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Gas Exchange Responses of Chesapeake Bay Tidal Marsh Species Under Field and Laboratory Conditions

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Summary. Laboratory and field gas exchange measurements were made on C_3 (*Scirpus olneyi* Gray) and C_4 (*Spartina patens* (Ait.) Mahl., *Distichlis spicata* (L.) Green) species from an irregularly flooded tidal marsh on the Chesapeake Bay. Laboratory measurements were made on plants grown from root stocks that were transplanted to a greenhouse and grown under high light and high nutrient conditions. The two C_4 species were similar in their laboratory gas exchange characteristics: both had higher net carbon exchange rates, higher mesophyll conductances, higher photosynthetic temperature optima and lower leaf conductances than the C_3 species. The laboratory photosynthetic water use efficiency of the C_4 species was approximately three times that of the C_3 species.

Field gas exchange responses of the above species were measured *in situ* in a Chesapeake Bay tidal marsh. Despite differences in biological potential measured in the laboratory, all three species had similar *in situ* carbon exchange rates on a leaf area basis. On a dry weight basis, leaves of the two C_4 species had about 1.4 times higher light saturated CO_2 assimilation rates than the C_3 species. Light saturation of CO_2 exchange occurred at photosynthetic photon flux densities of 80 n Einstein $cm^{-2}s^{-1}$, compared with 160 n Einstein $cm^{-2}s^{-1}$ in the laboratory grown plants. *Spartina patens* and *Scirpus olneyi* had similar daily CO_2 assimilation rates, but the daily transpiration rate of the C_3 species was almost twice that of the C_4 species. *Spartina patens* showed greater seasonal decrease in photosynthesis than *Distichlis spicata* and *Scirpus olneyi*. The two C_4 grass species maintained higher mesophyll conductances and photosynthetic water use efficiencies than the C_3 sedge.

Introduction

Since the discovery of C_4 photosynthesis (Kortschak et al. 1965; Hatch and Slack 1966) there has been much interest in elucidating the ecological significance of the C_3 and C_4 photosynthetic pathways. Research with species from temperate inland vegetation types, where C_3 and C_4 plants coexist in the same habitats, has shown that they often exhibit differences in seasonal activity. "Cool season" prairie grasses are generally found to be C_3 species while "warm season" grasses are most often C_4 species (Sims et al. 1978; Waller and Lewis 1979). Similarly, the catagories of "winter active" and "summer active" desert species often correspond to plants with C_3 and C_4 photosynthesis, respectively

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(Mooney et al. 1976; Mulroy and Rundel 1977). Temporal separation in these inland habitats appears to be related to possibly several adaptive differences between C_3 and C_4 plants (Williams 1974; Ehleringer 1978; Teeri and Stowe 1976).

In temperate coastal environments, the ecological significance of the C_3 and C_4 photosynthetic pathways is less well understood. These habitats are generally less seasonally variable than inland locations and temporal differences in activity between C_3 and C_4 plants are often lacking (Bjorkman 1975; DeJong 1978a; Long and Woolhouse 1978; Giurgevich and Dunn 1979).

The Kirkpatrick Marsh, located on the Rhode River of the Chesapeake Bay estuary system, is comprised of several plant communities that are dominated by both C_3 and C_4 species that do not exhibit temporal differences in activity. This marsh is fairly open, with daytime leaf temperatures during the summer months generally being above 28° C (Drake and Read 1981). Under these conditions it is expected that the photosynthetic potential of the C_4 marsh species would be greater than the C_3 species (Ehleringer and Bjorkman 1977). However, field measurements have shown that a community consisting of approximately equal proportions of a C_3 sedge (*Scirpus olneyi* Grey) and C_4 grasses (*Spartina patens* (Alt.) Mahl and *Distichlis spicata* (L.) Greene) had rates of canopy gas exchange and seasonal biomass accumulation similar to adjacent marsh communities consisting of only the same two C_4 grasses (Drake and Read 1981). Thus, although temperature and light conditions appear to be favorable for C_4 species there is no evidence to indicate that C_4 species have a distinct advantage over C_3 species at the canopy level of organization.

The purpose of this study was twofold: 1) to determine if there are differences in the biological potential for net carbon dioxide exchange (NCE) between C_3 and C_4 tidal marsh species grown under optimal conditions and measured in the laboratory, and 2) to determine how the potential for leaf NCE under optimal conditions relates to maximum leaf NCE rates measured in the field.

