

**Leaf production, shoot demography, and flowering of the
seagrass *Thalassodendron ciliatum* (Cymodoceaceae)
along the East African coast**

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Abstract

Several characteristics of *Thalassodendron ciliatum* populations were evaluated along the coasts of Kenya and Zanzibar Island, with the aim to study spatial variability in this species. The study is the first large-scale sampling effort to evaluate the status of *T. ciliatum* on the East African coast and provides a base line in future works. A reconstruction technique, which makes use of scars left by abscised leaves and flowers, was employed to determine leaf production, shoot demography and flowering frequency. Eight subtidal sites in different back-reef lagoons were sampled. Furthermore, samples were collected at a subtidal site that was not protected by a reef, a site with intertidal rock pools, and a subtidal site in a mangrove bay. Leaf-production rates were lowest for the *T. ciliatum* population of the subtidal site that was not protected by a reef and for the population from the intertidal rock pools (30 leaves shoot⁻¹ year⁻¹). At these sites, leaf lifespan was almost twice as long (94 days). Low leaf-formation rates seem to be compensated by long leaf lifespans to maintain similar numbers of standing leaves per shoot. Highest leaf-production rates were found at the mangrove-bay site (53 leaves shoot⁻¹ year⁻¹). The mangrove-bay population showed internodal lengths of almost 7 mm and stem lengths of almost 90 cm. The stems were two to four fold longer than those at the other sites. A short leaf lifespan of 51 days at the mangrove site indicates that the investment in stem growth occurs at the expense of leaf maintenance. Median ages of the populations varied almost four fold from 0.5 year to 1.8 years. Shoot recruitment and mortality rates differed significantly among sites. Differences could not be related to habitat type. All meadows in the present study were either expanding or in steady state. This suggests that, even though some sites were located near accumulations of beach hotels, the environmental quality in this region is still suitable for sustaining vigorous seagrass vegetation. Flowering frequencies were generally low. In addition, seedlings were not found in our study. Thus, sexual reproduction is of minor importance for the permanently submerged *T. ciliatum* populations, which reduces the ability to adapt to changes.

Keywords: Seagrass; Leaf production, Demography; Flowering; East Africa; *Thalassodendron ciliatum*

1. Introduction

In the tropics, shallow coastal areas are characterised by the existence of extensive seagrass meadows. The seagrasses are found in different habitats such as lagoons behind coral reefs that fringe the coast, mangrove bays or estuaries. The seagrass beds provide food and shelter for a variety of other organisms, including commercially important fish species, and thus constitute a valuable component of the nearshore ecosystem (Howard *et al.*, 1989). Since the last two decades, anthropogenic pressure, mainly derived from tourism development, is increasing exponentially along the East African coast (Shah *et al.*, 1997). This increase of the human population is rapidly changing the coastal zone. It may lead to deterioration of the marine environment and puts pressure on seagrass functioning (Johnson and Johnstone, 1995). At the same time, the local economy often depends on the presence of seagrass biotopes (Poiner *et al.*, 1989). The seagrass meadows along the East African coast might be sensitive to the transformation this coast is experiencing. Conservation of these habitats is therefore important. However, lack of base line information on the status of East African seagrass beds prevents forecasts of the future of seagrasses in this region.

For many tropical seagrass species, knowledge on spatial variability in population dynamics is scarce. A rapid assessment of seagrass dynamics can be obtained using the so-called reconstruction technique (Duarte *et al.*, 1994). The method is based on age determinations and can evaluate the vigour, expansion or decline of the beds. In seagrasses, new leaves are constantly being produced and old leaves are shed. Leaf scars from shed leaves remain visible on the stems. Internodal lengths between two successive leaf scars are longer during fast growth and smaller during periods of slow growth (e.g. Duarte and Sand-Jensen, 1990b). Variability in internodal length reflects seasonal variability in plant growth (Duarte *et al.*, 1994). These seasonal signals on the stems can be used to determine the leaf-production rate, and consequently the age of the shoots. Estimation of leaf-production rate, shoot recruitment and mortality, and flowering can reveal whether a population is expanding, declining or in steady state. The advantage of the reconstruction technique is that one can forecast meadow development from a single visit to the study site. However, the method must be used with caution, because determination of recruitment is

based on the proportion of shoots older than 1 year. Therefore, meadow development is estimated from the size of one cohort only, which limits the analysis (Kaldy *et al.*, 1999).

Thalassodendron ciliatum (Forsk.) den Hartog is a very common seagrass species in the Red Sea, the western Indian Ocean and the tropical part of the Indo-Pacific region (den Hartog, 1970). According to Den Hartog (1970) *T. ciliatum* is generally found in extensive and monotonous meadows. However, Johnstone (1984) observed a total of eight other species co-existing with *T. ciliatum*. *T. ciliatum* has horizontal as well as vertical rhizomes. The horizontal rhizomes show a distinct pattern in branching; every fourth node a new vertical rhizome or shoot is produced. A cluster of leaves is present at the top of each living stem. Knowledge on population structure in *T. ciliatum* is limited to estimates of leaf production rates at locations in Asia and Africa (Johnstone, 1984; Brouns, 1985; Hemminga *et al.*, 1995; Bandeira, 1997), stem-length distribution at two sites in Mozambique (Bandeira, 1996), and population dynamics at one site in Kenya (Duarte *et al.*, 1996).

This paper presents leaf production, shoot dynamics and flowering intensity of a number of *T. ciliatum* populations along the East African coast to determine the spatial variability in this species. Moreover, the study provides an evaluation of the present status of *T. ciliatum* at different localities that may be used as a base line in future works.

