

CARBON DIOXIDE ASSIMILATION, PHOTOSYNTHETIC EFFICIENCY, AND RESPIRATION OF A CHESAPEAKE BAY SALT MARSH

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SUMMARY

(1) Net CO₂ exchange and photosynthetically active radiation (PAR; 400–700 nm) were measured periodically between August 1974 and September 1979 in two salt marsh communities on Chesapeake Bay, U.S.A. One community had the two C₄ grasses, *Spartina patens* and *Distichlis spicata*, and the other included these grasses, as well as the C₃ sedge, *Scirpus olneyi*.

(2) Photosynthetic efficiency can be defined as the quotient of CO₂ assimilated during the day by a unit area of salt marsh and the total photon flux of PAR incident on that area. The mean value (%) of photosynthetic efficiency from June to August of the grass community (16.8 mmol Einstein⁻¹) was significantly greater than that of the mixed community (15.3 mmol Einstein⁻¹), but at the $P = 0.05$ level of significance the year-to-year differences within both communities were not statistically significant.

(3) In the grass community, photosynthetic efficiency per unit green biomass declined sharply from mid-May until early June. From late June until late September, the decline continued, but was linear and gradual in both communities.

(4) The maximum value for day-time net CO₂ assimilation per unit area of salt marsh, between sunrise and sunset, was 0.95 mol m⁻² and occurred in late June. During June, July, and August, net CO₂ assimilation by both communities accounted for $3.5 \pm 0.9\%$ of the incident PAR. Whole-season community net CO₂ assimilation was estimated using a regression equation for the seasonal course of photosynthetic efficiency and a model for incident solar radiation. The estimate of total CO₂ assimilation predicted by the model for the entire growing season (May to October) was 62 mol m⁻². The photosynthetic efficiency during June to August was 19% (1.9%) equivalent to 0.9% of total solar radiation.

(5) Community respiration was first measurable in early April. The rate of loss of CO₂ increased rapidly thereafter. The highest rate for a single night, from sunset to sunrise, was approximately 0.30 mol m⁻² and occurred during July. The mean value of night-time community respiration in June and July was 0.20 mol m⁻², which was approximately 30% of the mean net daily CO₂ assimilation at this time. The loss of CO₂ from April to December was 36 mol m⁻².

(6) The seasonal (May to October) daytime net assimilation of CO₂ exceeded seasonal (April to December) night-time net loss of CO₂ by 26 mol m⁻². Thus, the carbon balance in the salt marsh was positive and accumulation of CO₂ equivalent to a biomass of about 740 g m⁻² per year was available for storage within the system or for export to the adjacent estuary.

(7) Though the photosynthetic efficiency between June and August was 1.9%, the net ecosystem efficiency, allowing for CO₂ losses, for utilization of PAR during May to October was 0.8% equivalent to 0.4% of total solar radiation.

INTRODUCTION

The importance of a coastal salt marsh to the ecology of adjacent sea or estuary depends largely upon what happens to the salt marsh plant biomass. Carbon assimilated by photosynthesis has three possible fates. It may be: (i) returned to the atmosphere and interstitial waters, through the collective respiratory processes of the salt marsh community, as CO_2 or CH_4 ; (ii) accumulated within the sediments of the community; or (iii) exported as secondary production in the bodies of consumers or as dissolved and suspended carbon compounds or as detritus removed as the water recedes after high tide.

Evidence from some studies of detritus and carbon in tidal creeks supports the view that there is a net seasonal loss from coastal marshes into the sea (Odum & De La Cruz 1967; Nixon & Oviatt 1973), but a study of a brackish estuary found no net export (Heinle & Flemer 1976), and Woodwell *et al.* (1977) argue that some coastal marshes are net sinks for carbon.

A different approach is to determine whether or not there is a sufficient difference between seasonal community carbon assimilation and carbon loss to allow net accumulation or export.

Most salt marsh carbon balance studies have been based on measurements of primary production computed from changes in standing crop biomass of the plant community (Teal 1962; Keefe 1972; Williams & Murdock 1972). The value of salt marsh net primary production depends on the method used for calculation, and the five most commonly used methods applied to the same harvest data gave results differing by as much as 70% (Linthurst & Reimold 1978).

Our purpose in undertaking the work we report here was to determine the difference between net community CO_2 accumulated during the day and the amount lost at night for a typical season. We were primarily interested in the annual accumulation of carbon within the community—material that was potentially available for export to the adjacent estuary. To do this, we have constructed a model for net community CO_2 assimilation based on the seasonal patterns of solar radiation, community photosynthetic efficiency, and respiration.

THE STUDY AREA

Kirkpatrick marsh is on the Rhode River near the Smithsonian Chesapeake Bay Center for Environmental Studies, Edgewater, Maryland ($38^\circ 53' \text{N}$, $76^\circ 33' \text{W}$, Fig. 1). A general account of the area is given by Correll (1973). Two communities were studied: one is a stand of two grasses, *Spartina patens* (Ait.) Muhl. and *Distichlis spicata* (L.) Greene, and will be referred to here as the grass community. In this community, *Spartina patens* forms 50–100% of the total biomass. The other includes the sedge *Scirpus olneyi* Gray, in addition to *Spartina patens* and *Distichlis spicata* and will be referred to as the mixed community. Here, *Scirpus olneyi* dominates and forms 30–50% of the total biomass with *Distichlis spicata* more abundant than *Spartina patens*. Communities of these species occupy 40% of the total study area and are common around Chesapeake Bay. Measurements of steady state CO_2 exchange by single leaves of these three species were made at a range of ambient CO_2 concentrations between 0 and $300 \mu\text{l l}^{-1}$ in an open gas-exchange system. The CO_2 concentration at compensation point in high light flux was near $50 \mu\text{l l}^{-1}$ for the sedge and near $0 \mu\text{l l}^{-1}$ for the two grasses. This is strong evidence that the grasses possess the C_4 pathway of carbon reduction, but that the sedge does not (DeJong, Drake & Pearcy 1981).

Tides in this area have an amplitude of approximately 45 cm for a single cycle. During

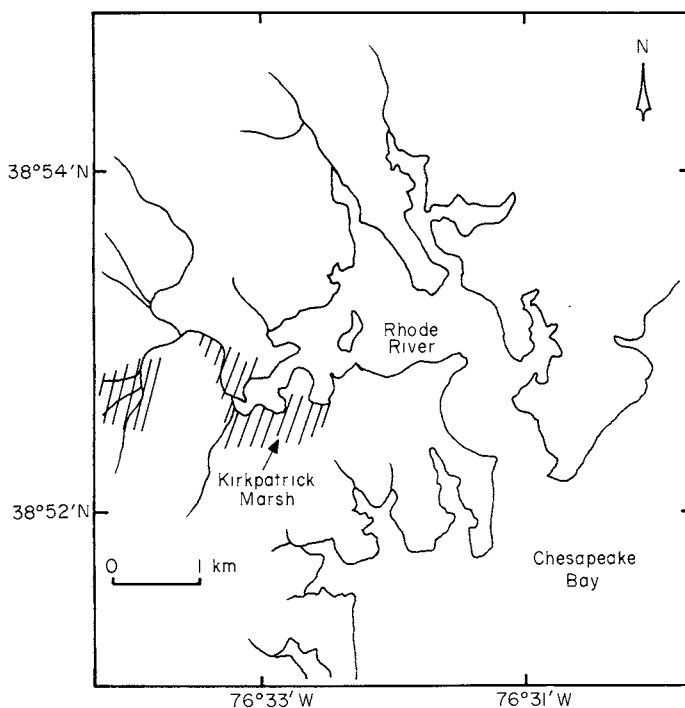


FIG. 1. Location of the field site. Salt marshes shown hatched.

the period January 1976 to December 1978, the range was 189 cm (Cory & Dresler 1980). Generally, the water level rises to within 10 cm of the surface of the marsh. Flooding is irregular. There is no detectable surface flow even during extreme high tide.