Materials and Methods

In October 1977, several patches of sod (1/16 m^2) were cut out of Kirkpatrick Marsh, a tidal marsh on the Rhode River of the Chesapeake Bay, placed in plastic bags, fumigated, and shipped by airmail to the University of California, Davis. Individual species were isolated and then placed in 13 cm plastic pots in a 30-6-12 mixture of sand, peat and vermiculite and set out in a greenhouse. The pots were watered regularly with deionized water and fertilized once a week with 2X Hoaglands

solution. Greenhouse temperatures ranged from 18° C at night to 27° C on cool overcast days and 33° C on clear warm days. Five weeks prior to gas exchange measurements, the plants were placed in an area of the greenhouse that had supplemental lighting of 160 n Einstein $cm^{-2}s^{-1}$ provided by two 1500 watt Sylvania metal-halide lamps. On the night prior to the gas exchange measurements, the plants were watered and transported to an I.S.C.O. E3A growth chamber and held there until the time of measurement.

All laboratory gas exchange measurements were made on an open system gas analysis apparatus that has been described in more detail elsewhere (DeJong 1978a). CO_2 exchange was measured with a Beckman Model 865 infrared gas analyzer. Water vapor concentrations were measured with a relative humidity sensor (Weather Measure Model HM 111) held at a constant temperature. Flow rates were monitored with an electronic mass flow meter (Technology, Inc., Model LFC-3). Leaf temperatures were measured with fine wire iron-constant an thermocouples. Light was provided by a 1,500-Watt metal-halide lamp (Sylvania) and a series of neutral-density filters. All gas exchange measurements were conducted on new tissue that had grown since shipment from the Kirkpatrick Marsh Study Site. Measurements on *Spartina* and *Distichlis* were made on four intact leaves inserted through the front of the assimilation chamber. Measurements on *Scirpus* were made on a pair of culms.

The light dependence of NCE was determined by first increasing the quantum flux up to near-saturating (200 n Einstein $cm^{-2}s^{-1}$) levels. After constant NCE was attained, quantum flux was decreased in steps to complete darkness with steady-state rates determined at each level. The temperature dependence of NCE was measured by initially establishing steady-state rates at 28° C. Then temperatures were increased in 3–4° C intervals until the optimum temperature for NCE had been exceeded. In other measurements, temperature was raised in steps to a point just above the optimum temperature and then decreased in 3–4° C intervals at 15° C.

The CO_2 dependence of NCE was determined by varying the CO_2 concentration of the entering airstream. After a steady-state NCE was attained at an initial concentration of 300 to 330 μl l^{-1} is was increased to 600 μl l^{-1} and then decreased in steps to approximately 300, 200, 125, 60, and 0 μl l^{-1}. The steady-state NCE was determined at each CO_2 concentration.

Field studies were carried out on Kirkpatrick Marsh on the Rhode River, Maryland, at the Chesapeake Bay Center for Environmental Studies. Descriptions of this site are found in Correll (1973) and Drake and Read (1981). Leaf gas exchange characteristics were determined with an open system gas exchange apparatus incorporating a chamber which enclosed the upper two-thirds of several attached leaves. The base of the chamber consisted of two pieces of plexiglas which, when clamped together over the leaves, formed an ellipse that fit tightly into the open end of a clear, 1.5 l, mylar bag. This material has a low permeability for CO_2 and water vapor but a relatively high transmittance for long-wave radiation, allowing for good radiation exchange. The leaves were held in place by monofilament line strung across a framework of thin stainless steel rod within the bag. Gas lines were connected through fittings mounted in the plexiglas. The volume of air in the bag was completely exchanged in about 0.4 min. In addition, a small mixing fan mounted on the lower piece of plexiglas provided for thorough mixing in the chamber. A small squirrel-cage fan on the outside of the chamber directed air across the chamber to maximize heat exchange between the open air and the outer walls of the chamber. This arrangement maintained leaf temperatures inside the chamber within ± 3° C

of leaf temperatures outside the chamber and permitted tracking of ambient temperature.

Leaf temperatures inside and outside the chamber were measured with 0.07 mm dia copper-constant an thermocouples on the adaxial surface of the leaves.

Incident photosynthetically active radiation (PAR) was measured by a radiometer (Li-Cor, Quantum sensor) placed under a piece of mylar of the same thickness as the chamber walls.

The gas circuit and data recording system used for field measurements was similar to that used by Drake and Read (1981) in measurements of gas exchange in a plant canopy, but modified to measure water vapor exchange and for working with a smaller assimilation chamber. Differential measurements of CO_2 and H_2O vapor concentrations were made with two infrared gas analyzers (Hartmann and Braun, URAS 2 and 2T). Ambient CO_2 concentrations were monitored with a third infrared CO_2 analyzer (Hartmann and Braun, URAS 2T), and ambient H_2O vapor concentrations were measured with a dew point hygrometer (E.G. & G Model 880).

