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**Production of the subtropical seagrass, *Halodule wrightii*
Aschers., in lower Laguna Madre, Texas**

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**PRODUCTION OF THE SUBTROPICAL
SEAGRASS, *HALODULE WRIGHTII* ASCHERS., IN
LOWER LAGUNA MADRE, TEXAS**

A Thesis

by

JOSEPH L. KOWALSKI

**Submitted to the Graduate School of the
University of Texas-Pan American
in partial fulfilment of the requirements for the degree of**

MASTER OF SCIENCE

December 1999

Major Subject: Biology

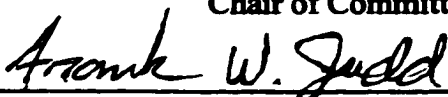
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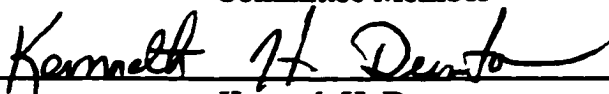
Terry C. Allison
Chair of Committee



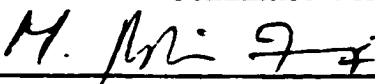
Frank W. Judd
Committee Member




Robert I. Lonard
Committee Member



Kenneth H. Dunton
Committee Member



Mohammed Farooqui
Chair of the Department of Biology



Jacob Chen
Dean of the College of Science and Engineering

December 1999

Kowalski, Joseph L., PRODUCTION OF THE SUBTROPICAL SEAGRASS, *HALODULE WRIGHTII* ASCHERS., IN LOWER LAGUNA MADRE, TEXAS. Master of Science (MS) Thesis, December 1999. 105 pp., 11 tables, 18 figures, 198 references.

The autecology of shoal grass, *Halodule wrightii* Aschers., was studied at 1.2 m depth from June 1995 to February 1997 in Lower Laguna Madre (LLM), Texas. *Halodule wrightii* in LLM received about 47% surface irradiance, but otherwise displayed lower growth rates and biomass in nutrient-poor rhizosphere and water-column environments compared to *H. wrightii* populations in other Texas estuaries. High tissue N content and low C:N ratios belied low growth dynamics. *Halodule wrightii* in LLM is probably nutrient limited. A high nutrient demand by *H. wrightii* in a nutrient-poor environment may explain, in part, its gradual displacement by *Thalassia testudinum* and *Syringodium filiforme* in LLM.

DEDICATION

This work is dedicated to my beloved wife, Nellie

ACKNOWLEDGMENTS

The compilation of this work would not have been possible without the dedicated support and friendship of my advisor, Dr. Terry C. Allison. His endeavors have made possible the logistical and financial completion of this study, and for this I am deeply appreciative. I learned a great deal about science in general and seagrass biology in particular from Dr. James E. Kaldy III, Dr. Kun-Seop Lee and Ms. Sharon Herzka. Jim, you in particular helped transform this experience from a mere scientific work to a valuable learning experience. Bust a move! Kun-Seop, thank you for all the stimulating discussions we had about seagrass biology and for the valuable comments on the thesis. I appreciate Christian Krull for being there through thick and thin, all the hours on the water and the stimulating discussions. I thank Jim White who was very helpful during the fieldwork, especially during the “clip experiment.” I thank Laurie H. Hirsch for a magnificent job processing samples. I appreciate the fellowship of Dr. Gary Marshall and Lyle Case, who were able hands on several field trips.

I am indebted to Dr. Ken Dunton for serving as an adjunct committee member, for ideas and thoughts on the “clipping problem”, and for the generous use of his lab. I thank you, Ken, for the added opportunities of working on seagrass projects beyond the scope of this work. These were invaluable learning experiences in their own right. I appreciate the extensive computational expertise and help of Susan Schonberg who assisted me in

data management and analysis. I thank Dr. Frank Judd for serving on my thesis committee and for the valuable discussions on statistical procedures and his scientific guidance. I also thank Dr. Robert Lonard for serving on my thesis committee and for his reviews and comments of this thesis and various other proposals I have written.

I offer my heartfelt appreciation to Don Hockaday, Director of The University of Texas-Pan American Coastal Studies Lab, for his assistance and the use of the lab and equipment. I am grateful to The Conrad Blutcher Institute from Texas A&M - Kingsville for providing the continuous water column and terrestrial light data. This research was funded by The Texas Higher Education Coordinating Board (Advanced Research Program Grant #003658-419) and a generous grant from The University of Texas-Pan American Faculty Research Council. I gratefully acknowledge a scholarship from The University of Texas - Pan American James-Ware-Foltz fund which was used to pay for the carbon and nitrogen elemental analysis.

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CHAPTER 1

SEAGRASS ECOLOGY AND *HALODULE WRIGHTII* ASCHERS. IN THE LAGUNA MADRE ECOSYSTEM: A LITERATURE SURVEY

Seagrass Adaptations to their Environment

Seagrasses are fully marine to estuarine flowering macrophytes capable of carrying out all of their life functions fully submersed (Dawes 1981). Arber (1920) was the first to examine seagrasses with freshwater plants and treat them as a homogenous group. Her monograph primarily focused on freshwater taxa and treats only general aspects of marine phanerogams in a single chapter. Life histories, water plant evolutionary origins, vegetative and reproductive organs of water plants in general and geographical distribution were considered. She listed four adaptations seagrasses have evolved to survive in a marine environment. These are the ability to grow and reproduce in saline waters, function normally and grow despite being completely submerged, develop a well-developed anchoring system to withstand wave action and tidal currents and carry out hydrophilous pollination and seed dispersal. Den Hartog (1977) added that each seagrass species must also be able to successfully compete with other seagrass species under more or less stable conditions. To adapt to complete submersion in a saline medium, seagrasses have evolved distinct morphological and physiological

characteristics. They have well-developed rhizomes that typically grow just beneath the substrate. From the rhizomes, vertical shoots branch which give rise to a varying number of typically blade-shaped leaves (Dawes 1981). Unlike terrestrial plants, seagrasses can take up nutrients directly from the water column through their leaves, in addition to their roots (Short and McRoy 1984), and they can use either CO_2 or HCO_3^- as a carbon source (Beer *et al.* 1977).

The Ecological Significance of Seagrasses

Temperate and tropical seagrasses often provide much of the fixed carbon used to drive estuarine secondary productivity. Despite the small area where seagrasses are found they are remarkably productive, generating large quantities of fixed carbon in their leaves, roots and rhizomes. Zieman and Wetzel (1980) reported productivity values of 500-1000 g C m⁻² year⁻¹ as typical of seagrasses. These values are comparable to some cultivated crops (Westlake 1963). High seagrass productivity drives direct and indirect (microbial) trophic structure of estuaries (Dawes 1981). Most seagrass carbon is made available to estuarine food webs as detritus (Odum *et al.* 1973; Phillips 1980).

Additionally, a large portion may be flushed out to sea and utilized in the nearshore zone (Fry and Parker 1979; Thresher *et al.* 1992). The importance of seagrass detritus to commercially important fisheries was suggested early this century by Peterson (1918) and detrital pathways and compounds have recently been studied (Tenore 1977; Peduzzi and Herndl 1991; Thresher *et al.* 1992; Opsahl and Benner 1993). Bacteria colonize senescent and detrital leaves and begin to degrade the plant material. The bacteria are subsequently

digested as the blade material passes through the guts of detrital grazers. Subsequent fecal material is then recolonized and the cycle begins anew until the blade is completely broken down (Fenchel 1977; Phillips 1978; Zieman and Zieman 1989).

Herbivores, such as green turtles, redhead and pintail ducks and manatees feed directly on living seagrasses, principally the root/rhizome fraction (Bjorndal 1980; McRoy and Helfferich 1980). McRoy and Helfferich (1980) cited seagrasses as a direct food source for numerous marine animals, including juvenile shrimp, fish and sea urchins which feed directly on the blades. Recent work has demonstrated that the seagrass - herbivore relationship may be more common than previously thought (Valentine *et al.* 1997) and that herbivory can even stimulate seagrass productivity (Valentine and Heck 1999).

Morgan and Kitting (1984), in an intensive study of seagrass leaf and epiphyte productivity and utilization of *H. wrightii* in Corpus Christi Bay, found many commercially important animals do not directly consume living seagrass tissue, but subsist mainly on its epiphytes, which can account for 50% of above-ground biomass. The canopy structure of seagrasses provides habitat for small and young animals, such as amphipods, isopods, polychaete annelids, shrimp, crabs and fish, the latter of which are particularly important commercial fauna (McMahan 1968; Kikuchi and Pérès 1977; Zieman and Zieman 1989; Tolan *et al.* 1997; Rooker *et al.* 1998). These animals commonly forage on epiphytic algae and epifauna which use the seagrass blades as a substrate (Phillips 1980; Morgan and Kitting 1984). Secondary production and diversity

is significantly greater in seagrass beds than in surrounding bare subtidal bottom habitats (Fredette *et al.* 1990; Corbisier 1994).

Seagrass leaves baffle and trap material suspended in the water column. This material is both inorganic, which is derived from terrestrial runoff, particulate organic matter (detritus) and phytoplankton. Seagrass leaves hinder sediment resuspension while the roots and rhizomes stabilize the sediments. Without the baffling and trapping effect of seagrass leaves, suspended materials are easily maintained in the water column, or resuspended, by wind-driven and tidal currents and wave action (Short and Short 1984; Fonseca and Cahalan 1992; Brown and Kraus 1997). Thus, seagrasses clear the water, provide shelter and produce diversity of habitat in what would otherwise be a structureless, monotypic feature (Phillips 1980). As a result, transplantation of seagrasses has been successfully attempted to recreate and restore rich habitat that improves water quality and biotic integrity (Thorhaug 1974; Fonseca *et al.* 1985; Fonseca *et al.* 1996a, b; Hammerstrom *et al.* 1998).

Seagrass Decline

Seagrasses require light to carry out photosynthesis; however, light availability for seagrass productivity is dependent on water quality and transparency (Dennison *et al.* 1993). There is a direct correlation between human encroachment and negative impact on water quality and productivity by seagrasses in shallow coastal waters with the resultant loss of seagrass habitat (Shepherd *et al.* 1989; Short *et al.* 1993; Dennison *et al.* 1993; Lapointe *et al.* 1994). As human populations continue to populate coastal areas, so will

degradation of these shallow habitats (Phillips 1978; Orth 1983). The two most cited anthropogenic agents involved in water quality affecting the seagrass environment are dredging and excess nutrient input. Wastewater effluent (urban, agricultural and industrial), dredging and disposal of dredged materials cause deterioration of water quality (Onuf 1994a; Chisholm *et al.* 1997). Reduced light availability for photosynthesis has caused direct and indirect mass mortality and structural change to seagrass populations worldwide (Thayer *et al.* 1975; Phillips 1978; Vant 1991; Dennison *et al.* 1993; Lapointe *et al.* 1994).

Australia, which possess the largest seagrass beds in the world, has lost over 45,000 hectares from as early as 1960 (Cambridge and McComb 1984; Walker and McComb 1992). Dredging and sediment loading effects on seagrass leaves have been implicated in five cases worldwide by Walker and McComb (1992). Giesen *et al.* (1990) attributed eutrophication and loss of almost all (>15,000 ha) *Zostera* beds from the Dutch Wadden Sea to excess nutrient input and dredging effects. Loss of a *Zostera* bed in England was caused by smothering by the epiphytic alga *Enteromorpha radiata* (den Hartog 1994).

In the United States, Chesapeake and San Francisco Bays have suffered severe loss of seagrass meadows with serious negative implications for commercially important species (Orth 1977, 1983; Zimmerman *et al.* 1991; Dennison *et al.* 1993). In both bays, the primary suspect of decline was increased light attenuation of the water column as a result of sediment resuspension due to dredging and phytoplankton blooms from nutrient loading (Dennison *et al.* 1993). Seagrass communities of Florida Bay have experienced a

large die-off over the past three decades with associated declines in commercial and sport fisheries. Proximate causes are proposed to be decreased freshwater flow and nutrient loading (Lapointe *et al.* 1994; Thayer *et al.* 1994). Effects of the die-off have led to increased resuspension of sediments and algal blooms, both of which attenuate light. Nutrient-rich effluent and runoff are prime causes promoting algal blooms and epiphyte loading of seagrass blades, both of which absorb, scatter and diffuse light available to seagrasses (Orth 1983). Recent algal blooms in New York coastal waters have negatively affected seagrass depth distribution, biomass and density (Dennison 1991).

Since June 1990, the Upper Laguna Madre (ULM), Texas, has periodically endured a large-scale phytoplanktonic bloom, a brown tide named *Aureoumbra lagunensis*, (Stockwell *et al.* 1993; DeYoe *et al.* 1997) which has degraded the underwater light environment and caused decreases in seagrass biomass and productivity (Dunton 1994, Onuf 1996a). Lower Laguna Madre (LLM), Texas, has generally been spared the manifestation of this bloom, although it has probably reached as far south as Port Isabel (located at the southern end of the basin) concurrent with the passing of northern cold fronts (Kaldy 1997). Maintenance dredging and open disposal of dredged material have been cited as the chief probable causes leading to decreased light availability for photosynthesis and the resultant loss of seagrass habitat in Laguna Madre (Merkord 1978; Onuf 1994a). Onuf (1994a) concluded that sediment resuspension, caused by wind-generated wave and tidal currents, were responsible for decreased light levels 10 months after dredging ceased in LLM. Where dredging was conducted nearby,

light attenuation was higher than normal which resulted in decreased productivity by *Thalassia testudinum* in Redfish Bay, Texas (Odum 1963).

Areal cover of *Halodule wrightii* in ULM has increased, but has declined 230 km² (60 percent) in LLM. *Thalassia testudinum* and *S. filiforme* have increased in areal coverage in LLM at the expense of *H. wrightii* (Quammen and Onuf 1993). If populations of *H. wrightii* continue to decline, a significant food resource for overwintering populations of waterfowl, principally redheads and pintails, will become increasingly threatened, as well as nursery habitat for juvenile fish and commercially important invertebrates (Mitchell *et al.* 1994; Michot and Chadwick 1994 Tolan *et al.* 1997; Welch *et al.* 1997; Rooker *et al.* 1998).

Seagrass losses in Texas have not been as severe or widespread as those reported for Chesapeake and San Francisco Bays; however, the Galveston Bay system has lost almost all (over 20 km²) of its seagrass beds within the past 40 years (Pulich and White 1991). Pulich and White (1991) attributed the losses to subsidence, erosion, dredge-and-fill on seagrass beds for commercial development and wastewater discharge, all of which lead to degradation of the underwater light environment.

The Laguna Madre Ecosystem

The Laguna Madre is a bar-built barrier estuary which formed approximately 4500 years ago (Rusnak 1960). It is the southernmost of Texas estuaries and stretches approximately 240 km, from near the Rio Grande River, north to the Nueces Estuary (Figure 1-1). The Laguna Madre is subdivided into upper (ULM) and lower (LLM)

portions, separated effectively by an aeolian sand sheet which is covered by a few centimeters of water only during high water periods. The sole link between ULM and LLM is the Gulf Intracoastal Waterway (GIWW). The northernmost extent of the LLM begins at the southern edge of the Kenedy Land Cut (also known as Saltillo Flats) and terminates at South Bay, near the mouth of the Rio Grande, a distance of about 90 km. LLM averages eight km in width with a mean depth of 1.2 m, although west of the GIWW depths to about three meters have been reported by Onuf (1994b). Five species of seagrass inhabit LLM: *Halodule wrightii*, *Thalassia testudinum*, *Syringodium filiforme*, *Halophila englemannii* and *Ruppia maritima*. *Halodule wrightii* is the most abundant species within the Laguna Madre as a whole, but *S. filiforme* is dominant in LLM (Quammen and Onuf 1993). *Ruppia maritima* and *H. englemannii* are locally abundant and typically occur in patches with *H. wrightii* (Pulich 1980a).

The Laguna Madre is still in relatively pristine condition compared to the estuarine waters of Florida and areas in Texas where seagrass habitat has been lost under anthropogenic stresses. However, even Laguna Madre has experienced human-induced changes and losses in its seagrass beds. Temporal alterations in climate, coupled with change in basin configuration (channelizing) have led to decreased salinities in Laguna Madre. As a result, successional change and shifts in seagrass species dominance and composition has occurred (Quammen and Onuf 1993). Change has been particularly acute in LLM. Prior to 1948, and the opening of the GIWW, salinities in the LLM frequently surpassed 40‰, with salinities of 80‰ not uncommon in shallow coves (Hedgepeth 1967). The LLM basin is enclosed by bar-built barrier islands (Padre Island

and Brazos Island) and has very restricted exchange with the Gulf of Mexico. Given the geomorphology of the basin, combined with sparse rainfall (< 70 cm yr⁻¹), low riverine drainage and strong prevailing southeasterly winds, hypersaline conditions were established. *Halodule wrightii* was the most abundant seagrass species in LLM prior to 1965 (Quammen and Onuf 1993). It is a pioneer plant (Phillips and Meñez 1988; Gallegos *et al.* 1994) and the most euryhaline of all the seagrasses found along the Texas coast (McMillan and Moseley 1967). *Thalassia testudinum*, a competitively superior species, is found in abundance only where salinities are close to that of the open ocean (Zieman and Zieman 1989; Fong and Harwell 1994). In LLM *T. testudinum* dominates areas adjacent to tidal passes and navigation channels connected with the Gulf of Mexico (Quammen and Onuf 1993). With the opening of the GIWW in 1948, exchange with waters from the Gulf of Mexico have ameliorated salinities closer to that of the open Gulf of Mexico (Quammen and Onuf 1993).

Taxonomy of the Genus *Halodule*

Although the numbers have changed over the years, seagrasses comprise 55 to 57 species worldwide which are placed in 12 genera, six families and two orders (Richardson 1995; Walters and Kiel 1996). As with all other seagrasses, *Halodule* is not a true grass (Family Poaceae), but is a flowering monocot. *Halodule* is dioecious, but reproductive structures are rarely present (den Hartog 1970). As a result, leaf width and tip morphology are commonly used to distinguish species (den Hartog 1964; Phillips *et al.* 1974). Historically, the genus *Halodule* has been placed in different families. Den

Hartog (1970), included it in the Potamogetonaceae for many years, while Tomlinson (1982) and Dahlgren *et al.* (1985) placed *Halodule* in the Cymodoceaceae. Richardson (1995) and Walters and Kiel (1996) assigned *Halodule* to the family Zannichelliaceae, but offered no references nor justification for the move. Tomlinson (1982) outlined a lucid comparison between the Cymodoceaceae and Zannichelliaceae which strongly supports the inclusion of *Halodule* into the Cymodoceaceae based on both morphologic and floristic characteristics. For this reason I follow the work of Tomlinson (1982) (Table 1-1).

Distribution of the Genus *Halodule*

Seagrasses are found at almost all latitudes, except for the high Arctic and Antarctica (Phillips 1980; Phillips and Meñez 1988). North America claims several genera of seagrasses, in both temperate and tropical latitudes. The most abundant genera of seagrasses in North America, as reported by Dawes (1981), are *Zostera*, *Thalassia*, *Phyllospadix*, *Syringodium*, *Halophila* and *Halodule*. Of these, *Zostera* and *Thalassia* are the most studied and best known. The genus *Halodule* is a pantropic to subtropic, polytypic taxon, but it is widely disjunct (Figure 1-2). Three *Halodule* species are currently recognized, *Halodule uninervis* and *H. pinifolia* from the Indo-Pacific and *H. wrightii* from the Caribbean Sea and Gulf of Mexico (Phillips *et al.* 1974; Phillips and Meñez 1988). *Halodule wrightii* occurs over a wide range of latitudes and diversity of habitats. It is found in the Gulf Stream waters of Bermuda, and as far north as the shallow, temperate waters of North Carolina (Phillips and Meñez 1988). *Halodule*

wrightii is most widely distributed in the Caribbean Sea, but is also found on the Pacific coasts of Mexico and Central America (McMillan and Phillips 1979a; Aguilar-Rosas and López-Ruelas 1985; Phillips and Meñez 1988). For many years there was a great lack of attention devoted to seagrass biology in much of South America (Phillips 1980; Dawes 1981). Recent research articles have focused on the biology and ecology of *H. wrightii*, principally from Brazil (Oliveira *et al.* 1983; 1997; Creed 1997; 1999).

Previous Studies on *Halodule wrightii*

LLM is a fertile ecological study area, because little research has been done on seagrasses there. Previous work in LLM has focused on general ecology and large-scale sampling and mapping. Early ecological works by Hedgepeth (1947), Breuer (1962) and Conover (1964) focused on general ecology and community structure. McMahan (1968) examined salinity tolerance and biomass of *Halodule wrightii* and *Syringodium filiforme* in LLM. McMillan conducted studies on the reproductive dynamics (1976, 1982, 1983), salinity and temperature tolerance (1979) and isozyme characteristics (1980) of *H. wrightii*. Merkord (1978), used aerial photography and transects to make detailed maps of seagrass distribution and abundance, while Chin (1978) mapped seagrass distribution off the mouth of the Arroyo Colorado.