The estuary is brackish. Salinity is lowest in May (<1‰) and highest during November (7‰) (Correll 1973). The water potential of interstitial water in the surface soil layers is approximately -0.5 MPa during June and decreases to about -0.8 MPa by late September (DeJong & Drake 1980b).

Mean maximum temperature, 29°C , occurs in July and mean minimum temperature, about -6°C , is in January.

There is virtually no available nitrate, except in tide water during spring (Correll 1973). Recent measurements of acetylene reduction by excised roots from this site suggest that a small proportion of the annual nitrogen requirement may be supplied by fixation by bacteria associated with the roots (Van Berkum & Sloger 1979).

The biomass in the top 50 cm of soil in these communities is approximately ten times the biomass of above-ground plant matter. The soil beneath the root zone is a dark grey silty clay.

We do not know whether the marsh is accumulating sediments; it does not seem to be accumulating peat.

METHODS

Measurements of biomass and leaf area

Gas exchange measurements were carried out in an area that was small in comparison with the total area of Kirkpatrick Marsh. In order to determine whether the section of the

community we chose for gas exchange measurements was representative of the stands of these communities throughout the marsh, we collected samples of above-ground biomass randomly in stands of the two communities throughout Kirkpatrick Marsh. Beginning in July 1973 and continuing to August 1974, above-ground biomass in five 0.25-m²-quadrats was harvested weekly. Green and dead leaves were separated, dried for 3 days at 60 °C, and weighed. During August the communities began to accumulate considerable amounts of dead plant matter. Dieback along stems and leaves of *Spartina patens* does not proceed uniformly from the tips and this made accurate determination of total green biomass of this species in the grass community increasingly difficult, so no results are given for that community after September.

Green biomass of all plants used in gas exchange measurements was harvested and these results are shown with the random harvest results for comparison.

Leaf area was measured in some samples using a Li-Cor leaf-area meter (Turitzin & Drake 1980). Leaf area per unit dry weight was used to estimate the foliage area index for the community.

Chamber for measuring CO₂ exchange

Net CO₂ exchange was measured by covering part of the plant community with a 'Plexiglas' ('Perspex') chamber and monitoring the difference in the CO₂ concentration of air before and after it passed through the chamber.

Profiles of CO₂ concentration through plant canopies during the day show that some of the CO₂ produced by the plants and soil is re-assimilated (Inoue 1968) and an additional amount is extracted from the atmosphere by photosynthesis. We measured net CO₂ exchange. This was positive (assimilation) during the day and negative (respiratory loss) during the night.

Assimilation chambers interfere with wind and with the radiation climate and this interference results in unnatural effects on leaf temperature, canopy gas exchange, and incident solar radiation. We have attempted to deal with these effects by using rapid air flow across the chamber, and by allowing for the measured difference between quantum flux density of solar radiation within and outside the chamber.

The square chamber surrounded 1 m² of the soil surface and, by addition of two vertical sections, its height could be varied from 30 to 150 cm. It was constructed of 3 mm 'Plexiglas' and inserted into a machined groove in a flange on top of an aluminium frame that could be pushed 5 cm into the soil (Fig. 2). A large squirrel cage fan blew air through the chamber at a variable rate (1.0×10^5 to 3.0×10^5 l h⁻¹), which, at maximum, was sufficient to change the volume of the empty chamber every 12 s. This rapid flow had two important consequences: (i) in full sunlight, the drop in CO₂ concentration across the chamber was about 10 µl l⁻¹; (ii) leaf temperature within the chamber was usually within 2 °C of leaf temperature of plants outside the chamber. Thus the 'greenhouse effect' of this chamber upon plants within it was rather small.

Leaf and air temperature within and outside the chamber were measured by copper-constantan thermocouple junctions made from wire of 0.08 mm diameter.

The quantum flux of incident photosynthetically active radiation (PAR) in the range 400 to 700 nm was measured at the top of the plant canopy within and outside the chamber by quantum meters (Li-Cor). The unit used here for PAR is the Einstein (1 Einstein = 1 mol (approximately 6×10^{23}) of photons). The quantum meters were calibrated periodically by comparing their output to that of six Eppley thermopiles fitted with filters to isolate the PAR region of the spectrum. Two radiometers were used for

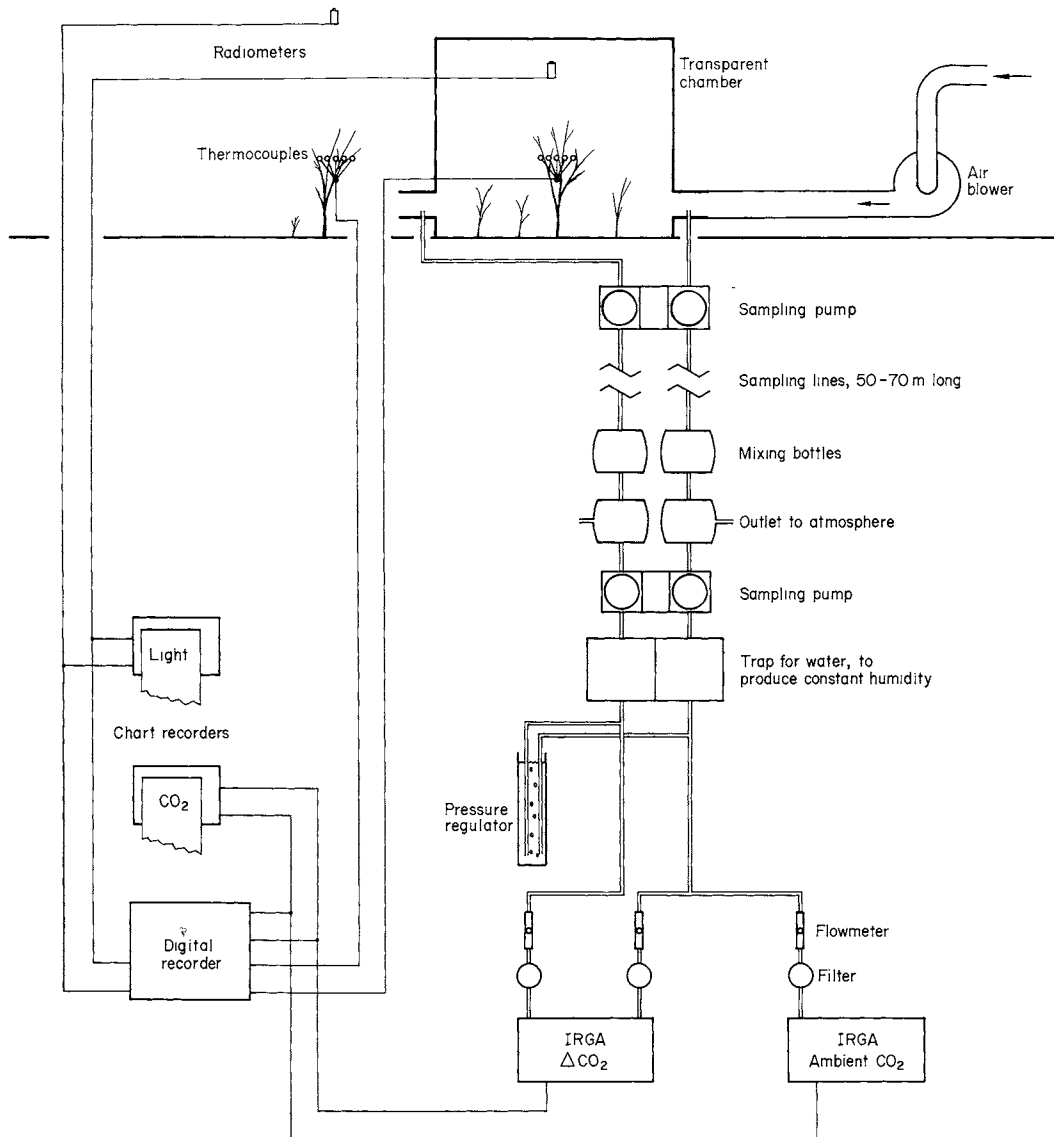


FIG. 2. Diagram of the gas exchange measuring circuit and associated recording equipment.