2. Material and methods

In March 1997, six sites in back-reef lagoons along the southern part of the Kenyan coast were sampled and in February 1998 sampling was carried out at five sites on Zanzibar Island: three sites in back-reef lagoons, one site that was not sheltered by a reef and one site in a mangrove bay (Fig. 1). The tidal range is 4 m at spring tide and 1 m at neap tide. All sampling sites were subtidal and located at the same depth (1.5 m below 0 Chart Datum, or 1.5 m below the lowest water level during an extreme spring tide), except for one of the lagoons on the Kenyan coast (Vipingo), where the site was intertidal (1.2 m above 0 Chart Datum) and the samples were collected in permanently submerged pools in the reef flat. *Thalassodendron ciliatum* occurred both in monospecific and in mixed meadows. Extensive monospecific meadows of at least more than 480 m long were found in the back-reef lagoons at Nyali and Watamu. In the lagoon at Roka, *T. ciliatum* was also the only seagrass species, but here it occurred in small patches of 30 m wide in between rocky areas. All

other sites had mixed populations where *T. ciliatum* patch size ranged from less than 1 m² to about 120 m in diameter. Co-occurring species were: *Thalassia hemprichii* (Ehrenb.) Aschers., *Syringodium isoetifolium* (Aschers.) Dandy, *Cymodocea serrulata* (R. Br.) Aschers. and Magnus., *Cymodocea rotundata* Ehrenb. and Hempr. ex Aschers., *Halodule uninervis* (Forsk.) Aschers., *Halodule wrightii* Aschers., *Halophila stipulacea* (Forsk.) Aschers., *Halophila ovalis* (R. Br.) Hook. F. and *Enhalus acoroides* (L. f.) Royle. At each site, samples of *T. ciliatum* shoots were collected at two to three different locations that were 30 to 120 m apart. Clumps of vertical shoots together with attached horizontal rhizomes were randomly removed from the sediment with a knife. When *T. ciliatum* occurred in patches, collection of shoots was restricted to the middle of the patches.

The leaf-production rate, age structure, recruitment and mortality rate of the different *T. ciliatum* populations were determined following Duarte *et al.* (1994). On minimally 100 living shoots per sample, the number of leaf scars from shed leaves were counted starting from the insertion point of the vertical rhizome in the horizontal rhizome, or in the vertical rhizome in case of a side branch. In addition, the number of attached leaves was counted. Leaves smaller than 1 cm (sheath excluded) were not included in the countings. The shoots were also examined for the presence of standing flowers or distinct scars left by the flowers on the stems to determine the flowering frequency and the age at which the shoot flowered (Duarte *et al.*, 1994). At Nyali, Kenyatta and Watamu, only the shoots collected for determination of the leaf-production rate were inspected for flower scars. At the other sites all shoots were examined for flower events. The flowering frequency is the number of flowering events per total number of leaves produced by all examined shoots. This frequency can be converted to years by dividing the total number of leaves produced with the number of leaves produced in a year. Flowering gives an indication of the upper threshold of sexual reproduction.

For each population, annual leaf-production rates were determined using the reconstruction technique. Per sampling site, 10 to 15 vertical shoots with the largest number of leaf scars (the oldest shoots) were selected. The number of standing leaves was recorded and the sequence of internodal lengths (i.e. distance between two successive leaf scars) was measured from the leaf cluster down to the insertion point of the vertical rhizome. For the Kenyan samples a dissecting microscope was used at a magnification of 16x fitted with a calibrated scale, and for the Zanzibar Island samples a 50-mm macro lens was used which was connected to a calibrated LEICA Image Analysis System. The sequence of vertical internodal lengths were smoothed (five-internode running average) to exclude

short-term variability. The sequence of internodal lengths was examined for the presence of annual signals, i.e. minimum and maximum. To exclude bias by interannual variability, only the last formed minima and maxima on the upper part of the stem were used. The number of leaf scars in a year cycle was considered to represent the number of leaves produced per year. The leaf production rate of *T. ciliatum* was expressed in g DW shoot⁻¹ yr⁻¹ by multiplication of the number of leaves produced with the weight of a mature leaf determined at each site. Earlier work showed that the 4th leaf can be considered representative of a mature leaf, while at the same time epiphytic overgrowth is still fairly low (Hemminga *et al.*, 1995). At each site, 1 to 5 samples were collected. Each sample consisted of ten 4th *T. ciliatum* leaves that were cut at the break point with the sheath, and cleaned with paper to remove any epiphytes. Prior to weighing, the leaves were dried at 60 °C for two days. The plastochrone interval (P.I.), or the average number of days between the formation of two successive leaves, was calculated from the leaf-production rate. To determine the average lifespan of the leaves for each study site, the plastochrone interval was multiplied by the number of standing leaves on a one year old shoot. Maximal stem lengths of *T. ciliatum* were determined from the sum of internodal lengths on the longest shoots.

The age of the *T. ciliatum* shoots expressed as total number of leaves produced (leaf scars plus attached leaves) was converted to years by dividing this value by the number of leaves produced per year. Per sample, the median shoot age was calculated. All *T. ciliatum* shoots were separated into age classes of 0.5 years to obtain the age distribution per sample. Exponential shoot mortality rates (M , in units yr⁻¹) were estimated as the slope of a linear regression fitted to the natural log-transformed age distribution using the equation:

$$N_t = N_0 e^{-Mt}$$

where N_0 and N_t are the number of shoots present at times 0 and t . The calculation of mortality rates is preferably based on the age distribution of dead shoots. However, in our study, this method was hampered by the fact that old shoots tended to be broken. The age distributions of living shoots was used as an alternative method to calculate mortality rates (Duarte *et al.*, 1994; Durako and Duarte, 1997). Annual shoot recruitment rates (R , in units yr⁻¹) were calculated from the proportion of living shoots older than one year using the equation:

$$R = \ln \sum_{t=0}^{\infty} N_t - \ln \sum_{t=1}^{\infty} N_t$$

in which $\sum_{t=0}^{\infty} N_t$ is the total number of shoots and $\sum_{t=1}^{\infty} N_t$ the number of shoots older than 1 year in

the age-distribution samples. The ratio between recruitment and mortality (R:M) can be considered as an indication of the colonisation state of a population for the next year. The following assumptions are made: when $R:M < 1$ the meadow is in decline, when $R:M > 1$ the population is expanding, and when $R:M = 1$ the seagrass bed is in steady state.

A one-way analysis of variance (ANOVA) was used to quantify the magnitude of local variability on *T. ciliatum* variables (Sokal and Rohlf, 1995). The significance of relationships between different *T. ciliatum* variables was determined with linear regression analyses (Sokal and Rohlf, 1995). Prior to each analysis, the data were tested for heteroscedacity with a Bartlett's test for homogeneity of variances (Sokal and Rohlf, 1995). Data that scored as significant were log-transformed, which yielded non-significant results in Bartlett's test. A Tukey-Kramer procedure was used as a post-hoc test for significance of differences between populations (Sokal and Rohlf, 1995). A significance level of 0.05 was set in all tests. The statistical analyses were conducted using the STATISTICA programme (StatSoft Inc., Tulsa, Oklahoma).

