REFERENCES

Photosynthetic Production and Biomass of the Subtropical Seagrass *Halodule wrightii* Along an Estuarine Gradient[1]

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ABSTRACT: Seasonal patterns of aboveground and belowground biomass, leaf chlorophyll (chl) content, and in situ differences in photosynthetic parameters were examined in the shoal grass *Halodule wrightii* along an estuarine gradient in the western Gulf of Mexico. Continuous measurements of biomass were collected over a 5-yr period (1989–1994) with respect to several abiotic factors in three estuarine systems that were characterized by significant differences in salinity and ambient dissolved inorganic nitrogen (DIN; NO_2^- + NO_3^-) regimes that ranged from 5–25‰ (0–80 μM DIN) in the Guadalupe estuary to 35–55‰ (0–9 μM DIN) in the upper Laguna Madre. Photosynthesis versus irradiance (*P* vs. *I*) parameters, measured from December 1989 to April 1991, showed no significant differences among the three sites, and there were no significant differences in leaf chlorophyll content and chl *a:b* ratios among sites over the entire 5-yr period. Saturation irradiance in *Halodule wrightii* is estimated at 319 μmoles photons m^{-2} s^{-1} based on measurements collected at the three sites over a 2-yr period. No strong seasonal variations were observed in total plant biomass, but root:shoot ratios (RSR) showed a clear pattern of maximum RSR values in winter and minimum values in summer. There were no significant differences in RSR among sites, and no consistent correlations could be established between plant parameters and sediment porewater NH_4^+, salinity, or temperature. Sediment porewater NH_4^+ values generally ranged from 50 μM to 400 μM (average 130–150 μM) but could not be correlated with significant differences in sediment composition between the sites. The high productivity of *Halodule wrightii* under a variety of light, nutrient, and salinity conditions explains its ubiquitous distribution and opportunistic strategy as a colonizing species. However, the persistence of a dense algal bloom in Laguna Madre coincident with low DIN levels (<5 μM) contradicts previously accepted relationships on nutrient stimulation of algal growth, and provides strong evidence that water quality parameters for estuarine seagrasses are decidedly estuarine-specific. Consequently, a knowledge of the long-term history of estuarine systems is critical to habitat managers, who are required to establish minimum water quality criteria for the protection of submerged aquatic vegetation in estuarine systems.

Introduction

There is little information on the production dynamics of submergent halophytes in the western Gulf of Mexico, despite the presence of over 719 km^2 of seagrass meadows between Corpus Christi and the Mexican border alone (Quammen and Onuf 1993). The unique physiography and gradient in climatic conditions of this area provide excellent opportunities to investigate the importance of various abiotic factors in regulating seagrass distribution. On the south Texas coast, an increase in seagrass cover on open-bay bottoms from less than 1% in Galveston Bay to 70–75% in Laguna Madre (Onuf personal communication) occurs in concert with a distinct gradient of decreasing freshwater

inflow and increasing salinity (Armstrong 1987). The change in seagrass cover is substantial, and consequently, over 85% of the 833 km^2 of seagrass meadows in Texas are located in the Laguna Madre, which is also characterized by the highest commercial finfish harvests in Texas (Texas Department of Water Resources 1982). The importance of seagrass meadows as nursery habitats in Gulf of Mexico coastal waters is well established, although the combined effects of freshwater inflow events on seagrass populations are not well defined.

The widespread occurrence of the shoal grass *Halodule wrightii* on the south Texas coast provided a unique opportunity to examine in situ differences in photosynthetic parameters and light-harvesting capabilities in plants subject to brackish and hypersaline conditions. The effect of salinity on measurements of photosynthesis has not been examined on entire plants in situ, although short-term experiments using isolated individuals have

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demonstrated that optimum growth rates in *Zostera marina* and *Thalassia testudinum* occur at salinities below that of seawater (Ogata and Matsui 1965; Biebl and McRoy 1971; Thayer et al. 1975; Zieman 1975). In situ observations of *Amphibolis antarctica,* an Australian seagrass, indicated that production declined at salinities above 57‰, and was maximum at 42‰ (Walker 1985). In upper Laguna Madre, salinities have historically ranged between 40‰ and 70‰, yet *H. wrightii* appears to have flourished under these conditions (Hedgpeth 1947, 1967).

This study also provided an opportunity to examine the long-term (5-yr) variations in the seasonal patterns of aboveground and belowground biomass in *Halodule wrightii* with respect to several abiotic parameters. The development and persistence of a brown tide algal bloom in Laguna Madre since early 1990 (Stockwell et al. 1993) has caused a 50% reduction in the amount of light available to benthic plants and a corresponding loss in seagrass productivity (Dunton 1994). High chlorophyll concentrations associated with the continued persistence of this bloom were found to be coincident with low inorganic nitrogen levels (<5 μM) in the water column and therefore contradict the current paradigm on the relationship between high nutrient concentrations and the resultant increase in phytoplankton growth at the expense of submerged vegetation (Wetzel 1975; Stevenson et al. 1993). The data presented in this paper thus provide valuable information in defining the relative importance of the major factors controlling seagrass distribution, which are largely estuarine-specific.

Study Area

Field studies were conducted within three estuarine systems along the south Texas coast, which were characterized by significant differences in freshwater inflow. From north to south, these were the Guadalupe, Nueces, and Laguna Madre estuaries (Fig. 1). Net inflows for each estuary range from a high of 2.54 km^3 yr^{-1} in the Guadalupe estuary to 0.51 km^3 yr^{-1} in the Nueces system, and -0.97 km^3 yr^{-1} in the hypersaline Laguna Madre (Armstrong 1987). Study sites established within each estuary included Blackjack Peninsula (GBP; 28°15′N, 96°47′W) in San Antonio Bay (Guadalupe estuary), East Flats (NEF; 27°49′N, 97°08′W) in Corpus Christi Bay (Nueces estuary), and site LM-151 (27°21′N, 97°22′W) in the Laguna Madre estuary. Water column, sediment, and plant biomass samples were collected at 1–3 mo intervals from May 1989 to December 1994 at LM-151 and from November 1989 to December 1994 at NEF and GBP near the deep edges of each meadow.
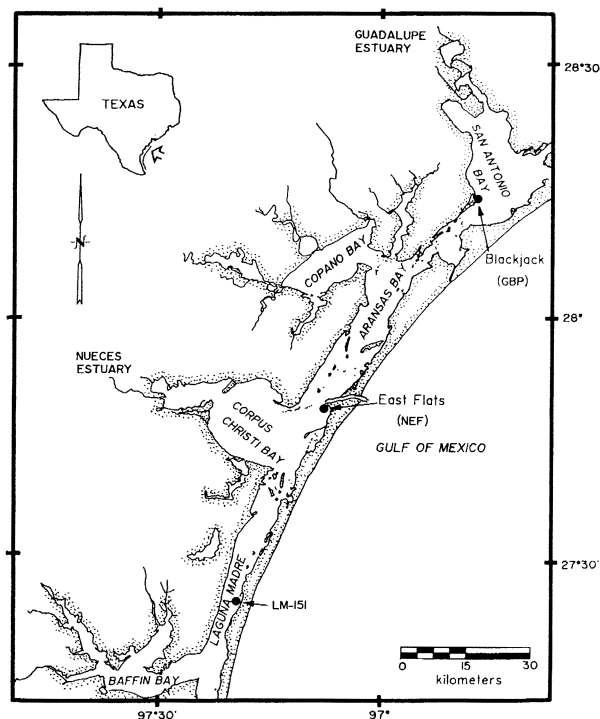

Fig. 1. The location of the study sites in south Texas (Blackjack Peninsula, GBP; East Flats, NEF; upper Laguna Madre, LM-151) along a gradient of decreasing freshwater inflow, from the Guadalupe estuary to Laguna Madre.

