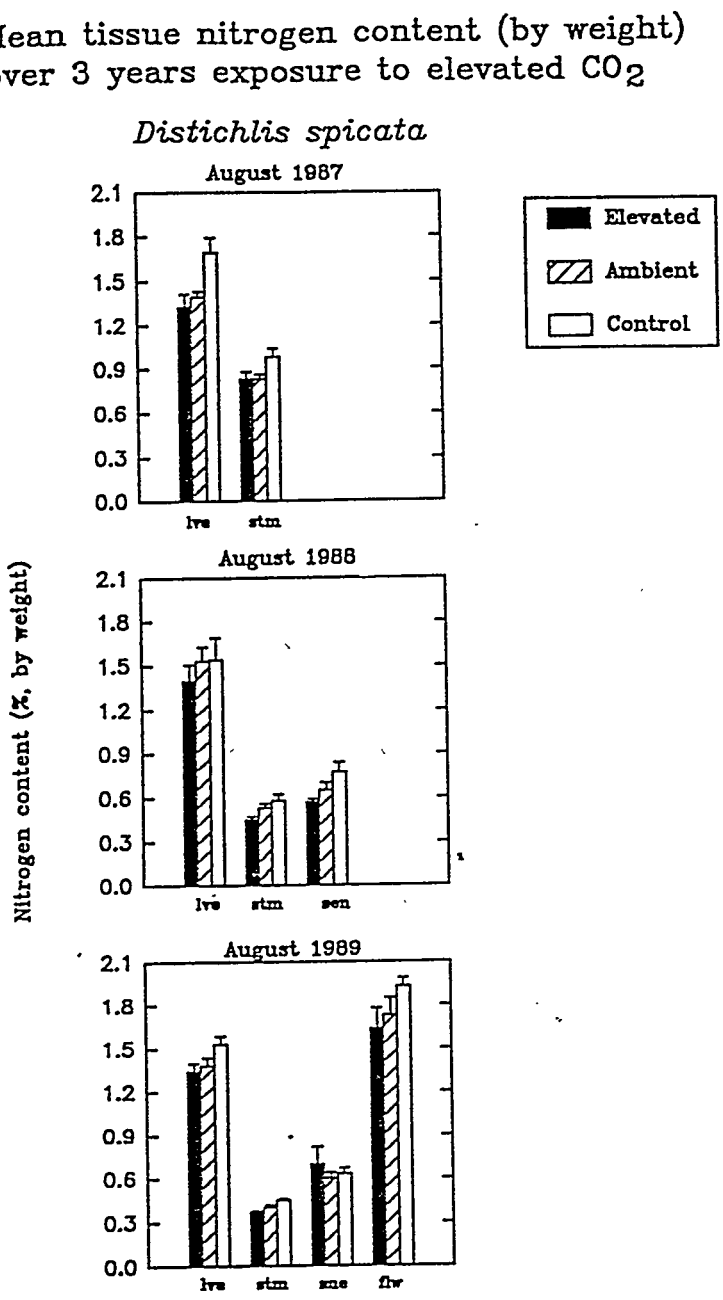

Figure 9.5

Mean tissue nitrogen content of Distichlis in the Mixed community over 3 years exposure to elevated CO_2. Data are expressed as a percentage by weight for Distichlis spicata grown in the Mixed community. Data are shown for leaves (lve), stems (stm), senescent (sen) and reproductive tissue (flw). All data are from analyses of dried tissue collected during the August/September harvest in 1987-1989.

Figure 9.6

Estimated annual carbon budgets for Scirpus in the Scirpus community, 1987-1989. Third order regressions were fit to data for total daily carbon uptake and total daily respiration of the elevated and ambient treatments of the Scirpus community. In most cases the R^2 of each regression was 0.8 or greater (see Table 9.x). The resulting equations were used to estimate carbon uptake and carbon loss for each day in the growing season. The sums of these estimates were used to calculate an approximate seasonal net carbon gain for each treatment for all three years.

