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Application of CO_2-porometer methods to assessment of components of photosynthetic production in estuarine ecosystems

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Abstract

A portable system for CO_2 gas exchange measurements is described that allows determination of net photosynthesis and transpiration rates as well as leaf conductance of salt marsh vascular plants, and photosynthesis rates of macrophytic algae and epibenthic algae of sediment cores during low tide periods of exposure. Carbon fixation processes of these several different types of organisms can be studied on the same day. Measurements may be carried out at an estuarine field site using controlled conditions of light, temperature, and air CO_2 partial pressure. Algal samples are enclosed in the cuvette for only a matter of minutes and do not dry significantly during measurement. The rapidity with which gas exchange rates of samples may be assessed will allow routine processing of many sediment cores. Thus, the distribution of producer populations can be studied with greater resolution than previously possible.

Introduction

Estuarine ecosystems are highly productive and extremely important to human activity (Wiegert *et al.*, 1981). To measure energy flow in such ecosystems, it is necessary to measure and understand the variations in carbon fixation carried out by phytoplankton, macrophytic algae, epibenthic microalgae, and vascular plants adapted to the salt marsh fringes of the estuary. Due to difficulties encountered in assessment of standing crops and determination of rates of carbon exchange in an environment continuously influenced by tidal flux, many large gaps remain in our understanding of photosynthetic primary production of estuaries and the dependence of primary production on environmental conditions and on diurnal and seasonal change in these conditions.

Near Lisbon, Portugal, the Tagus estuary covers an area of 32 000 ha. Within this, 11 380 ha are in the intertidal zone, 1 300 ha have salt marsh associations, and the rest are mud flats and oyster beds. Dense algal mats form about the stem bases of higher plant species in the marshes (cf. Zedler, 1982). The mud flats, when exposed, are richly populated with algae and cyanobacteria in some locations but overall distribution patterns remain obscure. Macroalgae cover approximately 70% of the ground surface area in oyster beds. The carbon fixation rates of epiphytic and epibenthic algae have in general been less extensively characterized in estuaries than those of the more accessible vascular plants, even though it is apparent that their contribution to total production is substantial (Zedler, 1980, 1982).

Until now, the methods that have been used reliably to provide estimates of carbon fixation rates of algae at such sites, have involved exposure of sediments or water columns to carbon sources labeled with ^{14}C (see Pomeroy *et al.*, 1981) or measurement of O_2 evolution (Gallagher and Daiber, 1973; Zedler, 1980). Exposure periods for both methods are relatively long and materials are enclosed in some type of cuvette, which is usually not climatized. Complex cuvette systems with ventilation and climate control have been used in studies of salt marsh vascular plant species (DeJong *et al.*, 1982; Giurgevich and Dunn, 1982) during low tide periods. To date, these have not proven practical for investigation of carbon uptake by algal species, most probably because the equilibration time of large cuvette systems is long and algal material placed in a cuvette tends to dry rapidly. We describe here preliminary experimentation with a new portable open-flow and steady-state gas exchange system which indicates that accurate rate determinations for macrophytic algae, epibenthic algae, and for higher plants are possible with a single device. Time periods for enclo-

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sure of the algal species are shortened to between one and two minutes so that drying during measurement is minimized. The measurement system provides the possibilities of working with different types of material on the same day, of maintaining climate conditions which track measured microclimate or are held constant with respect to all but a single variable in order to elaborate photosynthetic response to particular environmental factors, and of conducting on site measurements which minimize disturbance of the physiological state of the material. We demonstrate here typical CO_2 uptake rates measured with such a system for different types of producer organisms of the Tagus estuary.

Materials and methods

Plant material and study sites

The location of the Tagus estuary and of the study sites are shown in Fig. 1. Detailed studies are being carried out in the salt marshes at Esteiro de Corroios and Pancas near Lisbon. Further materials were collected at sites on the oyster beds of the estuary and the surrounding mud flats. Samples collected at remote locations were held at 4 °C in a freezer box while being transferred to a mobile field laboratory in Sobreda near Corroios.

