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Spatial Influences on Temporal Variations in Leaf Growth and Chemical Composition of *Thalassia testudinum* Banks Ex König in Tampa Bay, Florida

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SPATIAL INFLUENCES ON TEMPORAL VARIATIONS IN LEAF GROWTH AND CHEMICAL COMPOSITION OF *THALASSIA TESTUDINUM* BANKS EX KÖNIG IN TAMPA BAY, FLORIDA

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ABSTRACT   The importance of spatial influences on seasonal fluctuations in *Thalassia testudinum* leaf blade lengths and chemical constituents was demonstrated. Differences between samples from fringe and mid-bed for several constituents were significant and, if not accounted for, could affect the measurement of apparent seasonal cycles. Fringe-shoots, reflecting the influence of more intense grazing activity, had shorter leaf blade lengths, lower dry weights and carbohydrate levels, and higher protein levels than mid-bed shoots. Mid-bed rhizomes and roots had highest protein and ash levels reflecting possible sediment influence. Percent ash and protein in the rhizomes, and percent carbohydrate in the roots exhibited seasonal fluctuations, but the levels were different between fringe and mid-bed samples. Protein levels were greatest in shoots and roots, while carbohydrate levels were highest in rhizomes, illustrating the respective partitioning of biosynthetic and storage functions. The spatial differences seem to reflect gradients in biological and chemical interactions, and they may play an important role in trophic interactions in seagrass systems.

INTRODUCTION

Studies on chemical composition of several seagrass species have demonstrated the presence of annual cycles (Walsh and Grow 1972, Harrison and Mann 1975, Dawes et al. 1979, Dawes and Lawrence 1980). Walsh and Grow (1972) and Dawes and Lawrence (1980) showed that in the dominant Florida seagrass, *Thalassia testudinum*, protein levels generally were highest in spring and early summer, while carbohydrate, ash, and dry weight levels peaked in the fall. Rhizomes contained relatively large amounts of carbohydrates, and function as storage organs for nutrient reserves. In contrast, leaves and shoots usually had higher protein levels than rhizomes due to greater biosynthetic activity.

Most previous studies of seasonality in seagrasses have utilized random sampling techniques which assumed that seagrass meadows were uniform communities. However, when environmental or successional gradients are suspected in a plant community, sampling along transects is more appropriate than random sampling (Whittaker 1967). In this regard, Zieman (1972) reported lower leaf blade densities and shorter blade lengths at the fringe compared to the center of circular beds of *T. testudinum* in Biscayne Bay, Florida. Capone and Taylor (1977), also working in Biscayne Bay, found that the dry weight of leaves per short-shoot and the number of leaves per square meter were lower at the fringe of a *T. testudinum* bed than in the interior. They also reported higher N_2 fixation activity associated with intact foliage at the fringe. Additional spatial trends have been observed in temperate *Zostera marina* L. meadows (Fonseca 1981, Kenworthy 1981). Kenworthy (1981) noted the largest pools of sedimentary

nitrogen, finest sediments, and highest shoot production may be associated with the mid-bed regions of *Z. marina* meadows. He suggested that fringe areas represent colonizing stages of growth, while mid-bed regions illustrate later successional stages. Organic matter content of sediments and leaf area index (LAI) may also increase with distance into a bed (Fonseca 1981).

This study examined the spatial and temporal variations of chemical constituents in *T. testudinum* shoots, rhizomes, and roots. We utilized transect sampling to determine: (1) the allocation of chemical constituents within plant organs, (2) if spatial variations between the fringe and the interior of a seagrass bed differed significantly, and (3) if the spatial differences were large enough to obscure apparent seasonal patterns.

MATERIALS AND METHODS

Samples of *T. testudinum* were obtained monthly from a small circular seagrass bed (approx. 23 m dia) adjacent to Lassing Park ($27°45'$N, $82°38'$W) in Tampa Bay, Florida (see description of Beach Drive, SE, Phillips 1960). Samples were obtained using a posthole digger (approx. 15 cm dia by 20 cm deep). Eleven sample plugs were removed each month at alternate meters along transects which bisected the bed and extended from fringe to fringe. January's transect was oriented along the east-west axis of the bed. Subsequent transects were rotated 30 degrees so the bed was ultimately bisected by six transects which were sampled twice over the 12-month study period. Samples one and eleven represented the fringe of the bed while samples four through eight were considered the mid-bed region. Water depth and the length of the longest intact leaf blade from four randomly chosen shoots (short-shoots) were measured at each sample point. Water temperature and salinity were measured each month.