about 60% of the measurements in order to determine the effect of the Plexiglass chamber on PAR available to plants within the chamber and subsequent effect on daily light-dependent CO_2 assimilation. The quotient of readings from a radiometer outside the chamber to one within the chamber varied between 1.09 and 1.35 with the highest values occurring at low solar angles. The mean daily value was approximately 1.13. We recognize that this method of correcting for the effect of the chamber on quantum flux density does not fully account for geometrical effects of the chamber on light flux.

Another major influence of the chamber on the plants it covered was upon the boundary layer through which CO_2 , heat and water vapour must diffuse during exchange between the plant canopy and ambient air. The principal limitation in this respect was that wind

velocity within the chamber was constant. The velocity of air passing over leaves exterior to the chamber was, of course, changing moment by moment and this could not be duplicated within the chamber.

Gas sampling and measuring circuit

Two diaphragm pumps on the marsh fed sample gas streams from the inlet and outlet sides of the chamber into the gas sampling circuit (Fig. 2). This consisted of 50–70 m of 0.65-cm inner-diameter stainless steel tubing leading from the marsh to a laboratory (which housed the gas analysis and recording equipment) at the edge of the nearby forest. The gas circuit included a series of glass bottles (10 litre) which provided mixing volumes to damp oscillations in the background concentration of CO₂. The number of these bottles used depended on the amplitude and period of excursions in ambient CO₂ concentration; fewer were needed in windy conditions than in calm air. The final bottle in each line was open to the atmosphere. A second pump withdrew a gas sample from the final bottle and delivered it through copper condensing coils in a water bath at 1.0 °C (which produced constant water vapour concentration in the gas mixture), into flow meters and membrane filters and finally into the gas analysers (Hartman & Braun Models URAS 2 and URAS 2T). Zero for the differential analyser was checked automatically once an hour. Resolution of the difference in CO₂ concentration across the chamber was 0.1 μl l⁻¹. Constant pressure in the gas lines through the final section of the circuit was maintained by a water column connected to the gas circuit just before the flow meters. The dead volume of the whole gas-measuring circuit introduced a lag in detection of a change in CO₂ concentration in the chamber. A step change in concentration of 10 μl l⁻¹ at the chamber (produced during daylight by covering the chamber with a black cloth) required 3 min for the first indication at the gas analyser and 12 min for 95% response. The effect of the 3-min lag in the response of the gas measuring circuit was countered by offsetting the time when measurements were recorded by this amount and by computing hourly mean values for twenty measurements collected at 3-min intervals. At night, when more mixing bottles were used, response time was longer than 12 min, but since we were interested in the rate integrated over an hour, the longer lag was acceptable. At night, with lower wind speeds and net CO₂ efflux, the background CO₂ concentration often changed rapidly. In these circumstances, we took a mean value for only those hours when the random fluctuations in the signal were less than 20% of the hourly mean value.

The chamber was placed in one location, measurements were made for approximately a week, and the chamber was then moved. Experiments were not made when water covered the marsh or during especially windy or rainy weather. We sampled the two communities alternately. The stands on which we made gas exchange measurements were within 200 m of the field laboratory which housed the gas analyser and other equipment, but the stands were protected from trampling. Measurements were made when the equipment was not being used for other tasks, and when weather permitted, over a 6-year period from 1974 to 1979. Results from all years have been pooled to approximate a typical season. The total number of full days of measurement for photosynthetic efficiency was 125. The respiration results were collected on 125 nights in 1978 and 1979. This procedure is not ideal, but the technical difficulties of making such measurements in salt marsh are great, and we believe our procedure was adequate. Most of our measurements were made during June, July, and August, during which rates of CO₂ assimilation and loss were highest. The determination of the onset of photosynthesis in spring may be in error by up to two weeks. The flux of

CO₂ assimilation is so low in September and October that it can have only small effects on the balance between net CO₂ assimilation and net CO₂ loss for the season.

RESULTS

Biomass of green tissue

The dry weight of green tissue in the two communities used in this study is shown in Fig. 3. Foliage area index (FAI) in the grass canopy was estimated using the product of leaf surface area to dry weight quotient (determined on sub-samples of the total green biomass in the harvest (Turitzin & Drake 1980)) and above-ground biomass. Above-ground biomass increased in the random samples from the mixed community at the rate

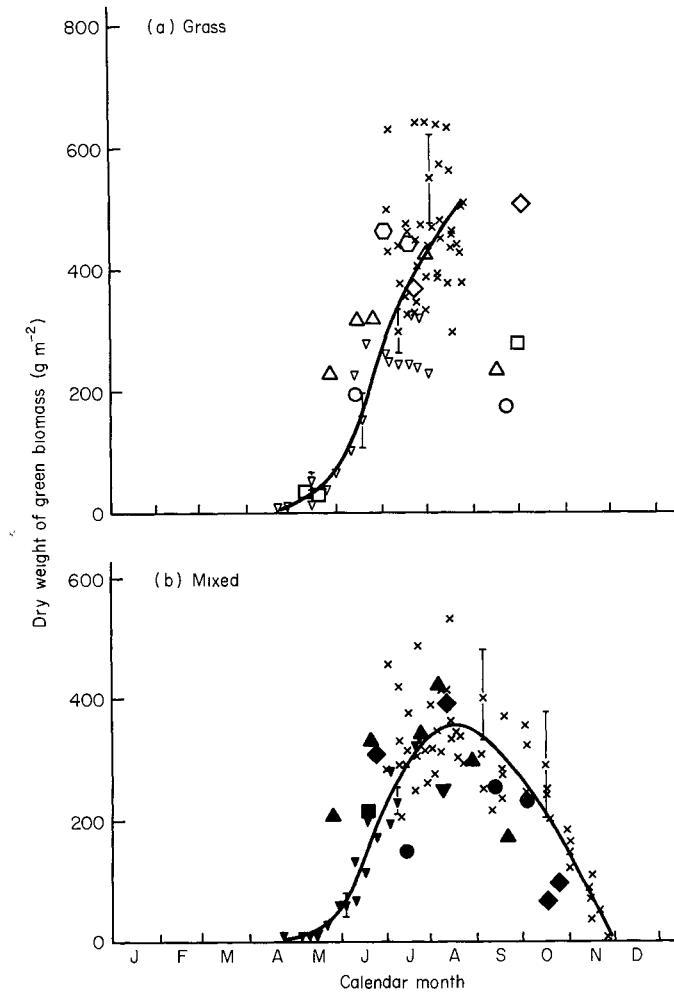


FIG. 3. Biomass in (a) the grass community (unfilled symbols) and (b) the mixed community (filled symbols) of the salt marsh on Chesapeake Bay. Small symbols, samples collected at random within either of the two communities over 25 ha; large symbols for biomass within the assimilation chamber. Symbols for years: x, 1973; ∇, 1974; ◇, 1975; △, 1976; ○, 1977; ○, 1978; □, 1979. Vertical bars are ± 1 S.E. ($n = 5$). The continuous curve is fitted by eye to the random samples.

of 4.5 g day^{-1} , and in the grass community at 5.0 g day^{-1} during June 1974. Mean standing crop (\pm S.E.) of green biomass in August and September 1973 was $414 \pm 48 \text{ g m}^{-2}$ in the grass community and $325 \pm 36 \text{ g m}^{-2}$ in the mixed community, equivalent to a mean FAI of 3.3 and 2.6 respectively.