At all three sites, sampling was conducted within monotypic stands of *Halodule wrightii* Aschers. At site NEF, *Halodule wrightii* was also found mixed with two other seagrasses, *Thalassia testudinum* and *Syringodium filiforme,* from ca. 0.5 m to 1.0 m. The maximum depth of *H. wrightii* distribution varied among locations. At GBP, the maximum depth penetration of *Halodule wrightii* was about 0.6 m, compared to 1.2 m at NEF. In Laguna Madre, *Halodule wrightii* extended to depths of 1.6–1.8 m (Onuf personal communication). Lunar tides seldom exceed 15 cm in this area of the Texas coast (Hedgpeth 1947) as reflected in the low variation in water depths (0.1–0.2 m) noted at the three sites over a 2–4 yr period (Dunton 1994). Sampling depths at each station were 0.4–0.6 m (GBP), 1.2 m (NEF), and 1.3 m (LM-151). The seagrass communities at each site were relatively protected from waves and adverse sea conditions by barrier islands or shoals that reduced fetch from prevailing southeasterly winds to 0.5 km or less.

Methods

PLANT BIOMASS AND LEAF CHLOROPHYLL CONTENT

Estimates of total plant biomass and shoot density were made at LM-151, NEF, and GBP following

the procedures outlined by Dunton (1990). Measurements were made at each site at 2–3 mo intervals from four replicate samples collected with a 9-cm diameter coring device. Samples were thoroughly cleaned of any epiphyte material in the laboratory and separated into aboveground and belowground live biomass to calculate root:shoot ratios and shoot density. Sorted material was dried at 60°C to a constant weight. Results are expressed as total biomass (gdw m^{-2}) of all shoot, rhizome, and root material collected in each core.

The initial procedure used (from May 1989 to October 1992) to measure leaf chlorophyll (chl) *a* and *b* content is as follows. Preweighed tissue samples were repeatedly ground in 90% cold acetone buffered with 0.05% MgCO$_3$ using chilled pestles and mortars with washed sea sand. The extract was made up to a known volume, centrifuged, and absorbances measured at 664 and 647 nm on a Shimadzu UV 160U spectrophotometer. Chl *a* and *b* concentration was then determined using the equations from Jeffrey and Humphrey (1975) for 90% acetone. After October 1992, an alternative extraction technique utilizing N,N-dimethyl formamide (DMF) was employed (Dunton and Tomasko 1994). This technique did not require grinding of plant tissue, thus saving time and effort as well as reducing potential sources of error. Preweighed tissue samples were extracted overnight in DMF; the resulting extract was measured as described above, and chl *a* and *b* content determined using the equations of Porra et al. (1989). Comparison of the results using the two techniques yielded no significant differences in chl *a* or chl *b* content (Dunton and Tomasko 1994).

In Situ Photosynthesis

Coincident measurements of photosynthesis versus irradiance (*P* vs. *I*) parameters for *Halodule wrightii* were examined in situ at each site from experimental incubations conducted at 2–4 mo intervals from December 1990 to April 1991 using the procedures of Dunton and Tomasko (1994). Photosynthetic incubations of whole plants (previously cleaned of algal epiphytes, if present) were conducted in situ using four 5.0-l chambers placed on the seabed by divers. The chamber contained a tapered opening for an oxygen probe and a small battery-powered submersible pump. The pump provided circular water movement within the chamber for 3-min periods at 2-min intervals; the pump was triggered by an external computer running in BASIC. Underwater photosynthetically active radiation (PAR; 400–700 nm) was measured at 5-s intervals and integrated every 5 min on a continuous basis using a LI-193SA spherical quantum sensor, which provided input to a LI-1000 datalogger (LI-COR, Lincoln, Nebraska).

Dissolved oxygen measurements were collected using an Endeco/YSI Type 1125 Pulsed Dissolved Oxygen System. The system utilized four YSI 1128 oxygen electrodes that were programmed to collect measurements of dissolved oxygen at 15-min intervals. Constant data output to a laptop computer (via RS-232 interface and using Endeco software) permitted the monitoring of oxygen tensions within the chambers and avoidance of saturating oxygen concentrations. If saturation occurred, oxygen levels were reduced 40–50% by bubbling N$_2$ into the chamber for 2–3 min. Any remaining gas bubbles were removed using the 1.2-cm diameter sampling port at the top of the chamber. Plants were incubated under natural daylight conditions, although neutral density shade cloth was occasionally deployed over the chambers to achieve a desired light level for incubations that generally ranged from 0.5 h to 1.5 h. At sites NEF and GBP (and LM-151 prior to July 1990), the contributions made by phytoplankton (based on light and dark bottle incubations) were usually insignificant (<5% of chamber photosynthesis); however, to avoid the necessity of making corrections for the oxygen contributions made by phytoplankton when chlorophyll levels were high, the water within the chambers was cycled sequentially through 10-μm and 1-μm filter cartridges for a 15-min period. This procedure effectively reduced chlorophyll concentrations in the chambers to negligible levels.

Photosynthetic rates were calculated from changes in dissolved oxygen concentrations in the chamber over the duration of each incubation as outlined by Dunton and Tomasko (1994). Gross photosynthetic rates were expressed in units of μmol O$_2$ (g dry wt leaf)$^{-1}$ h^{-1}. Photosynthesis versus irradiance data were fit to the hyperbolic tangent function of Jassby and Platt (1976):

$$P = P_{max} \tanh\left(\frac{\alpha I}{P_{max}}\right)$$

where P_{max} is the light-saturated rate of photosynthesis, α is the light-limited slope of the *P* vs. *I* curve, and *I* is the irradiance. All curve-fitting was performed statistically on a 486 PC using nonlinear least squares regression techniques (SAS Institute 1987). *P* vs. *I* parameters were estimated simultaneously using a derivative-free algorithm (the Dudly algorithm) of Ralston and Jennrich (1978). The saturation irradiance, I_k, was defined as P_{max}/α. Estimation of I_{cp}, the compensation irradiance for an entire plant (blades and their associated belowground tissues), was calculated from root:shoot ra-

tios (RSR) for *Halodule wrightii* and measurements of leaf and root-rhizome dark respiration rates. Total plant respiration was normalized to 1 g dry weight of leaf tissue and calculated from the respiratory demands of leaf tissue and root/rhizome tissue based on the proportion of root-rhizome tissue needed to support that leaf tissue (the RSR ratio) as described by Dunton and Tomasko (1994).

