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Progress Report of Research: EFFECTS OF ELEVATED CO<sub>2</sub> ON  
CHESAPEAKE BAY WETLANDS.  
II. Gas Exchange and  
Microenvironment in  
Open Top Chambers.

Submitted By: Dr. Bert G. Drake

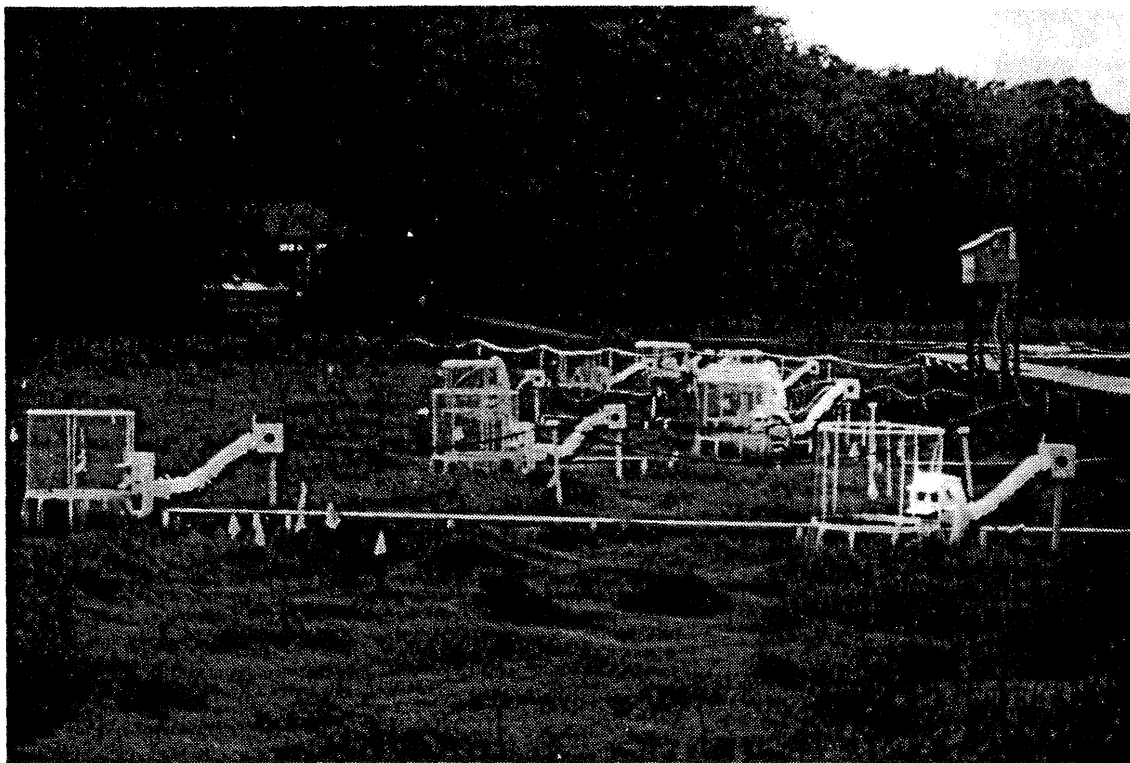
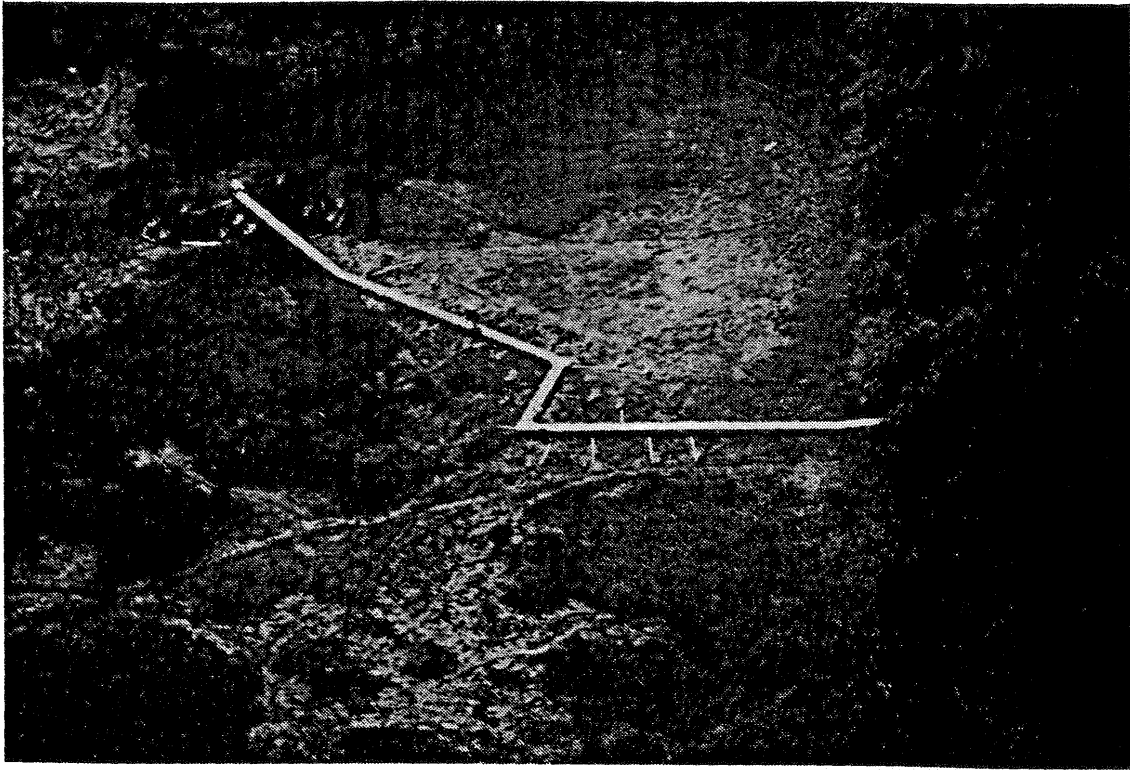
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View of the study site from the North. Kirkpatrick marsh is in the foreground and Chesapeake Bay is on the horizon.



Upper; walkway and plant communities.

Lower; chambers, walkway, and lab.

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## Executive Summary

The 1986 growing season was devoted to constructing and testing a system for producing test atmospheres of elevated CO<sub>2</sub> concentration in salt marsh vegetation. The species composition of these communities is ideal for testing the effects of elevated CO<sub>2</sub> on community structure: two are monospecific and the third contains the two species of the monocultures. The two major species differ in the capacity to respond to CO<sub>2</sub>: one is a C<sub>3</sub> sedge, Scirpus olneyii, and one is the C<sub>4</sub> grass, Spartina patens. Another C<sub>4</sub> grass Distichlis spicata, also occurs in the mixed community. Additional details of the site are given in a previous greenbook report, #034 Effects of Elevated Carbon Dioxide on Chesapeake Bay Wetlands. I. Description of the study site, July, 1986.

This report provides details of construction and performance of the four system components: exposure chambers, CO<sub>2</sub> dispensing, gas sampling and measuring circuit, and data acquisition and management. Special attention was given to the microenvironment within the chamber, particularly temperature. Highlights of the report are listed below.

1. Open top chambers, 1.2 m high by 0.8 m diameter, with a polyester film covering a framework of aluminum tubing, were set up in three plant communities. The chamber covering reduced solar radiation received by the plants within the chamber by about 10%. Ultra-violet radiation below 400 nm was reduced but the covering was neutral to all other radiation in the photosynthetically active part of the solar spectrum.

2. In order to optimize heat and gas exchange between the plant canopy and the air within the chamber, an air flow pattern was designed which incorporated a circulation loop. Air flow within the chamber is driven by two blowers: one introduces air from outside the chamber to the top of the plant canopy and the second draws air from the plenum around the base of the chamber and reintroduces it at the top of the plant canopy.

3. Air temperature within the open top chambers averaged 1.8 C higher than air temperature outside the chambers. The temperature increase was due mostly to heat added by the two blower motors, but differences between the microenvironment inside the chamber compared with the microenvironment of vegetation outside the chamber added complications to this generality. The major difference between the

microenvironment within the chamber and that in the vegetation outside the chamber was the absence of thermal stratification within the chamber. Stratification patterns are characteristic features of the boundary layer around vegetation during periods of low wind. These differences in temperature stratification patterns were responsible for both higher air temperatures within the chamber at night and lower temperatures within the chamber during the day compared to air temperatures at the top of the plant canopy outside the chamber. Closing the top to measure photosynthesis raised the air temperature within the chamber an additional 0.5 C.

4. Canopy temperatures inside the open top chambers measured by infra-red radiation thermometers were within  $\pm 1.0$  C of canopy temperatures outside the open top chamber during the day. At night, canopy temperatures inside the chamber were higher than canopy temperatures outside the chamber by as much as 3.5 C. In closed top chambers, canopy temperatures were always higher than canopy temperatures outside the chambers. This difference was approximately 1.5 C during the day and near 4.0 C at night.

5. CO<sub>2</sub> was added to air entering the chamber through a bank of manually operated flowmeters. Using this method, CO<sub>2</sub> concentration within the open top chamber could be maintained within  $\pm 10$  ppm of the target concentration which was taken to

be +260 ppm above normal/ambient for these tests.

6. Normal ambient CO<sub>2</sub> concentration was found to be stable near 340 ppm during the day, but at night it was variable, often reaching 500 ppm and occasionally 700 ppm.

7. Net ecosystem CO<sub>2</sub> exchange (NCE) tracked solar radiation. NCE was measured using a special top which reduced the ingress of air from outside the chamber. NCE was determined by measuring the drop in CO<sub>2</sub> concentration of air as it passed through the chamber and the air flow rate through the chamber, which was approximately 2100 l min<sup>-1</sup>.

8. Light response curves for NCE showed clear differentiation of the three community types during the end of the growing season when these tests were made. The Mixed community had the highest NCE and the Spartina community the lowest.

9. Elevated CO<sub>2</sub> concentration increased both maximum NCE and the initial slope of the light response curve in all communities. An unexpected result was that the relative increase in NCE was greatest in the C<sub>4</sub> community and least in the C<sub>3</sub> community. This result must be considered preliminary because the data were taken at the end of the growing season when the vegetation was senescent.

10. Elevated CO<sub>2</sub> also increased 24 hour ecosystem carbon



assimilation compared to ecosystem uptake in vegetation exposed to normal ambient CO<sub>2</sub> concentration.

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## INTRODUCTION

The increasing concentration of carbon dioxide in the earth's atmosphere has stimulated research into the likely consequence for global climate and the carbon cycle. The response of the world's vegetation to an increase in atmospheric  $\text{CO}_2$  is important to both climate and the carbon cycle. Recent work has indicated that due to deforestation, the world's vegetation should be considered a net source of carbon to the atmosphere rather than a sink (Houghton et al. 1983). But because many plant species substantially increase their rate of carbon fixation as ambient  $\text{CO}_2$  concentration rises, it is not clear what the net effect of these opposing trends will be on the global carbon budget. Carbon dioxide can also directly affect the way plants respond to climatic variables such as temperature and water (reviewed by Acock and Allen 1985). Further, the distribution and composition of plant communities is both influenced by, and can influence, local and regional climate (Salati and Vose 1984).

Most research into the direct effects of  $\text{CO}_2$  on vegetation has been conducted with crop plants under controlled or agronomic conditions. These studies have shed considerable light on the physiology of the  $\text{CO}_2$  response, and predictions concerning the effects of elevated  $\text{CO}_2$  concentrations on agricultural productivity have been based



on them. It is difficult to extrapolate from this body of work to unmanaged plants communities of diverse species composition because, although agricultural and wild species share much in common biochemically, those factors which distinguish crops from wild plants may also alter their responses to elevated  $\text{CO}_2$ . For example, the relative absence of stress under cultivation may allow agricultural species to better utilize increased  $\text{CO}_2$  as a substrate for photosynthesis than species in natural environments (Patterson and Flint 1982; Zangerl and Bazzaz 1984). Alternatively, the annual, determinate habit of many crop plants may limit their long term ability to use this additional carbon source. Indeterminate plants and those with a strong carbon sink in storage organs appear to respond most strongly to increased  $\text{CO}_2$  concentrations (Clough et al. 1981).

The literature on wild species and ecosystem responses to  $\text{CO}_2$  has recently been reviewed by Oechel and Strain (1985) and Bazzaz et al. (1985). These authors stress the variability in the effect of  $\text{CO}_2$  on photosynthesis and growth of different species, ranging from a net decrease in leaf photosynthesis and plant growth under elevated  $\text{CO}_2$  to substantial increases in both measures.

Some general trends are evident, however. Total community biomass should increase. Plants possessing the

C<sub>4</sub> pathway of photosynthesis typically show a relatively small growth response to elevated CO<sub>2</sub> and consequently will compete less well against plants with the C<sub>3</sub> pathway. Community composition should change, although the great diversity of species responses to CO<sub>2</sub> makes it impossible at present to predict exactly how it will change. Environmental variables which act to limit plant growth (e.g. low nutrient availability, extreme temperatures) will also decrease the magnitude of the response to elevated CO<sub>2</sub>. A notable exception to this rule is water availability. Increasing CO<sub>2</sub> increases plant water use efficiency, such that water stressed plants respond relatively more to CO<sub>2</sub> than do unstressed plants. Finally, such factors as growth form, species composition, life history, and phenotypic plasticity may all significantly affect the relationship between system response (either whole plant or ecosystem) and the response of component parts (organs or individuals).

It should be emphasized that these observations were based on a small number of studies conducted largely under controlled conditions. To overcome the limitations of our present body of knowledge, additional research must be carried out using plants grown under natural conditions and exposed to elevated CO<sub>2</sub> from emergence through senescence. In the absence of an adequate data base on wild species responses it will be impossible to make useful predictions concerning the impact of elevated CO<sub>2</sub> on unmanaged

ecosystems.

We are investigating the effects of elevated atmospheric CO<sub>2</sub> on a Chesapeake Bay salt marsh. Coastal and brackish wetlands border much of the eastern coast of North America, forming a distinctive series of communities from the Yucatan Peninsula to Newfoundland. These wetlands are recognized as critical habitat supporting coastal fisheries, wildlife, shoreline stabilization, and recreation. Some of these wetlands are also among the most productive of terrestrial plant communities. In most, substrates are low in oxygen and decomposition proceeds slowly, which results in substantial carbon accretion. Wetlands play an important role in the global carbon cycle because many sequester a relatively large fraction of their annual production.

The difficulty in extrapolating from the results of controlled environment studies to the behavior of wild species has led to the development of experimental systems for exposing plants to elevated CO<sub>2</sub> in the field. A widely used approach has been the enclosure of plants within a portable chamber whose atmosphere is then manipulated by the introduction of CO<sub>2</sub> or other gases (Drake et al. 1985). Our research program uses open top chambers to expose plants in the field to elevated CO<sub>2</sub> and to monitor plant and community responses to this treatment.

The design and performance of the open top chambers used in this study are discussed in detail in this report. These chambers are similar to those used by Rogers et al. (1983), but they differ in size and in the control of air flow around the enclosed vegetation. The microenvironment within the chambers is described, as are the CO<sub>2</sub> delivery system; sampling of gasses and measurement of CO<sub>2</sub> concentration; measurement of light and temperature; and data acquisition and analysis.

A necessary consequence of using chambers is the perturbation of the microenvironment of the system and this produces effects on the vegetation unrelated to the elevation of CO<sub>2</sub>. Open top chambers alter the canopy microenvironment by changing temperature, light, humidity, and wind (Heagle et al. 1979; Shinn et al. 1976; Olszyk et al. 1980). Temperature is higher, light attenuated, and humidity greater inside than outside the chamber. The effect of the chambers on crop growth has been evaluated by a number of authors (Heagle et al. 1979; Heggestad et al. 1980; Olszyk et al. 1980; Winestock et al. 1982). In each instance, while growth differences between inside and outside were found, they were random with respect to the chamber. Drake et al. (1985) reviewed the available data and concluded that the data reported in the open literature on this question do not permit a strong conclusion regarding the effect of open top chambers on growth or yield. However, personal

communications from other workers suggest that the chamber may have had a greater effect than can be known from data published to date.

Results from our analysis of the chamber microclimate are presented in this report. We measured air temperature, canopy temperature, CO<sub>2</sub> concentration, light quality and quantity, and wind speed inside and outside the chambers. Temperature effects, in particular, were complex and we have sought to identify chamber components which influenced the outside to inside temperature difference. We intend to test for the effects of our chambers on plant growth by the analysis of unchambered control sites. Plants in these sites will be treated identically to those in chambers receiving normal ambient CO<sub>2</sub> concentrations.

An important goal of this research is to determine the effect of elevated CO<sub>2</sub> on the salt marsh community carbon budget, that is, the balance between carbon assimilated during daylight hours less that lost through respiration during the night. In this high marsh, photosynthesis is carried out solely by macrophytes, while respiration comes from macrophytes plus a complex sediment fungal and microbial community. Drake and Read (1981) estimated that 60% of the 1750 g m<sup>-2</sup> produced on this salt marsh annually was lost by respiration. Of the remaining 40%, 33% was accumulated in marsh sediment and 7% was exported to the adjacent estuary

(Jordan et al. 1983).

These results can be used to examine the possible effects of an increase in primary productivity on carbon accretion by the high marsh ecosystem. Given a 10% increase in primary productivity with a doubling in atmospheric  $\text{CO}_2$  concentration, and no increase in decomposition or export rates, carbon accretion on the marsh would increase 27% above present rates. This sensitivity of accretion to small changes in carbon flux rates through the marsh illustrates the importance of accurately measuring community photosynthesis and respiration.

With respect to the salt marsh carbon budget, the following hypotheses will be tested.

- Elevated  $\text{CO}_2$  will increase net primary production. This effect will be greatest in communities containing  $\text{C}_3$  species.
- Elevated  $\text{CO}_2$  will increase the photosynthetic capacity of ecosystems with  $\text{C}_3$  species.
- Elevated  $\text{CO}_2$  will increase the rate of litter decomposition.

There will be two independent means to test these

hypotheses and quantify the marsh carbon budget. One involves the measurement of above and belowground plant growth and decomposition rates. The other is the direct monitoring of net  $\text{CO}_2$  uptake and release throughout the season by intact plant canopies and their associated sediment. These methods are complimentary. Short term effects of elevated  $\text{CO}_2$  on carbon flux are reflected in changes in instantaneous and daily net  $\text{CO}_2$  exchange rates while long term change in carbon pool sizes will be evident in measurements of plant biomass.

Integration of daily net carbon exchange over the entire growing season can also be used to estimate changes in total carbon pool size (Drake and Read, 1981). This is important, in that productivity estimates from the measurement of plant material are very sensitive to the particular method used (Linthurst and Reimold 1978). This is particularly true for estimates of belowground production (Good et al. 1982) and decomposition rates (Wieder and Lang 1982). Ecosystem gas exchange is thus a valuable independent reference for direct estimates of primary production.

This report discusses progress to date in the use of gas exchange measurements to address hypotheses 1 and 2 above. By continuous sampling of chamber inlet and exhaust gases we measured ecosystem net  $\text{CO}_2$  exchange as a function of incident light and calculated the integrated 24 hr carbon balance for

the three communities. Single leaf measurements of gas exchange were also made.

The data set on ecosystem gas exchange covers the period from mid-September through early November. Interpretation of results is consequently tentative. However, these results demonstrate our ability to track ecosystem photosynthesis accurately under normal ambient and elevated CO<sub>2</sub> conditions. Light response curves generated from these data were analyzed for maximum CO<sub>2</sub> exchange rates, respiration, quantum yields, and light compensation values. Seasonal trends in net ecosystem carbon balance were also obtained.



## CHAPTER 1

### THE CO<sub>2</sub> EXPOSURE AND MONITORING SYSTEM

The maintenance of elevated CO<sub>2</sub> environments and the monitoring of canopy gas exchange in the field required the development of four interrelated components. These were: I) an exposure chamber, II) a CO<sub>2</sub> monitoring system, III) a CO<sub>2</sub> dispensing system, and IV) a data acquisition, control and analysis system. In this chapter we present details of the design and construction of each of these components.

#### I) Exposure Chamber

##### A. Design

The chamber was designed to maintain a stable, elevated CO<sub>2</sub> concentration above a plant canopy, while keeping the micro-environment as close as possible to normal, ambient conditions. The small stature of the plants in the high marsh ecosystem (generally less than 1 m) allowed use of a relatively small chamber (Figure 1.1). Chambers were approximately 1.2 m tall by 0.8 m in diameter. Small chambers had the advantages of requiring less CO<sub>2</sub> to elevate

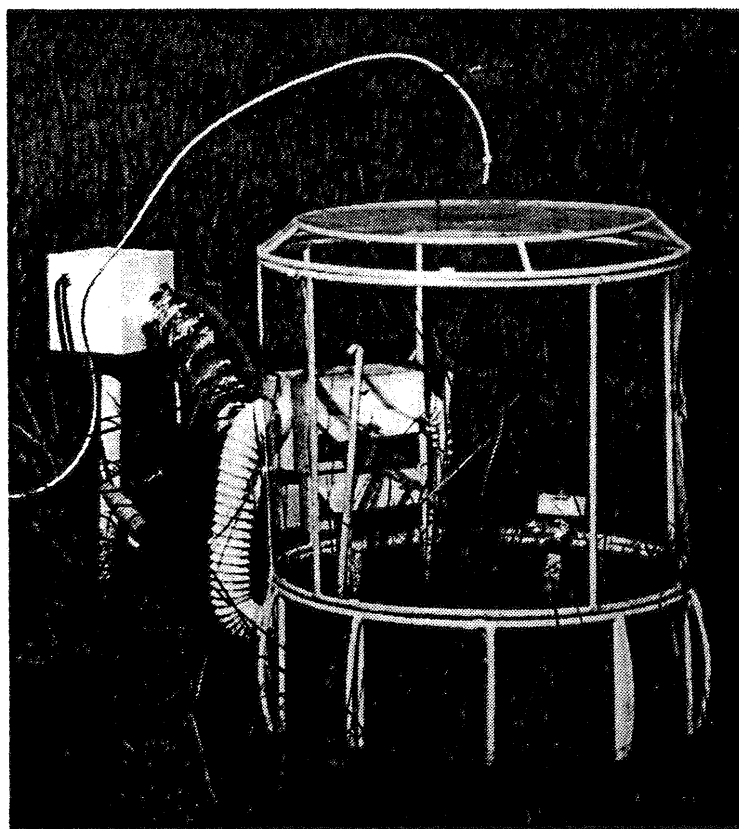
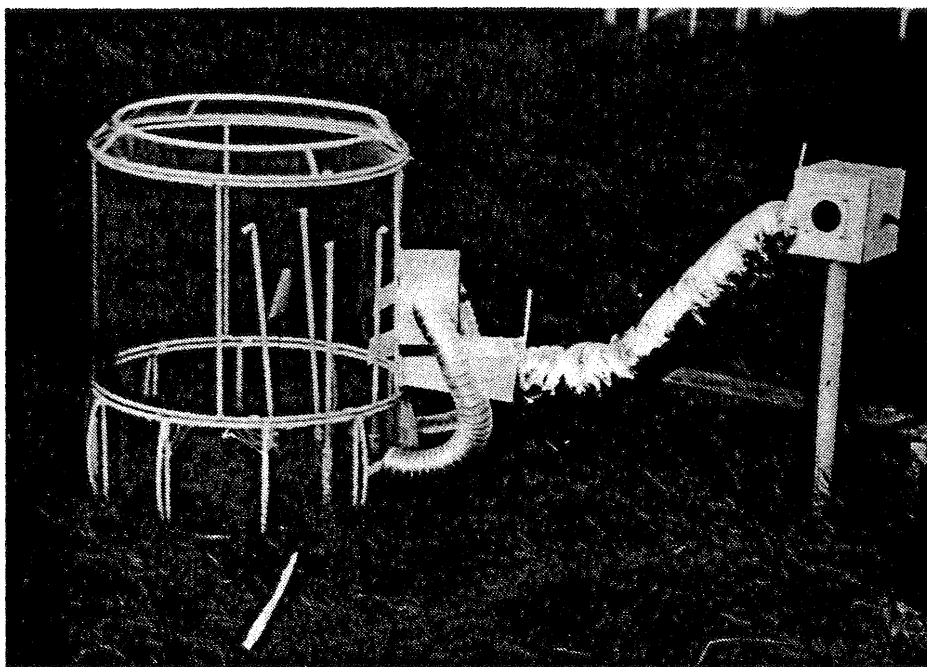


Fig 1.1 Exposure chamber in place on the salt marsh. A) In the open top configuration, B) in the closed top configuration. Tubes inside chambers are capped wells for sampling interstitial water.

