# Productivity aspects of three tropical seagrass species in areas of different nutrient levels in Kenya

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## Abstract

Previous work conducted in two seagrass areas of different nutrient status, along the Kenyan coast, has shown that the seagrasses were characterised by differences in the species composition and biomass of epiphytic algae. This study was undertaken to evaluate the productivity patterns of the seagrass species growing in these same sites. Studies were made on *Thalassodendron ciliatum* (Forskål) den Hartog, *Thalassia hemprichii* (Ehrenberg) Aschers and *Cymodocea rotundata* Ehrenberg and Hempr. ex Ascherson growing in the lagoons of Nyali and Vipingo, along the Kenyan coast, during the South East (SE) and North East (NE) monsoon periods. The results of this study revealed differences in the levels of nitrate within the water column, with Vipingo having lower levels of around 4 μM during the low tide period of the SE monsoon while nitrate levels in Nyali reached levels of 16 μM during the same period. Of the three seagrass species studied, *C. rotundata* had the highest shoot densities in both sites. The shoot densities of *C. rotundata* reached levels of 1300 shoots m$^{-2}$ compared to an average of 600 shoots m$^{-2}$ for both *T. ciliatum* and *T. hemprichii*. The stems of *T. ciliatum* were found to be 200 mm long in Nyali whereas those in Vipingo were 80 mm in length. Of the three seagrasses *T. ciliatum* and *T. hemprichii* showed significant differences in total leaf growth between the two sites. However, of these two species, only *T. hemprichii* showed distinct differences in leaf production and biomass when the two sites were compared. Leaves of *T. hemprichii* showed growth rates of 0.008 g dw shoot$^{-1}$ day$^{-1}$ in Nyali while the growth rate in Vipingo was 0.004 g dw shoot$^{-1}$ day$^{-1}$. Leaf production rates were approximately 0.005 g dw shoot$^{-1}$ day$^{-1}$ for *T. ciliatum* in both Nyali and Vipingo and that of *C. rotundata* was approximately 0.0015 g dw shoot$^{-1}$ day$^{-1}$ in the two sites. This suggests that of the three species studied, *T. hemprichii* may have been influenced by the nutrient input in Nyali. The abundance of epiphytes on the stems of *T. ciliatum* was higher in Nyali during both seasons; therefore we suggest that although the composition of epiphytic species is the main indicator of nutrient enrichment in these areas the enhanced productivity of *T. hemprichii* may be another indicator of the nutrient status of these study sites.

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## 1. Introduction

Seagrass beds cover extensive intertidal areas along the East African coast and, consequently, they are one of the first ecosystems to experience the effects of land based nutrient discharge (Mwashote et al., 1999). Studies that have documented the consequences of nutrient enrichment on seagrass beds show that there is enhanced seagrass growth in the initial stages of enrichment and a prolific growth of epiphytic algae, which then leads to shading of the leaves and eventually lowers the photosynthetic productivity of the seagrasses (Harlin and Thorne-Miller, 1981; Tomasko and Lapointe, 1991; Frankovich and Fourqurean, 1997).

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A previous study on the composition of epiphytic algae on some Kenyan seagrasses in nutrient impacted areas has shown differences in the composition and biomass of the epiphytic algae (Uku and Björk, 2001). The nutrient rich site (Nyali) was characterised by a higher abundance of fleshy macroalgae while the nutrient poor site (Vipingo) was characterised by an abundance of cyanobacteria (Uku and Björk, 2001). With this knowledge of differences in epiphytic composition, we conducted this study to compare seagrass productivity in the two sites. Growth patterns of *Thalassodendron ciliatum* (Forskål) den Hartog, *Cymodocea rotundata* Ehrenberg and Hemprich ex Ascherson, and *Thalassia hemprichii* (Ehrenberg) Ascherson were investigated from May 2001 to February 2002, covering the South East (SE) and North East (NE) monsoons. The epiphytic composition on the stems of *T. ciliatum* was also taken into consideration during this study.

## 2. Materials and methods

### 2.1. Study sites

This investigation was conducted in Nyali and Vipingo along the Kenyan coast. Nyali Beach (4°03′ S, 39°43′ E) is an important tourist centre located 2 km from Mombasa Island (Fig. 1). Town settlements and numerous beach hotels characterise the Nyali area. There are also several groundwater seepage points along the beach zone in the Nyali area. Vipingo (3°45′ S, 39°50′ E) is located 33 km from Mombasa Island. The site in Vipingo has a few residential houses along the beach and one beach hotel. The location of beach hotels and residential properties along Kenyan beaches means that septic tanks are located in porous limestone rocks close to the beach. This leads to an enhanced seepage of nutrient rich water into intertidal lagoons which impacts the intertidal seagrass beds (Uku, 1995). An earlier study in the two sites showed that nitrate levels in Nyali reached approximately 20 μM while levels in Vipingo were approximately 2 μM in August 1999 (Uku and Björk, 2001), indicating the differences in nutrient inputs in the two selected sites.

The tidal regime in these areas has a semi-diurnal periodicity and the tidal range is around 4 m (McClanahan, 1988; Obura, 2001). This means that there is a wide area of seagrasses exposed during the low tide periods. The three seagrasses, studied here, are found growing in intertidal areas close to the beach and are exposed during low tide. These species grow in monospecific patches in the study areas and exhibit different growth morphologies. *Cymodocea rotundata* and *Thalassia hemprichii* possess leaves extending from the substrate while *Thalassodendron ciliatum* has an upright lignified stem with leaves projecting from the terminal end of the stem.
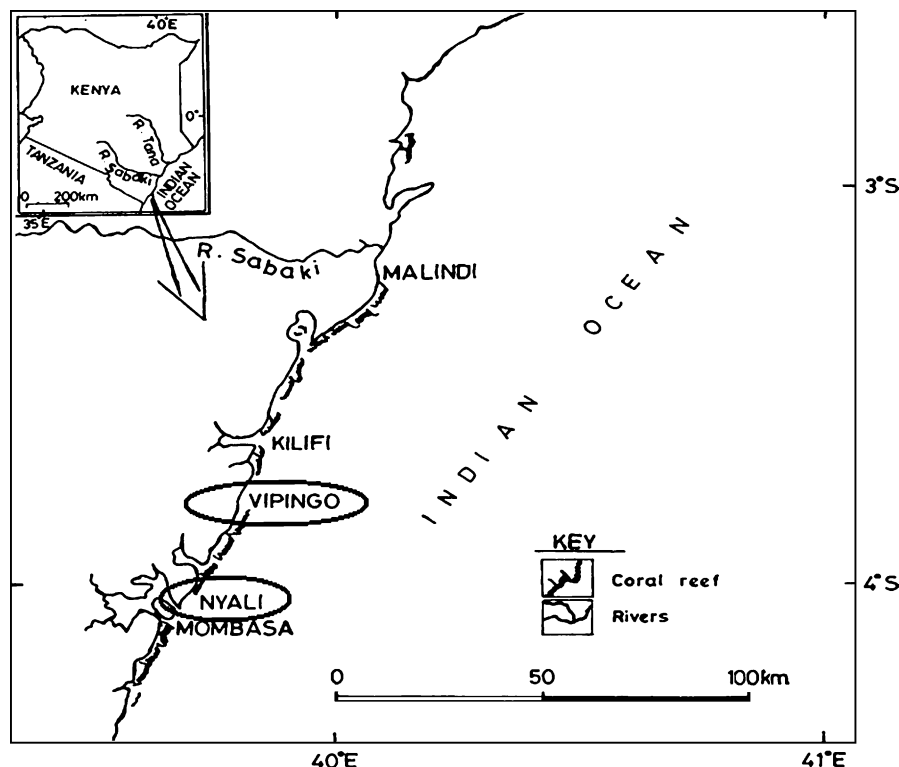


Fig. 1. Map of the Kenyan coast showing the location of Nyali and Vipingo.