WATER COLUMN AND SEDIMENT SAMPLING

Temperature, salinity, and water column DIN (as $NO_3^- + NO_2^-$) were measured from water samples collected at 1–3 mo intervals at each site. Temperature and salinity were taken directly within grass beds; salinity was measured using a refractometer (calibrated against known salinity standards) or with an Orion 140 salinometer. DIN was determined colorimetrically according to Parsons et al. (1984) from surface water samples collected within each grass bed.

From early 1990 through 1992, four sediment samples were collected at 2–3 mo intervals at each site. Samples were taken to a depth of 10 cm within beds of *Halodule wrightii*. Sediment grain size analysis was performed using standard geologic procedures (Folk 1964). Percent contribution by weight was measured for four components: rubble (e.g., shell hash), sand, silt, and clay. A 20-ml sediment sample was mixed with 50 ml of hydrogen peroxide and 75 ml of deionized water to digest organic material in the sample. The sample was wet sieved through a 62-μm mesh stainless steel screen using a vacuum pump and a Millipore Hydrosol SST filter holder to separate rubble and sand from silt and clay. After drying, the rubble and sand were separated on a 125-μm screen. The silt and clay fractions were measured using pipette analysis.

Interstitial porewater NH_4^+ concentrations were analyzed from four replicate samples of sediment collected to 10 cm depth on each visit with a 60 ml syringe. Sediment pore water was obtained by centrifugation (5,000 × g for 5–10 min) and then diluted (5–10:1) with ammonium-free seawater. Concentrations of NH_4^+ were determined using standard calorimetric techniques following the alternative method of Parsons et al. (1984).

STATISTICAL ANALYSES

Statistical analyses were performed on a 486 PC using a general linear model procedure (SAS Institute 1987). Significant differences in chlorophyll content, photosynthetic parameters, porewater NH_4^+, water column DIN, temperature, and salinity among sites were tested using a one-way ANOVA. When a significant difference for a main effect (p < 0.05) was observed, the means were analyzed
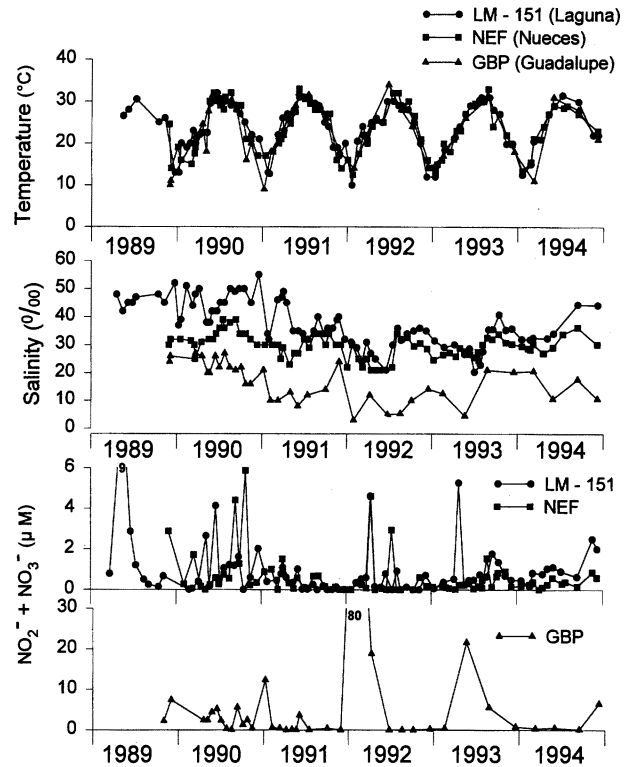

Fig. 2.   Seasonal and annual variations in temperature, salinity, and DIN ($NO_3^- + NO_2^-$) among three estuarine systems in south Texas from 1989 to 1994.

by a Tukey multiple-comparison test to determine significant differences among sampling sites.

Data were transformed when necessary to meet with assumptions of parametric statistics. Correlation coefficients were calculated using a least-squares fit between chlorophyll content or P_{max} with various physicochemical parameters (e.g., temperature, salinity, and porewater NH_4^+).

Results

WATER COLUMN PARAMETERS

Although there were no significant differences (p = 0.77) in water temperature among sites, distinct seasonal variations in temperature were noted within all three estuarine systems over the 5-yr period of study. Within grass beds, temperatures varied from average winter lows of 10°C to summer highs ranging between 31°C and 33°C (Fig. 2). In contrast, salinity and DIN ($NO_2^- + NO_3^-$) varied considerably over both temporal and spatial time scales. Salinities were significantly different (p = 0.0001) among all sites, ranging from 35‰ to 55‰ in upper Laguna Madre, from 25‰ to 35‰ in the Nueces estuary, and from 5‰ to 25‰ in the Guadalupe estuary. The overall trend in decreasing salinity noted at all sites from mid 1991
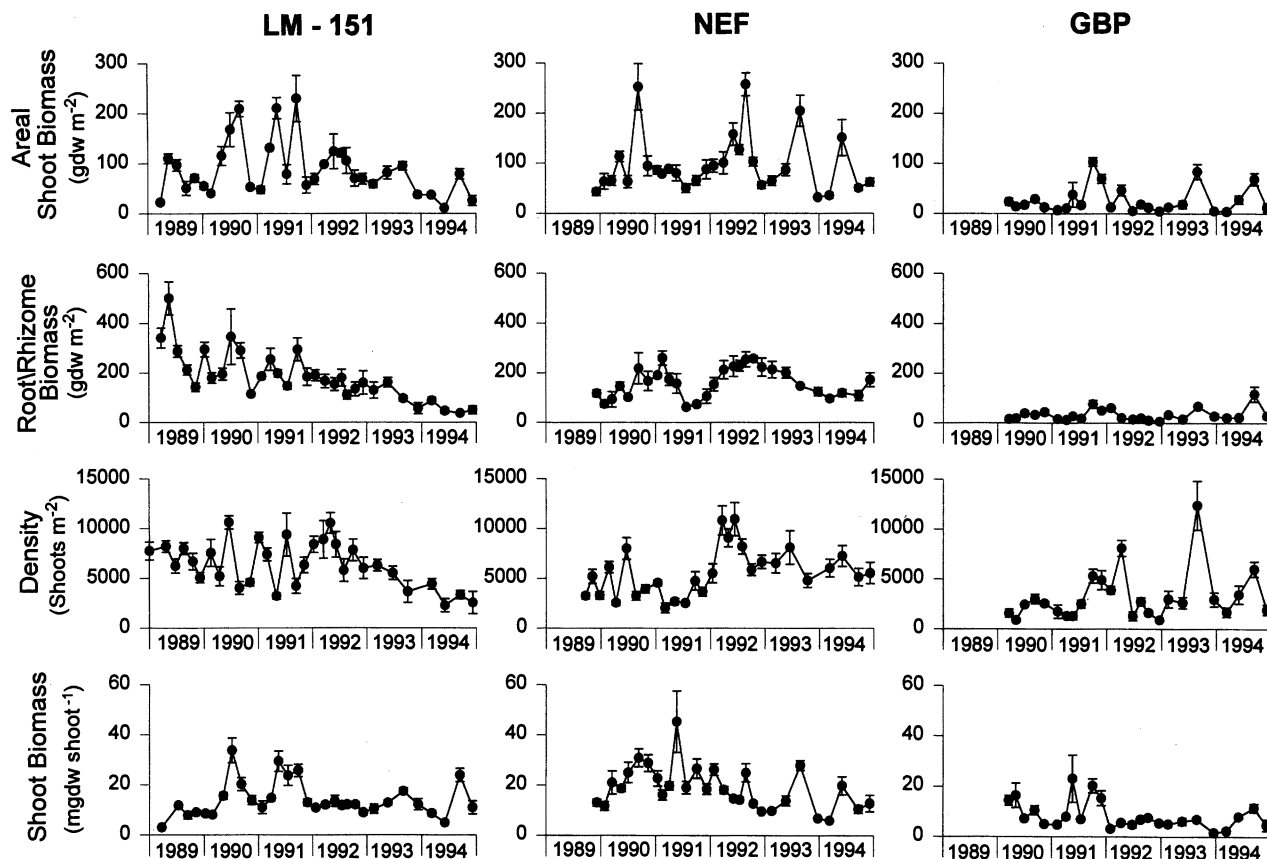
Fig. 3. *Halodule wrightii.* Indices of aboveground and belowground areal biomass, shoot density, and shoot biomass at sites LM-151, NEF, and GBP over the study period. Values are x̄ ± SE (n = 4).

