The Production of the Seagrass *Thalassia hemprichii* in Relation to Epiphytic Biomass

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Abstract
The growth of *Thalassia hemprichii* was investigated in relation to its epiphytic biomass during the dry season at Inhaca and Portuguese Islands in the south of Mozambique. Three sites were investigated, chosen due to their assumed difference in epiphytic biomass. Epiphyte species composition was not considered, but the epiphyte assemblages were mainly found to be layers of varying thickness lining the leaf surfaces, and large macroalgae were not present. The hypothesis was that the less epiphytic biomass the higher production of *T. hemprichii* would occur at the different sites. This was shown not to be the case for the prevailing epiphyte load on a “per shoot basis”, however the areal shoot density, above ground biomass and production was found to be greater where epiphytic biomass was lower despite smaller shoots. When compared to previous studies epiphytic biomass on *T. hemprichii* in the South Bay of Inhaca has increased greatly since 2001, meanwhile a large decrease in above ground biomass of seagrass has occurred. Whether these changes in biomasses are linked or not is difficult to say without further studies of rhizome growth and clonal recruitment, but it appears as though increased epiphyte load can have a negative impact on the areal production of *T. hemprichii*.

Introduction
Seagrass beds are ecologically and economically important habitats, and one of the most productive amongst the aquatic primary producer ecosystems (Duarte and Chiscano, 1999). Numerous studies conducted throughout the world demonstrate that seagrass systems sustain a higher density of organisms than do unvegetated areas (Edgar and Shaw, 1995 and Mattila et al., 1997), higher diversity and biomass than mangroves (Sheridan, 1997), and support fish populations in adjacent areas by acting as breeding grounds and nurseries (e.g. Joseph et al., 2006 and Gotceitas et al., 1997).

Seagrass leaves are known to be habitats to epiphytic organisms such as micro and macro algae, various prokaryotes and calcareous animals (e.g. Corlett and Jones, 2007, Wear et al., 1999, Uku et al., 2007 and Perry and Beavington-Penney, 2005). Epiphytes on seagrass leaves have been found to be both beneficial and detrimental to the host plants. Beneficial effects can be that heavy epiphytization has been shown to lessen desiccation, and hence leaf damage, during exposure to air (Penhale and Smith, 1977). Also epiphytes decrease water movement and thereby the erosion of sediment, which in turn allows for the seagrass to live in higher energy environments (Borowitzka et al., 1990).

A possible detrimental effect is for example increased attenuation of photosynthetically active radiation (PAR) with increasing epiphyte load, a factor that can have a large impact already at relatively low epiphyte densities (Brush and Nixon, 2002). Moreover, apart from only shading, high O$_2$ and low CO$_2$ conditions can be generated during daylight and anoxic conditions at night (Sand-Jensen et al., 1985), which may lead to difficulties for the plants to uphold normal photosynthetic rates. Other detrimental effects can be inhibition of NH$_4^+$ uptake by blocking the uptake sites (Cornelissen and Thomas, 2004). It has also been shown that heavily epiphytized leaves, already weakened by reasons mentioned earlier, are more receptive to sloughing due to increased drag (Fong et al., 2000).

Nutrient enrichment has been thought to pose a threat to seagrass beds around the world (e.g. Wear et al., 1999, Bowen and Valiela, 2001 and Short et al., 1995). In a study by Tomasko and Lapointe (1991) it was shown that *Thalassia testudinum*-beds at sites with increased levels of nutrients in the water column, had elevated levels of epiphytes, something that also was linked to the low shoot densities, leaf area indices and biomasses found in the meadows, which in turn lead to a low areal growth. Hauxwell et al. (2003) linked great losses of *Zostera marina* to nitrogen loading by increased standing stock of macroalgae, which caused severe light limitation to the shoots, especially newly recruited ones, and increased mortality by epiphyte shading. Implications were found that the low shoot densities in these areas were not only due to high mortality, but also low recruitment resulting from a lack of energy for translocation to new clones.