Plugs were washed free of sediment and separated into shoot, rhizome, and root fractions within 2 h of collection. Floral and faunal epiphytes were removed from the leaf blades by gently scraping under a stream of water. Each fraction was then blotted dry and weighed (fresh weight), dried at 60°C to constant mass, and reweighed to determine percent dry weight. The entire dried fractions were ground in a mill (screen size #40) and stored in a dessicator over $CaCl_2$ until the chemical analyses were performed.

Percent ash was determined by weight loss after combustion of duplicate 50-mg subsamples in a muffle furnace at 500°C for 4 h. Protein was measured after extraction of 30-mg subsamples with 1 N NaOH by Folin reagent using bovine serum albumin as the standard (Lowry et al. 1951). Soluble carbohydrate was measured after extraction of 10-mg subsamples with 5% hot trichloroacetic acid (TCA) by the phenol-sulfuric acid method (Dubois et al. 1956) using glycogen as the standard. Protein and carbohydrate analyses were done in triplicate. The levels of the constituents were expressed as percentage of dry weight.

Seasonal patterns were statistically analyzed using data pooled from all samples of a transect, whereas spatial distinctions were determined by pooled monthly data for each sample point. Normality of the data was assessed using Kolmogorov-Smirnov tests for normality ($p < 0.05$). Multivariate analyses of variance were performed to determine if chemical constituents exhibited significant ($p < 0.05$) temporal or spatial variation. If significant variation occurred, means were compared using Duncan's multiple range tests ($p < 0.05$). Calculations were performed using Statistical Analysis System (SAS) computer programs (Barr et al. 1976). The SAS/GCONTOUR procedure was used to generate a contour map of the circular bed utilizing water depth data.

RESULTS

Seasonal variations

Pronounced seasonal variations of salinity, water temperature, and leaf blade lengths were evident at Lassing Park. Although salinity fluctuated between 25 and 28 ppt for 75% of the year reaching highest levels during the early summer (Figure 1a), high rainfall amounts in late summer—early fall resulted in substantially reduced salinities. Water temperature (Figure 1b) and mean longest leaf blade lengths (Figure 2) exhibited similar seasonal patterns; they increased from spring to summer and decreased from fall to winter. Maximum leaf blade lengths decreased slightly during the summer (Figure 2), coincident with highest water temperatures, floral anthesis, and initial fruit development. Water temperatures ranged from 11.5°C to 31.5°C during the year, while leaf lengths varied from 13.4 cm to 23.3 cm.

Seasonal variability was also evident in the chemical composition of T. testudinum and the patterns were generally distinctive between plant organs (Table 1).
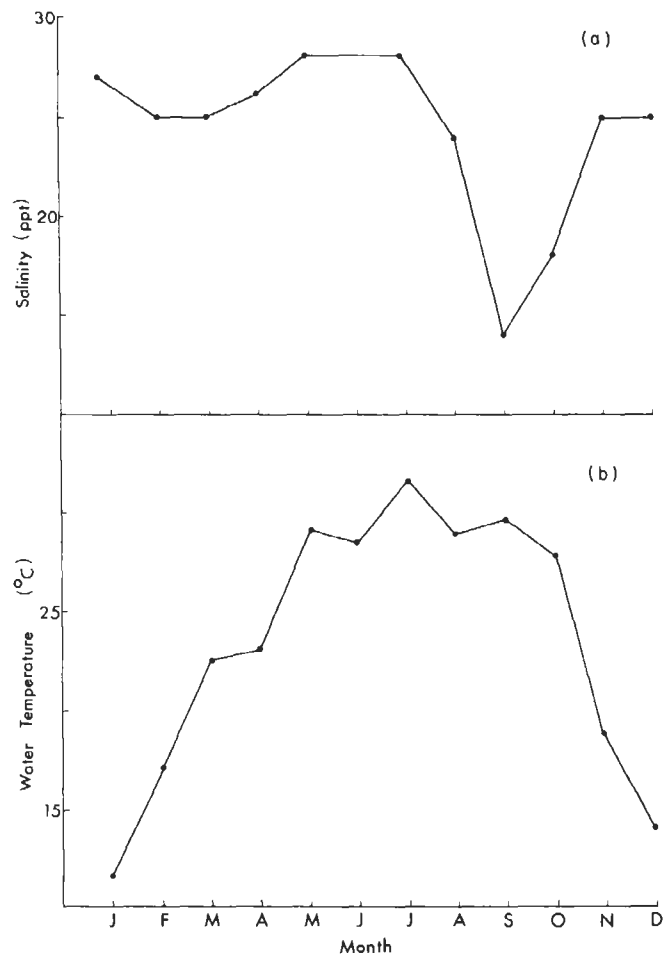