Gas exchange, PAR, and temperature measurements during the day

Measurements recorded at 3-min intervals in the grass community on 19 June 1977 are shown in Fig. 4. Although this day was especially clear and cannot be called typical of summer days, the results are used for illustration because they are clear cut and trends are easily seen. The net rate of CO_2 assimilation and the flux of PAR increased during the morning until approximately 12.00 hours, when both began to decline. The highest value

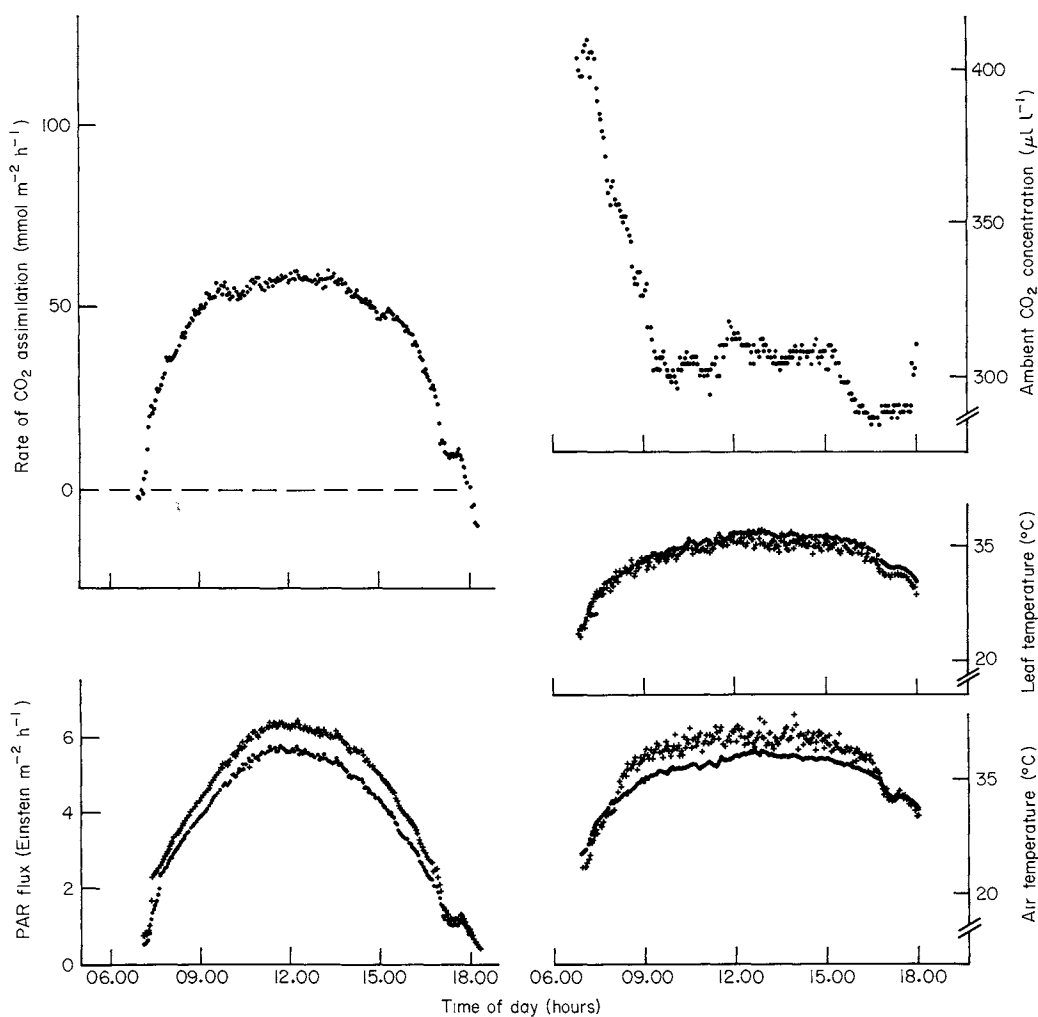


FIG. 4. Results on 19 June 1977 in the grass community in salt marsh on Chesapeake Bay. Symbols: ●, measurements made within the Plexiglas chamber, +, those made outside the chamber within the grass community. Measurements were recorded at 3-min intervals. Time is Eastern Standard Time.

of PAR outside the chamber on this day was $6.3 \text{ Einstein m}^{-2} \text{ h}^{-1}$. Maximum PAR at this latitude is approximately $7.1 \text{ Einstein m}^{-2} \text{ h}^{-1}$. Temperature was near $20 \text{ }^\circ\text{C}$ at 06.30 hours in the morning, but by noon, it had reached $35 \text{ }^\circ\text{C}$. The temperature of leaves inside the chamber was within $2 \text{ }^\circ\text{C}$ of that of leaves outside the chamber. (Leaf temperature often rose by as much as $15 \text{ }^\circ\text{C}$ during the morning.) Ambient CO_2 concentration declined from about $400 \mu\text{l l}^{-1}$ at 06.30 hours to about $300 \mu\text{l l}^{-1}$ at 13.00 hours.

Photosynthetic efficiency

Photosynthetic efficiency (%) is defined here as the quotient of total CO_2 assimilated during the day ($\text{mmol m}^{-2} \text{ day}^{-1}$) and total incident PAR ($\text{Einstein m}^{-2} \text{ day}^{-1}$). The mean and standard deviation of this quotient for June to August are shown in Table 1. Using a two way analysis of variance (Scheffe 1959), we found a small but statistically significant

TABLE 1. Photosynthetic efficiency (%) during June, July and August of 6 years for the two salt marsh communities on Chesapeake Bay. Photosynthetic efficiency is defined as the quotient of CO_2 assimilated and quanta of PAR absorbed, $(\text{mmol m}^{-2} \text{ d}^{-1})/(\text{E m}^{-2} \text{ d}^{-1})$.

Year	Grass community	Mixed community
	Mean \pm S.E. (n)	Mean \pm S.E. (n)
1974	17.3 ± 3.7 (3)	16.0 ± 2.8 (8)
1975	18.4 ± 3.9 (4)	10.8 ± 2.2 (5)
1976	17.3 ± 2.2 (14)	17.5 ± 6.0 (17)
1977	13.5 ± 3.2 (9)	—
1978	17.3 ± 4.4 (8)	—
1979	17.5 ± 0.1 (2)	13.8 ± 2.4 (15)
All years	16.8 ± 3.5 (40)	15.3 ± 4.7 (45)

All years and both communities: mean = 15.9 ± 4.1 (85).

