Production and carbon reserve dynamics of the seagrass *Thalassia testudinum* in Corpus Christi Bay, Texas, USA

Kun-Seop Lee, Kenneth H. Dunton*

University of Texas at Austin, Marine Science Institute, 750 Channelview Drive, Port Aransas, Texas 78373, USA

ABSTRACT: The seasonal production dynamics of *Thalassia testudinum* in Corpus Christi Bay, Texas (USA) were evaluated through measurements of biomass, leaf growth and carbohydrate carbon content from December 1993 to March 1995. Shoot density and biomass changed significantly with season; values ranged from 321 shoots m^{-2} (454 g dry wt m^{-2}) in March to 531 shoots m^{-2} (885 g dry wt m^{-2}) in September Biomass of individual plant parts was significantly different over the sampling period; rhizome tissues tended to have the highest biomass while root tissues had the lowest. However, leaf biomass was higher than that of rhizome tissues during summer. Leaf productivities showed significant seasonal variation that was strongly correlated with temperature, ranging from 0.07 g dry wt m^{-2} d^{-1} in December to 5.6 g dry wt m^{-2} d^{-1} in July. Chlorophyll (chl) concentrations were significantly higher and chl $a:b$ ratios lowest during the spring/summer period of maximum photosynthetic production and growth than during winter. Non-structural carbohydrate carbon content was highest in rhizome tissues (111 to 203 mg C g^{-1} dry wt) and lowest in leaf tissues (46 to 70 mg C g^{-1} dry wt), which is consistent with the rhizome's role as a carbon storage tissue. Rhizome carbohydrate carbon content increased rapidly during June and July, which coincided with high water temperatures, underwater irradiance and blade chl concentrations. During winter and early spring, rhizome carbohydrate carbon content dropped nearly 50%, suggesting that these reserves were mobilized for tissue maintenance and new growth in early spring. Estimated annual blade production of *T testudinum* in Corpus Christi Bay over the period of this study was 792 g dry wt m^{-2} yr^{-1}, equivalent to 253 g C m^{-2} yr^{-1} Overall, annual productivity appears to be primarily regulated by temperature and secondarily by irradiance, as reflected in the timing and magnitude of the strong seasonal variations in leaf productivity, total chl content, chl $a:b$ ratios and rhizome carbohydrate carbon content in *T testudinum*.

KEY WORDS: Seagrass · Biomass · Production · Non-structural carbohydrates · Chlorophyll · *Thalassia testudinum* · Carbon dynamics

INTRODUCTION

Seagrass meadows are among the most productive of plant communities (McRoy & McMillan 1977), providing habitat and food for a wide variety of flora and fauna (Heck & Westone 1977, Orth et al. 1984, Summerson & Peterson 1984, Huh & Kitting 1985). Although few herbivores consume seagrass directly (Ogden 1980, Mann 1988), a substantial fraction of seagrass carbon enters coastal and estuarine food webs through microbial transformation of litter and particulate detritus (Kenworthy & Thayer 1984, Mann 1988, Chin-Leo & Benner 1991, Peduzzi & Herndl 1991, Koepfler et al. 1993, Opsahl & Benner 1993).

Accurate assessment of total seagrass production is difficult since a substantial fraction of plant biomass is below-ground. However, net above-ground production of seagrasses having strap-like leaves can be easily estimated using leaf marking techniques (Zieman 1974, Vermaat et al. 1987). Leaf production shows clear seasonal trends with rates increasing in spring and summer and decreasing in fall and winter (Vermaat et al. 1987, Dunton 1994). In spring, when water

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*Addressee for correspondence.
 E-mail: dunton@utmsi.zo.utexas.edu

temperature and day length increase, leaf production rates increase primarily due to the creation of new leaves which are thought to originate mainly from stored carbon in the rhizomes, while higher leaf production rate in summer is due to growth of existing leaves (Dawes & Lawrence 1980, Dawes & Guiry 1992, Tussenbroek 1995).

Seasonal growth of seagrasses is probably regulated by insolation and temperature or an interaction of both (Wetzel & Penhale 1983, Dunton 1994). Some researchers have considered temperature as the primary factor controlling seasonal growth (Setchell 1929, Tutin 1942, Phillips et al. 1983). However, Sand-Jensen & Borum (1983) stated that water temperature did not correlate with seasonal trends in leaf productivities. In addition, endogenous circannual rhythms of leaf elongation have been suggested for *Posidonia oceanica*, *Thalassia testudinum* and *Halodule wrightii* (Ott 1979, Dunton 1994, Czerny & Dunton 1995).