Little attention has been devoted to *Halodule wrightii*, presumably because of its narrow blade widths (1 mm or less) (den Hartog 1970) and high shoot densities (>5000 m⁻²) (Tomasko and Dunton 1995) which makes it difficult to study. Dillon (1971) first reported productivity values for *H. wrightii* from North Carolina waters at 0.5 to 2.0 g C

$\text{m}^{-2} \text{ day}^{-1}$. Pulich (1980b, 1982a, 1982b, 1985, 1986, 1989) studied growth dynamics of *H. wrightii* relative to heavy metal cycling and sediment-nutrient dynamics in Corpus Christi Bay, Aransas Bay and Redfish Bay, and the upper Laguna Madre, and found the plant capable of rapid, colonizing growth of unvegetated highly reduced sediments. Mitchell (1987) found the effects of light intensity, salinity, cropping and the toxicity of the herbicide atrazine did not affect *H. wrightii* maintenance and growth. McMillan and Phillips (1979b) investigated morphological variation of *Halodule wrightii* along the Gulf of Mexico. They noted populations from turbid bays tended to have narrower leaves than populations occurring in clear waters. They suggested that variation between populations of this species is genetically controlled, but heavily influenced by local environmental conditions, such as temperature, light intensity and depth. McMillan (1980) compared nine enzyme systems using isozyme electrophoresis between populations of *Halodule* from the Gulf of Mexico (Texas) and the Indo-Pacific. His findings showed the populations are genetically different and suggest their divergence is a result of geographic isolation. In Texas, Phillips (1980) found that *H. wrightii* is more tolerant of sediment loading from dredging and cold stress, compared to the larger *Thalassia testudinum*. McMillan (1979) demonstrated the ability of *H. wrightii* to tolerate cold stress to 2 °C, and Hicks *et al.* (1998) documented survival of below-ground tissues of *H. wrightii* in temperatures to -10.6 °C in LLM. *Halodule wrightii* was not found to be adversely affected by nitrate enrichment by Burkholder *et al.* (1994) in mesocosm experiments and suggested that *H. wrightii* be used in transplant efforts because of its ability to withstand eutrophic conditions.

Morgan and Kitting (1984) determined *in situ* production rates of *Halodule wrightii* from Corpus Christi Bay using the ^{14}C method and found rates averaged about $2 \text{ mg C g}^{-1} \text{ h}^{-1}$, with leaf turnover times estimated between 34 and 37 days. They concluded that *H. wrightii* at that site was among the more productive North American seagrasses. Dunton (1990), was the first to examine *in situ* productivity of *H. wrightii* relative to light in the western Gulf of Mexico. He found leaf elongation rates were greatest from March to April in two shallow (0.4 m and 0.6 m) populations in Corpus Christi Bay. Dunton and Tomasko (1994) studied *in situ* photosynthesis versus irradiance (P vs I) parameters of *H. wrightii* with oxygen evolution chambers to determine whole-plant photosynthesis. They found laboratory-derived results of P vs I incubations overestimated maximum depth limits and areal primary productivity rates. Dunton (1994), in a five-year study of *H. wrightii* productivity and biomass from ULM, found suppressed shoot elongation rates as a result of decreased light levels caused by a "brown tide," named *Aureoumbra lagunensis* (DeYoe *et al.* 1997), although a seasonal rhythm of leaf growth persisted despite the greater light attenuation. He concluded biomass declines (nearly 50%) were more sensitive than leaf elongation rates to stresses imposed by lowered light levels, which dropped two-fold in ULM as a result of the brown tide bloom. Dunton (1994) found the maximum depth limit of *H. wrightii* to be 0.6 m and 1.3 m in San Antonio Bay and ULM, respectively, and that a quantum flux of 18% surface irradiance (SI) was insufficient to maintain a positive carbon balance for *H. wrightii*. Tomasko and Dunton (1995) conducted an extensive study on productivity, productivity measurement techniques, seasonal biomass and modeling of carbon budgets on *H. wrightii*, all relative to minimum

underwater light requirements in ULM. They found the clip-harvest method of productivity measurement seriously underestimated leaf productivity in *H. wrightii*, but that this method could be used when corrected for by inclusion of biomass and leaf turnover measurements in productivity calculations. Czerny and Dunton (1995) investigated effects of *in situ* light reduction on *H. wrightii* and *Thalassia testudinum* productivity, biomass, blade chlorophyll and sediment water ammonium concentrations in Corpus Christi Bay. Their experimental manipulation of underwater light showed *H. wrightii* under 10% and 14% SI died after 10 months of treatment and confirmed the finding that *H. wrightii* requires a minimum 18% SI for survival. Dunton (1996) found no differences in photosynthesis vs irradiance characteristics, blade chlorophyll content, root to shoot ratios and nutrient availability in *H. wrightii* from San Antonio Bay, Corpus Christi Bay and ULM, despite marked differences in salinity, dissolved inorganic nitrogen concentrations, and underwater light between basins. These data also suggest the inability of *H. wrightii* to manipulate its photosynthetic apparatus to specialize in a particular habitat.

Burkholder *et al.* (1994) demonstrated *Halodule wrightii* can proliferate under high levels (10 μ M) of nitrate enrichment. Creed (1997) showed 9 populations of *H. wrightii* from Rio de Janeiro, Brazil, were highly variable in shoot and leaf morphology and number, rhizome diameter and root density. He suggested genetic differences between populations could be responsible for the variation. These studies collectively demonstrate that *H. wrightii* is capable of wide phenotypic and genotypic plasticity among and within coastal waters and is tolerant of wide ecological conditions and

anthropogenic perturbations. It is not surprising that *H. wrightii* has been ascribed the role of colonizing species capable of growing in a wide range of habitats.

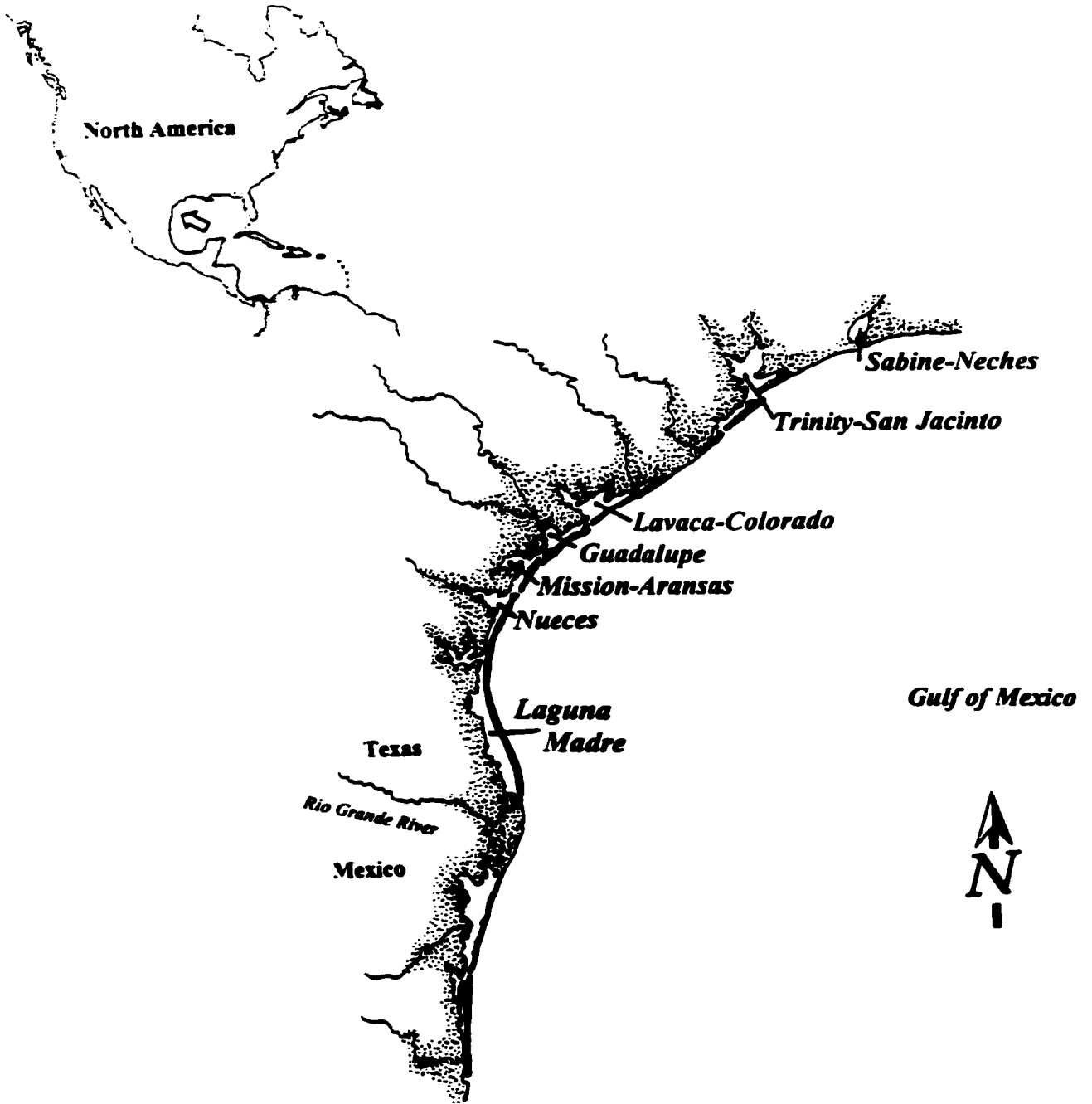


Figure 1-1. Map showing the location of the Laguna Madre of Texas in relation to other major Texas estuaries.

Table 1-1. Taxonomic standing of *Halodule wrightii* after the classification of Tomlinson (1982).

Category	Taxon
Kingdom	Plantae
Division	Anthophyta
Class	Monocotyledoneae
Order	Najadales
Family	Cymodoceaceae
Genus	<i>Halodule</i>
Species	<i>H. wrightii</i>

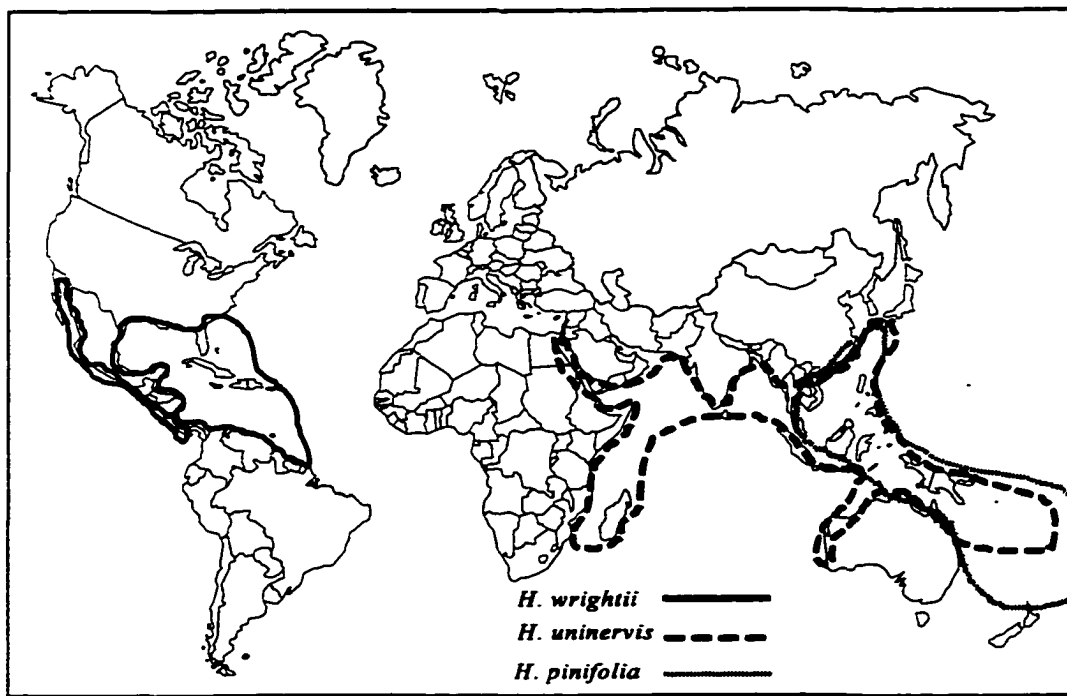


Figure 1-2. Worldwide distribution of the genus *Halodule* (after Phillips and Meñez 1988).

CHAPTER 2
SHOOT PRODUCTION AND SEASONAL BIOMASS OF
HALODULE WRIGHTII ASCHERS. IN RELATION TO
UNDERWATER LIGHT, LOWER LAGUNA MADRE, TEXAS

Introduction

There are seven major estuarine systems along 2290 km of Texas estuarine shoreline (Diener 1975; Figure 1-1). The ecological characteristics of each estuary along the Texas coast are controlled by local environmental conditions, such as precipitation and evaporation rates, salinity and proximity to riverine freshwater inflow; therefore, each estuary is ecologically unique (Armstrong 1987; Longley 1994; Dunton 1996). The Laguna Madre, the southernmost of Texas estuarine systems, is also the largest in surface area with about 214,545 ha at mean water level (Armstrong 1987). The Laguna Madre, divided into upper (ULM) and lower (LLM) portions, is situated adjacent to large agricultural and rangeland areas to the east and the Padre Island National Seashore to the west, thus, it is probably the least urbanized of Texas estuaries (Longley 1994). Seagrasses cover more than 75% of the bottom of the entire Laguna Madre, with *H. wrightii* responsible for nearly one-half of the coverage (Onuf 1996b). Seagrass abundance has been positively correlated with more than one-half the commercial finfish

harvest taken from its waters (Hedgepeth 1947). It is not surprising that the Laguna Madre has been responsible for 2.6 billion dollars in revenue to the state of Texas from sport and commercial fisheries (Fesenmaier *et al.* 1987).

Halodule wrightii (shoal grass) is a critical species in maintaining the unique ecological characteristics that define ULM and LLM where seagrasses are responsible for fueling heterotrophic activity in the system (Ziegler and Benner 1998). Like all seagrasses, *H. wrightii* fills the ecological roles of carbon producer and nursery habitat provider (Chapter 1). Its fate has been closely tied to that of recreationally important sciaenid fish species (Rooker *et al.* 1998), juvenile commercial species (Tolan *et al.* 1997; Welch *et al.* 1997), and duck species which use the rhizome and root portion of *H. wrightii* (Michot and Chadwick 1994; Mitchell *et al.* 1994; Woodin 1996). Consequently, a detailed understanding of shoal grass biology and ecology is critical to our understanding of the workings of LLM as an ecological unit, especially since differences between estuaries has been documented (Dunton 1996) and gradual change in LLM system dynamics has been documented and is predicted to continue (Quammen and Onuf 1993; Tolan *et al.* 1997).

Light is the most critical abiotic factor controlling the growth of seagrasses, when temperature and nutrients are not limiting (Short 1991; Dring 1992; Dunton 1994). The quantity of underwater light regulates plant density, depth distribution and productivity (Backman and Barilotti 1976; Zimmerman and Alberte 1991). Light is intimately tied to seagrass productivity, but few long-term *in situ* investigations have focused on the

seagrass-light relationship. This is especially true in LLM where in only the past three years have workers begun to explore this relationship (Herzka 1996; Kaldy 1997).

Historically, underwater light was quantified relative to Secchi disk readings, but Secchi disk measures light penetration not underwater irradiance. Estuaries commonly contain large amounts of organic matter which can add "color" (gelbstoff) and change Secchi disk readings. Despite the fact that the wavelengths of light visible to the human eye are almost identical to the photosynthetically active radiation (PAR) ($\approx 400\text{-}700\text{ nm}$) used by plants for photosynthesis, the difference between what the human eye perceives and the amount of PAR plants receive can be significant (Dennison 1991). Additionally, Secchi disk readings are instantaneous and, unless monitored constantly, can lead to erroneous assumptions about the underwater light environment to which the plant is exposed.

Continuous long-term underwater measurement of PAR is available and makes possible an understanding between the relationship of PAR and seagrass productivity (Dunton 1994; 1996; Czerny and Dunton 1995; Lee and Dunton 1996; Herzka and Dunton 1997; Kaldy 1997). Considering the importance of carbon fixation by marine macrophytes in driving trophic food levels in marine ecosystems, seagrass productivity and seasonal biomass dynamics in relation to underwater light should be examined. Because there is no long-term (seasonal) productivity and biomass studies on *Halodule wrightii* in LLM, especially in relation to its underwater light environment, I undertook a study of these basic parameters. Furthermore, because seagrasses have been shown to alter chlorophyll concentration in relation to changes in available light (Wiginton and

McMillan 1979; Dennison 1991; Czerny and Dunton 1995). I monitored seasonal changes in chlorophyll concentration. I hypothesized that *H. wrightii* shoot production, biomass dynamics and response to underwater PAR from LLM would be different from ULM because of between-basin differences. Although I did not sample from ULM, I compared my results to recent studies by Dunton (1990; 1994; 1996), Czerny and Dunton (1995) and Tomasko and Dunton (1995) on the biology of *H. wrightii*. The objectives of this study were to:

- 1) determine shoot production over a 21 month period,
- 2) monitor biomass patterns over a 21 month period,
- 3) examine the relationship between biomass and leaf production, and
- 4) monitor chlorophyll concentrations and chlorophyll *a:b* ratios as they relate to shoot production, seasonal biomass and underwater light.

Materials and Methods

Study Site

Field studies were conducted in the LLM, approximately 10 km north of Brazos Santiago Pass. The study site was situated about 500 m west of channel marker 107 (hereafter referred to as LLM 107) of the GIWW near the lower depth limit (about 1.2 m) of *Halodule wrightii* in LLM (Figure 2-1). The site was exposed to a fetch of about 5 km from the southeast where winds of 6-12 m sec⁻¹ (13-27 miles hour⁻¹) predominate for one-half of the year (Brown and Kraus 1997). Astronomical tides are about 20 cm in the Laguna Madre (Hedgepeth 1947), but strong atmospheric conditions (winds) caused

water levels to vary between 1.6 to 0.9 m at the study site. Northerly fronts, generally starting in October and lasting through April, can change wind speed and direction. During the 20% of the year associated with fronts, wind speeds can reach 12-17 m sec⁻¹. Current speed in the vicinity of LLM 107 is less than 10 cm sec⁻¹ for > 80% of the year (Brown and Kraus 1997). The study site was located within U.S. Army Corps of Engineers (USACOE) disposal area 234, but the exact age of the sediments at LLM 107 is not exactly known because the section dredged does not necessarily receive its own disposal. However, USACOE records over the past 20 years indicate dredging occurred in immediate vicinity of LLM 107 during the years 1979, 1981, 1983, 1985, 1987, 1989, 1991, and 1994 (Neil McLellan, USACOE, personal communication).

Water Column Physical and Chemical Measurements

Water temperature, salinity and depth were recorded with every visit to the study site using a bulb thermometer, hand-held refractometer and white PVC-pipe marked with graduations ("precision depth recorder"), respectively. However, the Conrad Blucher Institute for Surveying and Science at Texas A&M University - Corpus Christi operated an *in situ* continuous-monitoring platform (FIX 1; 26° 10' 45.2" N by 97° 15' 36.2") for water column measurements located about 2 km northwest of LLM 107 during the duration of this study. Because of the accuracy and precision of its equipment and continuous *in situ* measurements, I present their data, kindly supplied, for water column temperature, salinity, chlorophyll *a*, and surface photosynthetically active radiation (PAR). Technical details concerning water column sampling equipment deployed on FIX

1 are provided in Table 2-1 (for a full description see Brown and Kraus 1997). Water column total dissolved inorganic nitrogen ($\text{DIN} = \text{NO}_3^- + \text{NO}_2^- + \text{NH}_4^+$) values were collected monthly from November 1995 to November 1996. Samples were stored on ice in the field and during transport and frozen in the laboratory until processing. Four replicate samples were analyzed colorimetrically according to Parsons *et al.* (1984).

Underwater Light Measurements

Continuous underwater photon flux density (PFD) was measured using a LI-COR LI-193SA spherical (4π) quantum sensor providing input to a LI-1000 datalogger (LI-COR Inc., Lincoln, Nebraska, USA). The datalogger was placed in a weighted, clear polycarbonate housing (Ikelite, Model 5910, Indianapolis, Indiana, USA) and wired to a sensor cable through a molded underwater connector. The underwater sensor was positioned 25 to 30 cm above the sediment on a PVC pole, at canopy level, and covered by a clear plastic bag to protect the sensor surface from encrusting organisms. Results of measurements of PFD with and without the bag have shown effects of the bag to be insignificant (Ken Dunton, personal communication). The bag was changed with each sampling trip (not greater than three weeks in summer and six weeks in winter) to minimize fouling. The datalogger housing was partially buried to minimize fouling and reduce the chance of discovery by fishermen. Instantaneous PFD was measured at one minute intervals and integrated hourly.