3. Results and discussion

Leaf production

An example of a clear pattern in the sequence of internodal lengths along a vertical stem of *T. ciliatum* is shown in Fig. 2. Internodes were very large near the insertion point with the horizontal rhizome. These are the first internodes that were produced. The large lengths of internodes produced at the initial stage of shoot development has been related to rapid raising of the leaves on these young *T. ciliatum* shoots to the canopy level to reduce the effect of shading (Duarte *et al.*, 1996). Apart from the decline in internodal lengths as the shoot grows, the stem also showed rhythmic cycles in internodal lengths (Fig. 2). Two minima could be distinguished in a year, which allowed estimates of leaf production (arrow in Fig. 2). The bimodal pattern was demonstrated earlier for *T. ciliatum*, as well as several other tropical seagrass species, and is probably related to the variability in light conditions as a result of alternations between rainy and dry seasons (Duarte *et al.*, 1996; Vermaat *et al.*, 1995).

Production rates ranged from 29 to 53 leaves shoot⁻¹ yr⁻¹. The observed range of leaf-production rates encompasses other rates reported for *T. ciliatum* using leaf marking (Brouns, 1985; Hemminga *et al.*, 1995) or reconstructing techniques (Duarte *et al.*, 1996). Leaf production rates were lowest for the *T. ciliatum* population of the subtidal site that was not protected by a reef and for the population from the intertidal rock pools. A possible larger physical disturbance of these unprotected habitats may cause this difference. Highest leaf production rates were found at the mangrove bay site. Leaf production rate expressed in weight ranged from 1.4 to 3.0 g DW shoot⁻¹ yr⁻¹. Significant differences were observed between sites, but these differences were not related to habitat or meadow type.

The vertical shoots of *T. ciliatum* showed large variability in distance between two successive leaf scars, which resulted in significant differences in average internodal length between sampling sites (Table 1). The longest internodal length (6.9 mm) was observed on shoots collected at Chwaka, the mangrove bay. Other differences were much smaller (range of 2.3 to 3.6 mm) and not affected by habitat or meadow type. E.g. larger internodal lengths were found on shoots from the rock-pool site (Vipingo), two lagoonal sites with monospecific *T. ciliatum* meadows (Nyali and Watamu), and the unprotected site with a mixed meadow (Nungwi). Maximal stem length of *T. ciliatum* varied widely from 20 cm in one of the back-reef lagoons to almost 90 cm in the mangrove bay (Table 1). The latter stem length is much higher than the maximal stem length of 65 cm recorded for *T. ciliatum* by Den Hartog (1970). The large internodal lengths and long shoots observed in the mangrove bay suggest a strong investment in vertical shoot elongation.

The number of standing leaves on shoots increased rapidly during the first year of life, and levelled off afterwards (Fig. 3). Apparently, young shoots do not allocate much energy to maintenance of their leaves. They invest more in vertical rhizome growth to reach the level of improved light conditions. Duarte and Sand-Jensen (1990b) observed a similar increase in number of standing leaves and shoot length with increasing age for *Cymodocea nodosa* (Ucria) Aschers.. Habitat or meadow type did not influence the number of standing leaves on *T. ciliatum* shoots (Table 1).

Significant differences in leaf lifespan were observed between sites (Table 1). In the back-reef lagoons, the leaf lifespan was between 50 and 70 days. With 51 days, lifespan was short at the mangrove site. This short leaf lifespan indicates that investment in stem growth occurs at the

expense of leaf maintenance. At Vipingo and Nungwi, the intertidal rock pool site and the unprotected site, leaf lifespan was almost twice as long (94 days). The lifespan found at the intertidal site is much higher than the leaf lifespan of 30 to 45 days observed for other intertidal *T. ciliatum* populations (Bandeira, 1997; Johnstone, 1984). Low leaf-formation rates seem to be compensated by long leaf lifespans to maintain similar numbers of standing leaves per shoot.

The most striking differences were observed for the mangrove-bay population. There, we observed internodal lengths and stem lengths that were two to four fold longer, highest leaf production rates and leaf lifespans that were up to 45 % shorter than *T. ciliatum* from the other sites (Table 1). The light availability in the mangrove bay was less than in the coastal lagoons (pers. obs.). Thus, the population in the mangrove area strongly invests in vertical shoot elongation, which will rapidly raise the leaves to better light conditions. Apparently, this occurs at the expense of leaf longevity.

Shoot demography

The age distribution of living *T. ciliatum* shoots showed different patterns at the different sites (Fig. 4). Most of the living shoots in all populations, except the ones sampled at Wataumu and Tumbatu, were younger than one year. Median ages of the populations varied almost four fold from 0.46 year at Diani to 1.82 years at Watamu (Table 2). The median shoot age was highest at Watamu and significantly different from all other sites. Maximum age showed a smaller variability from 2.39 years at Kiwengwa to 5.09 years at Watamu (Table 2). No significant differences between sites were found. Vermaat et al. (1995) determined the age of six seagrass species in the Philippines. The maximal ages ranged from 0.21 for *Halophila ovalis* to 9.76 years for *Enhalus acoroides*. The same species are found along the East African coast. Thus, compared to co-occurring species, the shoots of *T. ciliatum* appear to have an intermediate life span.

Shoot recruitment and mortality rates differed significantly among sites, but these differences were not related to differences between habitats (Table 2). Recruitment rates were either the same or larger than mortality rates. Thus, all populations in the present study were either in steady state or expanding (Table 2). At Nyali, Kenyatta and Diani the sampling sites were located close to densely populated areas with large numbers of beach hotels, which may, in various ways, threaten the health of the seagrasses. However, our results suggest that the *T. ciliatum* meadows were not declining at

these sites. Compared to other species of similar size (Vermaat *et al.*, 1995; Marbà & Walker, 1999), mortality and recruitment rates of *T. ciliatum* shoots are fast. This indicates that *T. ciliatum* populations are maintained by a fast flow of shoots. In seagrass meadows, shoot proliferation is mainly coupled to clonal growth (Duarte & Sand-Jensen, 1990a). In *T. ciliatum*, the growth of horizontal rhizomes is slow (Duarte *et al.*, 1996). This observation, together with the fast flux of shoots observed in the studied *T. ciliatum* populations, reveals that branching of vertical stems is the main mechanism providing shoots in *T. ciliatum* meadows.