Figure 1. Seasonal fluctuations in (a) salinity and (b) water temperature at Lassing Park site.
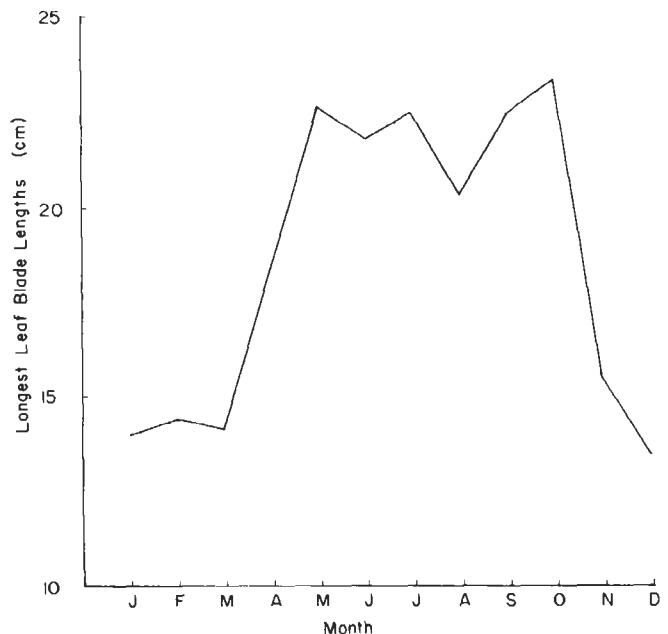

Figure 2. Seasonal fluctuations in maximum leaf blade lengths for Thalassia testudinum from Tampa Bay, Florida.

TABLE 1

Seasonal proximate analyses of *Thalassia testudinum* from Tampa Bay, Florida. Dry weight is expressed as a percentage of fresh weight.
Ash, protein, and soluble carbohydrate levels are expressed as percentage of dry weight.
Means of pooled transect samples ± one standard deviation are listed, n = 11.