To demonstrate potential fixation rates of representative higher plants, *Spartina maritima* (Curtis) Fernald (C_4 type of carbon fixation) and *Arthrocnemum fruticosum* (L.) Moq. (C_3 type of carbon fixation) were chosen. These species grow in close proximity in low areas of the marsh, *S. maritima* usually remaining flooded longer than *A. fruticosum* during tidal cycles. Epiphytic algal mats form under *A. fruticosum* and they are extremely dense and compact. For these preliminary measurements, fronds of the red alga *Bostrychia scorpioides* (Huds.) Montagne were separated from the mat by washing in sterilized sea water. *Ulva lactuca* L., which abundantly colonizes the oyster beds, was collected as a second example for the macroalgae. Epibenthic microalgae, including cyanobacteria, were considered only as total population samples and were collected by coring small areas of the mud surface. Sediment samples were collected from different locations of the exposed mud flats as well as under higher plant canopies in the salt marsh vegetation. A small plastic tube (internal cross section 3.5 cm^2) was pressed into the mud to a standardized depth (1 cm) imposed by a surrounding flange plate. The corer was then removed and extra mud shaved from the bottom of the column with a trowel. The cores were removed for study by lightly blowing into the tube, and were then inserted into an aluminum foil pan.

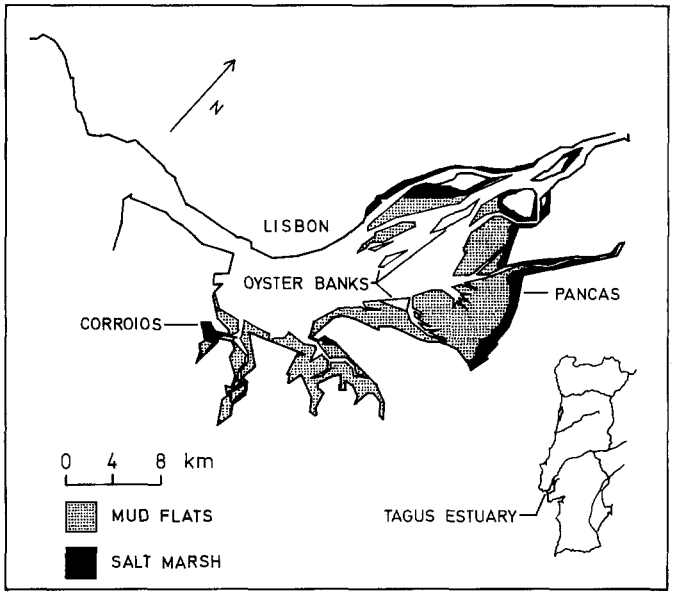

Fig. 1. Mud flat and salt marsh areas of the Tagus Estuary intertidal zone located near Lisbon, Portugal. Samples were collected from the sites indicated at Corroios, Pancas, and from the oyster banks. Inset map of Portugal indicates the geographic location of the Tagus Estuary

Gas exchange measurements

The gas exchange equipment is constructed in two models with either a non-climatized but ventilated cuvette for rapid comparative measurements under natural conditions (Schulze *et al.*, 1982; Lange *et al.*, 1984a) or a fully climatized cuvette with an artificial light source for response curve determinations (Lange *et al.*, 1984b). In the non-climatized model, the porometer cuvette is surrounded by a cylindrical radiation shield, and air temperature is held close to ambient air temperature by circulating air along the walls of the chamber through the shield with a fan. The lid is covered by a thin polyethylene film which is transparent in the visible region and which transmits some longwave radiation. The air within the cuvette is circulated by a small fan; the cuvette contains sensors for temperature (NTC thermistor and thermocouple) and air humidity. Even in situations with high solar radiation and longer exposure time, the temperature in the cuvette does not rise more than 3° or 4C° above ambient air temperature. The climatized cuvette is regulated to maintain constant temperatures through the use of Peltier heating and cooling elements. Under summer Mediterranean climate conditions, constant temperatures between 15° and 40 °C have been realized. A technical description of the equipment is available from Heinz Walz Meß- und Regeltechnik (Eichenring 10–14, D-8521 Effeltrich, FRG). Both systems are portable and may be powered in the field by a small generator.

Details of the cuvette construction have been reported by Lange *et al.* (1984a, b) for both climatized and non-climatized models. For measurements under natural environmental conditions, air is taken from an inlet situated to obtain well-mixed outside air, enters a buffer vessel, and is then split into two streams. One stream passes through the porometer cuvette[1] and to an infra-red analyser

[1] The gas exchange equipment described was designed originally to determine degree of opening of stomata in the sense of Darwin and Pertz (1911). While this is not always the case in the present application, the equipment is commercially available as a "porometer" and this designation has been retained.

