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REFERENCES

Seasonal Production and Biomass of the Seagrass, *Halodule wrightii* Aschers. (Shoal Grass), in a Subtropical Texas Lagoon

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Abstract A study of *Halodule wrightii* in a shallow subtropical Texas lagoon was performed to obtain seasonal data on its physiological ecology. Leaf production and biomass dynamics of *H. wrightii* were intensively monitored along with the underwater light environment at a 1.2-m depth study site over a 21-month period from June 1995 to February 1997. The annual photosynthetically active radiation (PAR) flux of 6,764 mol m^{-2} year^{-1} was more than twice as high as 2,400 mol m^{-2} year^{-1}, the minimum annual PAR required for maintenance of growth. As light intensity declined, blade chlorophyll a/b ratios increased suggesting that the plants were photo-adapting. Seasonal trends were evident in shoot growth and biomass. Compared to other *Halodule* populations in Texas, *H. wrightii* in LLM displayed slow growth and low biomass, high leaf tissue N content, and low C/N ratio but high N/P ratio of 38 suggesting that the plants were phosphorus-limited.

Keywords *Halodule wrightii* · Laguna Madre · Ecology · Underwater light · Nutrient limitation

Introduction

The Laguna Madre is the largest coastal embayment along the Texas (USA) coast with a surface area of more than 1,658 km^2 at mean sea level (TDWR 1983). This shallow, hypersaline, subtropical lagoon (mean depth of 1 m) is bordered on the east by a barrier island, Padre Island and on the west by semi-arid coastal prairie and rangeland of the

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Texas mainland. The lagoon has expansive seagrass meadows consisting largely of *Thalassia testudinum*, *Syringodium filiforme*, and *Halodule wrightii*.

The Laguna Madre is divided into the upper (ULM) and lower (LLM) basins, separated by a broad aeolian sand sheet which is covered by a few centimeters of water only during high water periods (Tunnell and Judd 2002). Exchange between the ULM and LLM is severely restricted and occurs via the Gulf Intracoastal Waterway (GIWW), a barge channel constructed in 1948 that cuts through the sand sheet (Ward 1997).

The LLM has two passes (Port Mansfield and Brazos-Santiago), one at each end, in contrast to the ULM which is connected to the Gulf of Mexico at the north end through Corpus Christi Bay which has two passes (Aransas and Packery) to the Gulf of Mexico. There is an almost fourfold greater water residence time in ULM compared to LLM (90 days) (Twilley et al. 1999). Although much of the Laguna Madre is hypersaline, the reduced circulation in the ULM has resulted in generally higher salinities than the LLM (TWQB 1975). For the period from 1962 to 1974, salinities were higher 68% of the time in the ULM than the LLM (TWQB 1975). Much of the ULM typically maintains salinities of 40‰ and higher most of the year (Dunton 1996; Solis and Powell 1999) while much of LLM has infrequently encountered salinities above 40‰ (Quammen and Onuf 1993). However, the average water temperature in the LLM is 1.7°C warmer (23.9 vs. 25.6°C from 1997 to 2007) than the ULM (DNR 2007). During the same 10-year period, the minimum (3.9 vs. 7.9°C) and maximum (34.1 vs. 34.3°C) water temperatures were also higher in the LLM (DNR 2007).

The basins have biological differences that are probably related to the temperature and salinity differences noted above. Hypersalinity has historically distinguished the

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composition and distribution of the euryhaline flora and fauna of both ULM and LLM (Breuer 1962). Allison (1987) reported differences in the molluscan community between the two basins that he attributed to salinity differences caused by increased flushing of the LLM compared to the ULM. In a macroalgal survey in which 74 species were found, Conover (1964) noted 13 species that occurred only in the ULM and 13 that occurred only in the LLM but did not speculate as to the cause(s). From June 1990 until 1997, ULM, unlike the LLM, had a continuous large-scale phytoplankton bloom, the Texas brown tide (DeYoe et al. 1997) which degraded the underwater light environment and caused significant decreases in seagrass biomass and productivity (Dunton 1994, Onuf 1996) and altered the zooplanktonic food pathways (Buskey and Stockwell 1993; Buskey et al. 1999; Ward et al. 2000). Greater circulation is probably why LLM has generally been spared the Texas brown tide.

The ULM seagrass community is dominated by the euryhaline seagrass *H. wrightii* (shoal grass) with *S. filiforme* (manatee grass) forming small, but expanding patches (Onuf 2007). In the LLM, *Halodule*, *Syringodium*, and *Thalassia* are more evenly represented but with an expanding distribution of *Thalassia* (Onuf 2007). Quammen and Onuf (1993) postulated that a gradual decline in the salinity of the LLM since construction of the two passes and the GIWW has caused a shift in seagrass species distributions. Specifically, *H. wrightii*, once the most abundant seagrass species in LLM prior to 1965, lost about 60% of its former range being displaced by *S. filiforme* and *T. testudinum* (Quammen and Onuf 1993).

In both ULM and LLM, *H. wrightii* is ecologically important. Its canopy is the preferred refuge and nursery habitat of juvenile Redfish (*Sciaenops ocellatus*), a recreationally important species (Rooker et al. 1998a, 1998b) and of juvenile commercial species, such as shrimp and crab (Tolan et al. 1997; Welch et al. 1997). Redhead ducks (*Aythya americana)* rely heavily on *H. wrightii* rhizomes and roots while overwintering along the Texas coast (Mitchell et al. 1994; Woodin 1996).

Despite considerable work on the biology of *H. wrightii* along the middle part of the Texas coast (Pulich 1980a, 1980b, 1982a, 1982b, 1985, 1986, 1989; Morgan and Kitting 1984; Dunton 1990; Dunton and Tomasko 1994; Dunton 1994, 1996, Tomasko and Dunton 1995; Czerny and Dunton 1995), there are no long-term autecological studies in the LLM. The physico-chemical differences notably salinity and temperature between the ULM and LLM suggest that there may be significant differences in shoal grass dynamics between the two basins. Dunton (1996) showed that *H. wrightii* exhibits different production dynamics among mid-Texas estuaries as a result of different physico-chemical environments although genetic differences may

also play a role (Angel 2002). Of the few studies on *H. wrightii* in LLM, none estimated seasonal or annual production or biomass dynamics. Consequently, a study of *H. wrightii* in the LLM was initiated to obtain seasonal data on its physiological ecology including shoot production rates, biomass changes, tissue nutrient fluctuations, leaf chlorophyll, and chlorophyll *a/b* ratios. In addition, the underwater light environment was documented during the study. A main objective of the study was to elucidate the relationship between plant physiology and the physical environment of the LLM, particularly underwater light. This information will be baseline data for LLM *H. wrightii* populations and could be useful to detect change in *H. wrightii* performance and possibly useful in the development of stress indicators for this species.

Methods

Study Site

Field studies were conducted in the LLM, approximately 10 km north of the Brazos-Santiago Pass (26° 9.0952' N, 97° 14.4322' W). The study site called LLM107 was situated about 500 m west of channel marker 107 on the Gulf Intracoastal Waterway near the lower depth limit (about 1.2 m) of *H. wrightii* in LLM. This site was selected because it had characteristics similar to a site used in a *H. wrightii* study in the ULM (Dunton 1994, Dunton 1996, Dunton and Tomasko 1994).

Water currents in the vicinity of LLM107 were <10 cm s^{-1} for more than 80% of the year (Brown and Kraus 1997). The site has a fetch of about 5 km from southeast winds of 6–12 m s^{-1} that are typical from May to October (Brown and Kraus 1997). From November to April, calm periods are interspersed with cold fronts during which northerly winds are strong (12–17 m s^{-1}) and air temperatures drop significantly and rapidly (Brown and Kraus 1997). Astronomical tides are about 20 cm in the Laguna Madre (Hedgepeth 1947) but, combined with the shallowness of the basin and strong winds, water levels vary between 0.9 to 1.6 m at the study site.

Physical and Chemical Measurements

Water temperature, salinity, light and in vivo chlorophyll *a* were collected continuously at a monitoring platform (FIX 1; N 26° 10.7533', W 97° 15.6033'), located 3.6 km north of the study site. Technical details concerning monitoring equipment and maintenance schedules at FIX 1 are provided in Brown and Kraus (1997). Field data (temperature, salinity, depth) were recorded at LLM107 during each sampling trip. Water column samples were collected monthly from No-

vember 1995 to November 1996 in quadruplicate for nutrient analysis. Unfiltered samples were stored on ice during transport then frozen until analysis. Nitrate-nitrite and ammonium analyses followed the protocols in Parsons et al. (1984).

Surface photosynthetically active radiation (PAR) data was collected using a LI-190SA terrestrial quantum sensor mounted on the monitoring platform and a LI-COR LI-1000 datalogger (LI-COR Inc., Lincoln, Nebraska, USA). Surface PAR data from the University of Texas-Pan American Coastal Studies Laboratory (12.2 km from study site) on South Padre Island was used from 2 September to 20 October 1995 because data were unavailable from FIX 1. Continuous subsurface PAR photon flux density (PFD) data was collected at LLM107 using a LI-193SA spherical (4π) quantum sensor positioned at seagrass canopy height and a LI-1000 datalogger protected in a waterproof housing (Ikelite, Model 5910, Indianapolis, IN, USA). To reduce fouling effects, the sensor was placed in a plastic bag and the bag was changed every 2 to 4 weeks. The plastic bag has been shown to not significantly alter light irradiance or quality (unpublished data). Instantaneous surface and underwater PFD were recorded as μmol m^{-2} s^{-1}, measured at 1-min intervals and integrated hourly. Because of instrument problems, underwater PFD data are lacking from 21 February through 28 April 1996 (66 days), and 11 August through 24 August 1996 (14 days). Attenuation of light (k) was calculated using the Bougert–Lambert law as used by McPherson and Miller (1987), k ln $(I_o/I_z)/z$, where I_o is the incident (surface) light intensity, I_z is the light intensity at depth z, the average depth at the site in meters, and k is the light attenuation coefficient (m^{-1}).

For the calculation of the annual underwater light budget, the period from 1 May 1996 to 30 April 1997 was selected because this period represented the most complete data set for both surface and underwater PFD although it did not correspond precisely with the biological sampling.

H_{sat}, the number of hours each day of irradiance-saturated photosynthesis, and H_{comp}, the number of hours of irradiance above the compensation irradiance (Dennison and Alberte 1982) were calculated based on saturation irradiance (I_k) (315 μmol m^{-2} s^{-1}) and whole plant compensation irradiance (I_{cp}) (80 μmol m^{-2} s^{-1}) values obtained from Dunton and Tomasko (1994).

Sediment Parameters

Sediment samples for grain size and ash-free dry weight analysis were collected in November 1996 and November 1997, using six replicate 60-mL modified syringe corers that sample to a depth of 10 cm. Grain size was analyzed according to the method of Folk (1980) using settling velocities of the size fractions to determine the percentages

of each fraction based on weight. Sediment ash-free dry weight was estimated using six replicate sediment samples by combusting dried samples at 500°C for 3 h. Pore water ammonium (NH$_4^+$) samples were collected every 3 months from November 1996 to November 1997 using a modified 60-mL syringe corer (n=4). Samples were placed in sealed bags, transported on ice, and stored frozen. Pore water was extracted by centrifugation of thawed homogenized samples and analyzed for NH$_4^+$ using the phenol–alcohol method described in Parsons et al. (1984).