Production dynamics of above-ground tissues of seagrasses are generally well documented, but the metabolic features and functional role of below-ground tissues in whole plant production dynamics are less well known (Kraemer & Alberte 1993). The below-ground portion of *Thalassia testudinum* can account for over 50% of the total biomass (Powell et al. 1989, Fourqurean & Zieman 1991), and is supported by photosynthetically derived carbon and oxygen (Smith et al. 1984, Caffrey & Kemp 1991, Ralph et al. 1992). Seagrass rhizomes serve as carbohydrate storage tissues, in the form of soluble carbohydrate carbon, that support growth and maintenance of other plant parts during periods of low photosynthetic production (Dawes & Lawrence 1979, 1980, Durako & Moffler 1985, Pirc 1985, Dawes & Guiry 1992). Therefore, production, metabolism and stored carbon content of below-ground tissues must be considered when deriving estimates of whole plant carbon balance (Fourqurean & Zieman 1991, Kraemer & Alberte 1993).

Pirc (1985, 1989) found that seasonal changes of rhizome carbohydrate concentrations in *Posidonia oceanica* and *Cymodocea nodosa* were characterized by seasonal maxima in summer and fall, with winter growth and maintenance supported by the mobilization of starch from the rhizome. In *Thalassia testudinum*, increases in rhizome carbohydrates in summer have been attributed to the production and storage of starch, while winter and spring decreases were linked to the utilization of these stored carbohydrates for growth and maintenance (Dawes & Lawrence 1979, 1980, Durako & Moffler 1985). Although carbohydrate carbon in below-ground tissues plays an important role in growth and survival of seagrass, little research has been conducted on carbohydrate carbon partitioning into different plant parts, particularly on a seasonal basis.

Since most of the work on *Thalassia testudinum* in the Gulf of Mexico has been conducted in Florida (USA), this study provides valuable comparative data on the biology of this species in Texas (USA). Our emphasis is focused on seasonal changes in plant biomass, carbohydrate carbon content, leaf chlorophyll, and leaf productivity in relation to coincident measurements of temperature and continuous measurements of underwater photosynthetically active radiation (PAR). We also examined seasonal changes in carbohydrate carbon partitioning into different plant parts encompassing leaves, rhizomes, short shoots and roots.

MATERIALS AND METHODS

Study site. The study site (East Flats) is located on the eastern side of Corpus Christi Bay (27° 49' N, 97° 7' W) and has been the focus of several recent investigations on south Texas seagrasses (Dunton 1990, 1994, Czerny & Dunton 1995). *Thalassia testudinum*, *Halodule wrightii* and *Syringodium filiforme* are the dominant seagrass species in this area. This study was conducted on a monotypic meadow of *T. testudinum* at an average water depth of 1.2 m. Sediments are composed of 78% sand and shell, 8% silt, and 14% clay and water temperatures generally range from 34°C in July and August to 13°C in January, with salinities varying between 27 and 32‰ (Dunton 1990, 1994).

Production and biomass measurements. Monthly measurements of shoot density, biomass, leaf chlorophyll content, carbohydrate carbon content and leaf production rates were made from December 1993 to March 1995. Four replicate biomass samples were collected with a 9 cm diameter coring device driven 15 to 20 cm into the sediments. Samples were thoroughly cleaned of epiphytes and sediments, separated into leaf (blade and sheath), short shoot (vertical rhizome), rhizome and root tissues, and dried at 60°C to a constant weight. Shoot density was estimated by counting the number of shoots inside a randomly thrown quadrat (0.05 m²; n = 4 to 8).

Leaf production rates were obtained using the blade marking technique (Zieman 1974, Kentula & McIntire 1986). Five sampling areas were marked with PVC poles in a monotypic *Thalassia testudinum* bed. Fifteen to 20 randomly chosen shoots around these poles were marked just above the bundle sheath with a hypodermic needle and collected after 12 to 16 d. Leaf production rate per shoot was determined by dividing the dry weight of new leaf tissue produced by the number of days since marking. Areal leaf production rates were obtained by multiplying shoot leaf production rates by the shoot density. Leaf production rate per shoot was

correlated with *in situ* water temperature and underwater irradiance measured during periods of leaf marking.

Chemical analyses. For determination of blade chlorophyll (chl) content, 6 replicate samples from each sampling date were collected and cleaned of epiphytes by gentle scraping in the laboratory. Preweighed leaf tissue was ground in 90% cold acetone buffered with 0.05% $MgCO_3$ using chilled pestles and mortars with washed sea sand. The extract was made up to a known volume, centrifuged, and absorbances measured at 750, 664 and 647 nm on a Shimadzu UV 160U spectrophotometer. Chl *a* and *b* contents were determined using the equations of Jeffrey & Humphrey (1975) for 90% acetone extractions.