The seagrass habitats on the east coast of Africa are of great importance, both in sustaining biological diversity and in providing the local populace with ecosystem goods and services. These terms are defined as “the benefits that humans derive, directly or indirectly, from ecological functions” (Costanza et al., 1997), with the use of fish and invertebrates for subsistence and profit being examples of such services. In Tanzania seagrass beds are considered one of the most productive fishing grounds in terms of catch per unit effort (de la Torre-Castro and Rönnbäck, 2004).
and in southern Mozambique meadows are exploited for net fishing and collection of invertebrates (Bandeira, 1995).

However, the seagrass beds of eastern Africa are still poorly studied, and a deeper understanding of these complex systems is needed to illuminate their current status and possible need for rectification in management, and thereby ensuring their long-term prosperity.

*Thalassia hemprichii* (Ehrenb.) Aschers is a tropical seagrass species that ranges from the shallow subtidal to below 10 meters in depth (Waycott et al. 2004), belonging to the family Hydrocharitaceae. The species is common and dominating in many seagrass associations in the western and eastern Indian Ocean (e.g. Gullström et al., 2002 and Prathep, 2003) as well as the western Pacific Ocean (e.g. Tanaka and Kayanne, 2007 and Vermaat et al., 1995).

Inhaca Island is located in the south of Mozambique and is approximately 42.5 km² (Muacanhia, 2003) with around 5000 inhabitants, but with increasing tourism and exploitation this number is likely to increase. Portuguese Island is a small uninhabited island, only 3.7 km² in size (Muacanhia, 2003), just west of Inhaca and almost connected to the larger island at spring low tide through a series of sand banks. The marine environment around the islands is diverse, and contains mangroves, sand flats, coral reefs, mud flats and seagrass beds all in close proximity. Seagrass meadows are fringing the island on three sides (fig.1) as well as covering much of the mudflats, which come to a total area of around 45 km² seagrass (Bandeira, 2000). The most common seagrass association around Inhaca and Portuguese Islands mainly consists of *T. hemprichii* and Halodule wrightii, but in which all three seagrass species of the area can be found, and this association spans over more than 40 per cent of the seagrass covered area (Bandeira, 2000).

The link between nutrient enrichment of shallow bays and increased epiphytic growth is in truth as complex as it is debated, and depends on numerous factors such as type and concentration of nutrients, grazing, light availability and temperature in many different constellations (e.g. Frankovich and Fourquarean, 1997, Williams and Ruckelshaus, 1993 and Neckles et al., 1993). However, since the nature of these interactions is highly variable, this possible link makes it important to investigate the sensitivity of *T. hemprichii*, as being one of the more dominant seagrasses around Inhaca, to this potential threat. At this time the rather small population and moderate tourism may not severely affect the nutrient input into the shallow waters around Inhaca and Portuguese Islands, but with increasing tourism and population, and the change in land use that this would bring, increased nutrient loading might result.

Three different intertidal sites, two in the South Bay of Inhaca Island and one east of Portuguese Island (fig.1), in the North Bay of Inhaca, of approximately the same tidal range were chosen due to their assumed varying amount of epiphytic biomass. The main aim of the study was to investigate the effect of epiphytic biomass, with “epiphytic biomass” here referring to diverse autotrophic and heterotrophic assemblages, on the production of the *T. hemprichii* shoots around Inhaca and Portuguese Island, with the hypothesis that higher epiphytic biomass will lead to decreased production. Epiphyte species composition was not investigated in this study, but has previously been shown around Inhaca to contain e.g. the crustose coralline algae *Hydroplithon farinosum*, as well as foraminifera such as *Peneroplis sp.* (Perry and Beavington-Penney, 2005). *T. hemprichii* has also been shown in associations with cyanobacteria (e.g. *Rivularia sp.*, *Synechococcus spp.* and *Trichodesmium sp.*), as well as various macroalgae (Uku, 2005). The secondary aim was to describe the meadows investigated and compare them to earlier research of the species to estimate the status of the *T. hemprichii* beds around Inhaca and Portuguese Islands.