Figure 9.7

Estimated annual carbon budgets for Spartina in the Spartina community, 1987-1989. Third order regressions were fit to data for total daily carbon uptake and total daily respiration of the elevated and ambient treatments of the Spartina community. In most cases the R^2 of each regression was 0.8 or greater (see Table 9.x). The resulting equations were used to estimate carbon uptake and carbon loss for each day in the growing season. The sums of these estimates were used to calculate an approximate seasonal net carbon gain for each treatment for all three years.

Chapter 9. Environmental Parameters.

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This chapter contains information about the conditions in the chambers and the surrounding environment. Figure 9.1 shows the mean temperatures in the soil and 3 m above the marsh over the course of the entire year. Figure 9.2 shows a comparison of temperatures in the different treatments of each community. With the exception of the mixed community during the daytime period, the temperatures in the elevated and ambient chambers were indistinguishable. The temperature difference between the chambered and control sites ranged from almost zero to 4.5 C. Table 9.1 and Figure 9.3 show the mean seasonal and mean daily absolute CO2 concentrations for each community and the ambient air.

Absolute CO2 Treatment, 1989					
Scirpus Chamber	Mean Seasonal [CO2]	Spartina Chamber	Mean Seasonal [CO2]	Mixed Chamber	Mean Seasonal [CO2]
SC 1E	683.3	SP 1E	685.6	MI 1E	687.4
SC 6E	685.8	SP 4E	684.1	MI 4E	684.7
SC 9E	682.6	SP 8E	687.5	MI 8E	686.5
SC 10E	681.0	SP 10E	686.6	MI 11E	687.8
SC 14E	678.6	SP 14E	691.4	MI 13E	687.1
Comm. Mean	682.8	Comm. Mean	687.1	Comm. Mean	686.5

Table 9.1 Mean seasonal CO_2 concentration for each elevated chamber and all the chambers in each community. Mean ambient concentrations over the season were 351 ppm (s.e. = 1.29).

Figure 9.5 shows the total daily rainfall recorded at the main laboratory of the Smithsonian Environmental Research Center several miles from the field site. Figure 9.4 shows the maximum and total photon flux recorded at the field site over the course of the entire year.

