FREE UNIVERSITY BRUSSELS
FACULTY OF SCIENCES
MANGROVE MANAGEMENT GROUP
Laboratory of General Botany and Nature Management

# Mangrove vegetation structure dynamics and regeneration

(*Thesis Philosophiae Doctor Scientiarum*)

[redacted]

FARID DAHDOUH-GUEBAS

**Proefschrift voorgelegd tot het behalen van de wettelijke graad Doctor in de Wetenschappen**

# FREE UNIVERSITY BRUSSELS

FACULTY OF SCIENCES
MANGROVE MANAGEMENT GROUP
Laboratory of General Botany and Nature Management

# Mangrove vegetation structure dynamics and regeneration

(*Thesis Philosophiae Doctor Scientiarum*)

**FARID DAHDOUH-GUEBAS**

**Proefschrift voorgelegd tot het**
**behalen van de wettelijke graad**
**Doctor in de Wetenschappen**

Voor het VLIZ
met hartelijke groeten,

Front cover :

Winning drawing in the Mangrove Drawing Competition 1996 (for 14-18 year-old youngsters) organised by the Small Fishers Federation of Lanka (SFFL), Pambala-Kakkapalliya, Sri Lanka. Drawn by W. Muditha Avanthie Livera from Sugathananda Vidiyaleiya (School) in Madampe.

*Courtesy of SFFL*

*Thesis Philosophiae Doctor Scientiarum* (PhD thesis) :

# Mangrove vegetation structure dynamics and regeneration

*thesis iunctus* (bijstelling / annex thesis) :

## Scientific research with a possible relevance in the framework of development cooperation, as evident from the geographic location of (part of) the research, is, at the level of the academic development of local scientists, insufficiently done in cooperation with research institutes from the country on which the research focuses.

by
**Farid DAHDOUH-GUEBAS**

Keywords : mangrove, vegetation structure, dynamics, regeneration, remote sensing, GIS, crab, propagule predation, PCQM, development cooperation, Kenya, Sri Lanka, Mauritania

Promoter : Prof. Dr. **Nico Koedam** (VUB)

Scientific Jury :

Prof. Dr. **Nanette Daro**
(Ecology and systematics Unit, VUB)
Prof. Dr. **Frank Dehairs**
(Analytical Chemistry Unit, VUB)
Prof. Dr. Ir. **Luc D'Haese**
(Belgian Technical Cooperation, BE)
Prof. Dr. **Nico Koedam**
(General Botany and Nature Management Unit, VUB)
Dr. **Jurgen F. Tack**
(Biodiversity Platform / Services of the Prime Minister, Scientific, Technical and Cultural Issues, BE)
Prof. Dr. **Ludwig Triest**
(General Botany and Nature Management Unit, VUB)
Prof. Dr. **Marc Van Molle**
(Geography Unit, VUB)
Prof. Dr. **Marco Vannini**
(Department of Animal Biology and Genetics 'Leo Pardi', Università degli Studi di Firenze, Italy)

Laboratory of General Botany and Nature Management, Mangrove Management Group,
Vrije Universiteit Brussel, Pleinlaan 2, B-1050 Brussels, Belgium
Tel. & Fax. + 32 02 629 34 13. E-mails : <fdahdouh@vub.ac.be><fdahdouh@freegates.be><apna@vub.ac.be>
URLs : http://www.vub.ac.be/APNA/staff/FDG/fdg.html and URL : http://home.freegates.be/fdahdouh/
Executive PhD summary available online through former URLs.

**To my entire family, who always supported me in my academic undertakings…**

***In memoriam Malawara Arachchige 'Alawattagoda' PEMADASA and Agrey OLUOCH***

*When you watch the ocean we were given,*
*And look at how the waves are driven,*
*Towards any tropical coast,*
*Towards a forest, towards a host.*
*Towards a ground made for breeding,*
*Where one is lodged or comes for feeding,*
*Where the water meets the land,*
*Where you only find this plant.*

*Once a seedling must have stranded,*
*Making this site so enchanted,*
*Lots of creeks, lots of roots,*
*Lots of curious floating fruits.*
*Unusual systems for dispersing,*
*Exotic life forms there for nursing,*
*Swimming, jumping, climbing trees,*
*Fish and crabs and more of these.*

*Many threats is what they face,*
*Try surviving their own ways,*
*All subjected to hard stress,*
*But still thriving nonetheless,*
*What on Earth is this unlike ?*
*Which plant is forming a living dyke ?*
*Who is it rooting in the sea ?*
*The mangrove tree,*
*The mangrove tree.*

# Table of Contents

**Table of Contents** ..... vi
**English Summary** ..... viii
**Nederlandse samenvatting** ..... ix
**Résumé Français** ..... x
**Deutsche Zusammenfassung** ..... xi
**Muhtasari** ..... xiii
**Summary in Sinhala** ..... xiv
**Summary in Tamil** ..... xvi
**General Introduction.** ..... 1
    Mangrove ecosystems ..... 3
    Mangrove services and mangrove threats ..... 4
    Objectives and layout ..... 5
        Research framework ..... 5
**Utilization of mangrove wood products around Mida Creek (Kenya) amongst subsistence and commercial users.** ..... 11
    Dahdouh-Guebas, F., C. Mathenge, J.G. Kairo & N. Koedam 11
**A review of the floral composition and distribution of mangroves in Sri Lanka.** ..... 29
    Jayatissa, L.P., F. Dahdouh-Guebas & N. Koedam 29
**High-resolution vegetation data for mangrove research as obtained from aerial photography.** ..... 49
    Verheyden, A., F. Dahdouh-Guebas, K. Thomaes, W. De Genst, S. Hettiarachchi & N. Koedam 49
**A note on the identification of mangroves from aerial photography in Kenya and Sri Lanka.** ..... 73
    Dahdouh-Guebas, F., A. Verheyden, L.P. Jayatissa & N. Koedam 73
**Four decade vegetation dynamics in Sri Lankan mangroves as detected from sequential aerial photography : a case-study in Galle.** ..... 85
    Dahdouh-Guebas, F., A. Verheyden, W. De Genst, S. Hettiarachchi & N. Koedam 85
**Two decade vegetation dynamics in Kenyan mangroves as detected from sequential aerial photography : a case-study in Gazi Bay.** ..... 105
    Dahdouh-Guebas, F., I. Van Pottelbergh, J.G. Kairo & N. Koedam 105
**An ordination study to view past, present and future vegetation structure dynamics in disturbed and undisturbed mangrove forests in Kenya and Sri Lanka.** ..... 123
    Dahdouh-Guebas, F., J.G. Kairo, L.P. Jayatissa & N. Koedam 123
**An explorative study on grapsid crab zonation in mangrove forests in Kenya.** ..... 139
    Dahdouh-Guebas, F., M. Verneirt, S. Cannicci, J.G. Kairo, J.F. Tack & N. Koedam139
**Propagule predators in Kenyan mangroves and their possible effect on regeneration.** 151
    Dahdouh-Guebas, F., M. Verneirt, J.F. Tack, D. Van Speybroeck & N. Koedam 151
**Propagule predation in Sri Lankan mangroves and its effect on vegetation structure.** 161
    Dahdouh-Guebas, F. 161
**Regeneration status of mangroves under natural and nursery conditions in Galle and Pambala, Sri Lanka.** ..... 185
    Dahdouh-Guebas, F., D.W.N. Thisera, A. Wickramasinghe & N. Koedam 185
**Are the northernmost mangroves of West Africa viable ? A case-study in the Parc National du Banc d'Arguin, Mauritania** ..... 207
    Dahdouh-Guebas, F. & N. Koedam 207

**Empirical estimate of the reliability of the use of the point-centred quarter method (PCQM) in mangrove forests.** ........ **227**
Dahdouh-Guebas, F. & N. Koedam 227
**General discussion.** ........ **251**
Research frameworks for studies on vegetation structure dynamics ........ 253
What encompasses 'dynamics' in the literature ? ........ 254
Data acquisition and analysis in studies on vegetation structure dynamics.... 254
Remote sensing ........ 254
Ground-truthing ........ 255
Types of vegetation structure dynamics in mangroves ........ 258
Mangrove regeneration and its constraints as an integrated application ........ 264
Reccommendations for future research on mangrove vegetation structure dynamics and regeneration (incl. regenerative constraints) ........ 266
**Epilogue** ........ **269**
Relevance of the work in the framework of development co-operation ........ 269
**General Conclusions** ........ **273**
**Bibliography** ........ **275**
**Appendices** ........ **289**
Appendix 1 : Field keys for Kenyan mangrove crabs ........ 291
Appendix 2 : Expertise and list of valorised research ........ 301
**Acknowledgements** ........ **309**
**Index** ........ **313**

# English Summary

The present PhD dissertation is composed of fourteen papers, preceded by a **general introduction** and followed by an epilogue that explains the entire research framework, including the links between the different case-studies, the local and global applicability of the results and the relevance of the work in the framework of development co-operation. The bulk of the research was carried out in four sites in Kenya and Sri Lanka : Gazi Bay and Mida Creek in Kenya, and Unawatuna-Galle and Pambala-Chilaw in Sri Lanka.

After a revision of the often controversial issue of the **floral composition of mangroves in Sri Lanka** (SW coast), followed by a synthesis of image attributes in the **interpretation of aerial photographs** in Kenya and Sri Lanka, a series of case-studies are presented which cover the study of **mangrove vegetation structure dynamics** (incl. zonation issues), mangrove regeneration and regenerative constraints (in particular propagule predation). Gazi and Galle appeared to be more disturbed than Mida and Pambala. The studies of these disturbed sites show different types of structural changes in vegetation over time, as well as the existence of interactions between the mangrove and terrestrial vegetation (sedges and coconut plantation). Parallel investigation of the adult, young and juvenile vegetation layers in combination with sequential aerial photography from the past allow an understanding of the dynamic processes and a **prediction of the future forest structure**, the latter subject to different scenarios (no change, mangrove cutting, natural hazards, etc.). This approach allows for the decision if a certain mangrove stand has the potential to successfully renew and rejuvenate or if anthropogenic pressure renders human interference such as restoration imperative. In the framework of re-afforestation programs the study of the fate of mangrove juveniles in rehabilitation plots is essential. Whereas the monitoring of **mangrove regeneration** provides information on the general status of mangrove juveniles, the study of **propagule predation** in particular has shown that crabs and gastropods may constitute a problem for the successful regeneration of mangroves in Kenya and Sri Lanka. Results also show how propagule predation is one link in the chain of events that leads to a particular vegetation structure (zoned or unzoned), and how hydrology and anthropogenic pressure may possibly influence it. The outcome therefore gives direct information for forest management issues by identifying the species, the areas and the processes that are likely to display higher propagule predation rates.

Another aspect of mangrove regeneration is more directed towards natural regeneration conditions, more specifically in **biogeographical limit situations** such as in the Parc National du Banc d'Arguin (Mauritania), a World Heritage Site where the mangroves of the West-African coast reach their northernmost distribution. As a biogeographically marginal, monospecific mangal in an area where freshwater availability has decreased over the last decades, concern about the survival of the mangroves has been expressed. However, except for inappropriate topographical conditions (mangroves growing in terrestrial locations, with little chance for propagule survival) the mangrove did not show signs of reduced vitality at its biogeographical limit, but even displayed a diversity of vegetation structure types (high trees, wide trees, shrub formations and 'sebkha' formations).

An empirical revisit of the **Point-Centred Quarter Method** (PCQM) prompted by fieldwork experience, tackles the problems associated with this method, such as ambiguous tree architectural settings for measuring the tree diameter, aggregation of trees or the over- or under-estimation of the density and the basal area. The factor by which the latter occurs, apparently is influenced by the vegetation structure of the forest.

The final paper provides an integrated **review of mangrove vegetation structure dynamics** based on existing literature as well as on the previous case-studies and summarises and defines the different types of vegetation structure dynamics.

# Nederlandse samenvatting

Deze doctoraatsthesis bestaat uit veertien manuscripten, voorafgegaan door een algemene inleiding en gevolgd door een epiloog dat het gehele onderzoekskader uitlegt, inclusief de verbanden tussen de verschillende case-studies, de lokale en globale toepasbaarheid van de resultaten en de relevantie van het werk in het kader van ontwikkelingssamenwerking. Het grootste gedeelte van het onderzoek werd uitgevoerd in vier sites in Kenia en Sri Lanka : Gazi Bay en Mida Creek in Kenia, en Unawatuna-Galle en Pambala-Chilaw in Sri Lanka.

Na een revisie van het vaak controversiële debat rond de floristische samenstelling van mangroven in Sri Lanka (zuid-west kust), gevolgd door een synthese van beeldattributen gebruikt in de interpretatie van luchtfoto's in Kenia en Sri Lanka, wordt een opeenvolging van case-studies gepresenteerd die de studie van de dynamiek van de vegetatiestructuur (incl. zonatie), mangrove-regeneratie en regeneratie-beperkende factoren (in het bijzonder propagulepredatie) overkoepelen. Gazi en Galle bleken meer verstoord dan Mida en Pambala. De studie van deze verstoorde sites tonen aan dat er zich in de tijd verschillende types structurele veranderingen in de vegetatie voordoen, en wijzen eveneens op het bestaan van interacties tussen mangrove- en terrestrische vegetatie (cypergrassen en cocosaanplantingen). Gelijktijdig onderzoek m.b.t. de adulte, de jonge en de juveniele vegetatielagen, in combinatie met sequentiële luchtfotografie uit het verleden, laten toe de dynamische processen te begrijpen en een voorspelling te doen m.b.t. de toekomstige structuur van het woud, deze laatste onder verschillende scenario's (geen verandering, mangrovekap, natuurlijke catastrofen, enz.). Deze aanpak laat toe om te beslissen of een bepaald mangrovebestand het potentieel heeft om op een successvolle manier te vernieuwen en te verjongen of dat de anthropogene druk een menselijk ingrijpen onder de vorm van bijv. restauratie noodzakelijk maakt. In het kader van herbebossingsprojecten is de studie van het lot van mangrovejuvenielen in rehabilitatieproefvlakken essentieel. Daar waar de monitoring van mangroveregeneratie informatie genereert over de algemene status van de mangrovejuvenielen, toont de studie van propagulepredatie aan dat in het bijzonder krabben en slakken een probleem kunnen vormen voor de successvolle regeneratie van mangroven in Kenya en Sri Lanka. Resultaten wijzen ook aan hoe propagulepredatie één schakel is in de keten van evenementen die tot een bepaalde vegetatiestructuur (gezoneerd of niet-gezoneerd) leidt, en hoe hydrologie of anthropogene druk dit mogelijk beïnvloeden. De uitkomst geeft dus directe informatie voor het bosbeheer door de soorten, de gebieden en de processen te identificeren die mogelijk leiden tot een meer intense propagulepredatie.

Een ander aspect van de mangroveregeneratie is gericht naar natuurlijke regeneratieomstandigheden, meer bepaald in de biogeografische limietsituatie zoals die van het Parc National du Banc d'Arguin (Mauretanië), een Wereld Heritage Site waar de mangroven van de West-Afrikaanse kust hun noordelijke areaalgrens bereiken. In deze biogeografisch marginale, monospecifieke mangrove, gelegen in een gebied waar de zoetwatervoorziening is gedaald gedurende de laatste decennia, was er bezorgdheid in verband met de overleving van de mangroven. Echter, met uitzondering van ongeschikte topografische condities (mangroven die groeien in terrestrische locaties, met weinig kans op overleving voor de propagulen) vertoonde de mangrove geen tekenen van een verminderde vitaliteit aan zijn biogeografische grens, maar zelfs een diversiteit in vegetatiestructuurtypes (hoge bomen, brede bomen, struikformaties en 'sebkha' formaties).

Een empirische herbeschouwing van de Point-Centred Quarter Method (PCQM) ingegeven door veldwerkervaring, behandelt de problemen die geassocieerd zijn aan deze methode, zoals dubbelzinnige boom-architectuur situaties voor het meten van de boomdiameter, aggregatie van bomen of de over- of onderschatting van de densiteit en de basale oppervlakte. De factor waarmee deze laatste gebeuren worden blijkbaar beïnvloed door de vegetatiestructuur van het woud.

Het laatste manuscript geeft een geïntegreerd overzicht van de dynamiek van de vegetatiestructuur van mangroven gebaseerd op bestaande literatuur evenals op voorgaande case-studies en vat de verschillende types van vegetatiestructuurdynamiek samen.

# Résumé Français

Cette thèse de doctorat se compose de quatorze manuscrits, précédés d'une introduction générale et suivis d'un épilogue ; ce dernier explique tout le cadre de recherche et comprend les liens entre les divers cas d'étude, l'applicabilité locale et globale des résultats et la pertinence du travail dans le cadre de la coopération au développement. Une grande part de la recherche a été effectuée dans quatre sites au Kenya et au Sri Lanka : Gazi Bay et Mida Creek au Kenya, et Unawatuna-Galle et Pambala-Chilaw au Sri Lanka.

Après une révision du sujet, souvent controverse, de la composition floristique des mangroves au Sri Lanka (côte Sud-Ouest), et la synthèse des attributs d'image utilisés dans l'interprétation de photos aériennes au Kenya et au Sri Lanka, une série de cas d'étude aborde différents aspects de l'étude de la dynamique de la structure de la végétation (incl. zonation), et de la régénération de la mangrove et de ses facteurs restrictifs (en particulier la prédation des semences). Gazi et Galle apparaissent plus perturbés que Mida et Pambala. L'étude de ces sites perturbés indique qu'au cours du temps, différents types de changements structuraux se sont produits dans la végétation, tels que l'apparition d'interactions entre les végétations de mangrove et de milieu terrestre (souchets et plantations de noix de coco). L'examen en parallèle des strates de végétation adulte, jeune et juvénile, en combinaison avec la photographie aérienne séquentielle de la situation antérieure de la végétation, permet de comprendre les processus de la dynamique et de faire des prédictions, à partir de différents scénarios (aucun changement, abattage de la mangrove, catastrophes naturelles, etc.), quant à la structure future de la forêt. Cette approche permet de déterminer si un certain stade de végétation a le potentiel de se renouveler ou de rajeunir, ou si la pression anthropogène rend une intervention humaine indispensable, par exemple sous la forme d'une restauration. Dans le cadre de projets de reboisement, l'étude du devenir des juvéniles de la mangrove dans les carrés de réhabilitation est essentielle. Alors que le monitoring de la régénération de la mangrove génère de l'information sur l'état général des juvéniles, l'étude de la prédation des semences en particulier, montre que les crabes et les gastropodes peuvent constituer un facteur limitant dans la régénération complète des mangroves au Kenya et au Sri Lanka. Les résultats montrent aussi comment la prédation des semences n'est qu'un maillon dans la chaîne d'événements qui mènent à une certaine structure de la végétation (zonée ou non), et comment l'hydrologie ou la pression anthropogène peut l'influencer. Donc, en identifiant les espèces, les terrains et les processus responsables d'une prédation plus intense des semences, les résultats fournissent des informations directes concernant l'aménagement de la forêt.

Un autre aspect de l'étude de la régénération de la mangrove concerne les conditions naturelles de régénération, en particulier en situation biogéographique marginale, comme c'est le cas dans le Parc National du Banc d'Arguin (Mauritanie), un Site d'Héritage Mondial où la mangrove de l'Afrique de l'Ouest atteint la limite septentrionale de sa distribution. Dans cette région de mangrove monospécifique et biogéographiquement marginale, où l'apport en eau douce a baissé durant ces dernières décennies, on peut s'inquiéter quant à la survie de celles-ci. Toutefois, à l'exception de conditions topographiques inappropriées (mangroves qui poussent dans des milieux terrestres, dont les semences ont peu de chance de survie), la mangrove ne montre pas de signe d'une vitalité réduite à sa marge biogéographique, mais, au contraire, une diversité au niveau de la structure de la végétation (arbres hauts ou larges, formation d'arbustes et formations 'sebkha').

Une revisite empirique de la Méthode des quadrants point-centré (Point-Centred Quarter Method, PCQM) inspirée par l'expérience sur le terrain, traite des problèmes qui sont associés à cette méthode, comme les situations ambiguës dans l'architecture des arbres pour la mesure du diamètre des troncs, l'agrégation d'arbres ou la sur- ou sous-estimation de la densité et de la surface basale. Le facteur avec lequel ce dernier se produit est apparemment influencé par la structure de la végétation de la forêt.

Le dernier manuscrit donne un aperçu intégré de la dynamique de la structure de la végétation de la mangrove basée sur la littérature existante comme sur les cas d'étude précédents, et récapitule les différents types de dynamique de la structure de la végétation.

# Deutsche Zusammenfassung

Die vorliegende Dissertation setzt sich aus vierzehn Veröffentlichungen zusammen, welchen eine generelle Zusammenfassung vorausgeht; anschließend folgt ein Epilog, der den gesamten Forschungszusammenhang einschließlich der Verknüpfungen verschiedener Fallstudien, die lokale und globale Anwendbarkeit der Ergebnisse und die Relevanz der Arbeit im Rahmen der Entwicklungszusammenarbeit erklärt. Die Forschungsarbeiten wurden hauptsächlich in vier Untersuchungsgebieten in Kenya und Sri Lanka durchgeführt: Gazi Bay und Mida Creek in Kenya und Unawatuna-Galle und Pambala-Chilaw auf Sri Lanka.

Nach einer Revision der oft kontrovers behandelten floristischen Zusammensetzung der Mangroven Sri Lankas (Südwest-Küste), folgt eine Synthese von Bildattributen zur Auswertung von Luftphotographien in Kenya und Sri Lanka; dann folgt eine Serie von Fallstudien zur Dynamik der Mangroven-Vegetationsstruktur (inklusive Fragen der Zonierung), Mangroven-Regeneration und zur Limitierung der Regeneration [insbesondere zur Prädation von Propagulen (Diasporen)]. Die Untersuchungsflächen von Gazi und Galle schienen mehr gestört zu sein als diejenigen von Mida und Pambala. Das Studium dieser gestörten Gebiete identifizierte sowohl verschiedene Typen struktureller Veränderungen über die Zeit als auch die Existenz von Interaktionen zwischen Mangroven und terrestrischer Vegetation („sedges“ und Kokosplantagen). Parallele Untersuchungen an reifen, in der Entwicklung befindlichen und junge und juvenile Vegetationsschichten in Kombination mit der Analyse serieller Luftphotographien aus früherer Zeit ermöglichen das Verständnis dynamischer Prozesse und Vorhersagen zukünftiger Waldstruktur, und zwar unter verschiedenen Szenarien (keine Änderung, Mangroven-Holzeinschlag, natürliche Gefährdungen, etc.). Dieser Ansatz befähigt zu Entscheidungen wie etwa ob ein bestimmter Mangroven-Bestand das Potential zur natürlichen Erneuerung und Verjüngung besitzt, oder ob anthropogener Druck menschliches Eingreifen wie die 'imperative Restauration' erfordert. Im Rahmen von Aufforstungsprogrammen sind in Rehabilitations-Plots durchgeführte Studien zum Schicksals von Mangroven-Keimlingen essenziell. Während ein Monitoring von Mangroven-Regeneration Informationen zum generellen Status von Mangroven-Keimlingen liefert, hat insbesondere das Studium der Vermehrungsstadien gezeigt, dass Krabben und Gastropoden ein Problem für die erfolgreiche Regeneration von Mangroven in Kenya und Sri Lanka darstellen können. Die Resultate zeigen außerdem, dass Prädation an Vermehrungsstadien ein Bindeglied in einer Ereigniskette ist, die zu einer bestimmten Vegetationsstruktur (zoniert/unzoniert) führt, und wie dieser Prozess durch Hydrologie und anthropogenen Druck möglicherweise beeinflusst wird. Über die Identifizierung von Arten, Gebieten und Prozessen mit wahrscheinlich höherer Propagulen-Prädation werden direkte Informationen zu Fragen des Forstmanagements geliefert.

Ein weiterer Aspekt des Studiums der Mangroven-Regeneration ist mehr auf die Bedingungen der natürlichen Regeneration ausgerichtet, speziell in biogeographischen Grenzsituationen wie dem 'Parc National du Banc d'Arguin' (Weltnaturerbe in Mauretanien), in dem die Mangroven der Westafrikanischen Küste ihre nördlichste Verbreitungsgrenze erreichen. Aufgrund dieser biogeographisch marginalen Lage, monospezifische Mangal in einer Region in dem die Verfügbarkeit von Süßwasser über die letzten Jahrzehnte abgenommen hat, wurden Befürchtungen über das Überleben der Mangroven geäußert. Doch außer aufgrund unzureichender topographischer Bedingungen (Mangroven wachsen in terrestrischen Standorten mit wenig Möglichkeiten für das Überleben von Vermehrungsstadien) zeigten die Mangroven keine Anzeichen reduzierter Vitalität an ihrer biogeographischen Grenze, ja enthüllten sogar eine Diversität an Vegetations-Struktur-Typen (Hohe Bäume, ausladende Bäume, Buschformationen und Sebkha-Formationen).

Eine empirische Wieder-betrachtung der 'Point-Centred Quarter' Methode (PCQM) - durch Erfahrungen aus Freilandarbeiten gestützt -, erhellt die Probleme die mit dieser Methode verbunden sind, wie undefinierte Baum-architekturelle Gegebenheiten bei der Baumdurchmesser-Messung, Aggregation von Bäumen oder Über- und Unterschätzung von Dichte und Grundfläche. Das Ausmaß des letzteren Problems ist ganz offensichtlich beeinflusst durch die Vegetationsstruktur des Waldes.

Die letzte Veröffentlichung liefert einen integrativen Überblick über Mangroven-Struktur-Dynamik basierend sowohl auf der existierenden Literatur als auch auf frühere Fallstudien und gruppiert und definiert die verschiedenen Typen von Vegetations-Struktur-Dynamik.

# Muhtasari

Kitabu hiki cha shahada ya juu ya Ph.D kinajumlisha nakala kumi na nne za taarifa kuhusu mikoko. Kazi hii ni kilele cha utafiti wangu wa shahada hii iliyo chukua mfululizo wa miaka minne kukamilisha. Kwanza kabisa kuna utangulizi wa utafiti wenyewe. Utangulizi huu unadokezea madhumini ya utafiti kwa jumla, na umuhimu wake nchini Kenya na ulimwenguni. Kazi kubwa ya utafiti huu ilifanyika katika pulu za Mida na Gazi nchini Kenya. Kazi iliyosalia ilifanyika sehemu za Gale na Pambala nchini Sri Lanka, na pia huko nchini Mauritania katika mbuga ya wanyama iitwayo Aruguini.

Utafiti huu umetumia mbinu za kisasa kueleza mambo muhimu katika misitu ya mikoko. Kwa mfano, jambo la mkusanyiko wa mikoko katika pwani limegusiwa. Hii ni pamoja na kusahihisha kazi ya hapo awali kuhusu mikoko ya Sri Lanka. Kwa jumla uharibifu wa misitu uliweza kuoneka katika vituo vya Gazi (Kenya) na Gale (Sri Lanka). Kituo cha Mida (Kenya) pamoja na kile cha Pambala (Sri Lanka), vilioneka vikiwa katika hali nzuri.

Kazi hii inachangia kuonyesha sababu za uharibifu wa mikoko katika nchi hizi, ikiwa pamoja na ukataji mbaya, ukosefu wa mbegu na hali ya kiangazi. Kama mapendekezo wakati wa kupanda mikoko, mwandishi ashauri utafiti kabambe ufanywe kuhuzu upotevu wa mbegu za mikoko kwa njia mbali bali. Pamoja na ukosefu wa mbegu unaotokana na uharibifu wa misitu, kuna uwezekano kwamba mbegu nyini huliwa na wanyama kama vile Kaa pamoja kobe hivyo kuchangia kutonawiri kwa mikoko.

Katika kituo cha Mauritania, ni kiangazi hasa ambacho kimechangia kudidimia kwa mikoko sehemu ya mbuga ya Aruguini, pwani kaskazini mwa bara la Afrika. Jambo la wazi ni kwamba eneo hili la Aruguini ndio mpaka wa mikoko kaskazini magharibi mwa Afrika. Kunauwezekano kwamba, mabadiliko ya hewa pamoja na ukosefu wa maji baridi yameadhiri sana usitawishaji wa mikoko katika mbuga hii. Anavyo onyesha mwadishi ni kwamba, japo mikoko ina mea kwa shida kule Aruguini, mazao yake hayakuonekana kupunguka.

Kwa kumalizia, mwandishi amegusia katika taarifa ya mwisho mojawapo ya taratibu alizo tumia katika utafiti wake. Mwisho kabisa ameunganisha nakala zote kumi na nne akijaribu kujibu swala la jadi kuhusu kusanyiko la mikoko katika pwani. Je, kwanini Mlilana unaota kando kando ya bahari hali Mchu na Mkandaa inaota katika sehemu karibu na nchi kavu ?

# Summary in Sinhala

## සිංහල සාරාංශය

මෙම ආචාර්ය උපාධි නිබන්ධනය පොදු හැඳින්වීමකට පසුව එන පර්යේෂණ නිබන්ධන 14කින් ද අවසානයේ ඒ සියල්ල පිළිබඳව වූ සමාලෝචනයකින් ද යුක්තය. එම සමාලෝචනයට පර්යේෂණ එකිනෙක අතර ඇති සම්බන්ධතාවය ද ප්‍රතිඵල වල දේශීය හා සමස්ථ ව්‍යාවහාරිකත්වය ද. සංවර්ධන සහයෝගිතා/ රාමුව තුල එහි අදාලත්වය ද ඇතුලත්වේ. පර්යේෂණ කටයුතු වලින් වැඩි කොටසක් සිදු කරන ලද්දේ ගාල්ලේ උණවටුන සහ හලාවත පම්බල යන ශ්‍රී ලංකාවේ ස්ථාන දෙකෙහිත්, ගාසි බොක්ක (Gazi bay) සහ මිඩා ඔය (Mida Creek) යන කෙන්යාවේ ස්ථාන දෙකෙහිත්ය. බොහෝවිට වාද විවාද වලට තුඩු දුන් මාතෘකාවක් වූ ශ්‍රී ලංකාවේ (දකුණු හා බටහිර වෙරළේ) කඩොලාන වල ශාක සංයුතිය දක්වන ලද ලැයිස්තු සංශෝධනය කිරීමකින් අනතුරුව ශ්‍රී ලංකාවේ හා කෙන්යාවේ කඩොලාන වල ගුවන් ඡායාරූප හඳුනාගැනීම සඳහා වූ ගුණාංග සංශ්ලේෂණයකින් ද ඉන් පසුව කඩොලාන වෘක්ෂලතාදියේ ව්‍යුහය (කලාපයන ද ඇතුළුව) ශාක වල පුනර්ධනය හා පුනර්වර්ධන සීමාකාරකයන් (විශේෂයෙන් බීජවල විලෝපනය) ද විස්තර කරන්නා වූ ශ්‍රේණියක් ද මෙහි ඉදිරිපත් වී ඇත. ඒ අනුව මිඩා සහ පම්බලට සාපේක්ෂව ගාසි හා ගාල්ල කඩොලාන වඩාත් හානි වී ඇති බව පෙනේ. මෙම හානියට පත් වූ ස්ථාන අධ්‍යයනයෙන්, වෘක්ෂලතාදියෙහි විවිධ මට්ටමේ ව්‍යුහමය වෙනස්වීම් කාලයත් සමග සිදුවන බව මෙන්ම කඩොලාන හා සාමාන්‍ය ගොඩබිම වෘක්ෂලතාදිය අතර අන්තර් ක්‍රියා පවතින බවද පෙනී යයි. අතීතයේ අනුගාමී කාලවල ගැණුනු ගුවන් ඡායාරූප අධ්‍යයනය හා බද්ධව සිදු කෙරුණු පරිණත මධ්‍යම හා ළපටි යන වෘක්ෂලතාදි ස්ථරයන්ගේ සමාන්තර අධ්‍යයනයන් මගින් ගතික, ක්‍රියා අවබෝධ කර ගැනීමටත් (වෙනස් වීමක් නැති කඩොලාන, ගස් කැපීම, ස්වාභාවික ආපදා ආදී වූ) විවිධ තත්ත්වයනට මුහුණ දෙන්නාවූ කඩොලාන වනාන්තරයන්හි අනාගත ව්‍යුහය පෙරැයීමටත් හැකියාව ලැබේ. කිසියම් කඩොලාන පද්ධතියකට නැවත සාර්ථකව හානිපූරණ තත්ත්වයට පත්වීමට විභවීය හැකියාවක් තිබේ නම් හෝ ඒ සඳහා වූ මානව ක්‍රියා කාරකම් ඒ වෙත යෙදෙන්නේ නම් හෝ හානිපූරණයන් පිළිබඳ තීරණ ගැනීමට මෙම ප්‍රවේශය ඉවහල්වේ. කඩොලාන පද්ධති නැවත පුනරුත්ථාපනය කිරීමේ ක්‍රියාදාම රාමුව තුල එම පුනරුත්ථාපන ස්ථාන වල ඇති ළපටි කඩොලාන ශාකයන්හි ඉරණම අධ්‍යයනය අත්‍යවශ්‍ය වේ. කඩොලාන පුනර්වර්ධනයේ අඛණ්ඩ නිරීක්ෂණය මගින් ළපටි කඩොලානයන් ගේ සාමාන්‍ය තත්ත්වය පිළිබඳ තොරතුරු සැපයෙන අතර විශේෂයෙන් බීජ පැළ(Propagules) විලෝපනය අධ්‍යයනය මගින් ශ්‍රී ලංකාවේ සහ කෙන්යාවේ කඩොලාන වල සාර්ථක පුනර්වර්ධනය පිළිබඳ ගැටට ඇති කිරීමට කකුළුවන් හා ගැස්ට්‍රොපෝඩාවන් මුල් වන බව ද පෙන්වා දී ඇත. බීජ පැළ වල විලෝපනය කිසියම් වෘක්ෂලතාදී ව්‍යුහයක් (කලාපනය වූ හෝ නො වූ) තීරණය කරන ක්‍රියා දාමයක එක් පුරුකක් වන්නේ කෙසේද යන්නත් මානවජන්‍ය පීඩනයන් හා ජල විද්‍යාත්මක

සාධක ඒ කෙරේ බලපාන්නේ කෙසේද යන්නත් ප්‍රතිඵල මගින් පෙන්වා දෙයි. ලෝකයේ කඩොලාන ව්‍යාප්තියේ උතුරු සීමාන්තයක් සේ සැලකිය හැකි, ලෝක උරුමයක් වූ මොරිටේනියා වේ the Parc National du Banc d'Arguin ජාතික වනෝද්‍යානයේ පිහිටි බටහිර අප්‍රිකානු වෙරළේ කඩොලාන, ස්වාභාවික පුනර්වර්ධනය කෙරේ වඩාත් යොමු වූ කඩොලාන පුනර්වර්ධනයේ තවත් අංශයන් වේ. පසුගිය දශක කිහිපයක් තිස්සේ මිරිදිය සැපයුම සීමා කෙරුණු ප්‍රදේශ වල පිහිටි, ජෛව භූගෝලීය සීමාවන් ලෙස සැලකිය හැකි ඒක විශේෂ කඩොලානයක් සේ එය සැලකිල්ලට ගෙන කඩොලානයන් ගේ නො නැසී පැවැත්ම පිළිබඳ අවශ්‍යතාවය විස්තර කර ඇත. කෙසේ වුව ද නුසුදුසු භූවිෂමතා තත්ත්වයන් (ප්‍රචාරක බීජ පැල නො නැසී පැවතීමට ඇති ඉඩ කඩ ඉතා අඩු භෞතික වාසස්ථාන) යටතේ දී හැර, කඩොලාන ඒවායේ ජෛව භූගෝලීය සීමාවන්හිදී ක්ෂීණ වූ ජීව බලයන් පෙන්වූයේ නැත. එපමණක් නො ව ඒවා (උස ගස්, පලල් ගස්, පඳුරු නිර්මාණයන් සහ 'Sebkha' නිර්මාණයන්ද ආදී වශයෙන් වූ) වෘක්ෂලතාදී ව්‍යුහ විවිධත්වයන් ද පෙන්වයි. ක්ෂෙත්‍ර කටයුතු වල පළපුරුද්ද විසින් පොළඹවනු ලදුව Point-Centred Quarter Method (PCQM) ක්‍රමයේ ව්‍යවහාරික සංශෝධනයක් භාවිත කිරීමෙන් එම ක්‍රමය හා බැඳුණු ගැටළු විසඳා ගැනීමට හැකි විය. ශාකයේ විෂ්කම්භය මැනීම කෙරෙහි බලපාන නො පැහැදිලි ශාක සැකසුම්, වෘක්ෂ ගොනුවීම්, ඝනත්වය හෝ පාදීය වර්ග ඵලය පිළිබඳ අධි තක්සේරු හෝ අව තක්සේරු වීම් ආදී මෙකී අධි හෝ අව තක්සෙරු වීම් කෙරේ හේතුවන සාධක කෙරෙහි වනාන්තරයේ වෘක්ෂලතාදී ව්‍යුහය බලපාන බව පෙනී යයි.

අවසාන නිබන්ධනය කඩොලාන වෘක්ෂලතාදී ව්‍යුහයේ ගතිකය පිළිබඳ දැනට පවතින තොරතුරු මෙන්ම පසුගිය අධ්‍යයනයන් හා සාරාංශකරයන් මත පදනම් වූ සමාලෝචනයන් ද සපයන අතරම විවිධ ආකාරයේ වෘක්ෂලතාදී ව්‍යුහ ගතිකයන් ද නිර්වචනය කරයි.

# Summary in Tamil

ஆங்கில சாரம்சத்தின் தமிழ் மொழிபெயர்ப்பு

பிரதான பதினான்கு பகுதிகளைக் கொண்டுள்ள இந்த கலாநிதி (PhD) பட்டத்திற்கான வெளியீடு ஓர் பொதுவான அறிமுகத்தினையும் அதனைத் தொடர்ந்து முழுதான ஆராய்ச்சிக் கட்டமைப்பையும் இறுதியாக முடிவுரையையும் உள்ளடக்கியுள்ளது. இவ் ஆராய்ச்சிக் கட்டமைப்புப் பகுதியானது வேறுபட்ட ஆராய்ச்சிக் கட்டமைப்புகளுக்கான தொடர்பினையும், ஆராய்ச்சியின் பயனாக பெறப்பட்ட தகவல்களின் சாத்தியமான உபயோகத்தினை உள்ளுர் ரீதியாகவும், புவியல் ரீதியாகவும் கூறப்பட்டுள்ளதுடன் இந்த ஆராய்ச்சியின் தொடர்பமைப்பு அபிவிருத்தி முயற்சியில் எவ்வாறு பங்களிப்பு செய்யும் என்பதையும் விளக்கியுள்ளது. இவ்வாறு பெறப்பட்ட தகவல்கள் பிரதானமாக நான்கு பிரதேசங்களில் மேற்கொள்ளப்பட்ட ஆராய்ச்சி மூலம் பெறப்பட்டவையாகும். அவை கென்னியாவில் ( Kenya ) உள்ள இரண்டு இடங்களான காசிவிரிகுடா ( Gazi Bay ), மிடா ஆற்றுக்கால் ( Mida Creek ) என்பனவும் இலங்கையிலுள்ள இரு இடங்களான காலியிலுள்ள உனவருன, சிலாபத்திலுள்ள பம்பல எனும் இடங்களுமாகும்.

கண்டல் தாவர சாகியத்தின் கட்டமைப்பும், ஆக்கக்கூறுகளும் சாதாரண தாவரச்சாகியத்தினை விட முரணான ஒன்றாகும். இத்தகைய தகவல்கள் வானிலிருந்து எடுக்கப்பட்ட புகைப்படங்களின் இயல்புகளை ஆராய்தலின் மூலம் பெறப்பட்டவையாகும். இதனை ஆராய்வதற்கு தொடர்ச்சியான ஆராய்ச்சித் தகவல்கள் / கற்கைகள் வெளியிடப்பட்டுள்ளன. இவை கண்டல் தாவர சாகியத்தின் கட்டமைப்பு இயக்கவியலையும், அவற்றின் (மீள்) உற்பத்தியாக்கலையும், உற்பத்திக்குரிய தடங்கல்களையும் (பிரதானமாக இனப்பெருக்க அலகுகளின் அழிவுகள்) உள்ளடக்கியுள்ளன. காசி ( Gazi ), காலி ( Galle ) ஆகிய இரு கண்டல் தாவரசாகிய கற்கை இடங்கள், மிடா ( Mida ) பம்பல ( Pambala ) ஆகிய இரு கற்கை இடங்களை விட கூடுதலான அளவில், சாதாரண சூழற்சாகியத்தை விட குழப்புநிலைக்குத் தள்ளப்பட்டுள்ளதாக காணப்படுகின்றது. காலப்போக்கில் ஏற்பட்ட வேறுபட்ட தாவரக் கட்டமைப்பு மாறுதல்களையும் அதேவேளையில் கண்டல்தாவர தொகுதிக்கும், அதனைச் சார்ந்த புல், தென்னை போன்ற நில வாழ் தாவர சாகியத்திற்கும் இடையேயான தொடர்பினையும் குழப்ப நிலைக்குள்ளாக்கியுள்ளன. ஆரம்ப கால கட்டங்களிலிருந்து தொடர்ச்சியாக பெறப்பட்ட வானிலிருந்து எடுக்கப்பட்ட புகைப்படங்களினதும், முதிர்ந்த, இளம் தாவரப் படைகளினது ஆராய்தலும் கண்டல் தாவர சாகியத்தின் இயக்கவியலுக்குரிய நிகழ்வுகளையும் எதிர்காலத்தில் இத்தாவரச் சாகியக்கட்டமைப்புகளின் ஒழுங்கமைப்பினையும் எதிர்வு கூறக் கூடிய ஓர் நிலைக்கு வழிவகுக்கும். புகைப்பட ஆய்வானது மாற்றமின்மை, கண்டல்தாவரம் வெட்டப்படுதல், இயற்கை அழிவு போன்றவற்றால் நிபந்தனைக் குட்பட்ட எதிர்கால நிலைமையை கூறும் இந்த எதிர்வு கூறலானது, கண்டல்தாவரத்தின் இயற்கை அழிவுகளையும், மனித தலையீடுகளையும்கூட எதிர்வுகூற உதவும். இவ்வகையான ஓர் அண்மித்த தகவல் சேகரிப்பு / ஆராய்ச்சி, கண்டல் தாவரசாகியத்தின் கட்டமைப்பலகின் வெற்றிகரமான மீள் உற்பத்தியையும், ஓர் இளமையான கட்டமைப்பாக மாறுவதற்குரிய நிலைமையினையும் கொண்டு வருதலுக்குரிய அழுத்தமான ஓர் தீர்மானத்தை எடுப்பதற்கு வழிவகுக்கும். ஆகவே கண்டல் தாவர மீள் உற்பத்தி / மீள் நடுகைக்குரிய திட்டமிடல் நிகழ்வுகள் பற்றிய நியமமான

கற்கைநெறி மிக அத்தியாவசியமான தொன்றாகும். அதே நேரத்தில் இத்தாவர சாகியத்தின் மீள் சீரபடுத்தலின் / மீள் உற்பத்தி பற்றிய கண்காணிப்பு மூலம் இளம் கண்டல் தாவரங்களின் பொதுவான நிலைப்பாடும் இனவிருத்தியலகுகளின் அழிவுக்குரிய காரணங்களும், கென்யா,சிறிலங்கா போன்ற நாடுகளில், பிரதானமாக நண்டுகள், தசைமூலம் நகர்வன (Gastropods) போன்றவற்றின் பங்களிப்பால் ஏற்பட்டதாக அமையலாம். இனப்பெருக்கவலகுகளின் அழிவுகள் / கவரப்படுகை எவ்வாறு ஓர் குறிப்பிட்ட தாவரக் கட்டமைப்பில் செல்வாக்கு செலுத்துகின்றன என்பதைப் பற்றியும், ( அதாவது சூழற் தொகுதியின் தொடர்ச்சியான சங்கிலி நிகழ்வுகளை எவ்வாறு பாதிக்கும் என்பதையும் ) அதேவேளை நீரியற் காரணங்களும், மானிட ஆய்வு ( Anthropogenic ) அழுத்தங்களும் எவ்வாறு இனப்பெருக்கவலகுகளின் அழிவில் செல்வாக்கு செலுத்துகின்றன என்பதனையும் முடிவுகள் எடுத்துக் காட்டியுள்ளன. இவற்றிலிருந்து பெறப்பட்ட முடிவுகள் காடுகளின் பேண்தகு முறையினைப் பற்றிய நேரடித்தகவல்களை வெளிக்காட்டியுள்ளன. அவை, இனங்களையும், வெற்றிகரமாக தங்களை நிலை நிறுத்திக் கொள்ளக்கூடிய நிலப்பரப்புகளையும் அதேவேளை இனப்பெருக்கவலகுகளின் விரைவான அழிதல் வீதத்தினையும் பற்றியவையாகும்.

கண்டல் தாவரங்களின் மீள் உற்பத்தி இயற்கை சூழல் நிலையில் முன்னெடுத்துச் செல்லப்படுகின்றது என்பது இன்னுமோர் அவதானிப்பு நிலையாகும். இது குறிப்பாக உயிரினப் புவியியலுக்குரிய சில இடங்களில் வரையறுக்கப்பட்டுள்ளது. உதாரணமாக ( Parc National du Banc d’Arguin- Mauritania), மொறிரானியாவிலுள்ள “டு பான்க் டி ஆர்குயின்” தேசிய பூங்கா, தாவரங்களில் பரம்பரைச் சொத்துப் பூமியாகும். இது மேற்கு ஆபிரிக்காவின் கரையோரப் பகுதியில் பரம்பியுள்ளது. தாவரவியல், புவியியல் ரீதியாக சிரமநிலைக்குத் தள்ளப்பட்டுள்ளதாலும் பல இடங்களில் கடந்த பல தசாப்தங்களாக நன்னீர் கிடைப்பது அருகி வருவதாலும் கண்டல் தாவரங்களின் நிலைபான இருப்பு சார்பாக கரிசனைகள் எழுந்துள்ளன. எனினும் சில சாதகமற்ற புவியியல் சூழ்நிலையில், மிகச் சொற்ப அளவிலான மீள் உற்பத்தி வசதிகளுடன் வளரும் கண்டல்தாவரங்களை விட ஏனையவை இனப்பெருக்கமடையும் தன்மையில் தனக்கு உரிய உயிரினப்புவியியலுக்கான எல்லையிலுள் எவ்வகையான வீழ்ச்சிகளையும் காண்பிக்கவில்லை. இவை பல்லினமான தாவரக்கட்டமைப்புக்களான உயர்வான மரங்கள், பருமனான மரங்கள், பற்றைபோல் வளர்தல் ஆகியவற்றுடன் “செப்கா” (Sebkha) வகையில் உண்டாகுதல் என்பவற்றை வெளிக்காட்டுகின்றன. களவேலை அனுபவங்களைக் கொண்டு “புள்ளி மையப்பட்ட கால் முறைமை” ( Point – Centered Quarter Method PCQM ) அனுகலில் ஏற்படும் பிரச்சனைகளான மரவிட்டத்தை அளவிடுதல், மரத் தொகை, மர அடிப்பகுதியின் அடர்த்தி சார்பான தவறான அனுமானம் ஆகியவற்றைத் தீர்க்கலாம். காடுகளின் தாவரவியல் கட்டமைப்பு அடர்த்தியில் செல்வாக்கு செலுத்துகின்றது.

இறுதியாக வெளியிடப்பட்டுள்ள ஆக்கம், தற்போது உபயோகத்திலுள்ள கண்டல் தாவரங்களின் இயக்கவியல், கட்டமைப்புக்குரிய தகவல்களை ஒருங்கிணைத்தும், இதற்கு முன் பெறப்பட்ட தகவல்களின் அடிப்படையிலும் ஒழுங்கமைக்கப்பட்டுள்ளதுடன், பலதரப்பட்ட தாவர வர்க்கங்களின் இயக்கவியலுக்குரிய கட்டமைப்புகளையும் வரையறுத்துள்ளது.

# Chapter I.

# General Introduction.

# GENERAL INTRODUCTION

Mangroves as a formation with their typical features have been reviewed extensively (Field, 1995, 2000; Stafford-Deitsch, 1996; Spalding *et al.*, 1997; Dahdouh-Guebas & Koedam, 2001; Dahdouh-Guebas *et al.*, 2001). In this introduction only a selected number of highlights of the mangrove ecosystem, which are important in the framework of the present study, will be given, followed by some of the threats faced by mangrove forests. Then, the objectives of the present study are formulated and shown as a scheme representing the separate units of this work. These separate units or case-studies are then extended one by one, each comprising its own introduction, objectives, study sites and methodology, all of which are specific to the respective case-study. The general discussion and epilogue link all of the case-studies, highlight the applicability of aspects of the study and suggest tracks of application in the framework of development-cooperation.

## MANGROVE ECOSYSTEMS

Mangrove forests, which are thriving in the intertidal zones of tropical countries flanking the equator on all continents, are ecotones between the marine and the terrestrial environment. Because of this particular location at the edge of both land and sea, much of the fauna and flora in the mangrove consists of specialized species. The mangrove ecosystem has a high primary production and locally (*e.g.* within a lagoon) supports an increased secondary and detrivorous production. Together with members of the Protista and Cyanobacteria, mangroves support virtually the entire primary production. Plant litter forms an important part of nutrients and energy necessary for breakdown by macrobenthos and micro-organisms in mangrove lagoons. The plant material is first transformed into particulate organic material by macro-invertebrates such as crabs and other macrobenthos, and is then enzymatically reduced to dissolved organic material. The full trophic dependence of the secondary producers and higher level organisms on the production of the mangrove, or alternatively, the prime contribution to food sources of the mangrove within the coastal ecosystems, is almost a paradigm. The issue of outwelling of mangrove material is increasingly revisited and some studies find outwelling is not always the case (Hemminga *et al.*, 1994; Marguillier *et al.*, 1997; Bouillon & Dehairs, in press; Bouillon *et al.*, in press, subm.a, subm.b) and sometimes even the opposite 'inwelling' may be true, *i.e.* the deposition of estuarine material in mangrove sediments (Bouillon *et al.*, submitted).

Mangroves also have a high rate of recycling within the ecosystem. In addition, the high productivity of the mangrove forest is supported by an increased supply of nutrients and by an availability of a large diversity in niches that are suited for the breeding, spawning, hatching and nursing of both sedentary and migratory marine species (*e.g.* Macintosh, 1988; Baran & Hambrey, 1998; Baran, 1999; Rönnbäck *et al.*, 1999; Blaber *et al.*, 2000; Nagelkerken *et al.*, 2000; Naylor *et al.*, 2000). Together with its importance with respect to the productivity of the mangrove trees themselves such as for wood (*e.g.* Dahdouh-Guebas *et al.*, 2000b; Chapter II), tannins or medicines (*e.g.* Premanathan *et al.*, 1999) at a local or global level, this can explain the economic importance of this ecosystem. However, despite the invaluable role played by the mangrove, this ecosystem has become very threatened. Rönnbäck (1999) states that the *undervaluation is partly due to the difficulty involved in placing a monetary value on all relevant factors, but lack of ecological knowledge and a holistic approach among those performing the evaluation may be even more important determinants.*

Mangrove trees have developed a number of morphological and physiological adaptations that make them very suited for the intertidal habitat. The most obvious feature is the development of aerial roots, under the form of pencil roots (*e.g. Avicennia*), peg roots (*e.g. Sonneratia*), knee roots (*e.g. Bruguiera*), plank roots (*e.g. Xylocarpus*) or prop roots (*e.g. Rhizophora*), associated with gas exchange. The fruits or propagules of many mangrove trees are viviparous, which means that a young individual starts growing leaves and a root while still attached to the parental tree, another morphological adaptation. Considering that the mangrove soil is relatively muddy, this means that when dropping at low tide, these propagules establish by the planting strategy (Van Speybroeck, 1992), whereby they actually plant themselves under the parental tree. During high tide on the other hand the propagule drops in the water and is transported by it (unless entangled), after which it strands elsewhere (stranding strategy of Van Speybroeck, 1992). This is an important factor when considering the spatio-temporal changes in stand structure and composition or 'vegetation structure dynamics' of the mangrove, as in the present study. The physiological adaptation necessary to cope with the salt water from the ocean is a mechanism to exclude salt (*e.g. Bruguiera, Lumnitzera, Rhizophora, Sonneratia*) or to secrete it (*e.g. Avicennia*) (Tomlinson, 1986). For a long time it was however a paradigm that mangroves need salt for their survival : they are facultative halophytes that can perfectly well thrive in freshwater, but they are often out competed by terrestrial vegetation under these conditions and are forced into habitats where the conditions are too harsh for terrestrial or freshwater plants (*i.e.* where the salinity is too high).

### MANGROVE SERVICES AND MANGROVE THREATS

People increasingly realise the important position that mangrove forests occupy along tropical and subtropical coasts. Apart from the above mentioned functions and services the benefits are emphasised, merely when negative consequences related to mangrove destruction become evident in a short time frame. One of the best examples is the function of mangroves as 'living dykes' preventing coastal erosion, a function which is unfortunately often neglected until the first intense storm after mangrove deforestation (Pearce, 1996, 1999). Removal of mangroves over the last few decades has dislocated the sedimentation of suspended matter supplied by rivers, which normally occurs within the mangrove, to the immediate surroundings of seagrass beds and coral reefs, which are often closely associated with the mangrove, but that will be adversely affected by such sedimentation processes.

The enormous ecological, social and economic importance of the mangrove (Clough, 1993; Pernetta, 1993a,b,c,d,e,f; Lefebvre & Poulin, 2000, United Nations University, 2000) as well as the ecological importance (biodiversity) of the coral reef demands that the mangrove ecosystem be managed in a sustainable way. Therefore regeneration programmes are playing an increasingly important role. The latter goes hand in hand with scientific research on the distribution strategies (Rabinowitz, 1978a,b; Van Speybroeck, 1992; Clarke & Myerscough, 1993; McGuinness, 1997a) and the restoration of mangroves (Teas, 1977; Lewis, 1982,1999; Field, 1996, 1998a, 1998b, 1999, 2000; Turner & Lewis, 1997; Lewis *et al.*, 1999; Stevenson *et al.*, 1999; Ellison, 2000; Erftemeijer & Lewis III, 2000; Lewis III, 2000; McKee & Faulkner, 2000). However, since mangrove management beyond the scale of community-based management types was non existent until the recent past, the scientific documentation of the evolution and the use of mangroves are very restricted. Besides a wider biogeographical analysis (universality of conclusions within a certain type of study) also a temporal analysis (historic evolution of the mangrove in a certain site) is required.

The possibilities and constraints of both natural and artificial mangrove regeneration hold a central position in mangrove research. Next to various physico-chemical factors required to allow the development of mangrove juveniles, the juveniles are supposed to establish in a certain area in the first place. This is often countered by propagule predation (Smith, 1987; Smith *et al.*, 1989; Osborne & Smith, 1990; McKee, 1995a; McGuinness, 1997b). The influence of the adult mangrove vegetation on the young and juvenile individuals has generally little been studied although it might generate relevant information for the evaluation of existing natural mangrove forests, particularly those under increasing anthropogenic pressure. At the same time it largely contributes to setup, protection and management of plantations in the framework of mangrove regeneration (*e.g.* Lee *et al.*, 1996). The role of propagule predation is important in all cases.

## OBJECTIVES AND LAYOUT

Human interference in mangrove areas has caused substantial changes in both physiognomy and species composition, and world-wide this ecosystem is subjected to an increasing anthropogenic stress. Nevertheless the ecological and derived socio-economical importance of mangroves was clearly established. A will to protect and manage the mangrove forests for their ecological services, as wildlife sanctuaries or for sustainable exploitation can be clearly discerned. This is however not matched by our understanding of factors governing their establishment, dynamics and regeneration, which impedes rational management plans.

The present research deals with the investigation of the regeneration potential of mangroves, and it is based on the study of the spatio-temporal vegetation structure of adult, young and juvenile mangrove individuals. It includes aspects of natural regenerative constraints.

The working hypothesis adopted states that young and juvenile trees predict future adult trees and indicate temporal and spatial dynamics. Since this hypothesis can only be tested on a decadal time scale (in the future), explorative and descriptive approaches have been used to understand their dynamics and to pinpoint a number of its causes.

### Research framework

The research framework in which the present PhD study fits, includes different researches, each of which constitutes a piece of the entire puzzle (Fig. 1). Underneath a general overview of this research framework will be given, followed by the specific questions (alternatively read : hypotheses) addressed in this PhD study (numbers refer to the research framework in figure 1).

This study starts with the mapping of the present vegetation structure through airborne remote sensing ⓿. Fieldwork in which we assess the horizontal and vertical distribution of adult, young and juvenile trees completes the analysis of the vegetation structure at present ❶. Retrospective investigation of the same area is done through sequential aerial photography from the past ❷. These three first steps constitute the basis of the present PhD research. The juvenile vegetation layer is subjected to regenerative constraints, amongst which propagule predation is investigated in-depth ❸. In combination with the evolution in the recent past of the mangrove and the present distribution of adult trees, both the young and the juvenile vegetation layer can be used to make a prediction for the future, which can be either positive or negative with respect to the extent or composition of the mangrove ❹. In case of a positive prediction we may still be interested in the assessment of the natural regeneration potential and make a comparative study between mangrove forests with various degrees of disturbance ❺. This is part of the research framework is only in part covered here and is predominantly investigated by Kairo (in prep.). In case of a negative prediction artificial regeneration and restoration may be necessary ❻. Two questions must be addressed then : first, which forest areas need rehabilitation, and second, which tree species are going to be used to rehabilitate those areas ? ❼ The study on propagule predation contributes to the answer on both questions. The steps introduced so far are part of the present research on mangrove vegetation structure dynamics and regeneration (footnote on original title : Dynamics and regeneration potential of mangroves : horizontal vegetation structure analysis of juvenile and adult individuals and research into regenerative constraints). The links with other research frameworks is given in grey in figure 1. The study of the genetic differentiation in the adult trees of various mangrove populations in part provides elements to answer the question of desirability of propagules from other populations for restoration (Abeysinghe, 1999) ❽. The investigation of hydrology in general or as a regenerative constraint in particular provides information to the rehabilitation of mangroves (Verheyden, in prep.) ❾. The questions that have often been forgotten by mangrove researchers and for which I designed a separate framework (carried out by Bosire, 1999, in prep.) are "What happens with the artificial regeneration plots 10 years from now ?", "How functional (*sensu oecologiae*) do these plantations become ?" and "Is there faunal and floral recruitment into the often monospecific plots ?". Therefore we compare the artificial forest with a natural mangrove and a naked area and investigate the environmental factors, the floristic succession and the faunistic recruitment ❿.

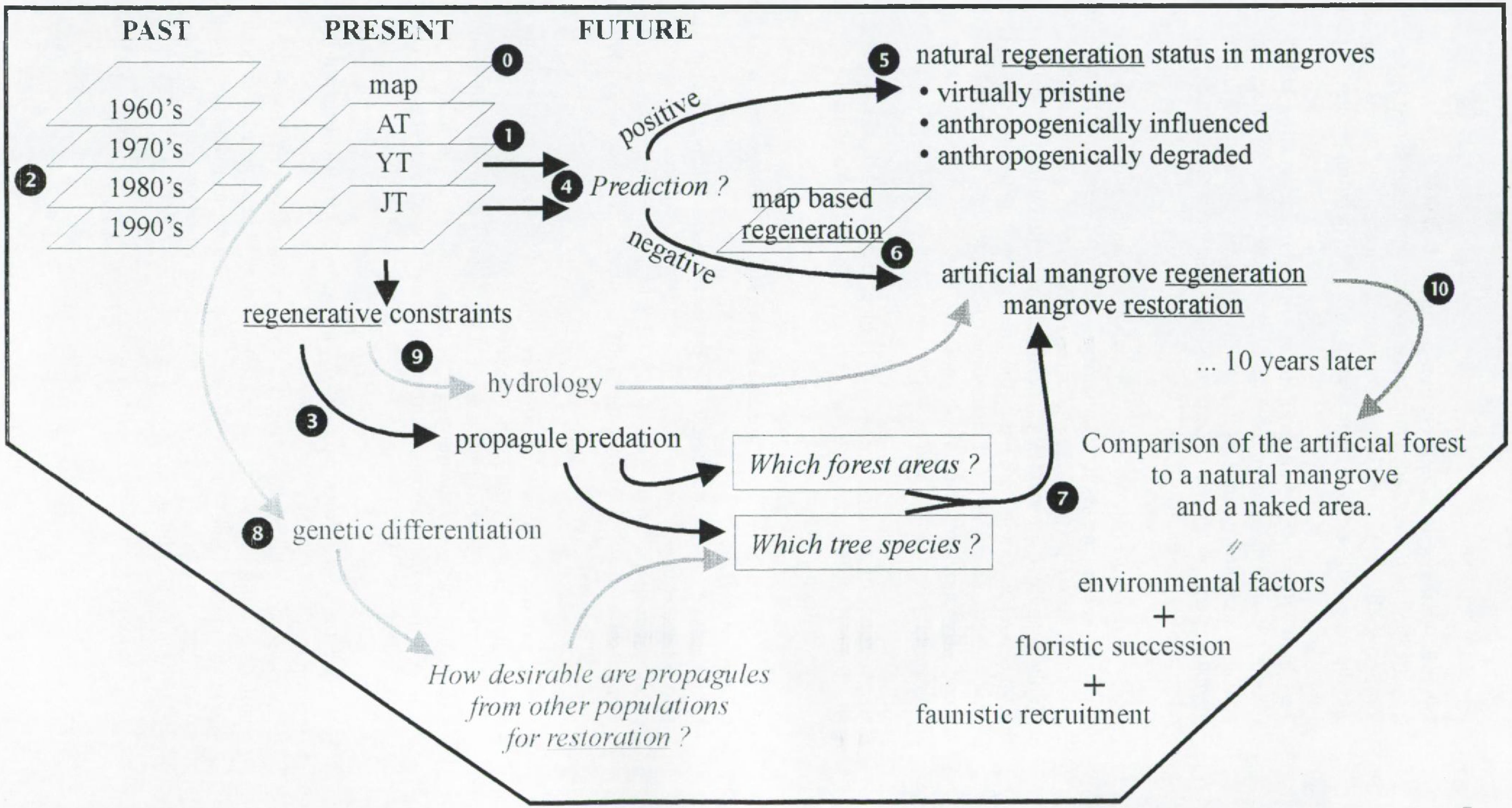
Central for the future in the restoration of mangroves is the possibility of executing a map-based regeneration programme that integrates the results of the different studies.

Concentrating on the present research, we can separate the objectives in two series. In a first series of objectives the research addresses the following questions for two study areas in both Kenya (Gazi Bay and Mida Creek) and Sri Lanka (Unawatuna-Galle and Pambala-Chilaw) :

- **What is the spatial vegetation structure of the mangroves ⓿❶ ?**
  Answering this question gives a basic description of the study areas in terms of physiognomy and floristic composition on a spatial scale. Using phytosociological approaches, completed with various measurements such as tree diameter, a fairly accurate description of the mangrove is generated. This is done for adult, young and juvenile individuals in several parallel respectively orthogonal transects. Through the use of geographic information systems (GIS) the vegetation structure is clearly visualised, and transect data are overlayed. Combining the qualitative GIS-output with correlation analysis and the use of ordination methods such as Detrended Correspondence Analysis (DCA) and Canonical Correspondence Analysis (CCA), the link between the adult, the young and the juvenile vegetation structure may be recognized. (CHAPTER VI, VII, VIII).

- **How has the mangrove area evolved ❷ ?**
  Sequential aerial photography, once more through use of GIS technology, yields information on the disturbance of the study areas in the first place. One of the objectives is to compare the vegetation structure and its dynamics in an undisturbed and in a disturbed mangrove forest. (CHAPTER VI, VII).

**Figure 1.** Example of the research framework in Kenya and Sri Lanka involving vegetation structure and its dynamics, natural and artificial regeneration incl. issues of regenerative constraints, conservation genetics, restoration and monitoring (see text).



- **What is the mangrove regeneration potential ❶❹❺❻ ?**
  Investigation of the juvenile abundance both on the parental tree and on the mangrove floor, for instance by monitoring juvenile rooting, produces insight in the reproductive phenology and the successful establishment, hence in the regeneration potential. (CHAPTER VIII, XII).

- **To which extent propagule predators constrain regeneration ❸❼ ?**
  Counts of burrows and/or individuals of propagule predators outlines the distribution of the predators and allows comparison with the different vegetation structures. Through plantations and preference experiments the predation intensity is examined as one of the regenerative constraints. (CHAPTER IX, X, XI).

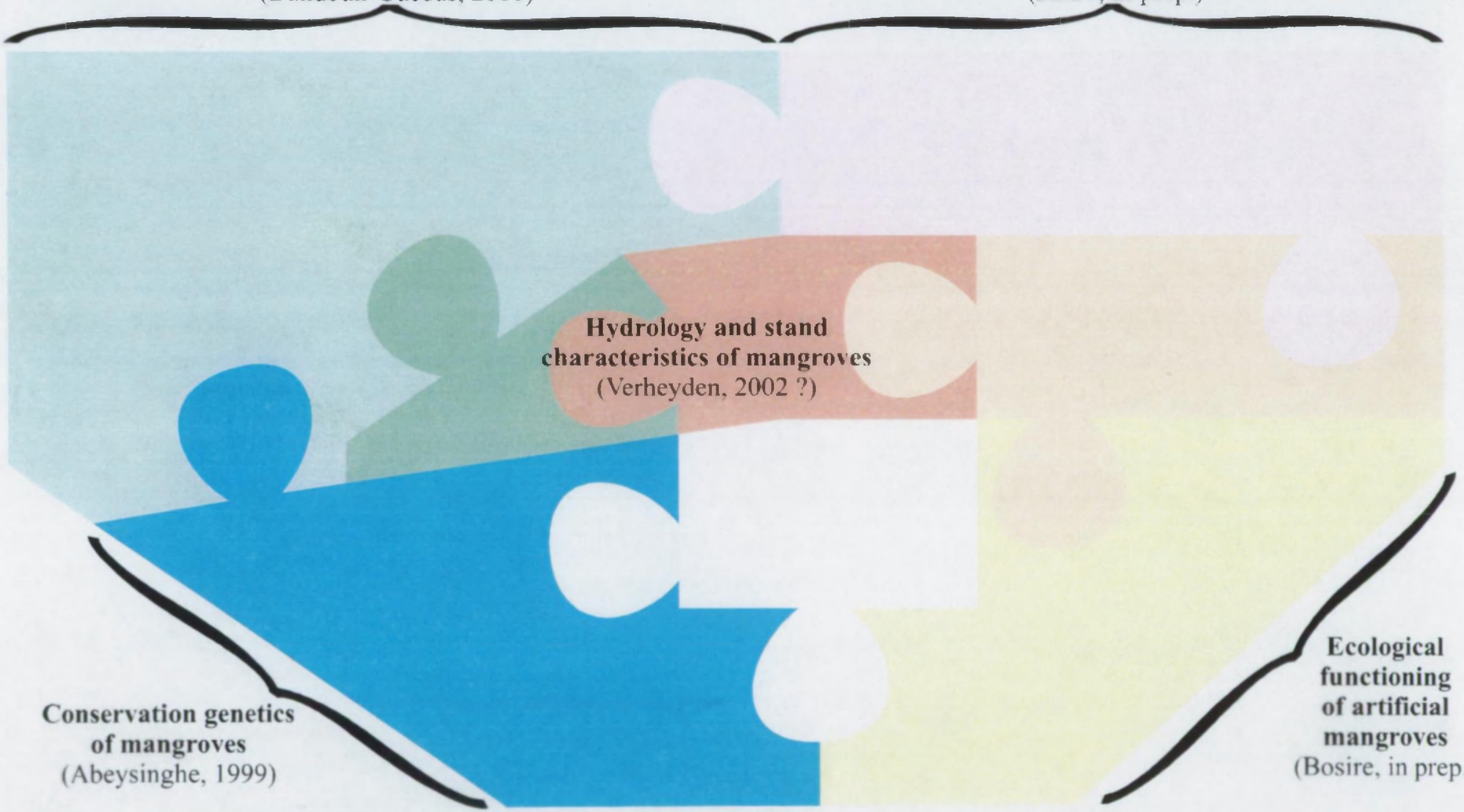
This research outline has the overall objective to purvey an approach to assess the mangrove ecosystem in its regeneration potential in a reliable way, and conclude whether human interference through artificial regeneration is necessary to guarantee the survival of a particular mangrove forest. The study of mangrove juvenile predators, as they often constitute a regeneration problem, is therefore inherent to this research. The realisation of this overall objective requires a full integration of the questions addressed above, which subsequently require intensive field work in an area relevant in general to the understanding of human interference in mangroves and specifically to the research objectives of this thesis.

A <u>second series of objectives</u> deals with subject areas that originated during the research tasks of the first series of objectives, either as interesting additional cases or as problem-solving for complex situations encountered :

- **What is the floral composition and distribution of mangroves in Sri Lanka ? (in support of ⓪❶❷)**
  Doubt arose as to which species were present in the Sri Lankan lagoons in which the above research was carried out, as well as in neighbouring lagoons, and at the same time publications of mangrove species lists for Sri Lanka reported data conflicting with the field reality. An in-depth field inventory for the South-West coast was executed for that purpose. (CHAPTER III).

- **Which are the features that can be recognised from airborne remote sensing imagery of mangrove areas ? (in support of ⓪❷)**
  In the framework of the identification of mangroves on aerial photographs, the question arose as to whether a 'compromise interpretation key' could be made, a key that resulted from a compromise in image attributes at species or genus level over the various study sites. (CHAPTER IV, V).

- **What is the vegetation structure of a mangrove at its biogeographical limit (comparative to ⓪❶) ?**
  Having seen the diversity in vegetation structures in countries located centrally (from a latitudinal point of view) in the distribution range, the vegetation structure at a biogeographical limit was questioned. A preliminary analysis of the northernmost mangrove vegetation of the West-African coast was done (Parc National du Banc d'Arguin, Mauritania). (CHAPTER XIII).



**Mangrove vegetation structure dynamics and regeneration**
(Dahdouh-Guebas, 2001)

**Mangrove regeneration ecology and restoration**
(Kairo, in prep.)

**Hydrology and stand characteristics of mangroves**
(Verheyden, 2002 ?)

**Conservation genetics of mangroves**
(Abeysinghe, 1999)

**Ecological functioning of artificial mangroves**
(Bosire, in prep.)

- **Which are the problems associated to the use of the Point-Centred Quarter Method (PCQM) for the study of mangrove vegetation (in support of future research on ❶❺❾❿) ?**
  Because of field experience the estimates of the tree density and basal area of mangrove vegetation using the established PCQ-Method were revisited and a number of problems to be solved where highlighted. (CHAPTER XIV).

The results of all the above objectives have been valorised as manuscripts engaged in a peer-review process, and are presented in the present dissertation in a logical sequence together with additional annexed material. It includes an introductory block, a case-study block and a recapitulate block as well as annexed material (numbers again refer to the research framework) :

## INTRODUCTORY BLOCK

**CHAPTER I :** General Introduction
**CHAPTER II :** Utilization of mangrove word products around Mida Creek (Kenya) amongst subsistence and commercial users.

## CASE-STUDIES

**CHAPTER III :** A revision of the floral composition and distribution of mangroves in Sri Lanka (⓿❶❷).
**CHAPTER IV :** High resolution vegetation data for mangrove research as obtained from aerial photography (⓿❷).
**CHAPTER V :** A note on the identification of mangroves from aerial photography in Kenya and Sri Lanka (⓿❷).
**CHAPTER VI :** Four decade vegetation dynamics in Sri Lankan mangroves as detected from sequential aerial photography : a case study in Galle (⓿❶❷).
**CHAPTER VII :** Two decade vegetation dynamics in Kenyan mangroves as detected from sequential aerial photography : a case study in Gazi Bay (⓿❶❷).
**CHAPTER VIII :** An ordination study to view past, present and future vegetation structure dynamics in disturbed and undisturbed mangroves forests in Kenya and Sri Lanka (⓿❶❷❹❺❻).
**APPENDIX I :** Field keys for Kenyan Mangrove Crabs (❸).
**CHAPTER IX :** An explorative study on grapsid crab zonation in mangrove forests in Kenya (❸).
**CHAPTER X :** Propagule predators in Kenyan mangroves and their possible effect on regeneration (❸❼).
**CHAPTER XI :** Propagule predation in Sri Lankan mangroves and its effect on vegetation structure (❸❼).
**CHAPTER XII :** Regeneration status of mangroves under natural and nursery conditions in Galle and Pambala, Sri Lanka (❺❻).
**CHAPTER XIII :** Are the northernmost mangroves of West Africa viable ? - a case study in the Parc National du Banc d'Arguin, Mauritania - (comparative to ❶❷)
**CHAPTER XIV :** Problems and possible solutions to the use of the Point-Centred Quarter Method (PCQM) in mangrove forests (in support of future research on ❶❺❾❿).

## RECAPITULATE BLOCK

**CHAPTER XV :** General discussion
**EPILOGUE**

# Chapter II.

# Utilization of mangrove wood products around Mida Creek (Kenya) amongst subsistence and commercial users.

Dahdouh-Guebas, F., C. Mathenge, J.G. Kairo & N. Koedam

In press

*Economic Botany* 54(4).

Please note that the version of this article consists of original galley proofs
whereas the published article will integrate some necessary updates and corrections.

# Utilization of Mangrove Wood Products around Mida Creek (Kenya) Amongst Subsistence and Commercial Users[1]

F Dahdouh-Guebas, C. Mathenge, J. G. Kairo, and N. Koedam

---

**Dahdouh-Guebas, F.** (*Laboratory of General Botany and Nature Management, Mangrove Management Group, Vrije Universiteit Brussel, Pleinlaan 2, B-1050 Brussel, Belgium*), **C. Mathenge** (*Laboratory of General Botany and Nature Management, Mangrove Management Group, Vrije Universiteit Brussel, Pleinlaan 2, B-1050 Brussel, Belgium*), **J. G. Kairo** (*Kenya Marine and Fisheries Research Institute, PO Box 81651, Mombasa, Kenya and Laboratory of General Botany and Nature Management, Mangrove Management Group, Vrije Universiteit Brussel, Pleinlaan 2, B-1050 Brussel, Belgium*), and **N. Koedam** (*Laboratory of General Botany and Nature Management, Mangrove Management Group, Vrije Universiteit Brussel, Pleinlaan 2, B-1050 Brussel, Belgium*). Utilization of Mangrove Wood Products around Mida Creek (Kenya) Amongst Subsistence and Commercial Users. *Economic Botany 54(4):508–522, 2000. Mida Creek (Kenya) comprises mangrove forests and other marine resources that are of economic, ecological, and environmental importance to the local village communities. In total 116 households (100 of which could be used for numerical analysis), which are estimated to correspond to a coverage of ca. 30% of the total Mida Creek population, were interviewed to assess the human reliance on mangrove resources in Mida Creek. The survey indicates that mangroves are a major resource of wood for house construction, fuel wood, charcoal, and boat building. Minor uses of mangrove products include pharmaceutical and medicinal applications, tanning material, and furniture making.* Rhizophora mucronata, Ceriops tagal, *and* Bruguiera gymnorrhiza *are the major resources for house construction and fuel wood, while* Sonneratia alba *and* Xylocarpus granatum *were reported to be useful for boat building and medicinal uses respectively. The survey further describes harvesting activities and house construction, and reveals species preferences within this one particular use. As a result of depletion of the supply and the banning of mangrove harvesting, the local people are turning to other wood materials and to poaching. In our view, local utilization patterns rather than global usefulness data are required to establish a conservation policy of both mangroves and users' subsistence requirements.*

*La ensenada de Mida (Kenya) posee bosques de manglar y otros recursos marinos de importancia económica, ecológica y ambiental para las comunidades de los pueblos. En total 116 hogares (100 de los cuales podrían ser usados para análisis numéricos) corresponden a una cobertura total del 24% de la totalidad de la población de ensenada de Mida. El sondeo indica que los manglares son la mayor fuente de madera para la construcción de casas y botes, combustible y carbón de madera. Usos menores de los productos de manglar incluyen aplicaciones farmacéuticas y medicinales, material de teñido y muebles.* Rhizophora mucronata, Ceriops tagal y Brugeuiera gymnorrhiza *son las principales fuentes para combustible y construcción de casas, mientras que* Sonneratia alba y Xylocarpus granatum *fueron reportados como aptos para la construcción de botes y usos medicinales respectivamente. El sondeo describe adicionalmente actividades de consecha y construcción de casas revelando preferencias de especies para este caso en particular. Como resultado de la destrucción del recurso y la prohibición de la cosecha de mangle, los pobladores se han inclinado por el uso de otras maderas y a la pesca furtiva. Consideramos que se requieren patrones de utilización local más que datos globales para establecer una política de conservación de manglares y requerimientos para la subsistencia de los usuarios.*

**Key Words:** mangrove; ethnobotany; wood; survey analysis; Kenya.

---

[1] Received 24 July 1999; accepted 21 March 2000.

*Economic Botany* 54(4) pp. 508–522. 2000

All over the world the mangrove ecosystem is threatened with destruction through various forms of human pressure (e.g., Farnsworth and Ellison 1997). The observed decline in Kenya is mainly a result of mangrove harvest exports as building material and fuel wood to Somalia, Saudi Arabia, and other Middle East countries (Rawlins 1957). Mangroves are well developed in many areas along the Kenyan coastline, particularly in creeks, bays, and estuaries. Estimates of total area of mangrove forest vary according to different sources. The Kenya Forestry Department lists 644 km², the World Mangrove Atlas 961 km² (Spalding, Blasco, and Field 1997), but the more rigorous studies made by Doute, Ochanda, and Epp (1981) indicate that there are 530 km² of mangroves along the Kenyan coast, the bulk of which are in Lamu (335 km²) with substantially smaller areas in Kwale (88 km²), Kilifi (66 km²) and Mombasa districts (20 km²). All nine typical East-African mangrove species occur along the Kenyan coast, i.e., *Avicennia marina* (Forsk.) Vierh., *Bruguiera gymnorrhiza* (L.) Lam., *Ceriops tagal* (Perr.) C.B. Robinson, *Heritiera littoralis* Dryand., *Lumnitzera racemosa* Willd., *Rhizophora mucronata* Lam., *Sonneratia alba* Sm., *Xylocarpus granatum* Koen, and *X. moluccensis* (Lamk.) Roem. (nomenclature according to Tomlinson 1986). However, on a local level not necessarily all of these are present (Dahdouh-Guebas et al. subm.).

The people of the Kenyan coast (Swahili community) are united by their common language (Kiswahili, but in the area of Mida Creek Giriama is common as well), common culture and religion (Islam), and common home, the coastal zone (Salim 1985). Most of these people have strong economic ties with the coastal ecosystems with which they interfere, as fishermen, as mangrove cutters, as coral collectors, and so forth.

The main reason for this study arose from some policy developments concerning environmental resources in Kenya in 1996, involving a proposal to lift a ban on mangrove export (initially in place in 1978, lifted in 1981 and again installed in 1982). Authorization for the exploitation and clearing of mangroves for any purpose has to be obtained from the Kenya Forestry Department at the Ministry of Environment and Natural Resources. In addition to controlling operations, all vehicles transporting mangrove poles must have a transit permit and timber statement. The local communities were affected in many ways by these measures as they have lived within the mangrove forests for several generations or visited them to make use of their resources. Restricting access through changes in property rights has been shown elsewhere to increase poverty (Reddy and Chakravarty 1999). The issues of indigenous resource rights and environmental conservation have been reported to be complementary as well as contradictory, as highlighted by Aagesen (1998).

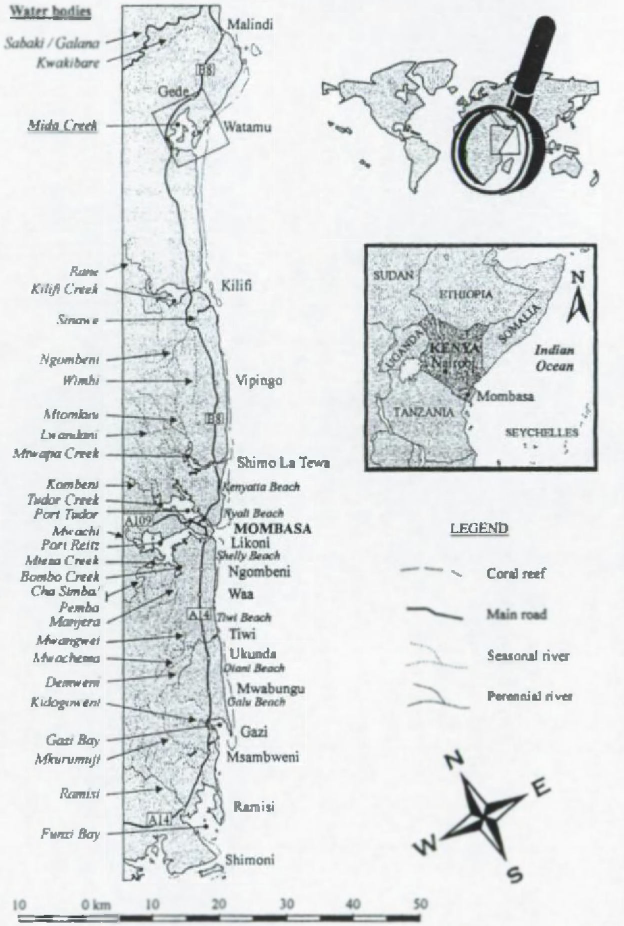
The objectives of this study were: (a) to provide data on the uses of mangroves by local communities within and around Mida Creek; (b) to assess the most significant use of the mangroves for these communities; (c) to investigate the local residents' perception of the current status of the mangrove forest; and (d) to examine the factors influencing frequency of harvesting activities, preferred harvesting areas, preferred species and actual organization of the harvesting activities. The combination of this information may give a clue to establish the community's dependence on the mangrove resource.

## DESCRIPTION OF THE SITES STUDIED

Mida Creek (03°21'S, 39°59'E) is located in Malindi district, 88 km north of Mombasa and approximately 25 km south of Malindi town (Fig. 1). The creek lies in a planigraphic area of 31.6 km² (Brakel, 1979).

In recognition of its scenery both above and below the water level Watamu Marine National Reserve in Mida Creek was declared a protected area, one out of the three protected areas with mangroves in Kenya (Spalding, Blasco, and Field 1997). It was established as a reserve in 1968, and gazetted under the Wildlife Conservation Management Act in 1976. In 1979, Watamu Marine National Reserve was designated the status of a Biosphere Reserve together with the adjoining coast (Kennedy 1988). Mida Creek has a number of distinct habitats comprising mangrove forest, sand flats, rock outcrops, seagrass beds, coral growths, and deep water. Unlike most of the coastal areas in Kenya, Mida Creek lacks overland freshwater input (cf. Fig. 1a).

Administratively the Mida Creek area was divided into two sublocations: Gede and Matsangoni. For the purpose of this study we considered the area bordered by the Mombasa-Malindi main road east, excluding the northwestward re-



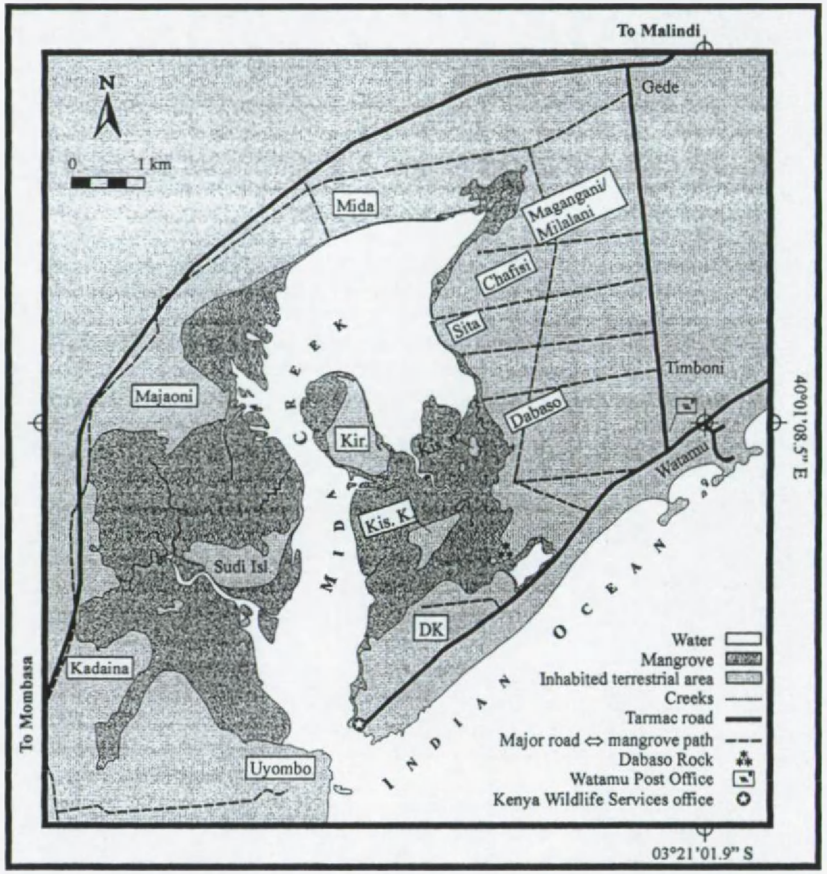


**Fig. 1a.** Location map of the southern part of the Kenyan coast. The rectangle around Mida Creek refers to Fig. 1b.

**Fig. 1b.** Detailed map of our study site Mida Creek (digitized from 11 aerial photographs) indicating the existing human settlements bordering the creek. The latter are seldom if ever indicated on maps, whether official or not. DK = Dongokundu, Kis. K. = Kisiwani Kubwa, Kis. n. = Kisiwani ndogo, Kir. = Kirepwe.

gions further away from the creek in the Gede sublocation. According to official records, the 1991 census for Kenya revealed the population of Mida Creek as approximately 23 000, of whom 60% are below the age of 16. An estimated 20% of this population live in the trade centers in Timboni and Gede and the Watamu tourist village, which are two to three km distant from the mangroves. Timboni is a small trading center that deals with mainly farm produce from Mombasa and up-country. It is also an important trading area for building materials like mangrove poles, bricks, gravel and cement. Gede on the other hand is an important historical village with 16th century ruins. In addition, it is a trade center for agricultural produce, and at present also the home of the Kipepeo Butterfly Project, that cultures the endemic Lepidoptera species of Arabuko Sokoke National Park, the largest block of indigenous coastal terrestrial forest in East Africa (KIFCON 1995). The people of these villages derive their livelihood from trading foodstuffs, building material, curios, and souvenirs to tourists and as government administration. Besides the villages that dot the area around the entire creek, the shore is lined with tourist lodges as well as properties owned by foreign residents (Hirsch and Mauser 1992).

## MATERIAL AND METHODS

Data collection was done by interviews at 116 households around the creek, systematically filling out questionnaires (Appendix 1), and through observation of everyday life in the households visited. One hundred questionnaires were used for numerical analysis (see below). Only one person per household was interviewed to avoid repetition from members of the same household, who could, however, interfere with the interview. Households were approached directly in the field, as topographic or administrative maps showing their distribution were unavailable. In densely populated areas, such as Uyombo and Dongokundu, systematic sampling was done by visiting every second household, whereas in sparsely populated areas all households were visited (e.g., Kisiwani Island and Chafisi). The settlements of Timboni and Gede were not included in the survey for reasons outlined in the introduction. Secondary data were pursued from official government records, but the archival research was restricted by the local authorities because of the highly unstable political situation at the time of data collection in the national election year 1997.

The interviews were conducted in Kiswahili and/or the local Giriama, depending on which of the languages the respondents felt more comfortable with. Often the elderly folk preferred to communicate in Giriama, whereas the middle-aged people and the youth felt more comfortable using Kiswahili. A guide, a local resident, facilitated moving around the creek reducing possible hostility, facilitating a comfortable reception and a fluent conversation with the respondents in the visited households. The information gathered was then filled out in questionnaire schedules in English. The questionnaire involved questions that sought to provide general information about the respondents, questions posed to reveal "the way of forest life" of the members of the community, i.e., how they conducted various activities in the forest and what kind of preferences they had, as well as questions aimed at bringing out the respondents' opinions concerning various issues (public opinion polls; Bailey 1987). The questionnaire had a semi-structured nature with short multiple-choice questions as well as some open-ended questions, the former of which mainly aimed at narrowing down the answer categories to facilitate and enhance data analysis. The interviews often began by assessing the understanding of the term mangrove to ensure that the respondent and interviewer were talking about the same concept and subject area. As it turned out, the respondents referred to the vegetation whenever they used the Kiswahili or Giriama term corresponding to mangrove *(mkoko)* rather than to the entire mangrove ecosystem.

In situations where cultural inhibitions limited or prevented the respondents from answering certain questions, visual observation was substituted as a method to acquire the required information. In the other situation observations were important to visually check and complete the respondent's answers. Some of the uses of mangroves were quite easily observable, e.g., making furniture, cooking utensils, fishing traps, canoes, and sailboats and in building houses. This observation technique provided supplementary information to that gathered in the interviews.

The few problems met during the survey related to the sensitivity of certain issues. Given the current policy on mangrove exploitation in Kenya, the entire subject has become a sensitive

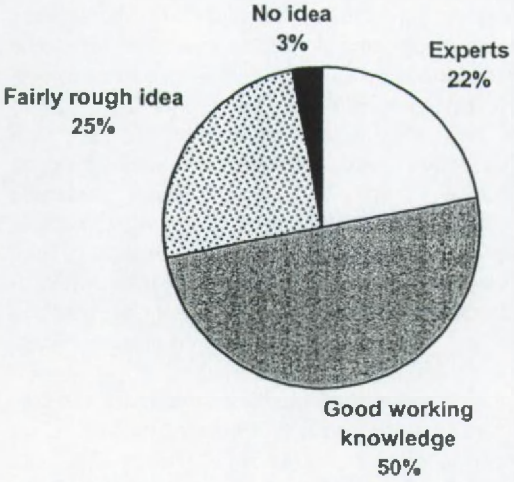


**Fig. 2.** Levels of knowledge on mangroves amongst the survey respondents.

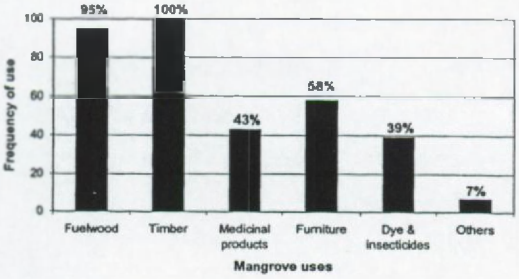


**Fig. 3.** Different uses of mangroves (n = 100 respondents).

one. Questions dealing with mangrove pole harvesting often result in a lot of suspicion, which made the gathering of information from outsiders rather complicated. Often it took a long conversation to win the confidence of the respondent so that they felt comfortable enough to answer questions. To obtain sensitive demographic data community leaders were approached.

In addition to the individual questionnaires a group interview with the Viriko-Vimoyoni Women's group, which owns a mangrove-harvesting permit, was done.

## RESULTS AND DISCUSSION

A total of 11 settlements can be mapped out distinctly from the study (Fig. 1). These settlements are immediately bordering the creek area, but are seldom, if ever, indicated on (official) maps, notwithstanding they form an important form of identity for the residents. Most residents were native to the area, having lived there for at least three generations. The main human settlements include: Dongokundu, Kisiwani, Dabaso, Sita, Chafisi, Magangani-Milalani, Mida, Majaoni, Kadaina, Uyombo, and Kirepwe (Fig. 1b).

From visual observation it was clear how much the villagers' lifestyle revolves around the mangrove ecosystem, on one hand because they are mainly fisher folk dependent on the functions of mangrove as breeding, spawning, hatching, and nursing grounds for many marine and lagoon animal species, and on the other hand because of the massive use of mangrove trees within their households.

### THE HOUSEHOLD ENTITY

Traditionally, a woman and her children share a house. Each homestead included one house for the man who is the family head, one for each of his wives and her children (the predominant Giriama culture in this area is polygamous), and one house for each of his adult sons, i.e., from the age of 15. Estimating from the fieldwork that a household comprises on average eight houses, each of which counts on average about six persons, the average household has approximately 48 persons. Considering the most recent official statistics of 23 000 persons inhabiting the area, and assuming that about 20% of these live outside the survey area based on the distribution of villages, the 116 households visited are estimated to cover 30% of the Mida Creek population. However, 16 questionnaires were excluded from the main analysis because of incompleteness, reducing the number of questionnaires suited for further analysis to 100, and the coverage to 26% of the population bordering the creek.

### MANGROVE KNOWLEDGE LEVELS

Different levels of knowledge became evident when interviewing the respondents (Fig. 2). First, experts, as they were referred to by others, who, when interviewed, were able to identify mangrove species using different physiognomic and morphological traits of the plants (e.g., roots, leaves, flowers, and propagules). Second, those who had a good working knowledge on the mangroves and could distinguish different mangrove species through the rooting system alone. These two first groups constituted the majority of respondents (72%). Third, those who

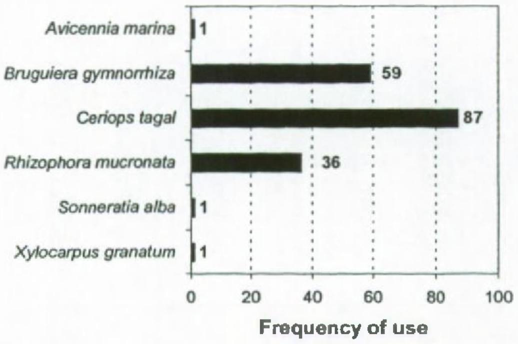


**Fig. 4.** Mangrove tree species used in house construction (n = 100 respondents).Mangrove wood as a source for construction along the Kenyan coast.

had a fairly rough idea and could acknowledge the existence of different species, but could almost never go beyond visually naming three species that were present in Mida Creek. Fourth, those with no idea at all, who knew what mangroves were but could not distinguish individual tree characteristics, much less name them.

## LOCAL USES OF MANGROVE TREES

Various tree species and tree parts of different sizes were used for different purposes, all of which have been summarized for each species in Table 1 and quantified in Fig. 3. The more direct uses of mangrove trees in making them into furniture of various sorts have been included entirely in Table 1.

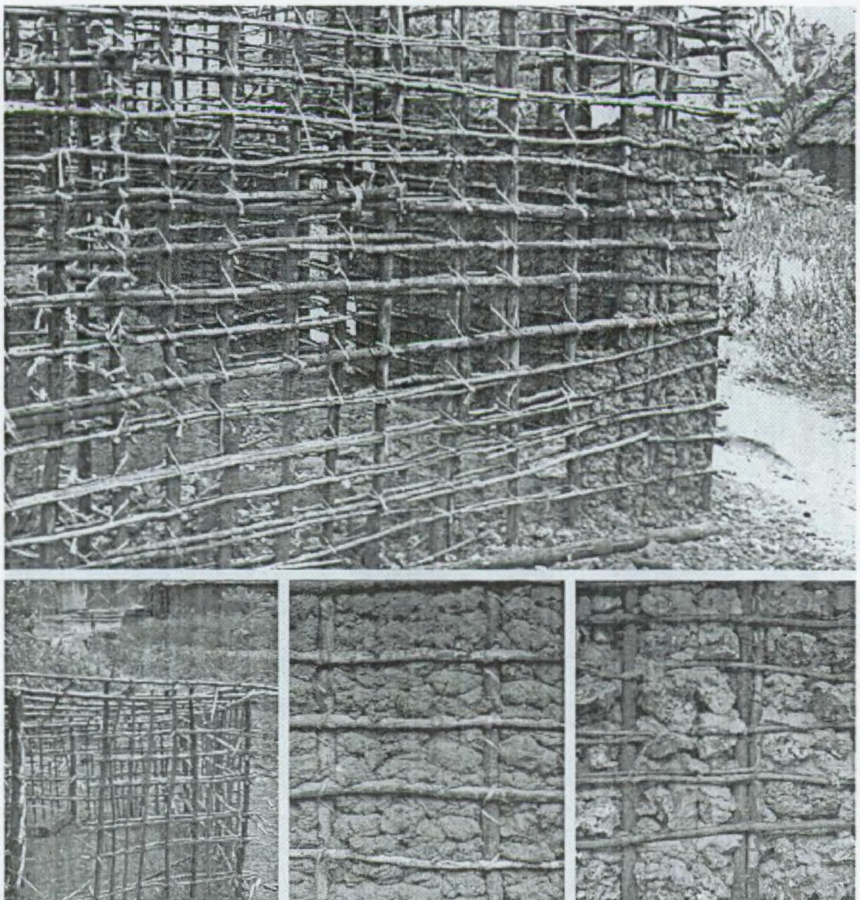
Fuel wood comprises firewood and can be turned into charcoal. Firewood is dead logs and branches washed ashore by the tides and gathered by the women, which implies that there is not a preferred species for this use. The making of charcoal, however, as it is for commercial purposes, involves felling trees favoring some species over others because of their heating quality. The whole process of cutting trees for commercial firewood and making charcoal is done by men, except for the actual selling of charcoal, which in the creek area is performed by women.

Medicinal products are mainly made from the bark of mangrove stems, which are crushed and blended with other ingredients or plant extracts before being boiled. Tree stems of different ages yield medicines for different ailments. *Rhizophora mucronata* roots are often valued for their curative properties for constipation, fertility-related or menstruation disorders. *Xylocarpus granatum* fruits are used as an ointment to soothe aching muscles and limbs resulting from injury, and mixed with other ingredients (e.g., chalk) they are also used as an ointment to cure skin disorders. An extract from the bark of roots is claimed to drive demons out from possessed persons, and in the case of *Rhizophora mucronata* roots, to have the power of bringing back lost family members. For both normal and paranormal applications the methods of preparation and proportions of various ingredients are closely guarded family secrets.

Dyes, including tanning compounds, are produced from the bark of *Rhizophora mucronata* stems, applied to the insides of canoes and boats and valued for their preservative quality. Dyes are also used to seal up the tiny pores in trays woven from reeds and palm leaves, used for storing flour from cereals, and to decorate sleeping mats, baskets, and trays. Among the school children and their teachers, dyes are used in school to produce tie-dye fabrics and clothes but the art is not pursued further for commercial purposes. The insecticide application of mangroves is reported to come mainly from green *Avicennia marina* logs which are very smoky when burnt, keeping away mosquitoes and other biting night insects. Their slow burning make them also popular with honey collectors or fishermen as they sit out on the beach at night, awaiting the right tide amplitude to set out fishing. However, the fishermen sometimes prefer to set the entire tree ablaze beginning with a hole at the base of the stem. These fishermen's fires are not extinguished so that they find the fire still burning the next nights until the entire tree is burnt out.

The use of mangroves as timber is the most important one (Fig. 3), either for house or boat construction. Simple one-man canoes are carved from heavy *Avicennia marina* logs. Larger vessels like the traditional dhows are built with ribs from *Sonneratia alba* logs. The paddles and oars to propel these boats forward are made from *pau* (see below) of *Bruguiera gymnorrhiza, Ceriops tagal,* or *Rhizophora mucronata,* the key features of these poles being their length and straight shape.

Although for some countries, different uses might be come out as most important, such as charcoal in Thailand (Aksornkoae, Paphavasit, and Wattayakorn 1993), the uses of mangrove



wood products generally correspond with those observed earlier by Kokwaro (1985) for the Kenyan coast. The most significant use of mangroves in Mida Creek as a source for house construction, is apparently also the case for other villages along the Kenyan coast (pers. obs.).

Our expectation that local people's opinions would, to a certain extent, vary depending on level of dependence (e.g., fishermen would perceive the most important use as being related to their occupation—fishing, boat construction, making of fishing traps, function as breeding ground for fish) is not supported since all respondents unanimously state house building as a prime use (Fig. 3). This is even more surprising when comparing the monthly income for mangrove cutters and fishermen: respectively 2500 KSh and 3500 KSh (Hirsch and Mauser, 1992. The exchange rate at the time of their research was 1 US $ = 32–35 KSh, whereas during the course of the present study and until present, it is 1 US $ = 70–74 KSh.). Only seven respondents included benefits like preservation of the environment by the mangroves, keeping sea storms and winds at bay by the mangrove tree fringe, and attracting rainfall (Fig. 3). This emphasizes the perception of the mangrove forest as being vegetation rather than the entire ecosystem.

## HOUSE CONSTRUCTION AS THE PRIME USE

The largest and most significant use of mangroves is in the form of poles used for house construction. Certain species are preferred over others namely: *Ceriops tagal*, *Rhizophora mucronata*, and *Bruguiera gymnorrhiza* (Fig. 4). These are favored because of their ability to grow long and straight, and each of these species occupies a particular place within the framework of a house. *Bruguiera gymnorrhiza* is preferred for the rooftops rather than for walls because it produces long yet strong enough poles for the roof. In addition, this species is cited as not lasting very long in the soil as it does not withstand moisture and saline soils. Most resistant to the soil conditions cited above is *Rhizophora mucronata* and is preferred for the walls and especially the thicker supportive poles and corner pillars of a house (Fig. 5). *Ceriops tagal* poles are much thinner and thus used as *fito* (Table 2; cf. Fig. 5) for creating an interweaving network in the walls and roofs. *C. tagal* was also used to make other houselike structures like shrines, cooking sheds outside the main house, and animal sheds and pegs (cf. Fig. 6). Classification of mangrove pole diameters and heights was given by Roberts and Ruara (1967) and the uses in a single house qualified and quantified per class according to our data in Table 2. Looking at the construction of a house from the utilization classes point of view we can summarize that the *boriti* are thick poles that go deep into the ground and that they are the main supports for the walls. At each side of the wall they are crossed by the *fito*. The fillings of the walls consisted of traditional clay (Fig. 7) or cemented dead coral rock (Fig. 8), whether or not finished with a more modern plaster treatment, depending on financial means. The latter provides a polished look exactly like that of a plastered modern brick house constructed with cement and stone or concrete bricks. The ceiling is made of *nguzo* and *boriti*, the former being thicker and heavier than the latter, which could be closely packed or evenly spaced out at one-foot intervals. The roof is composed of *pau* and *mazio*, which are long poles meeting at a common apex or at the same level at the top depending on the roof design (Fig. 9). Finally, the *vigingi* are used to support the roof extension that formed a kind of veranda just outside the main door and is used as a cool or dry sitting area. The most common roof fillings are dried coconut leaves woven into a thatch called *makuti* (Fig. 9). This material insulates the house adequately from the hot daytime sun. The *makuti* are placed in an overlapping manner directly onto the grid of mangrove poles and tied with strings made from some indigenous inland creepers, dried coconut leaves split into thin strips, or split roots of *Rhizophora*

←

**Fig. 5.** Top: Mangrove wall *skelet* (vertical *boriti* with horizontal *fito*, cf. Table 2) partially filled with mud.
**Fig. 6.** Center left: Small cooking shed made of *Ceriops tagal*.
**Fig. 7.** Center: Close-up of a mangrove wall filled with mud and clay and,
**Fig. 8.** Center right, a wall filled with dead coral and cement.
**Fig. 9.** Bottom: Roof with *nguzo* and *boriti* and covered with *makuti*.

TABLE 1. TRADITIONAL USES OF MANGROVES IN MIDA CREEK.

| Species name | Local names (Kiswahili, Giriama) | Uses | Parts used |
|---|---|---|---|
| *Avicennia marina* | mchu | bed posts, chair legs, table legs, fencing posts, charcoal, low quality commercial firewood, crushing pole, crushing mortar, serving dishes, drums, boat ribs, board games (bao) | thick stems |
| | | firewood (for home use) | dead stems |
| | | insecticides | green stems |
| *Bruguiera gymnorrhiza* | muia, mkoko wimbi | high quality commercial firewood, high quality charcoal, construction poles, roof supports, boat paddles, oars, handcart handles, axe handles, pounding poles | thick mature stems |
| | | drums, bee hives | old hollow stems |
| *Ceriops tagal* | mkandaa, mkoko mtune, mkoko mwekundu | construction poles, paddles, oars, medium quality commercial firewood | mature and young stems |
| | | dyes (incl. tanning compounds) | bark of stems |
| | | fishing traps | young flexible stems |
| *Lumnitzera racemosa* | kikandaa, mkaa pwani | medium quality commercial firewood and charcoal | mature stems, dead stems |
| *Sonneratia alba* | mlilana | canoes, boat ribs, paddles, masts, fishing net floats, timber for window and door frames, medium quality commercial charcoal and firewood | thick mature stems |
| *Rhizophora mucronata* | mkoko, mkoko mwenye | construction poles, high quality commercial charcoal, high quality commercial firewood | thick mature stems and young stems |
| | | dyes (incl. tanning compounds), medicines, ointments | bark of stems and roots |
| | | fishing traps | roots |
| | | weapons | young stems |
| *Xylocarpus granatum* | mkomafi | high quality timber for bed construction, window and door frames, medium quality commercial charcoal and firewood | mature stems |
| | | ointments | crushed fruits |

TABLE 2. CLASSIFICATION CATEGORIES OF DIFFERENT UTILIZATION CLASSES OF MANGROVE MOLES (ROBERTS AND RUARA 1967), QUALIFIED WITH RESPECT TO THE USE AND FOR A SINGLE HOUSE QUANTIFIED PER CATEGORY ACCORDING TO OUR DATA. THE UTILIZATION CLASSES ARE IDENTIFIED BY KISWAHILI WORDS USED LOCALLY (THERE IS NO TRANSLATION FOR THESE TERMS).

| Utilization class | Diameter range (cm) | Height (m) | Number required* | Use |
|---|---|---|---|---|
| *Fito* | 2.5–3.5 | >4 | 1000 | wall filling |
| *Pau-Mazio* | 4.0–11.5 | >4 | 92 | roof filling |
| *Boriti* | 11.5–13.5 | >4 | 32 | wall supports |
| *Nguzo* | 14.0–20.0 | >4 | 112 | ceiling and roof supports |
| *Vigingi* | 20.5–35.0 | <4 | 4 | supports and fencing |

* 20 poles = 1 score.

*mucronata*. From our own observations, we estimate that 90% of the houses in the villages around Mida Creek are of the traditional design, with a bare instead of a cement floor. The average house has an L-shape, consisting of three rooms with one main entrance into the house, and a perimeter of about 27 m.

According to the respondents, once constructed a house can last from one to over 30 years with an estimated average of eight years, depending greatly on the quality of poles and fillings used in the framework and especially whether or not the house has a cement floor and plastered walls. Also, environmental conditions such as soil drainage levels obviously are a factor. However, it should be highlighted that some houses built with mangrove wood in Lamu (further North) are more than a century old, and some near Fort Jesus (Mombasa) are reported to be several centuries old.

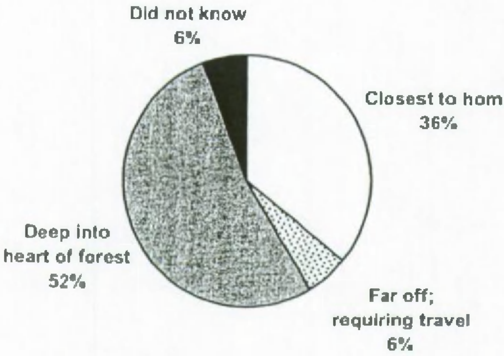


**Fig. 10.** Location of harvesting activity (n = 100 respondents).

## HARVESTING LOCATIONS

Pole harvesting activities occurred in different sections of the mangrove forest (Fig. 10). However, the actual harvesting locations were often a result of preferred species and pole size availability (cf. Fig. 4) rather than merely an element of accessibility to that section of the forest. Some parts of the creek reportedly had no mangroves that could be harvested, e.g., the Mida/Majaoni region (Fig. 1). As a result the villagers in this part of the creek indicated they traveled to the Kadaina and Uyombo area to harvest poles of suitable sizes. The closest forest region to Mida/Majaoni is the adjoining Sudi Island, which is left for tourism-related activity like pic-

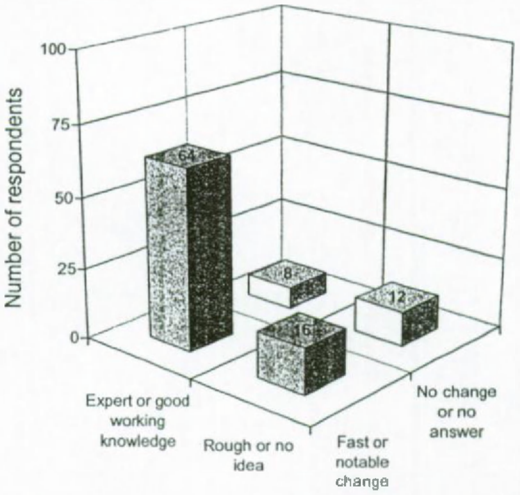


**Fig. 11.** Respondents' opinions on current forest status classified according to mangrove knowledge (n = 100 respondents).