**Method**

**Site description**

The three *Thalassia hemprichii* sites studied are located in the proximity of Inhaca Island (fig.1): One in the outer parts of the South Bay, henceforth called Saco, which is located on the mudflat fringing the southwest part of the bay (26,05°S, 32,93°E) and relatively close to land. Next site is situated on a mudflat at the entrance of the South Bay, called Banco (26,06°S, 32,94°E), which is separated from the Saco site by a tidal channel and a rather large unvegetated part of the mudflat, and in closer proximity Ponta Torres where oceanic water enters the bay. The last site is located east of Portuguese Island, here called PI (25,98°S, 32,92°E), which is a nature reserve at the far edge of the North Bay of Inhaca.

The growth of *Thalassia hemprichii* is patchy at the sites, with plants generally being located in deeper pools of the flats, in mostly monospecific stands. The tide is semi-diurnal and has a range of +2,2 to -0,7 meters (de Boer et al., 2000), and at spring low tide the minimum water level is 5-10 cm above the sediment, and thus the shoots are never completely exposed to air. However, the shoots at PI seem slightly more rigid than at Banco and Saco, why leaves sometimes partly extend over the water surface, whereas the leaves of the shoots at the latter sites float along the water surface (pers. obs.).
The climate is tropical to subtropical and has two distinct seasons: Winter, from April to September, which is cold and dry, and summer from October until March, which is warm and rainy (de Boer et al., 2000). The salinity and temperature have previously been shown to range between 30 - 39 psu and 20-29°C respectively (Paula et al., 1998 and Bandeira, 2000), with the average during the dry season being 36 psu and 24-25.5°C for the surface water (Paula et al., 2001).

**Sampling and analysis**

At each of the sites plant shoots of ten squares, each 0.25 m² in size, were marked with a 1.5 mm syringe needle using a punch hole leaf marking technique initially developed by Zieman (1974). Due to the patchy growth, the squares were chosen as randomly as possible but with the obligate criteria of existing seagrass shoots. The investigation was performed from the beginning of May to mid June, and each site was sampled at 4 different times at varying time intervals, due to favourable tides, but with the final sampling consistently being performed at day 29. Since the marking and sampling was performed by foot, it was limited to low tide. The treatment of samples was time-consuming, why the marking and sampling could not be performed simultaneously for the different sites. To try to eliminate the variation in growth due to different tides, i.e. periods of spring and neap tides, or difference in water depth during daylight, the sampling was performed over time instead of just once.

The sampling was performed as follows: Three to five shoots from each square were chosen more or less haphazardly, making a total of approximately 30 shoots per sampling. At first this number was 50, but due to time-limitations this number was decreased. As some of the square markers disappeared, due to unfortunate weather conditions,
more shoots were taken from the remaining squares. The shoots were placed in zip-lock bags filled with seawater during the transport, after which they were carefully dipped in brackish water (freshwater was not available) to avoid loosening of epiphytes but removing loose debris not attached to the leaves. The leaves of a shoot were then separated, placed in order of age and photographed. The epiphytes were removed by gently scraping the leaves with a flat bladed scalpel after which they were placed in eppendorf vials and frozen before being dried in 80°C for 24 hours. Once the leaves had been rid of epiphytes, they were once again rinsed in brackish water to eliminate all epiphyte remnants, after which they were measured for length, width, sheath length and growth. The number of leaves was noted as well as the presence of flowers. The outermost leaf or leaf sheath that had not grown was used as reference height regarding the growth, and for each leaf the difference between the reference height and the punch-hole was cut out and frozen for later drying in 80°C for 24 hours. After drying, the samples were weighed, and three samples from each site were burned in 550 ºC for six hours to obtain an ash free dry weight (AFDW) to dry weight (DW) ratio.

To be able to estimate the production per square meter in a non-destructive way, the number of shoots was counted in 30 randomly chosen squares (0.25 m² in size) per site. In order to calculate the standing stock a minimum of 15 unmarked shoots per site were randomly collected, and measured in the same way as above with the exception that the whole leaves were frozen. Once again three shoots per site were burned for AFDW:DW ratio. The ring cowrie, Cyprea annulus (Mollusca: Gastropoda), with and adult size of approximately 15-20 mm (Katoh, 1989), was observed to be the dominant relatively sedentary grazer found on the leaves, why also the number of ring cowries was counted in 30 randomly chosen squares (0.25 m²). Other gastropods found on the leaves were very rare, why they were not included.

