

Temporal variation of biomass and productivity of *Thalassia testudinum* (Hydrocharitaceae) in Venezuela, Southern Caribbean

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Abstract. Annual biomass and productivity of *Thalassia testudinum* were determined during a year at a seagrass bed located in the Parque Nacional Morrocoy, Venezuela. Leaf, rhizome and root biomass were determined monthly, together with short-shoot density, from February 1992 to January 1993, from nine replicated core samples. Productivity was measured using the methodology by Ziemann (1974) with minor modifications, and leaf turnover rate was calculated. Leaf biomass values ranged between 101.73 dry g m⁻² in February and 178.11 dry g m⁻² in August. Productivity ranged from 1.69 dry g m⁻² d⁻¹ in April and October to 3.30 dry g m⁻² d⁻¹ in July, showing two annual peaks: one in July and one in March. The leaf turnover rate showed the highest value in June (2.41% d⁻¹) and the lowest in May (1.23% d⁻¹). Sampling time differences in leaf biomass, productivity and turnover rate were statistically significant. Short-shoot density values varied between 811.10 shoots m⁻² in April and 1226.08 shoots m⁻² in December, but the differences were not significant along the year. These results indicated seasonal trends for leaf biomass, productivity and turnover rate of *T. testudinum* in the Southern Caribbean (latitude 10°N). Rev. Biol. Trop. 54(2): 329-339. Epub 2006 Jun 01.

Key words: tropical seagrasses, *Thalassia testudinum*, temporal variations, productivity, biomass.

Seasonal changes in productivity, biomass and density in natural populations of seagrasses have been determined for temperate and sub-tropical areas: e.g. *Thalassia testudinum* (Ziemann 1975); *Zostera marina* (Jacobs 1979, Aioi 1980); *T. testudinum* and *Syringodium filiforme* (Barber and Behrens 1985); *Amphibolis antarctica* and *Posidonia australis* (Walker and McComb 1988); *Posidonia oceanica* (Buia *et al.* 1992) and *Zostera noltii* (Vermaat and Verhagen 1996). However, these studies are scarce for tropical seagrasses (e.g. *Thalassia hemprichii*: Brouns 1985, 1987, Moriarty *et al.* 1990). Growth, production and distribution have been determined for *T. testudinum* (Banks ex König), species that dominates the highly productive seagrass meadows of the Caribbean Sea (e.g. Barbados: Patriquin 1973; Cuba: Buesa 1974, 1975; Jamaica: Greenway

1974; Mexico, Belize and Honduras: Tomasko and Lapointe 1991; Mexico: Gallegos *et al.* 1992, 1993, Marba *et al.* 1994, Espinoza 1996, Van Tussenbroek 1996 a,b, Van Tussenbroek *et al.* 1996; Venezuela: Pérez and Galindo 2000, Bone *et al.* 2001). Nonetheless, these studies are rarely concerned with seasonal variations of biomass and productivity. Recent information on seasonal patterns of growth and primary production of *T. testudinum* in the Caribbean Sea is limited to the study by Van Tussenbroek (1995) at Puerto Morelos, Mexico, 20°51' N latitude. This author reported that the leaf growth and primary production were significantly correlated with water temperature and/or the hours of daylight throughout the year. At 20°N latitude there is a seasonal difference on daylight of 2.6 hours (from 13.4 h to 10.8 h, Van Tussenbroek 1995). To our knowledge,

seasonal fluctuations have not been reported further South. Present work concerns a field research carried out during a year in a *T. testudinum* seagrass bed located in the Parque Nacional Morrocoy, Venezuela (10°50' N, 68°20' W), to characterize the annual variations for biomass, productivity, short-shoot density, leaf turnover rate, allocation of the biomass into the different parts of the plant, and determine possible relations with surface water temperature, surface salinity, dissolved oxygen and water transparency.