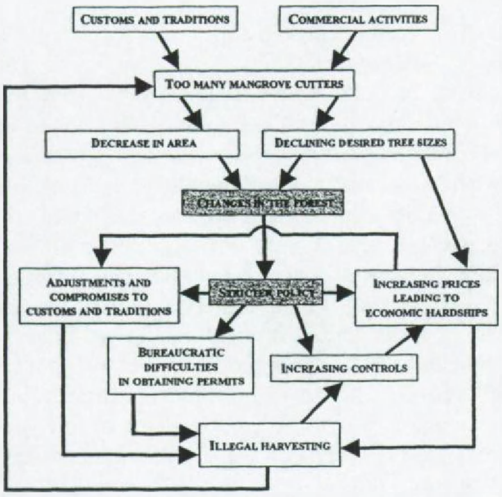


**Fig. 12.** General framework of harvesting activities and policy leading to the observed changes in Mida Creek. Note the loops forming a vicious circle.

nicking. Access is restricted and harvesting forbidden by the Kenya Wildlife Service (KWS). In other areas, especially the island regions of Kadaina, Kirepwe, and Kisiwani, the poles were harvested in the forest regions closest to the homesteads (often just outside of the compounds). Harvesting of mangrove trees usually took place whenever poles were required and not on any regular or seasonal basis. The organization of the harvesting activities varied according to different levels of formality. A local formally organized pattern of harvesting involves the interested party approaching a professional mangrove cutter with an authorized license to carry out cutting activities in the forest. Sellers' prices are from 105 KSh per score (1 score = 20 poles) for *pau*, to 1000 KSh per score for *vigingi* (Hirsch and Mauser 1992). A less formally organized harvesting activity comprises of the interested party personally harvesting the mangroves and seeking a permit from the Forestry Department for it. Licenses cost 300 KSh plus 3000 KSh per annum per licensee, however only 50% of the applicants actually obtain a license (Hirsch and Mauser 1992). The Forestry Department often stipulates the exact quantities of poles per any particular utilization class (Table 2). Officially, on average six scores per month are allowed to be cut, but actually eight times that amount is being extracted (Hirsch and Mauser 1992). The informally organized harvesting activity often took a longer time because the parties were not professionals, lacking skill, experience, and efficient equipment. Due to major difficulties in obtaining licenses most people relied on ordered consignments or opted to harvest illegally, which is at the owner's risk of getting caught and having the poles confiscated. The reported high prices of poles, from the dealers or directly from the professional cutters, also encouraged illegal harvesting to some degree. Information on the quantity of mangroves harvested was obtained when interviewing a professional mangrove cutter. He estimated that a nine-ton lorry was filled every time he went on an ordered consignment mission. Such an expedition occurred with a frequency of about one per month (three weeks of cutting and one week of rest). Estimating from this information, in a year there would be 13 such expeditions equaling about 117 tons of harvested mangrove poles for one professional mangrove cutter and his team. However, local people working with mangroves cutting teams of about 50 persons in Gazi, further south, reported about 10 filled lorries per week leaving their mangrove area in the 1960s (Abdulrahman Lali, pers. comm. 1999). These differences in figures may reflect the observed differences in disturbance between the Kenyan north and south coast, but must be considered in the context of the extent and status of the forest, the number of licenses in the area, and the size of the mangrove cutting team. In 1997 in Mida Creek there were four harvesting licenses, but local people reported that resource depletion forced the cutters to move to other areas. Another trend is that as demand actually increases as deduced from utilization patterns and population growth, while supply diminishes as indicated by the reported forest decline, combined with restriction of harvesting as a result of the ban, the locals may turn to other wood materials and to poaching. The degree to which this is admitted cannot reliably be estimated from inquiries.

## Mangrove Decline in Mida Creek

The majority of people state that the mangrove vegetation is declining (Fig. 11) and further analysis confirms that this is mainly the opinion of those with the highest mangrove knowledge (89% respondents with expert or good working knowledge). Statistical analysis ($\chi^2$-test) confronting this group of respondents versus the people with a rough or no idea on mangroves (Fig. 2, Fig. 11) in their reply on the decline of mangroves (fast or notable change against no change or no answer) corroborated this ($\chi^2 = 10\ 792$; d.f. = 1; $P < 0.01$). The main cause given for the observed change is a decline in desired sizes or in overall number of trees. Kairo and Gwada (1998) and Kairo et al. (n.d. a) observed a clear physiognomic difference of mangrove trees between the forest areas of Uyombo (Fig. 1, left) and Kirepwe (Fig. 1, right). The Uyombo region has been subjected to over-exploitation and as a consequence displays a large proportion of crooked trees (quality class 3), in contrast to Kirepwe (Kairo and Gwada 1998; Kairo et al., n.d. a).

Another indirect cause for decline is the increasingly complex procedures to obtain permits. The latter has been put into a framework of harvesting activities and cause of the observed changes (Fig. 12). Although a ban has been put on mangrove export the system would benefit only for a short term, since the local market also has high demands. The most important task for the Forestry Department would be to carry out a complete inventory of the mangrove resource in the whole country. The inventory should provide forest cover maps as well as data on the forest stocking rates for the main species. Such work is currently being done for Kiunga Marine National Reserve (Kairo et al., n.d. b) and Ramisi (Kairo and Gwada, in prep.). The major obstacle that has prevented rational use and conservation of mangroves in Kenya has been a management policy that consists of controls and prohibitions in the absence of the means to implement them (Ferguson 1993; Kairo 1996).

## CONSERVATION AND MANAGEMENT ISSUES

The wealth of the mangal was well appreciated by the local residents of Mida Creek and reflected in the realization for the need to conserve the forest area. There were various efforts to conserve and replant certain areas by organized groups of people, e.g., Dongokundu Mangrove Planters Association and Viriko/Vimoyoni Women's group. Some even expressed the wish to have stricter and a more rigid control of activities within the forest by the authorities concerned in order to give the forest time to recover. However, policies such as bans on all harvesting activities cannot be applied effectively without examining the consequences for local subsistence communities.

Numerous recommendations have been put forward concerning the direction and steps to be taken towards a mangrove management plan and a sound forestry management scheme to enable sustainable exploitation of the mangrove resources (Kenya Forestry Master Plan 1994). However, few of these, if any, have been implemented to date. A clear understanding of the nature and dynamics of local mangrove ecosystems will be the best guide to any restoration program (Field 1996), and thus necessitates fundamental as well as applied research to fully appreciate and understand and even manage this ecosystem and its utilization patterns. The approach to involve the local population by educating them on the value of the ecosystem to enable them to fully appreciate it, such as in Gazi Bay, Kenya (Kairo 1995) or in the Chilaw Lagoon-Mundel Lake-Puttalam area, Sri Lanka (SFFL 1997; Foell et al. 1999), is presently set up in Mida Creek through the Viriko/Vimoyoni Women's group. This form of environmental education introduces a sense of responsibility among residents on their activities within the forest, but an effective institutionalization of community-based natural resource management and conservation is essential (Agrawal and Gibson 1999). Special training for personnel of the Forestry Department and other authorities managing the mangrove forest area would also result in more appreciation of the value of the resource and hopefully change behavior and attitudes towards exploitation habits and patterns. Duraiappah (1998) also emphasizes that groups that adopt unsustainable activities must be given the incentives (compensation, rewards, taxes, and information provision) to stop. Forestry management programs, if put in place in Mida Creek, could result in success particularly now that the population is aware of the need to conserve mangroves. In southern Chile, self-determination and territorial rights are also important factors in the indigenous interests in and commitment to conservation of certain plant species (Aagesen 1998). However, in some cases, the conditions which are deemed to be necessary for the sustainable management of a resource appear to be undermined by increasing inequality and conflict (Adger et al. 1997), the latter as the result of the effects of the economic liberalization process in former centrally planned economies (Adger 1999).

Clough (1993) cites that economic indicators do not necessarily provide an adequate description of the contribution of mangrove ecosystems to the daily life and culture of people who have traditionally used mangrove areas. In our view local utilization patterns rather than global usefulness and utilization inventories are required to establish a conservation policy of both mangroves and users' subsistence requirements.

## CONCLUSION

The local residents of Mida Creek are dependent to a large degree on the mangrove resource, if the lack of economically acceptable alternatives for mangrove resource utilization is considered to cause dependence. The present study provides details on mangrove use that were never reported, such as the preference of wood types for different purposes within a certain use (construction). This shows that local rather than global utilization patterns constitute important sources of information. The majority of Mida Creek's people realize their mangrove forest is degrading and while some are turning to illegal practices (e.g., poaching) because of the bureaucratic difficulties in obtaining a cutting license, others wish to have stricter monitoring and enforcement of the existing mangrove forest policy. The present will and engagement of the local people to protect the mangrove should be an incentive for the government to put a Kenya Forestry Master Plan into action.

## ACKNOWLEDGMENTS

We are very grateful to B. Simpson and her entire staff that proved very encouraging and supportive during the fieldwork. Many thanks are due to the practical help of Vladica Sivcev in shaping the questionnaires, and to our local guide on the field. We also thank Willem Brakel, as well as two anonymous reviewers for their comments on the manuscript, and Adriana Sanchéz-Suaréz and Manzour Hazhon for the Spanish abstract. Research financed by the Fund for Collective Fundamental Research (FKFO) and with a specialization fellowship of the Flemish Institute for the advancement of scientific-techoological research in the industry (IWT). This work was presented on the Symposium on Recent Advances and Future Trends in Mangrove Research: Biodiversity, Genetics, Evolutionary Biology and Restoration (July 8–10, 1998, Toulouse, France).

## LITERATURE CITED

**Aagesen, D. L.** 1998. Indigenous resource rights and conservation of the monkey-puzzle tree (*Araucaria araucana*, Araucariaceae): a case study from southern Chile. Economic Botany 52(2):146–160.

**Adger, W. N.** 1999. Exploring income inequality in rural coastal Viet Nam. Journal of Development Studies 35(5):96–119.

**———, M. Kelly, N. H. Ninh, and N. C. Thanh.** 1997. Property rights and the social incidence of mangrove conversion in Vietnam. CSERGE Working Paper GEC 97–21. Centre for Social and Economic Research on the Global Environment, School of Environmental Sciences, University of East Anglia, Norwich, U.K.

**Agrawal, A., and C. C. Gibson.** 1999. Enchantment and disenchantment: the role of community in natural resource conservation. World Development 27(4):629–649.

**Aksornkoae, S., N. Paphavasit, and G. Wattayakorn.** 1993. Mangroves of Thailand: present status of conservation, use and management. Pages 83–132 *in* The economic and environment value of mangrove forests and their present state of conservation. International Tropical Timber Organisation/Japan International Association for Mangroves/International Society for Mangrove Ecosystems, Japan.

**Bailey, K. D.** 1987. Methods of social research. Collier Macmillon, London, U.K.

**Brakel, W. H.** 1979. Marine parks and recreation. Pages 409–433 *in* World Bank Tourism Pricing Policy Study for the Kenya Ministry of Tourism and Wildlife.

**Clough, B. F.** 1993. The status and value of mangrove forests in Indonesia, Malaysia and Thailand: summary. Pages 1–10 *in* The economic and environment value of mangrove forests and their present state of conservation. International Tropical Timber Organisation/Japan International Association for Mangroves/International Society for Mangrove Ecosystems, Japan.

**Dahdouh-Guebas, F., M. Verneirt, S. Cannicci, J. G. Kairo, and N. Koedam.** An exploratory study on grapsid crab zonation in zoned mangrove forests in Kenya. (submitted).

**Doute, R., N. Ochanda, and H. Epp.** 1981. A forestry inventory of Kenya using remote sensing techniques. Kenya Rangeland Ecological Monitoring Unit report, Nairobi, Kenya.

**Durraiappah, A. K.** 1998. Poverty and environmental degradation: a review and analysis of the nexus. World Development 26(12):2169–2179.

**Farnsworth, E. J., and A. M. Ellison.** 1997. The global conservation status of mangroves. Ambio 26(6):328–334.

**Ferguson, W.** 1993. A land(scape) ecological survey of the mangrove resource of Kenya (Draft Report). Technical Coperation Project (FAO TCP/KEN/0051) for the Forestry Department, Ministry of Environment and Natural Resources, Nairobi, Kenya.

**Foell, J., E. Harrison, and R. L. Stirrat.** 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, U.K.

**Gang, P. O., and J. L. Agatsiva.** 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.

**Hirsch, D. and A. Mauser.** 1992. The economic values of mangroves. Two case studies: Mida Creek and Funzi Bay. (Thesis). University of Amsterdam, Netherlands.

**Kairo, J. G.** 1995. *Community participatory forestry* for rehabilitation of deforested mangrove areas of Gazi Bay (Kenya). A first approach. Final technical report. University of Nairobi, Department of Botany, Nairobi, Kenya.

———. 1996. Towards alternative views of mangrove forestry in Kenya. *In* Supporting capacity building in forestry research in Africa. A. Ngeny-Mengech (ed.), International Foundation for Science (IFS), Nairobi, Kenya.

———, **and P. O. Gwada.** 1998. Mangrove of Mida Creek. Ecological survey of Mida Creek. Final technical report. Kenya Wildlife Services, Mombasa, Kenya.

———, **and** ———. Mangrove of Kwale district. Structural inventory. Kenya Wildlife Services, Mombasa, Kenya. (in preparation).

———, **and B. Kiryatu.** 2000. Mangrove management survey with and adjacent to Kiunga Marine National Reserve. WWF project KE0087.01, Technical Report. WWF EARO, Nairobi, Kenya/UNESCO, Nairobi, Kenya.

———, ———, **F. Dahdouh-Guebas, N. Koedam, D. Van Speybroeck, and C. Ochieng.** n.d. a. Natural regeneration status of mangrove forests in Mida Creek, Kenya.

———, **B. Kivyatu, J. Chruch, F. Dahdouh-Guebas, N. Koedam, and R. Höft.** n.d. b. Management survey of mangrove forests within the marine protected area of Kiunga, Kenya.

**Kennedy, A.** 1988. Mida Creek—a study of human impact. (Thesis) University of Edinburgh, Scotland, U.K.

**Kenya Forestry Master Plan.** 1994. Development Programmes. Ministry of Environment and Natural Resources, Nairobi, Kenya.

**KIFCON.** 1995. Arabuko Sokoke Forest and Mida Creek. The offical guide. Kenya Indigenous Forest Conservation Programme. Kenya Wildlife Service/Forestry Department, Nairobi, Kenya.

**Kokwaro, J. O.** 1985. The distribution and economic importance of the mangrove forests of Kenya. Journal of the East Africa Natural History Society and National Museum 75(188):1–10.

**Rawlins, S. P.** 1957. The East-African mangrove trade. Unpublished manuscript #51 of the National Museum of Kenya, Nairobi, Kenya.

**Reddy, S. R. C., and S. P. Chakravarty.** 1999. Forest dependence and income distribution in a subsistence economy: evidence from India. World Development 27(7):1141–1149.

**Roberts, R. W., and W. W. Ruara.** 1967. Lamu Mangrove Inventory. Forest Department, Nairobi, Kenya.

**Salim, A. I.** 1985. Kenya's people. People of the coast: Swahili. Evans Brothers Limited, Nairobi, Kenya.

**SFFL.** 1997. Performance report for the years 1994, 1995 and 1996. Small Fishers Federation of Lanka, Pambala, Kakkapalliya, Sri Lanka.

**Spalding, M., F. Blasco, and C. Field.** 1997. World mangrove atlas. The International Society for Mangrove Ecosystems, Okinawa, Japan.

**Tomlinson, P. B.** 1986. The botany of mangroves. Cambridge University Press, Cambridge, UK.

## APPENDIX 1

### QUESTIONNAIRE USED DURING THE FIELD SURVEY

1. What do you understand by the term mangrove?
2. What are the uses of mangrove within your household?
    a) Fuel-wood (firewood and charcoal)
    b) Timber (house and boat construction)
    c) Medicinal products (medicine and ointments)
    d) Furniture (chairs, tables, shelves, utensils, boat masts, paddles, fishing equipment)
    e) Food (for man and animal feeds)
    f) Others (specify)
3. Which of the above listed uses is the most used within your household?
4. Do you have a preferred species of mangrove for use as poles for house construction? If so, which one (vernacular names)?
5. How long do the houses last once constructed with mangrove poles, before they require replacing?
6. Where, within the forest, does the harvesting activity take place?
    a) long the forest edge, closest to home
    b) Deep in the heart of the forest
    c) In a forest region that is far off and requires traveling
    d) Do not know
7. How do you organize your harvesting?
8. How frequently do you visit the forest to harvest mangroves?
    a) At least once a month
    b) Once a month
    c) Twice a month
    d) Once in two months
    e) Whenever necessary (specify)
9. What is the size of your household?

10. Do you harvest mangroves for uses other than those within your household? If so, for what purposes?
    a) Small trading
    b) To stock in a commercial place
    c) Other uses (specify)
11. Do you buy mangrove poles? If yes, from whom?
12. Has it become easier or more difficult to harvest mangroves? Why do you think so? Has the forest changed?

# Chapter III.

## A review of the floral composition and distribution of mangroves in Sri Lanka.

Jayatissa, L.P., F. Dahdouh-Guebas & N. Koedam

Engaged in a peer-review process

# A review of the floral composition and distribution of mangroves in Sri Lanka.

Jayatissa, L.P.[1], F. Dahdouh-Guebas[2] & N. Koedam[3]

[1] *Department of Botany, University of Ruhuna, Matara, Sri Lanka, lpj@cc.ruh.ac.lk*
[2] *Laboratory of General Botany and Nature Management, Mangrove Management Group, Vrije Universiteit Brussel, Pleinlaan 2, B-1050 Brussels, Belgium, fdahdouh@vub.ac.be, nikoedam@vub.ac.be*

## Abstract

Recently published reports list numbers and distributions of mangrove species that outnumbers the actual number of species present in the field. The present study serves to review this literature, highlight the causes of such large species numbers of Sri Lankan mangrove species while providing an objective and realistic review of the mangrove species actually present in Sri Lanka today. This study is based on standardised fieldwork over a 4-year period using well-established diagnostic identification keys. The study indicates that there are at present 20 identified 'mangrove species' (major and minor components) and at least 18 'mangrove associates' along the Southwestern coast of the island, and addresses the importance of clearly defining these terms. The use of erroneous mangrove species compositions reported in the past for Sri Lanka has adversely affected interpretation in the framework of biogeography, remote sensing and biological conservation and management.

Keywords : mangrove, mangrove associates, species composition, biogeography, remote sensing, conservation, Sri Lanka.

## Introduction

Mangrove communities comprise a group of biotic components, including plants, animals and microbial organisms, which are highly adapted to intertidal environmental conditions. However, none of these can be identified as a community in a mangrove ecosystem without the actual mangrove plants (trees and shrubs), implying that the true mangrove vegetation is the major constituent of the ecosystem. Mangrove vegetation defines the landscape and participates directly or indirectly in the ecological processes that take place in this ecosystem (Lugo & Snedaker, 1974; Hamilton & Snedaker, 1984; Tomlinson, 1986). Therefore, knowledge of the exact species composition of mangroves in any country is a basic and important prerequisite in the understanding of all the aspects of structure and function of mangroves as well as its biogeographical affinities and their conservation and management. The past and present distribution of mangroves has been reviewed by several authors on a global level (*e.g.* Tomlinson, 1986; Ricklefs & Latham, 1993; Duke, 1995; Duke *et al.*, 1998; Ellison *et al.*, 1999). In this paper we focus on the local distribution of mangroves, namely in Sri Lanka.

The species richness of mangroves in many geographical areas is decreasing with time as a result of the destruction of mangrove forests and exposure to various anthropogenic stresses (Hamilton & Snedaker, 1984). The area and floristic composition of mangrove forests in Sri Lanka has also decreased at a high rate during the last few decades (De Silva & Balasubramaniam, 1984-85; Pernetta, 1993; Corea *et al.*, 1995; Dahdouh-Guebas *et al.*, 2000a; Dahdouh-Guebas *et al.*, 2000c), possibly leading to the local extinction of some rare species. Peculiarly, some recent documents from governmental and national institutes have reported a number of new records of mangrove species for Sri Lanka new for the record and these publications (*e.g.* Liyanage, 1997) have erroneous species identifications and a list of mangrove species far longer than what is present in reality. There is also a general trend amongst researchers to include mangrove associates or beach vegetation that occurs occasionally within the mangrove when reporting the total number of mangrove species. The danger of such reports, particularly of governmental origin (*e.g.* from a national Forest Department), is that authors seeking data on national mangrove species distribution can readily adapt them. Unfortunately, the inclusion of fictional and non-mangrove species counters the value of such biological data on the distribution of species and may lead to wrong conclusions in the framework of, for instance, biogeographical research.

The objectives of this study are to review the existing literature on Sri Lankan mangrove species and to provide an up-to-date list of the authentic floral composition of mangrove ecosystems in Sri Lanka, emphasizing 'mangrove species' and 'mangrove associates' (see below). The possible effects of erroneous mangrove species lists are discussed in the contexts of biogeography, remote sensing and biological conservation.

## Material & Methods

### *Mangrove definitions*

A good definition for mangrove plants is a pre-requisite to indicate the species richness of mangroves in any geographical area. Until present no absolute definition to distinguish clearly between the mangrove and non-mangrove species has been followed. This can in part be explained by the merging of mangrove vegetation with salt marshes, seashore vegetation, fresh-water marsh vegetation or other terrestrial vegetation bordering mangals and the introgression of eurytopic species. The non-mangrove vegetation generally occurs at the landward margins of mangroves or at the freshwater influx side.

To reduce some of the confusion, several authors have recognized two categories of plants in mangrove communities as 'plants, which are restricted to mangrove habitats' and 'plants, which are not restricted to mangrove habitats'. However, the terminology of these two categories varies according to the literature. Lugo & Snedaker (1974) and Arulchelvam (1968) for instance named them as 'true mangroves' and 'mangrove associates' whilst Saenger *et al.* (1983) and Ricklefs & Latham (1993) and designated them as 'exclusive mangroves' and 'non-exclusive mangroves'. These two groups have been further subdivided and separated in a more descriptive way by Tomlinson (1986) and named 'major mangrove components = true or strict mangroves', 'minor mangrove components' and 'mangrove associates'. In the present study we follow this division and, like Tomlinson (*loc. cit.*), use the term 'mangrove species' to refer to the first two groups. Duke (1992) prepared the ground for a better definition of what is a mangrove and what is not, and he highlights that the emphasis of the definition is on the species which 'normally' grow in the intertidal zone, 'normally' being defined on the basis of wide-ranging field observations. The definition Duke (*loc. cit.*) adopts for a mangrove is 'a tree, shrub, palm or ground fern, generally exceeding one half meter in height, and which normally grows above mean sea level in the intertidal zone of marine coastal environments, or estuarine margins. We decided however to consider the genus *Acrostichum* as a mangrove associate in this study, unlike Tomlinson (1986) or Duke (1992), for the following two reasons : first, it is by no means restricted to mangrove ecosystems in Sri Lanka (pers. obs.) and also elsewhere it has been reported to occur away from mangals (Adams & Tomlinson, 1979; Tomlinson, 1986); secondly, unlike all the other minor mangrove components, which are woody, it is a ground fern that does not allow the same scientific approach as for woody plants in the study of mangrove ecology (*e.g.* measurement of common forestry characteristics in virtually pure stands).

### *Fieldwork*

Along the coastal belt over a distance of approximately 390 km ranging from Palatupana (6° 14' N; 81°14' E) to Puttalam (8° 07' N; 81°46' E) all mangrove communities were visited and the species composition recorded (Fig. 1). At present, due to political disturbance, it is the only safely accessible part of the coastal belt. However, it represents all the climatic divisions (Mueller-Dombois, 1968) and most of the major soil types (Panabokke, 1967) characteristic of coastal areas in Sri Lanka. Mangrove populations along this section of the coast, and within each site those parts of the mangrove with different physiognomic aspects, were visited in a period from 1996 to 1999. All vascular plants and ferns were identified in the field using Duke & Bunt (1979), Tomlinson (1986), Duke & Jackes (1987), Banerjee *et al.* (1989), Duke (1991) and the Revised series of the Flora of Ceylon (Dassanayake & Fosberg, 1980; Dassanayake & Fosberg, 1981a, 1981b; Dassanayake & Fosberg, 1983 ; Dassanayake & Fosberg, 1985; Dassanayake & Fosberg, 1987; Dassanayake & Fosberg, 1991; Dassanayake & Fosberg, 1994; Dassanayake *et al.*, 1995; Dassanayake *et al.*, 1996; Dassanayake *et al.*, 1997; Dassanayake *et al.*, 1998), and herbarium specimens for all the true mangrove species and common mangrove associates were prepared. The fresh or herbarium specimens were checked against the ones present in the National Herbarium at the Royal Botanical Gardens in Peradeniya (Sri Lanka) and with collections from the Department of Botany at the University of Ruhuna. All sites have been visited at least once at the time of flowering of the different species to crosscheck identification with flower based diagnostic features. The total abundance of plants was estimated based on best professional judgment from field visits and field knowledge, and expressed as 'very common', 'common', 'rare' or 'very rare'. Seven mangrove lagoon communities covering a range of 270 kilometers (*i.e.* Lunama, Kalamatiya, Rekawa, Dondra, Unawatuna-Galle, Negombo and Pambala-Chilaw) along the coastal belt were studied in detail in the framework of related studies on mangrove ecology (Jayatissa, 1987; Ladavid, 1995; Thomaes, 1995; Verheyden, 1997; Zetterström, 1998; Dahdouh-Guebas *et al.*, 2000a; Dahdouh-Guebas *et al.*, 2000c; Verheyden *et al.*, subm.).

Altogether 43 mangrove communities bordering lagoons, estuaries and other coastal water bodies were recorded on the coastal belt from Palatupana to Puttalam. The mangrove area of the Puttalam lagoon was the largest in the area and its extent has been estimated to about 1800 ha (Kanakaratne *et al.*, 1984). Mangrove communities of moderate areas fringe the lagoons of Chilaw, Negombo and Rekawa. All the other mangrove communities were small and less than 100 ha in area. However, for some mangroves, it is quite difficult to determine the extent, as their boundaries are not clear. Particularly, some estuarine mangroves in the wet zone extend backward to cover extensive flood plains of rivers where mangrove associates (*e.g. Annona glabra* L., *Acrostichum aureum* L., *Cerbera manghas* L., *Dolichandrone spathacea* (L.f.) K. Schumann, etc.) are dominant and some true mangrove species are distributed sporadically.

## Results & Discussion

The mangrove communities from Palatupana to Puttalam, are probably representative for the mangrove communities in the whole of Sri Lanka, because they are located in areas representing all the climatic zones (Mueller-Dombois, 1968) and most of the major soil types (Panabokke, 1967). Climate and soil texture are two of the major factors affecting the composition and distribution of mangrove species. These mangroves constitute, apart from some major contiguous areas such as Negombo and Puttalam Lagoons, fairly small patches, possibly allowing for a great diversity of ecological conditions and management practices. In total we found 20 mangrove species along the Sri Lankan southwest coast, all of which were included already in the National Herbarium in Peradeniya.

### *Sri Lankan mangrove species observed in this study*

The diversity in mangrove species composition can be seen from Appendix I. The earlier report of 9 mangrove species for Chilaw Lagoon by the Wetland Conservation Project (1994) and its conclusion that the biological diversity in this lagoon could have been undervalued because of their incomplete species lists, proves very true when considering the 16 species reported in the this study. The higher species richness of mangroves in the intermediate climate zone as compared to the dry or wet climate zone (Tab. 1; Appendix I) is probably due to the fact that at least some environmental factors may not go to the extreme high or low levels in the intermediate zone and these moderate conditions may favour more a number of species. It is also possible that the variety of habitats available to mangroves is higher in intermediate rainfall areas because there is a mixture of wet and dry sites that would not be present either at the wet or dry end of the environmental spectrum.

Underneath we will focus on the globally polyspecific genera to highlight the diagnostic features we used to distinguish between species.

Within the *Avicennia* genus only *Avicennia alba* Blume, *A. marina* (Forsk.) Vierh. (or *A. marina* var. *marina*), *A. officinalis* L. and *A. rumphiana* Hallier f. appear in the Indo-Malaysia biogeographic region and only the former three species reach the Indian subcontinent (Duke, 1991; Duke *et al.*, 1998). In Sri Lanka the key diagnostic feature to distinguish *A. officinalis* from *A. marina* based are the rounded leaf tips of the former species. Although we did not observe *A. alba*, we know this species has propagules that are elongated and have a sharp tip, most remarkable within the entire genus.

Although there is some plasticity in *Bruguiera* (see further), we could distinguish well among species based on the flowers (and knowing the global distribution of the species). The three filamentous appendages on the petals, in open flowers as well as in closed immature flowers, were a diagnostic feature in differentiating *B. gymnorrhiza* (L.) Lamk. from *B. sexangula* (Lour.) Poir. We found the descriptions given in Tomlinson (1986) useful for this purpose, and also to distinguish between the two *Ceriops* species we used his diagnostic keys. Noteworthy at this point is the field knowledge of Mr. Daglas Thisera, who grew up in the mangrove and was active as a fisherman for 18 years after dropping out of school, and who then was selected as the Coordinator Mangrove Conservation and Education at the Small Fishers Federation of Lanka. This local man knows how to distinguish between species based on the integration of characteristics that go beyond what is currently translated into diagnostic keys. However, when a species is crosschecked with the latter, his answer always proved

correct. According to him it appears for instance that the density of the branches and of the leaf rosettes and the way they are from a physiognomic point of view is different in *B. sexangula* and *B. gymnorrhiza*.
Of the small-flowered *Bruguiera* species, only *B. cylindrica* (L.) Blume was encountered, which can be distinguished from *Bruguiera parviflora* Wight & Arnold ex. Griffith based on calyx and petal proportions, and from *Bruguiera hainesii* C.G. Rogers based on the same as well as on petal length.

Arulchelvam (1968) was the first to report that *Xylocarpus moluccensis* (Lamk.) Roem. occurs in Sri Lanka. However, according to the description and drawings given in his paper (*loc. cit.*), it is obvious that *Cynometra iripa* Kostel was misidentified as *Xylocarpus moluccensis*. The same mistake was followed by other authors as well (*e.g.* Pinto, 1986). Although De Silva & Balasubramaniam (1984) included both *X. moluccensis* and *C. iripa* in their list of mangrove species and referred to Arulchelvam's study (1968) without further taxonomic descriptions or localities given for either species, the original misidentification by Arulchelvam (*loc.cit.*) has not been corrected by them. Whereas Arulchelvam (*loc.cit.*) has reported that *X. moluccensis* (in reality *Cynometra iripa*) has been recorded in Batticaloa lagoon only (Sri Lankan East-Coast), this study now shows that, although still a very rare species, few specimens of *Cynometra iripa* are actually present in the lagoons of Rekawa and Puttalam (Fig. 1).

The presence of *Xylocarpus moluccensis* or *Xylocarpus mekongensis* Pierre in Sri Lanka remains doubtful. Although these species have been included into the list of mangrove species by several authors (*e.g.* Amarasinghe, 1996; Liyanage, 1997), no researcher has given a proper taxonomic description and other authors do not report its presence in publications featuring global mangrove distribution (Tomlinson, 1986; Duke, 1992; Spalding *et al.*, 1997; Duke *et al.*, 1998). A few trees of a *Xylocarpus* species that is not a mangrove but a halophyte, and that inhabits sandy shores (beach vegetation), were recorded from Unawatuna Bay on the Southwest coast of Sri Lanka as the sole location. Its characteristics fit well with the short description given by Tomlinson (1986) for *X. moluccensis*, but it has been identified as *X. rumphii* by Mabberley (1995). Amarasinghe (1996) and Liyanage (1997) also followed the same nomenclature, but categorized it as a 'mangrove species'. Unfortunately taxonomic descriptions of the less common *Xylocarpus* species are deficient because it has not been recognized until fairly recently that flowers are unisexual (Tomlinson, 1986).
Within the genus, *Xylocarpus granatum* Koenig can easily be distinguished on basis of its flaking bark and its very large fruits, at least 20 cm in diameter. In Kenya, many *X. granatum* fruits grow larger than this size (pers. obs.).

Although *Heritiera fomes* Buch.-Ham. occurs on the Indian subcontinent, based on our observations of an extended fruit with a single ridge we found *Heritiera littoralis* Dryand. to be the only representative species of its genus.

*Excoecaria indica* (Willd.) Muell.-Arg. was found in considerable numbers in the Tillawatawana Lagoon, Bentota Estuary and Gin Oya, and in smaller numbers in Pambala-Chilaw lagoon. It may be restricted to mangrove area or appear in the back mangrove where it blends with terrestrial vegetation. It is typically distinguished from *Excoecaria agallocha* L. by its green fruit the size of a cherry, and by its thorny trunk. It is however claimed that this species might have been recorded previously in Sri Lanka under the synonym *Sapium indicum*, the nomenclature of which was however not reported by Tomlinson (1986). It thus remains unclear whether or not this is the first time *E. indica* is being reported for Sri Lanka.

*Lumnitzera littorea* (Jack) Voigt (= *L. coccinea* Wight & Arnold) and *Scyphiphora hydrophyllacea* Gaertn.f. were recorded 40 years ago for the first time by Abeywickrema (1960) and have now become very rare species in Sri Lanka. At the moment, a few trees of *L. littorea*, with their typical red flowers, can be seen at one locality in one of the small islands in the Balapitiya estuary (fig. 1), but 40 years ago it was recorded in the Bentota river estuary as well (Abeywickrema, pers. comm.). A few trees of *Scyphiphora hydrophyllacea* are also restricted to one locality on the Kalpitiya Peninsula in Puttalam lagoon (Fig. 1).

*Sonneratia alba* J. Smith was recorded in this study as a species with a limited distribution in the dry climate zone and it appears to be replaced by *Sonneratia caseolaris* (L.) Engler in the wet zone.
*Sonneratia apetala* Buch.-Ham, which is perhaps the most distinctive species in its genus because of its tiny fruits, was not reported in this study. It was however recorded 20 years ago as a very rare species in Sri Lanka with a population of six trees near Muttur in the estuary of Koddiyar river (Macnae & Fosberg, 1981). However, no recent report exists to re-confirm this.

In our study we encountered only two known representatives of *Rhizophora* : *R. apiculata* Blume and *R. mucronata* Lamk., and identified these species based on the inflorescence and the propagules (*cf.* Duke & Bunt, 1979), and their relative positions with respect to the leaf rosette. We are however not familiar with other *Rhizophora* species that are potentially present in Sri Lanka (we think of *R. stylosa* Griff. which is present in India and of its possible hybrid *R.* x *lamarckii* Montr. formed together with *R. apiculata* as the second putative parent). In addition, Duke *et al.* (1998) state that major systematic problems exist with the *Rhizophora* genus.

The existence of mangrove hybrids must also be highlighted. A *Rhizophora* species that is probably a hybrid between *R. apiculata* and *R. mucronata* was found in the Pambala-Chilaw lagoon complex, one out of the three sites where both species occur together (Appendix I). This type of hybrid so far has been named twice : *Rhizophora* x *lombokensis* Baba and Hayashi 1994 (Baba, 1994), and *R. annamalai* Kathiresan (Kathiresan, 1995). Both reports aimed at naming the apparent new plant without providing much detail about the plant itself. The possible hybrid has not occurred in systematic contributions to mangrove literature any more since its report, but its existence was briefly highlighted in a study on the molecular phylogeny of mangroves (Parani *et al.*, 1997). The Sri Lankan putative hybrid is currently being investigated in-depth on a morphologic and genetic level by Jayatissa, Abeysinghe, Dahdouh-Guebas, Duke, Triest & Koedam (unpublished results).

Although no other mangrove hybrids were found during the course of this study, it should be highlighted that there are a number of sites where putative parents from existing hybrids occur together, meaning that the possibility for the respective hybrids to occur is always there. This is the case for *Lumnitzera* x *rosea* (Gaud.) Presl. (hybrid between *L. littorea* and *L. racemosa* Willd.) in Balapitiya, and *Sonneratia* x *gulngai* N.C. Duke (hybrid between *S. alba* and *S. caseolaris*) in Negombo Lagoon and in Pambala-Chilaw Lagoon. As for the possible putative hybrid between *Bruguiera gymnorrhiza* and *B. sexangula* that appears to exist in Sri Lanka, when such individuals originating from mixed *B. gymnorrhiza* – *B. sexangula* mixed stands are analysed on a genetic level, they all separate well, with no hybrid position between the two taxa (Abeysinghe *et al.*, 1999; Abeysinghe *et al.*, 2000).

### *Sri Lankan mangrove species reported in earlier studies and by the Forest Department*

Table 2 shows the species compositions of true mangroves in Sri Lanka according to different national and international reports as well as results observed in the present study. Note that more and more mangrove species are reported in more recent national reports. Also Duke (1992) reported a steady increase in species numbers from 19 to 39 for Australia over the last 23 years. However, there is a slight difference between the situation in Australia and Sri Lanka. If all the literature reports on the species composition in Sri Lankan mangroves were both accurate and precise, then this country counts 38 mangrove species (Tab. 2), which approximates the number of species in the most species diverse mangrove longitudinal sections in the world, *i.e.* between 135° E and 150° E (Tomlinson, 1986; Duke, 1992; Ellison *et al.*, 1999). If filtered according to our definition of 'mangrove species' the total number of species in Sri Lanka would still amount to 29 species. These are fascinating numbers, also because all these species are not only restricted to a longitudinal section inferior to 2°30', as compared to the 15° section mentioned above, but also to a small area of approximately 10 000 ha (Pemadasa, 1997), which in addition is fragmented to a high degree (De Silva & Balasubramaniam, 1984-85). The literature reports citing such high species numbers therefore necessitated a review (this study) of which species are present in Sri Lanka, what leads to the lists outnumbering the actual species composition and what are the scientific implications of such lists.

As described above, the 20 mangrove species reported in the present study are contrasting with an additional 9 to 18 species mentioned in earlier reports. It is a fact that this study was restricted to Southern and Western coasts of Sri Lanka, mainly because the other areas of the coasts are not accessible for researchers since 1983 due to the prevailing security situation. However, since all the reports that give additional species were published after 1983 as well, it implies that they were concentrated along the same coastal area as the present study and therefore the reliability of some of these must be questioned.

Five species out of the above mentioned additional species, *i.e. Avicennia alba*, *Bruguiera hainesii*, *Bruguiera parviflora*, *Kandelia candel* (L.) Druce and *Phoenix paludosa* Roxb., were included to the list of mangrove species in Sri Lanka for the first time by Rao (1984). It is not clear how these species were incorporated into this report, since a survey on mangroves in Sri Lanka was not actually conducted and the sole publication Rao (*loc. cit.*) referred to in order to obtain information on Sri Lankan mangroves is a paper by Jayawardene (1986). However, the latter publication does not list any of the above five species either. One could infer, without justification, that some of these species were included because of their presence in the neighbouring country India, such as *Kandelia candel* in the Ganges Delta.

Amarasinghe (1996) and Liyanage (1997) have given almost similar lists of mangroves in Sri Lanka including a number of species that were not recorded in our study. However, only the species given by Liyanage (1997), a publication by the Forest Department of Sri Lanka, will be taken into consideration here, since the list given by Amarasinghe (1996) was based on information received from the Forest Department and thus is subject to the same criticism.

It is clear that *Acanthus volubilis* Wall. was included into the list of mangroves in Sri Lanka by Liyanage (1997) as a result of obvious misidentification. According to Tomlinson (1986) and Banerjee *et al.* (1989) the diagnostic differences between *Acanthus ilicifolius* L. and *A. volubilis* are as follows : the corolla of *A. ilicifolius* is blue or violet, but rarely white, bracteoles are persistent, plants are robust and erect with spiny leaves, but some times leaves can be spineless. The corolla of *A. volubilis* on the other hand, is always white, bracteoles are absent, plants are usually unarmed and twining with delicate sprawling stems. The description and photographs given in Liyanage (1997) for *A. volubilis* reveal that the only character of the observed specimen used to identify the particular species as such is the white colour of the flowers, whereas this can be a feature of *A. ilicifolius* as well (see description; pers. obs.). In the present study, we have inspected herbarium and live specimens located in Pambala-Chilaw lagoon (one of our main research areas on mangrove ecosystems) of the plant claimed to be *A. volubilis* (*loc.cit.*) and confirm that it is a whitish flowered form of *A. ilicifolius*, based on diagnostic characteristics of flowers, fruits and general plant morphology (*e.g.* the same plant also carries purple flowers, the fruits are large, the plant is always very spiny). In addition, the purple colour of the stem, claimed to be another characteristic of *A. volubilis* (*loc.cit.*), are not evident from the photographs given and are but another very plastic morphological characteristic in our opinion, since *A. ilicifolius* specimens have been recorded with stems that are green in colour, purple or in between (pers. obs.). Sri Lankan field botanists who have identified *A. volubilis* in India, also confirm that the Sri Lankan specimens under question are not in line with the diagnostic characteristics of *A. volubilis* (Dr. P. L. Hettiarachchi, pers. comm., 1997). Rather, in some instances we were first dealing with an ambiguity between *A. ilicifolius* and *A. ebracteatus* Vahl. in Pambala. It must however be highlighted that a large plasticity exists between the members of this genus (Tomlinson, 1986).

Next to Rao (1987), also Liyanage (1997) reported the presence of *Avicennia alba* in Sri Lanka. However, unlike Rao (1987) who included the species into his list of mangrove species without further details, Liyanage (1997) has given a description and localities of the species with a technical drawing (Fig. 2). This description is not sharp enough to distinguish *A. alba* from the other two *Avicennia* species that occur in Sri Lanka. In the present study the localities given by Liyanage (*loc. cit.*) were re-visited (*i.e.* Puttalam and Seenimodara), but *A. alba* was not found there or anywhere else. Nevertheless, *A. alba*, if present, would be easily recognisable on basis of its elongated and pointed propagule (see previous section). The inclusion of *A. alba* by Liyanage (1997) into the list of mangrove species in Sri Lanka appears to be based on a specimen represented by a copy of the drawing given by Arulchelvam (1968) to illustrate *Avicennia officinalis* (but with slight alterations at leaf tips), and therefore should be rejected (Fig. 2).

*Ceriops decandra* (Griff.) Ding Hou was reported as a mangrove species in Sri Lanka by a few authors without giving a description or locality. Macnae and Fosberg (1981) also quote that they have not observed this species in Sri Lanka. Nevertheless, Liyanage (1997) lists Rekawa Lagoon (Fig. 1, Tab. 1) as he gives a description, an illustration and a locality for this species. However, our joint research experience on mangroves in this lagoon for the last 15 years (Jayatissa, 1987; Thomaes, 1996; Verheyden *et al.*, subm.) lead but to the identification of *Ceriops tagal* (Perr.) C.B. Robinson within this genus. Similar to the previous case, Liyanage (1997) apparently based his drawing on the photograph of *C. tagal* given in the same publication (Liyanage, 1997), but with slight changes in propagule root apex, the major characteristic for differentiation of *C. decandra*. The description given to illustrate this species does not correspond with the actual description of the species by Tomlinson (1986).

*Sonneratia ovata* Backer and *Sonneratia griffithii* Kurz were not recorded in the present study, but were reported by Liyanage (1997) as Sri Lankan mangrove species. The former species was reported as a very rare species observed in Negombo lagoon (*loc. cit.*). According to Tomlinson (1986), *S. ovata* is distinguished by a finely warted calyx, which forms a cup enclosing the base of the fruit, and a fruit apex that is depressed at the base of the style. Liyanage (1997) used the characteristic of the cup-shaped calyx in fruits with a depression at the base of the style to distinguish *S. ovata*, but a neither a photograph nor a drawing was given for this feature. Not only is it important to note that according to Tomlinson (1986) the cup-shaped calyx is a common character for *S. alba* as well, but even more important is that in their revision of the *Sonneratia* genus Duke & Jackes (1987) identified the cup-shaped fruit receptacle to differentiate *S. alba* and *S. x gulngai* from the other members within the genus (incl. *S. ovata*), the latter of which have flattened fruit receptacles. The isolated tree in Negombo lagoon, given in Liyanage (1997) as one of the few locations for *S. ovata*, was visited in the present study and identified as *S. alba*, based on the cup-shaped calyx, on the white petals and on our experience in Kenya.

According to Tomlinson (1986) and Banerjee *et al.* (1989), obovate or suborbicular leaves with conspicuous veins, prominent on the adaxial side, and scarcely developed petioles are some of the characteristics that help to distinguish *S. griffithii* from other *Sonneratia* species. The description and photograph given in Liyanage (1997) for *S. griffithii* suggest that veins are not conspicuous and that petioles are well developed. Another fact stated by Liyanage (1997) is that *S. griffithii* produces pencil-like pneumatophores, commonly found in *Avicennia* species. The photograph given by this author shows indeed pencil-like pneumatophores on the ground surrounding a *Sonneratia* tree (incl. its own peg roots), but the author failed to recognise that these roots originate from the *Avicennia* trees located on the background of the photograph. Therefore, it is clear that the inclusion of both *S. griffithii* and *S. ovata* by Liyanage (1997) is the result of a misidentification.

The mangrove associate *Acrostichum speciosum* Willd. was also reported as a very rare plant recorded only from Hikkaduwa and Akurala mangrove communities (*loc. cit.*). Also in this case the same communities visited in the framework of this study did not reveal the presence of this species there or elsewhere. The drawing given for *A. speciosum* in Liyanage (1997) is similar to the illustration of *A. aureum* and does not distinguish from the latter.

### *Erroneous species lists : what are the consequences for the study of mangroves ?*

The shortcomings of certain national publications mentioned above are extremely important for the scientific community because of their impact in the dissemination of information. Usually scientists seeking information on the distribution of plants in a particular country are directed to the Forest Department. If the information of such institutions is subject of misidentifications, intentional or unintentional, and the erroneous report of more and more mangrove species, this clearly goes at the expense of the quality of information.

In a biogeographical research framework the consequences of the interpretation of such erroneous data can hardly be overseen. For some species, an erroneous presence in Sri Lanka has little influence on their global biogeographical area as for instance in *Ceriops decandra* (Liyanage, 1997) or *Kandelia candel* (Rao, 1987). The latter, for instance, is also present in the Ganges Delta according to Tomlinson (1986) and along about 80% of the Indian coast according to Spalding *et al.* (1997). But for reports of *Sonneratia ovata* or *S. griffithii* (Liyanage, 1997), the impact is far greater and would include a disjunct global distribution pattern with Sri Lanka as a distant outlier. This of course depends on the scale on which this problem is analysed at. Adopting the wide biogeographic regions used by Duke (1992) and Duke *et al.* (1998) there is only a minor difference in the distribution of the above *Sonneratia* species with or without Sri Lanka as a point of occurrence, since they occur within the Indo-Malaysian region in both cases, and *S. ovata* in the Australasian region as well. However, on a smaller scale – but larger than the estuarine scale, hierarchically the next scale in the series of scales used by Duke *et al.* (1998) to discuss the distributional gradients of mangroves – there are peculiar implications. Figure 3 shows that *S. ovata* has a distribution from Thailand through the Malay Peninsula and Malay Archipelago (excl. Borneo) to the Gulf of Papua in New Guinea and into Queensland, whereas *S. griffithii* is restricted to the Andaman Sea, from the upper Malay Peninsula to Bengal. For both species, a presence in Sri Lanka lies relatively far outside their known biogeographical range. Similar discussions can be made for *Bruguiera hainesii* and *B. parviflora*, which are reported for Sri Lanka (*loc. cit.*).

Another implication of the report of erroneous data on species composition resides in the remote sensing of inaccessible or formerly uninvestigated mangrove areas. Considering the continuing unstable political situation in Sri Lanka, remotely sensed mangrove data from the lagoons located along the inaccessible parts of the country are likely to be used in the future. Verheyden *et al.* (subm.) proposed interpretation keys for aerial photography interpretations in three mangrove lagoons in Sri Lanka, which theoretically, in a phase prior to compulsory fieldwork, may be used to preliminary extrapolate to other lagoons. However, erroneous species compositions for those lagoons can easily lead to wrong interpretations in this context as well. For instance, the report of an *Avicennia* species, which displays a light grey or white tonality on aerial photographs, for a lagoon where in reality this genus is poorly represented (*e.g. A. alba* for Puttalam Lagoon by Liyanage, 1997), may lead to confusion with other species with a similar tonality such as the widespread *Excoecaria agallocha*.

Related to the previous discussion is the use of data on species composition for issues like conservation biology. Forests with different species compositions may require very distinct management practises, particularly when involving rare species. For example, a mangrove stand dominated by *E. agallocha*, a species that can resist human disturbance on decadal scale (Dahdouh-Guebas *et al.*, 2000a), probably requires a less strict management than a stand dominated by highly vulnerable mangrove species. Mangrove plants species also extend over a large range of environmental conditions, some of which may suit a particular species, but is fatal to another. Factors that may be decisive in the success or failure of mangrove rehabilitation measures are for instance hydrology (Elster, 2000), salinity (*loc. cit.*) or propagule predation (Weinstock, 1994; Dahdouh-Guebas *et al.*, 1997, 1998). Priorities on resource allocation for conservation may also be diverted by wrong species composition reports. Dealing with the same issue, Cormier-Salem (1999) also emphasized that the definition of 'mangrove species' is not solely an academic debate, but it has political and social implications as well. Apart from the definition of a mangrove in the context of species, she highlights the variability of 'mangrove area' delimitation, which can be defined in a floristic, a faunistic or a human context (*loc. cit.*).

Note that in a country like Sri Lanka (South-Western part), where the actual distribution of the mangrove communities is the result of an increased human-induced fragmentation (De Silva & Balasubramaniam, 1984-85), and where each mangrove community has been easily accessible for a long time, there is a significant relationship between the national reports of mangrove species totals over time. Such a paradoxical situation in these accessible areas can be explained by the national prestige associated to the discovery of additional species presumed by some scientists (pers. obs.), in this case in mangrove ecosystems. In addition, there seems to be an international competition, particular amongst certain researchers from developing countries, to report more and more mangrove species for a particular country and in this way impose a certain type of respect for a country's mangrove species richness. In the latter context the inclusion of mangrove associates or beach vegetation, which occurs occasionally within the mangrove, when reporting the total number of 'mangrove species' is a common trend.

Another problem is the reluctance of some senior scientists to perform fieldwork personally (pers. obs.), particularly within the 'awful' mangrove ecosystem, working with field officers instead. Double-checking is rarely, if ever, done and restricted to a distant visual inspection from the dry terrestrial vegetation or from a boat.

The above lacunas are major causes for the publication of erroneous lists of mangrove species. This is a great shame because, particular for developing countries, this leads to a generalised underestimation of the scientific capabilities of institutes, and the quality of some of the rigorous research papers (*e.g.* Abeywickrema, 1960; De Silva & Balasubramaniam, 1984-85; Dassanayake & Fosberg, 1981; Pemadasa, 1997) may become jeopardised. In addition, investigations on floristics and species composition are one of the few studies that can be carried out in developing countries easily and cheap, and this should not be compromised.

## Conclusion

The present study is intended to provide an objective and realistic revision of the mangrove species present in Sri Lanka, or at least its southwestern part, and to review and highlight the causes of misidentifications of Sri Lankan mangrove in the past. This study therefore required standardised fieldwork of different persons double-checking over a 4-year period using the existing diagnostic identification keys, herbaria and their Indo - East African field knowledge. The use of photographs to illustrate the 20 Sri Lankan mangrove species reported in this study was considered beyond the scope of this paper, but Appendix I provides details on the locations of each species reported.

Three mangrove species (*i.e. Lumnitzera littorea*, *Pemphis acidula* Forst. and *Scyphiphora hydrophyllacea*), one mangrove associate (*i.e. Cynometra iripa*) and one species of beach vegetation plant (*i.e. Xylocarpus rumphii*) were recognized in this study as very rare species (Tab. 1) of which the abundance is restricted to few trees at one or two localities in Sri Lanka. In addition to these very rare species, another three species of true mangrove (*i.e. Bruguiera cylindrica*, *Excoecaria indica* and *Sonneratia alba*) have been recognized as rare species. At the moment, all these species are at serious threat as no systematic attempt has been made to conserve them and educate the local people and to draw attention to their value and current situation. The conversion of mangrove forests for aquaculture purposes for instance (Dahdouh-Guebas *et al.*, 2000c) and pollution of mangrove lands is still going on unchecked (Foell *et al.*, 1999) and indicates many mangroves are 'outlaws'. Therefore the necessity of a urgent and serious attempt to conserve them *in situ* is emphasized.

## Acknowledgements

Many thanks are due to Dr. S. Hettiarachchi and the late Professor M.A. Pemadasa of the Department of Botany of the University of Ruhuna in Matara (Sri Lanka) and Professor B.A. Abeywickrema of the Department of Botany of the University of Colombo, Colombo (Sri Lanka) for their encouragement and help in this work. We are very grateful to Daglas Thisera for his practical help in the field and keen observation, and to Mr. Anuradha Wickramasinghe and the entire staff of the Small Fishers Federation of Lanka (SFFL) at the Mangrove Conservation and Demonstration Centre in Pambala – Kakkapalliya for the excellent logistics. Mr. U. Dhanasekara, Curator of the National Hebarium at the Royal Botanical Garden in Peradeniya is to be acknowledged for his help in comparing our herbarium species with the voucher specimens in the National Herbarium. Norman C. Duke and Robert E. Ricklefs are acknowledged for their critical comments on the manuscript. Research financed by the European Commission (Contract EBR IC18-CT98-0295), and with a specialisation fellowship of the Flemish Institute for the advancement of scientific-technological research in the industry (IWT). This research was presented on the "Symposium on Biodiversity : from genes to landscapes", 13-15 December 2000, Louvain-La-Neuve, Belgium.

**References**

See Bibliography

**Table 1.** Distribution of mangrove species (according to Tomlinson 1986, except the genus *Acrostichum*) and mangrove associates in five representative mangrove forests covering all the climatic zones of Sri Lanka. The indication of abundance includes all 43 mangrove communities (++ = very common; + = common; - = rare; -- = very rare). The asterisk * refers to an endemic species, the question mark ? to an as yet uncertain occurrence (see text).

| **Species** | **Wet Zone** | | **Intermediate Zone** | | **Dry Zone** | |
|---|---|---|---|---|---|---|
| | **Galle-Unawatuna** | **Balapitiya** | **Rekawa** | **Pambala-Chilaw** | **Puttalam** | **Abundance** |
| MANGROVE SPECIES | | | | | | |
| *Aegiceras corniculatum* (L.) Blanco | ● | | ● | ● | ● | + |
| *Avicennia marina* (Forsk.) Vierh. | ● | | ● | ● | ● | ++ |
| *Avicennia officinalis* L. | | | ● | ● | | ++ |
| *Bruguiera cylindrica* (L.) Blume | | | | ● | ● | - |
| *Bruguiera gymnorrhiza* (L.) Lamk. | ● | ● | ● | ● | | + |
| *Bruguiera sexangula* (Lour.) Poir. | ● | ● | ● | ● | | + |
| *Ceriops tagal* (Perr.) C.B. Robinson | | | ● | ● | ● | + |
| *Excoecaria agallocha* L. | ● | ● | ● | ● | ● | ++ |
| *Excoecaria indica* (Willd.) Muell.-Arg. | | | | ● | | -- |
| *Heritiera littoralis* Dryand. | ● | ● | ● | ● | ● | + |
| *Lumnitzera littorea* (Jack) Voigt | | ● | | | | -- |
| *Lumnitzera racemosa* Willd. | ● | ● | ● | ● | ● | ++ |
| *Nypa fruticans* (Thunb.) Wurmb. | | ● | ● | | | + |

| | | | | | | |
|---|---|---|---|---|---|---|
| *Pemphis acidula* Forst. | ● | | | | ● | -- |
| *Rhizophora apiculata* BL. | ● | ● | | ● | | + |
| *Rhizophora mucronata* Lamk. | | | ● | ● | ● | + |
| *Rhizophora annamalai* Kathiresan | | | | ? | | |
| *Scyphiphora hydrophyllacea* Gaertn.f. | | | | | ● | -- |
| *Sonneratia alba* J. Smith | | | | ● | ● | - |
| *Sonneratia caseolaris* (L.) Engler | ● | | | ● | | + |
| *Xylocarpus granatum* König | | | | ● | | + |
| Total number of mangrove species | **10** | **8** | **11** | **16** | **11** | |
| MANGROVE ASSOCIATES | | | | | | |
| *Acanthus ilicifolius* L. | ● | ● | ● | ● | ● | ++ |
| *Acrostichum aureum* L. | ● | ● | ● | ● | ● | ++ |
| *Annona glabra* L. | ● | ● | | ● | | + |
| *Barringtonia asiatica* (L.) Kurz. | ● | | | | | + |
| *Barringtonia racemosa* (L.) Spreng. | ● | ● | ● | | | + |
| *Callophyllum inophyllum* L. | ● | ● | ● | ● | ● | + |
| *Cerbera manghas* L. | ● | ● | ● | ● | ● | + |
| *Clerodendron inerme* (L.) Gaertn. | ● | ● | ● | ● | ● | ++ |
| *Cynometra iripa* Kostel | | | ● | | ● | -- |
| *Derris* spp | ● | ● | ● | ● | ● | + |
| *Dolichandrone spathacea* (L.f.) K. Schumann | ● | ● | ● | ● | | + |
| *Hibiscus tiliaceus* L. | ● | ● | ● | ● | ● | ++ |
| *Phoenix zeylanica* Trim.* | | ● | ● | ● | | + |
| *Premna integrifolia* Lam. (= *P. foetida* Reinw.) | ● | ● | ● | ● | ● | + |
| *Sphaeranthus amaranthoides* Burm. F. | | | ● | | ● | - |
| *Tamarix galica* L. | | | | ● | ● | - |
| *Thespesia populnea* (L.) Soland. ex.Corr. | ● | ● | ● | ● | ● | ++ |
| Total number of mangrove associates | **14** | **13** | **14** | **13** | **12** | |

**Table 2. Review of the species composition of mangroves as reported by various Sri Lankan authors.**
● = reported by other authors or in this study; O = recorded but not considered a true mangrove species. The total number of species for the present study has been computed with the species considered to be true mangroves only.

| Plants listed as mangrove species in scientific literature | Abeywickrema, 1960 | Arulchelvam, 1968 | De Silva & Balasubramaniam, 1984 | Nanayakkara, 1986 | Pinto, 1986 | Jayawardena, 1986 | Rao, 1987 | Amarasinghe, 1996 | Liyanage, 1997 | **Jayatissa *et al.* (THIS STUDY)** |
|---|---|---|---|---|---|---|---|---|---|---|
| *Acanthus ilicifolius* L. | ● | ● | ● | ● | ● | ● | ● | ● | ● | O |
| *Acanthus volubilis* Wall. | | | | | | | | ● | ● | |
| *Acrostichum aureum* L. | | | | | | | | ● | ● | O |
| *Acrostichum speciosum* Willd. | | | | | | | | ● | ● | |
| *Aegiceras corniculatum* (L.) Blanco | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● |
| *Avicennia alba* Blume | | | | | | | ● | ● | ● | |
| *Avicennia marina* (Forsk.) Vierh. | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● |
| *Avicennia officinalis* L. | ● | ● | ● | ● | ● | ● | | ● | ● | ● |
| *Bruguiera cylindrica* (L.) Blume | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● |
| *Bruguiera gymnorrhiza* (L.) Lamk. | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● |
| *Bruguiera hainesii* C.G. Rogers | | | | | | | ● | | | |
| *Bruguiera parviflora* Wight & Arnold ex. Griffith | | | | | | | ● | | | |
| *Bruguiera sexangula* (Lour.) Poir. | ● | | ● | | ● | ● | ● | ● | ● | ● |
| *Ceriops decandra* (Griff.) Ding Hou | ● | | ● | | ● | ● | ● | ● | ● | |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| *Ceriops tagal* (Perr.) C.B. Robinson | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● |
| *Cynometra iripa* Kostel | | | ● | | | | | | | ○ |
| *Dolichandrone spathacea* (L.f.) K. Schumann | | | | | | | | | | ○ |
| *Excoecaria agallocha* L. | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● |
| *Excoecaria indica* (Willd.) Muell.-Arg. | | | | | | | | | | ● |
| *Heritiera littoralis* Dryand. | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● |
| *Kandelia candel* (L.) Druce | | | | | | | ● | | | |
| *Lumnitzera littorea* (Jack) Voigt | ● | | ● | | | | ● | ● | ● | ● |
| *Lumnitzera racemosa* Willd. | ● | ● | ● | ● | ● | ● | | ● | ● | ● |
| *Nypa fruticans* (Thunb.) Wurmb. | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● |
| *Pemphis acidula* Forst. | | | | | | | | ● | | ● |
| *Phoenix paludosa* Roxb. | | | | | | | ● | | | |
| *Rhizophora apiculata* BL. | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● |
| *Rhizophora mucronata* Lamk. | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● |
| *Rhizophora annamalai* Kathiresan | | | | | | | | | | ? |
| *Scyphiphora hydrophyllacea* Gaertn.f. | ● | | ● | | | ● | ● | ● | ● | ● |
| *Sonneratia alba* J. Smith | | | ● | | ● | ● | ● | | ● | ● |
| *Sonneraria apetala* Buch.-Ham | | | ● | | ● | ● | ● | | | |
| *Sonneratia caseolaris* (L.) Engler | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● |
| *Sonneratia griffithii* Kurz | | | | | | | | ● | ● | |
| *Sonneratia ovata* Backer | | | | | | | | ● | ● | |
| *Xylocarpus granatum* König | | ● | ● | ● | ● | ● | ● | ● | ● | ● |
| *Xylocarpus moluccensis* (Lamk.) Roem. | | ● | ● | ● | ● | ● | ● | ● | | |
| *Xylocarpus mekongensis* Pierre | | | | | | | | ● | ● | |
| Xylocarpus rumphii | | | | | | | | ● | ● | ○ |
| Total number of species | **18** | **16** | **23** | **16** | **20** | **21** | **25** | **29** | **28** | **20**<br>**(+ 1?)** |

**Figure 1.** Map of Sri Lanka showing the different climatic zones (Mueller-Dombois, 1968) and some of the major cities along the coast. Dots represent the lagoons investigated (see Appendix I for numbers, and the names of five representative mangrove lagoons (Tab. 1) are indicated in frames.

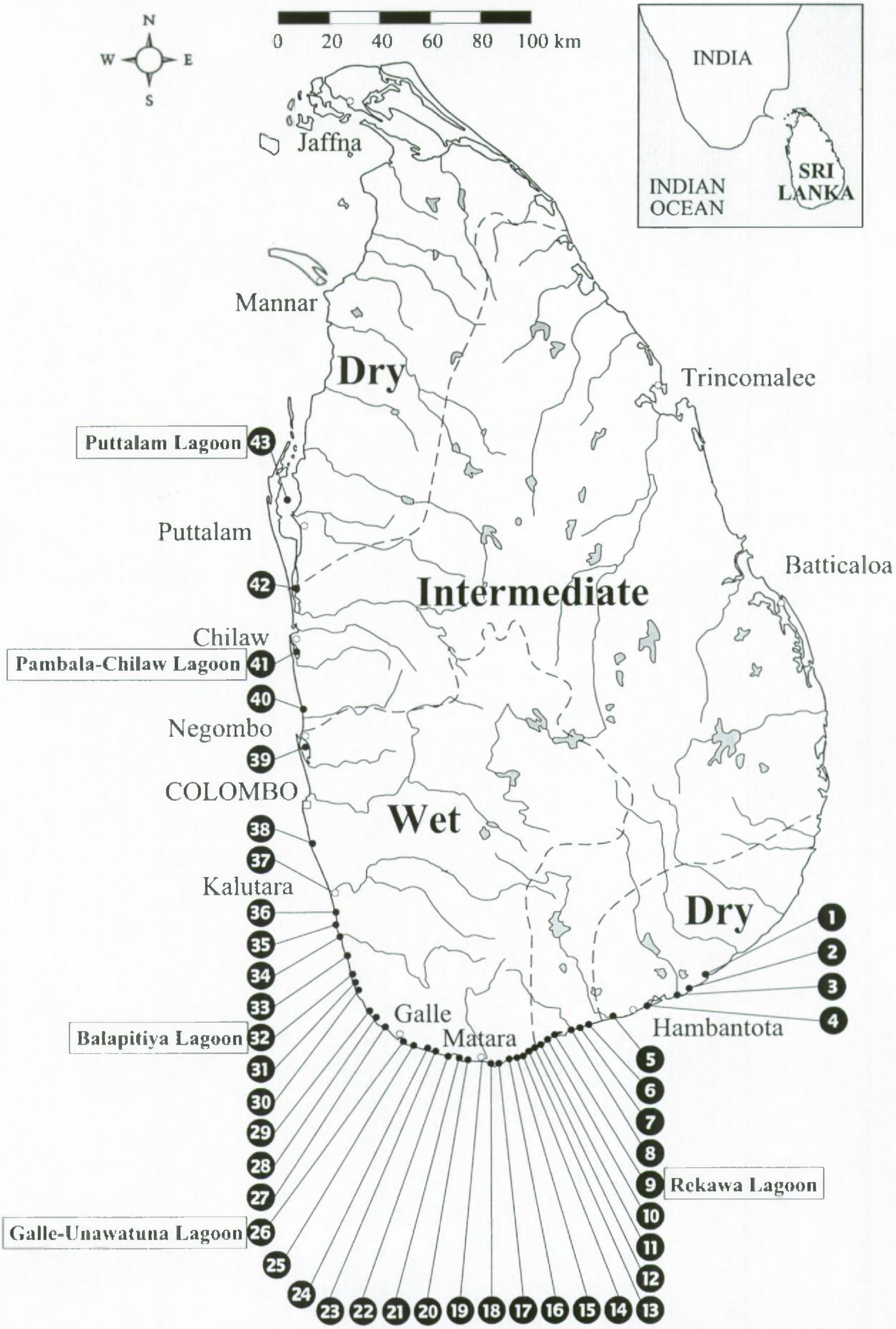
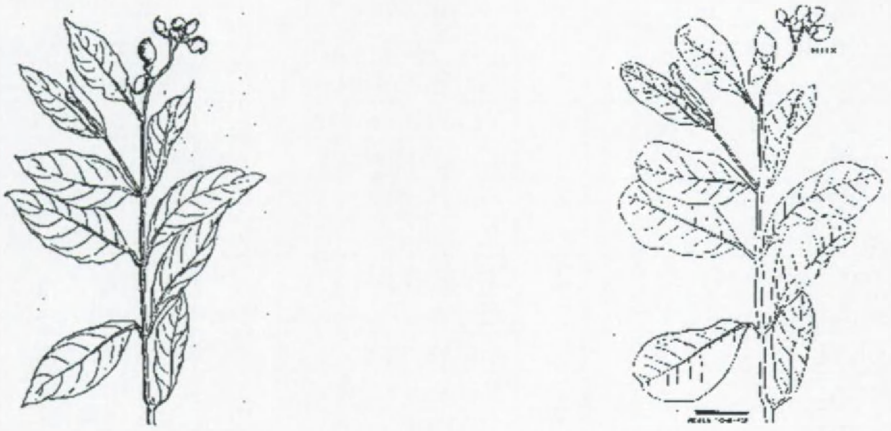


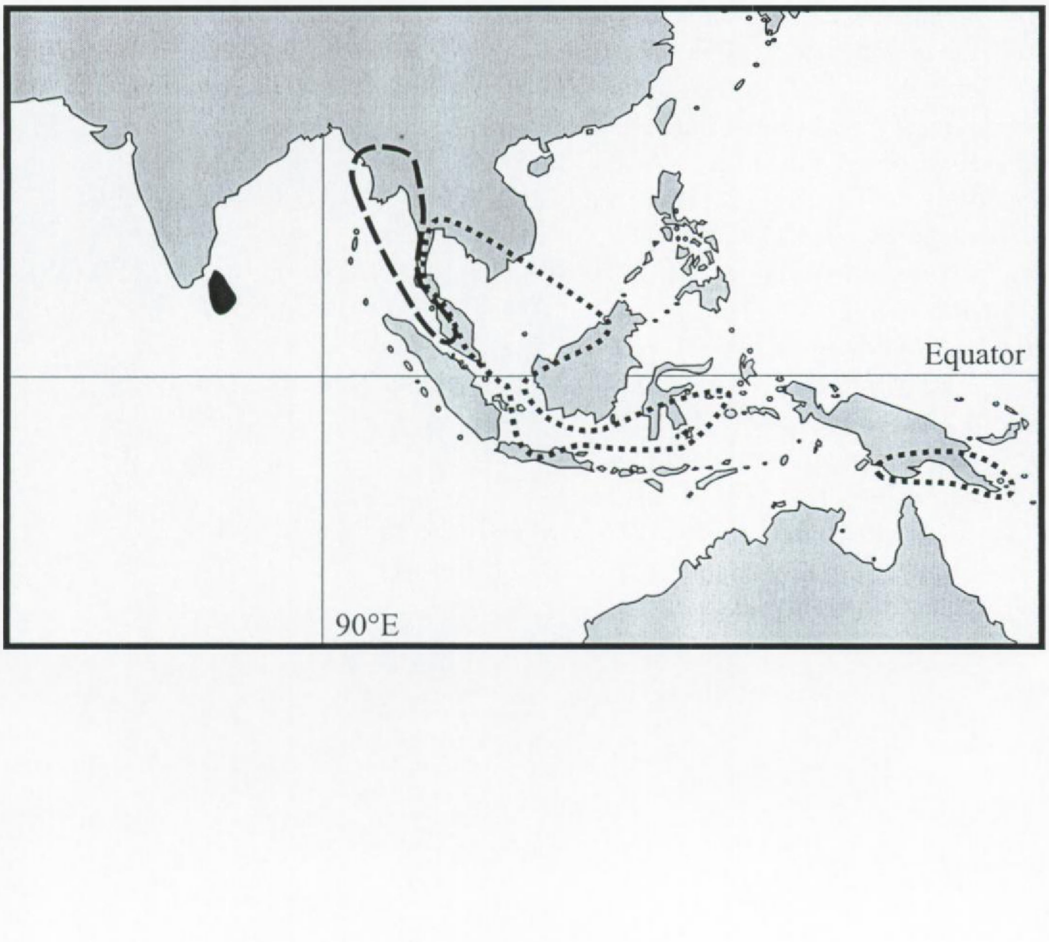
**Figure 2.** Example of the erroneous listing of species in Sri Lanka : the report of *Avicennia alba* (Liyanage, 1997), based on an original drawing of *Avicennia officinalis* (Arulchelvam, 1968), the latter of which, judging from the drawing, might very well be an *Avicennia marina* (*cf.* Tomlinson, 1986; Duke, 1991).



*A. officinalis* (Arulchelvam, 1968)

*A. alba* (Liyanage, 1997)

**Figure 3.** Distribution of *Sonneratia ovata* (dotted line) and *S. griffithii* (dashed line) with respect to the location of Sri Lanka (black) according to Spalding *et al.* (1997).



## APPENDIX I : Distribution of mangrove species in South-Western Sri Lanka.

The 43 mangrove sites visited are numbered as follows (in geographical order) :

| | | | | | |
|---|---|---|---|---|---|
| 1. | Palatupana L. | 16. | Suduwella | 31. | Madampa Ganga |
| 2. | Kirinda L. | 17. | Talalla | 32. | Balapitiya |
| 3. | Embilikala L. | 18. | Devinuwara L. | 33. | Kosgoda |
| 4. | Hambantota lewaya inlet | 19. | Nilwala Ganga E. | 34. | Bentota Ganga E. |
| 5. | Walawey Ganga E. | 20. | Garanduwa L. | 35. | Kaluwamodara |
| 6. | Lunama L. | 21. | Polwatumodara | 36. | Maggona |
| 7. | Kalametiya L. | 22. | Kapparatota | 37. | Kalu Ganga E. |
| 8. | Tillawatawana L. | 23. | Goiyyapana | 38. | Moratuwa Ganga E. |
| 9. | Rekawa L. | 24. | Koggala L. | 39. | Negombo L. |
| 10. | Kirama Oya mouth | 25. | Timbiri Ela | 40. | Gin Oya |
| 11. | Seenimodara canal mouth | 26. | Galle-Unawatuna | 41. | Pambala-Chilaw L. |
| 12. | Mawella L. | 27. | Ginganga E. | 42. | Mundel Lake |
| 13. | Kataketiya | 28. | Ratgama Oya | 43. | Puttalam L. |
| 14. | Dickwella | 29. | Hikkaduwa | | |
| 15. | Tondilay L. | 30. | Akurala | | |

Sinhala : Ganga = river; Ela = stream; Oya = large stream.
L. = lagoon; E. = estuary

In the present study the 20 mangrove species present between Palatupana and Puttalam (tab. 1) were observed in the following sites (numbers correspond to the table above) :

*Aegiceras corniculatum* (L.) Blanco : (5),(8) (9),(18),(20),(26),(33),(39),(41),(43)
*Avicennia marina* (Forsk.) Vierh. : (7-9),(12),(18),(26),(39-43)
*Avicennia officinalis* L. : (4),(9-11),(13),(14),(17),(18), (39),(41)
*Bruguiera cylindrica* (L.) Blume : (39),(41),(43)
*Bruguiera gymnorrhiza* (L.) Lamk. : (8-10),(18),(24),(26),(32),(34),(35),(38),(39),(41)
*Bruguiera sexangula* (Lour.) Poir. : (8-11),(13-41)
*Ceriops tagal* (Perr.) C.B. Robinson : (9),(39),(41),(43)
*Excoecaria agallocha* L. : (5-21),(23),(26-35),(39-43)
*Excoecaria indica* (Willd.) Muell.-Arg. : (8),(34),(41)
*Heritiera littoralis* Dryand. : (8-10),(13),(14),(24),(26),(29),(31),(34),(35),(39-41)
*Lumnitzera littorea* (Jack) Voigt : (32)
*Lumnitzera racemosa* Willd. : (1),(2),(4),(6-9),(11),(15),(18),(24),(26),(30),(32),(39), (41-43)
*Nypa fruticans* (Thunb.) Wurmb. : (8-10),(14),(17),(18),(19),(21),(29),(31),(32), (36),(40)
*Pemphis acidula* Forst. : (26),(43)
*Rhizophora apiculata* BL. : (14),(18),(19),(21),(24),(26-29),(31-35),(38-39),(41)
*Rhizophora mucronata* Lamk. : (8-10),(24),(39-41),(43)
*Scyphiphora hydrophyllacea* Gaertn.f. : (43)
*Sonneratia alba* J. Smith : (39),(41),(43)
*Sonneratia caseolaris* (L.) Engler : (5),(7),(8),(10-12),(14),(16-24),(26),(27),
(29),(30),(34),(36-41)
*Xylocarpus granatum* König : (21),(41)

# Chapter IV.

## High-resolution vegetation data for mangrove research as obtained from aerial photography.

Verheyden, A., F. Dahdouh-Guebas, K. Thomaes, W. De Genst, S. Hettiarachchi & N. Koedam

Engaged in a peer-review process

# High-resolution vegetation data for mangrove research as obtained from aerial photography.

Verheyden, A. [1,*] , F. Dahdouh-Guebas[1], K. Thomaes[1], W. De Genst[2], S. Hettiarachchi[3] & N. Koedam[1,‡].

[1] *Research Group of General Botany and Nature Management, Mangrove Management Group, Vrije Universiteit Brussel, Pleinlaan 2, B-1050 Brussel, Belgium.*
[2] *Center for Cartography and GIS, Department of Geography, Vrije Universiteit Brussel, Pleinlaan 2, B-1050 Brussel, Belgium.*
[3] *Department of Botany, University of Ruhuna, Matara, Sri Lanka.*

## Abstract

Remote sensing data provide valuable information for mapping vegetation and monitoring vegetation change. Moreover, they often constitute the only data source to study vegetation assemblages during the last decades. In the present methodological study, the applicability of aerial photographs for monitoring mangrove vegetation dynamics at high resolution was investigated. Satellite imagery was not considered since these data are only available for periods after 1970 and currently they show too coarse a resolution for the identification of mangrove tree genera. For the purpose of this study, vegetation maps of three mangrove forests in Sri Lanka (Galle, Rekawa and Pambala) were produced based on visual analysis of aerial photographs. The visual analysis was aided by applying an interpretation key constructed during a first fieldwork mission. Image attributes used for the identification of individual trees included: grey-values, texture, form and size of the crowns and the presence or absence of a shaded side. For the identification of species assemblages, the vegetation structure (i.e. the distribution of individual trees) appeared to be an important attribute. The accuracy and reliability of the vegetation maps were investigated during a second fieldwork mission. The aerial photographs proved to be very useful for the production of genus-based vegetation maps. The error analysis showed that density estimations (quantitative identification) based on aerial photography was not sufficiently accurate for the objectives of the study, but that the overall identification of vegetation assemblages (qualitative identification) was well as the boundaries between them coincided most satisfactory with the ground-truth data.

Keywords : mangrove, mapping, remote sensing, aerial photography, Sri Lanka.

## Introduction

Mangrove forests have been studied worldwide and, at present, considerable research effort is put in the assessment of the state of mangroves on a large scale (Spalding *et al.*, 1997). This includes the study of mangrove dynamics in time and space, the increase or decrease in areal extent, changes in species richness, regeneration capacity, *etc.* (*cf.* Dahdouh-Guebas *et al.*, 2000a). Remote sensing provides valuable information for mapping vegetation and monitoring vegetation change. Aside from the information given by the local population, it is often the only information available about the forests' history. Within the literature there is a tremendous emphasis on digital imagery and automated methods, despite the fact that in many cases human interpretation of photographic images is the only method of obtaining

---

[*] Research assistant, Fund for Scientific Research-Flanders (Belgium), Contractn° : G.0056.96
[‡] Corresponding author (e-mail: nikoedam.vub.ac.be)

information. Satellite imagery has been used to map and assess vast areas of mangroves (Aschbacher *et al.*, 1995, Ravan & Roy, 1997, Ramachandran *et al.*, 1998). However, the coarse resolution of these data sources rarely allows identification at the species or generic level, or the typology of assemblages necessary to detect changes within a mangrove forest (Holmgren & Thuresson, 1998). Aerial photographs still possess a much higher resolution and therefore give considerably more information, allowing a more detailed study of the local vegetation and floristics (Blasco *et al.* (1998). Smith *et al.* (1998) used multi-temporal aerial photographs to detect subtle seasonal changes in vegetation cover in a salt marsh system. Holmgren *et al.* (1997) could estimate forest characteristics, such as timber volume, from digital high altitude aerial photographs and the canopy dynamics of a tropical rainforest were investigated by Herwitz *et al.* (1998) with the aid of aerial stereo pairs.

Aside from the higher resolution, aerial photographs also have the advantage of being available over a larger time range, compared to satellite imagery. Photographs of war or shortly post-war times (WWII) are generally the earliest available. Time series of aerial photography give relevant information to study vegetation dynamics (Williams & Lyon; 1991; Miller *et al.*, 1996; Dahdouh-Guebas *et al.*, 2000a). The understanding of mangrove dynamics can lead to conservation and management directives, such as the establishment, protection and management of re-afforestation plots in the framework of regeneration and/or restoration projects, as described by Lee (1996).

The main objective of this study was to investigate the applicability of aerial photographs in the production of detailed mangrove vegetation maps to be utilized in the study of vegetation dynamics. This entails a two-phase procedure: first, a reliable determination key is generated for the interpretation of the photographs, and second, the determination of typologies of different species assemblages is done making use of this key. Both the identification of the mangrove (qualitative identification) and the tree density of the mangrove (quantitative identification) from the aerial photographs were confronted with the field reality and tested. The secondary objective of this study was to investigate the wider applicability of the interpretation key and to evaluate the feasibility of its use for the interpretation of aerial mangrove photographs from the past.

## Material & Methods

### *General approach*

The methodological procedure used in this study can be summarized as follows:

Phase 1: photographs were analysed visually and in the process of outlining the boundaries of assemblages that appeared different, useful image attributes to distinguish among these were searched for.

Phase 2: the data collected during the first fieldwork mission were superimposed on the aerial photographs to allow identification of individual trees and species assemblages.

Phase 3: using both the information from the visual analysis and the fieldwork a preliminary interpretation key was developed.

Phase 4: detailed vegetation maps were produced in a Geographic Information System (GIS) environment.

Phase 5: during the second fieldwork mission, data from representative areas of the forest were collected to check the accuracy of the vegetation maps.

Phase 6: error analysis and correction was performed, where necessary, on the vegetation maps and on the interpretation key.

Phase 7: the interpretation keys of the different study sites were compared to determine the wider or universal applicability of the keys.

Figure 1 gives an overview of the scientific approach of the study. In the following text, the numbers between brackets refer to the different steps in figure 1.

### *Description of the study sites*

Three mangrove forests were selected for investigation, based on their relative undisturbed character and their location in different climatic zones of Sri Lanka (Mueller-Dombois, 1968). For a site to be classified as relatively undisturbed, the site had to show a continuity of mangrove cover over four decades. The choice of sites in different climatic zones enabled us to draw conclusions about the wider applicability of the interpretation key, since different climatic zones show different vegetation compositions (De Silva & Balasubramaniam, 1985). The studied sites are located in Galle (06°01'N - 80°14'E), Rekawa Lagoon (06°03'N - 80°50' E) and Pambala (07°30' N-79°49' E).

The mangroves of Galle, sometimes referred to as the mangroves of Unawatuna, are located in the 'wet' climate zone of Sri Lanka (Fig. 2). They cover an area of 1.5 km$^2$ and are of the basin and riverine type according to the typology of Lugo & Snedaker (1974). The forest is located approximately 600 m from the Indian Ocean shoreline. Two rivers run through the forest, namely the Thalpe Ela discharging into the ocean, and the Galu Ganga, a tributary of the former. Interviews with the local population revealed that in 1982 the Galu Ganga was deepened and broadened and the sediment was used to construct an earthen road, which follows the river and continues through the mangrove forest. Furthermore, a dam was built where the Galu Ganga discharges in the Thalpe Ela in order to allow rice farming upstream. The dam was not operational between 1990 and 1997, but was repaired in 1998. The road and the dam may constitute an obstacle to the flow of water through the mangrove forest and may be influencing the vegetation in the long term. This makes the Galle mangroves an interesting site for the study of vegetation dynamics.

Rekawa Lagoon is located in the intermediate climatic zone (Fig. 2) and can be classified as a fringe forest type (Lugo & Snedaker, 1974). The lagoon is about 3.3 km long and 0.9 km wide with its long axis and running parallel with the ocean, into which it discharges through a meandering creek of about 1.6 km in length. However, the discharge is often blocked by a sand bar, which is frequently cleared by local farmers in order to improve freshwater run-off from the upstream paddy fields. A wide sand flat with coconut palms, *Cocos nucifera* L., separates the bulk of the lagoon from the Indian Ocean. Near its discharge point along the shore, three rivers feed the creek: the Kirama Oya, Urubokka Oya and Rekawa Oya. Disturbances include some wood harvesting and tanbark collection.

Pambala (Kakkapalliya) is situated in the intermediate climatic zone (Fig. 2) and is part of Chilaw lagoon, which is about 5 km long and 2 km wide. The mangroves in Pambala can also be classified as a fringe forest type (Lugo & Snedaker, 1974). The lagoon opens into the ocean at two sides, resulting in a daily influx of seawater into the lagoon. Pambala is recognized by the IUCN (1996) as a fairly undisturbed site.

Although Pambala and Rekawa are both located in the intermediate climatic zone (Mueller-Dombois, 1968), these two study sites are interesting for comparison. Pambala is situated in the northern section of the intermediate climatic zone and Rekawa in the southern (Fig. 2). The mangroves of Pambala are thus separated from those of Rekawa by a 'wet' climatic barrier, along the coast.

### *Visual interpretation of the aerial photographs*

Aerial black and white photographs of Galle and Rekawa (Fig. 3a; 3b) were obtained from the Department of Geography at the University of Ruhuna, Matara, while those of Pambala (Fig. 3c) were obtained from the Forest Department, Colombo. The most recent photographs were from 1994. All photographs originally had a scale of 1:20,000, but were photographically enlarged to facilitate investigation.

During visual analysis of the aerial photographs individual trees (1) were inspected for image attributes (grey value, texture, shape, *etc.*) (2). The attributes retained for the purpose of species identification were the following :

- Grey values : this attribute is regarded as a relative value, since light conditions can cause considerable differences. The shaded side of the crown is not taken into consideration to determine the grey value.
- Texture : here defined as the internal structure detected in one crown (*e.g.* smooth, grainy).
- The shape and size of the crown : the presence or absence of a shaded side, as an indication of the density and shape of the canopy.

The photographs were also analysed for species assemblages (3), which show a typical typology. To define and recognize species assemblages the 'structure' attribute was added for visual analysis of the photographs (4). The term 'structure' is here defined as the way the tree canopies are distributed with respect to each other, and can be compared to Lillesand & Kiefer's (1994) 'pattern' attribute. The main distinction between the assemblages therefore was a clear visual difference of image attributes on the aerial photographs.

Once species assemblages were defined and localized, preliminary vegetation maps were constructed, showing only the boundaries of different assemblages without taxonomic identification (5).

### *Fieldwork*

The first fieldwork mission took place during January-February 1996, for Galle and Rekawa and February 1997, for Pambala. The second fieldwork mission was carried out in January 1997, for Galle and Rekawa and April-May 1998, for Pambala. A gap of two to four years separates the ground-truth missions from the taking of the aerial photographs. The possibility of any discrepancies between the data of the field inventories and the aerial photographs due to this time gap is small; however, it cannot be completely excluded.

Species presence was recorded on a number of transects using the point-centred-quarter method or PCQM (Cottam and Curtis 1956) to detect the species assemblage (6). In this method the closest tree was recorded in each of four adjacent 90° quadrants in different sample points, and tree's $D_{130}$ was measured (term according to Brokaw & Thompson (2000), but formerly referred to as DBH, the diameter at breast height) for trees with a $D_{130}$ greater than 2.5 cm. Mangrove tree species nomenclature is according to Tomlinson (1986), Duke &

Jackes (1987) and Duke (1991). Attention was also given to the identification of individual trees (7), which could be easily located on the photographs (*e.g.* along the roads).

During the first fieldwork mission, one transect was investigated in Galle, seven in Rekawa, and five in Pambala. The second fieldwork mission included eight transects using the PCQM in Galle and a number of observational transects in Rekawa and Pambala. In Galle the absolute density and the relative density was calculated for each species assemblage separately. For this purpose, transects crossing different assemblages were overlaid with the vegetation contours (as obtained by visual analysis). The transects were split up and the sample points were attributed to the different vegetation assemblages for the calculation of the densities.

### *Production of the vegetation maps*

A preliminary interpretation key was constructed using the data collected from the first fieldwork mission and the image attributes selected during visual analysis (8). This key was used to taxonomically identify the species assemblages on the photographs (9) and produce the vegetation maps (10).

The scanned aerial photographs and the contours of the different assemblages were digitised in a GIS (MapGrafix) and converted to a grid (MapII) using Genamap. Relative density of species in each assemblage was obtained from the aerial photographs by counting individual trees.

### *Error analysis*

The purpose of the error analysis is to investigate whether the information obtained from fieldwork can be obtained from (less time consuming) aerial photograph interpretation. More specifically this research focuses on the recognition of the dominant tree species on one hand (qualitative identification) and their relative densities (quantitative identification). Using the data obtained during the second fieldwork mission (11), an error-analysis (12) was performed for the three vegetation maps. This analysis is threefold.

The relative densities as obtained from counting individual trees on the aerial photograph ('observed' values) were compared with those obtained from the fieldwork ('expected' values) using the G-test (Sokal & Rohlf, 1981).

The proportion of sample points, which varied between 39 and 322 according to the assemblage and the site, occupied by the species present in each of the vegetation assemblages was investigated. If a vegetation assemblage is labelled with an identification tag, then the representative species should take in the highest proportion.

Finally, he correct delimitation of the species assemblages was incorporated into the error analysis. For this purpose the data obtained from the transects were visualized in a GIS and superimposed on the vegetation maps. The resulting map was visually inspected for species assemblages detected during fieldwork but not on the photographs.

## Results

### *The interpretation keys*

Figures 4a, 4b and 4c show the final interpretation keys for Galle, Rekawa and Pambala, respectively. These do not show any fundamental difference from the preliminary keys produced after the first phase fieldwork missions, which is positive for the reliability of the keys. Specifically for Galle, a number of species could be added to the key after the second phase fieldwork missions. This was particularly due to the discovery of more species in the field when more transects were investigated.

### *The vegetation maps*

Figures 5a, 5b and 5c show the vegetation maps for Galle, Rekawa and Pambala, respectively. The maps focus on the mangrove vegetation. Terrestrial vegetation, rice farms and inhabited areas were all classified as non-mangroves. Plantations (*e.g.* coconut palms) and infrastructures (*e.g.* shrimp farms, roads) close to the mangroves, or interacting directly or indirectly with the mangrove ecosystem were added to the maps, since these could be important when studying dynamics. On the photograph a distinction could be made between homogenous assemblages (composed of one dominant genus and some individuals of other genera) and heterogeneous or mixed assemblages, in which two or more genera are co-dominant. In some cases the absolute density of some stands could be distinct. An obvious example is the recognition of open areas within the forest. These 'open' areas are usually not completely bare of vegetation, but contain very sparse individuals or young trees, the latter being hardly or not visible on the photographs. A less obvious example of difference in absolute density was the distinction between sparse and dense *Excoecaria* assemblage in Galle. This distinction was based on the relative distance between crowns, and thus it was based on the attribute 'structure'.

### *Error analysis*

Table 1 displays the values of the G-test results of the comparison between tree densities as obtained from visual analysis of the photographs and from fieldwork measurements for each assemblage. The results show that there was a significant difference between the remotely sensed and the field data in most of the cases, indicating that visual quantitative identification based on aerial photographs is not advised.

However, the results for the qualitative identification proved very satisfactory (Tab. 2). In a total of 10 assemblages analysed over the three sites, nine showed a highest proportion of the representative species, the best example being *Lumnitzera racemosa* Willd. trees occupying 74.10 % of the 139 sample points that lay in the *L. racemosa* forest patch. Mixed assemblages were not included since any species belonging to a mixed class leads to 100% correct data. Only the proportion of the Open Space in Galle, presumed to have predominantly empty sample points (= open space), has a rather unexpected highest proportion of *Excoecaria agallocha* L. individuals that are young and small adults and that cannot easily be distinguished on the aerial photograph. However, note that the density in the open space correctly reflects the 'open' character (Tab. 1).

Figure 6 a, b and c shows the overlay of the transects with the vegetation map. Each little compartment on the transect represents one tree, measured according to PCQM (the measured distance is not represented). Shifts of a maximum of 20 meters occur between the boundaries of the species assemblages as obtained from interpretation of the photographs and those visible from the overlaid transect data. On two occasions, small clusters of trees were noticed during the fieldwork (Fig. 6a; 6b), differing from those that were predicted to be the dominant species or genus. One is a *Bruguiera* cluster and the other is a *Rhizophora* cluster, both in an *Excoecaria*-dominated area.

## Discussion

The objective of this study was to investigate the applicability of aerial photographs to mangrove vegetation research and hence to determine whether information such as species assemblage, species composition of assemblages and relative densities of species could be obtained by interpretation of aerial photographs.

### *Image attributes*

For the identification of individual trees the following image attributes were retained: grey-values, texture, form and size of the crowns and the presence or absence of a shaded side. However not all attributes were useful for the identification of each species. The presence or absence of a shaded side, for example, was in Galle, useful to distinct the shrub *Clerodendron* from *Excoecaria*, but it was not useful for other genera. Depending on the species encountered in the study site, one might have to redefine or add image attributes. Overlap of these image attributes caused some problems to identify certain individuals. This was the case for the identification of *Bruguiera*. *Bruguiera* individuals overlap considerably in their image attributes with those of *Excoecaria* as well as with those of *Rhizophora*. For this reason *Bruguiera* trees were not detected when individual trees were counted. If only identification of individual trees is considered, the *Bruguiera-Excoecaria* mixed stand would have been mistaken for an *Excoecaria-Rhizophora* mixed stand. Using ‘structure’, a clear difference was noticed: *Rhizophora-Excoecaria* stands display connected crowns with greater height differences, while *Bruguiera-Excoecaria* stands are characterized by a loose canopy and a more uniform tree height. This appeared to be unrelated to the ages of the trees.

In mangrove forests, plant species richness is often low if compared to neighbouring terrestrial vegetation. Moreover, the species are often grouped in monospecific zones or patches. The importance of the structure-attribute seemingly increases when species show clear groupings and cannot be applied when a very homogeneous forest is investigated. In Sri Lanka the mangroves seldom, if ever, show a clear zonation, however, the forest shows patches of dominant species.

### *Error analysis*

Although the quantitative analysis (relative density) did not give good results, the qualitative analysis of the photographs (dominant genera, delimitation of the assemblages) appeared very satisfactory.

The failure to detect the species composition quantitatively is only partly due to overlap in image attributes in the interpretation key. This is the case for *Bruguiera*, which is undetectable as an individual, as is explained above. The overestimation of *Rhizophora* and *Excoecaria* when counted on the aerial photograph (Tab. 1), is thus partly due to misidentification of *Bruguiera* trees.
Another problem is the one of species occurring only sporadically. They were not included in the interpretation key, since insufficient individuals were encountered in order to clearly define the image attributes. In Galle, this was the case for *Heritiera littoralis* Dryand. After encountering this species in the field, detection on the aerial photograph was performed. Although a preliminary description of *Heritiera* included a white to light grey crown, with a blurred texture and a very distinct darker point in the middle of the crown (which could be the stem end or a crown gap), it was impossible to check the reliability of this description with other individuals.

Besides these interpretation errors or failures, the unsatisfactory outcome of the G-test might reflect the unsuitability of the PCQ-Method, which is directed to method used towards measuring stem characteristics (stem density, basal area), while features observed on the photographs are rather crown directed. This difference in measured features could have played an important role especially in *Rhizophora*-mixed stands. In Galle, *Rhizophora* clusters to form large colonies, giving them the typical 'cauliflower' structure, in which individual crowns were subjectively recognized. In mangrove forests, where different species within the adult vegetation layer of an assemblage show large height differences (this is seldom the case in Sri Lanka), the discrepancy between aerial photography interpretation and field method is larger because of over-topping of the trees (Dahdouh-Guebas *et al.*, pers. comm. 1999, subm.a). Nevertheless, the PCQM has other advantages such as the fast investigation of large areas.

The good results for the identification of assemblages (Tab. 2) proves the suitability of aerial photography for the identification of assemblages. Although in the case of the Open Space in Galle the highest proportion of sample points was taken in by *Excoecaria agallocha* trees, a closer look to the field situation showed that this was mainly the result of the relatively young age, although adults according to our definition. The justification for the tag, however, is supported by the very low density of trees (Tab. 1), *i.e.* an 'open space'.
One might argue that for the open space in Pambala the representative 'species' (= nil) is not very convincing as compared to other species, but the situation is similar to that of the open space in Galle. Actually, in Pambala the number of trees is so low that forest characteristics derived from the PCQ-Method (density, dominance, frequency) cannot even be calculated (Dahdouh-Guebas, 2001). The relatively high proportion of *Lumnitzera racemosa* and *Rhizophora* spp. is due to their close association with water fronts (and possible delineation errors as explained underneath) and isolated colonies within a water body.

Correct delimitation of the species assemblages was investigated visually by overlaying transect data with the vegetation maps. Small shifts of the boundaries between both data sets can be attributed to interpretation errors, digitising errors, lack of unequivocal reference points for the orientation of our transects, a discontinuous scale due to parallax, deviations in the true length of the transects due to a poor estimation of the dimension of impenetrable *Rhizophora* colonies or finally because of small changes which occurred in the period between the taking of the aerial photographs (1994) and the fieldwork (1996, 1997, 1998). These shifts, of maximum 20 meters, show the accuracy of the position of our boundaries.

From the two clusters of species detected during fieldwork, only the *Rhizophora* cluster could be recognized to a certain extent, when the aerial photograph was re-inspected, suggesting a digitisation error. However, due to the absence of an unequivocal situation for the above recognition, and the introgression of *Excoecaria* in the same area, we preferred to stick to the identification as an *Excoecaria* dominated forest patch. The undetected *Bruguiera* cluster is greatly due to the overlap of image attributes and to the fact that the clusters are too small to show a clear differentiated structure on the photograph.

### *Wider applicability of aerial photographs*

Between the different study sites the interpretation keys differ because of physiognomic variations for certain species, and because of the relative aspect of certain image attributes. For example, *Excoecaria agallocha* appears almost white on the aerial photographs of Galle, while it is darker on the photographs of Rekawa lagoon and Pambala, on which, *Avicennia marina* (Forsk.) Vierh. appears white instead. A physiognomic difference of *E. agallocha* between these two sites can in fact also be observed in the field. This suggests that the interpretation keys should only be used locally, if high accuracy is the objective. The term locally implies that the keys can be used in similar geographic units, in which the floristic composition of the forest resembles the one on which the key is based on. When used on a different geographic unit, the keys presented here can give preliminary results about the species possibly present. If white crowns are detected, with blurred texture and no distinct shape, the detected individual could be an *Excoecaria*, an *Avicennia* or a *Lumnitzera*. But if information about the species present in the area is available, a correct identification is possible. Basically, for photo interpretation all information is useful. Since mangroves often show a clear zonation, the position of the species in relation to the sea can be very important as well. Since clear zonation is virtually absent in Sri Lanka, this feature was not considered in this research. If a high degree of accuracy of the vegetation maps is required, the interpretation key should either be used only locally or for forests with similar species composition, or be calibrated for each new area.

With the aid of recent photographs and the interpretation key, mangrove vegetation dynamics can be studied using sequential aerial photography (*cf.* Dahdouh-Guebas *et al.*, 2000a). The photographs in a time series display differences in quality and sometimes in scale. These differences increase the difficulty of interpreting older photographs using the interpretation key, which is based on the most recent photograph only. However, a 'calibration' of the key for universality in time, as opposed to universality in space, is very easy to achieve in most circumstances.

For the calibration of the interpretation key, unchanged areas of the forest are compared on the different photographs. The available original photograph of Galle taken in 1974, for example, is very dark as compared to the one of 1994. The key can easily be calibrated when the attributes of unchanged areas, or areas showing minor changes are compared. Unchanged areas can be recognized on the photograph by using equiformity of the contours of the species assemblages as an indication. The resultant calibrated key will allow identification of assemblages in the more disturbed areas of the forest.

The calibration technique incorporates one assumption: the fact that the species composition remains the same in the forest over time. The problem does not emerge from the genera currently present, since these can be observed during fieldwork, but locally extinct genera will not be comprised in the interpretation key and will not be identified on the photograph. To assure minor changes in the forest and to enable calibration of the key one should make use of sequential aerial photography with the least possible time gaps. In this respect high-resolution satellite imagery would be very appropriate for the future.

The very rapid advancing technology gives hopeful results concerning the development of the acquisition of such data (McGraw *et al.*, 1998). However, in a recent remote sensing study that compared airborne and space-borne (e.g. SAR technology) data sources, the airborne data from imaging spectrometer (AISA), airborne ranging radar (HUTSCAT) and aerial photographs (1 : 20,000) were the most accurate data sources in the retrieval of forest stand attributes (Hyyppä *et al.*, 2000). In addition, automated delineation of individual tree crowns in forests (provided individual crowns can be distinguished) has recently been proven to be as reliable as visual interpretation in forests of central Sweden (Brandtberg & Walter, 1998), possibly a first step to a computer aided reliable interpretation of aerial photographs. The only recent available imagery that could challenge aerial photography for the future (not for the past) are the IKONOS space-born image with a 1 to 4 m resolution. However, the commercial nature of this satellite launched in September 1999, and consequently the very high prices charged, is a limiting factor that prevents the international scientific community to access these data.

The changes, which can be monitored with high reliability using sequential aerial photography, are increase and decrease in covered area of each species assemblage and changes in boundaries of the vegetation. In addition to the high value of aerial photographs in producing vegetation maps of mangroves with identification of species composition up to the generic level, sequential aerial photography has a high value for studying mangrove dynamics. Due to the relative low species richness of mangrove forests, this positive evaluation may not be extrapolated to floristically or structurally more diverse forests.

## Conclusion

This study showed that aerial photographs constitute a most valuable tool in producing accurate vegetation maps of mangrove forests with identification up to the generic level. Most individual trees could directly be recognized from the aerial photograph using the following image attributes: grey values, texture, crown form and size, presence or absence of a shaded side. Overlap of the image attributes of different genera caused some problems during interpretation of the photographs. In this case the generic composition of a species assemblage could indirectly be identified using the attribute 'structure'. Although the quantitative analysis (relative density) did not give good results and should therefore be investigated in the field only, the qualitative analysis of the photographs (dominant genera, delimitation of the assemblages) appeared very satisfactory. The interpretation keys show basic differences between locations and should therefore only be used locally or in mangrove areas with similar floristic composition.

## Acknowledgements

We would like to thank the late Prof. Dr. M.A. Pemadasa, Dr. L.P. Jayatissa and Mr. G.W.N. Tushira Kumara from the Department of Botany for their support, and the Department of Geography of the University of Ruhuna, Matara, and the Forest Department for access to the aerial photographs. Furthermore thanks is given to Mr. Anuradha Wickramasinghe, Director of the Small Fishers Federation of Lanka, Pambala-Kakkapalliya, Sri Lanka and his staff, in particular Mr Daglas Thisera (Co-ordinator Mangrove Conservation and Education, Mangrove Conservation and Demonstration Center) for their logistic support in the field. We also would like to thank Lic. G. Ladavid (Laboratory of Plant Physiology, VUB), D.W. Indunil Divilewattage, Saman Nishante and Fatuma Saidi for their field assistance. Research financed by the Fund for Scientific Research, Flanders (Belgium), by the European Commission and with a specialization fellowship of the Fund for Scientific Research-Flanders (FWO) and of the Flemish Institute for the advancement of scientific-technological research in the industry (IWT).

### References

See Bibliography

**Table 1.** Results from comparison of the relative densities as obtained from the visual analysis of the photographs (Obs) and from the fieldwork (Exp) for the different species assemblages using the G-test.

| Assemblage | Genera | Obs | Exp | G-value | d.f. | p-value |
|---|---|---|---|---|---|---|
| **EAd** | *Rhizophora* | 99 | 27 | 59.035 | 3 | $p < 0.001$ |
| | *Excoecaria* | 531 | 129 | | | |
| | *Bruguiera* | 0 | 14 | | | |
| | *Heritiera* | 0 | 6 | | | |
| **EAs** | *Rhizophora* | 0 | 0 | 1.746 | 1 | n.s. |
| | *Excoecaria* | 100 | 23 | | | |
| | *Bruguiera* | 0 | 1 | | | |
| **EA/B** | *Rhizophora* | | 8 | | not computable | |
| | *Excoecaria* | | 19 | | | |
| | *Bruguiera* | | 19 | | | |
| **R/EA** | *Rhizophora* | 116 | 26 | 59.375 | 2 | $0.001 < p < 0.01$ |
| | *Excoecaria* | 171 | 11 | | | |
| | *Bruguiera* | 0 | 1 | | | |
| **R** | *Rhizophora* | 76 | 34 | 1.787 | 2 | n.s. |
| | *Excoecaria* | 53 | 25 | | | |
| | *Bruguiera* | 0 | 1 | | | |
| **OS** | *Rhizophora* | 14 | 8 | 8.269 | 2 | $0.01 < p < 0.02$ |
| | *Excoecaria* | 61 | 70 | | | |
| | *Bruguiera* | 0 | 5 | | | |

Assemblages dominated by B = *Bruguiera* spp., E = *Excocaria agallocha*, R = *Rhizophora* spp. or co-dominated (indicated by /); OS = open space; d = dense; s = sparse.

**Table 2.** Percentage proportions of the sample points containing a particular species (columns) for each of the main vegetation assemblages (rows) in Galle, Rekawa and Pambala. Mixed assemblages were left out because any species can belong to a mixed class. For each vegetation assemblage the species that should take in the highest proportion, and in a majority of the assemblages does, is highlighted. Only the proportion of the Open Space in Galle, presumed to have predominantly empty sample points (= open space), has a rather unexpected highest proportion of *E. agallocha* individuals that are young and small adults and that cannot easily be distinguished on the aerial photograph. However, note that the density in the open space correctly reflects the 'open' character (Tab. 1).

| Assemblage | n | *A. cor* | *A. off* | *B. spp* | *C. tag* | *E. aga* | *H. lit* | *L. rac* | *R. spp* | *X. gra* | nil |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **Galle** | 666 | | | | | | | | | | |
| EA | 322 | --- | --- | 9.94 | --- | 60.56 | 1.86 | --- | 13.04 | --- | 14.60 |
| EA/B | 50 | --- | --- | 32.00 | --- | 34.00 | 0.00 | --- | 12.00 | --- | 22.00 |
| R | 165 | --- | --- | 5.45 | --- | 24.85 | 0.00 | --- | 52.12 | --- | 17.58 |
| OS | 129 | --- | --- | 3.10 | --- | 52.71 | 0.00 | --- | 5.43 | --- | 38.76 |
| **Rekawa** | 116 | | | | | | | | | | |
| LR | 39 | 17.95 | 10.26 | --- | 0.00 | 2.56 | --- | 61.54 | 0.00 | --- | 7.69 |
| R | 39 | 5.13 | 7.69 | --- | 5.13 | 2.56 | --- | 28.21 | 38.46 | --- | 12.82 |
| OS | 38 | 0.00 | 0.00 | --- | 0.00 | 0.00 | --- | 13.16 | 0.00 | --- | 86.84 |
| **Pambala** | 484 | | | | | | | | | | |
| LR | 139 | 0.00 | 7.19 | 3.60 | --- | 7.19 | --- | 74.10 | 1.44 | 0.72 | 5.76 |
| R | 261 | 0.38 | 3.83 | 11.88 | --- | 1.15 | --- | 5.36 | 71.65 | 0.00 | 5.75 |
| OS+water | 84 | 1.19 | 2.38 | 3.57 | --- | 3.57 | --- | 26.19 | 22.62 | 10.71 | 29.76 |

Assemblages dominated by B = *Bruguiera* spp., E = *Excocaria agallocha*, LR = *Lumnitzera racemosa*; R = *Rhizophora* spp. or co-dominated (indicated by /); OS = open space. The OS includes a few *Acrostichum aureum* and *Acanthus ilicifolius* dominated areas and where present was combined with the 'water' class since all these map classes should result in an absence of mangrove trees and a highest proportion of empty sample points (= nil).

**Figure 1.** Methodological framework used in this study. The numbers between parentheses refer to detailed descriptions of the stages in the text.

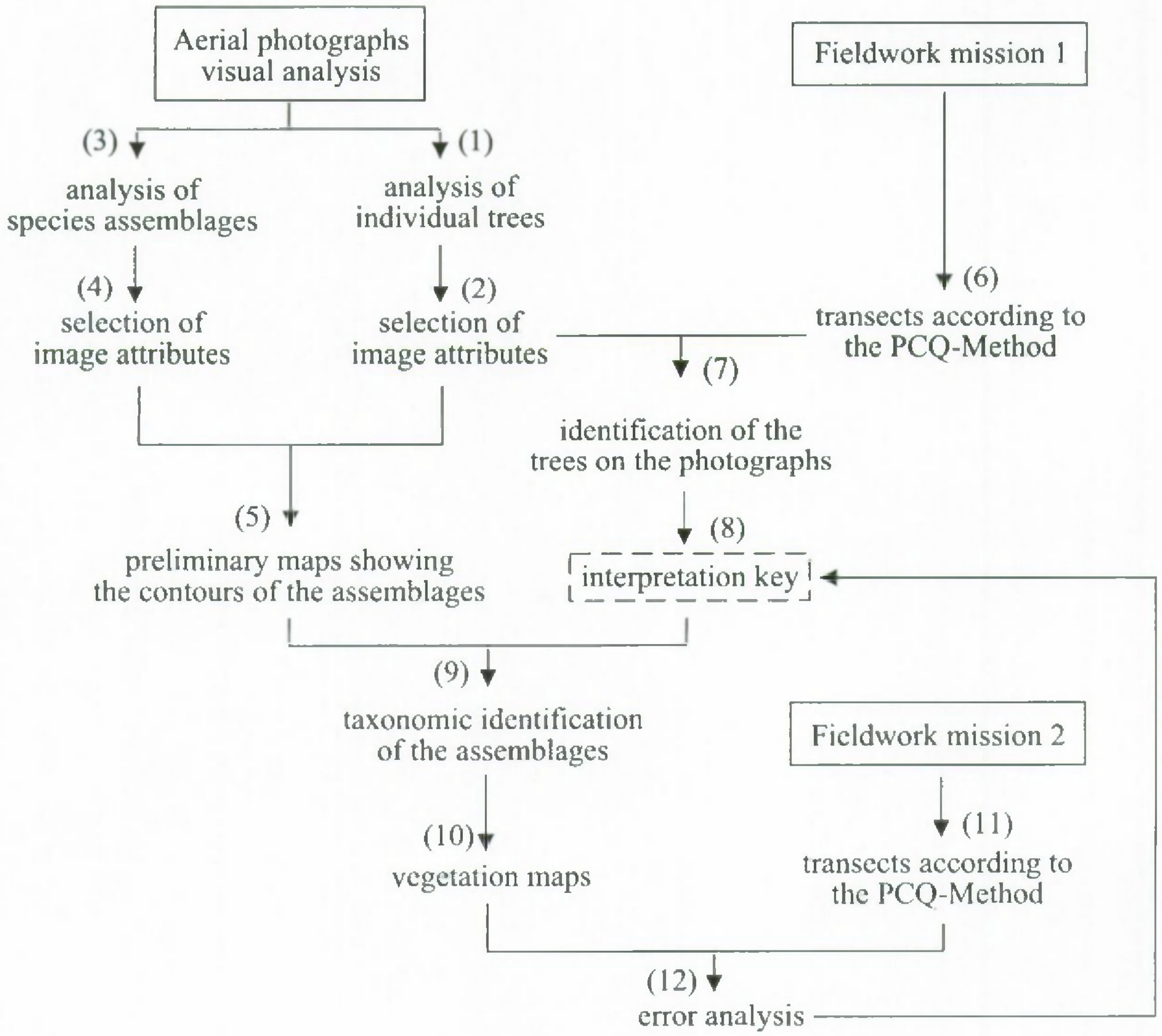


**Figure 2.** Location of the study sites in Sri Lanka and the distribution of the main climatic zones according to Mueller-Dombois (1968).