## 2.2. Sample collection and analysis

### 2.2.1. Physical characteristics of the study areas

Nutrient levels in the near shore areas were determined by collecting water samples, on a monthly basis, from both Nyali and Vipingo. Thirty water samples were collected during high and low tide periods from May 2001 to February 2002 (excluding October 2001). The content of nitrate, ammonium and phosphate was then determined using methods described in Parsons et al. (1984). The nutrients in the sediments were determined by collecting sediment samples, using a plastic corer, from a sediment depth of 10 cm. A total of five samples were obtained monthly from each specific seagrass patch. Pore water extraction was conducted following methods described by Mohammed (1998) where KCl extraction was used to extract nutrients that were adsorbed to the sediments. The nutrient content of the extracted water was determined using methods described by Parsons et al. (1984). During the study period, pH was measured, using a pH meter, from samples collected during the monthly low and high tide sampling periods. Salinity measurements were also made at the same time using a salinometer. All samples were analysed within 3 h after collection.

Water quality in the study sites was characterised by estimates of the biological oxygen demand (BOD), which is a measure of the oxygen used by microorganisms to decompose organic compounds in water (Tebbutt, 1983). For the BOD analysis, a total of 10 samples were collected monthly. The oxygen content of half of the samples was determined using the Winkler method described by Parsons et al. (1984). The remaining samples were incubated in the dark for 5 days, after which the dissolved oxygen content was determined. The difference between the initial oxygen content and the oxygen content after the 5-day incubation period was considered to be the BOD of the water samples.

Total suspended solids in the water column were determined by collecting 1-litre water samples from the water column during the high and low tide sampling periods. The total suspended solids were determined using methods described by Erftemeijer and Koch (2001). The sediment texture in the three seagrass patches was determined from sediment samples collected from a depth of 10 cm. A total of 10 samples were collected from each of the two sites, twice in each season, and methods described by Buchanan and Kain (1971) and Giere et al. (1988) were used to determine the sediment grain size. The organic matter content of the sediments collected during the study period was determined using combustion methods described by Erftemeijer and Koch (2001).

Water motion in the study sites was evaluated by deploying balls made of plaster of Paris in the field.

Control balls were kept in buckets outdoors for the duration of the period that the experimental balls were deployed in the field. The intensity of water motion was measured as the diffusion factor (DF) according to the formula: Diffusion Factor $= 100$ [(FIDW$-$FFDW)/CIDW$-$CFDW]/hours of exposure, where FIDW is the initial dry weight of the plaster ball, FFDW is the final dry weight of the plaster ball, CIDW is the initial dry weight of the control plaster ball, CFDW the final dry weight of the control plaster ball as described by Bandeira (2002). The diffusion factor is expressed as a percentage of weight loss per hour (Bandeira, 2002). A total of 18 balls were randomly deployed in the seagrass patches.

Temperature and light were measured using automated loggers (StowAway Tidbit and Light intensity loggers, respectively, Onset Computer Corp.) encased together in a waterproof transparent capsule. The loggers were anchored on a mangrove pole within the seagrass bed. The loggers were placed just under the water surface, and were located on top of the seagrass canopy. Sampling was conducted as the water approached low tide periods and the water depth averaged 1.5 m during the sampling occasions. Light and temperature readings were recorded at different times on different days. The data presented here represent a mean value of readings obtained from the different days during which the loggers were set for a duration of 1 h. Light measurements were recorded in Lumens square feet$^{-1}$ and temperature measurements were recorded in degrees Celsius. Light measurements given by the loggers were converted to µmol photons m$^{-2}$ s$^{-1}$ by calibrating the light logger against a PAR sensor. This was done by holding a PAR sensor next to the light loggers and taking measurements every minute for 15 min. This was repeated on different occasions in order to obtain a range of PAR estimates with which to undertake the calibration.

### 2.2.2. Seagrass characteristics in the study sites

The shoot density of the different seagrasses was determined by counting individual shoots within 0.0625 m$^2$ quadrats. The seagrass beds were selected on the basis of their proximity to groundwater outlets and random sampling was conducted in patches with maximum development of each species. The selected seagrass patches were intertidal and they were exposed during low tide periods. The seagrass *T. ciliatum* was found in pools that were covered with water during the low tide periods. A total of 10 randomly placed quadrats were counted for each seagrass on a monthly basis. Increases in leaf length, of each species, were obtained by the hole punch method described by Dennison (1990). Following this procedure, a hole was punched through all the leaves of an individual shoot using a leather punch. The hole was made just above the basal meristem region of

each shoot. A minimum of 30 shoots was punched for each species. After 4 days, a new mark was made just above the basal meristem. Leaf production parameters were calculated as described by Dennison (1990). The ratio of leaf material produced before marking to that produced after marking was divided by the time interval to give the relative production rate expressed as g $g^{-1} day^{-1}$. The leaf materials produced after marking for each shoot divided by the time interval yielded leaf production per shoot (g shoot$^{-1} day^{-1}$). Aerial production rate was calculated by multiplying the leaf production per shoot by the shoot density and was expressed as g m$^{-2} day^{-1}$. Leaf turnover time was estimated as the inverse of the relative leaf production rate.

Earlier studies documented a diverse assemblage of epiphytic macroalgae on the stems of *Thalassodendron ciliatum* (Semesi, 1988; Bandeira, 2000a; Uku and Björk, 2001; Leliaert et al., 2001) and during this study the dominant epiphytes found attached to the stems of the seagrass *T. ciliatum* were noted and their areas were estimated. Length and width measurements were made of *T. ciliatum* stems using a vernier calliper. Following recommendations by Littler and Arnold (1985) where areas can be calculated using appropriate geometric shapes, the areas of the stems were determined by using the formula for the surface area of a cylinder. The length and width of the filamentous red algae, encrusting coralline red algae and sponges found directly attached to the stem, were also measured using vernier callipers. The area of these epiphytes was then determined by assuming that they open out into a rectangle.

### 2.3. Statistical analysis

The data obtained were compared using one-way and two-way ANOVA to test for differences between sites and seasons for the parameters measured during this study. The $F_{max}$ test was used to determine homogeneity of variances (Sokal and Rohlf, 1995; Fowler et al., 1998). In cases where the variances were heterogeneous, logarithmic transformation was used to make the data homogeneous, after which the ANOVA was performed. The significance level was set at $P < 0.05$. Correlation analysis was conducted to determine the relationships between parameters that were found to be significant by the ANOVA analysis. The significance of the correlation results was determined, at a significance level of $P < 0.05$, using the *t*-test (Sokal and Rohlf, 1995).

## 3. Results

### 3.1. Physical characteristics of the study areas

The nutrient levels in the water column were usually higher during low tide in both sites (Table 1). Mean nitrate levels were higher in Nyali and there was a significant difference between the two sites during the SE monsoon ($F = 16.31$, $P < 0.05$) (Figs. 2A and 3A). Tidal variation in nitrate levels was also significant with both the high and low tide nitrate levels varying significantly between the sites during the SE monsoon ($F = 8.42$; $F = 11.85$, $P < 0.05$ for the high and low tide, respectively). Levels of ammonium and phosphate varied with the tides in the two sites but these levels were not significant when the two sites were compared (Figs. 2A and 3A). Other physical parameters that characterise the water column in the two sites are shown in Table 1. Although the variation in salinity was not significant there was a seasonal variation with lower values recorded during the SE monsoon. pH levels did not vary significantly between the sites or seasons. BOD varied significantly between the sites during the SE monsoon ($F = 36.1$, $P < 0.05$) with higher levels recorded in Nyali during this period. Although levels of total suspended matter in the water column were not significant there was