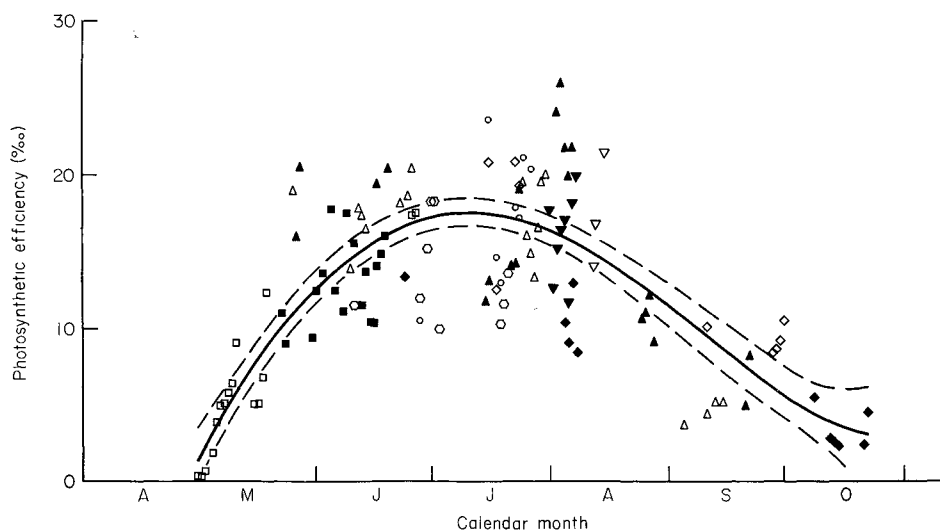


FIG. 5. Photosynthetic efficiency (%) of a unit area of salt marsh on Chesapeake Bay throughout the growing season. Symbols represent year of measurement and community as in Fig. 3. The continuous line is the fourth order polynomial regression and the broken lines are the 90% confidence interval for the regression. The regression equation is $Y = -97.0 + 98.5X + 6.44 \times 10^{-4}X^2 + 2.19 \times 10^{-5}X^3 + 4.16 \times 10^{-8}X^4$; $n = 125$, $R^2 = 0.62$.

difference ($P = 0.05$) between photosynthetic efficiency for the two communities (maxima 16.8 and 15.3 $\text{mmol Einstein}^{-1}$ for grass and mixed communities, respectively) but no significant difference ($P > 0.05$) between years within the same community. We used the months of June, July, and August for this analysis because the greatest overlap in the year-to-year measurements and most of the yearly carbon fixation occur during this period. Because there was so little difference between years or communities we calculated a single regression to describe the seasonal course of photosynthetic efficiency (Fig. 5). Photosynthetic efficiency rises during May to a maximum during the early part of July and declines to near zero by the end of October.

The mean photosynthetic efficiency for both communities and all years during June, July, and August was $15.9 \pm 4.1 \text{ mmol Einstein}^{-1}$. Given a value of $5.02 \times 10^5 \text{ J mol}^{-1}$ of CO_2 assimilated and $2.30 \times 10^5 \text{ J Einstein}^{-1}$ of incident PAR (Cartledge & Connor 1972) the mean daily photosynthetic assimilation of CO_2 accounted for $3.5 \pm 0.9\%$ of the energy of incident PAR during this period.

A measure of the extent to which the amount and physiological state of the green plant material affects the photosynthetic efficiency may be had by expressing the photosynthetic efficiency per unit biomass (Fig. 6). This measure declines linearly in both communities from June to September, and there is a statistically significant difference between the two communities: the mixed community is more efficient per unit biomass than is the grass community. In the grass community, photosynthetic efficiency per unit biomass is particularly high in early May.

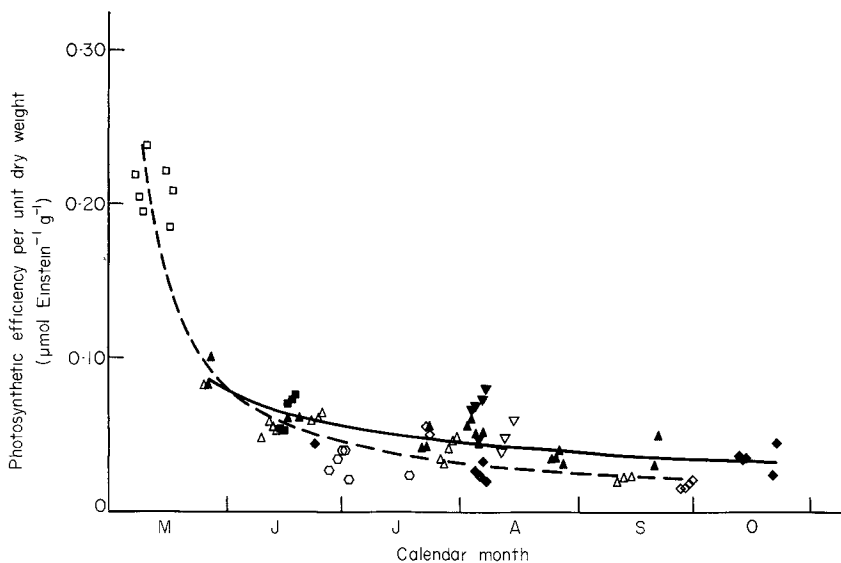


FIG. 6. The dependence of photosynthetic efficiency per unit dry weight of green biomass (Y) upon time of year ($X = \text{day in the year} - 120$). The data for the grass (---) and the mixed (—) community can be described by power functions. For the grass community $Y = 1.39 X^{-0.82}$; $n = 38$, $R^2 = 0.84$, and for the mixed community $Y = 0.45 X^{-0.50}$; $n = 38$, $R^2 = 0.41$. Symbols as in Fig. 3. For the difference between communities for the period June to September, $P = 0.1$.

Respiration

Figure 7 illustrates the time course of the average hourly rate of community CO_2 loss throughout several nights.

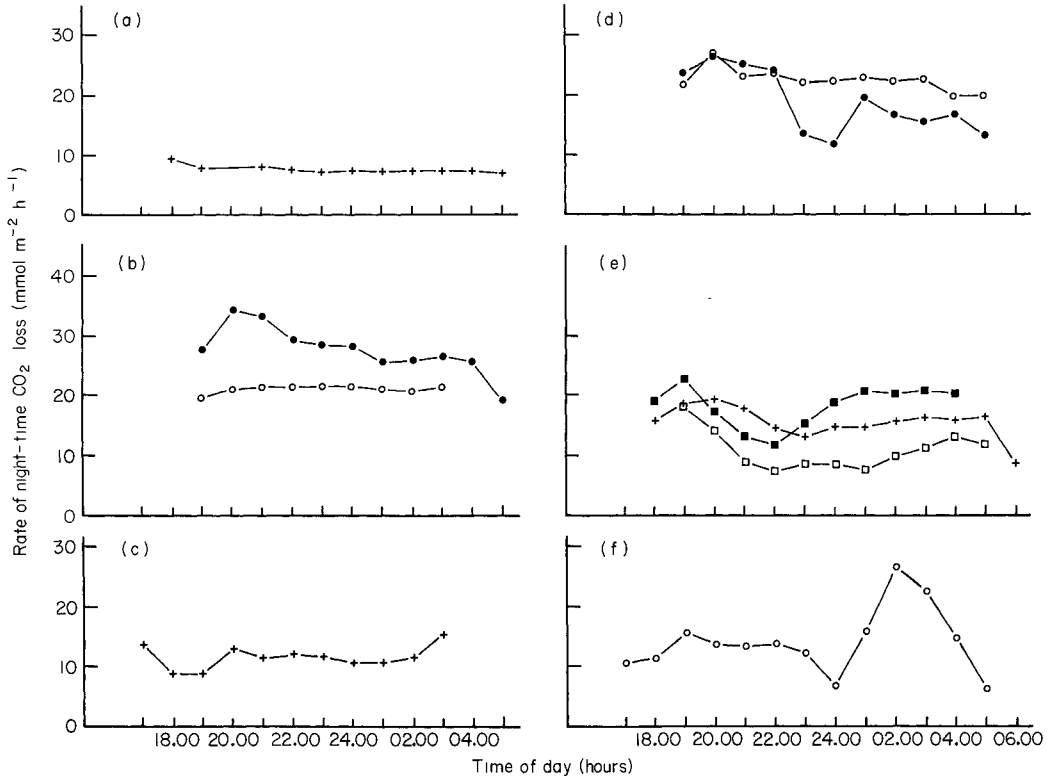


FIG. 7. Mean rate of CO_2 loss throughout the night for the two communities for several nights in 1978. Symbols: \circ and \bullet , grass community; $+$ and \square , mixed community. Results obtained within a few days of one another are on the same graph. (a) Mixed community, 12 May. (b) Grass community, 1 June (\circ), 5 June (\bullet). (c) Mixed community, 10 July. (d) Grass community, 13 July (\circ), 26 July (\bullet). (e) Mixed community, 8 September (\square), 9 September ($+$), 10 September (\blacksquare). (f) Grass community, 14 September.

