An ordination study to view vegetation structure dynamics in disturbed and undisturbed mangrove forests in Kenya and Sri Lanka

F. Dahdouh-Guebas[1,*], J.G. Kairo[2], L.P. Jayatissa[3], S. Cannicci[4] and N. Koedam[1]

[1]*Laboratory of General Botany and Nature Management, Mangrove Management Group, Vrije Universiteit Brussel, Pleinlaan 2, B-1050 Brussels, Belgium;* [2]*Kenyan Marine and Fisheries Research Institute, P.O. Box 81651, Mombasa, Kenya;* [3]*Department of Botany, University of Ruhuna, Matara, Sri Lanka;* [4]*Dipartimento di Biologia Animale e Genetica 'Leo Pardi', Università degli Studi di Firenze, Via Romana 17, I-50125 Firenze, Italy;* *Author for correspondence*

Abstract

The mangrove vegetation of a disturbed and undisturbed site in both Kenya and Sri Lanka was investigated in the field for three vegetation layers: adult trees, young trees, and juvenile trees. A minimum of 25 sample points, in which the vegetation was described and environmental factors (salinity, light intensity, land/water ratio, abundance of herbivorous crabs and snail abundance) were measured or estimated, were taken on each site. Detrended correspondence analysis (DCA) and canonical correspondence analysis (CCA) were used to summarize the data bulk, to investigate the vegetation dynamics (e.g., comparability of species distribution in the three vegetation layers), and/or to link the vegetation data to the environmental factors. Results showed that species clusters were relatively easy to delineate, whether mangrove zonation was present or not. Among the environmental factors, the abundance of propagule predators (mostly sesarmid crabs) contributed significantly to the variation in vegetation and could be an explanatory parameter for the observed vegetation data in a majority of sites. In the site where it was not, the most important factor in the ordination was the land/water ratio, which is important at the ecological level as well (link between water level and vegetation dynamics). However, none of the environmental factors could successfully explain the total variability in the vegetation data suggesting that other, more determining factors exist. Our results further provide information on the dynamic or non-dynamic nature of a forest and on its ability to rejuvenate, and may contribute to appropriate forestry management guidelines in the future.

Introduction

Vegetation dynamics, defined as changes in stand structure and composition over time, are a major aspect of vegetation ecology (e.g., Putz and Chan (1986); Smith and Huston (1989); Heil and Van Deursen (1996); Murali et al. (1998); Dahdouh-Guebas et al. (2000c)), yet such research has received little attention. Very often, the study of vegetation dynamics relies on remote sensing, combined with geographic information systems (GIS), and usually constitutes the only retrospective basis of comparison to actual vegetation data (Dahdouh-Guebas et al. 2000c). In addition, this type of research can gener-

ate results with direct application to forest management planning (e.g., Holmgren et al. (1997); Holmgren and Thuresson (1998)). Studying appropriate forestry variables and parameters and applying them to specific vegetation layers in a certain sequence can generate invaluable data on past, present, and even future vegetation structure dynamics.

Among the tools that are available to analyse vegetation data, ordination algorithms are an appropriate choice to explore the relationship between the vegetation structure and the environment (Kent and Coker 1992). However, in mangrove ecology, particularly in studies on vegetation dynamics, ordination algorithms have seldom been utilized (e.g., Ukpong (1995)). In

the past, vegetation dynamics have been deduced from ordinations focusing on one time stamp (e.g., from principal component analysis by Hobbs and Grace (1981)), but these analyses create problems that can be overcome by repetitive analysis over time. Studies of the mangrove vegetation using sequential aerial photography has shown that autogenous changes can occur in mangrove ecosystems (Dahdouh-Guebas et al. 2000c). Since mangroves become increasingly threatened by various human impacts (e.g., ITTO (1993); Pernetta (1993); IUCN (1996); Farnsworth and Ellison (1997); Kjerfve et al. (1997)Dahdouh-Guebas et al. (2000a, 2000b, 2000c (in press), 2001)), there is a need to investigate the mangrove vegetation with the purpose of predicting changes in the future. Adverse alterations in vegetation structure could then be countered in time by various forms of human interference, such as artificial rehabilitation.

In this study we investigate and compare the vegetation structure and composition from different vegetation layers of undisturbed and disturbed mangrove sites in Kenya and Sri Lanka using two ordination techniques. In order to interpret presence/absence and abundance data from different vegetation layers, we employed the use of detrended correspondence analysis and canonical correspondence analysis, to explore the comparability of species distribution in the different vegetation layers and to test the hypothesis that the environmental factors measured contribute significantly to the observed variability in the vegetation, respectively. In addition, we demonstrate how such an ordination study may reveal the vegetation structure dynamics, test the underlying explanatory hypotheses, and allow for prediction of future vegetation changes.

Description of the study sites

Single undisturbed and disturbed study sites were chosen in both Kenya and Sri Lanka (Figure 1). The Kenyan study sites were located in Mida Creek (3°20′ S, 40°00′ E) and Gazi Bay (4°26′ S, 39°30′ E). Mida Creek has a narrow opening towards the ocean located about 100 km north of Mombasa. The creek has no overland freshwater input, but benefits from a high groundwater outflow (Tack and Polk 1999). Gazi Bay, a mangrove bay widely open to the ocean, is located about 40 km south of Mombasa. Unlike Mida Creek, Gazi Bay is fed by two seasonal rivers. Mangroves in
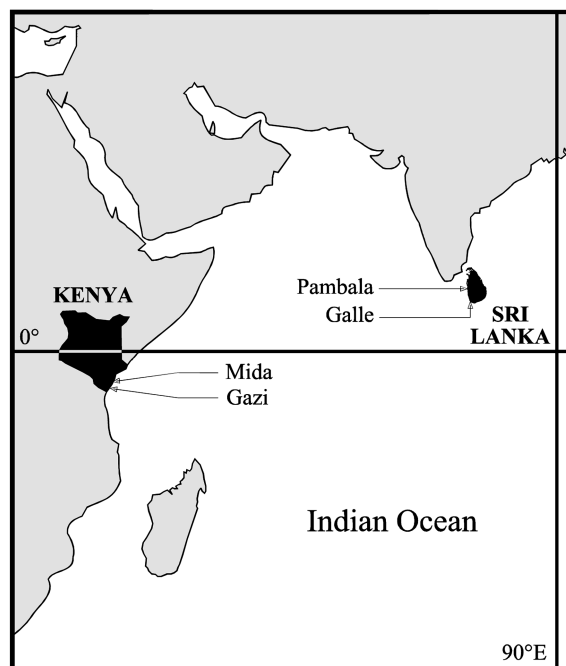

Figure 1. Map of the western part of the Indian Ocean showing the locations of our study sites in Kenya and Sri Lanka. For detailed cartographic material on these study sites we refer to Dahdouh-Guebas et al. (2000a, 2000b, in press); Gallin et al. (1989); Kairo (2001).

both Mida Creek and Gazi Bay constitute a fringing forest type (*cf*. Lugo and Snedaker (1974)). The mangroves in Gazi Bay have long been over-exploited for wood and, likewise, is disturbed. Although woodcutting is also occurring in Mida Creek (Dahdouh-Guebas et al. 2000a), the mangroves are much less affected in Mida Creek than in Gazi Bay (Kairo 2001).