Table 1

Water column characteristics in the study sites during the study period (mean±standard deviation)

| Physical factor | Nyali | | Vipingo | |
|---|---|---|---|---|
| | SE Monsoon | NE Monsoon | SE Monsoon | NE Monsoon |
| Nitrate μM (high tide)[a] | 5.9±1.8 | 3.0±3.2 | 2.6±1.8 | 1.1±0.9 |
| Nitrate μM (low tide)[a] | 16.7±4.6 | 4.6±2.6 | 4.4±3.5 | 1.6±0.5 |
| Ammonia μM (high tide) | 0.2±0.2 | 1.00±1.7 | 5.1±9.3 | 0.001±0.001 |
| Ammonia μM (low tide) | 3.7±4.3 | 1.3±0.9 | 1.5±1.1 | 1.3±0.9 |
| Phosphate μM (high tide) | 0.5±0.7 | 1.1±1.1 | 0.6±0.5 | 0.9±0.7 |
| Phosphate μM (low tide) | 0.6±0.6 | 0.9±1.0 | 0.6±0.4 | 0.6±0.8 |
| Salinity | 33.3±1.4 | 35.2±1.1 | 34.2±0.7 | 35.3±1.1 |
| PH | 8.4±0.3 | 8.3±0.2 | 8.4±0.3 | 8.2±0.03 |
| BOD (mg/l)[a] | 1.3±0.4 | 1.4±0.4 | 0.8±0.5 | 1.4±0.7 |
| Total suspended matter (g/l) | 0.03±0.02 | 0.02±0.004 | 0.03±0.005 | 0.02±0.00 |
| Plaster ball diffusion factor (%) | 15.6±1.00 | 28.6±8.9 | 18.8±2.6 | 16.4±6.2 |
| Temperature (ºC) | 30.0±3.7 | 33.6±4.3 | 29.0±2.2 | 32.5±2.8 |
| Light levels (μmol photons m$^{-2}$s$^{-1}$) | 152.7±182.8 | 329.9±290.9 | 70.3±72.8 | 190.4±202.9 |

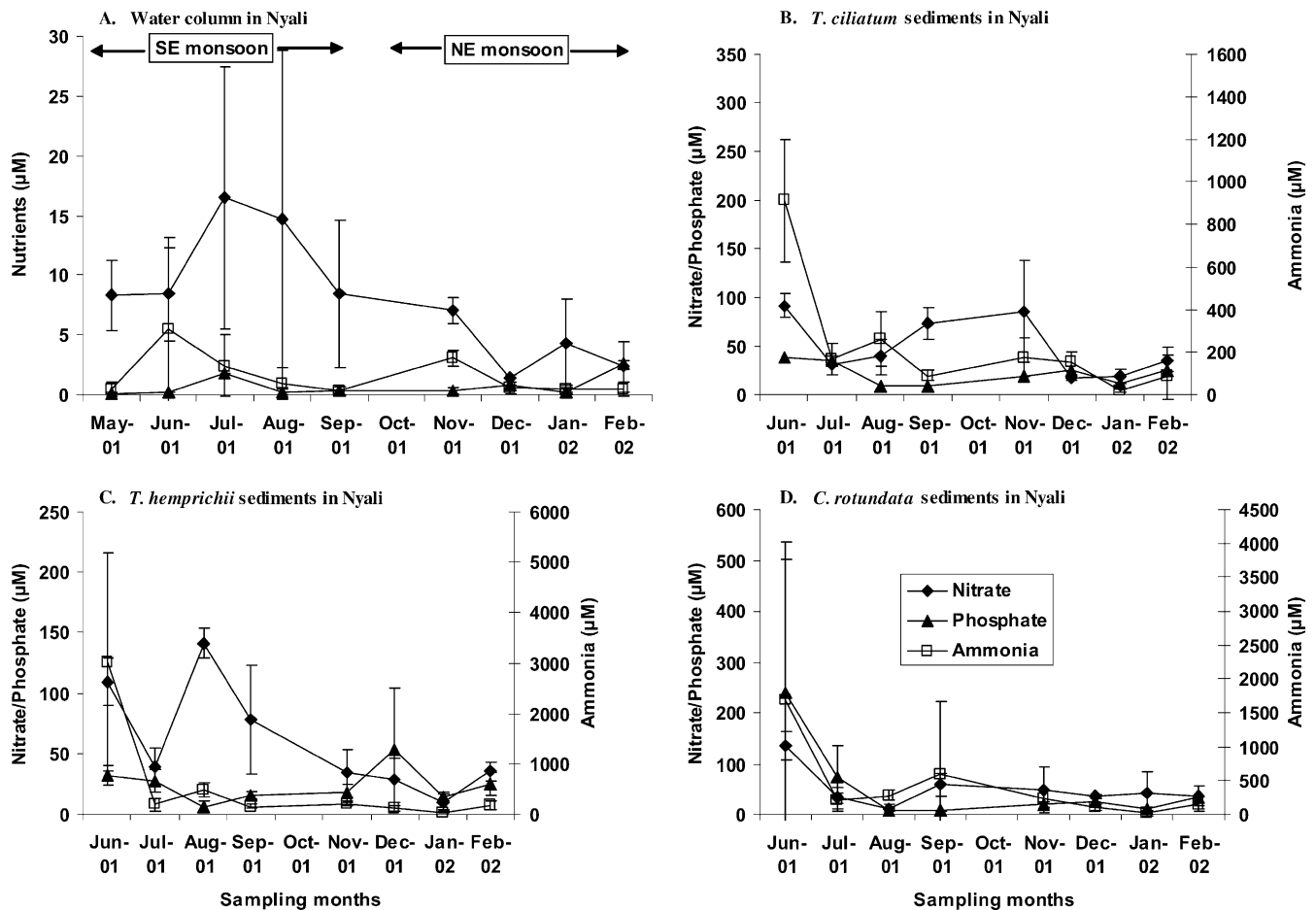[a] Significant differences between sites during the SE monsoon, P < 0.05.

Fig. 2. Mean nutrient levels in Nyali in (A) the water column and the sediments of seagrass beds dominated by (B) *Thalassodendron ciliatum*, (C) *Thalassia hemprichii* and (D) *Cymodocea rotundata* during the sampling period ($n = 30$ monthly for water column; $n = 5$ monthly for each of the sediment samples).

more suspended material in the water column during the SE monsoon. The plaster ball experiments revealed that there was no significant difference in the water motion between the sites or the seasons. There was an increase in temperature from the SE to the NE monsoon in the two sites but this was not significant. Light levels also increased from the SE to the NE monsoon in the two sites but this was also not significant. Light levels varied during the sampling period with low light levels such as 12 μmol photons $m^{-2} s^{-1}$ being recorded on cloudy overcast days of the SE monsoon and high light levels of up to 675 μmol photons $m^{-2} s^{-1}$ being recorded during bright sunny days.

The seagrass patches in Nyali were characterised by finer sediments compared to Vipingo however this difference in grain sizes was not significant. Although insignificant, there was a trend towards higher organic matter content in *Cymodocea rotundata* beds compared to the other species, during the SE monsoon. The sediments colonised by all seagrasses had high levels of ammonium during the SE monsoon (Table 2). For all

sediment nutrients there was an initial peak in June then a decline with the remaining months (Figs. 2B–D and 3B–D). In Vipingo sediment phosphate levels peaked in December in all the seagrass beds (Fig. 3B–D).

### 3.2. Seagrass density and productivity

Of the three seagrass species studied, *Cymodocea rotundata* showed the highest shoot densities, in the two sites, with up to 1500 shoots $m^{-2}$ (Fig. 4A, B and Tables 3–5). In the study sites, *Thalassodendron ciliatum* had the highest number of leaves on each shoot while *C. rotundata* had the lowest leaf count (Tables 3–5).