Biomass and Shoot Density Measurements

Four replicate biomass cores (9 cm core, 0.006 m^2 area), each at least 1-m apart, were collected weekly to monthly where grass cover appeared uniformly dense. Weekly sampling was typically done from spring to fall while monthly sampling occurred during winter. The PVC coring device was pounded 15 to 20 cm into the sediment to insure inclusion of rhizome and root material. Samples were washed of sediment through a 1-mm sieve immediately upon return to the lab and stored in sealed plastic bags and refrigerated until processing. In the laboratory, plant material was separated into above- and below-sediment fractions, the number of shoots per core counted, and multiplied by area (shoots m^{-2}). Leaves from all cores were cleaned of epiphytes by gently scraping with a scalpel (Dauby and Poulicek 1995), dried at 60°C to a constant weight and weighed to the nearest 0.001 g. Below-sediment to above-sediment biomass ratios (B/A) were calculated from dried samples. Results are expressed as dry weight of above-sediment, below- sediment, and total biomass per unit area (g dw m^{-2}). Biomass of individual shoots was determined by dividing the above-ground biomass by the shoot density of replicate cores (mg shoot^{-1}).

Shoot Production and Leaf Elongation Measurements

Leaf-clipping was used to estimate shoot leaf production (Kowalski et al. 2001). Briefly, a monotypic *H. wrightii* stand with uniform density and an area of 50 by 50 cm was marked off then clipped 1 to 3 cm above the sediment. A mean value for the height of remaining shoot stubble (termed initial clip-height) was determined in the field by collecting one 9-cm core (0.006 m^2) from the perimeter of the clipped area and measuring the stubble length of ten to 20 clipped shoots. Clipped shoots were allowed to re-grow for 1 to 3 weeks (spring and summer) or 4 to 6 weeks (fall and winter) and then four 9-cm diameter cores were harvested from each clipped plot. This method of clipping typically produced 10–30 shoots per core. Care was taken to clip new areas at least 2 m from previously clipped areas.

In the laboratory, the leaves of up to 30 clipped shoots were scraped of epiphytes, measured for leaf length to the nearest millimeter, dried (60°C), and weighed. Lengths of all leaves per shoot were pooled to calculate average length of re-grown leaves. The average initial clip height value was subtracted from the average length of re-grown leaves per shoot and divided by the re-growth time interval to give leaf elongation rate in mm day^{-1}. Shoot production (mg shoot^{-1} day^{-1}) was calculated by obtaining a clipped and re-grown leaf biomass to leaf length ratio multiplied by the mean stubble length (measured at clipping) divided by the re-growth period, divided by the number of shoots per core. This method accounts for the old growth leaf biomass remaining after clipping. Areal production (g m^{-2} day^{-1}) was calculated by multiplying shoot production by shoot density.

Elemental Analyses

Replicate biomass samples (leaves and below-ground tissue) were analyzed for carbon (C) and nitrogen (N) content using a Carlo-Erba Elemental Analyzer EA 1108. Biomass leaf samples were also analyzed for phosphorus (P) content using the method of Solorzano and Sharp (1980). Biomass samples (above- and below-sediment) from June, August and November 1995 and February 1996 were analyzed. Clipped leaves were analyzed for June, August, and November 1995; February, May, August, and December 1996 and February 1997 samples. Results are presented as percent C, P, and N content and C/N/P molar ratios. Monthly and annual C, P, and N incorporation budgets were calculated by numerical summation from daily production rates. Annual rates were summed from monthly estimates.

Blade Chlorophyll Analysis

Leaves were collected monthly for chlorophyll a and b quantification. Leaf material was transported on ice and frozen in the lab until processing. Blades were thawed and gently scraped with a scalpel to remove epiphytes. Chlorophyll was extracted by immersing 10 to 15 mg of leaf material in 5 mL of N, N-dimethylformamide. Six replicate samples were placed in the dark at room temperature (25°C) for 48 to 72 h. Samples were analyzed on a Shimadzu 160 UV spectrophotometer at 664 and 647 nm. Absorbance values at 750 nm were used to correct for turbidity. Leaf chlorophyll content was calculated according to the equations of Porra et al. (1989) and are expressed as mg chl g^{-1} dw leaf.

Statistical Analysis

Statistical and graphical analyses were performed using a general linear model procedure (SPSS, Inc. 1993, 1997). Data were tested for homogeneity and transformed when necessary to meet the assumptions of parametric statistics. Kruskal–Wallis one-way analysis of variance (ANOVA) tests were used for heteroscedastic data that were not transformed and for sediment grain size distribution. Parametric ANOVAs were used to detect significant differences in shoot elongation, biomass, and leaf chlorophyll content among sampling dates. Where significant differences were observed Tukey's multiple comparison post-hoc tests were used to determine significant differences among sampling dates (Sokal and Rohlf 1995). Correlation and regression analyses and t-tests were used to test for significant relationships between light, temperature, pore water NH$_4^+$ concentrations, and blade chlorophyll concentration and between shoot growth and shoot elongation. The alpha level was 0.05 for all statistical tests.

There were typically two sampling trips per month during the summer and one per month during the winter. The leaf elongation rates measured by clipping were not replicated. The quadruplicate core samples from each plot were pseudo-replicates. For comparison among seasons, we combined three sampling dates within a season (based on solar position) to achieve replication needed for parametric statistical analysis. Based on the results of Kowalski (1999) and Kowalski et al. (2001) on *H. wrightii* at the same site, no significant differences were found ($p>0.05$) in leaf elongation rates among two or three dates within the same 30-day period at the same location. Dunton (1990, 1994) also employed this method in his study of *H. wrightii* in the ULM.

Results

Physical and Chemical Parameters

Water temperature (°C) ranged from the low teens in the winter to the low 30 s in the summer and was seasonal ($F_{609, 20}=113.09$, $p<0.0001$; Fig. 1). Highest daily mean values recorded during summer months (July and August) were between 31 and 32°C. Lowest temperatures occurred during winter (January and February) with daily means ranging between 13 and 17°C. Short periods (2–3 days) of water temperatures below 10°C were recorded from January to February 1996, and December 1996 to January 1997, attendant with the passage of cold fronts. Periods of greatest precipitation during the study period were in late summer and fall (Fig. 1) and salinity lows coincided with peak precipitation periods. Salinity peaked in July–August 1996 with values between 36 and 38 ppt with lows between 24–26 ppt in November–December 1995 ($F_{609, 20}=89.58$, $p<0.0001$; Fig. 1).

Water column NO$_3^-$–NO$_2^-$ and NH$_4^+$ were low (<3 μM) during the entire sampling period ($F_{34, 11}=12.89$, $p<0.0001$
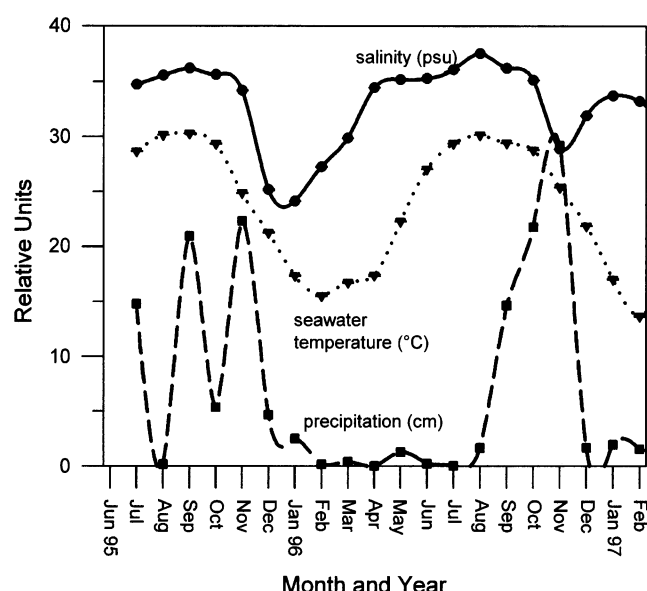
Fig. 1 Record of surface water temperature, precipitation, and surface water salinity from January 1995 to February 1997. Units are as follows: water temperature (°C); precipitation (cm); surface water salinity (parts per thousand = practical salinity units [psu]). Precipitation data from NOAA station at Brownsville, Texas. *Error bars* for temperature and salinity are smaller than *symbols*, except for precipitation means which lack error bars

for $NO_3^- - NO_2^-$ and $F_{34, 11} = 57.23$, $p < 0.0001$ for NH_4^+). Most months $NO_3^- - NO_2^-$ was 1 μM or less except November 1995 when values were between 2.0 and 2.5 μM. Mean water column chl *a* concentrations were low with values around 1.0 μg L^{-1} or lower for summer and early fall months. However, significant increases between 1 and 5 μg L^{-1} were recorded during late fall and winter ($F_{609, 20} = 21.19$, $p < 0.0001$), coincident with the passage of cold fronts. These pulses may have been related to entrained benthic microalgae and/or an increase in phytoplankton density from Texas brown tide cells brought in from the ULM.

Highest mean pore water NH_4^+ value occurred in February 1996 (70 μM) and lowest in August 1996

(9 μM). There were significant two- to threefold differences between spring and summer months compared to late summer and late fall ($F_{25, 4} = 16.07$, $p < 0.0001$). Percent organic content was low (about 1%) and not significantly different between samples collected in February and November 1996 ($F_{34, 11} = 57.23$, $p > 0.05$). Sediment grain size composition was 10% shell rubble (grain size $> 0\phi$, Folk 1980), 66% sand, 12% silt, and 12% clay.

Underwater PFD was high compared to other Texas bays (Table 1). On cloudless summer days, underwater quantum flux at canopy level was between 1,200 and 1,700 μmol m^{-2} s^{-1}. Highest daily underwater PFD means were recorded during summer months with values typically above 30 mol m^{-2} day^{-1}, with peaks as high as 45 mol m^{-2} day^{-1} (Fig. 2). Daily compensation irradiance of 5.74 mol m^{-2} day^{-1} (calculated from the average of December and February I_c values at 1.3 m site in Dunton 1996) or less occurred on 92 days (about 21%) of the 470 days of the monitoring period. The passage of winter cold fronts caused underwater PFD to drop to between 0 and 1 mol m^{-2} day^{-1}, but returned to pre-front levels of 15 to 20 mol m^{-2} day^{-1} 1–2 days after front passage. This corresponded to *k* values between 6 and 16 m^{-1} and a decline of 0 to 20% SI at canopy level. Percent surface irradiance at canopy level ranged from 0 to nearly 70% with the lowest values occurring largely during the colder months of the year and were associated with the passage of cold fronts (Fig. 3). Annual underwater PFD from 1 May 1996 to 30 April 1997 was 6,764 mol m^{-2} year^{-1} which corresponded to a mean of 45% SI and an annual mean attenuation coefficient of 1.16 (± 0.07 SE) m^{-1}. A moderately strong relationship between surface and underwater light was found in this study ($r^2 = 0.69$, $p < 0.0001$). Average values of H_{sat} and H_{comp} for the period from September 1995 to August 1996 (data missing for 21 Feb to 28 April) were 5.8 h and 8.6 h, respectively. The lowest and highest H_{sat} seasonal averages for the study period were 2.1 h (fall 1995) and 9.1 h (summer 1996).