Of the two mangrove forests investigated along the southwestern side of Sri Lanka, the first one was located in the Pambala area of Chilaw Lagoon, in Sri Lanka's intermediate climate zone (Mueller-Dombois 1968). The mangroves there are of the fringe type (c.f., Lugo and Snedaker (1974)), and have a rather irregular distribution along a complex of creeks (i.e., Marambettiya Ela, Bate Ela, Pol Ela, and Dutch Channel). Most freshwater influx originates from the Karambalan Oya catchment, whereas outflow to the sea is possible at Chilaw (07°35′48″ N, 079°47′25″ E) and Toduwawa (07°29′30″ N, 079°48′16″ E). The Pambala site is well preserved and has the greatest species diversity in Southwestern Sri Lanka (Jayatissa et al. 2002). Nevertheless, the mangroves in Chilaw Lagoon have recently been subjected to strong anthropogenic influences as a result of shrimp farming

(Foell et al. 1999; Dahdouh-Guebas et al. 2000c, in press).

The second Sri Lankan mangrove forest was located between Galle and Unawatuna (06°01′N – 80°14′E) in the wet climate zone of Sri Lanka (Mueller-Dombois 1968). This basin and riverine mangrove type (*cf.* Lugo and Snedaker (1974)) covers an area of 1.5 km^2 and is located at about 600 m from the Indian Ocean shore. Two rivers run through the mangrove forest–the Thalpe Ela, which discharges into the ocean, and the Galu Ganga, which is a tributary of the former. The mangrove forest in Galle has been subjected to anthropogenic influence over the last 50 years (Dahdouh-Guebas et al. 2000c).

All ten East-African mangrove species occur along the Kenyan coast - *Avicennia marina* (Forsk.) Vierh., *Bruguiera gymnorrhiza* (L.) Lam., *Ceriops tagal* (Perr.) C.B. Robinson, *Heritiera littoralis* Dryand., *Lumnitzera racemosa* Willd., *Pemphis acidula* Forst., *Rhizophora mucronata* Lam., *Sonneratia alba* Sm., *Xylocarpus granatum* Koen, and *X. moluccensis* (Lamk.) Roem. The common species present in Pambala (Sri Lanka) are *Aegiceras corniculatum* (L.) Blanco, *Avicennia officinalis* L., *Bruguiera gymnorrhiza*, *B. sexangula* (Lour.) Poir., *Excoecaria agallocha* L., *Lumnitzera racemosa*, *Rhizophora apiculata* Bl., *R. mucronata*, and *Xylocarpus granatum*. In Galle the common species are *B. gymnorrhiza*, *B. sexangula*, *E. agallocha*, *H. littoralis*, and *R. apiculata*. A considerable area in the forest was covered with the non-mangrove herbaceous species *Fimbristylis salbundia* (Nees) Kunth subsp. *pentaptera* (Nees) T. Koyama. For a more detailed description of the mangrove species and mangrove associates in Pambala and Galle, we refer to Jayatissa et al. (2002). The taxonomy and nomenclature of mangrove species are according to Tomlinson (1986); Duke and Jackes (1987); Duke (1991).

Apart from the more species diverse nature of mangroves in Sri Lanka, there are two other main differences between the Kenyan and Sri Lankan sites. The first is the spring tidal amplitude, which is more than 3.5 m in Kenya, but less than 1 m in Sri Lanka (Spalding et al. 1997); locally the tidal amplitude changes as little as 15 cm per week throughout the year (Dahdouh-Guebas et al. 2000c). The second difference concerns mangrove species zonation. In Kenya zonation is very pronounced in all mangrove areas, whereas in Sri Lanka species zonation is seldom present (i.e., very localized partial or semi-zonation). In both Sri Lankan sites, there was no slope in upper or lower intertidal areas. In contrast, Pambala contains a plateau with pools and Galle possesses a multitude of small islands and pools, primarily resulting from the burrowing activities of the mangrove mud lobster *Thalassina anomala* Herbst.

Methods

In each of the mangrove sites, sample points (Table 1) along parallel as well as orthogonal transects were chosen at 10 m intervals. In each sample point, 4 quadrants were established as in the Point-Centred Quarter Method of Cottam and Curtis (1956). The height and D_{130}, a new term coined by Brokaw and Thompson (2000) to deal with the unstandardised use of diameter at breast height (DBH), of the adult and young trees (Ht < 1.3 m or D_{130} < 2.5 cm) closest to the sample point were recorded in each quadrant (= quarter). Total vegetation coverage in the 5 × 5 m^2 quadrat (= square) nearest to the sampling point was estimated in each quadrant (as in the Braun-Blanquet relevé method). Measurements were taken in July 1996 for Mida Creek, in January 1997 for Galle, in February 1997 for Pambala, and in July 1997 for Gazi Bay.

In the same 5 × 5 m quadrats, mangrove juveniles; defined as propagules, seeds, or young plants with no more than 6 leaves; were identified and counted. At each sample point the following environmental factors were measured: salinity (using an Atago refractometer, S/Mill-E, Japan), light intensity (using a Lutron luxmeter, LX105, France), and, in the 10 × 10 m^2 area around the sample point, centre land/water ratio (visually estimated), crab burrow density, and *Terebralia palustris* L. snail density. All factors were investigated in March-April 1998 and November 1999 for both Galle and Pambala, in April 1999 for Gazi Bay, and in May 1999 for Mida Creek. The dry season is in January and February, whereas the peaks of the wet season are around May and November in both Kenya and Sri Lanka.

Vegetation data were inserted into two types of matrices – one based on presence/absence data (0 or 1), and the other based on abundance data, ranging from 0 – 4 per sample point (i.e., 4 quadrants together). For each of these two types of matrices, three sub-types of matrices were created, which included adult and young trees alone, or adult and young trees combined with juveniles based on either a separate input for each of the fieldwork expeditions or a com-

Table 1. Summary of the structural vegetation data for the 4 sites located in Kenya (KE) and Sri Lanka (LK).

Site	Disturbance	Number of sample points	Mangrove species present[1] (in order of importance[2])	Tree density (stems 0.1 ha^{-1})	Basal area (m^2/0.1ha)	Mean tree height (m)	Complexity Index (C.I.)[3]
Mida, KE	undisturbed	25	*C. tag, R. muc, A. mar, B. gym, X. gra*	107.6	0.697	8.9	3.3
Gazi, KE	disturbed	99	*R. muc, S. alb, A. mar, C. tag, B. gym*	89.2	2.144	5.6	2.5
Pambala, LK	undisturbed	127	*R. muc, L. rac, R. api, B. sex, A. off, E. aga, B. gym, X. gra, H. lit, A. cor*	191.5	1.012	6.2	12.0
Galle, LK	disturbed	116	*E. aga, R. api, B. gym, H. lit*	131.1	0.764	4.7	2.5

[1] *A. cor = Aegiceras corniculatum, A. mar = Avicennia marina, A. off = Avicennia officinalis, B. gym = Bruguiera gymnorrhiza, B. sex = Bruguiera sexangula; C. tag = Ceriops tagal, E. aga = Excoecaria agallocha, H. lit = Heritiera littoralis, L. rac = Lumnitzera racemosa, R. api = Rhizophora apiculata, R. muc = Rhizophora mucronata, S. alb = Sonneratia alba, X. gra = Xylocarpus granatum*

[2] Ranked according to the importance value of Curtis (1959)

[3] C.I. = the product of number of species, basal area (m^2 0.1 ha^{-1}), mean tree height (m) and tree density 0.1 ha^{-1} × 10^{-3} expressed in a 0.1 ha plot (Holdridge et al. 1971)

bination of all fieldwork expeditions. In our view the latter was most representative for the study of the mangrove vegetation structure dynamics, since the place (= quadrat) that a juvenile reaches is more important than the time (= fieldwork expedition) in which it reaches that particular quadrat. However, the spread of fieldwork expeditions indicate the annual variability of juvenile distribution. The separate matrices of adult and young trees tell us more about the relation with environmental variables, since the 'noise' that new juveniles with a compromised future might introduce in the matrices is removed.