CO<sub>2</sub> concentrations, having high chamber volume exchange rates, and allowing greater replication of experimental plots. In addition, these chambers could be used with closed tops for measurement of net CO<sub>2</sub> exchange. These chambers differed from those used by Rogers et al. (1983) principally in size and method of mixing air within the chamber.

Air circulation within the chamber is illustrated in Fig 1.2A. Component parts are identified in Fig 1.2B. Ambient air entered through the intake port of the remote blower. The air was blown through a 4" diameter delivery tube, an inlet plenum, and into the chamber through a louvered opening. A mixing blower located above the air inlet plenum pulled air down through the canopy and through a perforated wall into a lower plenum which was formed by the double walled bottom section of the chamber. From the lower plenum, air was drawn upward through 3" diameter mixing tubes into the mixing blower and then back out into the chamber to be re-mixed with chamber air before being exhausted out the frustum. In chambers with elevated CO<sub>2</sub> concentrations, pure CO<sub>2</sub> is injected at the intake port of the remote blower and thoroughly mixed with incoming air. A modified frustum with a narrow exit tube replaced the open frustum when the chamber was being used for net CO<sub>2</sub> exchange measurements (Figure 1.1B). With this modified frustum in place, chambers were referred to as "closed top".

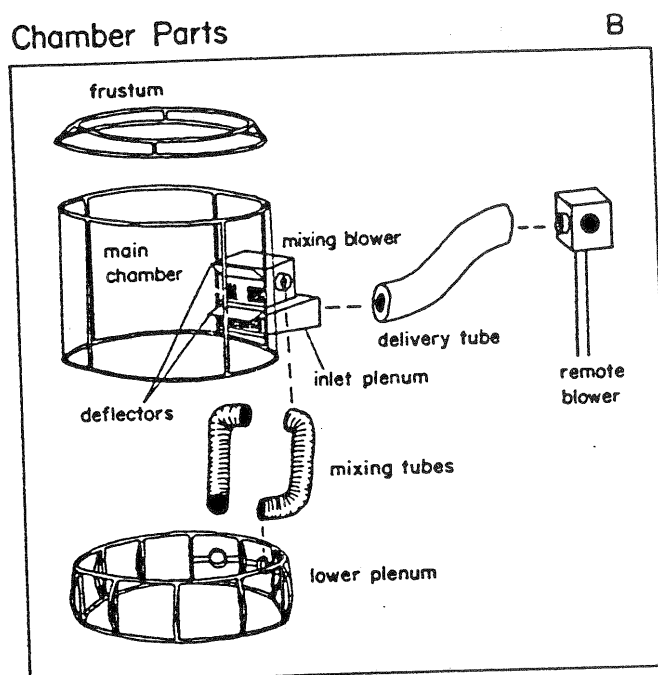
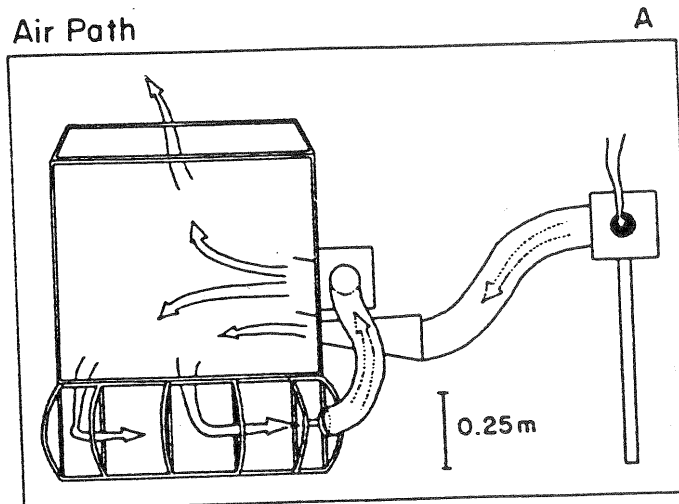


Fig 1.2 Detail of the open top chamber. A) Pathway of air through the chamber, B) chamber parts.

The remote blower determined the rate of air entering and leaving the chamber. High chamber volume exchange rates were achieved by combining a small chamber with a high capacity blower (ca.  $2800 \text{ l min}^{-1}$  free air rating). Chamber volume exchange rates were about 4.4 changes of chamber volume per minute (see Chapter 2). The mixing blower increased turbulence within the chamber. This pattern of air flow was intended to provide more mixing within the chamber and plant canopy than could be obtained using a single pass system. Mixing could be controlled to a degree by moving the deflectors mounted on the air inlet plenum. The high exchange rates and mixing were designed to maintain temperature and humidity close to ambient conditions and to reduce the influx of outside air into the chamber through the open top. Data on chamber performance are presented in Chapter 2.

## B. Construction

The chamber consisted of four parts: a double walled lower plenum, the main chamber which included the air inlet plenum and mixing blower, a frustum, and a remote blower (Figure 1.2B). A detailed parts list can be found in Appendix A.

The chamber frame was constructed of thin-walled aluminum tubing (8.5 mm ID) which was rolled and heli-arc

welded in the machine shop at the Smithsonian Environmental Research Center (Rockville). The frames were primed and painted with a polyurethane enamel paint to prevent weathering and salt corrosion. Painted frames were covered with a 75 um (300 guage) clear, polyester film. The film was taped to the aluminum frames with a 2.5 cm polyester tape. A power cord connected the two blowers and ran from the remote blower to a sheltered electrical outlet. Waterproof electrical couplings were used between the remote blower and mixing blower and between remote blower and power cord to allow easy removal of the chamber from the marsh during severe weather. The chambers were very sturdy, withstanding high winds and several thunderstorms as well as one hurricane and flood without damage.

## II CO<sub>2</sub> Monitoring System

Figure 1.3 shows the gas sampling circuit. "Reference" gas was sampled inside the chamber at the top of the canopy, or in the frustum exit tube during closed-top operation. "Sample" gas was sampled at the air inlet plenum. Color coded thermoplastic tubing was used throughout the gas circuit. A dual-head diaphragm pump drew a continuous sample of the reference and sample gas from each chamber to a nearby pump house. The gases were forwarded from the pump house to the lab and then through three one-gallon mixing volumes per

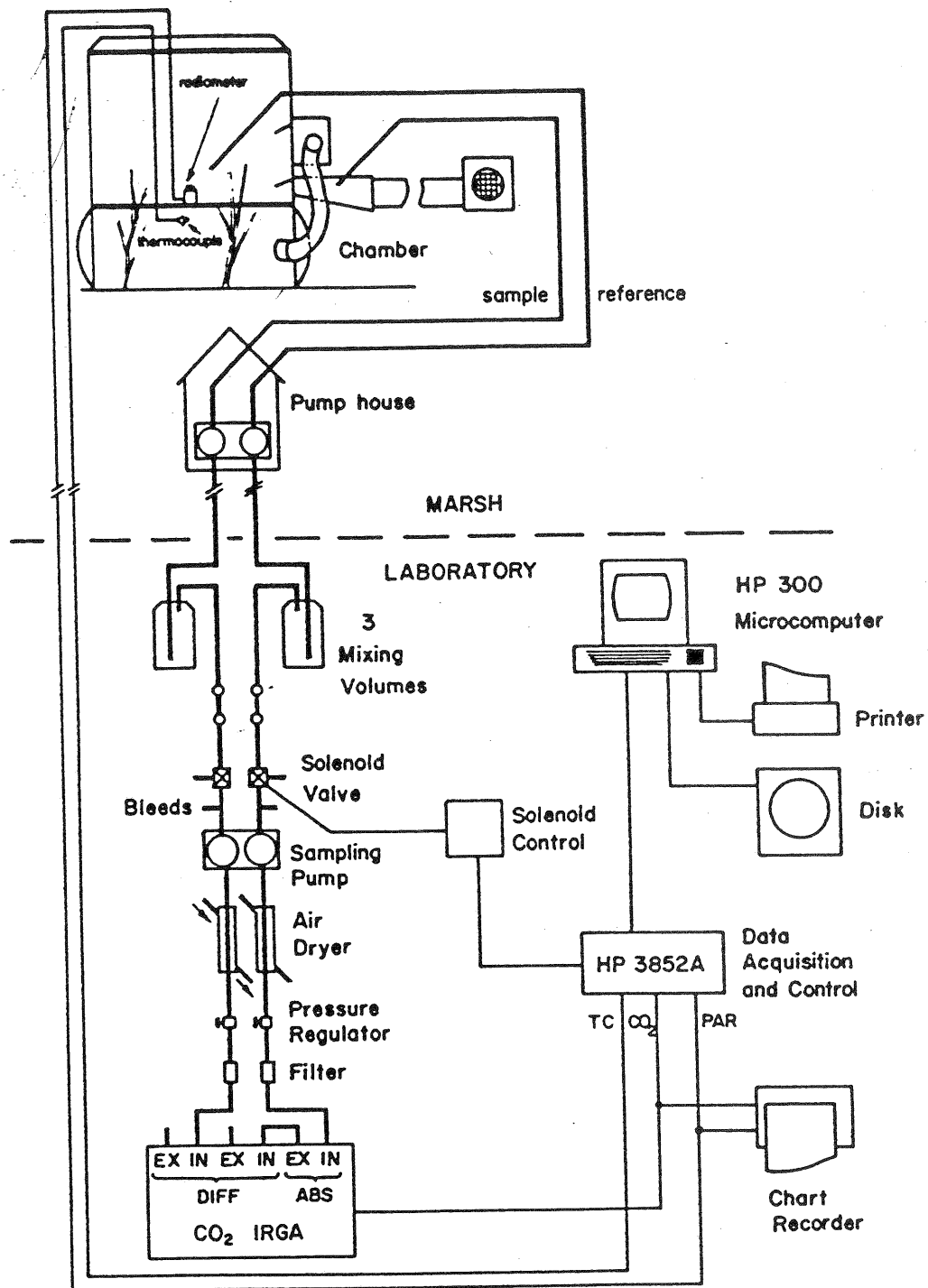


Fig 1.3 Schematic showing gas, light, and temperature sampling circuits and their computer interface.

line. The mixing volumes dampened fluctuations in the differential CO<sub>2</sub> signal caused by the time lag in sensing changes in the CO<sub>2</sub> concentration of air passing through the chamber. Gas then entered a three-way, nylon bodied solenoid valve which either exhausted the gas or shunted the gas into a manifold when actuated. Actuation of the solenoids was controlled by the data acquisition and control system.

Gas from the manifold was directed to the sampling pump which provided a constant flow rate of 2 l min<sup>-1</sup> to the infra-red CO<sub>2</sub> gas analyzer (IRGA). Excess gas from the solenoid manifold was exhausted upstream from the sampling pump. The gas was pushed through a two-tube dryer which removed water vapor by establishing a water vapor gradient across a hygroscopic membrane. Dry air to create the water vapor pressure gradient was generated by drawing air from the lab through chilled condensing coils maintained at 4 C. A filter before the coil generated a resistance, expanding air in the coil and depressing the dew-point. The air in the purge loop of the drying tube was moved at a higher rate, at lower pressure, and with lower dew-point than the gas in the test-loop. Filters just upstream from the IRGA removed particulate matter from the gas. The dry reference gas first entered an absolute gas analysis cell of the IRGA and then entered the reference side of a differential gas analysis cell. The dry sample gas entered the measurement side of the differential gas analysis cell. This allowed simultaneous



measurements of absolute and differential gas concentrations to be made.

Two features of this system allowed rapid and accurate measurement of the small differentials in  $\text{CO}_2$  concentration generated in the chamber. First, all gas lines were under positive pressure between the pump house and IRGA. Small leaks would therefore have no effect on the  $\text{CO}_2$  concentration of the sample gas and the loss of volume through such leaks would have no effect on the desired measurements. Second, the gas analyzer in the system (BINOS, model BIN 4b) had superior stability both in zero and sensitivity drift and had an extremely rapid response time (less than 15 seconds). With 30 chambers in operation, it will be possible to sample the  $\text{CO}_2$  concentration in each chamber at least every 15 minutes and potentially every 7.5 minutes.

### III $\text{CO}_2$ Dispensing System

Elevation of the  $\text{CO}_2$  concentration inside a chamber was accomplished by continuously injecting pure  $\text{CO}_2$  into the air stream entering the chamber. Figure 1.4 shows the gas dispensing circuit. A manually operated  $\text{CO}_2$  dispensing system was found to be adequate in larger chambers (Rogers, et al., 1983) and was also used in our system.

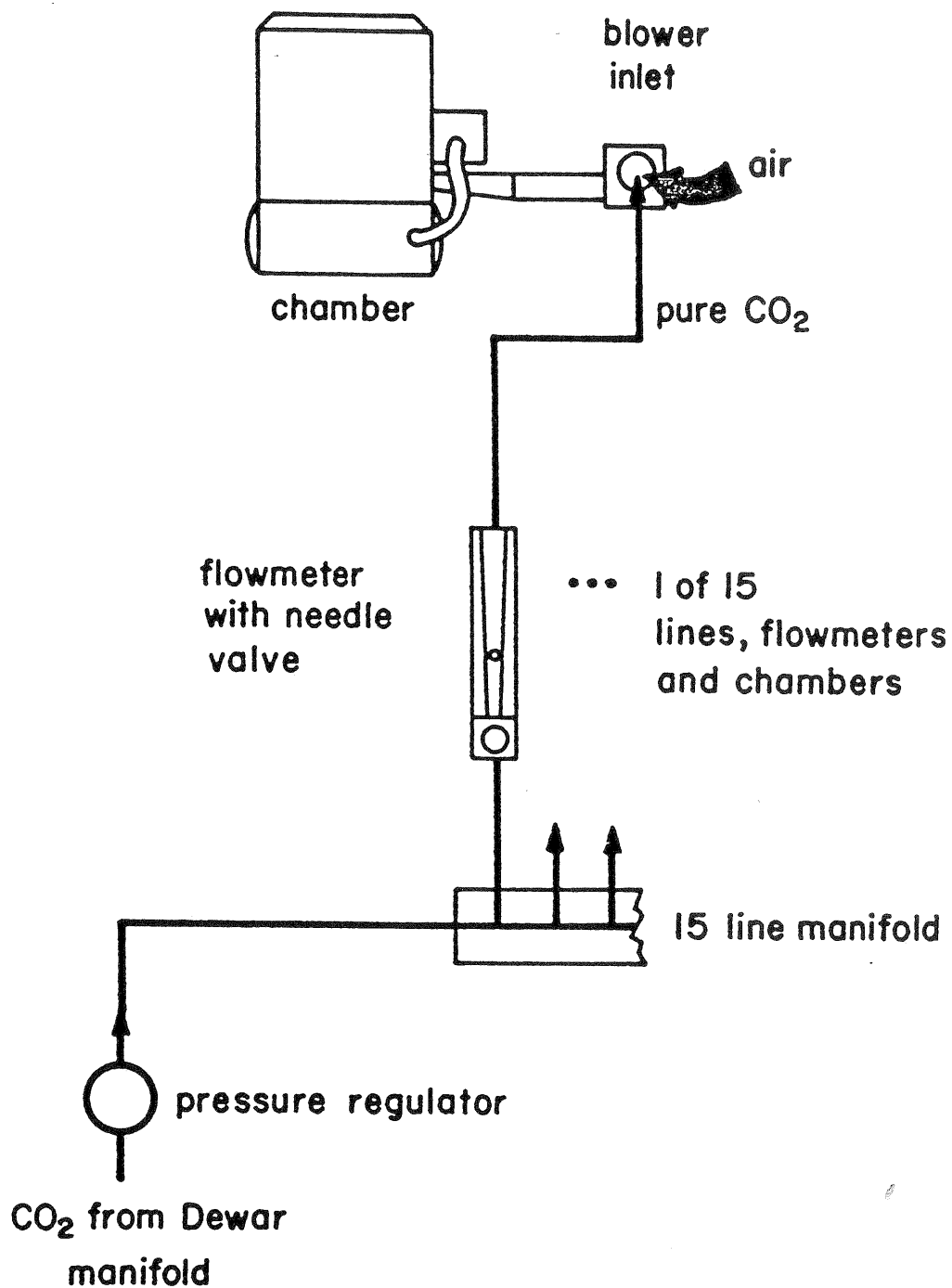


Fig 1.4 Carbon dioxide dispensing circuit. Flow of CO<sub>2</sub> to the chambers is controlled manually from the laboratory.

One hundred percent CO<sub>2</sub> was supplied by 380 lb capacity dewar flasks housed near the lab in a small shed. The dewars were connected to a custom manifold with a dual-guage pressure regulator. Carbon dioxide was fed under pressure to chambers through thermoplastic tubing. The CO<sub>2</sub> supply line fed a 15 line manifold in the lab. Flow to each chamber was controlled by a needle valve flowmeter.

#### IV Data Aquisition, Control and Analysis System

Figure 1.5 is a schematic of the data aquisition, control and analysis system. Analog signals from the gas analyzer (absolute and differential), quantum sensors, and weather station were digitized using a 20 input multiplexer coupled to an integrating digital voltmeter. Thermocouple signals were input through a compensated 20 input multiplexer.

The central unit controlling data acquisition was a Hewlett-Packard 3852A Data Aquisition/Control device. Two 16 channel relay boards in the HP 3852A switched a 5 volt signal which operated the solenoid switch box. Each HP 3852A channel was connected to an light emitting diode (LED), a manual switch and an optically-isolated relay located in the solenoid switch box (Fig. 1.6). When a signal was applied by the HP 3852A, the LED was lit, and the optically-isolated





relay allowed 120 VAC to actuate the solenoid. Solenoids could also be operated manually via the front panel switches of the solenoid switch box. Up to four days of CO<sub>2</sub> concentration and micro-climate data could be stored in the memory of the HP 3852A. A Campbell Scientific CR7 data acquisition and control system could be used as a backup to collect data, control solenoid switching, and transfer data to the micro-computer.

Data was transferred to a Hewlett-Packard 300 microcomputer for analysis, permanent storage, printing and graphing. Data for one week was stored on micro-floppy disks. A data manipulation package allowed graphing and statistical analysis of the data.

## CHAPTER 2

### SYSTEM PERFORMANCE

The 1986 growing season was devoted to constructing and testing system components described in Chapter 1. The most important function of the system was to maintain CO<sub>2</sub> concentrations 260 ppm above ambient, the target value for elevated CO<sub>2</sub> concentration. To do this it was necessary to monitor CO<sub>2</sub> concentration within the chamber. Another aspect of system performance which was tested was the measurement of ecosystem net CO<sub>2</sub> exchange (NCE). A closed top was used on the chamber when measuring NCE to prevent mixing of air inside the chamber with air from outside the chamber. Measurement of NCE required the ability to detect a small CO<sub>2</sub> concentration difference between reference and sample gas lines and to measure the flow rate of air through the chamber.

We also needed to understand the effect of the exposure chamber on the ecosystem micro-environment. The open top chamber alters the microenvironment of natural vegetation and plant responses to environmental factors are modified by their responses to CO<sub>2</sub>. In order to aid the interpretation of results we have characterized the environment inside the

chamber with respect to that outside the chamber, and included in our experiment an unchambered control site for each treatment chamber. In this chapter we report on the maintenance and monitoring of target CO<sub>2</sub> differences, the measurement of NCE, and the effect of the chamber on light quality and quantity, air and vegetation temperature, and wind speed.

## I. CO<sub>2</sub> concentration

### A. Absolute CO<sub>2</sub> concentration

Carbon dioxide concentrations were monitored throughout the day in six chambers. Two replicate chambers were located in each of the three communities. Prior to September 24 all chambers were exposed to normal ambient air. After September 24 one chamber in each community received ambient +260 ppm CO<sub>2</sub>. See Appendix B for details of this chronology.