(Binos, Leybold Heraeus, Hanau, FRG); the second serves as a reference gas for the analyser which works in the differential mode. Both CO_2 and H_2O exchange of the enclosed plant material is registered with this two-channel instrument. In the case of algal samples, the water signal is disregarded. Flow rates are monitored with a mass flow-meter; rates of 0.4 to 0.6 l min^{-1} are typical. A digital display provides differentials of CO_2 and H_2O partial pressures between cuvette and reference air stream, flow rate, air temperature, relative humidity of chamber air, and incident photosynthetically-active radiation (PAR). All signals are available as linear voltage outputs for data processing by small computer or line recorder monitoring. In the present investigation, data were read manually and CO_2 differential signals were recorded continually. Gas exchange data were then evaluated in the computing center of the University of Würzburg according to equations given by von Caemmerer and Farquhar (1981).

To illustrate the difference in production capacities of *Arthrocnemum fruticosum* and *Spartina maritima,* carbon dioxide dependencies of net photosynthesis were determined at constant saturating light intensity and for a constant leaf temperature. Air mixtures with different CO_2 partial pressures were produced by mixing a stream of CO_2-free air (CO_2 removed with soda lime) with a second stream of pure CO_2. Partial pressures of CO_2 between 0 and 4 000 μbar were mixed with a high degree of accuracy by varying the flow of the two gas streams with mass flow controllers (Tylan). By mixing CO_2-free air, nitrogen, and pure CO_2, the carbon dioxide dependencies at 1% oxygen were also determined.

The non-climatized porometer is shown in operation during measurement of gas exchange of leaves of *Spartina maritima* in the salt marsh in Fig. 2. In Fig. 2A, one sees the porometer cuvette supported on a clamp with a marked section of the blade of *S. maritima* inserted. The cuvette is sealed with closed foam rubber rings. One can also see the quantum sensor (LiCor, Lincoln, Nebraska), which is used to register incident photosynthetically active radiation. The general aspect of the Corroios measurement site is shown in Fig. 2B. The porometer equipment is supported on a small table; when not in use, the measurement cuvette is shaded and conveniently protected in a small basket. The air line to the cuvette first goes to a buffering vessel (polypropylene jug) and then to the pumping unit. The suspended electrical cable from the generator which powers the equipment is seen at the right of the figure. Dark areas around the basket are occupied by *S. maritima* and *Arthrocnemum fruticosum.* The taller plants of light color which appear in bunches are *Halimione portulacoides.*

Selected plant material is inserted into the porometer cuvette and then the lid is closed and sealed. Intact leaves of *Spartina maritima* and succulent stems of *Arthrocnemum fruticosum* were used to illustrate gas exchange determinations with higher plants. A layer of Terostat putty around the stem of *A. fruticosum* facilitated sealing of the cuvette. Loose mats of *Bostrychia scorpioides* fronds and the cores with epibenthic algae were placed on small aluminum pans and inserted onto a wire mesh support within the cuvette. Sections of the green alga *Ulva lactuca* were cut out and suspended on a frame. Exposure time was approximately three minutes (see also Fig. 4 below). Photosynthetic rates of *S. maritima* and *A. fruticosum* are expressed on a total surface area basis. Rates of algal photosynthesis are expressed on a mg chlorophyll, dry weight, or total surface area basis as indicated in the figures. To obtain the pigment content of the mud cores, they were extracted in 90% acetone, according to standard spectrophotometric methods recommended by the American Public Health Association (1971). Non-functional chlorophyll *a* was determined by an acidification of the