Using PC ORD for Windows (McCune and Mefford 1997), DCA (Detrended Correspondence Analysis: Hill and Gauch (1980)) or CCA (Canonical Correspondence Analysis: Ter Braak (1986, 1994)) were applied. The percentage of variance in the matrix that is explained by each axis was calculated. For the DCA this calculation was done *a posteriori* by calculating the coefficient of determination (r^2) between Euclidean distances in the ordination space and those in the original space. The environmental variables and parameters used in the CCA were selected according to their relevance as suggested in the scientific literature. Environmental variables included salinity (averaged if not significantly different between seasons), light intensity, land cover, and abundance of herbivorous crabs and snails. Monte Carlo tests were performed to determine the significance of the eigenvalues and of the species-environment correlations up to a significance level of 0.001 (= 999 runs).

It is essential to recall and emphasize at this point that DCA was used only to explore and view the data set. Independent from all causal factors, the distribution of tree species in adult, young, and juvenile vegetation layers in the DCA provides insight into the present and potential future vegetation dynamics. Past dynamics were reflected by frequency distributions in part based on D_{130} classes at 2.5 cm intervals. The CCA, on the other hand, was used as a hypothesis-testing technique to understand some of the determining environmental factors important in the establishment of a particular mangrove vegetation structure. After obtaining the CCA results, based on both vegetation and environmental data, the results from the DCA, based exclusively on vegetation data, was used once more to evaluate whether the environmental factors chosen contributed substantially to the total variability in vegetation.

Results

From the structural attributes of the vegetation, tree densities and forest heights are higher in the less disturbed forests (Table 1). This is true for basal area in the Sri Lankan site, but not in the Kenyan sites. Gazi, although disturbed, is dominated by *Rhizophora mucronata* with a presence of very large *Avicennia marina* and *Sonneratia alba* trees, the latter two species of which greatly influence the total basal area of the forest. Nevertheless, the undisturbed sites (Mida and Pambala) are structurally more complex than the disturbed sites (Gazi and Galle), according to the complexity indices (Table 1).

The variation in species data and the comparability of the distribution of species in the different vegetation layers in each of the sites were analysed in the DCA (Figure 2, Table 2), whereas the hypothesis-testing combination of species and environmental data is shown in the CCA (Figure 3, Table 3). For a majority of the ordinations (87%), those based on matrices with abundance data (0–4) had better explanatory power than those based on presence-absence values only. The exclusion of juveniles from the input matrices, explored in the research phase, did not alter the explanatory power of the ordination or the ease of interpretation substantially and are therefore not shown. Except for Pambala, the ordinations incorporating the juvenile trees can be interpreted without severe complications and the presence of the juveniles is important from a future vegetation structure stand point. For Pambala, the combination of many species and their juveniles render interpretation difficult and therefore the ordination was repeated omitting the juvenile trees (Figure 4, Table 4). The omission of the outliers formed by young *Heritiera littoralis* trees in this ordination, did likewise not affect the ordination results.

Although the species-environment correlations in the CCA were highly significant along the first axis, except for Mida Creek, and along the second axis, except for Mida Creek and Galle, the environmental variables measured explained but a small part of the variation in species data. Generally, the variance explained was low in all sites (Table 2). Nevertheless some remarkable patterns can be recognized. For instance, some species-environment associations can be recognized in the CCA and information on mangrove vegetation structural dynamics can be inferred based on both types of ordinations. However, such an inter-
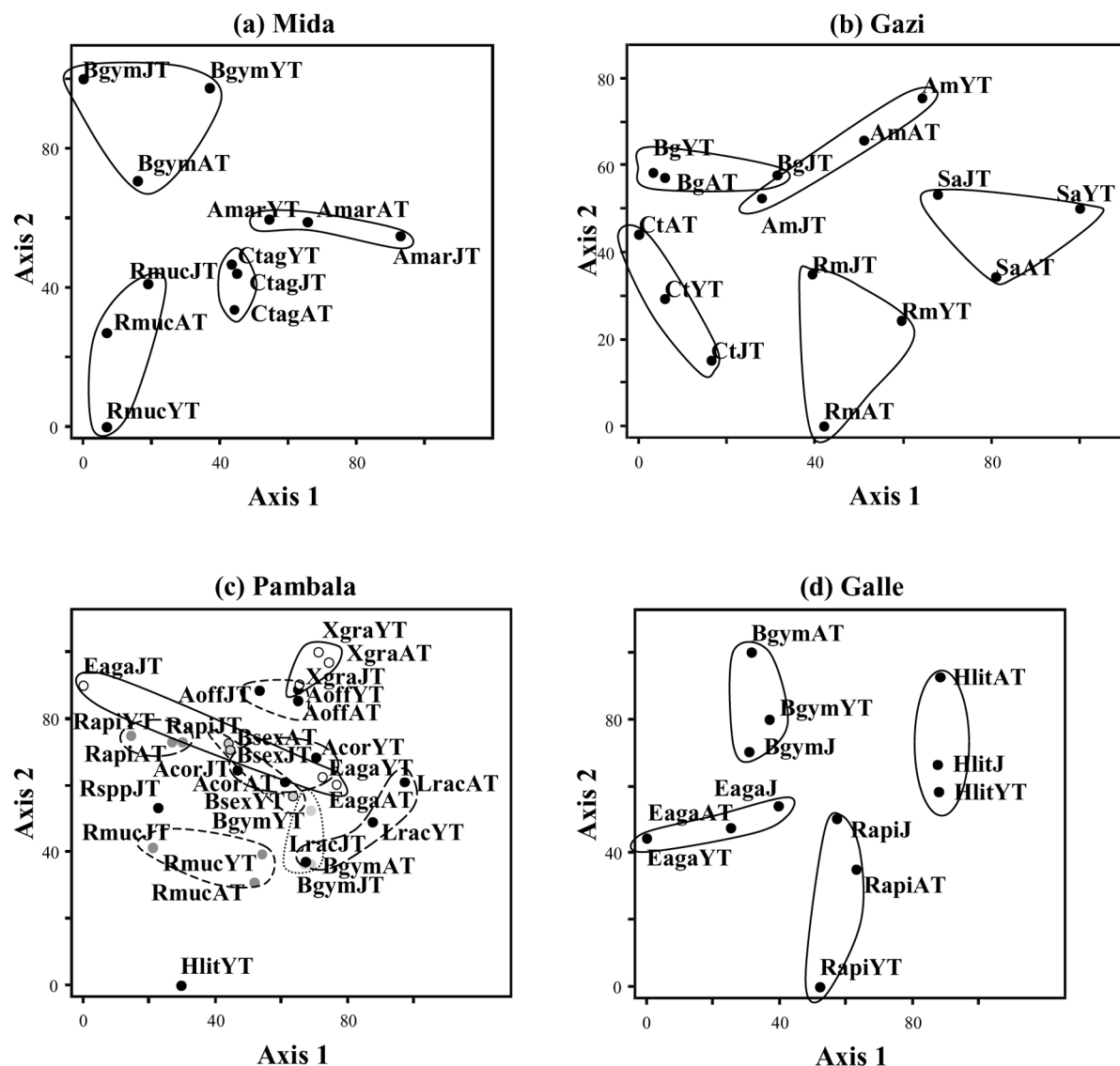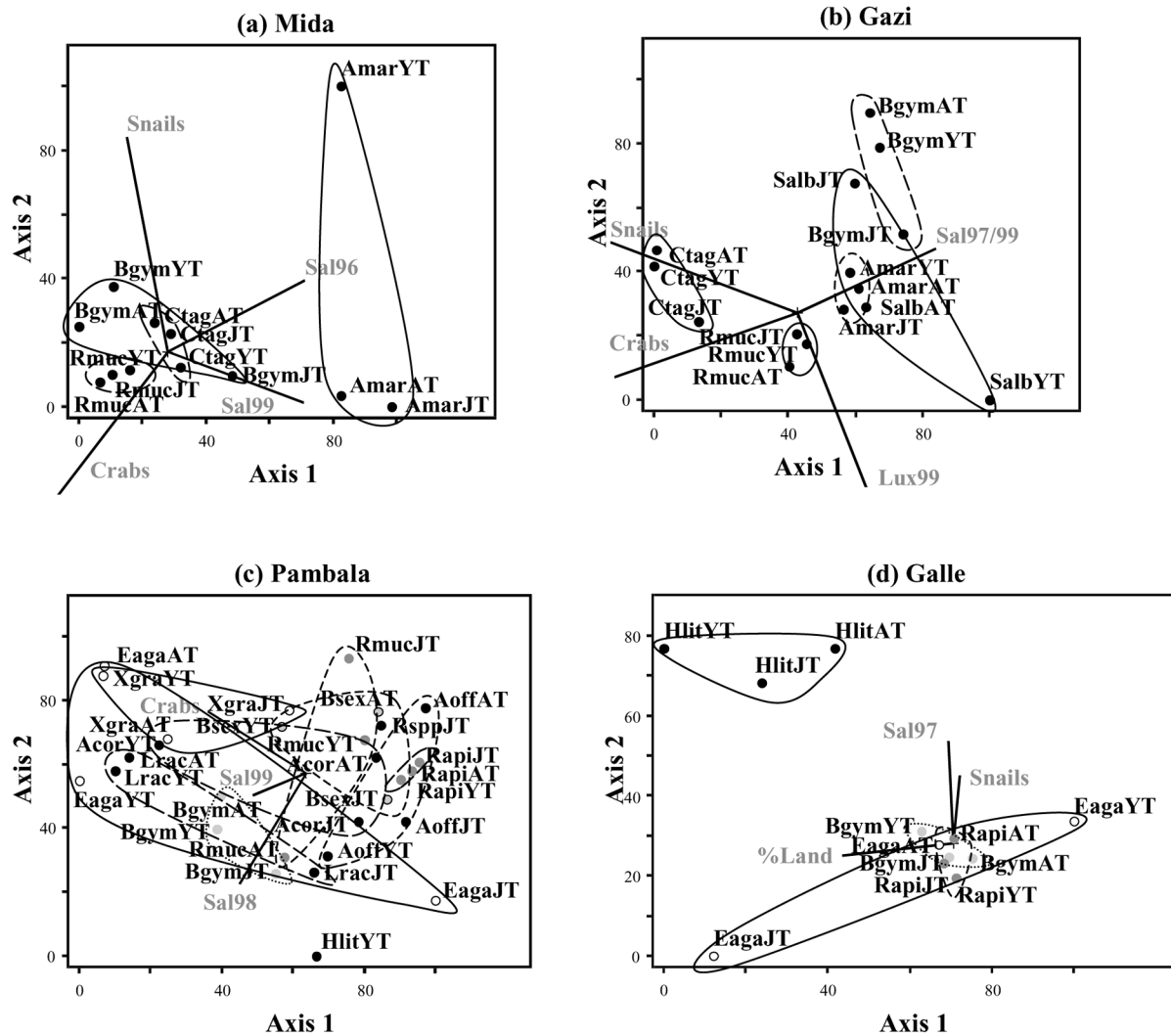
128