To complement the study a sampling of salinity, organic content of sediment and grain size were performed in October at Portuguese Island (S25° 58’ E032° 55’), Saco (S26° 03’ E032° 55’) and Banco (S26° 01’ E032° 54’). The salinity was measured with a handheld refractometer, the organic content by drying the sediment in 80°C for 24 hours followed by burning in 550°C for six hours and subtracting the AFDW from the DW. The grain size was determined by removing the organic material with hydrogen peroxide and then sieving and drying the fractions. The fractions of fine and medium sand were used as indicators of exposure, with a higher fraction of medium sand and lower fraction of fine sand meaning higher exposure than the opposite.

Calculations

Leaf surface (LS) is calculated as (leaf length* width). The shoot biomass, since whole shoots were not saved except for the 15 unmarked shoots, were obtained by ((biomass produced/ length produced)*shoot length). The shoot density is normalized to 1 m², leaf density is calculated as (average no. leaves shoot¹*shoot density) and LAI is (leaf density*average LS shoot¹) (n=30). The above ground biomass (AGB) is obtained by (shoot density*average shoot biomass). Epiphyte biomass per photosynthetic leaf surface (PLS) was chosen since epiphytes was only found on leaf parts outside leaf sheaths, and is calculated as (biomass of epiphytes shoot¹/ PLS shoot¹) (n=40, 37 and 40 for PI, Banco and Saco respectively). To be able to estimate the photosynthetic leaf surface (PLS) the assumption was made that the leaf sheath, which most commonly is covered by the remnants of previous leaves, is not photosynthetic, and that even though a younger leaf has photosynthetic surface it cannot be regarded as such if it is still covered by the sheaths of the older leaves. This of course is a crude estimation and does not take into account that leaves are not the same width for their full length, but the leaf width above the sheath was not extremely varying for any individual leaf. Hence the PLS is calculated as ((leaf length -sheath length)*leaf width) and added together for all leaves of a shoot. The areal epiphyte biomass is hence (average PLS shoot¹*average epiphyte biomass PLS¹*shoot density). Leaf growth is calculated as (length produced/ no. days since marking), shoot production as (biomass produced/ no. days since marking) and relative production rate (RPR) as (shoot production/ biomass shoot¹). Areal production is (average shoot production*shoot density). Per cent flowering is calculated by (shoots with flower/ all sampled shoots*100) and density of Cyprea annulus is normalized to 1 m².

For the LS, epiphyte biomass per PLS, leaf growth, shoot production and RPR the mean of each square at each sampling has been used, giving n=40, 35 and 40 for PI, Banco and Saco respectively. Regarding the shoot density, leaf density, LAI, areal epiphyte biomass, areal production and Cyprea annulus density, the number of squares from which they were calculated gave n=30.

Statistical analysis

In order to test the difference between T. hemprichii parameters measured a multivariate ANOVA was run on square averages for the variables where this was possible (n= 40, 35 and 40 for PI, Banco and Saco respectively): number of leaves, shoot length, shoot biomass, epiphyte biomass per PLS (ln values used for statistical analysis).
analysis) and shoot production. Multivariate ANOVA was also run on density (sqrt values used for statistical analysis), leaf density, LAI, areal epiphyte biomass (ln values used for statistical analysis), shoot production, RPR and areal production (n=30). Salinity, organic content and sand fractions were also run in a multivariate ANOVA (n=5).

Results

Table 1: Salinity, organic content of sediment, medium and fine sand fraction (average and SE) at PI Banco and Saco (n=5).

<table>
<thead>
<tr>
<th>Study areas</th>
<th>Salinity %</th>
<th>Organic content %</th>
<th>Medium sand fraction %</th>
<th>Fine sand fraction %</th>
</tr>
</thead>
<tbody>
<tr>
<td>Portuguese Island</td>
<td>3,8</td>
<td>1,29</td>
<td>0,08</td>
<td>79,0</td>
</tr>
<tr>
<td>Banco</td>
<td>3,84</td>
<td>0,04</td>
<td>1,23</td>
<td>65,5</td>
</tr>
<tr>
<td>Saco</td>
<td>3,84</td>
<td>0,04</td>
<td>1,26</td>
<td>75,3</td>
</tr>
</tbody>
</table>

Abiotic factors

The salinity and organic content of the sediment are similar between all sites (p=1,000). Considering medium and fine sand fractions Banco has a smaller fraction than PI and Saco of medium sand (p=0,003 and 0,028 respectively) and larger fraction of fine sand (p=0,000 and 0,004 respectively). PI has the largest fraction of medium sand and the smallest fraction of fine sand, but there is no significant difference between PI and Saco for either fraction.