The diurnal course of gas exchange, on several clear to partly cloudy days, was determined by calculating the running mean of five consecutive readings at 3-min intervals. Additionally, the seasonal course of gas exchange characteristics was determined from measurements taken from 10 to 15:00 h under full sinlight conditions. These data were analyzed by calculating the mean of five consecutive readings taken at 3 min intervals when temperature and light varied by less than 5% and CER rates were constant. A minimum of 3 such mean values were obtained for each short monitoring period. In each case, means were used to compensate for the lag time of the gas circuit which included the lag in response of the CO_2 analyser and that of transport and mixing of gas in the circuit.

The light response of CER was determined during periods of full sunlight when neutral density filters were used to obtain a range of quantum flux densities and the corresponding steady-state CER rates.

Net carbon exchange (NCE), transpiration (E), leaf conductance to water vapor (C_{H_2O}), leaf conductance to CO_2 (C_{CO_2}), and intercellular CO_2 concentration ($[CO_2]_{int}$) were calculated as outlined by Jarvis (1971). In the laboratory experiments, mesophyll conductance (C_m) was calculated from the initial, linear portion of the curve relating NCE to intercellular CO_2 concentration. In the field experiments, the residual conductance to CO_2 (C_r) was calculated from the difference between the leaf resistance and the total resistance to CO_2 flux (Jarvis 1971). Mesophyll and residual conductances measure the same parameter, but are given different labels to distinguish between the two methods of computation.

Results

Laboratory Measurements

The light response curves for NCE for *Spartina* and *Distichlis* were nearly identical, but both had higher maximum NCE than *Scirpus* (Fig. 1). NCE for all three species was essentially light-saturated at 200 nEinstein $cm^{-2}s^{-1}$. At low quantum fluxes little difference was apparent in NCE.

The dependence of NCE upon temperature was similar in the two C_4 species, *Spartina* and *Distichlis* (Fig. 2). Both species had temperature optima near 34° C, but it was broader in *Distichlis* than in *Spartina*. In comparison, *Scripus* had lower NCE above 25° C, but its much broader temperature response gave it considerably higher NCE rates at lower temperature.
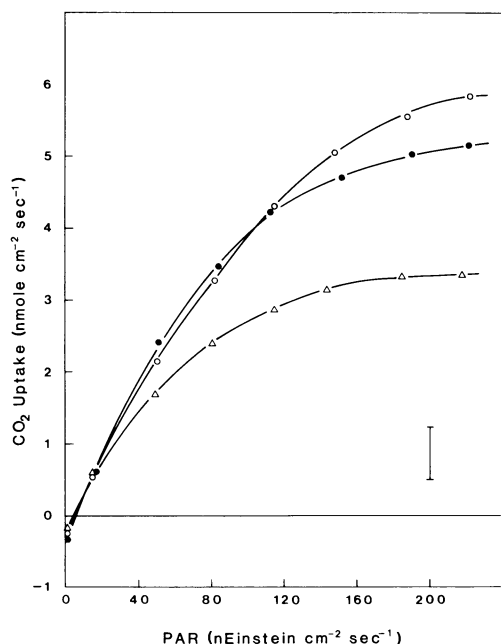
Fig. 1. The light response of net carbon dioxide exchange rate (NCE) in three greenhouse-grown marsh taxa: *Spartina patens* (●), *Distichlis spicata* (○), and *Scirpus olneyi* (△). Vertical bar represents the $LSD_{\alpha=0.05}$ where species approach light saturation

Fig. 2. The temperature response of NCE and leaf conductance to water vapor (C_{H_2O}) in the three greenhouse-grown marsh taxa: *Spartina patens* (●), *Distichlis spicata* (○), and *Scirpus olneyi* (△). Vertical bar represents the $LSD_{\alpha=0.05}$ near the photosynthetic temperature optima for each species

Leaf conductance to water vapor (C_{H_2O}) was virtually independent of temperature in all three species (Fig. 2); therefore, the dependence of NCE upon temperature was not caused by changes in stomata, but resulted from effects of temperature upon the photosynthetic apparatus within the leaf. The values for leaf conductance in the C_3, *Scirpus*, were twice those of the two C_4 species.