Dried plant material from biomass samples was used to determine total non-structural carbohydrate (starch + soluble sugars) carbon content in different plant parts. Total non-structural carbohydrates from leaf, horizontal rhizome, vertical rhizome and root were determined using the MBTH (3-methyl-2-benzothiazolinone hydrazone hydrochloride) analysis (Parsons et al. 1984, Pakulski & Benner 1992). Ground plant samples were hydrolyzed with dilute HCl. The hydrolyzed samples were neutralized with NaOH solution, followed by reduction to alditols with KBH_4. The alditols were oxidized with periodic acid solution to form 2 mol of formaldehyde per mol of monosaccharide. The aldehyde content was determined spectrophotometrically with MBTH. Absorbances were compared with a glucose standard and converted to equivalent carbon values (mg C g^{-1} dry wt).

Four replicate surface water samples for determination of water column dissolved inorganic nitrogen (DIN, $NO_3^- + NO_2^-$) were collected every month. DIN was determined colorimetrically according to Parsons et al. (1984).

Photon flux measurement. Photosynthetically active radiation (PAR, 400 to 700 nm) was collected continuously using an LI-193SA spherical quantum sensor that recorded PAR at canopy level in conjunction with an LI-1000 datalogger (LI-COR Inc., Lincoln, NB, USA) enclosed in an underwater housing. The underwater quantum sensor was cleaned regularly to minimize fouling. Photon flux density (PFD, μmol m^{-2} s^{-1}) was measured at 1 min intervals and integrated hourly. Daily PFD (mol m^{-2} d^{-1}) was calculated as the summation of quantum flux over each 24 h period.

Statistics. All values are reported as means ± 1 SE. Statistical analyses were performed on a microcomputer using a general linear model procedure (SAS Institute 1989). Significant differences in underwater irradiance, density, chl content, chl *a*:*b* ratios and leaf productivity among sampling times were tested using a 1-way ANOVA. A 2-way ANOVA was used to test significant differences in biomass and carbohydrate carbon content among sampling times and plant parts. When a significant difference among variables was observed, the means were analyzed by a Tukey multiple comparison test to determine where the significant differences occurred among variables.

RESULTS

Physical and chemical parameters

Underwater PFD, which was collected on a continuous basis from October 1993 to January 1995, exhibited a high degree of fluctuation (Fig. 1A). Average daily PFD ranged from 9.6 mol m^{-2} d^{-1} in April to 21.7 mol m^{-2} d^{-1} in July. Daily maximal PFD ranged from 50 to 1450 μmol m^{-2} s^{-1} and did not show a seasonal trend. The annual quantum flux at the seagrass canopy was 5382 mol m^{-2} yr^{-1}, which corresponded to 47% of surface irradiance (SI). In contrast, water temperature showed a strong seasonal trend ranging from 13°C in January to 30°C in August (Fig. 1B). Water column DIN concentrations, which were almost always less than 1 μM during the study period, did not show any distinct seasonal trend (Fig. 2).

Density, biomass and leaf production

Shoot (sht) density and total biomass showed significant seasonal variations ($p < 0.001$ and $p = 0.019$, respectively); values ranged from 321 shts m^{-2} (454 g dry wt m^{-2}) in March to 531 shts m^{-2} (885 g dry wt m^{-2}) in September (Fig. 3A). Biomass of individual plant parts was significantly different ($p < 0.001$; Fig. 3B). Leaf and root biomass also showed significant seasonal variation ($p < 0.001$ and $p = 0.0026$, respectively), but rhizomes and short shoots did not ($p = 0.777$ and $p = 0.418$, respectively). Leaf biomass was highest in September (355 g dry wt m^{-2}) and lowest in early April (81 g dry wt m^{-2}), while root biomass was highest in September (103 g dry wt m^{-2}) and lowest in late February (43 g dry wt m^{-2}). Seasonal changes in total biomass were closely correlated with variations in leaf biomass which showed higher annual variability as compared to that of other plant parts (Fig. 3A, B).