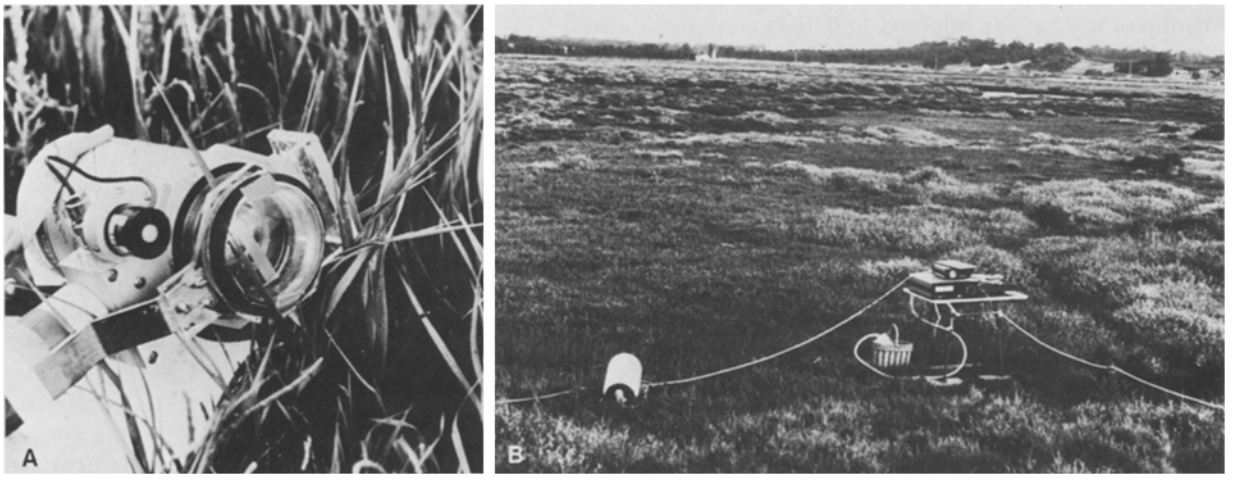

Fig. 2. (A) View of the porometer supported on a clamp with a blade of *Spartina maritima* inserted into the cuvette between foam rings. The small sensor next to the cuvette lid measures photosynthetically active radiation. (B) The porometer instrumentation as used during measurements in the salt marsh near Corroios. The measurement cuvette is protected in a small basket; a polypropylene container is used to buffer CO_2 partial pressure changes of the ambient air entering in the line from the left; power is supplied from a generator via the cable at the right; and the pumps, gas analyzer, recorder, and digital read-out units are supported on the small table

acetone extract, with one drop of 1N HCl added to the spectrophotometer cuvette (Lorenzen, 1967). Algal photosynthesis measurements were made with ambient air supplied to the cuvette and at a constant temperature. Light was provided as natural sun light or with Quartz halide projector lamps (General Electric, 12 V/75 W spot lamp).

Results

Responses of net photosynthesis (NP) to changes in internal leaf CO_2 partial pressure (P_i) and at 1 and 21% O_2 concentration are shown for *Spartina maritima* and *Arthrocnemum fruticosum* in Fig. 3. The data were obtained at saturating light intensity (1 800 μmol m^{-2} s^{-1} PAR) and at a constant leaf temperature of 31 °C. To compare the cylindrical stems of *A. fruticosum* with the flat blades of *S. maritima*, the rate of NP shown in Fig. 3 is expressed on the basis of total surface area of the sample included in the cuvette. No oxygen effect on photosynthesis was apparent for the C_4 grass species. In contrast, typical reduction of net photosynthesis with increase in O_2 content of the air and increase in leaf CO_2 compensation point was found for the C_3 succulent *A. fruticosum*. The results illustrate the large differences in potential photosynthesis occurring in these two sympatric species under conditions that are common during the summer (July 1983).

Under natural habitat conditions (350 μbar CO_2 and 21% oxygen in the air external to the leaves) at low tide on a sunny summer day, leaf conductance on a total surface basis of *Spartina maritima* was approximately 60 mmol m^{-2} s^{-1} as compared to 30 mmol m^{-2} s^{-1} for *Arthrocnemum fruticosum*. The large photosynthetic potential of *S. maritima* resulted in CO_2 uptake rates of approximately 7.5 μmol m^{-2} s^{-1} versus 0.8 μmol m^{-2} s^{-1} realized by *A. fruticosum*. A similar difference in photosynthetic CO_2 fixation is found when rates are expressed on a dry weight basis (0.16 nanomol mg^{-1} s^{-1} as opposed to 0.02 nanomol mg^{-1} s^{-1}). The differences in photosynthetic capacity and stomatal conductance result in large differences between species in leaf internal CO_2 partial pressure under natural conditions, which are 125 and 285 μbar, respectively, for *S. maritima* and *A. fruticosum*, i.e. they operate under natural conditions at very different points on their photosynthetic CO_2 response curve (Fig. 3). Due to lower leaf conductance, *A. fruticosum* transpired much less water at a leaf temperature of 31 °C than did *S. maritima* (0.7 mmol m^{-2} s^{-1} compared to 1.6 mmol m^{-2} s^{-1} – total surface area basis), but had a much less favorable transpiration ratio (transpiration rate/net photosynthesis rate approximately 1050 compared to 200 mol H_2O/mol CO_2 for *S. maritima*). From time-course measurements it appeared that the optimum temperature for net photosynthesis of *A. fruticosum* in July was considerably below 31 °C with rates for NP of approximately 2.2 μmol m^{-2} s^{-1}. *S. maritima* exhibited high rates at high temperatures as might be expected for this C_4 species.