Of the three seagrasses, *Thalassodendron ciliatum* had the highest leaf biomass (Fig. 5A,B) but it did not vary significantly between the sites. A drastic and unexpected decline in the leaf biomass of *T. ciliatum* occurred in January 2002 (Fig. 5A) accompanied and probably caused by a similar decrease in leaf production (Fig. 6B). The biomass of *Thalassia hemprichii* varied significantly with site during the two seasons ($F = 15.64$; $F = 58.89$
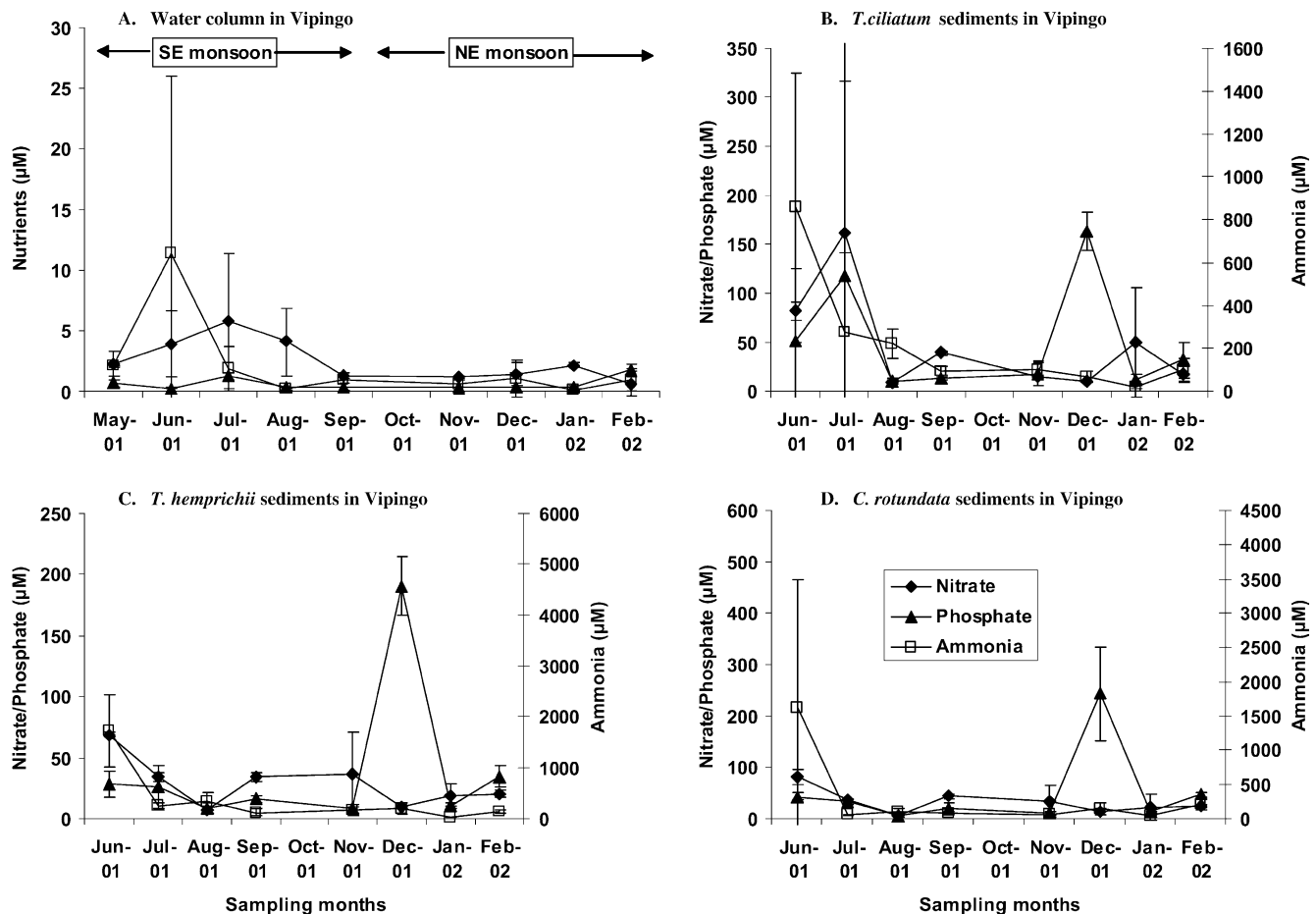
Fig. 3. Mean nutrient levels in Vipingo in (A) the water column and the sediments of seagrass beds dominated by (B) *Thalassodendron ciliatum*, (C) *Thalassia hemprichii* and (D) *Cymodocea rotundata* during the sampling period ($n = 30$ monthly for water column; $n = 5$ monthly for each of the sediment samples).

for the NE and SE monsoon, respectively, $P < 0.05$) with a higher biomass of this seagrass recorded in Nyali (Table 4).

Leaf production estimates showed that the growth of *Thalassia hemprichii* exceeded the growth of the other seagrasses, especially in Nyali, during the study period (Fig. 6A,B). The leaf production of this species varied significantly between the sites during the two seasons ($F = 633,489$; $F = 4,477,051$, $P < 0.05$ for the SE and NE monsoon, respectively). Total leaf growth within shoots was found to be significant for both *Thalassodendron ciliatum* and *T. hemprichii* (Table 3 & 4). In the case of *T. ciliatum* there was a significant difference in total growth between the two sites during the two seasons ($F = 101.76$; $F = 217.49$, $P < 0.05$ for the SE and NE monsoon respectively). However, for *T. hemprichii* the difference in total leaf growth within the shoots was only significant during the NE monsoon when the two sites were compared ($F = 121.11$, $P < 0.05$). The turnover time of the leaves on the shoots was highest for *T. ciliatum* whereas it was similar for the other two seagrasses (Tables 3–5).

The growth of individual leaves on the different seagrasses is shown in Fig. 7A–F. Leaf growth characteristics showed that the oldest leaves in *Thalassodendron ciliatum* (leaves 1–3) did not increase in length (Fig. 7A,B) while the highest growth was seen in leaves 6–8, which were younger in age. The other seagrasses only had one leaf that did not show growth increments. The leaves of *T. ciliatum* showed significant differences in growth when the two sites were compared ($F = 10.56$; $F = 10.55$, $P < 0.05$ for the SE and NE monsoon respectively). The seasonal difference in growth was most pronounced for *Thalassia hemprichii* (Fig. 7C,D) with an increase from the SE to the NE monsoon seen in Nyali. During the NE monsoon period, the difference in the growth of individual *T. hemprichii* leaves varied significantly between the sites ($F = 29.0$; $P < 0.05$).

The length of *Thalassodendron ciliatum* stems varied significantly between the two sites during the two seasons ($F = 52.61$; $F = 88.77$, $P < 0.05$ for the SE and NE monsoon, respectively). The diameters of the stems remained consistent with time (Table 3).

Table 2
Sediment characteristics in the different seagrass beds during the study period (mean±standard deviation)

| | Nyali | | Vipingo | |
|---|---|---|---|---|
| | SE Monsoon | NE Monsoon | SE Monsoon | NE Monsoon |
| Sediment grain size ($\phi$) | | | | |
| *T. ciliatum* | 2.2±0.1 Fine sand | 1.9±0.1 Medium sand | 1.5±0.4 Medium sand | 1.4±0.3 Medium sand |
| *T. hemprichii* | 2.1±0.2 Fine sand | 2.1±0.4 Fine sand | 1.7±0.2 Medium sand | 1.6±0.2 Medium sand |
| *C. rotundata* | 2.2±0.3 Fine sand | 2.2±0.4 Fine sand | 1.7±0.2 Medium sand | 1.6±0.1 Medium sand |
| Organic matter (g) | | | | |
| *T. ciliatum* | 4.1±2.3 | 2.6±0.8 | 3.4±1.5 | 3.7±1.4 |
| *T. hemprichii* | 4.1±1.5 | 3.1±0.9 | 3.9±2.5 | 3.6±1.4 |
| *C. rotundata* | 6.8±3.2 | 2.5±0.4 | 3.3±0.9 | 2.9±0.6 |
| Sediment nutrients ($\mu$M) | | | | |
| *T. ciliatum* | | | | |
| Ammonium | 358.1±376.2 | 109.2±70.7 | 363.0±338.4 | 72.0±36.9 |
| Nitrate | 58.8±28.9 | 39.5±31.9 | 72.8±66.0 | 22.8±18.0 |
| Phosphate | 22.8±16.2 | 20.2±6.7 | 48.5±49.8 | 56.4±71.7 |
| *T. hemprichii* | | | | |
| Ammonium | 203.8±204.7 | 129.8±68.8 | 609.3±748.5 | 131.7±73.5 |
| Nitrate | 91.9±43.4 | 26.6±11.5 | 36.0±25.9 | 21.1±11.4 |
| Phosphate | 19.9±11.9 | 28.5±17.5 | 19.7±9.1 | 60.9±86.9 |
| *C. rotundata* | | | | |
| Ammonium | 694.6±683.3 | 124.2±83.7 | 468.1±771.8 | 114.0±81.3 |
| Nitrate | 60.0±53.8 | 40.5±5.02 | 41.8±31.1 | 23.7±8.1 |
| Phosphate | 82.0±108.8 | 22.2±9.3 | 25.4±15.6 | 78.1±111.1 |

### 3.3. Distribution of epiphytes on the stems of *Thalassodendron ciliatum*

Macroalgal epiphytes found attached to the stems of *Thalassodendron ciliatum* in Nyali were encrusting coralline red algae, filamentous red algae and sponges during the SE monsoon (Table 6). Additionally, *Gracilaria corticata* (J. Agardh) J. Agardh and *Chaetomorpha crassa* (C. Agardh) Kützing were found during this period as secondary epiphytes, which were anchored onto the filamentous red algae. Sponges were also found attached as epiphytes on the stems of *T. ciliatum*.