MATERIALS AND METHODS

Study site. The study site is located at Las Luisas, within Parque Nacional Morrocoy (10°50' N, 68°20' W), a marine sanctuary covering 320 km², located on the western coast of Venezuela (Bone *et al.* 1998, Penchaszadeh *et al.* 2000). Monthly measurements of temperature and salinity done at Las Luisas, between August 1992 and November 1999, indicated annual mean values of $29.87 \pm 1.41^{\circ}\text{C}$ and $37.17 \pm 2.97\text{‰}$ (Bone *et al.* 2001). The rain regime is bimodal, with the minima between January and March and the maxima between September and December (Bone *et al.* 2001). Average annual precipitation from January 1968 to December 1995 was 1 148 mm (Pérez and Galindo 2000). The seawater at Las Luisas is oligotrophic, with low average concentrations of nitrites, nitrates and phosphates (Gutiérrez 1997). Transparency in the seagrass beds from Parque Nacional Morrocoy is low compared to other seagrass meadows in the Caribbean Sea (Bone *et al.* 2001). Sediments are mostly coarse and calcareous, and contain 10% organic matter (Guevara 1993). The mangrove *Rhizophora mangle* borders the shore of the study site. The submersed vegetation is largely comprised by *T. testudinum* accompanied by algae such as *Halimeda opuntia*, *H. incrassata*, *H. monile* and *Padina gimnospora*, with *H. opuntia* as the dominant green algae which forms a dense mat over the substrate (Pérez and Galindo 2000). Las Luisas was chosen as the study location

because it has a healthy looking and highly dense meadow of *T. testudinum*, fringing for almost 2 km a straight coastline. Along this fringe, the meadow extends from the mangrove border to more than 50 m offshore, on a flat slope from 0.5 to 3.0 m depth.

Environmental data. We obtained monthly measurements, taken between 10:00 and 11:00, of temperature, salinity, dissolved oxygen and water transparency. The environmental parameters were measured in three sites, 0.5, 1.5 and 3.0 m deep. Temperature was measured at 0.2 m above the canopy using a hand-held thermometer ($\pm 0.5^{\circ}\text{C}$). Salinity was measured using an optical refractometer ($\pm 1\text{‰}$) and dissolved oxygen was measured with a YSI recorder ($\pm 0.01 \text{ mg/l}$), at 0.2 m depth. Given the shallow depth of the study site, water transparency was measured by horizontal distance readings at 0.2 m deep, using the Secchi disk ($\pm 0.1 \text{ m}$). Sediment samples were taken at Las Luisas in March, June, August and November 1994, to determine their nutrient content. Total N was determined using the method by Jackson (1982) and total P was determined using the method by Murphy and Riley (1962).

Biomass and short-shoot density. Monthly samples of *T. testudinum* were taken at Las Luisas, from February 1992 to January 1993, in a sampling station 20 m offshore and 1.5 m deep. Nine replicated samples were collected with a corer (area 176.71 cm²), which was pushed to a depth of 40 cm into the sediment to obtain over 90% of rhizomes and roots (Pérez and Galindo 2000). Each core sample was placed into a fine-meshed bag and shaken underwater to remove most of the fine-grained sediment. Once in the laboratory, plant samples were washed on a 1 mm screen sieve and were separated from coarse shell material and bulky sediments by hand. Short-shoot number was recorded and plant material was separated into the fractions (CARICOMP 1994): green leaves (GL), sheaths (SH), short-shoots (SS), horizontal rhizomes (RH), roots (RO) and dead material (DM). Live blades were green,

whereas dead tissue was brownish in colour. Live rhizomes and short-shoots were firm in texture and live roots were whitish or grayish in colour and had a crisp texture (Van Tussenbroek 1998). Epiphytes were removed from leaves by moderate blade scraping followed by slight acidification (HCl 10% for 5 min), ensuring almost complete cleaning with very little damage of the blade (Dauby and Poulicek 1996). All plant fractions were rinsed thoroughly in freshwater and dried (60°C) until constant weight was obtained. The dry weight of each fraction and the number of short shoots were scaled to 1 m².