Table 1 Total annual quanta received by seagrasses from four Texas estuaries at various depths from 1989 to 1997

Estuary	Total irradiance (mol m^{-2} year^{-1})	Year(s) recorded	Depth (m)	Source
Guadalupe[a]	2,276	1990	0.4–0.6	Dunton (1994)
Nueces[a]	3,300–5,122	1990–1992	1.2	Dunton (1994)
Nueces[b] (Corpus Christi Bay)	5,382	1994	1.2	Lee and Dunton (1996)
Upper Laguna Madre[a]	2,162–5,672[c]	1989–1992	1.3	Dunton (1994)
Lower Laguna Madre[b] (FIX 2)	4,293–9,149	1995–1996	1.2	Kaldy (1997)
Lower Laguna Madre[b] (Deep)	2,924–7,041	1995–1996	1.7	Kaldy (1997)
Lower Laguna Madre[a] (LLM 107)	6,764	1995–1997	1.2	This Study

[a] Underwater light measurements from a *Halodule wrightii* meadow

[b] Underwater light measurements from a *Thalassia testudinum* meadow

[c] Variation in total annual underwater light resulting from a brown tide algal bloom

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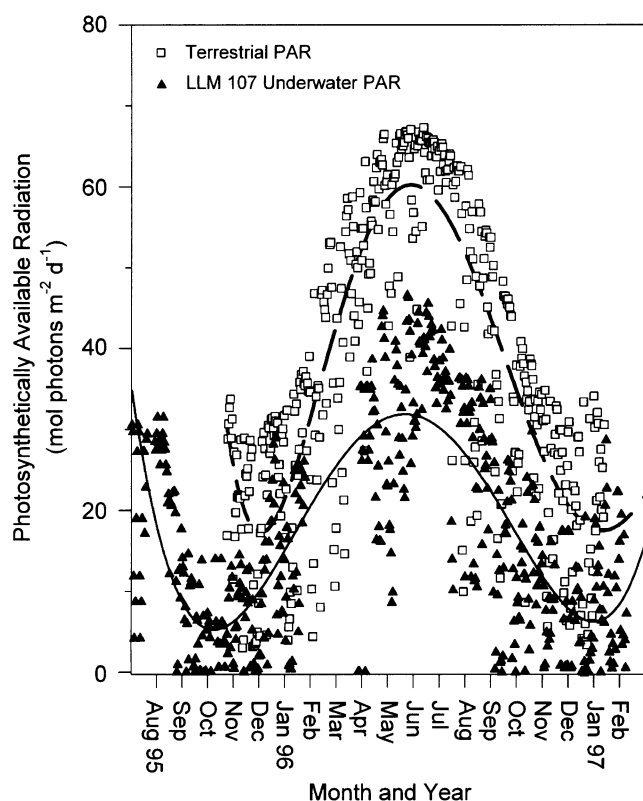
Fig. 2 Daily quantum flux density measurements collected from FIX 1 (surface PAR and underwater at canopy level from LLM 107 from August 1995 to February 1997. Best-fit regression lines generated from a tenth-order polynomial equation

Halodule Production

Biomass and Shoot Density There was a distinct seasonal trend in biomass with highest total biomass occurring in August 1995 and October 1996 (272 and 279 g dw m^{-2}, respectively) (Fig. 4). Lowest total biomass values were below 100 g dw m^{-2} and occurred in November 1995 and February 1996. Mean total biomass during the study was 185 (± 9) g dw m^{-2}. Below-ground biomass ranged from 91% and 46% of total biomass at LLM107 and was significantly different among months. Below-ground to above-ground (B/A) biomass allocation changed seasonally ranging between 2.3 (April 1996) and 15.7 (January 1997) (Fig. 4). There were significantly higher B/A values for December 1996, January and February 1997. Above-ground biomass of *Halodule* also showed significant seasonal variation (Fig. 4). Lowest means were recorded during the winters of 1996 and 1997 (17.15 and 14.54 g dw m^{-2}, respectively); highest values occurred in September 1995 (fall) and August 1996 (late summer) (56.96 and 50.07 g dw m^{-2}, respectively). *Halodule* shoot biomass varied significantly among seasons with highest values occurring in summer months, ranging from 8.07 mg dw shoot^{-1} in June 1995 to 3.15 mg dw shoot^{-1} in March 1996 (Fig. 4). There was

a strong and significant correlation between individual shoot biomass and above-ground biomass ($r=0.7245$, $p=<0.0001$).

Shoot density for *Halodule* at LLM107 fluctuated seasonally with lowest values in winter (Fig. 5). Shoot density ranged from 3,942 (January 1997) to 9,672 shoots m^{-2} (April 1996). April and May 1996 had the highest densities and were significantly greater than all other months. There was a significant seasonal pattern in leaf density for *H. wrightii*. Highest values were recorded for August 1995 (13,980$\pm$540 leaves m^{-2}) and July 1996 (14,752$\pm$ 700) while lowest values were found in January and February 1996 (8,290$\pm$1,457 and 8,128$\pm$1,017 leaves m^{-2}, respectively).

Leaf Elongation and Leaf Production Leaf elongation exhibited seasonal variation with highest rates during summer months and lowest rates during winter months (Fig. 6). Elongation rates greater than 3 mm day^{-1} were typical of early summer months during 1995 and 1996 and were significantly greater than slowest winter rates of <1 mm day^{-1} (SNK, $p<0.05$; Table 2). After peak summer growth,
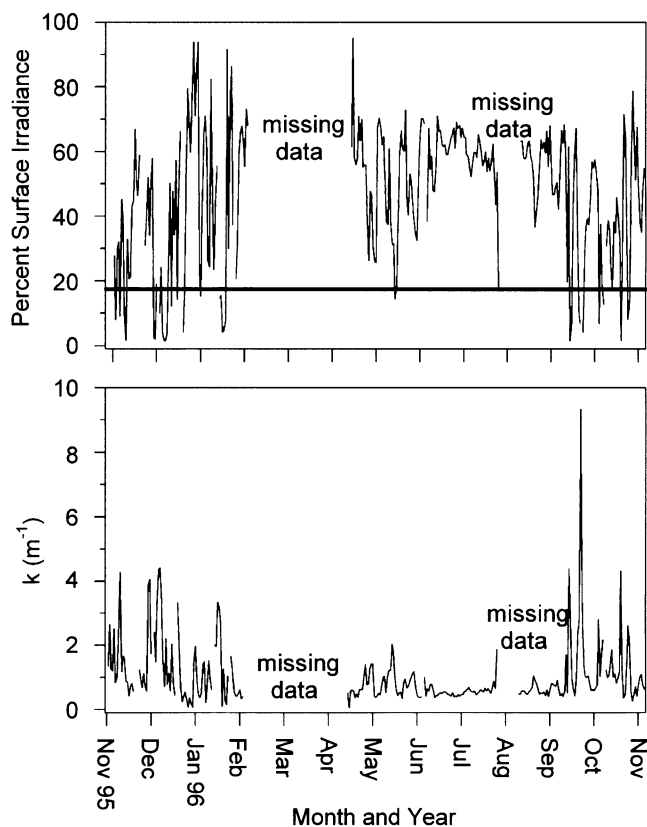
Fig. 3 Percent surface irradiance at canopy level and attenuation of light from surface (FIX 1) and underwater PAR (LLM107) data from August 1995 to February 1997 (*bottom panel*). *Horizontal line* on percent surface irradiance (% SI) graph represents 18% SI, the minimum % SI determined by Dunton (1994) for *Halodule wrightii*
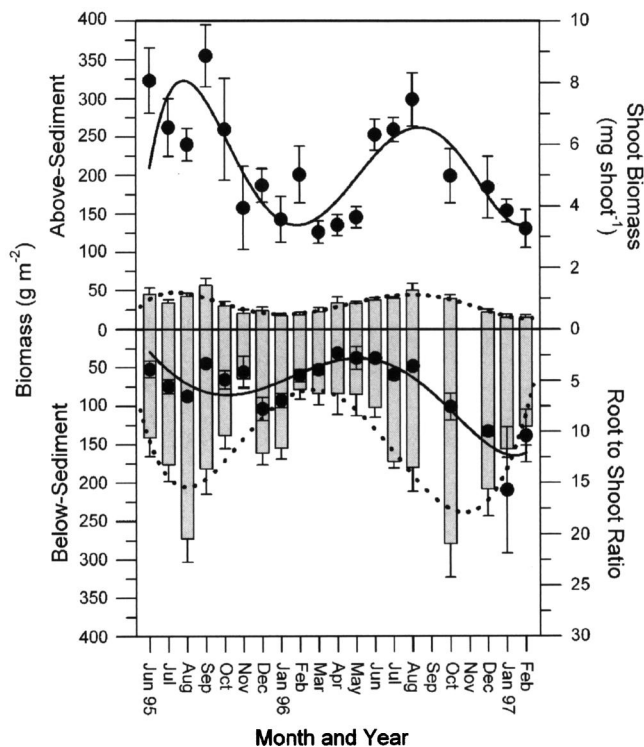
Fig. 4 Seasonal above-ground and below-ground biomass (*bars*), individual shoot biomass (*top panel, right y axis*), and above- to below-ground biomass ratio (*bottom panel, right y axis*) of *Halodule wrightii* at LLM 107 from June 1995 to February 1997. Note the *zero line* represents sediment surface

leaf elongation rates gradually diminished reaching a plateau around 1.5 mm day^{-1} (Fig. 6). Mean shoot production over the 21-month study period was 0.056 ($\pm$0.003) mg dw shoot^{-1} day^{-1}. Peak growth during 1995 exhibited a bimodal pattern (June and September) with rates between 0.101$\pm$ 0.009 mg dw shoot^{-1} day^{-1} and 0.110$\pm$0.010 mg dw shoot^{-1} day^{-1} (Fig. 6). Shoot production was significantly different between years (p=<0.001). Highest shoot production occurred in late spring and again in the fall and lowest production during winter months. There was a significant positive relationship (r^2=0.24, p<0.0001) between leaf elongation and shoot production.

Areal production was high from spring (May) to summer before winter decline (Fig. 7). Areal shoot production had highest values of 0.548$\pm$0.074 g dw m^{-2} day^{-1} in May 1995 and lowest values of 0.071$\pm$0.004 g dw m^{-2} day^{-1} during February 1997, a significant difference (SNK, p<0.05). Significant difference in areal production was found between 1995 and 1996 (p=0.031 and <0.001).

Tissue Carbon, Nitrogen, and Phosphorus Content Halodule leaf C content was generally high (range 41.3–42.7%) throughout the study with no seasonal pattern (Table 2). Below-ground tissue C was only slightly more variable ranging from 39.8% in June then declining steadily to a low of 34.4% in February (Table 2). Tissue N and P in both above- and below-ground tissues was highest in fall and winter with lower values in summer (Table 2). The C/N molar ratio for above- and below-ground tissues combined ranged from 14.8 to 45.3 and was highest in late summer

Fig. 5 Density of individual *Halodule wrightii* shoots from June 1995 to February 1997, LLM107
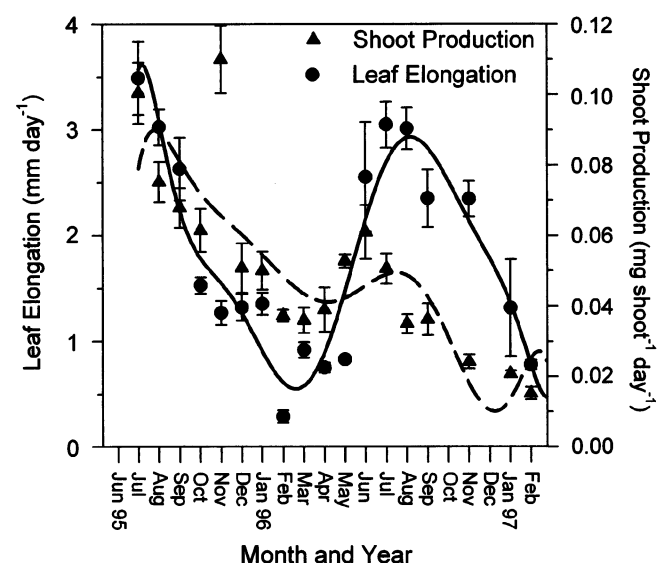
Fig. 6 *Halodule wrightii* leaf elongation and leaf production by individual shoots at LLM 107 from June 1995 to February 1997. Where no error bars appear, error is smaller than the symbol. Best fit lines from *sixth* order polynomial equations obtained from SigmaPlot, Inc. graphing software