A representative example of a 24 hr record of ambient CO<sub>2</sub> concentrations is shown in Fig 2.1A. The sampling frequency was once every three minutes. These data demonstrate the range in normal ambient CO<sub>2</sub> concentrations to which this plant community was exposed. Carbon dioxide concentrations above 500 ppm were not unusual at night. Variation in ambient CO<sub>2</sub> concentration at night was



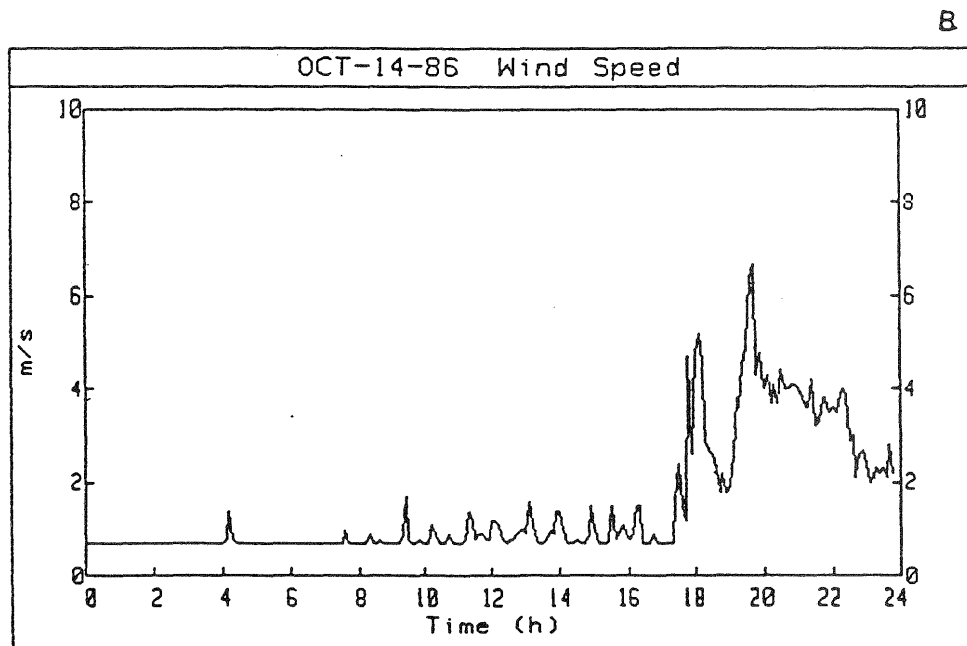
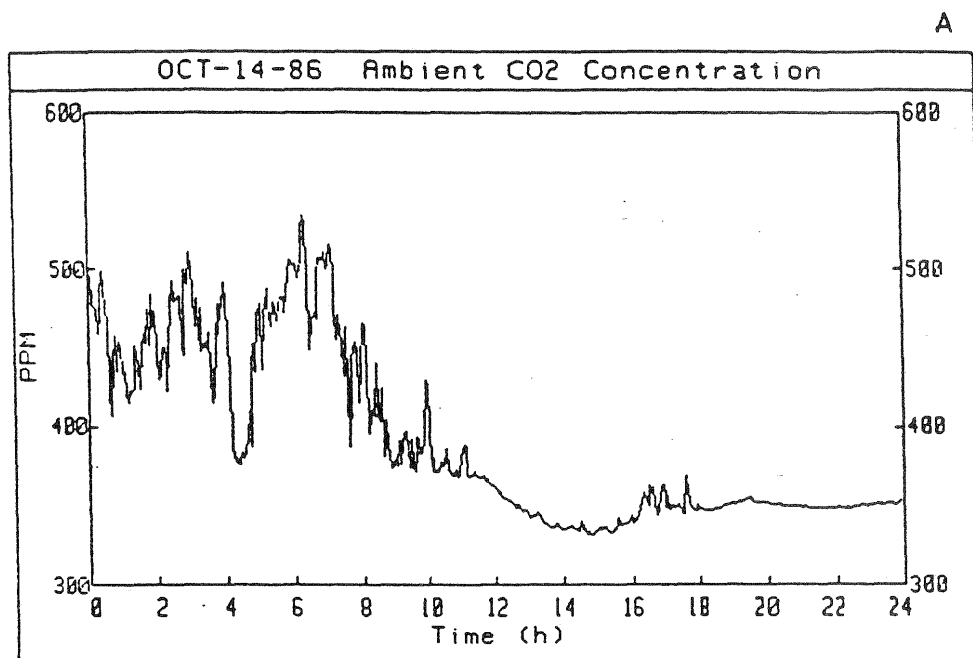


Fig 2.1 Ambient CO<sub>2</sub> concentration and wind speed in an open-top chamber. A. Ambient CO<sub>2</sub> concentration in an open-top chamber on Oct. 14, 1986. B. Windspeed for the same date measured with a cup anemometer located 3 m above the ground.

negatively correlated with wind speed; when there was little wind at night, ambient  $\text{CO}_2$  concentrations were high and variable. This pattern can be seen by comparing Figs 2.1A and 2.1B between 0 and 9 hrs. Carbon dioxide concentrations ranged between 370 and 540 ppm and wind velocities were less than  $1.0 \text{ m s}^{-1}$ . Wind velocity exceeded  $2 \text{ m s}^{-1}$  after 10 hrs and ambient  $\text{CO}_2$  concentrations remained near 350. On other nights with low wind velocities  $\text{CO}_2$  concentrations as high as 700 ppm were observed. During midday and during windy conditions at night,  $\text{CO}_2$  concentrations remained between 330 and 350 ppm.

The fluctuations in ambient  $\text{CO}_2$  concentration which we observed at night (Figure 2.1A), were almost an order of magnitude greater than those reported by Rogers et al.(1983). These large changes in  $\text{CO}_2$  concentration were probably due to the unusual topography of our research site. The Kirkpatrick marsh is surrounded on three sides by a forest of deciduous trees reaching approximately 35 m above the level of the marsh. This forms a basin into which  $\text{CO}_2$  settled at night and, when the air was still, concentrations could increase at ground level.

Elevated  $\text{CO}_2$  concentrations were maintained close to 260 ppm above ambient (the target difference) in both the open and closed top chambers in spite of large variations in ambient concentrations. Figure 2.2 shows a 24 hr record of

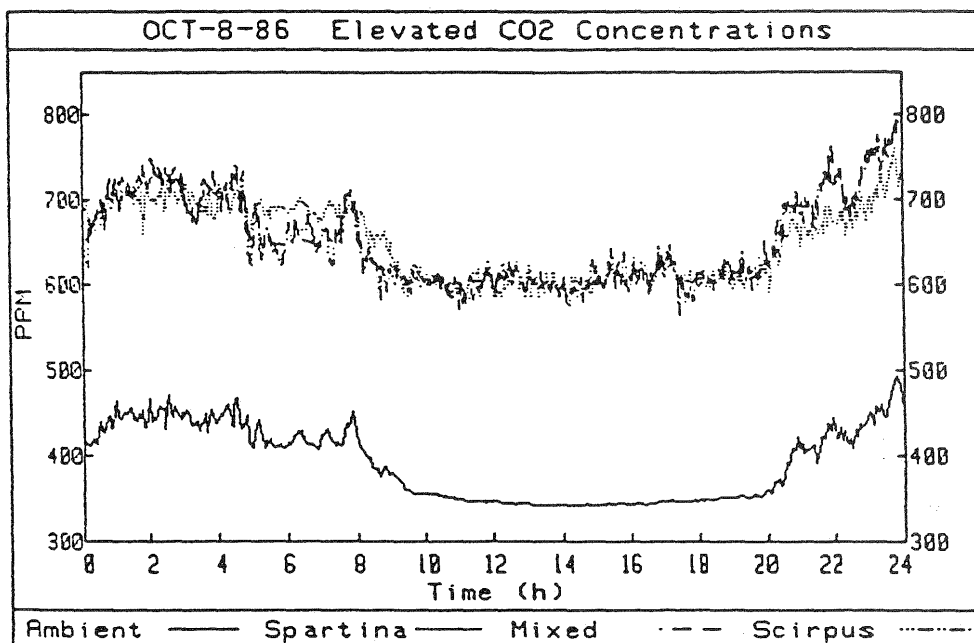


Fig 2.2 CO<sub>2</sub> concentration in an open-top chamber without CO<sub>2</sub> added (Ambient) and in open-top chambers from three communities with enough CO<sub>2</sub> added to elevated the concentration ca. 260 ppm above ambient.

CO<sub>2</sub> concentrations in three open top, +260 chambers compared with the record from an ambient chamber. Figure 2.3 shows the 24 hr record of CO<sub>2</sub> concentrations in three closed top, +260 chambers compared with the record from an ambient chamber. Differences in CO<sub>2</sub> concentration among the communities were small.

Few adjustments of the CO<sub>2</sub> dispensing rates in either open or closed top chambers were required to maintain the target CO<sub>2</sub> difference. Figures 2.4 A,B and 2.4 C,D show daily mean target CO<sub>2</sub> differences in open top chambers for the periods Oct 2-14 and Nov 7-28 respectively. Both 24 hr means and daytime means are presented. With practice, within day variability was less than  $\pm 10$  ppm.

In order to determine whether high or variable winds influenced the CO<sub>2</sub> concentration in open top chambers, we made comparisons of data in all three treatment chambers during periods of windy weather. Wind speed at the site was measured by a cup anemometer with windvane (R.M. Young Co., Traverse City, MI) located within the site at a height of 3 m above the marsh. Figure 2.5A shows the 24 hr record of CO<sub>2</sub> concentrations within the three +260 chambers compared to ambient concentrations. Wind velocity during the same period is shown in Fig 2.5B. Wind speed was typically  $2-4 \text{ m s}^{-1}$  during the day in the fall. CO<sub>2</sub> concentrations could be maintained within 25 ppm of the target level with wind speed

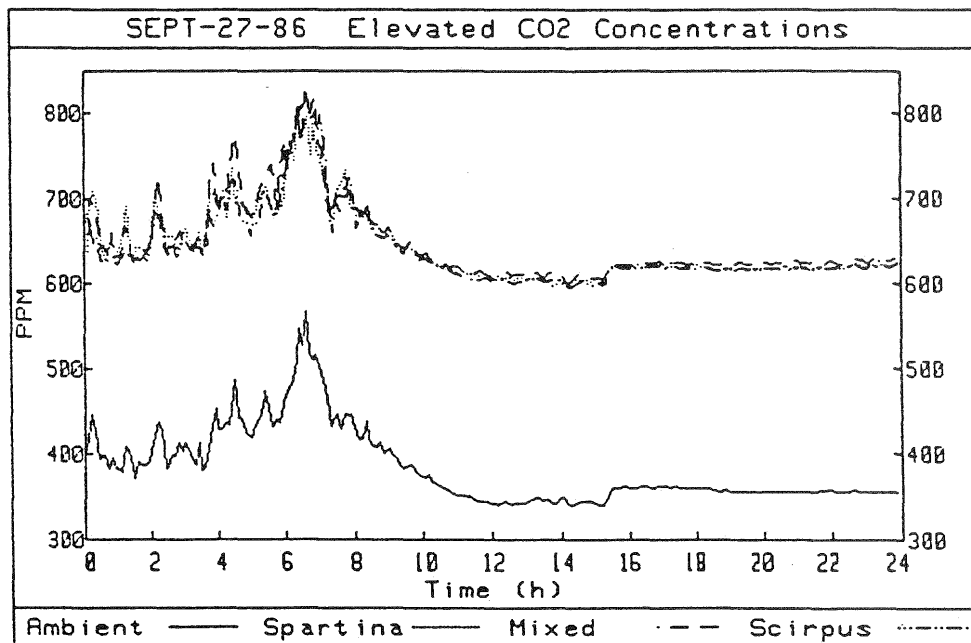


Fig 2.3 CO<sub>2</sub> concentration in a closed-top chamber without CO<sub>2</sub> added (Ambient) and in closed-top chambers from three communities with enough CO<sub>2</sub> added to elevated the concentration ca. 260 ppm above ambient.

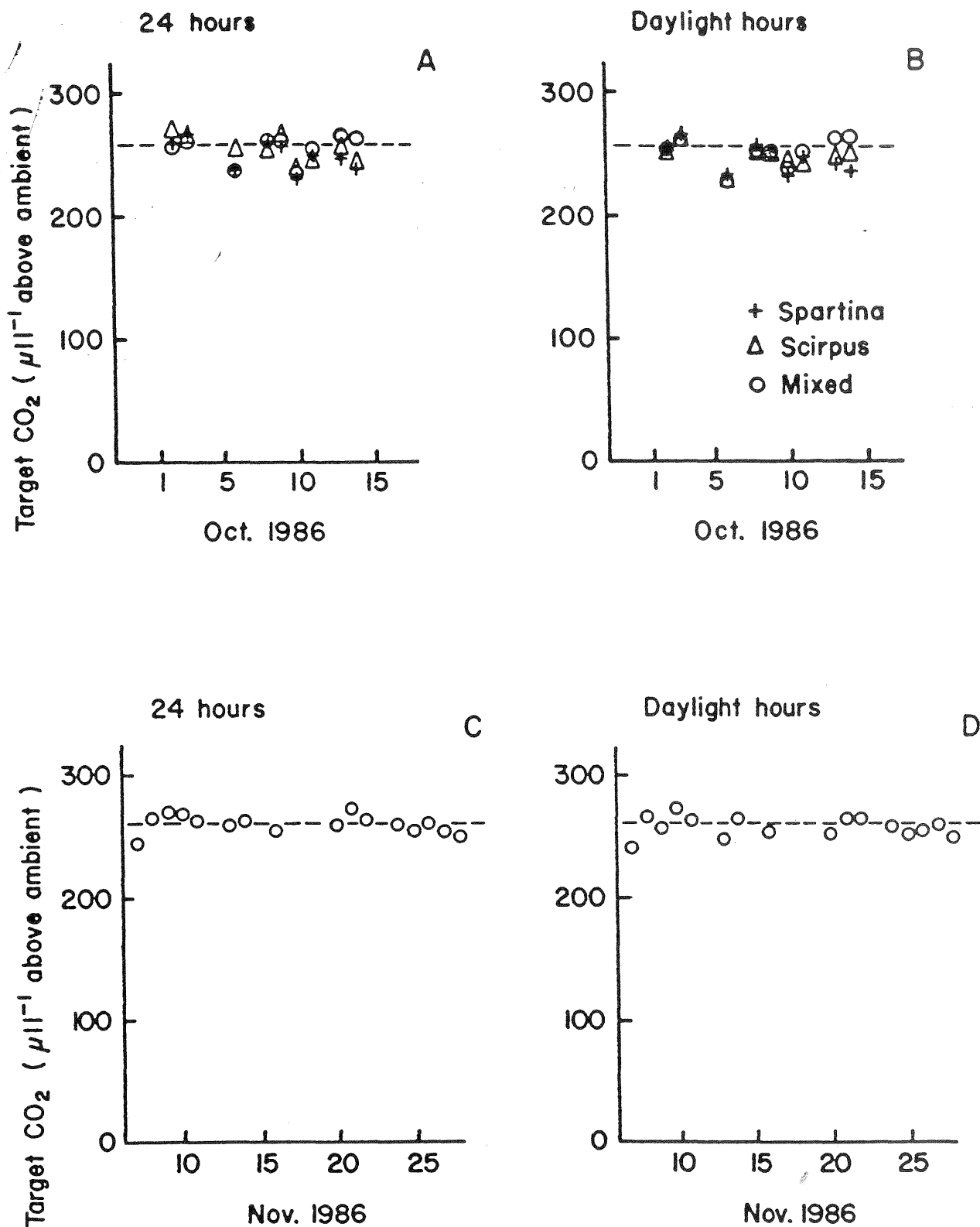


Fig 2.4 Mean daily target CO<sub>2</sub> concentrations in +260, open-top chambers. Twenty-four hr means were taken from midnight to midnight. Daylight means were taken from sunrise to sunset.

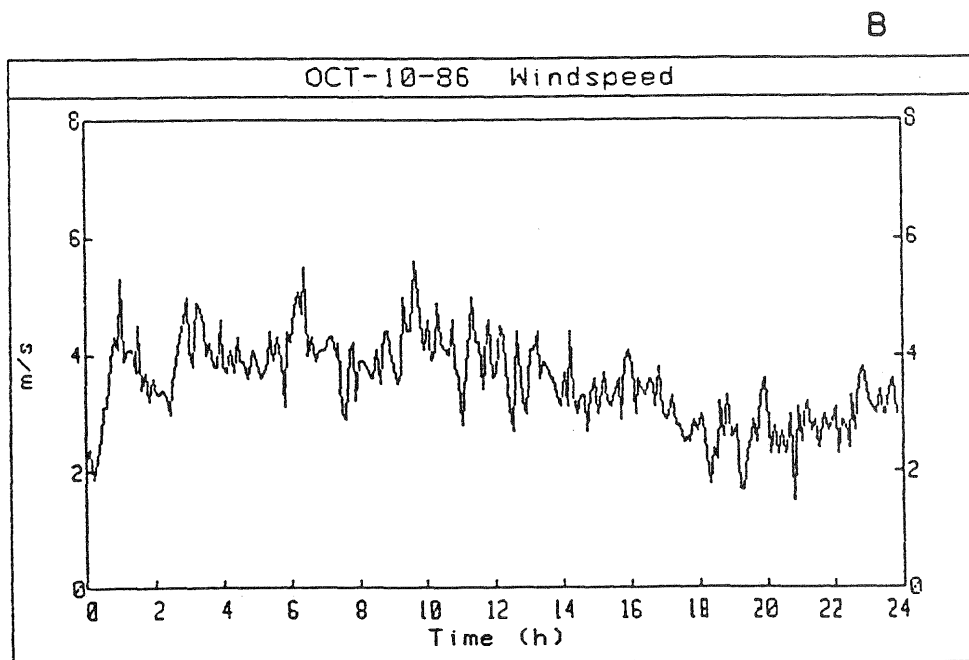
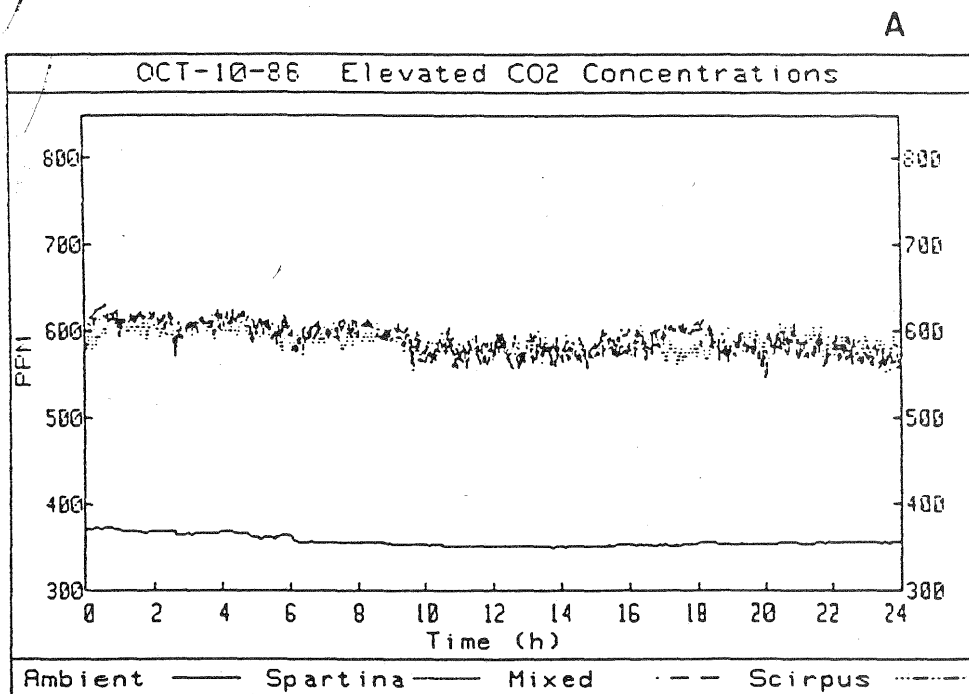


Fig 2.5 Effect of wind speed on maintenance of +260 CO<sub>2</sub> concentrations. A. CO<sub>2</sub> concentrations in an ambient, open-top chamber and in +260, open-top chambers from three communities. B. Wind speed.

as high as  $5 \text{ m s}^{-1}$ . Wind direction may also be an important parameter in the interpretation of results when we are exposing all test areas to  $\text{CO}_2$ . An example of a 24 hr record of wind direction and speed is shown in Fig 2.6.

Rogers et al. (1983) reported that they could maintain elevated  $\text{CO}_2$  atmospheres in large open top chambers within 10% of the desired values. Their chamber included a frustum to reduce incursion of outside air into the chamber and improve control of  $\text{CO}_2$  concentration above the plant canopy (Davis & Rogers, 1980). This feature was incorporated in our chambers (Fig 1.1).

#### B. $\text{CO}_2$ Requirements

The amount of  $\text{CO}_2$  needed to reach the target difference of 260 ppm above ambient was greater in the open top chambers than when the top was covered for measurement of net  $\text{CO}_2$  exchange. Open top chambers required about  $680 \text{ l CO}_2 \text{ day}^{-1}$  while closed top chambers required approximately  $373 \text{ l CO}_2 \text{ day}^{-1}$ . We estimated a seasonal use of 9000 lbs. of  $\text{CO}_2$  based on a 200 day growing season with 15 open top chambers receiving  $\text{CO}_2$ . This could be supplied by one dewar flask (380 lb capacity) per week.



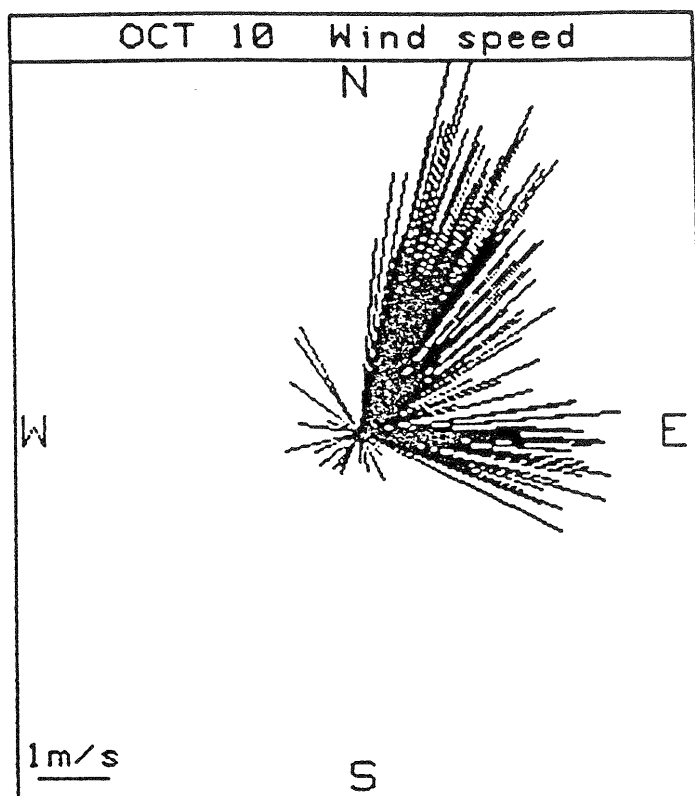


Fig 2.6 Wind speed and direction for a single 24 hr period. Direction of the line indicates average wind direction, length of the line indicates average wind speed. Data were collected every 30 sec and averaged over 15 min intervals. The blank area in the NNW quadrat was caused by a built-in "dead spot" in the wind vane potentiometer.

### C. Measurement of Net CO<sub>2</sub> Exchange

The first tests of the chamber were made to determine whether it could be used to measure net CO<sub>2</sub> exchange while in the open top configuration. These experiments showed that we could measure a CO<sub>2</sub> difference across the chamber under ambient CO<sub>2</sub> concentrations, but this difference was smaller than expected because of mixing of outside air into the chamber. There was also an increase in the signal noise when compared with measurements from closed top chambers. In chambers with +260 CO<sub>2</sub>, these problems were acute. The effect of mixing by ambient CO<sub>2</sub> in the +260, open top chambers was small relative to the maintenance of the target CO<sub>2</sub> difference (260 ppm) but large with respect to the measurement of a CO<sub>2</sub> concentration difference across the chamber which was usually of the order of 3-7 ppm in bright sunlight.