Coincident measurements of incident surface PFD was measured from FIX 1 using a LI-190SA terrestrial quantum sensor (2π) mounted above the platform and wired

to a LI-COR datalogger. Surface PFD was initially collected from the roof of a land station (The University of Texas - Pan American Coastal Studies Laboratory, South Padre Island, TX) from August 1994 to November 1995. However, these data were called into question as a result of suspected structural interference which may have resulted in the logging of lower than actual values. Thus, this data set was not used with the exception of the period 2 September to 20 October 1995 for reasons explained in the results. PFD was recorded as $\mu\text{mol m}^{-2} \text{s}^{-1}$ and downloaded on a personal computer for analysis. Data were transformed when necessary to $\text{mol m}^{-2} \text{day}^{-1}$, or $\text{mol m}^{-2} \text{month}^{-1}$ for statistical analysis. Attenuation of light (k) was calculated using the Bougert-Lambert law as used by McPherson and Miller (1987) and calculated as follows in Equation 1:

$$k = \frac{\ln(I_0/I_z)}{z} \quad (1)$$

where I_0 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}) (Kirk 1983). All sensors were calibrated at the factory and were accurate to $\pm 5\%$, traceable to National Bureau of Standards, with a precision of $\pm 0.01 \mu\text{mol photons m}^{-2} \text{s}^{-1}$.

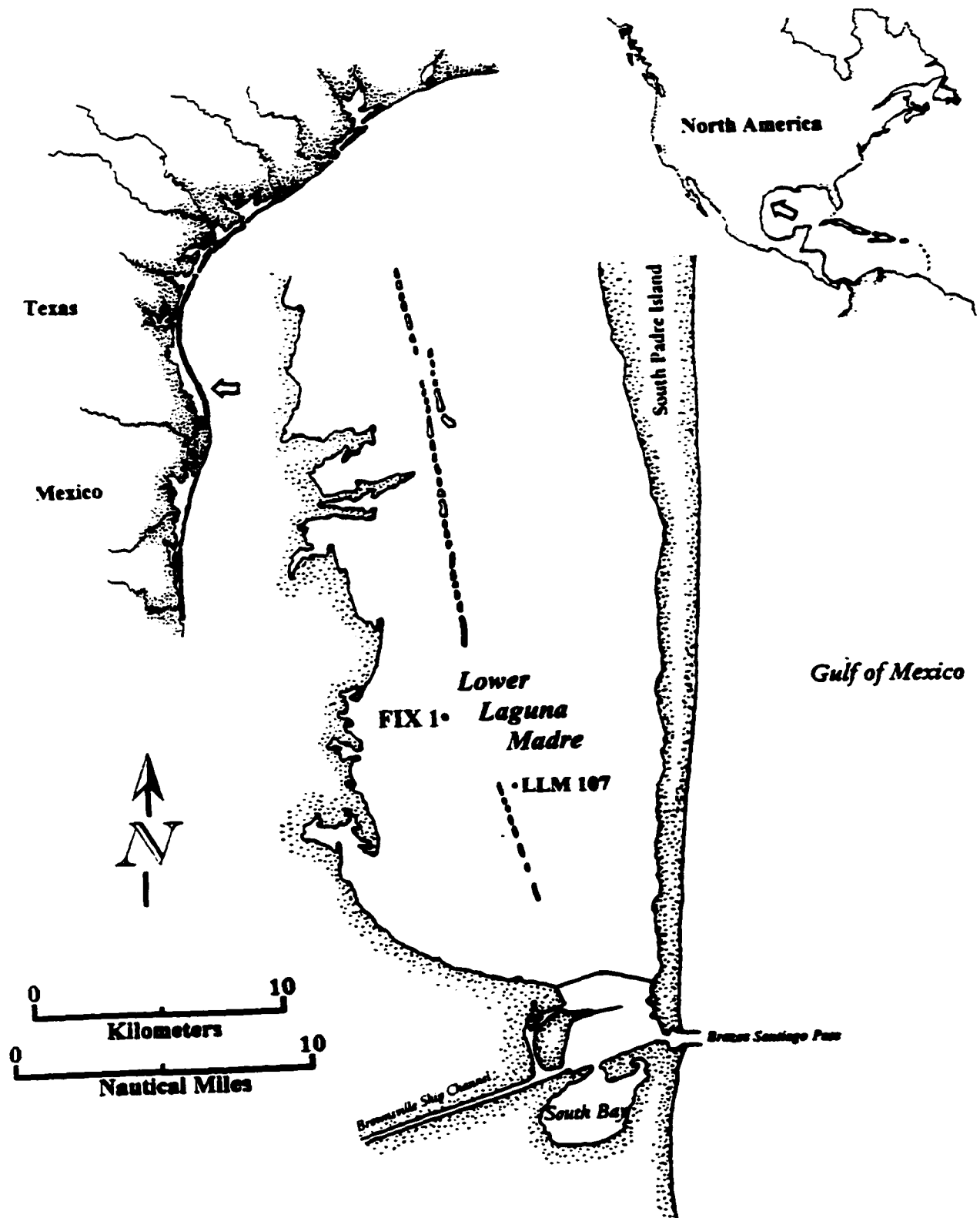


Figure 2-1. Detail of Lower Laguna Madre study area showing the location of the study site (LLM 107) and FIX 1.

Table 2-1. Water column parameters and equipment used on FIX 1 (after Brown and Kraus 1997). Platform was located approximately 2 km north of LLM 107. Data were recorded every 2 minutes with both instruments. Maintenance of equipment was weekly, weather permitting.

Water Column Parameter	Instrument
water temperature, salinity	H2O ^o Water Quality Multiprobe, Hydrolab ^o Corp. Austin, TX, USA
chlorophyll <i>a</i>	Aquatracka III Fluorometer, Chelsea Instruments, Surrey, UK

Sediment Parameters

Sediment samples for grain size and organic content were collected twice, during November 1996 and November 1997, using six replicate 60 mL modified syringe coring devices. Sediment grain size was analyzed for sand to silt to clay ratios according to the method of Folk (1964) which uses settling velocities of the size fractions to determine the percentages of each fraction based on weight. Sediment organic content was estimated using four replicate samples collected in February and November 1996. Organic content was determined as a percentage by drying samples to a constant weight and combusting at 500 °C for three hours. Porewater ammonium (NH_4^+) was sampled every three months from November 1996 to November 1997 using a modified 60 mL syringe corer ($n = 4$). Samples were placed in tightly sealed bags, stored on ice in the field and during transport and frozen in the lab before analysis. Porewater was extracted by centrifugation of thawed samples and analyzed for NH_4^+ according to the methods of Parsons *et al.* (1984).

Biomass, Shoot Density and Leaf Length Measurements

Four replicate biomass cores were randomly taken weekly to monthly where grass cover appeared uniform and dense. Cores were pounded 15 to 20 cm into the sediment to insure inclusion of all rhizome and most root material. Samples were washed of sediments through a 1 mm sieve immediately upon return to the lab and stored in zippered plastic bags and refrigerated until processing.

Halodule wrightii possesses basically the same architecture as other Laguna Madre seagrasses, with roots, horizontal rhizomes (long shoots), vertical shoots (short

shoots), and leaves. However, because of the small size of *H. wrightii* structures and the subsequent difficulty in separation of these structures, I consider all roots, rhizomes and nonphotosynthetic shoots, white to tan in color, collectively as below-ground biomass. All photosynthetic tissue is referred to as above-ground biomass.

In the laboratory, shoots were cut from rhizomes where tissue changed from green (photosynthetic) to white or tan, and the number of shoots per core were counted to determine shoot density (shoots m⁻²). Leaf length of all leaves per shoot was determined by measuring from where shoots were cut basally to the tips of leaves for samples collected from June 1995 to July 1996. Leaf samples for all sample dates were cleaned of epiphytic material by gently scraping with a scalpel. This process removes >90% of epiphytes at low density (Borum *et al.* 1984). Processed samples were dried at 60°C to a constant dry weight and weighed to the nearest 0.001 g. Below-ground to above-ground biomass ratios (B:A) were calculated from dried and weighed samples. Results are expressed as dry weight (dw) biomass (g) of above-ground, below-ground and total biomass and total biomass per unit area (g dw m⁻²).

Shoot Production and Leaf Elongation Measurements

Shoot production is defined as production of new leaf biomass per shoot per unit of time, while leaf elongation is the linear growth of new leaf tissue per shoot per unit of time. Measurements of shoot production and leaf elongation were made using a modified leaf-clipping technique described by Dunton (1990). A monotypic stand of *Halodule wrightii* that appeared uniformly distributed and dense was chosen for clipping on weekly

to monthly intervals. An area of about 30 by 30 cm was marked off and clipped approximately two to three cm above the sediment. A mean value of the height of remaining shoot stubble (termed initial clip height) was determined by harvesting one core from the clipped area and measuring the lengths of 10 to 20 clipped shoots. Clipped shoots were allowed to regrow over one to three week (spring and summer) or four to six week (fall and winter) intervals. Four replicate nine cm diameter cores from within the clipped areas were harvested after each regrowth period.

Clipped shoots were measured for leaf length, scraped of epiphytes and dried as previously described. Lengths of all leaves per shoot were measured and all measured leaves per core were pooled for an average length of all regrown leaves. The average initial clip height value recorded from the previous trip was subtracted from the average length of regrown leaves and divided by the time interval allowed for regrowth (Equation 2). Results for leaf elongation are expressed as mm day⁻¹.

$$\text{Leaf Elongation} = \frac{\text{mean regrown leaf length} - \text{initially clipped shoots (stubble length)}}{\text{time allowed for regrowth}} \quad (2)$$

Shoot production was calculated by obtaining a leaf biomass to leaf length ratio multiplied by the mean stubble length (measured at clipping) divided by the regrowth period, divided by the number of shoots per core (equation 3). This method accounts for the old growth leaf biomass remaining after clipping. Results are expressed as mg shoot⁻¹ day⁻¹.

$$\frac{(\bar{x} \text{ clip length}) (\text{dry weight})}{(\bar{x} \text{ regrown leaf length per core})(\text{regrowth time})(\# \text{ shoots per core})} \quad (3)$$

Areal production was determined by multiplying shoot production by shoot density m^{-2} and is expressed as $\text{g m}^{-2} \text{ day}^{-1}$. Monthly leaf turnover rates were calculated by dividing the above-ground biomass by monthly areal productivity estimates.

Elemental Analyses

Two replicate samples of regrown clipped leaves, leaf biomass and below-ground tissue were analyzed for carbon (C) and nitrogen (N) content using a Carlo-Erba Elemental Analyzer EA 1108. For each sample, one to three mg of finely-ground tissue was combusted at 1020 °C in a tin (Sn) container. Biomass samples (above- and below-ground) were analyzed from June, August and November 1995 and February 1996. Assays for regrown clipped leaves were made for June, August and November 1995; February, May, August and December 1996 and February 1997. Results are presented as percent C and N content and C:N molar ratios for all samples. Monthly and annual carbon budgets were calculated by numerical summation from daily rates. Annual rates were summed from monthly estimates.

Blade Chlorophyll Analysis

Leaves were collected monthly for chlorophyll concentrations. Leaf material was kept on ice immediately after collection and frozen in the lab until processing.

Approximately 10 to 15 mg of wet leaf material was immersed in 5 mL of N, N-dimethylformamide (DMF) in glass screw-top tubes. Before immersion in DMF, blades were gently scraped with a scalpel to remove epiphytes. Six replicate samples were made and placed in the dark at room temperature ($\approx 25^{\circ}\text{C}$) for 48 to 72 hours. Samples were analyzed on a Shimadzu 160 UV spectrophotometer at 664 nm and 647 nm. A DMF blank analyzed at 750 nm was used to correct for turbidity. Absorbances were calculated according to the equations of Porra *et al.* (1989). Results were expressed as mg chlorophyll g^{-1} dw.

Statistical Analysis

Statistical analyses were performed on a personal computer using a general linear model procedure (SPSS, Inc. 1993, 1997). Alpha was set at 0.05 for all statistical tests. 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. Parametric one-way ANOVAs were used to test for significant differences in shoot elongation, biomass and chlorophyll concentrations among sampling dates. Where significant differences were observed ($p < 0.05$), Student-Newman-Keuls (SNK) multiple comparison tests were used to determine significant differences between sampling dates (Sokal and Rohlf 1995). Correlation and regression analyses, as well as *t*-tests were used to test for significant differences ($p < 0.05$) between light and blade chlorophyll

concentration and between shoot growth and shoot elongation. Data points in figures, unless stated otherwise, are presented as means \pm 1 standard error (SE).

Results

Physical and Chemical Parameters

Water temperature varied greatly and was clearly seasonal over the 21 month study period (Figure 2-2A). Highest mean values recorded during summer months were between 31 and 32 °C. Lowest temperatures occurred during winter with means ranging between 13 and 17 °C. Short-term periods (two to three days) of water temperatures below 10 °C were recorded during January and February 1996 (6.47 and 4.96 °C, respectively), and December 1996 and January 1997 (5.05 and 3.14 °C, respectively), attendant with the passage of cold fronts. Periods of greatest precipitation in South Texas during the study period were in late summer and fall (NOAA 1997; Figure 2-2B) and salinity lows generally coincided with peak precipitation periods. Salinity showed seasonal peaks in summer with values between 36 and 38 ‰ which dropped during the fall and early winter of 1995 to between 24 and 26 ‰ (Figure 2-2C).

Mean water column chlorophyll *a* concentrations were generally low with values around 1 $\mu\text{g L}^{-1}$, or lower for summer and early fall months. However, increases between 1 and 5 $\mu\text{g L}^{-1}$ were recorded during late fall and winter, coincident with the passage of northerly cold fronts (Figure 2-3A). No attempt was made to determine the taxonomic composition of the phytoplankton measured, but the bulk of the biomass measured is attributed to a recently named chrysophyte (*Aureoumbra lagunensis*, DeYoe *et al.* 1997)

responsible for a “brown tide” from the ULM which was advected to the LLM as a result of northerly winds (Brown and Kraus 1997). Water column $\text{NO}_2^- + \text{NO}_3^-$ and NH_4^+ was low ($< 3 \mu\text{M}$) during the entire sampling period and significantly different by month (Table 2-2). Most months had values of $1 \mu\text{M}$ or less with November 1995 about two-fold greater than all other months sampled (Figure 2-3B, 2-3C).

Sand was the dominant sediment size class at LLM 107 at almost 70% of the total, followed by nearly equal percentages of silt, clay and shell rubble (Figure 2-4A). A non-parametric test between the two sample dates for sediment grain size showed significant differences among sand, rubble and clay fractions, but not silt (Table 2-3). Porewater NH_4^+ concentrations were well below $100 \mu\text{M}$ for all months sampled. There were significant two to three-fold differences between spring and summer months compared to late summer and late fall (Table 2-2; Figure 2-4B). Percent organic content was about 1% and not significantly different between samples collected in February and November 1996 (Table 2-3).

Surface PFD was collected from FIX 1 between 21 November 1995 to 13 February 1997, and from 21 June to the end of October 1997. Because of missing surface PFD data prior to 21 November 1995 and the 5 month gap in the data set from 14 February to 20 June 1997, I utilized the 365 day period between 1 December 1995 and 30 November 1996. There was a clear seasonal pattern in surface PFD with highest daily means ($>60 \text{ mol m}^{-2} \text{ d}^{-1}$) occurring during the summer months (June, July and August) of 1996. Lowest daily means were between 16 and $25 \text{ mol m}^{-2} \text{ d}^{-1}$ (January and February 1997; Figure 2-5). On an annual basis, surface PFD was $15,064.79 \text{ mol m}^{-2} \text{ year}^{-1}$.

Comparatively, underwater PFD was high, but variable on a daily basis. On cloudless summer days underwater quantum flux at canopy level was between 1200 and 1700 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Highest daily underwater means were recorded during summer months with values typically near 40 $\text{mol m}^{-2} \text{d}^{-1}$ (July 1996 and August 1997), although certain days during these periods could be greater than 45 $\text{mol m}^{-2} \text{d}^{-1}$. Lowest daily underwater mean PFD values ($<10 \text{ mol m}^{-2} \text{d}^{-1}$) occurred in all but summer months (Figure 2-5). The passing of northerly cold fronts during winter, accompanied by strong winds, caused underwater PFD to drop to less than 5 $\text{mol m}^{-2} \text{d}^{-1}$ for two to three days. This corresponded to k values between 6 and 16 m^{-1} and a decline of %SI at canopy level to between 0 and 20 (Figure 2-6). All but summer months in any year had days where underwater PFD was less than 1 $\text{mol m}^{-2} \text{d}^{-1}$. A complete underwater PFD data set from 1 May 1996 to 30 April 1997 was used to estimate an annual PFD of 6747 $\text{mol m}^{-2} \text{year}^{-1}$. To compare underwater to surface PFD, I chose the same time period, 1 December 1995 to 30 November 1996. Regrettably, for the dates 21 February through April 1996 (70 days), and 11 August through 24 August 1996 (14 days), underwater PFD data were lacking. I selected this time interval because both surface and underwater data sets have gaps and this time series represents the most complete data set for both surface and underwater PFD. For missing dates I selected data from either the previous, or following years for the same dates to calculate attenuation coefficients and percent irradiance. Paired t-tests of underwater PFD from LLM 107 between the months of January 1995/96, and October 1996/97 showed no differences between years ($p = 0.40$, $t = 2.15_{30}$; $p = 0.72$, $t = 0.37_{30}$, respectively). Using the replacement procedure described above, annual PFD

was $6986.73 \text{ mol m}^{-2} \text{ year}^{-1}$. This corresponded to a mean of 41.87% SI and an annual mean attenuation coefficient of $1.21 (\pm 0.06) \text{ m}^{-1}$ (Figure 2-7).

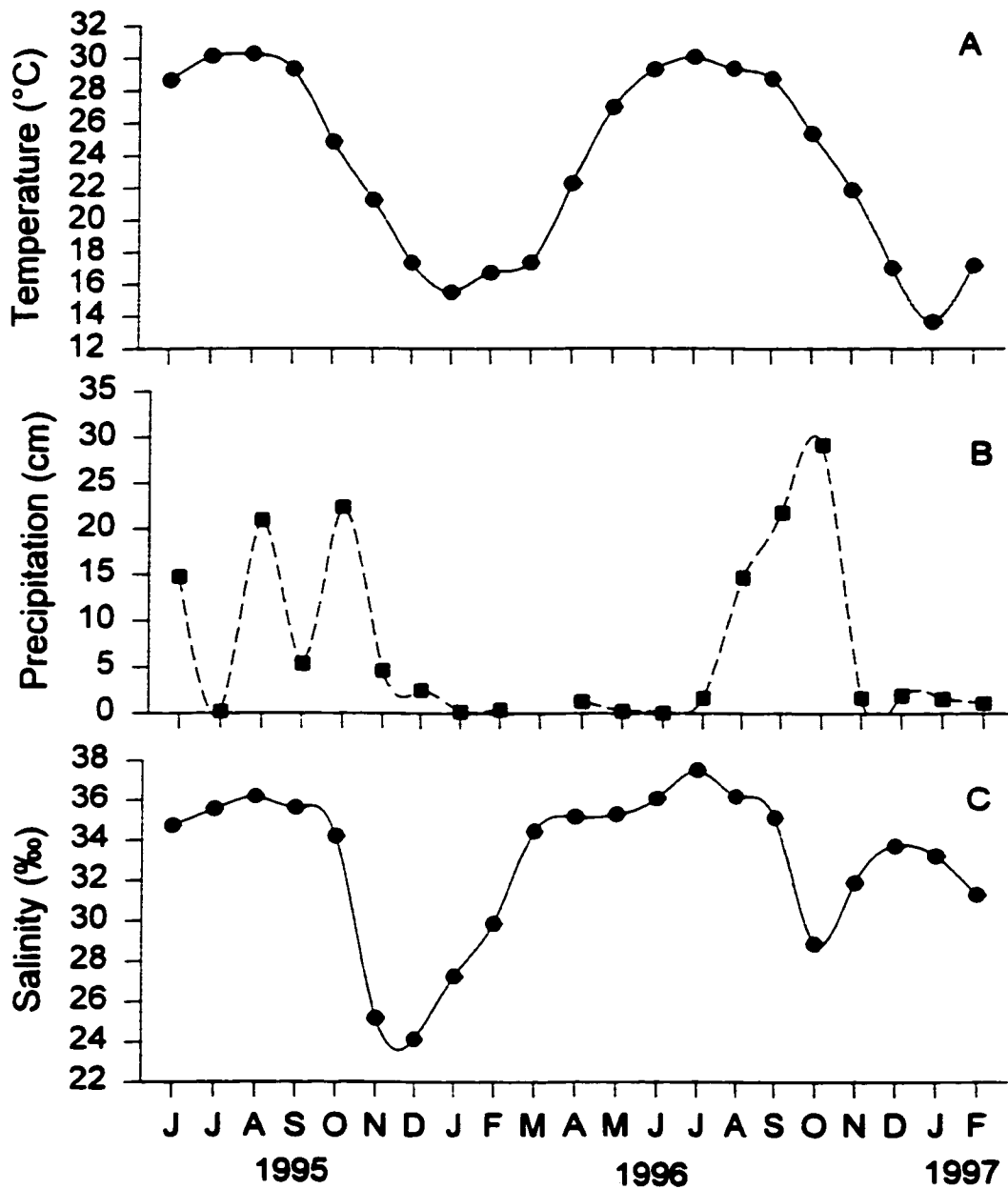


Figure 2-2. Record of surface water temperature (Panel A), precipitation from Brownsville, Texas (Panel B) and surface water salinity (Panel C) from January 1995 to February 1997. Error bars for temperature and salinity appear smaller than symbols, except for precipitation means which lack error bars.