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Table 2 Average tissue C, N, and P percent values and molar ratios for *Halodule wrightii* for samples collected at LLM 107 between June 1995 and February 1996

		% C	% N	% P	C/N	C/P	N/P
June 1995	Above	41.3 (0.1)	2.47 (0.1)	0.13 (0.03)	19.5 (0.5)	816 (183)	41.8 (8.3)
	Below	39.8 (5.8)	1.16 (0.26)	0.12 (0.00)	40.1 (2.9)	890 (123)	22.6 (4.7)
Aug 1995	Above	41.5 (0.26)	2.17 (0.01)	0.12 (0.00)	22.3 (0.03)	890 (32.1)	39.8 (1.5)
	Below	38.9 (0.00)	1.00 (0.01)	0.11 (0.02)	45.3 (0.54)	929 (158)	20.5 (3.2)
Nov 1995	Above	42.6 (0.96)	3.33 (0.14)	0.16 (0.02)	14.9 (0.27)	666 (48.6)	44.8 (2.5)
	Below	37.1 (1.5)	1.44 (0.11)	0.28 (0.14)	30.2 (3.5)	397 (219)	12.8 (5.7)
Feb 1996	Above	42.7 (0.70)	3.38 (0.19)	0.28 (0.07)	14.8 (1.1)	399 (107)	26.8 (5.3)
	Below	34.4 (4.7)	2.00 (0.53)	0.29 (0.06)	20.4 (2.6)	310 (18.6)	15.2 (1.0)

"Above" and "Below" refer to aboveground biomass and belowground biomass, respectively; $N=2$. Values in parentheses are standard deviations

and lowest in winter (Table 2). The N/P molar ratio for above- and below-ground tissues combined ranged from 21.0 to 32.2 and was highest in early summer and lowest in winter (Table 2).

Monthly leaf production ranged from 5.55 (Jan 1996) to 44.18 (Jun 1995) g dw m^{-2} month^{-1} with annual production being 242.7 g dw m^{-2} year^{-1} (Table 3). Highest monthly areal C production rates occurred in late spring and early summer and lowest rates were in winter (Table 3) while annual C incorporation was 94.83 ± 19.43 g C m^{-2} year^{-1}. Annual N incorporation was 6.84 ± 1.42 g N m^{-2} year^{-1} with highest monthly incorporation rates in early summer (1.11 g N m^{-2} month^{-1}) and lowest in winter (0.17 g N m^{-2} month^{-1}) (Table 3).

Blade Chlorophyll Blade chlorophyll *a* concentrations tended to be lowest in summer and highest in winter (Fig. 8) with high variability among months. Despite this variability, there was a significant difference among
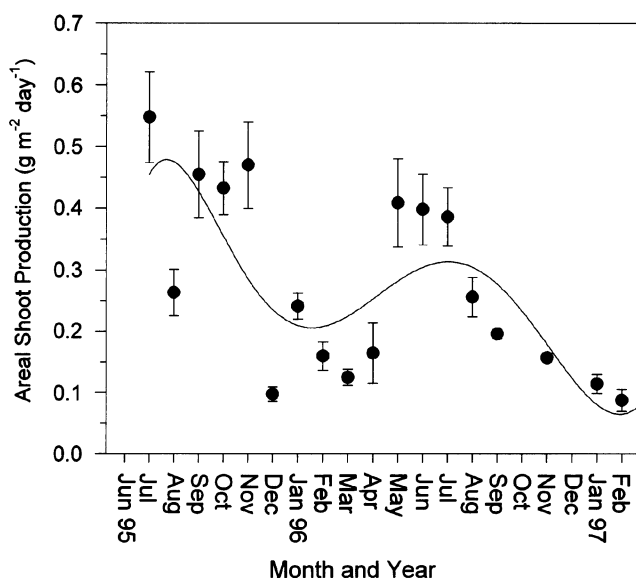
Fig. 7 *Halodule wrightii* areal production at LLM 107 from June 1995 to February 1997. Where no error bars appear, error is smaller than the symbol. Best fit lines from sixth order polynomial equations obtained from SigmaPlot, Inc. graphing software

months. Values ranged from 5.11 ± 0.51 mg chl g dw leaf^{-1} in July 1996 to 11.82 ± 0.65 mg chl g dw leaf^{-1} in February 1997, with a mean of 9.17 ± 0.24 mg chl g dw leaf^{-1} over the study. The chlorophyll *a* to *b* ratio was significantly different ($p<0.0021$) among months and showed a seasonal pattern with lowest values between 2.3 and 2.7 in summer and fall, and highest values, greater than 3.0, during winter (Fig. 8). Mean chlorophyll *a* to *b* over the study period was 2.8 ± 0.04. Seasonal changes in chlorophyll *a* to *b* ratio were attributable to greater variability of chlorophyll *b* than *a*, although the relationship was weak ($r=-0.25$, $p=0.012$).

Discussion

Seasonal Light and Growth of *Halodule*

Even at a depth of 1.2 m, the underwater light was likely not limiting on an annual basis to *Halodule* growth at LLM107. The annual PAR flux of 6,764 mol m^{-2} year^{-1} was more than twice as high as 2,400 mol m^{-2} year^{-1}, the minimum annual PAR required for maintenance of growth (Dunton 1994; Czerny and Dunton 1995). Average daily PAR flux was 19.14 mol m^{-2} day^{-1}. Winter underwater irradiances were lower than those of summer but were extremely low during periodic cold fronts when suspended sediments occluded the water column.

Annual underwater PAR from LLM107 was approximately 45% of surface PFD (15,065 mol m^{-2} year^{-1}), more than twofold higher than the 18–21% SI minimum suggested by Dunton and others (Dunton 1994; Czerny and Dunton 1995; Onuf 1996). Kenworthy and Fonseca (1996), using a different method, suggested an optimal range of 24% to 37% SI for *H. wrightii*. Our estimate still lies above their suggested optimal range.

Attenuation coefficients were less than 1 m^{-1} on nearly 65% of the days PAR data were collected. Average saturation irradiance for *Halodule* in three Texas estuaries was estimated to be 315 μmol photons m^{-2} s^{-1} (Dunton and Tomasko 1994) and between 200 to 300 μmol photons

Table 3 Monthly and annual estimates of leaf growth and carbon and nitrogen incorporation using unadjusted calculations for *Halodule wrightii* at LLM 107, Lower Laguna Madre, Texas

Values were interpolated between existing data points, assuming a linear response. Values represent means (±1 SE)

[a] units are g dw m^{-2} year^{-1}

Month	g dw m^{-2} mo^{-1}	g C m^{-2} mo^{-1}	g N m^{-2} mo^{-1}
Jun 1995	44.18 (13.03)	16.80 (4.95)	1.11 (0.32)
Jul	20.46 (3.50)	7.69 (1.29)	0.51 (0.09)
Aug	30.61 (4.91)	11.92 (1.89)	0.77 (0.12)
Sep	26.96 (4.04)	10.97 (1.64)	0.67 (0.11)
Oct	24.06 (4.37)	9.79 (1.78)	0.60 (0.12)
Nov	5.70 (0.96)	2.22 (0.38)	0.17 (0.03)
Dec	10.39 (2.29)	5.34 (0.90)	0.42 (0.08)
Jan 1996	5.55 (0.81)	2.16 (0.31)	0.17 (0.03)
Feb	7.64 (1.12)	0.31 (0.46)	0.25 (0.03)
Mar	10.66 (3.32)	4.36 (1.33)	0.36 (0.12)
Apr	22.44 (4.11)	9.14 (1.69)	0.75 (0.15)
May	34.09 (6.84)	14.13 (2.82)	1.05 (0.22)
Annual leaf production[a]	242.74 (49.30)[a]	94.83 (19.43)[a]	6.84 (1.42)[a]

m^{-2} s^{-1} in Indian River Lagoon, Florida (Rice et al. 1983). Dunton (1994) cited a H_{sat} for *Halodule* of 2 h as necessary for plant maintenance with 3 and 8 h needed to sustain spring and summer growth. The average H_{sat} at

Fig. 8 Blade chlorophyll (*top panel*) and chlorophyll *a* to *b* ratio in *Halodule wrightii* from LLM 107 from June 1995 to February 1997. *Dotted lines* represent 95% confidence intervals. Bottom chlorophyll *a* to *b* ratio graph with plot of water temperature throughout the sampling period

LLM107 was 5.8 h similar to the average H_{sat} for a *Halodule* site in the Upper Laguna Madre (ULM) (5.2 h) (Dunton 1994). In contrast, during the fall 1995, the average H_{sat} at LLM107 was 2.1 h suggesting that the plants may have been near the break even point during that period. With a H_{sat} of 5.8 h at 315 µmol photons m^{-2} s^{-1}, LLM107 *Halodule* plants would receive at least 6.58 mol photons m^{-2} day^{-1}. During active growth periods (May and July), daily PAR received by *Halodule* at LLM107 was in excess of 27.0 mol photons m^{-2} day^{-1}, two to three times higher than H_{sat}. The average H_{comp} at LLM107 for 1995–1996 was similar to that of a "healthy" *Halodule* site in the ULM (8.6 vs. 8.9 h, respectively) (Dunton 1994). During the study period, underwater PAR generally did not limit *Halodule* growth at LLM107.

The underwater light data for this study is one of the few long-term records for Laguna Madre seagrass beds and the first for a LLM *Halodule* meadow. *Halodule* at 1.2 m may be near its maximum depth limit in the LLM (Onuf 1996). *Halodule* in water deeper than 1.2 m had diminished biomass (35 g m^{-2}; Onuf 1996) compared to 185 g m^{-2} for *Halodule* at 1.2 m depth in this study but it is not known if this difference is due to less light or some other factor(s) singly or in combination such as competition or nutrient limitation. Kaldy and Dunton (2000) reported small patches of *Halodule* within *Thalassia* beds at 1.7 m on the western side of LLM. They concluded that 1.7 m was the maximum depth for *Thalassia* in LLM. Reduced biomass at deeper depths may due to a combination of low light coupled with competitive interactions between *Halodule* and *Thalassia* (*sensu* Tomasko 1992).

Light transmittance in the Laguna Madre is impacted by phytoplankton and wind-driven suspension of sediment. When the Texas brown tide algal bloom reduced underwater light levels in the ULM by more than 50%, *H. wrightii* biomass at 1.3 m declined by more than one-half (Dunton
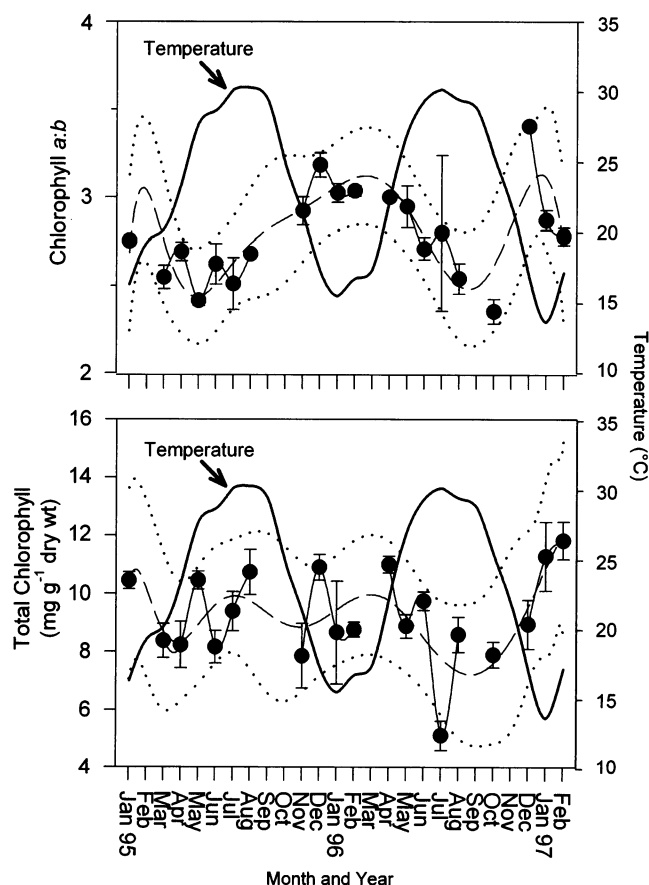
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1994). ULM *Halodule* populations in water less than 1 m deep were not impacted (Onuf 1996). The Arroyo Colorado, one of the most eutrophic waterways in Texas contributes large quantities of nitrogen and phosphorus to the LLM (TCEQ 2003). Areas of the LLM affected by Arroyo Colorado nutrient loading typically have high phytoplankton chlorophyll levels and reduced light penetration (DeYoe, unpublished data.). An on-going study is examining the influence of the Arroyo Colorado on the LLM seagrass community.