Leaf production and turnover rate. Leaf production was measured using the methodology proposed by Zieman (1974) with minor modifications. Each month nine 10 x 20 cm quadrates were placed at the sampling site. All the leaves on the short-shoots (vertical rhizomes) inside the frame were pierced at the “green-white border” with a metallic punch (2.5 mm in diameter). Short-shoots of *T. testudinum* produce leaves, consisting of a colourless sheath and a green photosynthetic blade (Van Tussenbroek 1998). Leaves are held tightly together by the bundle sheath. Above it, the leaves separate and become green, but below it leaves are still whitish. The “green-white border” is the zone of a leaf in which the white tissue becomes green (CARICOMP 1994). As the height of this border varies between external and internal leaves on the same short shoot, we pierced all the leaves at the green-white border level of the internal ones.

After 8 or 9 days, all the leaves on the short shoots inside the frame were harvested by cutting them under the green-white border of the internal leaves. Leaves samples were separated in two groups: 1) new leaves, without mark, and new leaf tissue emerged since marking (the section of the leaf from the mark down to the green-white border), and 2) old leaf tissue, parts of leaves present before marking, located above the mark. Leaf productivity (i.e. daily production, DProd) was calculated by dividing the biomass of group 1 by the period of

growth (8 to 9 days). The sum of the biomass of the two groups was used as the standing crop (StCrop) of the sample, and the turnover rate (percent of the leaf biomass that is replaced per day) was calculated as follows: Turnover rate = (DProd / StCrop).100

Data Analyses. Mean values of biomass, productivity, short-shoot density and turnover rates were compared by a one-way ANOVA with time as the main factor (Sokal and Rohlf 1981). All data were previously tested for assumptions of normality and homocedasticity.

RESULTS

Environmental data. The water temperature values were lowest in February and September ($27 \pm 0.0 - 27.3 \pm 0.5^\circ\text{C}$) and highest in June ($32 \pm 0.0^\circ\text{C}$), with an annual mean of $29.2 \pm 1.4^\circ\text{C}$ (Table 1). Salinity varied throughout the year between $35.3 \pm 0.4\text{‰}$ in April and January and $40.6 \pm 0.4\text{‰}$ in March, the annual mean was $37.1 \pm 1.5\text{‰}$. Dissolved oxygen fluctuated between $4.87 \pm 0.09 \text{ mg l}^{-1}$ in June and $7.20 \pm 0.16 \text{ mg l}^{-1}$ in December, with an annual mean of $5.70 \pm 0.73 \text{ mg l}^{-1}$. Water transparency ranged from $3.60 \pm 0.41 \text{ m}$ in September to $6.33 \pm 1.84 \text{ m}$ in December, with an annual mean of $4.69 \pm 0.83 \text{ m}$ (Table 1). Total N content in sediment was lowest in March ($2.35 \pm 0.98 \text{ mg g}^{-1}$) and highest in August ($10.28 \pm 2.35 \text{ mg g}^{-1}$) (Table 2). Total P content was lowest in August ($0.14 \pm 0.09 \text{ mg g}^{-1}$) and highest in November ($1.30 \pm 0.51 \text{ mg g}^{-1}$). N:P relation was lowest in March (3:1) and highest in August (73:1).

Biomass and short-shoot density. Total live biomass values fluctuated around an annual mean of $638.24 \pm 60.50 \text{ dry g m}^{-2}$ (Table 3), with the lower values in April (543.22 ± 92.15) and December (558.52 ± 85.30), and the highest in May (721.91 ± 116.94) (Fig.1). The differences between monthly values for the total biomass were not statistically significant (ANOVA, $F = 2.13$, $p = 0.14$). The biomass of

TABLE 1
Environmental data from Las Luisas, Parque Nacional Morrocoy, Venezuela, from February 1992 to January 1993. Average and standard deviation