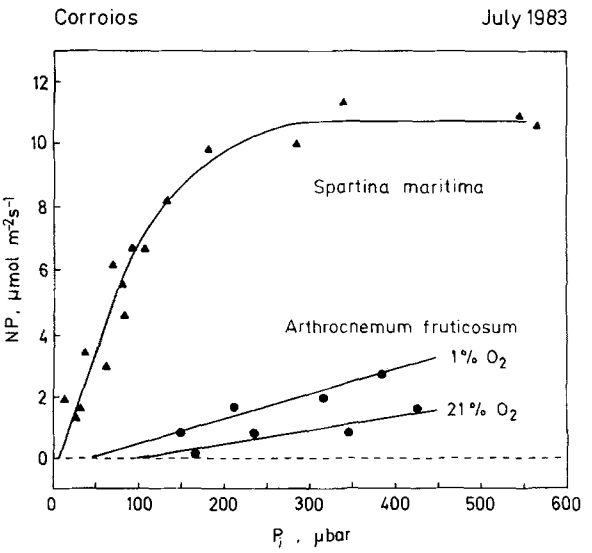

Fig. 3. Net photosynthesis rates (NP) of two salt marsh vascular plant species as a function of leaf intercellular CO_2 partial pressure (P_i). Triangular symbols were obtained with *Spartina maritima*, circular symbols with *Arthrocnemum fruticosum* at 1 and 21% oxygen as indicated. Light intensity was approximately 1800 μmol m^{-2} s^{-1} PAR, leaf temperature was 31°, and leaf to air water mole fraction difference was approximately 30 mbar bar^{-1}

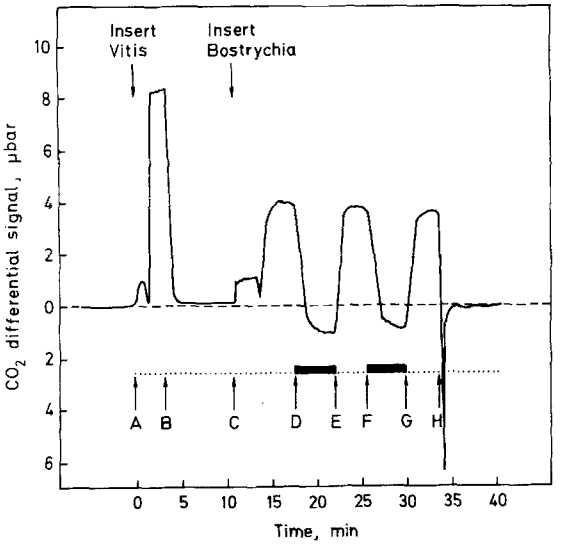

Fig. 4. Chart recording comparing the photosynthetic response of a leaf (*Vitis vinifera*) with that of the red alga *Bostrychia scorpioides* as viewed with the porometer methodology described. At times A and C, the cuvette was opened and material was inserted; at B and H the samples were removed; at D and F the sample was placed in the dark by covering the cuvette. During the remaining time, light intensity was approximately 650 μmol m^{-2} s^{-1} PAR

The response and sensitivity of the measurement system during observation of algal samples is illustrated in Fig. 4. In this figure a chart recording is shown that compares the response of a leaf with that of a compacted sample of the red alga *Bostrychia scorpioides*. The zero signal of the analyser is shown at time zero and indicated

at later times as a dashed line. At point A, approximately 10 cm^2 surface area of a *Vitis vinifera* L. leaf was inserted into the cuvette for demonstrative purposes. After a short disturbance, during which introduced air is flushed from the cuvette and pressure equilibrates, photosynthetic uptake of CO_2 commences and a steady-state uptake is rapidly established with a CO_2 reduction in the cuvette of 8 μbar. Upon removal of the leaf, at point B, the CO_2 signal rapidly falls back to the zero level.