Figure 2: Leaf surface per leaf (average and SE) of Thalassia hemprichii shoots at PI, Banco and Saco (n= 40, 35 and 40 for leaf 1).

Shoots, density and biomass

Banco and Saco have quite similar leaf lengths and widths, with the only exception being the two oldest leaves which are slightly shorter at Saco, whereas PI has both narrower and shorter leaves throughout, which makes the difference in leaf surface more pronounced (fig.2).

In tab.2 a number of shoot, density and biomass variables are shown. Number of leaves per shoot is at its lowest at Banco, and rather similar between PI and Saco, with the only significant difference being between Banco and Saco (p =0,012). The combined shoot length with all leaves included is shorter at PI than at Banco and Saco (p = 0,000), but similar between the latter two (p=1,000). Also a lower biomass per shoot is found at PI than at both Banco and Saco (p=0,000), and only slightly greater biomass at Banco than at Saco (ns). However the density of T. hemprichii is approximately double the number at PI than the other sites (p=0,000), but similar between Banco and Saco (p=1,000). The above ground biomass is significantly higher for PI than Banco and Saco (p=0,003) but highly insignificant between Banco and Saco (p=1,000). The leaf density is just like the shoot density approximately half of that at PI for Banco and Saco (0,000) and the leaf area index is significantly higher for PI than the latter two (p=0,006 and 0,007 respectively).
Table 2. Number of leaves, shoot length, shoot biomass, density, leaf density, leaf area index (LAI), above ground biomass (AGB), epiphyte biomass per photosynthetic leaf surface (PLS), areal epiphyte biomass, leaf growth, shoot production, relative production rate, areal production, flowering of Thalassia hemprichii and density of Cypraea annulus in the seagrass beds at PI, Banco and Saco (average and SE).

<table>
<thead>
<tr>
<th></th>
<th>Portuguese Island</th>
<th>Banco</th>
<th>Saco</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Number of leaves</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(leaves shoot⁻¹)</td>
<td>4,4</td>
<td>4,2</td>
<td>4,5</td>
</tr>
<tr>
<td><strong>Shoot length</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(mm)</td>
<td>382,8</td>
<td>12,4</td>
<td>530,4</td>
</tr>
<tr>
<td><strong>Shoot biomass</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(g DW shoot⁻¹)</td>
<td>0,12</td>
<td>0,006</td>
<td>0,20</td>
</tr>
<tr>
<td>(g AFDW shoot⁻¹)</td>
<td>0,09</td>
<td>0,005</td>
<td>0,15</td>
</tr>
<tr>
<td><strong>Density</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(shoots m⁻²)</td>
<td>475</td>
<td>17</td>
<td>234</td>
</tr>
<tr>
<td><strong>Leaf density</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(leaves m⁻²)</td>
<td>2177</td>
<td>78</td>
<td>970</td>
</tr>
<tr>
<td><strong>LAI</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(m² m⁻²)</td>
<td>1,42</td>
<td>0,05</td>
<td>1,16</td>
</tr>
<tr>
<td><strong>AGB</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(g DW m⁻²)</td>
<td>57,7</td>
<td>2,1</td>
<td>46,1</td>
</tr>
<tr>
<td>(g AFDW m⁻²)</td>
<td>43,9</td>
<td>1,6</td>
<td>35,5</td>
</tr>
<tr>
<td><strong>Epiphyte biomass per PLS</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(g DW cm⁻²)</td>
<td>0,0004</td>
<td>2,1E⁻⁰⁵</td>
<td>0,0019</td>
</tr>
<tr>
<td><strong>Areal epiphyte biomass</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(g DW m⁻²)</td>
<td>3,0</td>
<td>0,1</td>
<td>11,5</td>
</tr>
<tr>
<td>(g AFDW cm⁻²)</td>
<td>0,7</td>
<td>0,02</td>
<td>2,2</td>
</tr>
<tr>
<td><strong>Leaf growth</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(mm shoot⁻¹ day⁻¹)</td>
<td>8,2</td>
<td>0,3</td>
<td>11,9</td>
</tr>
<tr>
<td><strong>Shoot production</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(g DW shoot⁻¹ day⁻¹)</td>
<td>0,0025</td>
<td>0,0001</td>
<td>0,0044</td>
</tr>
<tr>
<td><strong>Relative production rate</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(g g⁻¹ DW day⁻¹)</td>
<td>0,022</td>
<td>0,0004</td>
<td>0,023</td>
</tr>
<tr>
<td><strong>Areal production</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(g DW m⁻² day⁻¹)</td>
<td>1,22</td>
<td>0,04</td>
<td>1,03</td>
</tr>
<tr>
<td>(g AFDW m⁻² day⁻¹)</td>
<td>0,92</td>
<td>0,03</td>
<td>0,79</td>
</tr>
<tr>
<td><strong>Flowering</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(% shoots with flowers)</td>
<td>8,7</td>
<td>0,6</td>
<td>0,7</td>
</tr>
<tr>
<td><strong>Cypraea annulus density</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(# m⁻²)</td>
<td>4,9</td>
<td>0,9</td>
<td>7,3</td>
</tr>
</tbody>
</table>