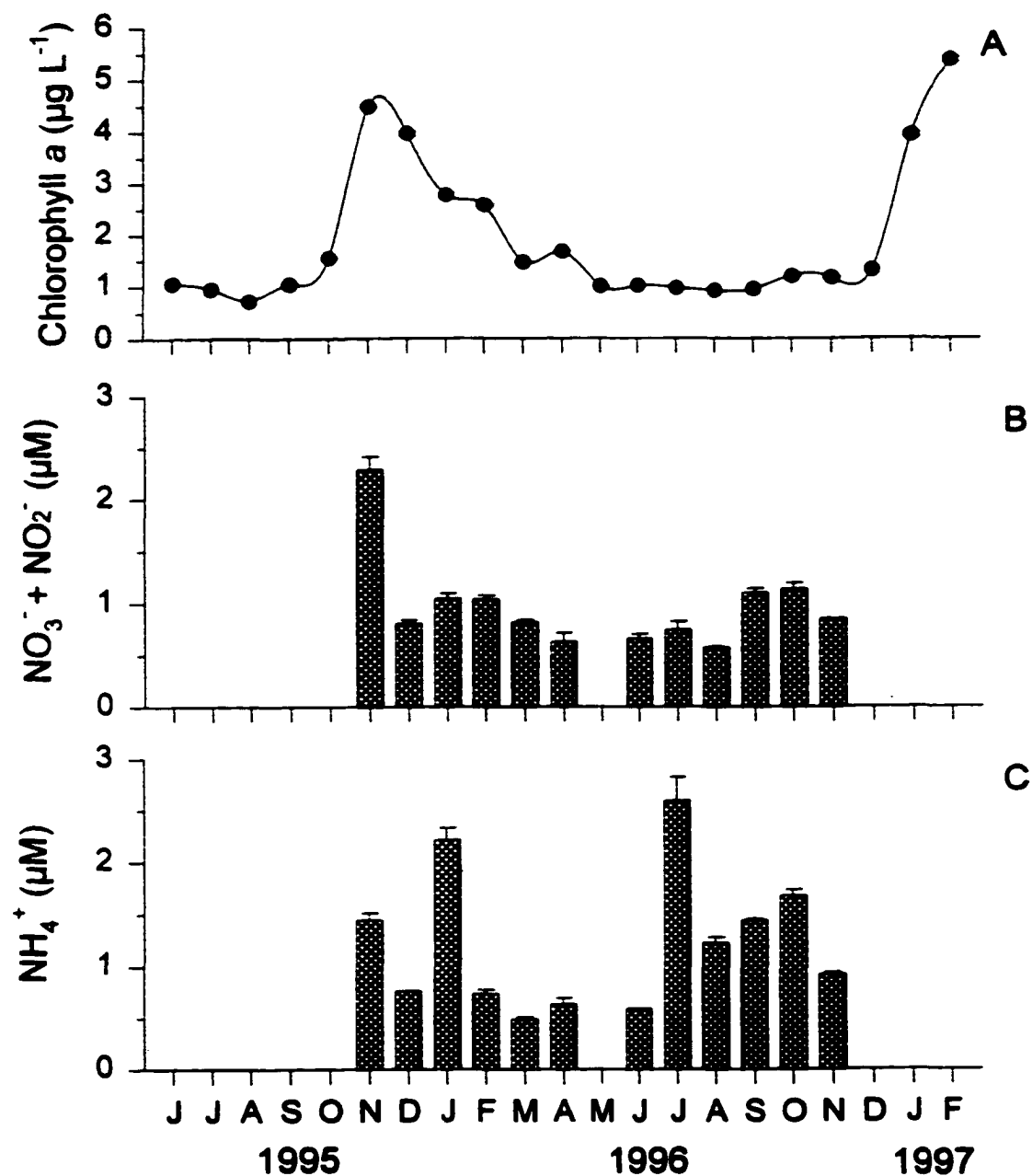


Figure 2-3. Water column chlorophyll *a* (Panel A) and dissolved inorganic nitrogen (DIN, nitrate + nitrite; Panel B, and ammonium; Panel C) concentrations recorded between June 1995 and February 1997 for chlorophyll *a*, and between November 1995 and November 1996 for DIN. Chlorophyll *a* samples were taken from FIX 1. DIN samples were collected from the study site (LLM 107).

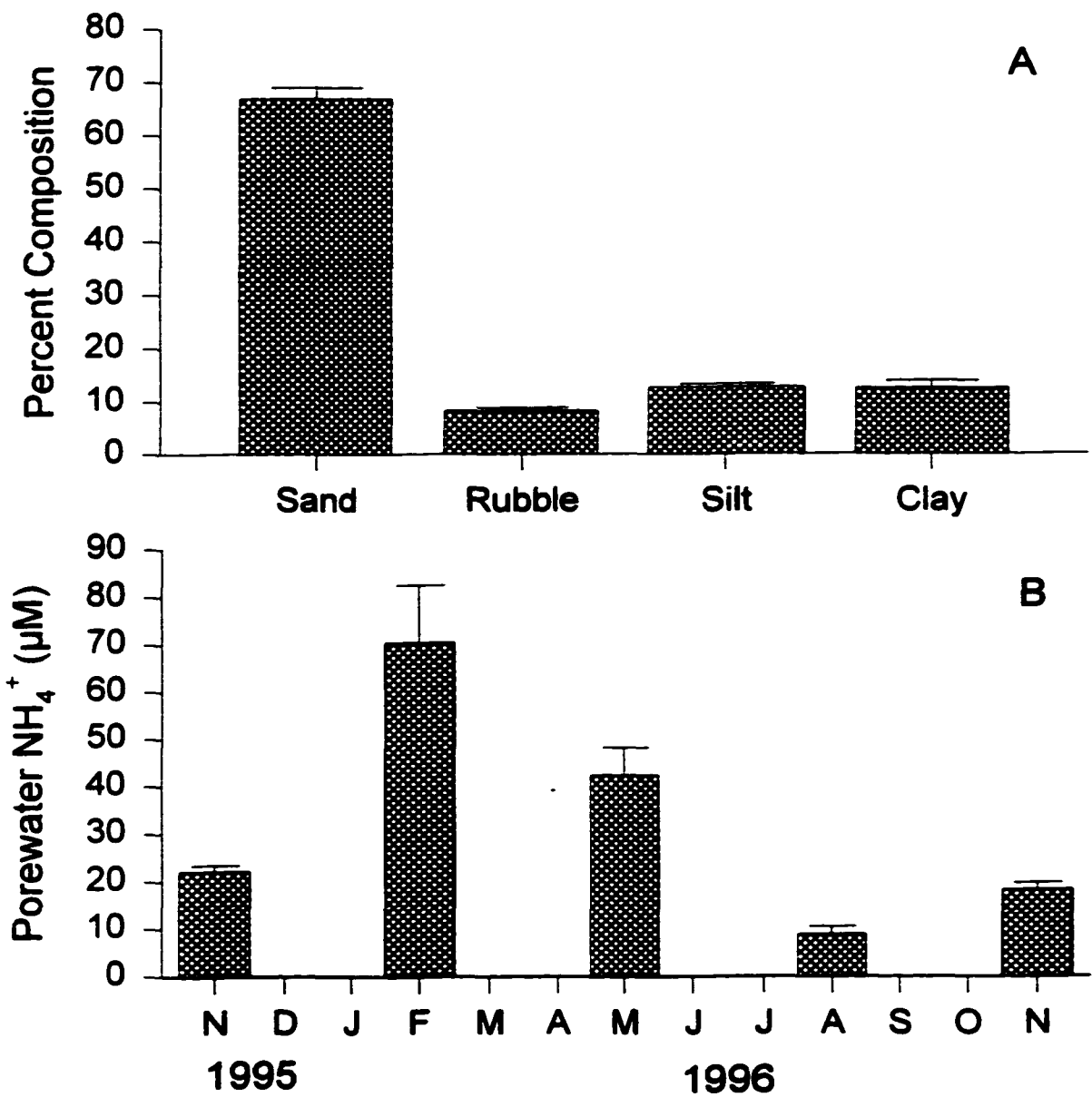


Figure 2-4. Sediment grain size distribution (Panel A) and sediment porewater ammonium concentrations from study site LLM 107. Sediment grain size based on samples collected in November 1995 and 1996. N = 6 for determination of each sediment parameter.

Table 2-2. Summary of ANOVA results for physical and chemical parameters at LLM 107. Physical and chemical parameters are the dependent variables with month as the independent variable. SS = sum of squares, df = degrees of freedom, MS = mean of squares.

Dependent	Source	SS	df	MS	F-ratio	P-value
Water Column NO ₂ ⁻ + NO ₃ ⁻	Month	1.93	11	0.18	12.89	<0.0001
Water Column NH ₄ ⁺	Month	17.27	11	1.57	57.23	<0.0001
Sediment NH ₄ ⁺	Month	14408.46	4	3602.12	16.07	<0.0001
Surface PFD ¹	Month	116424.83	19	6127.62	61.83	<0.0001
Underwater PFD	Month	81110.96	24	3379.62	56.43	<0.0001
Percent Irradiance	Month	87712.05	17	5159.53	12.46	<0.0001
Attenuation	Month	146.73	17	8.63	8.64	<0.0001

¹Photon Flux Density

Table 2-3. Summary of results of Kruskal-Wallis One-Way ANOVA for sediment grain size and sediment percent organic content. Samples (n = 6 for percent organic and grain size for both dates) were taken in February 1996 and November 1996 for organic content and November 1995 and 1996 for grain size.

Variable	df	Chi-Square	P-value
Percent Organic Content	1	0.64	0.4233
Sand	1	5.77	0.0163
Rubble	1	4.33	0.0374
Silt	1	0.10	0.7488
Clay	1	7.41	0.0065

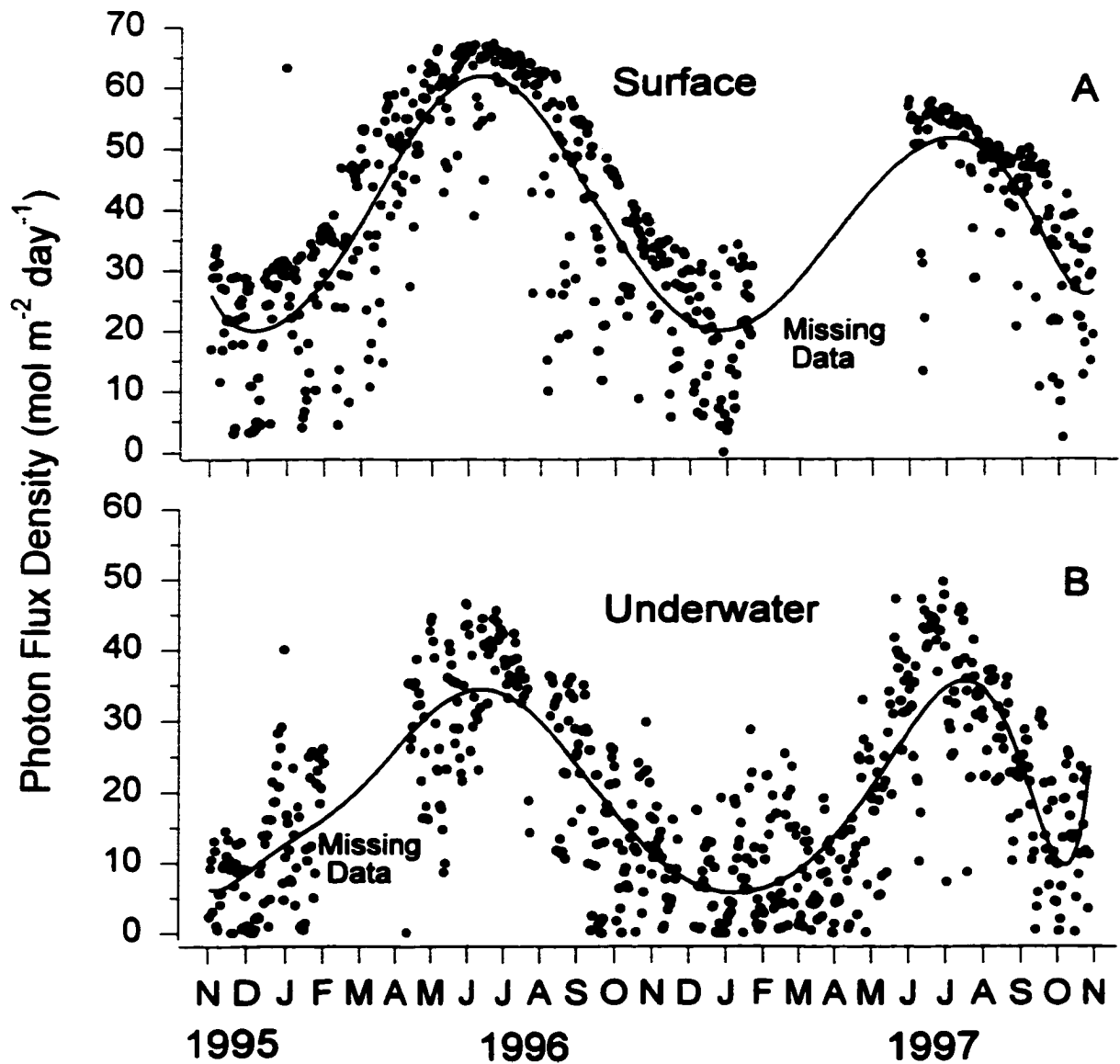


Figure 2-5. Daily surface photon flux density (PFD) measurements collected from FIX 1 (Panel A) and underwater PFD at canopy level from LLM 107 (Panel B) from November 1995 to November 1997 in Lower Laguna Madre. Regression lines generated from a tenth-order polynomial equation.

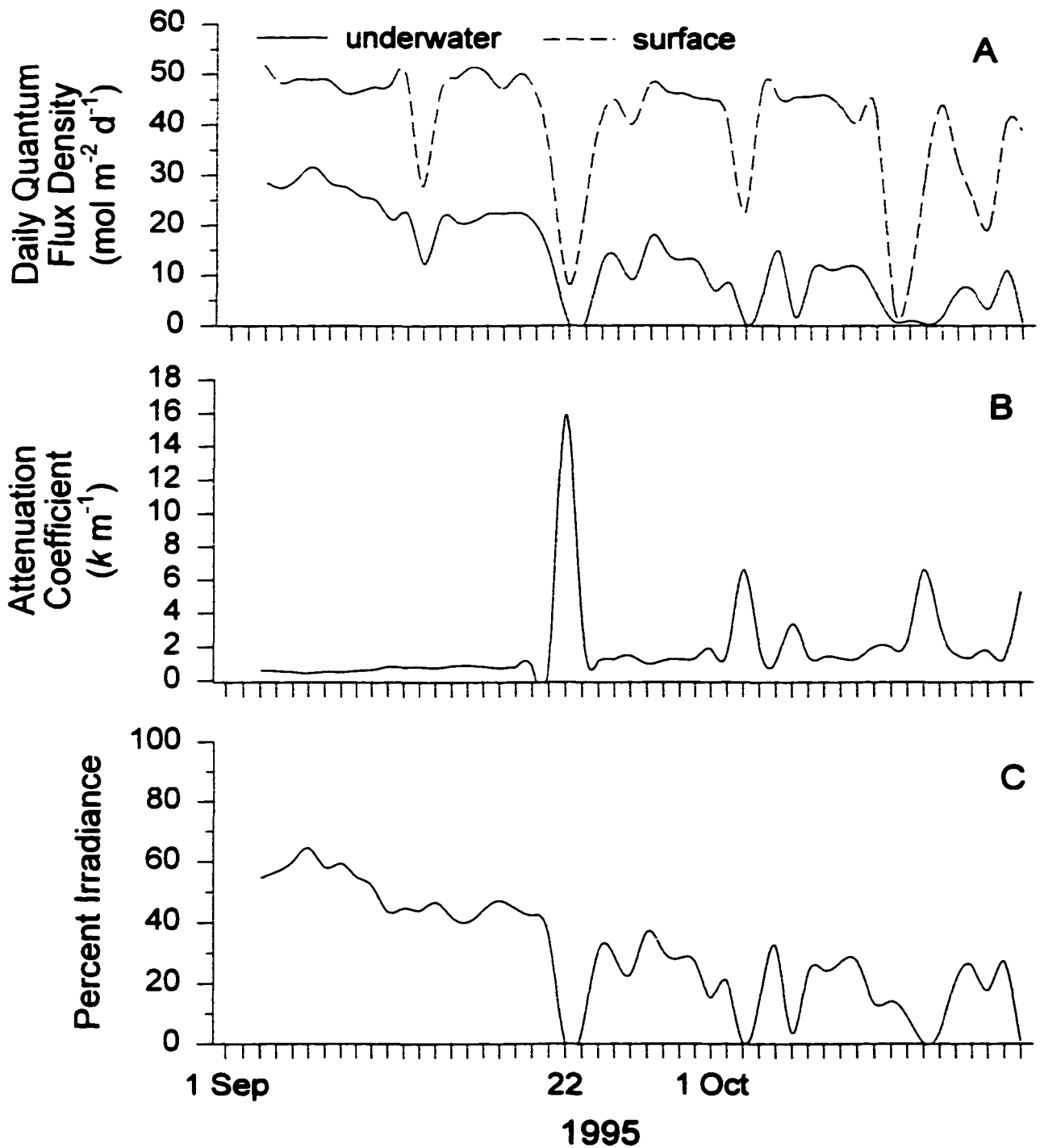


Figure 2-6. Surface and underwater PFD collected from FIX 1 and LLM 107 at canopy level from 2 September to 20 October 1995 during the passage of the first northerly front through South Texas which arrived on 22 September 1995 (Panel A). Light attenuation (Panel B) and percent surface PFD at canopy level (Panel C) are shown for the same time period.

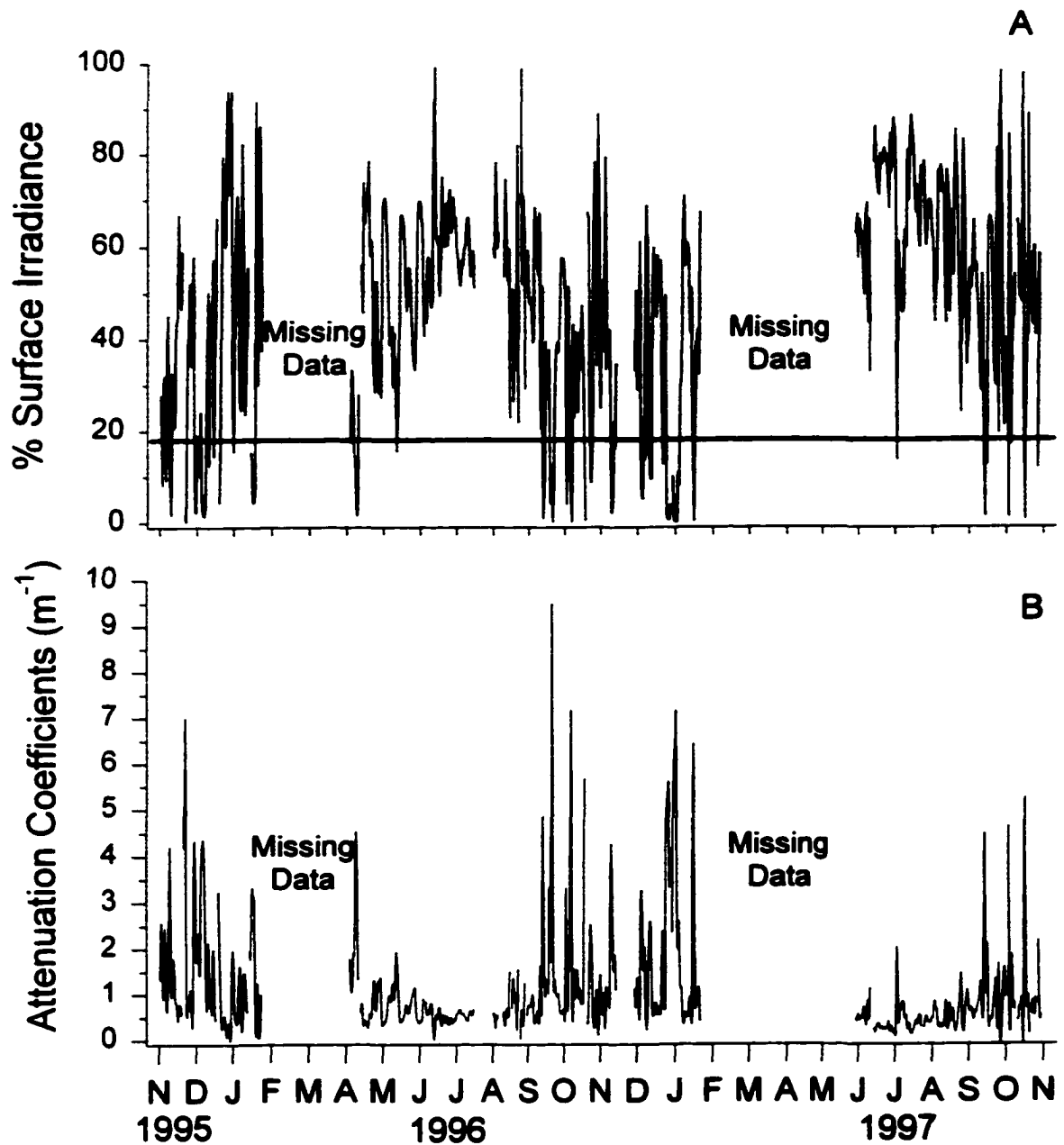


Figure 2-7. Calculated percent surface irradiance (%SI) at canopy level (Panel A) and light attenuation coefficients (Panel B) from surface (FIX 1) and underwater PFD (LLM 107) data, November 1995 to November 1997. Horizontal line on Panel A represents 18% SI, the minimum %SI determined by Dunton (1994).