On an annual basis, rhizome tissues accounted for about 40% of total biomass, while root tissues accounted for about 12% of total biomass. Biomass partitioning into leaf tissues significantly changed with season ($p < 0.001$); leaf tissues accounted for 17% of total biomass in April and 41% in July. Biomass partitioning into rhizome tissues did not change with season ($p = 0.08$).
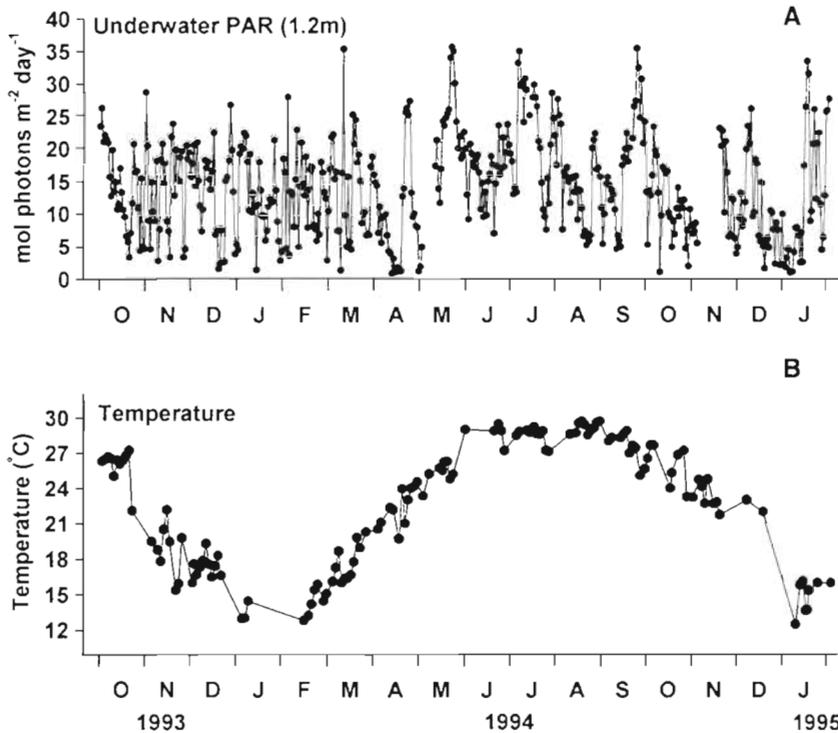
Fig. 1 (A) Daily irradiance recorded at canopy level and (B) water temperature in a *Thalassia testudinum* bed in Corpus Christi Bay (Texas, USA) from October 1993 to January 1995

Shoot production, as reflected by leaf growth (mg dry wt sht^{-1} d^{-1}), and areal leaf production (g dry wt m^{-2} d^{-1}) changed significantly with sampling time (p < 0.001), increasing during spring and summer, decreasing during fall, and approaching zero between December and February (Fig. 4). Leaf production was highest in July (12 mg dry wt sht^{-1} d^{-1} or 5.6 g dry wt m^{-2} d^{-1}) and lowest in December (0.2 mg dry wt sht^{-1} d^{-1} or 0.07 g dry wt m^{-2} d^{-1}), and was closely correlated with water temperature changes throughout the year (r^2 =
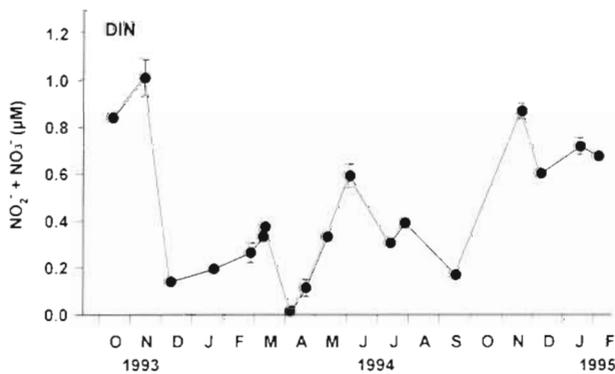

Fig. 2. Water column DIN (NO_3^- + NO_2^-) concentrations in Corpus Christi Bay from October 1993 to January 1995. Values are mean ± SE (n = 4). Where no error bars appear, SE is less than the size of the symbol
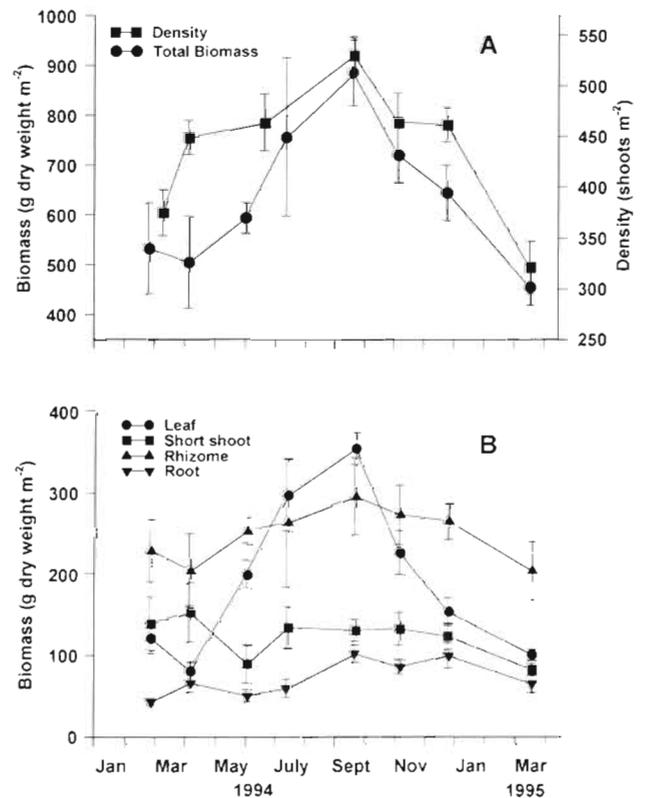