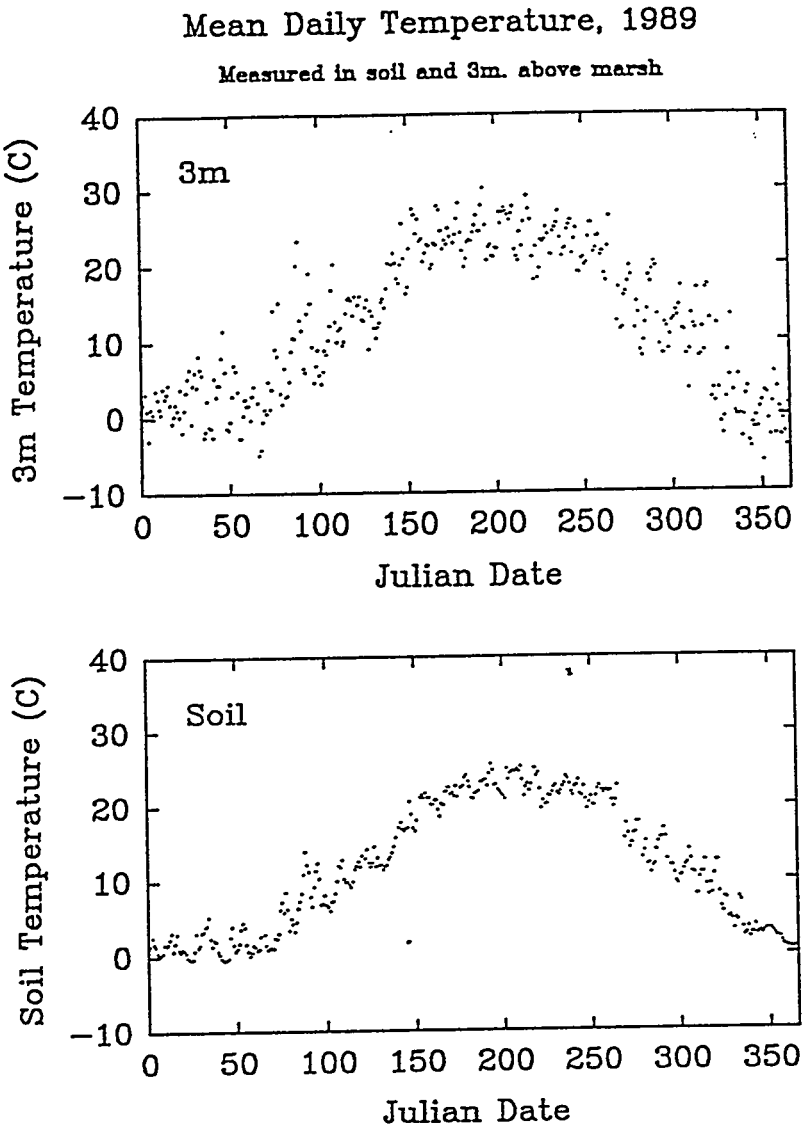

Figure 9.1

Mean temperatures in the soil and three meters above the marsh surface. (3m) Mean temperature over every twenty four hour period during 1989. (Soil) The mean soil temperature over every twenty four hour period during 1989.