(a) Mida

(b) Gazi

(c) Pambala

(d) Galle

Figure 2. Plots of the detrended correspondence analysis in Mida (a), Gazi (b), Pambala (c) and Galle (d). For Mida *Xylocarpus granatum* formed an outlier to the ordination and was therefore omitted from the input matrix. Points of one species are encircled and where necessary the points have been shaded to ease interpretation. See Table 2 for numerical results. See Fig. 4a for a simplified graph of Pambala. (AT = adult trees, YT = young trees, JT = juvenile trees, propagules and seeds, Acor = *Aegiceras corniculatum*, Amar = *Avicennia marina*, Aoff = *Avicennia officinalis*, Bgym = *Bruguiera gymnorrhiza*, Bsex = *Bruguiera sexangula*; Ctag = Ceriops tagal, Eaga = *Excoecaria agallocha*, Hlit = *Heritiera littoralis*, Lrac = *Lumnitzera racemosa*, Rapi = *Rhizophora apiculata*, Rmuc = *Rhizophora mucronata*, Rspp = *Rhizophora* juveniles that could not be identified unambiguously to species level, Salb = *Sonneratia alba*, Xgra = *Xylocarpus granatum*).

pretation can be performed independently from the indirect ordination (DCA) only (see discussion).

The species-environment correlations that can be recognized from the biplots in Figure 3, bearing in mind that the account of other non-measured biotic and abiotic factors remain to be elucidated but are different by site. One of the common results is the fact that species clusters usually appear where fewer her-

bivorous crabs and snails are present (Figure 3). The same can be observed more clearly in Figure 4b for Pambala, where the species associated with low crab abundances are all propagule producing species, namely: *Aegiceras corniculatum*, *Avicennia officinalis*, *Bruguiera gymnorrhiza*, *Rhizophora apiculata*, and *R. mucronata*. In Galle, crab abundance was so poorly associated with the second axis as compared
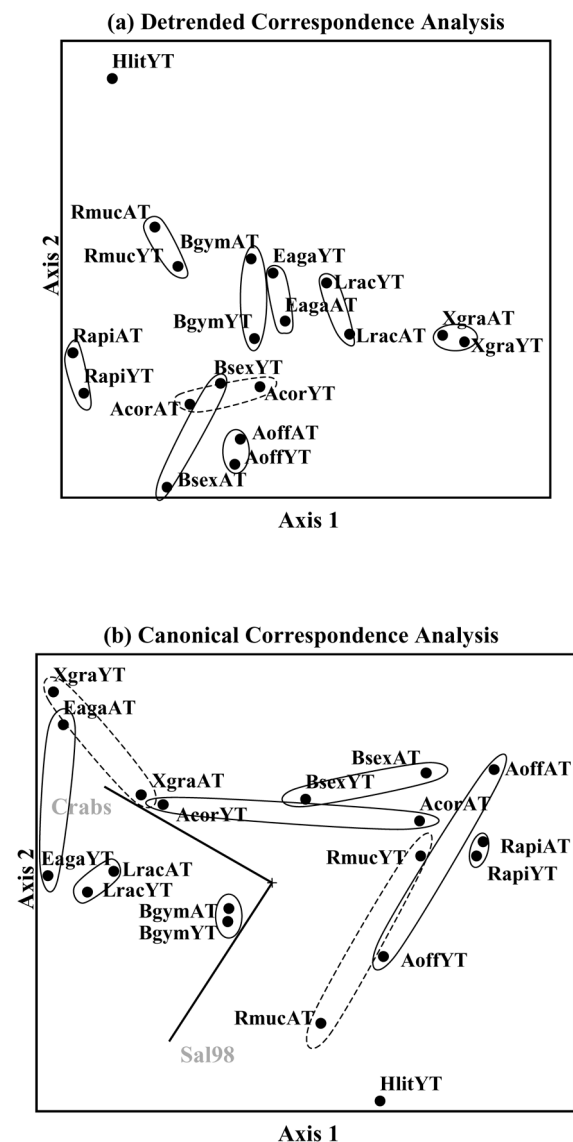
(a) Mida