to early 1993 is related to increased freshwater inflow that resulted from above-average rainfall during that period. Ambient DIN concentrations at GBP (0–80 μM) were significantly higher (p = 0.001) than concentrations (0–9 μM) at NEF and LM-151, which were not significantly different (p > 0.05). The variations in DIN reported here are similar to those reported by Dunton (1990) for the Guadalupe and Nueces estuarine systems.

PLANT BIOMASS, LEAF CHLOROPHYLL, AND SEDIMENT CHARACTERISTICS

Halodule wrightii exhibited large variations in both belowground and aboveground biomass within all three estuaries. Aboveground shoot biomass was usually highest in early autumn, approaching 200–300 gdw m^{-2} in some years at sites LM-151 and NEF and 100 gdw m^{-2} at GBP (Fig. 3). No strong seasonal trend could be detected in belowground biomass, although higher levels were often noted in summer or early autumn at GBP (to 70 gdw m^{-2}) and at LM-151 (300–550 gdw m^{-2}, 1989 to 1991 only). Average values of aboveground and belowground biomass and shoot density were signif-

icantly higher (p = 0.0001) at LM-151 and NEF than at GBP (Table 1). However, at LM-151, a long-term decline in plant biomass and density has been evident since 1991, one year following the onset of a brown tide algal bloom (Stockwell et al. 1993), which has continued unabated and has reduced underwater light levels significantly (Dunton 1994). At GBP, plants were collected at the deep edge of the seagrass bed (0.6 m) until April 1991; they were subsequently sampled at 0.4–0.5 m after the vegetation retreated to shallower depths. Corresponding values or shoot density were highly variable at all sites and showed little seasonality as depicted by ranges of ca. 1,000–12,000 shoots m^{-2}. Comparison of the allocation of dry weight biomass to individual shoots (mgdw shoot^{-1}) showed significant differences among all sites (p = 0.0001). Highest mean values (18.7 mgdw shoot^{-1}) were recorded at NEF; sites LM-151 and GBP had 13.9 mgdw shoot^{-1} and 8.4 mgdw shoot^{-1}, respectively (Table 1). As with shoot density, there was little evidence for distinct seasonal trends in shoot biomass, although values tended to be highest during the summer months.

TABLE 1. Summary of abiotic parameters in relation to biomass and leaf chlorophyll content in *Halodule wrightii* at three estuarine sites in south Texas. Values are x̄ ± SE (n). Numbers sharing the same letter (superscript) are not significantly different (p > 0.05).

Parameter	Site		
	LM-151	NEF	GBP
DIN (µM)	[a]0.8 ± 0.1 (70)	[a]0.6 ± 0.1 (76)	[b]5.1 ± 2.5 (37)
Salinity (‰)	[a]38 ± 0.9 (81)	[b]30 ± 0.5 (82)	[c]17 ± 1.2 (37)
Porewater NH_4^+ (µM)	[a]140 ± 17 (36)	[a]128 ± 14 (33)	[a]123 ± 10 (26)
Areal biomass (gdw m^{-2})			
Shoots	[a]88.0 ± 9.6 (32)	[a]96.9 ± 10.7 (29)	[b]26.8 ± 5.3 (25)
Root/rhizomes	[a]184.9 ± 17.8 (32)	[a]160.9 ± 11.1 (29)	[b]32.7 ± 5.1 (25)
Shoot biomass (mgdw shoot^{-1})	[a]13.9 ± 1.2 (31)	[b]18.7 ± 1.6 (29)	[c]8.4 ± 1.1 (25)
Shoot density (# m^{-2})	[a]6,351 ± 412 (31)	[a]5,551 ± 411 (29)	[b]3,201 ± 514 (25)
RSR	[a]2.9 ± 0.5 (32)	[a]2.0 ± 0.2 (29)	[a]2.2 ± 0.4 (25)
Total chlorophyll (mg g^{-1} dw)	[a]11.7 ± 0.5 (38)	[a]11.0 ± 0.5 (34)	[a]12.1 ± 0.7 (23)
Chlorophyll a:b	[a]2.4 ± 0.1 (38)	[a]2.4 ± 0.1 (34)	[a]2.7 ± 0.1 (23)

Strong seasonal trends were noted in RSR levels for *Halodule wrightii* within all three estuarine systems (Fig. 4). RSR values were highest during the winter months, generally ranging from 2 to 5, as compared with the summer months when values often decreased to less than 1. There were no significant differences (p = 0.22) in RSR among sites; however, in Laguna Madre, RSR has steadily decreased from winter values of >5 in 1989 and 1990 to about 2.3 in 1993 and 1994, which corresponds to a 50% reduction in underwater irradiance resulting from the continuous presence of the brown tide algal bloom (Dunton 1994). No similar long-term changes in RSR have been noted at NEF or GBP.