Month	Temperature (°C)	Salinity (‰)	Dissolved oxygen (mg l ⁻¹)	Transparency (m)
February	27.0 ± 0.0	36.6 ± 0.9	5.20 ± 0.43	4.13 ± 0.37
March	28.2 ± 0.2	40.6 ± 0.4	6.33 ± 0.38	4.10 ± 1.10
April	29.1 ± 0.3	35.3 ± 0.4	5.27 ± 0.25	4.10 ± 0.33
May	30.8 ± 0.3	36.3 ± 0.9	5.70 ± 0.22	4.20 ± 0.33
June	32.0 ± 0.0	37.1 ± 1.0	4.87 ± 0.09	4.63 ± 0.96
July	29.9 ± 0.3	38.3 ± 0.4	5.13 ± 0.25	4.30 ± 0.59
August	30.6 ± 0.6	36.3 ± 1.8	5.27 ± 0.21	5.73 ± 1.03
September	27.3 ± 0.5	37.3 ± 0.9	6.03 ± 0.26	3.60 ± 0.41
October	29.3 ± 1.15	38.6 ± 0.9	6.80 ± 0.29	5.73 ± 0.56
November	29.6 ± 0.3	37.3 ± 1.8	5.30 ± 0.36	4.93 ± 1.52
December	28.5 ± 0.5	36.3 ± 0.9	7.20 ± 0.16	6.33 ± 1.84
January	28.5 ± 0.5	35.3 ± 0.4	5.33 ± 0.41	4.43 ± 1.20
Average	29.2 ± 1.4	37.1 ± 1.5	5.70 ± 0.73	4.69 ± 0.83

the plant's fractions also fluctuated along the year (Table 3). The biomass of the green leaves fraction fluctuated between 101.73 ± 7.27 dry g m⁻² in December and 178.11 ± 10.81 dry g m⁻² in August (Table 3). The highest green leaves biomass was observed in April and August (Fig. 2). Biomass of the rhizome fraction ranged from 230.88 ± 101.5 dry g m⁻² in October to 321.05 ± 105.24 dry g m⁻² in June. Biomass of the roots fraction fluctuated between $37.70 \pm$

24.23 dry g m⁻² in April and 75.07 ± 25.28 dry g m⁻² in February. Biomass of dead material ranged from 44.97 ± 20.08 dry g m⁻² in April to 107.05 ± 77.52 dry g m⁻² in May (Table 3). From these, only the monthly variations of the biomass of the green leaves (ANOVA, F= 3.26, p = 0.042) and the dead material fraction (ANOVA, F= 4.13, p = 0.008) were statistically significant. Short-shoot density values fluctuated between 811.10 ± 174.93 shoots/m² in April and $1\ 226.08 \pm 96.18$ shoots/m² in December (Fig. 3), with an annual mean of $1\ 025.45 \pm 253.19$ shoots/m². Despite the fluctuations, the short-shoot density values did not show significant monthly variations (ANOVA, F= 1.24, p= 0.31).

TABLE 2
Total N and P content, and N:P relation in sediments at Las Luisas, Parque Nacional Morrocoy, Venezuela, from March to November 1994. Average and standard deviation

Month	Total N mg g ⁻¹	Total P mg g ⁻¹	N:P
March	2.35 ± 0.98	0.78 ± 0.23	3:1
June	9.27 ± 1.14	0.56 ± 0.10	16:1
August	10.28 ± 2.35	0.14 ± 0.09	73:1
November	6.44 ± 1.07	1.30 ± 0.51	4:1
Average	7.08 ± 1.36	0.69 ± 0.21	10:1

Leaf production and turnover rate. Leaf production was seasonal (Fig. 4), with two annual periods of higher productivity: one towards mid-year months (July-August) and the other one at the beginning of the year (January-March). Productivity ranged from 1.69 dry g m⁻² d⁻¹ in April and October to 3.30 dry g m⁻² d⁻¹ in July, with an annual mean of $2.35 \pm$

TABLE 3
Biomass (dry g m⁻²) of Thalassia testudinum at Las Luisas, Parque Nacional Morrocoy, from February 1992 to January 1993