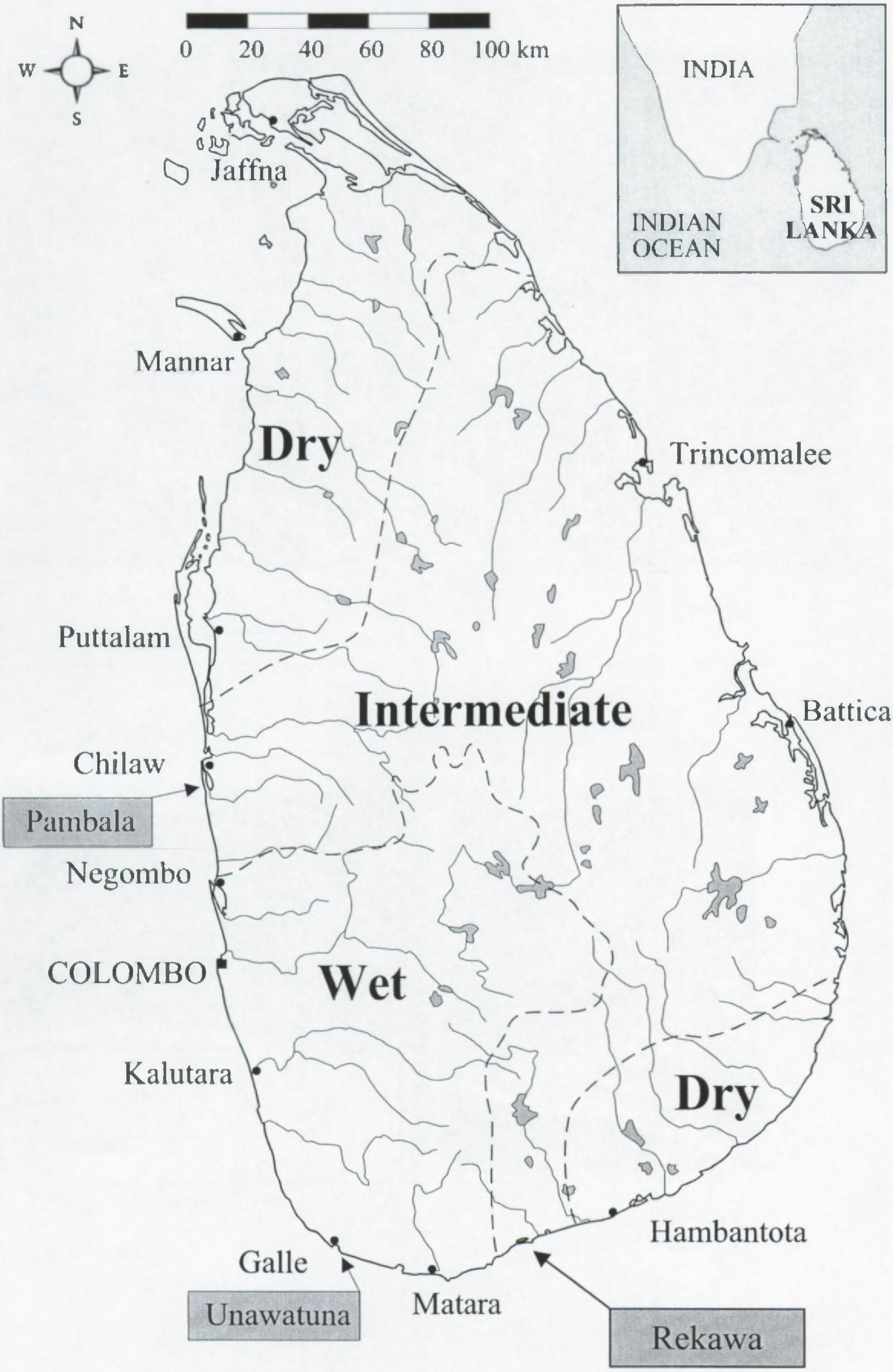


**Figure 3.** (a) Aerial photograph of the mangrove area in Galle (1994). (b) Aerial photograph of Rekawa lagoon (1994); (c) Aerial photograph of the study site in Pambala (1994). The black arrows point to the North.

(c)

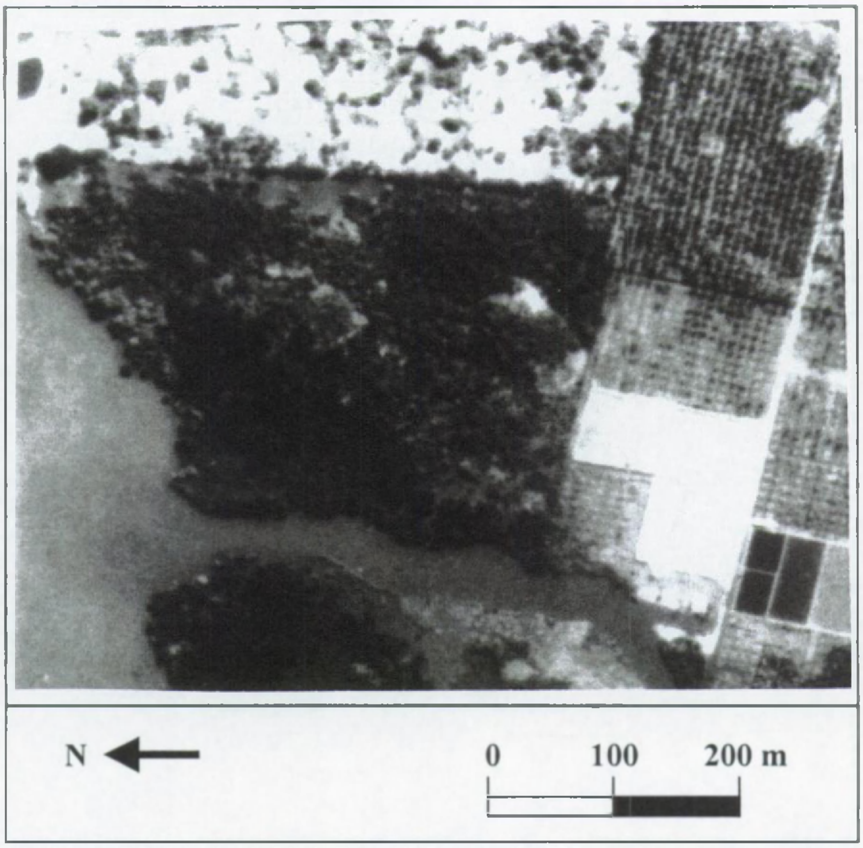
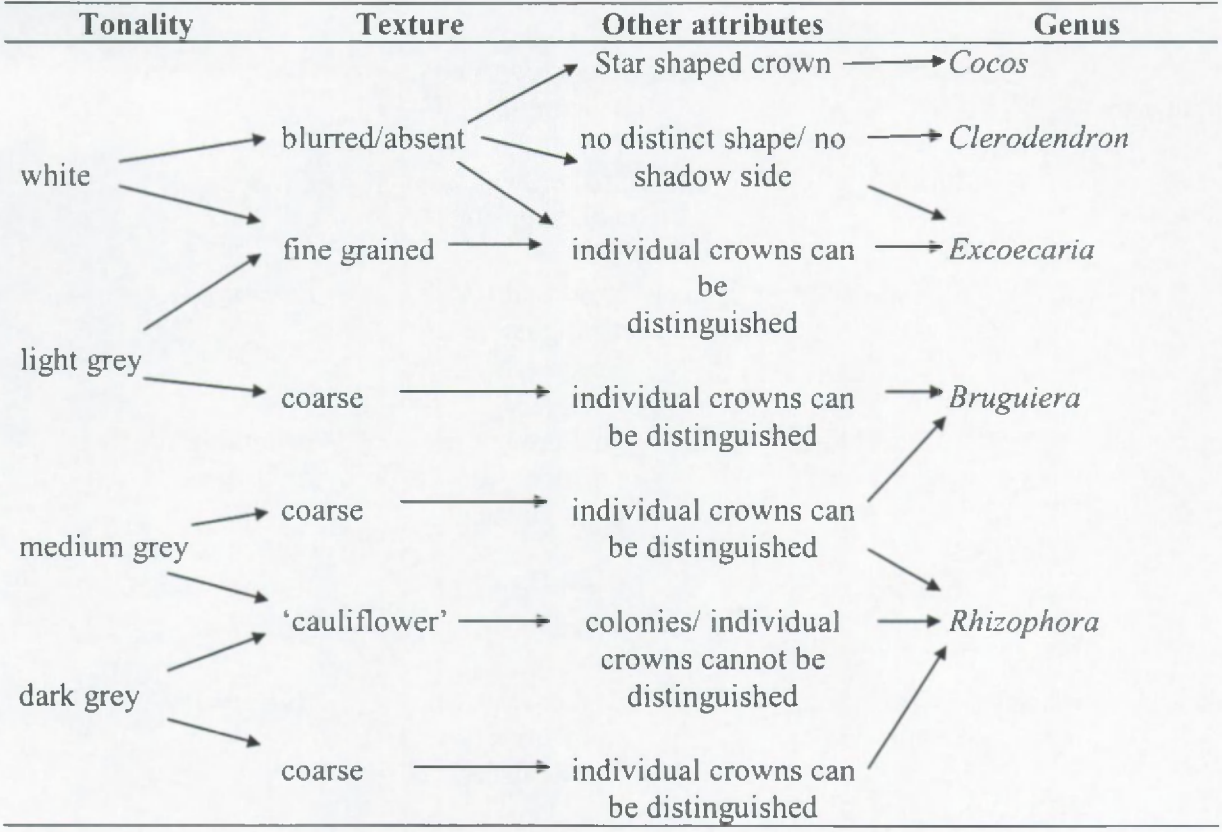


**Figure 4.** Interpretation keys for the mangroves of Galle (a), Rekawa (b) and Pambala (c). Compare figs 3 and 5 for examples illustrating the image attributes.

**(a) Galle**



**(b) Rekawa**

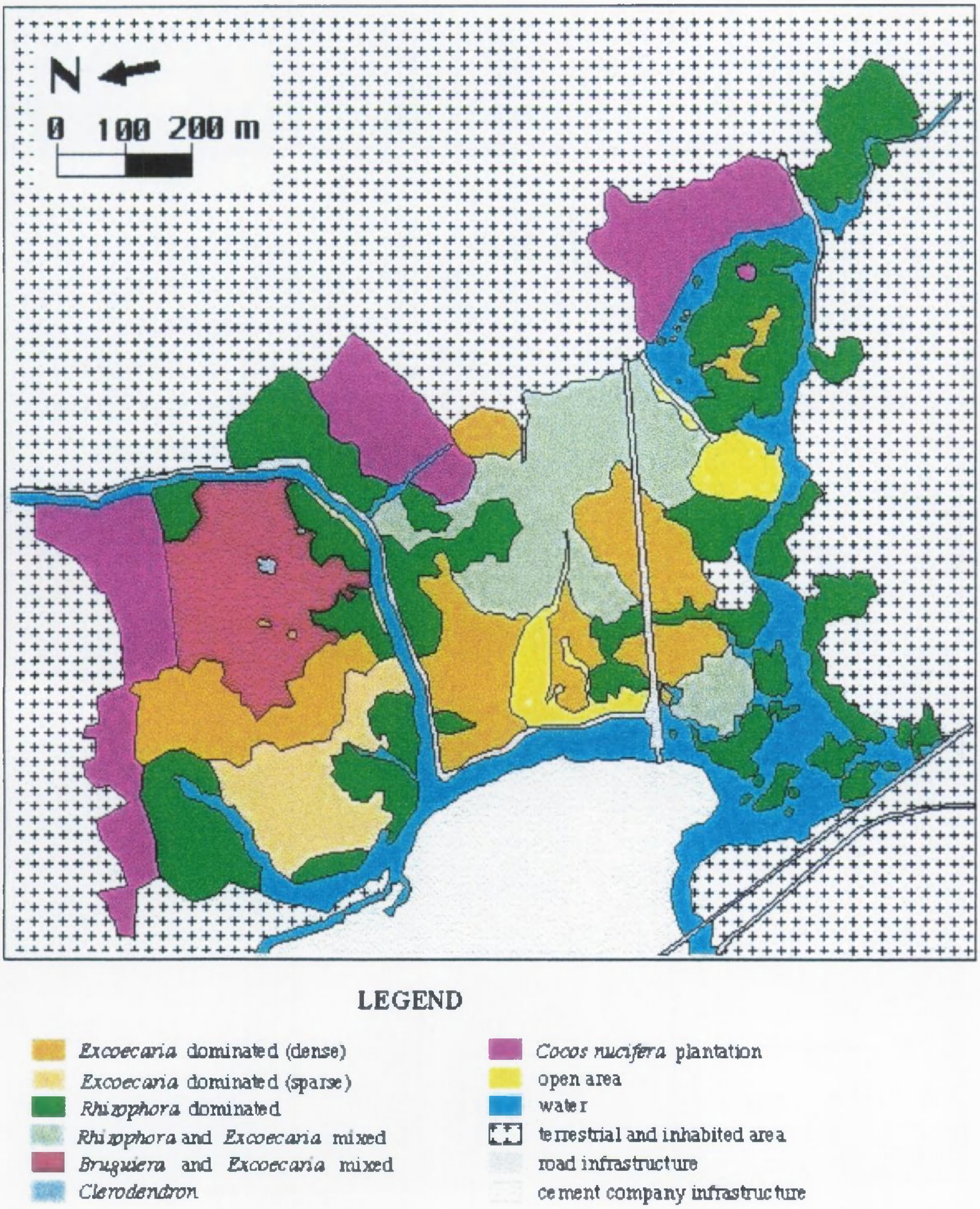
| Tonality | Texture | Other attributes | Genus |
|---|---|---|---|
| grey value 0 (white) | blurred/absent | Star shaped crown | *Cocos* |
| | blurred | individual crowns can be distinguished | *Avicennia* spp. |
| grey value 1 | fine grained | individual crowns can be distinguished | *Aegiceras* |
| grey value 2 | coarse | small crowns, difficult to distinguish from each other | *Lumnitzera* |
| grey value 3 | coarse/ 'cauliflower' | colonies | *Rhizophora* |
| grey value 4 (black) | smooth | individual crowns cannot be distinguished | *Ceriops* |

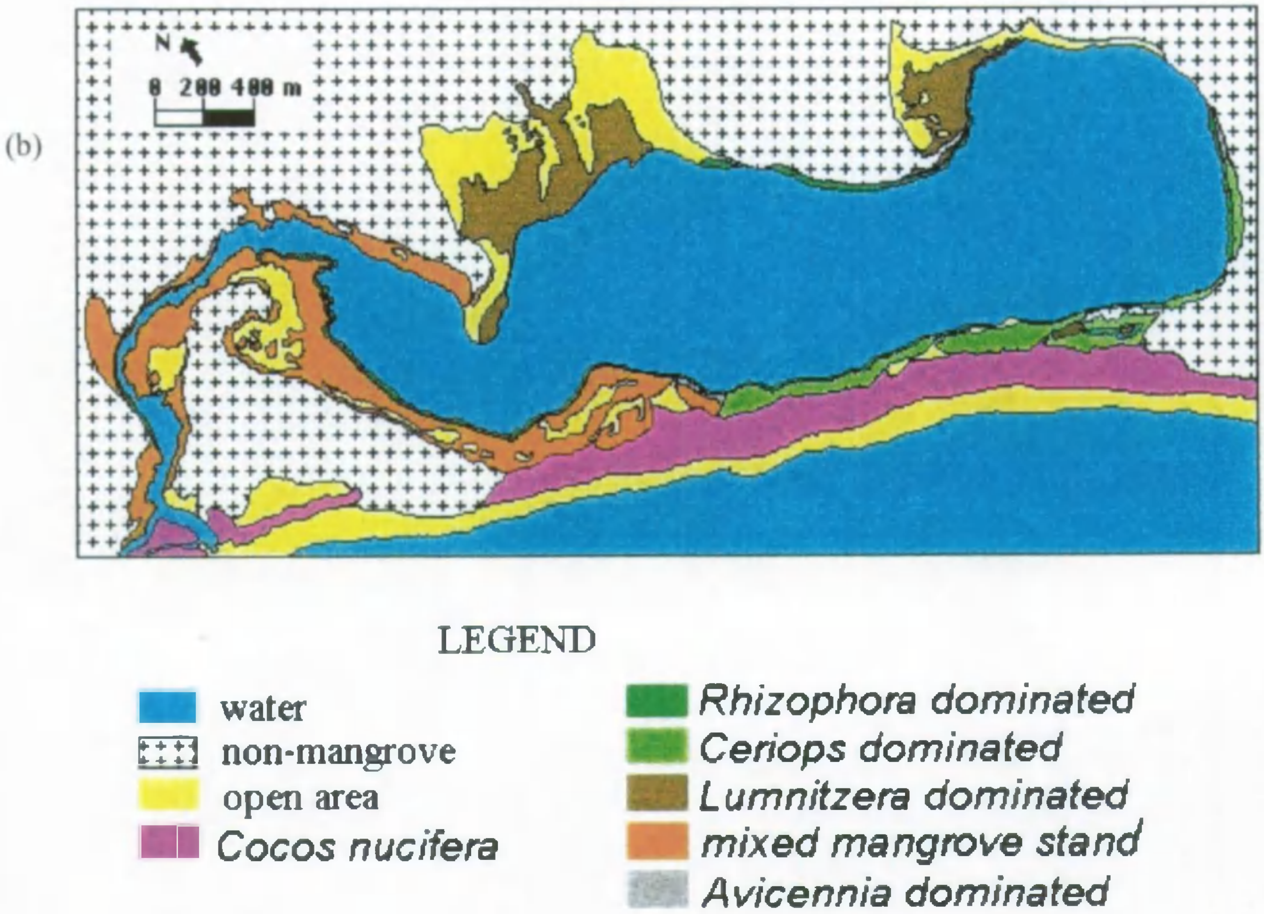
**(c) Pambala**

| Tonality | Texture | Other attributes | Genus |
|---|---|---|---|
| white | blurred/absent | Star shaped crown | *Cocos* |
| light grey | coarse | individual crowns can be distinguished | *Avicennia* spp. |
| | blurred | individual crowns can be distinguished | *Excoecaria* |
| medium grey | fine grained | small crowns, difficult to distinguish from each other | *Lumnitzera* |
| | coarse/ blurred | individual crowns are difficult to distinguished | *Bruguiera* or *Xylocarpus* |
| | blurred/absent | no distinct shape/ no shadow side | *Acrostichum or Acanthus* |
| dark grey / black | coarse/ 'cauliflower | individual crowns can sometimes be distinguished | *Rhizophora* |

**Figure 5.** Vegetation maps of 1994 for the mangroves of Galle (a), Rekawa (b) and Pambala (c).

(a)




(b)
N
0 200 400 m
LEGEND
water
non-mangrove
open area
*Cocos nucifera*
*Rhizophora dominated*
*Ceriops dominated*
*Lumnitzera dominated*
*mixed mangrove stand*
*Avicennia dominated*

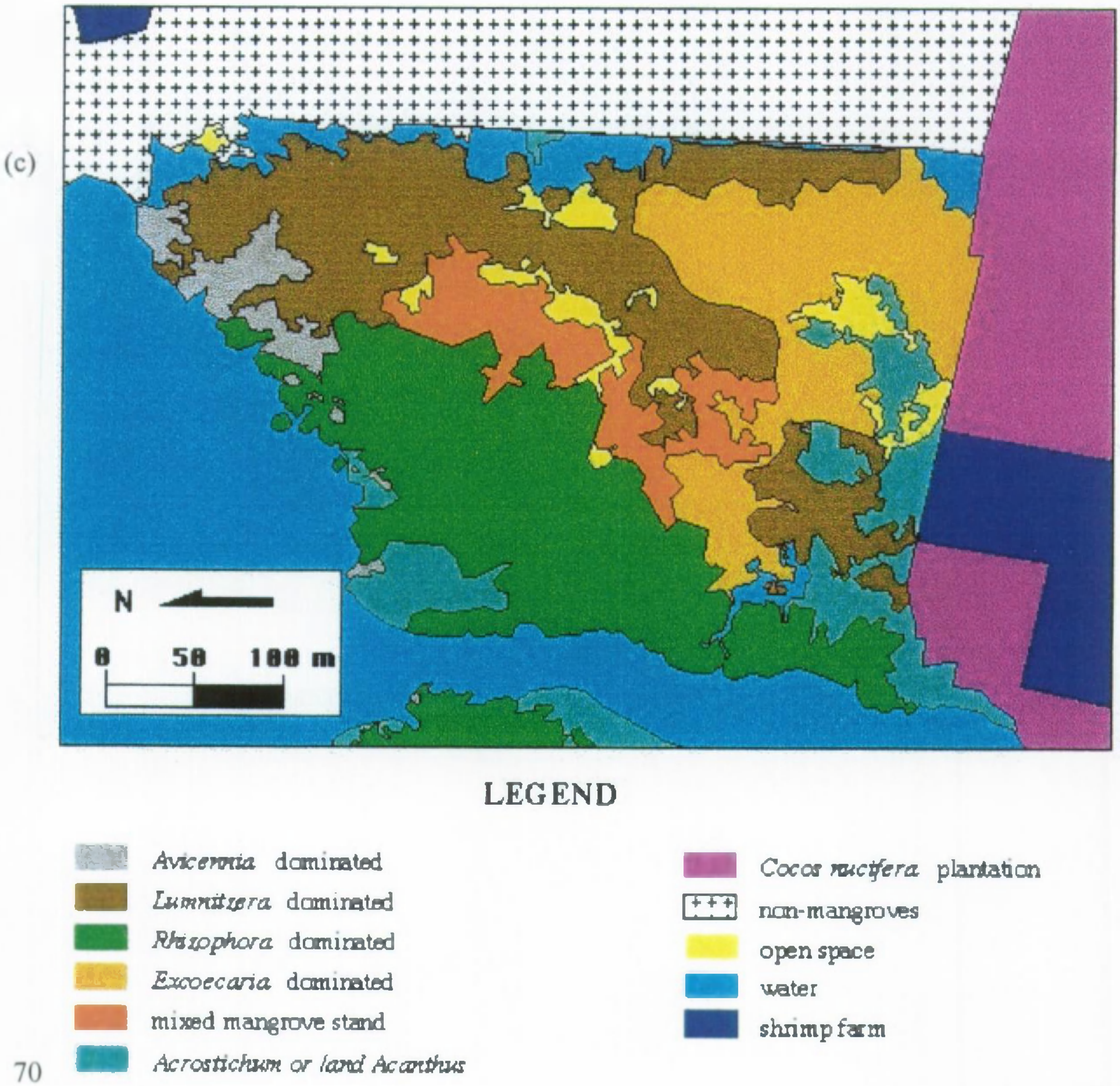
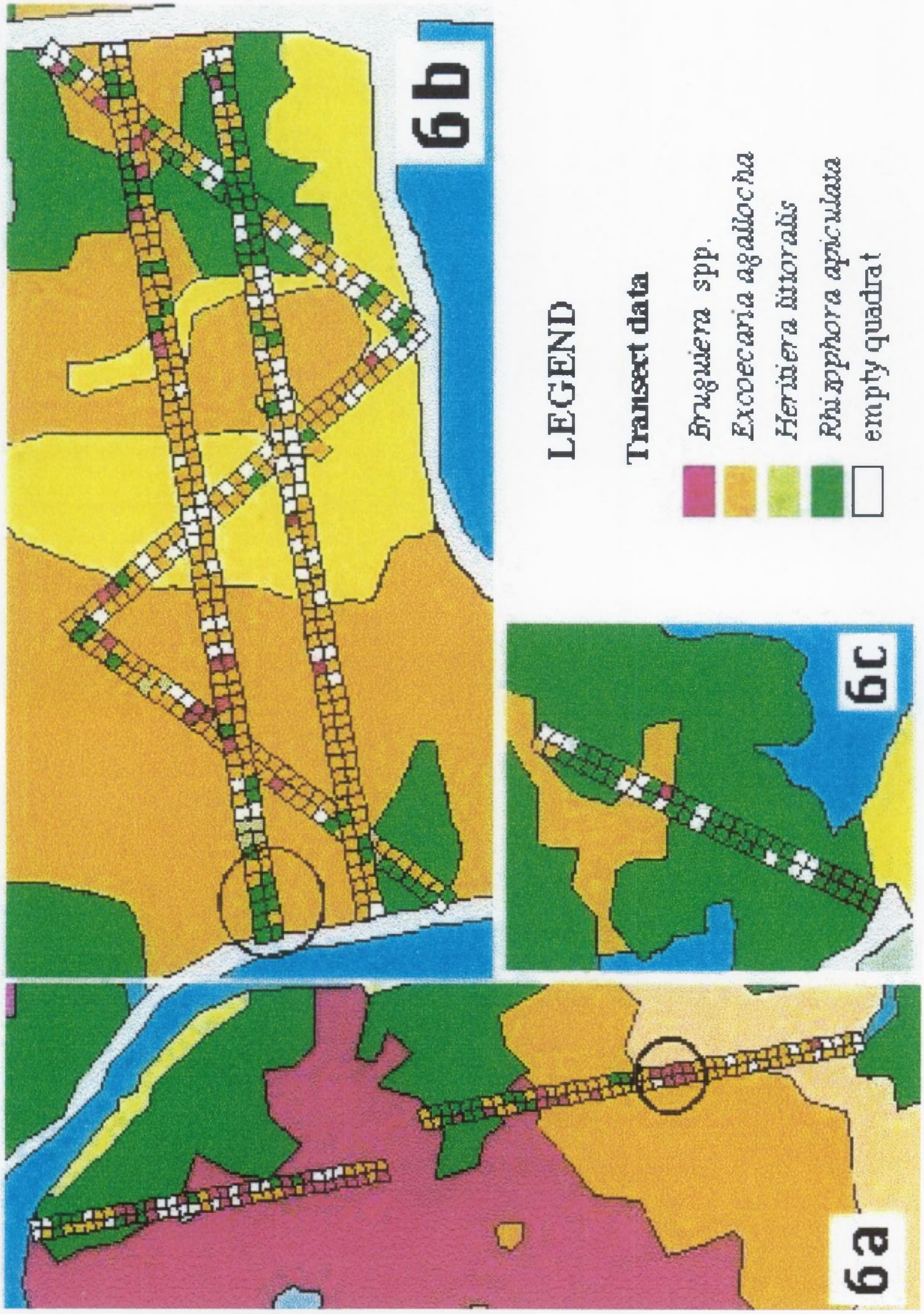

(c)
N
0 50 100 m
LEGEND
*Avicennia* dominated
*Lumnitzera* dominated
*Rhizophora* dominated
*Excoecaria* dominated
mixed mangrove stand
*Acrostichum or land Acanthus*
*Cocos nucifera* plantation
non-mangroves
open space
water
shrimp farm

**Figure 6.** Different species assemblages in the Galle area (1994) with fieldwork transects (1997) superimposed. Encircled are small assemblages, detected during the fieldwork, but not during visual analysis.



# Chapter V.

## A note on the identification of mangroves from aerial photography in Kenya and Sri Lanka.

Dahdouh-Guebas, F., A. Verheyden, L.P. Jayatissa & N. Koedam

In preparation

# A note on the identification of mangroves from aerial photography in Kenya and Sri Lanka.

Dahdouh-Guebas, F.[1], A. Verheyden[1], L.P. Jayatissa[2] 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] *Department of Botany, University of Ruhuna, Matara, Sri Lanka.*

Keywords : mangrove, vegetation structure, remote sensing, tonality, texture, structure, GIS, Kenya, Sri Lanka.

## Introduction

Air- or space-borne imagery are common data for investigating natural resources remotely. Particularly in difficultly accessible and penetrable habitats, such as mangrove forests, remote sensing is an efficient tool and provides preliminary results in a phase prior to compulsory fieldwork, or moreless final results on a scale larger than where the fieldwork is concentrated. The application of aerial photography has shown to be successful in the study of mangrove floristics (Verheyden *et al.*, subm.) and mangrove vegetation dynamics (Dahdouh-Guebas *et al.*, 2000a), allowing a more detailed study than possible with satellite imagery (Blasco *et al.*, 1998). Within literature there is a tremendous emphasis on digital imagery and automated methods, despite the fact that in many cases human interpretation of aerial photographic images and the ability to integrate different image attributes intuitively is the only way of obtaining information.

Keys to identify certain vegetation assemblages are usually applied to well delineated forests, leaving a more detailed comparison on the consistency of species identification on a wider scale virtually unchallenged. For mangroves, Verheyden *et al.* (subm.) discussed the wider spatial and temporal applicability of aerial photography and briefly highlighted the case of *Excoecaria agallocha* L. to illustrate differences in tonality for different mangrove lagoons in Sri Lanka.

The objective of the present study is to attempt a comparison of the consistency of all the image attributes (tonality, texture, structure and other attributes) in different mangrove lagoons located on two different continents : Gazi Bay and Mida Creek in Kenya, and Rekawa Lagoon, Galle-Unawatuna Lagoon and Pambala-Chilaw Lagoon in Sri Lanka.

## Material & methods

New keys for the interpretation of aerial photographs of Gazi Bay and Mida Creek were constructed using the image attributes 'tonality' (= the colour or grey value of a single image object), 'texture' (= the internal pattern of a single image object), 'structure' (= the way different image objects connect to each other) and 'other image attributes' (*e.g.* shape, shade, water- or landward location). Formerly established interpretation keys for the Sri Lankan lagoons (Verheyden *et al.*, subm.) have been amended here and consistently structured according to the above image attributes. The five resulting standardised interpretation keys were then used to further investigate the species that are recognisable as vegetation assemblages. It should be recalled here that the use of a mangrove species' name as an identification tag in the keys should be considered as a vegetation assemblage dominated by a certain species rather than as a pure stand. Species listed as 'mangrove species', according to Jayatissa *et al.* (subm.), and present in at least three out of the five sites, were then compared in their image attributes and a 'compromise key' was drafted. In the latter, the most common non-mangrove identification classes were included as well.

## Results

The most common non-mangrove image objects are water, sand, coconut trees (*Cocos nucifera* L.) and human infrastructure (Tab. 1). They are present in a majority of the sites and are characterised by unambiguously recognisable features within the photographic 'context'. Human infrastructure includes constructions (houses, buildings, industrial facilities) and tracks (railways, paths, roads and bridges). Other clearly recognisable man-made features are agricultural fields such as for example rice fields or coconut plantations, which are often found near mangroves. The 'compromise key' (Tab. 2) represents five common mangrove genera and when compared with the original identification keys, it shows that for a particular species none of the image attributes displays a strong plasticity.

## Discussion

Although identification keys are not meant to be applied to aerial photographs of regions that are not familiar (*e.g.* in other geographic units, in more or less diverse sites), the present study suggests that, at least for mangroves, they might be less plastic and possibly wider applicable than formerly assumed. Apart from the basic image attributes tonality, texture and structure, it appears that for the vegetation classes particularly spatial information can greatly help their identification and in certain cases even be decisive in the identification of vegetation assemblages that do not differ in tonality, texture or structure (Tab. 2d). Even in situations in which zonation is not or poorly present spatial information is very useful. Information with respect to crown shapes or height relative to the surrounding vegetation for instance, can help as well. All the above is further aided if knowledge about the species composition of a certain site exists, as pointed out by Verheyden *et al.* (subm.). It is also imperative to get access to correct information with regard to species composition, as erroneous species lists may lead to wrong interpretations in the framework of remote sensing (Jayatissa *et al.*, subm.).

Verheyden *et al.* (subm.) highlighted for *Excoecaria agallocha* physiognomic differences between Galle and Rekawa caused by the plasticity in tonality of this species. Although technical photographic differences are always a possible cause for observed differences in image attributes, in particular tonality, the underlying basis of the above observation is probably the location of these sites in different climatic zones. Temperature and humidity conditions, and their close association with soil salinity, are also known to affect mangrove height and together with environmental factors the vegetation structure of a forest (Dahdouh-Guebas & Koedam, in press; Dahdouh-Guebas *et al.*, subm.d). This has a direct influence on the attribute 'structure' in aerial photography, such as for *Avicennia marina* (Forsk.) Vierh. in

Gazi Bay (Tab. 1a). For *Rhizophora* species it seems that local environmental conditions may be more important than differences induced by climate. A continuous canopy is characteristic for this genus in all sites, yet within the mangrove area of Galle (Tab. 1d) it may feature different 'structure' attributes. This within-site variability may be due to the variability of micro-environmental settings, such as the topography. In Galle, the latter is influenced to a high degree by the mangrove mud lobster *Thalassina anomala* Herbst, which forms small islands and ponds. *Excoecaria agallocha* trees are always established on these islands whereas *Rhizophora apiculata* Bl. is located on the edges of the islands and is in part standing in the water. Hence, the general topography, whether or not anthropogenical (*e.g.* from abandoned coconut plantations), influences the 'structure' component, and the burrowing activity of *T. anomala* is one biotic factor that further shapes this image attribute. The 'texture' seems to be little influenced by local environmental conditions, but is instead characteristic of a particular species.

It seems that identification keys for the interpretation of aerial photographs of a certain mangrove area can be applied to another one in a preliminary phase, provided species compositions are, at least in part, overlapping. Fieldwork is a compulsory next phase, but due to the small variability of the image attributes it can probably be carried out in a relatively small area or over less ground truth points than presumed as 'standard' till now. Attention should however be drawn to the fact that only fieldwork can overcome the problems of misidentification due to optical interference (*e.g.* a black tonality and a white tonality which result in a grey tonality if present near each other). Also the relative importance of species should be estimated solely from fieldwork, because possible overtopping of one species by another is not visible from aerial photographs.

## Acknowledgements

Research financed by the European Commission (Contract EBR IC18-CT98-0295), the Fund for Scientific Research, Flanders (Belgium) and with a specialisation fellowship of the Flemish Institute for the advancement of scientific-technological research in the industry (IWT).

## References

See Bibliography

**Table 1.** Keys for the identification of vegetation in mangroves of Gazi Bay (a) and Mida Creek (b) in Kenya, and Rekawa (c), Galle (d) and Pambala (e) in Sri Lanka.

**(a) MIDA (03°20' S - 39°59' E)**

| Tonality | Texture | Structure | Other image attributes (*e.g.* shape, shade, location) | Identification |
|---|---|---|---|---|
| white | plain | plain | none | sand |
| light grey | coarse grain | discontinuous canopy | water side | *Avicennia marina* |
|  | coarse grain | discontinuous canopy or continuous canopy with crowns hard to distinguish | landward side | *Avicennia marina* |
| intermediate grey | fine grain | continuous canopy<br>crowns not visible separately | often landward side<br>often lower than surrounding vegetation | *Ceriops tagal* |
| dark grey | fine grain | continuous canopy<br>crowns not visible separately | often at water side<br>wide horizontal spatial range<br>sometimes clearly higher than surrounding vegetation | *Rhizophora mucronata* |
| primarily dark grey, but mixed with light and intermediate grey | coarse grain | dense but often with a discontinuous canopy | none | Mixed stand with *Rhizophora mucronata* and *Ceriops tagal* co-dominant |

N.B. the identification tag should always be considered as a vegetation assemblage dominated by a certain species, rather than as a pure stand.

N.B. a 'discontinuous canopy' implies that crowns are separately visible, but a 'continuous canopy' does not imply that separate crowns cannot be distinguished.

**(b) GAZI (04°25'S - 39°30' E)**
**(Dahdouh-Guebas, published by Van Pottelbergh (1999) by consent of former)**

| **Tonality** | **Texture** | **Structure** | **Other image attributes (*e.g.* shape, shade, location)** | **Identification** |
|---|---|---|---|---|
| white | plain or irregular | plain or irregular | none | sand |
| | irregular | irregular | often clearly man-made | infrastructure (tracks, constructions) |
| | coarse grain and/or blurred | discontinuous canopy | star-shaped crown<br>sparse and regular distribution | *Cocos nucifera* (coconut) |
| light grey | coarse grain | discontinuous canopy | water side and often higher than surrounding vegetation | *Avicennia marina* |
| | fine grain | discontinuous canopy or continuous canopy with crowns hard to distinguish | landward side | *Avicennia marina* |
| | variable | often discontinuous canopy | landward side or outside reach of mangrove vegetation | terrestrial vegetation |
| dark grey | fine grain and blurred | continuous canopy<br>crowns not separately visible | landward side<br>lower than surrounding vegetation | *Ceriops tagal* |
| | coarse grain<br>'peluche' texture | discontinuous canopy | amongst terrestrial vegetation<br>sparse and regular distribution | *Mangifera indica* (mango) |
| | coarse grain | discontinuous canopy | always at water side | *Sonneratia alba* |
| very dark grey or black | fine or coarse grain | continuous canopy with crowns hard to distinguish | aggregating / often at water side<br>wide horizontal spatial range | *Rhizophora* spp. |

N.B. the identification tag should always be considered as a vegetation assemblage dominated by a certain species, rather than as a pure stand.

N.B. a 'discontinuous canopy' implies that crowns are separately visible, but a 'continuous canopy' does not imply that separate crowns cannot be distinguished.

**(c) REKAWA (06°03' N - 80°50' E)**
**(Thomaes, 1996; elaborated by Verheyden *et al.*, subm.; amended underneath)**

| **Tonality** | **Texture** | **Structure** | **Other image attributes (*e.g.* shape, shade, location)** | **Identification** |
|---|---|---|---|---|
| white | blurred | discontinuous canopy | star-shaped crown | *Cocos nucifera* |
| white | blurred | discontinuous canopy | water or land side | *Avicennia* spp. |
| light grey | fine grain | crowns can be distinguished | none | *Aegiceras corniculatum* |
| **intermediate grey** | coarse grain | many small crowns hard to distinguish | none | *Lumnitzera racemosa* |
| dark grey | coarse grain 'cauliflower' texture | continuous canopy | none | *Rhizophora mucronata* |
| black | blurred | crowns not distinguishable | none | *Ceriops tagal* |

N.B. the identification tag should always be considered as a vegetation assemblage dominated by a certain species, rather than as a pure stand.

N.B. a 'discontinuous canopy' implies that crowns are separately visible, but a 'continuous canopy' does not imply that separate crowns cannot be distinguished.

### (d) GALLE (06°01'N - 80°13' E)
### (Thomaes, 1996; elaborated by Verheyden, 1997; amended underneath)

| **Tonality** | **Texture** | **Structure** | **Other image attributes (*e.g.* shape, shade, location)** | **Identification** |
|---|---|---|---|---|
| white | irregular | irregular | often clearly man-made | infrastructure (tracks, constructions) |
| | blurred | discontinuous canopy | star-shaped crown<br>sparse and regular distribution | *Cocos nucifera* (coconut) |
| | blurred | irregular | no typical shape<br>no shadow-side | *Clerodendron inerme* |
| | fine grain | discontinuous canopy | horizontal not spatially bound | *Excoecaria agallocha* |
| light grey | fine grain | discontinuous canopy | horizontal not spatially bound | *Excoecaria agallocha* |
| | coarse grain | discontinuous canopy | horizontal not spatially bound | *Bruguiera* spp. |
| intermediate grey | coarse grain | discontinuous canopy | horizontal not spatially bound | *Bruguiera* spp. |
| | coarse grain | discontinuous canopy | often at water side | *Rhizophora* spp. |
| | 'cauliflower' texture | continuous canopy with no separately visible crowns | aggregating / often at water side<br>wide horizontal spatial range | *Rhizophora* spp. |
| dark grey | 'cauliflower' texture | continuous canopy with no separately visible crowns | aggregating / often at water side<br>wide horizontal spatial range | *Rhizophora* spp. |
| | coarse grain | discontinuous canopy | aggregating / often at water side<br>wide horizontal spatial range | *Rhizophora* spp. |

N.B. the identification tag should always be considered as a vegetation assemblage dominated by a certain species, rather than as a pure stand.

N.B. a 'discontinuous canopy' implies that crowns are separately visible, but a 'continuous canopy' does not imply that separate crowns cannot be distinguished.

### (e) PAMBALA (07°30' N - 80°00' E)
### (Dahdouh-Guebas, published by Zetterström (1998) by consent of former)

| Tonality | Texture | Structure | Other image attributes (*e.g.* shape, shade, location) | Identification |
|---|---|---|---|---|
| white | plain or irregular | plain or irregular | none | sand or grassy plain |
|  | blurred | discontinuous canopy | star-shaped crown<br>sparse and regular distribution | *Cocos nucifera* (coconut) |
| light grey | coarse grain | discontinuous canopy | land or water side | *Avicennia* spp |
|  | blurred | discontinuous canopy | horizontal not spatially bound | *Excoecaria agallocha* |
| intermediate grey | very fine grain | continuous canopy with many crowns hardly distinguishable | often at landward side | *Lumnitzera racemosa* |
|  | coarse grain and /or blurred | crowns hard to distinguish | none | *Bruguiera* spp<br>*Xylocarpus* spp |
|  | none or blurred | none or regular | none | *Acrostichum aureum* |
|  |  |  | at water side | *Acrostichum aureum* or *Acanthus ilicifolius* |
| dark grey | coarse | continuous canopy<br>crowns separately visible or not so | aggregating / often at water side<br>wide horizontal spatial range | *Rhizophora* spp |

N.B. the identification tag should always be considered as a vegetation assemblage dominated by a certain species, rather than as a pure stand.

N.B. a 'discontinuous canopy' implies that crowns are separately visible, but a 'continuous canopy' does not imply that separate crowns cannot be distinguished.

**Table 2.** 'Compromise key' to identify some common species and features from aerial photographs of mangrove areas based on five mangrove lagoons in Kenya and Sri Lanka. See table 1 for the plasticity of the features.

| Species | Tonality | Texture | Structure | Other image attributes |
|---|---|---|---|---|
| *Avicennia* spp. | white or light grey | coarse grain | often discontinuous canopy | mostly along water side, but can also occur landward |
| *Bruguiera* spp. | light or intermediate grey | coarse grain / blurred | (dis)continuous canopy | horizontal not spatially bound |
| *Ceriops tagal* | intermediate or dark grey | fine grain / blurred | continuous canopy<br>crowns not visible separately | landward<br>lower than surrounding vegetation |
| *Excoecaria agallocha* | white or light grey | fine grain / blurred | discontinuous canopy | horizontal not spatially bound |
| *Rhizophora* spp. | intermediate or dark grey | coarse grain<br>'cauliflower' texture | continuous canopy, with sometimes distinguishable crowns | aggregating<br>often at water side<br>wide horizontal spatial range |
| *Cocos nucifera* | white | blurred | discontinuous canopy | 'star'-shaped crown |
| sand | white | plain or irregular | plain or irregular | none |
| water | black | plain or irregular | plain or irregular | waves can be present |
| human infrastructure | white | irregular | irregular | often clearly man-made |

N.B. the identification tag should always be considered as a vegetation assemblage dominated by a certain species, rather than as a pure stand.

N.B. a 'discontinuous canopy' implies that crowns are separately visible, but a 'continuous canopy' does not imply that separate crowns cannot be distinguished.

# Chapter VI.

# Four decade vegetation dynamics in Sri Lankan mangroves as detected from sequential aerial photography : a case-study in Galle.

Dahdouh-Guebas, F., A. Verheyden, W. De Genst, S. Hettiarachchi & N. Koedam

Published in

*Bulletin of Marine Science* 67(2): 741-759.

BULLETIN OF MARINE SCIENCE, 67(2): 741–759, 2000

# FOUR DECADE VEGETATION DYNAMICS IN SRI LANKAN MANGROVES AS DETECTED FROM SEQUENTIAL AERIAL PHOTOGRAPHY: A CASE STUDY IN GALLE

*F. Dahdouh-Guebas, A. Verheyden, W. De Genst,
S. Hettiarachchi and N. Koedam*

## ABSTRACT

In remote sensing, aerial photography is often indispensable, particularly in species-diverse mangroves, to identify species or genera or the typology of assemblages. Aerial photographs constitute a most valuable tool to study the dynamics of mangrove forests on a typology basis. They usually constitute the only retroactive basis of comparison to actual mangrove vegetation data. In the present study the dynamics of a mangrove area in southern Sri Lanka, namely Galle (06°01'N, 80°13'E), was investigated using sequential aerial photographs (1956, 1974 and 1994). To identify species or genera from aerial photographs a reliable determination key based on photographic features is needed. For the purpose of this study, a key proposed by Verheyden et al. (submitted) was used. Identification of species and genera from aerial photographs and a study of vegetation dynamics revealed that four sectors, each characterized by a particular vegetation dynamic, could be identified. Characteristic changes in these sectors consisted of either minor changes in composition, mangrove area increase or decrease, or major structural change. Furthermore, the results show that a dynamic interaction between mangroves and *Cocos nucifera* stands exists in the area. Ground truthing in each of the mangrove sectors confirmed the aerial photography interpretations. Quantitative and qualitative comparisons of field data on adult, young and juvenile trees result in a prediction of a transition of the *Excoecaria* dominated mangrove to a *Bruguiera* dominated one in one part, and an evolution towards a terrestrial vegetation elsewhere. These results point at fundamental floristic and structural changes in the mangroves of Galle, in a time scale of decades, both when comparing to the past and when predicting the future.

Mangrove forests have been studied worldwide, and at present, considerable research effort is put in the assessment of the state of mangroves on a country-, region- or world-wide scale. For many applications, remote sensing has proved to be a good tool to collect large sets of data in a fast and reliable way. Space-borne data have been used repeatedly to assess vast areas of mangroves (among others Aschbacher et al., 1995; Spalding et al., 1997; Ramachandran et al., 1998; Blasco et al., 1998), but the resolution of these data does not always allow us to identify species or genera or the typology of assemblages, required for the assessment of mangrove vegetation dynamics. Therefore such data sometimes provide insufficient information to study vegetation dynamics. Although providing less spectral information, aerial photographs can be used instead. Also in the framework of forestry planning, Holmgren and Thuresson (1998) conclude that satellite sensors contain little relevant information—though this can be expected to improve rapidly—and for forest management planning purposes there are often more efficient ways of collecting the information required. For our purpose, airborne remote sensing was shown to be appropriate (Verheyden et al., submitted).

Understanding of mangrove dynamics in a particular area is a prerequisite to conservation and management directives, such as the establishment, protection and management of reafforestation plots in the framework of regeneration projects (e.g., Lee et al., 1996; Caloz and Collet, 1997). There is a need for a methodology that allows us to make reliable predictions about the state of mangroves using a relatively small input from vegetation fieldwork, and to decide if a mangrove stand of a certain location has the potential to successfully renew and rejuvenate or if anthropogenic pressure renders human interference such as restoration imperative. It may be argued that artificial restoration for nature management purposes should be avoided whenever possible. Therefore, a monitoring system is needed to decide whether this human interference is desirable. A clear understanding of the nature and dynamics of local mangrove ecosystems will be the best guide to any restoration program (Field, 1996). The first step is to collect information about the actual state of the mangrove forest, emphasizing different vegetation layers, the importance of which has been properly highlighted by Murali et al. (1998), but also about past changes in a particular vegetation. Where such studies concentrate on the diversity of mangroves it is important to assess the appropriate spatial, taxonomic and temporal scale (Farnsworth, 1998). The second step is to integrate such findings into the management and decision-making process.

The objectives of the present study are to make a quantitative and qualitative evaluation of the mangrove vegetation and of the vegetation dynamics in a mangrove forest near Galle (Sri Lanka). The study aims at interpreting the results from the past and the present using aerial photography analysis and fieldwork on the adult vegetation and to extrapolate the interpretation to future dynamics through fieldwork on the young and juvenile vegetation. In the context of mangrove dynamics, as spatial changes in vegetation patterns over time, we explore the following idea: how dynamic can mangroves be and what could be the underlying basis of their dynamism?

## STUDY SITE

The mangrove area investigated is located in southern Sri Lanka, between Galle and Unawatuna (06°01'N,80°14'E). The mangroves of Galle, which are situated in the wet climate zone of Sri Lanka (Fig. 1), are located at about 600 m from the Indian Ocean shore (Fig. 2), cover a surface of 1.5 km$^2$ and are of the riverine and basin type (Lugo and Snedaker, 1974), the latter of which was claimed not to exist along the Sri Lankan West-Coast (De Silva and Balasubramaniam, 1984–85). Two rivers run through the mangrove forest: the Thalpe Ela, discharging into the ocean, and the Galu Ganga, a tributary of the former.

## MATERIALS AND METHODS

This research is the third phase in the ongoing research on mangrove dynamics (Fig. 3). The digitization of aerial photographs of the mangrove in Galle and their conversion into vector- and grid-based vegetation maps was done in a Geographical Information System (GIS) on a Macintosh platform, using MapGrafix, MapClass, GenaMap and MapII. Comparison of the vegetation maps (1956, 1974, 1994) resulted in the definition of four sectors in Galle depending on the degree and direction of change (Fig. 2), called Sector 1, Sector 2, Sector 3 and Sector 4. In each of these sectors more detailed investigations (both in the field and on the aerial photographs) were conducted (Fig. 3).

During a field campaign in January and February 1997, two transects were investigated in Sector 1 (170 and 210 m length), five transects in Sector 2 (330, 320, 170, 170 and 170 m length) and one transect in Sector 3 (170 m) (Fig. 2), making use of 10 m intervals and applying the Point-Centred

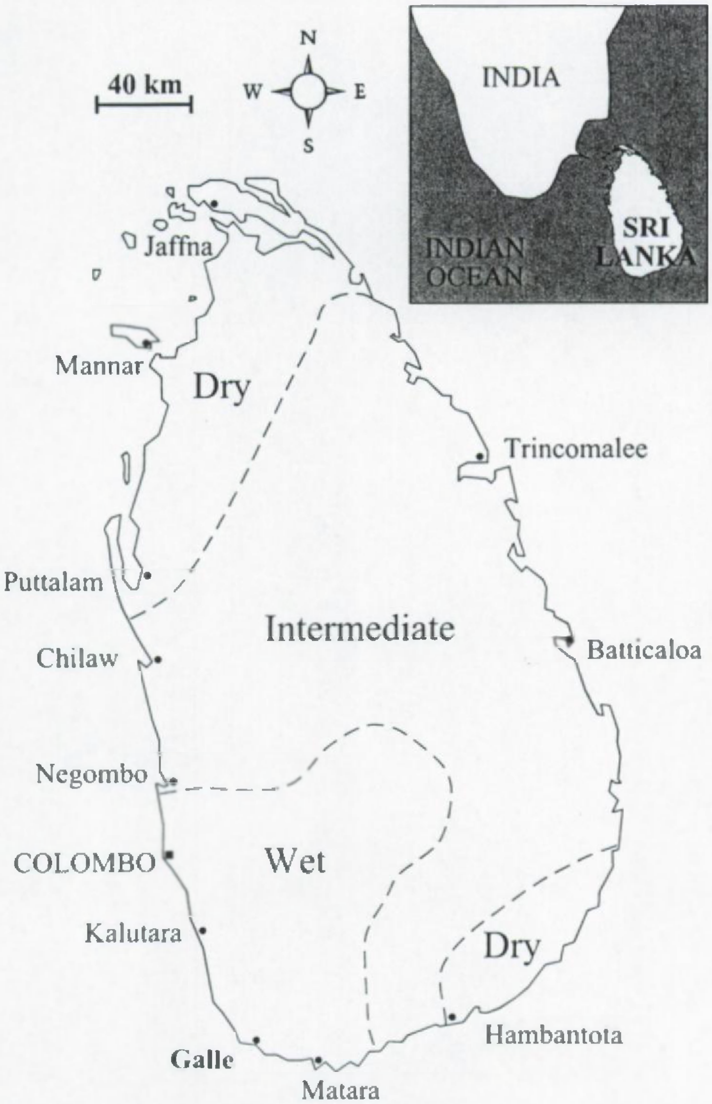


Figure 1. Map of Sri Lanka showing the climatic zones and some major cities along the coast, of which our study site Galle is printed bold. Climatic zones are after Mueller-Dombois (1968).

Quarter Method or PCQM (Cottam and Curtis, 1956). The tree species closest to the sample point was recorded in each quadrant (= quarter), its height and $D_{130}$ (term according to Brokaw and Thompson (2000), but formerly referred to as DBH, the diameter at breast height) were measured and the total cover abundance in the 5 m × 5 m quadrat (= square) nearest to the sampling point was estimated in each quadrant. Each of the transects was covered on three occasions within 3 d: to investigate adult mangrove trees, to investigate young mangrove trees (trees smaller than 1.3 m or with a $D_{130}$ <2.5 cm, but which already reached the sapling stage) and to investigate mangrove juveniles (propagules or seeds until they reached the stage of sapling, which is defined here as a young plant with more than six leaves). Considering our definition of a young tree, there was no

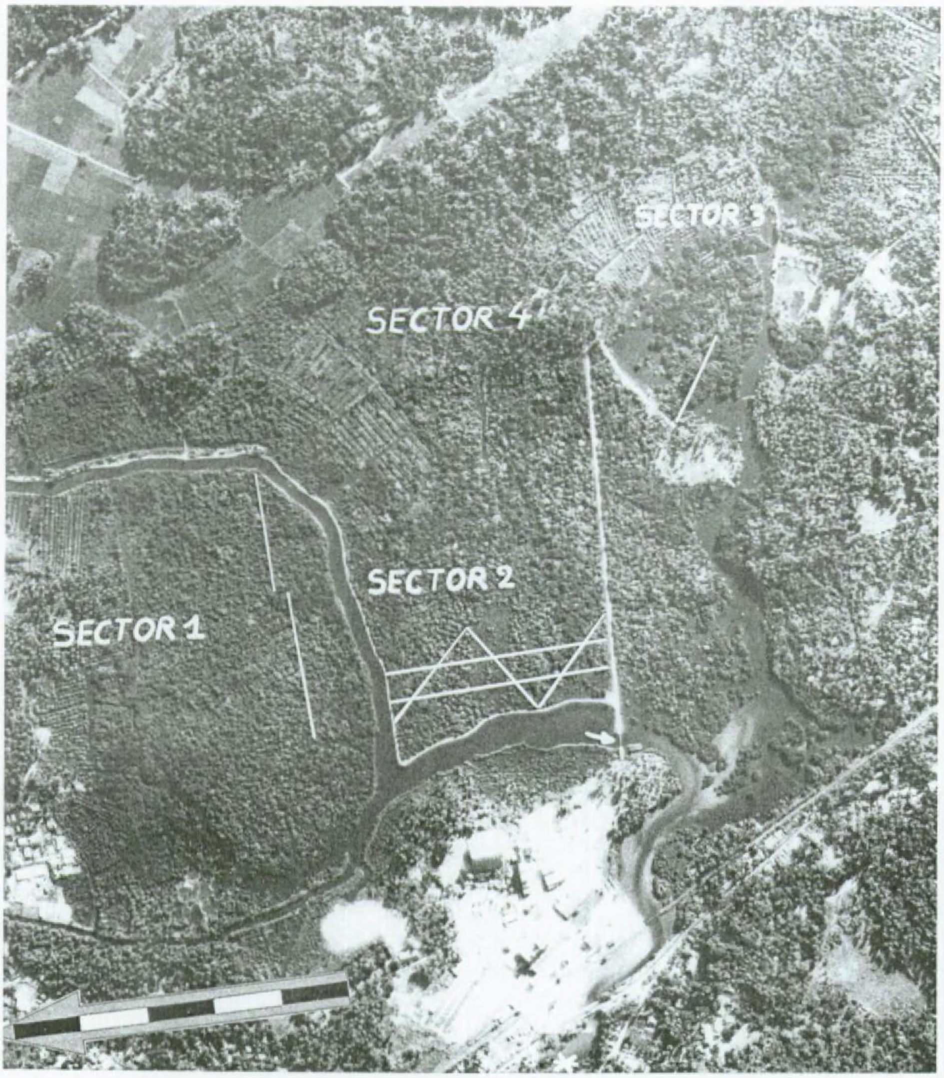


Figure 2. Aerial photograph of Galle showing the different sectors (please refer to the 'Results' section for detailed description of each sector). The white lines indicate the locations of the vegetation transects and the small white arrow beneath the transects in Sector 2 points to the dam (06°01'37.9"N, 080°14'50.5"E with an accuracy of 7 m). The only connection between the river (and mangrove) and the Indian Ocean is given by the white asterisk at the bottom of the photograph. The scale represents 500 m and is pointing to the north.

point in measuring the $D_{130}$ (or in a later stage calculating the basal area). Visual observations and interviews with local people were also carried out, whenever possible and for the whole duration of the field work mission, in order to gather information on the past condition of the mangroves in Galle.

Vegetation maps of 1956, 1974 and 1994 were digitized and overlay analyses were conducted for the digital vegetation maps of 1956 and 1974 and for 1974 and 1994 from which changes in surface area were calculated. The field transects were traced on photographic copies of the most recent aerial photograph (1994). Transect data for adult, young and juvenile mangrove species were visualized in separate GIS layers, superimposed on the vegetation map of 1994 and absolute numbers of

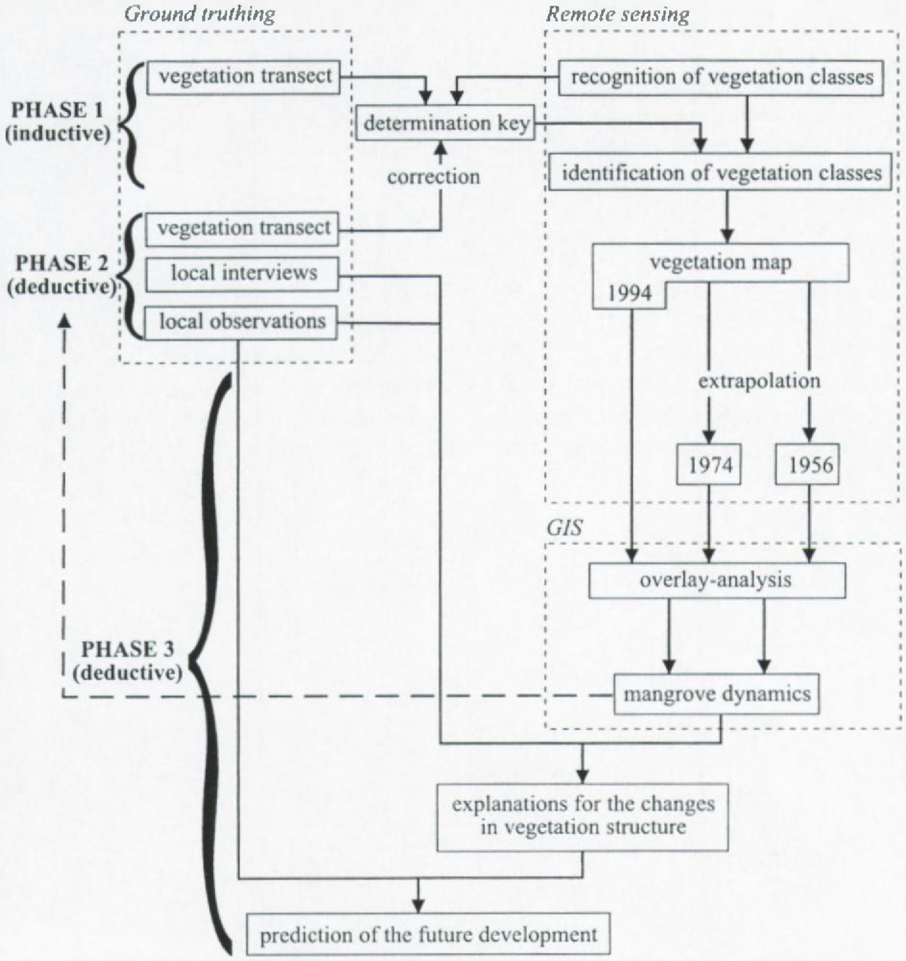


Figure 3. Scientific approach used in this study. In a first phase an inductive scientific approach was adopted to interpret aerial photographs based on a first field work mission (Verheyden et al., submitted). Different vegetation classes are recognized on aerial photographs, and with the help of a determination key and vegetation transects in the field, they are identified. The second phase was the deductive continuation of the first study, in which the previously established predictions were confirmed and investigated in detail, and a reliable determination key for the identification of mangrove genera was constructed (Verheyden et al., submitted; Table 1). In the present study the determination key was used to interpret aerial photographs for 1956 and 1974. By comparing all vegetation maps (1956, 1974, 1994), a view of the dynamics of the forest was obtained (see results) and together with local observations enabled us to gain insight in the hypotheses accounting for the observed dynamics and to make predictions for the future.

young and juveniles located in a certain forest patch were calculated (The terms 'forest patch' and 'vegetation class' have been used as synonyms with a rather geographical and ecological context for the former and a remote sensing context for the latter). From the PCQM data the relative density [$D_r$ = (number of individuals of species/total number of individuals) × 100], the relative dominance [(dominance of a species/Σ dominance for all species) × 100] and the relative frequency [(frequency of a species/Σ frequency of all species) × 100] were computed for the adult trees using the methods described by Cintrón and Schaeffer Novelli (1984) in order to calculate the importance value of Curtis (1959) or I.V. for each mangrove tree species. Relative density was calculated for young mangrove trees as well, but no importance value was given since the latter necessitates the $D_{130}$ in the process of its calculation (Curtis, 1959). A statistical analysis (G-test as described in Sokal and Rohlf, 1981) was performed on the absolute numbers of sample points located in a certain forest patch and containing a certain mangrove species in order to detect differences in abundance between the adult and young vegetation layer.

## RESULTS

Figure 4A–C shows the vegetation map for 1956, 1974 and 1994, respectively, on the basis of sequential aerial photographs. When comparing the aerial photographs or vegetation maps two by two in a chronological order, it can be seen that during the first period a second track appears along the coast, which runs between the mangrove forest and the ocean. Secondly, a large scale infrastructure (a factory of the Ruhunu Cement Company), was built close to the mangroves. The dam built during the second period

### LEGEND

**Transect data**

■ *Bruguiera gymnorrhiza*
░ *Excoecaria agallocha*
▨ *Heritiera littoralis*
▓ *Rhizophora apiculata*
□ empty quadrat

**Vegetation map data**

░ dense *Excoecaria agallocha*
□ sparse *Excoecaria agallocha* (only in map of 1994)
▓ dense *Rhizophora apiculata*
▒ sparse *Rhizophora apiculata* (only in map of 1956)
▒ *Bruguiera* spp. and *Excoecaria agallocha* mixed
▦ *Rhizophora apiculata* and *Excoecaria agallocha* mixed
××× *Cocos nucifera* plantation
□ open space
■ water
+++ terrestrial and inhabited area
■ traffic infrastructure
▩ cement company infrastructure

Figure 4A. Final vegetation maps of Galle for 1956. Refer to legend *(opposite page)* and to Table 1 on page 750 for map conventions for Figures 4 and 5.

(1974–1994), as well as the paths along the banks of the creek and through the mangroves, can be seen on the aerial photograph (Fig. 2) and on vegetation map of 1994 (Fig. 4C). Analysis of the sequential vegetation maps leads to a number of obvious conclusions:

- Galle has undergone heavy anthropogenic transformations in the past.
- Some mangrove species' coverage have decreased at the benefit of other mangrove species.
- A particular vegetation dynamic can be recognized in four different parts (hereafter called 'Sectors') of the mangrove forest (cf Fig. 2): Sector (1) minor changes in the vegetation occurred over time (38 yr period); Sector (2) major structural differences occurred over time (18 and 20 yr period); Sector (3) mangrove has invaded the sector (20 yr period); Sector (4) mangrove has disappeared from the sector (38 yr period).

Interviews with the local Area Watcher-in-Chief revealed that the banks of both rivers were artificially enlarged in 1982 and an earthen motorable track was constructed along them; another elevated track was constructed straight across the mangrove forest (Figs. 2,4C). Furthermore, in 1985 a dam was built where the Galu Ganga discharges in the Thalpe Ela, in order to allow rice farming upstream. However, the dam was not opera-

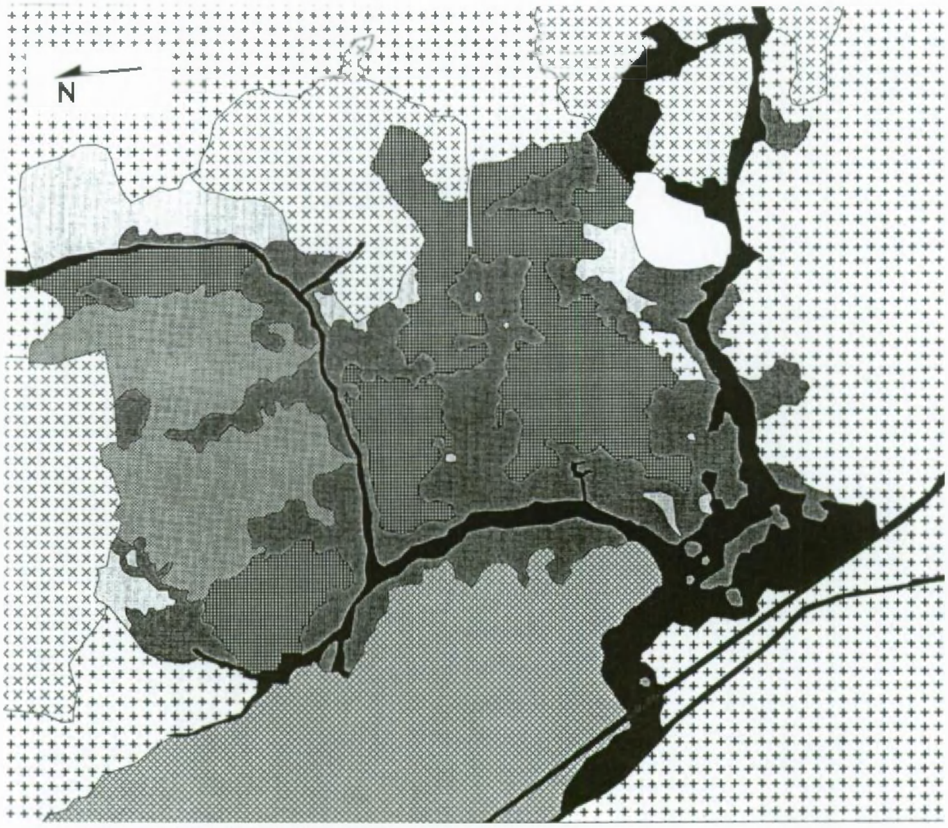


Figure 4B. Final vegetation maps of Galle for 1974. Refer to legend on page 746 and to Table 1 on page 750 for map conventions for Figures 4 and 5.

tional between 1990 and December 1997. Though not fully impeding water flow, the dam nevertheless constituted an obstacle to the water flow in the river. In February 1998 all elevated motorable tracks were renewed and enlarged.

The mangrove species which were observed in Galle are: *Bruguiera gymnorrhiza* (L.) Lam., *Bruguiera sexangula* (Lour.) Poir., *Excoecaria agallocha* L., *Heritiera littoralis* Dryand. and *Rhizophora apiculata* Bl. [nomenclature according to Tomlinson (1986)]. There were also a few occurrences of *Lumnitzera racemosa* Willd. and *Sonneratia caseolaris* (L.) Engler and a single tree of *Bruguiera cylindrica* (L.) Bl. and of *Ceriops tagal* (Perr.) C. B. Robinson was reported to be imported from another mangrove lagoon. Table 2 summarizes the surface areas for each vegetation class in 1956, 1974 and 1994. Calculating the areal extent of each vegetation class reveals that the surface cover (in ha) of *R. apiculata* stands have hardly changed between 1956 and 1994, but that the proportion of this species within the mangrove forest decreases. For *E. agallocha* stands, a loss of a few hectares over the 18-yr period 1956–1974 (Table 2) is followed by over a threefold increase the following 20 yrs (1974–1994). The structural changes that this implies, i.e. the shifts in the vegetation patches for each species or assemblage, can be seen from Figure 4, particularly in Sector 2: there *E. agallocha* has clearly become the dominant species. It is also present in the open space of Sector 2, which is a plain covered with

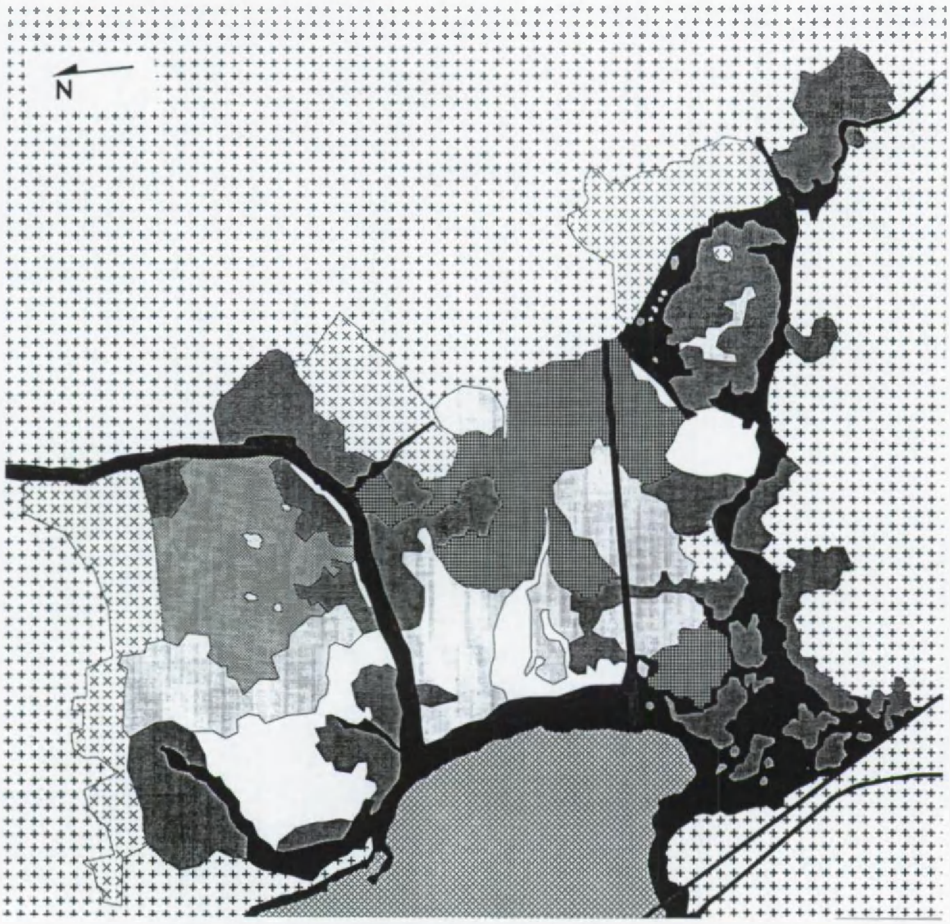


Figure 4C. Final vegetation maps of Galle for 1994. Refer to legend on page 746 and to Table 1 on page 750 for map conventions for Figures 4 and 5.

*Fimbristylis salbundia* (Nees) Kunth subsp. *pentaptera* (Nees) T. Koyama in the herbaceous vegetation layer (yet >1 m). Also the two area decreases of the *E. agallocha* and *Bruguiera* spp. mixed stand (Table 2), and the recent area decrease of *E. agallocha* and *R. apiculata* (Table 2) can be linked to the explosive dispersal of *E. agallocha* stands (Table 2, Fig. 4). The area of *Cocos nucifera* plantations has decreased remarkably (Table 2, Fig. 4), and from visual observations as well as from interviews with the local people we learned that neglect of the plantations was responsible for the decrease. Another observation, primarily relevant to the understory of the mangrove, is the considerable presence of the mangrove associates *Acrostichum aureum* L. and *Dolichandrone spathacea* (L.f.) K. Schumann and other terrestrial species. Together with *E. agallocha* these species occurred on small islands formed by the mangrove mud lobster *Thalassina anomala* Herbst, which is probably the major causative agent for the irregular topography in the mangrove forest (pools and islands up to 1.5 m height). The total mangrove cover of the forest under study, as detected from the aerial photographs, increased slightly (+5.7 ha or +12 % over a period of 38 yrs).

Table 1. Identification key for the various vegetation assemblages in Galle, Sri Lanka (06° 01'N, 80° 13'E) drafted by Thomaes (1996), elaborated by Verheyden (1997) and Verheyden et al. (submitted) and amended underneath.

| Tonality | Texture | Structure | Other image attributes (e.g. shape, shade, location) | Identification |
|---|---|---|---|---|
| white | irregular | irregular | often clearly anthropogenic | infrastructure (tracks, constructions) |
| white | blurred | discontinuous canopy | star-shaped crown<br>sparse and regular distribution | *Cocos nucifera* (coconut) |
| white | blurred | irregular | no typical shape<br>no shadow-side | *Clerodendron inerme* |
| white | fine grain | (dis)continuous canopy | horizontal not spatially bounded | *Excoecaria agallocha* |
| light grey | fine grain | (dis)continuous canopy | horizontal not spatially bounded | *Excoecaria agallocha* |
| light grey | coarse grain | (dis)continuous canopy | horizontal not spatially bounded | *Bruguiera* spp. |
| intermediate grey | coarse grain | discontinuous canopy | horizontal not spatially bounded | *Bruguiera* spp. |
| intermediate grey | coarse grain | discontinuous canopy | often at water side | *Rhizophora* spp. |
| intermediate grey | 'cauliflower' texture | continuous canopy with no separately visible crowns | aggregating / often at water side<br>wide horizontal spatial range | *Rhizophora* spp. |
| dark grey / black | 'cauliflower' texture | continuous canopy with no separately visible crowns | aggregating / often at water side<br>wide horizontal spatial range | *Rhizophora* spp. |
| dark grey / black | coarse grain | discontinuous canopy | aggregating / often at water side | *Rhizophora* spp.<br>wide horizontal spatial range |
| dark grey / black | plain or irregular | plain or irregular | 'waves' may be present | water |

N.B. The identification tag should always be considered as a vegetation assemblage dominated by a certain species, rather than as a pure stand.

N.B. A 'discontinuous canopy' implies that crowns are separately visible, but a 'continuous canopy' does not imply that separate crowns cannot be distinguished.

Table 2. Area covered by the various vegetation classes in 1956, 1974 and 1994 in Galle. The areas are expressed in hectares and as a percentage of the total mangrove cover (between brackets). The limits of the considered areas are real mangrove limits (the mangrove of Galle is completely covered by the photographs).

| Vegetation class | Area in 1956 (ha) | Area in 1974 (ha) | Area in 1994 (ha) |
|---|---|---|---|
| *Rhizophora apiculata* (dense + sparse) | 21.7 (45.3%) | 20.0 (40.4%) | 20.3 (37.8%) |
| *Excoecaria agallocha* (dense + sparse) | 7.8 (16.3%) | 5.0 (10.1%) | 18.4 (34.4%) |
| *E. agallocha* + *Bruguiera* spp. mixed | 11.7 (24.4%) | 9.4 (19.0%) | 6.3 (11.8%) |
| *E. agallocha* + *R. apiculata* mixed | 6.7 (14.0%) | 15.1 (30.5%) | 8.6 (16.0%) |
| **Total mangrove cover** | **47.9 (100%)** | **49.5 (100%)** | **53.6 (100%)** |
| *Cocos nucifera* plantation | 25.1 | 19.4 | 12.1 |
| Water bodies | 11.8 | 11.3 | 15.4 |

The distributions of adult and young mangrove trees resulting from the field work is shown in an overlay with the final vegetation map of 1994 in Figure 5. It was chosen to show only Sector 2 (Fig. 5) in this paper, because of its history of major structural changes. However, the results of the data on the other sectors can be found in table form (Tables 3,4). When superimposing the vegetation map and the transect data for adult trees (Fig. 5A), for young trees (Fig. 5B) and for juvenile trees (map not shown), it can be observed that the understory species are not necessarily the same as those dominating the canopy. In 35% of the sample point quadrants in Sector 2 where *E. agallocha* dominates the canopy, *B. gymnorrhiza* dominates the vegetation layer of young mangrove trees (Table 3). The relative density of these young *B. gymnorrhiza* trees is 70.6% as compared to 23.0% for young *E. agallocha* trees (Table 4B). In the open space, where the woody vegetation is very thin, *E. agallocha* is abundant in the young vegetation layer (77% of the sample point quadrants) and has a relative density of 77.1% (Table 4B). Although a considerable proportion of the quadrants is devoid of woody plants ('nil' in figure legends) in the young vegetation layer, in the area where *R. apiculata* dominates the canopy this 'nil'-proportion reaches 82% (Table 3; Fig. 5). Quantitative analysis of the transect data from Sector 1 can be found in Table 3 and Table 4A. Here *B. gymnorrhiza* dominates the young vegetation layer in each forest patch, with relative densities ranging between 72.7% and 100% as compared to ranges between 0% and 13.6% for *E. agallocha* and *R. apiculata*.

The young tree which was found in Sector 3 was a single *B. gymnorrhiza* (Table 3); therefore it was preferred to omit calculations of relative densities for the young trees in this sector. The high number of empty quadrats in all sectors for the juvenile mangrove trees, does not allow to recognize any associations between juvenile species composition and the adult vegetation structure. The only exception to this are the juvenile *B. gymnorrhiza* trees which take in 26% of the sample points of Sector 1 dominated by *Bruguiera* and *Excoecaria* adult trees.

The results of the statistical analysis (Table 5) show that the observed differences between the abundance of adult and young trees are highly significant.

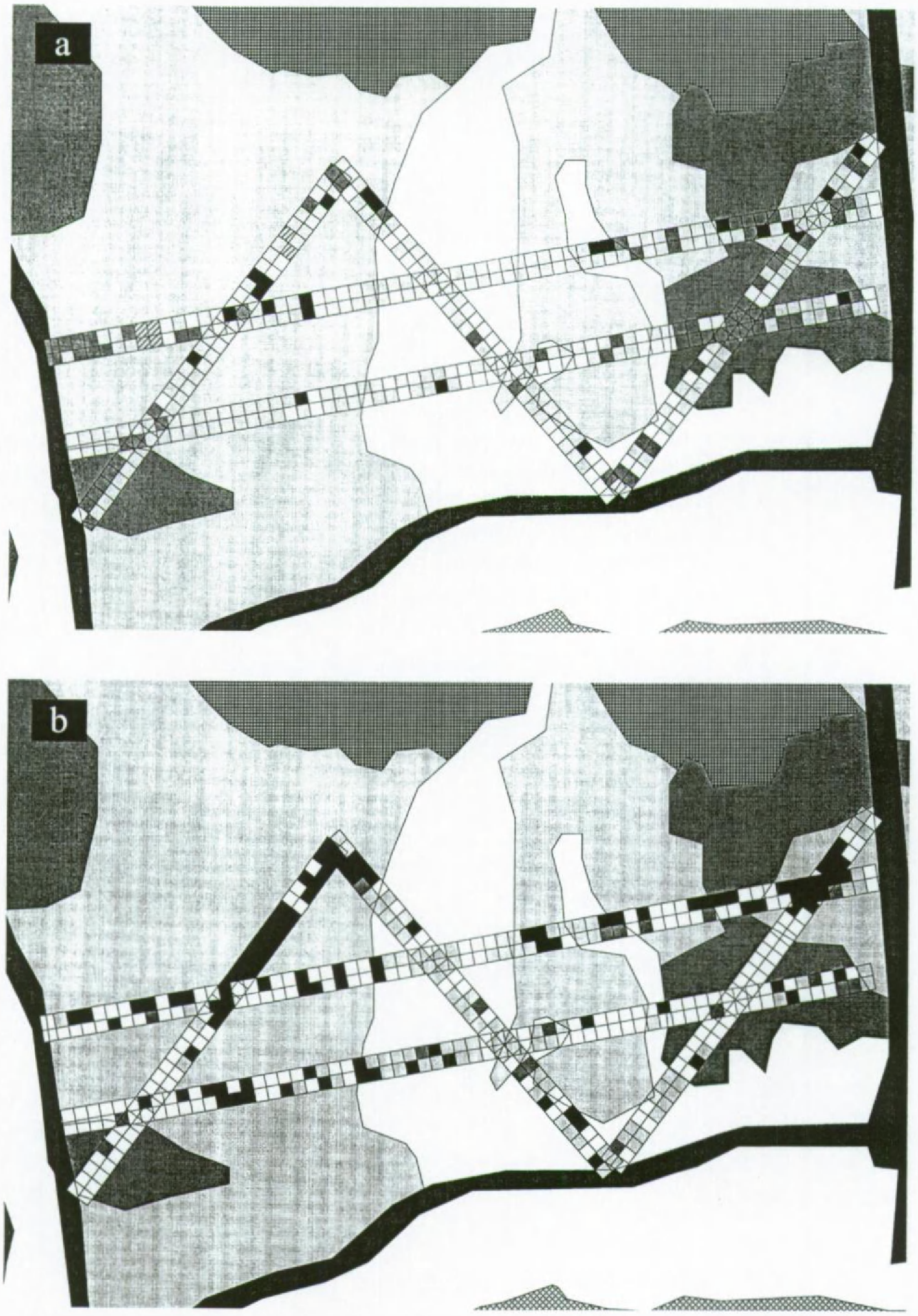


Figure 5. Overlay of the 1994 vegetation map (remote sensing) and the 1997 transect data (ground-truthing) for adult (a) and young (b) mangrove trees. Each block of four squares represents four PCQM quadrants with the PCQM sample point located in the centre. The pattern represents the tree nearest to the sample point and is considered to be dominant (for a detailed PCQM description see Cintrón and Schaeffer Novelli, 1984).

Table 3. Frequency of quadrants located in a certain forest patch (remotely sensed) and containing certain adult, young or juvenile tree species (ground truthed) in each of the sectors recognized in Galle.

| Sector | Sector 1 | | | Sector 2 | | | Sector 3 | |
|---|---|---|---|---|---|---|---|---|
| Forest patch | *B.* spp. + *E. aga* | *E. aga* | *R. api* | *E. aga* | *R. api* | open space | *E. aga* | *R. api* |
| **Adult trees** | | | | | | | | |
| *Bruguiera* spp. | 16 | 13 | 7 | 18 | 2 | 4 | 1 | 0 |
| *E. agallocha* | 17 | 37 | 9 | 158 | 32 | 68 | 0 | 3 |
| *H. littoralis* | - | - | - | 6 | 0 | 0 | - | - |
| *R. apiculata* | 6 | 3 | 14 | 37 | 36 | 7 | 2 | 36 |
| nil | 11 | 11 | 7 | 33 | 13 | 50 | 3 | 9 |
| # quadrants | 50 | 65 | 37 | 252 | 83 | 129 | 6 | 44 |
| **Young trees** | | | | | | | | |
| *Bruguiera* spp. | 28 | 16 | 14 | 89 | 7 | 14 | 0 | 1 |
| *E. agallocha* | 0 | 3 | 0 | 29 | 3 | 74 | 0 | 0 |
| *H. littoralis* | - | - | - | 2 | 0 | 0 | - | - |
| *R. apiculata* | 2 | 3 | 0 | 6 | 5 | 8 | 0 | 0 |
| nil | 20 | 43 | 23 | 126 | 68 | 33 | 6 | 43 |
| # quadrants | 50 | 65 | 37 | 252 | 83 | 129 | 6 | 44 |
| **Juvenile trees** | | | | | | | | |
| *Bruguiera* spp. | 13 | 5 | 4 | 6 | 5 | 1 | 0 | 0 |
| *E. agallocha* | 2 | 5 | 0 | 1 | 2 | 2 | 0 | 0 |
| *H. littoralis* | - | - | - | 0 | 0 | 0 | - | - |
| *R. apiculata* | 5 | 4 | 7 | 17 | 5 | 3 | 1 | 10 |
| nil | 30 | 51 | 26 | 235 | 77 | 123 | 5 | 34 |
| # quadrants | 50 | 65 | 37 | 252 | 83 | 129 | 6 | 44 |

*B.* = *Bruguiera*, *E. aga* = *Excoecaria agallocha*, *R. api* = *Rhizophora apiculata*, – = not observed in the respective sector.

## DISCUSSION AND CONCLUSION

Aerial photographs are useful in the study of mangrove vegetation (Dahdouh-Guebas et al., 2000; Verheyden et al., submitted). Application of actual identification keys on aerial photograph data from the past are the only way to gain insight into the history of that particular area, where vegetation has developed without any previous scientific record.

The results of this study have shown that Galle is a site with a dynamic past, both in terms of anthropogenic impacts and vegetation structure. Comparison of the final vegetation maps requires particular attention in order to explain the observed differences and alterations. The expansion and the disappearance of mangroves along the margins of the forest between 1956 and 1974 is mainly due to man. On one hand coconut plantations were neglected and colonized by mangroves, on the other hand mangrove forest is sacrificed in favor of extension of the coconut plantations. This trend is not observed for the banks of the Thalpe Ela river and the area close to the cement factory in Galle.

As for the previous period, the margins of the forest continued to change between 1974 and 1994. However, the change in the central area of the Galle mangroves (Sector 2) is much more pronounced: a considerable area of *R. apiculata* has been changed into an open space colonised with the herbaceous plant *F. salbundia* subsp. *pentaptera* and young

Table 4. Relative density (Dr) and importance value (I.V.; according to Cintrón and Schaeffer Novelli, 1984) from PCQM data for adult mangrove trees, and of relative density for young trees, for the species present in the various forest patches of Sector 1 (a), Sector 2 (b) and Sector 3 (c). Due to the small n value, Sector 3 does not display the relative density for the young mangrove trees.

**(a) Sector 1**

| Forest patch | *B.* spp. + *E. aga* | | | *E. aga* | | | *R. api* | | |
|---|---|---|---|---|---|---|---|---|---|
| | Adult Dr (%) | I.V. | Young Dr (%) | Adult Dr (%) | I.V. | Young Dr (%) | Adult Dr (%) | I.V. | Young Dr (%) |
| *Bruguiera* spp. | 41.0 | 2 | 93.3 | 24.5 | 2 | 72.7 | 23.3 | 3 | 100.0 |
| *E. agallocha* | 43.6 | 1 | 0 | 69.8 | 1 | 13.6 | 30.0 | 2 | 0 |
| *R. apiculata* | 15.4 | 3 | 6.7 | 5.7 | 3 | 13.6 | 46.7 | 1 | 0 |

*B.* = *Bruguiera*, *E. aga* = *Excoecaria agallocha*, *R. api* = *Rhizophora apiculata*.

**(b) Sector 2**

| Forest patch | *E. aga* | | | *R. api* | | | open space | | |
|---|---|---|---|---|---|---|---|---|---|
| | Adult Dr (%) | I.V. | Young Dr (%) | Adult Dr (%) | I.V. | Young Dr (%) | Adult Dr (%) | I.V. | Young Dr (%) |
| *Bruguiera* spp. | 8.2 | 3 | 70.6 | 2.9 | 3 | 46.7 | 5.1 | 3 | 14.6 |
| *E. agallocha* | 72.1 | 1 | 23.0 | 45.7 | 2 | 20.0 | 86.1 | 1 | 77.1 |
| *H. littoralis* | 2.7 | 4 | 1.6 | - | - | - | - | - | - |
| *R. apiculata* | 16.9 | 2 | 4.8 | 51.4 | 1 | 33.3 | 8.9 | 2 | 8.3 |

*E. aga* = *Excoecaria agallocha*, *R. api* = *Rhizophora apiculata*, – = not observed in the respective forest patch.

**(c) Sector 3**

| Forest patch | *R. api* | | |
|---|---|---|---|
| | Adult Dr (%) | I.V. | Young Dr (%) |
| *Bruguiera* spp. | 2.4 | 3 | - |
| *E. agallocha* | 7.1 | 2 | - |
| *R. apiculata* | 90.5 | 1 | - |

*R. api* = *Rhizophora apiculata*, – = not calculated.

Table 5. Results of the statistical comparison between the abundance of species in the young and adult vegetation layer for each of the forest patches in each of the sectors (G-test).

| Forest patch in each sector | G | d.f. | P |
|---|---|---|---|
| SECTOR 1 | | | |
| *Bruguiera* spp. + *E. agallocha* | 30.464 | 3 | < 0.001 |
| *E. agallocha* | 52.632 | 3 | < 0.001 |
| *R. apiculata* | 41.523 | 3 | < 0.001 |
| SECTOR 2 | | | |
| *E. agallocha* | 229.439 | 4 | < 0.001 |
| *R. apiculata* | 95.634 | 3 | < 0.001 |
| open space | 9.493 | 3 | < 0.050 |
| SECTOR 3 | | | |
| *E. agallocha* | not computable | | |
| *R. apiculata* | 64.655 | 3 | < 0.001 |

*E. agallocha* trees (Fig. 4C). Different explanations can account for this observation. First, construction of the dam and the roads isolated Sector 2 from the rest of the mangroves during the greater part of the year, a situation which implies hydrological changes among which a cut-off of ocean influences. *E. agallocha*, which is not a strict mangrove species according to Tomlinson (1986), is more tolerant to disturbances and could competitively benefit from human-induced stresses on the forest, which might explain its increase. Second, the presence of the cement factory causes the visible spread of cement dust on the mangroves in the area, especially on those located down wind, i.e., from the seashore land inward and therefore to the mangrove area where today we can observe the open space (pers. observ.). Light reflection induced by the white cement powder causing a decreased photosynthetic activity or chemical damage could explain the expansion of the more disturbance tolerant *E. agallocha* at the expense of true mangrove species. Third, local people mentioned illegal clear-cuttings in the mangrove forest, even though in situ only selective cuttings of *Rhizophora* roots along the paths were observed. Each of these hypotheses is acceptable, but in order to establish the exact causes, more research is needed: knowledge on the hydrology of the area and the influence of cement dust on mangrove vitality can help to support the hypotheses presented above. Finally, it cannot yet be excluded that a spontaneous succession constitutes an underlying basis for or at least contributes to the observed transition.

Next to the results of the airborne remote sensing of past situations in Galle, the information on young and juvenile mangrove trees can lead to predictions for the future. The high number of empty quadrants or quadrats for young and juvenile mangrove trees respectively, is expected since mangroves are known to be forests with a thin or no understory (Janzen, 1985; Lugo, 1985; Corlett, 1986; Snedaker and Lahmann, 1988). Moreover, understories have been observed to display high growth performance when gaps are created in the adult canopy (James G. Kairo, pers. comm., 1999). The identity of young trees with respect to the adult trees dominating the canopy suggests for Sector 2 a transition of the *E. agallocha* towards a *B. gymnorrhiza* dominated or co-dominated forest (Tables 3,4B). The same is observed for Sector 1 (Table 3,4A), but for this sector such results are less striking considering the co-dominance of *Bruguiera* spp. in the adult vegetation layer. These observations are supported by the significant differences ($P < 0.001$)

observed between the abundance of adult and young trees (Table 5). However, the suggested transition will only appear if there is a further input of juvenile *Bruguiera* spp. trees and if the young trees of this species survive. The former condition is not an evident outcome of this study (Table 3) and no prediction on the latter can be made. Final conclusions can be drawn only when juvenile inputs are surveyed for seasonal variations and young trees are assessed in their vitality during a long-term follow-up. For the open space, the suggested transition to an *E. agallocha* dominated forest, as concluded from the abundance of young trees of this particular mangrove species (Table 3), is more probable because of the anthropogenic events and the resistant character of this species, as highlighted above. In addition, the open space was the only exception where difference between the abundance of adult and young mangrove species was statistically less significant (Table 5). The low light conditions which reign in the *Rhizophora apiculata* dominated area are probably not the cause of the low proportion of young and juvenile trees present here: of all species present in Galle, Smith (1992) only lists *Rhizophora* species as a shade-intolerant. However, in the Pambala-Chilaw lagoon system, about 200 km north from Galle along the Sri Lankan west coast, the *Rhizophora* zone in the mangrove forest with a similar low-light condition displays the highest abundance of young and juvenile mangrove trees, including *Rhizophora* species (Dahdouh-Guebas, unpubl. results, 1998). The low abundance of juveniles in Galle might also in part be attributable to predation stress, which is known to affect the establishment of propagules in other mangrove regions (Smith et al., 1989; Robertson and Daniel, 1989; Robertson et al., 1990; McKee, 1995; Dahdouh-Guebas et al., 1997, 1998; McGuinness, 1997a,b). The behavior of crabs, snails, insects, porcupines as well as squirrels and other rodents, which affect *Rhizophora* and *Bruguiera* mangrove propagules mainly for feeding (pers. observ.), corroborates the above hypothesis. Data on propagule predation in Sri Lanka will be published as a separate paper (Dahdouh-Guebas, subm.).

Sector 3 merits particular attention, since this landward area, which was a coconut plantation in 1974, has been colonized completely by mangroves in 20 yrs time. The vegetation which can be found in this sector are mature impenetrable *R. apiculata* colonies, some *Clerodendron inerme* (L.) Gaertn. and *A. aureum* individuals, as well as remains of *C. nucifera*. It is remarkable how fast this change in vegetation type occurred in this 'terrestrial' area and it is equally remarkable how there is an almost complete lack of young trees in this sector. As for the juveniles, only *R. apiculata* was found both in the *E. agallocha* and in the *R. apiculata* dominated area, with 23% and 17% of the quadrats occupied, respectively (Table 3). As observed previously by Thomaes (1996) for Rekawa Lagoon on the south-east coast of Sri Lanka, also for Galle a dynamic interaction between coconut plantations and mangroves is apparent. A possible explanation for the vegetation dynamics observed in Galle 3, is the alteration of overland freshwater flow by the construction of the road straight through the mangrove forest and the dam at the end of this road. Since both the river and the ocean do not have free access to the complete mangrove forest as in previous decades (compare Fig. 4A,B with Fig. 4C), on one hand this concentrates sedimentation of the river in the area of Galle 3, and on the other hand it increases the salinity through seawater intrusion, two conditions which favor the establishment of mangroves. Due to these anthropogenic influences the development of mangroves in Galle 3 does not necessarily follow the classical vegetation stages as compared to other regions (e.g., Fromard et al., 1998).

The mangrove forest of Galle is subject to different dynamic processes, which can be summarized by the new term 'moving mosaic.' We suggest that such a vegetation dynamic is a dominant factor for change in mangroves which are characterized by an irregular topography (e.g., due to the burrowing activities of the mudlobster) instead of the more classical intertidal slope. The present study shows that a dynamic interaction between the terrestrial coconut stands and the mangrove exists. Importance values (Table 4) indicate that the present mangrove assemblages on the field correspond with those recognized on the aerial photographs, but future assemblages, as predicted from the abundance (Table 3) and relative densities (Table 4) of young mangrove trees, suggest the situation will be still different from the ones observed until now, with a possible transition to a *Bruguiera* dominated forest. The past explosive expansion of *E. agallocha*, not regarded as an exclusively mangrove component according to Tomlinson (1986), as well as the presence of mangrove associates and terrestrial species, casts doubt on the general trend in mangrove species composition of this forest. A transition of the Open Space into an *E. agallocha* dominated stand is even more probable. Although young *Bruguiera* trees are thriving vigorously, under the influence of man and the mangrove mud lobster, the destiny of this forest as a true mangrove can be questioned.

## ACKNOWLEDGMENTS

We are very thankful to the late M. A. Pemadasa and we thank L. P. Jayatissa and G. W. N. Tushira Kumara from the Department of Botany, University of Ruhuna, Matara, Sri Lanka, for their logistic support in the field. Many thanks are due to the local people of Unawatuna, Galle, Sri Lanka, in particular to the Area-Watcher-in-Chief Y. L. Michael Vijedasa and his family and to Attorney R. Koswattage for the hospitality and the invaluable information they could provide us with, and to F. M. Saidi and Indunil D. W. Divilewattage for their practical help in the field. We would also like to thank K. Kathiresan and an anonymous reviewer for a critical review of the manuscript. Research financed by the Fund for Scientific Research (FWO, Flanders), the Fund for Collective Fundamental Research (FKFO) and with a specialization fellowship of the Flemish Institute for the advancement of scientific-technological research in the industry (IWT). This work was in part presented on the Symposium on Mangrove Ecosystems: Biodiversity, Functioning, Restoration and Management (July 10–11, 1997, Toulouse, France).

## LITERATURE CITED

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

Blasco, F., T. Gauquelin, M. Rasolofoharinoro, J. Denis, M. Aizpuru and V. Caldairou. 1998. Recent advances in mangrove studies using remote sensing data. Mar. Freshw. Res. 49(4): 287–296.

Brokaw, N. and J. Thompson. 2000. The H for DBH. Forest Ecol. Manage. 129: 89–91.

Caloz, R. and C. Collet. 1997. Geographic information systems (GIS) and remote sensing in aquatic botany: methodological aspects. Aquat. Bot. 58: 209–228.

Cintrón, G. and Y. Schaeffer Novelli. 1984. Methods for studying mangrove structure. Pages 91–113 *in* S. C. Snedaker and J. G. Snedaker, eds. The mangrove ecosystem: research methods. UNESCO, Paris, France.

Corlett, R. T. 1986. The mangrove understory: some additional observations. J. Trop. Ecol. 2: 84–93.

Cottam, G. and J. T. Curtis. 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. Univ. Wisconsin Press, Madison, Wisconsin.

Dahdouh-Guebas, F. Propagule predation in Sri Lankan mangroves and its effect on vegetation structure dynamics. Presented on the Meeting on Mangrove Macrobenthos, 7–11 Sept. 2000, Mombasa, Kenya. (submitted).

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

_______________, __________, ________, D. Van Speybroeck and N. Koedam. 1998. Propagule predators in Kenyan mangroves and their possible effect on regeneration. Mar. Freshw. Res. 49: 345–350.

_______________, T. Zetterström, P. Rönnbäck, M. Troell and N. Koedam. 2000. Conservation of mangroves vs. development of shrimp farming in Pambala - Chilaw lagoon, Sri Lanka. *In* R. Flos and L. Creswell, compilers. Responsible aquaculture in the new millenium. European Aquacult. Soc., Spec. Publ. no. 28, Oostende, Belgium. 167 p.

De Silva, K. H. G. M. and S. Balasubramaniam. 1984–85. Some ecological aspects of the mangroves on the west coast of Sri Lanka. Ceylon J. Sci. (Bio. Sci.) 17–18: 22–40.

Farnsworth, E. J. 1998. Issues of spatial, taxonomic and temporal scale in delineating links between mangrove diversity and ecosystem function. Global Ecol. Biogeogr. Lett. 7: 15–25.

Field, C. D. 1996. Restoration of mangrove ecosystems. Int'l. Soc. Mangrove Ecosystems, Okinawa, Japan.

Fromard, F., H. Puig, E. Mougin, G. Marty, J. I. Betoulle and L. Cadamuro. 1998. Structure, above-ground biomass and dynamics of mangrove ecosystems: new data from French Guiana. Oecologia 115: 39–53.

Holmgren, P. and T. Thuresson. 1998. Satellite remote sensing for forestry planning - a review. Scand. J. Forest Res. 13: 90–110.

Janzen, D. H. 1985. Mangroves: where's the understory? J. Trop. Ecol. 1: 89–92.

Lee, S. K., W. H. Tan and S. Havanond. 1996. Regeneration and colonisation of mangrove on clay-filled reclaimed land in Singapore. Hydrobiologia 319: 23–35.

Lugo, A. E. 1985. Mangrove understory: an expensive luxury? J. Trop. Ecol. 2: 287.

__________ and S. C. Snedaker. 1974. The ecology of mangroves. Ann. Rev. Ecol. Syst. 5: 39–64.

McGuinness, K. A. 1997a. Dispersal, establishment and survival of *Ceriops tagal* propagules in a north Australian mangrove forest. Oecologia 109: 80–87.

_______________. 1997b. Seed predation in a tropical mangrove forest : a test of the dominance-predation model in northern Australia. J. Trop. Ecol. 13: 293–302.

McKee, K. L. 1995. Seedling recruitment patterns in a Belizean mangrove forest: effects of establishment ability and physico-chemical factors. Oecologia 101: 448–460.

Mueller-Dombois, M. 1968. Ecogeographic analysis of a climate map of Ceylon with particular reference to vegetation. The Ceylon Forester 8(3/4): 1–20.

Murali, K. S., R. Siddappa Setty, K. N. Ganeshaiah and R. Uma Shaanker. 1998. Does forest type classification reflect spatial dynamics of vegetation? An analysis using GIS techniques. Cur. Sci. 75(3): 220–227.

Ramachandran, S., S. Sundaramoorthy, R. Krishnamoorthy, J. Devasenapathy and M. Thanikachalam. 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. Cur. Sci. 75(3): 236–244.

Robertson, A. I. and P. A. Daniel. 1989. The influence of crabs on litter processing in high intertidal mangrove forests in tropical Australia. Oecologia 78: 191–198.

_____________, R. Giddins and T. J. Smith. 1990. Seed predation by insects in tropical mangrove forests: extent and effects on seed viablility and the growth of seedlings. Oecologia 83: 213–219.

Smith III, T. J. 1992. Forest structure. *In* A. I. Robertson and D. M. Alongi, eds. Tropical mangrove ecosystems. Amer. Geophys. Union, Washington D.C..

____________, H. T. Chan, C. C. McIvor and M. B. Robblee. 1989. Comparisons of seed predation in tropical tidal forests from three continents. Ecology 70(1): 146–151.

Snedaker, S. C. and E.J. Lahmann. 1988. Mangrove understory absence: a consequence of evolution? J. Trop. Ecol. 4: 311–314.

Sokal, R. R. and F. J. Rohlf. 1981. Biometry. The principals and practice of statistics in biological research. W. H. Freeman and Co, New York.

Spalding, M., F. Blasco and C. Field. 1997. World mangrove atlas. Int'l. Soc. Mangrove Ecosystems, Okinawa, Japan.

Thomaes, K. 1996. Voorbereidend onderzoek naar de bruikbaarheid van luchtfoto's voor mangroveanalyse en evolutie van mangrovegebieden in Sri Lanka. Thesis M.Sc. Biology, Vrije Universiteit Brussel, Brussels, Belgium. [in Dutch with English summary]

Tomlinson, C. B. 1986. The botany of mangroves. Cambridge Tropical Biology Series, Cambridge Univ. Press, Cambridge, New York.

Verheyden, A., 1997. Ruimtelijke analyse van flora and fauna in mangrovegebieden van Sri Lanka. Luchtfoto-interpretatie en GIS toepassing in het onderzoek naar mangrovedynamiek. Thesis M.Sc. Biology, Vrije Universiteit Brussel, Brussels, Belgium. [in Dutch with English summary]

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

DATE SUBMITTED: October 13, 1999. DATE ACCEPTED: July 20, 2000.

ADDRESSES: (F.D.-G., N.K.) *Laboratory of General Botany and Nature Management, Mangrove Management Group, Vrije Universiteit Brussel, Pleinlaan 2, B-1050 Brussels, Belgium;* (A.V.) *Research Assistant Fund for Scientific Research–Flanders, c/o Laboratory of General Botany and Nature Management, Mangrove Management Group, Vrije Universiteit Brussel, Pleinlaan 2, B-1050 Brussels, Belgium* (W.D.G.) *Centre for Cartography and GIS, Department of Geography, Vrije Universiteit Brussel, Pleinlaan 2, B-1050 Brussels, Belgium;* (S.H.) *Department of Botany, University of Ruhuna, Matara, Sri Lanka.* CORRESPONDING AUTHOR: (F.D.-G.) *Tel. + 32 2 629.34.20; Fax. + 32 2 629.34 13; E-mail: <fdahdouh@vub.ac.be>, <nikoedam@vub.ac.be>.*

# Chapter VII.

## Two decade vegetation dynamics in Kenyan mangroves as detected from sequential aerial photography : a case-study in Gazi Bay.

Dahdouh-Guebas, F., I. Van Pottelbergh, J.G. Kairo & N. Koedam

Engaged in a peer-review process

# Two decade vegetation dynamics in Kenyan mangroves as detected from sequential aerial photography : a case study in Gazi Bay.

F. Dahdouh-Guebas[1,*], I. Van Pottelbergh[1], J.G. Kairo[2,1] and N. Koedam[1]

[1] *Laboratory of General Botany and Nature Management, Mangrove Management Group, Vrije Universiteit Brussel, Pleinlaan 2, B-1050 Brussel, Belgium.*
[2] *Kenyan Marine and Fisheries Research Institute, Po Box 81651, Mombasa, Kenya.*
* *Corresponding author : Fax : + 32 02 629 34 13; E-mails : fdahdouh@vub.ac.be; nikoedam@vub.ac.be*

## Abstract

Gazi Bay (Kenya) comprises a mangrove system of 18 km$^2$ that is in part much anthropogenically degraded. This study provides a quantitative and qualitative evaluation of the degradation in terms of vegetation structure and dynamics in Gazi, using sequential aerial photography analysis in a geographical information system covering two decades, combined with ground truth information from the adult, young and juvenile vegetation layers as well as direct and indirect ordination analyses. Apart from confirmed anthropogenic degradation and visualised vegetation structure and changes in floristic composition of the frontal mangrove zone, it was shown that a sandy stretch is expanding at the expense of mangrove, whereas in the back mangrove changes are minor. Due to the ubiquity of *Rhizophora mucronata* in 1972 no zonation is discernible. However, both from a 1992 aerial photograph and from current field data an apparent zonation can be observed at present with a landward *Avicennia marina* zone, an *A. marina* - *Ceriops tagal* - *R. mucronata* mixed zone, a zone with either *R. mucronata* or seaward *A. marina* and a *Sonneratia alba* zone, with a high importance for *R. mucronata* in each of these zones and in each of the vegetation layers. Present dynamics, such as the apparent degradation of mangroves, initiated by man, but continuing even after the human impact has ceased, are discussed and possible future dynamics are predicted.

Keywords : mangroves, dynamics, aerial photography, GIS, multivariate analysis, Kenya

## Introduction

An understanding of vegetation dynamics in a particular area may be an important tool for conservation, restoration and sustainable exploitation purposes. Mangroves, which are often undervalued and presently destroyed as the result of various forms of human pressure (*e.g.* Farnsworth and Ellison, 1997), are known to display major structural changes in a small time frame (Dahdouh-Guebas *et al.*, 2000a). Therefore this ecosystem in particular requires insight into processes involved in the dynamic shifts in vegetation structure. There is a lack of data to define the original situation of the mangrove (apart from oral contributions from local people), and the investigation of the anthropogenic or endogenic factors involved in its dynamics are incomplete. Particularly in Kenya, where the adverse effect of predation on the initial regeneration of mangroves has been documented (Dahdouh-Guebas *et al.*, 1997, 1998), the experimental design of re-afforestation projects might benefit from this type of fundamental research. Furthermore it serves as a basis of decision-making in whether or not this human interference under the form of restoration is desired, by providing data on the potential of a mangrove stand to successfully renew and rejuvenate.

The objective of the present study is to make a quantitative and qualitative evaluation of the vegetation dynamics in a section of the mangrove forest in Gazi Bay (Kenya), emphasizing the anthropogenic degradation that has taken place. The study aims at interpreting the results from the past and the present using aerial photography analysis and fieldwork on the adult vegetation and to extrapolate the interpretation to future dynamics through fieldwork on the young and juvenile vegetation. In the context of mangrove dynamics, as spatial changes in vegetation patterns over time, we explore how dynamic mangroves can be and what could be the underlying factors of their dynamism.

## Area descriptions

Gazi Bay (4°26' S, 39°30' E), located about 40 km South of Mombasa, lodges over 615 ha of mangrove forest (Fig. 1), much of it subject to severe anthropogenic stresses (Kairo, 1995, pers. obs.). This study concentrates on a mangrove stretch adjacent to the village of Gazi, one of the most affected areas (Fig. 2). Kidogoweni and Mkurumuji, two seasonal rivers, are responsible for most of the overland freshwater input into the bay. All ten East-African mangrove species, *i.e. 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. (nomenclature according to Tomlinson, 1986; Duke & Jackes, 1987 and Duke, 1991), occur along the Kenyan coast and their presence has been reported in Gazi Bay. The latter was however not observed during the course of this study.