Fig. 3. *Thalassia testudinum*. Seasonal changes in (A) density and total biomass and (B) biomass of different plant components. Values are mean ± SE (n = 4 to 8)
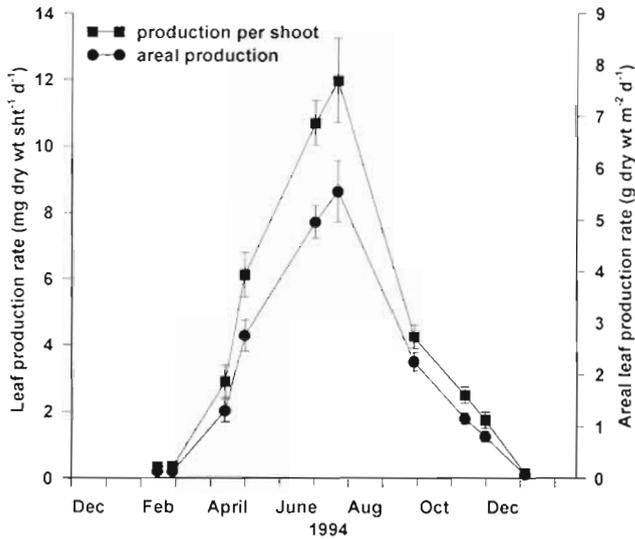
Fig. 4. *Thalassia testudinum*. Seasonal changes in leaf production rates per shoot and areal leaf production rate from February 1994 to January 1995. Values are mean ± SE (n = 5 to 16)

0.73). Productivity increased rapidly with increasing temperature during spring and summer and decreased rapidly with falling temperatures during fall and winter (Fig. 5A). On an annual basis, there was not a strong correlation between underwater irradiance and leaf productivity (r^2 = 0.41; Fig. 5B).

Chlorophyll

Total chl content from *Thalassia testudinum* leaf tissue changed significantly with sampling time (p = 0.004), ranging from 8.3 mg chl g^{-1} dry wt in June to 6.3 mg chl g^{-1} dry wt in February (Fig. 6). Chl content increased during spring, remained constant until early winter and decreased later in the winter. Chl *a:b* ratios also changed significantly with sampling time (p < 0.001), ranging from 2.9 in September to 3.2 in December (Fig. 6). In general, chl *a:b* ratios varied inversely with respect to total chl content, with highest values of total chl associated with higher proportions of chl *b* relative to chl *a*.

Non-structural carbohydrate carbon content

Total non-structural carbohydrate carbon content (based on 0.1 N HCl hydrolysis) was significantly different with sampling date (p < 0.001) and among different plant parts (p < 0.001). *Thalassia testudinum* had highest carbohydrate carbon content in mid-July and lowest in early June (Fig. 7). On an annual basis, aver-
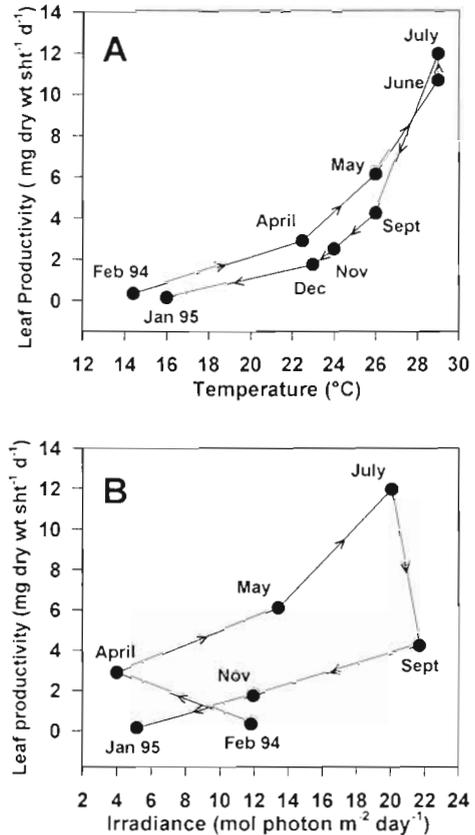

Fig. 5. *Thalassia testudinum*. Relationships between leaf productivity and (A) water temperature and (B) underwater irradiance from February 1994 to January 1995
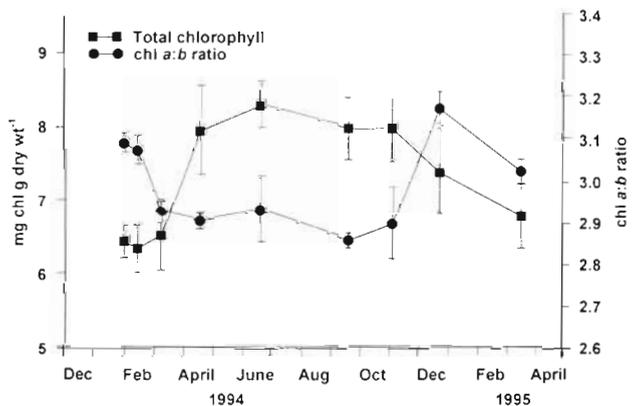