Narrowing the opening in the frustum to a centrally located 15 cm diameter x 30 cm tall "chimney" (Fig 1.1B) greatly reduced entry of outside air and allowed the measurement of a stable net CO<sub>2</sub> exchange signal. This modified frustum constituted a "closed top". Figure 2.7 shows a daytime record of canopy NCE from the ambient, Mixed community. Photosynthetically active photon flux (PPF) outside the chamber is also shown. Comparison of NCE and PPF

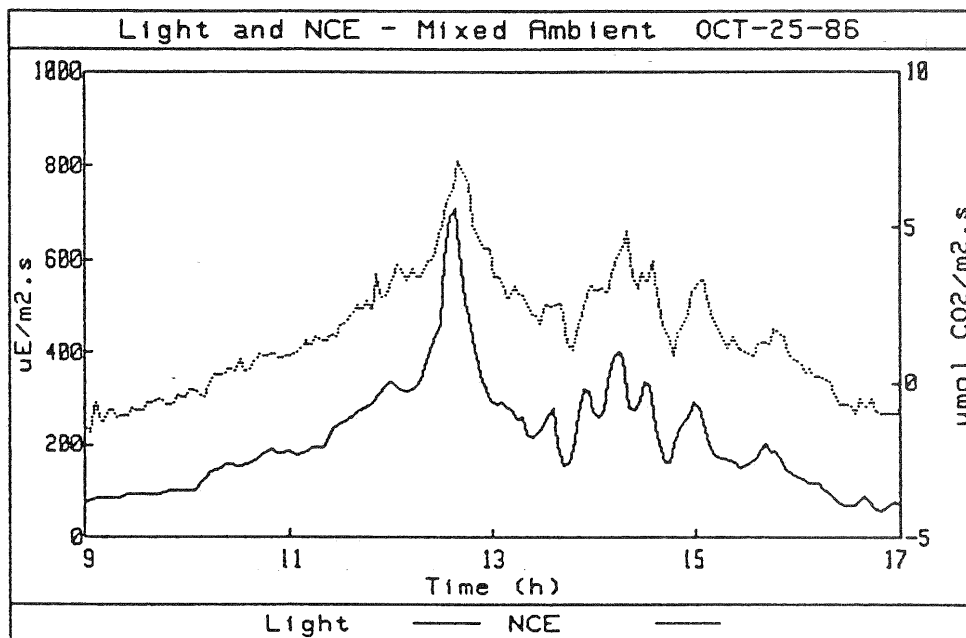


Fig 2.7 The relationship between PPF and net  $\text{CO}_2$  exchange (NCE) in a closed-top, ambient chamber in the Mixed community.

showed that NCE closely tracked PPF. Since plant photosynthetic rates respond rapidly to changes in light, this tracking indicated that we were measuring ecosystem photosynthesis.

Figure 2.8 shows a 24 hr record of NCE from the ambient Mixed community and the simultaneous record of the absolute CO<sub>2</sub> concentration from the same community. Between 0 and 17 hrs on Oct 26 the absolute CO<sub>2</sub> concentration was relatively stable around 350 ppm and measurements of NCE were also stable. When the CO<sub>2</sub> concentration began to fluctuate between 16 and 24 hrs (see earlier discussion of the correlation between wind speed and absolute CO<sub>2</sub> concentration) measurements of NCE became increasingly unstable. This was because changes in ambient CO<sub>2</sub> concentration (measured from the "sample" line at the inlet plenum) were detected by the IRGA before changes in CO<sub>2</sub> concentration of the same air volume at the chamber outlet ("reference" line). We were able to measure NCE during all daylight hours, and during nighttime when ambient CO<sub>2</sub> concentration was constant.

Although NCE was found to track PPF closely, small leaks of ambient air into +260 CO<sub>2</sub> chambers caused a positive offset in the differential CO<sub>2</sub> signal relative to zero (Fig 2.9A). Since we could not determine the precise magnitude of these leaks, the offset was corrected arithmetically by

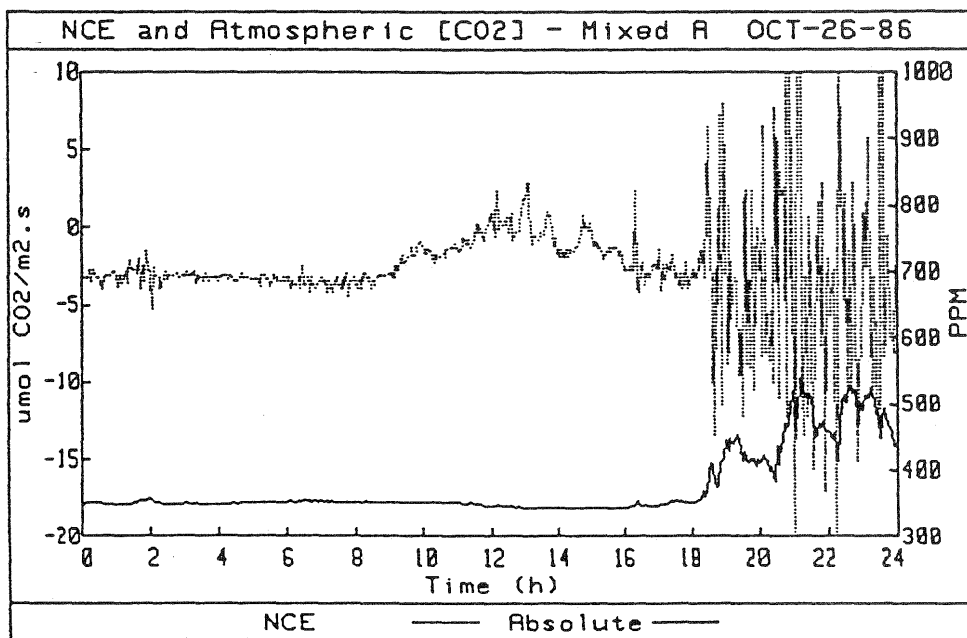


Fig 2.8 Absolute CO<sub>2</sub> concentration and net CO<sub>2</sub> exchange (NCE) in a closed-top chamber in the Mixed community.

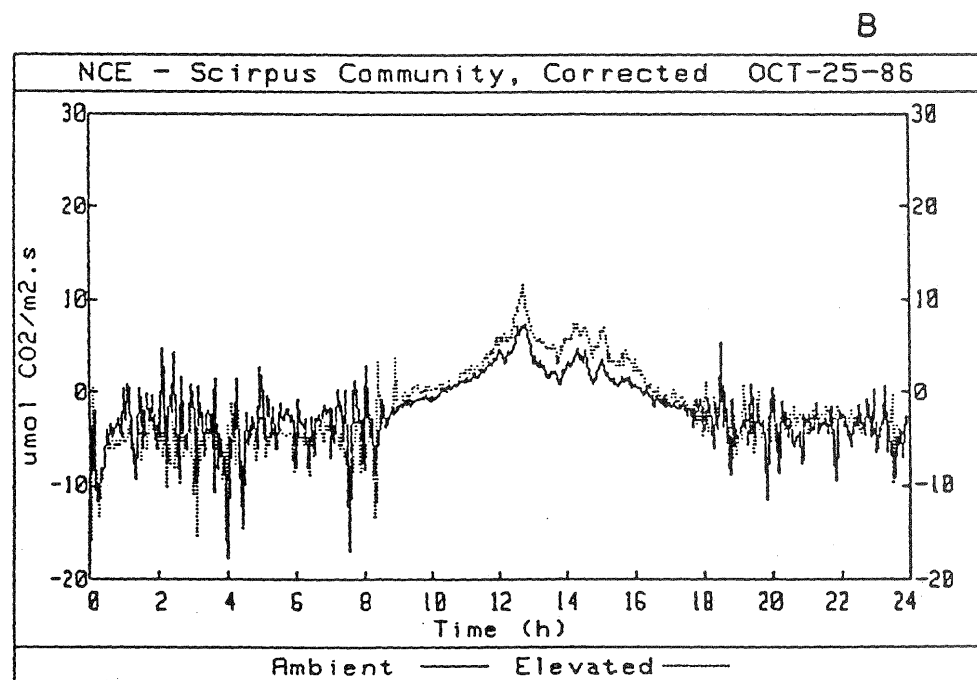
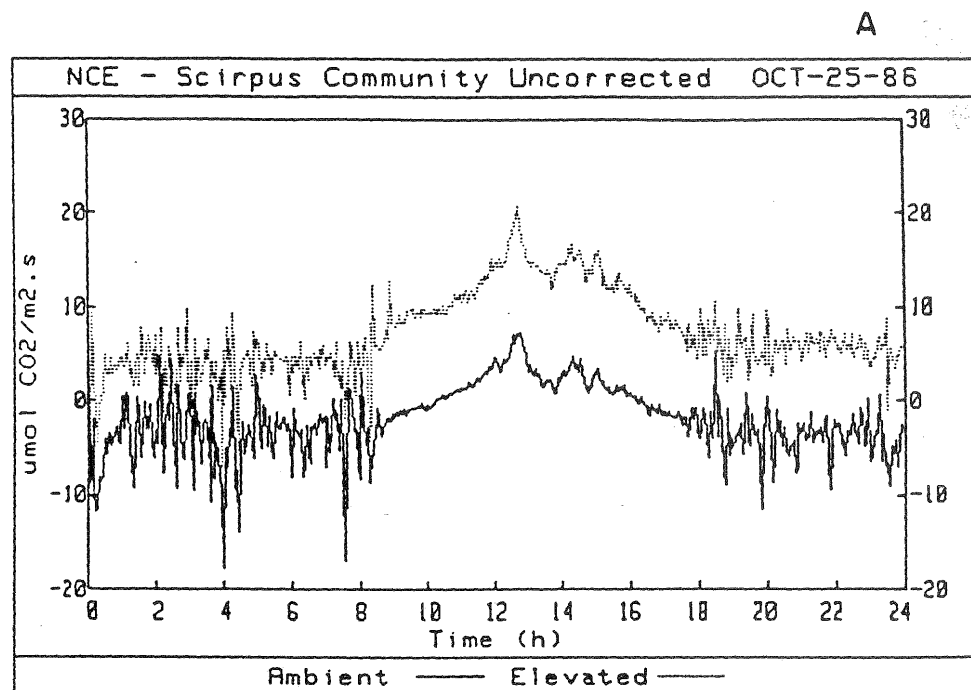


Fig 2.9 Method of correction for leaks in +260 chambers  
 A) positive offset in differential signal and B)  
 differential signal after nighttime respiration in +260  
 and ambient chambers was set equal.

making respiration in the +260 CO<sub>2</sub> treatment equal to respiration in the ambient treatment. Average nighttime respiration was then set equal for ambient and +260 chambers from the same community on the same day (Fig 2.9B). All NCE data from +260 chambers were treated in this way. We have since been successful in sealing the chambers against such leaks, although this was not achieved in time to collect NCE data. The effects of elevated CO<sub>2</sub> on plant respiration are poorly understood, with positive, negative, and neutral effects reported (Hrubec et al. 1985; Gifford et al. 1985).

## II. Chamber Microenvironment

### A. Light

#### 1. Light quality

The material used for the chamber covers (Melinex 071, ICI Americas Inc, Wilmington, Delaware) was developed for use in greenhouses. It was designed to be durable and to resist de-polymerization by ultra-violet light. Melinex has layers of UV stabilizers on both surfaces which retard degradation of the polymer. This suggested that Melinex had optical properties which might change the quality of solar radiation incident on the plants within the chamber.

A transmission spectrum for Melinex was run using a Cary

spectrophotometer (Fig 2.10). Multiplication of the solar spectrum by the transmission spectrum gave the spectral distribution of light reaching the plants inside the chamber. Curve A is the solar spectrum, normalized to 100% on the highest value, near 460 nm. Curve B is the transmission spectrum for Melinex which shows a sharp cut-off at 330nm but rises steeply to 80% transmission at 400nm. The effect of the spectral characteristics of Melinex on the solar spectrum reaching the plants is shown by curve C. Above ca. 380 nm there was very little effect on light quality. The manufacturers specifications indicated that Melinex had little effect on light quality up to 2100 nm. Longwave radiation above 3000 nm was reported to be affected by Melinex, about 25% was reflected and about 8% was absorbed.

## 2. Light quantity

The average transmission of Melinex in the 400-700nm band, the photosynthetically active region of the solar spectrum, was approximately 90% (Fig 2.10 and manufacturer's specifications). To further characterize chamber effects on light quantity, quantum sensors were placed at canopy height inside and outside the chamber. Photosynthetically active photon flux was monitored throughout the day. Figure 2.11A is a 24 hr record of incident PPF inside and outside a closed top chamber. PPF within the chamber was very close to PPF outside. Comparison of the data collected inside the chamber



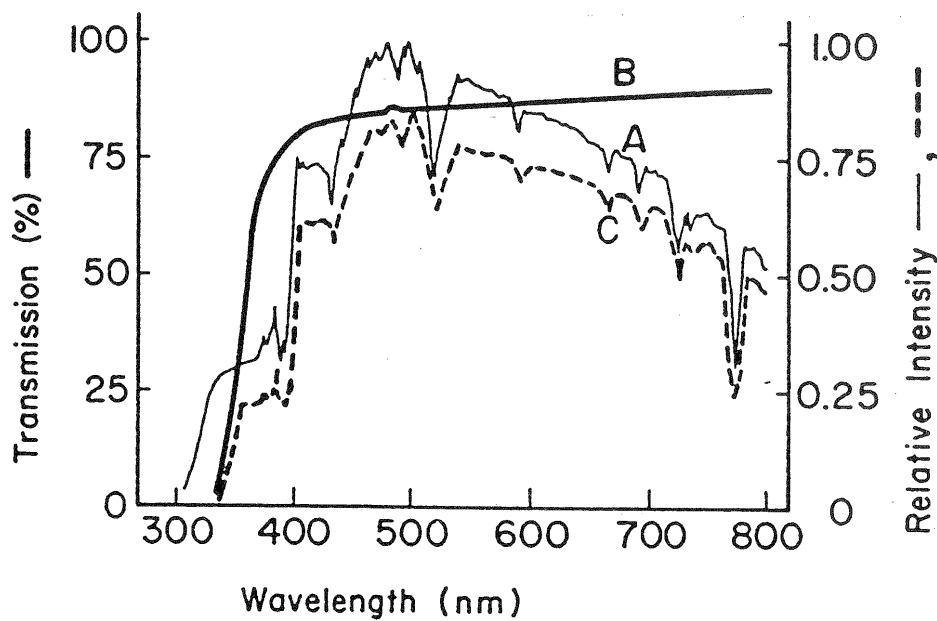


Fig 2.10 Effect of chamber covering on light quality. Light transimission characteristics of Melinex 071 (line B), relative intensity of sunlight (line A) and relative intensity of sunlight after having passed through Melinex 071 (line C).

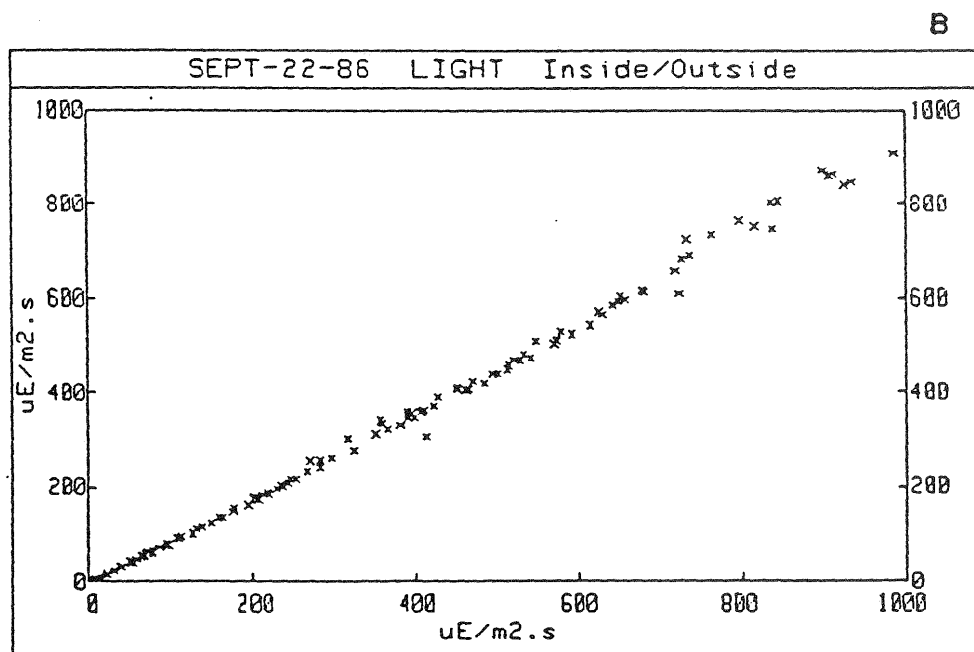
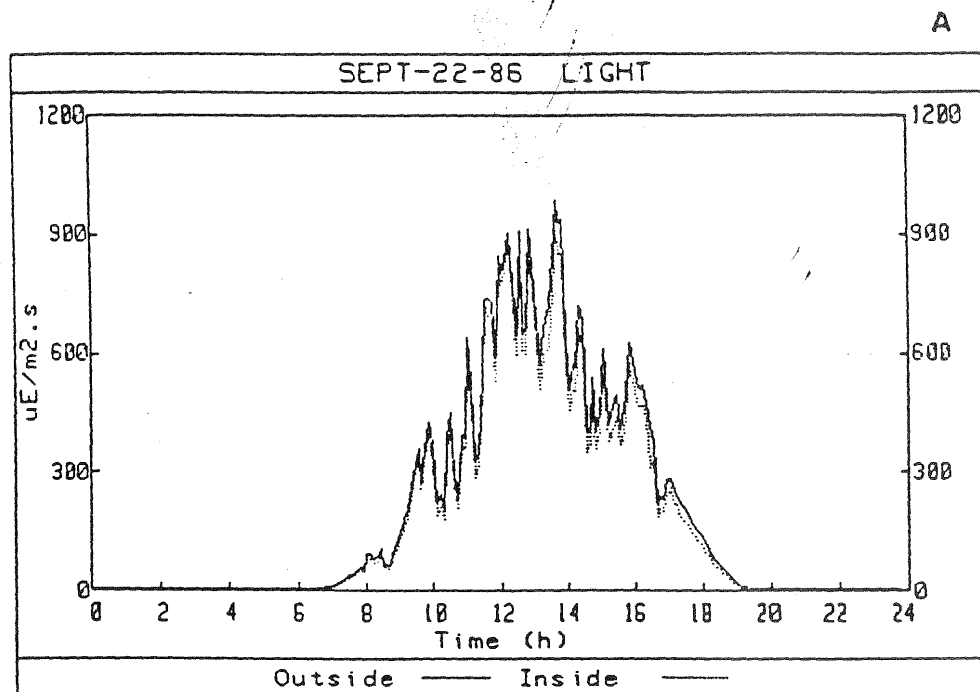


Fig 2.11 Effect of chamber covering on light quantity.  
 A. PPF outside and inside an open-top chamber. B.  
 Same data with light inside plotted on the Y-axis and  
 light outside plotted on the X-axis.

against that outside the chamber, confirmed that the reduction of PPF by the chamber was approximately 10% (Fig 2.11B).

It should be noted that the exact amount of the decrease in light quantity is a function both of solar elevation and the placement of the radiometer inside and outside the chamber. Material aging may also affect light attenuation by the chambers. We intend to measure light inside and outside the chambers throughout the course of our experiments. We will then be able to correct for the effect of the chamber on net CO<sub>2</sub> exchange if necessary. Other studies have reported a reduction in light intensity inside large open top chambers from 10 to 15% (Olszyk et al., 1980; Heagle et al., 1979; Unsworth 1982).

## B. Air movement

### 1. Wind speeds within the chamber

Wind speeds within the chamber were measured on an empty chamber sealed at the bottom. Measurements were made with a hot wire anemometer (Kurtz, model 1440M) at five levels within the chamber; 3, 15, 30, 60, and 90 cm from the bottom. At each level, measurements were made at five positions along two transects; one transect running from the center of the air inlet plenum to the opposite side of the

chamber and the other perpendicular to and intersecting the first transect in the center of the chamber. A total of 60 wind speed measurements were made. These measurements were repeated three times to test the effect of the deflectors on the wind speed profile within the chamber. Results are shown in Table 2.1.

Wind speeds ranged from  $3.2 \text{ m s}^{-1}$  directly in front of the blower to  $0.1 \text{ m s}^{-1}$  along the side of the chamber above the inlet plenum. In all three deflector configurations there were two areas of high wind speed in the chamber, one at the bottom of the chamber and the other at 30 to 60 cm above the bottom. In general, wind speeds in the bottom 30 cm of the chamber were highest when the inlet plenum deflector was down. We used the deflectors in the down position to insure effective circulation of air around the plant canopy.

## 2. Chamber volume exchange rate

The rate of volume exchange for an open top chamber was determined by dividing the air flow rate through the chamber by the chamber volume. Flow rates through the chamber were calculated by replacing the delivery tube with a 1.2 m length of aluminum pipe, measuring the average wind speed in the pipe and multiplying the wind speed by the cross sectional area of the pipe. Wind speed was measured using a hot wire

Table 2.1 Wind speed profile within the chamber. Each value represents the mean of 9 observations. The range of values is given in parentheses. The three experiments tested the effect of the position of the air deflectors on the wind speed profile. In Exp 1, both deflectors were positioned horizontally, in Exp 2, both were positioned down, and in Exp 3, the upper deflector was positioned up and the lower was positioned down.

Height above bottom [cm]	Exp 1	Exp 2 $\text{m s}^{-1}$	Exp 3
90	0.37 (0.1-0.7)	0.50 (0.2-0.8)	0.63 (0.4-1.1)
60	1.28 (0.4-2.9)	0.34 (0.2-0.7)	0.60 (0.3-0.9)
30	0.49 (0.5-0.8)	1.42 (0.4-3.2)	1.26 (0.3-2.3)
15	0.57 (0.3-0.9)	0.74 (0.4-2.0)	0.50 (0.3-0.7)
3	1.52 (0.8-2.0)	0.95 (0.5-1.7)	1.64 (0.5-2.3)

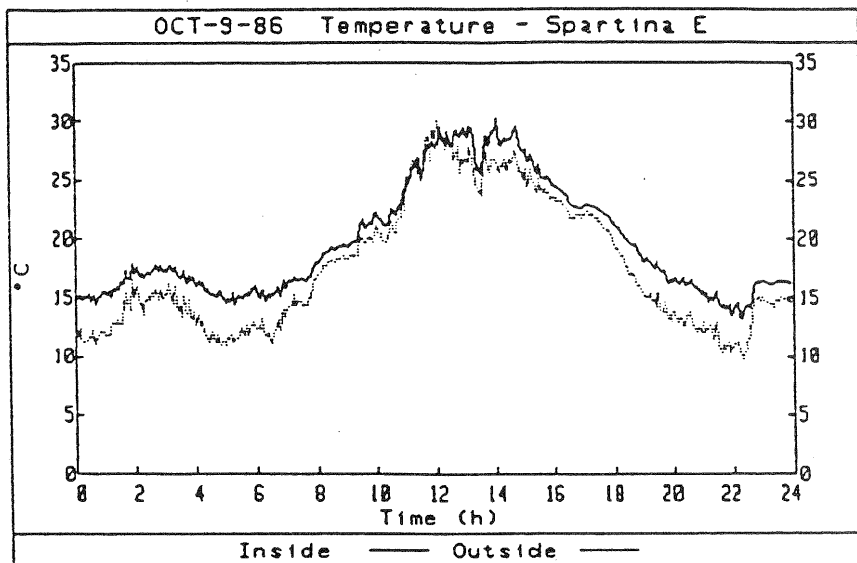
anemometer. Average flow rate for the six chambers was  $2091 \pm 52 \text{ l min}^{-1}$ . The chamber volume was  $480 \text{ l}$ , giving an exchange rate of  $4.4 \text{ changes min}^{-1}$  ( $0.073 \text{ s}^{-1}$ ).