**Epiphytic biomass**

Epiphytic biomass per photosynthetic leaf surface and areal epiphyte biomass is significantly lower at PI than the other sites (p=0,000), but rather similar between Banco and Saco (tab.2). Regarding the epiphyte assemblages can be said that no large macroalgae were found on the leaves at any of the sites, but rather the epiphytes lined the leaf surfaces in varyingly thick layers. However, calcium carbonate depositing epiphytes appeared more common at PI than the other sites.

**Production**

In tab.2 it is shown that leaf growth is significantly lower at PI than the other sites (p=0,000), as is the shoot production (p=0,000), however the relative production rate is similar between all sites (ns). Production of areal biomass per day is significantly higher for PI than Banco and Saco (p=0,032 and 0,004 respectively).

**Flowering and grazer density**

Flowering shoots were found in the random sampling, and the trend appears to be that PI had a higher percentage of flowering shoots during the sampling period (tab.2). At each of the other sites only one flower was found in the samples. The grazer predominantly found at the sites during low tide was Cypraea annulus (Ring cowrie), with the trend being that Banco had the greatest density followed by PI, and with Saco having the lowest density of cowries.
Discussion

To be able to compare the production of *Thalassia hemprichii* in relation to epiphytic biomass, it is first important to lay out the existing prerequisites for each site. The salinity and organic content was very similar for all sites (tab.1), but the higher percentage of medium sand and lower percentage of fine sand at PI indicates this site to be more exposed, followed by Saco, with Banco being the most sheltered site.

Apparent morphological differences of the shoots can be seen between the sites, with PI having a significantly smaller and lighter phenotype than both Banco and Saco, which are fairly similar in most aspects (fig.1 and tab.2) with the only significant exception for entire shoots being the number of leaves. The similarity of the sites in the South Bay of Inhaca continues for shoot density (tab.2), while PI has approximately twice their density. These phenotypic expressions and shoot densities have previously been linked to exposure gradient for *T. hemprichii* in Japan (Takada and Abe, 2002), where lower shoot density as well as longer and wider leaves were found at protected shores, something that is supported by the higher exposure gradient at PI. Higher shoot density has also been shown to coincide with lower canopy height for the species on Zanzibar (Eklöf et al., 2005 and Gullström et al., 2006). However, it appears that the shoot density at all sites around Inhaca is rather low, especially in the South Bay, where it is lower than almost all reported values (e.g. Uku and Björk, 2005, Jagtap, 2004 and Vonk et al., 2008). Low shoot densities has previously also been connected with nutrient loading and increased epiphytic biomass for other seagrass (Tomasko and Lapointe, 1991 and Hauxwell et al., 2003), and shading has been shown to induce longer leaves in *T. hemprichii* (Abu Hena et al., 2004).