During the SE monsoon, the epiphytic cover on the stems was 72% in Nyali while in Vipingo 33% of the *T. ciliatum* stem was covered by epiphytes (Table 6). In Nyali, the species composition changed in the NE monsoon and the epiphytic cover on the Nyali stems reduced to 66%. At the same time, more bare areas of the stems were exposed and the red algal epiphyte *Gracilaria corticata* disappeared from the stems. In Vipingo, the epiphytic cover on the stems of *T. ciliatum* was only 15% during the NE monsoon and the epiphytic species were not as many as those found in Nyali (Table 6). The stem area was found to be significantly
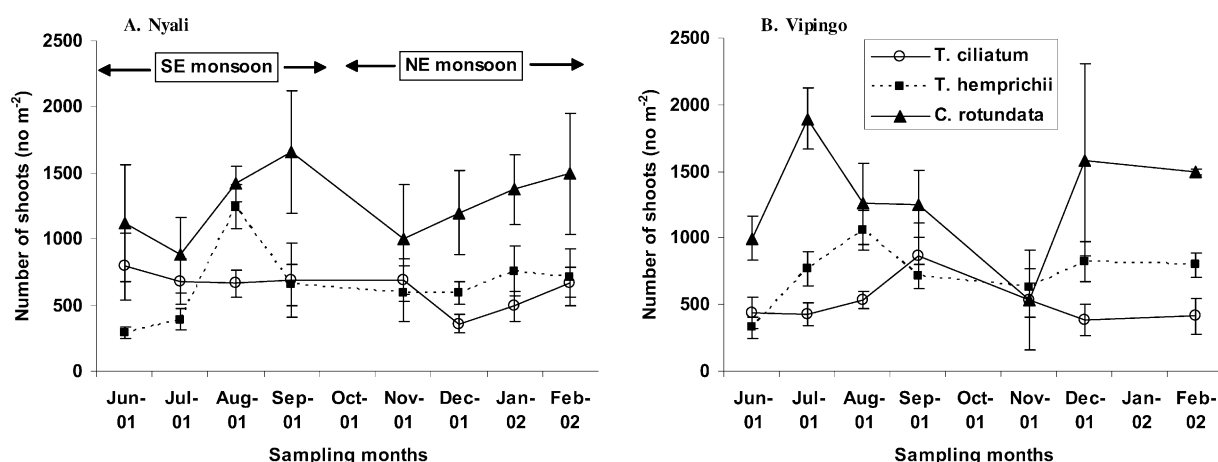


Fig. 4. Shoot densities of the three seagrasses in (A) Nyali and (B) Vipingo ($n=10$ quadrats for each seagrass sampled monthly).

Table 3

Characteristics of *T. ciliatum* found in Nyali and Vipingo during the study period (mean±standard deviation)

| Characteristic | Nyali | | Vipingo | |
|---|---|---|---|---|
| | SE monsoon | NE monsoon | SE monsoon | NE monsoon |
| No. of leaves per shoot | 8.6±0.8 | 8.2±0.9 | 8.6±0.8 | 8.8±0.3 |
| Total leaf biomass (g dw shoot$^{-1}$) | 0.3±0.0 | 0.3±0.1 | 0.2±0.1 | 0.2±0.03 |
| Total leaf biomass (g dw m$^{-2}$) | 176.7 | 154.8 | 119.4 | 84.2 |
| Shoot density (no shoots m$^{-2}$) | 706.6±58.6 | 552.7±157.2 | 568.6±205.1 | 443.7±77.1 |
| Leaf production (g dw shoot$^{-1}$ day$^{-1}$) | 0.005±0.005 | 0.006±0.003 | 0.005±0.002 | 0.004±0.001 |
| Leaf production (g dw shoot$^{-1}$ year$^{-1}$) | 1.8 | 2.2 | 1.8 | 1.5 |
| Relative growth rate (g g$^{-1}$ dw day$^{-1}$) | 0.02±0.002 | 0.02±0.01 | 0.02±0.01 | 0.02±0.01 |
| Aerial production (g dw m$^{-2}$ day$^{-1}$) | 3.7±2.4 | 3.1±1.8 | 2.9±2.4 | 1.8±0.6 |
| Production of new leaves (shoot day$^{-1}$) | 0.1±0.01 | 0.1±0.03 | 0.09±0.06 | 0.1±0.02 |
| Total leaf growth (mm shoot$^{-1}$ day$^{-1}$)[a,b] | 17.3±1.6 | 18.8±5.9 | 12.4±5.7 | 12.4±1.3 |
| Leaf turnover time (days) | 43.1±3.9 | 46.1±8.8 | 45.8±13.4 | 45.6±12.9 |
| Stem length (mm)[a,b] | 257.8±43.9 | 277.8±45.4 | 85.6±31.6 | 82.6±17.0 |
| Stem diameter (mm) | 3.4±0.8 | 2.4±0.4 | 2.9±0.7 | 2.5±0.3 |

[a] Significant differences between sites during the SE monsoon, $P<0.05$.
[b] Significant differences between sites during the NE monsoon, $P<0.05$.

different when the two sites were compared ($F=10.56$; $F=10.55$, $P<0.05$ for the SE and NE monsoon respectively). The differences in epiphytic cover were significant when the sites were compared ($F=20.56$; $F=6.66$, $P<0.05$ for the SE and NE monsoon, respectively) and the cover of epiphytes in Vipingo was significantly correlated to stem length ($r=0.83$).

## 4. Discussion

### 4.1. Physical factors

The results of the water column nutrient analysis confirm the fact that there is an influx of nitrates into the lagoon in Nyali and that the nutrient levels were highest during the low tide period. Higher nitrate levels recorded in Nyali during the SE monsoon are characteristic of nutrient elevation during the rainy season due to

river and surface runoff (Mwashote et al., 1999). Past evaluations of nutrient influxes into the Nyali lagoon found that nitrate levels at the beach sites, with underground water streams feeding the lagoon, varied between 5 and 200 μM, while the ammonium was found to be less than 16 μM and the phosphate levels were around 2 μM (Mwashote et al., 1999). The nutrient levels recorded in this study were within the range recorded for beach areas in Nyali. The nitrate level showed significant variation compared to the other nutrients indicating that the lagoon in Nyali is characterised by nitrate enrichment. This finding is confirmed by work on the nitrogen isotope signatures of *Thalassodendron ciliatum* (Kamermans et al., 2002) which showed that the groundwater is an important source of nitrogen for these plants. Worldwide estimates of water column nutrients in seagrass beds show that the average concentration of ammonium is 3.1 μM, the nitrate concentration is 2.7 μM while the average phosphate concentration is