The dependence of NCE upon intercellular CO_2 concentration was similar in the two C_4 species and differed from that of the C_3 species in the following ways: the initial slope was much steeper; saturation of NCE occurred at lower $[CO_2]_{int}$; and CO_2 compensation points were near 0 in the C_4 species (Fig. 3). Intercellular CO_2 levels at an ambient CO_2 of 300 µl l^{-1} were 80 to 120 µl l^{-1} in the C_4 species and 200 to 240 µl l^{-1} in the C_3 species. When CO_2 concentrations were raised to 600 µl l^{-1}, NCE rates were higher in *Scirpus* than in the two C_4 species (data not shown).

Field Measurements

The daily course of gas exchange responses and the environmental parameters for *Scirpus* and *Spartina* on two days in August, 1978 are shown in Figs. 4 and 5. Both days were relatively clear and thus similar with respect to PAR, T_L, and VPD, particularly during the afternoon hours. Measurements in the early morning are not presented because of high humidities and condensation which prevented measurements of water vapor exchange. However, NCE rates during this period were either similar to, or lower than, those measured later in the day. The NCE of both species was nearly constant between 1,000 and 1,600 h when PAR was high. Furthermore, these NCE rates were similar in both species. NCE appeared to be essentially independent of leaf temperature and VPD during this period. Because of the greater C_{H_2O} of *Scirpus* as compared to *Spartina* (1.0 vs. 0.5 cm s^{-1}), changes in leaf temperature and VPD had a proportionately greater effect on the transpiration rate of *Scirpus* than on *Spartina*. The daily
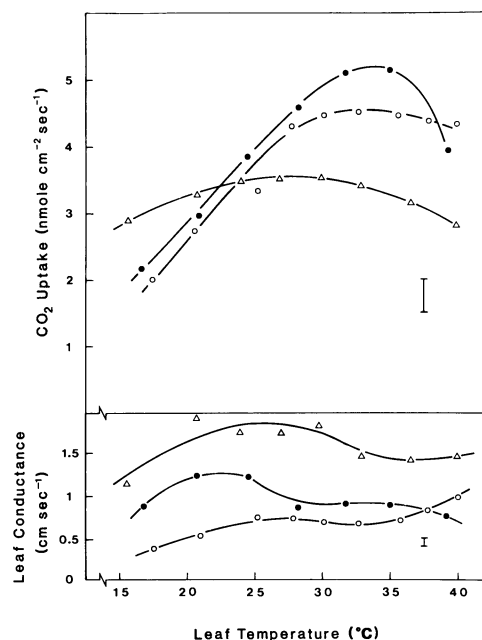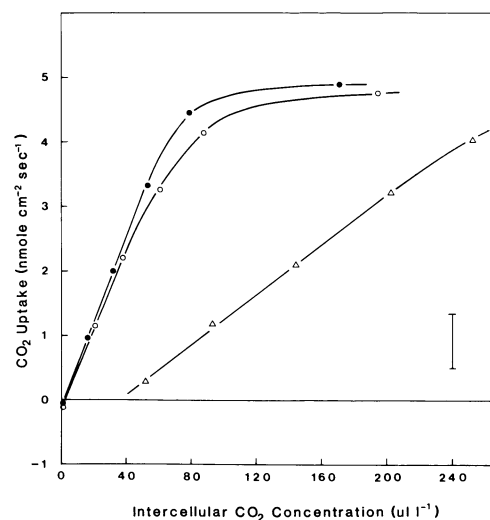

Fig. 3. The response of NCE to differing intercellular CO_2 concentrations in three greenhouse-grown marsh taxa: *Spartina patens* (●), *Distichlis spicata* (○), and *Scirpus olneyi* (△). Vertical bar represents the $LSD_{\alpha=0.05}$ near the point where *S. patens* and *D. spicata* approach CO_2 saturation

carbon exchange rates and transpiration rates for the periods of time shown in Figs. 4 and 5 are summarized in Table 2. On a daily basis, *Scirpus* assimilated about as much CO_2 as *S. patens*, but lost about twice as much water. As a consequence, *Spartina*, the C_4 species, had nearly twice the photosynthetic water use efficiency of *Scirpus*.