Total chlorophyll from *Halodule wrightii* leaf tis-
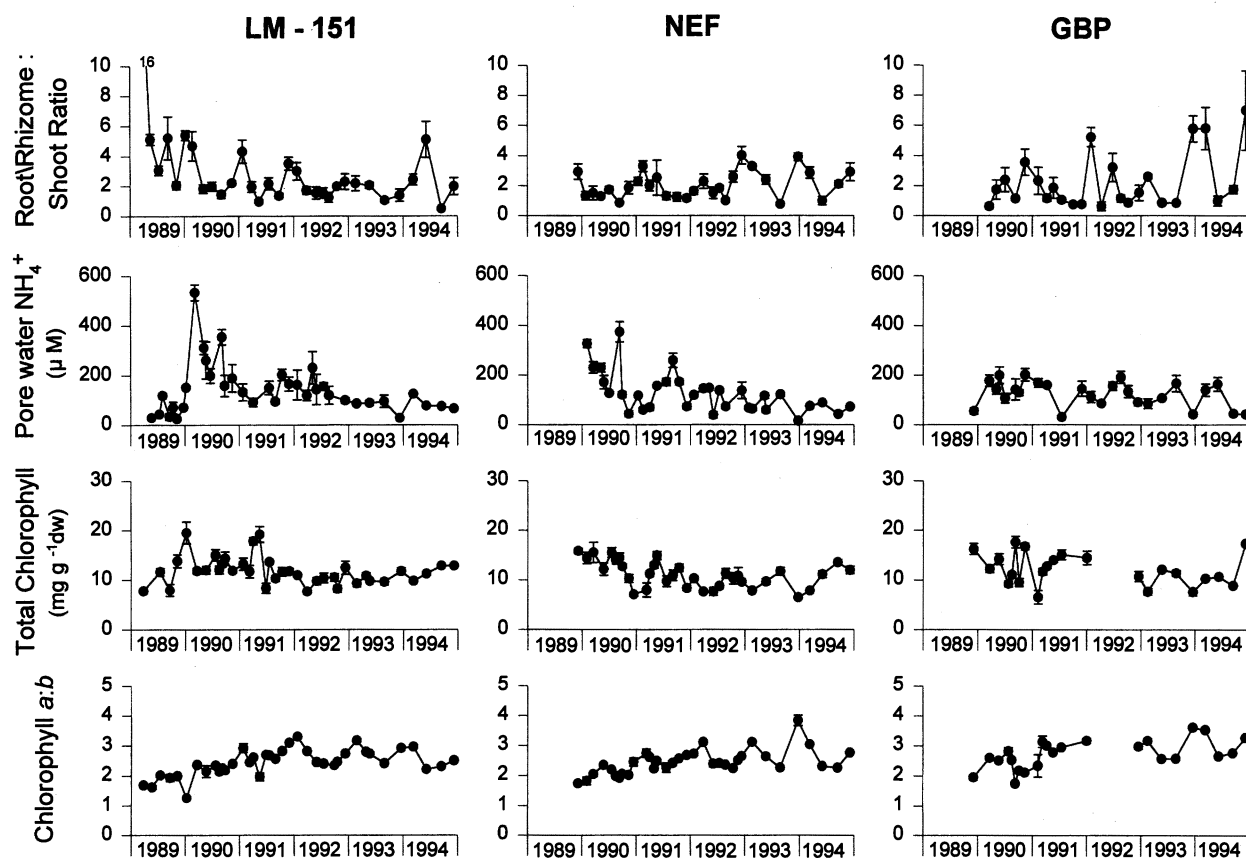

Fig. 4. *Halodule wrightii*. RSR values, sediment porewater NH_4^+ levels, total leaf chlorophyll, and blade chl a:b ratios over the study period. Values are x̄ ± SE (n = 4). Where no error bars appear, SE is less than the size of the symbol.
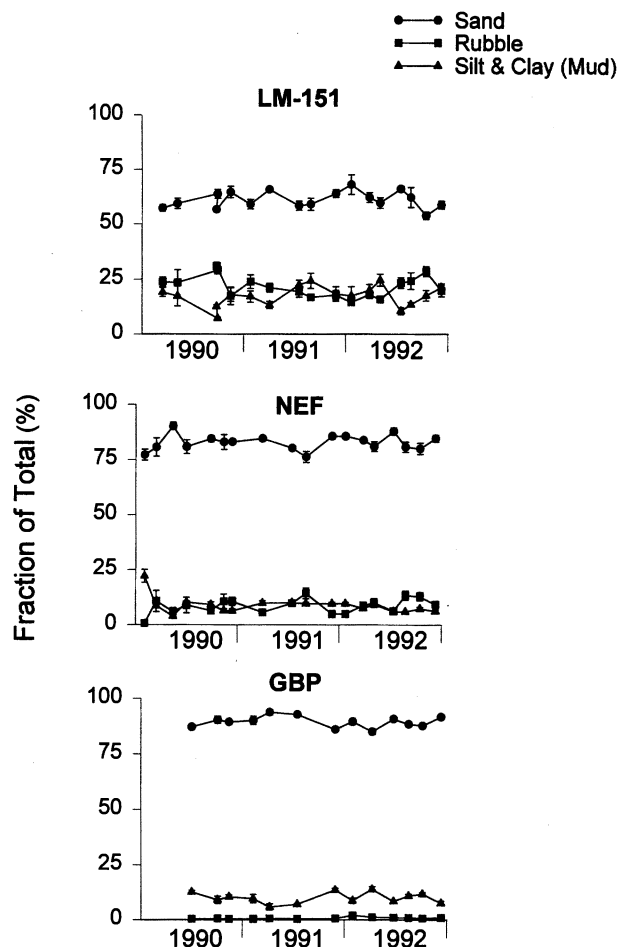
Fig. 5. Comparison of sediment grain size composition among sites between 1990 and 1992. Values are x̄ ± SE (n = 4, sand or rubble; n = 8, mud).

Porewater ammonium levels in *Halodule wrightii* grass beds were extremely variable and showed no seasonal trends. Average values ranged from ca. 25 μM to nearly 500 μM with no significant differences (p = 0.71) among sites. Correlation of porewater NH_4^+ with total chlorophyll and chl *a:b* ratios found no significant relationships for LM-151 or GBP (p > 0.05 and r^2 < 0.10); however, at NEF, total blade chlorophyll and chl *a:b* ratios were significantly correlated with sediment NH_4^+ (p = 0.004, r^2 = 0.30; p = 0.003, r^2 = 0.31, respectively).

Sediment grain size composition showed no strong seasonal variations over a 2-yr period at each of the study sites (Fig. 5). Sand was the predominant component at all sites, but the percentage differed significantly (p = 0.0001) among sites, with GBP having the highest sand content and LM-151 the lowest. Rubble and sand usually constituted over 84% of the sediment at all sites (Table 2), with mud (clay and silt) constituting the remaining fraction (10–16%). Silt and clay each contributed equivalent fractions (ca. 4–8%) to the overall percentage of material at each site.

IN SITU PHOTOSYNTHESIS

The *P* vs. *I* curves generated for *Halodule wrightii* from in situ incubations of whole plants at sites NEF and GBP (Fig. 6) were very similar to the curves reported previously for the same period at LM-151 (Dunton and Tomasko 1994). Photosynthetic relationships were explained well by the hyperbolic tangent function of Jassby and Platt (1976), with all curves exhibiting an r^2 > 0.95. No seasonal patterns in photosynthetic oxygen production were noted at the three sites (Table 3), although nearly all incubations were conducted at temperatures ranging from 17°C to 30°C and at salinities ranging from 10‰ to 50‰. Average P_{max} values tended to be higher at GBP than at sites LM-151 or NEF, but comparisons of photosynthetic parameter values among sites yielded no significant differences in either P_{max} (p = 0.41), α (p = 0.19), or I_k (p = 0.93).