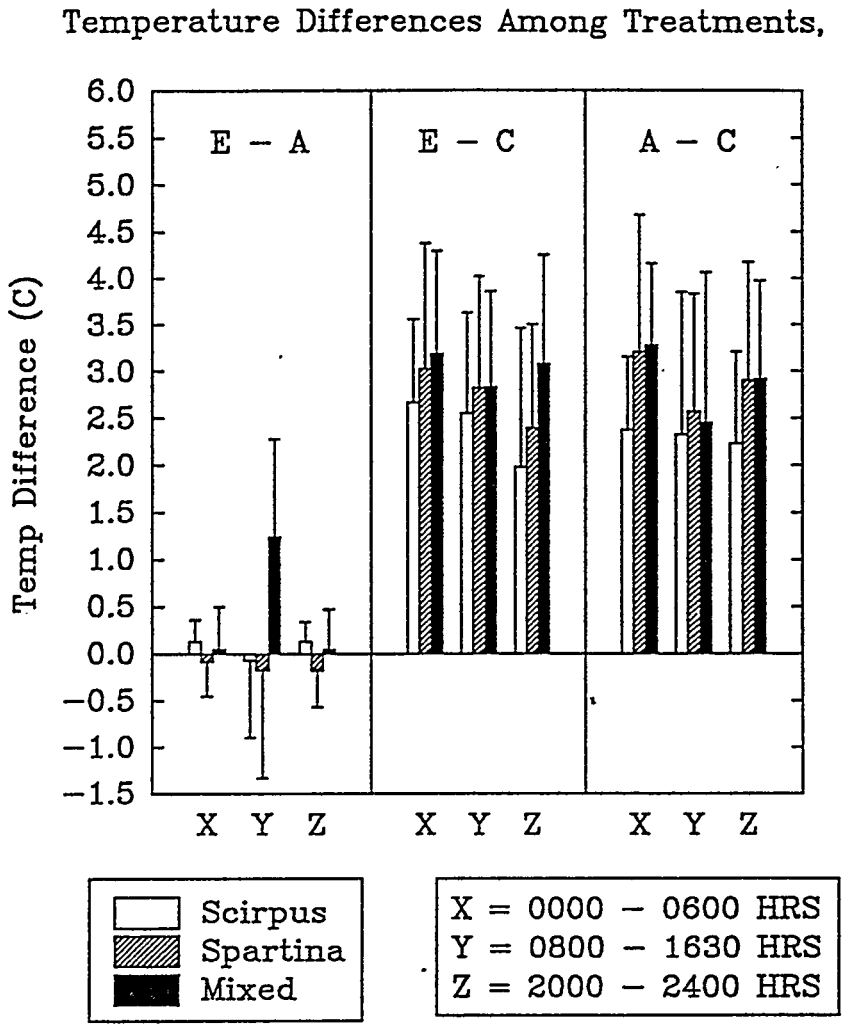

Figure 9.2

Temperature differences among treatments in the Scirpus, Spartina and Mixed communities, 1989. Temperature differences among the three treatments were calculated for the morning, daytime and night periods. Differences are shown above by time of day, treatment comparison and community. Among the chambered sites only the Mixed ambient showed any trend away from no difference. The chambered sites were clearly warmer than the control sites during all the time periods.