## Methods and material studied

### *Remote sensing and ground truth*

Two aerial photographs (1972-1992), obtained from the Kenyan Survey Department, were scanned and digitised on a Macintosh computer platform using the GIS-program MapInfo. The digitisation of the vegetation was based on the image attributes tonality, texture and structure (Dahdouh-Guebas *et al.*, in prep.a), as successfully applied to the identification of mangroves in the framework of mangrove vegetation dynamics research in the past (Dahdouh-Guebas *et al.*, 2000a; Verheyden *et al.*, subm.). The 1992 photograph was ground truthed in 1997, the time gap of five years being acceptable considered the absence of major visual differences on the field (pers. obs. since 1992 on a semestrial basis) and the absence of differences with the zonation studied in 1993 (*cf.* Dahdouh-Guebas *et al.*, subm.c). Ground truthing consisted of visits to all the areas outlined in the digitisation of the photograph as well as land-creek transects through the mangrove vegetation.

During a first field campaign in July-August 1997, 6 transects were investigated in the most affected part of our study site (Fig. 2), making use of 10 m intervals and applying the Point-Centred Quarter Method or PCQM (Cottam & Curtis, 1956) as described by Cintrón & Schaeffer Novelli (1984). The tree species closest to the sample point was recorded in each of the four quadrants, its height and diameter $D_{130}$ (term according to Brokaw and Thompson (2000), but formerly referred to as DBH, the diameter at breast height) were measured and the total cover abundance in the 5 x 5 m quadrat nearest to the sampling point was estimated in each quadrant (the sample point thus formed the common corner of the four quadrats located in the four quadrants). Each of the transects was covered on three occasions within three days : to investigate adult mangrove trees, to investigate young mangrove trees (trees smaller than 1.3 m or with a $D_{130} < 2.5$ cm, but which already reached the stage of sapling stage, which is defined here as a young plant with more than 6 leaves) and to investigate mangrove juveniles (propagules or seeds until they reached the stage of sapling). Considering our definition of a young tree, there was no point in measuring the diameter (or in a later stage calculating the basal area).

A second fieldwork mission to collect an extra set of data on mangrove juveniles was organised in March 1999 in order to detect possible seasonal variations in juvenile abundance. Along two additional transects (transect A and B), crossing the complete vegetation belt (incl. terrestrial vegetation) from the village to the creek, mangrove species were inventoried to visualise the land-sea zonation and to detect any zones not visible from the aerial photograph. In the present study the term ‘zonation’ is defined as banding of vegetation types with a certain, often monospecific floristic composition. Environmental factors such as salinity, light intensity, herbivorous crab abundance and snail abundance were also recorded. Visual observations and interviews with local people were also carried out, whenever possible and for the whole duration of the fieldwork missions. The free and open-ended interviews were carried out in Kiswahili with 13 persons (most of them > 40 years of age) belonging to 11 different households in Gazi - the total number of houses in Gazi is 119 (Vandeput, 1999) and on average one household occupies one house (pers. obs.) -. Particularly the past condition of the mangroves in the area under study and the changes that occurred were emphasised.

Vegetation maps of 1972 and 1992 were created and the field transects were traced on the most recent aerial photograph (1992). Transect data for adult, young and juvenile mangrove species were visualised in separate GIS layers, superimposed on the vegetation map of 1992 and absolute numbers of young and juvenile mangroves located in a certain vegetation class were calculated. From the PCQM data the relative density [$D_r$ = (number of individuals of species / total number of individuals)*100], the relative dominance [(dominance of a species / dominance for all species)*100] and the relative frequency [= (frequency of a species / sum of frequencies of all species)*100] were computed for the adult trees using the methods described by Cintrón & Schaeffer Novelli (1984) in order to calculate the importance value (I.V.) for each mangrove tree species. According to this method, the relative dominance is based on the tree diameter. Relative density and relative frequency were calculated for young and juvenile mangrove trees as well, and an importance value for these vegetation layers was calculated similar to that of the adult tree layers, however omitting the relative dominance, as mentioned above.

### *Statistical analyses*

The G-test (Sokal & Rohlf, 1981) was performed for the absolute numbers of sample points located in a certain vegetation class or zone and containing a certain mangrove species in order to detect differences in abundance between the adult and young vegetation layer. It was also used together with the $\chi^2$-test in order to test for significant seasonal differences in absolute juvenile densities.

To investigate the similarity in distribution between the elements of the different vegetation layers and to explore the links between vegetation and environmental factors, species ordinations were performed on the adult, young and juvenile mangrove distributional data. Since the places where juveniles can be found are of prime interest, regardless of the season in which they are found there, the data on mangrove juveniles of the fieldwork missions of 1997 and 1999 were combined. The input matrices were generated based on presence/absence data (0 or 1) and on abundance data (0 to 4) for each of the 99 sample points (the latter of which includes the four original quadrants). Using PC ORD for Windows (McCune & Mefford, 1997) Detrended Correspondence Analysis (Hill & Gauch, 1980) and Canonical Correspondence Analysis (Ter Braak 1986, 1994) were applied and the percentage of variance in the matrix that is explained by each axis was calculated. The environmental variables and parameters used in the CCA were salinity, light intensity, herbivorous crab abundance and snail abundance. Monte-Carlo tests (randomisation tests) were used to test the significance of the eigenvalues and the species-environment correlations.

## Results

### *Remote sensing and ground truth*

Both fieldwork and interviews with the village people reveal that over-harvesting is the main cause of mangrove decline. Remaining mangrove stumps in the field as well as declarations from locals revealed that *Bruguiera gymnorrhiza*, *Ceriops tagal* and *Rhizophora mucronata* are the preferred species for cutting. Figure 3 (a,b) shows the vegetation maps of 1972 and 1992 respectively, and when comparing them it is obvious that the vegetation density has decreased. However, this is not the case for the floristic composition. The open space in the upper left part of the vegetation map of 1972 (Fig. 3a) corresponds with bare sand and low beach vegetation but once formed a dense forest with the surrounding mangrove.

According to the local people, mangrove cutters started cutting in this area in 1964 because it was the thinnest and most easily accessible area in the forest, and the cleared area was then used to allow spotting of incoming *dhows* (traditional Arab boats, typically from Zanzibar and Lamu). Since then the area cut has expanded at the expense of mangrove (*cf.* Fig. 3b), which is still an on-going process with visible changes on the field between the expeditions of 1997 and 1999. The degradation of mangroves is initiated by man and a large part of the sandy stretch arose as a direct consequence of the logging activities. But more important is the further expansion of that stretch and further natural degradation of the mangroves around it after the human impact has ceased. At the most landward side the *Avicennia marina* fringe is also slightly reducing in area. However, within the mixed zone visible from the aerial photograph of 1972, individual *A. marina* trees have formed a real patch recognisable as a vegetation patch as such on the aerial photograph of 1992 (Fig. 3b). Within the rest of the mangrove forest *Ceriops tagal* seems to be the only other species that is expanding.

The forest section that was studied in detail is (partially) zoned from land to sea with a landward *Avicennia marina* zone, an *A. marina/Ceriops tagal/Rhizophora mucronata* mixed zone, a *R. mucronata* and/or seaward *A. marina* zone and finally a *Sonneratia alba* zone. This section of the forest is sloping downward to the creek. However, in the more landward areas, where topography is irregular with many small emerging areas even at high spring tide, zonation is less evident and species composition seems restricted first to

*C. tagal*, *A. marina* and *Lumnitzera racemosa* and more landward to the latter two species only. In these areas there is an occasional presence of other species, but a virtually total absence of *R. mucronata*, as also confirmed by transect A and B. The most landward species is *Avicennia marina*, but some locals remember *R. mucronata* to be the first mangrove tree species encountered on the way from the village to the fishermen's place (Fig. 2).

The quantified PCQM vegetation data from the zoned forest section outlined above, are given in table 1. It can be seen that *R. mucronata* is ubiquitous as an important species in all vegetation classes identified on the aerial photograph and in all vegetation layers (visible from the field work). The absolute densities of the juveniles was significantly different over the two seasons for the entire study site ($\chi^2 = 25.526$; d.f. 2; $p < 0.001$) and for the different forest patches, except for the *S. alba* zone ($G = 4.194$; d.f. = 2; n.s.).

### *Statistical analysis*

The results of the G-test (Tab. 2) show that the observed differences between the abundance of adult and young trees in each vegetation class are not significant, except for the most seaward zones (*Avicennia marina* and *Sonneratia alba*).

Figure 4 shows the ordination graph of the detrended correspondence analysis (DCA). It can be seen that the graph is not dominated by outliers and that species clusters can be easily distinguished. Although the ordination did not serve to view zonation, the latter can also clearly be deduced from the graph in figure 4. From land to sea we can indeed see the a mixed zone (*A. marina*, *B. gymnorrhiza* and *C. tagal*), a *R. mucronata* zone and a *S. alba* zone. The *A. marina* zone is disjunct as the most landward and the most seaward (together with *S. alba*) and therefore is located more central in the ordination plot. The eigenvalues for the first and second axis are 0.404 and 0.194 respectively and the variance explained by the same axes are 0.44 and 0.08 respectively. The cluster represented by *A. marina*, *B. gymnorrhiza* and *Sonneratia alba* are the most widespread. Particularly for these species clusters, the points for adult and young individuals tend to lay closer together, whereas those for the juveniles reach away from the adult and young individuals. For the other species the latter is less obvious. The variance does not change significantly when juvenile distributional data are omitted from the matrices.

In the direct ordination (CCA) the environmental variables and parameters used, failed to explain the observed variation in the vegetation data of the adult, young and juvenile mangroves. However, when the juvenile vegetation matrices are omitted, the remaining adult and juvenile distributional data clearly separate according to species, and to a certain extent according to environmental factors (Fig. 5). Adult and young *Avicennia marina* and adult *Sonneratia alba* are weakly negatively correlated with the first axis, whereas young *S. alba* and *Ceriops tagal* strongly positively correlate with it. Adult and young *Bruguiera gymnorrhiza* are strongly positively correlated with the second axis. The canonical coefficients, which are conceptually similar to the usual regression coefficients and represent the unique contribution of individual variables, as opposed to the simple correlation coefficient between a variable and an ordination axis, are highest for snail abundance with respect to the first axis (0.618) and for light conditions with respect to the second axis (-0.924). The correlation coefficients for the same environmental factors with respect to the same axes are 0.703 and –0.727 respectively. However, the total amount of variability in the species data that could potentially be "explained" by the environmental factors in this direct ordination is only 4.2 % and 2.8 % for the first two axes respectively. Monte Carlo tests showed that for the first axis the species-environment correlations were not significant ($p_{\text{Monte Carlo test}} = 0.106$), whereas for the second axis they were ($p_{\text{Monte Carlo test}} = 0.024$).

## Discussion and conclusions

From the analysis of the aerial photographs, from the field visits and from the interviews with local people it is clear that man is at the origin of the mangrove decline in Gazi, mainly through over-harvesting. The same conclusion was reached for the quality and natural regeneration of mangroves in Mida Creek further North along the Kenyan coast (Kairo *et al.*, in prep.). However, occasional natural hazards may further contribute to the reduction in mangrove area : the El-Niño rains of 1997 in Kenya for instance caused siltation and subsequently massive die-off of adult and young trees within a small *Rhizophora* stand in Gazi Bay was observed (pers. obs.). This *Rhizophora* stand, located in the upper right part of the vegetation map of 1992 (Fig. 3b), however is rejuvenating at present.

Despite the deteriorating status of the forest adjacent to the village, some species have expanded. The low spatial dynamics of the sand banks in the creek over time (*cf.* major sand banks in the creek on both aerial photographs) have made it possible for *Sonneratia alba* to establish on these banks, very close to the *S. alba* zone of the adjacent forest (at about 150 m). The low desirability of *A. marina* by mangrove cutters, like in Mida Creek (Dahdouh-Guebas *et al.*, 2000b), allowed this species to expand in the seaward zone, as compared to *Bruguiera gymnorrhiza*, *Ceriops tagal* and *Rhizophora mucronata* in decreasing order of preference by the local people.

Unlike previously reported, comparisons between the presence of adult and young mangrove trees in a disturbed forest with respect to the dominant species as detected from aerial photography in Sri Lanka (Dahdouh-Guebas *et al.*, 2000a), the same results for the forest studied in Gazi shows there is no significant difference, except for the *Avicennia marina* and *Sonneratia alba* zone (Tab. 2). The seaward position of these zones in Kenya - the landward fraction of the *Avicennia marina* zone is negligible (*cf.* Fig. 3b) - are responsible for a high dynamism which probably leads to the rare establishment of species, as compared to the more landward zones. On one hand this is also reflected in the absence of a significant seasonal difference between mangrove juveniles in the *S. alba* zone. On the other hand it is reflected in the low adult tree density for the *S. alba* zone (28.8 stems.ha$^{-1}$ only) as opposed to the *R. mucronata* zone (95.3 stems.ha$^{-1}$) and the mixed zone (205.2 stems.ha$^{-1}$), but it is less evident for the seaward *A. marina* zone (156.5 stems.ha$^{-1}$) because of the *R. mucronata* dominated understory. The root complex of the latter typically facilitates the trapping of propagules (pers. obs.).

Since *R. mucronata* is ubiquitous as an important species irrespective of the vegetation class or the vegetation layer, it can be concluded that fieldwork data not always correspond with remotely sensed data. This was reported earlier by Verheyden *et al.* (subm.) for Sri Lankan mangroves and was attributed to the difficulties of detection within a stand. However, in this case it is mainly due to canopy overgrowth of one species by another (*e.g.* *R. mucronata* by the huge seaward *A. marina*). This emphasizes once more that vegetation data interpreted through aerial photography necessitates fieldwork, within the adult vegetation even divided over different layers where necessary.

The distribution of young individuals is more related to that of adult trees than to the distribution of juveniles, particularly for *A. marina* and *B. gymnorrhiza* (Fig. 4). Their juveniles are thus generally spread over a wider area than that of adult trees, but survival (*cf.* young trees) only occurs near adult trees. For *B. gymnorrhiza* the same has been observed in Sri Lankan mangroves (Dahdouh-Guebas *et al.*, 2000a). Although there is no difference in rank for the importance of mangrove juveniles for the most common species, there is a seasonal variation in the absolute values.

Adult, young and juvenile individuals of one species can easily be distinguished from other species (Fig. 4). Combined with the results from the G-test (Tab. 2) this leads to our prediction that there are no major dynamic shifts in species distribution over 20 years time in Gazi Bay.
The omission of juveniles from the ordination matrices emphasised the separation between species clusters (Fig. 5). *S. alba* and *A. marina* adult trees indeed overlap in their distribution, whereas this is less obvious for their young trees : *A. marina* young trees can be found all the way to the landward side, but *S. alba* young trees are restricted to the *S. alba* vegetation zone.

*Avicennia marina* and *Sonneratia alba* seem to be positively correlated with salinity and negatively correlated with the abundance of herbivorous crabs and snails, whereas the opposite is observed for *Ceriops tagal*. The vegetation zones dominated by *A. marina* or *S. alba* are indeed devoid of snails, but the landward *A. marina* zone corresponds with the presence of the crab *Neosarmatium meinerti* De Man, known to predate intensely on propagules (Dahdouh-Guebas *et al.*, 1997). However, the number of plots in the narrow landward *A. marina* fringe (Fig. 3b) is probably too low compared to the number of plots in the seaward zone - the latter is not a home to *N. meinerti* – to overrule the observed correlation with crabs. The same is true for the salinity component. *Ceriops tagal* is less affected by salinity (Matthijs, Dahdouh-Guebas & Koedam, unpublished results, 1999), and more by predation by crabs (Dahdouh-Guebas *et al.*, 1998). *Bruguiera gymnorrhiza* seems to be most negatively correlated with light conditions. This corresponds with earlier reports regarding its shade tolerance (Smith III, 1992). It is unclear to which environmental variable the distribution of *Rhizophora mucronata* is most correlated, but in different locations within Gazi the border between the vegetation zone dominated by *Rhizophora mucronata* and that dominated by *Ceriops tagal* corresponds with the surface flooded during neap tide periods (pers. obs.), and consequently with the amount of time the vegetation is submerged.

In Gazi Bay, anthropogenic influences, through cutting for instance, leads to a direct loss of mangroves in a first stage, and a further natural degradation in a second stage. Yet, because this site is much impacted by the tidal regime, the degradation does not seem to have such a strong effect on zonation, as observed for instance in disturbed sites in Sri Lanka, where the tidal influence is less (Dahdouh-Guebas *et al.*, 2000a). We predict that under the current scenario the sandy stretch will expand due to a synergism between the selective cutting of trees (*e.g. Rhizophora*) and the subsequent intrusion of the sand into the mangrove. On one hand this might lead to the disappearance of the *Rhizophora* zone, which may be replaced by *Avicennia marina*, a species that can cope with the more arid conditions (high light intensity and dry soil) associated to the sandy stretch, as they do in the landward zone. However, although *A. marina* is known to thrive in a disjunct zone, it must be investigated to which extent trees of the seaward zone, having a different morphology as compared to the specimens from the landward zone (Dahdouh-Guebas *et al.*, subm.d), are able to stand conditions from the landward zone. The plasticity within the species may not necessarily be applicable to the individual.

Whether or not the *Rhizophora* zone is being replaced by *Avicennia*, another problem is that the frontal *Avicennia* and *Sonneratia* zone alone cannot stop the formation, and subsequent effects, of waves (pers. obs.), and the sand might slowly be washed away. Under the above 'no-change scenario' the landward mangroves are less likely to change substantially, but scenario's with greater impact, such as for example the alteration or disappearance of the small topographic differences present in Gazi today, will lead to a re-organisation of the mangrove zonation to a large degree. This would create the same scenario as a sea-level rise. A landward extension and a frontal regression have been predicted in general as a response of the mangrove ecosystem to sea level rise (Pernetta, 1993a; UNEP, 1994; Woodroffe, 1990, 1999). However, we do not expect the latter in our study site because of the current seaward zonation, which is already the result of the local topographic condition, *i.e.* sloping down towards the sea in this area only, a regularity absent in the more landward mangrove. Instead an enlargement of the most seaward zones is predicted.
Both under a no-change scenario and under a scenario that would alter the topography, human interference may be needed to prevent the sandy stretch from expanding. It might be preferable to replant large, but protected, areas with the more vulnerable mangrove species, such as *Rhizophora mucronata*. Small-scale re-afforestation programmes in Gazi Bay (Kairo, 1993, 1995) have shown to successfully (re)convert denuded or degraded mangrove areas into functional forest units (Bosire, 1999). This implies that both floral secondary succession (Bosire *et al.*, subm. b) and faunal recruitment (Bosire *et al.*, subm. a) can be observed within the regeneration plots. Solely this type of continuous monitoring of past and present mangrove vegetation, in natural forests as in rehabilitation areas, makes it possible to express a vision on mangrove dynamics and possibly predict the future vegetation structure. The in-depth study of the introgression between natural and artificially planted mangroves would be a new research challenge.

## Acknowledgements

We thank the people from the Kenya Belgium Project and the Kenyan Marine and Fisheries Research Institute (KMFRI) for providing logistic support. A lot of gratitude is due to the all people of Gazi, in particular family S. Ba'alawy for hosting us, Abdulhakim Abubakr Ali Jilo and Fatuma Mohamedi Saidi for their practical help in the field and Abdulbasit Mohamed Daghar, Fatuma Mohamedi Saidi, Samir Abubakr and Omari Juma Kisasi for their translation assistance during the interviews. Research financed with a specialisation fellowship of the Flemish Institute for the advancement of scientific-technological research in the industry (IWT), and by the Fund for Scientific Research (FWO). This work was in part presented on the Shallow Tropical Waters and Humans Conference (April 11-16, 1999, Naivasha, Kenya).

## References

See Bibliography

**Table 1a.** Relative density (DEr), relative dominance (DOr) and relative frequency (FRr) for the major vegetation classes identified on the aerial photograph.

| Vegetation class | ***A. marina* zone** | | | | | ***R. mucronata* zone** | | | | | ***S. alba* zone** | | | | | **Mixed zone** | | | | | **Open space** | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **DEr** | **DOr** | **FRr** | **IV** | **rank** | **DEr** | **DOr** | **FRr** | **IV** | **rank** | **DEr** | **DOr** | **FRr** | **IV** | **rank** | **DEr** | **DOr** | **FRr** | **IV** | **Rank** | **DEr** | **DOr** | **FRr** | **IV** | **rank** |
| **ADULT TREES** | | | | | | | | | | | | | | | | | | | | | | | | | |
| *A. marina* | 15.8 | 65.5 | 20.8 | 102 | 2 | 9.3 | 14.7 | 13.6 | 38 | 3 | 12.0 | 5.8 | 13.5 | 31 | 3 | 3.9 | 7.9 | 7.5 | 19 | 4 | 10.7 | 30.3 | 18.2 | 59 | 2 |
| *B. gymnorrhiza* | 3.0 | 0.2 | 5.7 | 9 | 5 | 0.0 | 0.0 | 0.0 | 0 | 5 | 0.0 | 0.0 | 0.0 | 0 | 4 | 3.9 | 0.7 | 5.7 | 10 | 5 | 0.0 | 0.0 | 0.0 | 0 | 5 |
| *C. tagal* | 15.8 | 5.8 | 18.9 | 41 | 3 | 5.3 | 0.7 | 6.8 | 13 | 4 | 0.0 | 0.0 | 0.0 | 0 | 4 | 22.3 | 7.3 | 24.5 | 54 | 3 | 7.1 | 9.6 | 9.1 | 26 | 4 |
| *R. mucronata* | 58.4 | 21.0 | 43.4 | 123 | 1 | 69.3 | 10.3 | 54.5 | 134 | 1 | 21.7 | 5.0 | 32.4 | 59 | 2 | 66.0 | 29.2 | 56.6 | 152 | 1 | 75.0 | 46.9 | 63.6 | 185 | 1 |
| *S. alba* | 6.9 | 7.5 | 11.3 | 26 | 4 | 16.0 | 74.3 | 22.7 | 113 | 2 | 66.3 | 89.2 | 48.6 | 204 | 1 | 3.9 | 54.9 | 5.7 | 64 | 2 | 7.1 | 13.2 | 9.1 | 29 | 3 |
| nil | | | 0.0 | | | | | 2.3 | | | | | 5.4 | | | | | 0.0 | | | | | 9.1 | | |
| **YOUNG TREES** | | | | | | | | | | | | | | | | | | | | | | | | | |
| *A. marina* | 1.1 | | 1.9 | 3 | 4 | 3.9 | | 6.3 | 10 | 4 | 9.0 | | 15.2 | 24 | 2 | 2.0 | | 3.5 | 5 | 3 | 7.4 | | 8.3 | 16 | 2 |
| *B. gymnorrhiza* | 3.2 | | 5.7 | 9 | 3 | 1.3 | | 3.1 | 4 | 5 | 0.0 | | 0.0 | 0 | 4 | 2.0 | | 3.5 | 5 | 3 | 0.0 | | 0.0 | 0 | 3 |
| *C. tagal* | 21.3 | | 26.4 | 48 | 2 | 5.3 | | 6.3 | 12 | 3 | 0.0 | | 0.0 | 0 | 4 | 34.7 | | 33.3 | 68 | 2 | 0.0 | | 0.0 | 0 | 3 |
| *R. mucronata* | 73.4 | | 54.7 | 128 | 1 | 85.5 | | 75.0 | 161 | 1 | 80.8 | | 63.6 | 144 | 1 | 59.4 | | 54.4 | 114 | 1 | 92.6 | | 75.0 | 168 | 1 |
| *S. alba* | 1.1 | | 1.9 | 3 | 4 | 3.9 | | 9.4 | 13 | 2 | 10.3 | | 12.1 | 22 | 3 | 2.0 | | 3.5 | 5 | 3 | 0.0 | | 0.0 | 0 | 3 |
| nil | | | 9.4 | | | | | 0.0 | | | | | 9.1 | | | | | 1.8 | | | | | 16.7 | | |
| **JUVENILE TREES 1997** | | | | | | | | | | | | | | | | | | | | | | | | | |
| *A. marina* | 25.8 | | 16.9 | 43 | 3 | 12.2 | | 17.8 | 30 | 2 | 0.1 | | 4.8 | 5 | 3 | 0.9 | | 9.7 | 11 | 3 | 42.8 | | 10.5 | 53 | 2 |
| *B. gymnorrhiza* | 0.0 | | 2.6 | 3 | 5 | 0.0 | | 4.4 | 4 | 4 | 0.1 | | 2.4 | 2 | 5 | 0.0 | | 1.4 | 1 | 4 | 0.0 | | 0.0 | 0 | 4 |
| *C. tagal* | 26.3 | | 19.5 | 46 | 2 | 3.6 | | 13.3 | 17 | 3 | 0.1 | | 4.8 | 5 | 3 | 44.3 | | 29.2 | 73 | 2 | 3.8 | | 21.1 | 25 | 3 |
| *R. mucronata* | 47.8 | | 42.9 | 91 | 1 | 84.1 | | 48.9 | 133 | 1 | 98.7 | | 35.7 | 134 | 1 | 54.7 | | 41.7 | 96 | 1 | 53.4 | | 42.1 | 96 | 1 |
| *S. alba* | 0.1 | | 5.2 | 5 | 4 | 0.0 | | 0.0 | 0 | 5 | 0.9 | | 7.1 | 8 | 2 | 0.0 | | 1.4 | 1 | 4 | 0.0 | | 0.0 | 0 | 4 |
| nil | | | 13.0 | | | | | 15.6 | | | | | 45.2 | | | | | 16.7 | | | | | 26.3 | | |
| **JUVENILE TREES 1999** | | | | | | | | | | | | | | | | | | | | | | | | | |
| *A. marina* | 64.1 | | 30.8 | 95 | 1 | 30.0 | | 15.6 | 46 | 2 | 5.4 | | 12.8 | 18 | 2 | 39.5 | | 21.6 | 61 | 2 | 83.1 | | 22.2 | 105 | 1 |
| *B. gymnorrhiza* | 0.0 | | 1.5 | 2 | 5 | 0.0 | | 2.2 | 2 | 4 | 0.1 | | 4.3 | 4 | 4 | 0.0 | | 1.4 | 1 | 4 | 0.0 | | 0.0 | 0 | 4 |
| *C. tagal* | 1.5 | | 18.5 | 20 | 3 | 1.4 | | 20.0 | 21 | 3 | 0.8 | | 6.4 | 7 | 3 | 14.6 | | 25.7 | 40 | 3 | 0.4 | | 11.1 | 12 | 3 |
| *R. mucronata* | 34.4 | | 41.5 | 76 | 2 | 68.6 | | 46.7 | 115 | 1 | 93.8 | | 29.8 | 124 | 1 | 45.9 | | 36.5 | 82 | 1 | 16.5 | | 22.2 | 39 | 2 |
| *S. alba* | 0.0 | | 1.5 | 2 | 4 | 0.0 | | 0.0 | 0 | 5 | 0.0 | | 4.3 | 4 | 5 | 0.0 | | 0.0 | 0 | 5 | 0.0 | | 0.0 | 0 | 4 |
| nil | | | 6.2 | | | | | 15.6 | | | | | 42.6 | | | | | 14.9 | | | | | 44.4 | | |

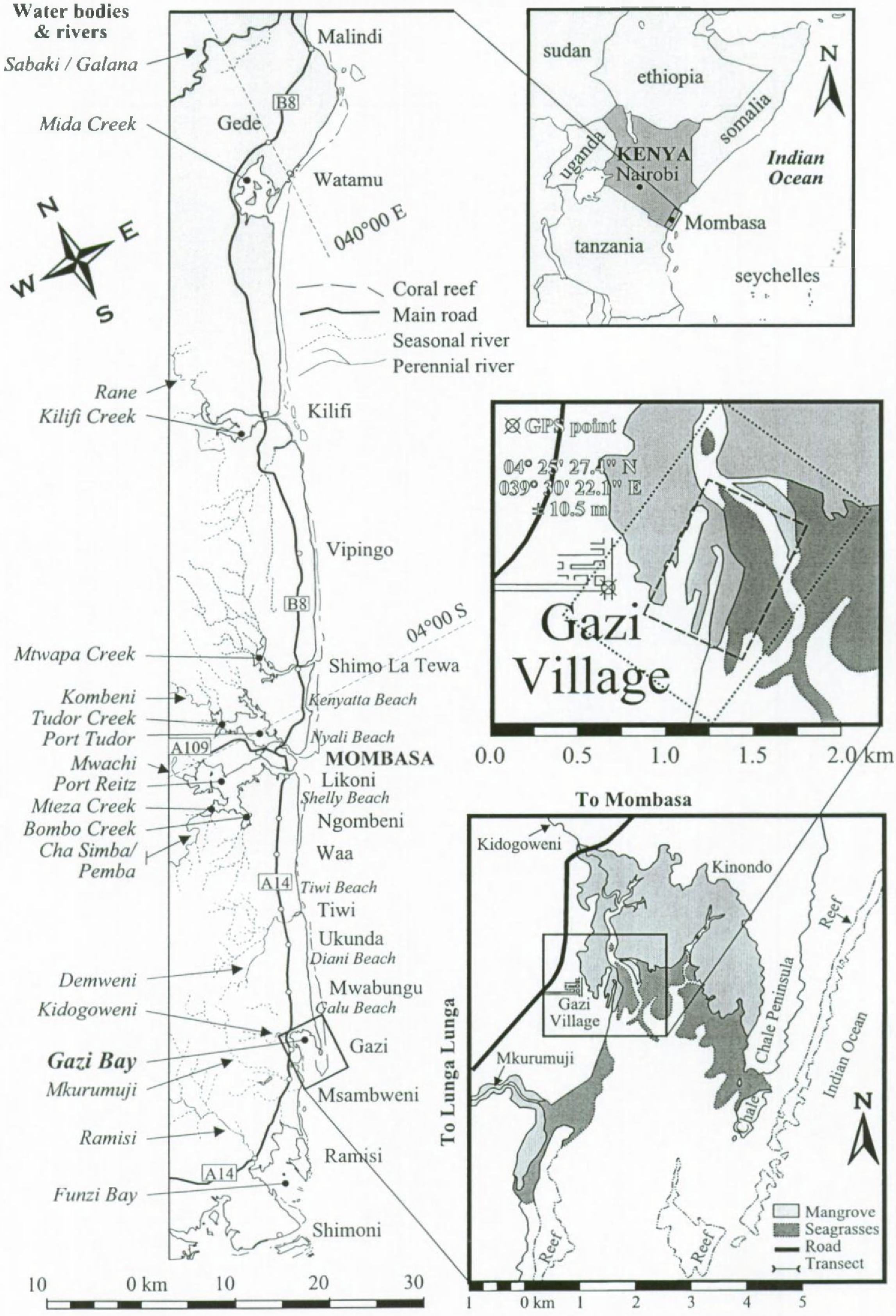
**Table 1b.** Relative density (DEr), relative dominance (DOr) and relative frequency (FRr) for the landward and seaward *A. marina* fringe separately and for all vegetation classes together.

| Vegetation class | Landward *A. marina* zone | | | | | Seaward *A. marina* zone | | | | | All classes | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | DEr | DOr | FRr | IV | rank | DEr | DOr | FRr | IV | rank | DEr | DOr | FRr | IV | rank |
| **ADULT TREES** | | | | | | | | | | | | | | | |
| *A. marina* | 23.5 | 73.9 | 19.0 | 116 | 1 | 13.2 | 28.8 | 21.9 | 64 | 2 | 10.3 | 16.5 | 14.5 | 41 | 3 |
| *B. gymnorrhiza* | 5.9 | 0.4 | 9.5 | 16 | 4 | 1.5 | 0.1 | 3.1 | 5 | 4 | 1.8 | 0.1 | 6.1 | 8 | 5 |
| *C. tagal* | 47.1 | 19.4 | 47.6 | 114 | 2 | 0.0 | 0.0 | 0.0 | 0 | 5 | 11.5 | 2.0 | 11.7 | 25 | 4 |
| *R. mucronata* | 20.6 | 5.6 | 19.0 | 45 | 3 | 76.5 | 51.3 | 59.4 | 187 | 1 | 55.9 | 11.6 | 44.7 | 112 | 1 |
| *S. alba* | 2.9 | 0.7 | 4.8 | 8 | 5 | 8.8 | 19.8 | 15.6 | 44 | 3 | 20.5 | 69.9 | 21.2 | 112 | 2 |
| nil | | | 0.0 | | | | | 0.0 | | | | | 1.7 | | |
| **YOUNG TREES** | | | | | | | | | | | | | | | |
| *A. marina* | 0.0 | | 0.0 | 0 | 4 | 1.6 | | 3.3 | 5 | 3 | 4.0 | | 7.6 | 12 | 3 |
| *B. gymnorrhiza* | 9.7 | | 13.0 | 23 | 3 | 0.0 | | 0.0 | 0 | 4 | 1.6 | | 4.7 | 6 | 5 |
| *C. tagal* | 51.6 | | 43.5 | 95 | 1 | 6.3 | | 13.3 | 20 | 2 | 15.7 | | 18.8 | 35 | 2 |
| *R. mucronata* | 38.7 | | 34.8 | 73 | 2 | 92.1 | | 73.3 | 165 | 1 | 75.0 | | 55.3 | 130 | 1 |
| *S. alba* | 0.0 | | 0.0 | 0 | 4 | 0.0 | | 0.0 | 0 | 4 | 3.7 | | 7.1 | 11 | 4 |
| nil | | | 8.7 | | | | | 10.0 | | | | | 6.5 | | |
| **JUVENILE TREES 1997** | | | | | | | | | | | | | | | |
| *A. marina* | 43.0 | | 25.0 | 68 | 2 | 0.2 | | 7.1 | 7 | 4 | 68.3 | | 10.8 | 79 | 1 |
| *B. gymnorrhiza* | 0.0 | | 0.0 | 0 | 4 | 0.1 | | 4.8 | 5 | 5 | 0.0 | | 2.7 | 3 | 5 |
| *C. tagal* | 44.7 | | 34.4 | 79 | 1 | 0.8 | | 9.5 | 10 | 2 | 7.5 | | 18.8 | 26 | 3 |
| *R. mucronata* | 12.3 | | 37.5 | 50 | 3 | 98.7 | | 50.0 | 149 | 1 | 24.2 | | 39.9 | 64 | 2 |
| *S. alba* | 0.0 | | 0.0 | 0 | 4 | 0.3 | | 9.5 | 10 | 3 | 0.0 | | 4.0 | 4 | 4 |
| nil | | | 3.1 | | | | | 19.0 | | | | | 23.8 | | |
| **JUVENILE TREES 1999** | | | | | | | | | | | | | | | |
| *A. marina* | 87.5 | | 34.8 | 122 | 1 | 42.7 | | 26.2 | 69 | 2 | 64.6 | | 21.7 | 86 | 1 |
| *B. gymnorrhiza* | 0.0 | | 0.0 | 0 | 4 | 0.0 | | 2.4 | 2 | 5 | 0.0 | | 2.4 | 2 | 4 |
| *C. tagal* | 5.4 | | 26.1 | 31 | 3 | 0.2 | | 14.3 | 14 | 3 | 2.4 | | 18.9 | 21 | 3 |
| *R. mucronata* | 7.1 | | 30.4 | 38 | 2 | 57.1 | | 50.0 | 107 | 1 | 32.9 | | 36.3 | 69 | 2 |
| *S. alba* | 0.0 | | 0.0 | 0 | 4 | 0.0 | | 2.4 | 2 | 4 | 0.0 | | 1.4 | 1 | 5 |
| nil | | | 8.7 | | | | | 4.8 | | | | | 19.3 | | |

**Table 2.** G-test results for the differences in species proportions of adult tree and young tree individuals in each of the vegetation classes.

| Vegetation class | G | d.f. | p-value |
|---|---|---|---|
| ***Avicennia marina*** **zone** | 30.363 | 5 | < 0.001 |
| ***Rhizophora mucronata*** **zone** | 10.250 | 5 | n.s. |
| ***Sonneratia alba*** **zone** | 66.830 | 3 | < 0.001 |
| **Mixed zone** | 7.089 | 5 | n.s. |
| **Open space** | 6.822 | 4 | n.s. |

**Figure 1.** Map of the Kenyan Coast (adapted from Dahdouh-Guebas *et al.*, 2000b) and of Gazi Bay, showing the area of mangrove, seagrass and coral reef (according to Slim, 1993). The location of our study site within Gazi Bay is shown approximately and the extent of the aerial photograph of 1972 (dashed line) and the one of 1992 (dotted line) is indicated as well (*cf.* Fig. 2). Scales and geographic coordinates have been indicated in this figure only.



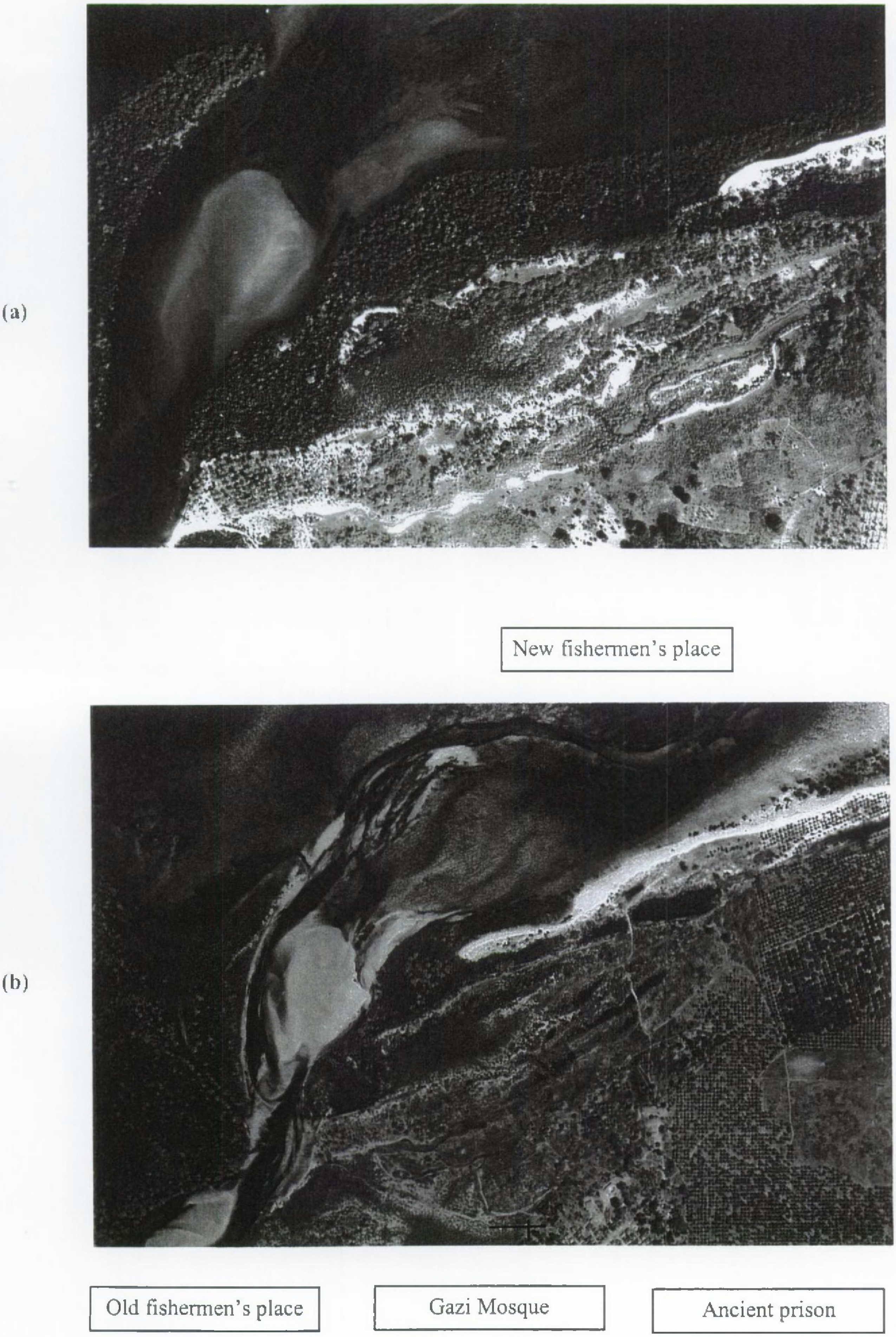


**Figure 2.** Aerial photographs of the study site taken in 1972 (a) and 1992 (b). The latter indicates important local features.

**Figure 3.** Vegetation maps of the study site for 1972 (a) and 1992 (b). The orientation of the photographs with respect to each other and to Gazi Bay is indicated in figure 1. The short black lines represent the location of the 6 transects and the area mainly under discussion in the text. The long black lines represent transects A and B. A dotted pattern represents an area with an open character, a dashed pattern an area that is degraded and a pattern with small lines the area outside our study field.

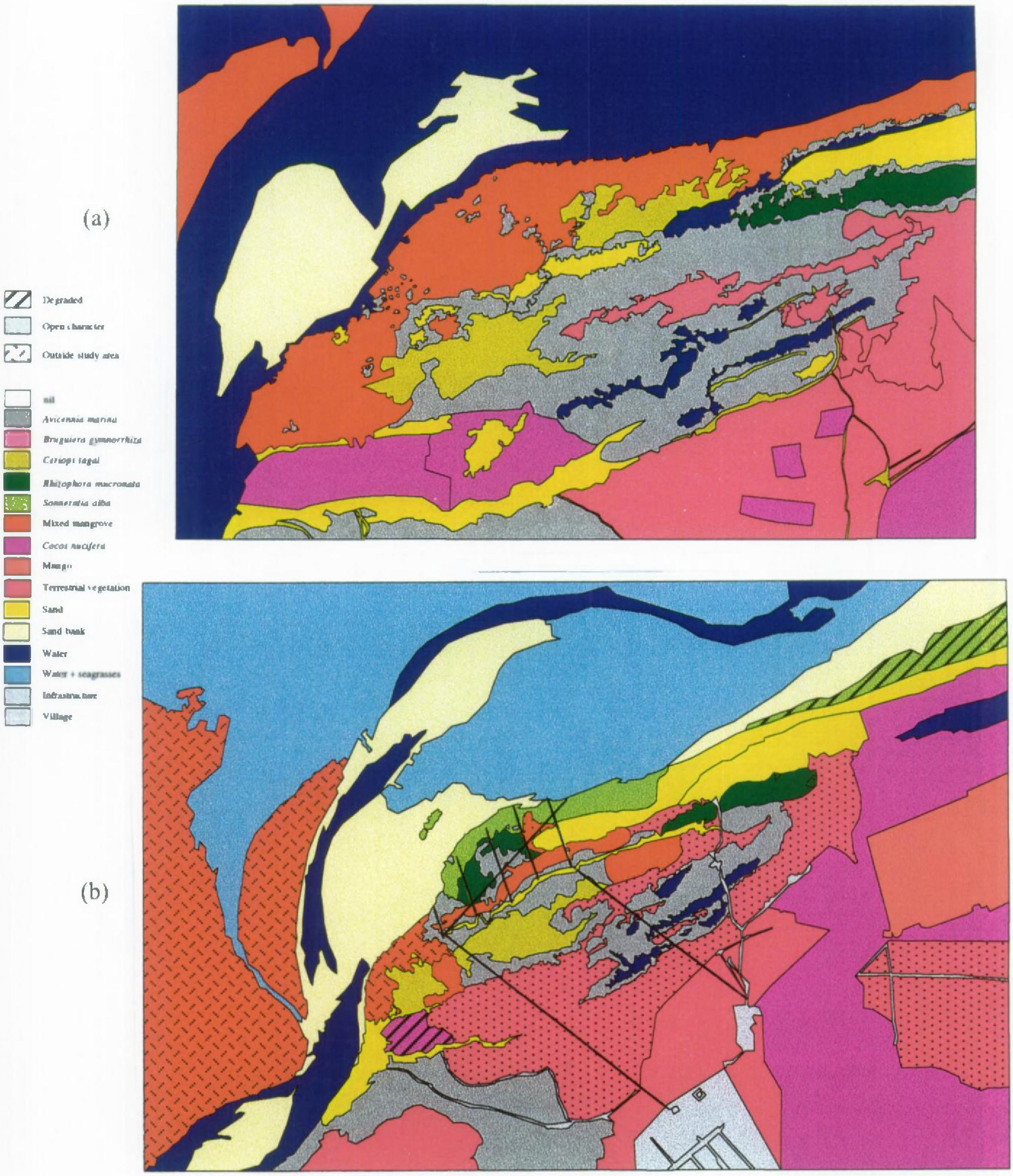


**Figure 4.** Results from the indirect species ordination (DCA) of the following presence/absence vegetation data in 99 sample points : adult trees (AT), young trees (YT) and juvenile trees (JT) recorded during the fieldwork expedition of 1997 (97) or 1999 (99). Am = *Avicennia marina*, Bg = *Bruguiera gymnorrhiza*, Ct = *Ceriops tagal*, Rm = *Rhizophora mucronata* and Sa = *Sonneratia alba*.

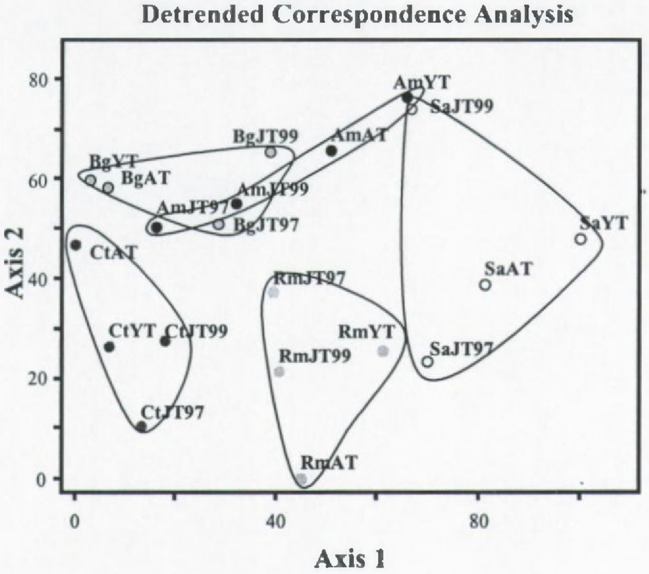
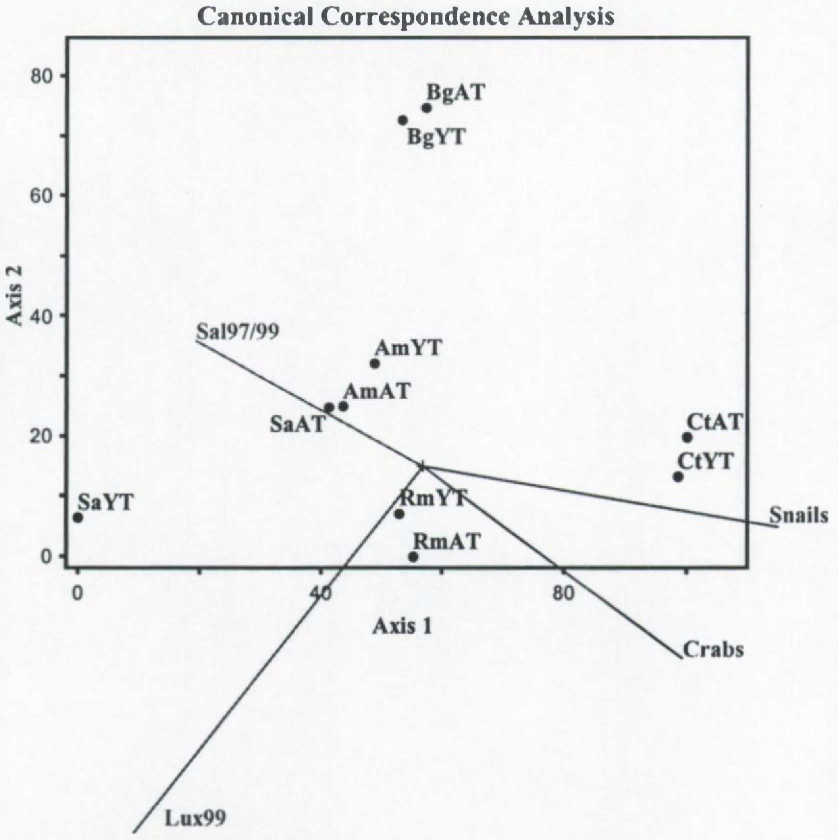


**Figure 5.** Results from the direct species ordination (CCA) of the adult and young presence/absence vegetation data in 99 sample points. Abbreviations are as in figure 4.



# Chapter VIII.

## An ordination study to view past, present and future vegetation structure dynamics in disturbed and undisturbed mangrove forests in Kenya and Sri Lanka.

Dahdouh-Guebas, F., J.G. Kairo, L.P. Jayatissa & N. Koedam

Engaged in a peer-review process

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

Dahdouh-Guebas, F.[1], J.G. Kairo[2], L.P. Jayatissa[3] 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.*

**Abstract**

The mangrove vegetation of a disturbed and an 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 in each site. Detrended correspondence analysis and canonical correspondence analysis were used to analyse the data and to link the vegetation data to the environmental factors. Results showed that species clusters were relatively easy to delineate, whether the mangrove was zoned or not. Among the environmental factors, the abundance of propagule predators (mostly sesarmid crabs) could be a major 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 takes in a high importance at the ecological level as well (link between water level and vegetation dynamics). However, none of the environmental factors could successfully explain the variability in vegetation data. The results of the study further provide information on the dynamic or static nature of a forest and on its ability to rejuvenate, contributing to appropriate forestry management guidelines.

Keywords : disturbance, crab, rehabilitation, DCA, CCA, forestry.

## Introduction

Vegetations have been increasingly investigated using remote sensing (*e.g.* Gang & Agatsiva, 1992; Cohen *et al.*, 1996; Ramachandran *et al.*, 1998; Dahdouh-Guebas *et al.*, 1999) and both 'reviews' and 'recent advances' are continuously reported in order to emphasize and compare the potential of various remote sensing technologies in the past and for the future (*e.g.* Rehder & Patterson, 1986; Tassan, 1987; Aschbacher *et al.*, 1995; Blasco *et al.*, 1998; Holmgren & Turesson, 1998; Hyyppä *et al.*, 2000). Vegetation dynamics, as changes in stand structure and composition, is one of the aspects of vegetation ecology (*e.g.* Putz & Chan, 1986; Smith & Huston, 1989; Heil & Van Deursen, 1996; Murali *et al.*, 1998; Dahdouh-Guebas *et al.*, 2000a), but as yet it has not received the attention it deserves. Vegetation dynamics is an important aspect of vegetation or forest science, since it integrates data from different moments in time. Very often the study of vegetation dynamics relies on remote sensing, combined with geographic information systems (GIS), since it usually constitutes the only retrospective basis of comparison to actual vegetation data (Dahdouh-Guebas *et al.*, 2000a). In addition, this type of studies can generate results that can be directly used in forest management planning (*e.g.* Holmgren *et al.*, 1997; Holmgren & Turesson, 1998).

Among the tools that are available to analyse vegetation data, ordination algorithms are appropriate to explore the relation between the vegetation structure and the environment (Kent & Coker, 1992). However, in mangrove ecology, particularly in studies on vegetation dynamics, such approaches have little been used (*e.g.* Ukpong, 1995). Whereas it is known that problems can be involved in the deduction of vegetation dynamics from PCA (Hobbs & Grace, 1981), this problem can be overcome by analysis through time rather than using data of one moment in time. Studies of the mangrove vegetation using sequential aerial photography has shown that autogenous changes can occur in mangroves (Dahdouh-Guebas *et al.*, 2000a). Since mangroves become increasingly threatened by various human impacts (*e.g.* ITTO, 1993; Pernetta, 1993a; IUCN, 1996; Farnsworth & Ellisson, 1997; Kjerve *et al.*, 1997; Dahdouh-Guebas *et al.*, 2000c), 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 the present study we investigate and compare the vegetation structure and composition of undisturbed and disturbed mangrove sites in Kenya and Sri Lanka using a combination of detrended and canonical correspondence analysis on presence/absence and abundance data, and show how such an ordination study may reveal the vegetation structure dynamics and allow us to predict future changes.

## Description of the study sites

An undisturbed and a disturbed site were chosen in both Kenya and Sri Lanka (Fig 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 is a creek with 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 & 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. Both the mangrove of Mida Creek and Gazi Bay constituted a fringing forest type (Lugo & Snedaker, 1974). The mangrove in Gazi Bay has long been (over)exploited for wood and is today regarded as a disturbed mangrove. Although woodcutting is also going on in Mida Creek (Dahdouh-Guebas *et al.*, 2000b), the mangrove is much less affected than in Gazi Bay.

Of the two mangrove forests investigated along the South-western side of Sri Lanka, the first one is located in the Pambala area of Chilaw Lagoon, in Sri Lanka's intermediate climate zone (Mueller-Dombois, 1968). The mangroves here are of the fringe type (Lugo & Snedaker, 1974), and have a rather irregular distribution along a complex of creeks (Marambettiya Ela, Bate Ela, Pol Ela and Dutch Channel). Most freshwater influx stems 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). This site is known to be well preserved for long and the most species diverse in South-Western Sri Lanka (Jayatissa *et al.*, subm.; Dahdouh-Guebas *et al.*, in prep.d). Nevertheless, the mangrove in Chilaw Lagoon has recently been subjected to strong anthropogenic influences as a result of shrimp farming (Foell *et al.*, 1999; Dahdouh-Guebas *et al.*, 2000c).

The second mangrove forest is 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 (Lugo & 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, namely the Thalpe Ela, discharging into the ocean, and the Galu Ganga, 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.*, 2000a).

The ten East-African mangrove species occur along the Kenyan coast, *i.e. Avicennia marina* (Forsk.) Vierh., *Bruguiera gymnorrhiza* (L.) Lam., *Ceriops tagal* (Perr.) C.B. Robinson, *Heritiera littoralis* Dryand., *Pemphis acidula* Forst., *Lumnitzera racemosa* Willd., *Rhizophora mucronata* Lam., *Sonneratia alba* Sm., *Xylocarpus granatum* Koen and *X. moluccensis* (Lamk.) Roem. The latter however is very rare. The common species present in Pambala are *Aegiceras corniculatum* (L.) Blanco, *Avicennia officinalis* L., *Bruguiera gymnorrhiza*, *Bruguiera 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.* (subm.). The nomenclature of mangrove species is according to Tomlinson (1986).

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), and locally the tidal amplitude is even as little as 15 cm in the course of one week (Dahdouh-Guebas, subm.). The second difference concerns the zonation. In Kenya zonation is very pronounced in all mangrove areas, whereas in Sri Lanka it is seldom present (*e.g.* very localized partial or semi-zonation). In both Sri Lankan sites, there was no slope with upper or lower intertidal areas. In Pambala is a plateau with pools, whereas in Galle is a multitude of small islands and pools, primarily resulting from the burrowing activities of the mangrove mud lobster *Thalassina anomala* Herbst.

## Material & methods

In each of the mangrove sites, sample points (Tab. 1) were chosen along parallel as well as orthogonal transects. In each sample point 4 quadrants were established as in the Point-Centred Quarter Method of Cottam & Curtis (1956). The height and $D_{130}$ (term according to Brokaw & Thompson (2000), but formerly referred to as DBH, the diameter at breast height) of the adult and young trees (trees smaller than 1.3 m or with a $D_{130} < 2.5$ cm, but which already reached the sapling stage) closest to the sample point was recorded in each quadrant (= quarter), were measured and the total cover abundance in the 5 x 5 m quadrat (= square) nearest to the sampling point was estimated in each quadrant (as in the Braun-Blanquet relevé method). This was done in July 1996 for Mida Creek, January 1997 for Galle, February 1997 for Pambala and July 1997 for Gazi Bay.

In the same 5 m x 5 m quadrats also the mangrove juveniles (propagules or seeds until they reached the stage of sapling, which is defined here as a young plant with more than 6 leaves) were identified and counted. At each sample point the following environmental factors were measured : salinity (using an Atago refractometer), light intensity (using a Lutron luxmeter), land/water ratio (visually estimated), crab burrow density and density of the snail *Terebralia palustris* L. These environmental factors as well as the mangrove juveniles were investigated during the above-mentioned fieldwork missions as well as 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 - February, whereas the peaks of the wet season are around May and even stronger around November in both Kenya and Sri Lanka.

The vegetation data were inserted into two types of matrices, one based on presence/absence data (0 - 1) and another on abundance data (0 - 4) per sample point (4 quadrants together). For each of these two types, 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 combination 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 & Mefford, 1997), DCA or Detrended Correspondence Analysis or (Hill & Gauch, 1980) and CCA or 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 the latter 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 and comprised salinity (averaged if not significantly different between seasons), light intensity, land cover, abundance of herbivorous crabs and snail abundance. Monte Carlo tests were performed to test the significance of the eigenvalues and of the species-environment correlations up to a significance level of 0.001 (= 999 runs).

## Results

From the structural attributes of the vegetation (Tab. 1) we can see that the tree densities and forest heights are higher in the less disturbed forests, as is the basal area in the Sri Lanka site, but not in Kenyan sites. Gazi, although disturbed, is dominated by *Rhizophora mucronata* with a presence of very large *Avicennia marina* and *Sonneratia alba* specimens, the latter two of which greatly influence the total basal area of the forest. Nevertheless, the undisturbed sites (Mida and Pambala) are structurally, according to the C.I., more complex than the disturbed sites (Gazi and Galle).

The variation in species data in each of the sites was analysed in the detrended correspondence analysis (Fig. 2 + Tab. 2) and species data in combination with environmental data in the canonical correspondence analysis (Fig. 3 + Tab. 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 for the discussion from a vegetation structure point of view (see further). For Pambala, the combination of many species and their juveniles render interpretation difficult and therefore the ordination was repeated omitting the juvenile trees (Fig 4 + Tab. 4). The omission of the outliers formed by young *Heritiera littoralis* trees in the latter as well, did not affect the ordination result.

Although the species-environment correlations in the CCA were 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 latter was low in all sites (Tab. 2). Nevertheless some remarkable patterns can be recognized. On one hand, some species-environment associations can be recognized in the CCA, and on the other hand, information on mangrove vegetation structure dynamics can be inferred based on both types of ordinations.

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, are different according to the sites. One of the common results is the fact that species clusters usually appear 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* (Fig. 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 to the second axis as compared to other environmental factors, that it did not even show on the biplot (Fig. 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 associated to 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 (Fig. 3d), reflects the field observation that the former two species are usually located on top of the small islands, whereas the latter is often growing on the margin of an island with roots in the water or entirely 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.

In addition to the ordinations, also frequency distributions $D_{130}$ classes at 2.5 cm intervals combined with frequency of juveniles during the fieldwork missions were made (Fig. 5). These results 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 cannot be said from the other species, which may explain the smaller $D_{130}$ classes represented. The frequency distribution for *Bruguiera gymnorrhiza* in Mida displays anomalies with twice two successive $D_{130}$ classes missing in between classes that are actually represented. Although no such patterns in $D_{130}$ classes are observed for *Rhizophora mucronata* or *Ceriops tagal* in the same site, their patterns are 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.

## Discussion

The ordinations provide new insight into the dynamics of the mangrove vegetation. As in the CCA, in the DCA the species clusters are also 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. Some species always have a restricted dispersal (species cluster with small coverage on the first axis), such as *Ceriops tagal* and *Rhizophora* species, whereas other species are distributed over considerable larger areas (species clusters with a wide coverage on the first axis), such as *Avicennia marina* and *Excoecaria agallocha*. For *Avicennia marina* this is clearly linked to its pioneering nature (*cf.* Osborne & Berjak, 1997). It spreads its seeds over a wider area than where they can actually establish. Therefore they display a distribution of juvenile trees that is less associated to that of the adult trees than that of young trees, which is also the case for *Avicennia officinalis*. In Gazi, the disjunct zonation of *A. marina* as a landward and a seaward fringe (*cf.* Dahdouh-Guebas *et al.*, subm.c, Dahdouh-Guebas *et al.*, subm.d) further explains it central and elongated position in the ordination graphs. Whether the same is true for *Heritiera littoralis*, young trees of which were observed in the section of Pambala where conspecific adult trees are absent, cannot be certified. 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 a phenomenon at the other side of the list of temporal succession events, namely the increase 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.*, 2000a). 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 appearance of species clusters where fewer herbivorous crabs and snails are present is in line with the observed predation intensity by these animals in Kenya (Dahdouh-Guebas *et al.*, 1997, 1998) and Sri Lanka (Dahdouh-Guebas, subm.). The land/water ratio in Galle taking in the highest important in the explanation of the variation in vegetation data is probably due to its high ecological importance concerning 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, interacting with propagule predation, it is a driving force in the dynamics of a mangrove forest (Dahdouh-Guebas, subm.).

*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 however 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, the latter of which can vary significantly between sites (Dahdouh-Guebas *et al.*, subm.c). 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, this is only the case for the most landward and the most creekward *Rhizophora* individuals, but probably the contact of both ends with water supplies the *Rhizophora* trees located further from the surface water. Whereas the influence of underground water supply on mangrove distribution has clearly been demonstrated by Tack & Polk (1999) for the Kenyan coast, this is still subject to further research (*e.g.* Song *et al.*, 1999). Another variable that probably plays a substantial role is the soil texture. It has recently been pointed out that this parameter 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 the same is true for mangrove species (Dahdouh-Guebas *et al.*, in prep.c). Also other edaphic characteristics such as nutrient availability may be important explanatory factors.

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 the people's higher preference in cutting for these species, as was established by Dahdouh-Guebas *et al.* (2000b).

The present study shows that ordinations can provide information with respect to the species composition and the dynamics of a vegetation assemblage by using different vegetation layers per species as an input, rather than single species. The dynamic or static nature of a particular forest is a direct result in this approach, 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 provide a possible indication on the destiny of a forest and may raise the awareness to protect or to rehabilitate a mangrove area.

## Acknowledgements

Many thanks are due to the fieldwork assistance of Fatuma M. Saidi, Daglas W.N. Thisera, Anouk Verheyden, Ilse Van Pottelbergh, Abdulhakim Abubakr Ali Jilo and Saman Nishante. Research financed by the European Commission (Contract EBR IC18-CT98-0295), and with a specialisation fellowship of the Flemish Institute for the advancement of scientific-technological research in the industry (IWT).

## References

See Bibliography

**Table 1.** Summary of the structural vegetation data for the 4 sites.

| Site | Number of sample points | Mangrove species present[1] (in order of importance[2]) | Tree density (stems/0.1ha) | Basal area ($m^2$/0.1ha) | Mean forest height (m) | Complexity Index (C.I.)[3] |
|---|---|---|---|---|---|---|
| **Mida** | 25 | *C. tag, R. muc, A. mar, B. gym, X. gra* | 107.6 | 0.697 | 8.9 | 3.3 |
| **Gazi** | 99 | *R. muc, S. alb, A. mar, C. tag, B. gym* | 89.2 | 2.144 | 5.6 | 2.5 |
| **Pambala** | 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** | 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 ($m^2.0.1ha^{-1}$), mean tree height (m) and number of stems.0.1 $ha^{-1}$ times $10^{-3}$ expressed in a 0.1 ha plot (Holdridge *et al.*, 1971)

**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 |

**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 are shaded. 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 are shaded. 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 ($p = 0.274$) |

**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), Gallin *et al.* (1989) and Verheyden *et al.* (subm.).

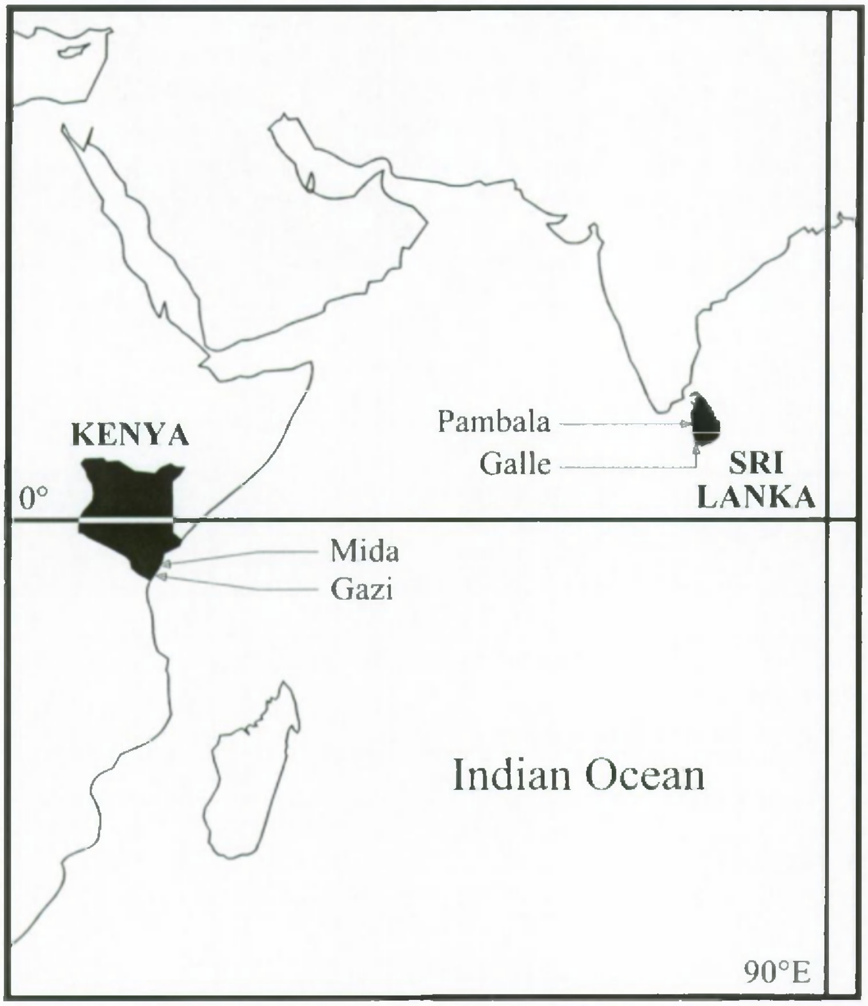
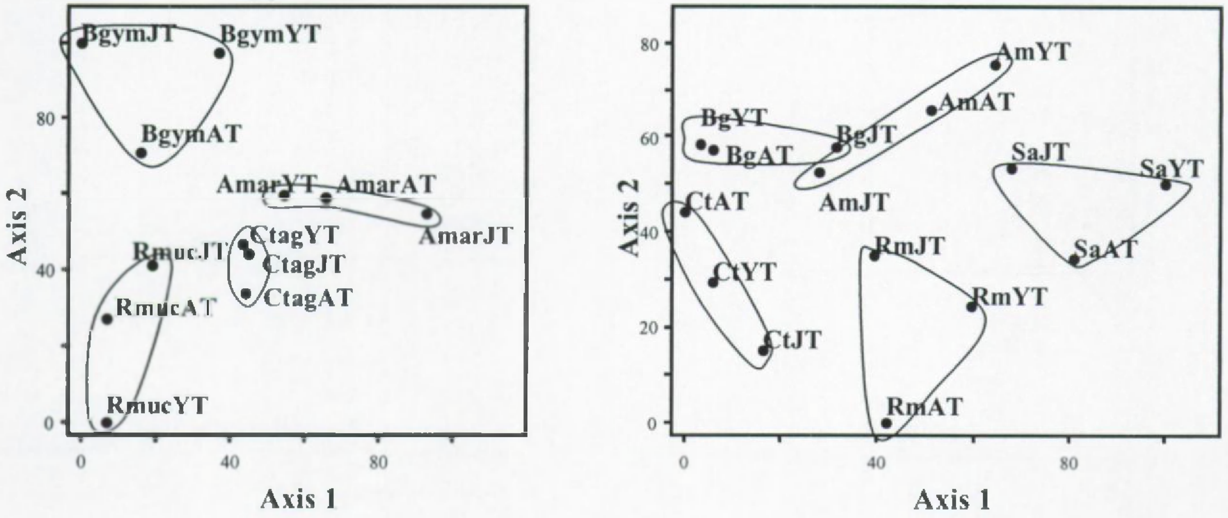


**Figure 2.** Plots of the detrended correspondence analysis in Mida (a), Gazi (b), Pambala (c) and Galle (d). For Mida *Xylocarpus granatum* formed an outlier to the ordination and was therefore omitted from the input matrix. Points of one species are encircled and where necessary the points have been shaded to ease interpretation. See table 2 for numerical results. (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*).

**(a) Mida** **(b) Gazi**



**(c) Pambala** **(d) Galle**

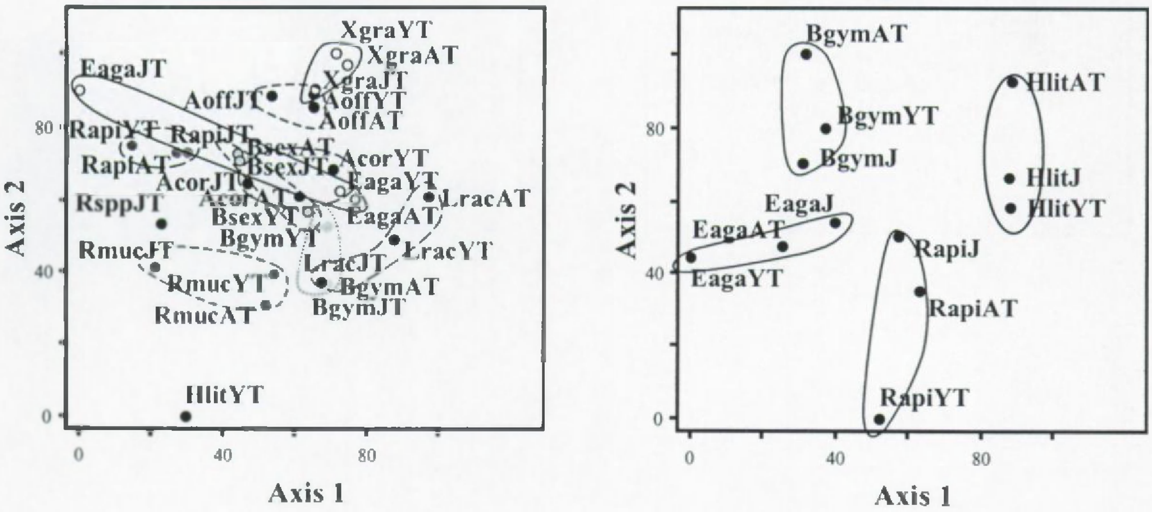
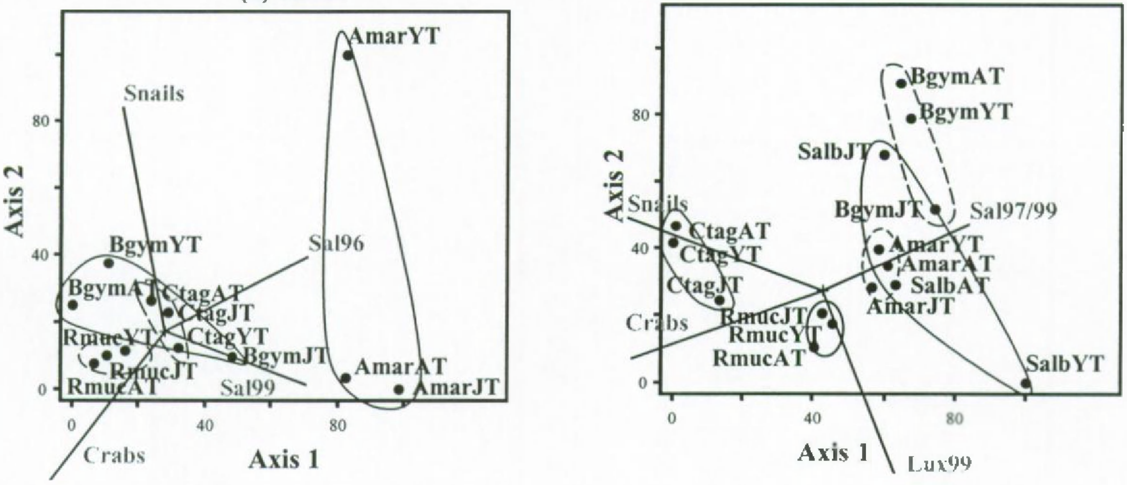
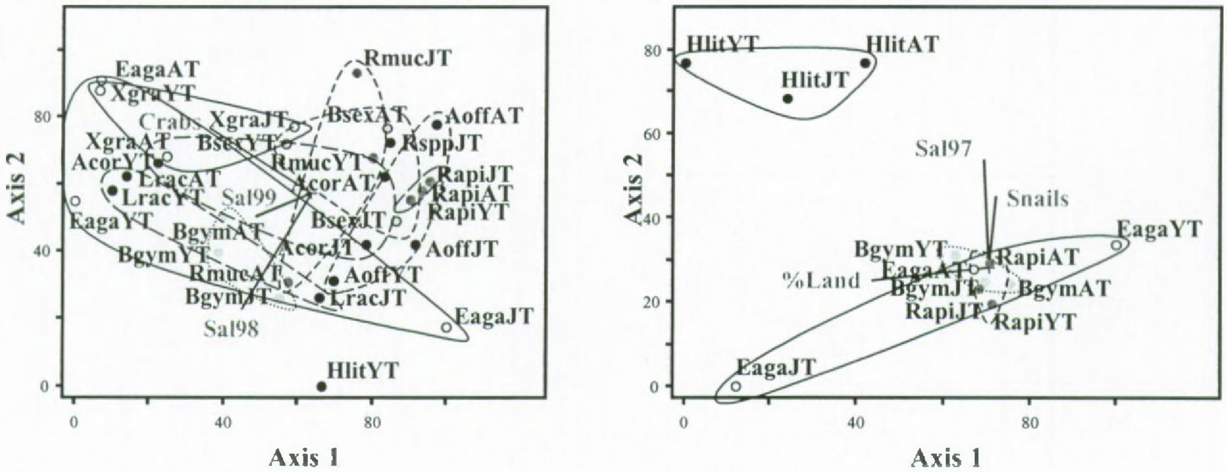


**Figure 3.** Biplots of the canonical correspondence analysis in Mida (a), Gazi (b), Pambala (c) and Galle (d). For Mida *Xylocarpus granatum* formed an outlier to the ordination and was therefore omitted from the input matrix. Points of one species are encircled and where necessary the points have been shaded to ease interpretation. See table 3 for numerical results. (%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).


(a) Mida

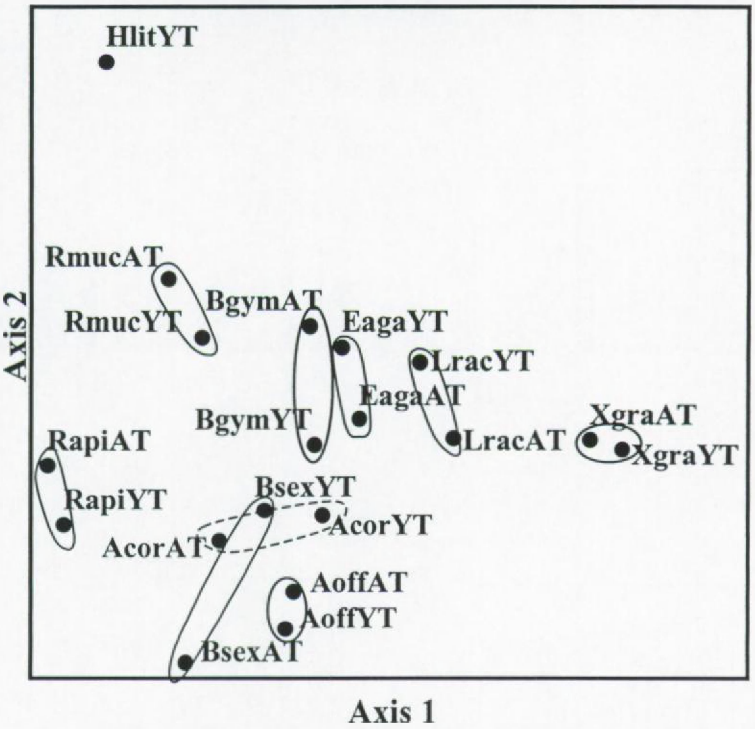
(b) Gazi


(c) Pambala

(d) Galle

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

**(a) Detrended Correspondence Analysis**



**(b) Canonical Correspondence Analysis**

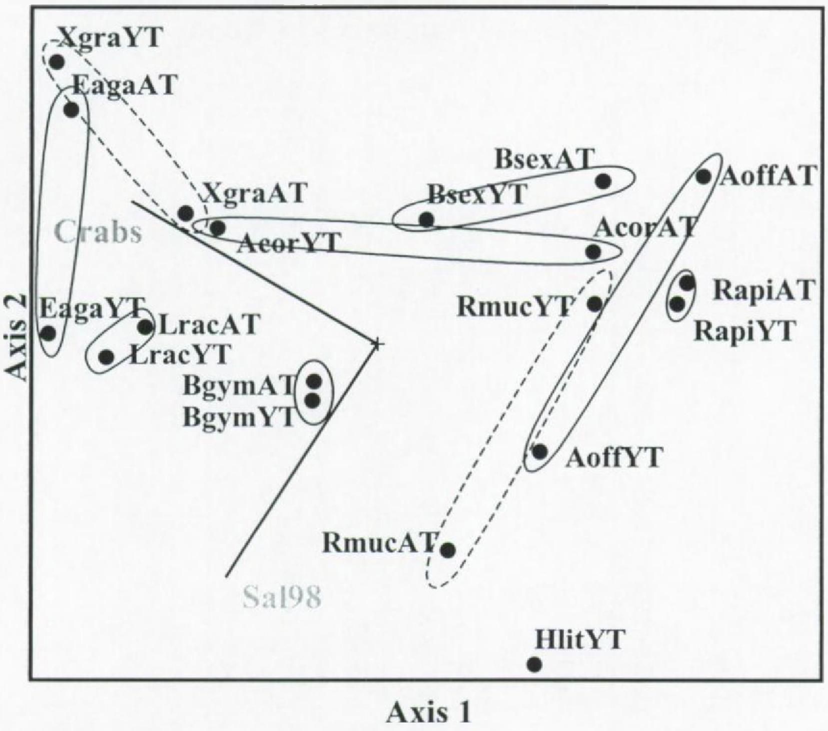
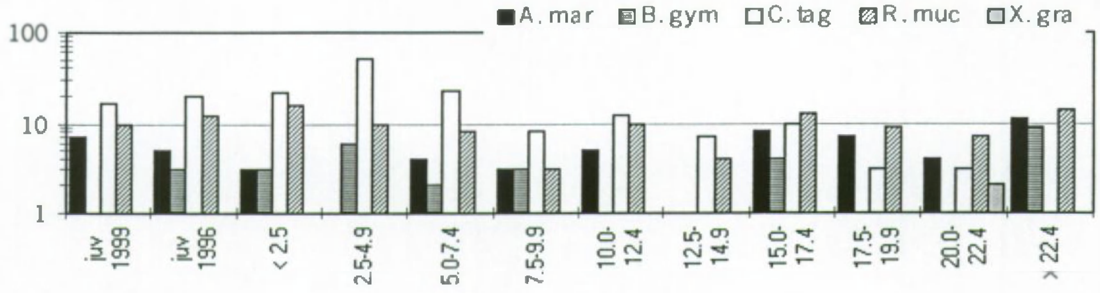
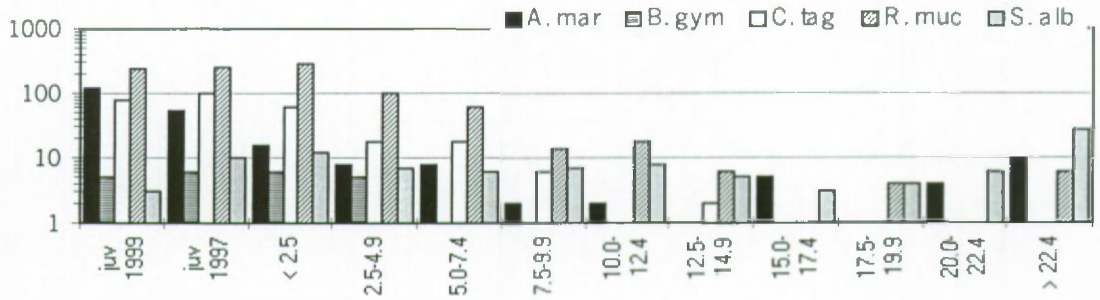


**Figure 5.** Frequency distributions of $D_{130}$ classes (at 2.5 cm intervals) combined with frequency of juveniles during the fieldwork missions. The right part of the frequency distributions provide information about the past of the forest, whereas the left part may be used to infer about the future.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

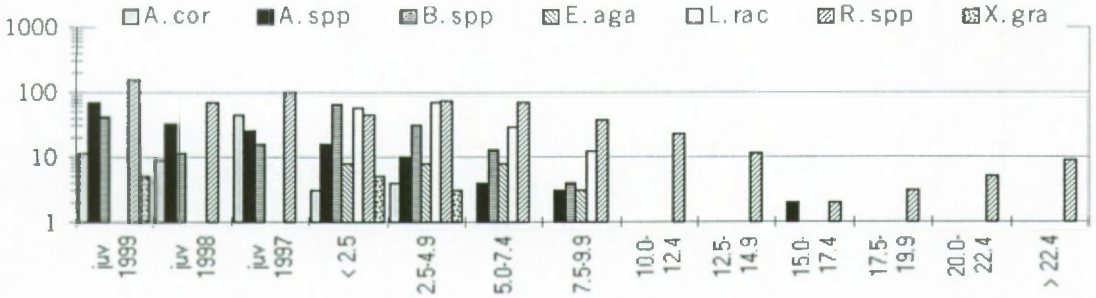
(a) Mida



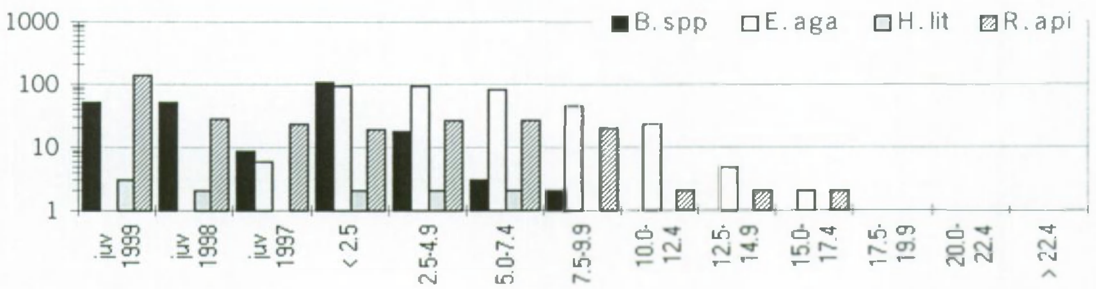
(b) Gazi



(c) Pambala



(d) Galle



# Chapter IX.

# An explorative study on grapsid crab zonation in mangrove forests in Kenya.

Dahdouh-Guebas, F., M. Verneirt, S. Cannicci, J.G. Kairo, J.F. Tack & N. Koedam

Engaged in a peer-review process

# An explorative study on grapsid crab zonation in Kenyan mangroves.

Dahdouh-Guebas, F.[1], M. Verneirt[1], S. Cannicci[2], J.G. Kairo[3], J.F. Tack[4] & N. Koedam[1]

[1] *Laboratory of General Botany and Nature Management, Mangrove Management Group, Vrije Universiteit Brussel, Pleinlaan 2, B-1050 Brussels, Belgium.*
[2] *Dipartimento di Biologia Animale e Genetica 'Leo Pardi', Università degli Studi di Firenze, Via Romana 17, I-50125 Firenze, Italia.*
[3] *Kenya Marine and Fisheries Research Institute, PO Box 81651, Mombasa, Kenya.*
[4] *Belgian National Science Foundation, c/o Laboratory of Ecology and Systematics, Mangrove Management Group, Vrije Universiteit Brussel, Pleinlaan 2, B-1050 Brussels, Belgium.*

### Abstract

Despite earlier efforts to understand the role played by grapsid crabs in mangroves, little evidence is available to substantiate their importance to contribute to the structuring and functioning of such systems. The present study provides some new data on the interactions between mangroves and crabs at the mangrove assemblage rather than at the species level. Floristic and faunistic relevés were made in Gazi Bay (2 sites) and Mida Creek (3 sites), 140km apart along the Kenyan coast, along five transects in a series of quadrats covering the width of the mangrove belts. Zonation of both mangrove vegetation and brachyuran fauna was described and height above datum and distance to the mainland (limit of non-flooded area) measured. The relation between the presence and the absence of crabs and trees was analysed using detrended correspondence analysis.
Synthesised, the mangrove tree zonation pattern contains four assemblages with a particular dominant species : a landward *Avicennia marina* zone, then a mixed zone with *Ceriops tagal*, *Rhizophora mucronata* and *Bruguiera gymnorrhiza*, followed by a *R. mucronata* zone and a *Sonneratia alba* zone, both of which can mix with *A. marina*. According to our results, the distribution of *Neosarmatium meinerti* and *Sesarma ortmanni* is linked to that of the landward *A. marina* zone and the distribution of *Metopograpsus thukuhar*, *Neosarmatium smithii*, *Sesarma guttatum* and *Sesarma leptosoma* corresponds to that of the *R. mucronata* zone. Ordination results show that there is one major underlying factor in the zonation of both crabs and trees, with most likely a complex multiple causality. In certain cases the association between crabs and trees are causal, whereas in other cases it can be the result of an independent restriction to the same zones by a common cause.

Keywords : mangrove, crab, Grapsidae, zonation, Detrended Correspondence Analysis, Kenya.

## Introduction

Descriptions of mangrove vegetation structure are available for many regions worldwide. In East-Africa Graham (1929), Walter & Steiner (1936), Kokwaro (1985), Ruwa & Polk (1986), Gallin *et al.* (1989), Ruwa (1990; 1993), Gang and Agatsiva (1992) and Van Speybroeck (1992) have investigated the vegetation or zonation pattern in mangrove forests. Most of these studies put a strong emphasis on the vegetation or plant cover alone. The study of the vegetation structure or assemblages on the other hand, provides data that are important in a broader ecological framework and can for instance also include faunistic aspects.

Mangrove fauna such as decapods (Smith, 1987a, 1987b; Smith *et al.*, 1989; Osborne and Smith 1990; Anon., 1991; Weinstock, 1994; McKee, 1995a; McGuinness, 1997b) have been reported worldwide to impact the recruitment of mangrove propagules to a large extent. For Kenya in particular Dahdouh-Guebas *et al.*(1997, 1998, 1999) have shown that grapsid crabs feed on mangrove propagules and can possibly be a threat to the early development of mangrove seedlings.

In the present study the aims are to describe the zonation of mangrove trees and grapsid crabs in two Kenyan coastal creek systems about 140 km apart, to emphasize the variability of mangrove tree zonation patterns between sites and to investigate whether the distribution of certain crab species is linked to the distribution of particular mangrove tree species. The term 'zonation' is defined here as banding of vegetation types with a certain, often monospecific floristic composition. Hypotheses on the complex multiple causality for the correlation between crabs and trees are discussed.

## Materials & Methods

### *Description of the sites studied*

The study areas were located in Gazi Bay (4°26' S, 39°30' E) and Mida Creek (3°20' S, 40°00' E), two well-studied water bodies along the 570 km long Kenyan coast (Fig. 1). Gazi Bay is an open creek located about 40 km South of Mombasa and fed by two seasonal rivers. Mida Creek, a creek with a narrow opening towards the ocean, is situated about 100 km North of Mombasa. Unlike Gazi Bay, Mida Creek has no overland freshwater input, but benefits from a high groundwater outflow (Tack & Polk, 1999).

Although subject to local variations, all eight East-African mangrove species described by Tomlinson (1986), as well as *Pemphis acidula* Forst. and *Xylocarpus mollucccensis* (Lamk.) Roem., occur along the Kenyan coast. In Gazi Bay, a natural, virtually undisturbed forest (subsequently called 'Covered'), as well as a forest with many marks of exploitation (subsequently called 'Cleared'), can be observed (Fig. 1). In Mida Creek Mida, Sita and Dabaso were investigated (Fig. 1). Al study sites were chosen from aerial photographs in order to ascertain a fringing forest type (following Lugo & Snedaker, 1974) and to be representative for the wider area. Gazi Bay and Mida Creek were chosen because of the considerable variability in the mangrove zonation.

## Methodology

All fieldwork was carried out between July and September 1993. Line transects down the slope and covering the complete width of the mangrove belt were drawn in order to investigate the zonation of the mangrove trees and crabs. The line transects consisted of a sequence of evenly spread, but non-connected quadrats of 5 x 5 m with in-between spaces of 1 to 15 m depending on the length of the transect. The mangrove vegetation in each quadrat was described by means of the relevé method of Braun-Blanquet (Westhoff & Van der Maarel, 1978; Van der Maarel, 1979), which describes the vegetation according to number and/or coverage degree of species for four different vegetation layers. Crabs were sampled according to a similar method using the ordinal scale from 0 to 5 (Tab. 1), which is known to generate reliable population estimates (Frith & Frith, 1977; Frith & Brunenmeister, 1980; Macintosh, 1988; Bosire *et al.*, 1999, Bosire *et al.*, subm.a). The crabs considered were predominantly herbivorous species only (Dahdouh-Guebas *et al.*, 1999), which are able to interfere with natural regeneration of mangroves. However, *Metopograpsus oceanicus* Jacquinot was omitted from the investigation because of its rarity in all sites and *Cardisoma carnifex* (Herbst) was not investigated. Occasional visual observations on the behaviour of the crabs were recorded to help formulating hypotheses on the causalities of their distribution. The sampling methods were completed with the distance to the mainland (*i.e.* limit non-flooded area) and the local topography, by means of the line method of Dawes (1981), whereby the height above datum of high tide was taken as a reference. These measurements were made in all sites within 24 hours. An observed tidal range within Mida Creek of more than 2.5 m, as compared to the reported 3.5 m outside the creek (Spalding *et al.*, 1997), indicates that differences between actual tidal amplitude and predictions, known to occur in some enclosed and shallow bay systems, were minimal.

Both the results of the floristic and faunistic relevés were fitted to the results of the topographic measurements. The association between the presence and absence of each of the mangrove crabs and mangrove trees in each sample point along the transects was investigated using Detrended Correspondence Analysis (Hill & Gauch, 1980) using PC ORD for Windows (McCune & Mefford, 1997).

## Results

The variability in mangrove zonation between the sites can be seen from figure 2 and even height above datum does not correspond with a certain mangrove assemblage (*e.g. cf. Rhizophora* between Gazi 'Covered' and Mida, and *Avicennia* between all sites, Fig. 2 and Tab. 2).

A synthesis of the zonation in our sites (Fig. 2) would comprise four zones, each having a dominant species. The first and landward zone has *Avicennia marina* as a dominant species, occasionally mixed with *Heritiera littoralis*, *Bruguiera gymnorrhiza* or *Ceriops tagal*. The second zone is a mixed zone in which *Ceriops tagal* is always found to be present, but not necessarily as the dominant species and often mixed with *Rhizophora mucronata* and *Bruguiera gymnorrhiza*, with an occasional presence of *Xylocarpus granatum*. The third zone is a *Rhizophora mucronata* zone, which is often monospecific, but which can be mixed with *Avicennia marina*. Sometimes *Ceriops tagal* thrives in the understory of this zone. The last and most seaward zone has *Sonneratia alba* as the dominant species, but like the former zone, it is found to mix with *Avicennia marina*, which therefore occurs in very different environments along the slope. As is expected in the natural environment the boundaries of these zones are not discrete but gradual.
*Neosarmatium meinerti* and *Sesarma ortmanni* are always restricted to the landward (*Avicennia*) zone and were observed in Mida and Gazi 'Covered' and Gazi 'Cleared' outside the range of the transect as a resident of the herbaceous vegetation on sandy substrate.

The ordination plot is shown in Figure 3 and the eigenvalues are 0.790, 0.386 and 0.171 for the first, second and third axis respectively. The variations explained by these first three axes are 23.0 %, 3.3 % and 1.0 % respectively. Although field data were introduced as independent data, the general zonation pattern of mangrove trees and crabs can be clearly discerned.
As can be observed from the clusters within the ordination graph (Fig. 3), together with *Heritiera littoralis* the species scores (hereafter 'SS') of *Neosarmatium meinerti* and *Sesarma ortmanni* according to the first axis are all within the same range (-159 – + 44). The disjunct zonation pattern of *Avicennia marina* (SS = 161) makes this tree species somewhat an outlier to the former cluster, but the landward *Avicennia* fringe can be considered part of it. *Bruguiera gymnorrhiza* (SS = 211) and *Ceriops tagal* (SS = 252) were not associated to any particular crab species. *Neosarmatium smithii* (SS = 386) was observed near *Rhizophora mucronata* trees (SS = 347), either in monospecific or mixed stands. *Sesarma guttatum* (SS = 351) was present in all sites and mostly over a wide range. However, like *N. smithii*, it seems to be associated with the *Rhizophora* zone. *Sesarma leptosoma* (SS = 374) was found less frequently and over a slightly smaller range than *S. guttatum*, but nevertheless in the same forest zones. *Sesarma leptosoma* was observed to climb the canopies of *Rhizophora mucronata* only. Also the crab *Metopograpsus thukuhar* (SS = 556) was observed less frequently and *Sesarma elongatum* (SS = 674) was only observed in Sita, both of them near creeklets. However, in the creeks near Dabaso these species were common in the *Rhizophora* zone. Only the distribution of *Neosarmatium meinerti* correlated with a restricted height above datum range (3 m and above).

### Discussion

The schematic site description and the vegetation data (Fig. 2) confirm the general zonation pattern of mangroves that exists along the Kenyan coast (Walter & Steiner, 1936; Gallin *et al.*, 1989). However, a new observation with respect to the species assemblages, of less importance here but of major importance in mangrove sustainable management and restoration frameworks, is the presence of *Ceriops tagal* in the understory of some *Rhizophora mucronata* dominated vegetation patches. Considering this, the importance lies in the fact that *R. mucronata* is a preferred species for house construction in Kenya (Dahdouh-Guebas *et al.*, 2000b), and that this harvested preferred species is therefore not necessarily the species that will regenerate. However, the variability in this zonation can be striking and earlier hypotheses that the height above datum is the determining factor in mangrove zonation (Walter & Steiner, 1936; Clarke & Hannon, 1970) or that tree species position along such a topographic gradient is a useful predictive tool (Watson, 1928) must be limited to their indicative value. Different floristic compositions in quadrats with a similar height above datum (Tab. 2), together with emersion curves for Kilindini (Mombasa) as published by Brakel (1982), show that some mangrove species can survive in areas with very different emersion times (6 to 12 hours per tidal cycle for *A. marina*, *C. tagal* and *R. mucronata*) and display disjunct zonation patterns with striking morphometric differences (*e.g. A. marina* in Gazi 'Covered'; Dahdouh-Guebas *et al.*, subm.d).

Similarly, the zonation of herbivorous crabs does not seem to be correlated with height above datum either. This is particularly well illustrated by the distribution of *Sesarma guttatum* and *Metopograpsus thukuhar*. The occurrence of the former varies from the landward zone (Sita), over the middle zone (Gazi 'Cleared') to the more seaward zones (Gazi 'Covered' and Mida). In Gazi 'Covered', Sita and Dabaso the abundance of *S. guttatum* does not increase or decrease gradually but instead jumps from many individuals and many burrows (coefficient 5, Fig. 2) to no individuals and no burrows (coefficient 0, Fig. 2). *Sesarma leptosoma* displays a true mangrove tree-dependence and has a typical vertical migrating behaviour – almost exclusively on *Rhizophora mucronata* - allowing them to feed on fresh leaves (Vannini & Ruwa, 1994; Cannicci *et al.*, 1996a, 1996b; Vannini *et al.*, 1997; personal observation).

The results from the ordination (Fig. 3) show that there is one main first axis explaining 23 % of the variability, possibly indicating that there must be one main responsible factor or set of factors for the observed distribution of tree and crab species. Mangrove tree species zonation has been correlated with different biotic and abiotic factors such as physiological adaptations to salinity and frequency of tidal inundation (Macnae, 1968), tidal flow and geomorphology (Thom, 1967), nutrient availability (Boto & Wellington, 1983), salinity of the soil (Naidoo, 1985), soil sulphide and redox levels (Hart, 1959; McKee, 1993; Matthijs *et al.*, 1999), competition between species (Ball, 1980; Clarke & Myerscough, 1993), tidal sorting of propagules (Rabinowitz, 1978a, 1978b; Clarke, 1993; Clarke & Myerscough, 1993), light availability to seedlings (Smith, 1987a) and predation of seedlings (Smith, 1987a, 1987b; Smith *et al.*, 1989; Osborne & Smith, 1990; Dahdouh-Guebas *et al.*, 1998). Clearly none of these hypotheses can be expected to adequately and solely account for the observed species distribution and it is clear that mangrove zonation is the result of a complex interaction between these different biotic and abiotic environmental factors. Therefore, most probably a complex multiple causality implying different factors underlie the first axis in the ordination (Fig. 3).

A possible causal relationship could be explained as a source of food for the crabs, whether direct or through mangrove-consuming intermediates, as source of protection among the mangrove root complex, as differentially beneficial conditions created by the root complex, such as oxygen conditions in the soil, soil compaction and consolidation, or, crabs and trees might simply require

similar environmental conditions, such as physico-chemical, tidal or edaphic conditions, restricting them to the same zones independently by a common cause. The results from the height above datum of species and the ordination results from our five sites (Fig. 3) suggest that the distribution of the crab species correlates better with the mangrove tree species present rather than with the height above datum, unlike Icely & Jones (1978) suggested for *Uca* species. However, on-going research by Ballerini *et al.* (2000) and Cannicci *et al.* (2000) reports no differential distribution in relation to mangrove tree species for sersarmid crabs within Mida Creek and suggests multivariate analysis to untangle the environmental factors such as temperature, salinity and soil granulometry that govern distribution of mangrove crabs.
The presence of the same crab species in *Ceriops tagal* and *Rhizophora mucronata* zones, as suggested in general for Kenyan mangroves by Ruwa (1997), must be rejected based on the results of this study.

The present study raises the question whether crabs influence the establishment of certain mangrove tree species. Lee (1998) recently reviewed the ecological roles that grapsid crabs play in mangrove ecosystems. One of the crabs' impacts is predation of mangrove propagules. A dominance-predation hypothesis was proposed by Smith (1987b), and confirmed by Smith *et al.* (1989) and Osborne & Smith (1990), who found an inverse relationship between seed predation and the dominance of a tree species in mangrove forest canopies. Although the above model was not supported for mangroves in Gazi Bay (Dahdouh-Guebas *et al.*, 1997), crabs and other propagule predators might still contribute to the establishment of the vegetation structure, rather than the zonation, of mangroves, and in turn be influenced by the mangrove's physical environment (*cf.* Lee, 1998, 1999) . Especially in mixed zones, but sometimes even in zones where one species is dominant, succession and future vegetation structure depends on the abundance and diversity of species : the species composition (and the dominance) in such a zone before and after a disturbance is not necessarily the same, but depends on the growing performance of the individuals in the understory and their competitive capacity. The investigation of a relationship between propagule predators and trees in mangroves in our opinion therefore necessitates an emphasis on the mixed nature or the assemblage where present, rather than the dominant species (*cf.* Walter & Steiner, 1936; Macnae, 1966).

## Acknowledgements

We would like to thank Prof. Dr P. Polk (VUB) and Prof. Dr M. Vannini (Università degli Studi di Firenze) for support, Dr E. Okemwa (Kenya Marine and Fisheries Research Institute) and Mrs. Y. Vermeulen (Kenya Belgium Project in Marine Sciences) for logistics in Kenya, and Mr. Francis Ayimba for field assistance. A lot of gratitude is due to all the local people, in particular family Ba'alawy from Gazi for being such a fine host family. Research financed by the Fund for Collective Fundamental Research (FKFO) and with a specialisation fellowship of the Flemish Institute for the advancement of scientific-technological research in the industry (IWT).

## References

See Bibliography

**Table 1.** Scale used to estimate the abundance of crab species based on both the frequency of individuals and burrows (see Fig. 2).

| **Coefficient** | **individual frequency ($m^{-2}$)** | **burrow frequency ($m^{-2}$)** |
|---|---|---|
| 0 | none | none |
| 1 | 1 individual | none |
| 2 | < 10 individuals | none |
| 3 | > 10 individuals | < 10 burrows |
| 4 | > 10 individuals | 10-20 burrows |
| 5 | > 10 individuals | > 20 burrows |

**Table 2.** Comparison of the adult vegetation type of different transects between quadrats with a similar height above datum.

| | Adult vegetation type in | | | | |
|---|---|---|---|---|---|
| **'Height above datum'-range** | **Gazi 'Covered'** | **Gazi 'Cleared'** | **Mida** | **Dabaso** | **Sita** |
| **2.60 – 3.10 m** | *C. tag. + B. gym. + X. gra. + A. mar* | *A. mar* | *A. mar.* | *A. mar* | *C. tag + A. mar + R. muc* |
| **2.10 – 2.60 m** | *C. tag. + B. gym. + R. muc. + A. mar* | *R. muc* | *A. mar* | *C. tag. + R. muc.* | no quadrat of similar height |
| **1.50 – 2.00 m** | *A. mar. + R. muc* | *R. muc + C. tag* | *A. mar + R. muc* | *R. muc* | *S. alb* |

*A. mar* = *Avicennia marina*, *B. gym* = *Bruguiera* gymnorrhiza, *C. tag* = *Ceriops tagal*, *R. muc* = *Rhizophora mucronata*, *S. alb* = *Sonneratia alba*, *X. gra* = *Xylocarpus granatum*.

**Figure 1.** Map of the Kenyan coast showing details of our study areas Gazi Bay and Mida Creek (adapted from Dahdouh-Guebas *et al.*, 2000b). On the Mida Creek map : Kir. = Kirepwe, Kis. = Kisiwani.

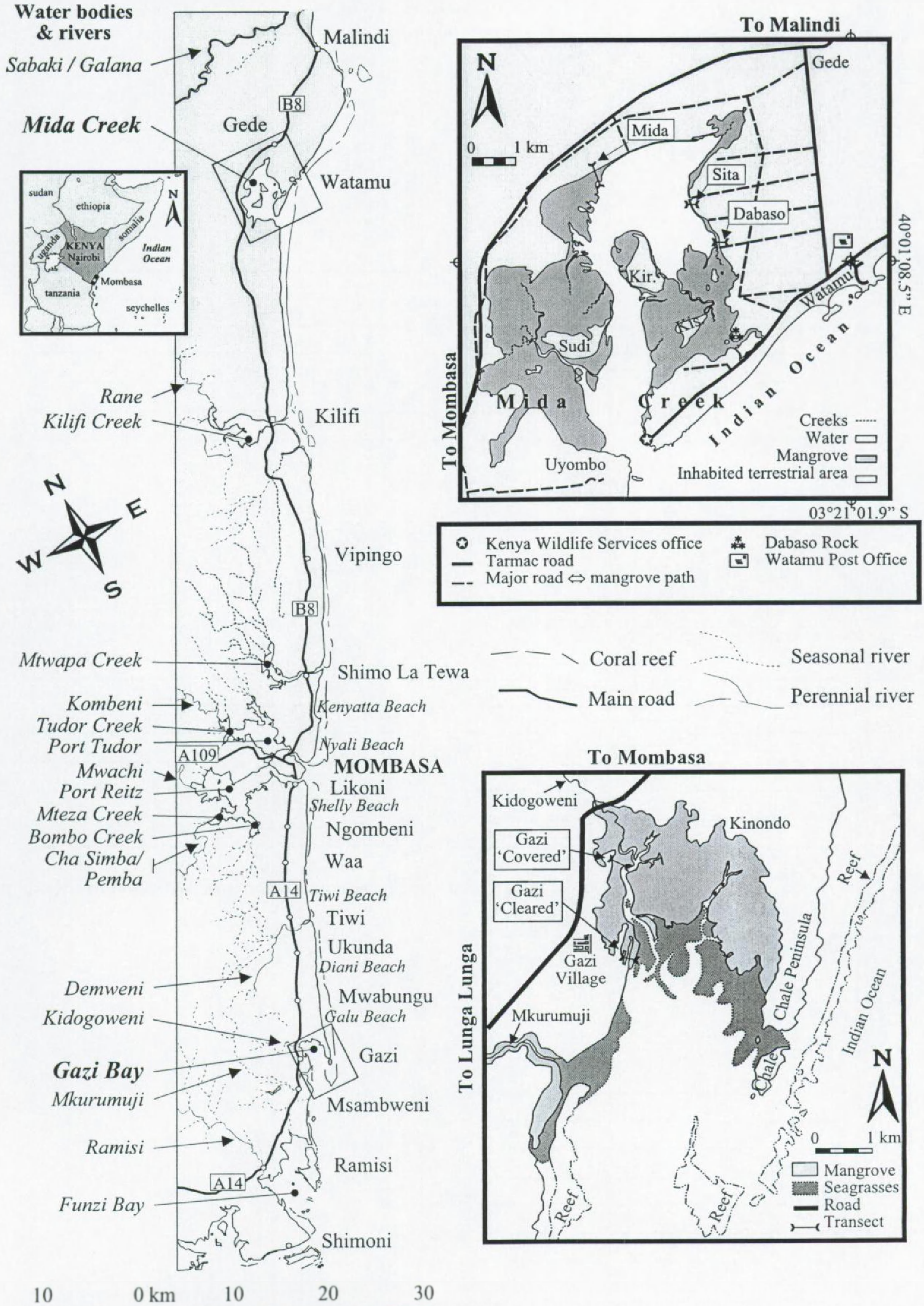


**Figure 2.** Topographic levels and schematic of the adult mangrove vegetation at the five study sites along the Kenyan coast. The distribution of the crabs along the transects is represented by the boxes on the lines and the abundance values, based on both the number of individuals and the number of burrows (as in table 1), are indicated within the boxes. *M. thu* = *Metopograpsus thukuhar*, *N. mei* = *Neosarmatium meinerti*, *N. smi* = *Neosarmatium smithii*, *S. gut* = *Sesarma guttatum*, *S. ort* = *Sesarma ortmanni*, *S. lep* = *Sesarma leptosoma* and *S. elo* = *Sesarma elongatum*.