Net community CO_2 balance

Net community CO_2 balance was estimated by subtracting the integrated values of net CO_2 loss at night from net CO_2 assimilation during the day. The seasonal trend for net CO_2 assimilation was estimated using the irradiance in the total solar spectrum calculated from a model (Goldberg, Klein & McCartney 1979) and the regression of photosynthetic efficiency on time of year (Fig. 5). Photosynthetic efficiency was corrected (by a method described below) to allow for the effect of the chamber on incident PAR. The values predicted by the solar radiation model were converted to units of quantum flux density in the photosynthetically active region (400–700 nm) by applying a conversion factor of $36.2 \mu\text{Einstein J}^{-1}$ (Loomis & Williams 1963). Use of this conversion is based on the assumption that irradiance in the 400–700 nm band is a constant proportion (47.5%) of total solar irradiance throughout the day. For daily or seasonal estimates this is acceptable (Stanhill & Fuchs 1977).

We could not make measurements during high tide and during especially windy and rainy weather. Our measurements were therefore biased for days of high solar radiation and so the non-linear dependence of CO_2 assimilation on PAR tended to produce an underestimate of the true whole-season photosynthetic efficiency. This would lead to an underestimate of total CO_2 assimilation which, in the context of our main objective, would

TABLE 2. Monthly mean values of PAR measured at the Kirkpatrick salt marsh on Chesapeake Bay during 1974 to 1978 compared with 8-yr monthly mean values at Rockville, Maryland (Klein & Goldberg 1974, 1976), and with monthly mean values predicted by a model of incident solar radiation (Goldberg, Klein & McCartney 1979). Monthly mean values measured at the field site are not significantly different ($P = 0.05$) from monthly mean values at Rockville or from values predicted by the model.

Month	Field site Mean \pm S.D. (<i>n</i>)	Rockville Mean \pm S.E. (<i>n</i> = 8)	Model
May	42.7 \pm 13.1 (16)	38.2 \pm 3.0	38.7
June	39.7 \pm 11.4 (31)	41.6 \pm 2.3	40.3
July	39.9 \pm 9.7 (12)	43.2 \pm 2.2	39.4
August	40.0 \pm 6.4 (7)	37.2 \pm 2.8	36.7
September	35.3 \pm 5.1 (5)	28.9 \pm 2.2	29.5

lead to an underestimate, rather than to an overestimate. We therefore compared monthly mean values of total daily PAR with monthly mean values from 8 yr of measurement at Rockville, Maryland (Klein & Goldberg 1974, 1976) and with the monthly mean value predicted by the model of incident solar radiation (Goldberg, Klein & McCartney 1979). These results are presented in Table 2. There were no statistically significant differences between the estimates made at the site and the others. We used the model of incident solar radiation as the basis for our estimate of seasonal net CO₂ assimilation, because it produced values of PAR closest to those measured at the field site.

We accounted for the effect of the reduction of PAR by the chamber for 85 of the 125 days used as follows. (1) A light response curve was constructed from hourly mean values of net CO₂ exchange and light flux within the chamber. (2) Simultaneous measurements of PAR outside the chamber were then applied to the light response curve to determine the

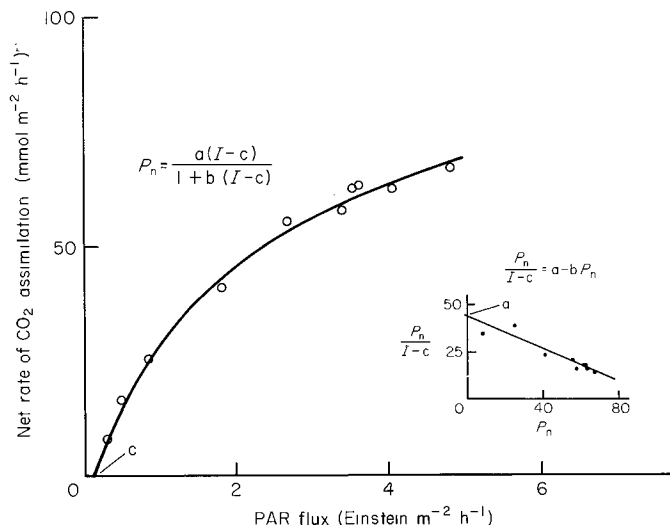


FIG. 8. The dependence of the net rate of CO₂ assimilation, P_n , upon the flux of incident photosynthetically active radiation (I), in the grass community on 19 July 1978. The values shown are the hourly mean values from Fig. 4. The value of c ($0.1 \text{ Einstein m}^{-2} \text{ h}^{-1}$) was determined by inspection of the recorder charts and those of a and b were found from the linear plot of $P_n/(I-c)$ against P_n (inset); $a = 43 \text{ mmol Einstein}^{-1}$, $b = 0.42 \text{ Einstein}^{-1} \text{ m}^2 \text{ h}$.

net rate of CO₂ exchange outside the chamber. The light response could be expressed by the relationship

$$P_n = \frac{a(I - c)}{1 + b(I - c)} \tag{1}$$

where P_n is the net rate of CO₂ assimilation, I is incident PAR, a is the initial slope of the light response curve, b is the slope of the relationship of $P/(I - c)$ plotted against P as the independent variable, and c is the light compensation value, the flux of PAR at which net CO₂ assimilation balances net CO₂ loss (Fig. 8). The constants a and b were determined