Table 4

Characteristics of *T. hemprichii* found in Nyali and Vipingo during the study period (mean±standard deviation)

| Characteristic | Nyali | | Vipingo | |
|---|---|---|---|---|
| | SE monsoon | NE monsoon | SE monsoon | NE monsoon |
| No. of leaves per shoot | 4.1±0.03 | 4.0±0.3 | 4.0±0.8 | 3.6±0.3 |
| Total leaf biomass (g dw shoot$^{-1}$)[a,b] | 0.2±0.03 | 0.2±0.02 | 0.09±0.05 | 0.06±0.04 |
| Total leaf biomass (g dw m$^{-2}$) | 109.3 | 139.2 | 64.5 | 59.9 |
| Shoot density (no shoots m$^{-2}$) | 643.2±428.2 | 662.8±85.5 | 716.4±229.4 | 749.3±105.2 |
| Leaf production (g dw shoot$^{-1}$ day$^{1}$)[a,b] | 0.008±0.002 | 0.008±0.006 | 0.004±0.001 | 0.004±0.002 |
| Leaf production (g dw shoot$^{-1}$ year$^{-1}$) | 2.9 | 2.9 | 1.5 | 1.5 |
| Relative growth rate (g g$^{-1}$ dw day$^{-1}$) | 0.05±0.01 | 0.04±0.01 | 0.05±0.01 | 0.06±0.02 |
| Aerial production (g dw m$^{-2}$ day$^{-1}$) | 5.5±4.9 | 5.3±0.5 | 2.4±1.04 | 3.3±1.1 |
| Production of new leaves (shoot day$^{-1}$) | 0.09±0.02 | 0.08±0.01 | 0.10±0.05 | 0.09±0.01 |
| Total leaf growth (mm shoot$^{-1}$ day$^{-1}$)[b] | 17.2±9.5 | 28.5±4.1 | 17.1±2.6 | 17.1±2.8 |
| Leaf turnover time (days) | 18.9±3.8 | 22.3±2.2 | 19.8±3.6 | 19.8±6.9 |

[a] Significant differences between sites during the SE monsoon, $P<0.05$.
[b] Significant differences between sites during the NE monsoon, $P<0.05$.

Table 5
Characteristics of *Cymodocea rotundata* found in Nyali and Vipingo during the study period (mean±standard deviation)

| Characteristic | Nyali | | Vipingo | |
| --- | --- | --- | --- | --- |
| | SE monsoon | NE monsoon | SE monsoon | NE monsoon |
| No. of leaves per shoot | 2.8±0.3 | 2.9±0.2 | 2.5±0.3 | 2.5±0.4 |
| Total leaf biomass (g dw shoot$^{-1}$) | 0.04±0.004 | 0.04±0.008 | 0.03±0.004 | 0.03±0.01 |
| Total leaf biomass (g dw m$^{-2}$) | 50.8 | 50.7 | 40.5 | 36.2 |
| Shoot density (no shoots m$^{-2}$) | 1269.9±339.6 | 1267.2±216.9 | 1350.9±382.2 | 1205.3±585.4 |
| Leaf production (g dw shoot$^{-1}$ day$^{-1}$) | 0.002±0.0005 | 0.002±0.0002 | 0.001±0.0006 | 0.001±0.0005 |
| Leaf production (g dw shoot$^{-1}$ year$^{-1}$) | 0.7 | 0.7 | 0.4 | 0.4 |
| Relative growth rate (g g$^{-1}$ dw day$^{-1}$) | 0.05±0.02 | 0.05±0.004 | 0.06±0.02 | 0.05±0.01 |
| Aerial production (g dw m$^{-2}$ day$^{-1}$) | 2.1±0.5 | 2.3±0.5 | 2.0±1.1 | 1.9±1.0 |
| Production of new leaves (shoot day$^{-1}$) | 0.08±0.02 | 0.07±0.03 | 0.07±0.06 | 0.06±0.02 |
| Leaf growth (mm shoot$^{-1}$ day$^{-1}$) | 12.8±1.6 | 14.9±1.8 | 10.0±9.1 | 11.7±2.0 |
| Leaf turnover time (days) | 19.2±5.1 | 20.7±2.4 | 20.4±9.6 | 19.7±4.3 |

0.35 μM (Hemminga and Duarte, 2000). The nitrate levels recorded in Nyali exceeded these averages.

Sediment nutrient levels were high and within the range found in studies of sediments within the Nyali lagoon (Mwashote et al., 1999; Marbà et al., 2002). Global estimates of pore water nutrients show that levels of ammonium reach 86 μM, those of nitrate are 3.4 μM while those of phosphate are 12 μM (Hemminga and Duarte, 2000). The levels recorded in our study were extremely variable and exceeded the global estimates. This is attributed to the method used where KCl was used to extract nutrients adsorbed to the sediment grains therefore giving an indication of how much was available to the seagrasses within the different beds. Though not significant, the sediment ammonium and nitrate levels were higher during the SE monsoon and this could be attributed to the effects of rainfall discharge through the ground water in the study areas.

The lower salinity that characterised the study sites from May to September 2002 was typical of the SE monsoon where rainfall discharge is high and the salinity can fall to 26 in some nearshore areas (McClanahan, 1988). The higher salinity recorded in the NE monsoon is also typical of this season. The pH levels were similar to those recorded in an earlier study in the two study areas (Uku and Björk, 2001). In spite of the nutrient inputs into the study site in Nyali, the BOD level remained below 5 mg O$_2$ L$^{-1}$ and these levels were similar to those recorded in other sites along the Kenyan coastline (Uku, 1995; Mwangi et al., 2001). The low BOD levels indicate that there is good flushing of nutrients from the Nyali lagoon and the variation in nutrient levels with the tides confirms that the residence time of nutrient inputs is low.

The SE monsoon is characterised by high cloud cover, decreased temperature and light levels as well as high current speeds (McClanahan, 1988). These characteristics were reflected in the light and temperature levels recorded during this study. Temperatures were lower during the SE monsoon while light reaching the upper canopy of the seagrass bed doubled in the NE monsoon period. The diffusion factors of the plaster balls exhibit
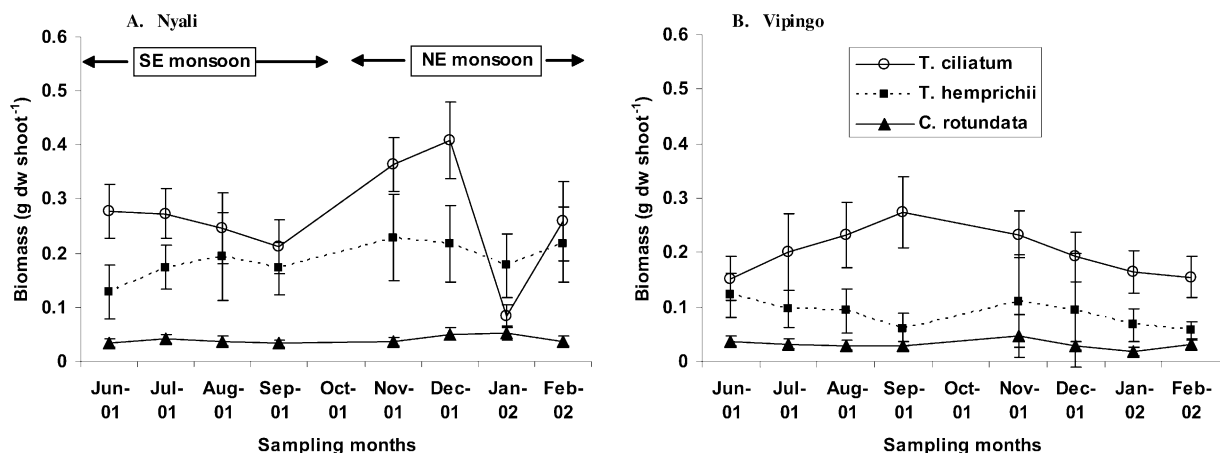