(b) Gazi

(c) Pambala

(d) Galle

Figure 3. Biplots of the canonical correspondence analysis in Mida (a), Gazi (b), Pambala (c) and Galle (d). For Mida *Xylocarpus granatum* formed an outlier to the ordination and was therefore omitted from the input matrix. Points of one species are encircled and where necessary the points have been shaded to ease interpretation. See Table 3 for numerical results. See Fig. 4b for a simplified graph of Pambala. (% Land = % land cover, the rest being water; Crabs = # herbivorous crabs m^{-2}; Snails = # snails m^{-2}; Sal = salinity and Lux = light intensity, both of them with mention of the year of sampling. Species legend as in Figure 2).

to other environmental factors, that it did not even show on the biplot (Figure 3d). In Galle, where tidal influence is minimal, a slope is absent and a mosaic of islands and pools is present. The land-water ratio is responsible for most of the variation in vegetation data (intraset correlation = −0.870). In the same site the association of *Excoecaria agallocha* and *Heritiera littoralis* with high land cover values, and that of *Rhizophora apiculata* with intermediate land cover values (Figure 3d), reflects the field observation that the former two species are usually located on top of the small islands, whereas *R. apiculata* is often grow-

ing on the margin of an island with roots in the water. In the zoned mangroves (Gazi and Mida) the species assemblage clusters are more separated and recognisable than in the semi-zoned (Pambala) or non-zoned (Galle) mangroves. Between the less disturbed sites (Mida and Pambala) and the disturbed sites (Gazi and Galle), no clear and relevant differences were found in the ordinations.

Frequency distributions based on D$_{130}$ classes at 2.5 cm intervals were combined with frequency distributions of juveniles during the fieldwork missions

(a) Detrended Correspondence Analysis

(b) Canonical Correspondence Analysis

Figure 4. Graphical output of the DCA (a) and the CCA (b) for adult and young mangrove trees in Pambala. (Legends as in Figures 2 and 3).

and are shown in Figure 5. It can be seen that for some species certain D_{130} classes are missing.

Discussion

Vegetation investigations have developed a greater dependence on remote sensing technology in recent years (e.g., Gang and Agatsiva (1992); Cohen et al. (1996); Ramachandran et al. (1998); Dahdouh-Guebas et al. (1999)), and 'reviews' and 'advances' that

Table 2. Eigenvalues and an assessment of how the variance explained is distributed among the primary axes of the detrended correspondence analysis in Mida (a), Gazi (b), Pambala (c) and Galle (d). The evaluation is performed by calculating the coefficient of determination (r^2) between distances in the ordination space and distances in the original space (see text). See figure 2 for graphical results.

(a) Mida	Axis 1	Axis 2	Axis 3
Eigenvalue	0.370	0.154	0.066
$r^2 \approx$ variance explained (%)	57.3	8.30	7.70
(b) Gazi	Axis 1	Axis 2	Axis 3
Eigenvalue	0.404	0.195	0.092
$r^2 \approx$ variance explained (%)	54.1	10.0	3.5
(c) Pambala	Axis 1	Axis 2	Axis 3
Eigenvalue	0.787	0.434	0.251
$r^2 \approx$ variance explained (%)	20.5	9.4	−3.7
(d) Galle	Axis 1	Axis 2	Axis 3
Eigenvalue	0.436	0.217	0.153
$r^2 \approx$ variance explained (%)	23.1	15.6	4.8

emphasize and compare the potential of various remote sensing technologies, case-studies, and future applications are being reported (e.g., Rehder and Patterson (1986); Tassan (1987); Aschbacher et al. (1995); Blasco et al. (1998); Holmgren and Thuresson (1998); Hyyppä et al. (2000)). In contrast to this growing literature base, our study proposes a slightly different approach and creates a similar but non-mapped output using ordination techniques to provide new insight into the past, present, and future vegetation structure of mangrove forests. Of particular importance are predictive capabilities for mangrove degradation. Mangrove areas may well have a luxurious vegetation cover and thus be mapped successfully, in the field, and in particular in the youngest layers of the understory, the situation may be different compared to the past (Kairo 2001). In fact, the understory of an extensive forest may indicate degradation.

As shown in the results, species clusters are clearly distinguishable and to a certain extent the zonation or semi-zonation present in the sites can be detected along a line that is closely associated to the first axis (Figure 2). Some species, such as *Ceriops tagal*, *Rhizophora apiculata* and *R. mucronata*, have restricted dispersal (species cluster with small coverage on the first axis), whereas others, such as *Avicennia marina* and *Excoecaria agallocha*, are distributed over considerably larger areas (species clusters with a wide coverage on the first axis). For *Avicennia ma-*

Table 3. Eigenvalues, variance in species data, and species-environment (Spp-Env) correlations for the primary axes from the canonical correspondence analysis in Mida (a), Gazi (b), Pambala (c) and Galle (d). The p-values from the Monte Carlo tests, which tested the significance of the eigenvalues and the Spp-Env correlations, are indicated between brackets and significant results with an asterisk. See Figure 3 for graphical results.

(a) Mida	Axis 1	Axis 2	Axis 3
Eigenvalue	0.097 (p = 0.317)	0.035 (p = 0.551)	0.011 (p = 0.766)
Variance explained (%)	10.3	3.7	1.2
Pearson Spp-Env correlation	0.536 (p = 0.702)	0.481 (p = 0.543)	0.408 (p = 0.402)
(b) Gazi	Axis 1	Axis 2	Axis 3
Eigenvalue	0.054 (p = 0.022)*	0.032 (p = 0.004)*	0.012 (p = 0.162)
% variance explained	3.7	2.2	0.9
Pearson Spp-Env correlation	0.505 (p = 0.028)*	0.423 (p = 0.025)*	0.327 (p = 0.095)*
(c) Pambala	Axis 1	Axis 2	Axis 3
Eigenvalue	0.348 (p = 0.001)*	0.130 (p = 0.002)*	0.067 (p = 0.002)*
% variance explained	7.4	2.8	1.4
Pearson Spp-Env correlation	0.693 (p = 0.031)*	0.666 (p = 0.001)*	0.418 (p = 0.258)
(d) Galle	Axis 1	Axis 2	Axis 3
Eigenvalue	0.127 (p = 0.001)*	0.039 (p = 0.055)	0.023 (p = 0.065)
% variance explained	6.6	2.0	1.2
Pearson Spp-Env correlation	0.636 (p = 0.001)*	0.364 (p = 0.204)	0.360 (p = 0.054)

Table 4. Eigenvalues and an assessment of how the variance explained is distributed among the primary axes of the DCA (a) and the CCA (b) in Pambala. The evaluation of the DCA is performed simply by calculating the coefficient of determination (r^2) between distances in the ordination space and distances in the original space (see text). The p-values from the Monte Carlo tests, which tested the significance of the eigenvalues and the Spp-Env correlations in the CCA, are indicated between brackets and significant results with an asterisk. See Figure 4 for graphical results.