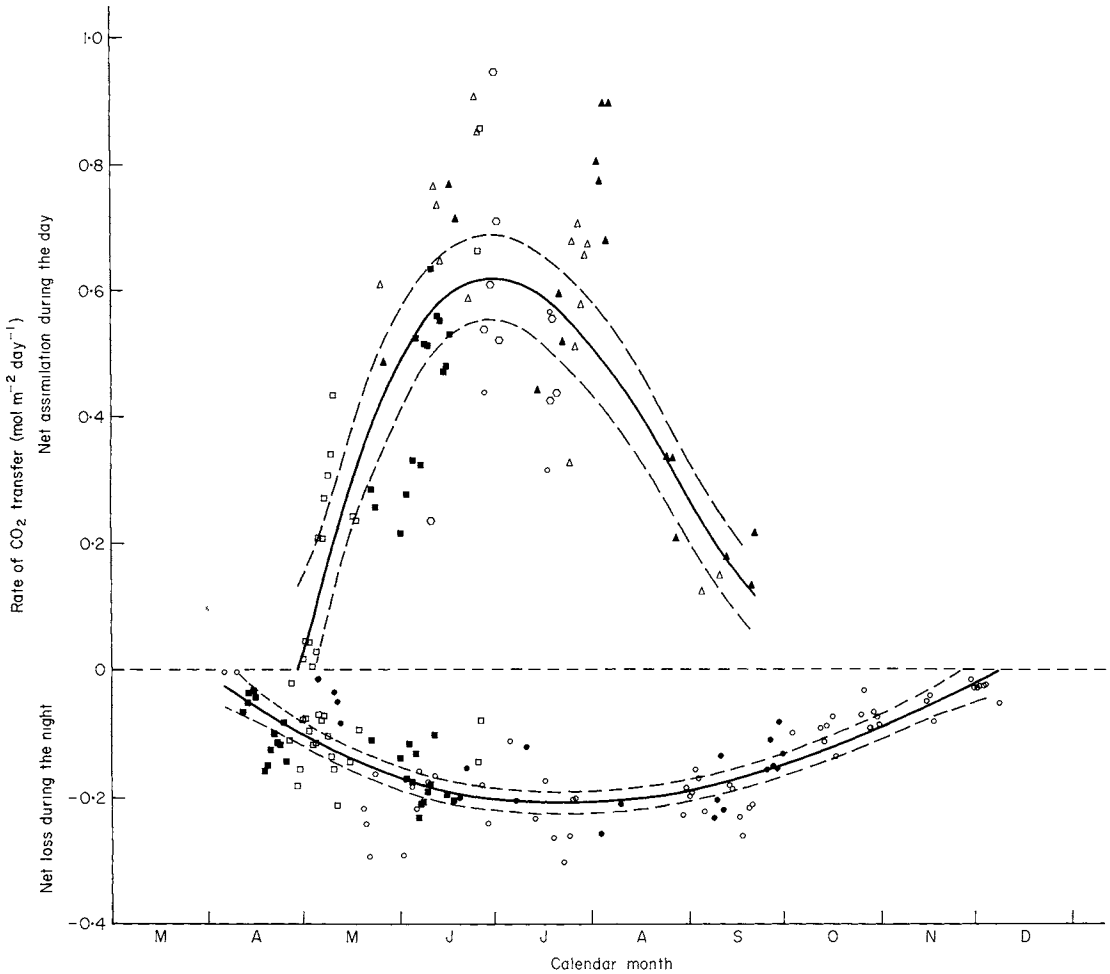


FIG. 9. Seasonal course of net CO₂ assimilation during the day and net CO₂ loss (shown negative) during the night. Measured values for net CO₂ assimilation corrected to allow for attenuation of PAR by the Plexiglas chamber. See text for details. Symbols as in Fig. 3. The continuous line through the net CO₂ assimilation results is the product of the polynomial regression describing the seasonal course of photosynthetic efficiency (Fig. 5) and total daily PAR computed from a model for incident solar radiation (Goldberg, Klein & McCartney 1979). The broken line is a similar product for the 90% confidence interval in Fig. 5. The continuous and dashed lines through the net CO₂ loss results are the third order polynomial regression and 90% confidence interval describing the dependence of net CO₂ loss (Y) on day in the year (X) ($Y = 466 + 7.3X - 2.3 \times 10^{-2}X^2 + 1.6 \times 10^{-5}X^3$; $n = 125$, $R^2 = 0.57$).

for each day from a plot of the linear transformation of Eqn 1 (Fig. 8). The constant c was taken directly from the recorder charts. This model was chosen because it has been commonly used (e.g. McCree 1971), the values for the constants can be compared with those obtained by others using single leaves or whole canopies, and because analysis of the seasonal trends in these constants helps in deciding which environmental factors influence the light response of the plant canopy. Details of the seasonal trends in the constants for the light response curves will be reported in another paper.

Observed values of net CO_2 assimilation, adjusted for the effect of the chamber on PAR flux, are shown in Fig. 9 with the calculated curve of net CO_2 assimilation. The reliability of this method for predicting seasonal CO_2 assimilation was tested by comparing observed values of net day-time CO_2 assimilation with calculated CO_2 assimilation. The correlation coefficient was 0.98. The difference between calculated and observed net CO_2 assimilation on the same day was plotted against the calculated value. The slope of the linear regression was 0.02, which was not significantly different from zero. The total observed day-time CO_2 assimilation for 75 days was 35.3 mol m^{-2} and the total calculated was 33.8 mol m^{-2} , a 4.5% difference. Thus, the predicted net CO_2 assimilation estimates the observed whole-season net assimilation fairly well, though it does not give a precise estimate for any given day. The total CO_2 assimilated, summed between May and October, was 62 mol m^{-2} .

Total CO_2 lost by the community during the night was determined by multiplying the mean rate for that night (Fig. 7) by the number of hours of darkness. The seasonal trend in net CO_2 lost by the community during darkness is shown in Fig. 9. The greatest rate of loss of CO_2 occurred during June and July. During the period from May to October there was a small but significant difference in CO_2 loss between the two communities. Yearly CO_2 loss was obtained by integration under the regression curve describing net CO_2 lost between April and December and gives 36 mol m^{-2} . The difference between net CO_2 assimilated (May to October) and seasonal net CO_2 lost (April to December) was 26 mol m^{-2} . Assuming that dry mass per CO_2 assimilated is 28.2 g mol^{-1} (Cartledge & Connor 1972) this is equivalent to a biomass of about 740 g.

Net ecosystem efficiency

The efficiency of community *assimilation* of CO_2 for the period May–October was estimated by dividing the energy equivalence of the calculated net CO_2 assimilation (Fig. 9) by calculated PAR during the same period. Total CO_2 assimilated was 62 mol m^{-2} (equivalent to a biomass of 1746 g m^{-2}); incident PAR was $7.1 \times 10^3 \text{ Einstein m}^{-2}$. Seasonal efficiency for the utilization of PAR energy in assimilation of CO_2 was therefore $100 (62 \times 5.02 \times 10^5) / (7.1 \times 10^3 \times 2.3 \times 10^5) = 1.9\%$. This is about 0.9% of total solar radiation for the same period. The net ecosystem efficiency for conversion of PAR to biomass (26.2 mol m^{-2}) stored in the system at the end of the growing season, or exported from the system, was 0.8%. This is about 0.4% of total incident solar radiation during the period April to December.

DISCUSSION

In order to demonstrate that the Kirkpatrick salt marsh may be a source of carbon for the adjacent estuary, it must first be shown that the marsh accumulates excess carbon after the seasonal demand of respiration by the plants and soil biota have been met. No single

method is without difficulties. The work reported here was necessarily restricted to a small area, but that area is similar to that of the marsh as a whole (Fig. 3). The sample chamber necessarily disturbs the plant microclimate, but we believe that the high rate at which air was pumped through the chamber minimized this disturbance and did not introduce great inaccuracy.

Photosynthetic efficiency

Photosynthetic efficiency of utilization of PAR in CO₂ assimilation averaged 15.9 ± 4.1 mmol Einstein⁻¹ during June, July, and August (Fig. 5). The range was 8.6 to 24.3 (Table 1). The mean value is equivalent to $3.5 \pm 0.9\%$ of the energy of incident PAR and about $1.7 \pm 0.5\%$ of total solar energy. Scatter in the seasonal time-course of photosynthetic efficiency is probably due to seasonal changes in biomass (Fig. 6), day-to-day variations in community respiration (Fig. 7), and the non-linear dependence of net CO₂ assimilation on PAR (Fig. 8).

Photosynthetic efficiency is defined here in terms of incident rather than absorbed photosynthetically active radiation because we did not measure reflectance and transmission in each of the sections of the community where we made gas exchange measurements. Absorption by the grass community is reported by Turitzin & Drake (1980) to be approximately 0.80 during July. Using this value to estimate photosynthetic efficiency per absorbed photon gives 20 mmol Einstein⁻¹.