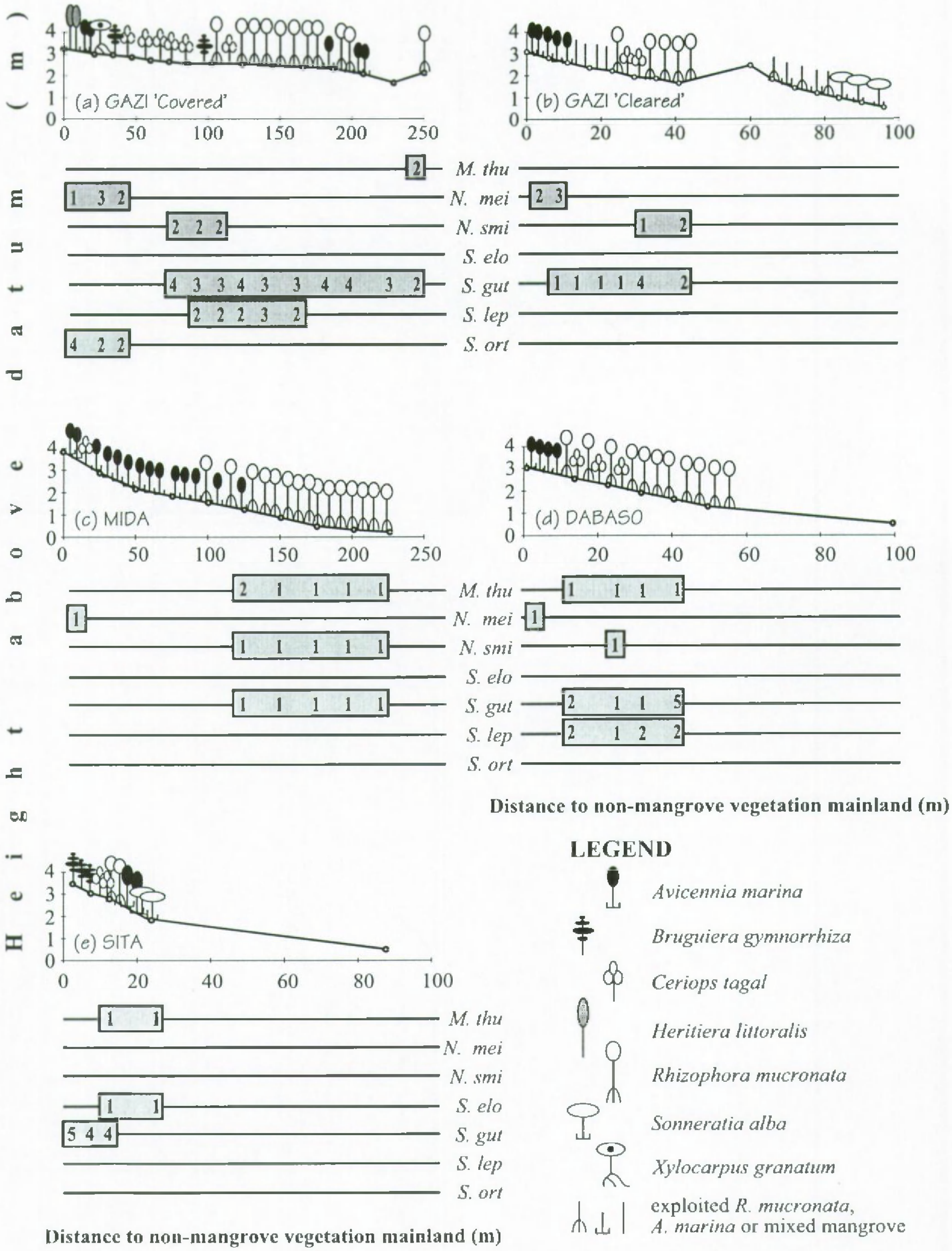
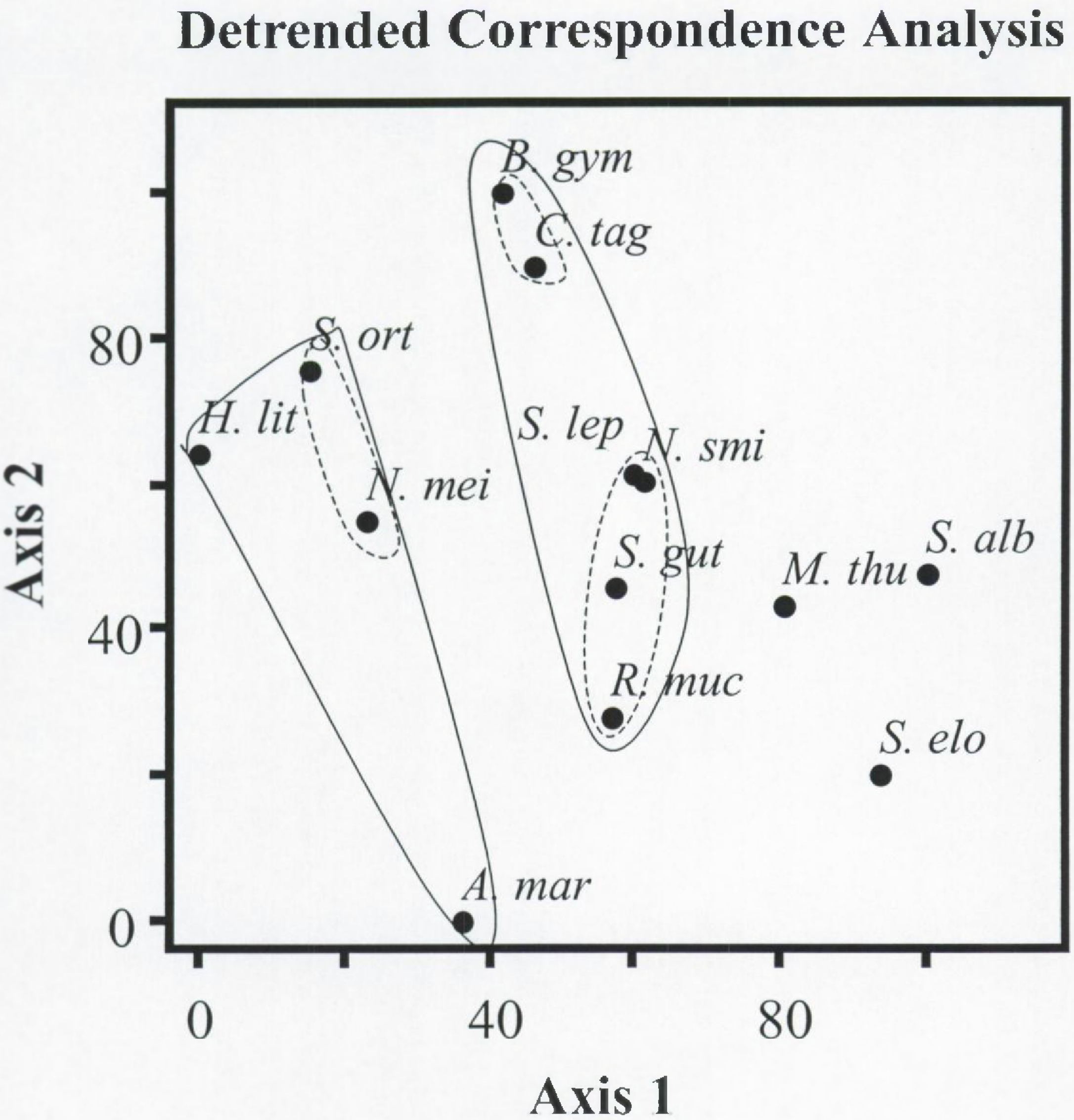


**Figure 3.** Results from the indirect species ordination (DCA) of the following presence/absence data in 43 sample points. Polygons, based on species scores with respect to the first axis, represent various degrees of species associations and were added to ease the visual interpretation. *A. mar = Avicennia marina, B. gym = Bruguiera gymnorrhiza, C. tag = Ceriops tagal, H. lit = Heritiera littoralis, R. muc = Rhizophora mucronata, S. alb = Sonneratia alba*, crab abbreviations as in figure 2.



# Chapter X.

## Propagule predators in Kenyan mangroves and their possible effect on regeneration.

Dahdouh-Guebas, F., M. Verneirt, J.F. Tack, D. Van Speybroeck & N. Koedam

Published in

*Marine and Freshwater Research* 49: 345-350

© CSIRO 1998 *Mar. Freshwater Res.*, 1998, **49**, 345–350

# Propagule predators in Kenyan mangroves and their possible effect on regeneration

F. Dahdouh-Guebas[A], M. Verneirt[A], J.F. Tack[B],
D. Van Speybroeck[C] and N. Koedam[A]

[A]*Laboratory of General Botany and Nature Management, Mangrove Management Group,*
*Vrije Universiteit Brussel, Pleinlaan 2, B-1050 Brussel, Belgium. email: fdahdouh@vub.ac.be*
[B]*Belgian National Science Foundation, c/o Laboratory of Ecology and Systematics, Mangrove Management Group,*
*Vrije Universiteit Brussel, Pleinlaan 2, B-1050 Brussel, Belgium.*
[C]*United Nations Environment Program, Coastal Resources Database and Atlas, PO Box 30552, Nairobi, Kenya.*

**Abstract.** Grapsid crabs can play a considerable role in the predation of mangrove propagules and possibly are a threat to the regeneration of mangroves, whether natural or artificial. Experiments consisting of artificial plantation of mangrove juveniles were set up in Gazi Bay (Kenya). Grapsid crabs, particularly *Neosarmatium meinerti* in the most landward fringe and *N. smithii* and *Sesarma guttatum* in the middle fringe of the mangrove forest, were found to be a regeneration-limiting factor. Almost 100% ($n = 40$) of the landward plantations were cleared. There was a slight initial preference for *Rhizophora* propagules lying horizontally on the mangrove floor, which simulates the position of a stranding propagule. In Mida Creek (Kenya) the snail *Terebralia palustris* was observed predating mangrove propagules. This study shows that crabs may affect the regeneration potential of mangroves, and snails might also be a factor in predation. A need to actively search for ways to protect re-afforestation plots from predators of mangrove tree juveniles is necessary.

*Extra keywords*: mangrove, regeneration, predation, crabs, *Terebralia palustris*, Kenya

## Introduction

Mangroves are a unique ecosystem with highly adapted plant species (facultative halophytes) thriving in the intertidal zone. In Kenya, mangrove tree species form more or less well defined zones (Walter and Steiner 1936; Macnae 1968; Chapman 1976; Ruwa and Polk 1986; Gallin *et al.* 1989; Gang and Agatsiva 1992; Ruwa 1990, 1993; Van Speybroeck 1992).

Several mangrove species have juveniles which further develop after fertilization when still on the parent tree, a phenomenon known as viviparity. When the propagule drops from the parent tree at low water, it can plant itself into the mud; this is termed the planting strategy (Van Speybroeck 1992). A second possibility is that the propagule falls in the water at high tide and then floats to another site where it settles and develops; this is termed the stranding strategy (Van Speybroeck 1992). Regeneration and colonization of a naked habitat is logically only possible by means of the stranding strategy. The planting strategy dominates in an undisturbed mangrove forest in Gazi Bay (Kenya), whereas the stranding strategy is dominant in an exploited and open forest (Van Speybroeck 1992).

Predation on mangrove juveniles can involve decapods (Smith 1987*a*, 1987*b*; Smith *et al.* 1989; Osborne and Smith 1990; Anon. 1991; McKee 1995; Dahdouh-Guebas *et al.* 1997; McGuinness 1997), snails (Smith *et al.* 1989; McKee 1995), insects (Robertson *et al.* 1990; Anon. 1991; Ellison and Farnsworth 1993), monkeys (Chan *et al.* 1984) and fish (Macnae 1969). Amongst these, predation by crabs or snails has been observed most frequently. This might be a threat, particularly to artificial regeneration plots in some mangrove areas, even though crabs are known to contribute to the dispersal of juveniles elsewhere (Thornton 1996).

It is important that the mangrove forest be maintained and that a sustainable management of this vegetation is pursued if there is a need for exploitation. The aim of this study is to assess crab pressure on mangrove propagule establishment in the light of restoration and regeneration of mangal ecosystems in Kenya. Preliminary data on gastropod pressure are also presented.

## Materials and methods

### *Site description*

The research was performed along the Kenyan coast in Gazi Bay (04°25'S,39°50'E), about 50 km south of Mombasa, and Mida Creek (03°20'S,40°00'E), about 100 km north of Mombasa (Fig. 1). Gazi Bay is a wide, open creek fed by two seasonal rivers. In contrast, Mida Creek has a very small opening to the ocean and is not fed by any overland fresh water. The field experiments were conducted from July to September 1993.

### *Predation by crabs*

Two transects were studied: one in an undisturbed mangrove area (250 m length), and one in a disturbed area (100 m). The disturbed area showed

1323-1650/98/040345

extensive gaps in the mangrove forest due to logging of the trees. Along each transect, 15 evenly dispersed quadrats of 5 × 5 m were outlined, the vegetation was described using the Braun-Blaquet relevé method, and in each plot 40 tagged mangrove juveniles were haphazardly planted. The proportion of the species reflected the actual proportions in the forest area and involved the species *Avicennia marina* (Forsk.) Vierh., *Bruguiera gymnorrhiza* (L.) Lam., *Ceriops tagal* (Perr.) C.B. Robinson, *Rhizophora mucronata* Lam., *Sonneratia alba* Sm. and *Xylocarpus granatum* Koen.; nomenclature according to Tomlinson (1986). Also, within each species 50% of the propagules planted represented the planting strategy (Van Speybroeck 1992), i.e vertical planting, and 50% were laid on the forest floor and tied with a nylon wire to a stick, simulating the stranding strategy.

The plantations in the disturbed and undisturbed area were regularly checked for 48 and 47 days respectively (usually at one-day intervals) and the juveniles were classified 'predated' according to one of the three possible ways proposed by Smith (1987*a*, 1987*b*): *(i)* the epicotyl was eaten, *(ii)* at least 50% of the hypocotyl was cut through, or *(iii)* the propagule was pulled into the burrow of a predator. Monitoring also involved visual observations of the crab fauna around the plantations at low tide.

Analyses of the data took into account the different zones of vegetation (order from landward to seaward side): for the undisturbed forest, *Avicennia* zone (plots 1 and 2; $n = 2$ plots), mixed zone (plots 3 and 4; $n = 2$), *Ceriops/Rhizophora* zone (plots 5 to 11; $n = 7$) and *Avicennia/Rhizophora/Sonneratia* zone (plots 12 to 15; $n = 4$); for the disturbed forest, *Avicennia* zone (plots 1 to 3; $n = 3$), *Ceriops/Rhizophora* zone (plots 4 to 9; $n = 6$), clear-cut zone (plots 10 to 12; $n = 3$) and *Avicennia/Rhizophora/Sonneratia* zone (plots 13 to 15; $n = 3$). Two-way analysis of variance (ANOVA unbalanced design) was used to compare propagule predation between the disturbed and undisturbed forest. Student's $t$-test was used to compare propagule loss by predation and by being washed away, propagule predation for horizontally and vertically placed juveniles, and propagule predation among species in each of the zones. Between-zone differences were investigated by one-way ANOVA.

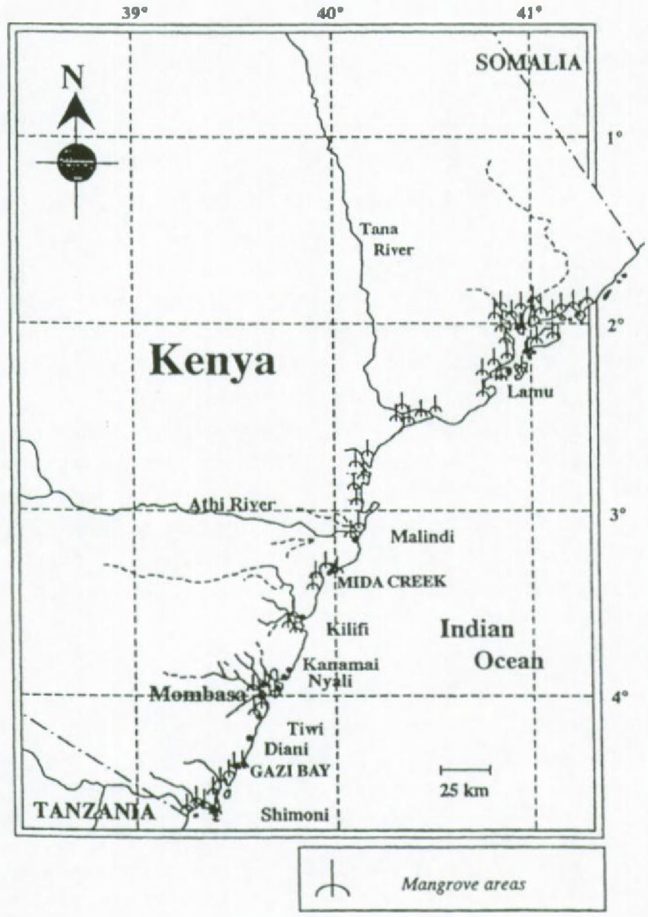


**Fig. 1.** Kenya coastline showing the mangrove areas (after Tack and Polk 1998). Study sites indicated in uppercase.

The dominance–predation hypothesis (Smith 1987*a*, 1987*b*) was tested for each mangrove species present in the undisturbed mangrove area; this hypothesis states that predation of propagules of a certain species is higher in areas where adult conspecifics are rare or absent than in those where adult conspecifics are dominant. To verify this, the point-biserial correlation coefficient $r_p$ test (Kent and Coker 1992) was performed on the data obtained after 13, 32 and 47 days of monitoring; this test is particularly appropriate in situations where one variable is in presence/absence or binary form (here 'dominance of adult trees') while the other variable is continuous (here 'predation intensity').

### *Predation by gastropods*

In Mida Creek the snail *Terebralia palustris* L. is present in large numbers and was observed preying on mangrove propagules. Therefore, a preliminary experiment was designed to investigate the impact of this gastropod on the propagule-producing mangrove species present: *Bruguiera gymnorrhiza*, *Ceriops tagal* and *Rhizophora mucronata*. In total, 33 propagules (9, 12 and 12 respectively) were planted in a plot in the mangrove forest and monitored for three days. For the first 5 h, the propagules were photographed at 1-h intervals. The experiment was repeated with 33 peeled propagules.

## Results

### *Predation by crabs*

Both in the disturbed and the undisturbed area, predation and washing away occurred (Fig. 2).

In the disturbed area propagule loss was high in three segments along the transect: propagules were washed away in the seaward section and predated in the other two segments (Fig. 2*a*). The same two predation segments could be recognized in the undisturbed area (Fig. 2*b*); in one, the crab *Neosarmatium meinerti* de Man was present and in the other the crabs *Neosarmatium smithii* H. Milne-Edwards and *Sesarma guttatum* A. Milne-Edwards were present. In the plots where predation was heavy (plots 1, 2 and 6 in Fig. 2*a*; plots 2, 3 and 7 in Fig. 2*b*), for both the disturbed and undisturbed mangrove area, the plateau in the rate of predation (Fig. 3*a* and Fig. 3*b* respectively) was reached within 10 days after the propagules were planted. In one of the plots in the disturbed area, predation was already 80% within 2 days (Fig. 3*a*). The juvenile mangrove trees survived if they reached 25 days after plantation, i.e. no more juveniles were predated. *Rhizophora mucronata* was the only species for which there existed a significant difference between horizontally and vertically placed propagules after 14 days ($r_p = 0.42$ ; $t = 2.43$ ; $P < 0.05$). However, this was only the case for the transect in the undisturbed mangrove area, and after 23 days no significant

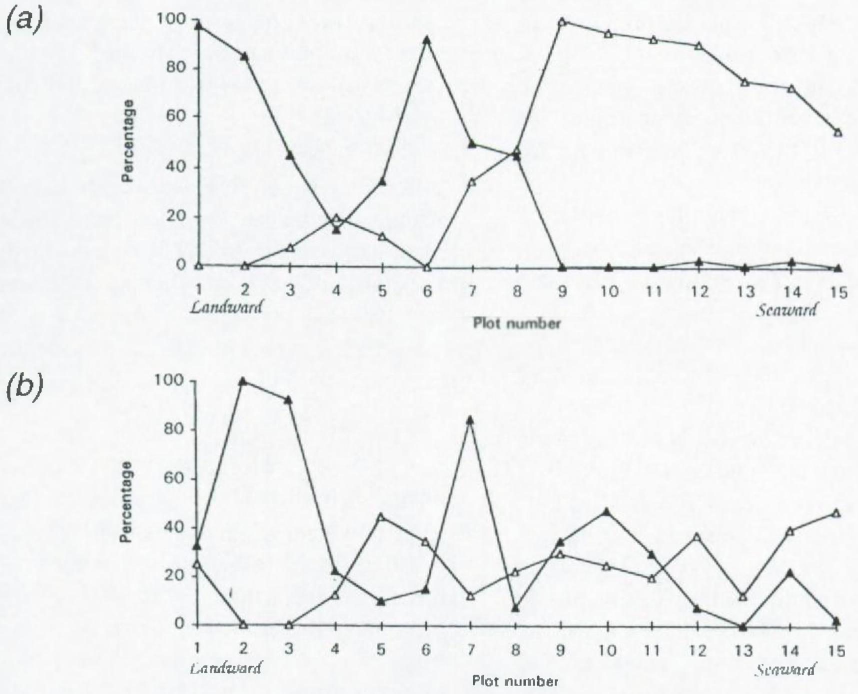


**Fig. 2.** Propagule loss (%) due to washing away and predation in *(a)* disturbed and *(b)* undisturbed mangrove forest after 48 and 47 days of monitoring respectively (Gazi Bay): △, washed away; ▲, predated.

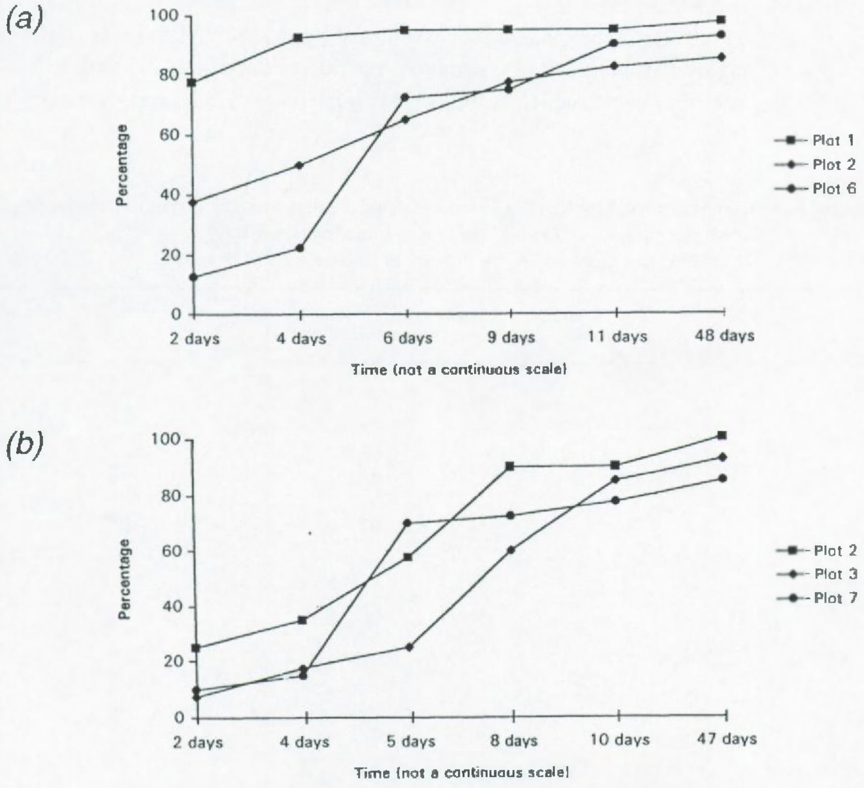


**Fig. 3.** Rate of predation in the plots with high propagule loss due to predation (Fig. 2) in *(a)* disturbed and *(b)* undisturbed mangrove forest (Gazi Bay).

difference was observed. Visual observations have pointed out that crabs may drag a horizontally placed propagule to their burrows before eating it, whereas predation on vertical propagules often occurred on the surface where the propagules were planted. However, when competition was too high the crabs tried to lift the propagule out of the substratum and drag it away.

In tests of the dominance–predation hypothesis, predation of propagules of a particular mangrove species was not correlated with the presence of an adult tree of the same species in one plot. The only exception was predation on *Rhizophora mucronata*. However, even for this species the correlation was only significant for the observations after 32 days ($r_p = 1.77$ ; $t = 2.27$ ; $P < 0.05$).

The ANOVA for the comparison between propagule predation in the disturbed and undisturbed forest showed that there is no difference between them ($F = 0.11$, d.f. 1; n.s.). Statistics for the comparison between propagule loss by predation and by being washed away and between propagule predation of horizontally and vertically placed juveniles have been summarized in Table 1. The significant differences between predation and washing away in each of the zones in the disturbed forest (Table 1*a*) indicate that it is either washing away or predation which is the main cause for propagule loss rather than a combination of the two. This can also be observed from Fig. 2*a*. As could have been expected already from Fig. 1*b*, the above-mentioned difference is not found in the undisturbed forest, but for the most seaward zone (Table 1*a*), and between-zone differences are absent. The global propagule loss is thus due to a synergism between predation and washing away, which is similar throughout the different zones, with some exceptions (Fig. 2*b*). None of the tests comparing propagule predation among species showed significant differences within any of the zones (results not shown).

*Predation by gastropods*

After 3 days, one *B. gymnorrhiza* and four *R. mucronata* propagules had been predated from the total of 33. The predation pressure in Mida Creek was clearly lower than that of the crabs in Gazi Bay. When the experiment was repeated with 33 peeled propagules, six propagules of each of the three species were predated, this representing a total predation of 54% (Table 2).

## Discussion

In the disturbed mangrove area in Gazi Bay, the high disappearance rate of juveniles from the seaward section due to washing away (Fig. 2*a*) was expected, since they were exposed to wave action.

In plot number 1, which was in a landward zone dominated by *Neosarmatium meinerti*, the rapid predation by this sesarmid crab (Dahdouh-Guebas *et al.* 1997) is confirmed. Dahdouh-Guebas *et al.* (1997) observed a 50% propagule clearance in less than 2 h and 85% after 24 h in plots where almost full elimination of propagules occurred. The initial significant difference in predation for horizontal and vertical *Rhizophora* propagules in the present study can be explained by the weight and size of the propagules which make vertically planted ones difficult to handle for the crabs. Once the horizontal lying propagules are cleared the crabs

**Table 1. Differences *(a)* in propagule loss for predation and for being washed away and *(b)* in propagule predation between horizontal and vertical placed juveniles, after 32 or 34 days of monitoring (Gazi Bay)**

Refer to 'Materials and methods' for the number of plots in each of the zones

| Source of variation | Undisturbed forest | | | Disturbed forest | | |
|---|---|---|---|---|---|---|
| | *t* | d.f. | *P* | *t* | d.f. | *P* |
| *(a)* predated *v.* washed away | | | | | | |
| *Avicennia* zone | 1.043 | 2 | n.s. | 4.743 | 4 | < 0.01 |
| Mixed zone | 1.624 | 2 | n.s. | – | – | – |
| *Ceriops/Rhizophora* zone | 0.785 | 12 | n.s. | 3.172 | 10 | < 0.01 |
| Clearcut zone | – | – | – | 64.086 | 4 | < 0.01 |
| *Avicennia/Rhizophora/Sonneratia* zone | 3.334 | 6 | < 0.02 | 10.505 | 4 | < 0.01 |
| Predation between zones | $F = 2.69$, d.f. 3, n.s. | | | $F = 8.38$, d.f. 3, $P < 0.005$ | | |
| Washing away between zones | $F = 2.81$, d.f. 3, n.s. | | | $F = 54.83$, d.f. 3, $P < 0.001$ | | |
| *(b)* horizontal *v.* vertical | | | | | | |
| *Avicennia* zone | 0.447 | 2 | n.s. | 0.177 | 4 | n.s. |
| Mixed zone | 1.193 | 2 | n.s. | – | – | – |
| *Ceriops/Rhizophora* zone | 0.753 | 12 | n.s. | 0.61 | 10 | n.s. |
| Clearcut zone | – | – | – | 0 | 4 | n.s. |
| *Avicennia/Rhizophora/Sonneratia* zone | 1 | 6 | n.s. | 1 | 4 | n.s. |
| Horizontal propagules between zones | $F = 5.81$, d.f. 3, $P < 0.01$ | | | $F = 5.76$, d.f. 3, $P < 0.01$ | | |
| Vertical propagules between zones | $F = 1.3$, d.f. 3, n.s. | | | $F = 3.6$, d.f. 3, $P < 0.025$ | | |

**Table 2. Preliminary observations of the cumulative number of propagules predated by snails after 1, 2 and 3 days (Mida Creek)**

| Species | Unpeeled propagules ($n$ = 33) | | | Peeled propagules ($n$ = 33) | | |
|---|---|---|---|---|---|---|
| | Day 1 | Day 2 | Day 3 | Day 1 | Day 2 | Day 3 |
| *Rhizophora mucronata* | 0 | 3 | 4 | 6 | 6 | 6 |
| *Bruguiera gymnorrhiza* | 0 | 1 | 1 | 3 | 5 | 6 |
| *Ceriops tagal* | 0 | 0 | 0 | 1 | 4 | 6 |

can switch to the vertical planted ones. Between-zone differences are probably due to differences in predator abundance in each of the zones; in zones where propagule predators are abundant, significant differences between the predation of horizontal and vertical propagules would be less likely since high competition results in a quick clearing of the experimental plantation. This can also explain why in the undisturbed forest there is a significant difference in predation on horizontal propagules between the zones, due to different predator abundances, whereas there is none for the vertical propagules (Table 1*b*), because predators are not excessively abundant in the undisturbed forest or they have more background input (non-experimental) from stranding propagules. Although absence of specificity in feeding behaviour was observed before (Dahdouh-Guebas *et al.* 1997), the lack of significance for the differences on the predation among species in the present study may be due to the small sample sizes.

The dominance–predation hypothesis cannot be supported in the present study, since predation levels in forest plots where certain adult mangrove tree species are dominant are not significantly different from the predation levels in forest plots where the trees do not occur. McGuinness (1997) has come to similar conclusions when investigating seed predation in a northern Australian mangrove forest. One may assume that under natural conditions a sufficient number of tree juveniles escapes predation. However, in artificial regeneration plots predation is a serious threat. An alternative hypothesis to explain how mangrove trees could overcome high predation rates follows from a personal observation on *Ceriops tagal* in Gazi Bay. Observations of over 500 mature propagules per tree at one time suggest that in natural conditions this mangrove tree might saturate the crabs by dropping a large number of propagules in a short period. Hence, the saturation method is a possible way to protect artificial regeneration plots. In Sulawesi, although standard re-afforestation methods require less dense plantation (50-cm intervals) the people prefer dense plantation (25-cm intervals) of *Rhizophora mucronata* in order to saturate predators (Weinstock 1994). Knowledge about the zones in which predation is highest (this study), particularly in a disturbed forest which may need artificial regeneration, and about the abundances of crabs in the different zones (the subject of further studies) will improve the choice of location for artificial plantations and their survival.

In Mida Creek the difference between peeled and unpeeled propagules in degree of predation by snails might suggest a possible toxicity, unpalatability or presence of an antinutritional factor in the peel. However, further research is required to investigate an actual preference as was observed for crabs (Dahdouh-Guebas *et al.* 1997). Although this study is preliminary, it suggests that crabs may not be the only invertebrates preying on mangrove propagules in Kenya and affecting their survival.

The effect of predation on natural regeneration in Kenya cannot yet be ascertained. Understanding the links between the zonation of brachyuran predators and the zonation of the mangrove tree species is a necessary step in understanding their ecological interactions.

## Acknowledgments

We thank the people from the Kenya Belgium Project and the Kenyan Marine and Fisheries Research Institute for logistic support, Professor Dr M. Vannini and Dr S. Cannicci from the Università degli Studi di Firenze (Italy) for the initial field training and preliminary experiments. Mr J. G. Kairo and F. Ayimba from the University of Nairobi are thanked for practical help in the field. Gratitude is due to all the people of Gazi, in particular family Ba'alawy. Research was financed by the Fund for Collective Fundamental Research (FKFO) and with a specialization fellowship of the Flemish Institute for the advancement of scientific–technological research in industry (IWT).

## References

**Anon.** (1991). UNDP/UNESCO Regional Project—Research and its application to the management of mangroves of Asia and the Pacific (RAS/86/120). In cooperation with the National Mangrove Committee of the National Research Council of Thailand. Bangkok, Thailand.

**Chan, H. T., Ujang, R., and Putz, F. E.** (1984). A preliminary study on the planting of *Rhizophora* species in an *Avicennia* forest at the Matang mangroves. In 'Prosiding Seminar II Ekosistem Mangrove'. (Ed. S. Soemodihardjo.) pp. 340–5. (Lembagu Ilmu Pengetahuan: Jakarta, Indonesia.)

**Chapman, V. J.** (1976). 'Mangrove Vegetation.' (J. Kramer: Vaduz, Liechtenstein.)

**Dahdouh-Guebas, F., Verneirt, M., Tack, J. F., and Koedam, N.** (1997). Food preferences of *Neosarmatium meinerti* de Man (Decapoda : Sesarminae) and its possible effect on the regeneration of mangroves. *Hydrobiologia* **347**, 83–9.

**Ellison, A. M., and Farnsworth, E. J.** (1993). Seedling survivorship, growth, and response to disturbance in Belizean mangal. *American Journal of Botany* **80**(10), 1137–45.

**Gallin, E., Coppejans, E., and Beeckman, H.** (1989). The mangrove vegetation of Gazi Bay (Kenya). *Bulletin de la Société Royal Botanique de Belgique* **122**, 197–209.

**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.

**Kent, M., and Coker, P.** (1992). 'Vegetation Description and Analysis. A Practical Approach.' (John Wiley: Chichester, UK.)

**Macnae, W.** (1968). A general account of the fauna and flora of mangrove swamps and forests in the Indo West Pacific region. *Advances in Marine Biology* **6**, 73–270.

**Macnae, W.** (1969). Zonation within mangroves associated with estuaries in north Queensland. In 'Estuaries'. (Ed. G. E. Lauff.) pp. 432–41. (American Association for the Advancement of Science: Washington DC.)

**McGuinness, K. A.** (1997). Seed predation in a tropical mangrove forest: a test of the dominance-predation model in northern Australia. *Journal of Tropical Ecology* **13**, 293–302.

**McKee, K. L.** (1995). Mangrove species distribution and propagule predation in Belize: an exception to the dominance-predation hypothesis. *Biotropica* **27**(3), 334–45.

**Osborne, K., and Smith, T. J.** (1990). Differential predation on mangrove propagules in open and closed canopy forest habitats. *Vegetatio* **89**,1–6.

**Robertson, A. I., Giddins, R., and Smith, T. J.** (1990). Seed predation by insects in tropical mangrove forests: extent and effect on seed viability and the growth of seedlings. *Oecologia* **83**, 213–19.

**Ruwa, R. K.** (1990). The effects of habitat complexities created by mangroves on macrofaunal composition in brackishwater intertidal zones at the Kenyan coast. *Discoveries and Innovation* **2**(1), March, 49–55.

**Ruwa, R. K.** (1993). Zonation and distribution of creek and fringe mangroves in the semi-arid Kenyan coast. In 'Towards the Rational Use of High Salinity Tolerant Plants'. (Eds H. Lieth and A. Al Masoons.) pp. 97–105. (Kluwer: Dordrecht.)

**Ruwa, R. K., and Polk, P.** (1986). Additional information on mangrove distribution in Kenya: some observations and remarks. *Kenya Journal of Science Series* B **7**(2),41–5.

**Smith, T. J.** (1987*a*). Effects of seed predators and light level on the distribution of *Avicennia marina* Forsk. in tropical tidal forests. *Estuarine Coastal Shelf Science* **25**(1), 43–52.

**Smith, T. J.** (1987*b*). Seed predation in relation to tree dominance and distribution in mangrove forest. *Ecology* **68**, 266–73.

**Smith, T. J., Chan, H. T., McIvor, C. C., and Robblee, M. B.** (1989). Comparisons of seed predation in tropical, tidal forests from three continents. *Ecology* **70**, 146–51.

**Tack, J. F., and Polk, P.** (1998). The influence of tropical catchments upon the coastal zone: modelling the links between groundwater and mangrove losses in Kenya, India and Florida. In 'The Sustainable Management of Tropical Catchments'. (Eds D. Harper and T. Brown.) (John Wiley: London, UK.)

**Thornton, I. W. B.** (1996). 'Krakatau: the Destruction and Reassembly of an Island Ecosystem.' (Harvard University Press: Cambridge, USA.)

**Tomlinson, P. B.** (1986). 'The Botany of Mangroves.' Cambridge Tropical Biology Series. (Cambridge University Press: Cambridge, New York.) p. 419.

**Van Speybroeck, D.** (1992). Regeneration strategy of mangroves along the Kenyan coast. *Hydrobiologia* **247**, 243-51.

**Walter, H., and Steiner, M.** (1936). The ecology of East African mangroves. *Zeitschrift für Botanik* **30**, 65–193.

**Weinstock, J. A.** (1994). *Rhizophora* mangrove agroforestry. *Economic Botany* **48**(2) 210–13.

Manuscript received 24 June 1997; revised 10 June 1998; accepted 6 July 1998

# Chapter XI.

## Propagule predation in Sri Lankan mangroves and its effect on vegetation structure.

Dahdouh-Guebas, F.

Engaged in a peer-review process

# Propagule predation in Sri Lankan mangroves and its effect on vegetation structure.

Dahdouh-Guebas, F.

*Laboratory of General Botany and Nature Management, Mangrove Management Group, Vrije Universiteit Brussel, Pleinlaan 2, B-1050 Brussels, Belgium, fdahdouh@vub.ac.be.*

**Abstract**

In mangrove forests characterised by zonation or that display a topographic slope with lower and upper intertidal areas, propagule predation has been highlighted as one of the hypotheses leading to the zonation present (dominance-predation hypothesis). In this paper, propagule predation was investigated in mangroves, where such zonation characteristics are absent, and related to data on vegetation structure.

In two sites (Galle-Unawatuna and Pambala-Kakapalliya, Sri Lanka), known to comprise forest patches dominated by different species as detected from aerial photographs (*Avicennia officinalis*, *Excoecaria agallocha*, *Lumnitzera racemosa*, *Rhizophora* spp., a Mixed and an Open Space), the predation of propagules from *A. officinalis*, *Bruguiera gymnorrhiza*, *Rhizophora apiculata* and *R. mucronata* was monitored in a total of 24 experimental plots, and within and between species and forest patches differences were compared. Influences from environmental factors (salinity, topography, water level) as well as from seasons were investigated. Predation by crabs, snails, insects and mammals was observed, and a significantly higher predation by crabs on *A. officinalis* than on other mangroves species was recorded, which did however not corroborate the dominance-predation hypothesis. Results also show a higher predation in *A. officinalis* and *E. agallocha* forest patches and in the Open Space, and in Galle as compared to Pambala. Many of the observed differences could be explained directly by propagule predator identity and abundance, and a theory on the control of propagule predation and dispersal by water level is introduced.

This study shows that in mangroves, where no continuous topographic slope or a conspicuous gradient in vegetation is present, propagule predators, in particular crabs and snails, also play a role in the shaping of the vegetation structure, but not necessarily through a dominance-predation relationship only.

Keywords : crab, dominance-predation hypothesis, gastropod, mangal, Sri Lanka.

## Introduction

The study of propagule predation in mangrove forests often tests a model explaining the zonation of mangroves based on predation in relation to tree dominance, known as the dominance-predation hypothesis proposed by Smith (1987a). Recent testing of this hypothesis along the Australia North coast (McGuinness, 1997b), in Malaysia (Smith *et al.*, 1989), in Kenya (Dahdouh-Guebas *et al.*, 1997, 1998), in Belize (McKee, 1995a), in Florida (Smith *et al.*, 1989), in Panama (*loc. cit.*) and in the Federated States of Micronesia (Allen *et al.*, in prep.) have all concentrated on zoned mangroves or which display a topographic slope between lower and upper intertidal areas. Results of some of these studies have indicated validity of the dominance-predation hypothesis (Smith *et al.*, 1989) whereas other studies its inapplicability (*e.g.* McKee, 1995a), raising questions for instance on the importance of crabs in mangroves (Smith *et al.*, 1991) or on the role played by propagule predators in the regeneration of mangroves (*e.g.* Siddiqi, 1995) or in the shaping the vegetation structure (Dahdouh-Guebas *et al.*, subm.c).

The objective of the present paper is, first, to investigate the phenomenon of propagule predation in mangroves with neither a topographic slope between upper and lower intertidal areas or a conspicuous gradient in vegetation, and, second, to explain the observations using environmental data as well as data with respect to vegetation structure. The validity of the dominance-predation hypothesis is explored and a new hypothesis on the establishment of the vegetation structure of mangroves is introduced.

## Material & Methods

### *Description of the study sites*

Two mangrove forests were investigated in Sri Lanka, along the Southwestern side of the island, where the spring tidal amplitude is less than 1 m (Spalding *et al.*, 1997), but locally rarely exceeds 15 cm in the course of one week (< 16 % of the time; personal measurements 1997-1999).

The first mangrove forest is located between Galle and Unawatuna (06°01'N - 80°14'E), in the wet climate zone of Sri Lanka (Mueller-Dombois, 1968; Fig. 1) and had a mean annual rainfall of 2379 mm over the last 50 years. This basin and riverine mangrove type (Lugo & 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, namely the Thalpe Ela, discharging into the ocean, and the Galu Ganga, a tributary of the former. The vegetation structure of the mangrove in Galle has been investigated in detail by Verheyden *et al.* (subm.) and Dahdouh-Guebas *et al.* (2000a), and comprises three distinct patches (a vegetation 'patch' is here defined as a ploygon with no determined shape or area and having a certain, often monospecific floristic composition) : one dominated by *Excoecaria agallocha* L., one dominated by *Rhizophora apiculata* Bl. (hereafter referred to as the zone dominated by *Rhizophora* spp. to allow comparison with the second mangrove site; see below) and an 'Open Space' in which the herb layer is dominated by *Fimbristylis salbundia* (Nees) Kunth subsp. *pentaptera* (Nees) T. Koyama. The mangrove forest in Galle has been subjected to anthropogenic influence over the last 50 years (Dahdouh-Guebas *et al.*, 2000a), the major one of which was the construction of a raised path through the mangrove as well as a dam on the Galu Ganga near its point of dicharge into the Thalpe Ela.

The second mangrove forest is located in the Pambala area of Chilaw Lagoon, located in Sri Lanka's intermediate climate zone (Mueller-Dombois, 1968), and had a mean annual rainfall of 1443 mm over the last 50 years. The mangroves here are of the fringe type (Lugo & Snedaker, 1974), and have a rather irregular distribution along a complex of creeks (Marambettiya Ela, Bate Ela, Pol Ela and Dutch Channel). Most freshwater influx stems 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). This site is known to be the most species diverse in South-Western Sri Lanka (Jayatissa *et al.*, subm.; Dahdouh-Guebas *et al.*, in prep.d). The vegetation structure of this mangrove forest has been studied in detail by Zetterström (1998), Verheyden *et al.* (subm.) and Dahdouh-Guebas (unpublished results), and comprises five distinct patches : one dominated by *Avicennia officinalis* L., one dominated by *E. agallocha*, one dominated by *Lumnitzera racemosa* Willd., one dominated by *Rhizophora mucronata* Lam. and *R. apiculata* (hereafter referred to as the zone dominated by *Rhizophora* spp.), and a 'Mixed' zone comprising *E. agallocha, L. racemosa, Heritiera littoralis* Dryand. and *Xylocarpus granatum* Koen. Other common species in Pambala, although never dominant or co-dominant, are *Bruguiera gymnorrhiza* (L.) Lam. and *B. sexangula* (Lour.) Poir. Occasionally *Aegiceras corniculatum* (L.) Blanco was observed. To a small extent some of the patches in Pambala could be regarded as constituting a semi-zonation (a vegetation 'zone' is then defined as a long band-like patch of vegetation with a certain, often monospecific floristic composition). The mangrove in Chilaw Lagoon has recently been subjected to strong anthropogenic influences such as clearing and pollution as a result of shrimp farming (Foell *et al.*, 1999; Dahdouh-Guebas *et al.*, 2000c).

In both mangrove forests there was no slope with upper or lower intertidal areas, but rather a plateau with water pools, the latter of which are many in Galle and few in Pambala. None of the forest patches or zones was isolated and inhibiting the natural input of propagules from elsewhere. Mangrove nomenclature follows Tomlinson (1986).

## Methodology

After exploratory experiments done in Galle in March 1998 (dry season), the main fieldwork expedition in Galle and Pambala was organised from October till December 1999 (wet season). In each of the vegetation assemblages outlined above, three predation plots of 5 m x 5 m were established. Within each plot a number of propagules of different species, in proportions reflecting the availability of propagules in the entire forest at the time of propagule collection, were tethered to plants or immobile debris using strong Ariadne twine. All propagules collected were mature and gathered fresh from the tree, except for *R. mucronata*. Propagules of the latter were not available in sufficient quantities fresh, and were therefore collected from the mangrove floor and from natural ponds instead, provided they did not show signs of decay, damage, predation or rooting. In Galle a single plot counted 10 propagules of *B. gymnorrhiza* and 10 of *R. apiculata*, whereas in Pambala it comprised 10 propagules of *A. officinalis*, 10 of *B. gymnorrhiza*, 5 of *R. apiculata* and 15 of *R. mucronata*. During the exploratory experiments carried out in Galle in 1998 only *B. gymnorrhiza* propagules were available and 20 of them were used per plot.

Every day (in Galle) or every other day (in Pambala), depending on the area of the study site, the plots were visited and the predation status was recorded for each of the propagules. Propagules were classified as 'predated' in any of the three cases defined by Smith (1987a, 1987b) : when the epicotyl was eaten, when at least 50 % of the hypocotyl was cut through or when the propagule was pulled into the burrow of a predator. If less than 50 % of the hypocotyl was cut through, the propagule was classified as 'damaged', whereas in all other cases it was classified as 'intact'. In a few cases the propagule had disappeared and was recorded as 'lost'. The experiment was ended when all the propagules were predated or when the frequency of propagules within each predation class had levelled off (*i.e.* after two weeks).

Two control experiments were established in order to check for the effect of freshness (do propagules from pools grow better than freshly gathered ones ?) and of predator damage (do intact propagules grow better than damaged ones ?) on the growth performance. For the former, 44 *R. mucronata* propagules, 22 freshly gathered and 22 taken from the mangrove soil and water ponds, were planted, and both the predation and development status were checked daily for two weeks, but the experiment revealed significant differences neither in predation effects between the two groups ($\chi^2 = 0.153$; d.f. = 1; n.s.) nor in growth performance (G = 10.561; d.f. = 6; n.s.). Similarly, the effect of predator damage was investigated by assessing 14 undamaged and 13 damaged *R. apiculata* propagules planted. The 'damaged' propagules were able to further develop just like 'intact' propagules (G = 2.482; d.f. = 4; n.s.; control experiment). Considering the absence of tidal effects or people in our plots, the 'lost' propagules were most probably 'predated' by stronger animals that were able to break the twine and take away the propagule. In addition not many propagules were 'damaged' or 'lost' (< 4 % and < 10 % of all species in all sites respectively). For this ecological and statistical reason respectively, the classes 'intact' and 'damaged' and the classes 'predated' and 'lost' were also tested combined during the statistical analysis. In Pambala, also *R. mucronata* and *R. apiculata* propagules formed a homogeneous entity for data on predation ($\chi^2 = 0.243$; d.f. = 1; n.s.; after 13 days) and were therefore combined in the further analysis on the predation status and referred to as *Rhizophora* spp. propagules.

In each of the forest patches between 13 and 64 points (depending on the size of the patch) were sampled for salinity (using an Atago refractometer), light intensity (using a Lutron luxmeter), land/water ratio (visual estimation), crab burrow density and density of the snail *Terebralia palustris* L. For the density of crab burrows, only burrows larger than 3 cm, and belonging to crabs likely to be propagule predators, were considered after reconnaissance surveys on the crabs' behaviour. During these reconnaissance surveys also other propagule predators were observed.

Rainfall data for Galle and Chilaw were available from the Meteorological Department in Colombo, and in addition the water level of the lagoon in Pambala was recorded daily from a fixed scale at the Mangrove Conservation and Demonstration Centre of the Small Fishers Federation of Lanka (SFFL). Use of these date-dependent variables was done taking into account the different starting dates for the experiments in the different forest patches. Information with respect to the past and present changes in the mangrove forest and with respect to adult, young and juvenile vegetation data (densities, frequencies, basal area, cover, etc.) were taken from published and unpublished studies done between 1997 and 1999 (Zetterström, 1998; Dahdouh-Guebas *et al.*, 2000a; Dahdouh-Guebas *et al.*, 2000c; Verheyden *et al.*, subm.; Dahdouh-Guebas *et al.*, in prep.d; Dahdouh-Guebas, unpublished results) and used where appropriate to visualise the link between propagule predation and the vegetation structure and its dynamics. The validity of the dominance-predation hypothesis (Smith, 1987a, 1987b) was tested for the species in the present study, but rather than only purely based on basal area, the dominance is reflected here by the importance value of Curtis (1959), which is based on measurements of density, frequency and basal area. These data were taken from Dahdouh-Guebas *et al.* (2000a) and measured or calculated as described therein.

Although *E. agallocha* is ubiquitous as a (co)dominant species, its litter was never observed to be consumed locally by the propagule predators present and it has small seeds instead of propagules like the other species, and was therefore not included in this study.

Statistical analyses using the $\chi^2$-test and the G-test (Sokal & Rohlf, 1981) were performed on the propagule predation classes for each day of observation on each of the following levels (in the results numbers between parenthesis refer to the statistical data in table 1) :

- between the three replicates within a particular species and within a particular forest patch (to justify whether the data for that species could be combined into one analysis for that forest patch and thus represented as one graph);
- between the different species within a particular forest patch;
- between the different forest patches within a particular species;

- between the *Excoecaria agallocha* forest patch of Galle and Pambala within *B. gymnorrhiza* and *Rhizophora* spp. species, and the same between the *Rhizophora* spp. forest patch in both sites.
- between the wet and the dry season (only applicable to *B. gymnorrhiza* in Galle).

The use of analysis of variance on the above data would violate some of the statistical assumptions made in these tests, since the data are structured in classes, and values are rather low.

## Results

### *Herbivores and predators*

In Galle, the predominant grapsid crab is cf. *Chiromantes bidens* Rathbun, but also *Neosarmatium meinerti* De Man is present, whereas in Pambala it is *N. meinerti*. Where present, these species usually occur in places with a rather high elevation, such as the *E. agallocha* patches, or the *Rhizophora* spp. forest patch in Galle, where the topography is raised by the burrowing activities of the mangrove mud lobster *Thalassina anomala* Herbst. *Cardisoma carnifex* Herbst was observed in Galle along the elevated paths through the mangrove, the highest elevations in the area. They have been observed predating on *Bruguiera gymnorrhiza* propagules artificially brought in their vicinity, but since the presence of this crab was never recorded within the mangrove forest, where the vegetation dynamics take place, and propagules were never observed to strand in their vicinity naturally, they were not investigated in detail. Propagules predated by snails had the epicotyl scraped off first in all cases, whereas in a few cases the hypocotyl was affected only later or not at all. Crabs on the other hand, seldom affect the epicotyl, but cut through the hypocotyl instead. Not only crabs and snails were observed predating on fallen propagules, but also rodents such as rats and squirrels, although it is not clear whether the latter only access fallen propagules or actually cause them to fall as well. Local people also reported the porcupine to consume mangrove propagules, and footprints of these animals were indeed found in the mangrove (pers. obs.). Finally, in Galle two species of insect (a coleopteran and a dipteran) have been observed to destroy *Bruguiera gymnorrhiza* propagules by breeding, hatching and nursing inside the hypocotyl, while the latter is still attached to the parental tree. More than 70 % of propagules were infested and at least half that percentage is expected not to survive because the hypocotyl is consumed or rotting from the inside (pers. obs.).

### *Differential predation patterns*

Analysis on the homogeneity of the replicates revealed that in a total of 24, in six cases 2 replicates out of 3 formed a homogeneous group, and in a majority of 16 cases (67 %) all three replicates formed a homogeneous group. Exclusively the homogeneous replicates were used for further analysis and considered a single, total observation that could be correctly represented as a single graph. Only in the predation of *B. gymnorrhiza* in the *E. agallocha* forest patch in 1998 and in the predation of *R. apiculata* in the open space in 1999, the three replicates appeared heterogeneous, displaying a rather high, an intermediate and a rather low predation intensity respectively. Therefore an average predation intensity was used for further analysis. For *B. gymnorrhiza* this calculated average did not differ significantly from the recorded predation intensity in 1999 in the same forest patch ($\chi^2 = 0.955$; d.f. = 1; n.s.; after 14 days). The results of the predation status have been given in figure 2.

The data collected in Galle in 1999 showed no significant differences between the predation status of *B. gymnorrhiza* and *R. apiculata* propagules in the *E. agallocha* forest patch (1) nor in the *Rhizophora* spp. forest patch (2), but large differences were observed in the Open Space (Fig. 2a; Tab. 1). In Pambala there was a large difference between the predation status of *A. officinalis* and the other species in each of the forest patches or zones (Fig. 2b). In the *Rhizophora* spp. zone the predation status between *B. gymnorrhiza* and *Rhizophora* spp. propagules showed also significant more predation on *B. gymnorrhiza* (3), but this was not the case in the *A. officinalis* forest patch (4), the *E. agallocha* forest patch (5), the *L. racemosa* forest patch (6) or the Mixed forest patch (7).

Between the forest patches in Galle the predation intensity was significantly higher in the Open Space and in the *Rhizophora* spp. forest patch as compared to the *E. agallocha* forest patch for propagules of *B. gymnorrhiza* (8), whereas in 1999 it was significantly higher in the *E. agallocha* forest patch and in the Open Space than in the *Rhizophora* spp. forest patch (9). For *Rhizophora apiculata* propagules the predation intensity was significantly higher in the *E. agallocha* forest patch than in the two other forest patches (10). In Pambala, there were no significant differences in predation status between the zones for *B. gymnorrhiza* propagules (11). For *A. officinalis* propagules the predation intensity after 9 days was higher than 60 % in all of the forest patches. Nevertheless, the predation intensity was significantly lower in the Mixed forest patch (12) as compared to the rest of the forest patches, and in the *Rhizophora* spp. forest patch it was likewise significantly lower than in the other three forest patches (13). For the *Rhizophora* spp. propagules the predation intensity was significantly higher in the *E. agallocha* forest patch (14) as compared to the rest of the forest patches.

After comparison between the two study sites it was found that the predation on *B. gymnorrhiza* and *Rhizophora* spp. in the *E. agallocha* forest patch (15) as well as in the *Rhizophora* spp. forest patch (16) was significantly higher in Galle than in Pambala.

Also the predation status of *B. gymnorrhiza* propagules in the dry season (March 1998) and the wet season (November 1999) in Galle was compared, and showed no significant differences in the *E. agallocha* forest patch (17). An initial (until 9 days after plantation) significant difference was observed in the Open Space with more predation in the wet season (18), after which no significant differences were found any more (19). In the *Rhizophora* spp. forest patch the opposite occurred and from the 11th day onwards significantly higher predation in the dry season was found (20).

### *Influence of environmental factors on predation*

The land/water ratio reflects the more accidented topography in Galle with many water pools and mud mounts, whereas in Pambala a rather plain non-sloping plateau is present (Tab. 2). In Pambala, the relationship between predation intensity and lagoon water level was very strong for all species in a majority of the forest patches, with $r^2$ ranging from 0.651 to 0.968 (Tab. 3). Considering that the water level is a date-dependent variable and the experiments were initiated on different days, and considering that the predation intensity is a cumulative figure, the original replica's for each of the forest patches were considered again and checked whether also a peek in rate of predation corresponded with a greater accessibility of the propagules at lower water levels. For all the *Avicennia officinalis* propagules, and for *Bruguiera gymnorrhiza* and *Rhizophora* spp. propagules in the *A. officinalis* and the *E. agallocha* forest patches these events coincided, as can in part be deducted from figure 2b.

The data on vegetation structure are given in Table 4, and the numerical data of propagule predation after 2 weeks have been indicated to allow an easy verification of the dominance-predation hypothesis. Keeping in mind that the species here are studied as an isolated case, whereas other species present were not included mainly because of the low availability of propagules and seeds, it appeared that the dominance-predation hypothesis was only valid with respect to the adult trees in the *Rhizophora* spp. forest patch in Pambala (Tab. 4b). Although introduced with respect to canopy dominance, and thus adult trees, the 'dominance-predation hypothesis', or at least a similar model, can be tested for the younger understory as well. However, there are biotic and abiotic factors that are not linked to predation, but that can prevent the respective trees to become dominant in the canopy, but since the younger uderstory has survived beyond the predation threat this should not compromise the hypothesis. In the latter case only the *Rhizophora* spp. forest patch in Galle (Tab. 4a) and the Mixed forest patch in Pambala (Tab. 4b) could be identified as forest patches where the 'dominance-predation hypothesis' is valid.

## Discussion

### *Herbivores and predators*

The results from this study show that propagule predation in Sri Lanka is not an occasional phenomenon and that grapsid crabs and snails are the main actors once the propagules fall. Various phytophagous insects were reported for mangroves in Thailand (Murphy & Meepol, 1990; Murphy & Rau, 1990; Murphy, 1990; Rau & Murphy, 1990), but they were clearly not exhaustive for the local forest. Ellison & Farnsworth (1993) reported that predation on *Rhizophora mangle* L. by a lepidepteran did not significantly affect plant growth. Predation on *Bruguiera gymnorrhiza* by adults and larvae of beetles (*Curculionidae*, *Scolytidae*) and by dipteran larvae have been reported before by Robertson *et al.* (1990), but contrary to our observations their experimental results indicated no adverse propagule growth or survival effects from these insects. However, scolytid beetles were also found to infest mangrove propagules of the Rhizophoraceae family, in particular *Rhizophora* spp., to such a degree that they could affect the botanical mangrove community structure (B. Brook, Meeting on Mangrove Macrobenthos, pers. comm. 2000).

### *Differential predation patterns*

In a large majority of cases the mangrove forest patches, which are homogeneous for the adult vegetation as detected from sequential aerial photography (Dahdouh-Guebas *et al.*, 2000a; Verheyden *et al.*, subm.), are homogeneous for predation effects as well (similar predation intensity for similar mangrove assemblages), whereas the few heterogeneous groups of replicates (33 %) remain unexplained, but could for instance indicate different micro-environmental settings on the substrate or different feeding behaviours within the same forest patch.

Many of the observed differences amongst species and forest patches can be explained by the abundance of propagule predators. On one hand, the absence of significant differences between the predation on *B. gymnorrhiza* and *R. apiculata* within the *E. agallocha* or within the *Rhizophora* spp. forest patch, two forest patches with a higher density of crabs (Tab. 2), is probably due to a higher degree of competition (pers. obs.). This situation leads to a fast predation on whichever propagule is accessible, an aselective behaviour that has been observed in high-density areas in Kenya for *Neosarmatium meinerti* (Dahdouh-Guebas *et al.*, 1997) as well as a more general pattern (Dahdouh-Guebas *et al.*, 1998). This should lead to a similar predation stress in the two forest patches, if it were not for the influence of the land/water ratio and especially of the water level, the latter of which always floods the *Rhizophora* spp. soil first. This is in agreement with the different predation intensity after 14 days in the wet season between these two forest patches.
On the other hand, the large difference between species observed within the Open Space in Galle, under the less competitive conditions that are present in that forest patch (Tab. 2), could be the expression of a preference, especially since the slowly moving *T. palustris* was never observed predating on *R. apiculata* propagules, and is responsible for the greater part of predation on *B. gymnorrhiza*. The latter was visible from the scraped-off epicotyl, contrary to observations on the same gastropod in Kenya during earlier studies (Dahdouh-Guebas *et al.*, 1998) where the specimens cut through the hypocotyl first. It is unclear to which extent there is a combined influence from crabs and snails.

For Pambala, the striking predation on *Avicennia officinalis* is in agreement with results on the same genus elsewhere (*e.g.* McGuinness, 1997b), but the dominance-predation hypothesis, which was supported by the results on *Avicennia* in Australia, Malaysia, Florida and Panama (Smith *et al.*, 1989), is rejected (Tab. 4b), as it was by McGuinness (1997b). The high predation must be the result of either a preference, whatever the competition situation is, or an ease of propagule handling by the predator. Further differences within forest patches, such as higher predation on *B. gymnorrhiza* in the *L. racemosa* forest patch, or between forest patches, such as the rather high predation in the *E. agallocha* forest patch or the rather low predation in the Mixed or the *Rhizophora* spp. forest patch, can also be linked directly to crab abundance (Tab. 2).

Although it is known that burrow counts overestimate the actual crab population (Crane, 1975; Frith & Brunenmeister, 1980; Bosire *et al.*, 1999, subm.a), the density of crabs cannot account for the significantly higher predation intensity of *B. gymnorrhiza* and *Rhizophora* spp. observed in Galle as compared to Pambala, on the contrary (Tab. 2). Rather than crab density, individual competition, as a result of the micro-topography, plays a role in this observation. In Galle, the accidented topography, which forms a mosaic of pools and small islands built by *Thalassina anomala*, restricts predators to the emerged locations and increases food competition (pers. obs.). In Pambala, although generally forest patches such as the *E. agallocha* or *Rhizophora* spp. dominated ones have a higher topography than other forest patches, just like in Galle, as a result of the absence of *T. anomala* in the lagoon, these higher areas are more spread and so are the propagule predators. Therefore, despite the lower crab burrow density for the entire forest patch in Galle and the higher one in Pambala, locally, predation is higher in Galle than in Pambala. A second biotic factor that plays a role is the presence of *Terebralia palustris* in Galle and not in Pambala. This species is known to consume mangrove propagules (Slim *et al.*, 1997) and to predate on propagules (Dahdouh-Guebas *et al.*, 1998), and obviously also poses a problem here. Finally, the presence of *Avicennia officinalis* in Pambala, together with the apparent preference for this species, and its absence in Galle also in part explains the observed differences in predation on the other species.

The predation stress in the *E. agallocha* forest patch is probably too high in order to find differences between wet and dry season. In the *Rhizophora* spp. forest patch the brachyuran propagule predators are probably more active in the dry season, because fewer propagules are available, whereas gastropods (Open Space) are known to be less active under drier conditions leading to significant differences in the first days after monitoring. However, eventually even snails predate the majority of propagules.

In a few cases only (Tab. 4), the pattern of differences in propagule predation among forest patches indicate that propagule predators could determine the distribution of the mangroves species according to the dominance-predation hypothesis (Smith 1987a, 1987b). However, when applied to the young vegetation layer, the validity of this hypothesis is initial (Tab. 4), and only long-term monitoring of the established propagules will show which biotic or abiotic factors will further determine their survival.

### *Influence of environmental factors on predation*

From all the environmental variables measured, water level of the lagoon in Pambala has the best relationship with the predation data and leads to the hypothesis that propagule predation and vegetation dynamics in areas without a topographic gradient and that are influenced little by tidal effects, can be largely controlled by differences in water level in the wet and dry season. The facts are that, first, between day 1, 2 or 3 and day 5, 6 or 7 after the initiation of the experiments in Pambala, a considerable drop in water level of more than 30 cm occurred, before which many crabs were observed to be retreated vertically on the mangrove roots. Second, parallel with the drop in water level an increase in propagule predation was recorded for all species in a majority of forest patches, which can in part be seen in figure 2b, and which is most clear for *A. officinalis*. It is important to recall at this point that the day of the initiation of the experiments (day 1) is not the same for each forest patch due to the size of the forest - visual combination of the data on water level and on predation intensity (Tab. 2b) is therefore not advisable - , but that the implied discrepancy with water level, obviously similar in all forest patches at a particular time, was corrected for in the regressions.

For the *E. agallocha* forest patch, predation on *A. officinalis* occurred right from the start of the experiment, thus before the drop in water level, which can be explained by this forest patch occupying the highest topographic levels, which are seldom, if ever, submerged. The theory proposed here (Fig. 3) states that when the water level is low (primarily during the dry season) propagules fall on the mangrove soil and may plant themselves or strand (planting and stranding strategy of Van Speybroeck, 1992), the latter of which are known to be predated more than the former (Dahdouh-Guebas *et al.*, 1997). However, with microtopographical situations such as in Sri Lanka there are more possibilities to strand, exposing the propagules more to propagule predators, which in turn are very mobile and predate considerably at low water levels. When the water level is high (primarily during the wet season), the forest is often permanently flooded for a period, and the propagules that fall under those conditions drift away through the water, and are much less likely to be affected by propagule predators, which at that time are stuck on the mangrove roots. Once the water table decreases again and propagules can establish, propagule predators further control this establishment, but to a lesser degree as compared to the dry season. Dahdouh-Guebas *et al.* (1997) found indeed a lower predation on mature propagules, a stage that may be reached during the dispersal period, and freshly gathered ones. Following establishment of a propagule, various environmental conditions, some of which are most pronounced and stressing during the dry season, will be responsible for the survival of a propagule, and later for the growth of the plant. It seems that the zonation, which is partially present in Pambala (semi-zonation), must be the result of the differences in salinity across the forest during the dry season (personal measurements during the period 1997-1999), but that the dispersion of propagules to lead to any 'zonation' in the first place, is controlled by the wet season (Fig. 3). Therefore, rather than the influence of many biotic and abiotic factors on a given location, it seems to be a chain of events (temporally separated influences of one or more biotic and abiotic factors) that leads to a particular mangrove vegetation structure or zonation.

### *Simulation of the anthropogenical influence on predation*

Although at the time of the predation experiments the water level was permanently low in Galle, which might explain the high predation intensity here, when the daily and seasonal water level fluctuations in figure 4 are considered, the above theory on the link between lagoon water level and propagule predation might be valid for this site as well. In addition the flooding of the entire forest, including the raised path through the mangrove and the dam, is a fact during certain periods of the year (Y.L. Michael Vijedasa, Chief-Area-Watcher, pers. comm.). A clear relationship of the water level as a function of rainfall arises when these two types of environmental data are combined monthly ($y = 0.0348x + 118.01$; $n = 30$; $r^2 = 0.429$; $p < 0.01$). An average over the period 1949-1998 shows the trends in the dry and the wet season (Fig. 4), but within a short period the different sub-seasons and their length do not necessarily correspond to that trend (*cf.* Fig. 4).

Based on unpublished results from measurements with respect to the water level it was concluded that an average monthly water level of 140 cm or above is likely to flood the mangrove forest in such a way that the different sections of the forest are connected more and propagules can float away more easily. On the other hand, an average monthly water level of less than 120 cm is likely to leave a considerable part of the mangrove emerged (but pools and islands are always present), rather preventing propagules from floating away easily and increasing the probability of predation. However, single flooding events that are not necessarily reflected in the monthly average, can occur as an exception to the above trend (Fig. 4).

Retrospective investigation of the trend in the monthly water level shows that there were only 2 flooding months (1.1 % of the time) since the raised path through the mangrove and the dam were built in 1985. Before that time (1949-1984), only 5 flooding months were recorded (1.2 % of the time) with the above minimum limit of 140 cm, but under absence of anthropogenic features that have a strong impact on the hydrology, such as the path or dam, this limit is too high. At 100 cm, which is enough to flood the forest under a lesser degree of anthropogenical disturbance based on present observations (100 cm is the absolute minimum level recorded over the period 1997-1999 and is located lower than the basis of the anthropogenic constructions), the proportion of flooding time was obviously 100 %, whereas on an intermediate level of 120 cm it was still 95.0 %. This indicates that the impact of anthropological constructions on the hydrology of the system was great enough to alter the frequency of flooding events, and since flooding probably plays a regulative role in the interaction between propagule predation and dispersion (Fig. 3), it follows that propagule predation may be anthropogenically regulated indirectly.

## Conclusion

From the present study it can be concluded that the reciprocal relationship between mangrove trees and crabs, as highlighted by Dahdouh-Guebas *et al.* (subm.c), indeed plays a role in the shaping of the vegetation structure together with other propagule predators, and a succession of as well as a synergism between factors (*e.g.* dispersion by water level followed by a selective propagule predation and later by different selective environmental conditions) will probably determine the final vegetation structure. Propagule predators, grapsid crabs and the gastropod *Terebralia palustris* in particular, therefore play, at least at one point in the process of propagule establishment, a role that will lead to a particular vegetation structure. Considering the link between water level and propagule predation, and since hydrological changes often are anthropogenic (*e.g.* the decrease in number of months with flooding as a result of dam and path construction), man may also indirectly affect propagule predation.

## Acknowledgements

Many thanks are due to Prof. Dr. Nico Koedam for the support during my PhD research. I am very grateful to Fatuma M. Saidi, Daglas Thisera and Y.L. Michael Vijedasa for their practical help in the field, and to Mr. Anuradha Wickramasinghe and the entire staff of the Small Fishers Federation of Lanka (SFFL) at the Mangrove Conservation and Demonstration Centre in Pambala – Kakkapalliya for the excellent logistics. Stefano Cannicci is acknowledged for his comments on the manuscript. Research financed by the European Commission (Contract EBR IC18-CT98-0295), and with a specialisation fellowship of the Flemish Institute for the advancement of scientific-technological research in the industry (IWT).

## References

See Bibliography

**Table 1.** Statistical results from 'within' and 'between' species, forest patches, sites and seasons comparisons. Since significance levels varied little over time (14 days of observations) the range of statistical values for the respective tests are given. Numbers between parentheses correspond to the numbers in the text.

| Place | Statistic value | d.f. | p-value | |
|---|---|---|---|---|
| **Predation between *R.* spp and *B. gym* (1999)** | | | | |
| **in Galle** | | | | |
| **in EA** | $0.062 < \chi^2 < 1.183$ | 1 | n.s. | (1) |
| **in R** | $0.003 < \chi^2 < 1.172$ | 1 | n.s. | (2) |
| **in Pambala** | | | | |
| **in AO** | $0.000 < \chi^2 < 3.049$ | 1 | n.s. | (4) |
| **in EA** | $0.025 < \chi^2 < 0.659$ | 1 | n.s. | (5) |
| **in LR** | $0.013 < \chi^2 < 0.388$ | 1 | n.s. | (6) |
| **in M** | $0.017 < \chi^2 < 0.047$ | 1 | n.s. | (7) |
| **in R** | $\chi^2 < 5.022$ | 1 | $p < 0.05$ | (3) |
| **Predation between forest patches** | | | | |
| **in Galle** | | | | |
| **for *B. gym* in 1998** | $6.690 < \chi^2 < 8.014$ | 2 | $0.01 < p < 0.05$ | (8) |
| **for *B. gym* in 1999** | $16.663 < \chi^2 < 28.482$ | 2 | $p < 0.001$ | (9) |
| **for *R.* spp in 1999** | $12.625 < \chi^2 < 28.457$ | 2 | $p < 0.01$ | (10) |
| **in Pambala (1999)** | | | | |
| **for *A. off*** | $19.334 < G < 34.393$ | 4 | $p < 0.001$ | (12) |
| | $10.138 < G < 17.692$ | 3 | $p < 0.02$ | (13) |
| **for *B. gym*** | $7.950 < G < 9.076$ | 4 | n.s. | (11) |
| **for *R.* spp** | $15.512 < G < 36.926$ | 4 | $p < 0.001$ | (14) |
| **Predation between Galle and Pambala (1999)** | | | | |
| **in EA** | $14.025 < \chi^2 < 59.494$ | 1 | $p < 0.001$ | (15) |
| **in R** | $3.889 < \chi^2 < 27.156$ | 1 | $p < 0.05$ | (16) |
| **Predation between dry and wet season (Galle)** | | | | |
| **in EA** | $1.546 < \chi^2 < 3.041$ | 1 | n.s. | (17) |
| **in OS** | $10.886 < \chi^2 < 15.476$ | 1 | $p < 0.001$ | (18) |
| | $0.162 < \chi^2 < 3.639$ | 1 | n.s. | (19) |
| **in R** | $3.985 < \chi^2 < 7.171$ | 1 | $p < 0.05$ | (20) |

Propagules : *A. off* = *Avicennia officinalis*; *B. gym* = *Bruguiera gymnorrhiza*; *R.* spp. = *Rhizophora* spp.
Forest patches : AO = *A. officinalis*; EA = *Excoecaria agallocha*; LR = *Lumnitzera racemosa*; M = Mixed; R = *Rhizophora* spp.; OS = Open Space.

**Table 2.** Land/water ratio (dry season), crab burrow density of the snail *Terebralia palustris* in different forest patches of Galle and Pambala.

| | **Land/water ratio (% land)** | **Crab burrow density (burrows.m$^{-2}$)** | ***T. palustris* density (snails.m$^{-2}$)** |
|---|---|---|---|
| **Forest patches in GALLE** | | | |
| ***E. agallocha*** | 43.3 | 3.5 | 1.9 |
| **Open Space** | 9.8 | 1.3 | 2.8* |
| ***Rhizophora* spp.** | 27.4 | 4.5 | 0.8 |
| **Forest patches in PAMBALA** | | | |
| ***A. officinalis*** | 95.0 | 5.0 | 0.0 |
| ***E. agallocha*** | 95.0 | > 10.0 | 0.0 |
| ***L. racemosa*** | 91.1 | 6.8 | 0.0 |
| **Mixed** | 85.0 | 3.2 | 0.0 |
| ***Rhizophora* spp.** | 89.0 | 2.0 | 0.0 |

* On bare mud the density of snails can reach ten times this value.

**Table 3.** Statistics for the linear relationship between daily predation intensity (%) and daily lagoon water level (cm) in Pambala during 4 or 5 days (depending on the location of the plots). The various combinations of forest patches for a particular species in the first column reflect the significant differences in predation intensity between forest patches outlined in the text and in table 1.

| **Predation status** | **$r^2$** | **equation** | **n** | **significance level of $r \neq 0$** |
|---|---|---|---|---|
| *A. off* in AO, EA & LR | 0.882 | $y = -1.8248x + 133.35$ | 5 | < 0.01 |
| *A. off* in M | 0.802 | $y = -1.127x + 70.046$ | 5 | < 0.02 |
| *A. off* in R | 0.651 | $y = -1.4x + 80.116$ | 4 | n.s. |
| *B. gym* in AO & R | 0.881 | $y = -0.3899x + 29.123$ | 4 | < 0.02 |
| *B. gym* in EA, LR & M | 0.947 | $y = -0.233x + 15.295$ | 5 | < 0.01 |
| *R.* spp. in AO, LR, M & R | 0.968 | $y = -0.1556x + 10.552$ | 4 | < 0.002 |
| *R.* spp. in EA | 0.922 | $y = -0.5706x + 40.435$ | 5 | < 0.01 |

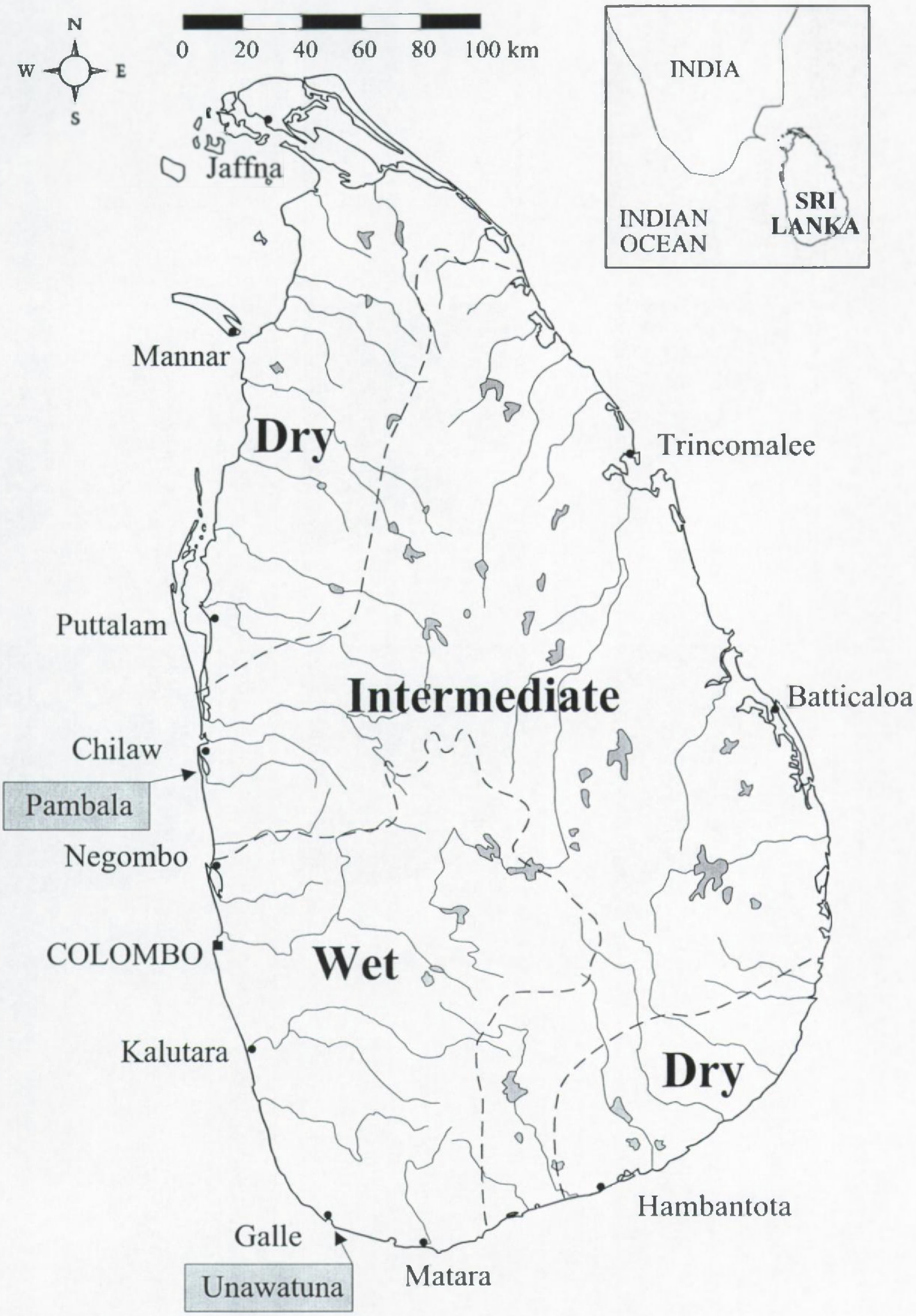
Propagules : A. off = *Avicennia officinalis*; B. gym = *Bruguiera gymnorrhiza*; *R.* spp. = *Rhizophora* spp.
Forest patches : AO = *A. officinalis*; EA = *Excoecaria agallocha*; LR = *Lumnitzera racemosa*; M = Mixed; R = *Rhizophora* spp.

**Table 4.** Relative density (De$_r$), relative frequency (F$_r$), relative dominance (Do$_r$) and the importance value (I.V.) of Curtis (1959) from PCQM transects on adult trees, young trees, and juveniles from 1997, 1998 and 1999 for the main forest patches in (a) Galle (Dahdouh-Guebas *et al.*, 2000a) and (b) Pambala (Zetterström, 1998; Dahdouh-Guebas, unpublished results). Also the predation intensity for each experimental species is given per forest patch, and shaded areas indicate a positive relationship with the 'dominance-predation hypothesis'.

| **(a) GALLE** | ***E. agallocha*** | | | | **Open Space** | | | | ***Rhizophora* spp** | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **De$_r$** | **F$_r$** | **Do$_r$** | **I.V.** | **De$_r$** | **F$_r$** | **Do$_r$** | **I.V.** | **De$_r$** | **F$_r$** | **Do$_r$** | **I.V.** |
| **ADULT TREES** | | | | | | | | | | | | |
| *B. gym* | 8.2 | 14.3 | 3.7 | 26 | 5.1 | 9.8 | 4.2 | 19 | 2.9 | 2.6 | 5.6 | 11 |
| R. *spp* | 16.9 | 22.9 | 17.0 | 57 | 8.9 | 9.8 | 8.1 | 27 | 51.4 | 52.3 | 44.4 | 148 |
| other species | 74.9 | 62.9 | 79.3 | 217 | 86.1 | 80.5 | 87.7 | 254 | 45.7 | 45.1 | 50.0 | 141 |
| **YOUNG TREES** | | | | | | | | | | | | |
| *B. gym* | 70.6 | 62.5 | | 133 | 14.6 | 24 | | 39 | 46.7 | 38.5 | | 39 |
| R. *spp* | 4.8 | 8.3 | | 13 | 8.3 | 12 | | 20 | 33.3 | 38.5 | | 20 |
| other species | 24.6 | 29.2 | | 54 | 77.1 | 64 | | 141 | 20 | 23 | | 43 |
| **PROPAGULES 01/1997** | | | | | | | | | | | | |
| *B. gym* | 13.6 | 22.2 | | 36 | 1 | 16.7 | | 18 | 0.7 | 16.7 | | 17 |
| R. *spp* | 86 | 66.7 | | 153 | 47.3 | 50 | | 97 | 78.9 | 50 | | 129 |
| other species | 0.3 | 11.1 | | 11 | 51.7 | 33.3 | | 85 | 20.4 | 33.3 | | 54 |
| **PROPAGULES 03/1998** | | | | | | | | | | | | |
| *B. gym* | 98.5 | 61.8 | | 160 | 87.4 | 62.5 | | 150 | 83.1 | 41.7 | | 125 |
| R. *spp* | 1.1 | 29.4 | | 31 | 12.6 | 37.5 | | 50 | 16.9 | 58.3 | | 75 |
| other species | 0.4 | 7.8 | | 8 | 0 | 0 | | 0 | 0 | 0 | | 0 |
| **PROPAGULES 11/1999** | | | | | | | | | | | | |
| *B. gym* | 20.7 | 40.4 | | 61 | 30.4 | 53.8 | | 84 | 0.1 | 9.5 | | 10 |
| R. *spp* | 79.3 | 54.4 | | 134 | 69.6 | 46.2 | | 116 | 99.9 | 90.5 | | 190 |
| other species | 0 | 5.3 | | 5.3 | 0 | 0 | | 0 | 0 | 0 | | 0 |
| **PREDATION INTENSITY AFTER 14 DAYS FOR ...** | | | | | | | | | | | | |
| ... *B. gym* | 93.3 % | | | | 93.3 % | | | | 43.3 % | | | |
| ... *R.* spp | 95.0 % | | | | 40.0 % | | | | 40.0 % | | | |

| (b) PAMBALA | *L. racemosa* | | | | Mixed | | | | *Rhizophora* spp | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | De$_r$ | F$_r$ | Do$_r$ | I.V. | De$_r$ | F$_r$ | Do$_r$ | I.V. | De$_r$ | F$_r$ | Do$_r$ | I.V. |
| ADULT TREES | | | | | | | | | | | | |
| *A. off* | 7.0 | 11.1 | 4.4 | 22 | 2.3 | 3.4 | 2.8 | 9 | 3.8 | 5.5 | 4.0 | 13 |
| *B. gym* | 1.6 | 3.7 | 1.2 | 6 | 14.0 | 20.7 | 2.8 | 37 | 3.0 | 5.5 | 0.9 | 9 |
| *R.* spp | 0.8 | 3.7 | 0.6 | 5 | 4.7 | 3.4 | 4.0 | 12 | 75.5 | 64.2 | 91.8 | 232 |
| other species | 90.7 | 81.5 | 93.8 | 266 | 79.1 | 72.4 | 90.3 | 242 | 17.7 | 24.8 | 3.3 | 46 |
| YOUNG TREES | | | | | | | | | | | | |
| *A. off* | 14.9 | 15.6 | | 31 | 0.0 | 0.0 | | 0 | 8.5 | 10.7 | | 19 |
| *B. gym* | 6.4 | 6.3 | | 13 | 25.8 | 23.8 | | 50 | 3.7 | 5.4 | | 9 |
| *R.* spp | 0.0 | 0.0 | | 0 | 0.0 | 0.0 | | 0 | 39.0 | 37.5 | | 77 |
| other species | 78.7 | 78.1 | | 157 | 74.2 | 76.2 | | 150 | 48.8 | 46.4 | | 95 |
| PROPAGULES 02/1997 | | | | | | | | | | | | |
| *A. off* | 88.2 | 66.7 | | 155 | 93.8 | 75.0 | | 169 | 8.2 | 10.1 | | 18 |
| *B. gym* | 0.0 | 0.0 | | 0 | 0.0 | 0.0 | | 0 | 0.1 | 3.8 | | 4 |
| *R.* spp | 0.0 | 0.0 | | 0 | 0.0 | 0.0 | | 0 | 79.9 | 45.6 | | 126 |
| other species | 11.8 | 33.3 | | 45 | 6.3 | 25.0 | | 31 | 11.9 | 40.5 | | 52 |
| PROPAGULES 04/1998 | | | | | | | | | | | | |
| *A. off* | 83.3 | 50.0 | | 133 | 0.0 | 0.0 | | 0 | 58.2 | 16.9 | | 75 |
| *B. gym* | 0.0 | 0.0 | | 0 | 88.2 | 66.7 | | 155 | 0.0 | 3.4 | | 3 |
| *R.* spp | 16.7 | 50.0 | | 67 | 0.0 | 0.0 | | 0 | 41.1 | 55.9 | | 97 |
| other species | 0.0 | 0.0 | | 0 | 11.8 | 33.3 | | 45 | 0.6 | 23.7 | | 24 |
| PROPAGULES 11/1999 | | | | | | | | | | | | |
| *A. off* | 94.2 | 55.6 | | 150 | 5.2 | 28.6 | | 34 | 15.5 | 17.2 | | 33 |
| *B. gym* | 0.0 | 0.0 | | 0 | 1.3 | 14.3 | | 16 | 0.0 | 6.1 | | 6 |
| *R.* spp | 3.4 | 11.1 | | 14 | 0.0 | 0.0 | | 0 | 83.5 | 46.5 | | 130 |
| other species | 2.4 | 33.3 | | 36 | 93.5 | 57.1 | | 151 | 1.0 | 30.3 | | 31 |
| PREDATION INTENSITY AFTER 13 DAYS FOR … | | | | | | | | | | | | |
| … *A. off* | 100.0 % | | | | 63.3 % | | | | 83.3 % | | | |
| … *B. gym* | 10.0 % | | | | 6.7 % | | | | 16.7 % | | | |
| … *R.* spp | 13.3 % | | | | 5.3 % | | | | 1.7 % | | | |

**Figure 1.** Map of Sri Lanka with the climate zones according to Mueller-Dombois (1968) showing the two study sites.



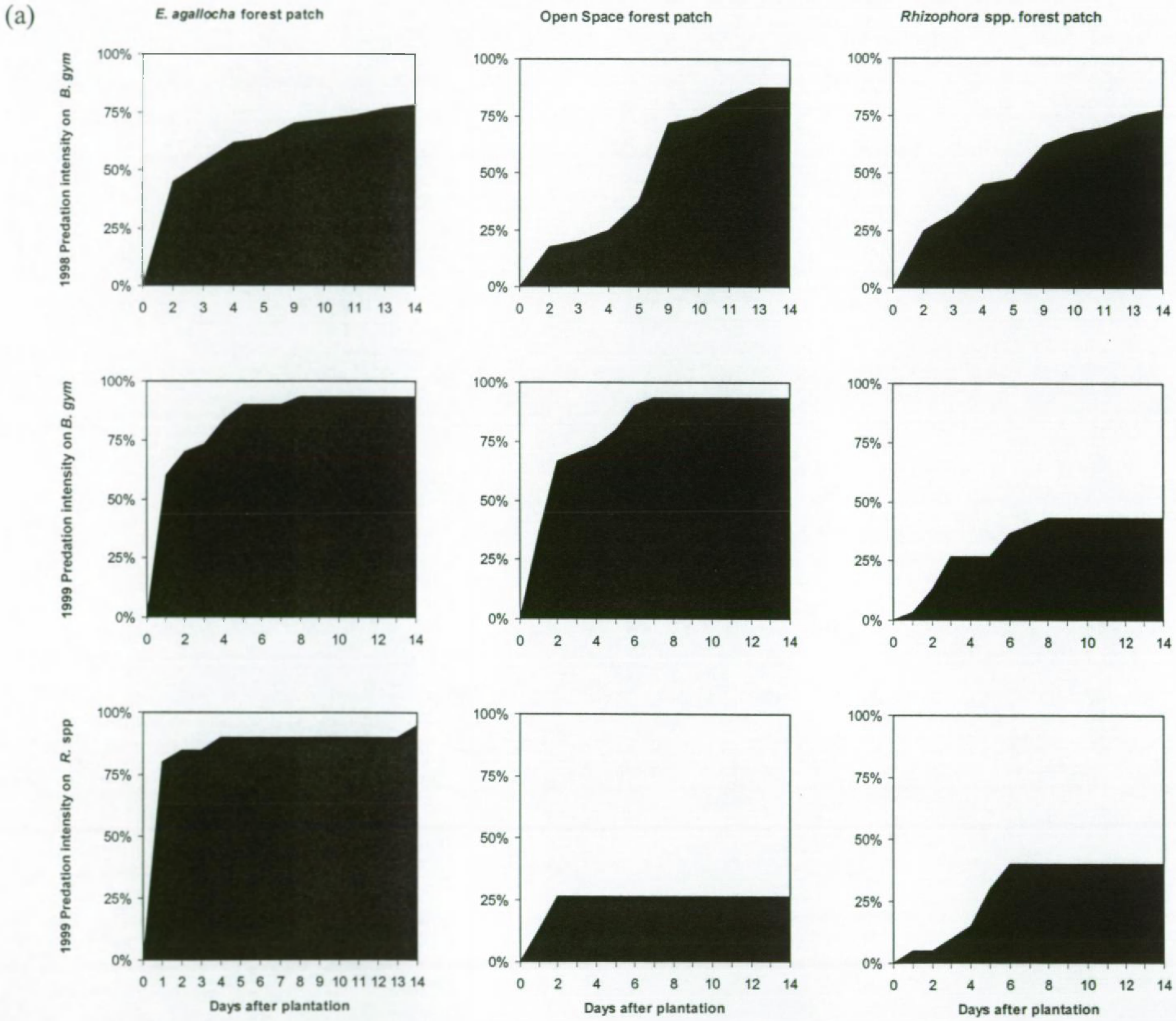


**Figure 2.** Predation status results (black = 'predated' and 'lost'; white = 'intact' and 'damaged') for propagules of *Bruguiera gymnorrhiza* (*B. gym*) for 1998 and 1999 and for propagules of *Rhizophora* spp. (*R.* spp) for 1999 in the tree forest patches in Galle (a), and for propagules of *Avicennia officinalis* (*A. off*), *B. gymnorrhiza* and *Rhizophora* spp. for 1999 in the five forest patches in Pambala (b).

(b)

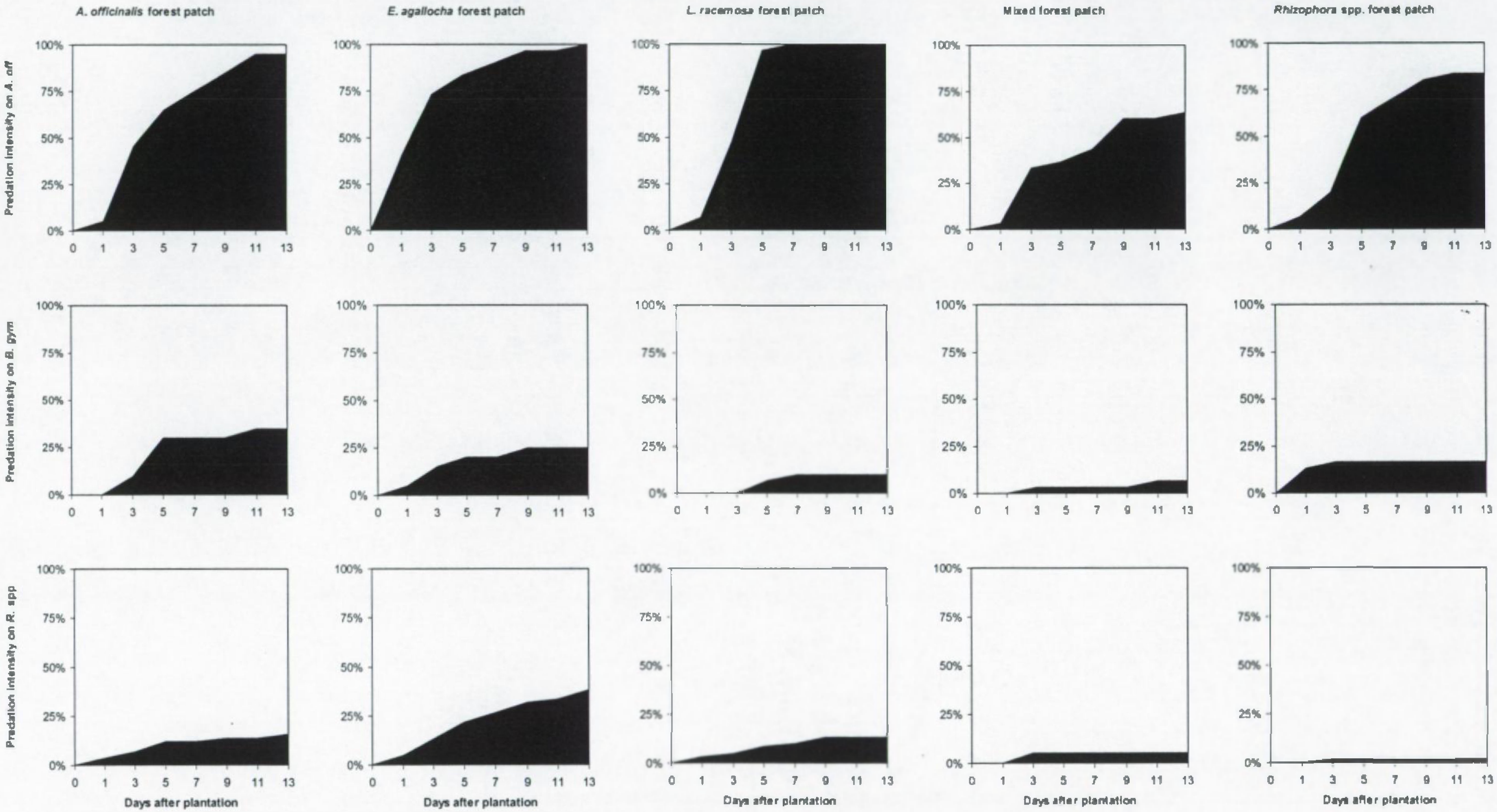

*A. officinalis* forest patch
*E. agallocha* forest patch
*L. racemosa* forest patch
Mixed forest patch
*Rhizophora* spp. forest patch
Predation intensity on *A. off*
Predation intensity on *B. gym*
Predation intensity on *R. spp*
100%
75%
50%
25%
0%
0
1
3
5
7
9
11
13
Days after plantation

**Figure 3.** Schematic of the synergistic role played by propagule predators, water level and environmental factors in the establishment of a certain vegetation structure in mangroves (see text for detailed explanation of the model).

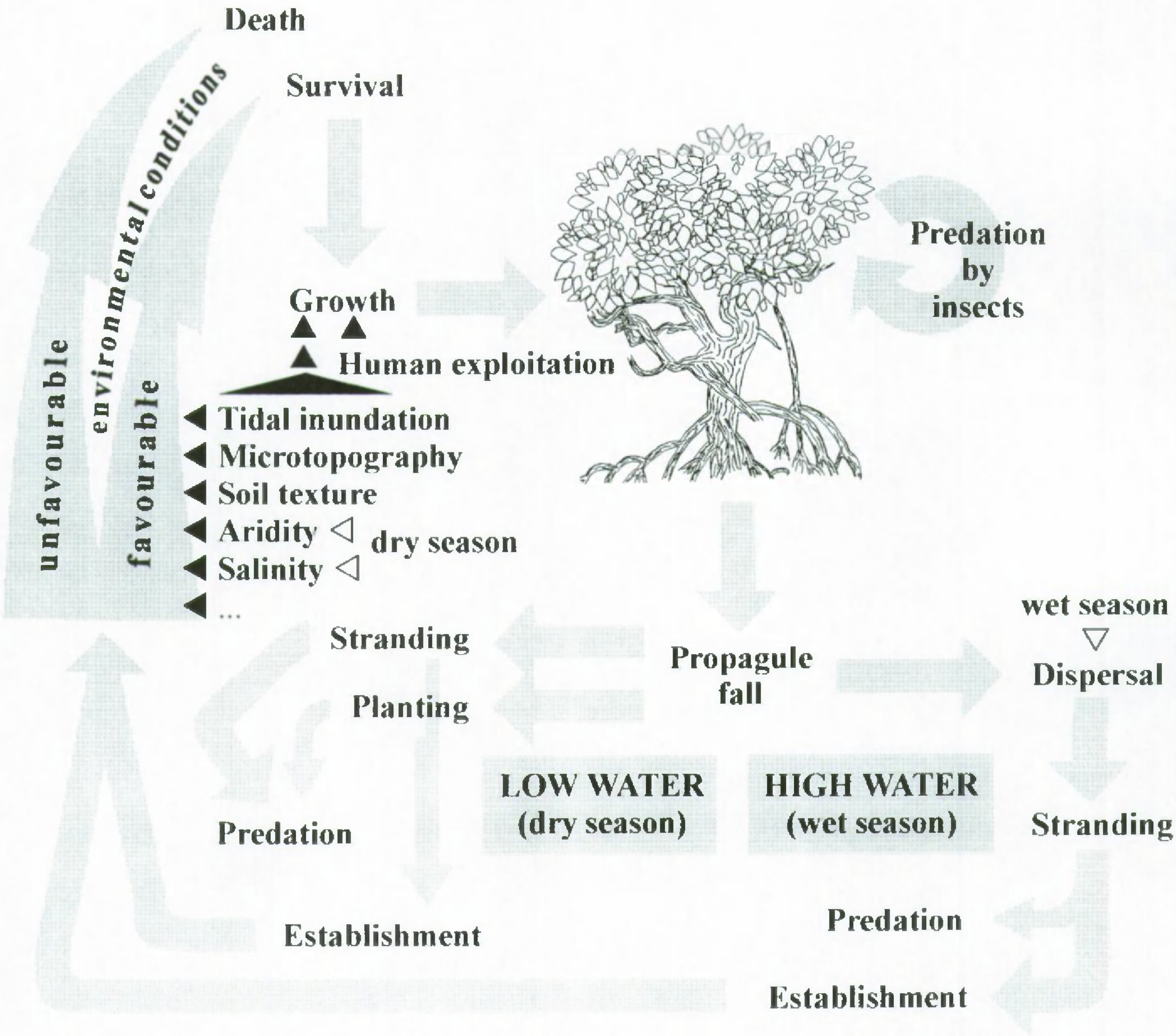
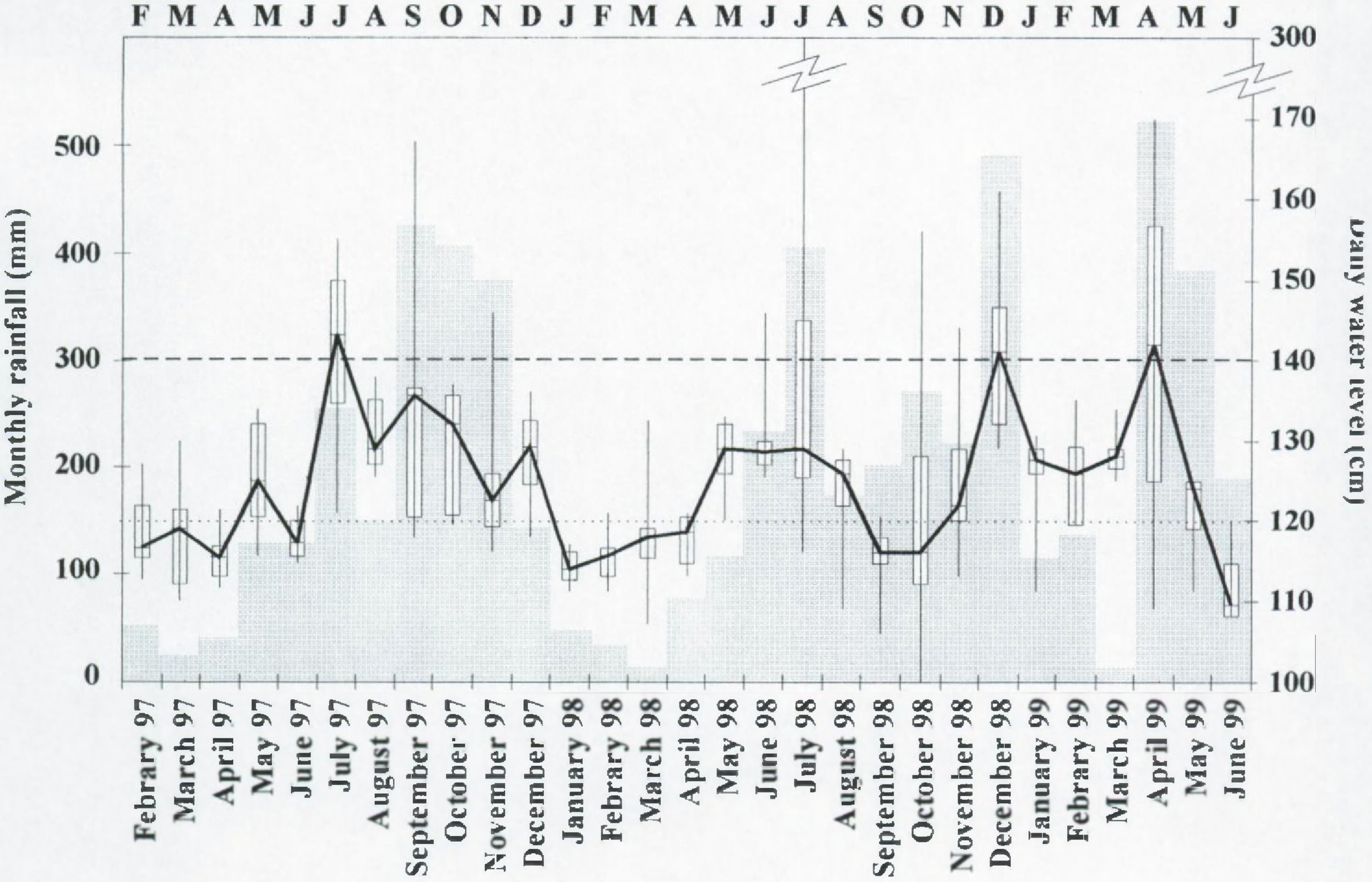


**Figure 4.** Monthly rainfall data (grey histograms) and daily water level fluctuations (solid line) measured at the concrete dam in the Galu Ganga in the mangrove forest of Galle between 24/01/1997 and 21/07/1999 (Dahdouh-Guebas, unpublished data). The dashed line in the graph indicates the minimum average monthly water level at which propagules are likely to float away, whereas the dotted line indicates the maximum average monthly water level at which propagules are likely to be predated.



# Chapter XII.

## Regeneration status of mangroves under natural and nursery conditions in Galle and Pambala, Sri Lanka.

Dahdouh-Guebas, F., D.W.N. Thisera, A. Wickramasinghe & N. Koedam

In preparation

# Regeneration of mangroves under natural and nursery conditions in Galle and Pambala, Sri Lanka.

Dahdouh-Guebas, F.[1], D.W.N. Thisera[2], A. Wickramasinghe[2] & N. Koedam[1]

[1] *Laboratory of General Botany and Nature Management, Mangrove Management Group, Vrije Universiteit Brussel, Pleinlaan 2, B-1050 Brussels, Belgium, fdahdouh@vub.ac.be, nikoedam@vub.ac.be*
[2] *Mangrove Conservation and Demonstration Centre, Small Fishers Federation of Lanka, Pambala-Kakapalliya, PO Box 1, Chilaw, Sri Lanka, sffl@sri.lanka.net*

## Abstract

Little is known about the fate of individual propagules from the moment it detaches from a tree, in particular : where, how quick and how well do they establish ? We try to answer in part how quick propagules are establishing. Therefore the regeneration of *Rhizophora mucronata*, *R. apiculata* and *Bruguiera gymnorrhiza* was investigated by measuring the root growth in forest patches with different species compositions in two mangrove forests in Sri Lanka (Unawatuna-Galle and Pambala-Chilaw). In addition, the height, number of leaves and leaf bud length of juveniles of the same species was monitored for 13 months every other week. Results show that the post-dispersal development status of the three mangrove species is influenced by the environmental conditions of the forest patch in which the propagules strand, suggesting that not only common abiotic variables such as light may have an impact on the development and establishment of propagules, but also for example the amount of leaf litter on the soil or the degree of soil consolidation. In the framework of artificial regeneration the comparison of our results with similar studies elsewhere emphasizes the plasticity of growth characteristics and shows that propagule size does not reflect growth performance.

Keywords : mangrove, regeneration, nursery, propagule predation, growth, rooting, phenology, Sri Lanka

## Introduction

In recent advances in mangrove research vegetation structure has been highlighted repeatedly (*e.g.* Jiménez & Sauter, 1991; Azariah, 1992; Pernetta, 1993a; Saifullah *et al.*, 1994; Fujimoto *et al.*, 1995; Ong *et al.*, 1995; Couto, 1996; Cantera & Arnaud, 1997; Imbert & Ménard, 1997; Osunkoya & Creese, 1997; El-Amry, 1998; Fromard *et al.*, 1998; Cole *et al.*, 1999; Cox & Allen, 1999; Duke & Khan, 1999), but in a majority of cases this 'structure' refers primarily to adult trees (> 65 % of the references above). Few studies have investigated the reproductive phenology of mangrove trees (Christensen & Wium-Andersen, 1977; Wium-Andersen & Christensen, 1978; Wium-Andersen, 1981; Duke *et al.*, 1984; Lopez-Portillo & Ezcurra, 1985; Duke, 1988, 1990), and much fewer have concentrated on the fate of mangrove propagules after falling from the parental tree. One of the most representative studies for the latter type of research is probably the one by Osunkoya & Creese (1997), who investigated the monospecific population structure, spatial pattern and seedling establishment of *Avicennia marina* (Forsk.) Vierh. var. *australasica* (Walp.) Moldenke in New Zealand, focussing on naturally occurring and on transplanted seedlings at different tidal positions and under different light conditions.

Within the above context there are three questions that have not been answered and that are important in the discussion on regeneration and zonation of mangroves. First, where do the propagules that fall from a particular tree establish ? Second, once fallen, how quick do propagules establish ? And third, once established, how strong is their establishment, *i.e.* which biotic or abiotic factors can succeed in removing propagules The first question necessitates the marking of propagules on the parental trees before they fall and requires regular monitoring of the marked propagules, the second question requires the monitoring of the rooting capabilities of propagules on the mangrove floor, and the third question requires both naturally fallen and artificially planted propagules exposed to different experimental designs.

In the present paper we will try to contribute to an answer to the second question. The main objective of this study is to investigate the short-term post-dispersal regeneration of individual seedlings (emphasizing their rooting capabilities) of some of the common mangrove species in Sri Lanka, and to verify how various forest patches characterised by a different species dominance influence this regeneration. The second objective is to investigate the growth performance of the same species under nursery conditions for a period of one year in order to view their suitability for mangrove rehabilitation purposes.

## Description of the study sites

Two mangrove forests were investigated along the South-western coast of Sri Lanka, where the spring tidal amplitude is reported to be inferior to 1 m (Spalding *et al.*, 1997), and where personal measurements (1997-1999; results not shown) reveal that the local weekly tidal amplitude is even inferior to 0.15 m for most of the time (84 %).
One mangrove forest is located between Galle and Unawatuna (06°01'N - 80°14'E), in the wet climate zone of Sri Lanka (Mueller-Dombois, 1968; Fig. 1) and had a mean annual rainfall of 2379 mm over the last 50 years. The forest is of the basin and riverine mangrove type according to Lugo & Snedaker (1974), covers a surface of 1.5 km$^2$ and is located at about 600 m from the Indian Ocean shore. Two rivers run through the mangrove forest : on one hand the Thalpe Ela, which is discharging into the ocean, and on the other hand the Galu Ganga, which is a tributary of the former. The vegetation structure of the mangrove in Galle has been investigated in detail by Verheyden *et al.* (subm.) and Dahdouh-Guebas *et al.* (2000a), and comprises three distinct types of patches (a vegetation 'patch' is here defined as having a certain, often monospecific floristic composition, and no determined shape or area) : one dominated by *Excoecaria agallocha* L., one dominated by *Rhizophora apiculata* Bl. (hereafter referred to as the zone dominated by *Rhizophora* spp. to allow comparison with the second mangrove site; see below) and an 'Open Space' in which the herb layer is dominated by *Fimbristylis sulbundia* (Nees) Kanth. Enum subspecies *pentaptera* (Nees). The mangrove forest in Galle has been subjected to strong anthropogenic influences over the last 50 years (Dahdouh-Guebas *et al.*, 2000a).
The other mangrove forest is located in the Pambala area of Chilaw Lagoon, located in Sri Lanka's intermediate climate zone (Mueller-Dombois, 1968), and had a mean annual rainfall of 1443 mm over the last 50 years. The mangroves here are of the fringe type (Lugo & Snedaker, 1974), and have a rather irregular distribution along a complex of creeks (Marambettiya Ela, Bate Ela, Pol Ela and Dutch Channel). Most freshwater influx stems 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). This site is known to be the most species diverse in South-Western Sri Lanka (Jayatissa *et al.*, subm.; Dahdouh-

Guebas *et al.*, in prep.d). The vegetation structure of this mangrove forest has been studied in detail by Zetterström (1998), Verheyden *et al.* (subm.) and Dahdouh-Guebas (unpublished results), and comprises five distinct patches or zones (a vegetation 'zone' is here defined as a band of vegetation with a certain, often monospecific floristic composition) : one dominated by *Avicennia officinalis* L., one dominated by *E. agallocha*, one dominated by *Lumnitzera racemosa* Willd., one dominated by *Rhizophora mucronata* Lam. and *R. apiculata* (hereafter both referred to as the zone dominated by *Rhizophora* spp.), and a 'Mixed' zone comprising *E. agallocha, L. racemosa, Heritiera littoralis* Dryand. and *Xylocarpus granatum* Koen. Other common species in Pambala, although never dominant or co-dominant, are *Bruguiera gymnorrhiza* (L.) Lam. and *B. sexangula* (Lour.) Poir. Occasionally *Aegiceras corniculatum* (L.) Blanco was observed. The mangrove in Chilaw Lagoon has recently been subjected to strong anthropogenic influences as a result of shrimp farming (Foell *et al.*, 1999; Dahdouh-Guebas *et al.*, 2000c).
In both mangrove forests none of the zones was isolated, such as to inhibit the natural input of propagules from elsewhere. Mangrove nomenclature follows Tomlinson (1986).

## Material & Methods

### *Regeneration under natural conditions*

After exploratory experiments done in Galle in March 1998 (dry season), the main field work in Galle and Pambala was organised from October till December 1999 (wet season). Propagules of *A. officinalis*, *B. gymnorrhiza*, *R. apiculata* and *R. mucronata* were collected in a mature stage and gathered fresh from the tree, except for *R. mucronata*. Propagules of the latter were not available in sufficient quantities fresh, and were therefore collected from the mangrove floor and from natural ponds instead, provided they did not show signs of decay, damage, predation or rooting. As a control experiment to check for the effect of freshness on the growth performance, 44 *R. mucronata* propagules, 22 freshly gathered and 22 taken from the mangrove soil and water ponds, were planted, and the development status was checked daily for two weeks, but there was no significant difference in growth performance (G-test : G = 10.561; d.f. = 6; n.s.).