Fig. 6. *Thalassia testudinum*. Seasonal changes in total chlorophyll concentration and chl *a:b* ratio in blades of plants collected from January 1994 to March 1995. Values are mean ± SE (n = 6)

age carbohydrate carbon content was highest in rhizome tissues (159 mg C g^{-1} dry wt) and lowest in leaf tissues (59 mg C g^{-1} dry wt). Rhizome and short shoot carbohydrate carbon content increased rapidly during
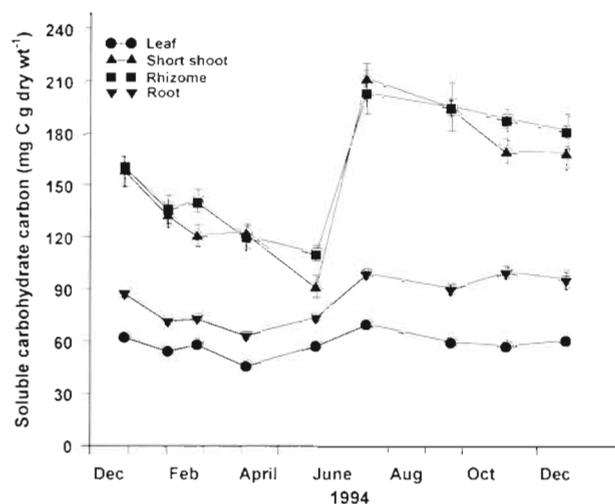
Fig. 7. *Thalassia testudinum*. Seasonal changes of total non-structural carbohydrate carbon content in leaf, short shoot, rhizome and root tissues. Values are mean ± SE (n = 4 to 5)

June and July, from 110 and 92 to 203 and 212 mg C g^{-1} dry wt, respectively, doubling over a 2 mo period. Levels decreased slightly during fall and decreased rapidly during winter and early spring. Total non-structural carbohydrate carbon content in leaves and roots showed little seasonal variation, with small increases during late spring and early summer, constant values in fall and early winter, and small decreases during late winter and early spring.

Total non-structural carbohydrate carbon estimated on an areal basis (g C m^{-2}) also varied significantly with sampling time (p < 0.001) and among different plant parts (p < 0.001). Total seagrass carbohydrate carbon was highest in September (115 g C m^{-2}) and lowest in April (51 g C m^{-2}). Non-structural carbohydrate carbon in rhizome ranged from 25 g C m^{-2} in April to 58 g C m^{-2} in September, and accounted for about 50% of total seagrass non-structural carbohydrate carbon throughout the year. Leaf carbohydrate carbon accounted for 8% of total seagrass carbohydrate carbon in April and 23% in June, while short shoot and root carbohydrate carbon accounted for an average of 25 and 8%, respectively, of total seagrass non-structural carbohydrate carbon in the seagrass bed.

DISCUSSION

Biomass and production

Thalassia testudinum in Corpus Christi Bay exhibited strong seasonal variations in density, biomass and leaf productivity, which increased during spring

and summer and decreased during fall and winter. Similar trends in seagrass standing crop and production have been reported for *T. testudinum* and other species earlier by several authors (Macauley et al. 1988, Dunton 1990, Thom 1990), and were attributed to changes in water temperature and insolation. Temperature has been considered as a major factor controlling seasonal growth (Tutin 1942, Phillips et al. 1983) because of its significant effect on the biochemical process involved in photosynthesis and tissue metabolism (Bulthuis 1987). However, some researchers have reported a poor correlation between water temperature and leaf productivity (Sand-Jensen & Borum 1983). In this study, there was a strong correlation between leaf productivities and water temperature. If plotted on a log scale, leaf productivity displayed an even stronger correlation with temperature (r^2 = 0.95), suggesting exponential changes in leaf productivity as a function of temperature. In contrast, with the exception of the late spring and summer periods, no relationship was apparent between leaf productivity and underwater irradiance. For example, leaf productivities increased from 0.4 to 2.9 mg dry wt sht^{-1} d^{-1} during early spring (February to April 1994) when underwater irradiance decreased from 12 to 4 mol m^{-2} d^{-1} (Fig. 5B). Based on these data, water temperature appears to regulate leaf productivity during fall to early spring, while both water temperature and underwater irradiance play a role during late spring and summer. Since early spring and winter growth appear to be supported by stored reserves in the below-ground tissues, temperature is probably a more important factor controlling seasonal growth than insolation because of its significant role in plant metabolism (Bulthuis 1987). Accordingly, underwater light reduction during the winter and early spring may affect seagrass production less than during summer (Czerny & Dunton 1995).