Flowering

T. ciliatum meadows can expand via horizontal rhizome growth and branching of vertical shoots, but the plants can also produce flowers. It was calculated that an average of 11 % of all inspected shoots had flowered (Table 3). Differences between populations were large, ranging from 0.2 % to 21.9 % of the shoots, but significant differences between populations were not found (Table 3). This was caused by the fact that the variation in abundance of flowering shoots within the populations was also large, as shown by high values for the standard errors (Table 3). These results indicate patchiness in flowering. An average proportion of 10% flowering shoots is commonly reported for other seagrass species as well (Table 1 in Gallegos *et al.*, 1992).

Flowering frequency also showed large variations, both within and among populations (Table 3). The lowest frequency was observed at Dongwe (0.01 flowers shoot⁻¹ year⁻¹) and the highest frequency (1.29 flowers shoot⁻¹ year⁻¹) was found at Chwaka (Table 3). This range is comparable to flowering frequencies observed in other seagrass species (Duarte *et al.*, 1997). The results suggest that sexual reproduction is of minor importance for the studied *T. ciliatum* populations. Examination of the age at which a shoot flowered revealed a minimum age between 0.5 and 1 year old (Table 3). This indicates that a maturation period is necessary to be able to flower. Similar maturation periods were observed for *Cymodocea nodosa* (9 months; Marbà and Duarte, 1995), *Cymodocea rotundata* and *Thalassia hemprichii* (0.5 to 1 year; Duarte *et al.*, 1997) and *Thalassia testudinum* Banks ex König (1 year; Gallegos *et al.*, 1992).

Most of the stems that flowered, did so more than once. The maximum number of flower scars on a single *T. ciliatum* stem was 21. This was observed on a stem that had produced 157 leaves. Flower scars tended to be clustered on the stems. In several cases, two or more of such clusters

were found on a stem and the time elapsed between two flowering events could be determined (Table 3). The cycle in flower production varied between 0.6 and 1.8 years. In addition, the time elapsed between two flowering events was not proportional to the number of leaves produced (linear regression $R^2 = 0.06$, $p > 0.05$). This suggests that the timing of flowering is not determined by the number of leaves produced, but by an external factor.

In Kenya, Cox (1991) observed that flowering of a *T. ciliatum* population in the low intertidal occurred at extremely low spring tides. Tides with differences of 3.7 m or more take place for three to four consecutive days each month in January, February, March, April and May and again in September, October, November and December (KBP tide table). In the present study, sampling was carried out in February and March. At several sites, flowers were visible on the stems just below the leaf clusters indicating that the latest flower formation took place 4 to 13 P.I. ago, or approximately 1 to 3 months earlier, i.e. in the period from November to January. These results suggest that the subtidal populations also show cycles in flower production which are attuned to the occurrence of low spring tides. Indeed, going back in time along the stems, most flower scars were observed at specific times, indicated by peaks in the frequency distribution (Fig. 5). Cox (1991) explains the timing of flowering by suggesting that, at extreme low tides, floating pollen can collide on the water surface with female stigmas emerging at the surface. The only population of the present study that was sampled at the intertidal level was located in rock pools that remained covered at low tide. The other populations were all located at 1.5 m below chart datum, i.e. 1.5 m below the water level at extreme low water spring. Thus, none of the studied populations will become exposed.

At Watamu, the peak at 2.5 years ago was higher than the peak at 1 year ago (Fig. 5). The age distribution of this site showed that more shoots of 1 year old were present in the sample, than 2.5 year old shoots (Fig. 4). Thus, the results indicate a lower sexual effort during the last flowering event. Seedlings were not found in our study, suggesting that pollination does not occur in subtidal populations. However, Kuo and Kirkman (1990) studied seedlings collected from subtidal populations of *T. pachyrhizum* den Hartog growing at 4 to 27 m depth in Australia. Apparently, this closely related species is able to produce seedlings without emerging at the water surface. In *Amphibolis antactica*, a species that has a morphology similar to *Thalassodendron*, Verduin *et al.* (1996) observed that pollination occurs under water. Why the East African subtidal *T. ciliatum*

populations invest in flower production without apparent successful reproduction remains to be explained.

Conclusion

This paper presents the first large scale sampling effort on the East African coast to evaluate the status of *T. ciliatum* meadows. All populations in the present study appeared to be either expanding or in steady state. This suggests that the environmental quality in this region is still suitable for sustaining vigorous seagrass vegetation. The lack of sexual reproduction may imply the presence of few genotypes, which reduces the ability to adapt to changes.

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Table 1. Average \pm SE, leaf production rates, internodal lengths, maximal stem lengths, number of standing leaves, and leaf life spans for the *Thalassodendron ciliatum* populations studied (msl = Kenyan mainland subtidal back-reef lagoon, isl = Zanzibar Island subtidal back-reef lagoon, isu = Zanzibar Island unprotected subtidal site, mil = Kenyan mainland intertidal rock pools in lagoon, ism = Zanzibar Island subtidal mangrove bay, * = monospecific meadow). Probability values from one-way analysis of variance to test for significant differences among populations are reported. Populations that share the same letter do not differ significantly from each other (Tukey-Kramer comparison test). N is given in brackets. When SE values are lacking the variable only has one value and is not included in the statistical analysis.