(a) DCA	Axis 1	Axis 2	Axis 3
Eigenvalue	0.788	0.465	0.301
$r^2 \approx$ variance explained (%)	32.8	13.6	1.5
(b) CCA	Axis 1	Axis 2	Axis 3
Eigenvalue	0.294 (p = 0.007)*	0.117 (p = 0.006)*	0.051 (p = 0.210)
% variance explained	5.7	2.3	1.0
Pearson Spp-Env correlation	0.634 (p = 0.025)*	0.476 (p = 0.054)	0.372 (p = 0.274)

rina this is clearly linked to its pioneer nature (*cf.* Osborne and Berjak (1997)). *A. marina* spreads seeds over a wider area than where they can actually establish. Therefore they display a distribution pattern for juvenile trees that is less associated to that for the adult trees than that for young trees. This same life history characteristic is true for *Avicennia officinalis*. This cannot be confirmed, however, for *Heritiera littoralis*, where young trees were observed in the section of Pambala where conspecific adult trees are absent. Adult *Heritiera* trees were observed in Pambala but outside the study area (pers. obs.). Contrary to the pioneering role played by these species, the same pattern observed for *E. agallocha* is explained by an in-crease of the terrestrial nature of the vegetation. *E. agallocha* is a disturbance resistant species (Tomlinson 1986) that can also easily colonise new areas over a small temporal scale (Dahdouh-Guebas et al. 2000c). It is always located at the highest topographical levels in the mangrove and therefore often associated to terrestrial non-mangrove species such as the herbaceous *Fimbristylis salbundia* subsp. *pentaptera* (pers. obs.). In total, less than half of the species clusters display the associated adult-young tree distribution as compared to the adult-juvenile tree distribution.

The results of the frequency distributions show that *Xylocarpus granatum* is not rejuvenating in

Mida, whereas it is a relatively new species in Pambala. Also, *Heritiera littoralis* can be considered to show a relatively recent establishment in Galle. Together with *Avicennia* and *Rhizophora* species, the above two species are known to grow to very tall trees in Kenya and Sri Lanka. This is not true for other species, which may explain the smaller D_{130} classes represented. The frequency distribution for *Bruguiera gymnorrhiza* in Mida (Fig. 5a) lacks two successive D_{130} classes in between classes that are actually represented. Although no such anomalous patterns in D_{130} classes are observed for *Rhizophora mucronata* or *Ceriops tagal* in the same site, their patterns were also more variable than expected. Comparing all sites confirms the degree of disturbance, since the less disturbed Mida and Pambala clearly have more and taller trees than Gazi and Galle. The observed D_{130} frequency distributions further revealed some differences between disturbed and undisturbed sites in terms of number and size of trees. In Mida, although a less disturbed site, the anomalous frequency distributions observed for *Bruguiera gymnorrhiza*, *Ceriops tagal*, and *Rhizophora mucronata* could be the result of a higher harvesting preference for these species, as was shown by Dahdouh-Guebas et al. (2000a); Kairo (2001). However, the species harvested are obviously preferred by man, but the species harvested are not necessarily the species that regenerate.

The appearance of species clusters in the CCA where fewer herbivorous crabs and snails are present, except for the species that are predated less or not at all, like *Excoecaria agallocha*, *Lumnitzera racemosa*, or *Xylocarpus granatum*, agrees with the observed predation intensity by these animals in Kenya (Dahdouh-Guebas et al. 1997, 2000b) and Sri Lanka (Dahdouh-Guebas 2001). The land/water ratio in Galle, which was the most important explanatory variable for vegetation data (Figure 3d), is probably due to its high ecological importance to vegetation dynamics. It was suggested recently that the water level in mangrove areas that lack a clear slope (and therefore hardly display zonation) is a major factor in the establishment of a particular vegetation structure and that, interacting with propagule predation, it is a driving force in the dynamics of a mangrove forest (Dahdouh-Guebas 2001). Sites with an irregular topography like Galle will create microhabitats for juvenile and adult mangroves and associated fauna that will change with different hydrological factors.

Rhizophora species are among the species that display distribution patterns that are difficult to link with the environmental factors measured in this study. Visual observations in Kenya (Mida and Gazi) have, in contrast, revealed that the vegetation zone dominated by *Rhizophora mucronata* and that dominated by *Ceriops tagal*, located at higher intertidal areas, corresponds with the upper topographical limit of the area flooded during neap tide periods and consequently with the time the vegetation is submerged. According to Brakel (1982) this elevation corresponds to at least 1 hour of immersion per tidal cycle, but this can vary significantly between sites (Dahdouh-Guebas et al., in press). Under the lower tidal influences in Sri Lanka, the conditions for *Rhizophora* are different and temporally irregular, but nevertheless also vary from permanent flooding by freshwater in the rainy season to very little flooding in the dry season. However, in Galle, many *Rhizophora* trees are in contact with pools. In Pambala, association with pools is only the case for the most landward and the most creekward *Rhizophora* individuals. Contact at both ends with water probably leads to a below-ground supply for the *Rhizophora* trees located farther from the surface water. Whereas the influence of groundwater supply on mangrove distribution has clearly been demonstrated by Tack and Polk (1999) for the Kenyan coast, in Sri Lanka no conclusive results have been found. Another variable that probably plays a substantial role is the soil texture. It has recently been found that soil texture is a major explanatory factor in the distribution of sesarmid crabs (Ballerini et al. 2000; Cannicci et al. 2000), and a recent study on rooting of mangrove species in Sri Lanka suggests that soil texture also influences the distribution of mangrove species (Dahdouh-Guebas et al. 2001). Other edaphic characteristics, such as nutrient availability, may be important explanatory factors but remain untested within ordination investigations.