The above ground biomass (AGB) is higher at PI, despite the lower biomass per shoot, due to the much higher shoot density, which in turn also explains the higher leaf density and leaf area index (tab.2). AGB appears to be very variable over the large scale distribution of the species, and does not appear to be closely connected to shoot size or density alone, but rather a combination of the two. In a review article by Duarte and Chiscano (1999), taking into account most measurements made until that date, the overall mean AGB was found to be 86.9 g dry weight per m². Compared to this value the AGB is rather low around Inhaca and Portuguese Islands, but when looking at individual studies it seems well within the range of the species (e.g. Vonk et al., 2008, Abu Hena et al., 2004 and Agawin et al., 2001). However, compared to two studies from 2001, which found AGB’s in the South Bay of Inhaca to be 142.2 g DW m⁻² (Martins and Bandeira, 2001) and approximately 60 g AFDW m⁻² (Paula et al., 2001), the biomass of the South Bay appears to have decreased a great deal. Although methods for biomass estimation varied, something that might contribute to the differences observed, this seems unlikely to explain the decrease of 68 and 40 per cent respectively. The leaf density at PI is somewhat greater than the 1542 leaves m⁻² previously recorded for the North Bay, which is the closest investigated area (Perry and Beavington-Penney, 2005). The leaf area index of *T. hemprichii* at PI is similar to a study in the North West Philippines with a LAI of 1.45 (Vermaat et al., 1995), and an LAI of 1.2 that was observed for the species dominating a mixed bed, is relatively similar to Banco and Saco. However, another study from the western Philippines show LAI’s of more than 5 (Rollon et al., 2001), compared to which all of the sites around Inhaca have low leaf area indices. It appears as though the LAI around Inhaca and Portuguese Islands is within the range, but at the lower parts of the scale, for the species.

The amount of epiphytic biomass per photosynthetic leaf surface is markedly lower at PI than the other sites (tab.2), partially supporting the basic assumption for the investigation of varying epiphytic load at the sites. This difference could be caused by a number of factors such as varying nutrient input (Borum, 1985), exposure (Strand and Weisner, 1996) and grazers (Fong et al, 2000), but since water column nutrients were not included in this study, and neither exposure nor grazers were more than crude estimations, it is difficult to elaborate. At best it can be concluded that PI, as the most exposed site, had an intermediate density of relatively sedentary grazers (*Cypraea annulus*) (tab.2), whereas Banco as the most sheltered site had the highest density, and Saco with intermediate exposure had a very low density of *C. annulus*. Schanz et al. (2002) found epiphyte biomass to be higher at exposed sites due to low grazer density caused by the hydrodynamic conditions, which apparently is not the case in Inhaca archipelago. Since Banco and Saco had very similar epiphytic biomasses, but differed in the amount of grazers investigated, it appears as though *C. annulus* is not exerting any great top-down effect, and hence is not the sole explanation of the difference in epiphytic biomass in this study. However, other grazers not accounted for here, for example herbivorous fish, might have greater impact on epiphytes. Strand and Weisner (1996) found that epiphyte biomass on *Pomatogeton pectinatus* decreased with increasing exposure gradient in eutrophicated lakes, something that could support exposure as being a reason for the lower epiphyte biomass found at PI. However, measurements of water column nutrients would be needed to clarify the difference observed between sites.
In a study by Brush and Nixon (2002) it was shown that epiphyte biomasses of one and two mg DW cm$^{-2}$ decreased incoming PAR to seagrass leaves down to 71 and 56 % respectively. Twilley et al. (1985) found radiation reduced to 90 and 59 % respectively, for the same biomasses. By these numbers PI, with its 0.4 mg DW cm$^{-2}$, would appear not to be at risk of greater PAR attenuation, but both Banco and Saco, with their 1.9 and 2.0 mg DW cm$^{-2}$ respectively, would run the risk of this affecting their production. The areal epiphyte biomass of the South Bay, which was found to be 2.1-2.2 g AFDW m$^{-2}$, compared to a previously reported biomass of between 0.0-0.4 g AFDW m$^{-2}$ (Paula et al., 2001), poses the question of whether the biomass was underestimated in 2001, or if there has been a rather large increase of epiphytic biomass in the bay. When considering that a decrease in above ground biomass of seagrass basically also means a decrease in available leaf surface, this could be interpreted as an even greater increase in epiphytic biomass per leaf surface, since there is now less leaf surface for the greater epiphyte load to occupy. When regarding the link that Tomasko and Lapointe (1991) found between elevated epiphyte levels and low shoot densities, biomasses and in turn low areal growth, it appears likely that a decrease in AGB and increase in areal epiphyte biomass occurring simultaneously are connected, and that the latter, at least partly, caused the former.