Exclusive of the high P_{max} obtained in January 1990 at LM-151 and the high I_k value recorded in March 1990 at NEF, gross P_{max} averaged 354 μmol O_2 (gdw leaf)$^{-1}$ h^{-1}, and I_k averaged 311 μmol photons m^{-2} s^{-1} (Table 3). No data on these parameters are available for March 1990 at LM-151 and October 1990 at NEF since maximum photon flux density (PFD) achieved during the entire incuba-

sue generally ranged from ca. 7.5 mg chl gdw^{-1} to 17 mg chl gdw^{-1}, with chl *a:b* ratios ranging from 1.6 to 3.8 over the 5-yr period of study within the three estuaries. There were no significant differences in total chlorophyll content among sites (p = 0.41), but the chl *a:b* ratio of GBP plants was significantly higher (p = 0.024) than that of plants at either NEF or LM-151. Chlorophyll content tended to be highest and chl *a:b* ratios lowest during the summer months, but this trend was not consistent at all sites within all years. Comparison of in situ water temperature with total chlorophyll and chl *a:b* ratios by site showed no significant relationships (p > 0.05) and low correlation coefficients (r^2 < 0.12).

Fig. 6. *Halodule wrightii. P* versus *I* curves. Relationship between photosynthetic oxygen production and PFD measured in situ for entire plants from December 1989 to April 1991 at stations NEF and GBP. Values are x̄ ± SE (n = 3 to 4). Note adjustment in y-axis scale between some months. Curves for LM-151 have been reported previously (Dunton and Tomasko 1994).
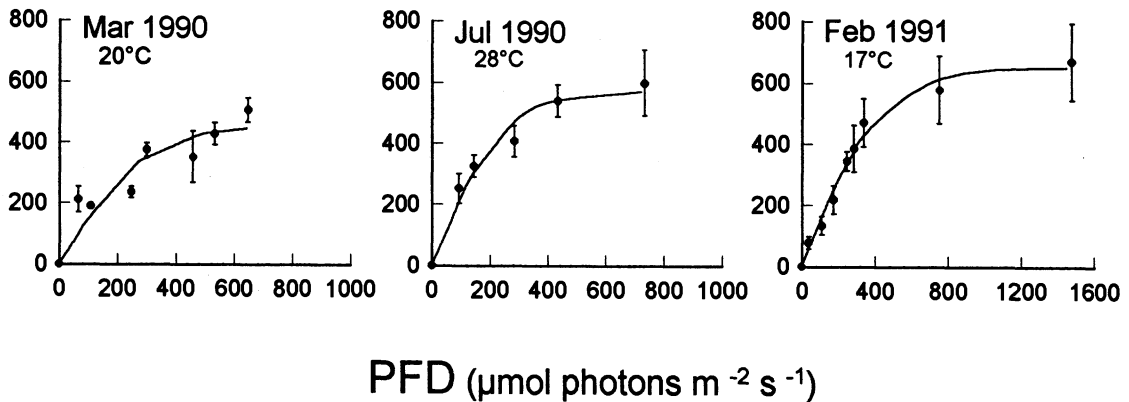
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NEF

Gross P (μmol O_2 g dry wt^{-1} hr^{-1})

PFD (μmol photons m^{-2} s^{-1})

GBP

PFD (μmol photons m^{-2} s^{-1})
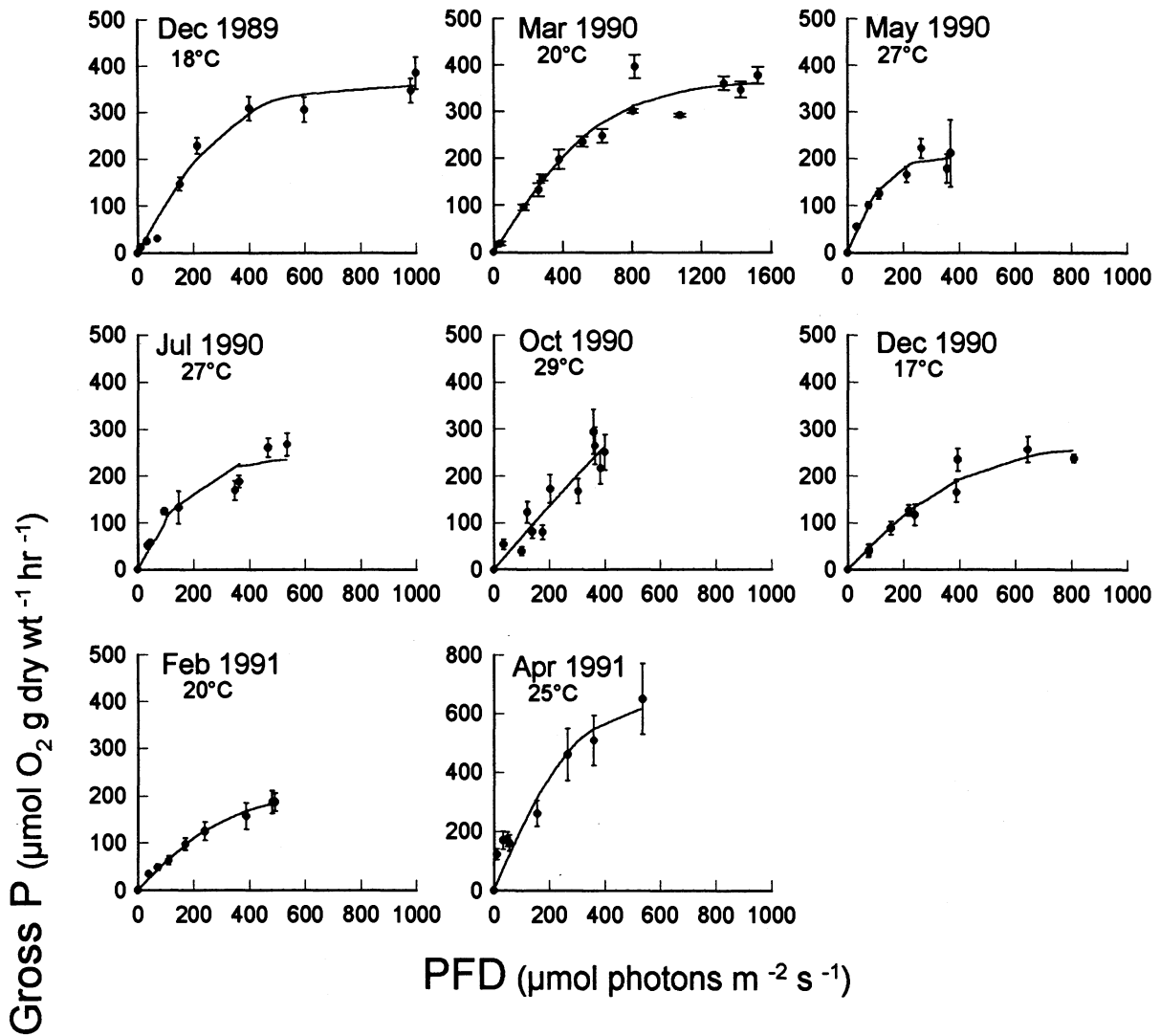
TABLE 2. Summary of grain size distribution ($\bar{x} \pm$ SE) and sediment porewater NH_4^+ from data pooled from all visits to each site. Values for sediment NH_4^+ are $\bar{x} \pm$ SE (n). Numbers sharing the same letter (superscript) are not significantly different (p > 0.05).