### C. Temperature

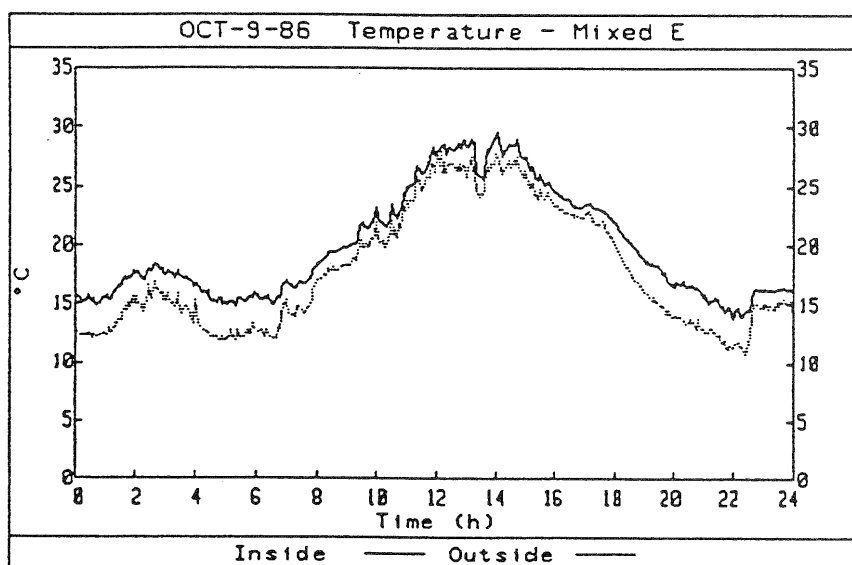
#### 1. Air temperature

One of our first observations about air temperature was that there was a temperature difference of about  $2 \text{ C}$  between the air within the chamber and the air outside, and that this increase was virtually constant at night but variable during the day. Because a temperature increase of this sort may be important to ecosystem processes, we made an effort to understand what physical processes within the chamber were causing this temperature increase. It was also hoped that through such understanding we could determine the best method to reduce these effects. By placing thermocouples at different locations within the chamber we determined where the rise in temperature occurred. Comparisons with outside temperatures helped us to understand the role of wind and radiant heating in the energy budget of the chamber.

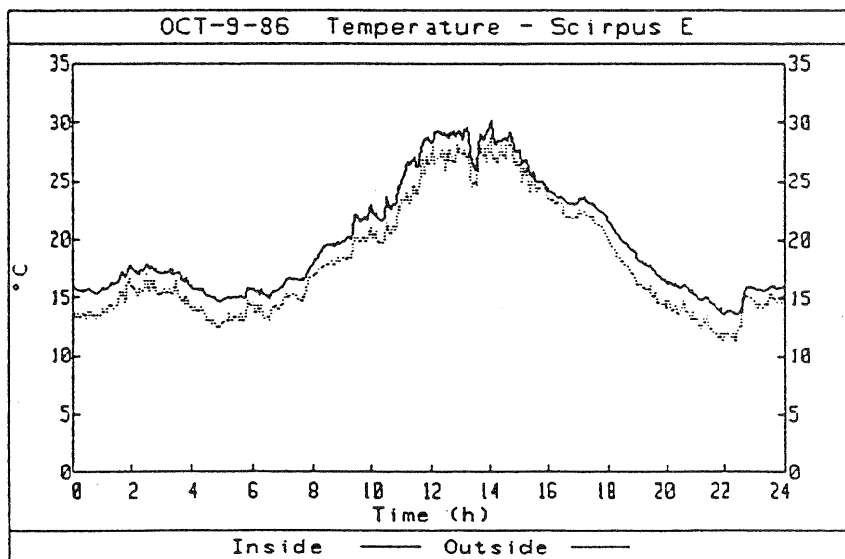
Twenty-four hr records of air temperatures inside and outside three open top chambers are shown in Fig 2.12. Air temperature was measured with  $24 \text{ ga}$  copper-constantan



A



B



C

Fig 2.12 Air temperatures at canopy height inside and

thermocouples positioned at the top of the plant canopy and shielded with aluminum foil. Figure 2.13 is a plot of the difference between inside temperature and outside temperature during the 24 hr period shown in Fig 2.12. Air temperatures within the chambers were less than 2.0 C above those outside the chambers during the day but closer to 3.0 C above outside air temperatures at night.

We wanted to determine the source of heat which caused the increase in air temperature as it passed through the chamber system. To do this we placed thermocouples at various points along the pathway of air through the chamber (Fig 2.14). The thermocouple positions are labeled as follows: RBI, immediately in front of the remote blower air intake; RBO, at the remote blower outlet; MBI, immediately upstream of the mixing blower; and MBO, at the mixing blower outlet. There were also thermocouples at the top of the plant canopy inside the chamber, CHM; and at canopy height outside the chamber, AMB.

Data shown in Figs 2.15, 2.17 and 2.18 are from the +260 chamber in the Mixed community on October 29. The chamber was in the open top configuration from 0 to 1800 hrs and closed top after 1800 hrs. This discussion will focus on data for the open top chambers since this is the configuration that chambers will be in most of the season. Figure 2.15A shows the 24 hr record of air temperatures



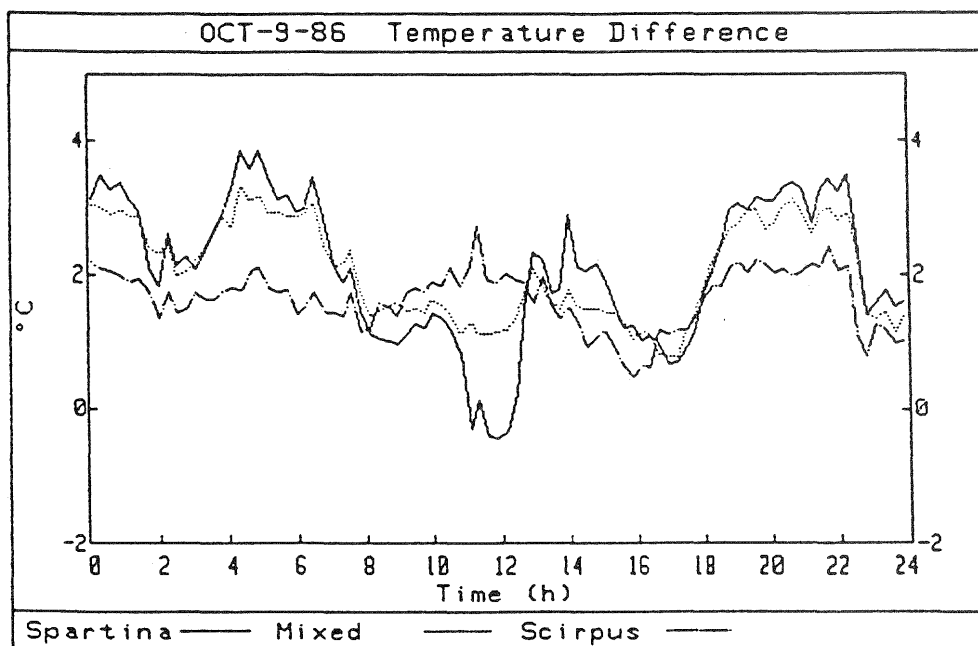


Fig 2.13 Difference in air temperature at canopy height from inside to outside open-top chambers in the three communities.

## Location of Thermocouples

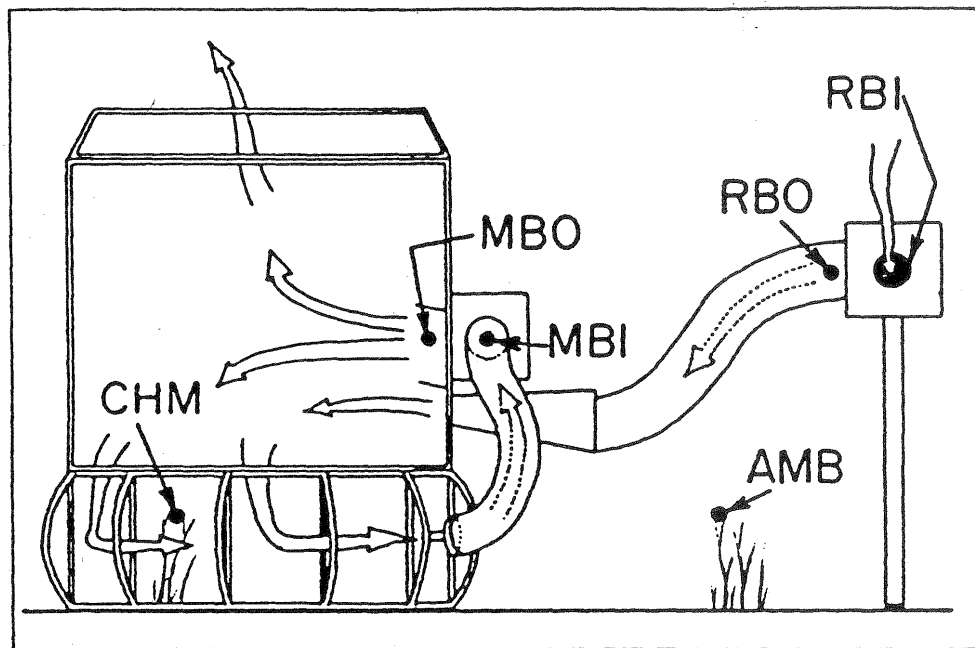


Fig 2.14 Location of shielded thermocouples in an open-top, +260 chamber in the Mixed community. Abbreviations are: AMB, ambient canopy; CHM chamber canopy; RBI, remote blower inlet; RBO, remote blower outlet; MBI, mixing blower inlet; and MBO, mixing blower outlet.

measured inside (CHM) and outside (AMB) the chamber. The difference between these temperatures (CHM-AMB) is shown in Fig 2.15B.

Air temperature increased about 1.2C as it passed each blower (Figure 2.16, RBO-RBI, MBO-MBI). These blowers consume approximately 61 and 74 watts respectively and this is slightly more than the amount of energy required to raise the temperature of dry air at STP by the amount observed.

The difference between inside and outside air temperatures at canopy height shown in Fig 2.15B ranged between -1.0 and 3.5 C and, therefore, could not be entirely explained by the relatively constant amount of heat added by the blowers. Temperature gradients in the boundary layer of the plant canopy outside the chamber also had an effect on the inside-outside temperature difference. Air drawn into the chamber by the remote blower came from a position much higher in the gradient than the location of the thermocouple outside the chamber measuring air temperature at the top of the plant canopy.

The following discussion is offered to clarify the interaction between solar radiation and wind with the effect of the chamber on air temperature. Temperature profiles above vegetated surfaces have been well documented (e.g. Rosenberg 1974). On sunny days, downward radiation heats the

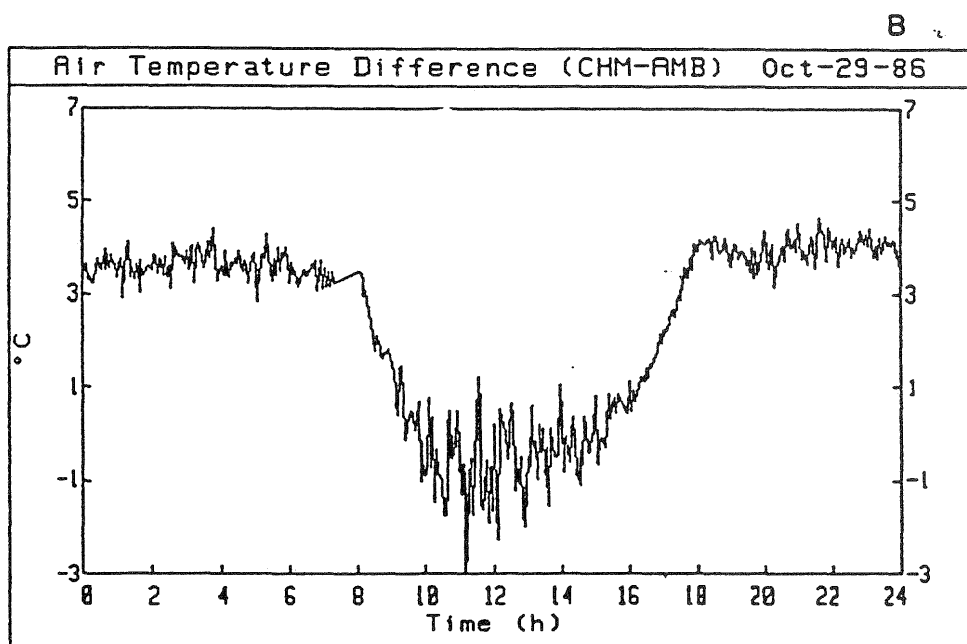
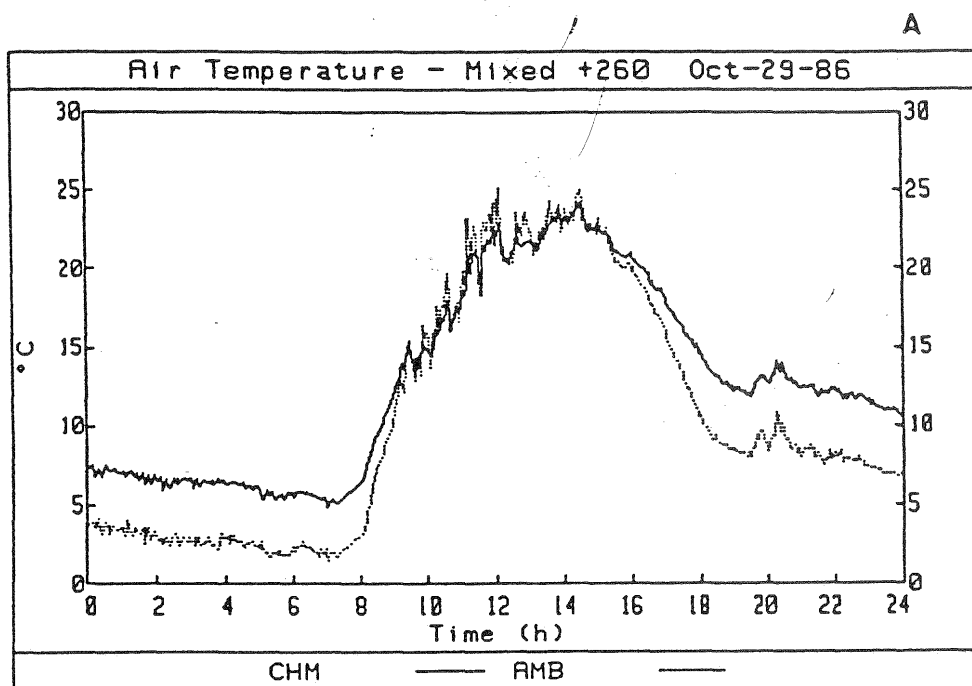


Fig 2.15 A. Air temperatures measured at the top of the canopy inside (CHM) and outside (AMB) a chamber in the Mixed community. B. the difference between CHM and AMB. The chamber was open-top from 0 to 1800 hrs and closed-top from 1800 to 2400 hrs.

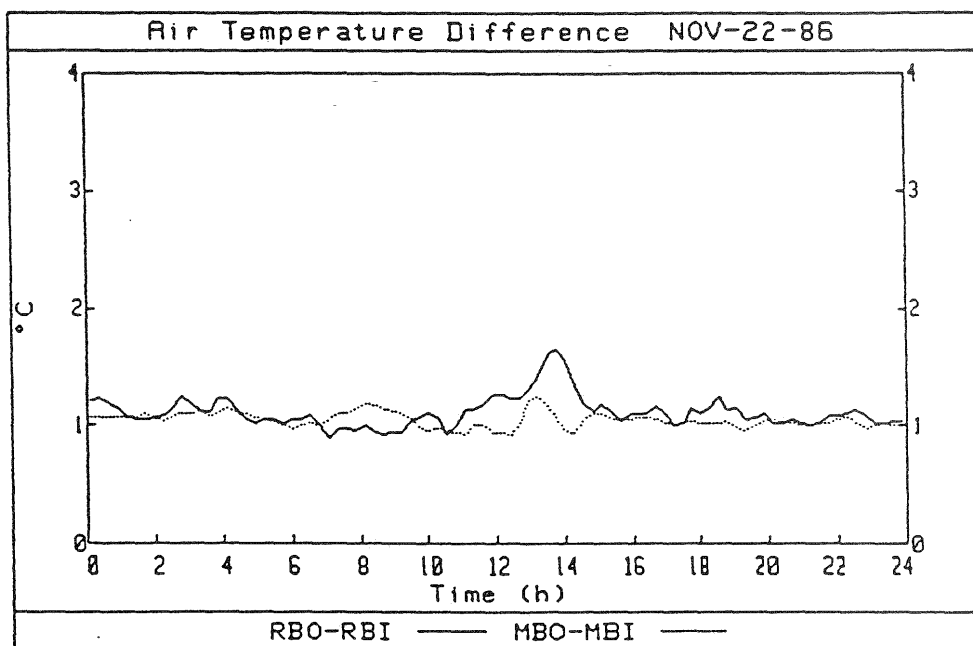


Fig 2.16 The increase in temperature of air passing through the remote (RBO-RBI) and mixing (MBO-MBI) blowers.

vegetation. This heat is dissipated by re-emission of longwave radiation, convection, and transpiration. If absorbed radiation is not balanced by losses of heat due to re-radiation and transpiration, the temperature of the vegetation rises and this establishes a temperature gradient in the boundary layer. This temperature gradient is the driving force for convective heat exchange. In this condition, air temperature is highest near the canopy surface and decreases with height above the canopy as heat is dissipated by convection. This temperature gradient, with the highest temperatures at ground level, is referred to as a lapse condition. On still, clear nights vegetation re-radiates more radiation than it receives and cools below air temperature. This establishes a temperature gradient with the lowest temperatures at ground level and is called a temperature inversion. Wind disrupts the boundary layer, increasing convective warming of the vegetation at night and cooling during the day. Cloudiness tends to balance radiation gains and losses during the day or night, making the temperature profile isothermal.

Data from this study illustrate these temperature gradients. Figure 2.17A shows the difference between the AMB and RBI thermocouples on a partly cloudy day. Temperatures at AMB were about 4 C warmer during the day and about 2 C cooler at night than at RBI. Since the AMB thermocouple was located 20 cm above the ground (at the top of the canopy) and

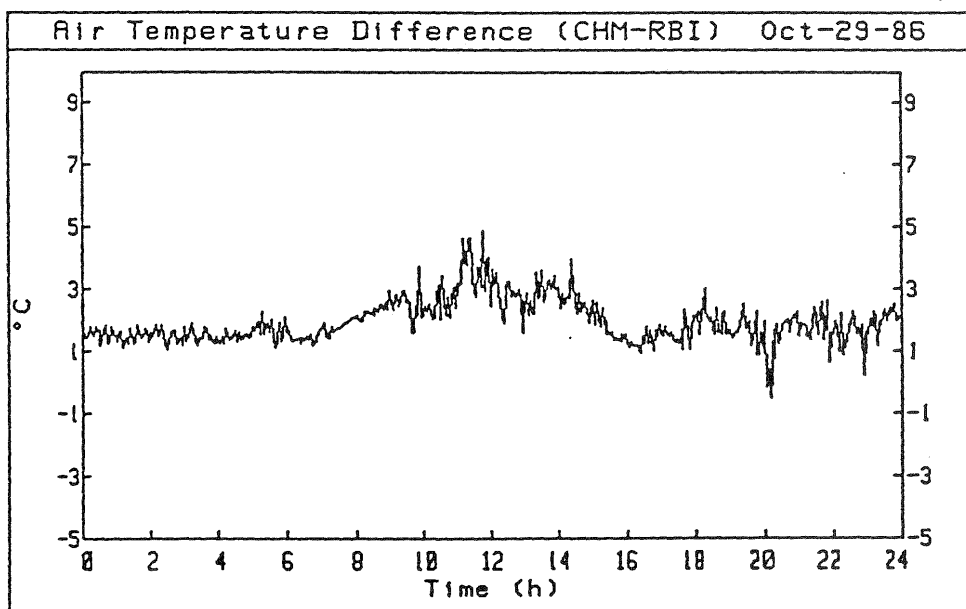
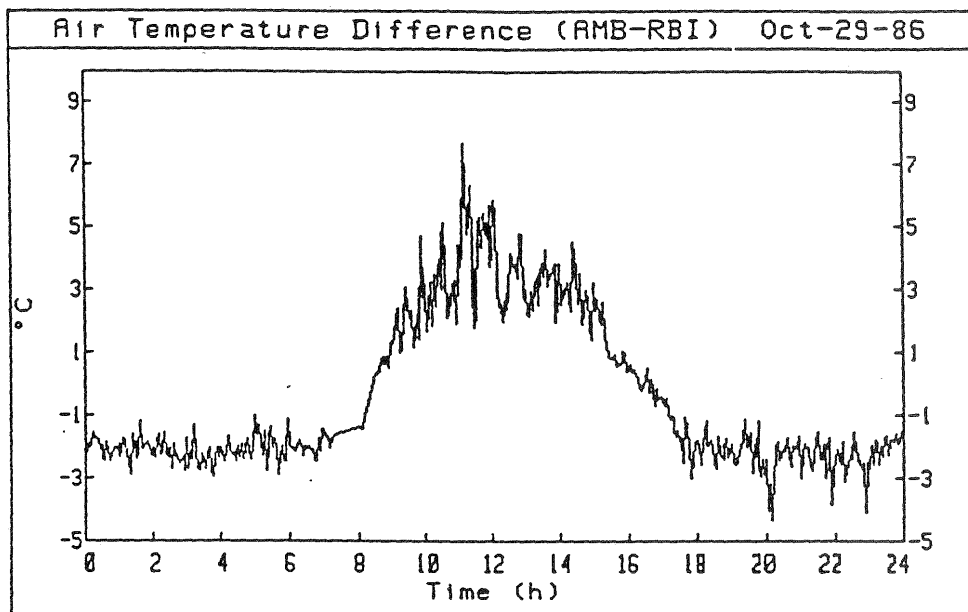


Fig 2.17 Air temperature difference between the top of the canopy outside the chamber (AMB) and at the remote blower inlet (RBI) (A) and top of the canopy inside the chamber (CHM) and RBI (B).

the RBI thermocouple (in the remote blower air inlet) was located 80 cm above the ground, these data indicated typical lapse conditions during the day, and a temperature inversion during the night. Thus, air entering the remote blower was cooler than air at canopy height outside the chamber (AMB) during the day and warmer than air at AMB at night.