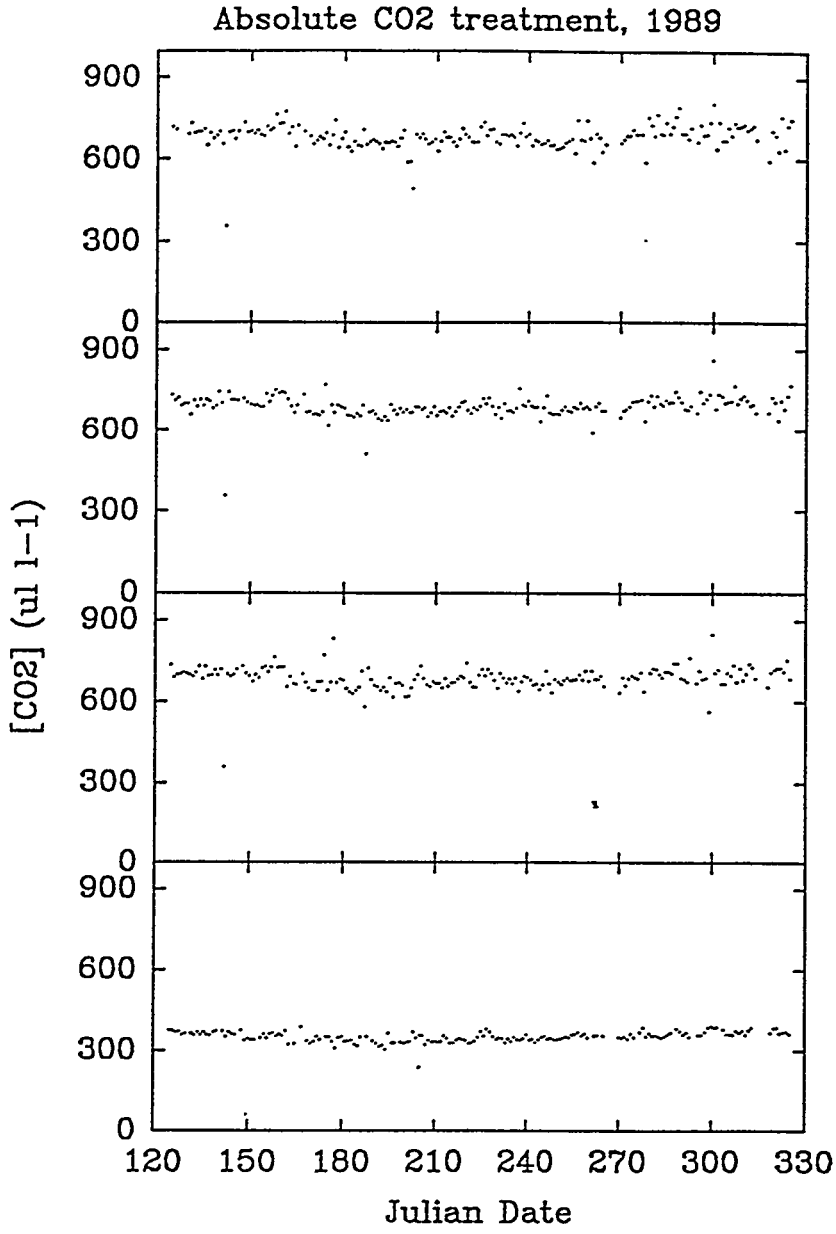

Figure 9.3

Mean daytime absolute CO_2 concentrations in the elevated treatment of each community and in the ambient air. The mean absolute CO_2 concentration for each treatment (elevated and ambient) was calculated by using all available data from all five chambers in the treatment. The mean ambient concentration was calculated using data from all three communities. In each case the mean concentration was calculated during the period 0800 - 1600.

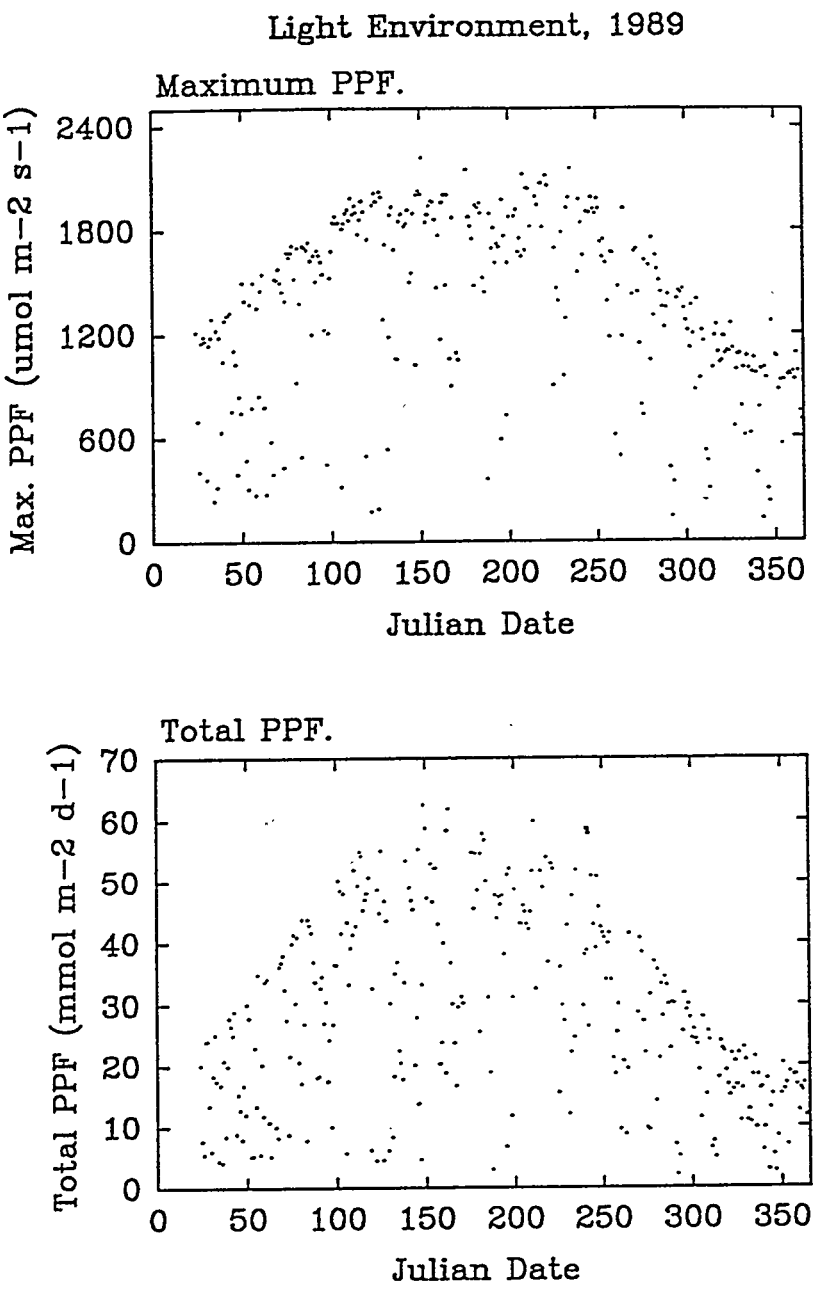

Figure 9.4

Maximum and total photon flux, 1989. The maximum (A) and total (B) photon flux were recorded at a site central to all three communities using two Eppley pyranometers.