This study shows that ordinations can provide information with respect to the dynamics of a vegetation assemblage by using different vegetation layers per species as an input, rather than single species. The dynamic or non-dynamic nature of a particular forest is captured by ordination approaches, and annual monitoring of the juveniles can reveal whether or not the forest is rejuvenating. The combination of a forest's dynamism and its rejuvenation provides a possible indication on the destiny of a forest and may raise the awareness to protect or to rehabilitate a mangrove area. Combined with remote-sensing and GIS and in-depth knowledge of silvicultural restoration techniques, the methodololgy used in the present
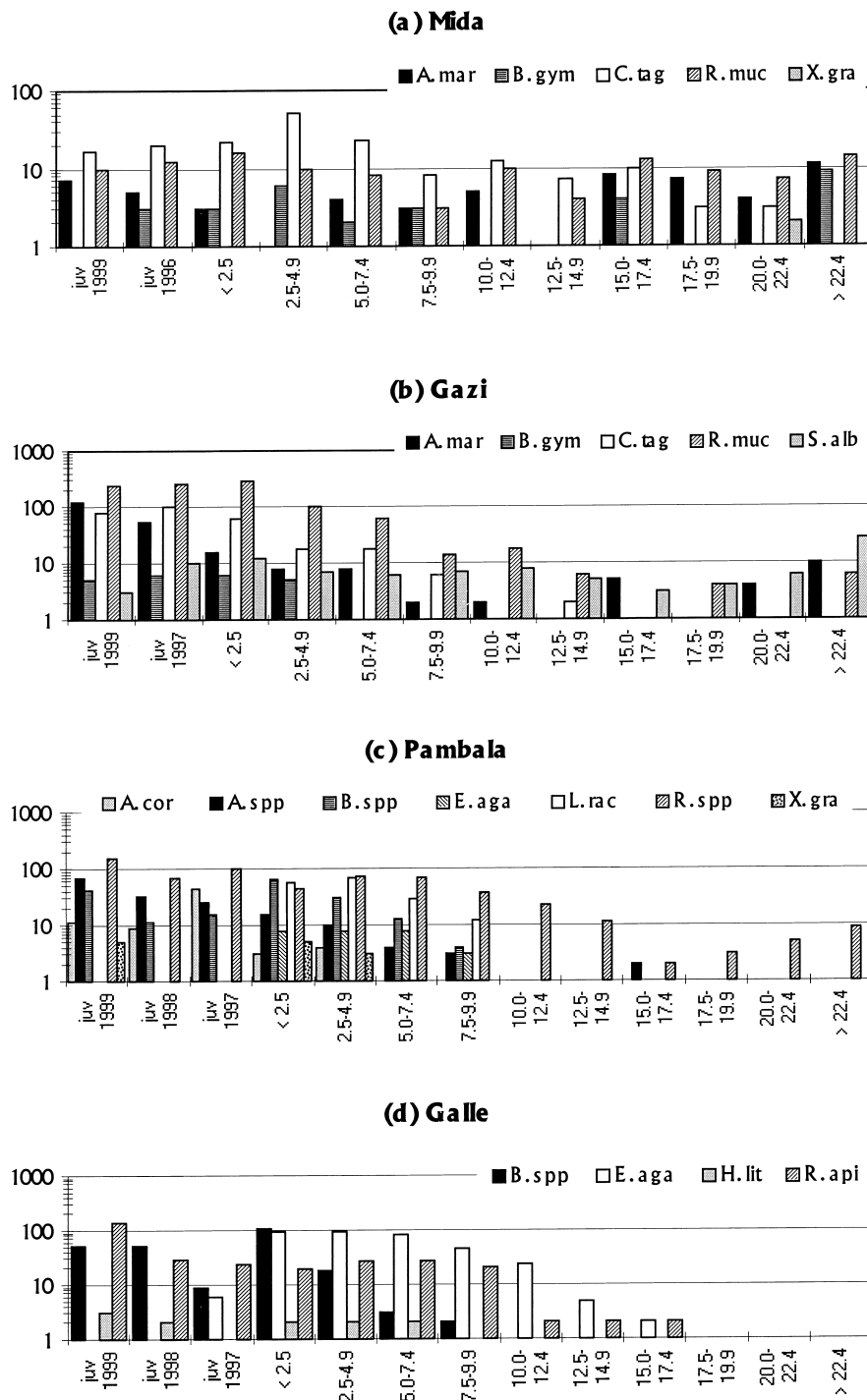
(a) Mida

(b) Gazi

(c) Pambala

(d) Galle

Figure 5. Frequency distributions of D_{130} classes (at 2.5 cm intervals) combined with frequency of juveniles during the fieldwork missions. The right part of the frequency distributions provide information about the history of the forest, whereas the left part may be used for inference about the future. The young *Heritiera littoralis* tree in Pambala was omitted because it does not display on the logarithmic scale.

study opens doors to the development of an early-warning system. Such a system may allow for the de-velopment of an emergency plan for declining man-

grove forests long before degradation symptoms are visible in the field.

Acknowledgements

References

Aschbacher J., Ofren R., Delsol J.P., Suselo T.B., Vibulsresth S. and Charrupat T. 1995. An integrated comparative approach to mangrove vegetation mapping using advanced remote sensing and GIS technologies: preliminary results. Hydrobiologia 295: 285–294.

Ballerini T., Macia A. and Cannicci S. 2000. Zonation of Mangrove Crabs at Inhaca Island (Mozambique): a new hypothesis. Abstract Volume of the Meeting on Mangrove Macrobenthos, 7-11 September, Mombasa, Kenya.

Blasco F., Gauquelin T., Rasolofoharinoro M., Denis J., Aizpuru M. and Caldairou V. 1998. Recent advances in mangrove studies using remote sensing data. Marine and Freshwater Research 49: 287–296.

Brakel W.H. 1982. Tidal patterns on the East African coast and their implications for the littoral biota. In: Proceedings of the Symposium on the Coastal and Marine Environment of the Red Sea, Gulf of Aden and Tropical Western Indian Ocean 2., pp. 403–418.

Brokaw N. and Thompson J. 2000. The H for DBH. Forest Ecology and Management 129: 89–91.

Cannicci S., Skov M.W. and Vannini M. 2000. The influence of abiotic and biotic factors on the distribution of mangrove crabs at Mida Creek (Kenya): a multivariate approach. Abstract Volume of the Meeting on Mangrove Macrobenthos, 7-11 September, Mombasa, Kenya.

Cohen W.B., Kushla J.D., Ripple W.J. and Garman S.L. 1996. An introduction to digital methods in remote sensing of forested ecosystems: focus on the Pacific Northwest, USA. Environmental Management 20: 421–435.

Cottam G. and Curtis J.T. 1956. The use of distance measures in phytosociological sampling. Ecology 37: 451–460.

Curtis J.T. 1959. The Vegetation of Wisconsin. An Ordination of Plant Communities. University of Wisconsin Press, Madison, Wisconsin, USA.

Dahdouh-Guebas F. 2001. Propagule predation in Sri Lankan mangroves and its effect on vegetation structure dynamics. In: Mangrove vegetation structure dynamics and regeneration. F. Dahdouh-Guebas. PhD Dissertation, Vrije Universiteit Brussel, Brussels, Belgium.

Dahdouh-Guebas F., Coppejans E. and Van Speybroeck D. 1999. Remote sensing and zonation of seagrasses and algae along the Kenyan coast. Hydrobiologia 400: 63–73.

Dahdouh-Guebas F., Mathenge C., Kairo J.G. and Koedam N. 2000a. Utilization of mangrove wood products around Mida Creek (Kenya) amongst subsistence and commercial users. Economic Botany 54: 513–527.

Dahdouh-Guebas F., Thisera D.W.N., Wickramasinghe A. and Koedam N. 2001. Regeneration status of mangroves under natural and nursery conditions in Galle and Pambala, Sri Lanka. In: Mangrove vegetation structure dynamics and regeneration. F. Dahdouh-Guebas. PhD Dissertation, Vrije Universiteit Brussel, Brussels, Belgium.

Dahdouh-Guebas F., Verneirt M., Tack J.F. and Koedam N. 1997. Food preferences in *Neosarmatium meinerti* de Man (Decapoda: Sesarminae) and its possible effect on the regeneration of mangroves. Hydrobiologia 347: 83–89.

Dahdouh-Guebas F., Verheyden A., De Genst W., Hettiarachchi S. and Koedam N. 2000b. Four decade vegetation dynamics in Sri Lankan mangroves as detected from sequential aerial photography: a case study in Galle. Bulletin of Marine Science 67: 741–759.

Dahdouh-Guebas F., Verneirt M., Tack J.F., Van Speybroeck D. and Koedam N. 1998. Propagule predators in Kenyan mangroves and their possible effect on regeneration. Marine and Freshwater Research 49: 345–350.

Dahdouh-Guebas F., Zetterström T., Rönnbäck P., Troell M. and Koedam N. 2000c. Conservation of mangroves vs. development of shrimp farming in Pambala - Chilaw lagoon, Sri Lanka. In: Flos R. and Creswell L. (eds), Responsible Aquaculture in the New Millenium. European Aquaculture Society, Oostende, Belgium, p. 167.