Seasonal Growth and Biomass of *Halodule*

Seagrass production and biomass maxima and minima attributed to seasonal changes in temperature and light is common (Duarte 1989) in temperate and tropical seagrass meadows (Sand-Jensen 1975; Ott 1980; Dennison 1987; Nelson and Waaland 1997; Brouns 1987; van Tussenbroek 1994, 1995, 1998). Seasonal changes in production and biomass of *Thalassia* and *Halodule* from subtropical Texas have been documented (Dunton 1996; Lee and Dunton 1996; Herzka and Dunton 1997; Kaldy and Dunton 2000, Pulich 1982a, 1985). In this study, *Halodule* from LLM showed a seasonal pattern of shoot production, biomass, B/A ratios, and leaf length. Highest above-ground biomass values of late summer and fall were the result of rapid late spring and early summer leaf growth which increased leaf area.

The highest below-ground biomass values of late summer and fall were due to the translocation of soluble carbohydrates from leaf to rhizome. Low below-ground biomass during winter and early spring occur as a consequence of use of stored C reserves for maintenance and growth during suboptimal conditions (Dawes and Lawrence 1980). The C content of below-ground tissues declined from late summer to spring while leaf C content remained relatively constant (Table 2). Similar conclusions for *Halodule* were made by Dunton (1994, 1996) from ULM and Corpus Christi Bay, Texas and by Kaldy et al. (2004) for LLM.

Compared to tropical Caribbean *Halodule* populations, leaf production and biomass values at LLM107 were low (Table 4). In coastal tropical waters, seasonal oscillations in temperature and light are dampened and annual values are higher compared to subtropical waters resulting in the potential for greater biomass accumulation. There are notable differences in biomass, leaf elongation, and shoot production of *Halodule* among Texas basins, especially between ULM and LLM (Table 4). It is noteworthy that there is a twofold, or more, difference in pore water NH_4^+ concentrations between ULM and LLM. Dunton (1994) found that *Halodule* from ULM, Corpus Christi Bay, and Guadalupe estuaries grew in sandy sediments with pore water NH_4^+ concentrations greater than 100 μM and prompted him to conclude those populations were not

nitrogen-limited. Pulich (1985) stated that pore water NH_4^+ in Upper Laguna Madre *Halodule* beds was 'impoverished' but also in the 100+ μM range. The low mean annual pore water NH_4^+ value of 32.3 μM from LLM107 may contribute to the low biomass and production at LLM107. It is unknown if low pore water NH_4^+ is widespread in the LLM.

Halodule at LLM107 experienced salinities ranging from 24‰ in winter to near 38‰ in summer, while populations from ULM having higher growth rates are commonly exposed to salinities above 40‰ (Dunton 1996). The salinity tolerance range for *H. wrightii* is 36 to 70 ppt (Koch et al., 2007). There was a noteworthy relationship between salinity and shoot productivity found in this study ($r^2=0.45$, $p=0.017$), however, lower salinity periods generally coincided with lower temperatures obscuring the relationship.

While light is the most critical factor that controls seagrass depth distribution, temperature has been cited as a factor regulating seagrass seasonal growth dynamics (Zieman 1975; Pérez and Romero 1992; Zupo et al. 1997; Lee and Dunton 1997). The upper temperature threshold in some seagrass species varies between 35 and 40°C (Bulthuis 1987) and between 0 and 2°C at the lower threshold for others (McRoy 1969), including *H. wrightii* (McMillan 1979). The relationship between water temperature and productivity ($r^2=0.53$, $p=0.007$, $n=12$) demonstrates the influence of water temperature on *Halodule* growth, especially since there was generally sufficient light at LLM107. The upper temperature limit of 35°C was never exceeded thus, it is likely that during peak growth periods of late spring and early summer water temperature was at, or near the optimal value for maximum production. Likewise, the lower temperature threshold of 2°C (McMillan 1979) was never approached to cause mass mortality of *Halodule*. During winter, low temperatures slowed growth through lowered metabolic activity. The warmer temperatures of late spring and early summer were likely less important in controlling shoot production because of endogenous circannual rhythms triggering growth which have been postulated for *Halodule* (Dunton 1994).

There was a strong and significant interrelationship between shoot production and collectively light, temperature, and salinity ($r^2=0.85$, $p=0.0117$). Light, temperature, and salinity were instrumental in regulating the leaf production and biomass dynamics of *Halodule* at LLM107. The effect of temperature appears to be more influential but that is likely due to greater annual variation in temperature than light or salinity.

Carbon and Nitrogen Incorporation

Halodule from LLM107 consistently exhibited lower production and biomass compared to populations from the western hemisphere at a similar depth (Table 2). On an annual basis, *Halodule* incorporated 46 g C m^{-2} $year^{-1}$

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Table 4 *Halodule wrightii* leaf production, biomass and density from different geographic locations

Geographic area (depth)	Shoot prod'n	Leaf areal Prod'n	Leaf elongation	Biomass	Shoot density	Time	Source
Indian River, Florida, USA							
0.20–0.40 m	—	1.3–3.0	2.2–8.5	23.6 (above)	—	Mar–Apr	Virnstein (1983)
San Antonio Bay, Texas, USA							
0.60 m	0.01–0.35	—	4–7<1	22–62 (total)	—	Apr–Sep winter	Dunton (1994)
(0.40–0.60 m)	—	—	—	100 (above)	1,000–12,000		Dunton (1996)
Upper Laguna Madre, Texas, USA							
1.3 m	0.05–0.3	—	4–7<1	200–500 (total)	—	Mar–Jun winter	Dunton (1994)
	—	—	—	200–300 (above) 300–550 (below)	1,000–12,000	Autumn	Dunton (1996)
Corpus Christi Bay, Texas, USA							
0.30–0.60 m	<0.001–0.23	—	<1–6	5–70 (above) 50–200 (below)	3,500–10,000	Annual range	Dunton (1990)
1.2 m	0.05–0.3	—	4–7	150–500 (total)	—	Annual range	Dunton (1994)
1.2 m	—	—	—	200–300 (above) 300–550 (below)	1,000–12,000	Annual range	Dunton (1996)
Matagorda Bay, Texas, USA							
(0.01–1.10 m)	—	—	—	34.6–115.7 (total)	—	Jul–Aug	Adair et al. (1994)
Alabama, Louisiana, Mississippi, USA							
0.6–1.37 m	—	—	—	80–1,220 (total)	300–3,200	Peak growth	Eleuterius (1987)
Laguna de la Mancha, Veracruz, Mexico							
–	—	—	—	38–62 (total)	1,824–2,669	Sep	Barriero-Guemes
Puerto Morelos Lagoon, Mexico							
(1.0–1.5 m)	—	—	—	519 (above)	14,872	Aug	Gallegos et al. (1994)
Redfish Bay, Texas, USA							
(0.05–0.55 m)	—	—	—	440 (total)	—	Aug	Pulich (1985)
Upper Laguna Madre, Texas, USA							
0.25–0.70 m	—	—	—	530 (total)	—	Sep	Pulich (1982)
Celestun Lagoon, Yucatan Peninsula, Mexico							
0.5–3.0 m	—	—	—	614–665 (total)	—	Aug	Herrera-Silviera (1994)
Indian River Lagoon, Florida, USA							
1.0 m	—	—	—	18.7 (above)	—	Annual mean	Jensen & Gibson (1986)
Tampa Bay, Florida, USA							
1.0 m	—	—	—	21.7 (above)	—	Annual mean	Jensen & Gibson (1986)
Little Bahama Bank, Bahamas							
1.0 m	—	—	—	5.9 (above)	—	Annual mean	Jensen & Gibson (1986)
Upper Laguna Madre, Texas, USA							
varied along transect	—	—	—	160 (total)	—	Jul–Nov	Onuf (1996b)
Coger Laguna Madre, Texas, USA							
Varied along transect	—	—	—	78 (total)	—	Jul–Nov	Onuf (1996b)
Coger Laguna Madre, Texas, USA							
1.2 m	0.015–0.056	0.071–0.304	0.52–3.49	33.86 (above); 152.07 (below)	96–315; 3,917–9,672	Annual range	This study

Units for shoot production are mg dw shoot^{-1} day^{-1}; for areal production, units are g dw m^{-2} day^{-1}; for elongation, units are mm day^{-1}. Units for biomass are g dw m^{-2} and units for density are shoots m^{-2}

(Table 3), which is more than threefold lower compared to *Halodule* from Florida (Virnstein 1982). Allowing for a correction of the 50% underestimation in leaf production associated with the clipping method (Tomasko and Dunton 1995; Kowalski et al. 2001), leaf C production still falls well below estimates for other small seagrass species (Hillman et al. 1989). Studies on the production dynamics of *Halodule* are few. Other studies have provided short-term C production rates (Dillon 1971; Morgan and Kitting 1984; Jensen and Gibson 1986; Dunton and Tomasko 1994) but did not attempt to calculate annual rates of leaf production. This work is the first to report an annual *Halodule* production budget.

Because light did not limit *Halodule* growth and temperature and salinity were generally favorable, an explanation for the low production and biomass at LLM107 is nutrient limitation. A direct relationship between seagrass productivity and the availability of inorganic nutrients necessary to sustain growth has been demonstrated (Hillman et al. 1989; Hemminga et al. 1991). Numerous studies have demonstrated the importance of both of water column and pore water nutrients for seagrass growth (e.g., Short 1987; Short et al. 1990; Bulthuis et al. 1992; Williams and Ruckelshaus 1993; Lee and Dunton 2000). Where nutrients have been demonstrated to be limiting, N is the macronutrient most often implicated in sediments of terrigenous origin, while P is typically limiting in carbonate sediment environments (Short 1987). Sediment in ULM and LLM is terrigenous in origin composed of fine quartz sand and silt (Rusnak 1960; Brown et al. 1980) and so might be expected to produce N limitation in *Halodule*.

Biomass B/A (below to above ground) ratios have been used to suggest nutrient-poor sediment status. Correlation between B/A ratios and soil nutrient concentrations have been well documented for terrestrial plants (Ingestad and Ågren 1991) and for the seagrass *T. testudinum* (Lee 1998). An increase in below-ground tissue increases root surface area for nutrient uptake (Short 1987; Gleeson 1993) and could offset low sediment nutrient levels. The mean B/A ratio of 5.5 for *Halodule* from LLM107 was nearly twice that of *Halodule* from ULM (2.9) and more than twofold greater than *Halodule* from Corpus Christi Bay (2.0) and Guadalupe estuary (2.2) (Dunton 1996) suggesting low pore water nutrient levels at LLM107. Pulich (1985) also measured biomass ratios for *Halodule* in ULM which ranged from ca. 2 (fall) to 4 (spring).