Site	Depth (m)	n	% Rubble	% Sand	% Silt	% Clay	% Mud (silt & clay)	Sediment NH_4^+ (μM)
LM-151	1.3	19	[a]19.4 ± 2.1	[a]64.1 ± 2.1	[a]8.3 ± 1.5	[a]8.2 ± 1.1	[a]16.5 ± 2.2	[a]146 ± 18 (33)
NEF	1.2	19	[b]9.0 ± 1.7	[b]81.5 ± 1.9	[b]4.7 ± 0.6	[b]4.8 ± 0.5	[b]9.5 ± 0.9	[a]134 ± 15 (30)
BPG	0.4–0.6	13	[c]0.8 ± 0.2	[c]89.3 ± 1.1	[a,b]5.8 ± 0.7	[b]4.1 ± 0.5	[b]9.8 ± 1.0	[a]129 ± 10 (23)

tion periods was less than 400 μmol m^{-2} s^{-1} due to low incident PAR. Values of relative quantum efficiency, α, had a range of 0.6–2.4 μmol O_2 (gdw leaf)$^{-1}$ h^{-1} (μmol photons m^{-2} s^{-1})$^{-1}$. Whole plant respiration generally ranged from ca. 40 μmol O_2 (gdw leaf)$^{-1}$ h^{-1} to 140 μmol O_2 (gdw leaf)$^{-1}$ h^{-1} (average 89 μmol O_2 (gdw leaf)$^{-1}$ h^{-1}). Average blade respiration from bottle incubations made during visits to the study site were 52 μmol O_2 gdw^{-1} h^{-1} (SE = 5.9, n = 9) compared to 17.2 μmol O_2 gdw^{-1} h^{-1} (SE = 2.6, n = 9) for root and rhizome tissue. Whole plant compensation irradiance (I_{cp}) generally ranged from ca. 60 μmol m^{-2} s^{-1} to 120 μmol m^{-2} s^{-1} (average 80 μmol m^{-2} s^{-1}).

Discussion

WATER QUALITY PARAMETERS AND SAV

Declines in seagrass habitat throughout the world is largely attributed to the deterioration of water quality, which is often correlated with nutrient enrichment from sewage or agricultural drainage, and underwater light reduction, which results from increased sediment loading, fouling by epiphytic algae, or nuisance phytoplankton blooms (Borum 1985; Twilley et al. 1985; Wetzel and Nec-

kles 1986; Dennison et al. 1993). Consequently, recent studies have focused on the establishment of quantitative levels of water quality parameters necessary to support submersed aquatic vegetation (SAV), particularly seagrasses (Dennison et al. 1993; Stevenson et al. 1993). In this study, information on sediment and water quality parameters were collected within three distinct seagrass habitats on the south Texas coast. The significant differences in salinity and nutrient regimes reflect a natural gradient of decreasing freshwater inflow from north to south (Armstrong 1987) and suggest that the establishment of minimum water quality criteria for the protection of SAV is strongly estuarine specific, even in adjacent estuarine systems.

In addition to the large differences in salinity and water column DIN, Dunton (1994) noted that average water transparency, as reflected in the diffuse light attenuation coefficient (k), was lower in the more northern Guadalupe estuary (2.5–3.8 m^{-1}) compared with the Nueces estuary and Laguna Madre (0.2–2.1 m^{-1}) to the south (Dunton 1994). Although high concentrations of chlorophyll a in Laguna Madre surface waters (60 μg l^{-1}) associated with a brown tide algal bloom nearly doubled average k values (from 0.7 to 1.2; Dunton

TABLE 3. *Halodule wrightii*. Seasonal variation in *P* versus *I* parameters for entire plants based on in situ measurements of oxygen evolution collected coincidentally at three sites along the Texas coast.

Date	Site	Temp (°C)	Salinity (‰)	P_{max} (μmol O_2 (gdw leaf)$^{-1}$ h^{-1})	R (μmol O_2 (gdw leaf)$^{-1}$ h^{-1})	α[a]	I_k (μmol m^{-2} s^{-1})	I_{cp} (μmol m^{-2} s^{-1})
December 1989/January 1990	NEF	18	32	358	132	1.0	341	125
	LM-151	22	39	1,104	141	2.4	453	58
March 1990	GBP	20	25	456	74	1.5	298	48
	NEF	20	30	366	94	0.6	642	164
	LM-151	20	48	—	70	0.6	—	—
May 1990	NEF	27	32	203	96	1.4	147	69
	LM-151	30	38	223	46	0.6	365	76
July 1990	GBP	28	22	574	142	2.3	245	61
	NEF	27	36	238	103	1.1	221	96
	M-151	28	45	331	120	1.0	321	116
October 1990	NEF	29	34	—	76	0.6	—	—
	LM-151	22	50	340	80	1.1	306	72
December 1990	NEF	17	30	267	40	0.6	437	66
February 1991	GBP	17	10	651	100	1.5	429	66
	NEF	20	30	204	45	0.6	334	73
	LM-151	12	32	140	37	0.5	286	75
April 1991	NEF	25	23	652	105	2.2	296	48
	LM-151	26	45	300	98	1.6	189	62

[a] μmol O_2 gdw^{-1} h^{-1} (μmol photons m^{-2} s^{-1})$^{-1}$.

1994), highest values for k were found in the Guadalupe estuary, which is characterized by generally low salinities and high ambient DIN concentrations. Large and frequent freshwater inflow events in the Guadalupe estuary probably contribute significantly to reduced water transparency and high k values through the influx of suspended solids, which are constantly resuspended in the shallow waters by winds and waves. In Laguna Madre, increases in light attenuation from elevated chlorophyll concentrations are clearly responsible for the decline in seagrass biomass and density at LM-151 and may eventually force *Halodule wrightii* to retreat into shallower (<1 m) water depths (see Dunton 1994 for discussion of light regimes at these stations). The differences in light availability are largely responsible for the differences in the maximum depth penetration of *Halodule wrightii*, based on the photosynthetic light requirements of this species (Dunton 1994; Dunton and Tomasko 1994).

Complications associated with high levels of algal epiphyte fouling were largely minimized through the examination of seagrass populations located on the deep edges of seagrass meadows, where light is often limiting for macroalgae at both GBP and NEF. Therefore, differences in the maximum depth distribution and biomass of *Halodule wrightii* examined in this study at the various estuarine sites is a product of variations in the underwater light environment and not physicochemical parameters. The significantly lower shoot biomass of *Halodule wrightii* at GBP compared to NEF or LM-151 is likely a reflection of light starvation. Although plants at GBP have retained relatively high shoot densities to maximize light capture, the allocation of carbon to each shoot is significantly lower than that of plants at NEF or LM-151 (the carbon content of dry weight for blade tissue is similar between sites; Dunton unpublished data), and consequently, the plants are unable to provide a large reservoir of carbon to belowground tissues.