In each of the vegetation patches outlined above, three regeneration plots of 5 x 5 m were established and propagules were attached to plants or immobile debris using strong Ariadne twine. In Galle a single plot counted 10 propagules of *B. gymnorrhiza* and 10 of *R. apiculata*, whereas in Pambala it comprised 10 propagules of *A. officinalis*, 10 of *B. gymnorrhiza*, 5 of *R. apiculata* and 15 of *R. mucronata*, the numbers depending on availability. During the preliminary experiments carried out in Galle in 1998 only *B. gymnorrhiza* propagules were available and 20 of them were used per plot.

Every day (in Galle) or every other day (in Pambala), depending on the area of the forest, the plots were visited and the development status was recorded for each of the propagules. For intact and damaged propagules the development status of the roots was classified into one of the following classes according to the longest root : no roots, roots < 1 cm, roots 1-3 cm, roots 3-5 cm, roots > 5 cm. During the experiments it became clear that the results of the natural regeneration of the propagules, had to be interpreted in an environmental context in which predation appeared to be a factor. Therefore, apart from the development classes defined above, a class 'predated' propagules, as defined by Smith (1987a, 1987b), was added, but only intact or damaged propagules were considered for further analysis. Fourteen undamaged and 13 damaged *R. apiculata* propagules, planted in a control quadrat to check for the effect of predator damage on the growth performance, were checked daily for two weeks but did not show significant differences in development status (G-test : G = 2.482; d.f. = 4; n.s.), indicating that damaged propagules conserve the same growth ability as intact propagules.

Also the development of the leaves was checked, but during the course of the experiment only one *B. gymnorrhiza* propagule developed a primary twig with two leaf pairs. The experimental monitoring was ended after two weeks, for this is known to be the most important period for establishment due to environmental influences such as predation or washing away (Dahdouh-Guebas *et al.*, 1998; Dahdouh-Guebas, subm.). In Pambala, where predation on *B. gymnorrhiza* and *Rhizophora* species has been reported to be lower (Dahdouh-Guebas, subm.), the development status of the propagules was checked again after 40 days. In Galle the latter was not done due to the higher predation intensity (between 80% and 98 % predation after 43 days in 1998).

In each of the forest patches between 13 and 64 points (depending on the size of the patch) were sampled for salinity (using an Atago refractometer), land/water ratio (visual estimation), propagule predator density (crabs and the gastropod *Terebralia palustris* L.) and vegetation cover. Rainfall data for Galle and Chilaw were obtained from the Meteorological Department in Colombo, and in addition the water level of the lagoon in Pambala was recorded daily from a fixed scale. Information with respect to the evolution of the mangrove forest and with respect to vegetation structure (densities, frequencies, basal area, cover, height, etc.) were taken from earlier studies done under our supervision between 1997 and 1999 (Zetterström, 1998; Dahdouh-Guebas *et al.*, 2000a, 2000c; Verheyden *et al.*, subm.; Dahdouh-Guebas *et al.*, subm.e; Dahdouh-Guebas, unpublished results) and used where appropriate to explain links with vegetation structure.

Statistical analysis using the $\chi^2$-test and the G-test (Sokal & Rohlf, 1981) was performed on the development status of the propagules after one week (7 or 8 days), after two weeks (13 or 14 days), and for Pambala also after 40 days of observation on all levels of 'within' and 'between' species, forest patches, sites and seasons (in the results numbers between parenthesis refer to the statistical data in table 1). Possible relationships between the rooting performance and the environmental variables were checked using correlation and regression analysis.

### *Regeneration under nursery conditions*

In order to investigate the development status on a longer term and in the framework of artificial mangrove regeneration, 30 *R. mucronata*, 10 *R. apiculata* and 9 *B. gymnorrhiza* propagules were planted in a nursery in September 1998, within natural *A. officinalis* vegetation in Pambala. Each propagule was put in a small plastic bag with a few holes (15 x 25 cm), which was filled with natural muddy mangrove soil from the nursery site. Each juvenile was checked every two weeks during 13 months for the following characteristics of which only the first two were used for further analysis : height, number of leaves and leaf bud length. The type of relationship with time was investigated through correlation and regression analysis.

## Results

The absence of a large tidal amplitude in Sri Lanka allows thick leaf litter beds to form, primarily in the forest patches dominated by *Rhizophora* spp. and *Bruguiera* spp., whereas in *L. racemosa* dominated forest patches the litter mainly consists of dead branches (pers. obs.). From visual observations we could discern an overall difference between naturally fallen propagules that were in direct contact with the mangrove soil, and those that were laying on the leaf litter beds. Although still subject to experimental verification, it seems that propagules in direct contact with the mangrove soil started to root much earlier than those laying on the leaf litter beds, and that among the propagules on the leaf litter beds those of *Bruguiera* are quicker in rooting and are twirling between the litter to reach the soil.

### *Regeneration under natural conditions*

Figure 2 graphically represents the results of the development of the propagules (rooting) in Galle (Fig. 2a) and Pambala (Fig. 2b). In 1998, the different forest patches in Galle did not show significant differences in the development of *B. gymnorrhiza* propagules after one week (1), but after two weeks there were significantly more classes with longer roots in the *Rhizophora* spp. forest patch than in the *E. agallocha* forest patch or the Open Space (2). For 1999, within the *E. agallocha* and the *Rhizophora* spp. forest patches there was no significant difference between the development status of *B. gymnorrhiza* and *R. apiculata* propagules (3), but in the Open Space, *B. gymnorrhiza* propagules had significantly more and longer roots than *R. apiculata* propagules (4). No significant differences in development status were visible between the forest patches for *B. gymnorrhiza* (5) or *R. apiculata* (6).

In Pambala, after one week there was no significant difference in development status for *A. officinalis* (7), and later so many propagules were predated (> 80% after 9 days) that the remaining numbers did not lend themselves to further statistical analyses. Within the *A. officinalis* forest patch, there was no significance 40 days after plantation (8). Within the *E. agallocha* forest patch the only significant between-species difference found was for the longer (but not 'more') *R. apiculata* roots as compared to the other species (9). In the three other forest patches there was a similar trend, with significantly more and longer roots for *R. mucronata* propagules as compared to the rest (10). This significance still existed after 40 days, but for the *Rhizophora* spp. forest patch (11).

For *B. gymnorrhiza* propagules there were significantly more and longer roots in the *E. agallocha* forest patch than in the rest after two weeks (12), and for *R. apiculata* the same was observed for the *A. officinalis* and *E. agallocha* forest patch as compared to the rest (13). These plots were checked again after 40 days and the earlier observed significant differences had disappeared for both *B. gymnorrhiza* (14) and *R. apiculata* propagules (15). *R. mucronata* propagules always had significant less and shorter roots in the *E. agallocha* forest patch as compared to the other forest patches (16).

After one week there were no significant differences between the *E. agallocha* or the *Rhizophora* spp. forest patch in Pambala and Galle with respect to the development status of *B. gymnorrhiza* or *R. apiculata* (17). After two weeks, too many propagules were predated in the *E. agallocha* forest patch to allow a sound statistical comparison. For the *Rhizophora* spp. forest patch there was no significant difference in the development status of *B. gymnorrhiza*

(18), whereas in Galle *R. apiculata* had significantly less and shorter roots as compared to Pambala (19).
Comparison of the development status of *B. gymnorrhiza* in the dry (1998) and wet season (1999) revealed no difference for the *E. agallocha* forest patch (20) or for the Open Space (21), but for the *Rhizophora* spp. forest patch there were always significantly more and longer roots in the dry season (22).

Spearman's rank correlation coefficient ($r_s$) for development status in the different forest patches after 40 days of observation for each of the species used ranged between 0.2 and 0.8 for the association with vegetation cover (Tab. 2) and between -0.3 and -0.5 for the association with wet season salinity (Tab. 2), and was not significant (n=5). Similarly, there was no significant difference for the relationship between development status of propagules (excl. predated propagules) on one side and land/water ratio or propagule predator density on the other side (Tab. 2).

### *Regeneration under nursery conditions*

The temporal evolution of the height and the number of leaves shows an expected strong positive relationship for *Rhizophora mucronata* ($y = 2317.7\text{Ln}(x) - 24222$; $r^2 = 0.89$; d.f. = 26; $p < 0.001$), *R. apiculata* ($y = 2632.3\text{Ln}(x) - 27581$; $r^2 = 0.69$; d.f. = 18; $p < 0.001$) and *Bruguiera gymnorrhiza* ($y = 1583.8\text{Ln}(x) - 16587$; $r^2 = 0.75$; d.f. = 26; $p < 0.001$) (Fig. 3). However, for *B. gymnorrhiza* the trend shows a drop in number of leaves and to a lesser degree also in height, which cannot be explained as a natural growth pattern.

## Discussion

A general observation is the absence of expanded leaves during the first weeks of juvenile growth. This indicates that all energy needed for establishment is stored in the hypocotyl and leaf photosynthesis contributes little in the energy requirements in the first stage of development.

### *Regeneration under natural conditions*

The better rooting status for *B. gymnorrhiza* in the *Rhizophora* forest patch as compared to the two other forest patches could be explained by the soil characteristics. Here, under dry conditions (dry season 1998) the soil remains muddy and easily penetrable, unlike the soil in the *E. agallocha* forest patch or the Open Space, the latter of which forms cracks (pers. obs.). During the wet season (wet season 1999) the soil in the *E. agallocha* forest patch is probably the most consolidated, but no significant difference in development of propagules between forest patches was observed. There was however a better development status for *B. gymnorrhiza* than for *R. apiculata* propagules in the Open Space. This could be the result of a better growth performance of *B. gymnorrhiza* under the good light conditions which are characteristic of the Open Space [on a cloudless day, the light intensity in the mangrove between 9 AM and 3 PM ranges between 128472 lux and 131617 lux with an average of 130156 lux on a location with no vegetation cover (n = 18) whereas it ranges between 1932 lux and 2376 lux with an average of 2106 lux on a location with a vegetation cover > 80 % (n = 13) (Dahdouh-Guebas, unpublished data)]. However, at this point it should be recalled that

*B. gymnorrhiza* is a shade tolerant species, whereas *R. apiculata* is shade intolerant (Smith, 1992).

Under the present high-predation pressure in Pambala, little can be said about *A. officinalis* except that experiments should be repeated under conditions in which propagule predators have been artificially removed from the experimental plots. However, even then its successful regeneration can be questioned, since Elster (2000) found 100 % mortality for *Avicennia germinans* (L.) Stearn and *Laguncularia racemosa* (L.) Gaertn. f. because of their delicate structure that is easily damaged by environmental influences such as water and wind. The general trend of *R. mucronata* having more and longer roots in a majority of the forest patches are not due to a more mature condition of these propagules (*cf.* control experiment in 'Material & Methods'). The cause as to why the above trend was not observed in the *Rhizophora* forest patch can be attributed to the darkest light conditions in this forest patch (Tab. 2) and to the shade intolerance of this species (Smith, 1992). However, this relationship cannot be generalised for Pambala, because many juvenile, young and adult mangrove trees, incl. those of shade intolerant species such as *Rhizophora apiculata* and *R. mucronata*, can be found in this darkest forest patch. A possible explanation for the above difference can be based on the actual light penetrating though the canopy (see further). The better rooting of *B. gymnorrhiza* and *R. apiculata* in the *E. agallocha* and/or the *A. officinalis* forest patches initially (after two weeks), can be linked on one hand to the lower amount of plant litter present on the mangrove soil hindering rooting. On the other hand, these observations could be the result of a bias by the stronger effect of predation for these two species in the forest patches considered here. The lower rooting performances of *R. mucronata* might be the result of a very consolidated soil – because of its high elevation the *E. agallocha* substrate is even emerged in the wet season – or simply because of unfavourable environmental conditions in this landward forest patch. However, during the time of field work in the wet season (November 1999) at least salinity, presumed to be the main environmental factor responsible for the establishment of the vegetation structure, was very similar in all forest patches, ranging between 0 and 6 ‰ (Tab. 2).

Since *B. gymnorrhiza* is a shade tolerant mangrove species (Smith, 1992) and total vegetation cover in the *E. agallocha* or the *Rhizophora* spp. forest patch between Galle and Pambala was similar, there was no expected difference in development status, as observed. For *R. apiculata*, expecting a similar lack of significance would not be correct since we are dealing with a shade intolerant species (*loc. cit.*) and light conditions rather than vegetation cover should be uncovered. The mangrove forest in Galle is low (< 6 m), and often with foliage developing within 3 m above the substrate, whereas in Pambala the majority of trees are rather high (> 8.5 m and up to 30 m) and foliage is more restricted to the canopy. This influences the light that penetrates through the canopy and makes the *Rhizophora* spp. forest patch in Galle much 'shadier' than in Pambala, a possible explanation for the significantly different development status of *R. apiculata* between the two sites. The issue of light is also important in gap-dynamics, which is believed to influence the vegetation structure more in Galle than in Pambala. It has been found indeed that major structural changes have taken place the last few decades in Galle, which is in part attributed to an increased anthropogenic pressure (Dahdouh-Guebas *et al.*, 2000a).

As for the between-forest patches comparison for Galle above, the better development of *B. gymnorrhiza* in the *Rhizophora* spp. forest patch during the dry season can be attributed to its lower topographic location and a less consolidated soil, whereas the *E. agallocha* forest patch, which is located higher, is more or less the same in the wet and dry season. Also the salinity can play a role in the topographically lower *Rhizophora* spp forest patch, where it can affect more the propagule growth. The salinity conditions during the dry season correspond more with the known conditions for growth of *B. gymnorrhiza*, which range between 8 and 34 ‰ (Smith, 1992).

The attempt to link the development status in Pambala after 40 days directly to biotic or abiotic environmental conditions (vegetation cover, salinity, land/water ratio and propagule predator density), characterised for each of the five forest patches, did not generate significant relationships. However, the role played by propagule predators in the mangrove of Galle and Pambala was clearly shown by Dahdouh-Guebas (subm), and also elsewhere they are known to have an impact on regeneration (Dahdouh-Guebas *et al.*, 1997, 1998).
Aquatic plants are known to have one major root that grows downward in sandy soil with few nutrients, whereas they are know to grow many secondary side-roots in soft nutrient-rich soils (Ludwig Triest, pers. comm.). Some observations in this study suggest the same might be true for the intertidal mangrove plants. In order to link rooting features to environmental conditions we therefore suggest future research to focus on one hand on soil characteristics such as soil texture and nutrient availability, and on the other hand on the size of the roots with respect to their position on the propagule.

The collection of density data with respect to naturally fallen propagules in 464 sample points in Galle and in 516 sample points in Pambala, visited during three times of the year (January-February 1997, March-April 1998 and October-November 1999), are indicated in Table 3 (Dahdouh-Guebas, unpublished data). Although the pattern over a full year has not been generated with the data from Table 3, it is partially clear and predictable that juvenile abundance patterns will not be exactly the same as those reported earlier, for example for the *Rhizophora* species by Gill & Tomlinson (1971), Christensen & Wium-Andersen (1977), Wium-Andersen (1981) and Kairo (1995). However, apparently the consistent pattern with the data presented in the above studies is the synchronisation of the release of propagules with the wet season, or rather with the end of the wet season, possibly indicating that heavy rains trigger abscission.

### *Regeneration under nursery conditions*

Whereas the net growth of the mangrove juveniles under nursery conditions displays a common pattern (Fig. 3), there are a number of similarities as well as differences with known data from other parts of the Indian Ocean region. First of all, it seems that propagules larger at the time of collection are not necessarily those with the best growing performance. Kairo (1995) reported for Kenya *Rhizophora mucronata* propagules, with a length between 30.3 and 54.5 cm at the time of collection, to have a mean height of 50.36 cm after 6 months, whereas our propagules, ranging from 24.5 to 48.5 cm at the time of collection, were on average 58.2 cm high after 6 months (Fig. 3a). For *Bruguiera gymnorrhiza* propagules ranging from 16.1 to 20.8 cm at the time of collection in Kenya (*loc. cit.*) and between 15.0 and 28.0 cm in Sri Lanka (Fig. 3c), displayed a similar mean height of 41.83 and 40.5 cm respectively after 6 months. Kairo (1995) reported for *Rhizophora mucronata* from Kenya a net growth of 20.06 ± 4.95 cm after six months and of 27.95 ± 6.18 cm after 9 months, whereas our data similarly display growth increments of 22.2 ± 8.41 and 26.63 ± 8.87 respectively (Fig. 3a). Likewise, for *Bruguiera gymnorrhiza* the same variables after the same period are 25.23 ± 5.09 cm and 45.68 ± 9.64 cm for Kenya (*loc. cit.*), and 23.03 ± 7.18 and 23.1 ± 3.99 for Sri Lanka respectively (Fig. 3c). These data are in agreement, except for the height of *B. gymnorrhiza* juveniles after 9 months, the latter probably due to the as yet unexplained adverse impact on this species during the experimental monitoring (Fig. 3c). For the same reason, the number of leaves is lower in Sri Lanka as compared to Kenya as well, but strangely enough this is also the case for *R. mucronata*, which generated 22.52 ± 7.28 leaves after 9 months in Kenya (*loc. cit.*) and only 13.00 ± 3.00 in Sri Lanka (Fig. 3a). For *Rhizophora apiculata* the average height increment of 25.6 cm in 4 months is already more than the maximum reported one of 16 cm per year (Kathiresan *et al.*, 1996). An average of 6 leaves per seedling after 6 months, however, will apparently lead to a figure per year much inferior to the 12 to 50 leaves per seedling after one year reported for the Southeast coast of India (*loc. cit.*, Kathiresan *et al.*, 2000).

None of the observed differences between Sri Lanka and Kenya can be directly linked to rainfall data. All experimental planting was done at the beginning of the rainfall peak in the wet season : in Sri Lanka this is September and in Kenya March-April (Kairo, 1995). The discontinuity in the development of *B. gymnorrhiza* in Sri Lanka (Fig. 3c), which is to lesser extents visible in the two *Rhizophora* species as well, at first sight appears not to be related to rainfall, because the rainfall pattern of 1999 seems not different from the average rainfall pattern over the last 50 years (Fig. 4). However, a slight delay in the start of the rains in 1999 with an average rainfall for March of only 57% of the 1950-1999 average for the same month, suggests that drought may have played a role. Physical damage or one or another type of pathogen are possible responsible for the discontinuous observations.

The present study shows that the post-dispersal development status of *Bruguiera gymnorrhiza*, *Rhizophora apiculata* and *R. mucronata* is influenced by the species composition and the environmental conditions of the forest patch in which the propagules strand. This study suggests that not only the common abiotic variables such as light may have an impact on the variables, but also for example the amount of leaf litter on the soil or the degree of soil consolidation.

## Acknowledgements

We are very grateful to Fatuma M. Saidi and Y.L. Michael Vijedasa for their practical help in the field and to Ludwig Triest for his critical comments on the paper. Research financed by the European Commission (Contract EBR IC18-CT98-0295), and with a specialisation fellowship of the Flemish Institute for the advancement of scientific-technological research in the industry (IWT).

## References

See Bibliography

**Table 1.** Statistical results from the rooting performance 'within' and 'between' species, forest patches, sites and seasons comparisons. Where significance levels varied little over time the results of statistical values for the respective tests were summarised as a range. Data after a given amount of time (w = weeks) on the other hand, have been indicated as a superscript. Numbers between parentheses correspond to the numbers in the text.

| Place | Statistic value | d.f. | p-value | |
|---|---|---|---|---|
| **Regeneration between *R.* spp and *B. gym* (1999)** | | | | |
| **in Galle** | | | | |
| **in EA and R** | $0.000 < G < 2.720$ | 1 | n.s. | (3) |
| **in OS** $^{2w}$ | $G = 5.335$ | 1 | $0.02 < p < 0.05$ | (4) |
| **in Pambala** | | | | |
| **in AO** $^{>5w}$ | $G = 10.142$ | 10 | n.s. | (8) |
| **in EA** | $G = 21.504$ | 8 | $0.001 < p < 0.01$ | (9) |
| **in LR, M and R** $^{2w}$ | $10.588 < G < 26.200$ | $2 < d.f. < 4$ | $0.001 < p < 0.02$ | (10) |
| **in R** $^{>5w}$ | $G = 13.174$ | 10 | n.s. | (11) |
| **Regeneration between forest patches** | | | | |
| **in Galle** | | | | |
| **for *B. gym* in 1998** $^{1w}$ | $G = 8.581$ | 6 | n.s. | (1) |
| **for *B. gym* in 1998** $^{2w}$ | $G = 20.244$ | 6 | $0.001 < p < 0.01$ | (2) |
| **for *B. gym* in 1999** $^{2w}$ | $G = 4.071$ | 4 | n.s. | (5) |
| **for *R. api* in 1999** $^{2w}$ | $G = 6.505$ | 6 | n.s. | (6) |
| **in Pambala (1999)** | | | | |
| **for *A. off*** $^{1w}$ | $G = 7.365$ | 9 | n.s. | (7) |
| **for *B. gym*** $^{2w}$ | $G = 21.266$ | 12 | $0.02 < p < 0.05$ | (12) |
| **for *B. gym*** $^{>5w}$ | $G = 14.159$ | 20 | n.s. | (14) |
| **for *R. api*** $^{2w}$ | $G = 27.791$ | 12 | $0.001 < p < 0.01$ | (13) |
| **for *R. api*** $^{>5w}$ | $G = 12.936$ | 16 | n.s. | (15) |
| **for *R. muc*** | $26.419 < G < 39.964$ | $12 < d.f. < 20$ | $0.001 < p < 0.02$ | (16) |
| **Regeneration between Galle and Pambala (1999)** | | | | |
| **all sp. in EA and R** $^{1w}$ | $0.801 < G < 3.740$ | 2 | n.s. | (17) |
| **B. gym in R** | $G = 1.741$ | 2 | n.s. | (18) |
| ***R. api* in R** | $G = 8.264$ | 3 | $0.02 < p < 0.05$ | (19) |
| **Regeneration between dry and wet season (Galle)** | | | | |
| **in EA** $^{1w}$ | $G = 1.844$ | 2 | n.s. | (20) |
| **in OS** $^{2w}$ | $G = 0.628$ | 1 | n.s. | (21) |
| **in R** $^{2w}$ | $G = 21.492$ | 3 | $p < 0.001$ | (22) |

Propagules : *A. off* = *Avicennia officinalis*; *B. gym* = *Bruguiera gymnorrhiza*; *R. api* = *Rhizophora apiculata*; *R. muc* = *Rhizophora mucronata*

Forest patches : AO = *A. officinalis*; EA = *Excoecaria agallocha*; LR = *Lumnitzera racemosa*; M = Mixed; R = *Rhizophora* spp.; OS = Open Space.

**Table 2.** Land/water ratio (dry season), soil salinity, total vegetation cover and propagule predator density in different forest patches of Galle and Pambala. The value between brackets indicates the cover excluding the sedge *Fimbristylis salbundia* subsp. *pentaptera*.

| | **Land/water ratio (% land)** | **Soil salinity (‰)** | | **Vegetation cover (%)** | **Predator density (individuals.m$^{-2}$)** |
|---|---|---|---|---|---|
| | | **dry season** | **wet season** | | |
| **Forest patches in GALLE** | | | | | |
| ***E. agallocha*** | 43.3 | 32.7 | 4.5 | 59.2 | 5.4 |
| **Open Space** | 9.8 | 29.4 | 5.2 | 65.1 (30.8) | 4.1 |
| ***Rhizophora* spp.** | 27.4 | 30.5 | 5.1 | 74.9 | 5.3 |
| **Forest patches in PAMBALA** | | | | | |
| ***A. officinalis*** | 95.0 | 25.0 | 1.0 | 65.0 | 5.0 |
| ***E. agallocha*** | 95.0 | 32.7 | 5.0 | 60.0 | > 10.0 |
| ***L. racemosa*** | 91.1 | 28.7 | 4.3 | 62.1 | 6.8 |
| **Mixed** | 85.0 | 27.2 | 0.7 | 52.9 | 3.2 |
| ***Rhizophora* spp.** | 89.0 | 24.3 | 2.1 | 73.6 | 2.0 |

**Table 3.** Absolute (mean ± standard deviation per m$^{-2}$) and relative (%) densities of naturally fallen propagules from the dominant propagule producing species in Galle (464 sample quadrats) and Pambala (516 sample quadrats). Relative densities are indicated between brackets. (Dahdouh-Guebas, unpublished data).

| | ***A. officinalis*** | ***B. gymnorrhiza*** | ***R. apiculata*** | ***R. mucronata*** |
|---|---|---|---|---|
| **GALLE** | | | | |
| **January 1997** | - - - | 0.0023 ± 0.0243 | 0.0078 ± 0.0555 | - - - |
| | - - - | (9.6 %) | (85.3 %) | - - - |
| **March 1998** | - - - | 0.4306 ± 2.8310 | 0.0242 ± 0.1432 | - - - |
| | - - - | (96.8 %) | (3.0 %) | - - - |
| **November 1999** | - - - | 0.0841 ± 0.4670 | 0.3231 ± 1.1240 | - - - |
| | - - - | (9.0 %) | (91.0 %) | - - - |
| **PAMBALA** | | | | |
| **February 1997** | 0.0123 ± 0.0979 | 0.0005 ± 0.0030 | 0.0145 ± 0.0164 | 0.0236 ± 0.0288 |
| | (12.1 %) | (0.1 %) | (31.7 %) | (43.1 %) |
| **April 1998** | 0.0786 ± 0.5450 | 0.0022 ± 0.0263 | 0.0264 ± 0.1028 | 0.0048 ± 0.0397 |
| | (61.0 %) | (0.3 %) | (36.6 %) | (1.6 %) |
| **November 1999** | 0.1245 ± 0.4933 | 0.0016 ± 0.0131 | 0.1877 ± 0.6158 | 0.4502 ± 0.9519 |
| | (20.7 %) | (0.0 %) | (41.8 %) | (36.1 %) |

Figure 1. Map of Sri Lanka with the climate zones according to Mueller-Dombois (1968) showing the two study sites.

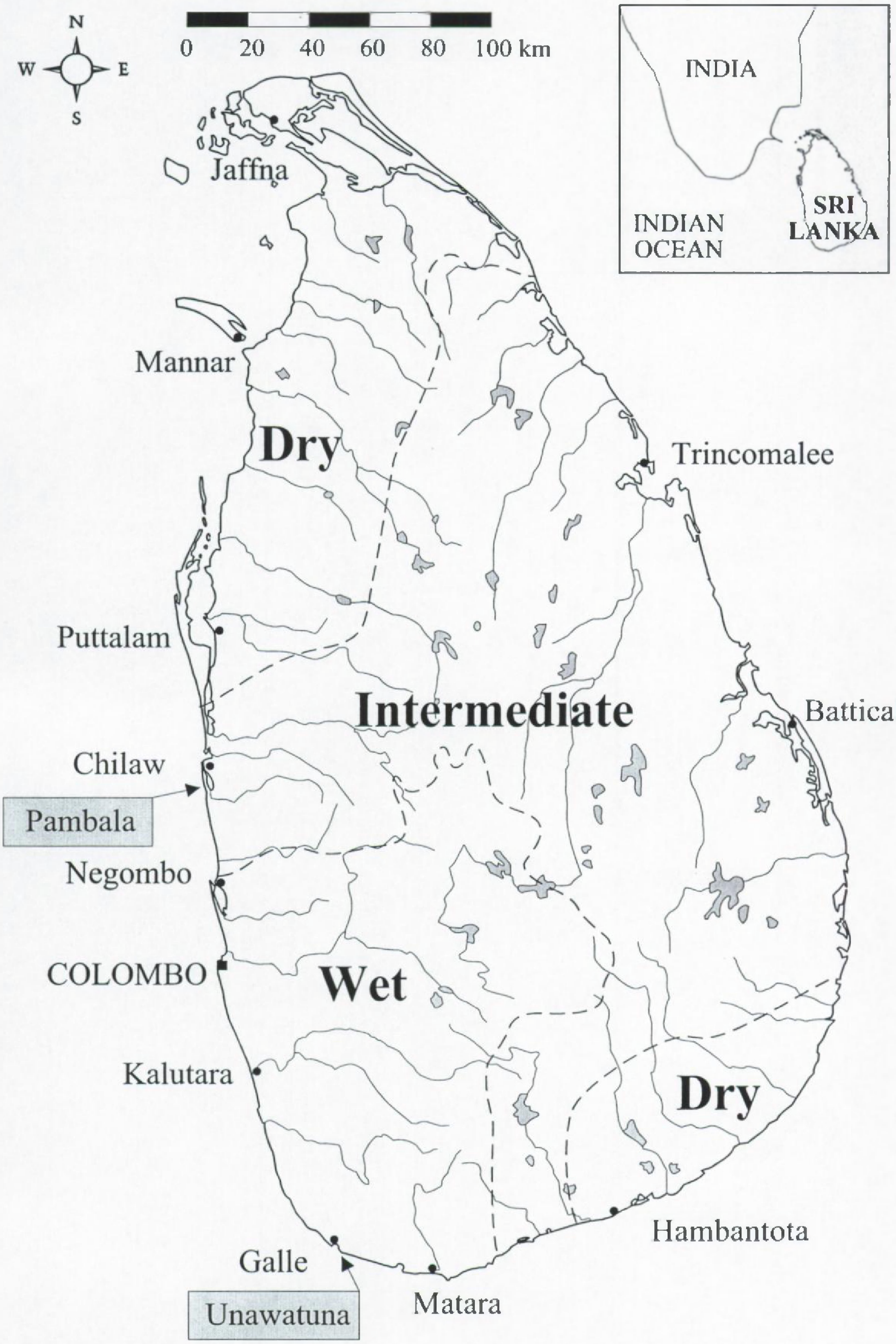
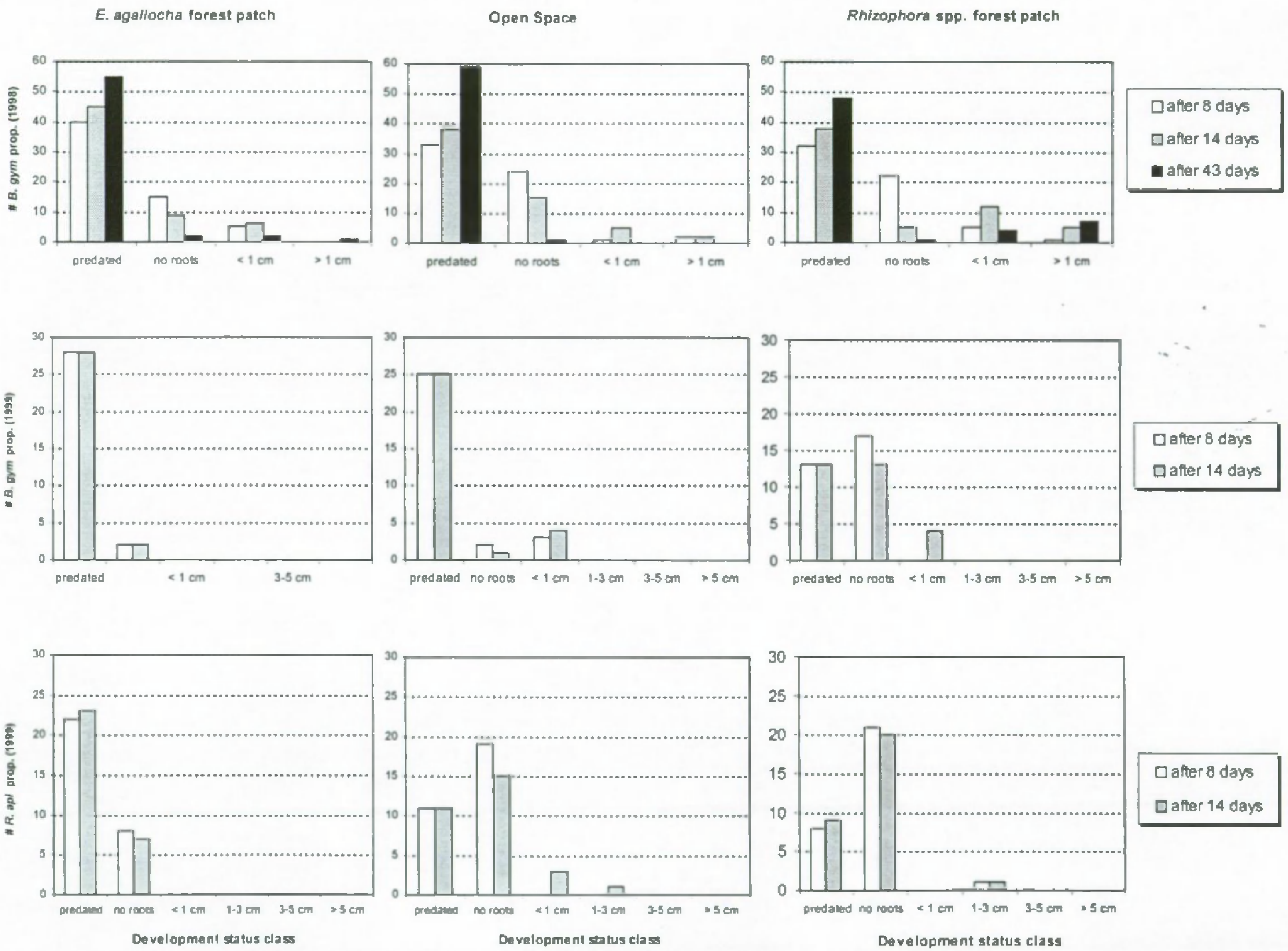


**Figure 2.** Root development status results of propagules of *Bruguiera gymnorrhiza* (*B. gym*) for 1998 and 1999 and of propagules of *Rhizophora apiculata* (*R. api*) for 1999 in the three forest patches in Galle (a), and of propagules of *Avicennia officinalis* (*A. off*), *B. gymnorrhiza*, *R. apiculata* and *R. mucronata* (*R. muc*) for 1999 in the five forest patches in Pambala (b).

(a)



(b)

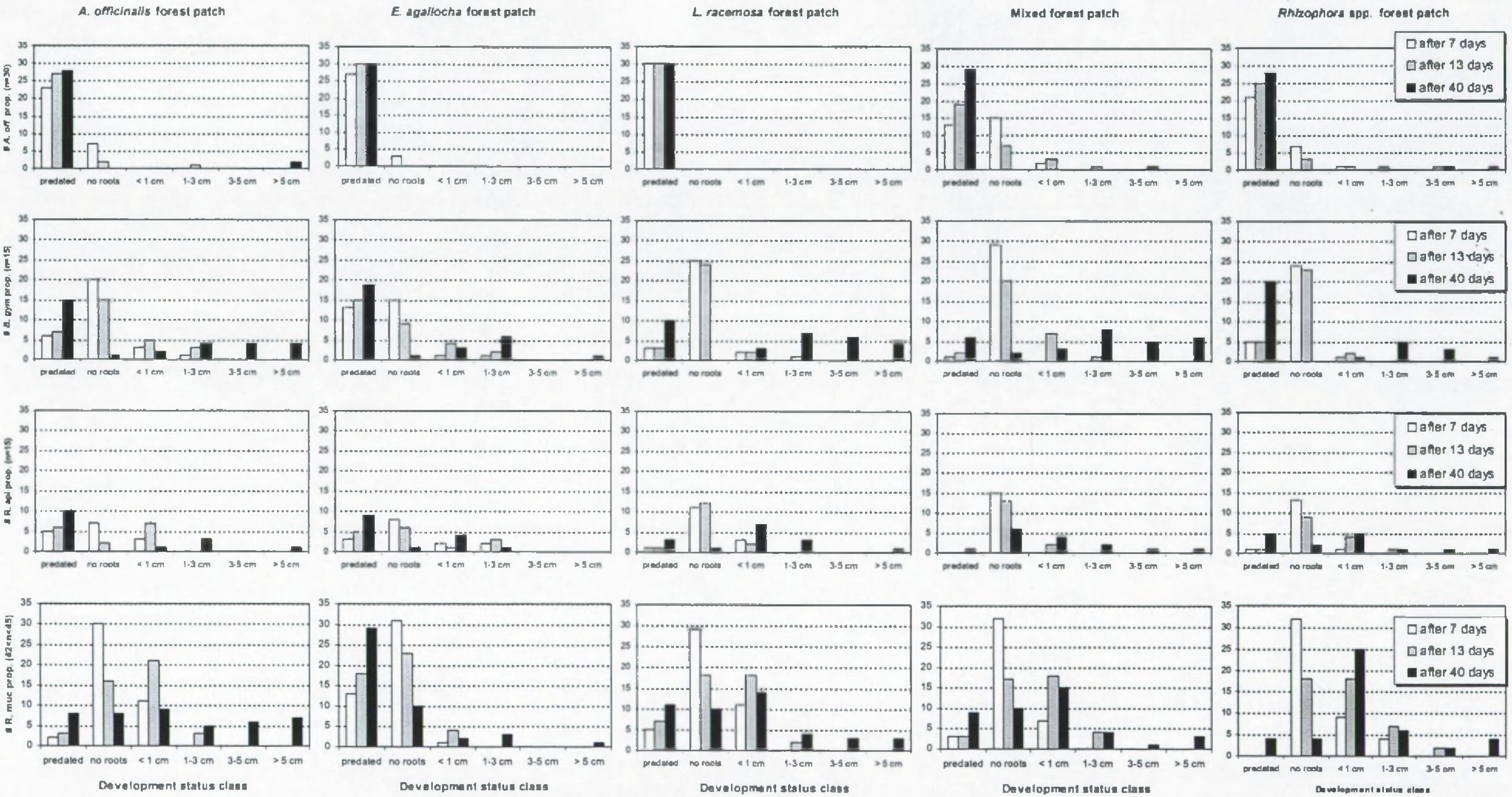
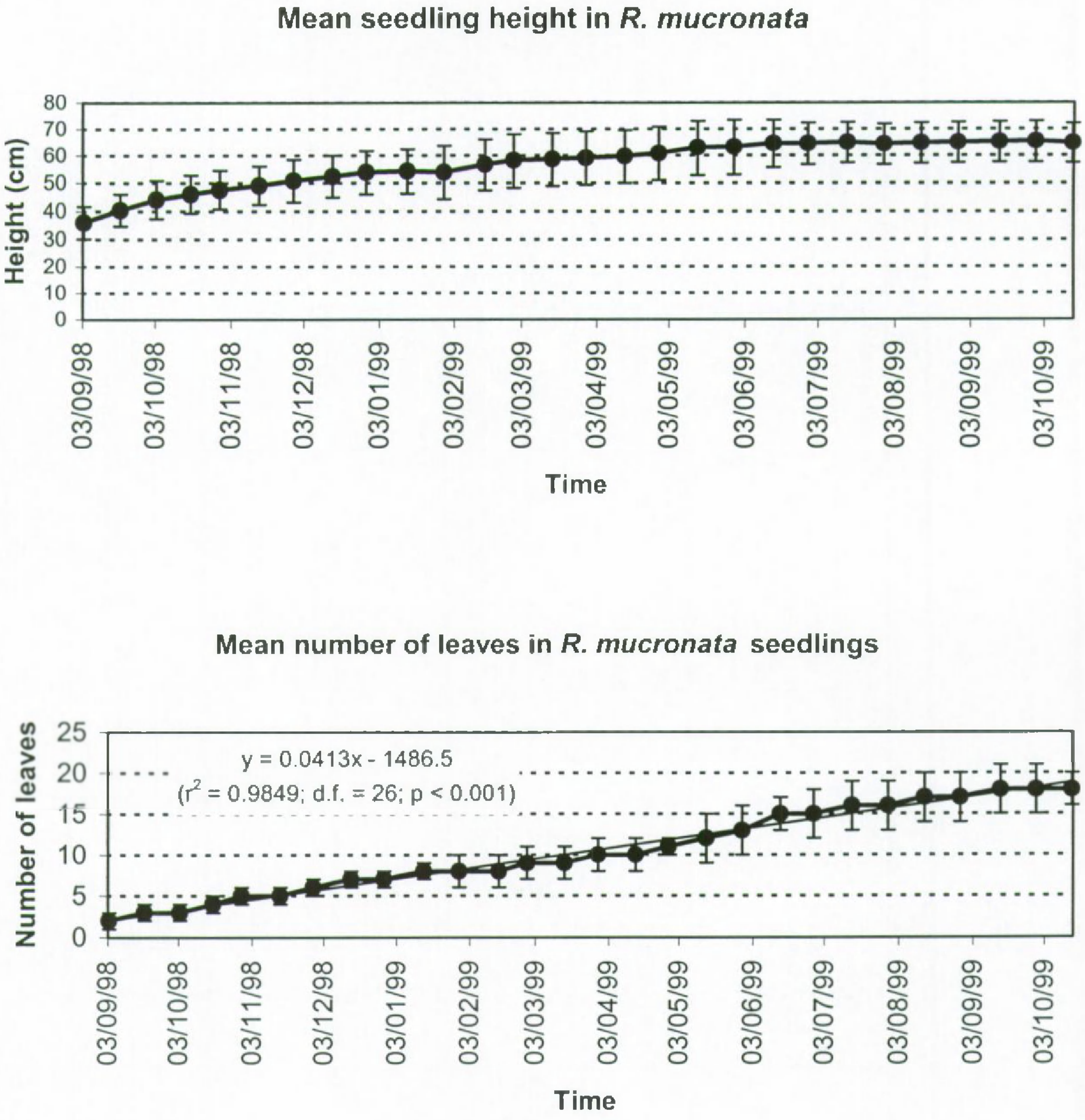
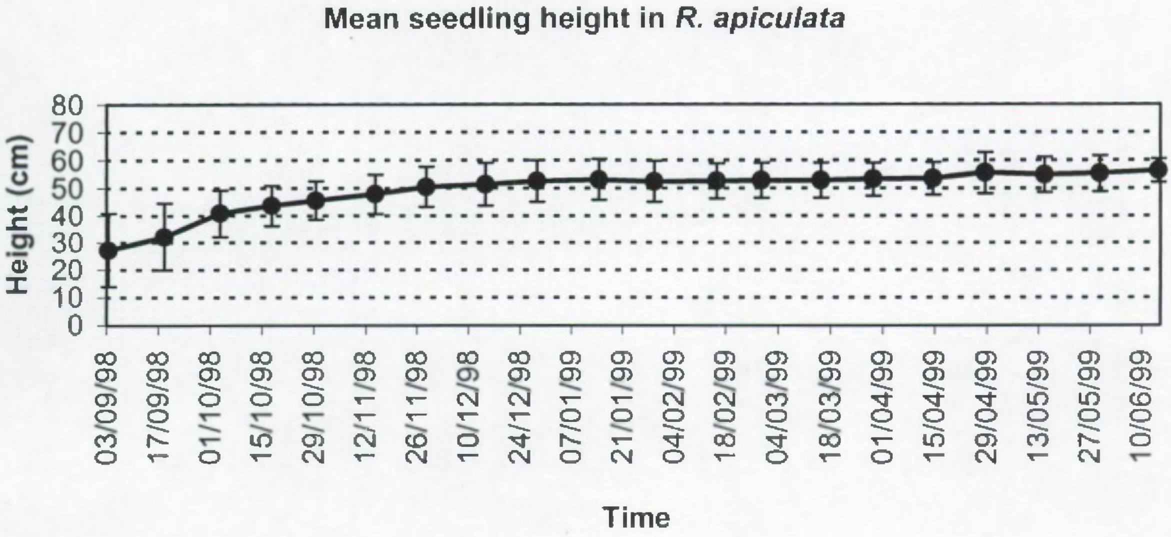

*A. officinalis* forest patch
*E. agallocha* forest patch
*L. racemosa* forest patch
Mixed forest patch
*Rhizophora* spp. forest patch
# A. off prop. (n=30)
# B. gym prop. (n=15)
# R. api prop. (n=15)
# R. muc prop. (42<n<45)
0
5
10
15
20
25
30
35
predated
no roots
< 1 cm
1-3 cm
3-5 cm
> 5 cm
Development status class
☐ after 7 days
▨ after 13 days
■ after 40 days

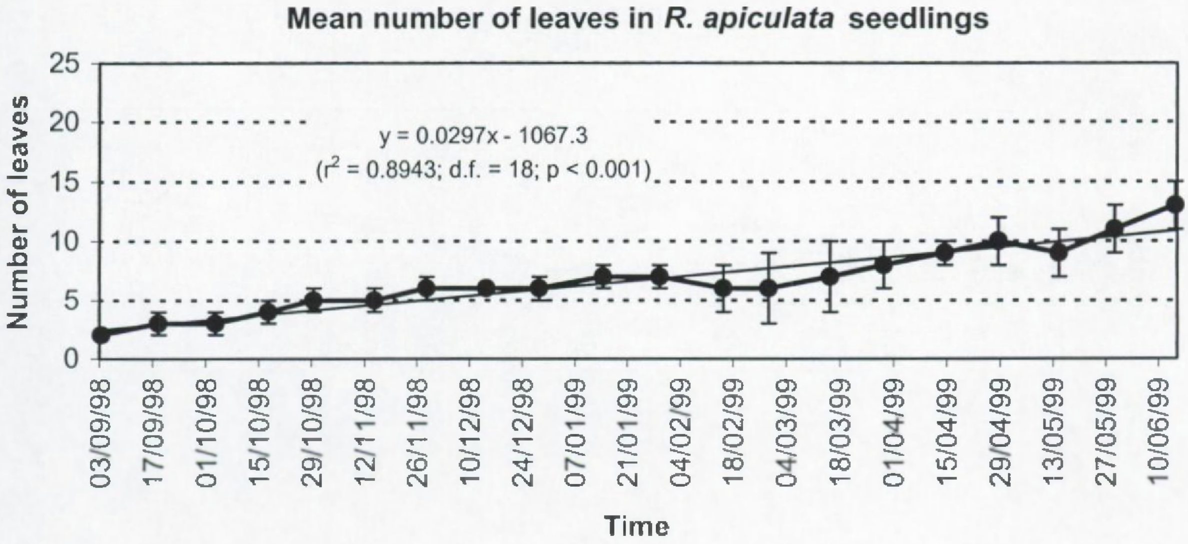
**Figure 3.** Evolution of the height and the number of leaves over a period of 13 months for 30 *Rhizophora mucronata* (a), 10 *R. apiculdta* (b) and 9 *Bruguiera gymnorrhiza* propagules (c). The regression line and its equation, as well as the coefficient of determination and its significance are given for the linear regressions. The error bars represent standard deviations.

(a)

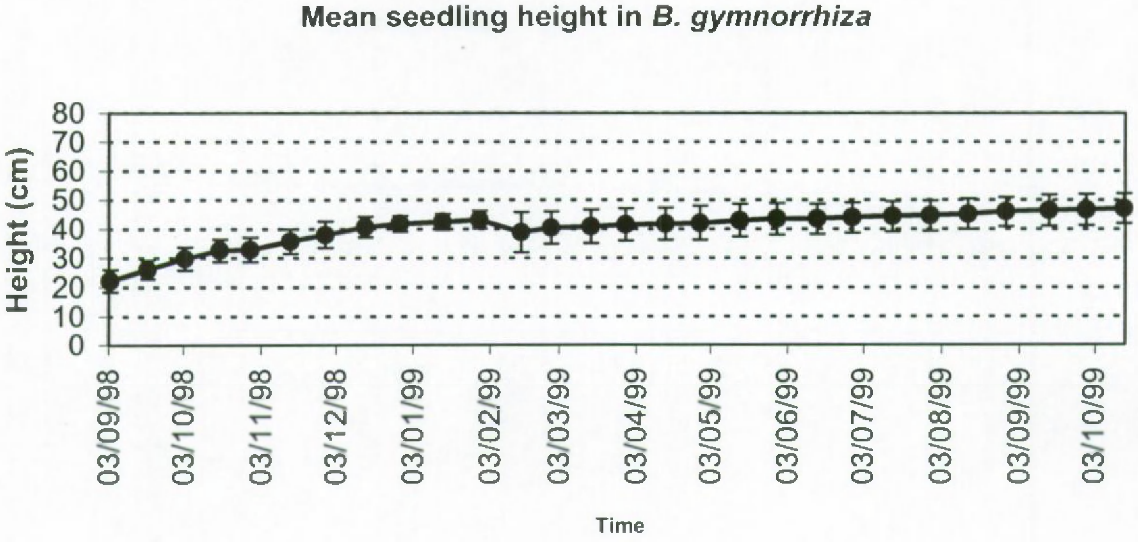


(b)

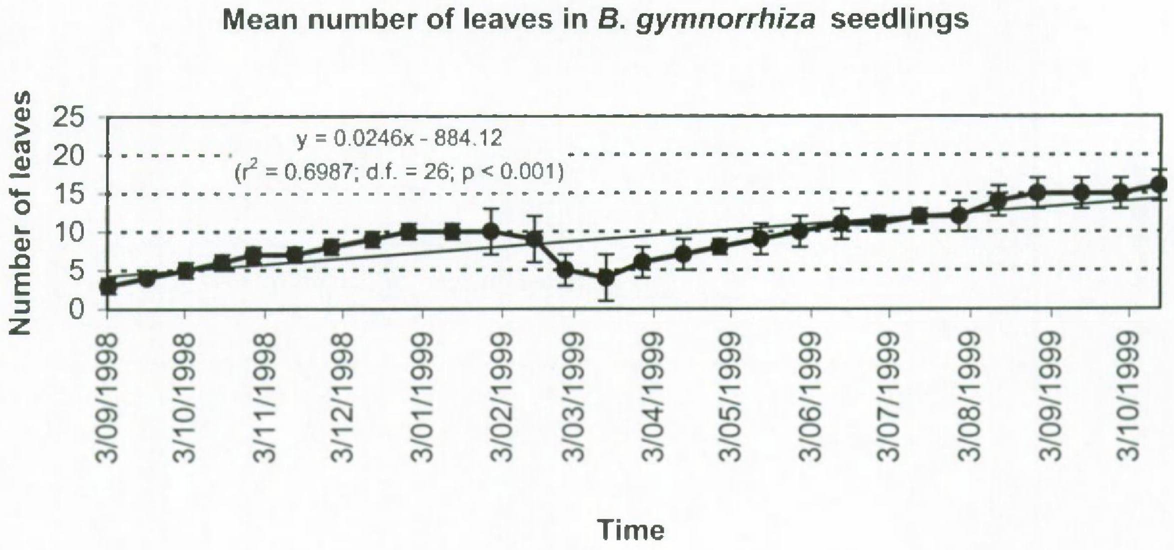

Mean seedling height in *R. apiculata*
Height (cm)
0
10
20
30
40
50
60
70
80
03/09/98
17/09/98
01/10/98
15/10/98
29/10/98
12/11/98
26/11/98
10/12/98
24/12/98
07/01/99
21/01/99
04/02/99
18/02/99
04/03/99
18/03/99
01/04/99
15/04/99
29/04/99
13/05/99
27/05/99
10/06/99
Time


Mean number of leaves in *R. apiculata* seedlings
Number of leaves
0
5
10
15
20
25
y = 0.0297x - 1067.3
($r^2$ = 0.8943; d.f. = 18; p < 0.001)
03/09/98
17/09/98
01/10/98
15/10/98
29/10/98
12/11/98
26/11/98
10/12/98
24/12/98
07/01/99
21/01/99
04/02/99
18/02/99
04/03/99
18/03/99
01/04/99
15/04/99
29/04/99
13/05/99
27/05/99
10/06/99
Time

(c)

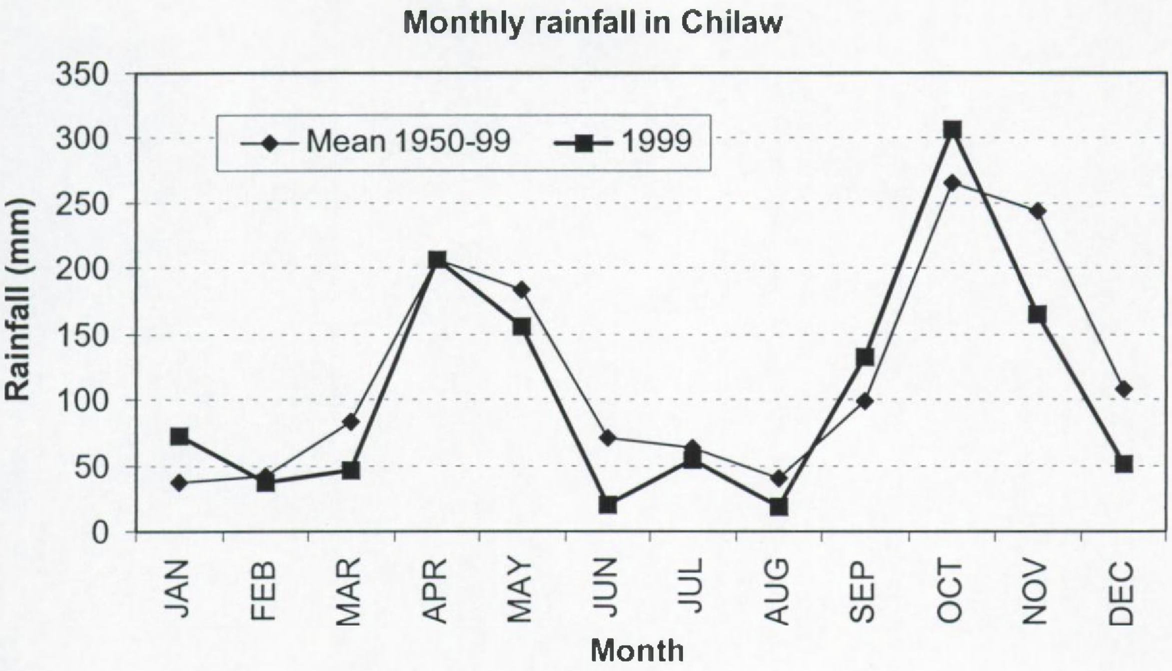


Mean seedling height in *B. gymnorrhiza*



Mean number of leaves in *B. gymnorrhiza* seedlings

**Figure 4.** Rainfall pattern in Chilaw in 1999 as compared to the average rainfall pattern over the last 50 years.



# Chapter XIII.

## Are the northernmost mangroves of West Africa viable ? A case-study in the Parc National du Banc d'Arguin, Mauritania.

Dahdouh-Guebas, F. & N. Koedam

In press for

*Developments in Hydrobiology*

# Are the northernmost mangroves of West Africa viable ?
## - a case study in Banc d'Arguin National Park, Mauritania -

Farid Dahdouh-Guebas & Nico Koedam

*Laboratory of General Botany and Nature Management, Mangrove Management Group, Vrije Universiteit Brussel, Pleinlaan 2, B-1050 Brussel, Belgium (E-mail : fdahdouh@vub.ac.be, nikoedam@vub.ac.be).*

### Abstract

In the Parc National du Banc d'Arguin (PNBA) in Mauritania, the mangroves of the West-African coast reach their northernmost distribution and comprise exclusively *Avicennia germinans*. As a biogeographically marginal, monospecific mangal in an area where freshwater availability has decreased over the last decades, concern about the survival of the mangroves, has been expressed. As yet, a description was lacking and no data regarding the fitness of *A. germinans* in the PNBA were available.

The mangrove and associated vegetation nearby Cape Timiris (southern border of the PNBA) was mapped in January 1998 and described for the adult, young and juvenile vegetation layer, along the lagoon perimeter of about 4 km. Physiognomic aspects of the mangroves were compared with those of a mangrove formation on the tidal island of Eizin further North and with those of the northernmost mangrove system, in Iouik. Three different formations were found (tall trees, wide trees and shrubs) with 'trees' as small as 30 cm flowering profusely. There were no site-related differences in leaf morphological characteristics. Propagules were available in large numbers but germinated successfully only where protected from the main Sahara wind currents and from the sun. Experiments to investigate the effects of predation or aridity (air exposure) on germination showed an absence of predator influences and that drought did affect viability of propagules. Release of propagules at the time of spring tides may favour colonisation of new areas. Future management plans can consider the collection and broadcasting of fresh propagules, as well as favouring free play of hydrodynamics (incl. flooding, breaching of barries) in the system.

Except for inappropriate topographical conditions (mangroves growing in terrestrial locations, with little chance for propagule survival) *A. germinans* did not show signs of reduced vitality at its biogeographical limit.

Keywords : mangrove, *Avicennia germinans*, physiognomy, regeneration, predation, biogeography, Mauritania.

## Introduction

Most mangroves are found between the Tropic of Cancer and the Tropic of Capricorn on all continents. Along the West-African coast mangroves reach their northernmost distribution in the Banc d'Arguin National Park, Mauritania, being composed exclusively of *Avicennia germinans* (L.) Stearn 1958 (= *Avicennia nitida* Jacq. 1760, = *Avicennia tomentosa* Jacq. 1760, = *Avicennia africana* Palisot de Beauvois 1805, according to Tomlinson, 1986). Stretched over more than 180 km Mauritanian coastline (around 20°N) and covering 12,000 km$^2$ (Gowthorpe, 1993), the Parc National du Banc d'Arguin (hereafter called PNBA) comprises desert, coastal swamps, small islands and shallow coastal waters. The austerity of the Sahara desert and the biodiversity and productivity of the upwelling marine system in a land and seascape of exceptionally contrasting natural value have seen that this site was inscribed as a World Heritage Site in 1989. A wide variety of migratory birds spend the winter in the PNBA (Ens *et al.*, 1990), and the monk seal and several species of sea turtle and dolphin, the latter of which are reported to assist fishermen in attracting and containing shoals of fish (Kane *et al.*, 1993), can also be found there (among others Wolff *et al.*, 1993a) and in the adjacent Cap Blanc satellite reserve.

World-wide human interference in mangrove areas has caused substantial changes in both physiognomy and species composition. The ecological and derived socio-economical importance of mangrove areas is however established clearly and a will to protect and manage the mangrove ecosystems in general (*e.g.* Charter for Mangroves, Field, 1995), and for the PNBA in particular (N'Gaïdé & Nicoll, 1994; Campredon & Gawler, 1998) can be discerned clearly. This is not matched by our understanding of factors governing mangrove establishment, dynamics and regeneration, an ignorance that impedes rational management plans. Socio-economically the mangroves are of little importance to the fisher folk villages in the PNBA Rather, its biogeographical interest must be considered. It is alarming that, according to Mahé (1985) and Gowthorpe (1993), the region of the PNBA testifies of the past existence (5,000 – 4,000 B.P.) of a more extended mangrove ecosystem (*e.g.* around Cape Timiris and Bay of St. Jean). Together with a poor regeneration of mangroves highlighted in the General Plan for Research in the PNBA (Greth, 1994), this could indicate that the disappearance of mangroves at this latitude is inevitable.

The aim of the present study is to provide a description of the mangrove vegetation around Cape Timiris as a reference basis, and to compare it with preliminary descriptions for all other mangrove systems currently known within the PNBA Descriptions of the vegetation, its structure and its current state, and aspects of regeneration were considered. Factors that could interfere with regeneration, such as aridity or predation stress, were experimentally approached.

## Description of the sites studied

The more detailed part of the study was done in and around the Lagoon of Cape Timiris or Râs Timirist (19°23' N), located a few kilometers North-West of the village of Nouâmghâr (also referred to as Mamghar) (Fig. 1). One part of the lagoon is locally called Al'Ain, Arab for 'eye', because of the eye-shaped form of the lagoon. We will further refer to this section of the lagoon as Al'Ain, and to the small islet in the middle of Al'Ain as 'Iris'.
Along the Bay of Saint Jean sites lodging mangroves were studied, as well as the northernmost mangrove system a few kilometres north of the village of Iouik (also spelled as Iwik) (Fig. 1). Finally, an inventory was made of the vegetation along two transects on the tidal island of Eizin (Fig. 1). This island is located north of the island of Tidra, between the islands of Niroumi and Arel, as indicated by Gowthorpe (1993).

## Materials and methods

Field work was carried out between 18 January and 2 February 1998 and included the spring tide of 28/01/98. Results reported here (*e.g.* salinity, reproductive phenology, predatory stresses) should thus be interpreted within the frame of this time. Some of these biotic and abiotic factors might be different during other times of the year or during other years. However, there is on average little seasonal variation in temperature and precipitation in coastal Mauritania (Walter *et al.*, 1957). Although a mean precipitation of 24 mm is reported, some years are without any (Dia *et al.*, 1997). Some of the observations were purely descriptive, and were intended to form a basis for further research. In order not to interfere with mangrove regeneration, sampling of propagules was kept deliberately small. The term 'propagule' is frequently used to identify the viviparous structures of numerous mangrove tree species, however, according to some, the structure of the diaspore of *Avicennia* does not allow the application of this term.

A copy of the Map of West-Africa at scale 1 : 200,000 from the French National Geographic Institute (feuille NF-28-11-VIII) was redrawn, enhanced and corrected for Cape Timiris using a compass and one-meter steps after reconnaissance surveys. The maps from the entire lagoon and from the Iris in particular were digitised and combined with our vegetation data described underneath, in order to produce the first maps on a linear scale exceeding that of the currently available maps by more than 40 times.

Every mangrove tree or colony was described (density, colony diameter, diameter at breast height, tree height, reproductive phenological status) around the 4 km long circumference of Cape Timiris lagoon complex, with particular attention to Al'Ain. The Iris was considered to be representative for Al'Ain because of the presence of all different physiognomies for *Avicennia germinans* in a small area of approximately 2,500 $m^2$ : relatively large adult trees, shrubs, young plants and saplings (individuals with maximum 3 leaf pairs). Therefore the vegetation of this islet was determined and described in detail. The same was done for a transect of about 200 m, crossing Al'Ain from the Atlantic coast to the Iris, at one-meter intervals.

The few mangroves along the Bay of St. Jean (south-eastern side) were described like the ones around Cape Timiris. The vegetation of the eastern side of the lagoon, which opens to the Bay of St. Jean at its southern bank, was described on a plot of 200 $m^2$. Since this bay does not have a name on the topographic map we will refer to it as Flamingo Bay, because of the continuous presence of flamingos during our field work there. This area is located at 5 km East Northeast from the Life Base at Nouâmghâr on the road to Iouik.
Each single mangrove tree located in the creek system to the North of Iouik was described like the mangroves around Cape Timiris.

On Eizin, the plant species along two line transects of 400 m were recorded at one meter intervals. The transects were oriented close to the WNW-ESE direction and the centre of the first transect (-77° N) was crossing the start of the second one (-102° N). Mangrove trees were described like those around Cape Timiris.

In all sites length and width of 25 to 197 leaves per population from 11 to 25 different trees per population were measured (different sites were assumed to comprise different populations). A distinction was made between flowering and non-flowering branches, and alternating the left and right leaf of the third leaf pair from the apex was taken for measurement.

On five randomly selected and individually marked branches of a tree, three generations of flowers were followed over a period of 6 days in order to estimate the duration of flowering. The first generation (existing flowers of unknown age) was counted on day 1 or 2, whereas the second and third generation started on day 3 and day 4 respectively.

Three artificial short term plantations, with 10 to 20 mangrove propagules each, were followed in order to check for propagule predation : underneath adult *Avicennia germinans* trees, in the intertidal zone dominated by the fiddler crab *Uca tangeri* Eydoux and in the infralittoral dominated by the predator *Callinectes marginatus* A. Milne-Edwards. In seven artificial plantations, with 8 to 33 propagules each, germination of the propagules was followed : in a sand basin (approximately 50 x 50 x 40 cm) dug into the soil, along a land-water transect within transparent PVC bottles from mineral water (1.5 l), and along a land-water transect within small nylon bags (5 x 10 cm, < 1 mm mesh size), all of these experimental settings exposed to the tides. Another plantation was made underneath an adult *Avicennia germinans* tree and one more inside dead coastal seagrass heaps, both of them only susceptible to spring high waters. For the remaining three plantations, propagules were submerged into a humid, saline environment for 5 days after one of the following treatments :

- TREATMENT A : collection of fresh and mature propagules found on or underneath an adult individual and exposed to air and sun for 24 h (n=16);
- TREATMENT B : collection of fresh and mature propagules found on or underneath an adult individual and submerged in a humid, saline (49 ‰) environment for 24 h (n=17);
- TREATMENT C : collection of dried/desiccated seeds found on the soil in a zone invaded by desert sand and submerged into a humid, saline environment for 24 h (n=15).

Finally, the root systems of 19 saplings were exposed to verify whether the plant originated from a propagule or from the cable root of another mangrove. The choice of the individuals was such that they apparently seemed to follow below ground cable roots, suggesting development from the latter.

Salinity (using an Atago hand refractometer), light intensity (using a Lutron luxmeter) and topography (using water tubes and recording differences in height at regular intervals) were measured and described in every site.

## Results

### *Distribution of mangrove stands*

The location, vitality and physiognomy of the mangroves around Cape Timiris is shown in figs 2 and 3. To visualise the vitality, the mangrove vegetation was subdivided into four classes according to their density and regeneration state:

- dense mangrove, forming a visual screen (*cf.* Fig. 3c);
- intensely regenerating mangrove, which has a high presence (> 0.05 $m^{-2}$) of small individuals or saplings, defined as a young plant with more than 6 leaves;
- mangrove in a depauperate state with desiccated or malformed leaves or propagules.
- mangrove in an apparently 'normal state', which includes mangroves that do not fall into one of the former categories.

The mangroves located on the Iris are shown in detail in the box in figure 2, and in figure 4 the different assemblages of vegetation, including *Avicennia germinans*, *Arthrocnemum macrostachyum* (Moric.) Moris & Delp., *Salicornia senegalensis* A. Chev., *Suaeda* sp., *Sesuvium portulacastrum* (L.) L. and *Zygophyllum gaetulum* Emberger & Maire subsp. *waterlotii* (Maire) Dobignard, Jacquemoud & Jordan (nomenclature according to Lebrun, 1998). Salinities measured within Al'Ain around 26 January 1998 are mapped in figure 5.

### *Stand characteristics*

The vegetation of the transect crossing Al'Ain from the Atlantic coast to the Iris corresponds with that observed on the Iris (Fig. 3), except for *Z. gaetulum* subsp. *waterlotii* which was absent along the transect.

The junction between a marine creeklet (with the predator *Callinectes marginatus* at 3 - 4 specimens.m$^{-2}$) and the mangrove-seagrass intertidal zone with the prey crab species *Uca tangeri* (> 50 specimens.m$^{-2}$) at the connection between Flamingo Bay and the Bay of St. Jean, makes this a site with strong interactions between predator and prey, and among predators. The present densities observed for *C. marginatus* – about the same densities were observed in Al'Ain - are 3 to 10 times higher than previous records of 1 specimen per 1 – 10 m$^2$ (Wolff *et al.*, 1993b).

In and around our experimental relevé the soil consists of a peaty substrate, originating from accumulations of dead *Zostera noltii* Hornem. and *Cymodocea nodosa* (Ucria) Aschers. (amongst others) seagrass accumulations, on a sandy soil layer, which are brought to the surface by *U. tangeri*. In and around our experimental relevé this crab seems to play an important role in mixing organic and inorganic material in the soil by its burrowing activities. The total cover of the vegetation in our plot of 200 m$^2$ was 70 %, of which 65 % was located in the herb layer, dominated by *Sesuvium portulacastrum* (about 60 %) and some *Suaeda* sp. individuals (about 5 %). The remaining 5 % was in the shrub layer (1 m and above), where one *Arthrocnemum macrostachyum* and one *Avicennia germinans* individual were present.

In Iouik, at the northernmost biogeographical limit, the mean height (± S.D.) of the 11 *A. germinans* trees or colonies present, was 1.32 ± 0.60 m, and the flowering and fruiting percentages were 72.7 % and 36.4 % respectively. The same parameters for the 41 trees along the two 400 m transects on Eizin was 1.16 ± 0.26 m, 97.6 % and 65.9 % respectively. Apart from *Avicennia germinans* only two plant species were present along these transects : cf. *Spartina maritima* (Curt.) Fern. and *Zostera noltii*. The transects are shown in figure 6 (a and b). Elsewhere on Eizin also *Sporobolus virginicus* (L.) Kunth was observed.

### *Flowering and leaf characteristics*

The record on *Avicennia germinans*' flowering period is shown in figure 6.
Figure 7 shows the association between leaf width and length for all leaf samples. There was no difference between leaves originating from flowering branches and leaves originating from non-flowering branches, or between leaves from different sites (confronting linear regressions between sites gave the following ANCOVA results : F (intercept) = 0.939; d.f. = 3 & 357; n.s.; and F (slope) = 1.365; d.f. = 3 & 360; n.s.). The data in figure 7 do not show a distinction based on shape either. Leaf shapes of *A. germinans* mangroves could be typified approximately within a range from a short elliptical shape (about 2.5 times longer than wide) to a lancet shape (more than 4 times longer than wide), but these types did not associate with particular sites.

Results from visual observations have been included directly into the discussion section.

### *Predation and germination experiments*

The results of the predation experiments on the *Uca tangeri* mudflat, under adult *A. germinans* trees and in dead seagrass accumulations are shown in table 1. Of the 20 propagules in the *Callinectes marginatus* area 7 propagules or labels were lost during the spring high tide. Of the remaining propagules, one had rotten, two had split and nine had germinated by the following day. The results of the germination experiments in the basin and along the transects are given in table 2. The results of germination experiments with *A. germinans* propagules with pericarp closed, which were submerged after various treatments are : 12 (75 %), 2 (12 %) and 15 (100 %) with no change, and 4 (25 %), 15 (88 %) and 0 (0 %) with a split pericarp, for treatment A, B and C respectively, indicating highly significant differences between dry seeds or seeds exposed to air and sun and fresh seeds ($\chi^2 = 28.321$; d.f. = 2; $p < 0.001$). Exposure of the root system of 19 saplings with a distance to the nearest adult tree ranging from 0.5 to 9.5 m revealed that 17 were originating from propagules (showing no possible connection to any cable root), whereas no conclusive result could be obtained on the remaining two.

## Discussion

Compared with *Avicennia marina* (Forsk.) Vierh. growing in the United Arab Emirates at about 25°N (ElAmry, 1998), *Avicennia germinans* apparently does well at the Banc d'Arguin National Park, at least in Al'Ain and Iouik, the northernmost population. From the point of view of general appearance, the Eizin population appears to perform less well in that it is rather stunted and crooked. Hardly any dead wood and no sign of exploitation or grazing was observed in any of the sites. Although the mangrove is generally small in size and even displays a dwarf growth, there seems to be regeneration in the middle of stands, judging from propagule production or the density of juveniles. Saplings were found in depressions protected from wind and waves, and inundated at (spring) high tides, except in the daily flooded Eizin island. Some young plants less than 40 cm tall were already flowering luxuriously, yet without ever bearing fruits, unlike taller trees observed at the same time.

### *Flowering in* **Avicennia germinans**

Although single flowers of *A. germinans* can flower for at least 5 days, we could not discern a clear phenology. There is no indication for a maximum flowering period and potential for propagule production, some flowers desiccate quickly, others remain for longer periods. Considering the number of flowers per inflorescence and the individual flowering time, the inflorescences indicate flowering for at least several weeks. A majority of the flowers did not appear to form propagules. Similarly, for *Avicennia marina* it has been reported that one third of the flower primordia survive to become open flowers, but only 3 % survive to produce viable fruits (Clarke, 1995). At the PNBA, the flowers were visited (but not necessarily pollinated) by ants, flies, butterflies and wasps (the latter observed only in Iouik) in decreasing order of frequency of casual observations. A long flowering period is not necessarily correlated to a long fertility period.

### *Propagule production in* A. **germinans**

Propagule production is irregular : certain individuals produce no propagules, while nearby others produce many. Inflorescences might seem desiccated after the flowering period. Whereas *Avicennia germinans* has been reported to reach a reproductive stage when plants are 2 to 3 m tall elsewhere (Lescure, 1980), in the PNBA shrubs of 1 to 1.5 m can be as fertile as trees. However, no propagules were observed on plants of less than 1 m, even though these were often flowering profusely. Where observed, propagules seemed to grow protected from the main Sahara wind currents, which have been reported to blow up to 8 m $sec^{-1}$ in the PNBA (Monod, 1977). It is possible that for the whole mangrove of the PNBA propagule production is rather restricted (*i.e.* intense flowering and propagule density not correlated). It is common that plant species at their biogeographical limit display a decreased fertility, preceded by a geographically decreasing flowering, as for instance in *Avicennia marina* (Duke, 1990). The latter was not observed, but decreased fertility could be a problem for *Avicennia germinans* in the PNBA

### *Predation of* A. **germinans** *propagules*

Recently, much evidence of the possible impact of brachyuran fauna on mangrove regeneration (among others McKee, 1995a, 1995b; McGuinness, 1997b; Dahdouh-Guebas *et al.*, 1998) has been published. However, in the PNBA no predation was observed in the intertidal zone occupied by *Uca tangeri*, which implies also the absence of predation by birds or fish in this area. The experimental problem encountered due to water dynamics (waves, tides) in the infralittoral zone occupied by *Callinectes marginatus* and the consequent loss of propagules and labels did not affect the interpretability of the results. Indeed, the propagules that were recovered (65 %), did not show any sign of predation, which would imply the absence of predation by fish or other crustaceans as well. The artificial plantations under the adult *A. germinans* tree and in dead seagrass accumulations also remained intact, leading to the overall conclusion that in the PNBA predation at the early stage is not a factor in the establishment of its mangroves.

### *Germination of* A. **germinans** *propagules*

A problem for mangrove regeneration in the PNBA is the dropping of propagules in environments that limit their development, often dry desert sand. In addition, an air and sun exposure of 24 h, which is compared to a natural situation, a 'mild' treatment, is enough to kill the propagules. This short-term die-off has been observed for *Avicennia marina* also (Osborne & Berjak, 1997). On the accumulations of dead seagrasses (*Cymodocea nodosa* and *Zostera noltii*) or under parental trees, naturally germinated propagules were observed. At the western side of the island of Tidra for the second consecutive year a small *Avicennia* population of young individuals (0.5 – 1 m height and flowering) was reported on dead seagrass accumulations (Tom van Spanje & Otto Overdijk, pers. comm., 1998). Many young plants were also observed in sebkhas[§], located behind the mangrove amongst the terrestrial vegetation and only flooded via small creeks at spring tides. It is during such spring tides that propagules are transported into these sebkhas and develop further.

---

[§] *sebkha*, a common wetland type in arid or semi-arid regions, is a North-African vernacular name for a natural, shallow, salty depression.

Submerged in water with a salinity between 40 and 50 ‰, both naturally fallen and artificially gathered propagules develop (splitting and shedding of the pericarp, rooting of the radicle and opening of the cotyledons) within a few hours. This ability is conserved for at least a week when the propagule is kept in humid, saline and shaded conditions. This development is the reaction of a living propagule and not a mechanical one due to water absorption, since propagules that were collected in sand or which were exposed to the sun did not behave in the same way.

### *Growth of* **A. germinans**

Often fresh, green shoots are observed on the plants. Apart from these, other leaves are frequently covered with a layer of red dust. A majority of the leaves have salt crystals on their adaxial surface (which is typical for *Avicennia,* Tomlinson, 1986), which redissolved in the morning dew, causing very high NaCl concentrations (> 120 ‰). The leaves of *A. germinans* did not show traces of herbivory by camels, goats, gazelles, insects, gastropods or any other animals (though most mangroves are easily accessible by land), neither did they show signs of disease. Grasshoppers and dragonflies were observed in the foliage of the mangroves. Occasional deformations of the mangrove leaves seemed to have been caused by mechanical injuries (wind) or by desiccating atmospheric condition in the early stage of leaf development. Pore or open water salinity is not a differential factor for the vitality of the mangrove. One could expect a relationship between salinity and mangrove vitality, height, flowering, leaf area, and so forth, but such a relationship was not apparent, even though interstitial and water salinity varies between 40 and 80 ‰, with peaks up to 100 ‰. A relationship between salinity and tree height for instance was absent ($r = 0.19$; d.f. = 7; n.s.), yet for other *Avicennia* species a clear relationship between these variables has been observed (Dahdouh-Guebas *et al.*, pers. comm. 1999, subm.d). The most probable relationship is that between salinity and seedling growth, as reported for *Avicennia alba* Blume (Dourado & Fong, 1983).

Leaf dimensions varied widely although there was no evidence from this study that larger leaves were likely to desiccate or that long, narrow leaves were more fragile. The leaf dimensions were not related to soil salinity (possible drought stress).

Randomly amplified polymorphic DNA (RAPD) analysis of 30 leaf samples of different *A. germinans* individuals for each of the populations visited, done in the Genetic Diversity Unit of the laboratory of General Botany and Nature Management at the Free University of Brussels, preliminarily suggests that, based on genetic characteristics, the *A. germinans* population from Eizin slightly differentiates from the mainland populations at Iouik, Bay of St. Jean and Cape Timiris (Abeysinghe, 1999).

Although Mauritanian mangroves may be under biogeographical retreat, there is, on the basis of our 1998 survey, no indication of an immediate threat to their survival. However, to maintain the mangroves, the management of the PNBA may consider a number of recommendations. First, the dynamics of small creeks and of the coastal dunes should be preserved and interference of motorable tracks with the system, as actually happens, should be avoided. Second, one could also consider the artificial dispersion of propagules, broadcasting them in the lagoon water, particularly those from the desertified zone in the southern extreme of Al'Ain, where no propagules apparently have any chance of survival. Depending on the degree of interference desired, a regeneration plot may be considered. However, for a region of high biogeographical importance for *Avicennia germinans* such as the PNBA, the genetic diversity pattern, and the northernmost occurrence and vitality of this species throughout the entire Atlantic biogeographical region or smaller geographic scales (*cf.* Duke *et al.*, 1998) must be further investigated.

## Acknowledgements

We are very grateful to Mr G. Hatti, Director of the Parc National du Banc d'Arguin, and to Prof. dr J.Cl. Lefeuvre, President of the Scientific Council of the PNBA, for the necessary authorisations to operate within the National Park, to Prof. dr. J.J. Symoens and Prof. dr. A. Robyns from the Foundation for the Promotion of Scientific Research in Africa, for support and Mr Abou Gueye, Chief of the Iouik Life Base, and particularly Mr Sall Alassane Mamadou, Chief of Nouâmghâr Life Base, for logistics and field assistance. We also thank Karen and Prof. dr. Olivier Hamerlynck for valuable information and hospitality, Prof. dr. Wim J. Wolff for scientific literature on the P.N.B.A, and an anonymous reviewer for help in improving the manuscript. The Foundation for the Promotion of Scientific Research in Africa, the Fund for Scientific Research (FWO) and the Vrije Universiteit Brussel (VUB) are acknowledged grateful for financial contributions. A specialisation fellowship of the Flemish Institute for the advancement of scientific-technological research in the industry (IWT) was granted to the first author. This work was presented on the "Science and Sustainable Management of Tropical Waters" Conference, 11-16 April 1999, Naivasha, Kenya and on the 15th Biennial International Conference of the Estuarine Research Foundation "Where THE River Meets the Sea", 25-30 September 1999, New Orleans, U.S.A.

## References

See Bibliography

**Table 1.** Results of experiments on the predation of *A. germinans* propagules in Al'Ain (Cape Timiris). The numbers given are cumulative (since beginning of experiment).

**(a) Predation site located on *Uca tangeri* mudflat**

| Date | Intact propagules | | | Lost propagules |
|---|---|---|---|---|
| | pericarp closed | pericarp split | rooting | |
| 21/01/98 (initial) | 10 | 0 | 0 | 0 |
| 22/01/98 | 10 | 0 | 0 | 0 |
| 23/01/98 | 10 | 0 | 0 | 0 |
| 24/01/98 | 10 | 0 | 0 | 0 |
| 25/01/98 | 10 | 0 | 0 | 0 |
| 26/01/98 | 5 | 5 | 0 | 0 |

**(b) Predation site located under adult *Avicennia germinans***

| Date | Intact propagules | | | Lost propagules |
|---|---|---|---|---|
| | pericarp closed | pericarp split | rooting | |
| 21/01/98 (initial) | 10 | 0 | 0 | 0 |
| 22/01/98 | 10 | 0 | 0 | 0 |
| 23/01/98 | 8 | 0 | 0 | 2 |
| 24/01/98 | 8 | 0 | 0 | 2 |
| 25/01/98 | 8 | 0 | 0 | 2 |
| 26/01/98 | 8 | 0 | 0 | 2 |

**(c) Predation site located in dead seagrass accumulations**

| Date | Intact propagules | | | Lost propagules |
|---|---|---|---|---|
| | pericarp closed | pericarp split | rooting | |
| 20/01/98 (initial) | 8 | 0 | 0 | 0 |
| 21/01/98 | 8 | 0 | 0 | 0 |
| 22/01/98 | 8 | 0 | 0 | 0 |
| 23/01/98 | 7 | 0 | 1 | 0 |
| 24/01/98 | 7 | 0 | 1 | 0 |
| 25/01/98 | 6 | 0 | 1 | 1 |
| 26/01/98 | 4 | 2 | 1 | 1 |

**Table 2.** Results of germination experiments on *A. germinans* in a basin and along the transects in Al'Ain (Cape Timiris). Spring tide was on 28/01/1998.

**(a) Propagules contained in a 50 x 50 x 40 cm sand basin**

| Date | Intact propagules | | | Lost propagules |
|---|---|---|---|---|
| | closed | open | germinating | |
| 22/01/98 | 18 | 0 | 0 | 0 |
| 22/01/1998 after 2h | 16 | 2 | 0 | 0 |
| 22/01/1998 after 4h | 14 | 4 | 0 | 0 |
| 23/01/1998 AM | 7 | 11 | 0 | 0 |
| 23/01/1998 PM | 7 | 11 | 0 | 0 |
| 24/01/98 | 7 | 11 | 0 | 0 |
| 25/01/98 | 6 | 12 | 0 | 0 |
| 26/01/98 | 3 | 11 | 0 | 4 |

**(b) Propagules contained in transparent PVC bottles along transect**

| Date | Number of open propagules of an initial 3 | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | B1 | B2 | B3 | B4 | B5 | B6 | B7 | B8 | B9 | B10 | B11 |
| 22/01/98 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 23/01/98 | 0 | 0 | 2 | 1 | 2 | 2 | 2 | 2 | 3 | 3 | L |
| 24/01/98 | 0 | 0 | 2 | 1 | 2 | 2 | 2 | 3 | 3 | 3 | L |
| 25/01/98 | 0 | 0 | 1 | L | 3 | 2 | 2 | 3 | 3 | 3 | L |
| 26/01/98 | 1 | L | L | L | L | L | L | L | L | L | L |

B1 = landside; B11 = seaside of intertidal zone; L = all propagules lost.

**(c) Propagules contained in nylon bags along transect**

| Date | Number of open propagules of an initial 3 | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | B1 | B2 | B3 | B4 | B5 | B6 | B7 | B8 | B9 | B10 | B11 |
| 22/01/98 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 23/01/98 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 2 | 1 | 2 |
| 24/01/98 | 0 | 0 | 0 | 3 | 1 | 1 | 3 | 1 | 3 | 2 | 2 |
| 25/01/98 | 0 | 0 | 1 | 3 | 3 | 3 | 3 | 2 | 3 | 3 | 3 |
| 26/01/98 | 0 | 0 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 |

B1 = landside; B11 = seaside of intertidal zone.

**Figure 1.** The southern part of Banc d'Arguin National Park (Mauritania, N.-Africa) and the location of our study sites. The connection between Flamingo Bay and the Bay of St. Jean has been given in detail (not on scale).

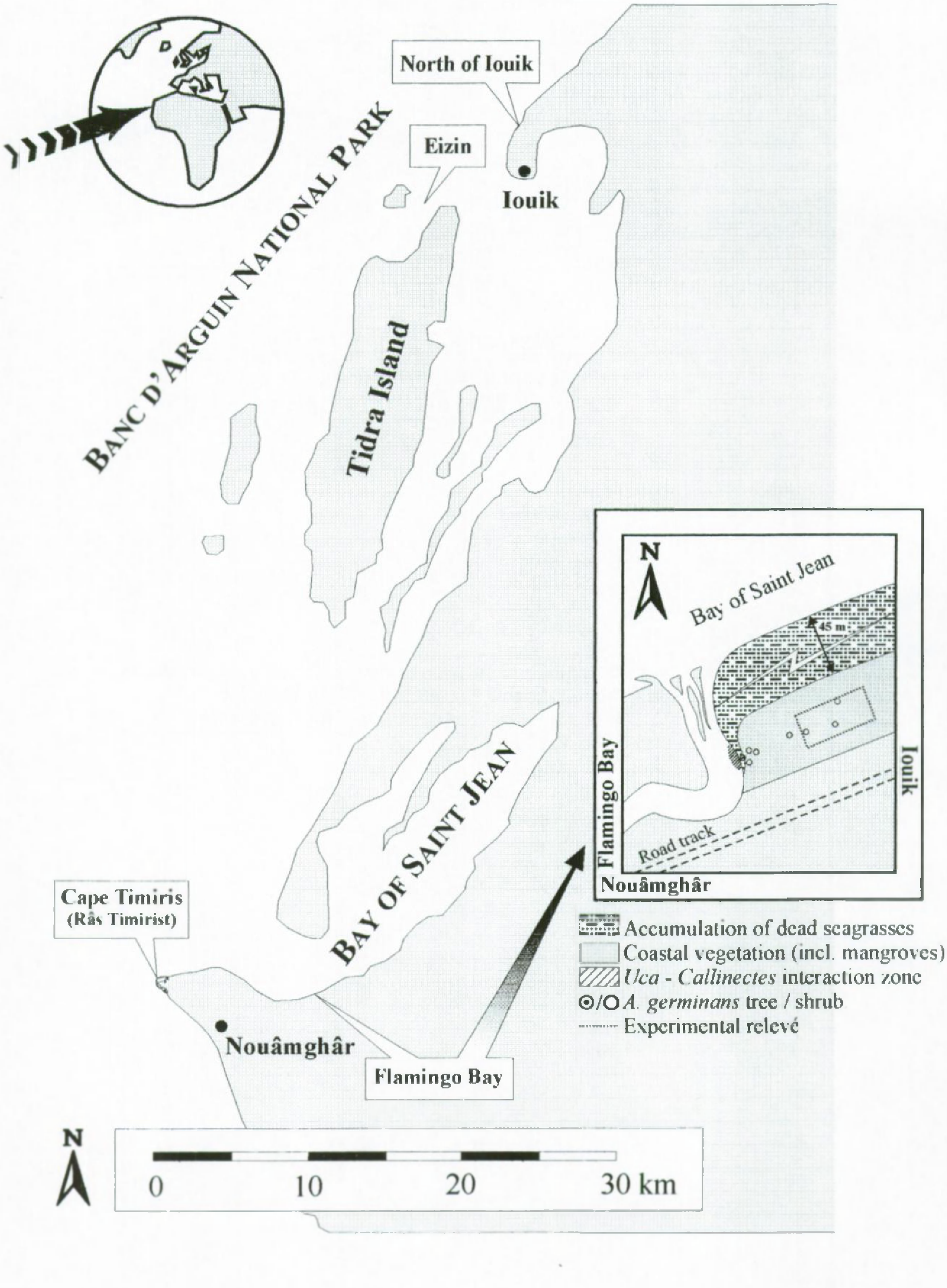


**Figure 2.** Physiognomy of the mangroves (trees, shrubs, young plants or saplings) and their vitality around Cape Timiris. Except for the trees in general and for all plants on the detailed map of the 'Iris', the mangrove vegetation symbols do not necessarily correspond with actual numbers of individuals, but are rather a relative representation.

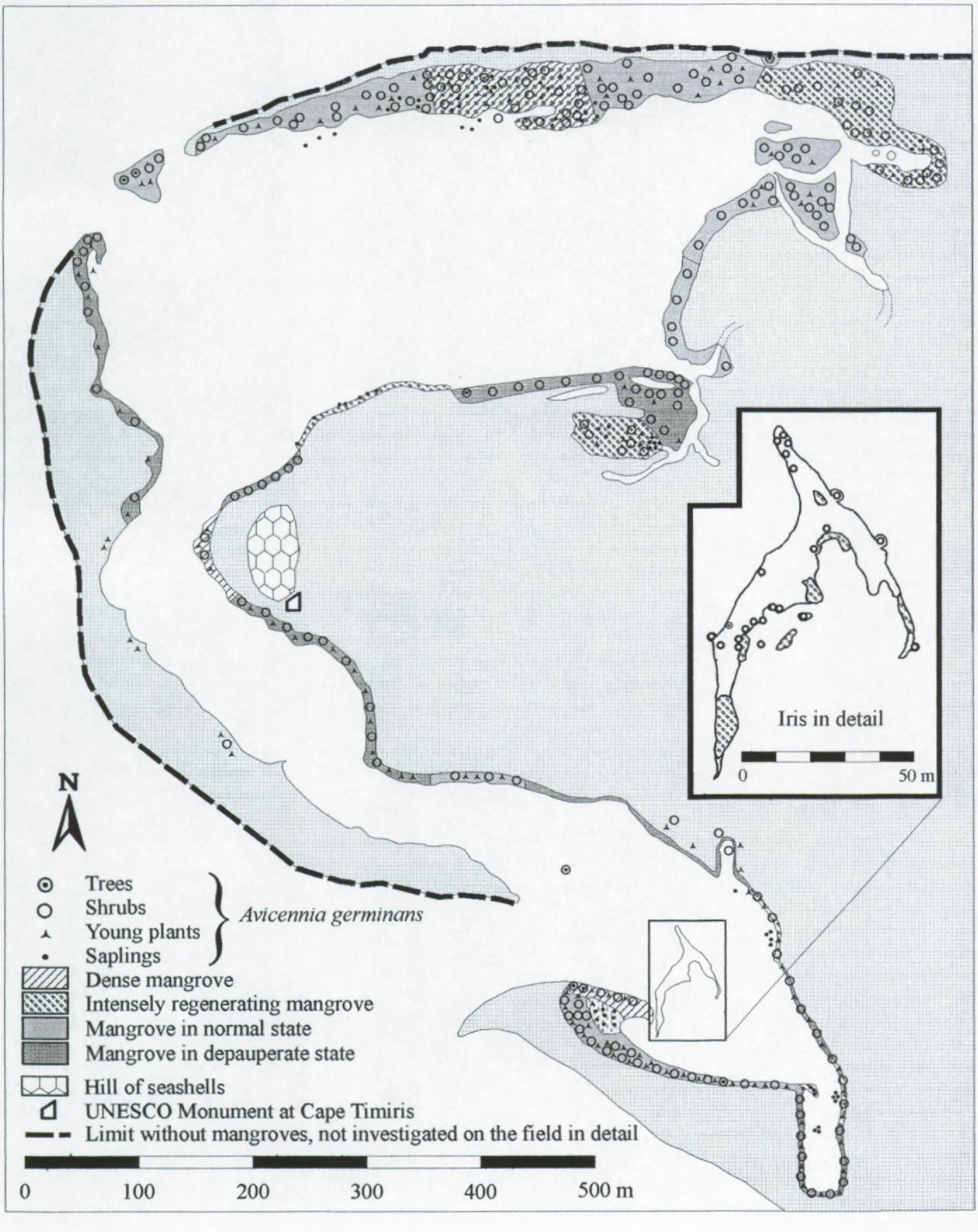


**Figure 3.** Physiognomies of *Avicennia marina* in Banc d'Arguin National Park. a) Tall, adult tree with height of 4.8 m (Cape Timiris, Atlantic shore). b) Wide, adult tree with a height of 1.2 m (Eizin). c) Dense, shrub formation of 1.4 m height on average (Cape Timiris lagoon). d) Sebkha formation of 0.8 m height on average (Cape Timiris lagoon, photograph taken towards desert). All of these *Avicennia* types were able to flower.

**Figure 4.** Vegetation assemblages (both mangrove and non-mangrove) on the 'Iris' in Al'Ain (Cape Timiris).

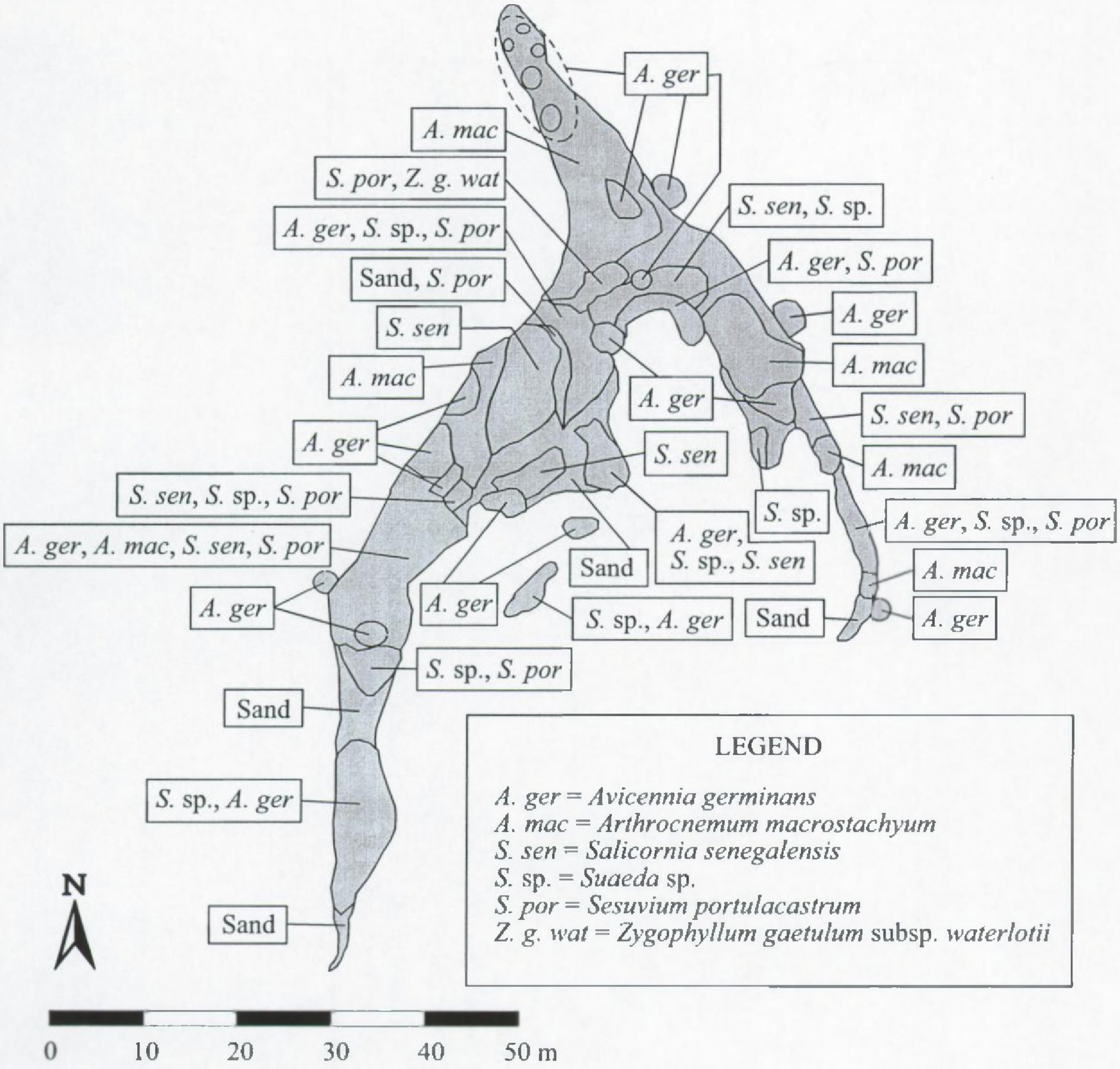


**Figure 5.** Salinity map (in ‰) from the southern section of Al'Ain (Cape Timiris) around January 26, 1998.

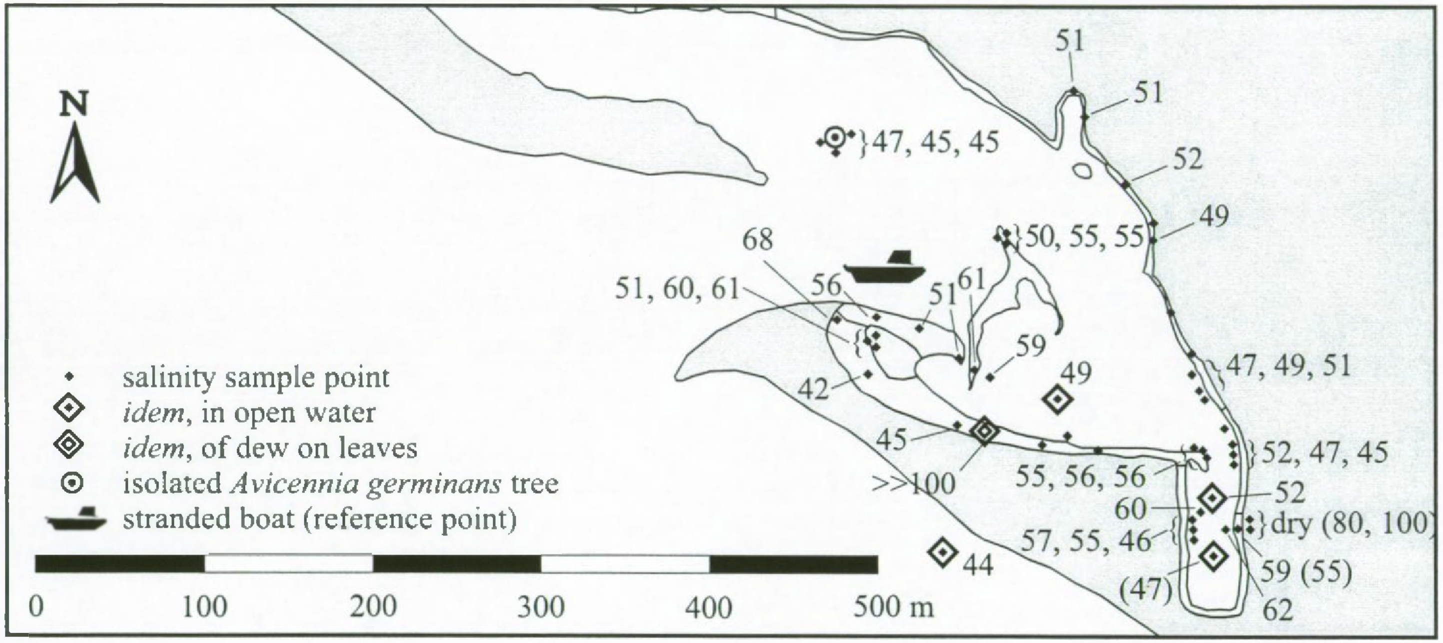


**Figure 6.** Evolution of the mean number of flowers on 5 branches (± standard deviation for the total number of flowers) of *Avicennia germinans* as a function of the time (in days).

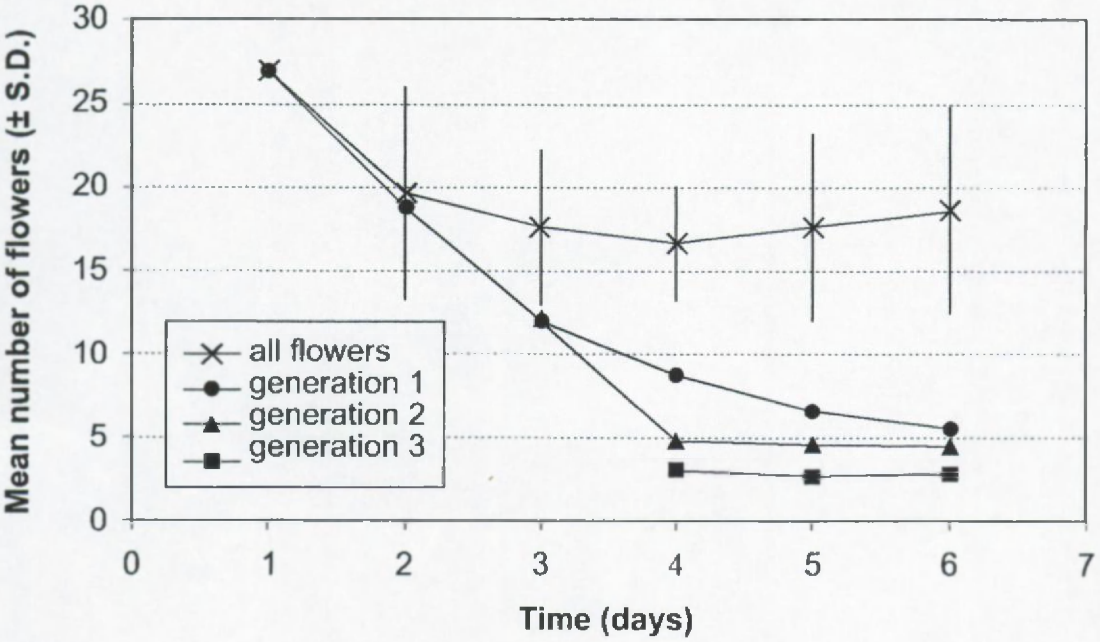
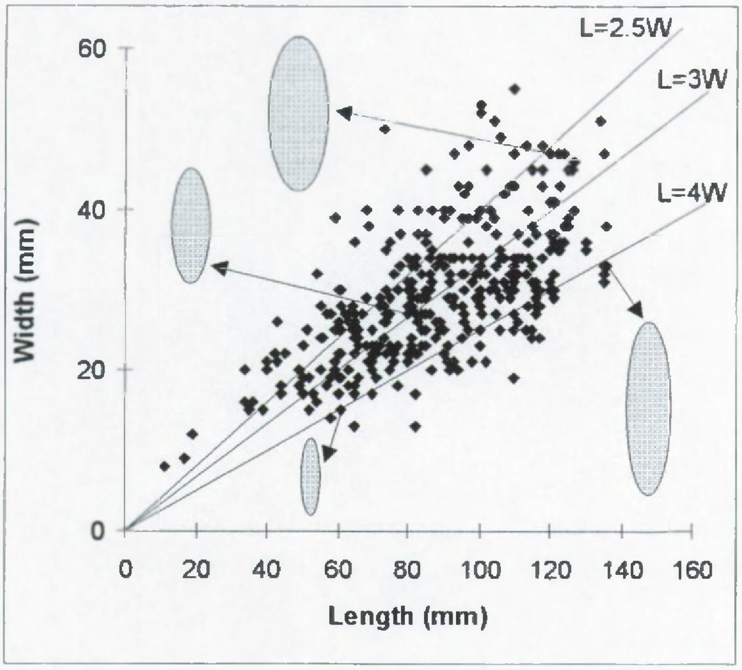


**Figure 7.** Association between the length and width of 364 *Avicennia germinans* leaves sampled around Cape Timiris, in Flamingo Bay, in Iouik and on Eizin. The three lines indicate three length/width (L/W) ratios and shaded areas show some typical leaf shapes.



# Chapter XIV.

## Empirical estimate of the reliability of the use of the point-centred quarter method (PCQM) in mangrove forests.

Dahdouh-Guebas, F. & N. Koedam

Engaged in a peer-review process

# Empirical estimate of the reliability of the use of the Point-Centred Quarter Method (PCQM) in mangrove forests.

Dahdouh-Guebas Farid and Koedam Nico

*Laboratory of General Botany and Nature Management, Mangrove Management Group, Vrije Universiteit Brussel, Pleinlaan 2, B-1050 Brussel, Belgium. Tel. + 32 02 629.34.22, Tel. & Fax. + 32 2 629.34.13, E-mail : fdahdouh@vub.ac.be, nikoedam@vub.ac.be, University URL : http://www.vub.ac.be/*

## Abstract

This study analyses problems that follow from the use of the Point-Centred Quarter Method (PCQM) in mangroves, due to aggregation of trees, ambiguous settings for measuring the distance to sample point or the tree diameters, and over- or underestimation of structural parameters of the forest. An empirical approach is followed, giving estimates of deviation from measured values. The analysis is carried out on digitised field maps that represent the exact position, stem diameter, height and cover of mangrove trees and roots in three sites located in Kenya and Sri Lanka, which comprise different types of tree aggregation and density. Replicated PCQM approaches were applied using sample points located *at random* or along transects in all sites. Various forest structural parameters were calculated, and an analysis of the sample point patterns and aggregation was done. The study indicates that theoretically old trees being surrounded by young ones amongst *Rhizophora* root complexes, and that the case of multiple stemmed trees such as *Excoecaria agallocha*, might lead to an underestimation of the basal area and an erroneous importance value of species. Results indicate that there can be a considerable over- or underestimation of the density and the basal area and that the factor by which this occurs is different according to the forest structure. Contrary to the reported expectation, the PCQM provides the most correct forest structure parameters in dense, aggregated forests. Forest structure limitations to the PCQ-Method can be partially overcome by the choice of sample point pattern ('*at random*' or 'along transect'), with transects being more appropriate in general. Since the PCQ-Method apparently cannot be carried out according to the book, the present study provides suggestions on how to overcome problematic settings.

Keywords : mangrove, PCQM, multi-stemmed trees, aggregation, density, basal area, Kenya, Sri Lanka.

## Introduction

The analysis of forest structure requires that forest density and biomass be estimated. The Point-Centred Quarter Method (PCQM) of Cottam & Curtis (1956) yields quantitative data by the selection of trees closest to reference points as an estimate of numbers and distribution, and it is a method suggested to be appropriate for calculating derived values allowing the investigation of forest structure in mangroves (Cintrón & Schaeffer-Novelli, 1984). On basis of these, various forest structure parameters can be calculated. Motivations to use of the PCQM above other plot-less methods or above plot-based relevé methods not only include the statistically sound quantitative basis, but also logistic factors such as ease and speed with which the fieldwork can be executed in these tide-dependent ecosystems. Although tree aggregation, as well as size-concentric tree organisation, a very frequent phenomenon in mangroves, has been recognised as a possible problem to the PCQ-Method (Cottam & Curtis, 1956; Cintrón & Schaeffer-Novelli, 1984), the method has been widely applied. Until present no effort was attempted to evaluate this or other PCQM-associated limitations.

As a result of mangrove fieldwork experience on basis of the PCQ-Method amongst others, we have realised that the use of the PCQ-Method in mangrove ecosystems is shrouded in more problems than commonly highlighted, if at all. Dense root systems entangle propagules, which may establish, thus creating a situation in which the first stem encountered by the investigator starting from a reference point is very often a younger and thinner tree or a secondary stem of a tree, and not the main stem from the species with the dense roots. Not only may this lead to an underestimation of the basal area calculated with the tree diameter or other parameters, but possibly also to an erroneous species importance value, since the propagules stuck in the root complex and developed into stems are not necessarily of the same species. This situation for example occurs in *Rhizophora* species, with younger individuals of the same or other species surrounding *Rhizophora*.

Multiple stemmed tree species such as *E. agallocha*, which comprises a number of thick central stems surrounded by many thin stems, may also lead to an underestimation of the basal area. In addition, multiple stems, together with cut stems or ambiguous root and stem settings, may lead to problems for measuring diameters and yielding representative data. The latter is very frequent in *Rhizophora* species and necessitates that a number of questions be answered : Where does one individual stop and another start ? How must stems that are interconnected over a large area be approached ? What if such connections break and the individual stems continue to grow separately ? Where should the stem diameter be measured with respect to prop roots ? Figure 1 gives an overview of these possible settings together with the problem of cut stems. Cutting (rather than logging) is often encountered in mangrove forests on which local people depend. If the PCQ-Method were applied in a rigorous way, a tree with a root complex on which a total of 10 stems originate should be considered only once. However, if the root connections break, the stems must be considered as separate trees. Apart from the fact that it is very tedious to untangle the tree connections, this would obviously give rise to a distance and a tree diameter that are not always correct, and, even worse, not always consistent. The tree diameter should be measured 30 cm above the highest aerial root, but woody mangrove roots that are well established in the soil may originate high in the stem or canopy (Fig. 2 a,c). It is obvious that the tree diameter will not be measured from a canopy branch.

The above extremes highlight the existence of a variety of realistic settings between these cases and the ideal PCQM setting, which should therefore be examined.

In the present study we investigate which situations are actually encountered in the field and how settings of different trees or the architecture of a single tree may jeopardise the PCQ-Method. We use simulations of the PCQ-Method on real data, mapped from three mangrove forests from Kenya and Sri Lanka, to assess the influence of sampling method and forest complexity on the accuracy of common PCQM-derived forest structure parameters (*e.g.* density, basal area). Our strategy is not to solve the questions addressed earlier, because these depend on arbitrary decisions, but rather to compare real density and values derived from PCQM measurements.

## Material & Methods

### *Description of the study sites*

Three sites were selected in the Indian Ocean region (Fig. 3) because their vegetation structure and vegetation dynamics have been studied intensively by our laboratory and have shown to cover the classical zoned mangrove forest (Gazi, Kenya), the partially zoned mangrove forest (Pambala, Sri Lanka) and the mosaic mangrove forest (Galle, Sri Lanka), and PCQM-related sampling problems have been experienced in each of these forests.