At point C, the cuvette was reopened and the sample of *Bostrychia scorpioides* inserted. The disturbance of the analyzer signal is greater due to the necessity of fully opening the cuvette. Again a rapid attainment of steady-state CO_2 uptake is observed. With approximately 170 mg dry weight of algae, the response signal at 28 °C and 650 μmol m^{-2} s^{-1} PAR is quite strong, indicating a reduction in cuvette CO_2 approximately 50% of that obtained with the leaf material. At points D and F the sample was placed in the dark by covering the cuvette with black cloth, and at points E and G the cloth was removed. During the dark periods, respiration rates are measured accurately and reproducibly. Similarly, CO_2 uptake rates in the light were reproducible despite exposure of the samples to ventilation in the cuvette for more than 20 min. Reliable estimates of the CO_2 uptake rate may be obtained in approximately three minutes. Upon removal of the material (H), the zero signal is again rapidly obtained.

Using either natural sunlight or an artificial light source, light response curves may be obtained by inserting neutral density filters between the light source and the measurement cuvette. Such responses are shown as determined in April 1984 for *Bostrychia scorpioides* and for the green alga *Ulva lactuca* in Fig. 5. As seen from Fig. 5, differences in the characteristics of the response curves (such as light saturation value), as well as differences in CO_2 uptake rates, are thus rapidly established.

Rates of gas exchange of sediment cores were determined in the dark and in the light, with the difference assumed to result from algal photosynthesis. Since the gas exchange rates of individual samples can be assessed within minutes, a relatively large number of cores may be processed and an attempt may be made to understand patterning that explains in part the large variation in rates observed. Samples collected in July 1983 from the mud flats of a drainage channel exhibited gas exchange rates at high light intensity (approximately 1 000 μmol m^{-2} s^{-1} PAR) which varied between −1.5 μmol m^{-2} s^{-1} and more than 5.0 μmol m^{-2} s^{-1}. Nevertheless, total chlorophyll content of the samples was the same order of magnitude and we must assume that the differences in CO_2 uptake are the result of differences in the distribution of algal cells with depth in the cores (see Pomeroy *et al.*, 1981). This suggests that the methods under discussion may be used with greater resolution to determine how sedimentation processes and algal mobility determine CO_2 fixation on the mud flats.

In the case of sediment samples collected from under salt marsh vascular plants, where the soil is more stabilized, a correlation was found between chlorophyll content of the samples and observed CO_2 uptake rate as shown in Fig. 6. Variability was large, and recognizable differences in coloration of the samples could be used to predict gas exchange characteristics of individual cores. The highest

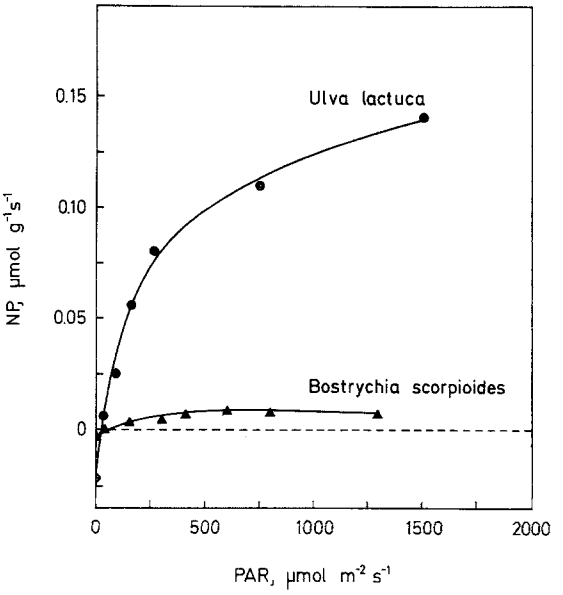

Fig. 5. Net photosynthesis rates (NP) of two algal species as a function of incident PAR. Triangular symbols were obtained with green alga *Ulva lactuca*, circular symbols with the red alga *Bostrychia scorpioides*. Air temperature was 25 °C