The dependence of NCE upon different levels of photosynthetically active radiation for *Spartina*, *Distichlis,* and *Scirpus* in June 1978 is shown in Fig. 6. The maximum rates of NCE were 2.0, 1.8, and 1.5 nmol cm^{-2}s^{-1} for *Spartina, Scirpus,* and

Table 1. A summary of the gas exchange characteristics of three Chesapeake Bay tidal marsh species measured on greenhouse grown plants. Net carbon dioxide exchange rates (NCE), leaf conductance (C_{H_2O}), and mesophyll conductance (C_m) are mean values measured at the photosynthetic temperature optimum (T_{opt}) for each species. The ratio of NCE to transpiration (NCE/E) was determined using a standard 15 mb vapor pressure deficit at the temperature optimum for each species. NCE's are given as mean values at saturating light and ambient CO_2 concentration near 300 μl l^{-1}

	Intercellular CO_2 Compensation point ($l\,l^{-1}$)	NCE (nmol cm^{-2}s^{-1})	NCE (mol gdw^{-1}s^{-1})	T_{opt} (C)	C_{H_2O} (cm s^{-1})	C_m (cm s^{-1})	NCE/E (mgCO$_2$/gm H$_2$O)
Scirpus olneyi (C$_3$)	40	3.72	420	28	1.61	0.49	9.4
Distichlis spicata (C$_4$)	0	5.11	1,096	34	0.77	1.52	27.6
Spartina patens (C$_4$)	0	5.16	1,050	34	0.75	1.25	28.7
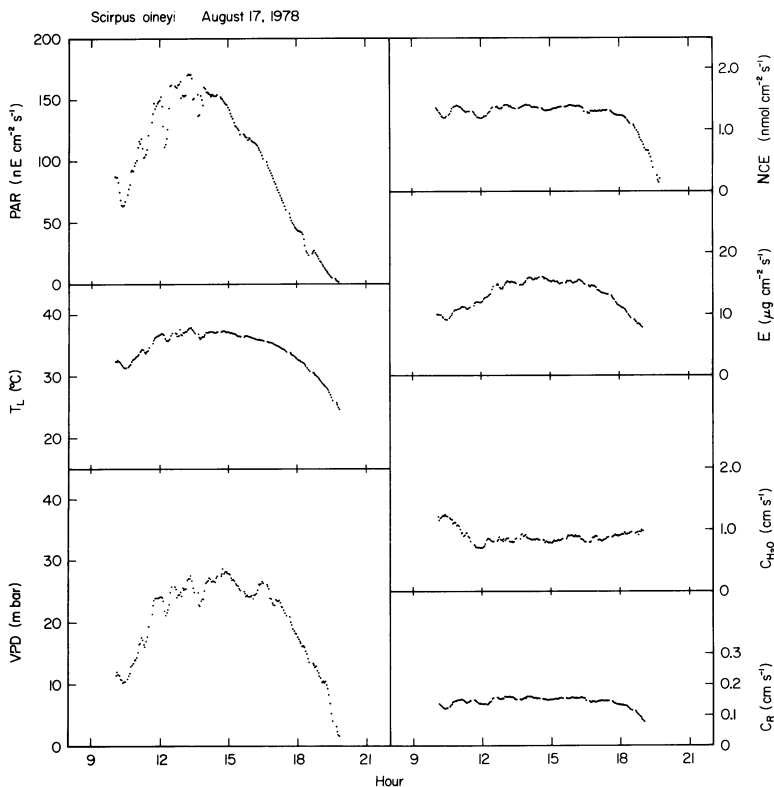
Fig. 4. The daily pattern of photosynthetically active radiation (*PAR*), vapor pressure deficit (*VPD*), and leaf temperature (T$_L$), net carbon dioxide exchange rate (*NCE*), transpiration (*E*), leaf conductance to water vapor (C$_{H_2O}$) and mesophyll conductance calculated as a residual (C$_R$) on August 17 for the C$_3$ sedge *Scirpus olneyi*. Data were collected at three minute intervals

Distichlis, respectively. All three species approached light saturation at approximately 80 n Einstein cm^{-2}s^{-1}, and had light compensation values near 2.5 n Einstein cm^{-2}s^{-1}.

Figure 7 shows seasonal changes in the light-saturated NCE and gas exchange characteristics for the three species. There was a substantial decline in NCE through August and September for *Spartina*, while *Distichlis* and *Scirpus* maintained much more constant NCE rates throughout the period. Measurements made in June gave slightly higher rates for *Scirpus*, but no significant difference from the August rates for *Spartina* and *Distichlis*. Interestingly, both C$_4$ species showed substantial decreases in C$_R$ and increases in [CO$_2$]$_{int}$ from August through September. [CO$_2$]$_{int}$ of the C$_3$ species was always higher than in the C$_4$ species and remained relatively constant through August and September. Occasional measurements of gas exchange characteristics on *Kosteletskya virginica*, a broad-leaved C$_3$ species, had similar patterns of conductances and [CO$_2$]$_{int}$ as *Scirpus*, whereas a third C$_4$ species, *Cyperus odoratus*, exhibited patterns similar to *Distichlis* and *Spartina* (data not shown).