Population	No. of leaves produced (shoot ⁻¹ yr ⁻¹)	Leaf P.I. (d)	Leaf production (g DW shoot ⁻¹ yr ⁻¹)	Internodal length (mm)	Maximal stem length (cm)	Number of standing leaves on 1 yr old stem	Leaf life span (d)
Nyali (msl*)	45.4 \pm 1.9 acd (8)	8.1 \pm 0.3 ad (8)	2.3 \pm 0.1 ab (4)	3.6 \pm 0.2 a (10)	40.2 \pm 1.9 beg (10)	6.9	56.2 \pm 2.3 ad (8)
Watamu (msl*)	41.0 \pm 2.1 abc (7)	9.1 \pm 0.5 ac (7)	2.5 \pm 0.1 ab (5)	2.9 \pm 0.1 ad (10)	54.0 \pm 2.1 a (10)	7.8	70.6 \pm 3.8 abc (7)
Kenyatta (msl)	45.8 \pm 2.3 acd (5)	8.1 \pm 0.4 ad (5)	2.5 \pm 0.1 ab (2)	2.4 \pm 0.1 d (10)	27.7 \pm 0.8 defhi (10)	6.3	50.8 \pm 2.8 ad (5)
Roka (msl*)	38.5 \pm 2.5 abcd (2)	9.5 \pm 0.6 abcd (2)	2.4 \pm 0.1 ab (2)	2.3 \pm 0.1 d (10)	23.7 \pm 0.8 dfhi (10)	6.9	65.7 \pm 4.2 abcd (2)
Diani (msl)	49.0 \pm 2.2 ad (10)	7.6 \pm 0.3 ad (10)	3.0 \pm 0.2 b (5)	2.7 \pm 0.2 bd (10)	35.2 \pm 0.9 egghi (10)	7.4	56.1 \pm 2.5 ad (10)
Kiwengwa (isl)	38.0 \pm 2.6 abc (4)	9.7 \pm 0.6 abcd (4)	1.8 \pm 0.1 a (3)	2.5 \pm 0.1 d (15)	20.5 \pm 1.5 fi (15)	6.8	66.2 \pm 4.3 abd (4)
Tumbatu (isl)	42.0 \pm 2.0 abc (14)	9.0 \pm 0.5 ac (14)	2.4 \pm 0.2 ab (3)	2.4 \pm 0.1 d (15)	37.1 \pm 1.6 gh (15)	7.2	64.5 \pm 3.2 a (14)
Dongwe (isl)	43.4 \pm 1.5 ac (13)	8.5 \pm 0.3 ac (13)	2.5 \pm 0.2 ab (3)	2.6 \pm 0.1 d (15)	30.9 \pm 2.0 ghi (15)	7.2	61.5 \pm 2.2 ad (13)
Nungwi (isu)	28.8 \pm 1.7 b (5)	12.9 \pm 0.8 b (5)	1.9 \pm 0.2 a (3)	3.0 \pm 0.2 ad (10)	32.4 \pm 1.5 bdegghi (10)	7.3	93.9 \pm 5.6 b (5)
Vipingo (mil)	32.5 \pm 4.5 bc (4)	11.8 \pm 1.4 bc (4)	1.4 (1)	3.6 \pm 0.3 ab (12)	26.8 \pm 0.8 hi (12)	8.0	94.5 \pm 11.4 bc (4)
Chwaka (ism)	52.6 \pm 1.2 d (15)	7.0 \pm 0.2 d (15)	2.5 \pm 0.3 ab (3)	6.9 \pm 0.4 c (15)	87.4 \pm 3.0 c (15)	7.3	51.1 \pm 1.2 d (15)
<i>p</i> of ANOVA	< 0.0001	< 0.0001	< 0.01	< 0.01	< 0.01		< 0.0001

Table 2. Average (\pm SE) median and maximum shoot age, shoot recruitment and mortality rate and the ratio between recruitment and mortality of the *Thalassodendron ciliatum* populations studied (msl = Kenyan mainland subtidal back-reef lagoon, isl = Zanzibar Island subtidal back-reef lagoon, isu = Zanzibar Island subtidal unprotected site, mil = Kenyan mainland intertidal rock pools in lagoon, ism = Zanzibar Island subtidal mangrove bay, * = monospecific meadow). Probability values from one-way analysis of variance to test for significant differences among populations are reported (ns is not significant). Populations that share the same letter do not differ significantly from each other (Tukey-Kramer comparison test).

Population	Median shoot age (yr)	Maximum shoot age (yr)	Shoot recruitment rate R (ln units yr ⁻¹)	Shoot mortality rate M (ln units yr ⁻¹)	R:M	N
Nyali (msl*)	0.51 \pm 0.02 ad	2.49 \pm 0.08	1.36 \pm 0.11 ab	0.72 \pm 0.01 ab	1.89 \pm 0.17 ab	2
Watamu (msl*)	1.82 \pm 0.22 b	5.09 \pm 0.04	0.42 \pm 0.04 a	0.31 \pm 0.02 b	1.37 \pm 0.17 a	3
Kenyatta (msl)	0.65 \pm 0.10 acd	2.49 \pm 0.34	1.13 \pm 0.12 ab	0.68 \pm 0.06 ab	1.66 \pm 0.10 a	3
Roka (msl*)	0.80 \pm 0.08 acd	2.74 \pm 0.09	1.11 \pm 0.20 ab	0.65 \pm 0.09 ab	1.72 \pm 0.23 a	3
Diani (msl)	0.46 \pm 0.07 a	2.80 \pm 0.70	1.96 \pm 0.27 b	0.79 \pm 0.21 ab	2.70 \pm 0.40 b	3
Kiwengwa (isl)	0.86 \pm 0.02 acd	2.39 \pm 0.46	0.97 \pm 0.10 a	0.98 \pm 0.26 a	1.08 \pm 0.17 a	3
Tumbatu (isl)	1.17 \pm 0.02 c	4.18 \pm 0.18	0.46 \pm 0.02 a	0.46 \pm 0.04 ab	1.00 \pm 0.04 a	3
Dongwe (isl)	0.85 \pm 0.12 acd	3.51 \pm 0.76	0.89 \pm 0.17 a	0.61 \pm 0.09 ab	1.44 \pm 0.11 a	3
Nungwi (isu)	0.99 \pm 0.09 cd	3.54 \pm 0.87	0.76 \pm 0.15 a	0.78 \pm 0.24 ab	1.06 \pm 0.20 a	3
Vipingo (mil)	0.63 \pm 0.08 acd	3.22 \pm 1.12	1.51 \pm 0.54 ab	0.75 \pm 0.20 ab	1.96 \pm 0.19 ab	2
Chwaka (ism)	0.56 \pm 0.07 ad	3.01 \pm 0.23	1.18 \pm 0.09 ab	0.62 \pm 0.07 ab	1.91 \pm 0.08 ab	3
<i>p</i> of ANOVA	< 0.0001	ns	< 0.001	< 0.05	< 0.001	