Halodule is reported to have a high nutrient (N and P) requirement and is commonly associated with high nutrient environments (Fourqurean et al. 1992). Powell et al. (1989) found *Halodule* from Florida Bay had a median N value of about 2%. The leaf N content for *Halodule* from LLM107 is among the highest reported for this species (avg=2.84%, SD=0.57). This is about the same as the leaf N content of *Halodule* from ULM (spring and fall avg=2.9%, Pulich 1982a; avg=2.71%, Dunton, unpublished data) where N is not believed to limit growth (Dunton 1996). The amount of N incorporated into leaf tissue by *Halodule* is estimated at 3.2 g N m^{-2} year^{-1}. Whole plant daily N incorporation ranged from 14 mg m^{-2} day^{-1} during peak growth in June 1995 to 2.7 mg m^{-2} day^{-1} in November 1995. The high leaf N content argues against N as being the limiting nutrient. Since N incorporation rate is a function of N supply and plant need, that parameter is not a reliable indicator of N limitation unless one of the factors is controlled.

Previous LLM seagrass studies and results from this study have shown low water column DIN and sediment NH$_4^+$ concentrations (Herzka and Dunton 1997; Kaldy 1997; Lee 1998). Kaldy and Dunton (2000) speculated that *Thalassia* in the LLM, with reduced photosynthetic performance, rapid nutrient turnover times and high B/A ratios, was likely N-limited. Lee and Dunton (2000) found that *T. testudinum* responded positively to in situ addition of N by increasing growth rates and leaf lengths and N content in leaf tissue, and decreasing B/A and C/N ratios. Plants from low nutrient environments tend to have higher C/N ratios than plants from high nutrient environments (Atkinson and Smith 1983; Duarte 1990). For seagrasses, N/P ratios above 25–30 are indicative of P limitation (Duarte 1990; Fourqurean and Cai 2001). *Halodule* from LLM107 had a year-round mean C/N molar ratio of 17.9, compared to 17.1 for a "healthy" *Halodule* population from ULM (Dunton, unpublished data). The annual average leaf N/P ratio of 38 (range 27 to 45) suggests P limitation. In contrast to *Thalassia* at nearby sites, it seems likely that *Halodule* at LLM107 is P-limited. Since the optimal N/P ratios for *Thalassia* and *Halodule* are not known, it is possible that each could be limited by a different nutrient in the same locale. The strongest evidence of nutrient limitation is a physiological response to addition of the limiting nutrient. Lacking that information, a comparison of nutrient ratios to critical (optimal) ratios as determined under experimental conditions is needed. In the absence of either type of information, conclusions regarding N or P limitation are tentative.

Besides P, micronutrients might also explain the low growth rates of *Halodule* at LLM107. Pulich (1982a, 1985) examined the sediment micro- and macronutrient dynamics of *Halodule* from the mid-Texas coast and found the plant required significant amounts of soluble Mn (0.1–0.4 μg mL^{-1}) and substantial sulfate reduction activity (0.2–1.0 mM). Moderate reducing conditions promote dissolution of phosphate, as well as micronutrients, in interstitial pore water (Pulich 1989). Although a need for significant sulfate-reduction activity was postulated, H$_2$S levels above 1 mM were concluded to be toxic to *Halodule* (Pulich 1989). If micronutrients are not at sufficiently high levels or sulfate reduction activity is depressed or excessive, growth

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may be limited. Other sediment factors could also impact *Halodule* performance including toxic bacterial by-products like phenols, organic acids, and reduced iron and manganese (Koch 2001). High organic matter content is also thought to be inhibitory but the mechanism is not clear (Koch 2001).

Blade Chlorophyll

H. wrightii from LLM107 demonstrated mild seasonal changes in total blade chlorophyll content and chlorophyll *a*/*b* ratio (Fig. 8). Total chlorophyll and chlorophyll *a*/*b* ratios were negatively but weakly correlated with temperature in this study ($r=-0.32$, $p=0.001$, and -0.35; $p<0.001$, respectively). Dunton and Tomasko (1994) noted a similar but non-significant trend at a 1.3-m deep study site in the Upper Laguna Madre where total chlorophyll content increased and chlorophyll *a*/*b* ratios decreased during the colder months.

Alteration of total chlorophyll concentration and chlorophyll *a* to *b* ratios is a common adaptation to changes in irradiance by submersed freshwater and marine angiosperms (Wiginton and McMillan 1979; Dennison and Alberte 1982; Barko and Filbin 1983; Al-Hamdani and Francko 1992; Pizarro and Montecino 1992; Abal et al. 1994; Czerny and Dunton 1995; Shafer 1999). It has been suggested that variations in blade chlorophyll levels are, in part, controlled by seasonal temperature changes in *H. wrightii* and *T. testudinum* (Czerny and Dunton 1995; Dunton 1996; Lee and Dunton 1997).

Many photoautotrophs, from cyanobacteria to higher vascular plants, adjust their photosystem stoichiometry to optimize photosynthetic performance (Chow et al. 1990). Increases in chlorophyll *b* relative to chlorophyll *a* during colder temperatures have been seen in *H. wrightii* populations from Texas and the Caribbean Sea (Wiginton and McMillan 1979), as well as algae and cucumber leaves (Tanaka et al. 1991; Maxwell 1994, 1995; Ohtsuka et al. 1997). Alteration of chl b/a ratio could be a photoadaptive response to high light during low temperature to dissipate excess PAR. These documented mechanisms, if they occur in seagrasses, could offer insight into the chlorophyll dynamics found in this, as well as numerous other studies, as photoadaptation to the combined effects of temperature and irradiance (Drew 1978; Pirc 1986; Czerny and Dunton 1995; Lee and Dunton 1996; Kaldy et al. 2004). Experimental verification of the occurrence of this mechanism in seagrasses is needed.

Conclusions

The seagrass *Halodule* displayed strong seasonal trends in shoot production and biomass at LLM107. Water temper-

ature explained most of the variability in shoot production and low water temperature was responsible for depressed winter growth. On an annual basis, it appears that *Halodule* is not light limited at LLM107; however, short-term light limitation may occur during the cold months of the year associated with high sediment re-suspension events spawned by the passage of cold fronts. Changes in shoot growth correlated positively with salinity and temperature. *Halodule* shoot production and biomass in LLM were lower compared to other *Halodule* populations in Texas, as well as worldwide. The most likely factor is nutrient limitation, specifically P limitation. Reasons for this conclusion include high below- to above-ground biomass ratios suggest enhanced nutrient scavenging, high leaf N content with leaf N/P ratio values in excess of 30.

Despite the comparatively lower biomass of *Halodule* in LLM, its wide distribution in LLM (Onuf 2007) and that the Laguna Madre ecosystem as a whole is net autotrophic underscores the importance of *Halodule* as an important habitat for larval fish and invertebrate communities. Its ecological importance may become more apparent in the face of change occurring to the species composition in this ecosystem (Onuf 2007). In recent history, change in seagrass species coverage including loss of *Halodule* has been attributed to long-term salinity change and associated competitive interactions (Quammen and Onuf 1993). New potential tropical benthic green algae competitors have appeared (DeYoe and Hockaday, 2001; Kowalski et al. 2007). In the past 20 years, south Texas has experienced tremendous population increases which will likely result in higher nutrient loading and recreational boat traffic. The impact of these changes on *H. wrightii* is not known, but this study provides critical baseline information for future studies.

References

Abal, E.G., N. Loneragan, P. Bowen, C.J. Perry, J.W. Udy, and W.C. Dennison. 1994. Physiological and morphological responses of the seagrass *Zostera capricorni* Aschers.to light intensity.

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Journal of Experimental Marine Biology and Ecology 178: 113–129. doi:10.1016/0022-0981(94)90228-3.

Al-Hamdani, S., and D.A. Francko. 1992. Effect of light and temperature on photosynthesis, elongation rate and chlorophyll content of *Nelumbo lutea* (Willd.) Pers. seedlings. *Aquatic Botany* 44:51–58. doi:10.1016/0304-3770(92)90080-3.

Allison, T.E. 1987. Molluscan communities of the Laguna Madre, Texas: Man's Impact. Proceedings from the 5th Symposium of Coastal and Ocean Management (Coastal Zone '87). Am. Soc. Civil Engineers, Seattle, Washington, May 26–29, 1987.

Angel, R. 2002. Genetic diversity of *Halodule wrightii* using randomly amplified polymorphic DNA. *Aquatic Botany* 1592: 1–10.

Atkinson, M.J., and S.V. Smith. 1983. C:N:P ratios of benthic marine plants. *Limnology and Oceanography* 28: 568–574.

Barko, J.W., and G.J. Filbin. 1983. Influence of light and temperature on chlorophyll composition in submersed freshwater macrophytes. *Aquatic Botany* 15: 249–255. doi:10.1016/0304-3770(83)90072-4.

Breuer, J.P. 1962. *An ecological survey of the Lower Laguna Madre of Texas, 1953–1959*. 8: 153–183. The University of Texas: Publications of the Institute of Marine Science.

Brouns, J.J.W.M. 1987. Aspects of production and biomass of four seagrass species (Cymodoceoideae) from Papua, New Guinea. *Aquatic Botany* 27: 333–362. doi:10.1016/0304-3770(87)90073-8.

Brown, J.L.F., J.L. Brewton, T.J. Evans, J.H. McGowen, W.A. White, C.G. Groat, and W.L. Fisher. 1980. *Environmental Geologic Atlas of the Texas Coastal Zone-Brownsville-Harlingen Area.*. Austin: Bureau of Economic Geology—The University of Texas at Austin.

Brown, C. A., N.C. Kraus. 1997. Environmental monitoring of dredging and processes in Lower Laguna Madre, Texas. Texas A&M University-Corpus Christi/Conrad Blucher Institute Technical Report TAMU-CC-CBI-96-01.

Bulthuis, D.A. 1987. Effects of temperature on photosynthesis and growth of seagrasses. *Aquatic Botany* 27: 27–40. doi:10.1016/0304-3770(87)90084-2.

Bulthuis, D.A., D.M. Axelrad, and M.J. Mickelson. 1992. Growth of the seagrass *Heterozostera tasmanica* limited by nitrogen in Port Phillip Bay, Australia. *Marine Ecology Progress Series* 89: 269–275. doi:10.3354/meps089269.

Buskey, E.J., and D.A. Stockwell. 1993. Effects of a persistent "brown tide" on zooplankton populations in Laguna Madre of south Texas. In *Toxic Phytoplankton Blooms in the Sea*, eds. T.J. Smayda, and Y. Shimizu, 659–666. New York: Elsevier Science Publishers.

Buskey, E.J., K.H. Dunton, and P.L. Parker. 1999. Variations in stable carbon isotope ratio of the copepod *Acartia tonsa* during the onset of the Texas brown tide. *Estuaries* 22: 995–1003. doi:10.2307/1353078.

Chow, W.S., A. Melis, and J.M. Anderson. 1990. Adjustments of photosystem stoichiometry in chloroplasts improve the quantum efficiency of photosynthesis. U.S.A Proceeding of the National Academy of Science 87: 7502–7506. doi:10.1073/pnas.87.19.7502.

Conover, J.T. 1964. The ecology, seasonal periodicity and distribution of benthic plants in some Texas lagoons. *Botanica Marina* v 7: 4–41.