When regarding production parameters both the leaf growth and shoot production (tab.2) are significantly lower for PI than the other sites, but this could partly be expected when looking at the size difference between the shoots, as previously shown for the species (Uku and Björk, 2005). However, the areal production is higher at PI, something that reflects on its higher AGB. Due to PI's lower epiphytic biomass one would expect a higher relative production rate at that site compared to the sites in the South Bay. This however is not the case, but rather the relative production rate is basically the same for all sites, i.e. the shoots produce approximately the same biomass per already existing biomass per day. A possible reason for this might be that the prevailing epiphyte load is not great enough to affect the production of the shoots. On the other hand, Hauxwell et al. (2003) found that Zostera marina shoots under severe light limitation grew equally well on a “per shoot basis”, but implications were found that the low shoot densities were not only due to high shoot mortality, but that affected shoots lacked excess energy to translocate to branching shoots. When comparing the relative production rate in Inhaca archipelago to other studies, it appears rather low, as most other studies present RPR’s of above 0.04 (e.g. Uku and Björk, 2005 and Abu Hena, 2004). The overall mean for the areal production of $T$. hemprichii around the world is 3.7 g DW m$^{-2}$ day$^{-1}$ (Duarte and Chiscano, 1999), and compared to this also the areal production around Inhaca and Portuguese Islands is rather low.

Regarding flowering in $T$. hemprichii, the percentage of shoots with flowers is much greater at PI than the sites in South Bay. Whether this is due to variation within flowering season at the different locations, or a higher tendency to flower at PI is hard to say. By visual observation the meadow at PI seemed to be flowering and bearing fruits during the full time of the investigation, whereas flowers were much more rarely found at Banco and Saco, starting from the beginning of June. Martins and Bandeira (2001) observed more frequent flowering in the South Bay during the dry period, from April to September, however this study was performed between May and June, which makes it difficult to say whether a change in this pattern has occurred.

To summarize the condition of the $T$. hemprichii- beds in Inhaca archipelago, in comparison to the species elsewhere, one can conclude that they seem within the range of the species for most variables, however at the lower parts of the scale for density, biomass and relative production rate. When compared within the archipelago it seems that the meadow at PI is doing rather well, while the South Bay might be in need of further investigations to illuminate whether the low shoot density and biomass found is related to low recruitment and high mortality due to epiphytic growth.

Concerning future monitoring of the meadows around Inhaca and Portuguese Islands, some issues should be addressed. It could be argued that areal production would be a better parameter for seagrass growth than leaf growth and shoot production, since the latter two largely depend on the size of the shoots, whereas areal production gives an estimation that combines the shoot size, relative production rate and density. Hauxwell et al. (2003) suggested shoot density and meadow area as adequate variables for $Zostera marina$ monitoring, after finding lowered areal production mainly depending on a decreased shoot density and not a change in shoot productivity. This seems a reasonable suggestion also for $T$. hemprichii around Inhaca and Portuguese Islands, but with additional care to note the phenotypic expression of the different meadows.

Conclusions

To conclude the study: It appears that $Thalassia hemprichii$ is not affected by the prevailing epiphyte load around Inhaca on a “per shoot basis”. However the shoot density, AGB and hence the areal production, is higher at the site with less epiphytic biomass. It seems that a decrease of AGB in the South Bay, appearing simultaneously with a large increase in epiphytic biomass, is a sign
that epiphyte load might still affect seagrass above ground biomass and areal productivity in a negative way. Future studies should focus on areal growth, not only for above ground material, but also for rhizomes, to see whether the low shoot densities in the South Bay is related to low clonal recruitment.

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