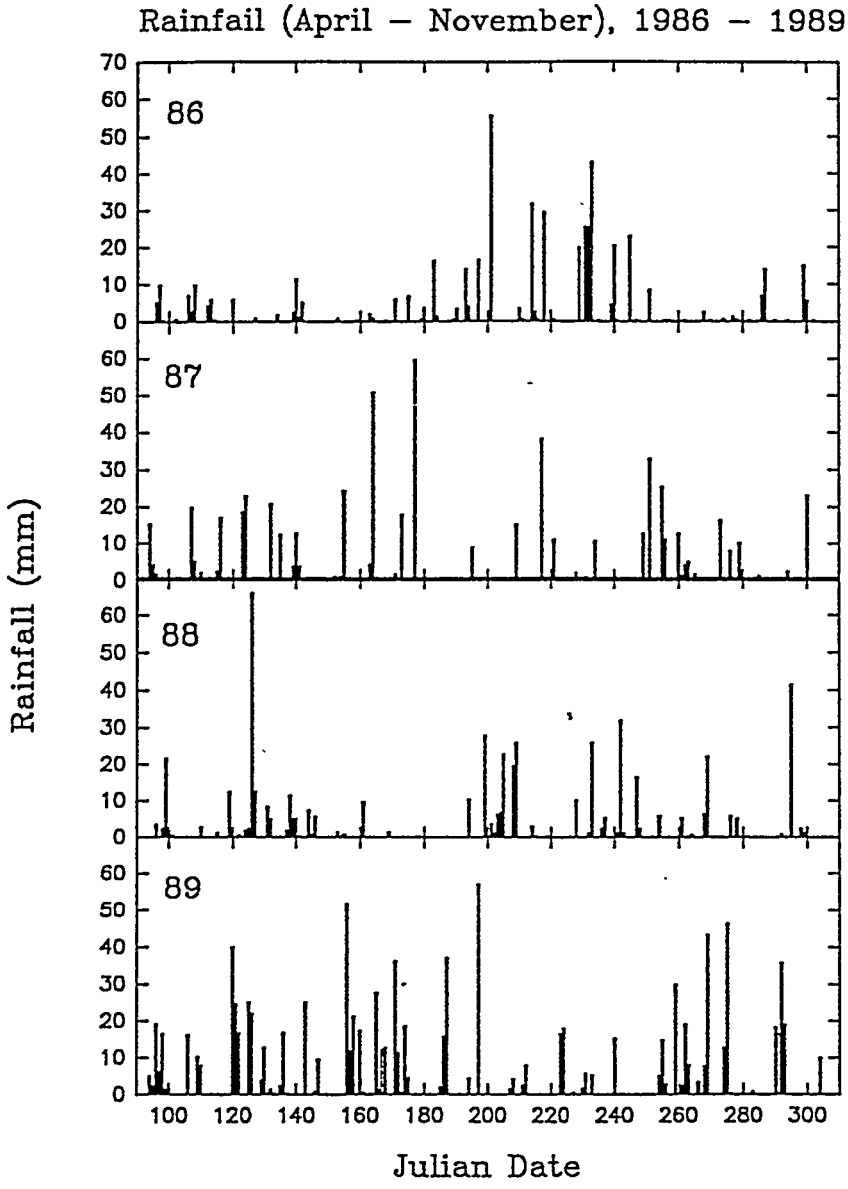

Figure 9.5

Total rainfall, April - November, 1986-1989. Rainfall was measured at the Smithsonian Environmental Reasearch Center main laboratory some four miles from the field site.