Component	Months											
	Jan	Feb	Mar	Apr	May	Jun	Jly	Aug	Sep	Oct	Nov	Dec
Shoots												
Dry weight	11.88	10.63	10.46	10.55	9.64	10.44	10.28	10.49	10.28	10.49	9.97	9.99
±	1.15	0.99	0.94	1.02	0.61	0.81	0.69	0.40	0.78	0.86	0.72	0.84
Ash	42.7	24.6	25.1	28.5	34.0	34.5	30.2	25.9	25.7	26.1	27.0	28.2
±	7.3	5.3	4.4	2.6	4.1	3.8	2.5	2.9	1.4	2.2	3.6	5.6
Protein	4.0	2.8	3.3	3.4	2.4	3.3	3.0	4.2	5.1	4.0	3.6	3.2
±	1.3	1.1	0.9	1.0	0.7	1.3	1.1	1.0	2.4	1.4	0.8	1.0
Carbohydrate	9.9	16.1	14.5	11.8	11.9	13.5	10.8	13.8	14.3	16.1	14.5	13.3
±	2.5	6.6	2.9	1.7	1.7	2.4	1.4	4.0	3.1	3.7	3.6	3.8
Rhizomes												
Dry weight	15.78	16.30	16.36	15.98	15.15	16.03	16.89	16.85	16.74	15.84	15.87	16.14
±	3.21	0.78	0.91	0.87	1.62	1.33	0.96	1.37	2.04	0.83	0.86	0.68
Ash	26.7	21.6	22.7	23.7	23.9	23.4	21.4	19.5	20.5	19.4	21.4	21.5
±	5.1	1.2	1.7	2.1	1.4	2.4	1.3	2.0	2.1	1.4	1.5	1.2
Protein	2.8	1.7	1.2	1.3	1.3	1.5	1.2	1.2	2.4	1.5	1.3	1.0
±	1.0	0.6	0.4	0.7	0.4	0.9	0.7	0.3	0.9	0.4	0.3	0.3
Carbohydrate	19.4	24.7	23.2	23.7	22.8	21.6	26.5	31.8	30.8	30.4	28.1	27.5
±	4.4	5.3	5.1	1.9	4.6	5.9	6.2	8.6	6.5	6.6	4.5	4.3
Roots												
Dry weight	–	13.02	14.58	14.32	13.16	13.33	12.88	11.22	11.49	11.98	11.77	12.29
±		1.00	1.80	1.52	1.65	1.56	0.94	1.28	1.52	1.93	0.84	1.22
Ash	–	31.9	31.4	36.1	33.6	32.5	30.5	26.5	26.6	25.7	26.4	25.8
±		3.7	6.3	7.5	3.8	3.7	3.3	1.8	1.7	3.8	1.9	5.9
Protein	–	3.6	3.5	3.0	4.0	3.9	3.9	4.7	4.6	4.3	5.0	4.2
±		0.8	0.9	1.3	1.4	0.8	1.4	1.0	1.5	1.0	1.2	1.4
Carbohydrate	–	9.9	9.4	12.0	10.5	12.0	12.1	12.6	15.1	12.1	13.4	11.7
±		1.7	1.4	2.2	2.1	3.2	3.0	3.1	3.5	2.7	1.9	1.9

Dry weights of shoots were significantly greater in January than in any other month and lowest in May. The highest dry weights in rhizomes occurred in late summer—early fall and were also lowest in May. Root dry weights, highest during the spring, decreased significantly during the summer, reaching minimum values in the fall. Shoots had the lowest dry weights (9.5–11.8%) and rhizomes had the highest (15.1–16.9%); roots were intermediate (11.2–14.6%). Ash levels exhibited seasonal patterns that were similar in all three organs. Low ash levels were present during early spring and fall, while highest levels occurred during late spring—early summer with a peak in January. This pattern corresponded with fluctuations in salinity (compare Figure 1a and Table 1). Ash levels were highest in shoots (24–42%) and lowest in rhizomes (19–27%); roots were again intermediate (25–36%).

Carbohydrate levels in shoots exhibited a bimodal seasonal pattern with peaks in February and October (Table 1). The seasonal pattern exhibited by both rhizomes and roots was slightly different; levels were lowest during spring then increased significantly during the late summer—early fall. Carbohydrate levels in shoots and roots ranged from 9 to 16.5%; levels in rhizomes were significantly higher (19–32%). Protein levels in shoots and rhizomes were lowest in spring and highest in January and September. Root levels were low in spring and increased through fall. Protein levels of shoots and roots (2–5%) were similar and always higher than those of rhizomes (1–3%).

Spatial variations

The seagrass bed we sampled had a "domelike" profile and water depth decreased approximately 10 cm from fringe to mid-bed, a lateral distance of about 10 m (Figure 3). Except for fringe samples, leaf lengths also tended to decrease toward the interior of the bed (Figure 4). The relatively short leaf blade lengths of fringe short-shoots, although in deeper water, were attributed to grazing activity which is more prevalent along fringe areas of these seagrass beds (personal observation).

Dry weight levels of shoots were significantly greater (10.5–10.9%) in the interior of the bed than on the fringe (Table 2). Roots exhibited the opposite trend and rhizomes showed no significant differences across the bed. Ash levels in shoots decreased significantly from the landward fringe (33.3%) to the seaward fringe (27.9%) (Table 2), while rhizomes had highest ash levels in the interior of the

bed (22.3—23.0%) and the lowest levels at the fringe (21.0 and 21.3%). Ash levels in roots fluctuated across the bed with little apparent pattern, but highest levels occurred in the mid-bed region.