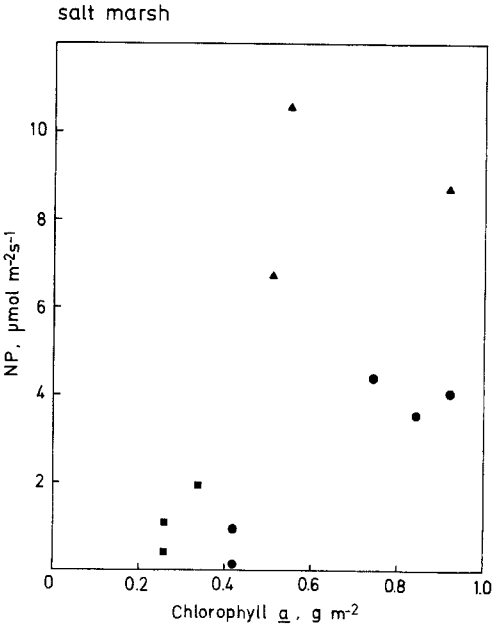

Fig. 6. Net photosynthesis rates (NP) of sediment cores taken from under the plants in the salt marsh as a function of chlorophyll *a* content. Triangular symbols are for samples collected beneath *Spartina maritima;* square symbols are for samples collected below *Arthrocnemum fruticosum* and *Halimione portulacoides*. Air temperature was 30 °C. Samples collected from less well-defined areas based on vegetation type are indicated as solid circles

rates of CO_2 uptake were found in samples collected below rather open canopies of *Spartina maritima* (triangular symbols in Fig. 6), while the lowest rates were obtained with samples collected below closed *Arthrocnemum fruticosum* and *Halimione portulacoides* canopies (square symbols in Fig. 6).

Discussion

Since the data on gas exchange rates reported here are few and have been selected to demonstrate capabilities of the measurement equipment, it is inappropriate to draw conclusions at this time about the ecophysiology of the species studied. Nevertheless, the similarity or difference in measured rates to those which have been obtained in other studies is of importance when evaluating the potential of the instrumentation described. The necessary comparison may be made by referring to only a few recent investigations which were designed to collect information on photosynthesis of organisms of estuarine ecosystems during the low tide period when these are exposed to the atmosphere.

Pearcy and Ustin (1984) investigated the regulation of gas exchange of *Spartina foliosa* Trin. and the succulent *Salicornia virginica* L. taken from the salt marsh of California. The CO_2 uptake rates which they observed were considerably higher than those found for plants from the salt marsh in Corroios. However, the plants used in that study were grown in aerated saline nutrient solution. As found for the plant species studied here, *Spartina foliosa* exhibited a high optimum temperature typical for C_4 metabolism, while the optimum temperature for the C_3 succulent *S. virginica* was approximately 25 °C. Leaf internal CO_2 partial pressure estimates determined for the two species studied from the salt marsh in Portugal were similar to those obtained for their C_4 and C_3 counterparts in California. Pearcy and Ustin (1984) reported that rates of CO_2 uptake by leaves of *S. foliosa* were several times higher than those of *S. virginica,* but that this difference was diminished at high salt concentrations which depressed the photosynthesis rates of *S. foliosa.* In contrast, the data presented in our Fig. 3 illustrate much larger differences in the potential photosynthetic capacities of *Spartina maritima* and *Arthrocnemum fruticosum.* In addition, Pearcy and Ustin found that the leaf conductance of the C_3 succulent *S. virginica* was even greater than that of *S. foliosa* at all levels of salinity, which suggests that this C_3 species was less conservative with water than the C_4 plant. *A. fruticosum* used water much more sparingly than did *S. maritima* in the Portugal salt marsh.

These apparent differences in regulation of leaf function lead one to question whether in fact the species studied are so different or whether growth conditions play a strong role in determining leaf conductance and CO_2 uptake rates. The latter possibility calls attention to the importance of investigating gas exchange characteristics in the natural habitat of the plants, which is certainly possible with the porometer equipment described. Additional difficulties are, of course, encountered when attempting to evaluate gas exchange characteristics in natural situations. These techniques are limited to application during intertidal periods, but may be used in combination with other techniques to assess the relative importance of high-tide and low-tide photosynthesis. Leaf orientation and self-shading must be taken into account. The small-sized, easily-positioned instrumentation described here allows one to overcome these problems to some extent. The boundary layer resistance of leaves is decreased to approximately 0.2 s cm^{-1} due to strong ventilation of the cuvette. Final estimations of CO_2 uptake under natural conditions should be based on rates corrected for actual boundary layer conditions.