Gazi Bay (4°26' S, 39°30' E), located about 40 km South of Mombasa, lodges over 615 ha of mangrove forest, much of it subject to severe anthropogenic stresses (Kairo, 1995; Dahdouh-Guebas *et al.*, subm.a). Kidogoweni and Mkurumuji, two seasonal rivers, are responsible for most of the overland freshwater input into the bay. All nine East-African mangrove species, *i.e. Avicennia marina* (Forsk.) Vierh., *Bruguiera gymnorrhiza* (L.) Lam., *Ceriops tagal* (Perr.) C.B. Robinson, *Heritiera littoralis* Dryand., *Lumnitzera racemosa* Willd., *Rhizophora mucronata* Lam., *Sonneratia alba* Sm., *Xylocarpus granatum* Koen and *X. moluccensis* (Lamk.) Roem. (all mangrove nomenclature according to Tomlinson, 1986), occur along the Kenyan coast and their presence has been reported in Gazi Bay.

Two mangrove forests were investigated in Sri Lanka, along the Southwestern side of the island, where the spring tidal amplitude is less than 1 m (Spalding *et al.*, 1997), but locally rarely exceeds 15 cm in the course of one week (Dahdouh-Guebas, subm.).

The first mangrove forest studied in Sri Lanka is located in the Pambala area of Chilaw Lagoon, located in Sri Lanka's intermediate climate zone (Mueller-Dombois, 1968). The mangroves here are of the fringe type (Lugo & Snedaker, 1974), and have a rather irregular distribution along a complex of creeks (Marambettiya Ela, Bate Ela, Pol Ela and Dutch Channel). Most freshwater influx stems 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). This mangrove lagoon is known to be the most species diverse in South-Western Sri Lanka (Jayatissa *et al.*, subm.; Dahdouh-Guebas *et al.*, in prep.d) and the local area of Pambala comprises *Aegiceras corniculatum* (L.) Blanco, *Avicennia marina*, *A. officinalis* L., *Bruguiera cylindrica* (L.) Bl., *B. gymnorrhiza*, *B. sexangula* (Lour.) Poir., *Excoecaria agallocha* L., *E. indica* (Willd.) Muell.-Arg., *Heritiera littoralis*, *Lumnitzera racemosa*, *Rhizophora apiculata* BL., *R. mucronata* and *Xylocarpus granatum*. The mangrove in Chilaw Lagoon has recently been subjected to strong anthropogenic influences as a result of shrimp farming (Foell *et al.*, 1999; Dahdouh-Guebas *et al.*, 2000c).

The second mangrove forest studied in Sri Lanka is located between Galle and Unawatuna (06°01'N - 80°14'E), in the wet climate zone of this country (Mueller-Dombois, 1968; Fig. 2). This basin and riverine mangrove type (Lugo & 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, namely the Thalpe Ela, discharging into the ocean, and the Galu Ganga, a tributary of the former. The vegetation structure of the mangrove in Galle consists of *Bruguiera gymnorrhiza*, *B. sexangula*, *Excoecaria agallocha*, *Heritiera littoralis* and *Rhizophora apiculata*. A few occurrences of *Lumnitzera racemosa*, *Bruguiera cylindrica* (L.) Bl. and *Ceriops tagal* have been reported as well (Dahdouh-Guebas *et al.*, 2000a). The mangrove forest in Galle has been subjected to anthropogenic influence over the last 50 years and displays what has been labelled as a 'moving-mosaic' vegetation dynamic (*loc. cit.*).

In mangrove forests of both Pambala and Galle there was no slope with upper or lower intertidal areas, but rather a plateau with pools, the latter of which are few in Pambala and many in Galle.

### *Methodology*

In each of the above sites a sampling area of 1,000 $m^2$ (for Gazi approx. 625 $m^2$) was marked out using coconut rope that formed a grid of 1 $m^2$ cells. Within this area the $D_{130}$ (term according to Brokaw & Thompson (2000), but formerly referred to as DBH, the diameter at breast height) of all mangrove trees higher than 1.3 m were measured. The exact position of stems with a $D_{130}$ greater than 2.5 cm was indicated on paper, which had the same wire-grid structure printed beforehand, with mention of the species identity and the $D_{130}$. Also the extent of prop roots and water bodies was drawn to scale on the paper. The total coverage of the canopy in all quadrats of 10 m x 10 m within each sampling areas was between 80 and 100 %.

For all species present within the sampling area, between 40 and 272 trees per species were selected in the forest and for each tree the $D_{130}$ and the height (using a Suunto hypsometer) was recorded in order to check whether a relationship between these two variables exists. The coefficient of determination ($r^2$) was tested (t-test) and was found to be significant for *B. sexangula* ($p < 0.01$) and highly significant ($p < 0.005$) for all the other species (*A. marina*, *B. gymnorrhiza*, *C. tagal*, *E. agallocha*, *L. racemosa*, *R. apiculata* and *R. mucronata*) and a regression was done to generate an equation. This equation was then used to extrapolate a height for each tree in the sampling area based on its $D_{130}$.

The sheets were then scanned and digitised using graphical software (CorelDRAW version 7.373) in a multi-layer system (as in a geographic information system). The top layer consisted of a new grid (cell resolution = 1 $m^2$) with letters and numbers to identify the cells. In order to include cells in any analysis, they were selected by a random number generator. The Point Centred Quarter Method was performed on the vegetation data using 20 randomly selected sample points. For each quadrant the nearest tree was identified and the distance of the sample point to the centre of that tree was automatically calculated to millimeter level (original scale) by the software and put into a spreadsheet program together with the species identity, the $D_{130}$ and the tree height (field data). The millimeter resolution is much higher as compared to a field measurement but constitutes no problem for the further analysis. Ten such '*at random* PCQM simulations' were done for each site. The term 'simulation' is used here to indicate that this PCQM analysis did not take place in the field but on a computer; it should be recalled however that the digitised vegetation data exactly represent the actual situation in the forest. In a second phase, the sampling area was covered with ten transect lines (making sure that all sections of the forest were included), and the sample points of the *at random* PCQM simulations were re-sampled, following the transect and systematically moving away from either side of the transect line over the whole length until 20 points were re-sampled (band transect). Ten such 'transect PCQM simulations' were done for each site as well, but for Pambala. There, because of the very sparse nature of the mangrove, the selection of 20 *at random* points already covered the entire forest (< 2.5 % of the forest available for possible additional points), implying that the results of the transect PCQM simulations would be identical to those of the *at random* PCQM simulations. In all simulations the rule of thumb that every quadrant contained at least one tree (by not applying a distance limit) and that a particular tree was not considered by more than one sample point within a simulation was respected. For each simulation the following parameters were calculated : the stem density and basal area for each species and for the entire stand, the stand height, the complexity index of Holdridge *et al.* (1971) [= the product of number of species, basal area ($m^2.0.1ha^{-1}$), mean tree height (m) and number of stems.0.1 $ha^{-1}$ times $10^{-3}$ in a 0.1 ha plot] and the relative density [$De_r$ = (number of individuals of species / total number of individuals)*100], the relative dominance [$Do_r$ = (dominance of a species / dominance for all species)*100], the relative frequency [$F_r$ = (frequency of a species / sum of frequency of all species)*100] and the importance value of Curtis (1959) for each species. For each set of 10 simulations (= 200 sample points) the total cell cover was calculated and the aggregation pattern of these sample points compared with that resulting from a selection of 200 sample points without limitations with respect to the PCQ-Method. The control consisted of the calculation of the above parameters for one plot the size of the entire sampling area.

Although the two main PCQM limitations in the selection of trees were respected (*i.e.* first, a particular tree was selected only once per simulation, and second, each quadrant had to contain a tree), we were also interested in the error that could arise when these conditions were not met. For the first rule to be broken, we located only four trees in the corners of a theoretical rectangular map of 1,000 $m^2$, and made 10 *at random* PCQM simulations of 20 sample points each. Hence, each sample point considered the same four trees and each of the trees was thus selected 20 times in the same simulation. The same was done for three theoretical maps comprising only one tree : a map with the tree in the centre, a map with the tree in the middle of the greater side of the rectangle and a map with the tree in one of the corners. For these simulations each sample point thus considered the same tree in one quadrant while the other three quadrants remained empty. For these simulations, an algebraically derived density correction that takes into account the empty quadrants, as suggested by Verheyden (1997), was applied. The further analysis with regard to the 'transect PCQM simulations', as well as the calculation of the various forest structure attributes, was carried out as described above. However, only 5 instead of 10 transect PCQM simulations were performed.

In all sites mangrove trees likely to lead to problems when applying the PCQ-Method were also drawn by hand in the field, indicating problematic features such as cut stems, multiple stems or ambiguous root and stem settings for measuring diameters.

In order to check for the influence of the root system on the spatial distribution of young trees (attraction of propagules as highlighted in the introduction), the number of young stems standing amongst *Rhizophora* roots and those standing away from these roots were counted, taking into account the surface taken in by the roots. To identify a 'young tree', the median $D_{130}$ of all trees in each study site was rounded to the nearest five-fold, and this number was taken to be the maximum diameter for a 'young tree'. For all sites the latter maximum $D_{130}$ for a young tree was equal to 5 cm (thus the median of all trees was between 2.5 cm and 7.4 cm for each site).

### *Statistical analysis*

Analyses and comparisons of the forest structure parameters concentrated on three levels :

- *at random* PCQM simulation *versus* transect PCQM simulations;
- a very aggregated situation (Galle) *versus* a less aggregated situation (Gazi, Pambala)
- a dense, less aggregated forest (Gazi) *versus* a sparse, less aggregated forest (Pambala)

In addition, the complexity index of the different forests eased an integrated comparison between sites.

The aggregation patterns of 200 *at random* sample points were compared between the theoretical simulation (without PCQM limitations) and our three field sites (with PCQM limitations). Aggregation classes were established by counting the number of cells in each structure that is formed by adjacent cells (adjacent with sides only, not with corners). The difference between the distributions of the number of cells per aggregation class was tested using the Kolmogorov-Smirnov test. In order to quantify the aggregation of sample points we calculated an aggregation index (A.I.) using the following formula :

$$\text{A.I.} = 1 - ( P / 4 A )$$

where

P = total number of cell sides that are part of the perimeters of aggregation structures

A = total number of cells in the aggregation structures (~ cell area)

4 A = maximum number of cell sides for a given cell area A

P / 4 A = measure of cell scatter (= 'scatter index S.I.')

The aggregation index varies between 0 and 1. However, it is important to note that $\text{A.I.}_{max}$ is dependent on the situation and that the more cells are involved, the higher is $\text{A.I.}_{max}$ for that situation : *e.g.* in a simple situation comprising two cells the A.I. varies between 0 (two separate cells) and 0.25 (two adjacent cells), but in a more complex situation comprising 100 cells the A.I. varies between 0 (100 separate cells) and 0.9 (a single structure of 10 x 10 cells). Whereas the $\text{A.I.}_{min}$ always equals 0 (a completely scattered pattern of cells with no aggregation structures), the $\text{A.I.}_{max}$ thus reaches its maximum value of 1 in a situation where an infinite number of cells form a single structure. The aggregation index can thus be calculated for any series of sample points and is easily comparable between sites, regardless the number of cells.

## Results

From the maps a number of between-site differences are clear (Fig. 4). The mangrove in Galle is visually very aggregated (Fig. 4b), whereas for Gazi (Fig. 4a) and Pambala (Fig. 4c) the mangrove trees are more regularly spread. Between the latter forests there is however a difference in density : the overall forest in Pambala is overall much sparser than in Gazi (114.7 stems per 0.1 ha *vs.* 204.7 stems per 0.1 ha).

The comparison of the spatial distribution of young trees in presence and in absence of *Rhizophora* roots clearly confirmed in practice the theoretical possibility that the root complex of *Rhizophora* entangles propagules as suggested in the introduction. The surface that a young tree had at its disposal in an area with roots was significantly smaller by a factor of 0.35, 0.09 and 0.05 for Gazi, Pambala and Galle respectively, as compared to an area without roots. This means that a 5 m x 5 m plot located away from *Rhizophora* roots and containing 1 young tree, would comprise between 3 and 20 young trees if it were located amongst *Rhizophora* roots.

The results of the relative forest structure attributes are given in box-plots (Fig. 5) and show that the relative values generally are somewhat more clustered for the *at random* PCQM simulations than for the transect PCQM simulations in dense forests (Gazi and Galle). Since the true values are based on a single evaluation of the forest area, the relative frequency, which considers all species present, must not be compared with the values from the simulations. Where the PCQM simulation has selected locally rare species, their low relative values are often represented more accurately by the PCQ-Method than the higher values of the more common species (Fig. 5). However, these rare species can also be missed in a simulation resulting in the erroneous absence of the species (minimum value = zero). The real relative density and the relative dominance of the dominant species in dense forests (*R. mucronata* in Gazi and *E. agallocha* in Galle) are systematically underestimated, whereas that of the other species is either accurate or overestimated. However, this is not the case in the sparser forest of Pambala where all relative forest structure attributes are most accurate.

The over- or underestimation for the absolute density and basal area by the PCQ-Method, shown as factors in table 1, can vary substantially. However, for both theoretical and real forests the results show that the overall forest structure and complexity influences this factor (Tab. 1). For the relative values of the different species in each of the sites results are not shown because no general trend was visible. However, *Bruguiera* spp. systematically showed larger coefficients of determination for the association between C.I. on one hand, and the over- or underestimation factor for the relative density, relative dominance or relative frequency on the other hand. Despite the use of a density correction for the theoretical simulations with a single tree (see material & methods), there was still an over- or underestimation of the density (Fig. 6 and Tab. 1), although it resulted in values closer to the real values.

Also the aggregation of PCQM sample points depends on the forest structure. A dense, aggregated forest like Galle will allow sample points to be located near each other, whereas a sparse, less aggregated forest like Pambala will not (Fig. 7). The comparison of aggregation patterns of sample points of Gazi, Galle, Pambala and an *at random* selection of 200 sample points shows that there is little difference in the overlap of cells between the three sites (13 – 17.5 %), but the aggregation is different between the sites (Fig. 8). The distributions of the aggregation patterns tested (Fig. 8), were not significantly different between the *at random* and the Gazi sample points ($D = 0.101$; $n = 17$; n.s.), between the *at random* and the Galle sample points ($D = 0.128$; $n = 17$; n.s.) or between the Pambala and Gazi sample points ($D = 0.082$; $n = 17$; n.s.), but highly significant between the *at random* and the Pambala sample points ($D = 0.250$; $n = 17$; $p < 0.001$), between the sample points of Galle and Pambala ($D = 0.384$; $n = 17$, $p < 0.001$) or between those of Galle and Gazi ($D = 0.213$; $n = 17$; $p < 0.001$). We can consider the random set of sample points to originate from a forest with an infinite number of trees that will compromise the selection of PCQM sample points by the possible selection of a particular tree twice under no condition. The aggregation patterns are more scattered in dense forests with more single- and double-cell structures, whereas they are more aggregated in sparse forests with more or larger multi-cell structures (Fig. 8), at least for the forests studied.

The drawings of tree architecture of *Rhizophora mucronata* in figure 2 are examples of problematic settings encountered during our fieldwork in both countries. In Kenya also *Bruguiera gymnorrhiza* trees can be found growing with very abnormal architectures, often as the result of cutting by people (pers. obs.).

## Discussion

The results from this study suggest that there are two problems that need to be solved : on one hand ambiguous situations for the choice of the stem closest to the sample point (which influences the density) and for the exact location of the measurement of its diameter (which influences the basal area) in the field, and on the other hand over- or underestimation of structural forest parameters. The comparison of the real values and values obtained after applying the PCQM indicate a deviation up to a factor 2 for density and up to a factor 6 for basal area, depending on the forest structure and on the type of PCQM approach used (*at random* or transect).

The results of the comparison of the spatial distribution of young trees with respect to the root complex of *Rhizophora* species suggest that the entanglement of propagules by the root complex of *Rhizophora* does significantly influence the intended *at random* choice of stems in the PCQ-Method. Since one or few adult trees attract many young trees, it is virtually impossible to attribute an equal chance of being selected to each (adult) stem and therefore complete randomness cannot be reached. This seems to be more pronounced in sites that are less affected by tides (such as Pambala and Galle) than in those that are under a daily tidal influence (such as Gazi), and is most probably affected by the tidal amplitude as well.

It seems that there is little opportunity to follow a diameter or distance measurement by the book, but each tree should be approached separately and the researcher should adopt a 'best professional consistency'. We suggest that in multiple stemmed trees such as *Excoecaria agallocha*, only the greater central trees are considered on the field and an average of their diameters is computed to prevent underestimation of a species' basal area and relative dominance. In a related study on mangrove dynamics in Galle (Dahdouh-Guebas *et al.*, 2000a), where also the present study was carried out, the mangrove was sampled according to the above suggestion and resulted in a relative dominance of 73.8 % for *E. agallocha*, whereas the true value is 73.7 % (this study). An *at random* or transect PCQM approach according to the book (strictly stem nearest to sample point) generates a value 71.2 % and 68.7 % respectively in the same, but larger, forest patch. The differences do however not jeopardise the rank of this species within the relative dominances of all species.

The suggestion for *E. agallocha* made above should not be generalised to species that are linked through more complex root systems such as *Rhizophora*. In the latter, stems that are not attached directly to each other should be considered separate individuals, even if they are clearly connected indirectly through the root complex. The underlying ecological justification for this is that each of these stems is connected to enough roots to assure the ability to further develop if the connections with other stems is broken.

During the fieldwork, it is most advisable to make sure that each quadrant contains a tree whatever its distance, instead of adopting a distance limit, as the latter will need to be corrected in a later phase (*e.g.* Verheyden, 1997).

PCQM results seem more accurate (factors in table 1 closer to one) in more complex forests than in less complex forests. Contrary to the claim made by Cottam & Curtis (1956) that aggregated trees with open spaces between them will not give an accurate density, the present study suggests that the PCQ-Method is more accurate in case of an aggregated forest. However, only when more sites are investigated, preferably spread over all existing mangrove typologies, significant trends can be recognised and actual 'PCQM accuracy correction factors' to correct the over- or underestimation of PCQM results according to the forest complexity, can be established. At present, we can only indicate the general trend that would be followed by such correction factors (Fig. 9). Apart from other motivations to use a particular approach for the description of the vegetation, the solutions that choice of the PCQM approach in the field (at random or transect) bring, can be commented more in detail. Generally, if the aim is accuracy (Fig. 9), a transect PCQM approach is better than an *at random* PCQM approach for both density and basal area (values closer to real values but more variability). If on the other hand the aim is precision (Fig 9), the opposite is valid (less variability but values less close to real values). The higher variability for the transect PCQM approach is however reduced since transects are seldom, if ever, established without replicates. If the mangrove displays different zones or patches (visible from aerial photography for instance) it is advisable to subdivide the transects accordingly and make PCQM calculations for each zone or patch separate. This results in a description that can both be used by research units that are interested in the different zones or patches (*e.g.*vegetation assemblages in Dahdouh-Guebas *et al.*, 2000) and by those interested in the entire forest (Kairo, 1993; Kairo *et al.*, in prep.b).

The choice of the approach according to the density and the research objectives can also be directed (Fig. 9). The results from the theoretical simulations suggest that in forests with extreme simplicity (*e.g.* very sparse, young, low, monospecific forests) the *at random* PCQM approach generates more precise as well as more accurate results.

In addition, the outcome of these simulations seem to question whether or not it matters that an individual tree is measured twice. Cottam & Curtis (1956) did not use any method of mutual exclusion in the location of sampling points, but Cintrón & Schaeffer Novelli (1984) indicated the selection of any tree twice as a limitation to the PCQ-Method. The theoretical simulations in the present study, in which each of 4 trees were selected 20 times, seem to indicate that this may be true in forests with a lot of empty space (*cf.* simulations with trees in the corners). However, it is greatly influenced by the complexity of the forest, since a forest with a single tree in the centre or at the side, apparently leads to an overestimation of the density. Only the variation in position of the unique tree in the forest accounted for a variation in over- or underestimation of the density of 360 % to 400 % and of the basal area of 347 % to 414 %, depending on the PCQM approach used.

The results showed that the aggregation of PCQM sample points, and therefore the ease with which the PCQ-Method can be applied in mangroves, also depends on the forest structure. In very sparse forests a sample point located in a certain area of the forest will automatically exclude possible sample point locations nearby and force them to be located in areas that are denser instead. This leads to the situations and patterns observed in figs 7 and 8. The lack of significance in the comparison of the frequency of aggregation classes between a dense aggregated forest (Galle) and a complete theoretical *at random* simulation is another indication that aggregated forests do not necessarily form a limitation to the PCQ-Method. Contrary to our mangrove situation, in a study of spatial patterns in terrestrial forests, including dry deciduous to wet evergreen forests, Condit *et al.* (2000) found that the trees themselves were more aggregated than a random distribution, when considering the relative neighbourhood density as a measure of aggregation (this is a measure based on the number of neighbouring trees and the area in concentric circles around individual trees, and standardised using the mean density of a given species across the area).

It is obvious that the complete measurement of all trees as in the present study is ideal, but highly time consuming and not applicable in real forest surveys. Further investigation of the possible limitations and their solutions to the use of the Point-Centred Quarter Method in mangrove forests should in our opinion concentrate on the establishment of the so-called 'PCQM accuracy correction factors' and their wide applicability. The variation in basal area or biomass that can occur for measurements of the tree diameter taken at different places on a mangrove tree, particularly in *Rhizophora* species, similarly to the study of Brokaw & Thompson (2000) on more conventional tree architectures in temperate forests, constitutes invaluable information for the establishment of more transparent procedures in measuring this diameter.

### Acknowledgements

We are very grateful to the people from Gazi (Kenya), in particular family S. Ba'alawy, and to the staff of the Small Fishers Federation of Lanka (Pambala-Kakkapalliya, Sri Lanka), in particular Mr. Anuradha Wickramasinghe (Director), for hosting us. We thank Daglas W.N. Thisera (Coordinator Mangrove Conservation and Education, SFFL), Fatuma M. Saidi and Sandra Matthijs for their practical help in the field. Research financed by the European Commission (Contract EBR IC18-CT98-0295), and with a specialisation fellowship of the Flemish Institute for the advancement of scientific-technological research in the industry (IWT).

### References

See Bibliography

**Table 1.** Factor for the over- or underestimation of the true density and basal area by the PCQ-Method sampled *at random* or along a transect in theoretical and real mangrove forests with varying complexity indices (C.I.). For each of the forest types the sites are ordered with increasing complexity.

| **Forest** | **C.I.** | **Density** | | **Basal area** | |
|---|---|---|---|---|---|
| | | ***at random*** | **transect** | ***at random*** | **transect** |
| **THEORETICAL FORESTS** | | | | | |
| One tree in centre | 0.000123 | 1.8 | 2.0 | 5.2 | 5.8 |
| One tree at side | 0.000123 | 1.3 | 1.4 | 3.8 | 4.1 |
| One tree in corner | 0.000123 | 0.5 | 0.5 | 1.5 | 1.4 |
| Four trees in corners | 0.001904 | 0.1 | 0.1 | 0.4 | 0.4 |
| **REAL FORESTS** | | | | | |
| Gazi | 0.9 | 2.1 | 1.7 | 6.2 | 6.2 |
| Pambala | 2.8 | 1.5 | 1.5 | 2.4 | 2.4 |
| Galle | 3.4 | 0.8 | 1.0 | 2.2 | 1.8 |

**Figure 1.** Schematic (side view on top and aerial view underneath) showing an ideal situation (t = 0) of a *Rhizophora* mangrove and its further evolution to highlight the following problems and possible solutions to the use of the Point Centred Quarter Method : a standardisation of + 30 cm along the stem for the measurement of the '$D_{130}$' (t = 1-4), measurement of the diameter with respect to cut stems (t = 2-4) and with respect to developing roots (t = 2), and the measurement of the distance d from the (flagged) sample point (t = 4). The figure also shows that in a future moment in time, the closest tree to a sample point will not be one of the central *Rhizophora* stems, but one of the aggregated propagules that will develop into young trees (possibly belonging to another genus). Black lines in bold indicate the theoretical possibilities of diameter measurement; 't = 0' stands for time at a certain moment in time and higher numbers for later moments in time.

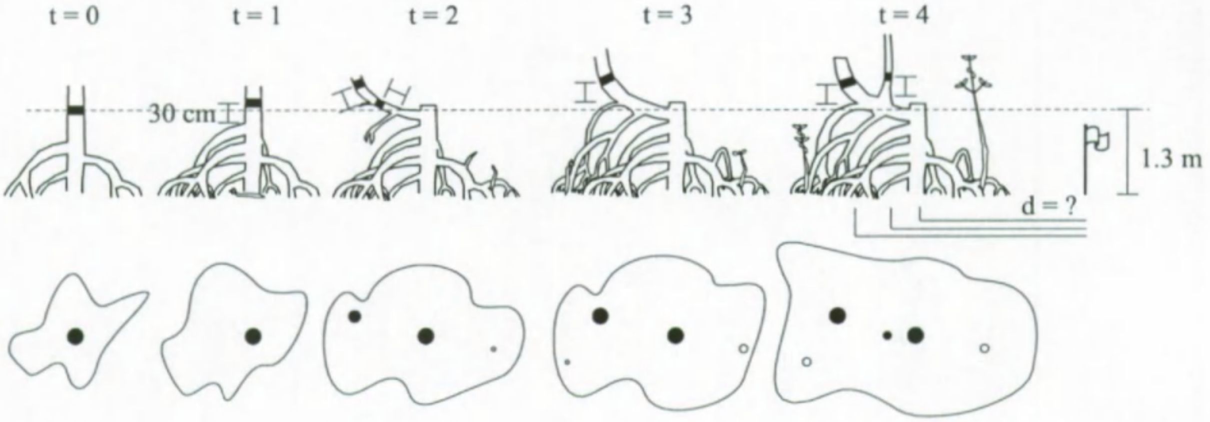


**Figure 2.** Three examples of *Rhizophora mucronata* trees drawn in the mangrove of Pambala (a,b) and Gazi (c) to highlight the architectural complexity of this genus (*cf.* central stem and in diameter choice). Black lines in bold indicate theoretical possibilities of diameter measurement.

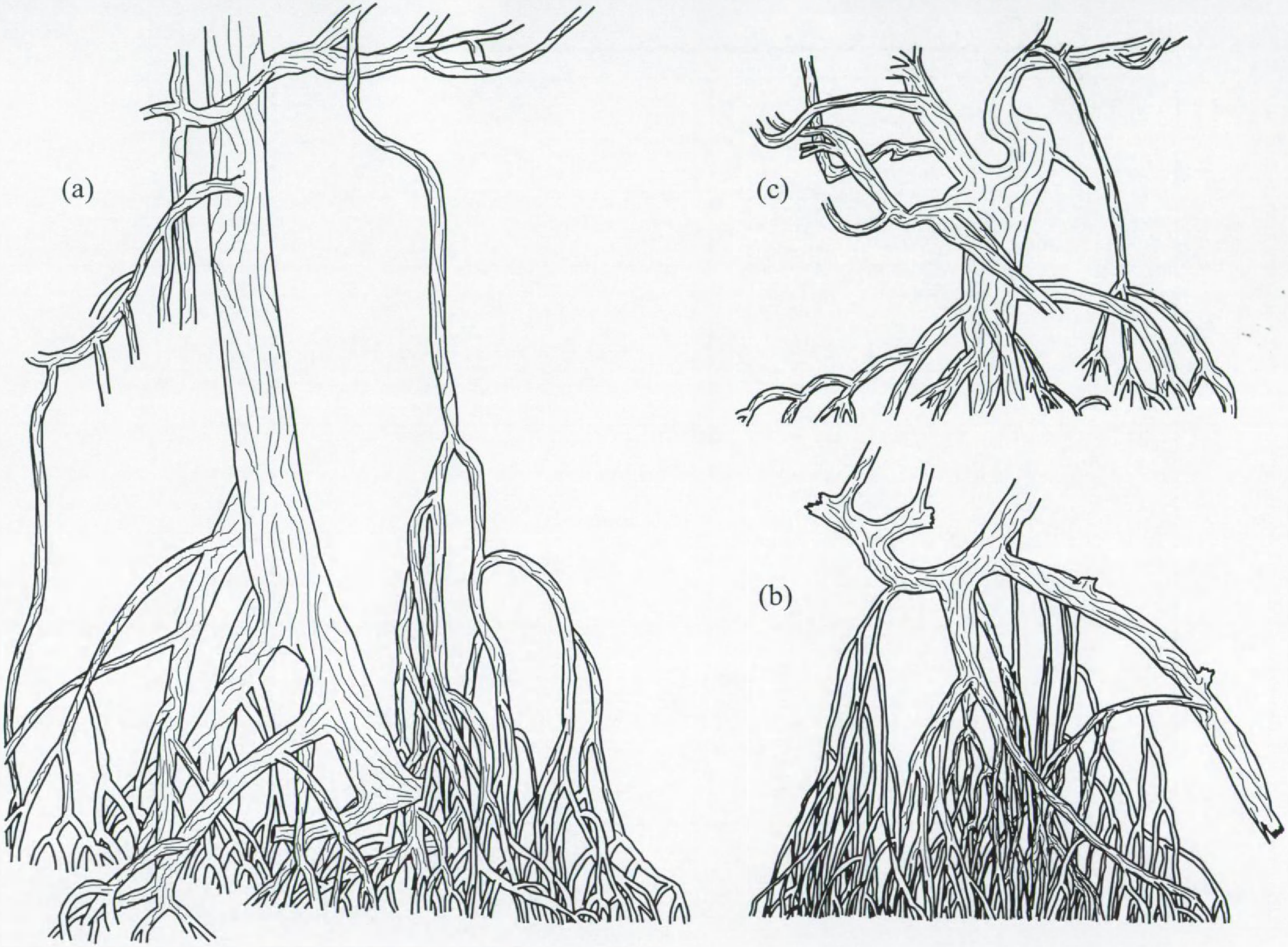


**Figure 3.** Map of the western part of the Indian Ocean showing the locations of our study sites in Kenya and Sri Lanka.

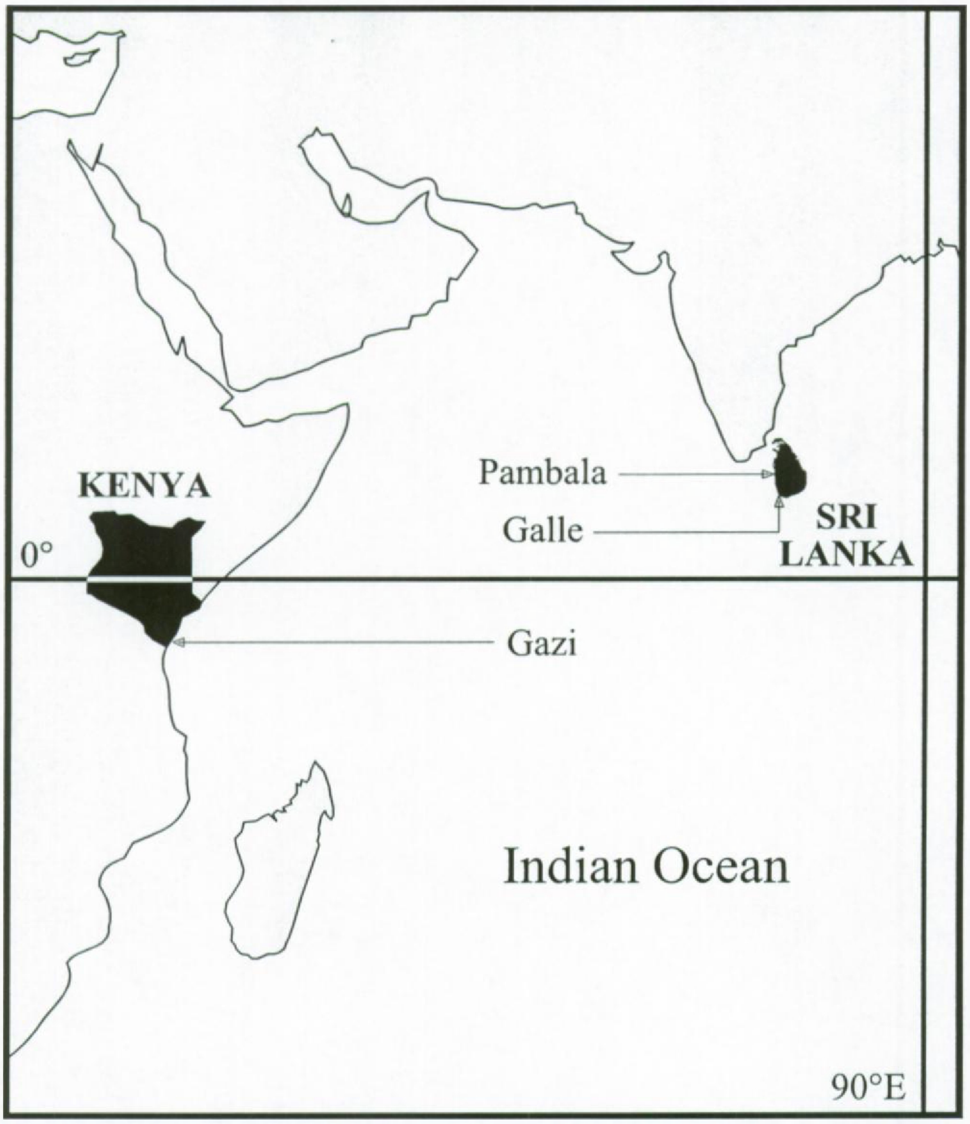
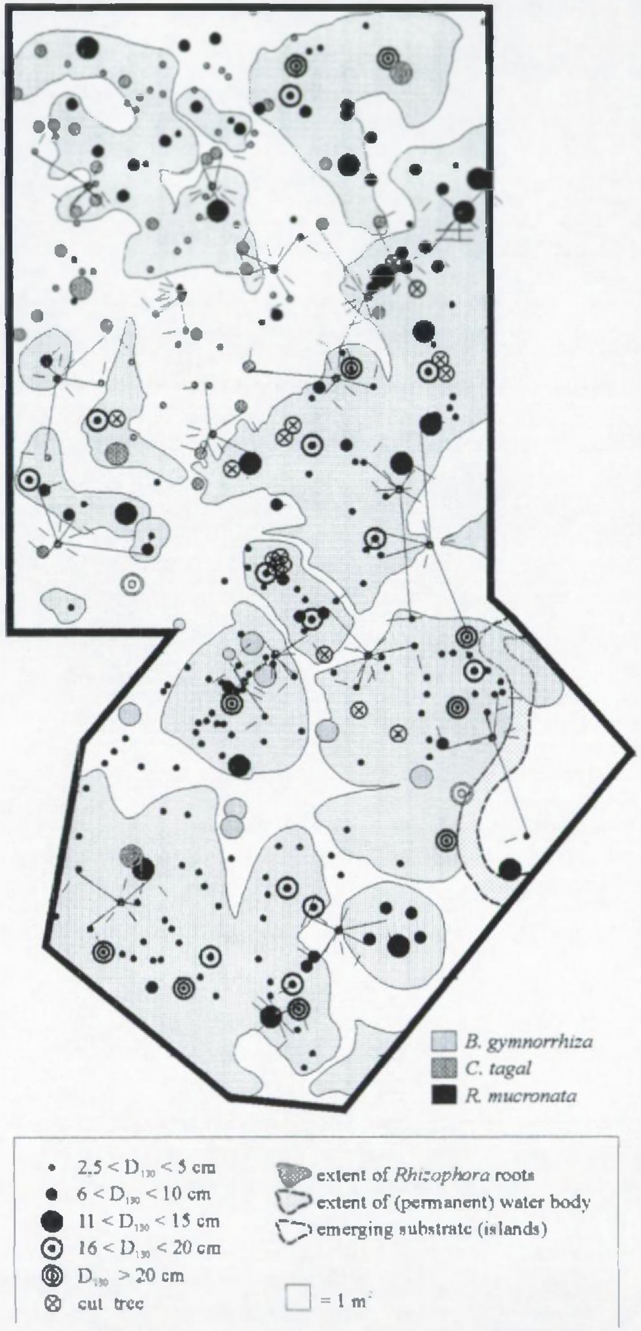
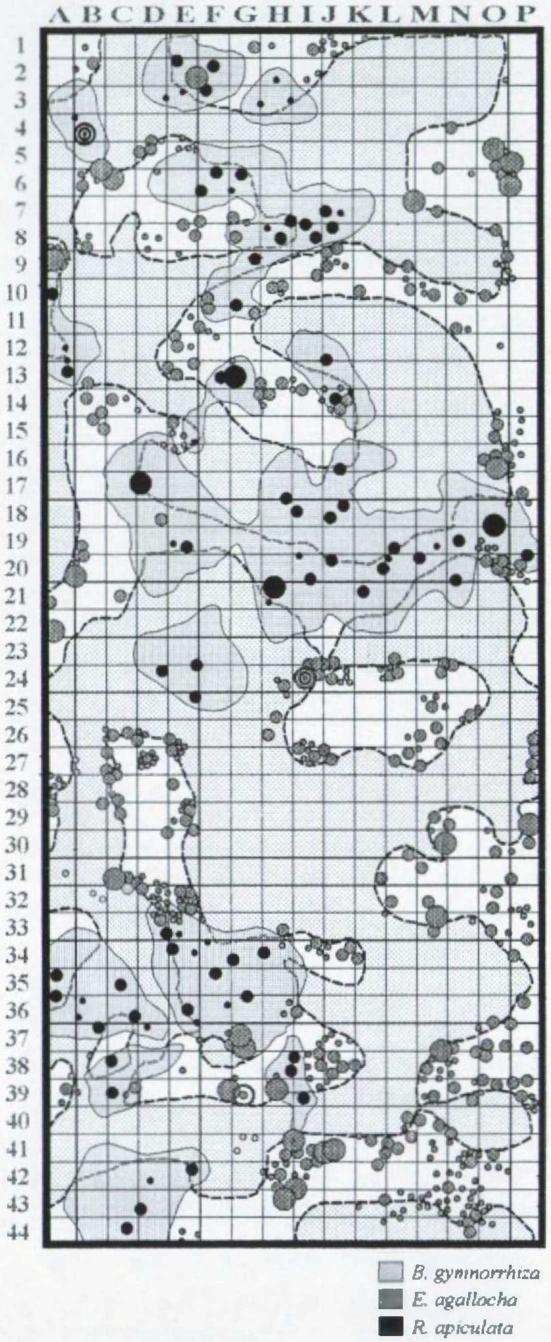


**Figure 4 (next page).** Mangrove forest maps for (a) Gazi (± 625 $m^2$), (b) Galle (1,000 $m^2$) and (c) Pambala (1,000 $m^2$). The map for Gazi also shows a completed example of an *at random* PCQM simulation. The maps for Galle and Pambala show the grid letters and numbers.


B. gymnorrhiza
C. tagal
R. mucronata
2.5 < D130 < 5 cm
6 < D130 < 10 cm
11 < D130 < 15 cm
16 < D130 < 20 cm
D130 > 20 cm
cut tree
extent of Rhizophora roots
extent of (permanent) water body
emerging substrate (islands)
= 1 m²


A B C D E F G H I J K L M N O P
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44
B. gymnorrhiza
E. agallocha
R. apiculata

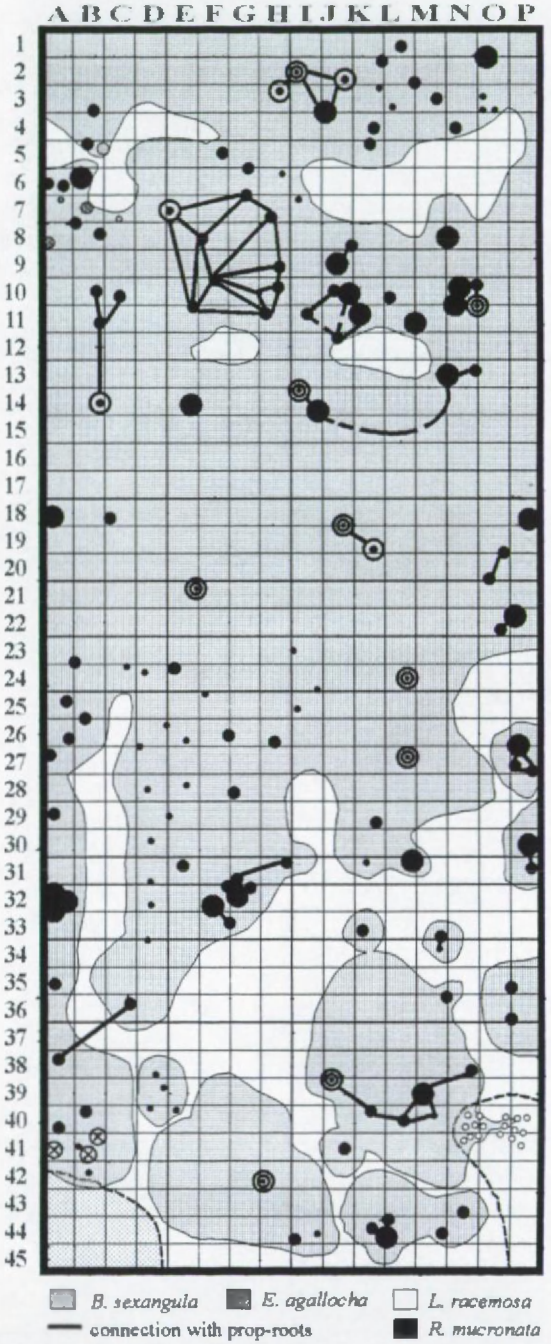

A B C D E F G H I J K L M N O P
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45
B. sexangula
E. agallocha
L. racemosa
connection with prop-roots
R. mucronata

**Figure 5.** Box plots showing the relative density, the relative dominance and the relative frequency for each species for the *at random* and the transect PCQM simulations in Gazi, Galle and Pambala. The exact values of the real situation in the forest are indicated between brackets. The boxes represent the data between the 25th and the 75th percentile whereas the lines extend to the minimum and maximum values.

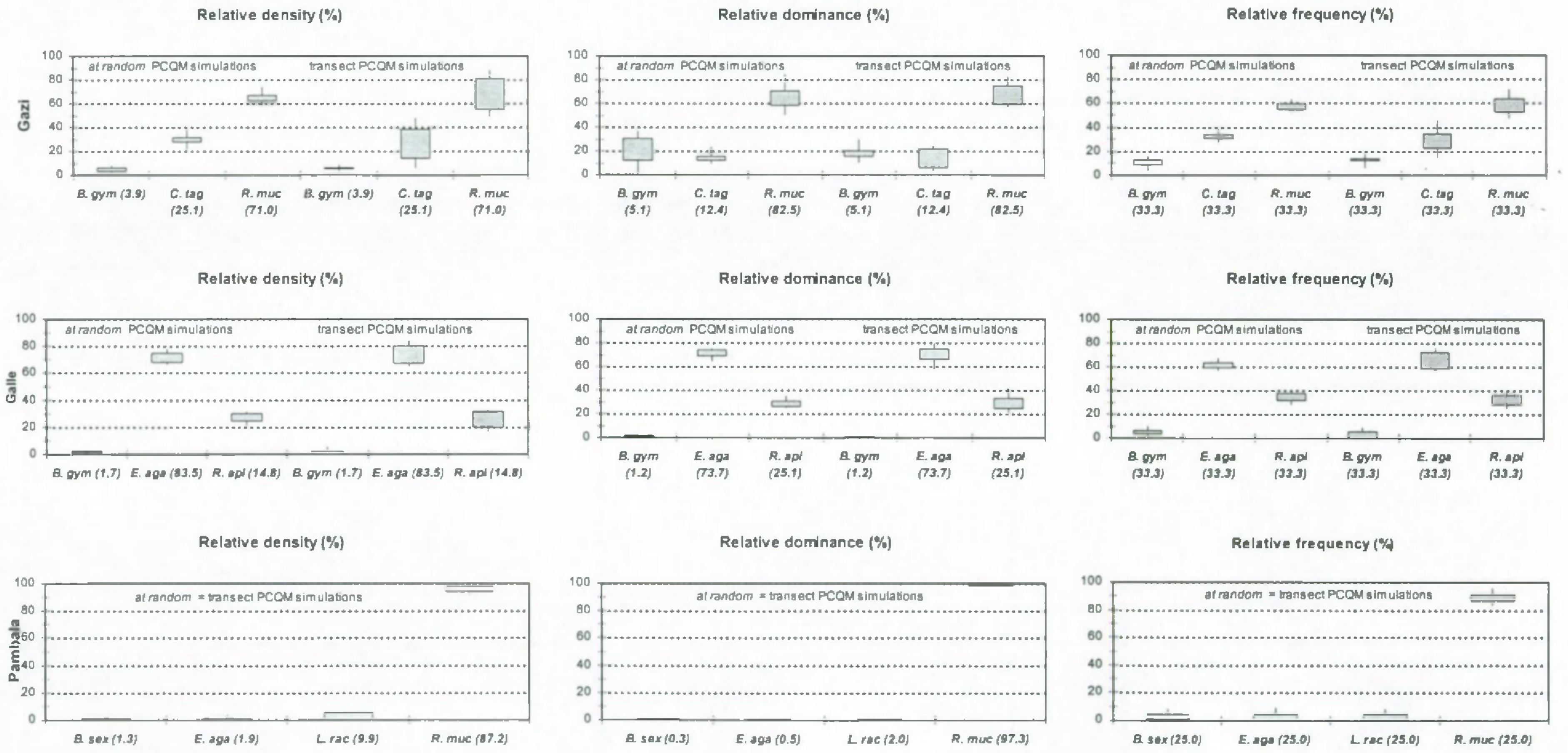


**Figure 6.** Box plots showing the total absolute density and basal area for the *at random* and the transect PCQM simulations in Gazi, Galle and Pambala, and for the four theoretical simulations with four trees and with a single tree. The exact values of the real situation in the forest are indicated between brackets. The boxes represent the data between the 25th and the 75th percentile whereas the lines extend to the minimum and maximum values.

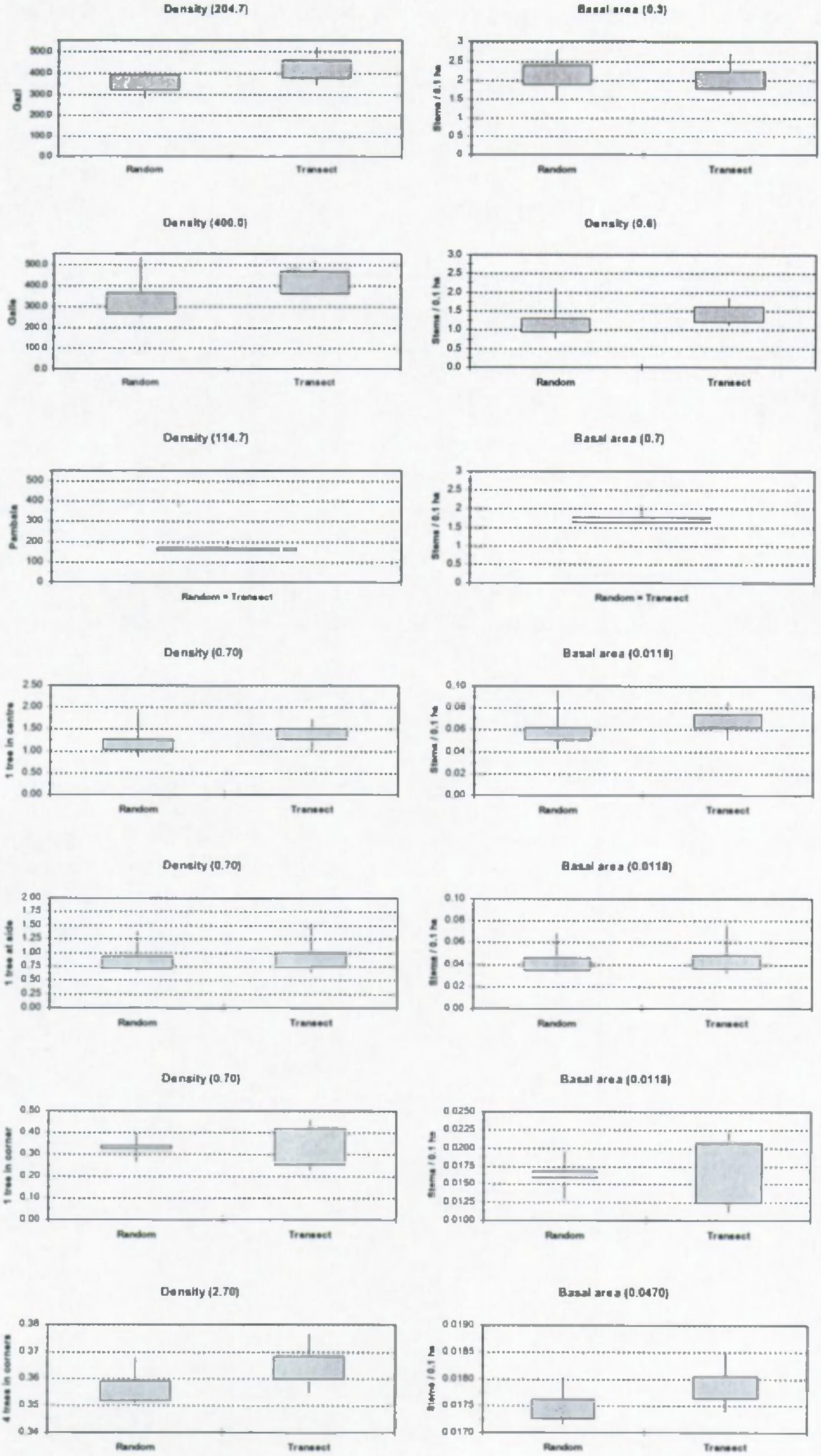


**Figure 7.** Effect of mangrove aggregation and density on the Point-Centred Quarter Method. Each PCQM sample point is represented by a star, whereas the four PCQM quadrants are shown in dashed lines. The closest tree in each quadrant is encircled and connected to the respective sample point with a line. In Pambala (a), sample points that could be located relatively far from each other (> 9 m) still consider a same tree (located in grid cell E21) because of the very sparse vegetation structure. In Galle (b) the forest is very dense and aggregated, and sample points les than 2 m from each other may exist without a limitation to the method. However, note that the central stem in grid cell D27 (Galle) can never be selected due to aggregation. For the legend refer to the maps in Figure 4 from which the cells are extracted.

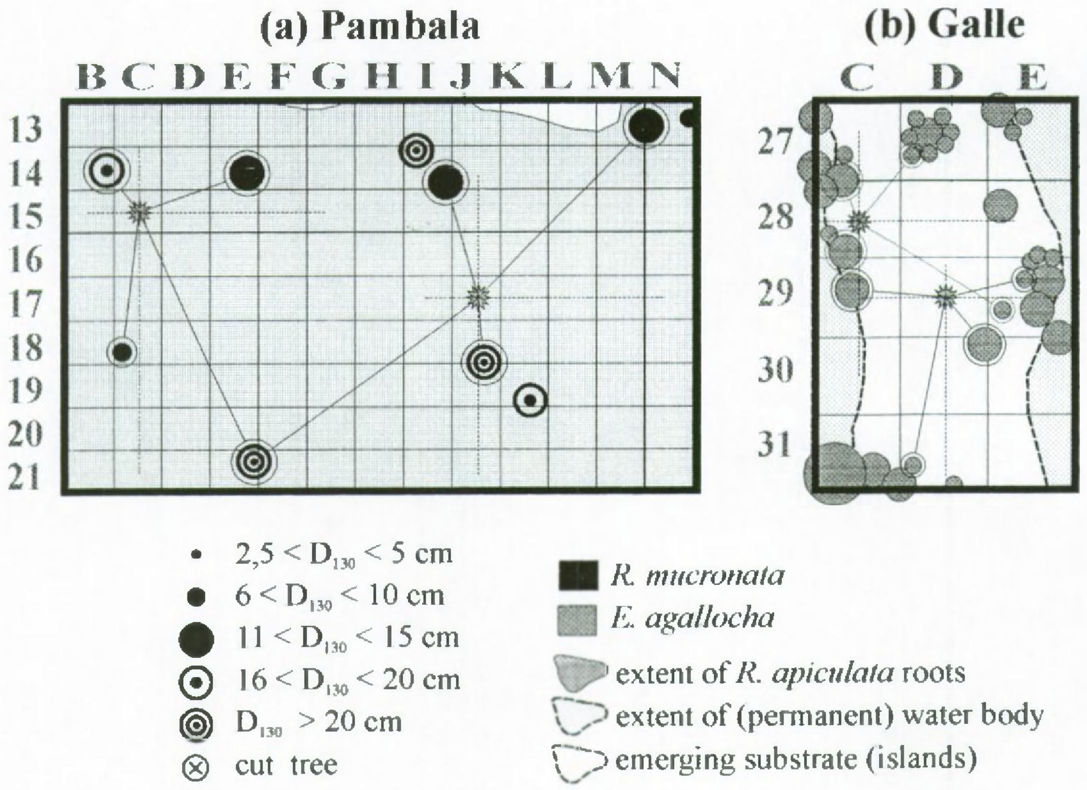


**Figure 8.** Aggregation patterns and coverage of the forest surface by sample points after 10 *at random* selections of 20 sample points each, in four situations : a theoretical selection of the cells in a total of 720 without limitations (a), and a selection of the cells in a total of 619 for the forest of Gazi (b), in a total of 704 for the dense forest of Galle (c) and in a total of 720 for the sparse forest of Pambala (d), both subject to the PCQM limitation that a tree can be selected only once within a simulation of 20 sample points. Amongst the sample points there was an overlap of 14 % for (a) and (c), of 17.5 % for (b) and of 13 % for (d). The frequency distributions of the aggregation structures as well as the aggregation indices (A.I.) are given below.

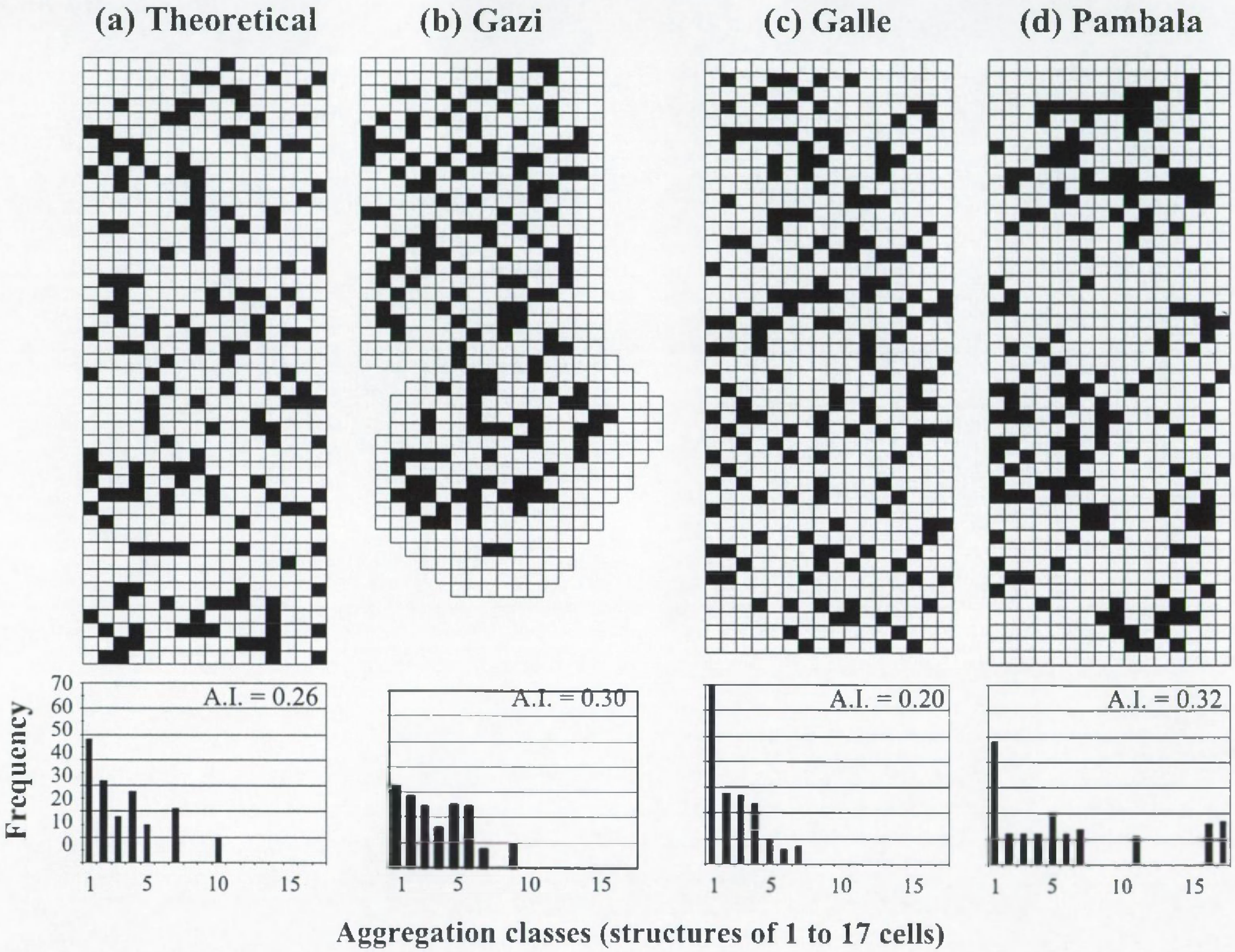
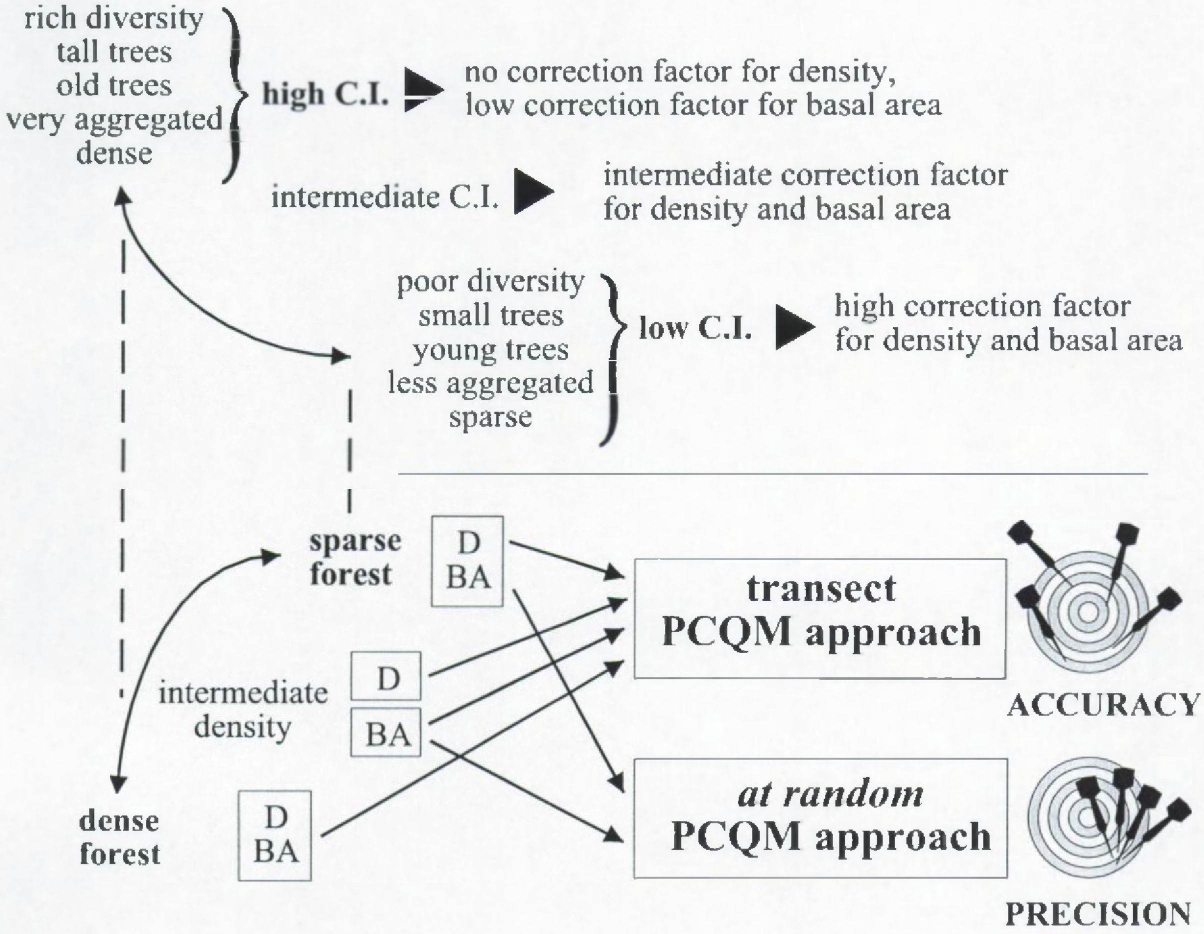


**Figure 9.** Variation of the suggested correction factor for the over- or underestimation of the density and the basal area by the PCQ-Method with respect to the complexity if the forest (C.I.). Underneath, the variation of the PCQM approach used (*at random* or transect) is given according to the density of the forest and the research purpose, the latter considering density more important than basal area (D), or *vice versa* (BA). The results of this study show that there is a precision-accuracy nuance between the transect and the *at random* approach.



# Chapter XV.

# General discussion.

# GENERAL DISCUSSION

## RESEARCH FRAMEWORKS FOR STUDIES ON VEGETATION STRUCTURE DYNAMICS

It is known that, because of direct factors such as exploitation and clear cutting (Kairo, 1995) and because of indirect factors such as siltation and groundwater fluxes (Tack & Polk, 1999), mangrove forests are adversely affected both quantitatively and qualitatively all around the globe (*e.g.* Pernetta, 1993a,b,c,d,e; Rützler & Feller, 1996). Research groups are trying to quantify this decline from different angles using remote sensing. However, it is equally important to link this analysis to fieldwork that monitors the qualitative changes as well. The latter aims for example at the selective unsustainable utilization or exploitation of certain mangrove tree species or at the patterns of succession, both of which can lead to a change in floristic composition or vegetation structure. Research on changes in mangrove forests and on the regeneration potential, including solutions to keep the latter at a level allowing forest rejuvenation must necessarily be considered.

Only recently the importance of mangroves has been acknowledged and efforts to restore them arose. Understanding mangrove vegetation structure dynamics in a particular area is a prerequisite to conservation and management directives, such as the establishment, protection and management of re-afforestation plots in the framework of regeneration projects (e.g. Lee, 1996; Caloz & Collet, 1997). Dahdouh-Guebas *et al.* (2000a) emphasize that there is a need for a methodology that allows to express reliable predictions about the state of mangroves using a relatively small input from vegetation field work, and to decide whether a mangrove stand at a certain location has the potential to successfully renew and rejuvenate or whether anthropogenic pressure renders human interference such as restoration imperative. A monitoring system is needed to decide whether human interference is desirable, since artificial restoration may be appreciated less than natural regeneration. Field (1998b) stated that 'natural regeneration of mangroves should be the first choice of any rehabilitation programme, unless there is irrefutable evidence that it will be unsuccessful'. A clear understanding of the nature and dynamics of local mangrove ecosystems will be the best guide to any restoration programme (Field, 1996). The first step is to collect information about the actual state of the mangrove forest, emphasizing different vegetation layers, but also about past changes in that particular vegetation. Where such studies concentrate on the diversity of mangroves it is important to assess on the appropriate spatial, taxonomic and temporal scale (Farnsworth, 1998). The second step is to integrate such findings in the management and decision-making process.

It has been shown that remote sensing and GIS-based forestry studies can generate results that can be directly used in forest management planning (*e.g.* Holmgren *et al.*, 1997; Holmgren & Turesson, 1998). Applicable findings (when focusing on vegetation layers of different age) can for instance include the prediction of future changes in the mangrove forests. In addition, combination of these data with local and global ecosystem data (biological, hydrological, physico-chemical, geographical,…), socio-geographical or –economic data, particularly in a GIS environment, allows to assess future changes under different scenarios (*e.g.* exploitation, conversion, natural catastrophes or sea level rise) and to adopt conservation strategies by interfering appropriately, if at all.

## WHAT ENCOMPASSES 'DYNAMICS' IN THE LITERATURE ?

A verification of the term 'dynamics' in recent literature on marine science or forestry, relevant to the study of general mangrove ecology, reveals that this term is being used in an environmental, a faunal or a floral context. In an environmental context it has been used to refer to nutrient dynamics (Rice & Tenore, 1981; Newell, 1984; Blair, 1988; Tam *et al.*, 1990; Chen & Twilley, 1999), DOC dynamics (Velimirov, 1986), sediment or detritus dynamics (Brakel, 1984; Flores-Verdugo *et al.*,1987) and hydrodynamics (Wolanski, 1992; Kitheka *et al.*, 1995; Kitheka, 1997). In a faunal context 'dynamics' has referred to behavioural clustering dynamics (Gherardi & Vannini, 1992), community dynamics (Syms & Jones, 2000) and spatial and temporal dynamics (Lugomela, 1995). In a vegetation context 'spatial and temporal dynamics' has been used as well (Smith & Huston, 1989; Murali *et al.*, 1998), next to litter dynamics (Brown, 1984; Twilley *et al.*, 1997), biomass dynamics (de Boer, 2000), canopy dynamics (Herwitz *et al.*, 1998) and population dynamics (Fromard *et al.*, 1998; Jiménez & Sauter, 1991; Clarke, 1995).

In a number of cases terms as 'mangrove forest dynamics' (Smith *et al.*, 1991), 'vegetation dynamics' (Heil & Van Deursen, 1996; Dahdouh-Guebas *et al.*, 2000a) or simply 'dynamics' (Putz & Chan, 1986) have been used, all of these intending more or less 'changes in stand structure and composition'. It is in the latter context that the present paper is written, more precisely : '*changes in stand extent, structure and composition*'. Although to scientists who are focusing on vegetation it is evident that these simple terms have the above meaning, to others these terms might seem less meaningful. Therefore we suggest to adopt the term 'vegetation structure dynamics' for 'changes in stand structure and composition', both spatial and temporal.

## DATA ACQUISITION AND ANALYSIS IN STUDIES ON VEGETATION STRUCTURE DYNAMICS

### Remote sensing

In the past two decades remote sensing technology has been given a leading role in the acquisition of data on vegetation (*e.g.* Gang & Agatsiva, 1992; Cohen *et al.*, 1996; Ramachandran *et al.*, 1998; Dahdouh-Guebas *et al.*, 1999, 2000a, 2000c) and both 'reviews' and 'recent advances' are continuously reported in order to emphasize and compare the potential of various remote sensing technologies in the past and for the future (*e.g.* Rehder & Patterson, 1986; Tassan, 1987; Aschbacher *et al.*, 1995; Blasco *et al.*, 1998; Holmgren & Turesson, 1998; Hyyppä *et al.*, 2000).

The integration of data on vegetation structure dynamics from different moments in time has become almost entirely dependent on remote sensing (*e.g.* Heil & Van Deursen, 1996; Murali *et al.*, 1998; Dahdouh-Guebas *et al.*, 2000a), which usually constitutes the only retrospective basis of comparison to actual vegetation data (Dahdouh-Guebas *et al.*, 2000a). Assessment of factors related to the mangrove on a large scale (global or regional distribution, cartographic inventories, land-use conversion, conservation) and investigation of the regional or global extent of mangroves (*e.g.* Spalding *et al.*, 1997), largely rely on satellite imagery. For periods of time starting before the existence of space-borne sensors, aerial photography will often provide the essential and the only data on changes in vegetation. Whereas aerial photography, in addition, has been of an unequalled quality in the study of vegetation structure dynamics until present, the launch of IKONOS, the first commercial Very High Resolution (VHR) Earth

Observation satellite in September 1999 by Space Imaging (US), probably marks the beginning of a new remote sensing era providing both panchromatic and multi-spectral images with a 1 m to 4 m resolution. This type of resolution combined with the multi-spectral character of the imagery (incl. near-infra-red) may provide alternatives to the as yet unsolutioned inability of identification of mangroves on a species level (Verheyden *et al.*, subm.; Dahdouh-Guebas *et al.*, in prep.a).

However, for the present research only aerial photographs were available and their applicability to the investigation of mangrove vegetation and the study of mangrove vegetation structure dynamics was positively evaluated (*loc. cit.*). However, a providing correct mangrove tree species list is essential (Jayatissa *et al.*, subm.) and eventually fieldwork must be carried out.

## Ground-truthing

Fieldwork or ground truthing, which remains imperative in remote sensing studies, has concentrated on the adult vegetation in many case-studies (Spalding *et al.*, 1997), but great benefit arises when combining these data with other vegetation layers (Murali *et al.*, 1998; Dahdouh-Guebas *et al.*, 2000a, subm.a). Next to overlays between map data originating from different moments in time in a GIS-environment (Geographical Information System) and a quantification of changes that occurred in the past (*e.g.* Verheyden, 1997), an overlay of a map with data from present-day vegetation layers (*e.g.* as plots or transects) may provide insight into the present and possibly future dynamics of the mangrove (Dahdouh-Guebas, *et al.*, 2000, subm.a).

If the vegetation layers with adult, young and juvenile trees are considered there can be either an absence or a presence for each of these. Table 1 summarises the possible combinations of vegetation layers and defines the type of vegetation structure dynamics that can form the basis for such combinations.

A forest, or a species within a forest, without adult individuals has a pioneering or colonising nature (colonisation dynamic type, hereafter referred to as C-type or displaying C-dynamics). Examples of species with a colonising nature are *Avicennia* and *Sonneratia*. A less obvious example, but encountered on beaches away from mangroves in both Kenya and Sri Lanka, is *Bruguiera gymnorrhiza* (pers. obs.). From the case-study of Galle (Dahdouh-Guebas *et al.*, 2000a) it is clear that in Sector 3 *Rhizophora apiculata* must have had a colonising nature in the past.

A forest with a presence of adult trees and an absence of either young or juvenile ones is declining (degradation dynamic type or D-type / D-dynamics). It is remarkable that this can be illustrated with the very same Sector 3 of Galle at present, since no young or juvenile trees were found during the recent fieldwork missions (*loc. cit.*). Another example to illustrate a D-type is the condition of the Parc National du Banc d'Arguin in Mauritania, where adult *Avicennia germinans* trees usually do not show young or juvenile trees in their understory (Dahdouh-Guebas & Koedam, in press). A forest with adult trees and without either young or juvenile ones may be threatened with decline as well, unless there is a transient lack of younger specimens or an accelerated growth. The latter can be very acute in forest areas where *Rhizophora mucronata* dominates the canopy, *Ceriops tagal* dominates the young understory and a mix of both species is dominating the juvenile understory. When canopy

**Table 1.** Presumed future status of a forest with an incomplete or complete vertical vegetation structure (not all vegetation layers represented in the field) on a monospecific or assemblage formation basis as theoretically derived from field data.

| AT | YT | JT | Description | Term |
|---|---|---|---|---|
| 0 | 1 | 0 | INCOMPLETE VERTICAL VEGETATION STRUCTURE<br>forest **colonisation** | → **C-TYPE DYNAMICS** |
| 0 | 0 | 1 | | |
| 0 | 1 | 1 | | |
| 1 | 0 | 0 | long-term lack of rejuvenation<br>actual **decline** of forest | → **D-TYPE DYNAMICS** |
| 1 | 1 | 0 | short-term lack of rejuvenation<br>threatening **decline** of forest in the distant future, unless acute, transient decline | |
| 1 | 0 | 1 | incipient rejuvenation or long rejuvenation cycle<br>threatening **decline** of forest in the near future, unless growth is accelerated (*e.g.* canopy gaps in Kenya, Kairo *et al.*, in prep.) | → **J-TYPE DYNAMICS** |
| 1 | 1 | 1 | COMPLETE VERTICAL VEGETATION STRUCTURE<br>How has vertical vegetation structure changed in the past ?<br>**Static forest** or **dynamic forest** (*cf.* table 2) | |

0 = absent; 1 = present; AT = adult trees; YT = young trees; JT = juvenile trees

**Table 2.** Status of a forest in a spatio-temporally static or dynamic nature (as evident from retrospective research), judging from the similar (=) or dissimilar ( ≠ ) distributions of adult trees (AT), young trees (YT) and juvenile trees (JT) in the field. Note that both a spatio-temporally static and dynamic nature are supported by a underlying steady-state mechanisms. The bullets represent exclusive options. Underlined examples for the respective situations have been taken from existing studies.

| | | ACTUAL FIELD DATA | | | | |
|---|---|---|---|---|---|---|
| | | **AT = YT = JT** | **AT = YT ≠ JT** | **AT = JT ≠ YT** | **AT ≠ YT = JT** | **AT ≠ YT ≠ JT** |
| **RETROSPECTIVE RESEARCH** | **Static forest** | • normal **rejuvenating** forest<br>(Dahdouh-Guebas *et al.*, subm.a, subm.b) | • **rejuvenating** forest, with elements of a dynamic forest nature, in which JT are spread over a wider area than where they can actually establish | • **declining** forest, in which YT fail to find areas appropriate to grow in and JT largely originate from AT, but possibly will be aborted<br>• (shift to **dynamic** nature) | • **declining** forest, in which YT fail to find appropriate areas to grow and JT largely originate from YT<br>• **change** in **static** nature<br>• (shift to **dynamic** nature) | • **declining** forest<br>• **change** in **static** nature<br>• (shift to **dynamic** nature) |
| | **Dynamic forest** | • **declining** forest<br>• (shift to **static** nature)<br>Dahdouh-Guebas *et al.*, 2000a, subm.b) | • **rejuvenating** forest, with elements of a static forest nature, in which JT are spread over a wider area than where they can actually establish | • **rejuvenating** forest with elements of a static forest nature, in which JT largely originate from AT | • **rejuvenating** forest with elements of a static forest nature, in which JT largely originate from YT | • normal **rejuvenating** forest<br>Dahdouh-Guebas *et al.*, 2000a, subm.b) |

N.B. Juvenile trees can originate from either young or adult trees, which can however not be unequivocally established.

gap formation occurs due to the logging of *R. mucronata*, which is a highly preferred species by the local population in Mida Creek (Dahdouh-Guebas *et al.*, 2000b), *C. tagal* is actually the species that pre-empts the gap in the canopy (Kairo *et al.*, in prep.b). What is preferred is logged, but what is logged is therefore not necessarily what will regenerate.

A forest with adult, young and juvenile trees is generally rejuvenating (rejuvenation dynamic type or J-type / J-dynamics). However, it may also be declining depending on the similarity in distribution of adult, young and juvenile trees. Whereas the term 'decline', as used above, refers to a decline of age structure on a particular place and will be referred to as 'vertical decline', this term can also be used with respect to the area coverage of a forest or species, hereafter called 'horizontal decline'. If this horizontal decline is purely surface bound we refer to 'quantitative horizontal decline', which is not considered at this stage. When all vegetation layers are represented in the field we will obviously also refer to J-dynamics, but if there are significant shifts in species composition from 'mangrove species' towards 'non-mangrove species' we will refer to 'qualitative horizontal decline'. This should be taken *sensu lato* and applies in case of both shifts from strict or major mangrove components towards the minor mangrove components and shifts from mangroves species in general towards mangrove associates or non-mangrove species.

Table 2 is showing how the data from the past on the spatially static or dynamic nature of a forest can be combined with distribution data from the present from all vegetation layers in order to evaluate the status of the mangrove as being spatially static (*i.e.* without spatial changes over time) or spatially dynamic (*i.e.* with spatial changes over time). It must be highlighted however that a spatially static forest does not imply a static nature of all processes. As a matter of fact there is a steady-state condition underlying the spatially static or spatially dynamic nature of a forest. A spatially static forest such as Sector 1 in the mangrove of Galle (Dahdouh-Guebas *et al.*, 2000a) supports rejuvenation and other processes in its understory.

A spatially static forest with a similar distribution of adult, young and juvenile trees, for instance, is obviously rejuvenating : the younger trees develop close to the adult ones but the vegetation patches themselves do not displace. In case of a strong dissimilarity between the above distributions the spatially static forest might be declining and possibly requiring human interference, whereas in case of a spatially dynamic forest dissimilar distributions might be perfectly normal (Tab. 2).

This type of analysis, the results of which can be shown using a clear and highly qualitative graphical design, can be supported by a parallel statistical analysis that is based on the same type of data and generates more quantitative and testable results (Figs 1 and 2). Detrended correspondence analysis (DCA), canonical correspondence analysis (CCA) and non-linear multi-dimensional scaling (NMDS) are particularly adapted tools for this type of research, which in addition also allow to include environmental data that may help in the explanation of the observed vegetation structure (Cannicci *et al.*, 2000; Dahdouh-Guebas *et al.* subm.a, subm.b).

## TYPES OF VEGETATION STRUCTURE DYNAMICS IN MANGROVES

Basically, the vegetation structure of mangroves can be typified as zoned on one hand (*e.g.* in the Kenyan sites), with a vegetation 'zone' defined as a long band-like patch of vegetation, or as non-zoned on the other hand, which then displays a mosaic pattern of 'vegetation patches', the latter defined as a polygon with no determined shape or area (*e.g.* Galle, Sri Lanka). In some cases however, zonation may be very irregular or restricted to a particular part of the tidal gradient, and be termed as a 'partial' or 'semi-zonation' (*e.g.* Pambala, Sri Lanka). Both 'zones' and 'patches' would have a certain, often monospecific floristic composition. However, there are also a number of recurrent mangrove assemblages, such as the ones listed by Macnae (1968). This author points out that Walter & Steiner (1937) named the zones that they observed in East-Africa after the dominant tree in the assemblage, a way of identifying zones or patches that is still much in use today (*cf. e.g.* Gallin *et al.*, 1989).

Whereas the zonation-issue and particularly the causes of its formation have been much debated in the history of mangrove research, little has been said about vegetation structure dynamics, let alone terming some of the types. Dahdouh-Guebas *et al.* (2000a) introduced the term 'moving mosaic' (Figs 1 and 3) for the type of vegetation structure dynamic that displays relatively large vegetation patches to apparently 'move' from one area in a mangrove forest to another area (disappearance and appearance), or put alternatively : for the type of vegetation structure dynamic that displays a certain area of a forest that changes in species composition over time, and may even interact with terrestrial vegetations such as sedges and coconut plantations. A vegetation structure dynamic displaying vegetation patches to extend or to grow, rather than to 'move around', can similarly be termed a 'growing mosaic'. Dahdouh-Guebas *et al.* (2000a) suggest that a moving mosaic vegetation structure dynamic may be typical for mangroves that are characterised by an irregular topography instead of the frequently encountered intertidal slope. In areas where mangroves are clearly zoned, changes in vegetation structure often follow a rather pronounced intertidal slope (Dahdouh-Guebas *et al.*, subm.a). The vegetation structure dynamics that occur under these circumstances can be typified as 'shifting zones' (Fig. 3), if the zones are displaced entirely, or as 'growing zones' (Figs 2 and 3) if the zones are becoming larger (positive growth, *e.g.* seaward grey patches in Gazi, Fig. 2) or smaller (negative growth, *e.g.* landward grey patches in Gazi, Fig. 2). Some clear examples of the latter types of transgressive (sometimes introgressive) vegetation structure dynamics can be found as responses of mangroves to selective cutting by people (Dahdouh-Guebas *et al.*, 2000b, subm.a; Kairo *et al.*, in prep.), to sea-level change or to altered tidal hydrodynamics (Woodroffe, 1990, 1995, 1999; Wilton, 1999), and to natural events (Stevens & Montague, 1999; Wilton, 1999; Nguyen *et al.*, 2000). In the latter two cases, however, the 'shifting zone' concept applies to the entire mangrove ecosystem rather than to vegetation assemblages specifically.

Vegetation structure dynamics of mangroves is also associated to succession, particularly in a situation in which a naked or denuded habitat is colonised and further develops. We recognise three categories : floristic accretion, floristic invasion and floristic dominance/extinction (Fig. 4). 'Floristic accretion' occurs when a first pioneering species is in part responsible for the development of new adjacent zones, mostly located more landward. This is the case for pioneering mangrove species such as *Avicennia* or *Sonneratia*. 'Floristic invasion' occurs when an established zone is invaded by another species that develops within the original zone and forces the original species to retreat (Fig. 2). This may be the process underlying the double zonation often observed in *Avicennia marina* (*e.g.* Dahdouh-Guebas *et al.*, subm.d). Finally, in a particular vegetation structure comprising different assemblages with a dominant species, one may develop to become the dominant assemblage at the expense of other species or assemblages (Fig. 1). We term this case 'floristic dominance' with respect to the dominating species and 'floristic extinction' with respect to the retreating and disappearing ones. In some case floristic invasion and floristic dominance may be difficult to distinguish, or an interaction between both may exist (*cf.* Fig. 1). The ease with which these

**Figure 1.** Example of past (a,b), present (c,d) and possible future dynamics (d) in Unawatuna-Galle (Sri Lanka) adapted from a remote sensing study (Dahdouh-Guebas *et al.*, 2000a) and from an ordination study (Dahdouh-Guebas *et al.*, subm.b). Colours represent different mangrove assemblages, except 'white' (= inhabited and terrestrial area), grey (= human infrastructure) and 'purple' (= coconut plantations).

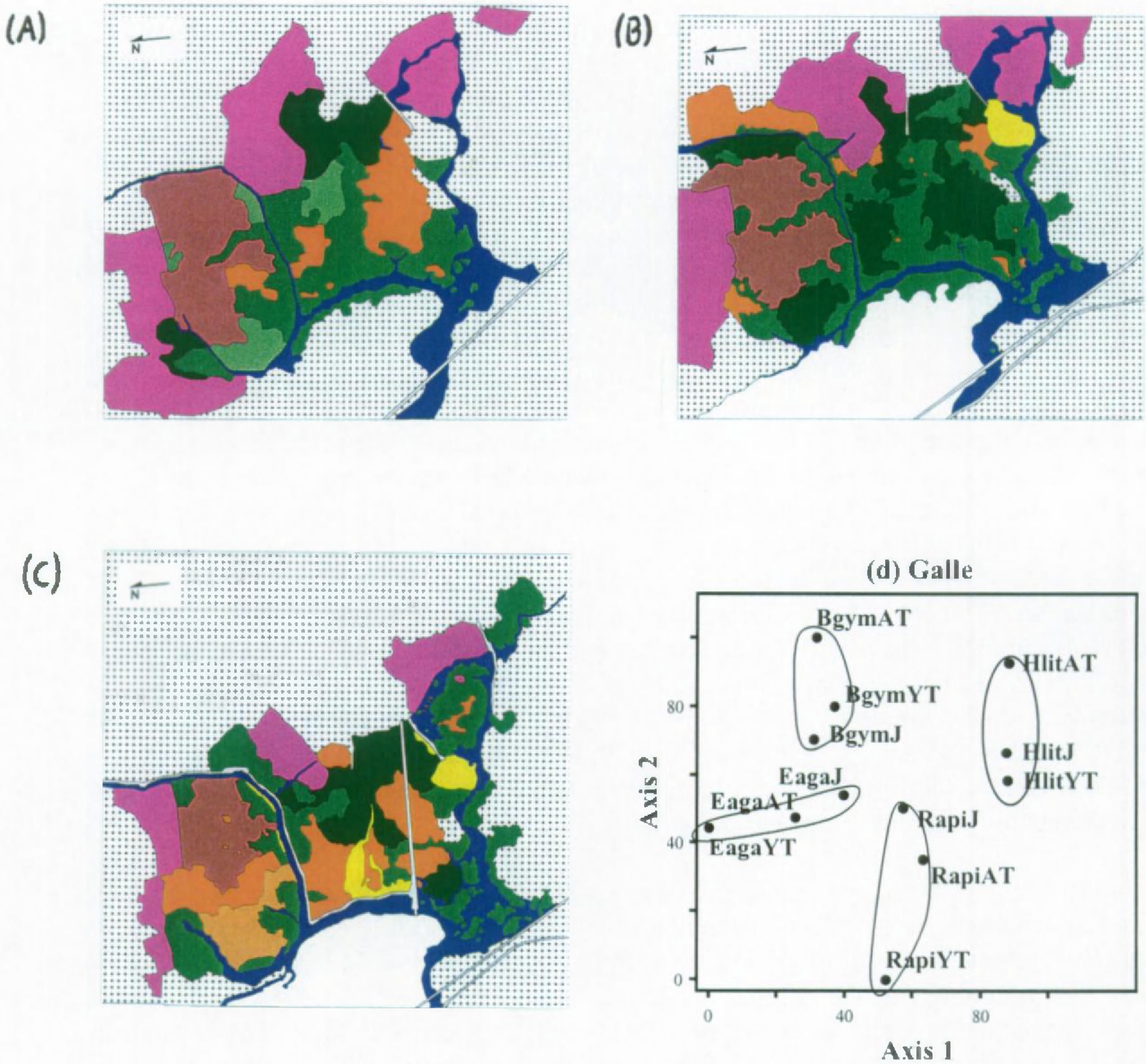
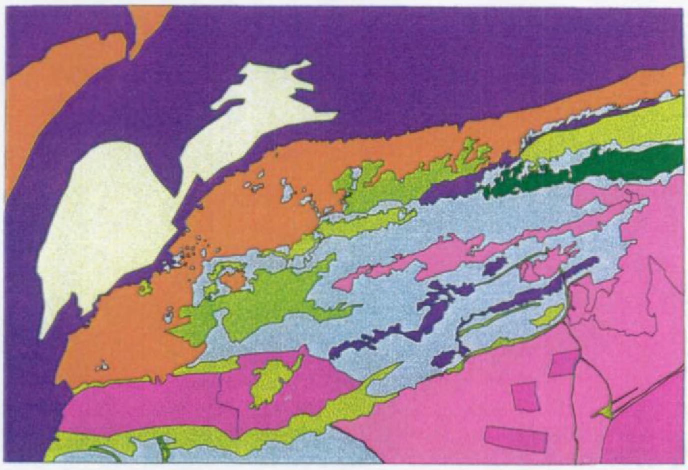
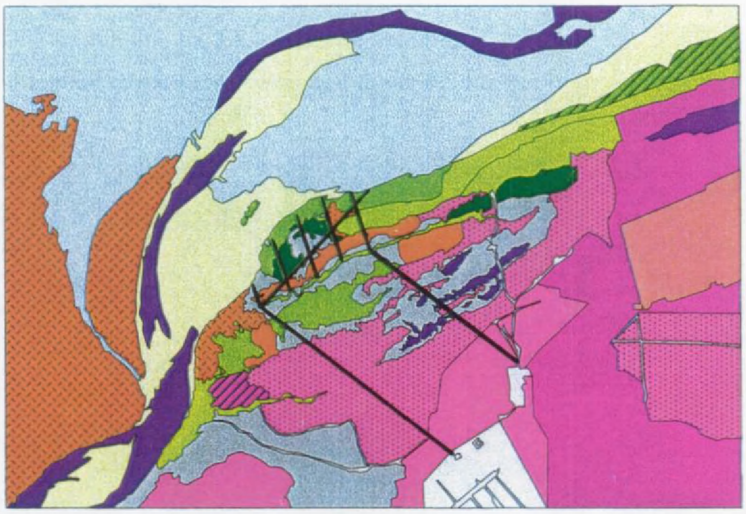


**Figure 2.** Example of past (a), present (b,c) and possible future dynamics (c) in Gazi Bay (Kenya) adapted from a remote sensing study (Dahdouh-Guebas *et al.*, subm.a) and from an ordination study (Dahdouh-Guebas *et al.*, subm.b). Colours represent different mangrove assemblages, except 'pink' (= terrestrial vegetation), grey (= human infrastructure) and 'purple' (= coconut plantations).

(a)



(b)



(b) Gazi

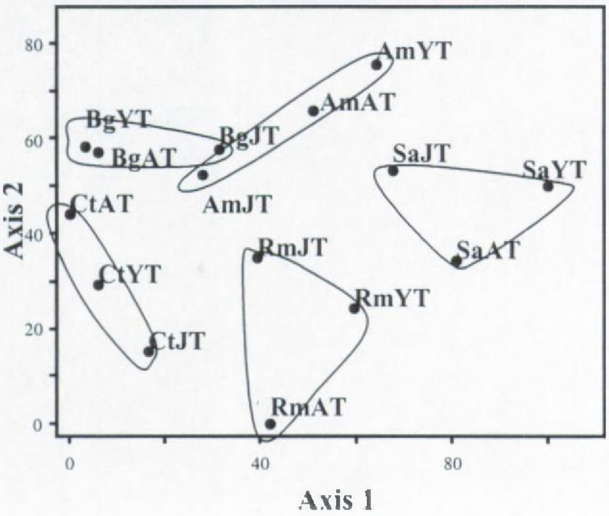


**Figure 3.** Types of spatio-temporal vegetation structure dynamics. Each row represents a forest area on three different and chronologically ordered moments in time ($t_1$, $t_2$ and $t_3$). The shades represent different mangrove tree species.

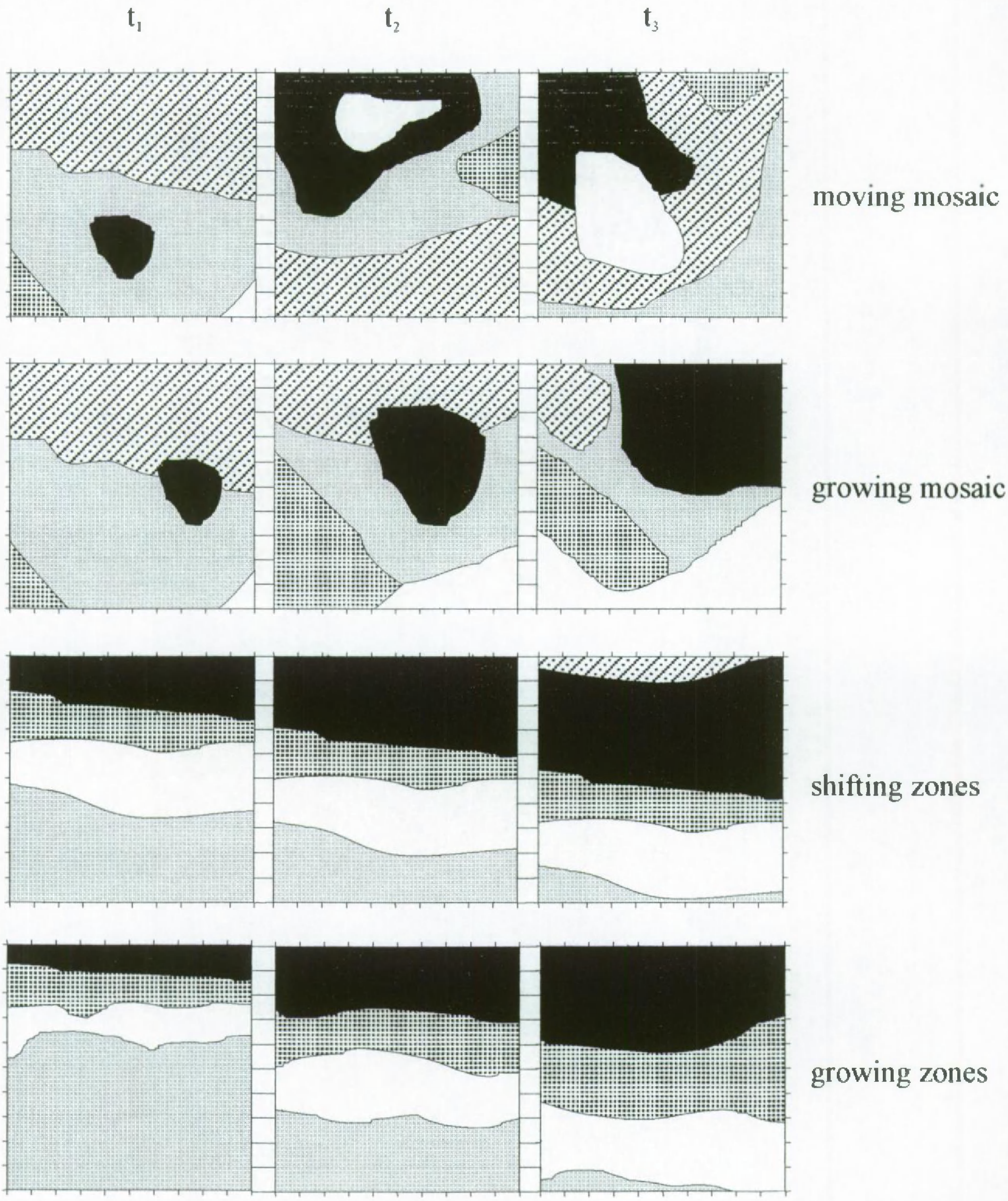
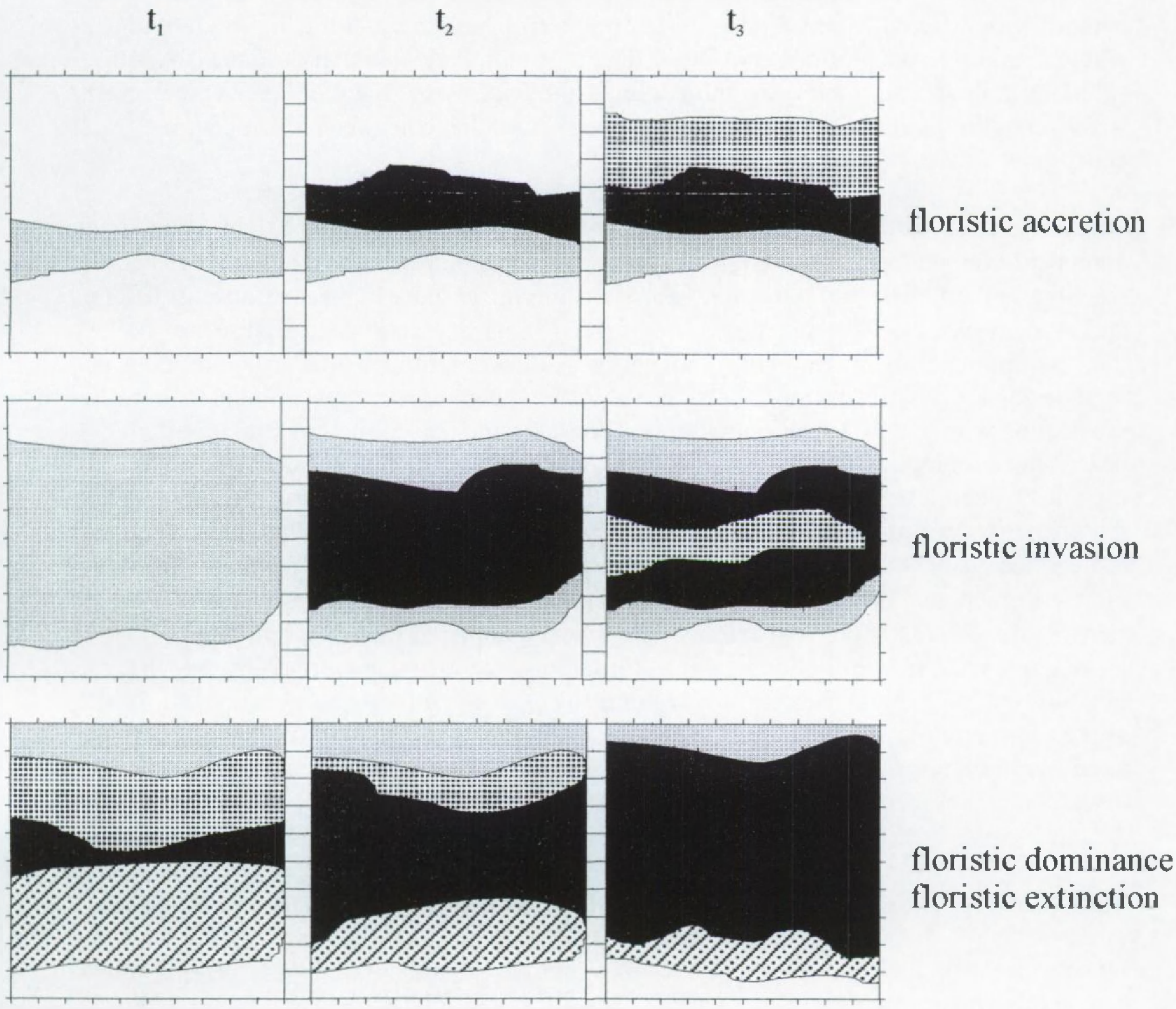


**Figure 4.** Types of spatio-temporal floristic succession in vegetation structure dynamics : floristic accretion, floristic invasion and floristic dominance/extinction



process can be distinguished in part also depends on the regularity with which imagery can be obtained.

Whereas the vegetation structure dynamics at lower latitudes take place against the background of the multispecific nature of the mangrove stands (incl. the 'behaviour' of forest patches with different compositions with respect to one another), at the highest latitudes where mangroves occur it is somewhat different. In the Parc National du Banc d'Arguin (PNBA), at the northern biogeographical limit of mangroves along the West-African coast, *Avicennia germinans* is the sole mangrove tree species that constitutes the mangrove ecosystem.

'Vegetation structure dynamics' as defined above (*i.e.* changes in stand extent, structure and composition) must be interpreted in its context. Basically, the 'extent' has still the very same meaning in the PNBA, but the scale we are considering at these higher latitudes is different and in many cases we are considering fragmented small populations on a large area rather than continuous fringes. Contrary to mangroves at lower latitudes, the 'structure' does not include zonation issues, mosaics or other vegetation patches on a substantial area, because we are dealing with a monospecific mangrove. For the same reason there is little point in describing a 'composition', unless all the non-mangrove beach and sebkha vegetation is included. Therefore 'vegetation structure' is limited to the extent and fragmentation of the few mangrove populations left and to their physiognomy. Whereas the latter has not been an issue in Kenya or Sri Lanka (probably because there are other vegetation features that are more conspicuous), in Mauritania the different mangrove physiognomies were the most remarkable features of the vegetation structure and comprised four different types : high tree formations, wide tree formations, 'shrub' formations and 'sebkha' formations, which were obviously no phases in a vegetation development. The sole possible case would be for the sebkha formation to evolve into a shrub formation. Whether this is actually the case requires a long-term monitoring, preferably using aerial photography if useful, and is subject to future research.

## MANGROVE REGENERATION AND ITS CONSTRAINTS AS AN INTEGRATED APPLICATION

Investigations on the status of mangroves in Kenya revealed that three types of forest states can be recognised : mangrove in a virtually pristine condition (Kiunga and Lamu, North Kenyan coast; Kairo *et al.* 1999), mangrove that is anthropogenically adversely influenced (Mida Creek and other creeks between Mombasa and Malindi, central Kenyan coast) and mangrove that is anthropogenically degraded (Gazi Bay and other creeks between Mombasa and Vanga, South Kenyan coast) (Kairo, in prep.). In South-West Sri Lanka the occurrence of mangrove forests in a highly fragmented way, is mainly due to man as well (De Silva & Balasubramaniam, 1984-85). Studies based on sequential aerial photography in both countries have shown that the dynamics in vegetation structure in sites disturbed by man probably requires human interference to rehabilitate the mangrove (Dahdouh-Guebas *et al.*, 2000a, subm.a). A prediction following from combination with investigations on the distribution of young and juvenile trees confirm this (Dahdouh-Guebas *et al.*, subm.b). The above study therefore leads to a suggestion of both forest areas and tree species that should be considered in artificial regeneration.

However, both areas and species are exposed to a number of threats. Certain mangrove areas are subject to high propagule predation rates (Smith *et al.*, 1989; McKee, 1995a; McGuinness, 1997b; Dahdouh-Guebas *et al.*, 1997, 1998; Dahdouh-Guebas, subm.). This biotic factor affects the choice of the site in mangrove restoration. Understanding such constraints to mangrove regeneration obviously contributes to an improvement and a development at the level of artificial plantations and silviculture (Gong & Ong, 1995). Dahdouh-Guebas *et al.* (1999b), Ballerini *et al.* (2000), Cannicci *et al.* (2000) and Dahdouh-Guebas *et al.* (subm.c) provide a first step in the understanding of crabs' feeding behaviours by analysing the diets of crabs and their zonation in the forest with respect to mangrove trees.

Experimental designs to analyse the phenomenon of propagule predation were set up by *e.g.* Smith *et al.* (1989), Osborne & Smith (1990), McKee (1995a), McGuinness (1997b), Dahdouh-Guebas *et al.* (1997, 1998), Steele *et al.* (1999), Dahdouh-Guebas (subm.) and Allen *et al.* (in prep.). The results found in the present study are summarized in table 1.

**Table 1.** A synthesis of the findings on propagule predation in Kenya and Sri Lanka (Dahdouh-Guebas *et al.*, 1997, 1998; Dahdouh-Guebas, subm.).

| KENYA | SRI LANKA |
|---|---|
| **differential predation among forest <u>zones</u> :** more predation in landward and *Rhizophora* dominated zones | **differential predation among forest <u>patches</u> :** more predation in *Excoecaria* dominated patches |
| **no differential predation among mangrove <u>propagules</u> :** all species are predated | **differential predation among mangrove <u>propagules</u> :** *Avicennia* predated more than *Buguiera*, which in turn is predated more than *Rhizophora* |
| **differential predation among mangrove <u>crabs</u> :** more predation by *Neosarmatium* spp. and *Sesarma* spp | **differential predation among mangrove <u>crabs</u> :** more predation by *Neosarmatium* spp. and *Chiromanthes* spp. |

Also propagule predation by other animals seems to affect tree species to different degrees, for instance propagules from *Rhizophora apiculata* Bl. seem to be much less appreciated by the snail *Terebralia palustris* L. than those of *Bruguiera gymnorrhiza* (L.) Lam (Dahdouh-Guebas, subm.). Predation or parasitism by insects was observed in *B. gymnorrhiza*, but not in other species (*loc. cit.*).

In the PNBA in Mauritania, the two main crab species observed were *Uca tangeri* Eydoux and *Callinectes marginatus* A. Milne-Edwards, which are an algal feeder and an animal predator respectively. Propagule predation was not observed at all in the PNBA (Dahdouh-Guebas & Koedam, in press).

It has also been shown how propagule predation and vegetation structure dynamics may be inter-linked through hydrology. The model that Dahdouh-Guebas (subm.) introduced for this link, is inspired on the phenomenon of propagule predation but includes elements from vegetation structure dynamics as well. It is briefly repeated here.

The model starts from an adult tree or forest with mature propagules. Before the propagules fall from the tree, predation or parasitism by insects may occur. When a propagule falls there are two possible situations with respect to the water level : low water and high water. The theory states that when the water level is low (predominantly during the dry season), propagules that fall on the mangrove soil plant themselves (planting strategy of Van Speybroeck, 1992) or have more possibilities to strand (stranding strategy of Van Speybroeck, 1992), exposing them more to propagule predators, which in turn are very mobile and predate considerably. The predation of planted propagules (vertical) is initially lower than from

stranded (horizontal) propagules (Dahdouh-Guebas *et al.*, 1997). Some of the propagules are not predated, initially survive and establish. When the water level is high (predominantly during the wet season), the forest is often permanently flooded for a period, and the fallen propagules drift away through the water. They are much less likely to be affected by propagule predators, which at that time are stuck on the mangrove roots. When the water level lowers, predation might still take place, but is less. Dahdouh-Guebas *et al.* (1997) indeed found that mature propagules are predated less than freshly gathered ones. Therefore, more propagules establish after a period of dispersal, during which such a mature stage can be reached. The propagules that establish are exposed to either favorable or unfavorable environmental conditions. These are influenced by environmental factors such as tidal inundation, microtopography, soil texture, aridity and salinity among others, some of which may be inter-linked. Propagules developing under unfavourable conditions will die, whereas those developing under favourable conditions will survive, further develop and grow into an adult tree. As a matter of fact, the post-establishment situation is less simple than introduced here, because between the stage of propagule and that of an adult tree there are many other events. One point in the model is that the zonation, which is partially present in Pambala, must be the result of differences in salinity along the tidal gradient during the dry season, but that the dispersion of propagules to lead to any zonation in the first place, is controlled by the wet season. Once the water level lowers again and propagules can establish, propagule predators further control this establishment. Propagule predation may thus be one link in the chain of events leading to a particular vegetation structure.
In the PNBA, the lack of success of *Avicennia germinans* North of the very last tree (which still produces numerous propagules) could be of a climatic nature (frost frequency) as reported for this species along the North-American West coast (Stevens, 1999).

Based on the study of vegetation structure dynamics, propagule predation, etc… the question as to which forest area needs rehabilitation can actually be answered by providing a map-based regeneration scheme. Within the issue of the mangrove tree species that can be used for regeneration the results of studies on genetic differentiation can be integrated (*e.g.* Abeysinghe, 1999), answering questions such as "To which degree do different or fragmented populations differentiate on a genetic level ?" and "How desirable is it then to collect propagules from a well rejuvenating, but distant population ?".

In mangrove regeneration studies, a most recent and new focus lies in the monitoring of re-afforested plots as a measure of the success of rehabilitation and of the degree of restoration of the original ecological functions or an alternative stable condition (Bosire, 1999; McKee & Faulkner, 2000; Bosire *et al.*, subm.a, subm.b). As a matter of fact rehabilitation plots aim at a restoration of the natural habitat, which can be assessed by monitoring the secondary succession into the often monospecific artificial mangrove stands, as well as the macrofaunal recruitment in it.

### RECCOMMENDATIONS FOR FUTURE RESEARCH ON MANGROVE VEGETATION STRUCTURE DYNAMICS AND REGENERATION (INCL. REGENERATIVE CONSTRAINTS)

A first door to future research was opened with the revisit of the Point-Centred Quarter Method or PCQM (Dahdouh-Guebas & Koedam, subm.). In order to understand mangrove vegetation structure dynamics, monitoring and fieldwork is required, the latter of which necessitates the application of certain methods to acquire the data needed. The PCQM is a widely used method to derive forest parameters such as density and basal area. However, for forest characteristics measured at a particular time to be interpreted within the framework of mangrove vegetation structure dynamics, it is essential that they represent as closely as possible the actual field conditions, or give a good estimation of the errors involved. Dahdouh-Guebas & Koedam (subm.) highlight a number of problems associated to the PCQ-Method, make a first attempt at tackling these issues and open the door to future empirical research that can be checked with actual field observations. The investigation of more sites will lead to the establishment of 'PCQM accuracy correction factors' (*sensu* Dahdouh-Guebas & Koedam, subm.). An in-depth comparison between different PCQM 'rules' (*e.g.* selection of closest stem *versus* selection of central stem) and their effects on the accuracy of derived forest structure parameters is also still unchallenged.

The abundance of mangrove juveniles on the tree and on the mangrove floor have never been investigated in an integrative manner. Phenology studies have always concentrated on characteristics of leaves, flowers and fruits when these were still attached to the parental tree, and terminated when these structures detached. This approach leaves the question as to which propagules establish where unanswered. In the study of vegetation structure, its establishment and its dynamics, the answer to this question may be very valuable.

Similarly, the assessment of the natural propagule predation as opposed to the experimental propagule predation may provide more insight into the relationship between propagule predation and vegetation structure. So far, propagule predation studies concentrated on experimentally planted propagules, leading to figures of 100% predation. However, in natural situations it is very unlikely that propagule predators will jeopardise the survival of the plants that form their habitat at a large scale. Mast seeding with predator saturation may be an escape mechanism.

The regular marking of cohorts of mature propagules, the monitoring of their dispersal and of their fate on the mangrove floor, integrates and fills the latter two gaps in scientific research on mangrove vegetation structure and propagule predation.

With respect to remote sensing, the study of vegetation structure dynamics using the new very high resolution space-borne imagery (*e.g.* IKONOS satellite) must be purchased, but the commercial nature of these data and the extremely high prices associated to this imagery is at present a block to the use of these data for many academic research groups in both industrialised and developing countries.

# Epilogue

## RELEVANCE OF THE WORK IN THE FRAMEWORK OF DEVELOPMENT CO-OPERATION

One thousand years ago, the human world population counted less than 500 million people. By 1650 this figure doubled a first time, by 1850 a second time and by 1975 a third time (Fisher, 1980). Now, at the turn of the second millennium, the world population numbers more than 6 billion people. On one hand this implies that natural resources are under a threat of over-exploitation and under the potential threat of depletion, unless the people using them understand the need for a sustainable use. Even under the latter circumstances, the population explosion may (have) be(en) too big for any sustainable use to generate positive results. On the other hand it becomes increasingly difficult and may even constitute an ethical problem to restrict people from using resources. As just one example, in mangrove forests local people may be dependent on the resources (Dahdouh-Guebas *et al.*, 2000b). Restricting access to natural resources through changes in property rights has been shown to increase poverty (Reddy and Chakravarty, 1999) and increasing inequality and conflict therefore undermine the conditions which are deemed to be necessary for the sustainable management of a resource (Adger *et al*, 1997). In Vietnam, a former centrally planned economy, the inequality is the result of the effects of the economic liberalization process (Adger, 1999). Agrawal & Gibson (1999) state that an effective institutionalisation of community-based natural resource management and conservation is essential. This is corroborated by Aagesen (1998) reporting that self-determination and territorial rights are important factors in the indigenous interests in and commitment to conservation of certain plant species (Aagesen, 1998). Duraiappah (1998) also emphasizes that groups that adopt unsustainable activities must be given the incentives (compensation, rewards, taxes, and information provision) to stop. Omodei-Zorini & Contini (2000) and Omodei-Zorini *et al.* (2000) showed for instance that people around a Kenyan mangrove forest would stop exploiting the mangrove if they were given cattle.