No significant correlation (r^2 = 0.065, p = 0.475) was found between leaf productivities and ambient DIN. Dunton (1996) reported that pore water ammonium levels in the study site (East Flats) were extremely variable and showed no seasonal trend. Therefore, water column DIN and sediment ammonium probably were not major controlling factors for seasonal growth in this study area.

Leaf production reflected seasonal changes in leaf biomass, increasing during spring and summer and decreasing during fall and winter. On the other hand, rhizome biomass was relatively constant throughout the year. Additionally, although root tissue exhibited significant seasonal variation, it accounts for a small portion of total seagrass biomass and hence does not have a noticeable effect on total biomass. Therefore, seasonal changes in *Thalassia testudinum* total bio-

mass occurred as a consequence of variations in leaf biomass. More metabolically active plant tissues, namely the leaf (photosynthetic organ) and root (nutrient absorption site), showed significant seasonal biomass variations, while the rhizome storage tissue did not.

To accurately estimate carbon balance, a better understanding of below-ground tissue dynamics is necessary, since below-ground tissues can constitute a significant portion of total plant biomass. However, few complete annual measurements of the *Thalassia testudinum* biomass divided into different plant parts have been reported; most research has been concerned with standing crop and conducted only for a short time period. Zieman (1975) reported that *T. testudinum* leaf tissues accounted for 15 to 22% of total biomass and the remainder was root and rhizome. However, as noted here, the partitioning of biomass to above- and below-ground tissues can show strong seasonal trends. In summer, leaf tissues can account for about 40% of total biomass, but only 15 to 20% during winter (rhizome biomass remains fairly constant at 40% throughout the year). Such distinct seasonal variations in the partitioning of above- and below-ground tissues can be critical in determinations of annual carbon balance in *T. testudinum*.

Seagrass communities contribute significantly to the primary production of shallow coastal ecosystems (Kentula & McIntire 1986, Roman & Able 1988, Peduzzi & Herndl 1991). To estimate the role of seagrasses in the carbon budget of a coastal ecosystem, the annual primary production of seagrasses has been estimated (Roman & Able 1988, Pergent & Pergent-Martini 1991, Gallegos et al. 1993). In this study, an annual blade production of 792 g dry wt m^{-2} yr^{-1} was calculated by adding measurements of leaf productivity for the entire annual period. It must be noted that blade production did not include sheath production. Preliminary elemental analysis indicated that about 32% of total dry weight was attributed to carbon. Thus, the annual blade production of 792 g dry wt m^{-2} yr^{-1} is equivalent to 253 g C m^{-2} yr^{-1}.

Shoot density of *Thalassia testudinum* in Corpus Christi Bay was similar to those reported for most other geographical areas (Table 1). Although biomass values for Cancun (Mexico) were similar to values from the present study, total biomass in the present study was much higher than values reported from Egmont Key and Anclote Key, Florida. Compared to low leaf biomass reported in Belize and Puerto Morelos (Mexico), leaf biomass in Corpus Christi Bay was almost 10-fold higher. Leaf productivities in Corpus Christi Bay were also high in comparison with values from other geographical areas, except for those in Cancun (Table 1). Biomass and leaf productivities appeared to vary as a function of water depth, sediment characteristics and temperature. Local environmental parameters are probably the most important determinators of biomass and productivity in this subtropical species.

Table 1 *Thalassia testudinum*. Density, biomass and leaf production at various geographical locations

Area (Depth)	Density (sht m^{-2})	Biomass (g dry wt m^{-2})	Leaf production (mg dry wt sht^{-1} d^{-1})	(g dry wt m^{-2} d^{-1})	Time	Source
Egmont Key, Florida, USA						
(0.4 m)	659 ± 82	217.7	17.88 ± 5.58		June	Dawes & Tomasko (1988)
(2.5 m)	1128 ± 224	107.6	7.24 ± 2.56		June	Dawes & Tomasko (1988)
Anclote Key, Florida						
(1 m)	454 ± 102	73.7	3.05 ± 1.55		July	Dawes & Tomasko (1988)
(2.5 m)	285 ± 109	80.0	3.52 ± 2.49		July	Dawes & Tomasko (1988)
Belize						
(0.5 m)	117–404	17.3–49.2[a]	1.6–6.1		May–June	Tomasko & Lapointe (1991)
(2.0 m)	106–260	22.3–48.6[a]	1.9–6.1		May–June	Tomasko & Lapointe (1991)
Honduras						
(0.5 m)	372 ± 19				May–June	Tomasko & Lapointe (1991)
(2.0 m)	324 ± 4				May–June	Tomasko & Lapointe (1991)
Puerto Morelos, Mexico						
(2.5–4.5 m)	547–661	24.5–57.0[a]		0.88–1.46	Annual mean	Tussenbroek (1995)
Cancun, Mexico	480–1222	482–1160		6.38 ± 2.3		Gallegos et al. (1993)
Florida Bay				0.05–3.42	Summer	Zieman et al. (1989)
Playa Habana, Cuba				1.6–18.1		Buesa (1974)
U.S. Virgin Islands	80–200		0.4–1.2	0.03–0.3	April–Nov	Williams (1988)
Corpus Christi Bay, Texas						
(1.2 m)	321–531	454–885	0.15–11.96	0.07–5.55	Seasonal	Present study