Carbohydrate and protein levels in shoots and roots were
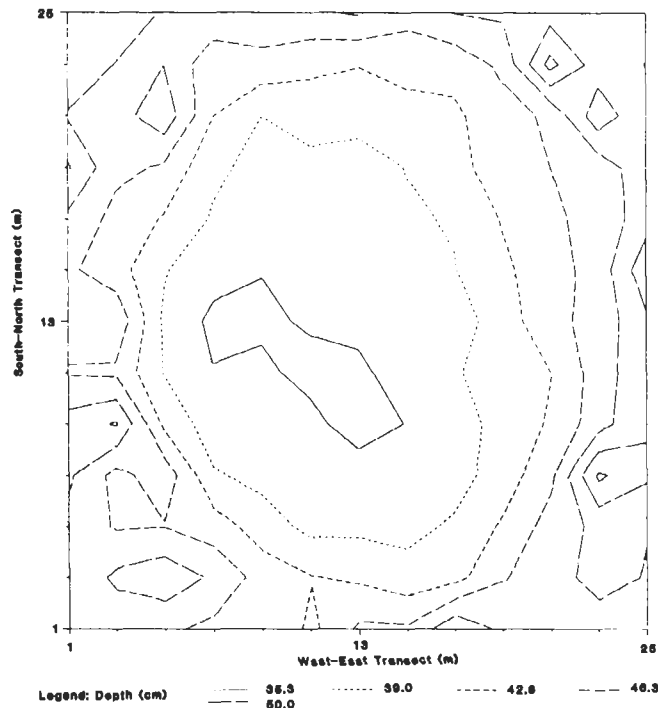

Figure 3. Depth profile of the circular *Thalassia testudinum* bed at Lassing Park showing mounded bed form.
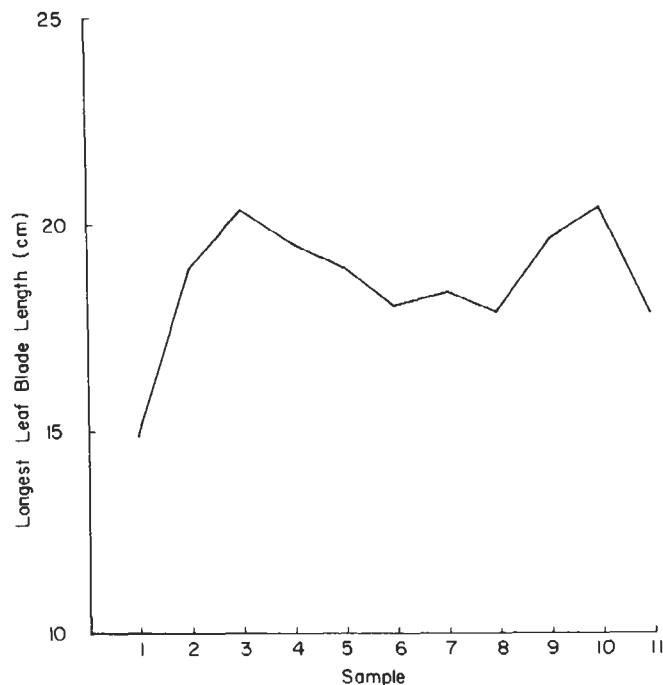

Figure 4. Spatial variation in maximum leaf blade length of *Thalassia testudinum* along transects through the circular bed.

inversely related along transects (Table 2). Carbohydrate levels of shoots were significantly lower at the fringe (10.9 and 12.6%) than in the interior (13.2—14.4%, except for sample #4). The opposite was true for protein levels. Root carbohydrate levels were significantly greater at the fringe while protein levels were significantly lower. Spatial variations in rhizome carbohydrate and protein were distinctive. The seaward fringe rhizomes had significantly more carbohydrate than the rest of the bed; but the interior had significantly higher protein levels.