Table 3. Average (\pm SE) abundance of flowering shoots, flowering frequency and time elapsed between flowering events of the *Thalassodendron ciliatum* populations studied (msl = Kenyan mainland subtidal back-reef lagoon, isl = Zanzibar Island subtidal back-reef lagoon, isu = Zanzibar Island subtidal unprotected site, mil = Kenyan mainland intertidal rock pools in lagoon, ism = Zanzibar Island subtidal mangrove bay, * = monospecific meadow, Nd = no data: the three sites at which only old shoots were examined were excluded, as these old shoots will give an overestimation of the proportion of shoots flowering in the population). Probability values from one-way analysis of variance to test for significant differences among populations are reported (ns is not significant). Populations that share the same letter do not differ significantly from each other (Tukey-Kramer comparison test). N is given in brackets. When SE values are lacking the variable only has one value and is not included in the statistical analysis.

Population	Abundance of flowering shoots (% of total # shoots)	Flowering frequency (# flowers shoot ⁻¹ yr ⁻¹)	Time elapsed between flowering events (years)	Minimum age at which shoot flowers (years)	Median age at which shoot flowers (years)
Nyali (msl*)	Nd	Nd	0.68 \pm 0.23 a (6)	0.29	1.22
Watamu (msl*)	Nd	Nd	1.34 \pm 0.02 b (29)	0.27	1.54
Kenyatta (msl)	Nd	Nd	1.00 \pm 0.11 ac (4)	0.22	1.28
Roka (msl*)	14.6 \pm 8.4 (3)	0.43 \pm 0.21 (3)	0.80 (1)	0.55	1.20
Diani (msl)	5.6 \pm 4.9 (3)	0.46 \pm 0.43 (3)	1.82 \pm 0.79 bc (2)	0.66	0.87
Kiwengwa (isl)	4.9 \pm 4.9 (3)	0.20 \pm 0.20 (3)	0.59 (1)	0.32	0.77
Tumbatu (isl)	21.0 \pm 4.9 (3)	0.49 \pm 0.12 (3)	0.94 \pm 0.07 ab (28)	0.15	1.28
Dongwe (isl)	0.2 \pm 0.2 (3)	0.01 \pm 0.01 (3)	1.08 (1)	1.43	2.01
Nungwi (isu)	15.5 \pm 8.3 (3)	0.28 \pm 0.25 (3)	0.87 \pm 0.10 a (9)	0.39	1.23
Vipingo (mil)	2.6 \pm 2.6 (2)	0.20 \pm 0.20 (2)	1.48 (1)	0.71	2.20
Chwaka (ism)	21.9 \pm 5.0 (3)	1.29 \pm 0.15 (3)	0.71 \pm 0.04 a (39)	0.13	0.84
<i>p</i> of ANOVA	ns	ns	< 0.0001		

Figure legends

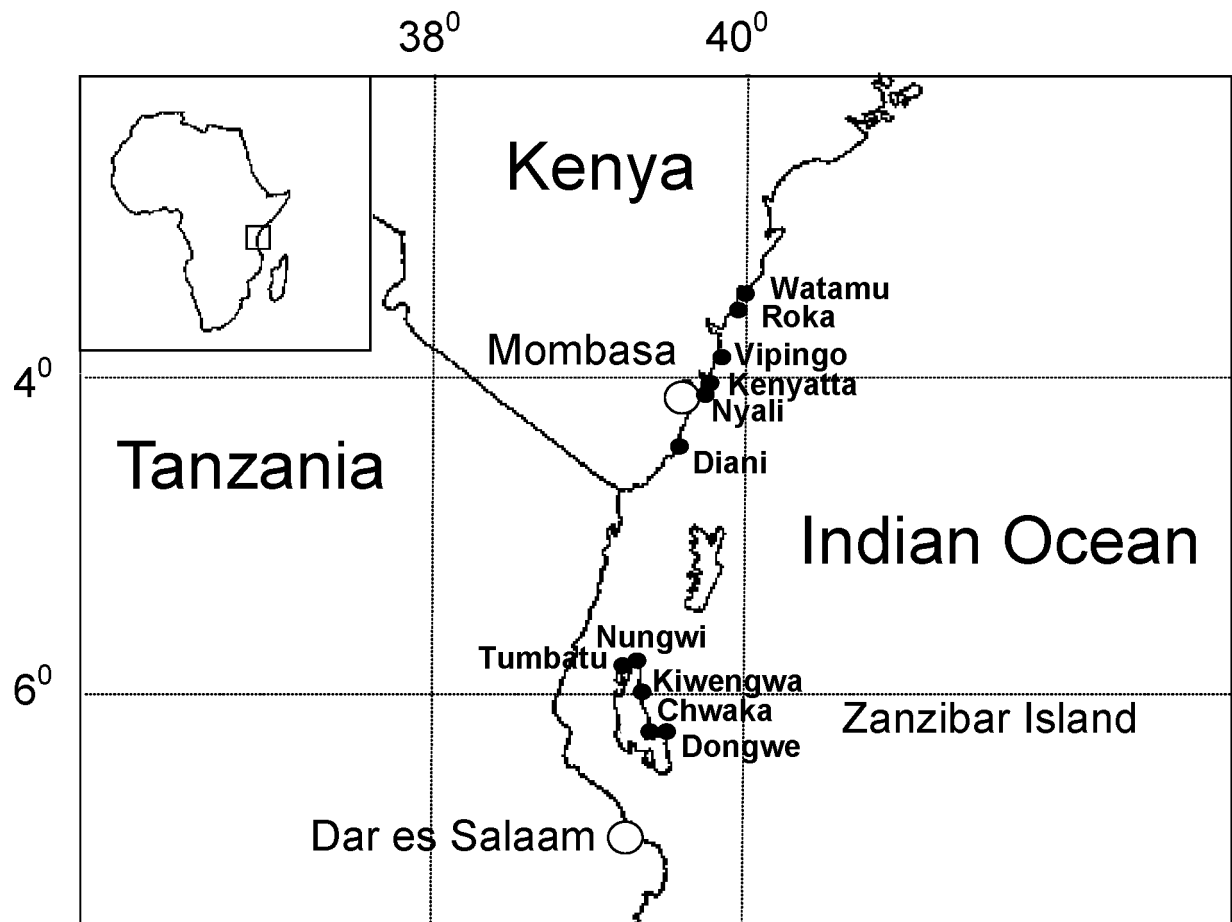
Fig. 1. Map of study sites along the Kenyan coast and on Zanzibar Island.