Dahdouh-Guebas F., Zetterström T., Rönnbäck P., Troell M., Wickramasinghe A. and Koedam N. 2002. Recent changes in landuse in the Pambala-Chilaw Lagoon complex (Sri Lanka) investigated using remote sensing and GIS: conservation of mangroves vs. development of shrimp farming. Environment, Development and Sustainability (in press).

Dahdouh-Guebas F., Verneirt M., Cannicci S., Kairo J.G., Tack J.F. and Koedam N. An explorative study on grapsid crab zonation in mangrove forests in Kenya. Wetlands Ecology and Management (in press).

Duke N.C. 1991. A systematic revision of the mangrove genus *Avicennia* (Avicenniaceae) in Australasia. Australian Systematic Botany 4: 299–324.

Duke N.C. and Jackes B.R. 1987. A systematic revision of the mangrove genus *Sonneratia* (Sonneratiaceae) in Australasia. Blumea 32: 277–302.

Farnsworth E.J. and Ellison A.M. 1997. The global conservation status of mangroves. Ambio 26: 328–334.

Foell J., Harrison E. and Stirrat R.L. 1999. Participatory approaches to natural resource management – the case of coastal zone management in the Puttalam District. Summary findings of DFID-funded research 'participatory mechanisms for sustainable development of coastal ecosystems' (Project R6977), School of African and Asian studies. University of Sussex, Falmer, Brighton, UK.

Gallin E., Coppejans E. and Beeckman H. 1989. The mangrove vegetation of Gazi bay (Kenya). Bulletin de la Société Royal Botanique de Belgique 122: 197–207.

Gang P.O. and Agatsiva J.L. 1992. The current status of mangroves along the Kenyan coast: a case study of Mida Creek mangroves based on remote sensing. Hydrobiologia 247: 29–36.

Heil G.W. and Van Deursen W.P.A. 1996. Searching for patterns and processes: modelling of vegetation dynamics with geographical information systems and remote sensing. Acta Botanica Neerlandica 45: 543–556.

Hill M.O. and Gauch H.G. 1980. Detrended correspondence analysis: an improved ordination technique. Vegetatio 42: 47–58.

Hobbs R.J. and Grace J. 1981. A study of pattern and process in coastal vegetation using principal component analysis. Vegetatio 44: 137–153.

Holdridge L., Grenke W.C., Hatheway W.H., Liang T. and Tosi J.A. 1971. Forest Environment in Tropical Life Zones. Pergamon Press, NY, pp. 747.

Holmgren P. and Thuresson T. 1998. Satellite remote sensing for forestry planning – a review. Scandinavian Journal of Forest Research 13: 90–110.

Holmgren P., Thuresson T. and Holm S. 1997. Estimating forest characteristics in scanned aerial photographs with respect to requirements for economic forest management planning. Scandinavian Journal of Forest Research 12: 189–199.

Hyyppä J., Hyyppä H., Inkinen M., Engdahl M., Linko S. and Zhu Y.H. 2000. Accuracy comparison of various remote sensing data sources in the retrieval of forest stand attributes. Forest Ecology and Management 128: 109–120.

ITTO 1993. The economic and environmental value of mangrove forests and their present state of conservation. Prepared for the International Tropical Timber Organisation. Japan International Association for Mangroves and International Society for Mangrove Ecosystems, Okinawa, Japan.

IUCN 1996. Conservation management plan for ten selected mangrove sites in southwestern Sri Lanka. IUCN, Gland, Switzerland, November 1996.

Jayatissa L.P., Dahdouh-Guebas F. and Koedam N. 2002. A review of the floral composition and distribution of mangroves in Sri Lanka. Botanical Journal of the Linnean Society 138: 29–43.

Kairo J.G. 2001. Ecology and Restoration of Mangrove Systems in Kenya. PhD Dissertation, Vrije Universiteit Brussel, Belgium.

Kairo J.G., Gwada P.O., Dahdouh-Guebas F., Koedam N., Van Speybroeck D. and Ochieng C. Natural regeneration status of Mangrove Forests in Mida Creek. (in preparation) (unpublished).

Kent M. and Coker P. 1992. Vegetation Description and Analysis. A practical Approach. John Wiley & Sons, Chichester, UK.

Kjerfve B., de Lacerda L.D. and Diop E.H.S. 1997. Mangrove Ecosystem Studies in Latin America and Africa. UNESCO, Paris, France.

Lugo A.E. and Snedaker S.C. 1974. The ecology of mangroves. Annual Review of Ecology and Systematics 5: 39–64.

McCune B. and Mefford M.J. 1997. Multivariate Analysis of Ecological Data. Version 3.09. MjM Software, Gleneden Beach, Oregon, USA.

Mueller-Dombois D. 1968. Ecogeographic analysis of a climate map of Ceylon with particular reference to vegetation. The Ceylon Forester 8: 3–20.

Murali K.S., Siddappa Setty R., Ganeshaiah K.N. and Uma Shaanker R. 1998. Does forest type classification reflect spatial dynamics of vegetation? An analysis using GIS techniques. Current Science 75 : 220–227.

Osborne D.J. and Berjak P. 1997. The making of mangroves: the remarkable pioneering role played by seeds of *Avicennia marina*. Endeavour 21: 143–147.

Pernetta J.C. 1993. *Marine protected areas needs in the South Asian Seas Region. Sri Lanka.* A Marine Conservation and Development Report. IUCN, Gland, Switzerland, vii + 67 pp.

Putz F.E. and Chan H.T. 1986. Tree growth, dynamics, and productivity in a mature mangrove forest in Malaysia. Forest Ecology and Management 17: 211–230.

Ramachandran S., Sundaramoorthy S., Krishnamoorthy R., Devasenapathy J. and Thanikachalam M. 1998. Application of remote sensing and GIS to coastal wetland ecology of Tamil Nadu and Andaman and Nicobar group of islands with special reference to mangroves. Current Science 75: 236–244.

Rehder J.B. and Patterson S.G. 1986. Mangrove mapping and monitoring. In: Damen M.C.J., Smit G.S. and Verstappen H.Th. (eds), Symposium on Remote Sensing for Resources Development and Environmental Management. ITC, Enschede, The Netherlands, pp. 495–497.

Smith T. and Huston M. 1989. A theory of the spatial and temporal dynamics of plant communities. Vegetatio 83: 49–69.

Spalding M., Blasco F. and Field C. 1997. World Mangrove Atlas. The International Society for Mangrove Ecosystems, Okinawa, Japan, 178 pp.

Tack J.F. and Polk P. 1999. The influence of tropical catchments upon the coastal zone: modelling the links between groundwater and mangrove losses in Kenya, India and Florida. In: Harper D. and Brown T. (eds), Sustainable management in tropical catchments. John Wiley & Sons Ltd, London, UK.

Tassan S. 1987. Evaluation of the potential of the Thematic Mapper for marine application. International Journal of Remote Sensing 8: 1455–1478.

Ter Braak C.J.F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67: 1167–1179.

Ter Braak C.J.F. 1994. Canonical community ordination. Part I: Basic theory and linear methods. Ecoscience 1: 127–140.

Tomlinson P.B. 1986. The Botany of Mangroves. Cambridge University Press, Cambridge, UK, 419 pp.

Ukpong I.E. 1995. An ordination study of mangrove swamp communities in West-Africa. Vegetatio 116: 147–159.

Verheyden A., Dahdouh-Guebas F., Thomaes K., De Genst W., Hettiarachchi S. and Koedam N. High resolution vegetation data for mangrove research as obtained from aerial photography. (submitted).