Czerny, A.B., and K.H. Dunton. 1995. The effect of *in situ* light reduction on the growth of two subtropical seagrasses, *Thalassia testudinum* and *Halodule wrightii*. *Estuaries* 18: 418–427. doi:10.2307/1352324.

Dauby, P., and M. Poulicek. 1995. Methods for removing epiphytes from seagrasses: SEM observations on treated leaves. *Aquatic Botany* 52: 217–228. doi:10.1016/0304-3770(95)00500-5.

Dawes, C.J., and J.M. Lawrence. 1980. Seasonal changes in the proximate constituents of the seagrasses: *Thalassia testudinum, Halodule wrightii*, and *Syringodium filiforme. Aquatic Botany* 8:371–380. doi:10.1016/0304-3770(80)90066-2.

Dennison, W.C., and R.C. Alberte. 1982. Photosynthetic responses of *Zostera marina* L. (Eelgrass) to *in situ* manipulations of light. *Oecologia* 55: 137–144. doi:10.1007/BF00384478.

Dennison, W.C. 1987. Effects of light on seagrass photosynthesis, growth and depth distribution. *Aquatic Botany* 27: 15–26. doi:10.1016/0304-3770(87)90083-0.

DeYoe, H.R., and D. Hockaday. 2001. Range extensions of the seaweeds *Codium taylorii* Silva and *Caulerpa prolifera* (Forsskal) Lamouroux in the lower Laguna Madre, Texas. *Texas J. Science* 53(2): 190–192.

DeYoe, H.R., D.A. Stockwell, R.R. Bidigare, M. Latasa, P.W. Johnson, P.E. Hargraves, and C.A. Suttle. 1997. Description and characterization of the algal species *Aureoumbra lagunensis* gen. et sp. nov. and referral of *Aureoumbra* and *Aureococcus* to the Pelagophyceae. *Journal of Phycology* 33: 1042–1048. doi:10.1111/j.0022-3646.1997.01042.x.

Dillon, C.R. 1971. *A comparative study of the primary productivity of estuarine phytoplankton and macrobenthic plants. Ph.D. Dissertation*. 112. Chapel Hill: University of North Carolina.

DNR (Division of Nearshore Research). 2007. Texas Coastal Ocean Observation Network data base. lighthouse.tamucc.edu/TCOON/HomePage. Accessed June 2006.

Drew, E.A. 1978. Factors affecting photosynthesis and its seasonal variation in the seagrasses *Cymodocea nososa* (Ucria) Aschers, and *Posidonia oceanica* (L.) Delile in the Mediterranean. *Journal of Experimental Marine Biology and Ecology* 31: 173–194. doi:10.1016/0022-0981(78)90128-4.

Duarte, C.M. 1989. Temporal biomass variability and production/biomass relationships of seagrass communities. *Marine Ecology Progress Series* 51: 269–276. doi:10.3354/meps051269.

Duarte, C.M. 1990. Seagrass nutrient content. *Marine Ecology Progress Series* 67: 201–207. doi:10.3354/meps067201.

Dunton, K.H. 1990. Production ecology of *Ruppia maritima* L. s.l. and *Halodule wrightii* Aschers. in two subtropical estuaries. *Journal of Experimental Marine Biology and Ecology* 143: 147–164. doi:10.1016/0022-0981(90)90067-M.

Dunton, K.H. 1994. Seasonal growth and biomass of the subtropical seagrass *Halodule wrightii* in relation to continuous measurements of underwater irradiance. *Marine Biology* 120: 479–489. doi:10.1007/BF00680223.

Dunton, K.H. 1996. Photosynthetic production and biomass of the subtropical seagrass *Halodule wrightii* along an estuarine gradient. *Estuaries* 19: 436–447. doi:10.2307/1352461.

Dunton, K.H., and D.A. Tomasko. 1994. *In situ* photosynthesis in the seagrass *Halodule wrightii* in a hypersaline subtropical lagoon. *Marine Ecology Progress Series* 107: 281–293. doi:10.3354/meps107281.

Folk, R.L. 1980. *Petrology of sedimentary rocks*. Austin: Hemphill Publishing Co.

Fourqurean, J.W., J.C. Zieman, and G.V.N. Powell. 1992. Relationships between porewater nutrients and seagrasses in a subtropical carbonate environment. *Marine Biology* 114:57–65.

Fourqurean, J.W., and Y. Cai. 2001. Arsenic and phosphorus in seagrass leaves from the Gulf of Mexico. *Aquatic Botany* 71: 247–258. doi:10.1016/S0304-3770(01)00193-0.

Gleeson, S.K. 1993. Optimization of tissue nitrogen and root-shoot allocation. *Annals of Botany* 71: 23–31. doi:10.1006/anbo.1993.1003.

Hedgepeth, J. 1947. The Laguna Madre of Texas. Transactions of the 12th North American Wildlife Conference. p. 364–380.

Hemminga, M.A., P.G. Harrison, and F. van Lent. 1991. The balance of nutrient losses and gains in seagrass meadows. *Marine Ecology Progress Series* 71: 85–96. doi:10.3354/meps071085.

Herzka, S.Z., and K.H. Dunton. 1997. Seasonal photosynthetic patterns of the seagrass *Thalassia testudinum* in the western Gulf of Mexico. *Marine Ecology Progress Series* 152: 103–117. doi:10.3354/meps152103.

Hillman, K., D.I. Walker, A.W.D. Larkum, and A.J. McComb. 1989. Productivity and nutrient limitation. In *Biology of Seagrasses—A Treatise on the Biology of Seagrasses with Special Reference to the Australian Region*, eds. A.W.D. Larkum, A.J. McComb, and S.A. Shepherd, 635–685. New York: Elsevier Volume Aquatic Plant Studies 2.

Ingestad, T., and G.I. Ågren. 1991. The influence of plant nutrition on biomass allocation. *Ecological Applications* 1: 168–174. doi:10.2307/1941809.

Jensen, P.R., and R.A. Gibson. 1986. Primary production in three subtropical seagrass communities: A comparison of four autotrophic components. *Florida Scientist* 49:129–141.

Kaldy III, J.E. 1997. Production dynamics, reproductive ecology and demography of *Thalassia testudinum* (turtle grass) from the Lower Laguna Madre, Texas. Ph.D. Dissertation. The University of Texas at Austin.

Kaldy, J.E., and K.H. Dunton. 2000. Above- and below-ground production, biomass and reproductive ecology of *Thalassia testudinum* (turtle grass) in a subtropical coastal lagoon. *Marine Ecology Progress Series* 193: 271–283. doi:10.3354/meps193271.

Kaldy, J.E., K.H. Dunton, J.L. Kowalski, and K.-S. Lee. 2004. Factors controlling seagrass revegetation onto dredged material deposits: A case study in Lower Laguna Madre, Texas. *Journal of Coastal Research* 20: 292–300. doi:10.2112/1551-5036(2004)20[292:FCSROD]2.0.CO;2.

Kennworthy, W.J., and M.S. Fonseca. 1996. Light requirements of seagrass *Halodule wrightii* and *Syringodium filiforme* derived from the relationship between diffuse light attenuation and maximum depth distribution. *Estuaries* 19: 740–750. doi:10.2307/1352533.

Koch, E.W. 2001. Beyond light: Physical, geological, and geochemical parameters as possible submersed aquatic vegetation habitat requirements. *Estuaries* 24: 1–17. doi:10.2307/1352808.

Koch, M.S., S.A. Schopmeyer, C. Kyhn-Hansen, C.J. Madden, and J.S. Peters. 2007. Tropical seagrass species tolerance to hypersalinity stress. *Aquatic Botany* 86: 14–24. doi:10.1016/j.aquabot.2006.08.003.

Kowalski, J.L., D.L. Hockaday, G.H. Boza, and H.R. DeYoe. 2007. Re-discovery of the tropical green macroalga, *Penicillus capitatus* Lamarck (Chlorophyta: Bryopsidales), in Lower Laguna Madre, Texas. *Texas Journal of Science V* 59(4):305–310.

Kowalski, J.L., H.R. DeYoe, T.C. Allison, and J.E. Kaldy. 2001. Productivity estimation in *Halodule wrightii*: comparison of leaf-clipping and leaf-marking techniques, and the importance of clip height. *Marine Ecology Progress Series* 220: 131–136. doi:10.3354/meps220131.

Kowalski, J.L. 1999. *Production of the subtropical seagrass, Halodule wrightii Aschers., in Lower Laguna Madre, Texas.* MS Thesis. Edinburg: The University of Texas-Pan American.

Lee, K.-S. 1998. Nitrogen Budget of the Seagrass *Thalassia testudinum* in the Western Gulf of Mexico. Ph.D. Dissertation. The University of Texas at Austin.

Lee, K.-S., and K.H. Dunton. 1996. Production and carbon reserve dynamics of the seagrass *Thalassia testudinum* in Corpus Christi Bay, Texas, USA. *Marine Ecology Progress Series* 143: 201–210. doi:10.3354/meps143201.

Lee, K.-S., and K.H. Dunton. 1997. Effects of *in situ* light reduction on the maintenance, growth and partioning of carbon resources in *Thalassia testudinum* Banks ex König. *Journal of Experimental Marine Biology and Ecology* 210: 53–73. doi:10.1016/S0022-0981(96)02720-7.

Lee, K.-S., and K.H. Dunton. 2000. Effects of nitrogen enrichment on biomass allocation, growth, and leaf morphology of the seagrass *Thalassia testudinum*. *Marine Ecology Progress Series* 196:39–48.

McMillan, C. 1979. Differentiation in response to chilling temperatures among populations of three marine spermatophytes, *Thalassia testudinum, Syringodium filiforme* and *Halodule wrightii*. *American Journal of Botany* 66: 810–819. doi:10.2307/2442468.

McPherson, B.F., and R.L. Miller. 1987. The vertical attenuation of light in Charlotte Harbor, a shallow subtropical estuary, southwestern Florida. *Estuarine Coastal and Shelf Science* 25: 721–737. doi:10.1016/0272-7714(87)90018-7.

McRoy, C.P. 1969. Eelgrass under Arctic winter ice. *Nature* 224: 818–819. doi:10.1038/224818a0.

Maxwell, D.P., S. Falk, C.G. Trick, and N.P.A. Huner. 1994. Growth at low temperature mimics high-light acclimation in *Chlorella vulgaris*. *Plant Physiology* 105:535–543.

Maxwell, D.P., D.E. Laudenbach, and N.P.A. Huner. 1995. Redox regulation of light-harvesting complex II and *cab* mRNA abundance in *Dunaliella salina*. *Plant Physiology* 109:787–795.

Mitchell, C.A., T.W. Custer, and P.J. Zwank. 1994. Herbivory on shoalgrass by wintering redheads in Texas. *Journal of Wildlife Management* 58: 131–141. doi:10.2307/3809559.

Morgan, M.D., and C.L. Kitting. 1984. Productivity and utilization of the seagrass *Halodule wrightii* and its attached epiphytes. *Limnology and Oceanography* 29:1066–1076.

Nelson, T.A., and J.R. Waaland. 1997. Seasonality of eelgrass, epiphyte, and grazer biomass and productivity in subtidal eelgrass meadows subjected to moderate tidal amplitude. *Aquatic Botany* 56: 51–74. doi:10.1016/S0304-3770(96)01094-7.

Ohtsuka, T., H. Ito, and A. Tanaka. 1997. Conversion of chlorophyll *b* to chlorophyll *a* and the assembly of chlorophyll with apoproteins by isolated chloroplasts. *Plant Physiology* 113:137–147.

Onuf, C.P. 1996. Biomass patterns in seagrass meadows of the Laguna Madre, Texas. *Bulletin of Marine Science* 58:404–420.