Temperature gradients existed outside the chamber but probably not inside the chamber because of the high turbulence and air flow pattern generated by the blower system. This was demonstrated by the fact that the difference between the air temperature at canopy height inside the chamber (CHM) and at the entrance to the remote blower (RBI) was nearly constant (Fig 2.17B). The air temperature at CHM was about 1.5 C warmer than RBI at night and about 3 C warmer than RBI during the day.

Effects of the chamber on the energy budget of the vegetation within it can be summarized as follows. First, convective and latent heat exchange are promoted by the constant and increased air circulation inside the chamber which forces air downward through the canopy (Fig 1.1A and see discussion of air movement below). This effect probably increases convective and transpirational cooling of the vegetation within the chamber compared with the vegetation outside the chamber during the day. Second, downward shortwave radiation is eliminated in the UV region and



reduced / 10% in the visible and near-IR regions (Fig 2.11B). This reduces the radiant heat load on the canopy during the day. Third, the chamber covering reflects some longwave radiation emitted from the plant canopy. This effect is probably most effective at night in reducing radiant heat loss to the sky. These factors tend to keep the range of the difference between air temperature at the entrance to the remote blower and that within the chamber relatively small. The collective effect of these factors was to make the air temperature inside the chamber warmer than ambient temperature at night but relatively close to and sometimes less than air temperature outside the chamber during the day (Fig 2.15B). This analysis suggests that the warmer temperatures within the chamber at night might be reduced by adding a tube to the remote blower inlet to collect air from near the canopy surface.

Based on this analysis of the temperatures inside and outside the chamber, we would expect that factors that would accentuate lapse conditions outside the chamber during the day, e.g. bright sunshine with low wind speeds, or disrupt the inversion layer at night, e.g. strong winds, would tend to reduce the temperature difference between CHM and AMB. Figure 2.18A shows the relationship between wind speed and temperature differences at night on Oct 9. During periods when the wind speed was less than  $0.7 \text{ m s}^{-1}$  the temperature difference was ca. 3 C. As soon as wind speed increased,

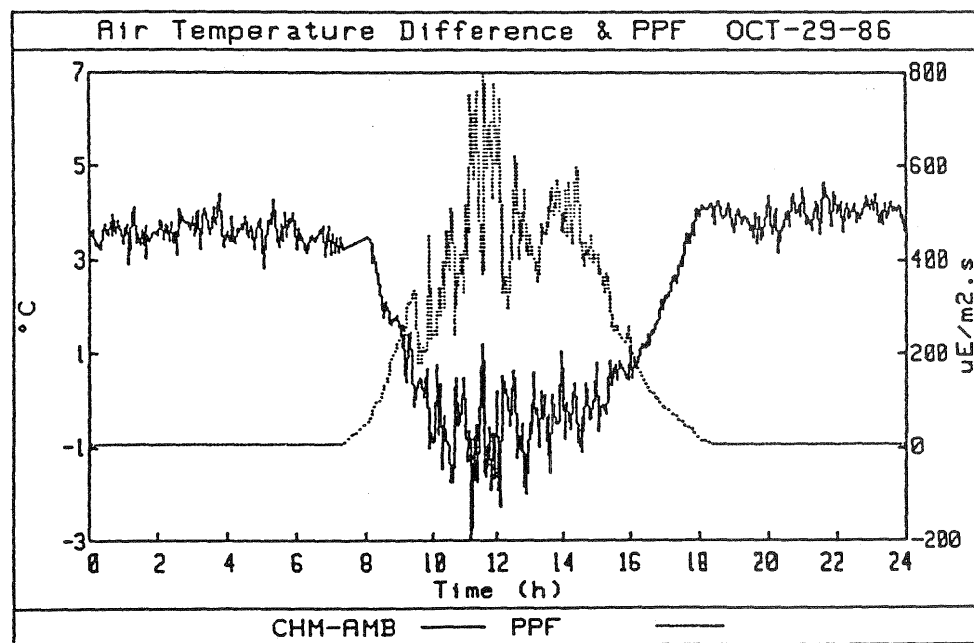
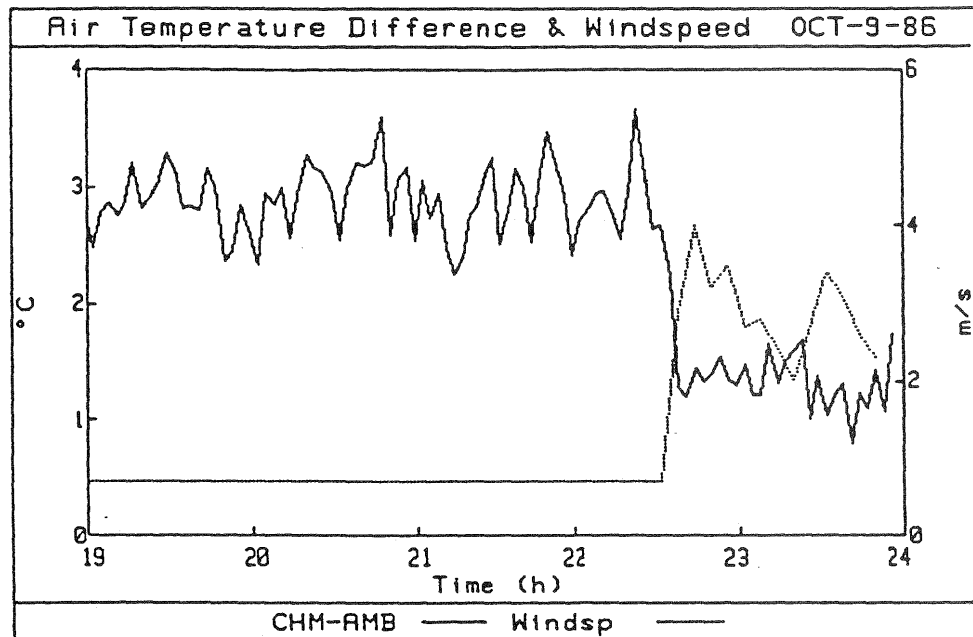


Fig 2.18 Air temperature difference between the top of the canopy inside the chamber (CHM) and outside the chamber (CHM) and its relationship to A) wind speed, and B) PPF.

the temperature difference dropped to about 1 C. Figure 2.18B shows the relationship between PPF and air temperature difference. Air temperature differences decreased as PPF increased, with the most negative differences corresponding to the highest PPF.

In order to examine the day to day mean value of the difference between air temperatures inside compared to outside the chambers, we determined mean values of data sampled every 3 minutes for 5 to 7 days, divided the results into day and night, and compared the two chamber configurations in three different communities. The results of this comparison are shown in Table 2.2. Nighttime data for this table were collected from 0 hrs to sunrise and from sunset to 24 hr. Daytime data were from PPF values above  $100 \mu\text{E m}^{-2} \text{ s}^{-1}$ .

In open top chambers, the daytime range of mean air temperature differences was 1.3 to 2.1 C for the three community types. The range at night was 1.6 to 2.2 C. The temperatures in the Scirpus community were higher than in the Spartina community, and this difference was found to be statistically significant (Table 2.2). At night, no statistically significant differences were found although the trends in the means were toward lowest temperature in the Scirpus community.

Table 2.2 Air temperature difference (inside-out) measured at canopy height in three communities Spartina (Sp), Scirpus (Sc) and Mixed (Mx). Means and standard deviations were derived from average daytime and nighttime temperature differences. Average daytime temperature differences were calculated from ca. 170 observations and nighttime from ca. 240 observations. Ranges were from 15 min. averages.

Config- uration	Commun- ity	DAY				NIGHT			
		Mean	s.d.	N	Range	Mean	s.d.	N	Range
Open-top	Sp	1.3	.14	7	-.4-+2.9	2.2	.77	7	.8-4.2
	MX	1.7	.27	7	.8-2.7	2.1	.62	7	.8-3.5
	Sc	2.1	.56	6	.4-3.6	1.6	.46	6	.7-2.5
Closed- top	Sp	2.3	.28	6	.4-4.0	2.6	.37	6	1.6-3.7
	Mx	2.2	.66	6	-.2-+4.3	2.5	.47	6	1.7-4.6
	Sc	2.7	.51	5	1.7-5.2	2.0	.24	6	1.5-3.0

In closed top chambers, the trends were the same as for the open top chambers but the statistically significant differences were at night. The overall temperature difference was about 0.5 C greater in the closed top chamber than in the open top chamber.

Other studies have reported 0 to 2 C temperature differences for open top chambers (Mandl et al., 1973; Kats et al., 1976; Heagle et al., 1979; Olszyk et al., 1980). Nighttime temperature differences were not reported in the previously cited studies.

## 2. Canopy temperature

Air temperature is an important factor in the energy budget of a vegetation canopy but physiological processes such as photosynthesis and respiration are directly dependent on tissue temperature. Canopy temperatures were measured on several days between Sept 6 and Nov 3 using a hand-held, infra-red thermometer. A Barnes Engineering, model PRT-10 was used in September and a Everest Interscience, model 210 was used in October and November. Mean canopy temperatures inside and outside open top and closed top chambers for several days are presented in Table 2.3. Air temperatures inside and outside the chambers, as well as windspeed and PPF are also given.

Table 2.3 Comparison of canopy and air temperatures inside and outside open and closed top chambers. Canopy temperature was measured using an infra-red radiation thermometer. Air temperatures were measured with shielded copper-constantan thermocouples located at the top of the canopy in the mixed community. PPF ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) was measured with a quantum sensor located outside a chamber in the Spartina community.

		Canopy temperature (C)				Air Temp. (C)		
Date	Time	Inside	In-Out	S.D.	N	Inside	In-Out	PPF
Open-top chambers								
Sept 6	~3:00	27.4	-0.20	1.32	33	---	---	---
Sept 9	~3:00	25.6	-0.73	1.51	31	---	---	---
Sept 11	~2:00	28.1	-0.27	0.34	27	---	---	---
Oct 3	10:15	23.7	0.85	0.50	18	---	---	---
	13:50	26.1	0.55	0.61	18	27	1.0	320
	16:04	26.3	0.21	0.96	18	27	1.5	220
Oct 20	14:20	20.7	-0.68	1.52	19	---	---	---
Oct 22	11:30	20.4	-0.20	0.75	18	24	0.0	760
Oct 23	19:27	14.4	2.98	1.03	18	17	3.0	0
Oct 24	7:08	9.3	2.12	0.68	18	---	---	---
Oct 29	6:10	2.4	3.6	0.49	3	5.5	3.5	0
	16:40	14.2	3.5	0.40	3	16	3.5	50
Closed-top chambers								
Oct 28	12:02	24.3	1.6	----	1	24	1.0	720
	15:15	19.0	1.7	----	1	20	1.5	220
	20:40	5.4	4.2	----	1	8	4.0	0
Oct 30	5:30	8.3	4.3	----	1	26	3.0	95
	14:55	23.9	2.6	----	1	26	3.0	95
Nov 3	11:42	18.6	-0.6	----	1	18	-1.0	760

Canopy temperature differences (inside - outside) in open top chambers during periods of moderate to high light were between -0.73 and 0.85 C. During periods of low light, or at night, canopy temperature differences in open top chambers ranged from 2.1 to 3.6 C. The range of canopy temperature differences was within the range of air temperature differences observed in early October and November. Air and canopy temperature differences in open top chambers were always within 1 C of each other, but canopy temperatures inside the chambers were always slightly less than air temperatures. Canopy temperature differences in closed top chambers were slightly higher at night than in open top chambers. Air and canopy temperature differences in closed top chambers were also within 1 C of each other. The difference between air temperature inside and outside the chamber was a good indicator of canopy temperature difference.

## CHAPTER 3

### CARBON DIOXIDE EXCHANGE AND CARBON BUDGET

Production by natural ecosystems is expected to increase with a rise in atmospheric  $\text{CO}_2$  concentration (Bazzaz et al. 1985) due mainly to an expected increase in photosynthesis and water use efficiency. An increase in ambient  $\text{CO}_2$  concentration usually results in increased intercellular  $\text{CO}_2$  concentration and, at least in  $\text{C}_3$  plants,  $\text{CO}_2$  fixation rates also increase (and sometimes in  $\text{C}_4$  plants too, see Bazzaz et al. 1985). While there is some uncertainty as to whether individual leaf photosynthetic rates will increase after prolonged exposure to  $\text{CO}_2$ , canopy photosynthesis always seems to increase (Acock and Allen 1985; Oechel and Strain 1985). Uncertainty is the handmaiden of practically all information so far obtained in the study of the effects of  $\text{CO}_2$  on vegetation with few exceptions. One of the exceptions is the effect of  $\text{CO}_2$  on stomata. Stomata of all plants grown under natural conditions in which ambient humidity is not unnaturally high during growth respond to  $\text{CO}_2$  by closing. The extent of closing is dependent on the  $\text{CO}_2$  concentration and varies with species and especially between  $\text{C}_3$  and  $\text{C}_4$  plants, but the effect is always the same: elevated  $\text{CO}_2$  reduces water loss and increases water use efficiency.



Direct effects of  $\text{CO}_2$  on photosynthesis and water use efficiency will account for part but not all of the ecosystem response to  $\text{CO}_2$ . Less well understood are the indirect effects of  $\text{CO}_2$  on canopy structure and the allocation of carbon and inorganic nutrients among different plant parts. Examination of both the direct and indirect effects, as well as their interaction, will be necessary to understand the responses of natural plant communities to elevated  $\text{CO}_2$ .

In this chapter we present data on ecosystem and single leaf net  $\text{CO}_2$  exchange under field conditions. Light response curves for the plant communities and for single leaves are analyzed for differences between species and for the effects of elevated  $\text{CO}_2$ . Data on integrated 24 hr carbon dioxide assimilation under ambient and elevated  $\text{CO}_2$  are also presented. These results illustrate the approach we will take, but must be considered preliminary since they were collected during the period of canopy senescence between late September and early November. Nonetheless, they serve to demonstrate the capabilities of the gas exchange system and its use in understanding the effects of elevated  $\text{CO}_2$  on the marsh ecosystem.

## I Ecosystem Net CO<sub>2</sub> Exchange

The measurement of CO<sub>2</sub> exchange presented here is a net measurement which includes the flux of CO<sub>2</sub> from the atmosphere to the leaves of green plants in the canopy, CO<sub>2</sub> arising from respiration within those same leaves, CO<sub>2</sub> arising from respiration by non-photosynthetic plant tissue including belowground roots and rhizomes, and CO<sub>2</sub> arising from soil and dead plant matter. This is therefore a measurement of ecosystem net CO<sub>2</sub> exchange and it is the measurement desired for determination of the ecosystem carbon balance. No effort is made to distinguish the sources and sinks described above. This is a technically difficult task and beyond the objectives of this study, although it may well be the subject of future research in the salt marsh ecosystem. Wetlands plants have an abundance of aerenchymous tissue and an unknown amount of respiratory CO<sub>2</sub> originating in the roots and rhizomes is transported to the leaves through lacunae. This CO<sub>2</sub> originating in the belowground organ is assimilated by photosynthetic tissue. Although this constitutes an important source for CO<sub>2</sub> in photosynthesis of wetlands plants, carbon re-cycled in this manner is neither a gain or a loss in the ecosystem carbon budget.

## A. Light response characteristics

Light response curves for the three communities were constructed by combining daytime ecosystem net CO<sub>2</sub> exchange (NCE) data with simultaneous measurements of photosynthetically active photon flux (PPF). The data points were obtained by averaging NCE and PPF over 15 min intervals. This was necessary because NCE data were obtained for each chamber only once every three minutes throughout the day while data for PPF were being recorded every 30 seconds. Figures 3.1 and 3.2 show representative results from September 22 and October 25 respectively. September 22 preceded the date that CO<sub>2</sub> was elevated (see Append B) and all six chambers were under ambient conditions. On October 25, three chambers had been exposed to ambient +260 CO<sub>2</sub> for 30 days. These data illustrate the accuracy with which NCE could be monitored with the chambers in closed top configuration.

The six light response curves from September 22 were plotted together to illustrate the differences in NCE among the three communities under normal ambient CO<sub>2</sub> and to gauge within community variability (Fig 3.3A). Maximum NCE was highest in the Mixed community (ca 20  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) and lowest in the Spartina community (ca 10  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ). The replicate Scirpus and Spartina chambers were quite uniform in

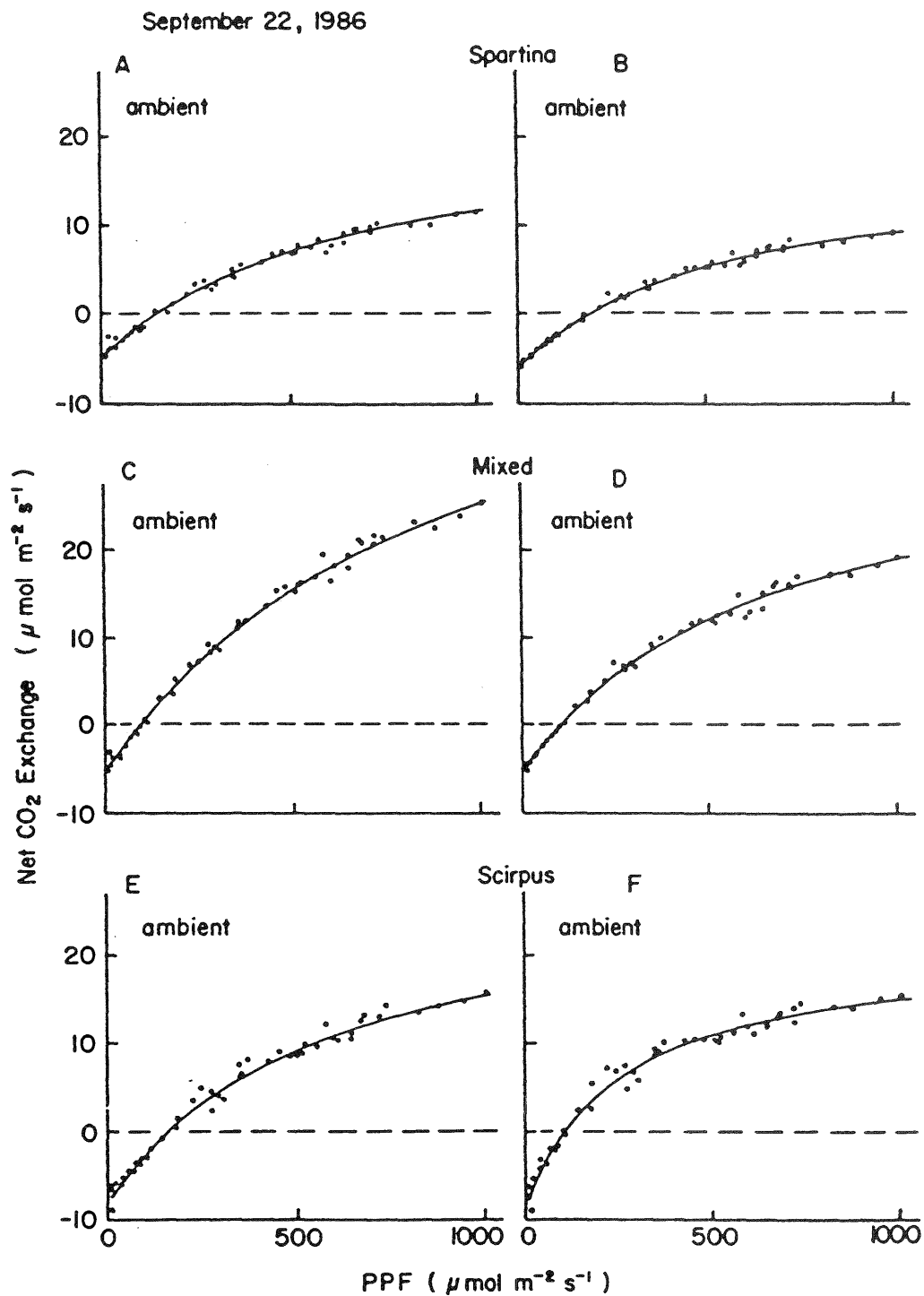


Fig 3.1 Canopy light response curves for three salt marsh communities under ambient CO<sub>2</sub> concentrations. 100% *Spartina patens* community (A,B), 100% *Scirpus olneyi* community (E,F) and a mixed community of *S. patens*, *S. olneyi* and *Distichlis spicata* (C,D). Curves were fit using least squares regression.

October 25, 1986

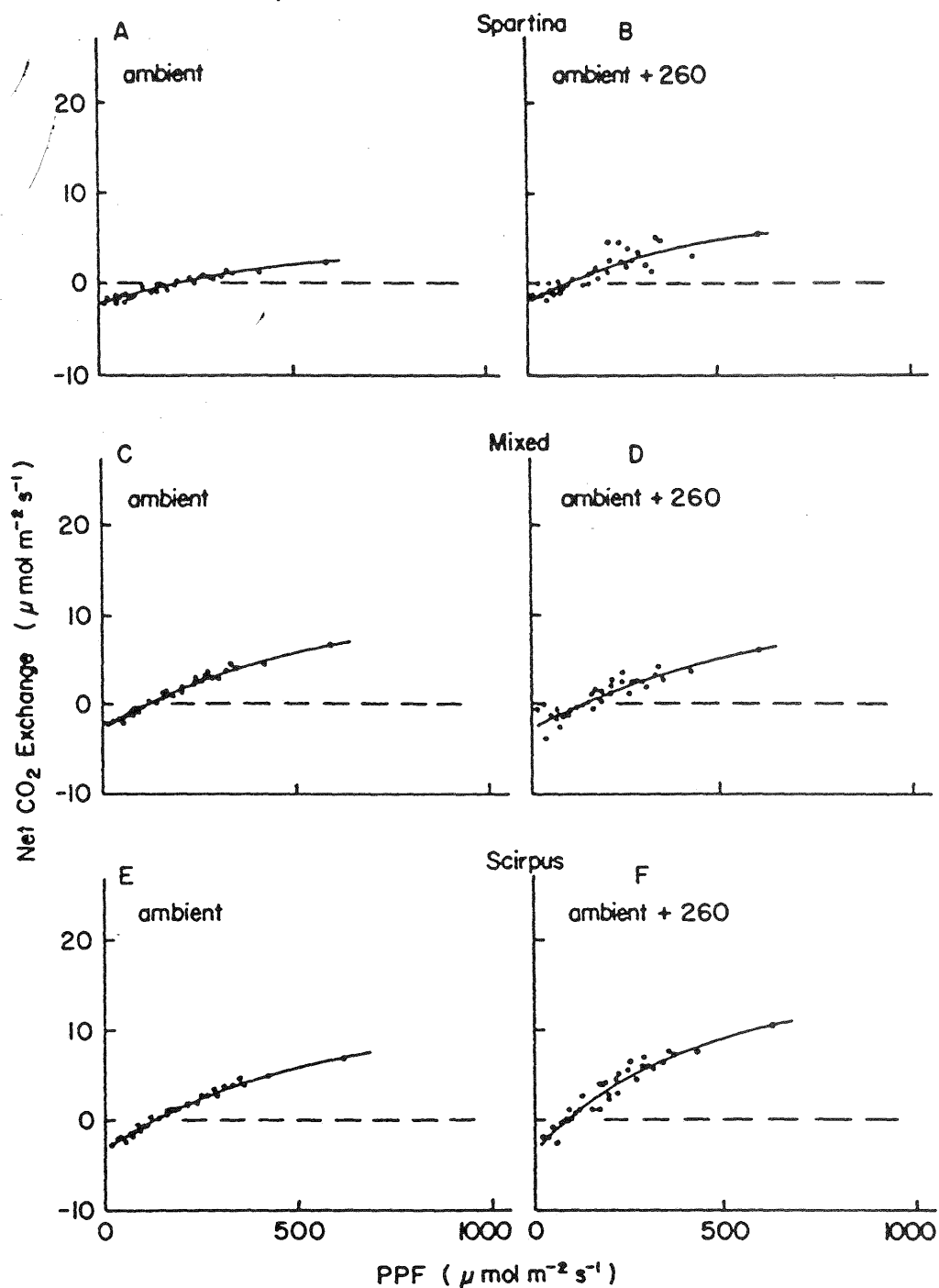


Fig 3.2 Canopy light response curves for three salt marsh communities under ambient (A,C,E) and ambient +260 ppm CO<sub>2</sub> (B,D,F) concentrations.