Fig. 2. Sequence of internodal lengths recorded for the three oldest *Thalassodendron ciliatum* shoots sampled at Diani, Kenya.

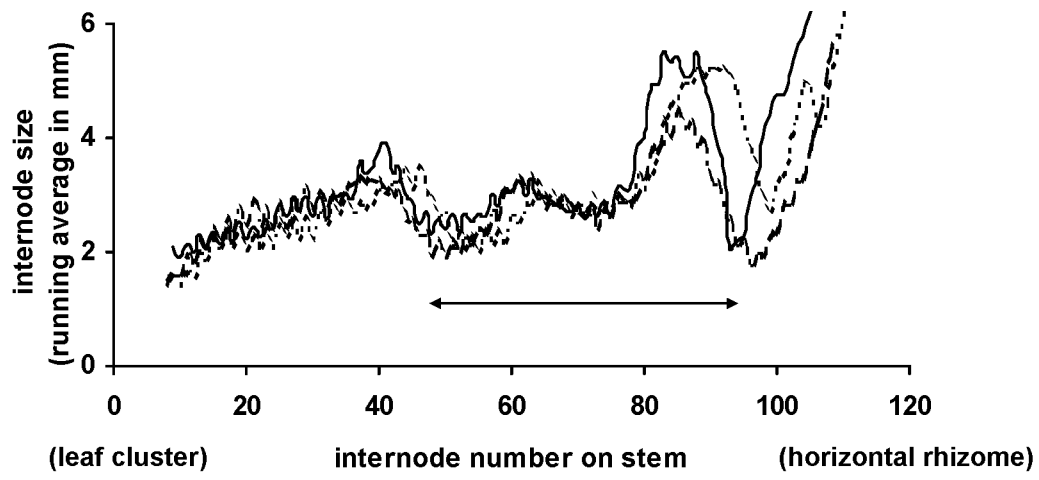
Fig. 3. Relation between shoot age and number of standing leaves for *Thalassodendron ciliatum* shoots sampled at Nungwi, Zanzibar Island.

Fig. 4. Shoot age structure of living shoots of different *Thalassodendron ciliatum* populations along the Kenyan coast and on Zanzibar Island.

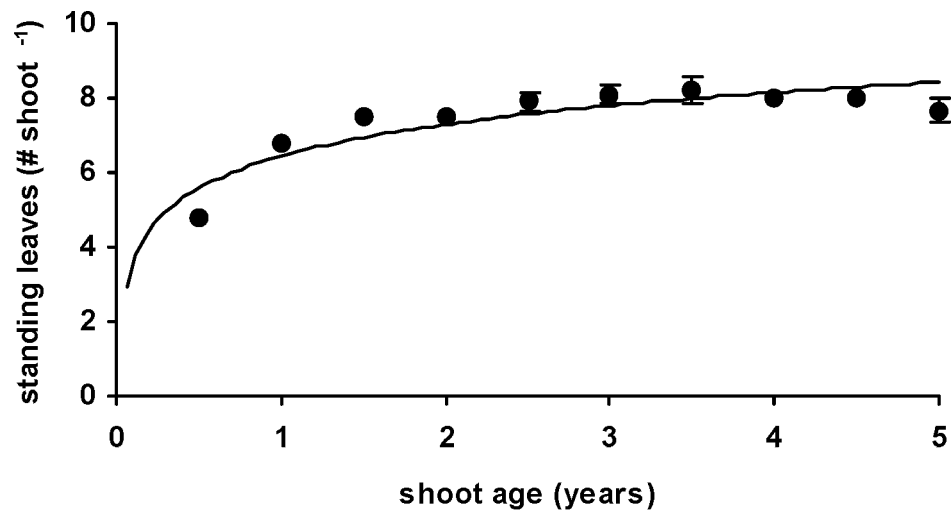
Fig. 5. Time elapsed since a flower was produced for different *Thalassodendron ciliatum* populations along the Kenyan coast and on Zanzibar Island.