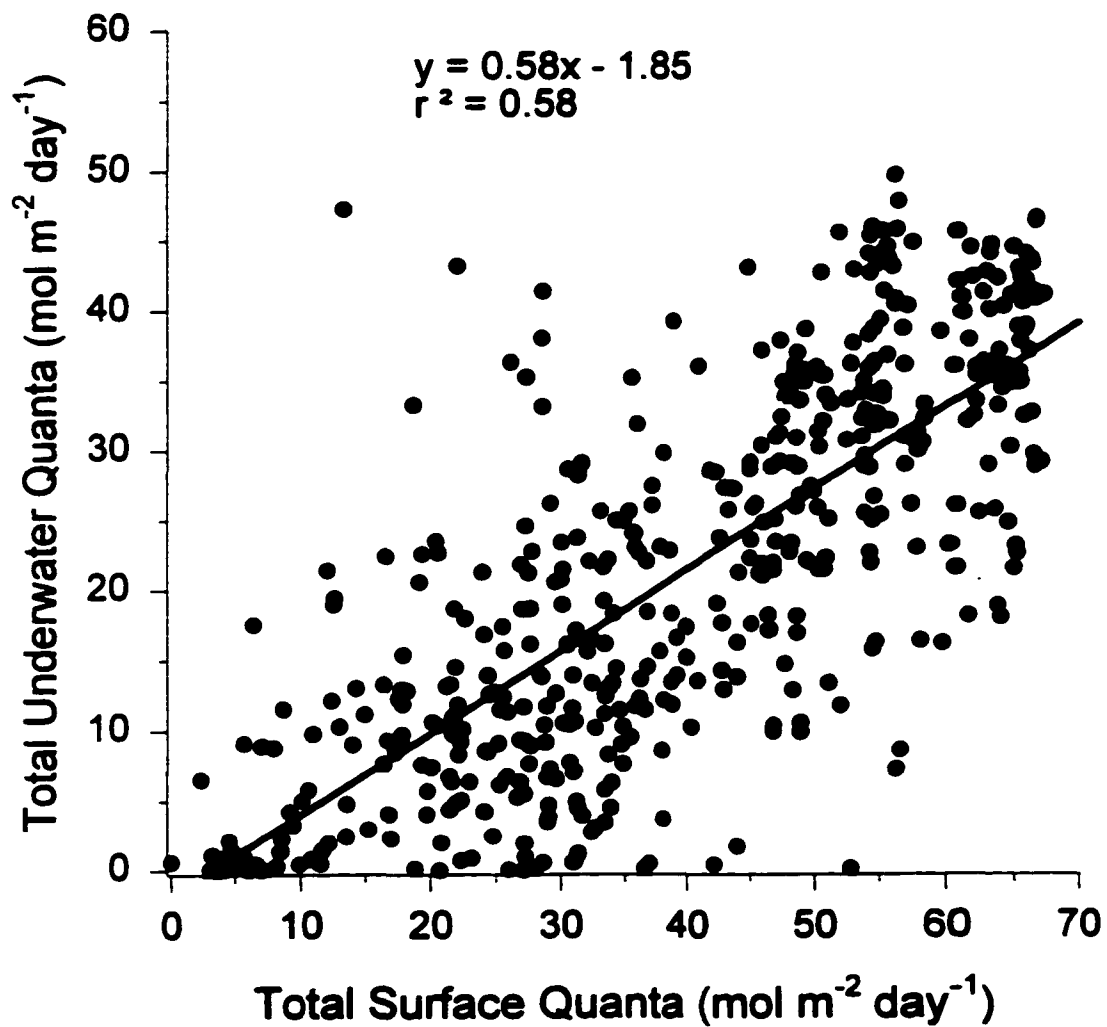


Figure 2-8. Relationship between underwater (LLM 107) and surface (FIX 1) PFD. Data from November 1995 to November 1997 (n = 491).

Biomass and Production of *Halodule wrightii*

There was a significant three-fold difference in *Halodule wrightii* total biomass (above- and below-ground fractions) with season. Highest values were around 318 g dw m⁻² during late summer and early fall. Lowest total biomass values were below 100 g dw m⁻² and coincided with late fall and winter months (Table 2-4; Figure 2-9A). Mean value total biomass was 185.41 (± 8.94) g dw m⁻². Below-ground biomass constituted between 91 and 46% of total biomass at LLM 107 and was significantly different among months (Table 2-3; Figure 2-9B). Highest values occurred in August 1995 and October 1996 (272.33 and 279.32 g dw m⁻², respectively). Below-ground to above-ground (B:A) biomass allocation was seasonal ranging between 2.3 (April 1996) and 15.7 (January 1997). There were significant differences between the winter 1996 months (December 1996, January and February 1997) and most other sample dates (Table 2-3; Figure 2-9C). Above-ground biomass of *H. wrightii* at LLM 107 showed significant seasonal variation (Table 2-4; Figure 2-9A). Lowest means were recorded during winter 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 wrightii shoots averaged 2.58 (± 0.05) leaves shoot⁻¹ during the study and values ranged between 2.14 (November 1995) and 3.13 (July 1996) leaves shoot⁻¹. There was no seasonal pattern to the number of leaves per shoot, nor a significant difference between months (Table 2-4; Figure 2-10A). Biomass of individual *H. wrightii* shoots was statistically significant among seasons, ranging from 8.07 mg shoot⁻¹ in June 1995 to 3.15 mg shoot⁻¹ in March 1996 (Table 2-4; Figure 2-10B). 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 wrightii* at LLM 107 showed wide, but no strong seasonal pattern; however, density was generally lowest in winter. Values ranged between 3942 (January 1997) and 9672 (April 1996) shoots m^{-2} , and was not significantly different between most months. However, April and May 1996 had the highest densities and were significantly greater than all other months (Table 2-3; Figure 2-11). There was a significant seasonal pattern in areal leaf density for *H. wrightii* (Table 2-4). Highest values were recorded for August 1995 (13980.16 ± 540.03) and July 1996 (14752.32 ± 700.38) while lowest values were found in January and February 1996 (8290.56 ± 1457.01 and 8128.00 ± 1017.36 , respectively) (Figure 2-11).

Halodule wrightii leaf length by rank order (youngest to oldest) was not significantly different among months (Table 2-5). *Halodule wrightii* shoots never possessed more than five leaves per shoot (Figure 2-12A) and leaf length for all leaves except the oldest (number five) were significantly different among months (Table 2-5).

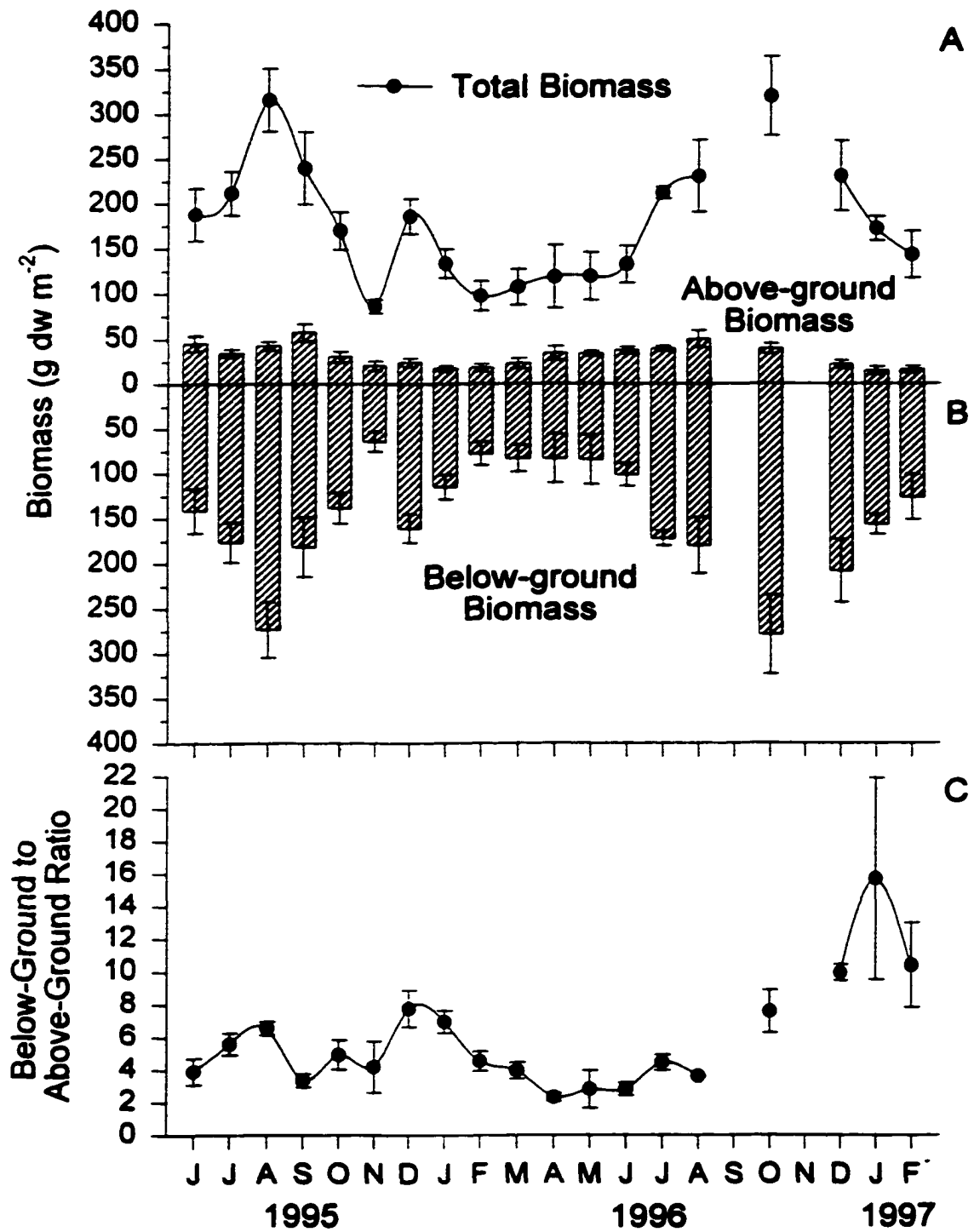


Figure 2-9. Seasonal above-ground (Panel A), below-ground (Panel B) and total biomass (Panel A), with below-ground to above-ground biomass ratio (Panel C) of *Halodule wrightii* at LLM 107 from June 1995 to February 1997.

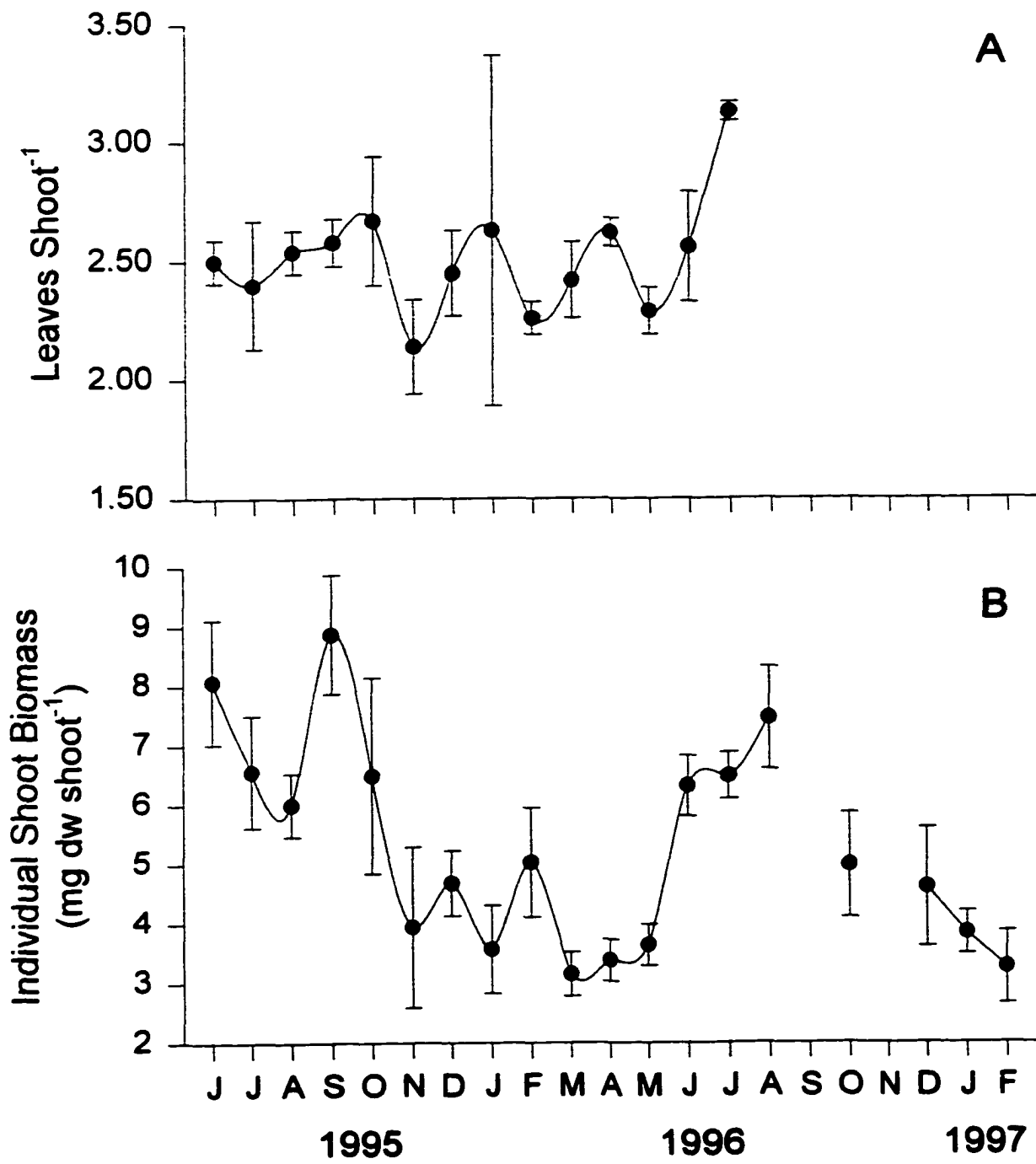


Figure 2-10. *Halodule wrightii* leaf number per shoot (Panel A) and individual shoot biomass (Panel B), LLM 107. Data for leaf number per shoot are from June 1995 to July 1996. Data for shoot biomass are from June 1995 to February 1997.

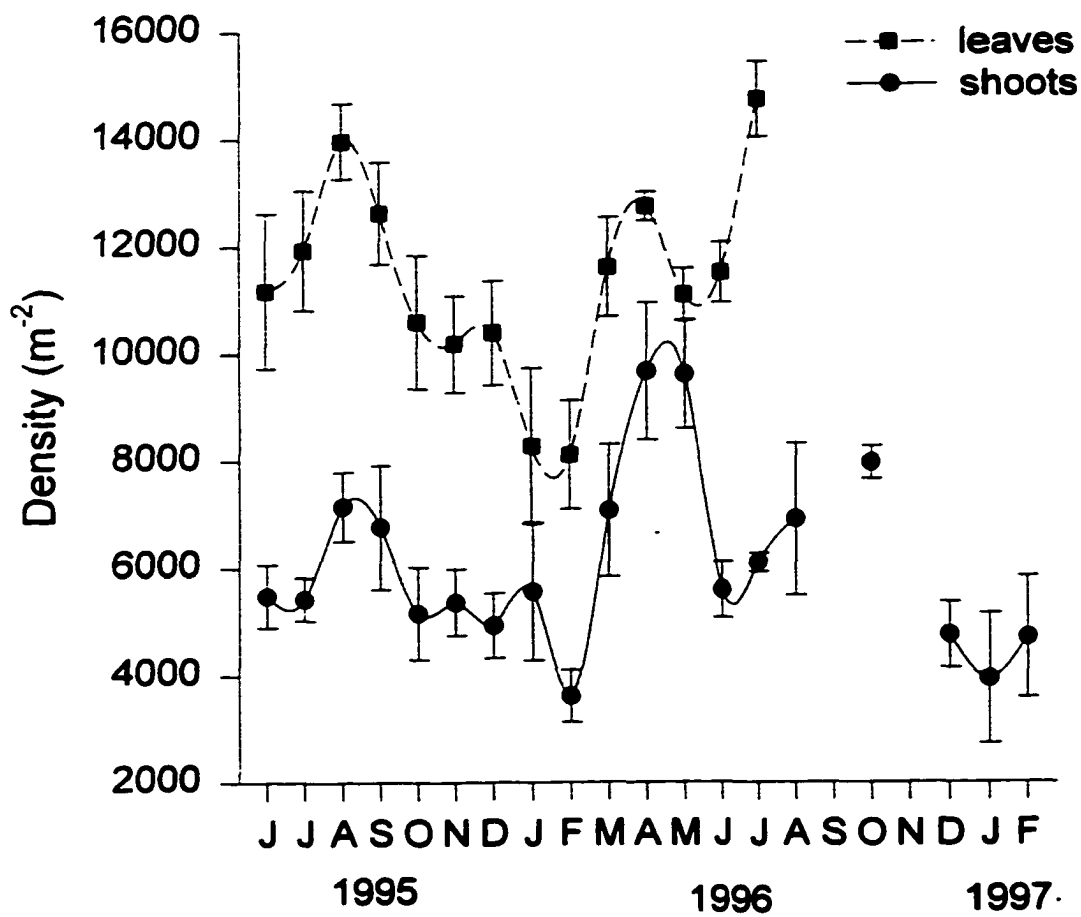


Figure 2-11. *Halodule wrightii* areal shoot and leaf density from June 1995 to February 1997, LLM 107.