Month	GL	SH+SS	RH	RO	TLB	DM
February	107.80 ± 10.44	234.81 ± 68.16	275.80 ± 114.25	75.07 ± 25.28	623.99 ± 56.23	75.10 ± 14.32
March	132.03 ± 8.52	260.41 ± 96.94	262.85 ± 120.55	62.36 ± 32.64	668.33 ± 104.25	67.80 ± 15.67
April	153.82 ± 12.24	198.13 ± 72.73	222.56 ± 96.32	37.70 ± 24.23	543.22 ± 92.15	44.97 ± 20.08
May	113.89 ± 9.48	265.11 ± 101.24	311.38 ± 87.59	74.97 ± 37.55	721.91 ± 116.94	107.05 ± 77.52
June	130.27 ± 7.63	286.24 ± 92.38	321.05 ± 105.24	46.52 ± 19.13	711.33 ± 206.21	65.88 ± 9.81
July	108.56 ± 17.34	211.88 ± 78.53	245.38 ± 92.05	54.46 ± 21.33	620.27 ± 95.16	64.90 ± 13.44
August	178.11 ± 10.81	307.50 ± 136.94	274.32 ± 78.34	55.19 ± 22.87	711.91 ± 194.52	47.28 ± 17.27
September	148.06 ± 7.98	247.85 ± 76.03	232.75 ± 95.40	49.01 ± 19.76	626.11 ± 78.28	80.61 ± 21.62
October	118.83 ± 12.56	197.25 ± 84.04	230.88 ± 101.05	43.19 ± 23.65	590.04 ± 148.13	59.27 ± 17.14
November	132.88 ± 8.34	258.24 ± 99.14	294.29 ± 112.10	47.71 ± 30.12	681.55 ± 234.63	58.94 ± 21.32
December	101.73 ± 7.27	214.04 ± 98.21	233.86 ± 98.23	44.38 ± 14.66	558.52 ± 85.30	60.15 ± 19.08
January	106.39 ± 9.46	236.74 ± 57.84	246.60 ± 77.67	58.80 ± 22.06	601.73 ± 99.21	56.00 ± 19.89

Green leaves (GL), sheaths and short-shoots (SH + SS), rhizomes (RH), roots (RO), total live biomass (TLB) and dead material (DM). Average and standard deviation.

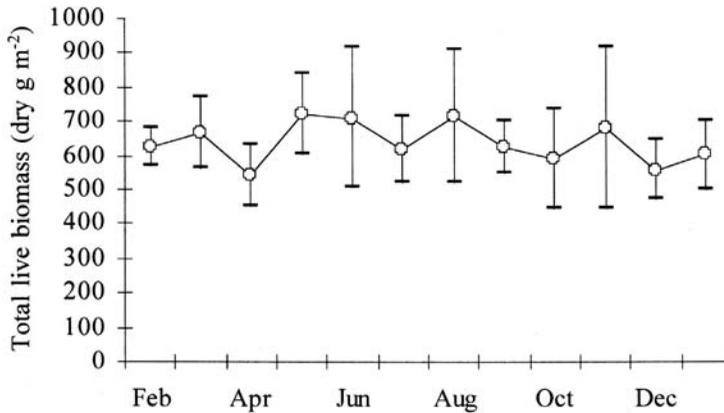


Fig. 1. Average total live biomass of *Thalassia testudinum* at Las Luisas, Parque Nacional Morrocoy, from February 92 to January 93. Bars represent standard deviation.

0.72 dry g m⁻² d⁻¹. These differences were statistically significant (ANOVA, F= 3.05, p= 0.01). The turnover rate (Fig. 5) showed the highest values in June (2.41% d⁻¹) and July (2.24% d⁻¹), and the lowest ones in May (1.23% d⁻¹) and November (1.47% d⁻¹), showing a similar significant temporal trend as for productivity (ANOVA, F= 4.44, p = 0.001).

DISCUSSION

Our sampling location may be affected by hypersaline water flows coming from adjacent shallow mangrove lagoons (from 48‰ in March to 56‰ in November). The highest leaf productivity for *T. testudinum* at Las Luisas was found in July, when the salinity was 38.3

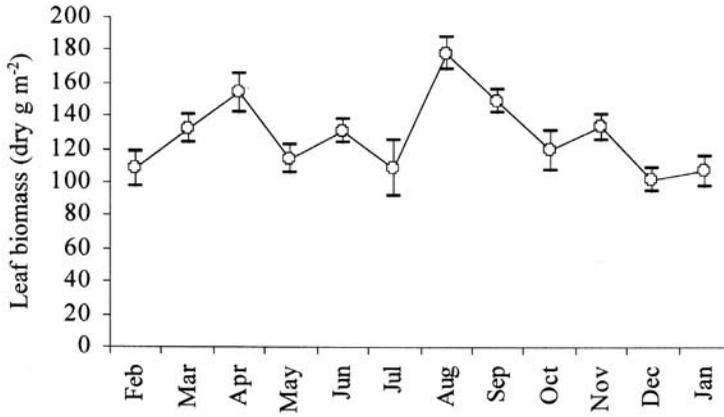


Fig. 2. Average leaf biomass of *Thalassia testudinum* at Las Luisas, Parque Nacional Morrocoy, from February 92 to January 93. Bars represent standard deviation.