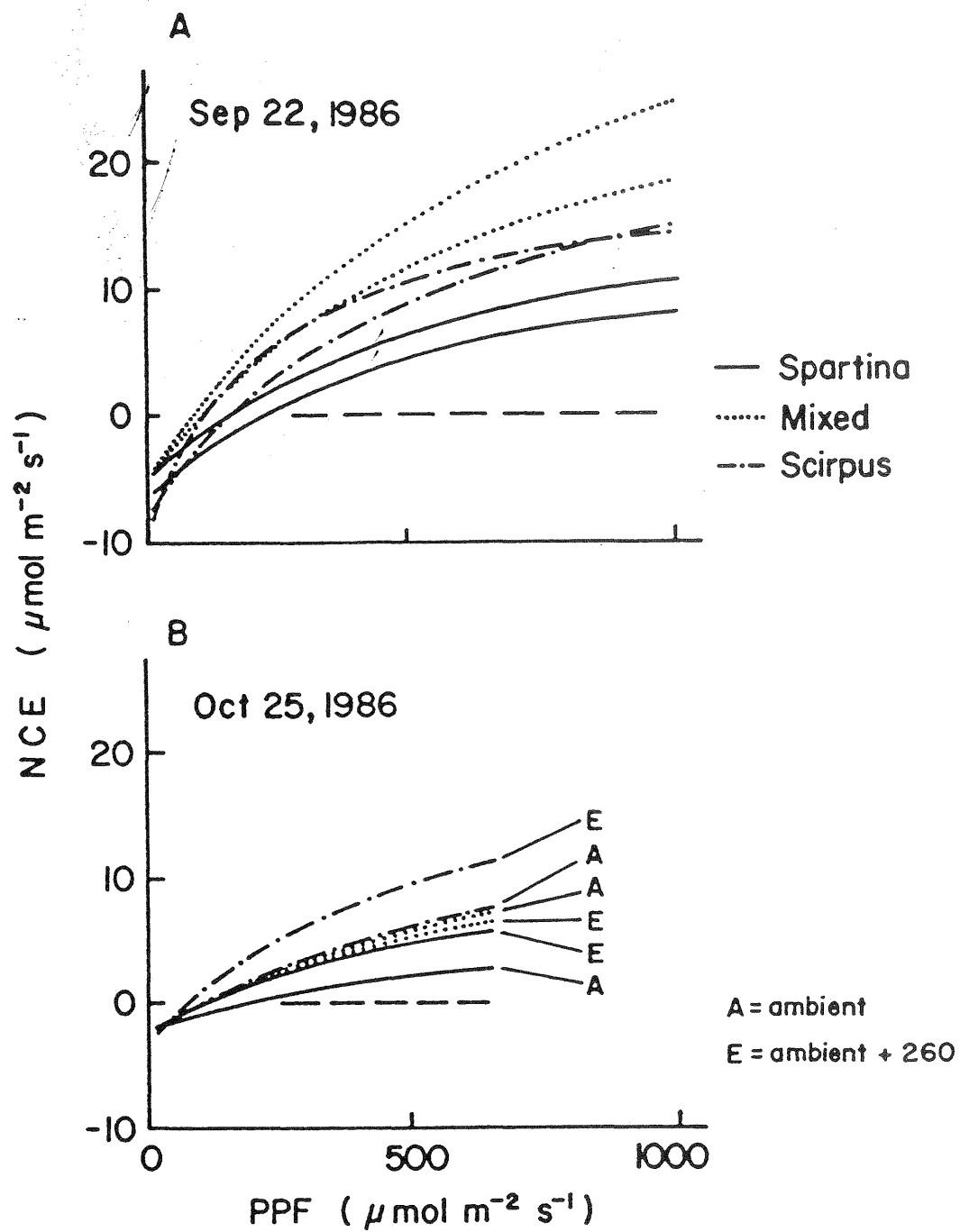


Fig 3.3 Comparison of canopy light response curves from Sept. 22 (A) and Oct. 25 (B).

their responses while the Mixed chambers were more variable. After CO<sub>2</sub> had been elevated (Fig 3.3B, October 25), the Spartina community continued to show the lowest NCEmax, regardless of CO<sub>2</sub> concentration, but the Scirpus community had higher uptake rates than did the Mixed community. Within a community, chambers with +260 CO<sub>2</sub> had higher NCEmax than chambers at ambient CO<sub>2</sub> concentration.

The model we fit to the light response data is shown in Fig 3.4. Dark respiration (R), the light compensation point (c), quantum yield (Q), and maximum net CO<sub>2</sub> exchange rate (NCEmax) were calculated using this model. R equals the y intercept, c the x intercept, Q the slope at c, and NCEmax the net CO<sub>2</sub> exchange at maximum PPF (PPFmax) for that day. Table 3.1 lists these parameters of ecosystem gas exchange for 10 days between September 17 and November 1.

Several trends were apparent from the data from Table 3.1. Maximum NCE under ambient CO<sub>2</sub> increased from September 17 to September 29 and then decreased in steps through the end of the season. The Spartina community had the lowest NCEmax throughout the measurement period. The Mixed community had the highest NCEmax in September but was about equal to the Scirpus community after October 17. These trends were similar to those reported by Drake (1984) for two communities located near the present study site. He documented a decline in NCEmax from about 10  $\mu\text{mol m}^{-2} \text{ sec}^{-1}$

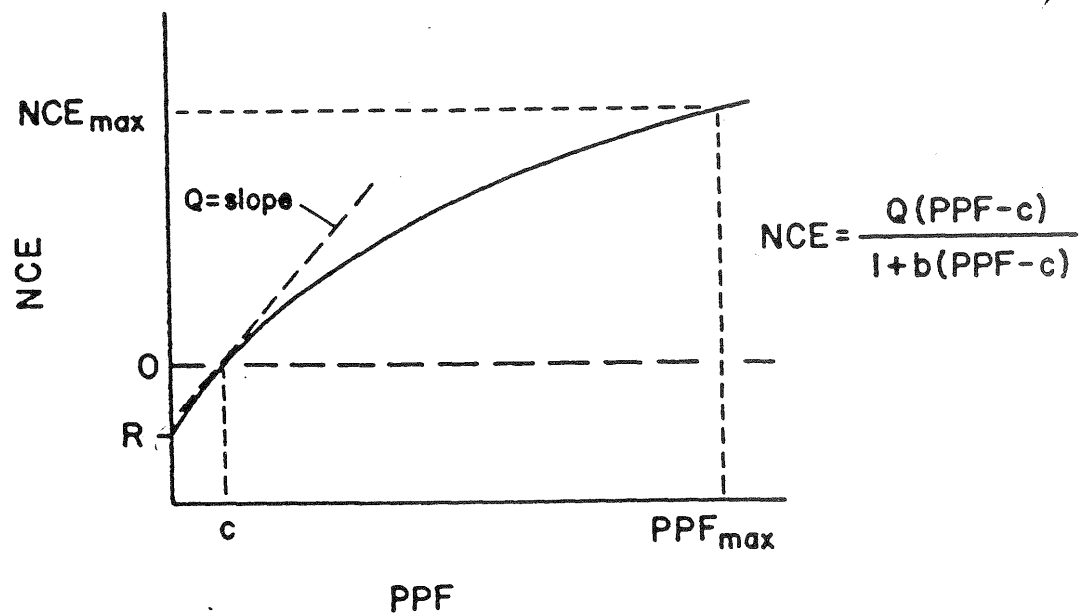


Fig 3.4 Mathematical model used to analyze light response curves. NCE = net CO<sub>2</sub> exchange, PPF = photosynthetically active photon flux, R = dark respiration, Q = quantum yield and c = light compensation point. b is a constant.



Table 3.1/ Canopy light response characteristics from the Spartina (Sp), Mixed (Mx), and Scirpus (Sc) communities under ambient (A) and +260 CO<sub>2</sub> concentrations.

Date	Community	NCEmax	R	Q	C	PPFmax
Sep 17	Sp A	7.2	1.7	0.007	230	1200
	Sp E	5.3	1.6	0.006	244	1200
	Mx A	14.8	1.6	0.018	84	1200
	Mx E	12.0	0.8	0.013	63	1200
	Sc A	11.9	2.4	0.024	89	1200
	Sc E	11.3	1.8	0.026	64	1200
Sep 18	Sp A	8.5	1.9	0.048	33	1200
	Sp E	---	---	-----	--	----
	Mx A	17.3	1.4	0.067	19	1200
	Mx E	14.0	2.1	0.059	32	1200
	Sc A	12.4	4.5	0.055	64	1200
	Sc E	12.4	3.4	0.070	39	1200
Sep 22	Sp A	11.3	4.7	0.027	142	1000
	Sp E	9.0	6.1	0.023	194	1000
	Mx A	24.9	5.3	0.054	89	1000
	Mx E	18.7	5.3	0.046	101	1000
	Sc A	15.4	7.7	0.040	152	1000
	Sc E	15.0	8.0	0.057	103	1000
Sep 28	Sp A	8.7	2.0	0.036	51	450
	Sp E	---	---	-----	--	----
	Mx A	15.4	2.8	0.044	64	450
	Mx E	---	---	-----	--	----
	Sc A	10.2	3.9	0.040	88	450
	Sc E	-----	---	-----	--	----
Sep 29	Sp A	12.4	4.0	0.037	92	850
	Sp E	-----	---	-----	--	----
	Mx A	25.3	4.3	0.064	62	850
	Mx E	-----	---	-----	--	----
	Sc A	12.5	5.5	0.043	103	850
	Sc E	-----	---	-----	---	----

(Table 3.1 continued)

Oct 17	Sp A	3.0	2.2	0.011	142	650
	Sp E	6.7	---	0.046	38	650
	Mx A	8.9	3.5	0.031	94	650
	Mx E	11.6	---	0.057	51	650
	Sc A	6.9	3.9	0.123	21	650
	Sc E	13.0	---	0.035	47	650
Oct 24	Sp A	2.8	1.4	0.008	148	700
	Sp E	---	---	-----	---	---
	Mx A	8.9	2.7	0.026	92	700
	Mx E	9.7	---	0.069	47	700
	Sc A	8.6	3.7	0.030	101	700
	Sc E	---	---	-----	---	---
Oct 25	Sp A	2.3	2.3	0.009	205	600
	Sp E	5.4	---	0.019	105	600
	Mx A	6.5	2.7	0.019	116	600
	Mx E	5.9	---	0.018	133	600
	Sc A	6.8	3.4	0.022	130	600
	Sc E	10.3	---	0.037	80	600
Oct 28	Sp A	2.4	0.2	0.006	36	800
	Sp E	---	---	-----	--	---
	Mx A	8.8	1.1	0.020	55	800
	Mx E	11.4	---	0.023	48	800
	Sc A	9.5	2.3	0.016	128	800
	Sc E	10.6	---	0.025	85	800
Nov 1	Sp A	1.9	3.9	0.010	190	550
	Sp E	1.6	---	0.009	299	550
	Mx A	6.3	2.5	0.020	113	550
	Mx E	6.9	---	0.026	84	550
	Sp A	3.9	4.8	0.020	151	550
	Sp E	7.7	---	0.066	97	550

in September to about  $4 \text{ } \mu\text{mol m}^{-2} \text{ sec}^{-1}$  in mid-October, in both a mixed and a Spartina community.

We were interested in examining whether +260  $\text{CO}_2$  had any effect on NCE over time. However, the seasonal decline in NCE made it difficult to directly compare NCEmax before and after  $\text{CO}_2$  was elevated. We therefore normalized NCEmax with respect to measurement date by calculating the ratio of +260 NCEmax to ambient NCEmax within a community for a given date. Before  $\text{CO}_2$  was elevated the NCEmax ratio from the replicate ambient chambers was less than 1 (Fig 3.5A). After  $\text{CO}_2$  was elevated to +260 in one chamber in each community this ratio increased 44% in the Mixed community, 67% in the Scirpus community and 135% in the Spartina community. Thus, +260  $\text{CO}_2$  had a positive effect on the mean values of light saturated and light limited NCE in all three communities.

The initial slope of the light response curve, or quantum yield (Q), from ambient communities showed a general trend of high values ( $0.04\text{-}0.07 \text{ mol mol}^{-1}$ ) in September declining to lower values ( $0.005\text{-}0.02 \text{ mol mol}^{-1}$ ) through October and November (Table 3.1). This decline was likely due to senescence of leaf tissue and changes in canopy structure leading to less efficient light utilization in photosynthesis (Turitzin and Drake 1981). The Spartina community declined earliest and reached the lowest values of the three communities. In general, Q increased under +260

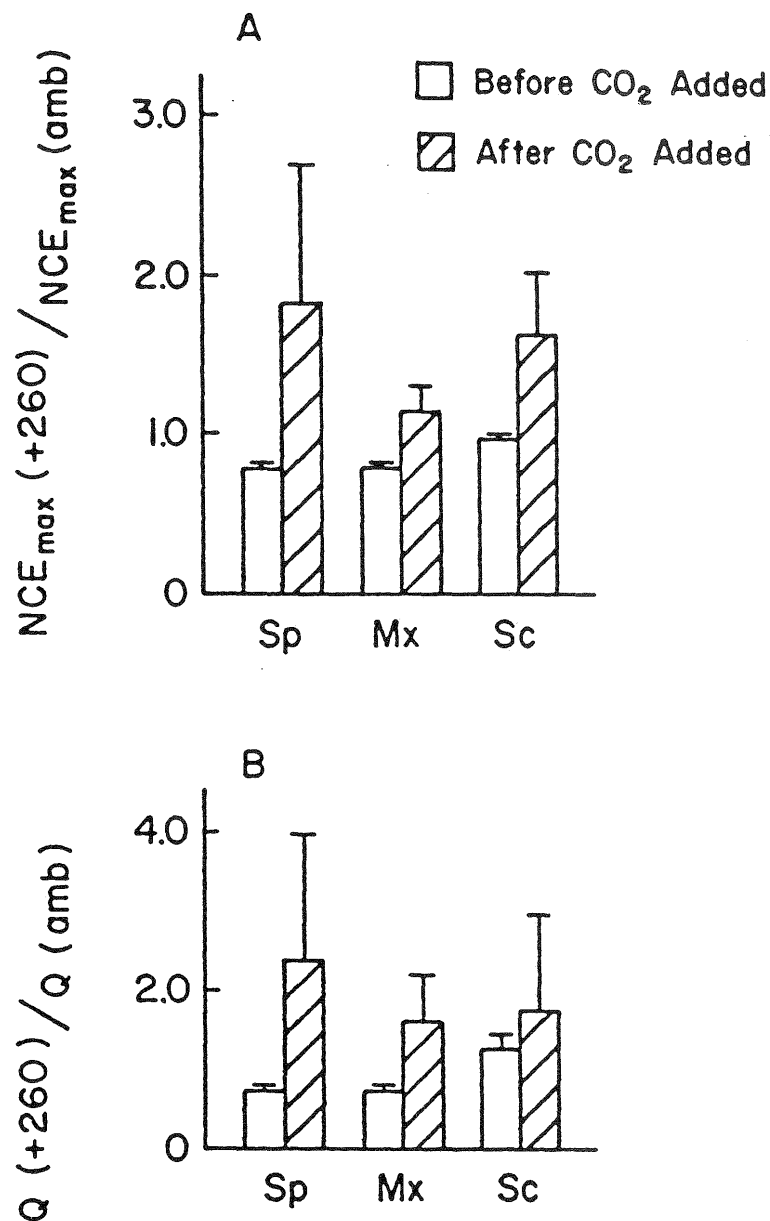


Fig 3.5 Effect of ambient +260 CO<sub>2</sub> on maximum net CO<sub>2</sub> exchange (A) and quantum yield (B). Sp = Spartina community, Mx = Mixed community and Sc = Scirpus community. Vertical bars = s.d. Effect of CO<sub>2</sub> on NCE<sub>max</sub> ratios was significant in the Mixed and Scirpus communities ( $p < 0.05$ ) but not in the Spartina community. Effect of CO<sub>2</sub> on Q ratios was not significant in any of the communities.

CO<sub>2</sub> relative to ambient concentrations (Fig 3.5B). We have insufficient data to evaluate seasonal trends in Q from +260 canopies. Drake (1984) reported Q between 0.01 and 0.03 mol mol<sup>-1</sup> for similar communities under normal ambient CO<sub>2</sub> concentrations during these months. He also noted a decline in Q between September and November, particularly in the mixed community.

Community respiration was variable between September and November, showing no clear seasonal trend (Table 3.1). Mean R during this time was 2.2, 2.8, and 4.2 umol m<sup>-2</sup> s<sup>-1</sup> for the ambient Spartina, Mixed, and Scirpus communities respectively. Evaluation of R from +260 communities was not meaningful due to the assumption of equality with ambient communities as discussed in Chapter 2. Drake (1984) reported R values between 3.0 and 4.0 umol m<sup>-2</sup> s<sup>-1</sup> for similar communities measured between June and August. Light compensation point (c) was also variable, with no clear trends among communities, with time, or with CO<sub>2</sub> concentration (Table 3.1).

#### B. Integrated 24 hour CO<sub>2</sub> exchange

The daily carbon budget of the ecosystem within a chamber was determined by integrating NCE over an entire day. Daytime, nighttime and 24 hr integrated NCE was determined on several days from September 28 to November 6 (Table 3.2).

Daytime NCE was computed as the integrated value of ecosystem NCE from the time NCE became positive in the morning until NCE became negative at night. Nighttime NCE was determined by multiplying the mean nighttime respiration rate (estimated from periods at night when the gas exchange signal was relatively stable) by the nighttime duration (defined as the end of the daytime period until dawn the next day). The sum of daytime (positive) and nighttime (negative) NCE equalled 24 hr NCE.

Figure 3.6 shows 24 hr NCE for ambient chambers during late September and early October, and for ambient and elevated chambers from mid-October to early November. The most prominent feature of the 24 hr NCE in the ambient chambers was that NCE was positive or near 0 in late September but was negative from October 17 through November 6. During late September the Mixed community had the highest 24 hr NCE and the Scirpus community had the lowest. This was largely due to differences in daily uptake since nighttime losses were quite similar during this period (Table 3.2). Low NCE in all communities on September 28 was probably due to low light and low maximum temperatures on that day (see Fig. 3.7).

Elevated CO<sub>2</sub> appeared to have increased 24 hr NCE in some instances. The Scirpus and Spartina communities both showed positive 24 hr NCE under +260 CO<sub>2</sub> on a day when 24 hr

Table 3.2 Daytime, nighttime and 24 hr integrated Net CO<sub>2</sub> Exchange. Plant communities were: Spartina (Sp), Mixed (Mx), and Scirpus (Sc) under normal ambient (Amb) and +260 CO<sub>2</sub> concentrations.

Date	Community	Net CO <sub>2</sub> Exchange (mol m <sup>-2</sup> day <sup>-1</sup> )		
		Daytime	Nighttime	24 hr
Sep 28,	Sp Amb	0.149	-0.098	0.051
	Sp +260	-----	-----	-----
	Mx Amb	0.224	-0.202	0.022
	Mx +260	-----	-----	-----
	Sc Amb	0.153	-0.207	-0.053
	Sc +260	-----	-----	-----
Sep 29	Sp Amb	0.246	-0.113	0.132
	Sp +260	-----	-----	-----
	Mx Amb	0.507	-0.113	0.374
	Mx +260	-----	-----	-----
	Sc Amb	0.271	-0.197	0.075
	Sc +260	-----	-----	-----
Oct 1	Sp Amb	0.358	-0.331	0.027
	Sp +260	-----	-----	-----
	Mx Amb	0.599	-0.246	0.362
	Mx +260	-----	-----	-----
	Sc Amb	0.236	-0.236	0.0
	Sc +260	-----	-----	-----
Oct 17	Sp Amb	0.029	-0.108	-0.079
	Sp +260	0.170	-0.108	0.063
	Mx Amb	0.113	-0.167	-0.054
	Mx +260	0.156	-0.167	-0.011
	Sc Amb	-----	-----	-----
	Sc +260	0.343	-0.108	0.235
Oct 25	Sp Amb	0.006	-0.115	-0.109
	Sp +260	0.047	-0.115	-0.068
	Mx Amb	0.048	-0.179	-0.131
	Mx +260	0.038	-0.179	-0.140
	Sc Amb	0.050	-0.115	-0.065
	Sc +260	0.160	-0.115	0.045
Nov 3	Sp Amb	0.009	-0.102	-0.093
	Sp +260	-----	-----	-----
	Mx Amb	0.047	-0.115	-0.069
	Mx +260	0.039	-0.115	-0.076
	Sc Amb	0.028	-0.143	-0.115
	Sc +260	0.039	-0.143	-0.104
Nov 6	Sp Amb	0.004	-0.057	-0.053
	Sp +260	-----	-----	-----
	Mx Amb	0.040	-0.128	-0.087
	Mx +260	0.039	-0.128	-0.089
	Sc Amb	0.017	-0.128	-0.111
	Sc +260	0.049	-0.128	-0.079

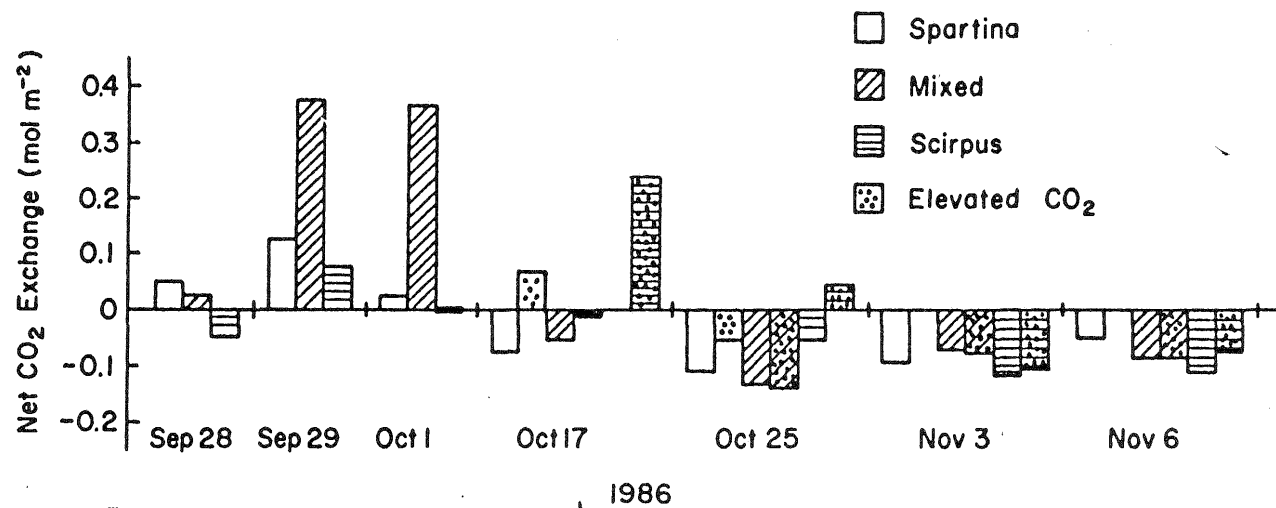


Fig 3.6 Twenty-four hr net CO<sub>2</sub> exchange for three salt marsh communities between Sept 28 and Nov 6, 1986. Plants were first exposed to ambient +260 CO<sub>2</sub> on Sept. 24.