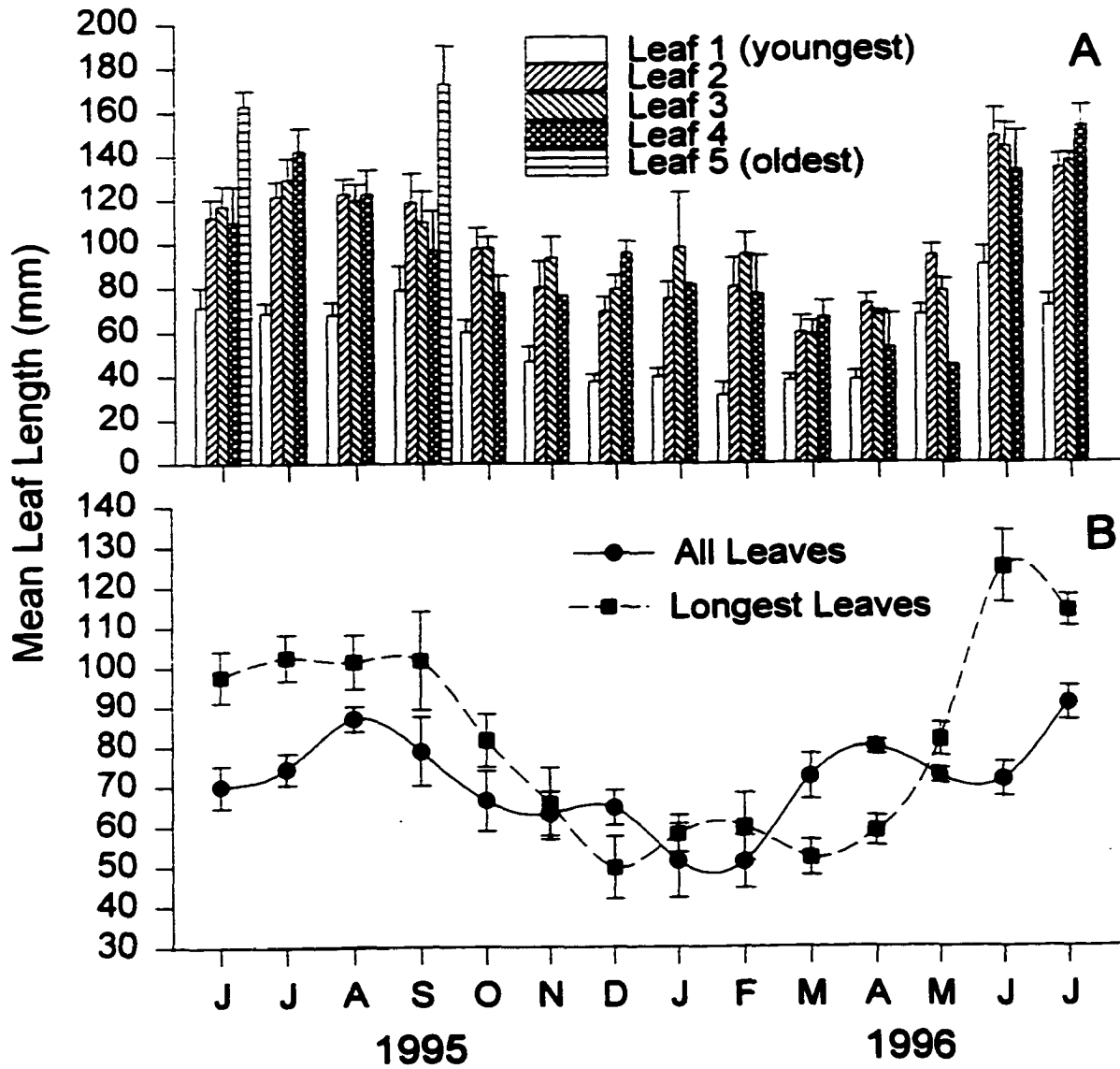


Figure 2-12. *Halodule wrightii* length of leaves by rank order (Panel A) and mean leaf length (Panel B) at LLM 107 from June 1995 to July 1996.

Table 2-4. Summary of ANOVA results for seagrass biomass and shoot parameters at LLM 107. Seagrass parameters are the dependent variables with month as the independent variable. SS = sum of squares, df = degrees of freedom, MS = mean of squares.

Dependent	Source	SS	df	MS	F-ratio	P-value
Total Biomass	Month	444953.99	18	24719.67	4.28	<0.0001
Above-Ground Biomass	Month	15565.41	18	864.75	3.30	0.0001
Below-Ground Biomass	Month	364850.34	18	20269.46	4.74	<0.0001
Shoot Biomass	Month	339.95	18	18.89	3.59	<0.0001
Below:Above Ratio	Month	925.56	18	51.42	5.17	<0.0001
Density	Month	258056578.1	18	14336476.56	3.49	<0.0001
Leaves Shoot ⁻¹	Month	4.92	18	0.38	1.56	0.1148
Leaves m ⁻²	Month	219751455.4	18	16903958.10	3.06	0.0011

Leaf elongation exhibited seasonal variation with highest rates during summer months and lowest rates during winter months (Figure 2-13A). Elongation rates greater than 3 mm d^{-1} were typical of early summer months during 1995 and 1996 and were significantly greater than slowest winter rates of $<1 \text{ mm d}^{-1}$ (SNK, $p < 0.05$; Table 2-5). After peak summer growth leaf elongation rates tended to gradually diminish to about 1.5 mm d^{-1} where rates leveled off in the fall (Figure 2-13A). Mean shoot production over the 21 month study period was $0.056 (\pm 0.003) \text{ mg dw shoot}^{-1} \text{ d}^{-1}$. Peak growth during 1995 exhibited a bimodal pattern with rates between $0.101 \pm 0.009 \text{ mg dw shoot}^{-1} \text{ d}^{-1}$ and $0.110 \pm 0.010 \text{ mg dw shoot}^{-1} \text{ d}^{-1}$ (Figure 2-13B). Shoot production was significantly different between years ($t_{30} = 12.66$; $p = <0.001$). Highest shoot production occurred in late spring and again in the fall and lowest production during winter months. There was a significantly positive relationship ($p < 0.0001$) between leaf elongation and shoot production (Figure 2-14).

Areal production was high from spring (May) to summer then it dropped during winter months (Figure 2-13C). Areal shoot production had highest values of $0.548 \pm 0.074 \text{ g dw m}^{-2} \text{ d}^{-1}$ in May 1995 and lowest values of $0.071 \pm 0.004 \text{ g dw m}^{-2} \text{ d}^{-1}$ during February 1997, a significant difference (SNK, $p < 0.05$; Table 2-5). Significant difference in areal production was found between years ($t_{14} = 2.40$ for summer and $t_{11} = 5.42$ for winter; $p = 0.031$ and <0.001 , respectively).

Carbon and Nitrogen Content

Carbon content in *Halodule wrightii* above-ground biomass was nearly constant (between 41.26 and 42.70%) over an annual period, while below-ground biomass C content was highest in summer and declined steadily throughout the year to its lowest values in winter (Table 2-6). Nitrogen content in both above- and below-ground tissues showed the opposite relationship with peak content in fall and winter and lowest content in summer (Table 2-6). The ratio of C to N was seasonal for both above- and below-ground tissues, with highest values in late summer and lowest values in winter (Table 2-6).

Leaf C content was generally high for all months and there was no seasonal pattern. Peak C content in clipped *Halodule wrightii* leaves occurred in August 1996 and lowest values were in June 1995 (Table 2-7). Areal C production with the adjusted method was more than two-fold lower compared to the unadjusted method. Highest monthly areal production rates occurred in late spring and early summer, and lowest monthly rates of production were in winter (Tables 2-8). Annually, C production was $45.59 \pm 7.66 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Table 2-8).

Blade Chlorophyll Concentration

Total blade chlorophyll concentrations tended to be lowest in summer and highest in winter (Figure 2-16A). Clear seasonal pattern was obscured by a high degree of variability among months. Despite this variability, there was a significant difference among months (Table 2-5). Values ranged from $5.11 \pm 0.51 \text{ mg g dw leaf}^{-1}$ in July 1996 to

11.82 ±0.65 mg g dw leaf¹ in February 1997. The ratio of chlorophyll *a* to *b* was significantly different among months and showed a clear seasonal pattern with lowest values, between 2.3 and 2.7 in summer and fall, and highest values, greater than 3.0, during winter (Table 2-5; Figure 2-16B).

Table 2-5. Summary of ANOVA results for seagrass leaf elongation, shoot and areal production parameters, total blade chlorophyll and chlorophyll *a:b* ratios at LLM 107. Seagrass parameters are the dependent variables with month as the independent variable. SS = sum of squares, df = degrees of freedom, MS = mean of squares.

Dependent	Source	SS	df	MS	F-ratio	P-value
Elongation	Month	110.09	18	6.12	13.17	<0.0001
Shoot Production	Month	0.0682	18	0.004	13.82	<0.0001
Areal Production	Month	2.45	18	0.14	7.44	<0.0001
Total Blade Chlorophyll	Month	285.12	15	19.01	4.75	<0.0001
Chlorophyll <i>a:b</i> ratio	Month	4.63	15	0.31	2.69	0.0021

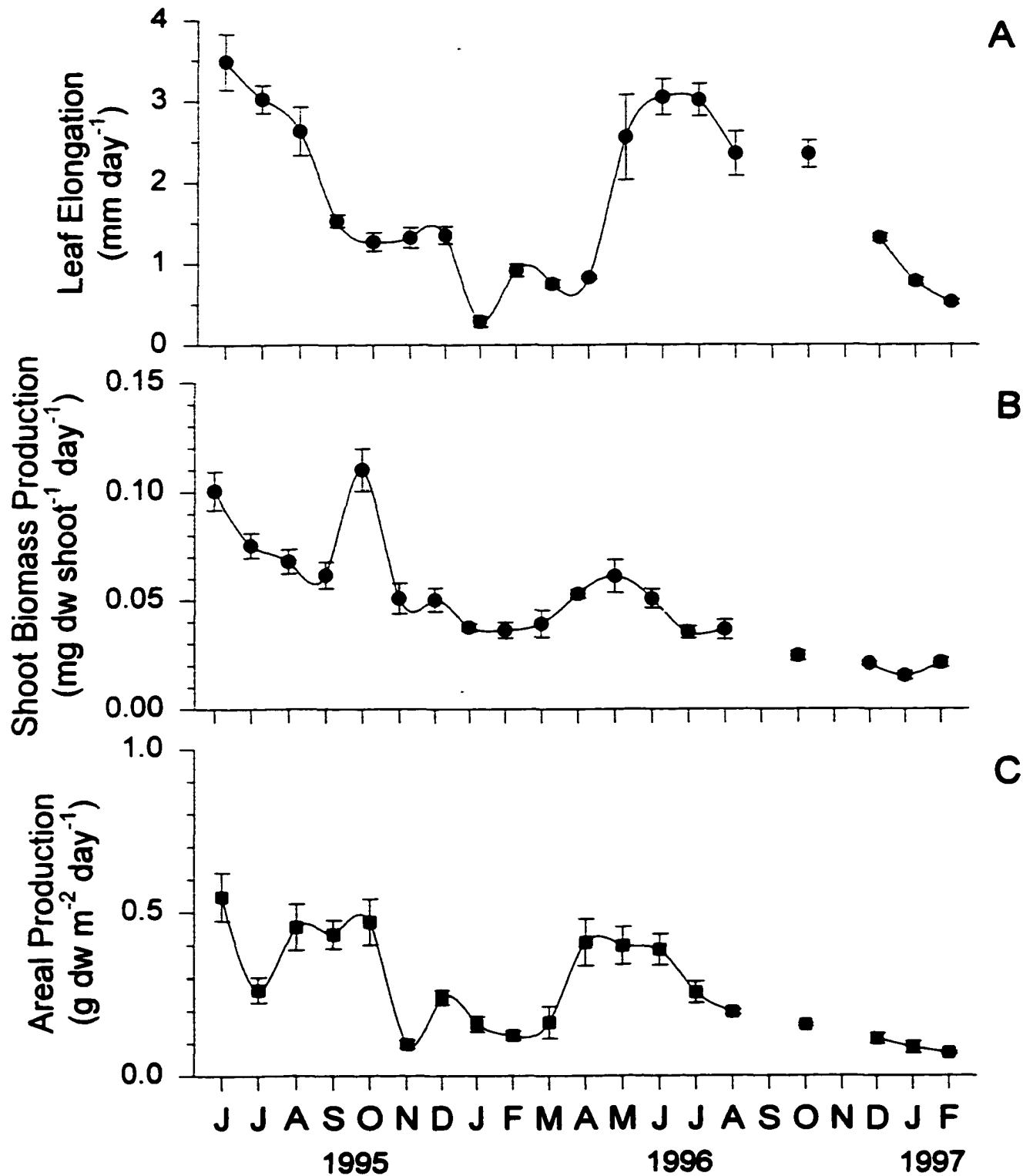


Figure 2-13. *Halodule wrightii* leaf elongation (Panel A), shoot biomass production (panel B), and areal production (Panel C) at LLM 107 from June 1995 to February 1997. Where no error bars appear, error is smaller than the symbol.

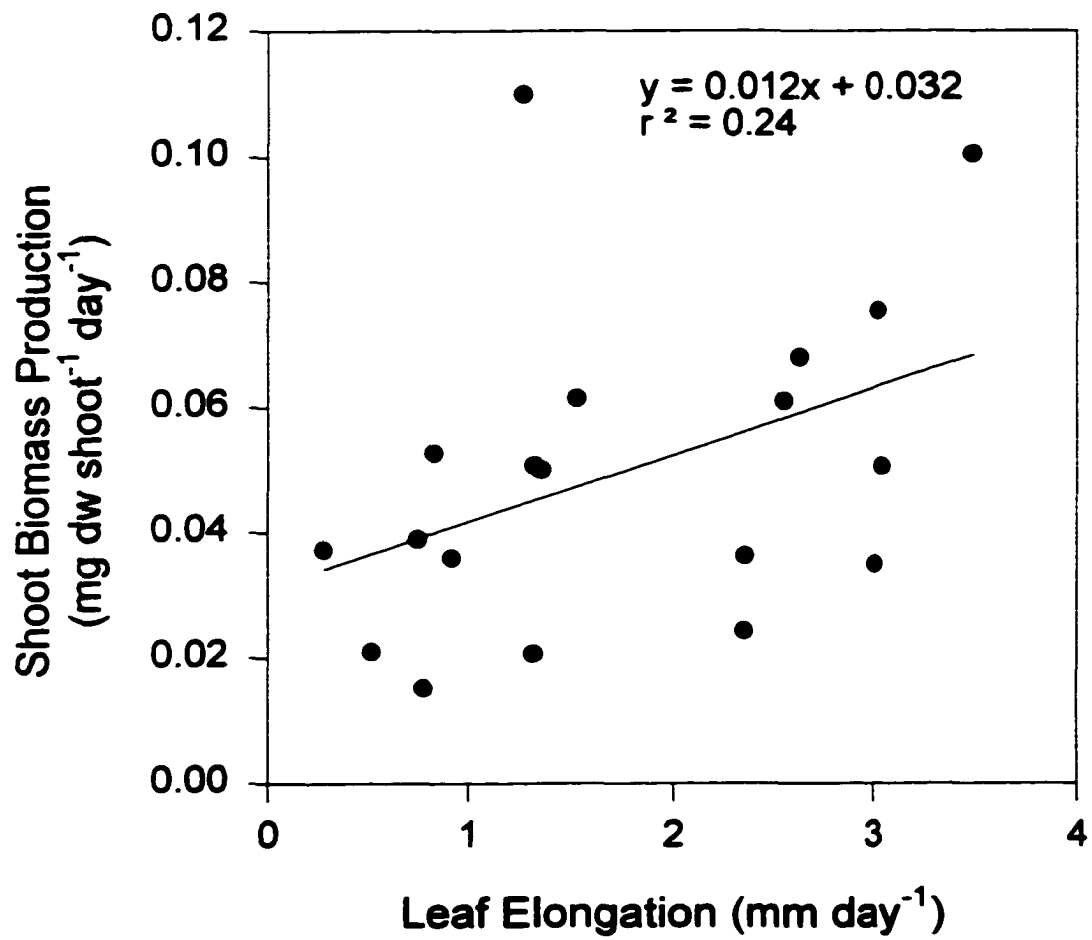


Figure 2-14. Relationship between shoot biomass production and leaf elongation for *Halodule wrightii* from LLM 107.

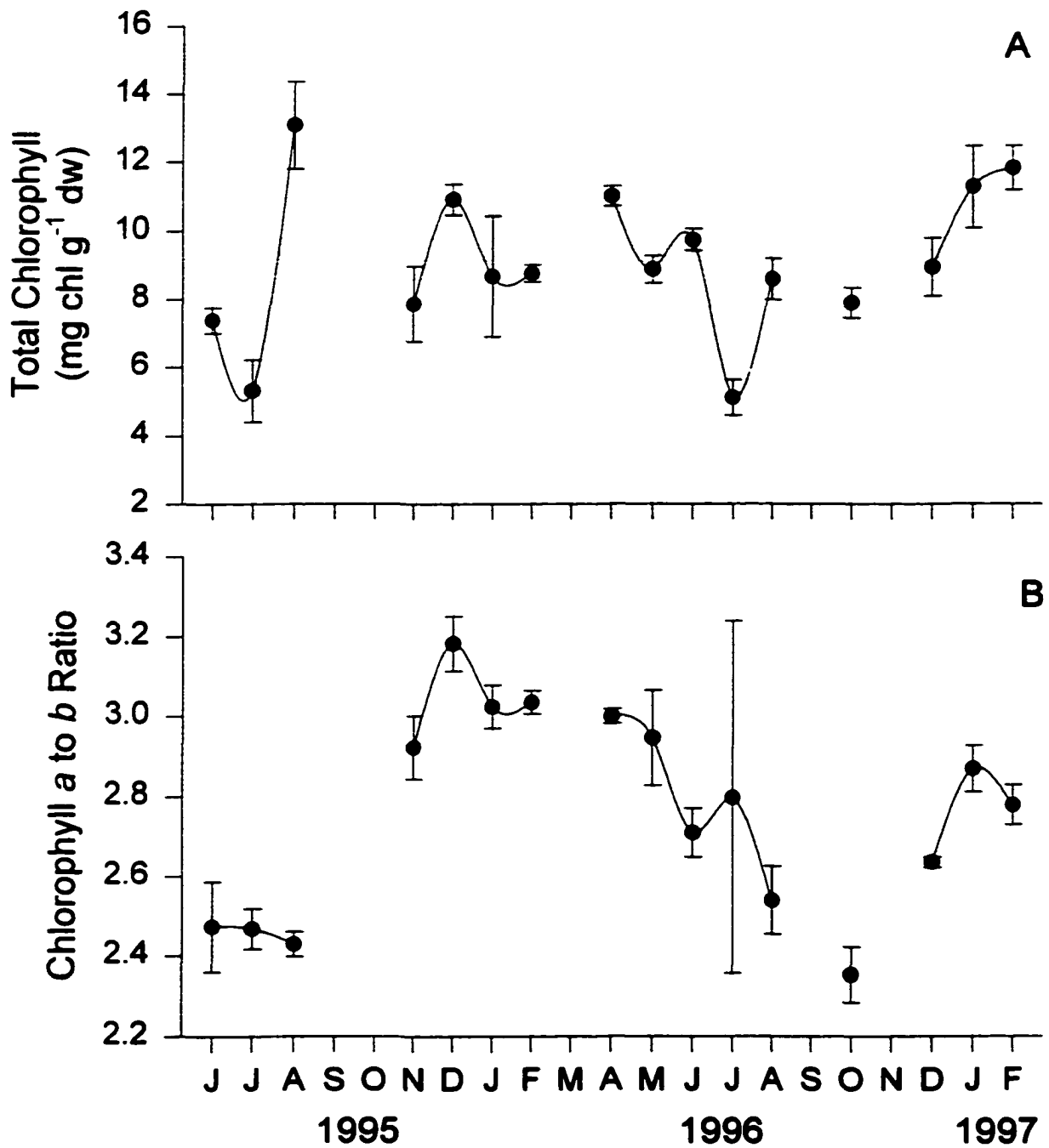


Figure 2-15. Blade chlorophyll (Panel A) and chlorophyll *a* to *b* ratio in *Halodule wrightii* from LLM 107 from June 1995 to February 1997.

Table 2-6. Percent carbon, nitrogen and calculated C:N molar ratios for *Halodule wrightii* above- and below-ground (biomass) tissue from LLM 107 in Lower Laguna Madre, Texas. Values are means \pm 1 SE, n = 2.

Date	Above %C	Below %C	Above %N	Below %N	Above C:N	Below C:N
2 Jun 95	41.26 (0.07)	39.79 (4.13)	2.47 (0.05)	1.17 (0.18)	19.46 (0.38)	40.13 (2.07)
19 Aug 95	41.50 (0.18)	38.86 (0.003)	2.17 (0.008)	1.00 (0.008)	22.33 (0.02)	45.29 (0.38)
12 Nov 95	42.56 (0.68)	37.13 (1.05)	3.34 (0.10)	1.44 (0.08)	14.89 (0.19)	30.17 (2.49)
17 Feb 96	42.70 (0.50)	34.38 (3.35)	3.38 (0.13)	2.00 (0.37)	14.75 (0.75)	20.44 (1.86)

Table 2-7. Percent carbon, nitrogen and calculated C:N molar ratios for *Halodule wrightii* clipped leaf tissue from LLM 107 in Lower Laguna Madre, Texas. Values are means \pm 1 SE, n = 2.

Date	%C	%N	C:N
2 Jun 95	38.04 (0.99)	2.51 (0.03)	17.66 (0.23)
19 Aug 95	40.69 (0.05)	2.45 (0.07)	19.09 (0.50)
12 Nov 95	39.15 (2.79)	3.07 (0.18)	14.84 (0.20)
17 Feb 96	40.79 (0.53)	3.34 (0.04)	14.26 (0.37)
18 May 96	41.71 (0.29)	2.99 (0.08)	16.26 (0.26)
24 Aug 96	42.13 (0.12)	2.51 (0.06)	19.57 (0.42)
7 Dec 96	41.78 (0.29)	3.38 (0.01)	14.43 (0.07)
1 Feb 97	39.13 (0.09)	3.35 (0.11)	13.62 (0.41)

Table 2-8. Monthly and annual estimates of leaf growth and carbon and nitrogen incorporation 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).