Fig. 5. Biomass of the three seagrasses in (A) Nyali and (B) Vipingo (*n*=10 quadrats for each seagrass sampled monthly).
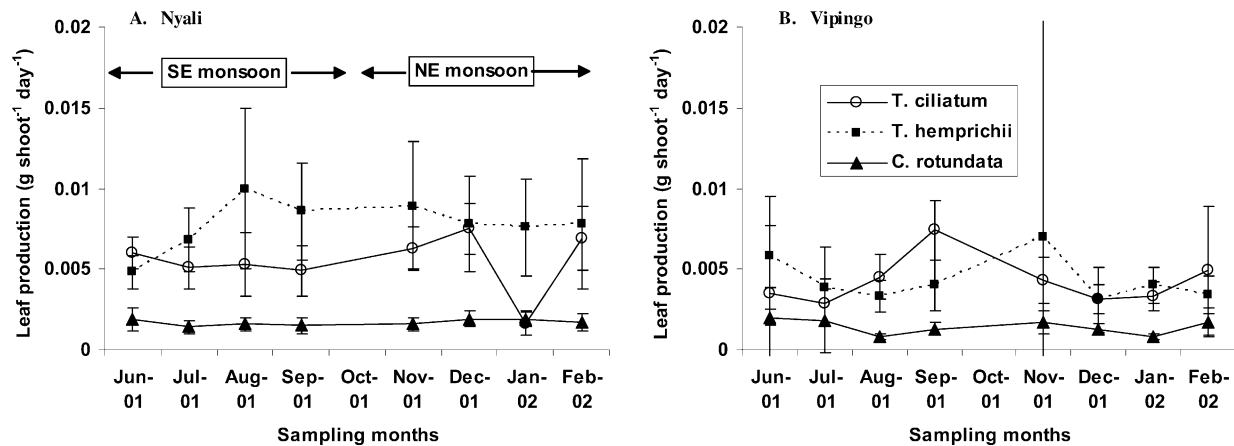
Fig. 6. Leaf production rates of the three seagrasses in (A) Nyali and (B) Vipingo ($n = 30$ shoots for each seagrass sampled monthly).

values that were close to those recorded by Bandeira (2002) for sandy habitats of *Thalassodendron ciliatum*. The lack of difference in water motion between the sites indicates that the currents within the two sites were relatively similar.

## 4.2. Seagrass growth characteristics

Of the 12 seagrass species found along the East African coast, most studies have concentrated on *Thalassodendron ciliatum ciliatum* (Forsk.) den Hartog due to its dominance while other species found in association with it have been less studied. The shoot densities of *T. ciliatum* reported in this study were close to the $888 \pm 103.12$ shoots m$^{-2}$ previously reported for sandy areas in Mozambique (Bandeira, 2000a). Estimates of the growth of *T. ciliatum* within the Nyali lagoon by Ochieng and Erftemeijer (1999) showed that this species had an average shoot growth rate of $13.4 \pm 1.4$ mm shoot$^{-1}$ day$^{-1}$ and a relative growth rate of $0.0142 \pm 0.0029$ g g$^{-1}$ dw day$^{-1}$. These estimates are lower than those reported in this study for Nyali and the difference may be attributed to the fact that our study was conducted on intertidal *T. ciliatum* beds in Nyali that were directly influenced by nutrient inputs. The seagrasses studied by Ochieng and Erftemeijer (1999) were found within deeper subtidal regions of the lagoon. Leaf production estimates were within the range of 0.0043 to 0.0106 g dw shoot$^{-1}$ day$^{-1}$ reported for *T. ciliatum* beds in rocky and sandy substrates in Mozambique (Bandeira, 2000b). The average leaf production rates for *T. ciliatum* along different sites of the East African coast, reported by Kamermans et al. (2002), was between 1.4 and 3.0 g dw shoot$^{-1}$ yr$^{-1}$ and the shoot production estimates made in this study lie within this range. The drastic drop in leaf biomass and leaf production of *T. ciliatum* in Nyali during the month of January 2002 could be attributed to increased herbivory caused by a proliferation of sea urchins in this area.

The stem diameters recorded in this study for both sites were higher than those recorded by Bandeira (2000b). The length of *Thalassodendron ciliatum* stems in Nyali was higher than that reported for this seagrass in Mozambique. The stems of *T. ciliatum* in Vipingo were within the range of $6.96 \pm 0.51$ cm reported for the sandy areas by Bandeira (2000b). Though *T. ciliatum* stems were significantly longer in Nyali they were within the range of stem lengths recorded in Kenyan lagoons (Kamermans et al., 2002). Stem height is a function of age (Borowitzka et al., 1990) but studies using reconstruction techniques to determine the age of *T. ciliatum* shoots along the East African coast showed that *T. ciliatum* shoots found in intertidal sites in Vipingo were similar in age to those found in subtidal areas in Nyali (Kamermans et al., 2002). In the study by Kamermans et al. (2002), the stem length was up to $40.2 \pm 1.9$ cm in Nyali compared to $26.8 \pm 0.8$ cm in Vipingo. In view of these findings we can assume that the shoots of *T. ciliatum* found in our study sites were similar in age. Water coverage has been observed to determine shoot height in intertidal areas along the East African coast (pers. obs.) and an evaluation of tidal height during a neap tide period, in November 2002, revealed that the average tidal height in Nyali was $1.25 \pm 0.68$ m while in Vipingo it was $0.75 \pm 0.64$ m. Although all *T. ciliatum* patches were submerged in pools it may be that the depth of the pools influenced the height of this species in our study sites.

A comparison of shoot densities of *Thalassia hemprichii* with estimates from different parts of the world revealed that the number of shoots recorded for this species in our study area were similar to the 860 shoots m$^{-2}$ recorded by Brouns (1987a) in a mixed seagrass meadow in Papua New Guinea. Studies in the Philippines show that shoot densities of *T. hemprichii* can be as high as 1300–1800 shoots m$^{-2}$ (Rollon et al., 2001) and they can also be as low as $533.2 \pm 17.9$ shoots m$^{-2}$ (Agawin et al., 2001). The lower limit is comparable
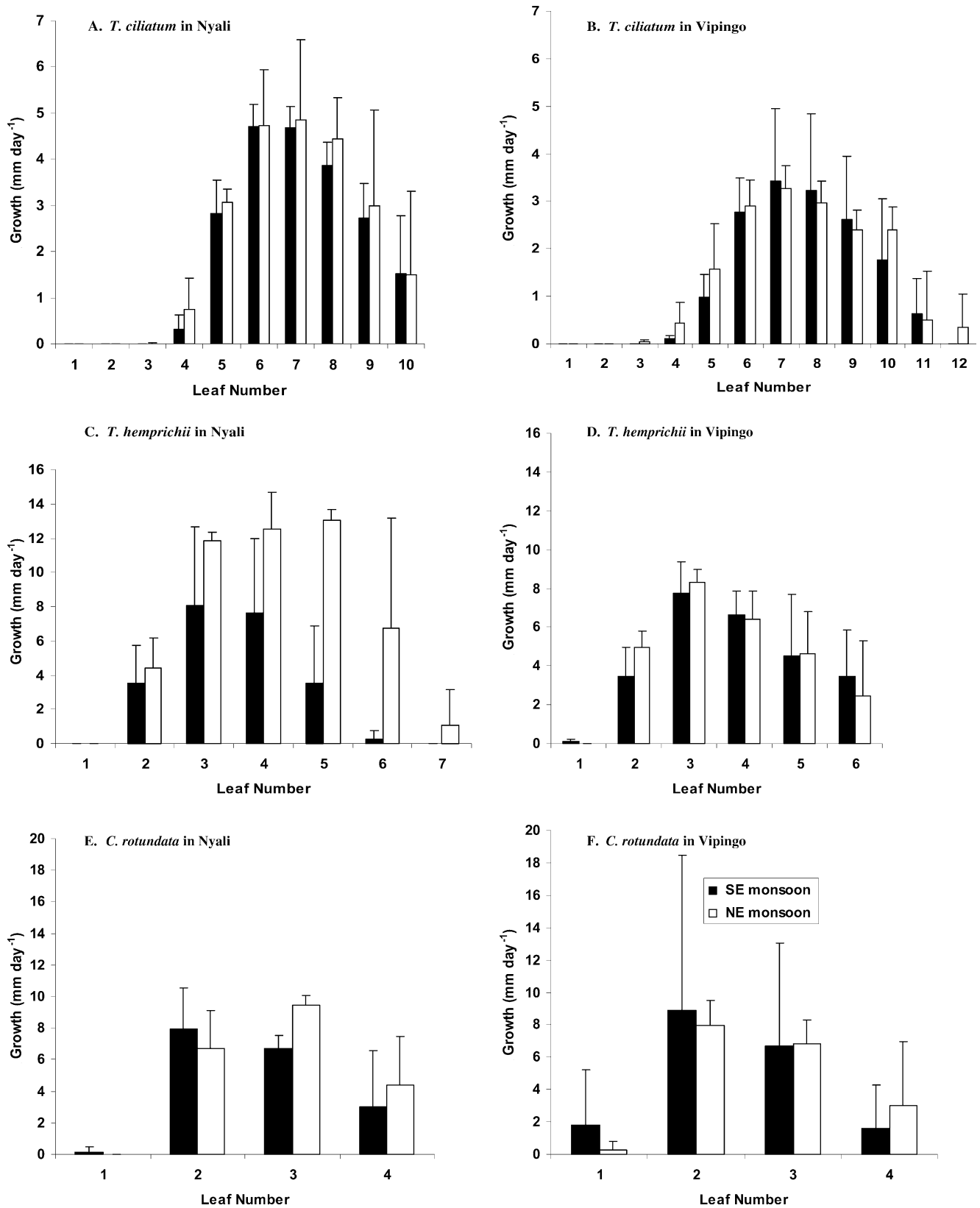
Fig. 7. The growth rate of individual leaves of (A) *T. ciliatum* in Nyali, (B) *T. ciliatum* in Vipingo, (C) *T. hemprichii* in Nyali, (D) *T. hemprichii* in Vipingo, (E) *C. rotundata* in Nyali, and (F) *C. rotundata* in Vipingo (*n* = 30 shoots for each seagrass sampled monthly). Leaf number is ordered from the oldest to the youngest leaf on each stem.