Analyses of variance indicated samples obtained at the fringe of this *T. testudinum* bed had mean levels significantly different than those obtained from the interior for dry weight in shoots, percent ash and protein in the rhizomes, and percent carbohydrate and protein in roots. No significant synergistic interactions occurred between the month of sampling and sample location.

DISCUSSION

Seasonal variations

Seasonal patterns observed in this study, based on pooled transect data, agree closely with those previously reported for *T. testudinum* using random sampling techniques. Maximum leaf lengths of *T. testudinum* at Lassing Park exhibited a bimodal seasonal pattern with peaks in May and October. Phillips (1960) reported a similar pattern and suggested that leaf lengths in this species correspond with water temperatures. The transient summer depression of leaf lengths we observed coincided with highest water temperatures, rapidly falling salinities, and period of floral anthesis. Zieman (1975) also observed a decrease in leaf lengths during summer, but attributed it to the shunting of energy resources of the plants into the formation of sexual reproductive structures, sexual reproduction apparently decreasing the energy available for vegetative growth. Yet he stated that sexual reproduction in *T. testudinum* was not extensive. Reproductive short-shoot density estimates range 1—15% for most south and central Florida *T. testudinum* populations (Phillips 1960, Thorhaug and Roessler 1977, Grey and Moffler 1978); therefore, only a small portion of the shoots would be involved in this reproduction related sag phenomenon. In contrast, reproductive shoot densities at Lassing Park range 14—75% (Moffler et al. 1981), so a physiological shift could be substantial in this population. The entire community was exposed to the extremes of highest water temperatures and lowest salinities and our observations indicated that both vegetative and reproductive shoots exhibited summer dieback. When water temperatures approach summer maxima in Tampa Bay, *T. testudinum* leaves become soft and flaccid then break off because of protoplasmic breakdown and accelerated bacterial activity (Phillips 1960). Salinity decreases also reduce leaf growth in this species (Phillips 1960, McMillan and Moseley 1967). Therefore, the combination of

TABLE 2

Proximate analyses of transect samples of *Thalassia testudinum* from Tampa Bay, Florida. Dry weight is expressed as a percentage of fresh weight. Ash, protein, and soluble carbohydrate levels are expressed as percentage of dry weight. Means of pooled monthly collections ±one standard deviation are listed, n = 12 for shoots and rhizomes, n = 11 for roots.

Component	Transect Sample										
	1	2	3	4	5	6	7	8	9	10	11
Shoots											
Dry weight	10.07	10.15	10.37	10.50	10.84	10.88	10.78	10.50	10.26	10.54	9.55
±	1.10	0.53	0.75	1.53	0.92	0.90	0.71	0.66	0.81	0.89	0.96
Ash	33.3	30.6	29.9	30.3	28.7	29.1	28.2	27.5	29.5	28.1	27.9
±	10.8	6.1	5.6	7.9	5.8	6.6	6.9	6.5	4.8	4.0	3.6
Protein	3.8	2.5	3.5	3.7	3.6	3.6	3.2	3.9	3.4	3.3	4.2
±	2.2	1.0	1.4	1.0	1.4	1.2	1.1	1.9	1.2	1.0	0.9
Carbohydrate	10.9	14.8	13.2	11.8	13.2	14.2	14.4	13.4	13.5	14.9	12.6
±	2.4	4.4	2.6	4.0	3.3	3.2	4.2	4.4	3.6	4.8	3.4
Rhizomes											
Dry weight	16.32	16.10	16.55	15.99	15.41	16.61	16.32	16.12	16.04	16.25	16.22
±	0.99	1.14	0.86	0.77	2.37	1.84	1.75	1.13	0.98	1.37	1.96
Ash	21.3	21.4	22.4	22.0	23.0	22.3	22.4	22.6	22.3	22.1	21.0
±	2.9	2.0	2.5	2.2	5.6	2.4	1.9	2.2	2.5	2.7	2.4
Protein	1.1	1.2	1.2	1.7	1.9	1.5	1.8	1.9	1.4	1.7	1.9
±	0.5	0.4	0.5	0.9	0.8	0.6	1.0	0.9	0.8	0.7	0.9
Carbohydrate	25.1	26.7	26.4	24.7	25.2	25.4	27.1	25.1	26.2	23.5	30.2
±	4.6	6.1	5.1	6.4	9.2	4.6	6.4	5.6	6.1	4.9	10.3
Roots											
Dry weight	13.46	12.66	12.76	12.18	12.74	12.22	12.74	12.55	12.78	12.53	13.50
±	2.18	1.57	2.15	0.97	2.16	1.88	1.25	0.92	2.41	1.16	1.90
Ash	31.1	30.2	28.3	30.7	32.0	29.9	28.9	28.5	29.7	29.2	28.4
±	6.6	7.9	2.5	3.3	6.4	4.2	4.2	4.0	5.4	5.2	8.1
Protein	3.0	4.1	4.3	4.8	4.1	4.2	4.6	4.0	4.2	4.4	3.3
±	1.4	1.2	1.5	1.0	1.1	1.6	1.2	0.8	1.3	0.9	1.0
Carbohydrate	14.5	11.1	12.10	11.7	11.0	11.0	10.9	10.6	12.3	12.0	13.2
±	2.3	1.9	2.6	2.7	3.4	2.1	3.4	2.5	2.8	2.5	2.6