Net ecosystem efficiency of conversion of PAR, after allowing for CO₂ loss at night, was 0.8%, which is about 0.4% for total solar radiation. Vegetable crops convert 2.2–4.5% of PAR into plant matter (Sale 1973; Loomis & Gerakis 1975), and Bray (1961) reports that a *Picea omorika* (Bolle) plantation converted 3.3% of total solar radiation year-round. The net ecosystem efficiency for conversion of total solar radiation of North Carolina *Spartina* marshes averaged 0.46% in April and 0.36% between July and November (Blum, Seneca & Stroud 1978), and Teal (1962) reported a value of 0.62% for a Georgia *Spartina* marsh.

The very steep decline during May in photosynthetic efficiency per unit dry weight (in the grass community) suggests two hypotheses to account for limitations in the efficiency of CO₂ and light harvesting by these communities: (1) individual leaves may be most efficient in spring and their efficiency declines thereafter; and (2) seasonal changes in canopy structure have a direct effect on light and CO₂ harvesting.

Three factors that may influence the photosynthetic efficiency of individual leaves in the salt marsh environment are water potential, salinity, and nitrogen stress.

We have repeatedly found that on clear days, plant water potentials in the species studied here, decline to values of about -3.0 to -4.0 MPa. Soil water potential in these communities never declines below about -0.8 MPa (DeJong & Drake 1981). Low plant water potential has been shown to reduce the rate of photosynthesis in some species in which the loss of capacity for carbon reduction was due to loss of photochemical activity of the chloroplasts (Boyer 1971; Mohanty & Boyer 1976). Salinity reduces stomatal aperture in halophytes as well as mesophytes (Gale 1975).

There appears to be an interaction of effects of salinity and light upon photosynthesis in salt marsh species. Kuramoto & Brest (1979) report that photosynthesis in *Spartina foliosa* and *Distichlis spicata* is reduced by growth in, or exposure to, low water potential. In high light flux, however, *S. alterniflora* did not lose its photosynthetic capacity, even when grown in water as saline as sea water (Longstreth & Strain 1977).

The productivity of salt marshes is thought to be nitrogen limited (Gallagher 1975; Valiela, Teal & Persson 1976). Nitrogen deficiency causes reduction of the photosynthetic efficiency of leaves of both C_3 and C_4 plants (Nevins & Loomis 1970; Medina 1970, 1971). The three species in this study showed reduction in capacity to harvest CO_2 at high light flux in the field, when compared to the same species grown on double strength Hoagland's solution (DeJong, Drake & Pearcy 1981).

Foliage area index (estimated from biomass) is below 1.0 during early May but exceeds 2 in June when the decline in photosynthetic efficiency becomes linear (Figs 3 and 6). Most of the leaves of this community are erect at the beginning of the season, but an increasing number fall over during mid-summer until all the leaves in the community are horizontal by late-August (Turitzin & Drake 1981). The effect of this change in canopy structure upon photosynthetic efficiency is substantial and probably operates through effects on canopy gas exchange rather than upon distribution of light within the canopy (Turitzin & Drake 1981).

The differences between the two communities with respect to photosynthetic efficiency per unit biomass (Fig. 6) may be a consequence of the difference in canopy structure. The mixed community is less compact and remains vertical throughout the season.

Although we treat photosynthetic CO_2 assimilation and night-time CO_2 loss as though they were completely separate processes, day-time respiration influences photosynthetic efficiency. The measurements we report are the net exchange of CO_2 from canopy, soil and roots. Day-to-day variations in net loss of CO_2 at night are substantial (Figs 7 and 9), and it is difficult to imagine that factors influencing CO_2 loss at night do not operate during the day as well.

Thus, the combined effects of canopy density, reduced light penetrating to lower layers within the canopy, seasonal decreases in water potential and nitrogen supply, seasonal increases in salinity, and respiration may all play a role in the seasonal loss of photosynthetic efficiency by these two communities.

Respiration

The rates of CO_2 loss we measured ranged between 10 and 30 $mmol\ m^{-2}\ h^{-1}$, and Teal & Kanwisher (1961) reported the uptake of O_2 in a Georgia salt marsh was between 8.9 and 14 $mmol\ m^{-2}\ h^{-1}$. Values for respiration from crops and soil (Mogensen 1977; Monteith, Szeicz & Yabuki 1964) are also within the range of measurements we report in Fig. 6.

Approximately 60% of the net seasonal community carbon gain ($62\ mol\ m^{-2}$) was lost at night or during the spring and autumn when the net rate of CO_2 assimilation was low (Fig. 9). Monteith, Szeicz & Yabuki (1964) reported that the night-time loss amongst crop plants varied between 11 and 40% of the daytime gain. During June and July in the present study, calculated CO_2 assimilation per day was approximately $0.58\ mol\ m^{-2}$ and mean loss at night about $0.20\ mol\ m^{-2}$ or about 34% of daily uptake (Fig. 9).

We have detected very little loss of CO_2 during March and December, the months which are the beginning and end of the active period for the plant communities in Kirkpatrick Marsh. Measurements were not made in January and February, but the possibility of substantial CO_2 loss then is remote, even though there must be respiration at a rate too slow to be detected with our methods. We estimate that during the growing season, after allowing for respiration, about $26\ mol\ m^{-2}$ remains in the system or is exported. If this amount were to be metabolized during January and February, respiration rate would have to average $18\ mmol\ m^{-2}\ h^{-1}$ —about the same rate as measured in mid-summer (Fig. 9).

Losses of carbon from the system in forms other than those measured in this study may occur, but probably represent an insignificant fraction of that accumulated during the growing season. An increase in CO_2 dissolved in waters that flood salt marshes has been measured (Teal 1967). Whether or not this is sufficient to represent a loss different from the losses from the whole community into air during slack tide is not known. Evolution of methane (CH_4) from brackish marshes in Delaware has been reported to be in the range of $1.22 \mu\text{l cm}^{-2} \text{ day}^{-1}$ during summer depending on redox state and flooding of soils (Swain 1975; Atkinson & Hall 1976). These rates are equivalent to about 0.5 to $10 \text{ mmol m}^{-2} \text{ d}^{-1}$, which would represent a maximum loss of less than 5% that lost as CO_2 in mid-summer (Fig. 9).

Biomass accumulation estimated from gas exchange

Increase in green biomass over the 30 day period in June is approximately $4.5 \text{ g m}^{-2} \text{ d}^{-1}$ for the mixed and $5.0 \text{ g m}^{-2} \text{ d}^{-1}$ for the grass community (Fig. 3). During this same period, CO_2 accumulation calculated from the gas exchange results is approximately $0.4 \text{ mol m}^{-2} \text{ d}^{-1}$, which is equivalent to a biomass accumulation of about $11.3 \text{ g m}^{-2} \text{ d}^{-1}$. Thus, aerial biomass accumulation accounts for 40–45% of net community CO_2 accumulation. Root growth in *Spartina patens* is reported to be 0.15 to 4.0 times shoot growth (Gosselink 1970; Valiela, Teal & Persson 1976).

The increase of above-ground biomass (Fig. 3) is probably a good estimate of total above-ground primary production during June and July for the plant communities in this study, because at that time there are few dead leaves. Our results therefore suggest a root/shoot quotient of 1.1.

We conclude from all our results that about 60% of the 1750 g m^{-2} produced on this salt marsh between May and October may be lost by respiration. The remaining 40% may accumulate or be lost by export.

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