Month	g dw m ⁻² mo ⁻¹	g C m ⁻² mo ⁻¹	g N m ⁻² mo ⁻¹
Jun 1995	16.99 (3.51)	6.46 (1.33)	0.43 (0.11)
Jul	8.14 (1.30)	3.09 (0.50)	0.21 (0.04)
Aug	14.11 (2.19)	5.51 (0.84)	0.35 (0.06)
Sep	12.98 (1.86)	5.28 (0.76)	0.32 (0.05)
Oct	14.57 (2.17)	5.92 (0.71)	0.36 (0.06)
Nov	2.73 (0.36)	1.06 (0.15)	0.08 (0.00)
Dec	7.49 (0.96)	2.92 (0.37)	0.23 (0.03)
Jan 1996	4.80 (0.71)	1.88 (0.28)	0.15 (0.03)
Feb	3.22 (0.34)	1.32 (0.14)	0.11 (0.00)
Mar	5.10 (1.52)	2.08 (0.62)	0.17 (0.06)
Apr	12.27 (2.13)	5.00 (0.87)	0.41 (0.06)
May	12.34 (2.64)	5.09 (1.09)	0.39 (0.08)
Annual Leaf Production ^a	114.73 (19.68) ^a	45.59 (7.66) ^a	3.21 (0.56) ^a

^aunits are g m⁻² yr⁻¹

Discussion

Seasonal Light and Growth of *Halodule wrightii*

The underwater PFD of 6986 mol m⁻² yr⁻¹ estimated for this study falls within the range for other recent studies on the ecology of *Thalassia testudinum* in LLM at similar depths, which ranged between 4292 and 9149 mol m⁻² yr⁻¹ (Herzka and Dunton 1997; Kaldy 1997; Table 2-10). Annual underwater PFD from this study equates to 41.87% of surface PFD (15,065 mol m⁻² yr⁻¹), more than two-fold above the 18% SI minimum light requirements for *H. wrightii* (Dunton 1994; Czerny and Dunton 1995; Kenworthy and Fonseca 1996; Onuf 1996a), and explains the good relationship between surface and underwater light at LLM 107 ($r^2 = 0.69$, $p < 0.0001$; Figures 2-7 and 2-8). The relative lack of seasonality in the underwater light environment in other Texas estuaries (Czerny and Dunton 1995; Lee and Dunton 1997), including ULM (Dunton 1996), was not found at LLM 107 (Figure 2-5). High underwater PFD were present throughout winter months despite the passage of wind events (northers) which resuspended sediments, occluded the water column and caused attenuation coefficients to rise to between 6 and 16 m⁻¹ (Figure 2-6B). After the passage of these high turbidity events, underwater PFD levels typically returned to sufficiently high levels within a matter of a few days to sustain growth (Figures 2-6A).

The underwater light environment at LLM 107 was probably the factor least limiting for *Halodule wrightii* growth at LLM 107. Table 2-10 shows a range of total annual light received by seagrasses at or near their maximum depths along selected Texas estuaries. By comparison, the underwater PFD at LLM 107 was sufficient to support an

extensive, dense *H. wrightii* meadow throughout the study (Figures 2-10 and 2-11). The total annual amount of underwater light received by *H. wrightii* at LLM 107 was high, almost three times more than $2400 \text{ mol m}^{-2} \text{ yr}^{-1}$, the minimum annual PFD required for maintenance of growth (Dunton 1994; Czerny and Dunton 1995). Attenuation coefficients were less than 1 m^{-1} on nearly 65% of the days PFD data were collected (Figure 2-7B). More importantly, the number of hours plants at LLM 107 received saturation irradiance (H_{sat}) was probably high. This aspect of underwater PFD incorporates the minimum number of hours of saturation irradiance needed for a seagrass to achieve maximum production (Dunton (1994). Average saturation irradiance for *H. wrightii* in three Texas estuaries has been estimated at $319 \text{ } \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ (Dunton and Tomasko 1995) and between 200 to $300 \text{ } \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ in Indian River Lagoon, Florida. (Rice *et al.* 1983). Dunton (1994) cited an H_{sat} of two hours as necessary for plant maintenance, but between three and eight hours to sustain greatest spring and summer growth. With an H_{sat} of five hours, plants would receive a minimum of $5.74 \text{ mol photons m}^{-2} \text{ d}^{-1}$. Indeed, the lowest average PFD during December 1995 from LLM 107 was $5.81 \text{ mol photons m}^{-2} \text{ d}^{-1}$. This was also a time of low water temperatures ($<16 \text{ }^\circ\text{C}$) (Figure 2-2A) and subsequent slow growth (Figure 2-13). Lowered respiration rates have been found during periods of low temperature in *H. wrightii* (Dunton and Tomasko 1995). If H_{sat} were 12 hours, daily irradiance would be nearly $13.78 \text{ mol photons m}^{-2} \text{ d}^{-1}$. Daily PFD received by *H. wrightii* at LLM 107 during the most active growth period was two-fold higher at $27.51 \text{ mol photons m}^{-2} \text{ d}^{-1}$ (May 1996) and $39.36 \text{ mol photons m}^{-2} \text{ d}^{-1}$

(July 1996). Thus, it appears that underwater PFD rarely, if ever, limits *H. wrightii* growth at LLM 107 for extended periods.

The 25 month data set of underwater light recorded for this study represents one of the few long-term *in situ* studies for Laguna Madre seagrass beds and the first from a *Halodule wrightii* meadow in LLM. This is especially important in LLM because *H. wrightii* at 1.2 m is apparently close to its maximum depth penetration (Onuf 1996b). The greatest *H. wrightii* biomass in LLM found by Onuf (1996b) was in the 0-119 cm depth range (78 g m⁻²). *Halodule wrightii* reported in water deeper than 1.2 m on the western side of LLM had diminished biomass (35 g m⁻²; Onuf 1996b) compared to 185 g m⁻² for *H. wrightii* at 1.2 m depth in this study (Table 2-11). Underwater PFD undoubtedly is the major determinant of the maximum depth distribution of seagrasses (Dennison 1987; Dunton 1994). Kaldy (1997) worked in stands of *Thalassia testudinum* at 1.7 m on the western side of LLM and reported small patches of *H. wrightii* growing where *T. testudinum* was the most abundant species. He also concluded that the deeper *T. testudinum* population was at its maximum depth penetration in LLM. It appears, then, that the *H. wrightii* meadow at LLM 107 at 1.2 m depth represented one of the deepest continuous meadows in LLM and that the reduced biomass at the deeper populations may be the result of a comparatively lower light environment and competitive interactions between these two species (*sensu* Tomasko 1992).

The long-term underwater PFD data recorded in this study has system-wide implications for *Halodule wrightii*. ULM and LLM basins have a mean depth of about 1 m and most of the bottom of each basin is covered with seagrasses. If the %SI at LLM

107 at 1.2 m depth was 47%, seagrass populations at or below this threshold are probably received ample light to sustain growth and secondary production. Evidence for this can be found in ULM where a temporally extensive brown tide algal bloom has reduced underwater light levels by more than 50% and caused *H. wrightii* biomass to decline by more than one-half at 1.3 m, near its maximum depth (Table 2-10; Dunton 1994). Despite the bloom, *H. wrightii* populations in 1 m, or shallower water from ULM persist (Onuf 1996a).

Table 2-10. Total annual quanta received by seagrasses from four Texas estuaries at various depths from 1989 to 1997.

Estuary	Total Irradiance (mol m ⁻² yr ⁻¹)	Year(s) Recorded	Depth (m)	Source
Guadalupe ¹	2276	1990	0.4-0.6	Dunton (1994)
Nueces ¹	3300-5122	1990-1992	1.2	Dunton (1994)
Nueces ² (Corpus Christi Bay)	5382	1994	1.2	Lee and Dunton (1996)
Upper Laguna Madre ¹	2162-5672 ^a	1989-1992	1.3	Dunton (1994)
Lower Laguna Madre ² (FIX 2)	4293-9149	1995-1996	1.2	Kaldy (1997)
Lower Laguna Madre ² (Deep)	2924-7041	1995-1996	1.7	Kaldy (1997)
Lower Laguna Madre ¹ (LLM 107)	6987	1995-1997	1.2	This Study

¹ Underwater light measurements from a *Halodule wrightii* meadow.

² Underwater light measurements from a *Thalassia testudinum* meadow.

^a Variation in total annual underwater light resulting from a brown tide algal bloom.

Seasonal Growth and Biomass of *Halodule wrightii*

Seagrass production and biomass maxima and minima attributed to seasonality is a common and worldwide phenomenon (Duarte 1989). Temperate seagrass meadows often exhibit distinct seasonal patterns in production and biomass, typically correlated with seasonal insolation and temperature (Sand-Jensen 1975; Ott 1980; Dennison 1987; Nelson and Waaland 1997). Tropical latitudes, where temperature and photoperiod vary little, have also been shown to display seasonal variation (Brouns 1987; van Tussenbroek 1994; 1995; 1998). Seasonal variation of production and biomass of *Thalassia testudinum* and *Halodule wrightii* from subtropical Texas has likewise been documented (Dunton 1996; Lee and Dunton 1996; Herzka and Dunton 1997; Kaldy 1997). *Halodule wrightii* from LLM in this study showed distinct seasonal 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, likewise seen in *H. wrightii* from ULM (Dunton 1996). The increase in above-ground tissue biomass was due to increases in leaf length and not generally an increase in the number of leaves per shoot, although it was in the summer and fall that as many as five leaves per shoot could be found (Figure 2-12A). The lack of a clear seasonal rhythm in shoot and leaf density throughout the study may not be a great determinant in the production dynamics of *H. wrightii* in LLM. However, the high densities of these parameters at LLM 107 (Figure 2-11) must be important to fish and invertebrate larvae which specifically use the canopy of *H. wrightii* as a refuge and food source (Tolan *et al.* 1997; Rooker *et al.* 1998).

The highest below-ground biomass values of late summer and fall can probably be explained by the translocation of photosynthate produced during summer. Translocation of soluble carbohydrates from leaf to rhizome has been documented for *H. wrightii*, as well as for *Thalassia testudinum* and *Syringodium filiforme* (Dawes and Lawrence 1980; Lee and Dunton 1996; Rey and Stephens 1996). Low below-ground biomass during winter and early spring occur as a consequence of use of stored reserves for maintenance and growth during nonoptimal conditions (Dawes and Lawrence 1980). As a result, the C content of below-ground tissues probably declined from summer to winter while leaf C content remained relatively constant (Table 2-6). Similar conclusions for *H. wrightii* biomass were made by Dunton (1994; 1996) from ULM and Corpus Christi Bay, Texas and by Dunton and Kaldy (1997) for LLM.

Compared to Caribbean populations of *Halodule wrightii*, biomass values from LLM 107 were low (Table 2-11). Seasonal oscillations, while present in tropical coastal waters, can be greatly dampened. Longer photoperiods and water temperatures which typically vary within a few degrees provide for a longer growing season, resulting in greater biomass accumulation which is less affected by seasonal perturbations, such as low water temperature. The great biomass and shoot production differences of *H. wrightii* between Texas basins is more difficult to explain, especially between ULM and LLM whose subtidal seagrass meadows share a number of similar abiotic factors. One striking difference lies in the two-fold, or more, difference in porewater NH_4^+ concentrations between ULM and LLM. Dunton (1994) found that *H. wrightii* from ULM, Corpus Christi Bay and Guadalupe estuaries grew in sandy sediments with porewater NH_4^+

concentrations greater than 100 μM and prompted him to conclude those populations were not nitrogen limited. The low mean annual porewater NH_4^+ value of 32.3 μM from LLM 107 is among the lowest documented and probably accounts for biomass and production differences between ULM and LLM meadows.

The unimodal response in leaf elongation in this study differed from the bimodal pattern observed by Dunton (1994) for the middle-Texas coast, but the initial timing of first growth in May and June for all populations was identical (Figure 2-13). Shoot production of *H. wrightii* from LLM was more than two-fold lower than those of other populations from Texas estuaries of similar depth (Table 2-10). This may be a result of the cumulative effect of the wounds produced by clipping and the subsequent regrowth of leaves in a nutrient-poor environment.

Blade Chlorophyll Concentrations

Nutrient availability and light availability can affect chlorophyll content (Dring 1994). The poor relationship between total blade chlorophyll content and porewater NH_4^+ concentrations ($r^2 = 0.04$, $p = 0.283$) has also been observed in other Texas *Halodule wrightii* populations (Dunton 1996), but probably for different reasons. Blade chlorophyll concentrations of *H. wrightii* from ULM and Corpus Christi Bay (11.7 and 11.0 mg g^{-1} dw, respectively) were comparatively higher than the population from LLM 107 (9.3 mg g^{-1} dw). Underwater PFD was lower and porewater NH_4^+ concentrations higher in ULM and Corpus Christi Bay *H. wrightii* meadows (Dunton 1996) compared to *H. wrightii* from LLM 107 which had higher underwater PFD in a lower porewater NH_4^+

environment. This relationship is consistent with the observation that greater PFD generally corresponds to lower chlorophyll concentrations in aquatic vascular plants (Barko and Filbin 1983; Pizarro and Montecino 1992; Czerny and Dunton 1995; Lee and Dunton 1997). The LLM population, with comparatively more underwater PFD, did not require greater concentrations of total blade chlorophyll for light capture.

Halodule wrightii, like other aquatic plants, has been found to increase the amount of chlorophyll *b* relative to chlorophyll *a* in low light environments (Wiginton and McMillan 1979; Barko and Filbin 1983; Lee and Dunton 1997). Winter increases in chlorophyll *a:b* found in this study contradict this trend. The lack of seasonal pattern in the total blade chlorophyll concentrations in *H. wrightii* and inconsistent chlorophyll *a:b* ratios is due to the high underwater PFD budget at LLM 107.

Table 2-10. *Halodule wrightii* and selected species leaf production, biomass and density from different geographic locations. 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.

Species	Area (Depth)	Leaf Production			Biomass		Density (shoots m ⁻²)	Time	Source
		Shoot	Areal	Elongation	(g dw m ⁻²)				
<i>H. wrightii</i>	Indian River, Florida, USA (20-40 cm)	-	1.3-3.0	2.2-8.5	23.6	(above)	-	Mar-Apr	Vimstein (1983)
<i>H. wrightii</i>	San Antonio Bay (Guadalupe Estuary), Texas, USA (60 cm)	0.01-0.35	-	4-7 < 1	22-62	(total)	-	Apr-Sep winter	Dunton (1994)
	(40-60 cm)	-	-	-	100	(above)	1000-12,000		Dunton (1996)
<i>H. wrightii</i>	Upper Laguna Madre, Texas, USA (1.3 m)	0.05-0.3	-	4-7 < 1	200-500	(total)	-	Mar-Jun winter	Dunton (1994)
		-	-	-	200-300 300-550	(above) (below)	1000-12,000	autumn	Dunton (1996)
<i>H. wrightii</i>	Corpus Christi Bay (Nueces Estuary), Texas, USA (30-60 cm)	< 0.001-0.23	-	< 1-6	5-70 50-200	(above) (below)	3500-10,000	annual range	Dunton (1990)
<i>H. wrightii</i>	(1.2 m)	0.05-0.3	-	4-7	150-500	(total)	-	annual range	Dunton (1994)
<i>H. wrightii</i>	(1.2 m)	-	-	-	200-300 300-550	(above) (below)	1000-12,000	annual range	Dunton (1996)
<i>H. wrightii</i>	Matagorda Bay, Texas, USA (1-110 cm)	-	-	-	34.6-115.7	(total)		Jul-Aug	Adair <i>et al.</i> (1994)

Table 2-10 (continued). *Halodule* sp. and selected species leaf production, biomass and density from different geographic locations. 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.

Species	Area (Depth)	Leaf Production			Biomass (g dw m ⁻²)	Density (shoots m ⁻²)	Time	Source
		Shoot	Areal	Elongation				
<i>H. wrightii</i>	Alabama, Louisiana, Mississippi, USA (0.6-1.37 m)	-	-	-	80-1220 (total)	300-3200	peak growth	Eleuterius (1987)
<i>H. wrightii</i>	Laguna de la Mancha, Veracruz, Mexico	-	-	-	38-62 (total)	1824-2669	Sep	Barriero-Guemes and Balderas-Cortes (1991)
<i>H. wrightii</i>	Puerto Morelos Lagoon, Mexico (1.0-1.5 m)	-	-	-	519 (above)	14,872	Aug	Gallegos <i>et al.</i> (1994)
<i>H. wrightii</i>	Redfish Bay, Texas, USA (5-55 cm)	-	-	-	440 (total)	-	Aug	Pulich (1985)
<i>H. wrightii</i>	Upper Laguna Madre, Texas, USA (25-70 cm)	-	-	-	530 (total)	-	Sep	Pulich (1982)
<i>H. wrightii</i>	Celestun Lagoon, Yucatan Peninsula, Mexico (0.5-3.0 m)	-	-	-	614-665 (total)	-	Aug	Herrera-Silveira (1994)
<i>H. wrightii</i>	Indian River Lagoon, Florida, USA (1.0 m)	-	-	-	18.7 (above)	-	annual mean	Jensen and Gibson (1986)
<i>H. wrightii</i>	Tampa Bay, Florida, USA (1.0 m)	-	-	-	21.7 (above)	-	annual mean	Jensen and Gibson (1986)
<i>H. wrightii</i>	Little Bahama Bank, Bahamas (1.0 m)	-	-	-	5.9 (above)	-	annual mean	Jensen and Gibson (1986)

Table 2-10 (continued). *Halodule* sp. and selected species leaf production, biomass and density from different geographic locations. 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. Asterisks denote cm² day⁻¹.

Species	Area (Depth)	Leaf Production			Biomass		Density	Time	Source
		Shoot	Areal	Elongation	(g dw m ⁻²)	(shoots m ⁻²)			
<i>H. wrightii</i>	Upper Laguna Madre, Texas, USA (varied along transect)	-	-	-	160	(total)	-	Jul-Nov	Onuf (1996b)
<i>H. wrightii</i>	Lower Laguna Madre, Texas, USA (varied along transect)	-	-	-	78	(total)	-	Jul-Nov	Onuf (1996b)
<i>Thalassia testudinum</i>	Lower Laguna Madre, Texas, USA (varied along transect)	-	-	-	373	(total)	-	Jul-Nov	Onuf (1996b)
<i>Syringodium filiforme</i>	Lower Laguna Madre, Texas, USA (varied along transect)	-	-	-	138	(total)	-	Jul-Nov	Onuf (1996b)
<i>Halophila engelmannii</i>	Lower Laguna Madre, Texas, USA (varied along transect)	-	-	-	6	(total)	-	Jul-Nov	Onuf (1996b)
<i>T. testudinum</i>	Lower Laguna Madre, Texas, USA								
	(1.2 m)	-	0.5-3.5*	0.15-1.4	800-1400	(total)	1300-2200	annual range	Kaldy (1997)
	(1.7 m)	-	0.5-2.0*	0.2-1.6	250-700	(total)	700-1600		
<i>H. wrightii</i>	Lower Laguna Madre, Texas, USA								
	(1.2 m)	0.015-0.056	0.071-0.304	0.52-3.49	33.86	(above)	96-315	annual range	This Study
					152.07	(below)	3917-9672		

Influence of Salinity, Temperature and, Light on *Halodule wrightii* Growth

McMillan and Moseley (1967) and McMahan (1968) found *Halodule wrightii* to be a widely euryhaline species, however, their studies shed no light on optimal salinity for maximum production. This is an important consideration since Walker (1985) found *Amphibolis antarctica*, growing in Shark Bay, Australia, is also euryhaline, but has optimal production at 42‰. *Halophila ovalis*, another euryhaline species, did not exhibit optimal production when salinity fell below 15‰ for extended periods (Hillman *et al.* 1995). *Halodule wrightii* at LLM 107 experienced salinities ranging from 24‰ in winter to near 38‰ in summer, while populations from ULM have higher growth rates and are commonly subjected to salinities above 40‰ (Dunton 1996). There was a strong and significant correlation between salinity and shoot productivity found in this study ($r = 0.67$; $p = 0.017$; Figure 2-16A). It is possible that, though tolerant of low salinity periods, optimal leaf production does not occur during these periods. That low salinity and low temperature generally occurred together demonstrates the difficulty of drawing ecologically meaningful conclusions from long-term, *in situ* field conditions and underscores the need for controlled experiments that are able to separate the interactive effects of temperature and salinity on the growth of *H. wrightii*.