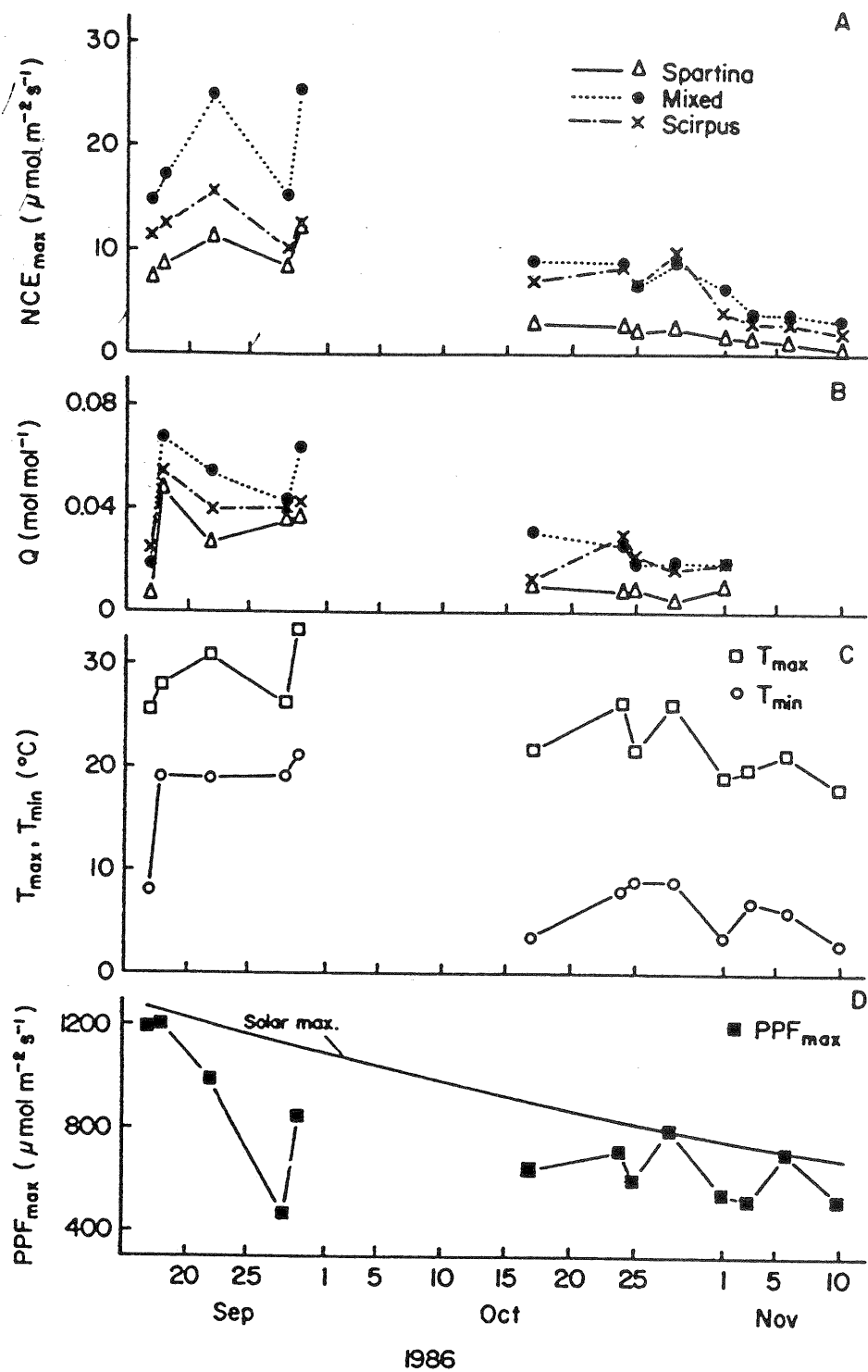


Fig 3.7 Seasonal trends in net CO<sub>2</sub> exchange (A), quantum yield (B), temperature (C) and PPF (D).

NCE from the corresponding ambient community was negative (Fig 3.6).

Similar patterns of daytime and nighttime NCE in mixed communities at ambient CO<sub>2</sub> concentrations on this salt marsh were reported by Drake & Read (1981). These authors observed a maximum daily CO<sub>2</sub> uptake in mid-summer of approximately 0.7 mol m<sup>-2</sup> day<sup>-1</sup> which declined to near zero in late September and then to approximately -0.12 mol m<sup>-2</sup> day<sup>-1</sup> in mid-October. After mid-October 24 hr NCE gradually became less negative, approaching zero in early December.

#### C. Seasonal and temperature effects on net CO<sub>2</sub> exchange

Maximum NCE and Q declined between September 17 and November 10 in all three communities (Fig 3.7A,B). The decline in NCE<sub>max</sub> prior to November 1 was pronounced in the Spartina and Mixed communities but appeared slight in the Scirpus community. During September, daily NCE<sub>max</sub> in the three communities appeared well correlated with maximum daily temperature (Figs 3.7, 3.8). The highest daily NCE<sub>max</sub> occurred during days with temperatures between 31 and 33 C. Changes in Q did not correlate as well with environmental variables, although very low Q values on September 17 did correlate with an unusually low minimum temperature on that day (Fig 3.7B,C).

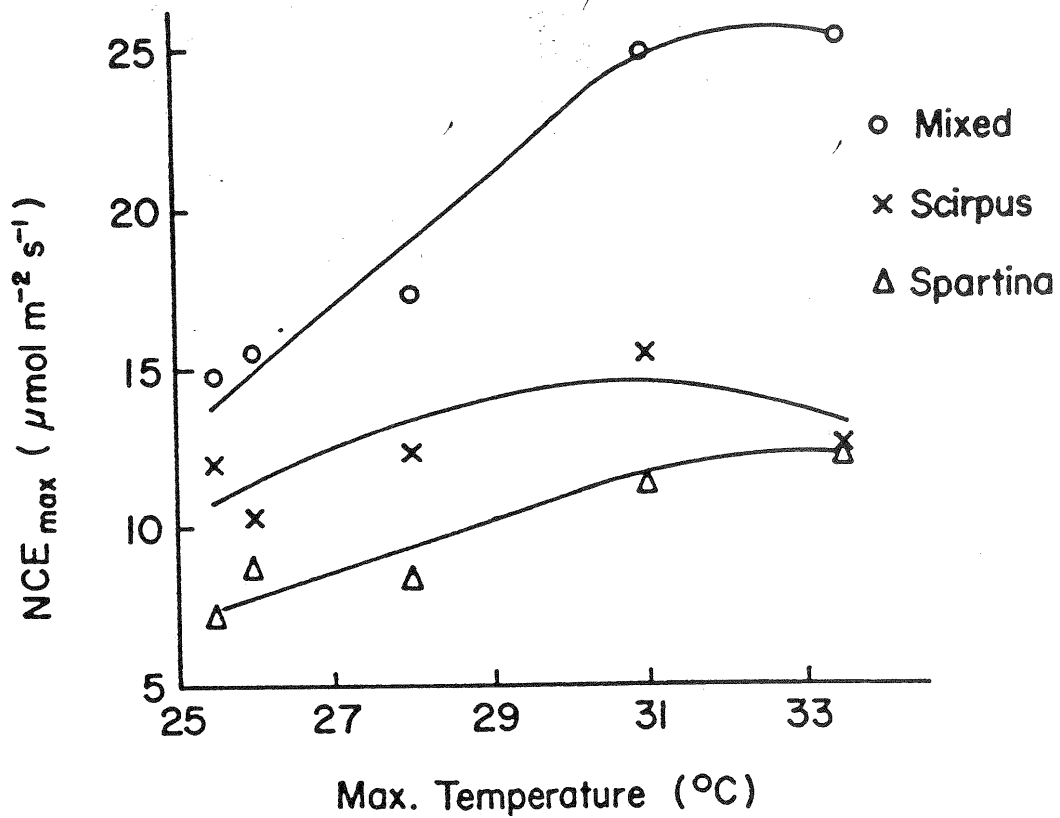


Fig 3.8 Relationship between maximum net CO<sub>2</sub> exchange and maximum daily temperature in three salt marsh communities. Lines were fit by eye.

DeJong et al. (1982) observed that NCEmax in S. patens grown in the lab was sensitive to temperatures between 15 and 30 C, but that NCEmax in S. olneyi was very insensitive to temperature. This may help explain why NCEmax in the Scirpus community in our study declined less markedly during October in the field than did NCEmax in the Spartina and Mixed communities. Drake (1984) observed declines in NCEmax in mixed communities in this salt marsh which were comparable to the declines in Fig 3.7. However, Drake (1984) did not observe substantial seasonal declines in Q in a S. patens dominated community.

## II Single Leaf Photosynthesis

Photosynthetic light response characteristics of single leaves from plants growing near the chamber sites were measured between July 3 and July 25, 1986. Steady state gas exchange was monitored in situ using an ADC LCA-2 portable infra-red gas analyser and an ADC PLC leaf chamber. Plants were selected at random and the youngest fully expanded leaf used for measurement. Single leaf net CO<sub>2</sub> exchange (A) was monitored until steady state was reached in full sun. Incident light was then reduced by covering the chamber with a series of neutral density filters. Total time for measurement of each leaf was approximately 15 min. The ADC PLC leaf chamber does not control leaf temperature.

Temperature differences between chamber /and air were typically small, between 1 and 3 C.

Representative light reponse curves for S. patens, S. olneyi, and D. spicata are shown in Fig 3.9. These data illustrate several important points concerning the field response of photosynthesis in these plants. In general, we saw very little difference in the maximum rates of net CO<sub>2</sub> exchange (A<sub>max</sub>) attained by the three species. Under controlled, laboratory conditions the C<sub>4</sub> species S. patens and D. spicata showed A<sub>max</sub> 75% higher than the C<sub>3</sub> species S. olneyi (DeJong et al. 1982, Table 3.3). In the field, however, numerous environmental factors combine to restrict photosynthetic capacity. Our data show no significant difference in A<sub>max</sub> among the three species whether measured in pure or mixed communities (Table 3.3). The strongest trend in these data was towards higher A<sub>max</sub> in plants from the mixed community. This trend was also noted in canopy gas exchange measurements (Fig 3.7). Figure 3.9 also illustrates that photosynthesis in these species in the field is not light saturated.

A number of photosynthetic light response characteristics were calculated from the light response curves and are presented in Table 3.3. The results of DeJong et al. (1982) are also included for comparison. Dark respiration was somewhat lower than reported by DeJong et al.

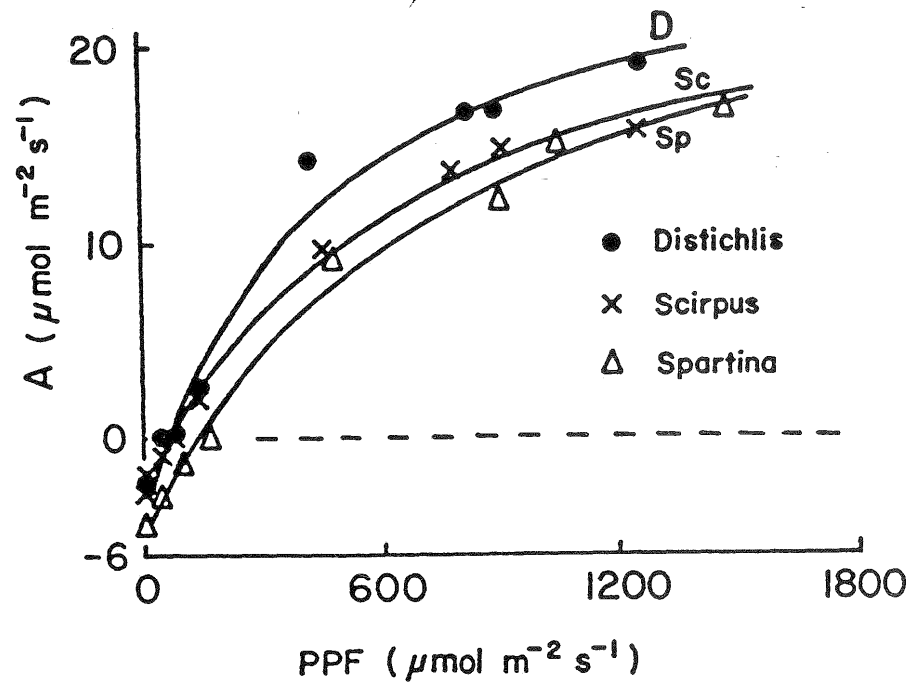


Fig 3.9 Representative single leaf light response curves from three salt marsh species. Curves were fit by least squares regression.

Table 3.3 Light response characteristics of single leaves measured in the field. A), this study, B) data from DeJong et al. (1982). Species measured were: Scirpus oleyi (Sc), Spartina patens (Sp), and Distichlis spicata (D) from monospecific (Sc, Sp) or mixed (MSc, MSp, MD) communities.

Species	R	C umol m <sup>-2</sup> s <sup>-1</sup>	Amax	Q mol mol <sup>-1</sup>	n
A)					
Sc	-2.9 (0.22)	75.5 (6.60)	14.9 (1.55)	0.034 (.0018)	8
MSc	-3.2 (0.50)	82.6 (13.35)	15.2 (1.43)	0.037 (.0077)	4
Sp	-4.3 (0.20)	119.0 (10.83)	15.9 (1.37)	0.033 (.0038)	9
MSp	-6.0 (0.62)	110.8 (16.27)	17.3 (5.70)	0.048 (.0141)	4
MD	-4.4 (0.52)	84.0 (13.51)	17.6 (3.81)	0.045 (.0052)	3
-----					
B)					
Sc					
Field	-2.0	25	18	0.033	
Greenhouse	-2.5	100	37	0.047	
Sp					
Field	-2.0	25	20	0.085	
Greenhouse	-3.0	100	52	0.047	
D					
Field	-2.0	25	15	0.050	
Greenhouse	-3.0	100	51	0.047	

and varied significantly among species. Spartina patens and D. spicata had higher respiration rates than did S. olneyi. This difference could be due to the higher energetic costs of the C<sub>4</sub> pathway or reflect different osmoregulatory costs associated with drought and salinity stresses. Additional research is necessary to clarify this. Light compensation point and quantum yield did not vary among species and were similar to values reported by DeJong et al. (1982).

### III Discussion

The results presented in this chapter demonstrate our ability to monitor ecosystem net CO<sub>2</sub> exchange and to use these data in quantifying community carbon budgets. Net CO<sub>2</sub> exchange followed incident light levels very closely, enabling us to construct light response curves for communities under ambient and +260 CO<sub>2</sub> concentrations (Figs 3.1, 3.2). Maximum NCE was relatively high in September in all three ambient communities, declining thereafter until the end of the measurement period in November (Table 3.1, Fig 3.7). The Spartina community consistently had the lowest NCE<sub>max</sub>. Single leaf measurements of NCE and light response characteristics were similar to previously reported data (Table 3.3).

Data from +260 communities were more limited but they



indicated an increase in NCEmax in all communities by +260 CO<sub>2</sub> concentrations (Table 3.1, Fig 3.5). The positive response of NCE in the C<sub>4</sub> community to elevated CO<sub>2</sub> was, in general, contrary to laboratory studies of single leaves but not entirely unexpected. A similar response of C<sub>4</sub> canopies to elevated CO<sub>2</sub> has been observed previously by Drake (unpublished). The mechanism of this response is unclear but could be related to CO<sub>2</sub> gradients within the Spartina canopy. Improvement of midday plant water status by elevated CO<sub>2</sub> could also result in higher NCEmax. No single leaf measurements were made from +260 communities.

Ambient community carbon budgets calculated from integrated daily NCE data showed seasonal changes entirely in agreement with our expectations and previously published reports. Twenty-four hr NCE was positive in all communities in September, becoming negative in October (Fig 3.6). Preliminary results from +260 communities suggested that elevated CO<sub>2</sub> improved the daily carbon budget, possibly extending the period of positive net daily CO<sub>2</sub> uptake later into the season (Fig 3.6).

## APPENDIX A

### PARTS LIST FOR CONSTRUCTION OF OPEN TOP CHAMBER

#### A. Frame

1. Aluminum tubing; 8.5 mm ID, 2 mm wall thickness
2. Paint; Sherwin Williams HI-Bild Aliphatic Polyurethane Enamel-Pure
3. Covering; Melinex 071, ICI, Wilmington DE
4. Tape to attach covering; 3M Polyester, 1" #853

#### B. Remote Blower

1. Electric blower; Dayton shaded pole #4C015B, attached with 8 10/32 - 1/2" stainless steel bolts, 2 wire nuts #74B, 1 fork terminal #14RB-6f, electrical cord (75 cm); ExCel #14/3 SO 3/4" service connector  
8, 1/2"X 6 panhead sheet metal screws  
Woodhead watertight super safeway cord caps;  
2 females #15W47, 1 male #14W47  
Variable length ExCel 14/3 SO cord to power  
Spec master nylon #5366-N male cord cap

#### C. Mixing Blower

1. Electric blower; Dayton shaded pole #4C443A  
6, 10/32 - 1/2" stainless steel bolts  
1 fork terminal, 3 wire nuts  
30 cm ITT 16 AWG wire, 75 cm ExCel 14/3 SO cord  
2 Halex LSI service connectors  
Woodhead watertight super safeway male cord cap  
8, 1/2" - #6 panhead phillips sheet metal screws  
10X10 cm hardware cloth

#### D. Air Ducts

1. Delivery tube; Certflex 25, class 1 insulated duct 90cm length, 10 cm ID. 2, 50 cm cable ties.
2. Mixing tubes; 2 marine ventilation ducts, 80 cm length 8 cm ID. 4 35 cm cable ties.

### PARTS LIST FOR CO<sub>2</sub> SAMPLING SYSTEM

- A. Thermoplastic tubing - Imperial Clevite Inc., Fluid Components Div., Chicago, IL; type: Impolene 44-pp, 1/4" O.D. (12,000 ft each of black and white).
- B. Dual-head diaphragm pumps - Thomas Industries; model: 2107CA14-TFE (30).
- C. Mixing volumes - 1 gallon glass jugs (180).

- D. 3-way solenoid valves - Automatic Switch Co., Florham Park, NJ; model: 8360A77, Acetal body, 120 VAC, 3/32" orifice, 1/4" compression fittings (80).
- E. Solenoid manifold - custom made at SERC; Delrin tapped for 1/8" NPT fittings (8 pieces).
- F. Solenoid rack - custom made at SERC; welded 1/8" aluminum plate (2 pieces).
- G. Drying tubing - Perma Pure Products Inc., Toms River, NJ; model: MD-250-48pp, 0.1" I.D., 1/4" compression fittings (2).
- H. Filters - Balston Inc., Lexington, MA.; model: DFU, grade DQ (2).
- I. Infra-red gas analyzer - Inficon Leybold-Heraeus Inc., E. Syracuse, NY; model: Binos 4B.2, dual channel CO<sub>2</sub>. Channel 1 - 0 to 1000 ppm absolute, channel 2 - -10 to +10 ppm differential. (1).

#### PARTS LIST FOR CO<sub>2</sub> DISPENSING SYSTEM

- A. Dispensing tubing - Imperial Clevite Inc., Fluid Components Division, Chicago IL; type: Polyflo, 1/4" O.D. (6000 ft).
- B. Dispensing manifold - custom made at SERC, Delrin tapped for 1/8" NPT fittings (1).
- C. Flowmeters - Brooks Instrument Div., Emerson Elec. Co., Hatfield PA; model: Sho-rate 150, R-2-15-A tube, tantalum ball, #4 needle valve (15).

#### PARTS LIST FOR DATA ACQUISITION AND STORAGE

- A. Solenoid switch box - custom made at SERC, 1 manual switch, 1 LED and 1 optically isolated relay (operated by 5 VDC, switches 120 VAC) for each of 40 channels (1).
- B. Data acquisition/control unit - Hewlett-Packard Corp., Loveland Instrument Div., Loveland, CO; model: HP 3852A, with 1 Mbyte memory, 2 general purpose switch, 1 Integrating DVM, 1 TC compensated MUX and 1 MUX card (1).
- C. Data acquisition/control unit (backup) - Campbell Scientific Inc., Logan, UT; model: CR-7X, with Excitation and Analog Input w/RTD cards (1).
- D. Micro-computer - Hewlett-Packard Corp., Fort Collins,

CO; model HP 310, 98580A bundled system, 10 Mbyte  
Winchester, dual 1/4" floppy drive, Inkjet Printer  
(1).

## APPENDIX B

### TIMETABLE FOR 1986 SEASON

DATE	COMMENTS
Apr-Jun	Construction of boardwalk and lab; chamber testing; vegetation sampling for baseline data (covered in previous report).
Jul-Sep	Construction and testing of CO <sub>2</sub> sampling and dispensing systems; covering chamber frames; start daily data logging with single chamber in mixed community on Aug 23.
Sep 17	Start of full time data logging with 6 chambers: Sp Amb, Sp +260, Mx Amb, Mx +260, Sc Amb and Sc +260.

DATE	OPEN-TOP	CLOSED-TOP	ELEVATED CO <sub>2</sub>
Sep 17		All chambers	No chambers
Sep 24		↓	↓
			+260 chambers
Oct 2	All chambers		
	↓		
Oct 16		All chambers except as noted	
		↓	
Oct 22-24	Mx +260		
Oct 29	Mx +260		
Nov 6-29	Mx +260		
Dec 2		↓	↓
			No chambers
Dec 18		all chambers removed from marsh	↓

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