Discussion

Comparison of the photosynthetic responses of the C$_3$ and C$_4$ species under field and laboratory conditions reveal several similarities and differences. First, for all species light saturated photosynthetic rates were substantially higher under laboratory conditions than in the field. The laboratory plants were grown at high light, high nutrient levels, and moderate temperatures, or in other words, conditions that were probably close to optimum for these species. Thus, the laboratory photosynthetic rates are probably close to the biological potentials for these species. On the other hand, the much lower field photosynthetic rates reflect limitations imposed by the tidal marsh environment.

In contrast to the laboratory plants, where photosynthetic rates of the C$_4$ grass species were substantially higher than those of the C$_3$ *Scirpus*, we found little difference in photosynthetic capacity in the field, either in terms of light saturated photosynthetic rates or in daily totals of CO$_2$ uptake. However, other charactistic differences between the C$_3$ and C$_4$ plants were little
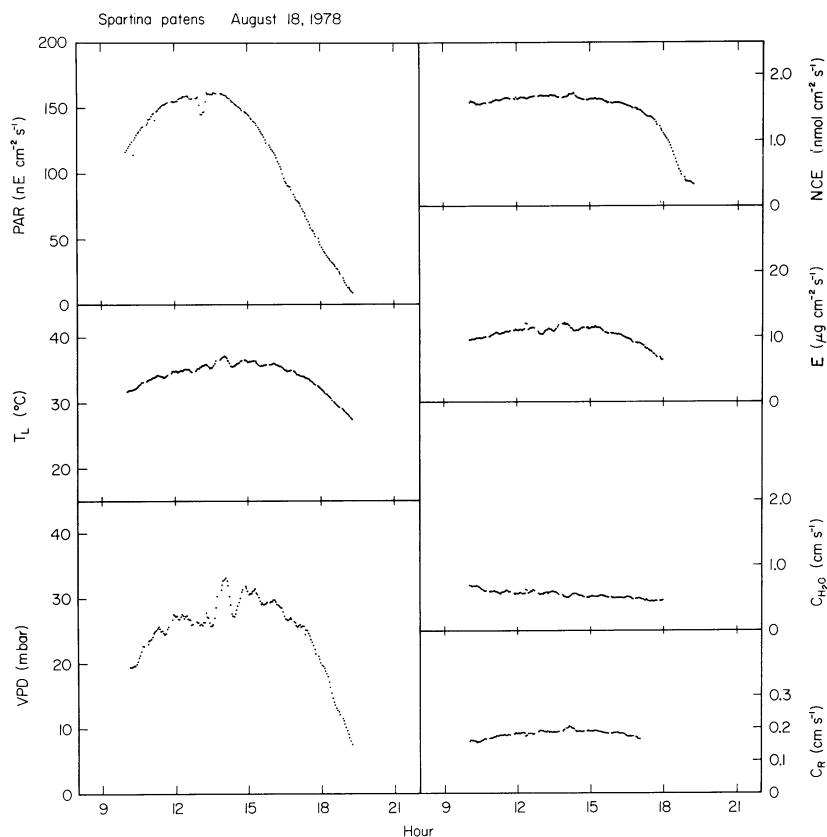
Fig. 5. The daily pattern of PAR, VPD, T_L, NCE, E, C_{H_2O} and C_R on August 18 for the C_4 grass *Spartina patens*. Data were collected at three minute intervals

Table 2. Daily totals for net carbon dioxide exchange (NCE), transpiration (E), and photosynthetic water water use efficiency (NCE/E) for plants growing in their natural tidal marsh habitat. Measurements were for the same periods as for data shown in Fig. 4 and 5

	NCE (mg $cm^{-2}d^{-1}$)	E (gm $cm^{-2}d^{-1}$)	NCE/E (mg CO_2/gm H_2O)
Scirpus olneyi (C_3)	1.9	0.32	6.0
Spartina patens (C_4)	2.1	0.18	11.7

changed under field as compared to laboratory conditions. Under both conditions, the C_4 species generally maintained lower leaf conductances and higher mesophyll or residual conductances. As a consequence of these differences, the C_4 species maintained higher water use efficiencies than the C_3 *Scirpus*. In these respects, these C_3 and C_4 plants did not differ, either under laboratory or field conditions, from the well-documented patterns of differences observed in other species (Bjorkman 1973; Black 1973).