While light is demonstrably one of the most critical factors that controls seagrass depth distribution, it did not appear to greatly influence growth of *Halodule wrightii* at LLM 107 ($r = 0.32$; $p = 0.314$; Figure 2-16B). Temperature controls the upper and lower thresholds of photosynthetic activity (Bulthuis 1987) and has been cited as a regulating factor of 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 *Halodule wrightii* (McMillan 1979). The relationship between water temperature and productivity ($r = 0.73$, $p = 0.007$; Figure 2-16B) correlated strongly and illustrates the influence of water temperature on *H. wrightii* growth, especially since there was sufficient PFD at LLM 107 throughout the year. The two-fold differences in water temperatures was clearly seasonal (Figure 2-2A), but never exceeded the upper temperature limit of 35 °C, above which production could potentially be depressed. Thus, it is likely that the peak growth periods of late spring and early summer were not limited by high temperatures, and were at, or near the optimal range for maximum production during these periods. Likewise, the lower temperature threshold of 2 °C was never approached, at least for periods necessary to cause mass mortality to *H. wrightii* (McMillan 1979). During winter, low temperatures probably were most limiting to growth through lowered metabolic activity. However, the warmer temperatures of late spring and early summer, while important, were likely a less important factor in shoot production. Reasons for this rationale include the role of endogenous circannual rhythms which could initiate spring growth and which has been postulated for *H. wrightii* (Dunton 1994), as well as for *Posidonia oceanica* (Ott 1979).

Light, temperature and salinity were instrumental in regulating the leaf production and biomass dynamics of *H. wrightii* at LLM 107, but the influence of temperature seems paramount. There was a strong and significant interrelationship between shoot production and light, temperature and salinity ($r^2 = 0.85$; $p = 0.0117$).

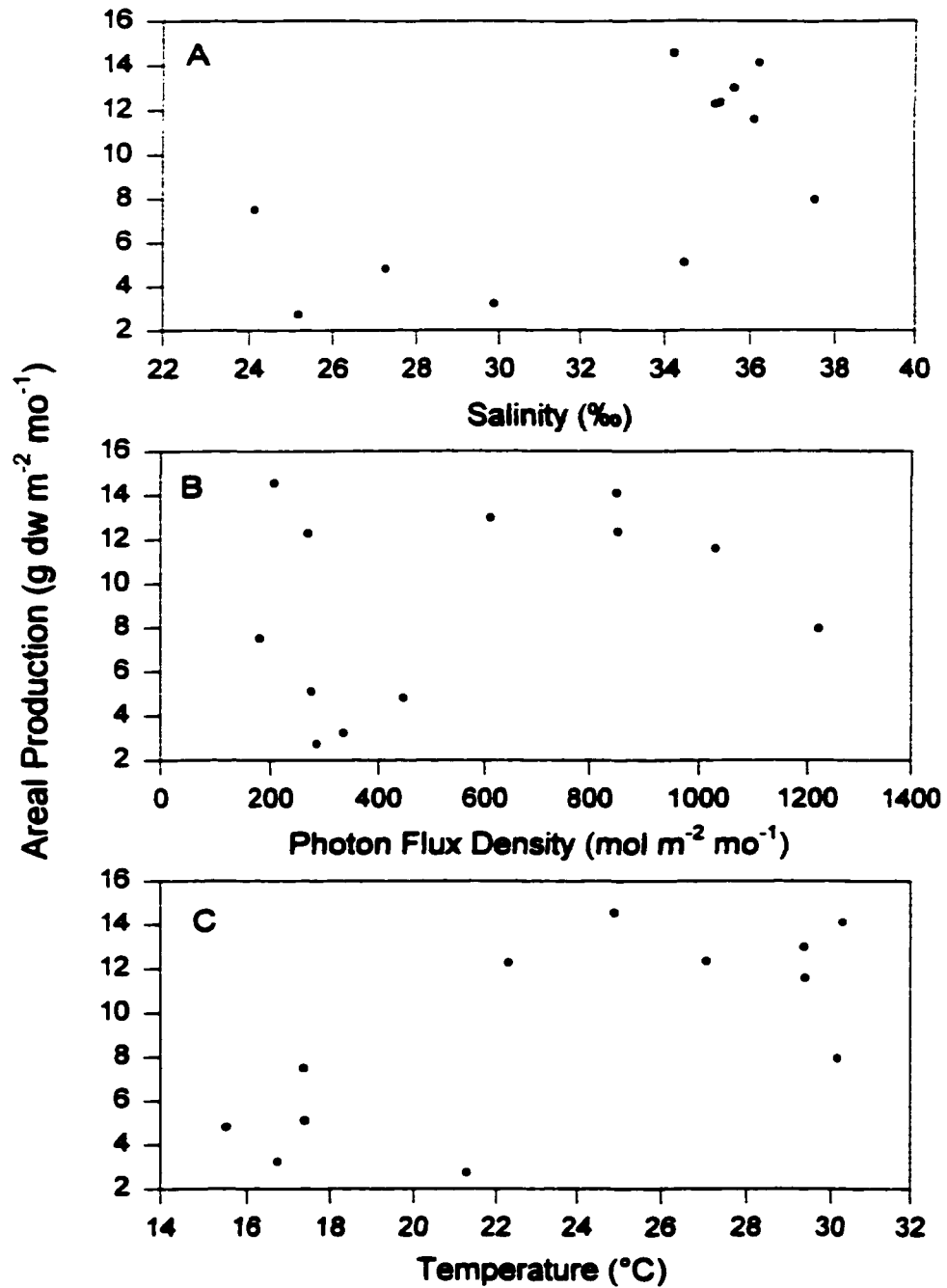


Figure 2-16. Relationships between *Halodule wrightii* monthly areal production and salinity (Panel A), photon flux density (PFD) (Panel B), and water temperature (Panel C). Salinity, PFD, and water temperature data points represent monthly means. Areal production data points were taken from an annual production budget from LLM 107.

Carbon and Nitrogen Incorporation

Halodule wrightii from LLM 107 typically displayed considerably lower production and biomass dynamics compared to populations from the western hemisphere at a similar depth (Table 2-11). On an annual basis, *Halodule wrightii* fixed 46 g C m⁻² year⁻¹ (Table 2-9), which is more than three-fold lower compared to *H. wrightii* from Florida (Virnstein 1982) and more than four-fold lower than *Thalassia testudinum* from LLM (Kaldy 1997). Allowing for a correction of the 50% underestimation in leaf production associated with clipping Tomasko and Dunton (1995), leaf C production still falls well below above-ground estimates for other colonizing or small species (Hillman *et al.* 1989). Numerous researchers have provided short-term included 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. To my knowledge, research into the production dynamics of *H. wrightii* are few and this work represents the first intensive study with an annual production budget estimate for *H. wrightii*.

The annual mean C content of *Halodule wrightii* leaves (40%) was greater than that of ULM *H. wrightii* (38%; Dunton, unpublished data). Given high N content, greater amounts of C would have been needed to structurally complex the N to a physiologically useful form (Atkinson and Smith 1983; Duarte 1990; Vitousek and Howarth 1991).

Halodule wrightii uses nonstructural carbohydrate content (NSCC) from the rhizomes to support winter and peak spring growth (Dawes and Lawrence 1980; Dunton and Kaldy 1997). There were more than two-fold decreases in below-ground biomass over the study period, yet the C content of these tissues varied little on a seasonally. Much of the

biomass lost seasonally from below-ground tissues of *H. wrightii* in LLM was probably in the form of NSCC (Dunton and Kaldy 1997). This discrepancy may be explained as a function of the sampling frequency for the respective parameters. Biomass was generally sampled monthly, while biomass C assays were done quarterly.

Because light did not appear to limit *H. wrightii* growth annually and temperature and salinity were most influential seasonally, the simplest explanation for these differences is nutrient limitation. There is a direct relationship between seagrasses productivity and the availability of inorganic nutrients necessary to sustain growth (Hillman *et al.* 1989; Hemminga *et al.* 1991). Numerous studies have experimentally demonstrated this relationship, both of nutrients in the water column and sediment porewater (e.g., Short 1987; Short *et al.* 1990; Bulthuis *et al.* 1992; Williams and Ruckelshaus 1993; Udy and Dennison 1997; Lee 1998). 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 environments (Short 1987). Nitrogen availability in finer-grained sediment is generally greater than on coarser-grained sediment (Short 1987). The bulk of sediment in ULM and LLM is typically fine quartz sand and silt (Rusnak 1960; Brown *et al.* 1980).

Halodule wrightii is reported to have a high nutrient requirement and is commonly associated with high nutrient environments (Fourqurean *et al.* 1992). Powell *et al.* (1989) found *H. wrightii* from Florida Bay had a median value of about 2%. The leaf N content for *H. wrightii* from LLM 107 is among the highest reported for this species (2.17 to 3.38%; \bar{x} = 2.95%). This is higher than the leaf N content of *H. wrightii* from

ULM ($\bar{x} = 2.71$; Dunton, unpublished data) where N is not believed to limit growth (Dunton 1996). The amount of N incorporated into leaf tissue by *Halodule wrightii* is estimated at $3.2 \text{ g N m}^{-2} \text{ year}^{-1}$, but this estimate does not reflect total metabolic plant requirements which are likely higher (Table 2-8). The amount of N *H. wrightii* incorporated into new leaf tissue was considerably lower than the threshold of $6.6 \text{ g N m}^{-2} \text{ year}^{-1}$ estimated for leaf tissue of seagrasses worldwide (Hemminga *et al.* 1991). Daily N incorporation in *H. wrightii* ranged from 14 mg N m^{-2} during peak growth in June 1995 to 2.6 mg N m^{-2} in November 1995. These values fall well below the general daily N requirements for *Zostera marina* ($150 - 574 \text{ mg N m}^{-2} \text{ mg day}^{-1}$) and *Thalassia testudinum* ($10 - 450 \text{ mg N m}^{-2} \text{ mg day}^{-1}$) (Hemminga *et al.* 1991; Kaldy 1997). The low rates of N incorporation I calculated are a function of daily leaf production rates, which are comparably low to *H. wrightii* populations elsewhere (Table 2-11). The most likely reason for the reduced rates in shoot growth and low biomass for *H. wrightii* at LLM 107 is limitation of a macronutrient, probably N. Because of the relative metabolic importance of N, and for reasons discussed below, I describe several lines of evidence to support an argument for N limitation in *H. wrightii* at LLM 107.

Previous studies from LLM, and results from this study, have consistently demonstrated low water column DIN and sediment NH_4^+ concentrations (Herzka 1996; Herzka and Dunton 1997; Kaldy 1997; Lee 1998; Figures 2-3 and 2-4, this study). Kaldy (1997) speculated that *Thalassia testudinum*, with comparatively reduced photosynthetic performance, leaf height, N content, rapid nutrient turnover times and high B:A ratios,

was likely nitrogen limited. Lee (1998) tested this nutrient limitation hypothesis and found *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. The nutrient ratios (to C) and content of tissues, particularly leaves, has been suggested as a proxy for determination of nutrient limitation (Duarte 1990; Hemminga *et al.* 1991). Plants from low nutrient environments also tend to have higher C:N ratios than those from high nutrient environments (Atkinson and Smith 1983; Duarte 1990). *Halodule wrightii* from LLM 107 had a year-round mean C:N molar ratio of 17.86, compared to 17.13 from ULM (Dunton, unpublished data). Using tissue N content and C:N ratios to determine the presence or absence of N limitation, *H. wrightii* at LLM 107 may not appear to be N limited at any time during the study. However, Duarte (1990) warned that nutrient values reported for species other than *Zostera marina* should be viewed as conservative estimates based on the limited number of measurements made for most species. Thus, the low productivity and biomass estimates, high B:A ratios, and sediment porewater NH_4^+ concentrations argue strongly in favor of N limitation for *H. wrightii* from LLM 107, despite the relatively high C and N tissue content, and low C:N ratios (Table 2-7) that *H. wrightii* displayed compared to *H. wrightii* populations of the middle Texas coast (Pulich 1985; Dunton 1996; Table 2-11).

A possible explanation for high leaf N content may be nutrient use efficiency (NUE) in a low porewater NH_4^+ environment. NUE is a function of the mean residence time (MRT) of a nutrient in a leaf population and nutrient productivity (annual leaf productivity per unit of nutrient in the population; Chapin 1980). In general, slower-

growing species have longer mean nutrient residence times and slower nutrient productivity. A terrestrial analogy has been documented for plants in nutrient-poor soils that had as high, or higher tissue nutrient content than plants from nutrient-rich soils under controlled conditions (Chapin 1980; Vitousek 1982). This hypothesis has been tested in seagrasses (Cambridge 1996). Thus, it is not unreasonable to find species with slower growth rates, or genotypically different populations of the same species, in low nutrient environments. The turnover time of the leaves of a population provides insight into the MRT of a nutrient within the leaves. Leaf turnover rates for *Halodule wrightii* at the study site varied from 30 days during peak growth to more than 100 days during cooler water temperatures, with a mean turnover time of 61 days. This mean is two-fold longer than Morgan and Kitting (1984) found for *H. wrightii* in Corpus Christi Bay, Texas, who worked with a population in shallow water (60 cm) from June to December. *Halodule wrightii* might remobilize nutrients from older, senescing leaves for reallocation to newer leaf tissues. Remobilization and translocation of mineral resources would decrease the dependence of the plant on external nutrient pools, as has been found in several seagrass species for N and P (Pederson *et al.* 1997; Stapel and Hemminga 1997), and documented for C in *Thalassia testudinum*, *Syringodium filiforme* and *Zostera marina* (Dawes and Lawrence 1979; Dawes and Guiry 1992; Lee and Dunton 1996; Rey and Stephens 1996; Lee 1998).

Biomass B:A ratios have also been used to suggest nutrient-poor sediment status. In such cases, an increase in below-ground tissue maximizes root surface area for nutrient uptake (Short 1987; Gleeson 1993). This is important in LLM where nutrient turnover

has been estimated at 1.25 to 2.50 day⁻¹ (Kaldy 1997; Ziegler 1998). Relationships between B:A ratios and soil nutrient concentrations have been well documented for terrestrial species (Ingestad and Ågren 1991), and recently for seagrass species (Lee 1998). The mean B:A ratio of 5.5 for *H. wrightii* from LLM 107 (Figure 2-9) was nearly twice that of *H. wrightii* from ULM and more than two-fold greater than *H. wrightii* from Corpus Christi Bay and Guadalupe estuary (2.9, 2.0, and 2.2, respectively, Dunton 1996).

Other possibilities to explain the low growth dynamics of *Halodule wrightii* at LLM 107 could lie in the role of sediment micronutrients. Pulich (1982a; 1985) examined the sediment micro- and macronutrient dynamics of *Halodule wrightii* 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). Micronutrient and sulfate reduction dynamics are unstudied in LLM *H. wrightii* seagrass meadows and if not at sufficiently high levels may restrict optimal growth. These factors could work synergistically to maintain growth dynamics below that of other Texas *H. wrightii* populations despite concentrations of sediment pore NH₄⁺. It is here that current flow differences between ULM and LLM could be important. Based on geomorphology and connection with the Gulf of Mexico, ULM likely has considerably more restricted water flow compared to LLM. Brown and Kraus (1997) found a year-round mean for currents in the vicinity of FIX 1 (outside a seagrass bed) to be 4 cm sec⁻¹. A current speed of 1 cm sec⁻¹ within a seagrass bed was considered high by Koch (1999) and the hydrodynamic shear stresses caused by wind-induced wave action can affect the diffusive flux of nutrients from the interstitial sediment porewater (Oldham and Lavery 1999). This

interdependent effect has recently been suggested for determining growth dynamics in *Thalassia testudinum* seedlings (Koch 1999) and could explain, in part, the low porewater NH_4^+ concentrations. High current speeds might also influence residence time of detrital material, allowing less organic matter to accumulate and resulting in a subsequent lower rate of nutrient remineralization. Additionally, the possibility of denitrification processes could contribute to sufficient N loss from the rhizosphere of *H. wrightii*, as has been demonstrated in *H. uninervis* (Shieh and Yang 1997). This factor should not be ignored.

It is possible that the LLM 107 population is of a sufficiently dissimilar genotype from other *Halodule wrightii* populations along the Texas coast that its production performance is phenotypically different enough to cause the observed differences. Indeed, there is tacit evidence that distinct genotypes of *H. wrightii* may exist within LLM. Dunton and Kaldy (1997) found *H. wrightii* shoots transplanted from shallow, high-light environments died when placed on dredge disposal sediment. They speculated that plants from low light environments may have survived, although the transplanted shoots were also exposed to high NH_4^+ concentrations (to 900 μM) in the transplant sediments. Genetic differences between populations of *H. wrightii* was suggested by Creed (1997) to explain significant morphological differences in nine populations from Brazil. Recent work on the genetic structure of *Posidonia oceanica* from the Mediterranean Sea shows that genetic differences between populations can occur as a result of local physical differences and geographical distance (Procaccini and Mazzella 1998). *Halodule wrightii* is reported to flower and produce seeds infrequently (Phillips and Meñez 1988). If genetic differentiation between ULM and LLM *H. wrightii* populations has occurred it could

explain some of the variation in production dynamics between these populations. This hypothesis needs to be tested. If supported, this aspect of seagrass biology will add another dimension to attempts to manage submerged wetlands. Understanding and documenting genetic differences of the seagrasses of Texas estuaries poses interesting questions for future research efforts, particularly *H. wrightii*.

Conclusions

The seagrass *Halodule wrightii* displayed strong seasonal trends in shoot production and biomass at LLM 107. Water temperature explained most of the variability in shoot production and low water temperatures were responsible for depressed winter growth. The influence of underwater PAR on shoot growth and biomass was minimal because of its abundance throughout the study period and I do not believe it limits *H. wrightii* growth. Changes in salinity correlated positively with shoot growth, but co-varied with water temperature, making generalizations difficult. *Halodule wrightii* shoot production and biomass dynamics in LLM were considerably lower compared to other populations along the Texas coast, as well as worldwide, probably due to nutrient limitation (likely N). Reasons for this conclusion include

- 1) sufficient PAR to maintain a positive carbon balance throughout the year,
- 2) low shoot production rates and biomass,
- 3) high below- to above-ground biomass ratios, and
- 4) low sediment porewater NH_4^+ concentrations.

High N and C content in leaf tissue may be explained by the ability of *H. wrightii* to translocate N from older, senescing tissue to younger, actively growing leaves, as has been shown for other seagrass species. It is possible that the high N demand by *H. wrightii* in LLM has contributed to its displacement by *Thalassia testudinum* and *Syringodium filiforme*. A system-wide increase in circulation and subsequent salinity decrease has enabled the more robust *T. testudinum* and *S. filiforme* to outcompete *H. wrightii*. However, with the presence of these larger species, with significantly larger storage organs, competition may also be occurring in the ability to grow in a nutrient-poor rhizosphere.

Despite the comparatively lower biomass of *Halodule wrightii* in LLM, its wide distribution in LLM (Onuf 1996b) and the fact that the Laguna Madre ecosystem as a whole is net autotrophic during the year explains the importance of *H. wrightii* as an important habitat for larval fish and invertebrates communities and continues to underscore its ecological importance in the face of change occurring to the species composition in this ecosystem. *Halodule wrightii* covers approximately 45% of 480 km² of LLM bay bottom (Hedgepeth 1967; Onuf 1996b). Based on these figures and the results from this study, I estimate that *H. wrightii* incorporates 7.4×10^4 kg C year⁻¹ and 5.2×10^3 kg N year⁻¹. This study is the first to provide an annual production budget for *H. wrightii* in the western Gulf of Mexico and it identifies areas where knowledge of the ecology of *H. wrightii* is wanting.

Seagrass habitat value extends beyond the ecological considerations as a direct or indirect food source, epiphytic substratum, or biogeochemical agent. Fesenmaier *et al.* (1987) valued the Laguna Madre at nearly 2.6 billion dollars annually to the state of Texas based on sport and commercial fisheries alone. Constanza *et al.* (1997) placed a \$19,004 ha⁻¹ value on seagrass habitat based on recreational and cultural values. *Halodule wrightii* comprises 45% of the 75% seagrass cover of a total area of 214,545 ha in the Laguna Madre (Armstrong 1987; Onuf 1996b). Based on these figures, the seagrass *H. wrightii* alone has a worth estimated at \$1.38 x 10⁹. Considering the ecological and economic information reported herein, natural resource managers should take all necessary steps to protect and preserve seagrass habitat, especially that of *H. wrightii*, in LLM.

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VITA

Joseph L. Kowalski was born on 10 June 1959 in Shreveport, Louisiana, to Lawrence and Theresa Kowalski. After spending 10 years away from school, most of these in the printing industry, he received his GED in 1986. Joseph entered The University of Texas - Pan American in 1987 and received his B.S. in biology in 1991, graduating with honors. He began teaching high school science at James "Nikki" Rowe High School after graduation, a position he holds to the present. Joseph entered graduate school at The University of Texas - Pan American in 1995.

Permanent Address: 6021 North 35th Street, McAllen, Texas 78504

This thesis was typed by the author.