environmental factors and an innate biological rhythm results in a summer dieback which may be expected annually. Minimal leaf lengths during the winter are likewise due to a combination of environmental factors. Leaf kills occur when the shoots are desiccated during extremely low tides associated with the passage of cold fronts. In addition, the plants are relatively dormant due to low water temperatures at this time, so recovery is slow.

Seasonal fluctuations in the chemical constituents of *T. testudinum* also reflected the influence of temperature and salinity on the growth characteristics of this species. Dry weight levels in shoots decreased as water temperatures and leaf lengths increased, during periods of maximal growth, then leveled off during the summer dieback, a period of limited growth. Dry weight levels in rhizomes increased from spring to summer, reflecting changes in resource allocation from shoot growth to nutrient storage in rhizomes (Dawes and Lawrence 1980). The dry weight patterns of the roots suggested a lag in seasonal growth relative to the shoots.

Ash levels in all three organs exhibited very similar seasonal patterns that corresponded to that of salinity. Lowest ash levels in seagrasses previously have been attributed to the presence of new shoot growth, which lacks calcareous epiphytes (Harrison and Mann 1975, Dawes et al. 1979). This does not apply to the patterns we found because most epiphytes were removed from the leaf blades prior to analyses. The similarity of the seasonal patterns in above- and below-ground organs suggests the possible influence of an environmental factor. Salinity influences ash levels in other marine plants (Durako and Dawes 1980); it may also be responsible for the observed seasonal fluctuations in *T. testudinum* since the relatively high ash levels of seagrasses are due to the presence of sea salt in their aerenchyma (Dawes 1981).

Seasonal variations in carbohydrate and protein levels between above- and below-ground organs again reflected the functional relationship of shoots, rhizomes, and roots. Rhizomes act as storage organs for nutrient reserves in *T. testudinum* (Walsh and Grow 1972, Dawes and Lawrence 1979). Increases in carbohydrate levels from spring to fall probably result from the translocation of photosynthate in the form of starch from shoots to rhizomes (Dawes and Lawrence 1979). Carbohydrate levels were always highest

in rhizomes while protein levels, which were relatively low due to the inclusion of both living and dead tissue in our samples, were always highest in shoots and roots. These patterns exemplify the partitioning of biosynthetic activity and storage among organs. They also illustrate the intermediate nature of the roots that had seasonal carbohydrate fluctuations similar to those of the rhizome, but protein and carbohydrate levels comparable to those of the shoots. Patriquin (1972) suggested nitrogen requirements for *T. testudinum* growth could be satisfied by uptake in the sediment root layer. This was determined using yield-supply correlations of leaves, rhizomes, and interstitial waters. Fixation of molecular nitrogen in the rhizosphere seems to be responsible for the supply of nitrogen required for observed production rates (Patriquin and Knowles 1972, Capone et al. 1979). Our observations of relatively high protein levels in the roots may reflect the conversion of fixed nitrogen into organic compounds.