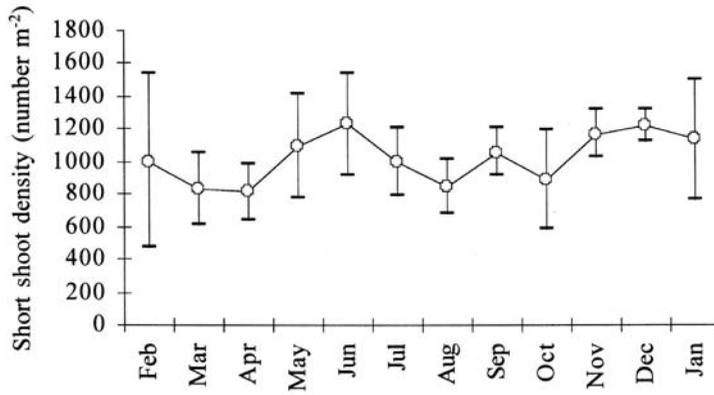


Fig. 3. Average short shoot density of *Thalassia testudinum* at Las Luisas, Parque Nacional Morrocoy, from February 92 to January 93. Bars represent standard deviation.

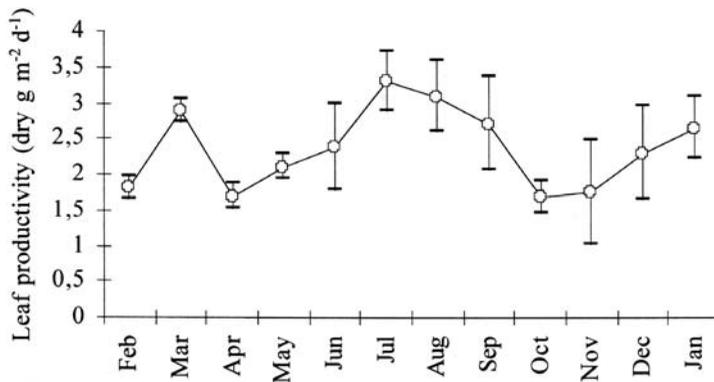


Fig. 4. Average leaf productivity of *Thalassia testudinum* at Las Luisas, Parque Nacional Morrocoy, from February 92 to January 93. Bars represent standard deviation.

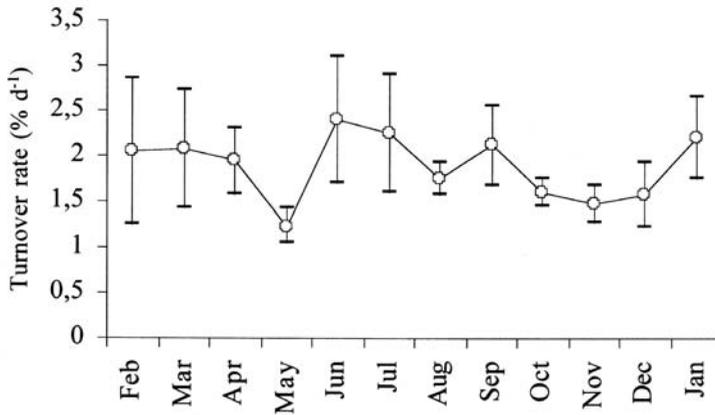


Fig. 5. Average leaf turnover rate of *Thalassia testudinum* at Las Luisas, Parque Nacional Morrocoy from February 92 to January 93. Bars represent standard deviation.