The rates of CO_2 uptake obtained for macrophytic algae from the Tejo Estuary are similar to rates that have been reported previously for algal samples from other locations. King and Schramm (1976) investigated the photosynthetic rates of green, brown, and red algae of the Baltic Sea region. They found that on a dry weight basis, the green alga *Ulothrix* sp. Kutzing exhibited CO_2 uptake rates which were approximately eight times as high as those of the red alga *Phycodrys* sp. Kutzing. With porometer methods, we determined at light saturation that the green alga *Ulva lactuca* fixed CO_2 at rates almost ten times greater than the red alga *Bostrychia scorpioides* (Fig. 5). As with *U., U. lactuca* appears to approach light saturation at greater than 500 μmol m^{-2} s^{-1} PAR.

Bostrychia scorpioides also reached light saturation at relatively high light intensity. This may result in part due to light penetration effects in the matted sample used. The effect is, nevertheless, interesting and relevant since these algae are even more densely matted in their natural situation. Further study of the actual light-climate situation of algal mats should be conducted. Measurements of CO_2 exchange may then be possible that allow an even more accurate assessment of the algal mat contribution to photosynthetic production of the estuary ecosystem than has been possible to date.

The degree of wetness of algae can influence their photosynthetic rate in air. For the purpose of these experiments, samples were moistened before insertion into the cuvette. As shown in Fig. 5, diffusion resistance due to water content did not appear to change rapidly under these conditions. While this allows us to have confidence in the methodology, water content is expected to play a greater role in determining net photosynthesis rates during intertidal cycles under natural conditions. As in the case of lichens (Lange *et al.,* 1984 a), samples must then be rapidly weighed, inserted into the cuvette for the short measurement period, and returned to their natural exposure.

Rates of CO_2 uptake of sediment cores measured with porometer methodology were assessed as the difference between CO_2 exchange rates in the light and in the dark. Apparently due to the patchiness in distribution of producers and consumers in these sediment samples, the actual net CO_2 exchange rates of individual cores were in

some cases negative in the light (loss of CO_2) and in others considerably positive. Since additional surface of the cores was exposed to the air by extraction and insertion into the porometer cuvette, there is no reason to believe that the exchange rates in the light alone reflect the *in-situ* situation of the cores as a whole. However, since the core surfaces are not disturbed, accurate determinations of photosynthetic CO_2 uptake are obtained from the light-dark difference for the conditions prevailing in the measurement cuvette. This offers the possibility of studying environmental effects on the algal contribution to production during low tide by subjecting samples to variations in light and temperature climates.

In general, the rates of CO_2 uptake measured for sediment cores were relatively high, equalling in some cases leaf photosynthesis rates on a surface area basis. The highest rates measured for individual cores on the mud flats, as well as below plants in the salt marsh, were five to ten times higher than rates obtained by Gallagher and Daiber (1973, see also Pomeroy *et al.*, 1981) for sediment cores from a Delaware salt marsh. Both studies were conducted at approximately 30 °C and at saturating light intensity. Gallagher and Daiber (1973) determined oxygen exchange of submerged cores and possibly transport resistances for CO_2 to the fixation sites were high. Further investigation, comparing these methodologies and rates obtained for the same cores, submerged and exposed, is required. The high rates of CO_2 fixation obtained in the present study do not imply equally high rates for large areas of the salt marsh due to the extreme patchiness in algal distributions. Rather the porometer methodology offers the opportunity of describing this mosaic better and incorporating such descriptions into an overall picture of carbon input to the estuarine ecosystem.

The transportable gas exchange measurement system described here offers a valuable potential as a tool for use in investigations of primary production in estuarine ecosystems. An apparatus which allows the study of vascular plant and algal materials without modification and during the same experimental period can aid in unifying information on photosynthetic response of these organisms. New experimental designs seem possible for gathering data which could illustrate, in detail, energy exchange of salt marsh and mud flat communities and trapping of energy by carbon fixation.

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