Several factors may account for the differences in photosynthetic capacity between the laboratory and field plants. No salinity was added to the nutrient solutions in the laboratory, whereas the field plants experienced moderate levels, especially late in the season (DeJong and Drake 1981). Salinity has been shown to depress photosynthesis in some halophytes although the levels required are generally quite high (DeJong 1978b; Pearcy and Ustin 1981). Soil water potentials in Kirpatrick Marsh were
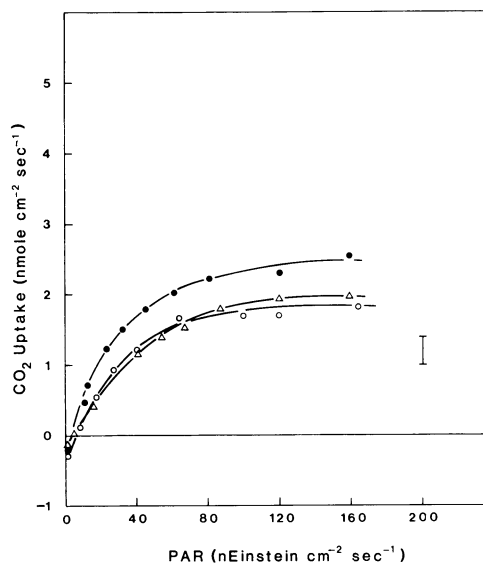
Fig. 6. The light response of NCE in three field-grown marsh taxa (*Spartina patens* ●, *Distichlis spicata* ○, *Scirpus olneyi* △) measured in June 1978. Vertical bars represent $LSD_{\alpha=0.05}$ where species approach light saturation

between -0.2 and -0.8 mPa indicating that salinities were not especially high. It is, therefore, unlikely that salinity in this marsh can account for the reduced photosynthetic rates. In the west-coast salt marsh species, *Spartina foliosa* and *Scirpus robustus*, photosynthesis was not reduced at 10 and 20 ppt salinities (-0.53 and -1.17 mPa soil osmotic potential), respectively, although
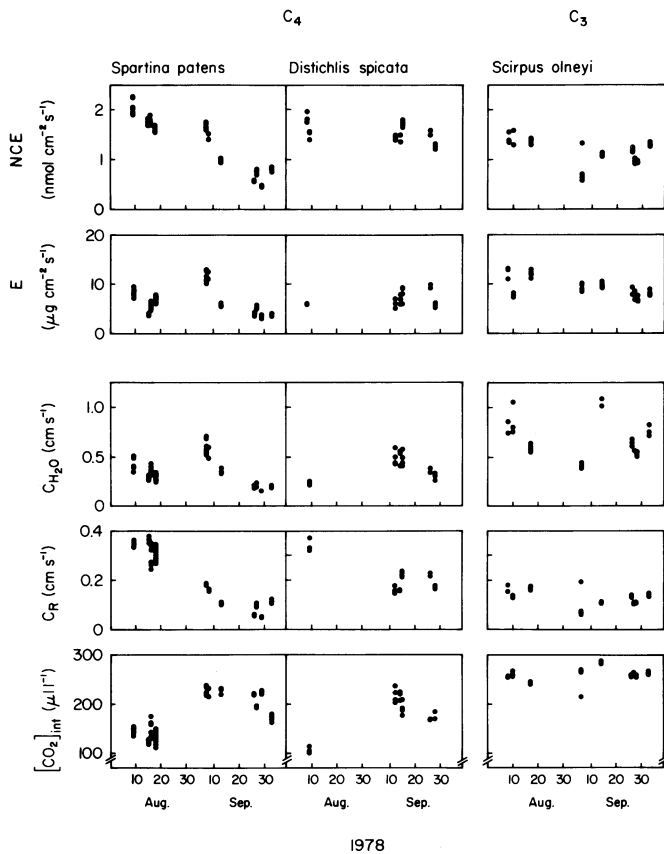
Fig. 7. Seasonal changes in net carbon dioxide exchange rate (*NCE*), transpiration (*E*), leaf conductance to water vapor (C_{H_2O}), mesophyll conductance calculated as a residual (C_R) and intercellular CO_2 concentration $[CO_2]_i$ in the two C_4 grasses *Spartina patens* and *Distichlis spicata* and the C_3 sedge, *Scirpus olneyi*. Each point is the mean of 5 measurements taken at 3-min intervals

higher levels were inhibitory (Pearcy and Ustin 1981). In *Spartina anglica*, sea water salinities stimulated photosynthetic rates over those of controls grown in unsalinized nutrient solutions (Mallot et al. 1975). Similarly, no inhibition of photosynthesis of *Spartina alterniflora* occurred at 30 ppt salinities and high growth light intensities, while the same salinity was inhibitory when the plants were grown at low light (Longstreth and Strain 1977).