Onuf, C.P. 2007. Laguna Madre. In Handley, L., Altsman, D., and DeMay, R., eds., 2007, Seagrass Status and Trends in the Northern Gulf of Mexico: 1940–2002: U.S. Geological Survey Scientific Investigations Report 2006-5287, 267 p.

Ott, J.A. 1980. Growth and production of *Posidonia oceanica* (L.) Delile. P.S.Z.N.I. *Marine Ecology* 1: 47–64. doi:10.1111/j.1439-0485.1980.tb00221.x.

Parsons, T.R., Y. Maita, and C.M. Lalli. 1984. *A manual of chemical and biological methods of seawater analysis*. New York: Pergamon Press.

Pérez, M., and J. Romero. 1992. Photosynthetic response to light and temperature of the seagrass *Cymodocea nodosa* and the prediction of its seasonality. *Aquatic Botany* 43: 51–62. doi:10.1016/0304-3770(92)90013-9.

Pirc, H. 1986. Seasonal aspects of photosynthesis in *Posidonia oceanica*: Influence of depth, temperature and light intensity. *Aquatic Botany* 26: 203–212. doi:10.1016/0304-3770(86)90021-5.

Pizarro, G.M., and V. Montecino. 1992. Primary productivity maintenance through chlorophyll *a* changes in *Elodea potamogeton* during an annual cycle. *AquaticBotany* 43: 231–248. doi:10.1016/0304-3770(92)90069-U.

Porra, R.J., W.A. Thompson, and P.E. Kriedemann. 1989. Determination of accurate extinction coefficients and simultaneous equations for assaying chlorophylls *a* and *b* extracted with four different solvents: verification of the concentration of chlorophyll standards by atomic absorption spectroscopy. *Biochimica et Biophysica Acta* 975: 384–394. doi:10.1016/S0005-2728(89)80347-0.

Powell, G.V.N., W.J. Kennworthy, and J.W. Fourqurean. 1989. Experimental evidence for nutrient limitation of seagrass growth in a tropical estuary with restricted circulation. *Bulletin of Marine Science* 44:324–340.

Pulich, W.M. Jr 1980a. Ecology of a Hypersaline Lagoon: The Laguna Madre. In *Proceedings of the Gulf of Mexico Coastal Workshop*, eds. P.L. Fore, and R.D. Peterson, Vol. FWS/OBS-80/30:103–122. Albuquerque: U.S. Fish and Wildlife Service.

Pulich, W.M. 1980b. Heavy metal accumulation by selected *Halodule wrightii* Asch. populations in the Corpus Christi Bay area. *Contributions in Marine Science* 23:89–100.

Pulich, W.M. 1982a. Edaphic factors related to shoalgrass (*Halodule wrightii* Aschers.) production. *Botanica Marina* 25:467–475.

Pulich, W.M. 1982b. Culture studies of *Halodule wrightii* Aschers. Edaphic requirements. *Botanica Marina* 25:477–482.

Pulich, W.M. 1985. Seasonal growth dynamics of *Ruppia maritima* L. sl. and *Halodule wrightii* Aschers. in southern Texas and evaluation of sediment fertility status. *Aquatic Botany* 23: 53–66. doi:10.1016/0304-3770(85)90020-8.

Pulich, W.M. 1986. Variations in leaf soluble amino acids and ammonium content in subtropical seagrasses related to stress. *Plant Physiology* 80:283–286.

Pulich, W.M. 1989. Effects of rhizosphere macronutrients and sulfide levels on the growth physiology of *Halodule wrightii* Aschers. and *Ruppia maritima* L. s.l. *Journal of Experimental Marine Biology and Ecology* 127: 69–80. doi:10.1016/0022-0981(89)90209-8.

Quammen, M.L., and C.P. Onuf. 1993. Laguna Madre: seagrass changes continue decades after salinity reduction. *Estuaries* 16: 302–310. doi:10.2307/1352503.

Rice, J.D., R.P. Trocine, and G.N. Wells. 1983. Factors influencing seagrass ecology in the Indian River Lagoon. *Florida Scientist* 46:276–286.

Rooker, J.R., S.A. Holt, M.A. Soto, and G.J. Holt. 1998a. Postsettlement patterns of habitat use by sciaenid fishes in subtropical seagrass meadows. *Estuaries* 21: 318–27. doi:10.2307/1352478.

Rooker, J.R., G.J. Holt, and S.A. Holt. 1998b. Vulnerability of newly settled red drum (*Scianops ocellatus*) to predatory fish: is early-life survival enhanced by seagrass meadows? *Marine Biology* 131: 145–151. doi:10.1007/s002270050305.

Rusnak, G.A. 1960. Sediments of Laguna Madre, Texas. In *Recent Sediments, Northwest Gulf of Mexico*, eds. F.P. Shepard, F.B. Phleger, and T.H. van Andel, 153–196. Tulsa: American Association of Petroleum Geologists.

Sand-Jensen, K. 1975. Biomass, net production and growth dynamics in an eelgrass (*Zostera marina* L.) population in Vellerup Vig, Denmark. *Freshwater Biological Laboratory* 14:185–201.

Shafer, D.J. 1999. The effects of dock shading on the seagrass *Halodule wrightii* in Perdido Bay, Alabama. *Estuaries* 22: 936–943. doi:10.2307/1353073.

Short, F.T. 1987. Effects of sediment nutrients on seagrasses: literature review and mesocosm experiment. *Aquatic Botany* 27: 41–57. doi:10.1016/0304-3770(87)90085-4.

Short, F.T., W.C. Dennison, and D.G. Capone. 1990. Phosphorus-limited growth of the subtropical seagrass *Syringodium filiforme* in carbonate sediments. *Marine Ecology Progress Series* 62: 169–174. doi:10.3354/meps062169.

Sokal, R.R., and F.J. Rohlf. 1995. Biometry. 3rd ed. Hampshire: W. H. Freeman and Company.

Solis, R.S., and G.L. Powell. 1999. Hydrography, mixing characteristics, and residence times of Gulf of Mexico estuaries. In *Biogeochemistry of Gulf of Mexico Estuaries*, eds. T.S. Bianchi, J.R. Pennock, and R. R. Twilley, 29–61. New York: John Wiley and Sons.

Solorzano, L., and J.H. Sharp. 1980. Determination of total dissolved phosphorus and particulate phosphorus in natural waters. *Limnol. Oceanogr* 25(4):754–758.

SPSS, Inc. 1993. *SPSS for Windows Base System User's Guide Release 6.0*. Chicago: SPSS, Inc.

SPSS, Inc.. 1997. *Sigma Plot 4.0 for Windows Reference Guide*. Chicago: SPSS, Inc.

Tanaka, A., Y. Yamamoto, and H. Tsuji. 1991. Formulation of chlorophyll-protein complex during greening. 2. Redistribution of chlorophyll among apoproteins. *Plant Cell Physiology* 32:195–204.

TCEQ (Texas Commission on Environmental Quality).. 2003. *Pollutant loading and dissolved oxygen dynamics in the tidal segment of the Arroyo Colorado (Draft Report)*. 68. Austin: TCEQ.

TDWR (Texas Department of Water Resources). 1983. *Laguna Madre Estuary: A Study of the Influence of Freshwater Inflows*. 270. Austin: Texas Department of Water Resources Report LP-182.

Tolan, J.M., S.A. Holt, and C.P. Onuf. 1997. Distribution and community structure of ichthyoplankton in Laguna Madre seagrass meadows: potential impact of seagrass species change. *Estuaries* 20: 450–464. doi:10.2307/1352357.

Tomasko, D.A. 1992. Variation in growth form of shoal grass (*Halodule wrightii*) due to changes in the spectral composition of light below a canopy of turtle grass (*Thalassia testudinum*). *Estuaries* 15: 214–217. doi:10.2307/1352694.

Tomasko, D.A., and K.H. Dunton. 1995. 271–278. Primary productivity in *Halodule wrightii*: a comparison of techniques based on daily carbon budgets. *Estuaries* 18. doi:10.2307/1352638.

Tunnel Jr., J.W., and F.W. Judd. Eds. 2002. The Laguna Madre of Texas and Tamaulipas. College Station: Texas A&M University Press, 346 p.

Twilley, R.R., J. Cowan, T. Miller-Way, P.A. Montagna, and B. Mortazavi. 1999. Benthic nutrient fluxes in selected estuaries in the Gulf of Mexico. In *Biogeochemistry of Gulf of Mexico Estuaries*, eds. T.S. Bianchi, J.R. Pennock, and R.R. Twilley, 163–209. New York: John Wiley and Sons.

TWQB (Texas Water Quality Board). 1975. Water Quality Segment Report for Segment No. 2491, Laguna Madre. Texas Water Quality Board Report No. WQS-14. 38 pp.

van Tussenbroek, B.I. 1994. Spatial and seasonal variability in biomass and leaf morphology of the manatee grass, *Syringodium filiforme* in a tropical coral reef lagoon. Anales del Instituto de Ciencias del Mar y Limnologia. *Universidad Nacional Autónoma de México* 21:15–22.

van Tussenbroek, B.I. 1995. *Thalassia testudinum* leaf dynamics in a Mexican Caribbean coral reef lagoon. *Marine Biology* 122: 33–40. doi:10.1007/BF00349275.

van Tussenbroek, B.I. 1998. Above- and below-ground biomass and production by *Thalassia testudinum* in a tropical reef lagoon. *Aquatic Botany* 61: 69–82. doi:10.1016/S0304-3770(98)00058-8.

Virnstein, R.W. 1982. Leaf growth of the seagrass *Halodule wrightii* photographically measured *in situ*. *Aquatic Botany* 12: 209–218. doi:10.1016/0304-3770(82)90017-1.

Ward, G.H. 1997. *Processes and trends of circulation with the Corpus Christi Bay National Estuary Program study area*. Austin: Texas Natural Resource Conservation Commission Volume CCBNEP-21.

Ward, L.A., P.A. Montagna, R.D. Kalke, and E.J. Buskey. 2000. Sublethal effects of Texas brown tide on *Streblospio benedicti* (Polychaeta) larvae. *Journal of Experimental Marine Biology and Ecology* 248: 121–129. doi:10.1016/S0022-0981(00)00157-X.

Welch, J.M., D. Rittschof, T.M. Bullock, and R.B. Forward Jr. 1997. Effects of chemical cues on settlement behavior of blue crab *Callinectus sapidus* postlarvae. *Marine Ecology Progress Series* 154: 143–153. doi:10.3354/meps154143.

Wiginton, J.R., and C. McMillan. 1979. Chlorophyll composition under controlled light conditions as related to the distribution of seagrasses in Texas and the U.S. Virgin Islands. *Aquatic Botany* 6: 171–184. doi:10.1016/0304-3770(79)90060-3.

Williams, S.L., and M.H. Ruckelshaus. 1993. Effects of nitrogen availability and herbivory on eelgrass (*Zostera marina*) and its epiphytes. *Ecology* 74: 904–918. doi:10.2307/1940815.

Woodin, M.C. 1996. Wintering ecology of redheads (*Aythya americana*) in the western Gulf of Mexico region. *Gibier Faune Sauvage, Game and Wildlife* 13:653–665.

Zieman, J.C. 1975. Seasonal variation of turtle grass, *Thalassia testudinum* König, with reference to temperature and salinity effects. *Aquatic Botany* 1: 107–123. doi:10.1016/0304-3770(75)90016-9.

Zupo, V., M.C. Buia, and L. Mazzella. 1997. A production model for *Posidonia oceanica* based on temperature. *Estuarine, Coastal and Shelf Science* 44: 483–492. doi:10.1006/ecss.1996.0137.