$\pm 0.4\%$. In March, when salinity reached $40.6 \pm 0.4\%$, no decrease in leaf productivity was recorded. On the contrary, an increase of this variable was detected with respect to the previous month. At Florida Bay, Zieman (1975) found *T. testudinum* maximum productivity at 30‰. Salinity values found at Las Luisas in the high productivity months were greater than the ones reported by Zieman (1975) as being optimal for *T. testudinum* growth in subtropical areas. Nonetheless, it is possible that optimal leaf productivity was not reached at Las Luisas due to sustained high annual salinity values at this locality, frequently greater than 36‰.

Water temperature at the study site varied between 27°C and 32°C, with the lowest values at the beginning of the year and the highest around the middle months. Water temperature in July, the month of the highest mean leaf productivity value ($3.34 \text{ dry g m}^{-2} \text{ d}^{-1}$) was $29.9 \pm 0.3^\circ\text{C}$. Zieman (1975) indicated that 30°C corresponds to the optimum for *T. testudinum* growth. *T. testudinum* production has been positively related to the increase of temperature between 20°C and 30°C in subtropical zones (Zieman 1975, Barber and Behrens 1985); over 30°C, growth decrease is expected (Bulthuis 1987). However, in this study the leaf production of *T. testudinum* was significantly increased in June, when the water temperature reached up to 32°C. A similar behavior has been

reported for *Cymodocea nodosa* (Drew 1978, Pérez and Romero 1992). Barber and Behrens (1985) found variations in leaf biomass turnover rate of *T. testudinum* from the west coast of Florida twenty times higher than the average value when the water temperature increased 14°C, from 18 to 32°C. Despite a 5°C difference found in our study, between February and June, no change in leaf biomass turnover rate was detected in those same months. On the contrary, in this study the lowest leaf biomass turnover rate was found in May when the water temperature was $30.8 \pm 0.3^\circ\text{C}$.

The possible relations between environmental parameters and biological variables were not evident in this study. Environmental data were taken only once a month; these parameters can fluctuate from day to day in a month, especially in shallow coastal areas such as the study site. The growth and dimensions of the seagrass depend on the salinity, temperature and light regime; thus more accurate environmental data are required before conclusions about the absence or presence of correlations between environmental and seagrass growth and morphometric parameters can be drawn.

We did not find significant variations of total biomass and shoot density of *T. testudinum* at Las Luisas (10°N) along the year but we found significant changes of leaf biomass and productivity, with the same annual pattern of

temporal variability for both variables: maxima at the mid-year months and minima at the end of the year. The highest green leaves biomass was observed in April and August, probably as a consequence of the increased productivity in March and July. We compared our results with the available data on seasonal growth of *T. testudinum* and *T. hemprichii* (Ehrenb.) Ascherson within tropical areas (Table 4). From these data it appeared evident that the significant variations were found only when monthly sampling was done. In Puerto Morelos, Mexico (20°-21° N) Van Tussenbroek (1995) reported that shoot density of *T. testudinum* displayed an upward trend from summer to winter rather than a seasonally fluctuating one, but found seasonal variations of leaf growth, leaf biomass and leaf production, minimum during winter and maximum during summer months, with a similar pattern as the seasonal variability in growth and production of *T. testudinum* that has been reported in South Florida

(25° N) (Zieman 1974, 1975, Thorhaug and Roessler 1977) and for other seagrasses elsewhere at temperate areas (Duarte 1989). We agree with the proposal of Van Tussenbroek (1995) that a monthly sampling scheme is probably necessary to detect seasonal variability at tropical latitudes.

Several authors have showed the importance of nutrient availability for seagrass growth and production (e.g. Orth 1977, Short 1983 1987; Powell *et al.* 1989, Short *et al.* 1990, Pérez *et al.* 1991, 1994, Pérez and Romero 1994). Nutrient availability is controlled locally by land inputs, sediment dynamics and type (Short 1987, Hemminga *et al.* 1991), and influences of associated biota (Aller 1980, Yamada and Kayama 1987). The results of the studies of De Mahieu and Ojeda (1989) and Gutiérrez (1997) done at Las Luisas suggest that the concentration of nitrogen compounds in the water column is sufficient to sustain the productivity of the system. This is not the case

TABLE 4
Comparison between data of growth variables of *T. testudinum* and *T. hemprichii* from tropical locations