Spatial variations

When transect data were analyzed with respect to sample position, it was evident that location had a decided effect on some of the parameters studied. We found a direct relationship between maximum leaf lengths and water depths (except at the fringe which was heavily grazed) similar to that reported by Phillips (1960), but contrary to the inverse relationship for circular beds in Biscayne Bay reported by Zieman (1972). Sediment depths are evidently the factor controlling leaf blade lengths in Biscayne Bay, since the circular patches occur over depressions in the bedrock surrounded by a thin veneer of sediments (Zieman 1972). Sediment trapping by these circular beds, evidenced by the decrease in water depth at the center of the beds, was very important for maximum development of the community. Patch beds can also form when small clumps of seagrasses grow laterally while accumulating sediments and organic matter (Kelly 1980). The circular bed at Lassing Park, which seems to conform more to the lateral growth model, had a domelike depth contour (see Figure 3) and expanded radially approximately 1 meter during the study period.

Kelly (1980) found that leaf blade cropping by herbivores forms a "halo" effect around seagrass beds. The circular bed at Lassing Park exhibited this feature, and samples obtained from the fringe had distinctive chemical patterns that reflected the influence of cropping. Highest protein and lowest carbohydrate levels were observed for fringe shoots. By cropping the leaf blades, herbivores may provide themselves with a higher energy food source. Dawes and Lawrence (1979) also observed high protein and low carbohydrate levels in experimentally cropped short-shoots of *T. testudinum* which they attributed to new leaf production. Increasing the proportion of young leaf blade tissue by cropping may be effective in increasing the efficiency of energy transfer between *T. testudinum* and herbivores. Healthy *T. testudinum* releases about 1.3% of its gross production as dissolved organic carbon (DOC) (Brylinsky 1977). The release of DOC increases tremendously in senescent tissues. This soluble material may then be absorbed by plankton (Turner 1978) and sediment heterotrophs (Brylinsky 1977), increasing the trophic complexity of carbon transfer.

A depletion of soluble carbohydrates in *T. testudinum* rhizomes in response to defoliation has been reported (Dawes and Lawrence 1979), but we noted an increase in carbohydrate levels of the roots and the seaward fringe rhizomes. *Myriophyllum spicatum,* a freshwater macrophyte, also increases the percentage of soluble carbohydrate in the roots in response to cropping (Kimbel and Carpenter 1981). These variable results indicate differences in allocation of proximate constituents (affecting relative proportions) rather than differences in biosynthesis.

High protein levels in fringe shoots may also be due, in part, to higher nitrogen availability in the phyllosphere of this region of the bed. Capone and Taylor (1977) found that nitrogen fixation activity of epiphytized leaves can be 20% higher at the fringe phyllosphere of a *T. testudinum* bed compared to the interior of the bed, while activity associated with intact foliage may be three times higher. This relatively high activity compensates for the less effective trapping and recycling of nitrogen from detritus at the fringe (Capone and Taylor 1977).

Rhizosphere nitrogen availability, the amount of organic matter and silt-clay in the sediments may increase with lateral distance into a seagrass bed (Fonseca 1981, Kenworthy et al. 1982). Our data indicated the proximate composition of below-ground organs may be affected by these changes in sedimentary characteristics. Ammonium regeneration is highest where organic matter in the sediments is high (Iizumi et al. 1982), and uptake of ammonium by seagrass roots is greatest in highly organic substrata (Short 1983). Thus, the high protein levels of mid-bed rhizomes and roots in *T. testudinum* may be due to increased nitrogen availability and assimilation, while elevated ash levels may indicate higher interstitial salinities or solute concentrations resulting from increases in organic and inorganic ions.

CONCLUSIONS

Spatially related parameters can influence seasonal fluctuations in chemical constituents of *Thalassia testudinum.* Although seasonality dominated changes in the levels for most chemical constituents, others, such as shoot dry weight and root protein levels, were significantly affected spatially but not temporally. In addition, some constituents that exhibited significant seasonal fluctuations had distinctive patterns between fringe and mid-bed samples. Therefore, the presence of gradients across seagrass beds needs to be considered in future investigations of these communities.

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