Table 6
Composition of dominant epiphytes that covered the stems of *T. ciliatum* in Nyali and Vipingo

| Epiphytic composition | Nyali | | Vipingo | |
|---|---|---|---|---|
| | SE monsoon | NE monsoon | SE monsoon | NE monsoon |
| | Encrusting red algae, filamentous red algae, sponge, *Chaetomorpha crassa*[a], *Gracilaria corticata*[a], *Ulva* sp.[a] | Encrusting red algae, filamentous red algae, sponge, *Chaetomorpha crassa*[a], *Ulva* sp.[a] | Encrusting red algae, sponge | Encrusting red algae |
| Stem area (cm$^2$)[a,b] | 17.9±7.3 | 12.8±4.3 | 5.5±2.7 | 5.3±2.3 |
| Area of epiphytes on stems (cm$^2$)[b,c] | 12.8±4.4 | 8.4±7.0 | 1.8±2.1 | 0.8±0.9 |
| % Epiphytic cover | 72 | 66 | 33 | 15 |

Areas are expressed as mean ± standard deviation.

[a] Epiphytes that are attached onto other epiphytes at different points along the stems.

[b] Significant differences between sites during the SE monsoon, $P < 0.05$.

[c] Significant differences between sites during the NE monsoon, $P < 0.05$.

to the shoot densities recorded in this study. Agawin et al. (2001) reported the leaf biomass of *T. hemprichii* to be 45.7±17.9 g dw m$^{-2}$. The shoots in Nyali exceeded this biomass estimate while those in Vipingo where close to this biomass level. The leaf appearance rate in *T. hemprichii* was reported to be 0.11±0.005 shoot$^{-1}$ day$^{-1}$ (Agawin et al., 2001) and this was similar to the rate of new leaf production in the SE monsoon for *T. hemprichii* in Vipingo. Shoot growth estimates made by Erftemeijer et al. (1993) showed that *T. hemprichii*, in Barang Lompo Indonesia, grew at a rate of 1.57 cm shoot$^{-1}$ day$^{-1}$. *Thalassia hemprichii* in this study grew at a similar rate in Nyali during the SE monsoon but there was a twofold increase in the NE monsoon period. A similar increase in the biomass of *T. hemprichii* was noted in February 2000 (Uku and Björk, 2001) indicating that this is a consistent feature of this species. Although we attribute this increase to nutrient inputs, other physical factors may have influenced the growth of this species. As these physical factors were sampled periodically, it is difficult to make comparisons.

In the case of *Cymodocea rotundata*, shoot densities reported by Brouns (1987b), from seagrass beds on Papua New Guinea, reached a maximum of 1770 shoots m$^{-2}$ and similar densities were reported in this study. In contrast, lower shoot densities of 155.8±20.30 shoots m$^{-2}$ were reported by Agawin et al. (2001) for seagrass beds in the Philippines. The appearance of leaves for *C. rotundata* recorded by Agawin et al. (2001) was 0.09±0.005 shoot$^{-1}$ day$^{-1}$ and this was similar to the estimate for the production of new leaves made in this study. The changes in shoot density of this species were also reported in an earlier study (Uku and Björk, 2001). In as much as the shoot densities for *C. rotundata* fluctuated in our study, its biomass and leaf production rates were relatively constant compared to the other two species, indicating a strong adaptation to the intertidal zone.

A limitation of this study is that productivity estimates made could not be compared to those made in early studies such as Brouns (1987a,b). This is because the seagrass material collected in this study was not ashed to produce estimates of ash free dry weight (AFDW) while this was the method used in earlier studies. The earlier study by Uku and Björk (2001) in the same sites showed significant differences in leaf biomass of the three species when the sites were compared, which was not the case in this study. In this study, *T. ciliatum* and *C. rotundata* did not show differences in biomass and this could be explained by the fact that this study was conducted over a longer time period such that monthly differences became less prominent.

### 4.3. Distribution of epiphytic algae on the stems of Thalassodendron ciliatum

There was an alternation of epiphytic species on the stems of *Thalassodendron ciliatum* in Nyali with the seasons. The absence of *Gracilaria corticata* in Nyali during the NE monsoon is an indication of the typical species shift between the monsoon periods as described by Moorjani (1977). However species such as the encrusting coralline red algae, the filamentous red algae and *Ulva* sp. appeared to be unaffected by this seasonal shift. The stems of Vipingo did not exhibit such a wide array of macroalgal epiphytes and studies in Australia on the seagrass *Amphibolis griffithii*, which also has a lignified stem, show that the number of epiphytic algae increases with increasing seagrass height (Borowitzka et al., 1990). This could explain why the shorter plants in Vipingo had fewer epiphytes. In this study, the significant correlation of epiphytic cover to variation in stem height in Vipingo is a confirmation of this. Nevertheless, earlier studies on the species composition of epiphytic algae on *T. ciliatum* show that some of the epiphytes that are persistent in Nyali such as *Ulva* sp. are associated with the nutrient inputs in this site (Mwaluma et al., 1999; Uku and Björk, 2001).

## 5. Conclusions

In conclusion, the findings of this study show that the different species exhibited differences in biomass, leaf number and stem dimensions when the two sites were compared. Of the three seagrasses, and *Thalassia hemprichii* showed significantly higher total leaf growth per shoot in Nyali, the nutrient rich site. *T. hemprichii* also showed significantly higher leaf biomass and leaf production in the Nyali site. The fact that the growth of *T. hemprichii* increased in the NE monsoon period after nutrient inputs of the SE monsoon suggests that there is a time lag in the response of this species to nutrient inputs. However, we cannot rule out the possibility that other environmental factors may have influenced the high productivity of *T. hemprichii* particularly in the NE monsoon period. Although, the stems of *Thalassodendron ciliatum* found in Nyali were much longer than those found in Vipingo, the length is within estimates reported for this species in Kenyan lagoons which suggests that stem height may not be linked to nutrient enrichment. Therefore, in conclusion, we suggest that apart from previously reported differences in epiphytic algae that were found to characterize these sites, enhanced seagrass productivity may also be an indicator of nutrient enrichment in these areas.

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