Species	Site and latitude	Sampling Frequency	Shoot Density n° m ⁻²	Leaf Biomass g m ⁻²	Leaf Production g m ⁻² d ⁻¹	Turnover rate % d ⁻¹	Reference
<i>T. hemprichii</i>	Papua New Guinea, 8° S	monthly	430-2060	22 - 56*	2.77 - 5.53**	2.6 - 3.7*	Brouns 1985
<i>T. hemprichii</i>	Papua New Guinea, 8° S	monthly	av. 860	56*	2.5*	nd	Brouns 1987
<i>T. hemprichii</i>	Gulf of Carpentaria Australia, 14° S	quarterly	av. 600	61	0.3 gC/mg/d***	nd	Moriarty <i>et al.</i> 1990
<i>T. testudinum</i>	Cuba, 22-23° N	quarterly	nd	90.9	4.57	1.2	Buesa 1975
<i>T. testudinum</i>	Jamaica, 18° N	quarterly	av. 941	248.6	5.95	nd	Greenway 1974
<i>T. testudinum</i>	Puerto Morelos Mexico, 20-21° N	monthly	547-743	24.5 - 57.0*	0.88 - 1.15*	nd	Van Tussenbroek 1995
<i>T. testudinum</i>	Las Luisas Venezuela, 10° N	monthly	av. 982	av.110.96*	av.2.35*	av.1.87*	this study

Data represents annual means except where more than one value is shown, which indicates local variations. (*) significant variation in time, (**) significant variation only in one study site, (***) determined from rates of lacunal gas production, (av.) average, (nd) data no available.

for phosphates, which seems to be the limiting nutrient during most of the year as reported by Gutiérrez (1997), who found a N:P relation of 16:1 in the water column only for June and suggested a co-limitation for both nutrients at Parque Nacional Morrocoy, depending on the season of the year.

Annual variations in leaf biomass and primary production of *T. testudinum* at Las Luisas could be related to differences in nutrient content of the sediment, as reported by Fourqurean *et al.* (1992) for the same species in a subtropical environment. Our results about nutrient availability in the sediments at Las Luisas indicated a N:P relation of 16:1 in June, while nitrogen might be limitant in March and November (3:1 and 4:1, respectively) and phosphates in August (73:1). Nonetheless, if we consider the relation N:P = 30:1 proposed by Atkinson and Smith (1983) for macrophytes, we would also have nitrogen limitation for June. To explain the decline in sediment nutrient concentrations in *P. oceanica* meadows following periods of fast growth, Alcoverro *et al.* (1995) proposed the possibility that nutrient limitation could result from nutrient depletion due to uptake by the plants, with the subsequent effect on plant growth. This argument would contribute to explain why *T. testudinum* leaf productivity decrease following high productivity periods during the mid-year months at Las Luisas. This possibility and the effect of nutrient input in the rainy season or nutrient depletion in the drought season over growth and production of *T. testudinum* at the study site is currently being studied.

RESUMEN

Durante un año se determinaron mensualmente la productividad foliar, la densidad de tallos cortos y la biomasa de hojas, tallos cortos, rizomas y raíces de *Thalassia testudinum*, en una "pradera" localizada en el Parque Nacional Morrocoy, Venezuela. Los valores de biomasa foliar estuvieron entre 101.73 g/m² en febrero y 178.11 g/m² en agosto, los de productividad foliar se ubicaron entre 1.69 g/m²/d en abril y octubre y 3.30 g/m²/d en julio, mostrando dos picos anuales, uno en julio y otro en marzo. La tasa de recambio foliar mostró el mayor valor en

junio (2.41%/d) y el menor en mayo (1.23%/d). Tales diferencias fueron estadísticamente significativas durante el año para todas estas variables. La densidad de tallos cortos fluctuó entre 811.10 tallos/m² en abril y 1 226.08 tallos/m² en diciembre, pero las diferencias no fueron significativas a lo largo del año. Estos resultados indicaron una tendencia estacional para la biomasa foliar, la productividad foliar y la tasa de recambio de las hojas de *T. testudinum* en el Caribe Sur, a 10° N de latitud.

Palabras clave: algas marinas tropicales, *Thalassia testudinum*, variaciones temporales, productividad, biomasa.

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