Nutrients, especially nitrogen, are often found to be limiting productivity in tidal marshes and could account for the lower photosynthetic rates under field conditions in Kirpatrick Marsh. Inorganic nitrogen fertilization has been shown to stimulate productivity or biomass accumulation in high marsh *Spartina alterniflora* communities (Gallagher 1975; Broome et al. 1975). Furthermore, urea application increased above ground standing crops of both *Spartina patens* and *Distichlis spicata* in a high marsh in Massachusetts (Valiela and Teal, 1974), and Haines and Dunn (1976) have shown significant interactions between nitrogen level and salinity effects on growth of *Spartina alterniflora* in solution cultures in a greenhouse. While little is known about the specific effects on photosynthesis of the species studied here, in general, nitrogen nutrition has been shown to strongly influence photosynthetic rates. Medina (1970, 1971) found much lower rates of photosynthesis, mesophyll conductances, and RuBP carboxylase activities in *Atriplex patula* grown in low as compared to high nitrogen content culture solutions and sug-

gested that nitrogen levels influence photosynthesis via an effect on RuBP carboxylase activities. Plants possessing C_4 photosynthesis generally have higher nitrogen use efficiencies (photosynthetic rate per unit leaf nitrogen) than C_3 species (Brown 1978). However, decreases in leaf nitrogen have a proportionally greater effect on photosynthetic rate in C_4 than in C_3 grasses (Bouton and Brown 1980; Wilson 1976). In the measurements reported here photosynthetic rates in the field as compared to the laboratory were clearly reduced more in the two C_4 species, *Spartina* and *Distichlis*, than in the C_3 species, a pattern which is consistent with the responses of C_4 and C_3 species to nitrogen.

The differences in NCE between field and greenhouse grown plants may also be a response to differences in average growth irradiance. Plants used in the laboratory analysis were grown for a 16-h photoperiod under supplemental greenhouse lighting of 160 n Einstein $cm^{-2}s^{-1}$. Those plants also approached light saturation of 160 n Einstein $cm^{-2}s^{-1}$. The field grown plants in this study approach light saturation at 80 n Einstein $cm^{-2}s^{-1}$. The average daylight photosynthetic photon flux density through September, within 50 km of the study site, is approximately 80 n Einstein $cm^{-2}s^{-1}$ (estimated from data of Klein and Goldberg (1976) and Loomis and Williams (1963)). It is well established that growth irradiance can have significant effects on the photosynthetic characteristics of leaves (Bjorkman 1975; Jurik et al. 1979). The lower average growth irradiance of the marsh as compared to the light supplemented greenhouse may have stimulated the development of leaves with lower photosynthetic maxima in the field.

Measurements on the intact canopies have revealed that NCE per unit of land surface reached a maximum near July 1 and then declined throughout the remainder of the year (Drake and Read 1981). Since single leaf NCE only declined in *Spartina* after Sept. 1 and was relatively constant in the other species, this cannot account for the decreases in canopy NCE. Turitzen and Drake (1980) showed that seasonal changes in canopy structure and light extinction are probably more important in determining the seasonal changes in canopy NCE than are differences at the single leaf level.

Drake and Read (1981) have measured NCE of whole canopies in Kirpatrick Marsh using a 1 m^3 chamber. No differences in photosynthetic rates between a pure C_4 community (90% *Spartina*, 10% *Distichlis*) and a mixed C_3 and C_4 community (38% *Scirpus*, 32% *Spartina*, 30% *Distichlis*) were apparent. Our results show that the lack of significant differences at the canopy level can be attributed to the lack of an expression of the differences in maximum NCE between the C_3 and C_4 species under field conditions. Maximum whole canopy NCE per unit of leaf area were only 0.66 and 0.64 nmol $cm^{-2}s^{-1}$ in the mixed and pure communities, respectively. These much lower rates, as compared to the single leaf measurements, reflect canopy influences on light extinction. A nearly 8-fold reduction in NCE occurs from the single leaf level under optimum conditions in the laboratory to the average leaf in a marsh community due to limitations imposed by the environment and the canopy. Gifford (1974) has pointed out that often the marked differences in performance between C_3 and C_4 plants decrease as increasing levels of organization from the primary carboxylation steps to short-term crop growth rates are reached. The data presented here show a similar trend for species within a given tidal marsh community. Thus, the ecological significance of the differences between the two photosynthetic pathways relative to the tidal marsh habitat are not evident from field carbon exchange measurements even though the biological potential for photosynthesis of the C_4 species is much greater than the C_3 species.

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