[a]Leaf

Chlorophyll

Chlorophyll (chl) concentrations in seagrasses fluctuate with variations in temperature and light regime (Wiginton & McMillan 1979, Dennison & Alberte 1982, 1985, Macauley et al. 1988, Abal et al. 1994). Seagrasses typically respond to light reduction by increasing chl content and decreasing chl $a:b$ ratios (Wiginton & McMillan 1979, Dennison & Alberte 1982, 1985, Abal et al. 1994, Lee & Dunton 1996). However, we observed high chl concentrations and low chl $a:b$ ratios during the period of high underwater irradiance. These measurements are not in agreement with seagrass photoadaptation in response to underwater light stress, suggesting plants in this study area are not light limited.

Instead, the seasonal changes in total chl content and chl $a:b$ ratios noted in this study are similar to those noted by Macauley et al. (1988), who noted that *Thalassia testudinum* blade chl concentrations were highest and chl $a:b$ ratios lowest during summer and early fall. These results provide evidence that variations in chl were related to water temperature and not to photoadaptive responses to changes in underwater irradiance. Chl is probably synthesized during high production periods (e.g. summer) to enhance light harvesting.

Leaf productivity and rhizome non-structural carbohydrate carbon content were closely correlated with chl content. The maximum chl concentration during June and July coincided with peaks of leaf productivity and rhizome carbohydrate carbon content. Photosynthesis was directly proportional to chl content in *Posidonia oceanica* (Drew 1978) and the highest P_{max} corresponded with a peak in total leaf chl in *Halodule wrightii* (Dunton & Tomasko 1994). It is likely that increases in leaf productivity and rhizome carbohydrate carbon content are a consequence, at least in part, of increased photosynthesis in response to higher blade chl content.

Non-structural carbohydrate carbon dynamics

Measurement of the distinct seasonal changes in non-structural carbohydrate carbon content, as reported in this study, provides valuable information for modeling the whole plant carbon balance in *Thalassia testudinum*. Many researchers have calculated whole plant carbon balance based on estimates from laboratory measured photosynthesis vs irradiance (P vs I) curves and the respiration rates of different plant parts to understand seagrass growth and survival under different environmental conditions (Zimmermann et al. 1989, 1991, Fourqurean & Zieman 1991). However, laboratory measurements of seagrass photosynthesis with leaf segments cannot always be extrapolated into the field (Dunton & Tomasko 1994). In experiments with *Zostera marina*, Zimmermann et al. (1989) noted that respiration rates calculated from the incubation of root and rhizome tissues in the laboratory vary as a function of oxygen concentration in the incubation medium. Consequently, total plant respiration can be overestimated since rhizome and root tissues are usually located in anoxic sediments, not in a well ventilated water column.

Seagrass rhizome tissues usually act as photosynthate storage tissue (Dawes & Lawrence 1979, Durako & Moffler 1985, Pirc 1985, 1989). Stored carbon can be used to meet respiratory demands and can contribute to plant growth when carbon demands exceed photosynthesis. Photosynthetic carbon accumulates as non-structural carbohydrate in the rhizome tissues when photosynthesis exceeds the carbon demands from respiration and growth. Therefore, the increase in rhizome carbohydrate carbon content indicates a positive whole plant carbon balance against respiration and growth, while a decreased rhizome carbohydrate carbon indicates a negative carbon balance. In this study, rhizome carbohydrate carbon content increased dramatically during June and July, indicating periods of positive carbon balance. This rapid increase in rhizome carbohydrate carbon content coincided with high water temperatures and underwater irradiance, as well as high chl concentrations, low chl $a:b$ ratios and high leaf biomass. Since the plants experienced optimal environmental and biological conditions for high photosynthetic production, there was a net storage of non-structural carbohydrate carbon in the rhizome tissues. During winter and spring, the plants showed a negative whole plant carbon balance as rhizome carbohydrate carbon content decreased rapidly. The rapid decrease of carbohydrate carbon contents during spring was probably due to spring leaf growth (Dawes & Lawrence 1979, Durako & Moffler 1985, Pirc 1985, 1989). Tissues not used for storage of carbon, particularly leaf and root material, did not show strong seasonal trends in carbohydrate carbon content.

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