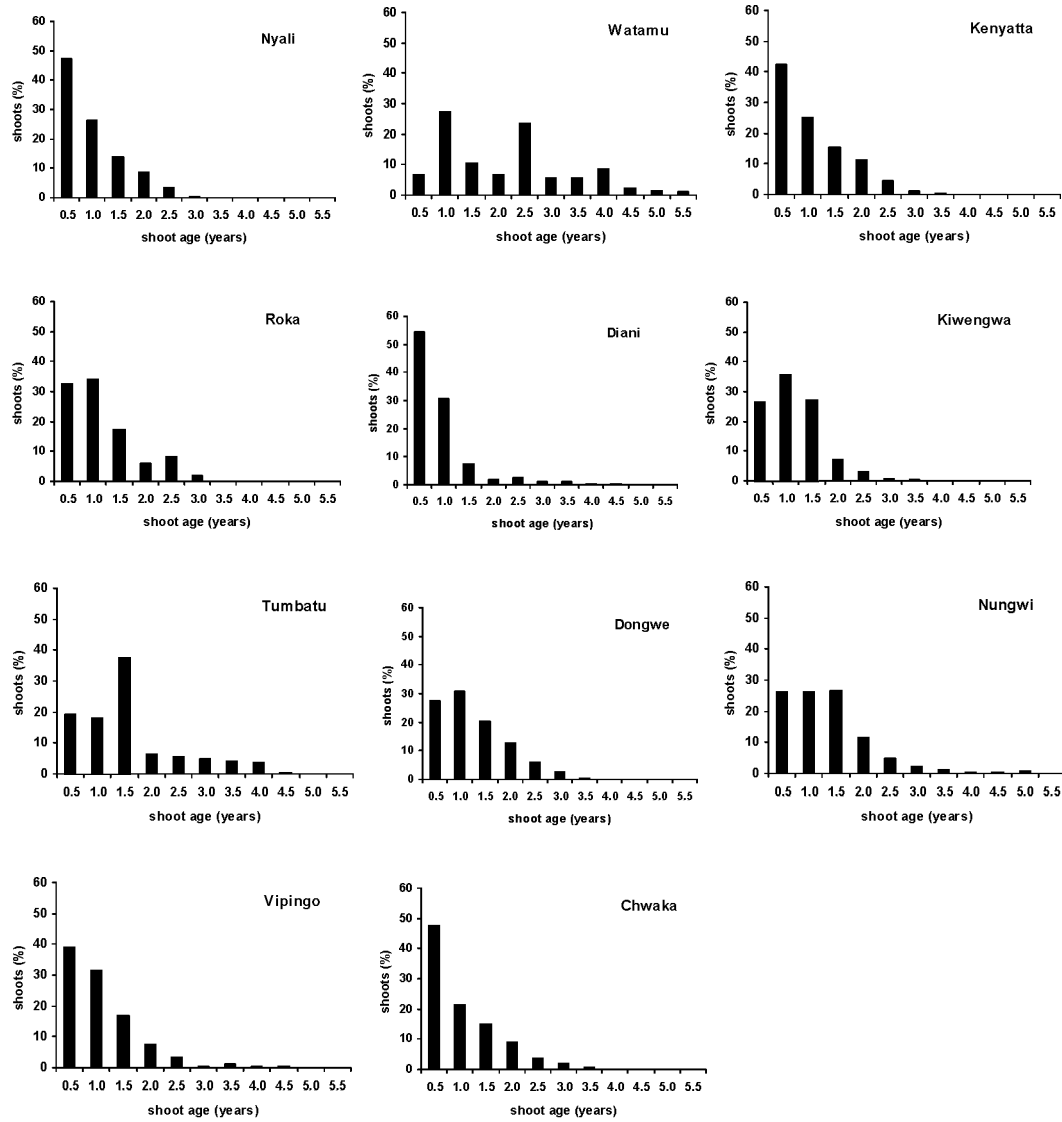
Kamermans *et al.* Fig. 1

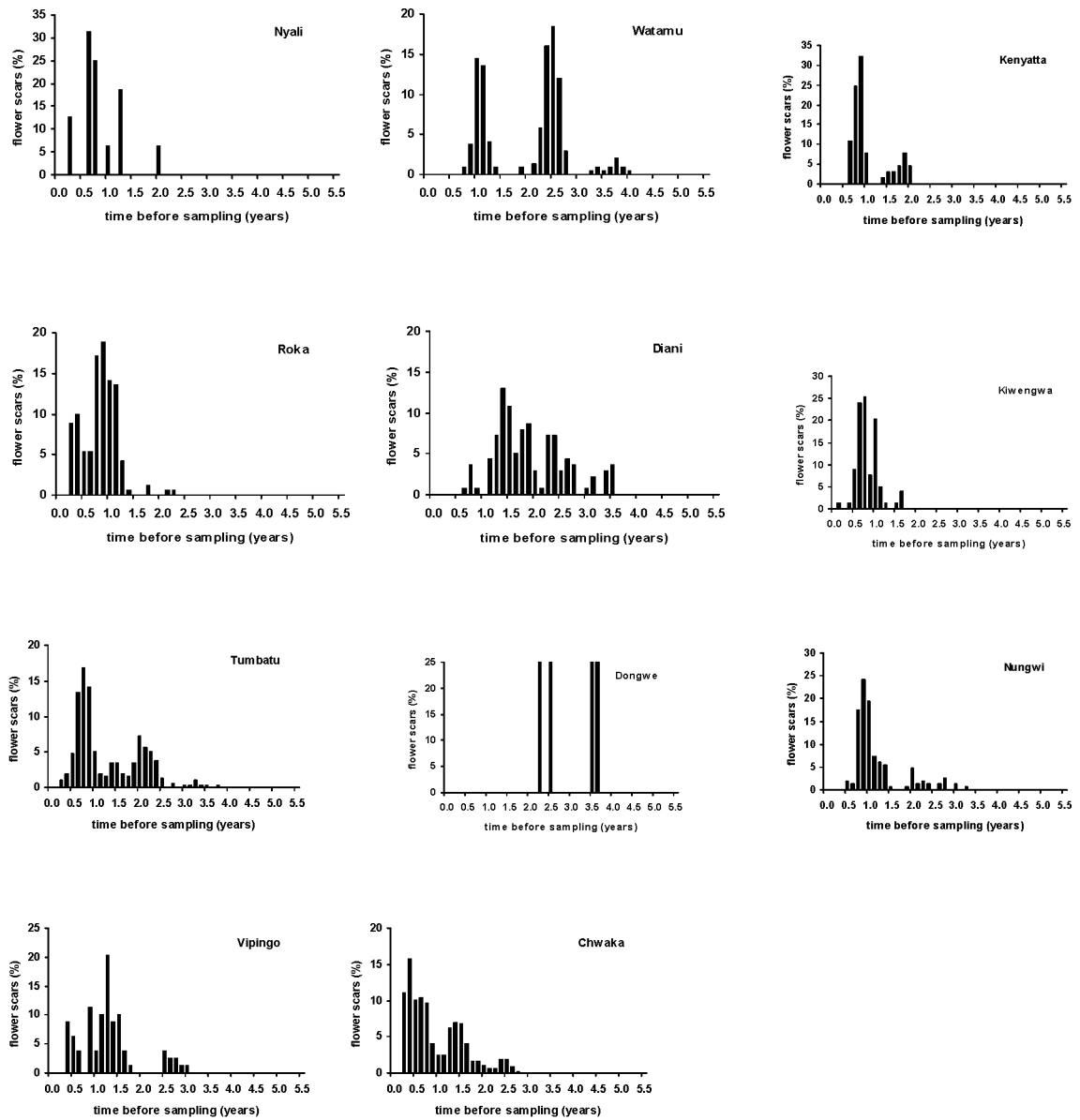


Kamermans *et al.* Fig. 2



Kamermans *et al.* Fig. 3

Kamermans *et al.* Fig. 4



Kamermans *et al.* Fig. 5