In summary, the results of this study suggest it is unlikely that differences in salinity or water column DIN contribute to differences in the maximum depth distribution of *Halodule wrightii*. No significant differences in photosynthetic parameters were noted among populations at the three estuarine sites and indices of RSR, which appear to be indicative of overall plant health based on the allocation of biomass to belowground structures (storage), were also not significantly different among sites. Similarly, Burkholder et al. (1994) demonstrated that, in contrast to *Zostera marina*, neither *Halodule wrightii* nor *Ruppia maritima* were adversely affected by increased (10 μM NO_3^--N) nutrient loading as reflected in measurements of

shoot production, leading to the conclusion that these species may be appropriate choices in transplant efforts in nitrate-enriched waters. Dunton (1990) also noted that the growth dynamics of *Ruppia maritima* were not affected by large differences in salinity or DIN levels in an earlier comparison of populations from the Guadalupe and Nueces estuaries. Instead, as pointed out by numerous workers, the effects of increased nutrient loading on SAV is more often related to light reduction caused by epiphytic algae (Silberstein et al. 1986; Tomasko and Lapointe 1991).

PLANT PHYSIOLOGICAL RESPONSES

Long-term continuous measurements of chlorophyll content with respect to seasonal variations in temperature or sediment porewater ammonium concentrations revealed no consistent correlation over the 5-yr study period. Total chlorophyll content tended to be highest and chl $a{:}b$ ratios lowest in summer, as recognized in this study and by Czerny (1994) for *Halodule wrightii*. However, no significant correlation could be established with respect to water temperature at any one site. This observation was not unexpected since *Halodule wrightii* does not appear to photoadapt in response to changes in underwater irradiance (Dunton and Tomasko 1994; Czerny 1994), unlike *Zostera marina* (Dennison and Alberte 1985).

Porewater NH_4^+ levels were extremely variable among all sites, and with one exception, there were no significant correlations between sediment NH_4^+ and leaf chlorophyll content. A significant correlation between NH_4^+ and total leaf chlorophyll and chl $a{:}b$ ratios was noted at site NEF, but the calculated r^2 was relatively low (<0.40). The high sediment NH_4^+ concentrations (130–150 μM) at all sites in contrast with the low average DIN concentrations in the water column (ca. 5 μM at NEF and LM-151) indicate that leaves are probably of minimal importance in nutrient uptake. Previous studies have also documented the secondary importance of leaf uptake since seagrass roots are exposed to considerably higher levels of reduced inorganic nitrogen, particularly NH_4^+ (Dennison et al. 1987; Fourqurean et al. 1992). The average sediment NH_4^+ concentrations reported in this study (ca. 130–150 μM) are unlikely to be limiting to *Halodule wrightii* productivity; Fourqurean et al. (1992) found no evidence for nitrogen limitation in *Halodule wrightii* populations exposed to average NH_4^+ concentrations of 160 μM. It was also noted that significant differences in grain size composition between sites were not coincident with any significant change in sediment porewater NH_4^+.

Little variation in P vs. I parameters in *Halodule wrightii* was noted among sites over the experimen-
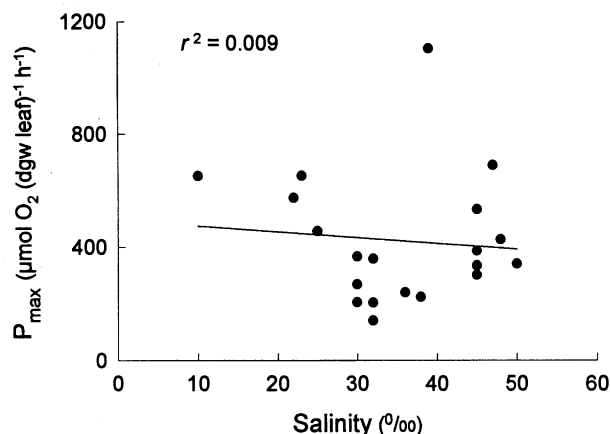
Fig. 7. *Halodule wrightii*. Relationship between water salinity and corresponding values of P_{max} collected in situ from photosynthetic incubations of entire plants. Data is derived from Table 1 (Dunton and Tomasko 1994) and Table 2 (this study).

TABLE 4. *Halodule wrightii*. Summary of photosynthetic parameters for entire plants based on measurements collected in situ from three locations in south Texas. Data are pooled from Dunton and Tomasko (1994) and this study. Values are $\bar{x} \pm SE$ (n = 19–22).

$P_{max(gross)}$	R		I_k	I_{cp}
μmol O$_2$ (gdw leaf)$^{-1}$ h^{-1}		α^a	(μmol m^{-2} s^{-1})	
422 ± 51	95 ± 8	1.2 ± 0.1	319 ± 19	81 ± 7

[a] μmol O$_2$ gdw^{-1} h^{-1} (μmol photons m^{-2} s^{-1})$^{-1}$.

tal period. This most likely reflects the inconsequential effects of different salinity and nutrient regimes on photosynthesis at each site. Although P_{max} values tended to be higher at site GBP, this may be related to the experimental problems associated with a very shallow and turbid water column. The extremely high P_{max} value recorded in January 1990 at LM-151 is enigmatic and corresponded with a winter peak in total leaf chlorophyll and low chl $a:b$ ratios (Dunton and Tomasko 1994). In situ measurements of photosynthesis on entire plants exposed to significantly different salinity regimes have not been reported previously in seagrasses, although in situ observations of *Amphibolis antarctica* found highest shoot productivity at 42‰. In *Halodule wrightii*, values of P_{max} showed no significant correlation with salinity (Fig. 7), based on measurements reported here and by Dunton and Tomasko (1994). It is apparent that the continued persistence of *Halodule wrightii* within the three estuarine systems is more related to changes in root and shoot biomass and depth of colonization than to photosynthetic characteristics.

The high productivity of *Halodule wrightii* under a variety of light, nutrient, and salinity conditions explains its nearly ubiquitous distribution and dominance in the western Gulf of Mexico. Its perennial nature and importance as the principal food source for overwintering ducks (McMahan 1969; Cornelius 1977) also indicate that *Halodule wrightii* should be the species to choice in transplant efforts focused on the restoration of seagrass habitats, as suggested by Burkholder et al. (1994). Therefore, a knowledge of its photosynthetic light requirements (Table 4) is critical in assessing the effect on the productivity of this species to changes in water transparency resulting from chronic algal

blooms (Dunton 1994) such as the brown tide in the upper Laguna Madre (Stockwell et al. 1993). The persistence of this bloom is coincident with low inorganic nitrogen levels (<5 μM) and the inability of the brown tide organism to utilize nitrate (DeYoe and Suttle 1994), despite measurable levels of NO$_3^-$ (up to 5 μM) in the water column. Its apparent dependence on NH$_4^+$ as an inorganic N source (DeYoe and Suttle 1994), despite the low concentrations of NH$_4^+$ in Laguna Madre (<2 μM; Dunton unpublished data), contradicts previously accepted relationships on nutrient stimulation of algal growth and continues to challenge our abilities to successfully manage and protect seagrass habitats from further loss and degradation.

ACKNOWLEDGMENTS

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