It is in our tradition to establish human settlements along waterways and coastlines (Fig. 1). Whereas the industrialised countries have been able to develop large cities away from the coast, in developing countries the vicinity of water bodies for many cities is still very pronounced. The coastal zone of most tropical and subtropical developing countries also host mangrove forests, which are important on different eco-socio-economic[**] levels. They constitute a place to live and a place to live from. Many settlements are located within the mangrove and in some countries such as Thailand or Tanzania entire villages may built on poles (Kajia, 2000). The people use mangrove wood for construction (houses, boats, furniture) and as fuel (charcoal, firewood), and other mangrove products range from the making of ointments and dyes to the making of fishing gear (*cf.* Stafford-Deitsch, 1996; Dahdouh-Guebas *et al.*, 2000b). A majority of the people living along the coast live from fishing or at least consume fish. Since mangroves act as breeding, spawning, hatching and nursing grounds for many marine animal species a direct link between the mangrove cover on one hand and both the lagoon and offshore fishery on the other hand has been found, and several areas have witnessed a decrease in production from fisheries with more intense mangrove destruction (Baran & Hambrey, 1998; Baran, 1999; Naylor *et al.*, 2000). One of the main reasons for destruction of these forests is shrimp aquaculture, largely under influence of the world's more industrialised countries, but clearly at the expense of poor people in developing countries. For the sake of the livelihoods of the communities depending of the

---

[**] referring to ecological, sociological and economical.

mangrove and on fisheries it is therefore essential that the mangrove ecosystem be protected worldwide.

Assessment and understanding of mangrove extent, evolution, regeneration and restoration is done in a framework of development cooperation (*cf.* Fig. 5 in Dahdouh-Guebas & Koedam, in prep.). At this point it must be emphasized that there is a clear difference between field- and goal-oriented development cooperation on one hand and fundamental and applied scientific research relevant in the framework of development cooperation on the other hand. Field-orientation generally focuses on those countries that are least developed or most in need of international aid, while goal-orientation concentrates on a number of actions that can easily be translated into direct benefits for local people. Belgian International Cooperation for example prioritises five sectors in its development cooperation – basic health care, education and training, agriculture and food security, basic infrastructure and community building – and three crosscutting themes – promotion of equal opportunities for women and men, environmental management, social economy – (BTC, 1999). It is clear that the present research does not fit into any of the sectors and can only be squeezed into the 'environmental management' theme. So, there is still a missing link between the research aspect and the field- and goal-oriented development cooperation. In the same context, on one hand it is claimed that previous knowledge has been ignored and that more and more obscure aspects of mangrove ecosystems are being subjected to examination (Field, 1998b), whereas on the other hand mangrove ecologists tend to be primarily concerned with the intrinsic nature of their research rather than in initiating the use of their findings in the management of mangrove rehabilitation projects (Field, 1999). This 'missing link' can best be established within a holistic forum (*e.g.* human ecology) that is understandable by decision-makers (*cf.* Rönnbäck, 1999). The filling of this missing link requires a separate investigation that integrates the finding in management plans and is beyond the scope of this thesis. However, underneath an attempt will be made to situate the different research aspects better in the framework of development cooperation and local and global management.

The results of scientific research fall apart into different case studies, each of which is an important piece in the whole research framework that has a development relevance. However, it is difficult to present this relevance for every single manuscript presented as a separate study. Therefore the relevance of the key manuscripts presented in the present dissertation, complemented with some of the manuscripts prepared in the same research framework but not included in this work (Appendix 2), is summarised briefly underneath.

- 'Utilization of mangrove wood products around Mida Creek (Kenya) amongst subsistence and commercial users' (Chapter II) :

  *relevant in assessing the* ***local utilization patterns*** *and establishing the* ***degree of dependence*** *of local people on the mangrove resource*;

- 'High resolution vegetation data for mangrove research as obtained from aerial photography' (Chapter IV), 'A note on the identification of mangroves from aerial photography in Kenya and Sri Lanka' (Chapter V) and 'Remote sensing and zonation of seagrasses and algae along the Kenyan coast (Dahdouh-Guebas *et al.*, 1999a) :

  *relevant in assessing the possible tools which can be used to* ***monitor coastal ecosystems*** *and the levels at which this can be done, as well as the actual distribution and composition of these ecosystems*;

- 'Conservation of mangroves *vs.* development of shrimp farming : investigation of the recent evolution of Pambala (Chilaw Lagoon, Sri Lanka) using remote sensing and GIS' (Dahdouh-Guebas *et al.*, 2000c; Dahdouh-Guebas *et al.*, subm.e) :

  *relevant in highlighting the **rate of mangrove destruction** and the **ecological footprint of shrimp farming**, and therefore the **carrying capacity of the environment***;

- 'Four decade vegetation dynamics in Sri Lankan mangroves as detected from sequential aerial photography : a case study in Galle' (Chapter VI), 'Two decade vegetation dynamics in Kenyan mangroves as detected from sequential aerial photography : a case study in Gazi Bay' (Chapter VII) and 'An ordination study to view past, present and future vegetation structure dynamics in disturbed and undisturbed mangroves forests in Kenya and Sri Lanka' (Chapter VIII) :

  *relevant in understanding the **evolution of mangrove vegetation structure** dynamics and to **make predictions for the future** to anticipate artificial restoration*;

- 'Propagule predators in Kenyan mangroves and their possible effect on regeneration' (Chapter X), 'Food preferences in *Neosarmatium meinerti* de Man (Decapoda : Sesarminae) and its possible effect on the regeneration of mangroves' (Dahdouh-Guebas *et al.*, 1997) and 'Propagule predation in Sri Lankan mangroves and its effect on vegetation structure' (Chapter XI) :

  *relevant in the framework of mangrove regeneration for finding the **crab species** and **mangrove areas** that are most likely to display propagule predation and for finding the **mangrove species** that is most likely to be **adversely affected by propagule predation***;

- 'Regeneration status of mangroves under natural and nursery conditions in Galle and Pambala, Sri Lanka' (Chapter XII) and 'Natural regeneration status of mangrove forests in Mida Creek, Kenya' (Kairo *et al.*, in prep.) :

  *relevant in the framework of mangrove regeneration for **monitoring the status of mangrove regeneration** in natural and nursery conditions on a short and a long term*;

- 'Recovery process of a restored mangrove system in Kenya : a floral perspective' (Bosire *et al.*, subm. b) and 'Macrofaunal recruitment in a restored mangrove system in Kenya' (Bosire *et al.*, subm. a) :

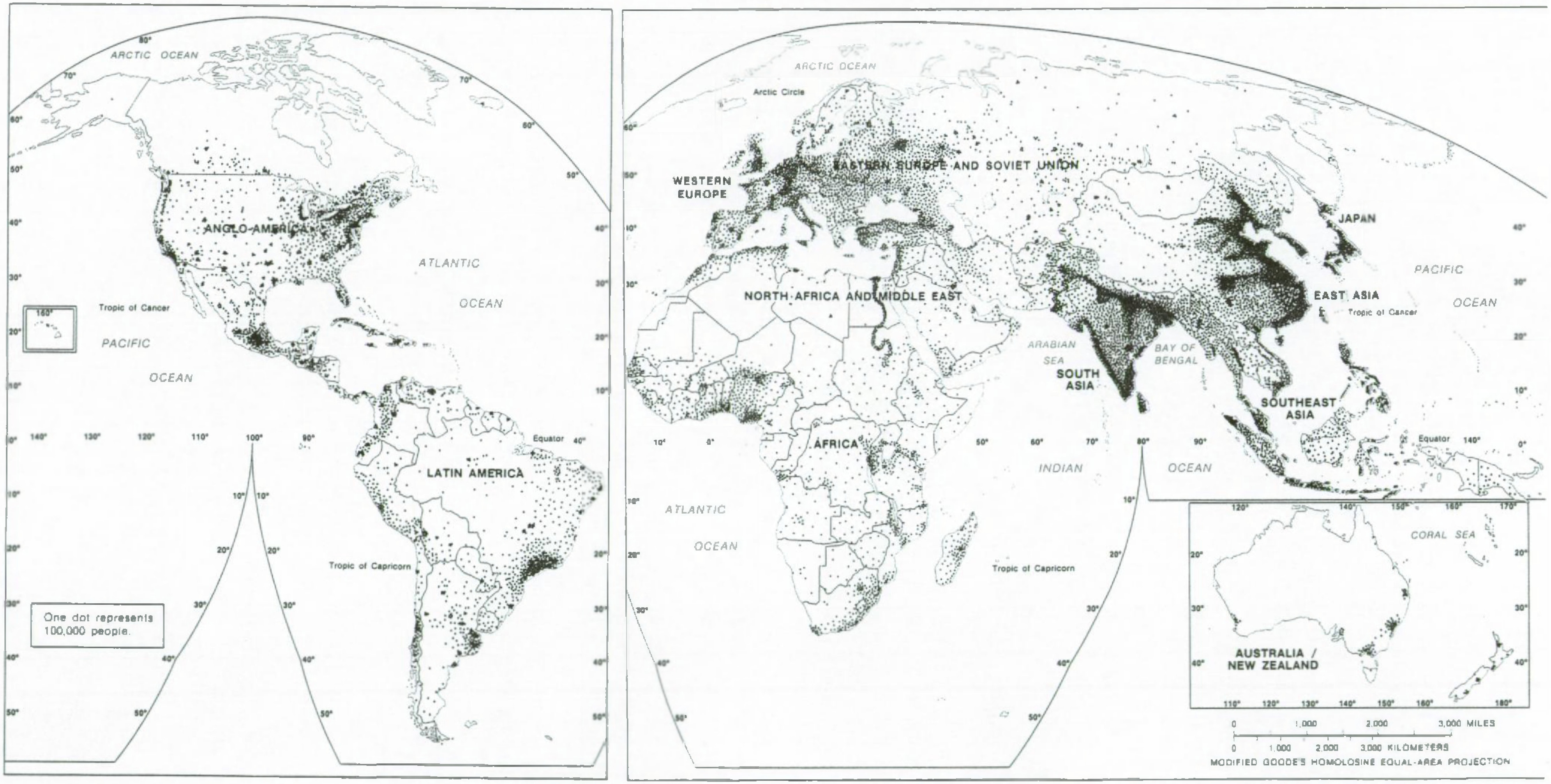
  *relevant in the evaluation of how similar the **functions and services of a restored mangrove** forest are as compared to the natural mangrove*;

- Are the northernmost mangroves of West Africa viable ? - a case study in the Parc National du Banc d'Arguin, Mauritania – (Chapter XIII) :

  *relevant in understanding **factors that limit the distribution of mangroves**.*

**References**
See Bibliography

**Figure 1.** World population distribution (Fisher, 1980). A majority of the population is located near water bodies (lakes, rivers, oceans).



# General Conclusions

- **Which are the features that can be recognised from airborne remote sensing imagery of mangrove areas ?**
  Identification of mangroves from airborne remote sensing has shown to penetrate to the assemblage or genus level. Species identification is a possibility if the local species composition is known, but not if there are several genus members. The latter may be compromised if erroneous species lists are provided, for instance for new mangrove areas. A synthesis of all the sites studied indicates the plasticity of some image attributes and the consistency of others.

- **What is the spatio-temporal vegetation structure of the mangroves ?**
  In our study sites the horizontal vegetation structure has been found to comprise 'zoned' or 'mosaic' forest patches, depending on the tidal amplitude. The 'moving mosaic', 'growing mosaic', 'shifting zones' or 'growing zones' dynamics, some of which associated to our study sites, each comprise a particular evolution of the vegetation. The floristic 'accretion', 'invasion' or 'dominance/extinction' describe the way in which the floristic diversity is enriched or extinct as a result of the dynamics. The vertical vegetation structure does not always comprise an adult, young and juvenile vegetation layer, and the various combinations of vegetation layers, on the species or assemblage level, can be an indication for the future vegetation structure. The qualitative analysis of the vegetation structure using remote sensing and GIS combined with the quantitative analysis using ordinations, is a complementary approach that allows predictions that can be used directly in management or forestry plans.

- **What is the mangrove regeneration potential and to which extent are propagule predators a constraint to regeneration ?**
  The short-term regeneration potential (measured through *e.g.* rooting performance) has been found to differentiate between species and forest patches. It is under strong influence of differential propagule predation in our study sites (differences between species, between forest patches and between sites), and was found to vary with the mangrove lagoon water level in the non-tide dominated sites. A model was proposed in which propagule predation is presented as one link in the chain of events that leads to a particular vegetation structure.

- **What is the vegetation structure of a mangrove at its biogeographical limit ?**
  The mangroves of the Parc National du Banc d'Arguin display four different growth forms of the vegetation : high trees, wide trees, shrub formations and sebkha formations comprising mangroves. Although under stressful conditions, there was no decreased flowering and only slightly decreased fruiting, the main problem being the fruits falling in sites with unfavourable conditions.

- **Which are the problems associated with the use of the PCQM for the study of mangrove vegetation ?**
  The PCQ-Method may lead to an inconsistent over- or underestimation of the density and the basal area of the mangrove, depending on the forest structure (dense / sparse, aggregated / non aggregated), which can be partially solved by the choice of a 'transect' or '*at random*' PCQM approach. Architecture of trees or colonies limits the applicability of the PCQM by the book.

## Bibliographical Errata

~~Striketrough~~ = erroneous, Underline = to be added

**Bosire**, J.O., ~~2004 ?~~ Floristic and faunistic recovery process of restored mangrove ecosystems in Kenya. PhD dissertation, Vrije Universiteit Brussel, Brussels, Belgium. (**in preparation**).

**Gong**, W.K. & J.E. **Ong**, 1995. The use of demographic studies in mangrove silviculture. *Hydrobiologia* 295: 255-261.

**Kairo**, J.G., ~~2001~~. *Ecology and restoration of mangrove systems in Kenya.* PhD dissertation, Vrije Universiteit Brussel, Brussels, Kenya. (**in preparation**).

**Lee**, S.Y., **1998**. Ecological role of grapsid crabs in mangrove ecosystems : a review. *Marine and Freshwater Research* 49: 335-343.

**Lee**, S.Y., **1999**. Tropical mangrove ecology : Physical and biotic factors influencing ecosystem structure and function. *Australian Journal of Ecology* 24: 355-366.

**Verheyden**, A., ~~2002 ?~~ Quantitative and qualitative influence of groundwater on the mangrove. PhD dissertation, Vrije Universiteit Brussel, Brussels, Kenya. (**in preparation**).

**Wilton**, K.M. & N. **Saintilan**, **1999**. Mangrove transgression into saltmarsh in Southeastern Australia. Oral presentation on the 15th Biennial International Conference of the Estuarine Research Federation 'Where THE River Meets the Sea', Sept. 25-30, New Orleans, LA, U.S.A. (in the text bulk wrongly referred to as Wilton, 1999).

# Bibliography

Underneath you can find a total bibliography compiled from the different chapters of the present PhD dissertation.

**Aagesen**, D.L., **1998**. Indigenous resource rights and conservation of the monkey-puzzle tree (*Araucaria araucana*, Araucariaceae) : a case study from southern Chile. *Economic Botany* 52(2): 146-160.

**Abeysinghe**, P.D., **1999**. *Conservation genetics of mangroves : morphology and DNA polymorphism in a geographical context*. PhD dissertation, Vrije Universiteit Brussel, Brussels, Belgium.

**Abeysinghe**, P.D., L. Triest, B. De Greef, N. Koedam & S. Hettiarachi, **1999**. Genetic differentiation between *Bruguiera gymnorhiza* and *B. sexangula* in Sri Lanka. *Hydrobiologia* 413: 11-16.

**Abeywickrema**, B.A., **1960**. Estuarine vegetation of Ceylon. In : *Proceedings of the Abidjan symposium on the humid tropics*. UNESCO, Paris, France : 207-210

**Adams**, D.C. & P.B. **Tomlinson**, **1979**. *Acrostichum* in Florida. *American Fern Journal*, 69: 42-46.

**Adger**, W.N., **1999**. Exploring income inequality in rural coastal Viet Nam. *Journal of Development Studies* 35(5): 96-119.

**Adger**, W.N., M. Kelly, N.H. Ninh & N.C. Thanh, **1997**. *Property rights and the social incidence of mangrove conversion in Vietnam*. CSERGE Working Paper GEC 97-21. Centre for Social and Economic Research on the Global Environment, School of Environmental Sciences, University of East Anglia, Norwich, U.K.

**Agrawal**, A. and C.C. **Gibson**, **1999**. Enchantment and disenchantment : the role of community in natural resource conservation. *World Development* 27(4): 629-649.

**Aksornkoae**, S., N. Paphavasit & G. Wattayakorn, **1993**. Mangroves of Thailand : present status of conservation, use and management. In : *The economic and environment value of mangrove forests and their present state of conservation*. International Tropical Timber Organisation / Japan International Association for Mangroves / International Society for Mangrove Ecosystems, Japan: 83-132

**Allen**, J.A., K.W. Krauss & R.D. Hauff. Factors limiting the intertidal distribution of the mangrove species *Xylocarpus granatum*. **(in preparation)**.

**Amarasinghe**, M. D., **1996**. *Mangroves in Sri Lanka*. Mangrove Information Centre of Small Fishers Federation, Pambala, Sri Lanka.

**Anon.**, **1991**. *UNDP/UNESCO Regional Project-Research and its application to the management of mangroves of Asia and the Pacific (RAS/86/120)*. In cooperation with the National Mangrove Committee of the National Research Council of Thailand. Bankok, Thailand.

**Arulchelvam**, K., **1968**. Mangroves. *The Ceylon Forester*, 8 (3&4): 59-92.

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

**Atuke**, D.M., **2000**. *Structure and growth form in a mangrove forest as influenced by the ecological and environmental factors, Gazi Bay, Kenya*. MSc. Ecological Marine Management thesis, Vrije Universiteit Brussel, Brussels, Belgium.

**Azariah**, J., H. Azariah, S. Gunasekaran & V. Selvam, **1992**. Structure and species distribution in Coringa mangrove forest, Godavari Delta, Andhra Pradesh, India. *Hydrobiologia* 247: 11-16.

**Baba**, S., **1994**. New natural hybrid in *Rhizophora*. *Mangroves, newsletter of the International Society of Mangrove Ecosystems* 13: 1.

**Bailey**, K.D. **1987**. *Methods of Social Research*. Collier Macmillon, London, U.K.

**Ball**, M. C., 1980. Patterns of secondary succession in a mangrove forest of South Florida. *Oecologia* 44: 226-235.

**Ballerini**, T., A. Macia & S. Cannicci, **2000**. Zonation of mangrove crabs at Inhaca Island (Mozambique) : a new hypothesis. In : *Abstract Volume of the Meeting on Mangrove Macrobenthos*, 7-11 September, Mombasa, Kenya: 9-10.

**Banerjee**, L.K., A.R.K. Sastry & M.P. Nayar, **1989**. *Mangroves in India. Identification manual*. Botanical Survey of India, Calcutta, India.

**Baran**, E. & J. **Hambrey**, **1998**. Mangrove conservation and coastal management in southeast Asia : What impact on fishery resources ? *Marine Pollution Bulletin* 37 (8-12): 431-440.

**Baran**, E., 1999. A review of quantified relationships between mangroves and coastal resources. *Phuket Marine Biology Centre Research Bulletin* 62: 57-64.

**Blaber**, S.J.M., D.P. Cyrus, J.-J. Albaret, V.C. Chong, J.W. Day, M. Elliott, M.S. Fonseca, D.E. Hoss, J. Orensanz, I.C. Potter & W. Silvert, **2000**. Effects of fishing on the structure and functioning of estuarine and nearshore ecosystems. *Journal of Marine Science* 57: 590-602.

**Blair**, J.M., **1988**. Nitrogen, sulfar and phosphorus dynamics in decomposing deciduous leaf litter in the southern appalchians. *Soil biol. Biochemistry* 20(5): 693-701.

**Blasco**, F., T. Gauquelin, M. Rasolofoharinoro, J. Denis, M. Aizpuru & V. Caldairou, **1998**. Recent advances in mangrove studies using remote sensing data. *Marine and Freshwater Research* 49(4): 287-296.

**Bosire**, J.O., **1999**. *Floristic and faunistic secondary succession in a mangrove ecosystem in Kenya*. MSc. Ecological Marine Management thesis, Vrije Universiteit Brussel, Brussels, Belgium.

**Bosire**, J.O., **2004 ?** Floristic and faunistic recovery process of restored mangrove ecosystems in Kenya. PhD dissertation, Vrije Universiteit Brussel, Brussels, Belgium.

**Bosire**, J.O., F. Dahdouh-Guebas, J. G. Kairo & N. Koedam, **1999**. Faunal and floral secondary succession in a restored mangrove system in Kenya. Personal communication on the 15th Biennial International Conference of the Estuarine Research Foundation "Where THE River Meets the Sea", 25-30 Sept., New Orleans, U.S.A.

**Bosire**, J.O., F. Dahdouh-Guebas, J.G. Kairo & N. Koedam. Macrofaunal recruitment in a restored mangrove system in Kenya. (**submitted a**).

**Bosire**, J.O., F. Dahdouh-Guebas, J.G. Kairo & N. Koedam. Recovery process of a restored mangrove system in Kenya : a floral perspective. (**submitted b**).

**Boto**, K. G. & J. T. **Wellington**, **1983**. Phosphorus and nitrogen nutritional status of a northern Australian mangrove forest. *Marine Ecology Progress Series* 11: 63-69.

**Bouillon**, S. & F. **Dehairs**. Estimating spatial and seasonal phytoplankton $\delta^{13}C$ variations in an estuarine mangrove ecosystem. Isotopes in Environmental and Health Studies (**in press**).

**Bouillon**, S., A.V. Raman & F. Dehairs. Primary producers sustaining the invertebrate community in an intertidal mangrove forest (Coringa Sanctuary, Andhra Pradesh, India) : results from carbon and nitrogen stable isotopes. (**submitted a**)

**Bouillon**, S., A.V.V.S. Rao, F. Dahdouh-Guebas, N. Koedam & F. Dehairs. Sources of organic carbon in mangrove sediments : variability and possible implications for ecosystem functioning. (**submitted b**).

**Bouillon**, S., P. Chandra Mohan, N. Sreenivas & F. Dehairs. Sources of suspended matter and selective feeding by zooplankton in an estuarine mangrove ecosystem, as traced by stable isotopes. Marine Ecology Progress Series. (**in press**).

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

**Brakel**, W.H., **1979**. Marine Parks and Recreation. In : *World Bank Tourism Pricing Policy Study for the Kenya Ministry of Tourism and Wildlife*: 409-433.

**Brakel**, W.H., **1984**. Seasonal dynamics of suspended-sediment plumes from the Tana and Sabaki Rivers, Kenya: Analysis of Landsat Imagery. *Remote Sensing of the Environment* 16: 165-173.

**Brandtberg**, T. & F. **Walter**, **1998**. Automated delineation of individual tree crowns in high spatial resolution aerial images by multiple-scale analysis. *Machine Visions and Applications* 11: 64-73.

**Brokaw**, N. & J. **Thompson**, **2000**. The H for DBH. Forest Ecology and Management 129: 89-91.

**Brown**, S., **1984**. Mangrove leaf litter production and dynamics. In : *The mangrove ecosystem : research methods*. Snedaker, S.C. & J.G. Snedaker, eds. UNESCO, Paris, France : 231-238.

**BTC**, **1999**. *Annual report of the Belgian Technical Cooperation*. Belgian Technical Cooperation, Brussels, Belgium.

**Caloz**, R. & C. **Collet**. **1997**. Geographic information systems (GIS) and remote sensing in aquatic botany : methodological aspects. *Aquatic Botany* 58: 209-228.

**Campredon**, P. & M. **Gawler**, **1998**. A visionary plan for the Banc d'Arguin. *People & the Planet* 7(2).

**Cannicci**, S., M.W. Skov & M. Vannini, **2000**. The influence of abiotic and biotic factors on the distribution of mangrove crabs at Mida Creek (Kenya) : a multivariate approach. In : *Abstract Volume of the Meeting on Mangrove Macrobenthos*, 7-11 September, Mombasa, Kenya: 20-21.

**Cannicci**, S., R. K. Ruwa, S. Ritossa & M. Vannini, **1996b**. Branch fidelity in the tree crab *Sesarma leptosoma*. *Journal of Zoology* 238(4): 795-801.

**Cannicci**, S., S. Ritossa, R. K. Ruwa & M. Vannini, **1996a**. Tree fidelity and hole fidelity in the tree crab *Sesarma leptosoma*. *Journal of Experimental Marine Biology and Ecology* 196(1-2): 299-311.

**Cantera**, J.R. & P.M. **Arnaud**, **1997** . Structure et distribution des associations de mangrove de deux baies de la côte pacifique de Colombie. In : *Mangrove Ecosystem Studies in Latin America and Africa*. B. Kjerfve, L.D. de Lacerda and E.H.S. Diop (eds), UNESCO, Paris, France: 71-97.

**Chan**, H.T., R. Ujang and F.E. Putz, **1984**. A preliminary study on the planting of *Rhizophora* species in an *Avicennia* forest at the Matang mangroves. In : *Prosiding Seminar II Ekosistem Mangrove*. S. Soemodihardjo, ed. Lembagu Ilmu Pengetahuan, Jakarta, Indonesia: 340-345.

**Chapman**, V.J., **1976**. *Mangrove vegetation*. J. Kramer Verlag, Vaduz, Liechtenstein.

**Chen**, R. & R.R. **Twilley**, **1999**. Patterns of mangrove forest structure and soil nutrient dynamics along the Shark River Estuary, Florida. *Estuaries* 22(4): 955-970.

**Christensen**, B. & S. **Wium-Andersen, 1977**. Seasonal growth of mangrove trees in southern Thailand. I. The phenology of *Rhizophora apiculata* Bl. *Aquatic Botany* 3: 281-286.

**Cintrón**, G. & Y. **Schaeffer Novelli, 1984**. Methods for studying mangrove structure. In : *The mangrove ecosystem : research methods*. Snedaker, S.C. & J.G. Snedaker, eds. UNESCO, Paris, France: 91-113.

**Clarke**, L. D. & N. J. **Hannon, 1970**. The mangrove swamp and salt marsh communities of the Sydney district. III. Plant growth in relation to salinity and waterlogging. *Journal of Ecology* 58: 351-369.

**Clarke**, L. D. & P. J. **Myerscough, 1993**. The intertidal distribution of the grey mangrove (*Avicennia marina*) in southeastern Australia : the effects of physical conditions, interspecific competition and predation on propagule establishment and survival. *Australian Journal of Ecology* 18: 307-315.

**Clarke**, L. D., **1993**. Dispersal of grey mangrove (*Avicennia marina*) propagules in southeastern Australia. *Aquatic Botany* 45: 195-204.

**Clarke**, P.J., **1995**. The population dynamics of the mangrove *Avicennia marina*, demographic synthesis and predictive modelling. *Hydrobiologia* 295: 83-88.

**Clough**, B.F. **1993**. The status and value of mangrove forests in Indonesia, Malaysia and Thailand : summary. In : *The economic and environment value of mangrove forests and their present state of conservation*. International Tropical Timber Organisation / Japan International Association for Mangroves / International Society for Mangrove Ecosystems, Japan: 1-10.

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

**Cole**, T.G., K.C. Ewel & N.N. Devoe, **1999**. Structure of mangrove trees and forests in Micronesia. *Forest Ecology and Management* 117: 90-109.

**Condit**, R., P.S. Ashton, P. Baker, S. Bunyavejchewin, S. Gunatilleke, N. Gunatilleke, S.P. Hubbell, R.B. Foster, A.Itoh, J.V. LaFrankie, H.S. Lee, E. Losos, N. Manokaran, R. Sukumar & T. Yamakura, **2000**. Spatial patterns in the distribution of tropical tree species. *Science* 288: 1414-1418.

**Corea**, A.S.L.E., Jayasinghe, J.M.P.K., Ekaratne, S.U.K. & R. Johnstone, **1995**. Environmental impact of prawn farming on Dutch Canal : the main water source for the prawn culture industry in Sri Lanka. *Ambio*, **24**(7-8): 423-427.

**Corlett**, R. T., **1986**. The mangrove understory : some additional observations. *Journal of Tropical Ecology* 2: 84-93.

**Cormier-Salem**, M.C., **1999**. The mangrove : an area to be cleared… for social scientists. *Hydrobiologia* 413: 135-142.

**Cottam**, G. & J.T. **Curtis**, **1956**. The use of distance measures in phytosociological sampling. *Ecology* 37(3): 451-460.

**Couto**, E.C.G., **1996**. Caracterização estrutural do manguezal da foz da gamboa do Maciel (Paranaguá-PR.). *Arq. Biol. Tecnol.* 39(3): 497-507.

**Cox**, E.F. & J.A. **Allen**, **1999**. Stand structure and productivity of the introduced *Rhizophora mangle* in Hawaii. *Estuaries* 22(2A): 276-284.

**Crane**, J., **1975**. *Fiddler crabs of the world. Ocypodidae : Genus Uca.* Princeton University Press, New Jersey, U.S.A.

**Curtis**, J.T., **1959**. *The vegetation of Wisconsin. An ordination of plant communities.* University of Wisconsin Press, Madison, Wisconsin, U.S.A.

**Dahdouh-Guebas**, F. Propagule predation in Sri Lankan mangroves and its effect on vegetation structure dynamics. In : *Abstract Volume of the Meeting on Mangrove Macrobenthos*, 7-11 Sept. 2000, Mombasa, Kenya. **(submitted)**.

**Dahdouh-Guebas**, F. & N. **Koedam**, **2001**. Mangroven, wandelende dijken. *Eos* (in press).

**Dahdouh-Guebas**, F. & N. **Koedam**. Empirical estimate of the reliability of the use of the Point-Centred Quarter Method (PCQM) in mangrove forests. **(submitted)**.

**Dahdouh-Guebas**, F. & N. **Koedam**. Mangrove vegetation structure dynamics : a review. **(in preparation)**.

**Dahdouh-Guebas**, F. & N. **Koedam**. Are the northernmost mangroves of West Africa viable ? - a case study in the Parc National du Banc d'Arguin, Mauritania - *Developments in Hydrobiology* **(in press)**.

**Dahdouh-Guebas**, F., **2001**. Mangrove vegetation structure dynamics and regeneration. PhD dissertation, Vrije Universiteit Brussel, Brussels, Belgium. (This study).

**Dahdouh-Guebas**, F., A. Verheyden, L.P Jayatissa & N. Koedam. A note on the identification of mangroves from aerial photography in Kenya and Sri Lanka. **(in preparation a)**.

**Dahdouh-Guebas**, F., A. Verheyden, L.P. Jayatissa, D.W.N. Thisera, A. Wickramasinghe & N. Koedam. Mangrove species distribution and zonation in the Pambala - Chilaw Lagoon complex (Sri Lanka), an invaluable but threatened site. **(in preparation b)**.

**Dahdouh-Guebas**, F., A. Verheyden, W. De Genst, S. Hettiarachchi & N. Koedam, **2000a**. Four decade vegetation dynamics in Sri Lankan mangroves as detected from sequential aerial photography : a case study in Galle. *Bulletin of Marine Science* 67(2): 741-759.

**Dahdouh-Guebas**, F., C. Mathenge, J.G. Kairo & N. Koedam, **2000b**. Utilization of mangrove wood products around Mida Creek (Kenya) amongst subsistence and commercial users. *Economic Botany* 54(4). (in press).

**Dahdouh-Guebas**, F., D.W.N. Thisera, A. Wickramasinghe & N. Koedam. Regeneration status of mangroves under natural and nursery conditions in Galle and Pambala, Sri Lanka. (**in preparation c**).

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

**Dahdouh-Guebas**, F., I. Van Pottelbergh, J.G. Kairo & N. Koedam. Two decade vegetation dynamics in Kenyan mangroves as detected from sequential aerial photography : a case study in Gazi Bay. Poster presentation on the Tropical Shallow Waters and Humans International Conference, 11-16 April 1999, Naivasha, Kenya. (**submitted a**).

**Dahdouh-Guebas**, F., J.G. Kairo, L.P. Jayatissa & N. Koedam. An ordination study to view past, present and future vegetation structure dynamics in disturbed and undisturbed mangrove forests in Kenya and Sri Lanka. (**submitted b**)

**Dahdouh-Guebas**, F., L.P. Jayatissa, A. Verheyden, D.W.N. Thisera, A. Wickramasinghe & N. Koedam. Mangrove species distribution and diversity in the Pambala - Chilaw Lagoon complex (Sri Lanka), an invaluable but threatened site. (**in preparation d**).

**Dahdouh-Guebas**, F., M. Giuggioli, A. Oluoch, M. Vannini & S. Cannicci, **1999b**. Feeding habits of non-ocypodid crabs from two mangrove forests in Kenya. *Bulletin of Marine Science* 64(2): 291-297.

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

**Dahdouh-Guebas**, F., M. Verneirt, J.F. Tack, D. Van Speybroeck & N. Koedam, **1998**. Propagule predators in Kenyan mangroves and their possible effect on regeneration. *Marine and Freshwater Research* 49(4): 345-350.

**Dahdouh-Guebas**, F., M. Verneirt, S. Cannicci, J.G. Kairo & N. Koedam. An explorative study on grapsid crab zonation in mangrove forests in Kenya. (**in preparation e**).

**Dahdouh-Guebas, F.**, R. De Bondt, P. Abeysinghe, J. G. Kairo, L. Triest & N. Koedam, **1999c**. Ecologic-comparative study of the disjunct zonation pattern of *Avicennia marina* (Forsk.) Vierh. in Gazi Bay (Kenya). Personal communication on the 15th Biennial International Conference of the Estuarine Research Foundation "Where THE River Meets the Sea", 25-30 September 1999, New Orleans, U.S.A. (**in prepapartion f**).

**Dahdouh-Guebas**, F., S. Bouillon, J.F. Tack & N. Koedam, **2001**. The empire of crabs. *Natuur & Techniek* (in press).

**Dahdouh-Guebas**, F., T. Zetterström, P. Rönnbäck, M. Troell & N. Koedam, **2000c**. Conservation of mangroves vs. development of shrimp farming in Pambala - Chilaw lagoon, Sri Lanka. In : *Responsible Aquaculture in the New Millenium*. Rosa Flos and Leroy Creswell (comp.), European Aquaculture Society, Special Publication n° 28, Oostende, Belgium: 167.

**Dahdouh-Guebas**, F., T. Zetterström, P. Rönnbäck, M. Troell & N. Koedam. Conservation of mangroves *vs*. development of shrimp farming : investigation of the recent evolution of Pambala (Chilaw Lagoon, Sri Lanka) using remote sensing and GIS. (**submitted c**).

**Dassanayake**, M.D & F.R Fosberg & D. Clayton, **1994**. *A revised handbook to the flora of Ceylon. Volume VIII.* Amernd Publishing Co. Pvt Ltd, New Delhi, India.

**Dassanayake**, M.D & F.R **Fosberg, 1980**. *A revised handbook to the flora of Ceylon. Volume I.* Amernd Publishing Co. Pvt Ltd, New Delhi, India.

**Dassanayake**, M.D & F.R **Fosberg, 1981a**. *A revised handbook to the flora of Ceylon. Volume II.* Amernd Publishing Co. Pvt Ltd, New Delhi, India.

**Dassanayake**, M.D & F.R **Fosberg, 1981b**. *A revised handbook to the flora of Ceylon. Volume III.* Amernd Publishing Co. Pvt Ltd, New Delhi, India.

**Dassanayake**, M.D & F.R **Fosberg, 1983**. *A revised handbook to the flora of Ceylon. Volume IV.* Amernd Publishing Co. Pvt Ltd, New Delhi, India.

**Dassanayake**, M.D & F.R **Fosberg, 1985**. *A revised handbook to the flora of Ceylon. Volume V.* Amernd Publishing Co. Pvt Ltd, New Delhi, India.

**Dassanayake**, M.D & F.R **Fosberg, 1987**. *A revised handbook to the flora of Ceylon. Volume VI.* Amernd Publishing Co. Pvt Ltd, New Delhi, India.

**Dassanayake**, M.D & F.R **Fosberg, 1991**. *A revised handbook to the flora of Ceylon. Volume VII.* Amernd Publishing Co. Pvt Ltd, New Delhi, India.

**Dassanayake**, M.D, F.R. Fosberg & D. Clayton, **1995**. *A revised handbook to the flora of Ceylon. Volume IX.* Oxford LIBH publishing Co. Ltd, New Delhi, India.

**Dassanayake**, M.D, F.R. Fosberg & D. Clayton, **1996**. *A revised handbook to the flora of Ceylon. Volume X.* Oxford LIBH publishing Co. Ltd, New Delhi, India.

**Dassanayake**, M.D, F.R. Fosberg & D. Clayton, **1997**. *A revised handbook to the flora of Ceylon. Volume XI.* Oxford LIBH publishing Co. Ltd, New Delhi, India.

**Dassanayake**, M.D, F.R. Fosberg & D. Clayton, **1998**. *A revised handbook to the flora of Ceylon. Volume XII.* Oxford LIBH publishing Co. Ltd, New Delhi, India.

**Dawes**, C. J., **1981**. *Marine Botany*. John Wiley & Sons, New York, USA.

**de Boer**, W.F., **2000**. Biomass dynamics of seagrass and the role of mangrove and seagrass vegetation as different nutrient sources for an intertidal ecosystem. *Aquatic Botany* 66: 225-239.

**De Bondt**, R., **1995**. *Het disjuncte patroon van* Avicennia marina *(Forsk.) Vierh. Langs de oostkust van Afrika (Kenya, Gazi Bay).* Een ecologisch vergelijkende studie. Biology Thesis, Vrije Universiteit Brussel, Brussels, Belgium.

**De Silva**, K.H.G.M. & S. **Balasubramaniam**, 1984-85. Some ecological aspects of the mangroves on the west coast of Sri Lanka. *Ceylon J. Sci. (Bio. Sci.)*, 17-18: 22-40.

**Deschuytter**, V., **2000**. *Vegetatiepatroon van de mangroven in Sri Lanka en fysico-chemische stressfactoren.* Lic./MSc Biology thesis, Vrije Universiteit Brussel, Brussels, Belgium.

**Dia**, A.T., F. Colas & G. de Wispelaere, **1997**. Contribution à l'étude des milieux naturels du littoral mauritanien. In : *Environnement et littoral mauritanien.* Colas, F. (ed.), Actes du colloque, 12-13 juin 1995, Nouakchott, Mauritanie. CIRAD, Montpellier, France: 39-45.

**Dourado**, F. & F.W. Fong, **1983**. Dispersal, establishment and early growth characteristics of two mangrove species, *Avicennia alba* Blume and *Bruguiera parviflora* Wight. *Int. J. Ecol. envir. Sci.* 9: 47-52.

**Doute**, R., N. Ochanda and H. Epp, **1981**. *A Forestry inventory of Kenya using remote sensing techniques.* Kenya Rangeland Ecological Monitoring Unit report, Nairobi, Kenya.

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

**Duke**, N.C. & J.S. **Bunt**, **1979**. The genus *Rhizophora* (Rhizophoraceae) in North-eastern Australia. *Australian Journal of Botany* 27: 657-678.

**Duke**, N.C. & M.A. **Khan**, **1999**. Structure and composition of the seaward mangrove forest at the Mai Po Marshes Nature Reserve, Hong Kong. In : *Proceedings of the International Workshop on the Mangrove Ecosystem of Deep Bay and the Mai Po Marshes, Hong Kong.* S.Y. Lee, ed. Hong Kong University Press, Hong Kong.

**Duke**, N.C., **1988**. Phenologies and litter fall of two mangrove trees, *Sonneratia alba* Sm. and *S. caseolaris* (L.) Engl., and their putative hybrid, *S.* x *gulngai* N.C. Duke. *Australian Journal of Botany* 36: 473-483.

**Duke**, N.C., **1990**. Phenological trends with latittude in the mangrove tree *Avicennia marina*. *Journal of Ecology* 78: 113-133.

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

**Duke**, N.C., **1992**. Mangrove floristics and biogeography. In : *Tropical Mangrove Ecosystems.* A.I. Robertson and D.M. Alongi, eds., Washington D.C., USA: 63-100.

**Duke**, N.C., **1995**. Genetic diversity, distributional barriers and rafting continents – more thoughts on the evolution of mangroves. *Hydrobiologia* 295(1-3): 167-181.

**Duke**, N.C., J.S. Bunt & W.T. Williams, **1984**. Observations on the floral and vegetative phenologies of North-eastern Australian Mangroves. *Australian Journal of Botany* 32: 87-99.

**Duke**, N.C., M.C. Ball & J.C. Ellison, **1998**. Factors influencing biodiversity and distributional gradients in mangroves. *Global Ecology and Biogeography Letters* 7: 27-47.

**Durraiappah**, A.K., **1998**. Poverty and environmental degradation : a review and analysis of the nexus. *World Development* 26(12): 2169-2179.

**ElAmry**, M., 1998. Population structure, demography and life tables of *Avicennia marina* (Forssk.) Vierh. at sites on the eastern and western coasts of the United Arab Emirates. *Marine and Freshwater Research* 49(4): 303-308.

**Ellison**, A.M. & E.J. Farnsworth, **1993**. Seedling survivorship, growth, and response to disturbance in Belizean mangal. *American Journal of Botany* 80(10): 1137-1145.

**Ellison**, A.M., E.J. Farnsworth & R.E. Merkt, **1999**. Origins of mangrove ecosystems and the mangrove biodiversity anomaly. *Global Ecology and Biogeography* 8: 95-115.

**Elster**, C., **2000**. Reasons for reforestation success and failure with three mangrove species in Colombia. *Forest Ecology and Management* 131: 201-214.

**Ens**, B.J., T. Piersma, W.J. Wolff & L. Zwarts, **1990**. Homeward Bound : problems waders face when migrating from the Banc d'Arguin, Mauritania, to their northern breeding grounds in spring. *Ardea* 78 (1/2): 364 pp.

**Erftemeijer**, P. & R.R.R. **Lewis III, 2000**. Planting mangroves on intertidal mudflats : habitat restoration or habitat conversion ? In : *Enhancing Coastal Ecosystem Restoration for the 21st Century.* Proceedings of Regional Seminar for East and Southeast Asian Countries : Ecotone VIII, Ranong and Phuket Provinces, Southern Thailand.

**Farnsworth**, E. J., **1998**. Issues of spatial, taxonomic and temporal scale in delineating links between mangrove diversity and ecosystem function. *Global Ecology and Biogeography Letters* 7: 15-25.

**Farnsworth**, E.J. & A.M. **Ellison**, **1997**. The global conservation status of mangroves. *Ambio* 26(6): 328-334.

**Ferguson**, W., **1993**. *A Land(scape) Ecological survey of the mangrove resource of Kenya* (Draft Report). Technical Coperation Project (FAO TCP/KEN/OO51) for the Forestry Department, Ministry of Environment and Natural Resources, Nairobi, Kenya.

**Field**, C.D., **1995**. *Journey amongst mangroves.* International Society of Mangrove Ecosystems, Okinawa, Japan. 140 pp.

**Field**, C.D., **1996**. *Restoration of Mangrove Ecosystems.* International Society for Mangrove Ecosystems, Okinawa, Japan.

**Field**, C., **1998a**. Rationales and practices of mangrove afforestation. *Marine and Freshwater Research* 49(4): 353-358.

**Field**, C.D., **1998b**. Rehabilitation of mangrove ecosystems : an overview. *Marine Pollution Bulletin* 37(8-12): 383-392.

**Field**, C.D., **1999**. Mangrove rehabilitation : choice and necessity. *Hydrobiologia* 413: 47-52.

**Field**, C.D., **2000**. Mangroves. In : *Seas at the Millenium : an environmental evaluation.* C. Sheppard, ed. Pergamon, Amsterdam, The Netherlands.

**Fisher**, J.S., **1980**. *Geography and development. A world regional approach.* Merrill Publishing Company, Columbus, Ohio, U.S.A.

**Flores-Verdugo**, F.J., J.W. Day Jr. & R. Briseño-Dueñas, **1987**. Structure, litter fall, decomposition, and detritus dynamics of mangroves in a Mexican coastal lagoon with an ephemeral inlet. *Marine Ecology Progress Series* 35: 83-90.

**Foell**, J., E. Harrison & R.L. Stirrat, **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, U.K.

**Frith**, D. W. & C. B. **Frith**, **1977**. Observations on fiddler crabs (Ocypodidae: Genus *Uca*) on Surin Island, Western Peninsular, Thailand, with special reference to *Uca tetragonon* (Herbst). *Phuket Marine Biological Centre Research Bulletin* 18: 1-14.

**Frith**, D. W. & S. **Brunenmeister**, **1980**. Ecological and population studies of fiddler crabs (Ocypodidae: Genus Uca) on a mangrove shore at Phuket Island, Western Peninsular, Thailand. *Crustacea* 39(2): 157-189.

**Fromard**, F., H. Puig, E. Mougin, G. Marty, J.I. Betoulle & L. Cadamuro, **1998**. Structure, above-ground biomass and dynamics of mangrove ecosystems : new data from French Guiana. *Oecologia* 115: 39-53.

**Frusher**, S. D., R. L. Giddins & T. J. Smith III, **1994**. Distribution and abundance of grapsid crabs (Grapsidae) in a mangrove estuary : effects of sediment characteristics, salinity tolerances, and osmoregulatory ability. *Estuaries* 17(3): 647-654.

**Fujimoto**, K., R. Tabuchi, T. Mori & T. Murofushi, **1995**. Site environments and stand structure of the mangrove forest on Pohnpei Island, Micronesia. *Japan Agricultural Research Quarterly* 29(4), pp. 275-284.

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

**Gang**, P.O. & J.L. **Agatsiva**, **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.

**Gherardi**, F. & M. **Vannini**, **1992**. Hermit crabs in a mangrove swamp : clustering dynamics in *Clibanarius laevimanus. Marine Behavioural Physiology* 21: 85-104.

**Gill**, A.M. & P.B. **Tomlinson**, **1971**. Studies on the growth of red mangrove (*Rhizophora mangle* L.). 3. Phenology of the shoot. *Biotropica* 3 (2): 109-124.

**Gowthorpe**, P., **1993**. *Une visite au Parc National du Banc d'Arguin. Itinéraires ~ Présentation des principales composantes naturelles.* Parc National du Banc d'Arguin, Nouakchott, Mauritania. 193 pp.

**Graham**, R. M., **1929**. Notes on the mangrove swamps of Kenya. *Journal of the East African Natural History Society* 36: 157-165.

**Greth**, A., **1994**. *Plan Directeur de Recherche pour le Parc National du Banc d'Arguin.* Conseil Scientifique du Banc d'Arguin, Nouakchott, Mauritania. 55 pp.

**Hamilton**, R.S. & S.C. **Snedaker**, **1984**. *Handbook for mangrove area management.* Commission on Ecology, IUCN, Gland, Switzerland.

**Hart**, M.G.R., **1959**. Sulphur oxidation in tidal mangrove soils. *Plant and Soil* 11 (3): 215-236.

**Heil**, G.W. & W.P.A. **Van Deursen**, **1996**. Searching for patterns and processes : modelling of vegetation dynamics with geographical information systems and remote sensing. *Acta Botanica Neerlandica* 45(4): 543-556.

**Hemminga**, M.A., F.J. Slim, J. Kazungu, G.M. Ganssen, J. Nieuwenhuize & N.M. Kruyt, **1994**. Carbon outwelling from a mangrove forest with adjacent seagrass beds and coral reefs (Gazi Bay, Kenya). *Marine Ecology Progress Series* 106: 291-301.

**Herwitz**, S. R., R. E. Slye & S. M. Turton, **1998**. Co-registered aerial stereopairs from low-flying aircraft for the analysis of long-term tropical rainforest canopy dynamics. *Photogrammetric Engineering and Remote Sensing* 64(5): 397-405.

**Hill**, M. O. & H. G. Gauch, **1980**. Detrended correspondence analysis: an improved ordination technique. *Vegetatio* 42: 47-58.

**Hirsch**, D. & A. **Mauser**, **1992**. The Economic Values of Mangroves. Two case studies: Mida Creek and Funzi Bay. (Thesis). University of Amsterdam, Netherlands.

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

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

**Holmgren**, P. & T. **Thuresson**, **1998**. Satellite Remote Sensing for Forestry Planning-A Review. *Scandinavian Journal of Forest Research* 13: 90-110.

**Holmgren**, P., T. Thuresson & S. Holm, **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., H. Hyyppä, M Inkinen, M. Engdahl, S. Linko & Y.H Zhu, **2000**. Accuracy comparison of various remote sensing data sources in the retrieval of forest stand attributes. *Forest Ecology and Management* 128: 109-120.

**Icely**, J.D. & D.A. **Jones**, **1978**. Factors affecting the distribution of the Genus *Uca* (Crustacea : Ocypodidae) on an East African shore. *Estuarine and Coastal Marine Science* 6: 315-325.

**Imbert**, D. & S. **Ménard**, **1997**. Structure de la végétation et production primaire dans la mangrove de la Baie de Fort-de-France, Martinique (F.W.I.). *Biotropica* 29(4): 413-426.

**ITTO**, **1993**. *The economic and environmental value of mangrove forests and their present state of conservation*. Prepared for the International Tropical Timber Organisation by 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, November 1996, Gland, Switzerland.

**Janzen**, D.H., **1985**. Mangroves : where's the understory ? *Journal of Tropical Ecology* 1: 89-92.

**Jayatissa**, L.P., **1987**. *Phytosociology of some coastal water bodies in Sri Lanka with particular emphasis on three lagoons*. M.Phil thesis, University of Ruhuna, Matara, Sri Lanka.

**Jayatissa**, L.P., F. Dahdouh-Guebas & N. Koedam. A review of the floral composition and distribution of mangroves in Sri Lanka. **(in preparation)**.

**Jayewardene**, R. P., **1986**. Sri Lanka. In : *Mangroves of Asia and the Pacific : Status and Management*. (ed. by R.M. Umali, P.M. Zamora, R.R. Gotera, R.S. Jara, A.S. Camacho and M. Vannucci), pp 219-230. UNESCO/UNDP, Manila, Philippines.

**Jayewardene**, R.P., **1985**. The mangroves of Sri Lanka. *Bakawan (Newsletter of the Regional Mangrove Information Network for Asia and the Pacific)* 4(1): 8-10.

**Jiménez**, J.A. & K. **Sauter**, **1991**. Structure and dynamics of mangrove forests along a flooding gradient. *Estuaries* 14(1): 49-56.

**Kairo**, J.G. & P.O. **Gwada**, **1998**. *Mangrove of Mida Creek. Ecological survey of Mida Creek*. Final technical report. Kenya Wildlife Services, Mombasa, Kenya.

**Kairo**, J.G. & P.O. **Gwada**. *Mangrove of Kwale district*. Structural inventory. Kenya Wildlife Services, Mombasa, Kenya. **(in preparation)**.

**Kairo**, J.G., **1993**. *Artificial regeneration and sustainable yield management of mangrove forests in Gazi Bay, Kenya*. M.Sc. Thesis Botany, University of Nairobi, Nairobi, Kenya.

**Kairo**, J.G., **1995**. *Community participatory forestry for rehabilitation of deforested mangrove areas of Gazi Bay (Kenya). A first approach*. Final technical report. University of Nairobi, Department of Botany, Nairobi, Kenya.

**Kairo**, J.G., **1996**. Towards alternative views of mangrove forestry in Kenya. In : *Supporting capacity building in forestry research in Africa*. A. Ngeny-Mengech (ed.), International Foundation for Science (IFS), Nairobi, Kenya.

**Kairo**, J.G., **2001**. *Ecology and restoration of mangrove systems in Kenya*. PhD dissertation, Vrije Universiteit Brussel, Brussels, Kenya. (in preparation).

**Kairo**, J.G. & B. **Kivyatu, 2000**. *Mangrove management survey within and adjacent to Kiunga Marine National Reserve.* WWF project KE0087.01, Technical Report. WWF (EARO)/ Unesco, Nairobi, Kenya.

**Kairo**, J.G., B. Kivyatu, J. Chruch, F. Dahdouh-Guebas, N. Koedam and R. Höft, 1999. Management survey of mangrove forests within the marine protected area of Kiunga, Kenya. Presentation on the 15th Biennial International Conference of the Estuarine Research Foundation "Where THE River Meets the Sea", 25-30 September 1999, New Orleans, U.S.A. (published as Kairo & Kivyatu, 2000).

**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 b)**.

**Kajia**, Y., **2000**. *Assessment of the effects of rice cultivation in the mangrove forests of the Rufiji Delta (Mainland Tanzania).* MSc. Ecological Marine Management thesis, Vrije Universiteit Brussel, Brussels, Belgium.

**Kanakaratne**, M.D., W.R.T. Perera & B.U.S. Fernando, **1984**. An attempt at determining the mangrove coverage around Puttalam lagoon in Sri Lanka through remote sensing techniques. In : *Proceedings of the 4th Asian Conference on Remote Sensing*, Colombo, Sri Lanka.

**Kane**, H.A., L. Hoffmann & P. Campredon, **1993**. Fishermen of the desert. In : *The law of the mother : protecting indigenous peoples in protected areas.* Kemf, E. (ed.) Sierra Club Books, San Francisco, USA.

**Kathiresan**, K., **1995**. *Rhizophora annamalai* : a new species of mangroves. *Environment & Ecology* 13(1): 240-241.

**Kathiresan**, K., N. Rajendran & G. Thangadurai, **1996**. Growth of mangrove seedlings in the intertidal area of Vellar estuary, southeast coast of India. *Indian Journal of Marine Sciences* 25: 240-243.

**Kathiresan**, K., N. Rajendran & V. Palaniselvam, **2000**. Growth of *Rhizophora apiculata* in degraded areas of Ariyankuppam estuary, along Pondicherry coastline, southeast coast of India. *Indian Journal of Marine Sciences* 29: 86-88.

**Kennedy**, A., **1988**. *Mida Creek – a study of human impact.* (Thesis) University of Edinburgh, Scotland, U.K.

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

**Kenya Forestry Master Plan**, **1994**. *Development Programmes.* Ministry of Environment and Natural Resources, Nairobi, Kenya.

**KIFCON**, **1995**. *Arabuko Sokoke Forest and Mida Creek. The offical guide.* Kenya Indigenous Forest Conservation Programme. Kenya Wildlife Service / Forestry Department, Nairobi, Kenya.

**Kitheka**, J.U., **1997**. Beach groundwater flow dynamics and coastal circulation : an examination of flow processes at Nyali and Diani Beaches. In : *Antropogenically induced changes in groundwater outflow and quality, and the functioning of Eastern African nearshore ecosystems (GROFLO).* Contract No. IC18-CT96-0065, First Annual Progress Report of the INCO Project: 11-18.

**Kitheka**, J.U., B.O. Ohowa, B.M., Mwashote, W.S. Shimbira, J.M. Mwaluma & J.M. Kazungu, **1995**. Water circulation dynamics, water column nutrients and plankton productivity in Gazi Bay (Kenya) . In : *Interlinkages between Eastern-African coastal ecosystems.* Contract No. TS3*-CT92-0114, Final Report: 95-121.

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

**Kokwaro**, J. O., **1985**. The distribution and economic importance of the mangrove forests of Kenya. *Journal of the East Africa Natural History Society and National Museum* 75(188): 1-10.

**Ladavid**, G., **1995**. *Fysico-chemische stressfactoren in mangrovebodems (relatie tot vegetatiestructuur) en optimalisatie van diversiteitsanalyse van mangrovesoorten.* Bio-Engineer Thesis, Vrije Universiteit Brussel, Brussels, Belgium.

**Lebrun**, J.P., **1998**. Catalogue des plantes vasculaires de la Mauritanie et du Sahara occidental. *Boissiera (Mémoires de botanique systématique, Conservatoire et jardin botanique de Genève)* 55 : 322.

**Lee**, S. K., W. H. Tan & S. Havanond, **1996**. Regeneration and colonization of mangrove on clay-filled reclaimed land in Singapore. *Hydrobiologia* 319 : 23-35.

**Lefebvre**, G. & B. **Poulin**, **2000**. Determinants of avian diversity in neotropical mangrove forests. In : *Biodiversity in wetlands : assessment, function and conservation, volume 1.* B. Gopal, W.J. Junk & J.A. Davis, eds., Backhuys Publishers, Leiden, The Netherlands.

**Lescure**, J.P., **1980**. Ecological aspects of the mangrove forest in French Guiana. In : *Memorias del seminario sobre el estudio cientifico e impacto humano en el ecosistema de manglares.* UNESCO, Oficina Regional de Ciencia y Tecnologia para America Latina e el Caribe, Montevideo, Uruguay: 76-93.

**Lewis III**, R.R., **1982**. Mangrove forests. In : *Creation and Restauration of Coastal Plant Communities.* R.R. Lewis III, ed., CRC Press:154-171.

**Lewis III**, R.R., **1999**. Key concepts in successful ecological restoration of mangrove forests. In : *Proceedings of the TCE-Workshop No. II, Coastal Environmental Improvement in Mangrove/Wetland Ecosystems*, 18-23 august 1998, Danish – SE Asian Collaboration in Tropical Coastal Ecosystems (TCE) Research and Training. NACA, PO Box 1040, 10903 Bangkok, Thailand: 19-32.

**Lewis** III, R.R., **2000**. Ecologically based goal setting in mangrove forest and tidal marsh restoration. *Ecological Engineering* 15: 191-198.

**Lewis**, R.R., P.A. Clark, W.F. Fehrings, H.S. Greenings, R.O. Johansson & R.T. Paul, **1999**. The rehabilitation of the Tampa Bay Estuary, Florida, USA, as an example of successful integrated coastal management. *Marine Pollution Bulletin* 37(8/12): 468-473.

**Lillesand**, T. M. and R. W. **Kiefer**, **1994**. *Remote sensing and image interpretation.* (3rd ed.). John Wiley & Sons, Inc, New York, USA.

**Liyanage**, S., **1997**. *Mangrove plant communities in Sri lanka.* Forest Department of Sri lanka, Colombo, Sri Lanka.

**López-Portillo**, J. & E. **Ezcurra**, **1985**. Litter fall of *Avicennia germinans* L. in a one year cycle in a mudflat at the laguna de Mecoacán, Tabsco, Mexico. *Biotropica* 17(3): 186-190.

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

**Lugo**, A.E., **1985**. Mangrove understory : an expensive luxury ? *Journal of Tropical Ecology* 2: 287.

**Lugomela**, C.V., **1995**. Spatial and temporal dynamics of phytoplankton biomass and species composition in Chwaka Bay, Zanzibar. In : *Interlinkages between Eastern-African coastal ecosystems.* Contract No. TS3*-CT92-0114, Final Report: 166-172.

**Mabberley**, D.J., **1995**. Meliaceae. *A revised handbook to the flora of Ceylon. Volume IX* (ed. by Dassanayake, M.D., F.R. Fosberg & W.D. Clayton), pp 229-300. Amernd Publishing Co. Pvt Ltd, New Delhi, India.

**Macintosh**, D.J., **1988**. The ecology and physiology of decapods of mangrove swamps. *Symposium of the Zoological Society of London* 59: 315-341.

**Macnae**, W. & F.R. **Fosberg**, **1981**. Rhizoporaceae. *A revised handbook to the flora of Ceylon. Volume III* ( ed. by M.D. Dassanayake & F.R. Fosberg), pp 487-500. Amernd Publishing Co. Pvt Ltd, New Delhi, India.

**Macnae**, W. & F.R. **Fosberg**, **1981**. Sonneratiaceae. *A revised handbook to the flora of Ceylon. Volume III* ( ed. by M.D. Dassanayake & F.R. Fosberg), pp 450-453. Amerind Publishing Co Pvt. Ltd., New Delhi, India.

**Macnae**, W., **1966**. Mangroves in Eastern and Southern Australia. *Australian Journal of Botany* 14(1): 67-104.

**Macnae**, W., **1968**. A general account of the fauna and flora of mangrove swamps and forests in the Indo West Pacific region. *Advances in Marine Biology* 6: 73-270.

**Macnae**, W., **1969**. Zonation within mangroves associated with estuaries in north Queensland. In : *Estuaries.* G.E. Lauff, ed. American Association for the Advancement of Science, Washington D.C., USA: 432-441.

**Mahé**, E., **1985**. *Contribution à l'étude scientifique de la région du Banc d'Arguin. Peuplements avifaunistiques.* PhD thesis. Université de Science et Technique du Languedoc, France. 576 pp.

**Malley**, D.F., **1978**. Degradation of mangrove leaf litter by the tropical sesarmid crab *Chiromanthes onychophorum. Marine Biology* 49: 377-386.

**Marguillier**, S., G. van der Velde, F. Dehairs, M.A. Hemminga & S. Rajagopal, **1997**. Trophic relationships in an interlinked mangrove-seagrass ecosystem as traced by $\delta^{13}$C and $\delta\ ^{15}$N. *Marine Ecology Progress Series* 151: 115-121.

**Mathenge**, C., **1998**. *Exploitation of mangroves from a subsistence perspective. Case study : Mida Creek.* MSc. Human Ecology thesis, Vrije Universiteit Brussel, Brussels, Belgium.

**Matthijs**, S., **1995**. *Relatie tussen de zonatie van de mangroven in Gazi Bay (Kenia) en de redoxtoestand en samenhangende factoren.* Biology Thesis, Vrije Universiteit Brussel, Brussels, Belgium.

**Matthijs**, S., J. Tack, D. Van Speybroeck & N. Koedam, **1999**. Mangrove species zonation and soil redox state, sulphide concentration and salinity in Gazi Bay (Kenya), a preliminary study. *Mangroves and Salt Marshes* 3: 243-249.

**McCune**, B. & M. J. **Mefford**, **1997**. *Multivariate Aanalysis of Ecological Data.* Version 3.09. MjM Software, Gleneden Beach, Oregon, U.S.A.

**McGraw**, J. B., T. A. Warner, T. L. Key & W. R. Lamar, **1998**. High spatial resolution remote sensing of forest trees. *Tree* 13(8): 300-301.

**McGuinness**, K.A. **1997a**. Dispersal, establishment and survival of *Ceriops tagal* propagules in a north Australian mangrove forest. *Oecologia* 109: 80-87.

**McGuinness**, K.A. **1997b**. Seed predation in a tropical mangrove forest : a test of the dominance-predation model in northern Australia. *Journal of Tropical Ecology* 13: 293-302.

**McKee**, K.L. & P.L. **Faulkner**, **2000**. Biogeochemical functioning of restored and natural mangrove forests in Southwest Florida, USA. *Restoration Ecology* 8: 247-259.

**McKee**, K.L., **1993**. Soil physiochemical patterns and mangrove species distribution - reciprocal effects ? *Journal of Ecology* 81: 477-487.

**McKee**, K.L., **1995a**. Mangrove species distribution and propagule predation in Belize : an exception to the dominance-predation hypothesis. *Biotropica* 27 (3) : 334-345.

**McKee**, K.L., **1995b**. Seedling recruitment patterns in a Belizean mangrove forest : effects of establishment ability and physico-chemical factors. *Oecologia* 101: 448-460.

**Micheli**, F., **1993**. Feeding ecology of mangrove crabs in North Eastern Australia : mangrove litter consumption by *Sesarma messa* and *Sesarma smithii*. *Journal of Experimental Marine Biology and Ecology* 171: 165-186.

**Miller**, D. L., F. E. Smeins & J.W. Webb, **1996**. Mid-Texas coastal marsh change (1939-1991) as influenced by lesser snow goose herbivory. *Journal of Coastal Research* 12: 462-476.

**Monod**, T., **1977**. Le Parc National du Banc d'Arguin et l'histoire, le cadre général, flore et végétation du PNBA In : *Richesse du Parc National du Banc d'Arguin (Mauritanie).* Association de soutien du Parc National du Banc d'Arguin, Versailles, France.

**Mueller-Dombois**, D., **1968**. Ecogeographic analysis of a climate map of Ceylon with particular reference to vegetation. *The Ceylon Forester*, VIII (3&4)(New Series): 1-20.

**Murali**, K.S., R. Siddappa Setty, K.N. Ganeshaiah & R. Uma Shaanker, **1998**. Does forest type classification reflect spatial dynamics of vegetation ? An analysis using GIS techniques. *Current Science* 75(3) : 220-227.

**Murphy**, D.H. & M.T. **Rau**, **1990**. Ground mesofauna of the Khlong Ngau transects. *Mangrove Ecosystems Occasional Papers* 7: 9-13.

**Murphy**, D.H. & W. **Meepol**, **1990**. Timber beetles of the Ranong mangrove forests. *Mangrove Ecosystems Occasional Papers* 7: 5-8.

**Murphy**, D.H., **1990**. The recognition of some insects associated with mangroves in Thailand. *Mangrove Ecosystems Occasional Papers* 7: 15-24.

**Mwangi**, E., **2000**. *Distribution of* Terebralia palustris *(Linnaeus, 1767) and* Littorina subvittata *(Reid, 1986) in relation to vertical and horizontal migration.* MSc. Ecological Marine Management thesis, Vrije Universiteit Brussel, Brussels, Belgium.

**N'Gaïdé**, H. & M. **Nicoll**, **1994**. *Plan Directeur pour le Parc National du Banc d'Arguin (1994-2003).* Parc National du Banc d'Arguin, Nouadhibou, Mauritania. 67 pp.

**Nagelkerken**, I., G. van der Velde, M.W. Gorissen, G.J. Meijer, T. van 't Hof & C. den-Hartog, **2000**. Importance of mangroves, seagrass beds and the shallow coral reef as a nursery for important coral reef fishes, using a visual census technique. *Estuarine Coastal and Shelf Science* 51(1): 31-44.

**Naidoo**, G., **1985**. Effects of waterlogging and salinity on plant - water relations and on the accumulation of solutes in three mangrove species. *Aquatic Botany* 22: 133-143.

**Nanayakkara**, V.R., **1987**. The mangroves of Sri Lanka - An initial study. *Vidurava (Bulletin of the NARESA of Sri lanka)*, **9**(1): 1-3.

**Naylor**, R.L., R.J. Goldburg, J.H. Primavera, N. Kautsky, M.C.M. Beveridge, J. Clay, C. Folke, J.Lubchenco, H. Moony & M. Troell, **2000**. Effect of aquaculture on world fish supplies. *Nature* 405(29): 1017-1024.

**Newell**, S.Y., **1984**. Carbon and nitrogen dynamics in decomposing leaves of three coastal marine vascular plants of the subtropics. *Aquatic Botany* 19: 183-192.

**Nguyen**, V.L., T.K.O. Ta & M. Tateishi, **2000**. Late Holocene deposital environments and coastal evolution of the Mekong River Delta, Southern Vietnam. *Journal of Asian Earth Sciences* 18: 427-439.

**Omodei-Zorini**, L. & C. **Contini**, **2000**. A multicriterion analysis for the sustainable use of natural resources in mangrove ecosystems with the involvement of local community. In : *Proceedings of the 4th European Symposium on European Farming and Rural Systems Research and Extension into the Next Millennium*, Volos, April 3-7.

**Omodei-Zorini**, L., C. Contini, F. Barbosa, N.S. Jiddawi, J. Ochiewo, R Polidori & J.P. Shunula, **2000**. A participatory analysis for a sustainable mangrove management. *Abstract Volume the International Meeting of Mangrove Macrobethos*, September 7-11, Mombasa, Kenya.

**Ong**, J.E., K.W. Gong & B.F. Clough, **1995**. Structure and productivity of a 20-year-old stand of *Rhizophora apiculata* Bl. mangrove forest. *Journal of Biogeography* 22: 417-424.

**Osborne**, D.J. & P. **Berjak**, **1997**. The making of mangroves : the remarkable pioneering role played by seeds of *Avicennia marina*. *Endeavour* 21(4): 143-147.

**Osborne**, K. & T. J. **Smith III**, **1990**. Differential predation on mangrove propagules in open and closed canopy forest habitats. *Vegetatio* 89:1-6.

**Osunkoya**, O.O. & R.G. **Creese**, **1997**. Population structure, spatial pattern and seedling establishment of the grey mangrove *Avicennia marina* var. *australasica*, in New Zealand. *Australian Journal of Botany* 45: 707-725.

**Panabokke**, C.R., **1967**. *Soils of Ceylon and fertilizer use.* Metro Printers, Colombo, Sri Lanka.

**Parani**, M., C.H. Rao, N. Mathan, C.S. Anuratha, K.K. Narayanan & A. Parida, **1997**. Molecular phylogeny of mangroves III. Parentage analysis of a *Rhizophora* hybrid using random amplified ploymorphic DNA and restriction fragment length plymorphism markers. *Aquatic Botany* 58(2): 165-172.

**Pearce**, F., **1996**. Living sea walls keep floods at bay. *New Scientist* 150(2032): 7.

**Pearce**, F., **1999**. An unnatural disaster - Clearing India's mangrove forests has left the coast defenceless. *New Scientist* 164(2211) : 12.

**Pemadasa**, M.A., **1997**. *Green mantle of Sri Lanka*. Tharangee Printers, Colombo, Sri Lanka.

**Pernetta**, J.C., **1993a**. *Mangrove forests, climate change and sea level rise: hydrological influences on community structure and survival, with examples from the Indo-West Pacific*. A Marine Conservation and Development Report. IUCN, Gland, Switzerland.

**Pernetta**, J.C., **1993b**. *Marine Protected Area Needs in the South Asian Seas Region. Volume 1 : Bangladesh*. A Marine Conservation and Development Report. IUCN, Gland, Switzerland.

**Pernetta**, J.C., **1993c**. *Marine Protected Area Needs in the South Asian Seas Region. -Volume 2 : India*. A Marine Conservation and Development Report. IUCN, Gland, Switzerland.

**Pernetta**, J.C., **1993d**. *Marine Protected Area Needs in the South Asian Seas Region. Volume 3 : Maldives*. A Marine Conservation and Development Report. IUCN, Gland, Switzerland.

**Pernetta**, J.C., **1993e**. *Marine Protected Area Needs in the South Asian Seas Region. Volume 4 : Pakistan*. A Marine Conservation and Development Report. IUCN, Gland, Switzerland.

**Pernetta**, J.C., **1993f**. *Marine Protected Area Needs in the South Asian Seas Region. Volume 5 : Sri Lanka*. A Marine Conservation and Development Report. IUCN, Gland, Switzerland.

**Pinto**, L., **1986**. *Mangroves of Sri Lanka*. Natural resource, energy and science authority of Sri Lanka, Colombo, Sri Lanka.

**Premanathan**, M., R. Arakiki, H. Izumi, K. Kathiresan, M. Nakano, N. Yamamoto & H. Nakashima, **1999**. Antiviral properties of a mangrove plant, *Rhizophora apiculata* Blume, against human immunodeficiency virus. *Antiviral Research* 44: 113-122.

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

**Rabinowitz**, D., **1978a**. Dispersal properties of mangrove propagules. *Biotropica* 10(1): 47-57.

**Rabinowitz**, D., **1978b**. Early growth of mangrove seedlings in Panamá, and an hypothesis concerning the relationship of dispersal and zonation. *Journal of Biogeography* 5: 113-133.

**Ramachandran**, S., S. Sundaramoorthy, R. Krishnamoorthy, J. Devasenapathy and M. Thanikachalam, **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(3): 236-244.

**Rao**, A.N., **1987**. Mangrove ecosystems of Asia and the pacific. *Mangroves of Asia and the Pacific : Status and Management*. (ed. by R.M. Umali, P.M. Zamora, R.R. Gotera, R.S. Jara, A.S. Camacho and M. Vannucci), UNESCO/UNDP, Manila, Philippines: 1-48.

**Rau**, M.T. & D.H. **Murphy**, **1990**. Herbivore attack on mangrove plants at Ranong. *Mangrove Ecosystems Occasional Papers* 7: 25-36.

**Ravan**, S.A. & P.S. **Roy**, 1997. Satellite remote sensing for ecological analysis of forested landscape. *Plant Ecology* 131: 129-141.

**Rawlins**, S.P., **1957**. The East-African mangrove trade. Unpublished manuscript #51 of the National Museum of Kenya, Nairobi, Kenya.

**Reddy**, S.R.C. & S.P. **Chakravarty**, **1999**. Forest dependence and income distribution in a subsistence economy : evidence from India. *World Development* 27(7): 1141-1149.

**Rehder**, J.B. & S.G. **Patterson**, **1986**. Mangrove mapping and monitoring. In : *Symposium on Remote Sensing for Resources Development and Environmental Management*, Enschede, The Netherlands: 495-497.

**Rice**, D.L. & K.R. **Tenore**, **1981**. Dynamics of carbon and nitrogen during the decompostition of detritus derived from estuarine macrophytes. *Estuarine, Coastal and Shelf Science* 13: 681-690.

**Ricklefs**, R.E., & R.E. **Latham**, **1993**. Global patterns of diversity in mangrove floras. In : *Species diversity in ecological communities. Historical and geographical perspectives*. R.E. Ricklefs and D. Schluter, eds., University of Chicago Press, Chicago: 215-233.

**Roberts**, R.W. & W.W. **Ruara**, **1967**. *Lamu Mangrove Inventory*. Forest Department, Nairobi, Kenya.

**Robertson**, A. I., R. Giddins & T.J. Smith. **1990**. Seed predation by insects in tropical mangrove forests: extent and effects on seed viablility and the growth of seedlings. *Oecologia* 83: 213-219.

**Robertson**, A.I. & P.A. **Daniel**, **1989**. The influence of crabs on litter processing in high intertidal mangrove forests in tropical Australia. *Oecologia* 78: 191-198.

**Rönnbäck**, P., **1999**. The ecological basis for economic value of seafood production supported by mangrove ecosystems. *Ecological Economics* 29: 235-252.

**Rönnbäck**, P., M. Troell, N. Kautsky & J.H. Primavera, **1999**. Distribution pattern of shrimps and fish among *Avicennia* and *Rhizophora* microhabitats in the Pagbilao mangroves, Philippines. *Estuarine, Coastal and Shelf Science* 48: 223-234.

**Rützler**, K. & I.C. **Feller**, **1996**. Caribbean mangrove swamps. *Scientific American* 274(3): 70-75.

**Ruwa**, R.K. & P. **Polk**, **1986**. Additional information on mangrove distribution in Kenya : some observations and remarks. *Kenya Journal of Science Series* B 7 (2): 41-45.

**Ruwa**, R.K., **1990**. The effects of habitat complexities created by mangroves on macrofaunal composition in brackishwater intertidal zones at the Kenyan coast. *Discovery and Innovation* 2 (1): 49-55.

**Ruwa**, R.K., **1993**. Zonation and distribution of creek and fringe mangroves in the semi-arid Kenyan coast. In : *Towards the rational use of high salinity tolerant plants*. H. Lieth and A.A. Al Masoom (eds.) Kluwer Academic Publishers, Dordrecht, The Netherlands.

**Ruwa**, R.K., **1997**. Zonation of burrowing crabs in the mangroves of the east coast of Kenya. In : *Mangrove Ecosystem Studies in Latin America and Africa*. B. Kjerfve, L.D. de Lacerda and E.H.S. Diop (eds.), UNESCO, Paris, France: 316-324.

**Saenger**, P., E.J. Hegerl & J.D.S Davie, **1983**. *Global status of mangrove ecosystems*. IUCN Commision on Ecology Papers 3. International Union for Conservation of Nature and Natural resources.

**Saifullah**, S.M., S.S. Shaukat & S. Shams, **1994**. Population structure and dispersion pattern in mangroves of Karachi, Pakistan. *Aquatic Botany* 47: 329-340.

**Salim**, A.I. **1985**. *Kenya's People. People of the Coast : Swahili*. Evans Brothers Limited, Nairobi, Kenya.

**SFFL**, **1997**. *Performance Report for the Years 1994, 1995 and 1996*. Small Fishers Federation of Lanka, Pambala, Kakkapalliya, Sri Lanka.

**Slim**, F.J., **1993**. Interlinkages between Eastern-African coastal ecosystems workshop, Zanzibar, Tanzania: 4p.

**Slim**, F.J., M.A. Hemminga, C. Ochieng, N.T. Jannink, E. Cocheret de la Morinière & G. van der Velde, **1997**. Leaf litter removal by the snail *Terebralia palustris* (Linnaeus) and sesarmid crabs in an East African mangrove forest (Gazi Bay, Kenya). *Journal of Experimental Marine Biology and Ecology* 215: 35-48.

**Smith III**, T.J., **1987a**. Effects of seed predators and light level on the distribution of *Avicennia marina* Forsk. in tropical tidal forests. *Estuarine Coastal and Shelf Science* 25(1): 43-52.

**Smith III**, T.J., **1987b**. Seed predation in relation to tree dominance and distribution in mangrove forest. *Ecology* 68(2): 266-273.

**Smith III**, T.J., **1992**. Forest structure. In : *Tropical Mangrove Ecosystems*. A.I. Robertson and D.M. Alongi (eds) American Geophysical Union, Washington D.C., USA: 101-136.

**Smith III**, T.J., H T. Chan, C.C. McIvor & M.B. Robblee, **1989**. Comparisons of seed predation in tropical, tidal forests from three continents. *Ecology* 70(1): 146-151.

**Smith III**, T.J., K.G. Boto, S.D. Frusher & R.L. Giddins, **1991**. Keystone species and mangrove forest dynamics : the influence of burrowing by crabs on soil nutrient status and forest productivity. *Estuarine, Coastal and Shelf Science* 33: 419-432.

**Smith**, G.M., T. Spencer, A.L. Murray & J.R. French, **1998**. Assessing seasonal vegetation change in coastal wetlands with airborne remote sensing: an outline methodology. *Mangroves and Salt Marshes* 2: 15-28.

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

**Snedaker**, S.C. & E.J. **Lahmann**, **1988**. Mangrove understory absence : a consequence of evolution ? *Journal of Tropical Ecology* 4: 311-314.

**Sokal**, R.R. & **Rohlf**, F.J., **1981**. *Biometry. The principals and practice of statistics in biological research*. W.H. Freeman and Co, New York, United States of America.

**Song**, X., I. Kayane, T. Tanaka & J. Shimada, **1999**. Conceptual model of the evolution of groundwater quality at the wet zone in Sri Lanka. *Environmental Geology* 39(2): 149-164.

**Spalding**, M.D., F. Blasco & C.D. Field, **1997**. *World Mangrove Atlas*. The International Society for Mangrove Ecosystems, Okinawa, Japan. 187 pp.

**Stafford-Deitsch**, J., **1996**. *Mangrove : the Forgotten Habitat*. Immel Publishing Limited, London, UK.

**Steele**, O.C., K.C. Ewel & G. Goldstein, **1999**. The importance of propagule predation in a forest of non-indigenous mangrove trees. *Wetlands* 19(3): 705-708.

**Stevens**, P.W., **1999**. *The vacillation between saltmarsh and mangrove communities at the transition between temperate and subtropical climate in Florida*. MSc Thesis, University of Florida, Gainesville, Florida, USA.

**Stevens**, P.W. & C.L. **Montague**, **1999**. The vacillation between saltmarsh and mangrove communities at a transition between temperate and subtropical climate. Personal communication on the 15th Biennial International Conference of the Estuarine Research Federation 'Where THE River Meets the Sea', Sept. 25-30, New Orleans, LA, U.S.A.

**Stevenson**, N.J., R.R. Lewis & P.R. Burbridge, **1999**. Disused shrimp ponds and mangrove rehabilitation. In : *An International Perspective on Wetland Restoration*, W. Streever (ed.), Kluwer Academic Publishers, Dordrecht, The Netherlands: 277-297.

**Stolk**, M.E., **2000**. *Patterns of mangroves use in Hoanh Bo District, Quang Ninh Province, Northern Vietnam.* MSc. Human Ecology thesis, Vrije Universiteit Brussel, Brussels, Belgium.

**Syms**, C. & G.P. **Jones**, **2000**. Disturbance, habitat structure, and the dynamics of a coral-reef fish community. *Ecology* 81(10): 2714-2729.

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

**Tam**, N.F.Y., L.L.P. Vrijmoed & Y.S. Wong, **1990**. Nutrient dynamics associated with leaf decomposition in a small subtropical mangrove community in Hong Kong. *Bulletin of Marine Science* 47(1): 68-78.

**Tassan**, S., **1987**. Evaluation of the potential of the Thematic Mapper for marine application. *International Journal of Remote Sensing* 8(10): 1455-1478.

**Teas**, H.J., **1977**. Ecology and restoration of mangrove shorelines in Florida. *Environmental Conservation* 4(1): 51-58.

**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.

**Thom**, B.G., **1967**. Mangrove ecology and deltaic geomorphology, Tabasco Mexico. *Journal of Ecology* 55: 301-343.

**Thomaes**, K., **1996**. *Voorbereidend onderzoek naar de bruikbaarheid van luchtfoto's voor mangrove-analyse en evolutie van mangrovegebieden in Sri Lanka.* Biology Thesis, Vrije Universiteit Brussel, Brussels, Belgium.

**Thornton**, I.W.B., **1996**. *Krakatau : the destruction and reassembly of an island ecosystem.* Harvard University Press, Cambridge, USA.

**Tomlinson**, P.B, **1986**. *The Botany of Mangroves.* Cambridge University Press, Cambridge, U.K. 404 pp

**Turner**, R.E. & R.R **Lewis**, **1997**. Hydrologic restoration of coastal wetlands. *Wetlands Ecology and Management* 4 (2): 65-72.

**Twilley**, R.R., M. Pozo, V.H. Garcia, V.H. Rivera-Monroy, R. Zambrano and A. Bodero, **1997**. Litter dynamics in riverine mangrove forests in the Guayas River estuary, Ecuador. *Oecologia* 111: 109-122.

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

**UNEP**, **1994**. *Assessment and monitoring of climatic change impacts on mangrove ecosystems.* UNEP Regional Seas Reports and Studies N° 154. United Nations Environmental Programme, Nairobi, Kenya.

**United Nations University**, **2000**. *Asia-Pacific cooperation on research for conservation of mangroves.* Proceedings of an international workshop, 26-30 March 2000, Okinawa, Japan. The United Nations University, Tokyo, Japan.

**Van der Maarel**, E., **1979**. Transformations of cover-abundance values in phytosociology and its effects on community similarity. *Vegetatio* 39: 97-114.

**Van Pottelbergh**, I., **1999**. *Mangrovedynamiek door teledetectie van temporeel sequentiële luchtfoto's : een studie in Gazi Bay, Kenya.* Lic. Biology thesis, Vrije Universiteit Brussel, Brussels, Belgium.

**Van Speybroeck**, D., 1992. Regeneration strategy of mangroves along the Kenya coast : a first approach. *Hydrobiologia* 247: 243-251.

**Vandeput**, S., **1999**. *De haalbaarheid van een kleinschalig ecotoeristisch project in Gazi.* Menselijke Ecologie Thesis (Human Ecology), Vrije Universiteit Brussel, Brussels, Belgium.

**Vannini**, M. & R.K. **Ruwa**, **1994**. Vertical migrations in the tree crab *Sesarma leptosoma* (Decapoda, Grapsidae). *Marine Biology* 118: 271-278.

**Vannini**, M., A. Oluoch & R. K. Ruwa, **1997**. Tree-climbing decapods of Kenyan mangroves. In : *Mangrove Ecosystem Studies in Latin America and Africa.* B. Kjerfve, L.D. de Lacerda and E.H.S. Diop (eds), UNESCO, Paris, France: 325-338.

**Velimirov**, B., **1986**. DOC dynamics in a Mediterranean seagrass system. *Marine Ecology Progress Series* 28: 21-41.

**Verheyden**, A., **1997**. *Ruimtelijke analyse van flora and fauna in mangrovegebieden van Sri Lanka. Luchtfoto-interpretatie en GIS toepassing in het onderzoek naar mangrovedynamiek.* MSc Biology Thesis, Vrije Universiteit Brussel, Brussels, Belgium.

**Verheyden**, A., **2002 ?** Quantitative and qualitative influence of groundwater on the mangrove. PhD dissertation, Vrije Universiteit Brussel, Brussels, Kenya. (in preparation).

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

**Verneirt**, M., **1994**. *Faunistische factoren in de regeneratie van de Oostafrikaanse mangrove - een case-study in Gazi, Kenya -.* Biology Thesis, Vrije Universiteit Brussel, Brussels, Belgium.

**Vrancken**, D., **1999**. *Studie naar de mogelijke impact van ferale buffels op de mangroven van de East-Godavari Delta*. Lic. Biology thesis, Vrije Universiteit Brussel, Brussels, Belgium.

**Walter**, H. & M. **Steiner**, **1936**. Die Ökologie der Ost-Afrikanischen Mangroven. *Zeitschrift für Botanik* 30: 65-193.

**Walter**, H., E. Harnickenn & D. Mueller-Dombois, **1957**. *Climate diagram maps of the individual continents and the ecoligal climatic regions of the Earth*. Springer-Verlag, Berlin, Germany.

**Watson**, J.G., **1928**. Mangrove forests of the Malay Peninsula. *Malayan Forest Records* 6: 1-275.

**Weinstock**, J.A., **1994**. *Rhizophora* mangrove agroforestry. *Economic Botany* 48(2) : 210-213.

**Westhoff**, V. & E. **Van der Maarel**, 1978. The Braun-Blanquet approach. In R.H. Whittaker, (ed.) *Classification of plant communities*. W. Junk Publishers, The Hague: 287-399.

**Wetland Conservation Project**, 1994. *Wetland site report. Chilaw Estuary*. Wetland Conservation Project - Sri Lanka. Central Environmental Authority, Colombo, Sri Lanka / Euroconsult, Arnhem, The Netherlands.

**Williams**, D.C. & J.G. **Lyon**, **1991**. Use of a geographical information system database to measure and evaluate wetland change in the St. Marys River, Michigan. *Hydrobiologia* 219: 83-95.

**Wilton**, K.M. & N. **Saintilan**, **1999**. Mangrove transgression into saltmarsh in Southeastern Australia. Oral presentation on the 15th Biennial International Conference of the Estuarine Research Federation 'Where THE River Meets the Sea', Sept. 25-30, New Orleans, LA, U.S.A.

**Wium-Andersen**, S. & B. **Christensen**, **1978**. Seasonal growth of mangrove trees in southern Thailand. II. Phenology of *Bruguiera cylindrica*, *Ceriops tagal*, *Lumnitzera littorea* and *Avicennia marina*. *Aquatic Botany* 5: 383-390.

**Wium-Andersen**, S., **1981**. Seasonal growth of mangrove trees in southern Thailand. III. Phenology of *Rhizophora mucronata* Lamk. and *Scyphiphora hydrophyllacea* Gaertn. *Aquatic Botany* 10: 371-376.

**Wolanski**, E., **1992**. Hydrodynamics of mangrove swamps and their coastal waters. *Hydrobiologia* 247: 141-161.

**Wolff**, W.J., A.G. Duiven, P. Duiven, P. Esselink, A. Gueye, A. Meijboom, G. Moerland & J. Zegers, **1993b**. Biomass of macrobenthic tidal flat fauna of the Banc d'Arguin, Mauritania. *Hydrobiologia* 258: 151-163.

**Wolff**, W.J., J. van der Land, P.H. Nienhuis & P.A.W.J. de Wilde, **1993a**. The functioning of the ecosystem of the Banc d'Arguin, Mauritania : a review. *Hydrobiologia* 258: 211-222.

**Woodroffe**, C.D., **1990**. The impact of sea-level rise on mangrove shorelines. *Progress in Physical Geography* 14(4): 483-520.

**Woodroffe**, C.D., **1995**. Response of tide-dominated mangrove shorelines in northern Australia to anticipated sea-level rise. *Earth Surface and Landforms* 20: 65-85.

**Woodroffe**, C.D., **1999**. Response of mangrove shorelines to sea-level change. *Tropics* 8(3): 159-177.

**Zetterström**, T., **1998**. *Sustainable Coastal Resource Utilization vs. Commercial Shrimp Production. A case study of mangrove conservation and expansion of shrimp farms in Pambala, Sri Lanka, using GIS as a tool*. MSc. Human Ecology thesis, Vrije Universiteit Brussel, Brussels, Belgium.

# Appendices

# APPENDIX 1 : FIELD KEYS FOR KENYAN MANGROVE CRABS

Cannicci, S., F. Dahdouh-Guebas & L. Montemagno, 1997. **Field keys for Kenyan Mangrove Crabs.** Museo Zoologico "La Specola" of the University of Florence, Firenze, Italy.

Available online through the following URLs :

http://www.specola.unifi.it/mangroves/

http://www.vub.ac.be/mangrove/

# FIELD KEYS FOR KENYAN MANGROVE CRABS

by: Museo Zoologico "La Specola" of the University of Florence
v. Romana 17, 50125 Florence, Italy

by
**S. Cannicci, F. Dahdouh-Guebas, L. Montemagno**
(first author) tel. : ++39 55 2288204/1 fax : ++39 55 222565
e-mail : scann@eurorock.dbag.unifi.it

## INTRODUCTION

These keys are intended to be mainly used in field, by non-specialists. For this reason characters have not been used if only visible under microscope (such as the reproductive apparatus details). We also will reduce the morphological terminology to a minimum (see Figs. 1 and 2).

The keys apply to Kenya but can easily be applied to any mangrove crabs from central Somalia to Tanzania. More species are known from Madagascar, southern Mozambique and Natal where, on the other hand, some of the northern species are missing. We hope soon to be able to produce a keyword for the whole East Africa.

We only have considered the species which have been found in mangroves as constant inhabitants (such as *Sesarma guttatum*) or anyway as frequent "intruders" (es. : *Grapsus fourmanoiri*). It is quite possible that other "intruders" may occasionally be found, coming from adjacent biotopes (intertidal mud flats, rocky flats, sheltered cliffs, etc.) which will obviously not fit within these keys. Please remember that, in no cases keys will be able to substitute the specialist's experience and professional literature.

Here are quoted the main sources used for preparing these keys :

Crane, J., 1975. Fiddler crabs of the world. Princeton, N. J.; Princeton University Press.

Crosnier, A., 1965. Crustacés Dècapodes. Grapsidae et Ocypodidae. Faune Madagascar 18: 1-143.

Hartnoll R. G., 1975. Grapsidae and Ocypodidae (Decapoda: Brachyura) of Tanzania. Journal of Zoology 177: 305-328

Macnae W., 1968. A general account of the fauna and flora of the mangrove swamps and forest in the Indo-West Pacific region. Advances in marine Biology 6: 73-270

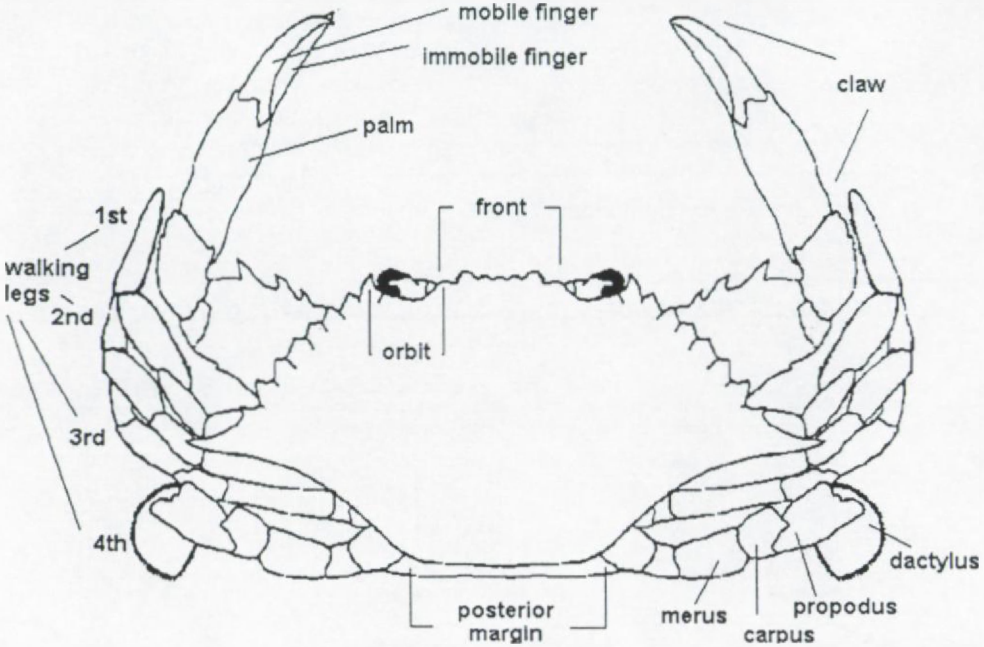
Sakai T., 1976. Crabs of Japan and the adjacent seas. Kodansha Ltd., Japan

Vannini M. & Valmori P., 1981. Researches on the coast of Somalia. The shore and the dune of Sar Uanle. 30. Grapsidae (Decapoda Brachyura). Monitore Zoologico Italiano NS (Supplemento) 14: 57-101

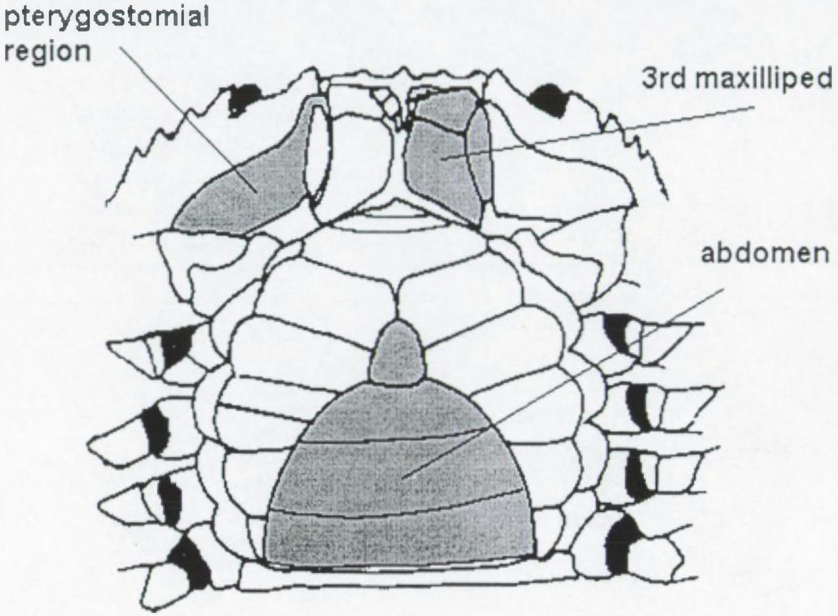
Vannini M. & Valmori P., 1981. Researches on the coast of Somalia. The shore and the dune of Sar Uanle. 30. Ocypodidae and Gecarcinidae (Decapoda Brachyura). Monitore Zoologico Italiano NS (Supplemento) 14: 199-226

**Terminology** :

Crabs, being Decapods, have 10 visible (5 pairs) thoracic appendix (pereiopods or pereopods). The first pair are called chelae, claw or hands. The following 4 pairs can be called walking legs . The 1st, 2nd, 3rd and 4th walking legs correspond thus to the 2nd, 3rd, 4th and 5th pereiopods. In the following text will we use the terms claw and 1st - 4th walking legs. The claw has two fingers : an immobile (the expansion of propodus) and a mobile one (dactylus). Here, they will always be called mobile and immobile finger.



semi-schematic representation of a swimming crab (upper view)



semi-schematic representation of a swimming crab (lower face)

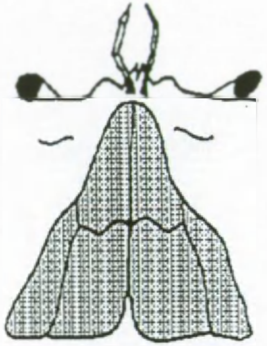
# KEYS

1) - buccal frame triangular ........................ (fig. 1a) .... (Calappidae) .......... 2

2) - walking legs all largely flattened, carapace with two prominent lateral spines ................................................ *Matuta lunaris*

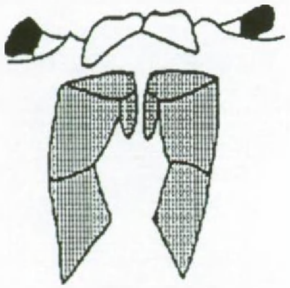
- walking legs not flattened, slender, carapace box-like, claws crested ................................................ *Calappa haepatica*

- buccal frame rectangular ...................... (fig. 1b, 1c) ............................3



*1a) Matuta lunaris*

*1b) Portunus pelagicus*



*1c) Metopograpsus oceanicus*

3) - last pair of walking legs paddle-like, much more flattened than the other legs....... (Portunidae) .......................................................................... 4

- last pair of walking legs never like above ................................................. 6

4) - carapace with 5 antero-lateral teethes, claws subequal, medium size species .............. (fig. 2a) ..........*Thalamita crenata*

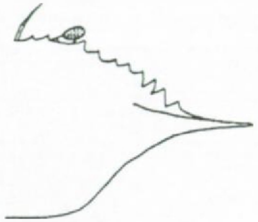
- 9 antero-lateral teeth, large species .......................................................... 5

5) - antero-lateral teethes subequal, claws stout and massive, one moderately larger than the other ........................................ (fig. 2b) ............... *Scylla serrata*

- the ninth antero-lateral tooth about three times longer than the others, claws long, slender and subequal ........................................... (fig. 2c) ........ *Portunus pelagicus*

*2a) Thalamita crenata*

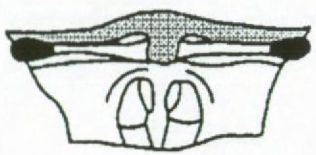
*2b) Scylla serrata*



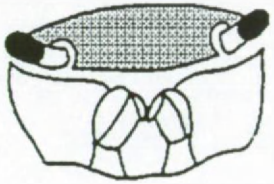
*2c) Portunus pelagicus*

6) - front much narrower than orbit ........... (fig. 3a) ...... (Ocypodidae) ...... 7

- front not narrower than orbit ............... (fig. 3b) ................................ **20**



*3a) Uca sp.*



*3b) Neosarmatium meinerti*

7) - carapace evidently globose, corrugated, buccal frame very large, nearly of the same size of the carapace itself, small species............................................................ *Dotilla fenestrata*

- carapace not globose, buccal frame normal size....................................... 8

8) - well visible hair tufts bordering a cavity between the base of 3rd and 4th walking legs ............................................ 9

- any special structure nor hair at the base of the 3rd-4th walking legs ...................................... (Genus *Macrophthalmus*) ............ 15

9) - carapace squarish, adult eyestalks ending with a styliform process ..................................... *Ocypode ceratophthalmus*

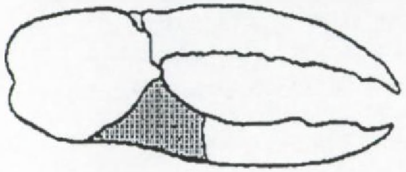
10) - no diagonal ridge on the palm (internal face)

of the major claw .................................. (fig. 4a) .................................. 11
- an evident ridge of tubercles on the palm
of the major claw ............................... (fig. 4b) .................................... 12

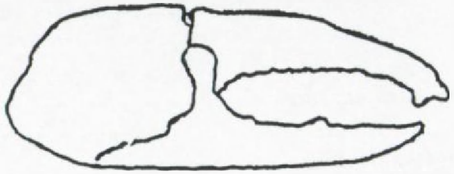
major claw internal face

*4a) Uca inversa* *4b)Uca urvillei*

11) - major claw pale, an orange patch restricted at
the base of immobile finger ................. (fig. 5a) ............... *Uca tetragonon*
- major claw uniformly pinkish or yellow-pink, tip of
mobile finger with an evident subterminal tooth ... (fig. 5b) ..... *Uca inversa*



*5a) Uca tetragonon*



*5b) Uca inversa*

12) - large species, a long groove on the external face
of both fingers of the major claw ........ (fig. 5c) ....................... *Uca urvillei*
- medium or small species with no
groove on the mobile finger ..................................................................... 13

13) - medium species, immobile finger orange, noticeably flattened, sabre-like,
with a long groove on its external face .. (fig. 5d) ... *Uca vocans hesperiae*

major claw external face

*5c) Uca urvillei* *5d) Uca vocans hesperiae*

- small species, immobile finger slender and never orange,
a thin grove on the lower external face of major claw immobile
finger only in *Uca annulipes*...................................................... 14

14) - a roughly triangular depression on external base of the
immobile finger , internal crest rounded ; cross section
of both fingers, round ...... (fig. 5e) ....................... *Uca chlorophthalmus*

*5e)* **external face** ***Uca chlorophthalmus*** **major claw** **internal face**

- no triangular depression, palm crest triangular, major
claw uniformly pink (from pale to reddish pink);
a vertical groove bordering a ridge on the claw outer face,
near the mobile finger; cross section of both fingers,
flattened ......................................... (fig. 5f) ........... *Uca annulipes*

*5f)* **external face** ***Uca annulipes*** **major claw** **internal face**

15) - eyestalks largely exceeding the length of the carapace .......................... 16
- eyestalks never exceed the carapace ........................................................ 17

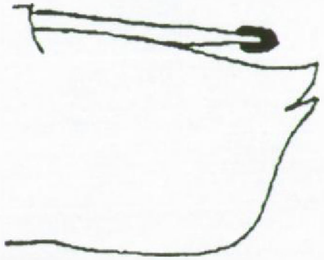
16) - eyestalk exceeding the orbit for about 1/4 of the orbit length ............................................ *Macrophthalmus milloti*
- eyestalk exceeding the orbit for about the whole orbit length ........................................ *Macrophthalmus verreauxi*

17) - carapace obviously much wider than long (width/length ratio =>* 1.5)........................................................................ 18
- carapace squarish (width/length ratio about 1.2) .. *Macrophthalmus boscii*

18) - carapace nearly twice as wide as long (width/length ratio about >=2) ...................................................................... 19
- carapace width/length ratio about 1.5, orange patches on the pterigostomial region ......................... *Macrophthalmus depressus*

19) -, antero-lateral carapace angle with two notches, inner face of male propodus with a tooth .......(fig. 6a,b,c) .. *Macrophthalmus grandidieri*
carapace angle with a single notch, inner face of male propodus without a toot.............. (fig. 6d) .. *Macrophthalmus parvimanus*

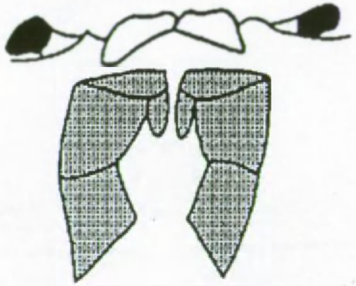
*6a,b,c)* ***Macrophthalmus grandidieri***



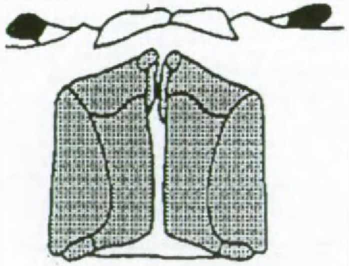
*6d)* ***Macrophthalmus parvimanus***

20) - brown, smooth, rounded ("inflated-like") carapace, black hair on walking legs carpus and propodus, terrestrial, large species, 3rd maxillipeds not meeting in the middle line ....................... (Gecarcinidae) ......... *Cardisoma carnifex*
- carapace not so ............................................................................................ 21

21) - carapace squarish, in certain cases slightly converging backwards *(Metopograpsus* spp., *Sesarma leptosoma)*, 3rd maxillipeds not meeting in the middle line ...................... (fig. 7a) .......... (Grapsidae) .................. 22
- antero-lateral margins and front aligned on a continuous arch, 3rd maxillipeds meeting in the middle line ..................... (fig. 7b) .......... (Xanthoidea) ................ 44



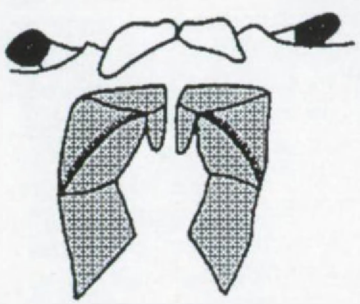
*7a)* ***Metopograpsus tuhukar***



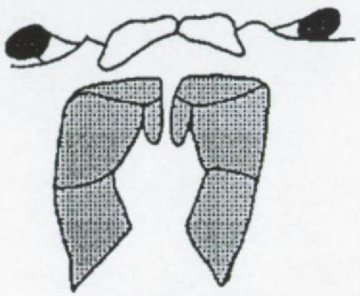
*7b)* ***Portunus pelagicus***

22) - 3rd maxilliped merus with a hairy crest, pterigostomial regions covered with a reticulated pattern ..... (fig. 8a) ..... (Sesarminae) ........... 24
- 3rd maxilliped merus without crest, pterigostomial regions

smooth or irregularly haired .. (fig. 8b) .................................................. 23

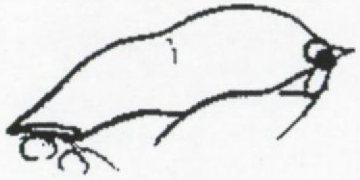


8a) *Neosarmatium meinerti*



8b) *Metopograpsus oceanicus*

23) - front strongly bent downwards (fig. 9a).......... (Grapsinae) .................... 36
- front continuing the carapace
convexity ................................ (fig. 9b) ........... (Varuninae) ................ 40



9b) *Varuna litterata*

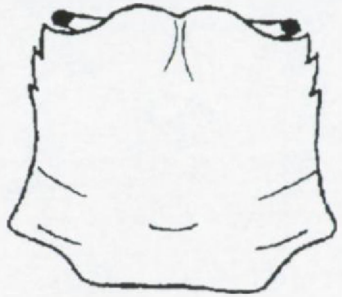
9a) *Metopograpsus oceanicus*

24) - front not abruptly bent ........ (fig. 10a) .................................................. 25
- front abruptly bent (90° or more) ......... (fig. 10b) ................................ 26

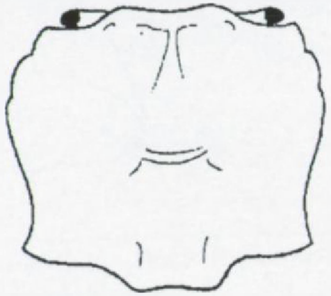
10a) *Sarmatium crassum*

10b) *Neosarmatium meinerti*

25) - front rounded, inner orbital angles smoothed,
carapace smooth, thick and convex, two teeth behind
the antero-lateral one. (fig. 11a) .................................... *Helice leachi*
- front squared, inner orbital
angles prominent .................. (fig. 11b) ...................... *Sarmatium crassum*



11a) *Helice leachi*



11b) *Sarmatium crassum*

26) - no teeth behind the antero-lateral one .................................................. 27
- one or more teeth behind the antero-lateral one .................................. 31

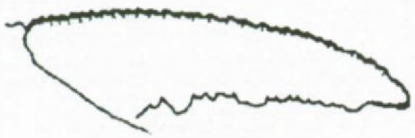
27) - carapace evidently longer than wide, tufts of hair in
the anterior region, legs flattened ................................ *Selatium elongatum*
- carapace squarish or wider than long .................................................... 28

28) - carapace fully covered by short tufts of hair,
small species .............................................................. *Sesarma villosum*
- carapace almost glabrous ............................................................................ 29

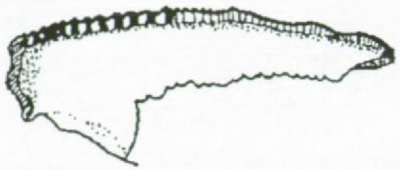
29) - walking leg propodus 3 times longer than dactylus, carapace smooth,
evidently converging backwards .............................. *Sesarma leptosoma*
- walking leg propodus of about the same length as
dactylus, carapace feebly converging backwards ..................................... 30

30) - orange claws ; tubercles on the upper margin of
claw mobile finger, uniform ......... (fig. 12a) ................. *Sesarma ortmanni*
- pale-purple claws, tubercles on the upper margin of claw mobile finger
not uniform ......................... (fig. 12b) ....................... *Sesarma eulimene*

**mobile finger**



*12a) Sesarma ortmanni*



*12b) Sesarma eulimene*

31) - one tooth behind the antero-lateral one (with a possible small accessory notch) .................................................................. 32
- two evident teeth behind the antero-lateral one ................................. 34

32) - row of tubercles on the inner palm ..................................................... 33
- no row of tubercles on the inner palm, medium species, claws dark purple-red with red mobile finger tips, internal palm bright-orange .......................................... *Sesarma guttatum*

33) - large species, carapace squarish, claws with red carpus and base of propodus; mobile finger and internal palm, pale yellow ................................................ *Neosarmatium meinerti*
- medium species, carapace diverging backwards, traces of a third teeth behind the second one ............ *Sesarma impressum*

34) - massive species (carapace length/thickness about 1.3) a spine on the claw mobile finger .................... *Neosarmatium smithi*
- carapace regularly flattened (length/thickness about 1.7), no spines on the mobile finger ................................................................ 35

35) - carapace squarish, mottled, legs flattened, walking legs tips very short (propodus/dactylus ratio, 1.5)...................... *Selatium brocki*
- carapace diverging backwards, smooth anduniformly coloured, legs not flattened, walking legs tips very long (propodus/dactylus ratio, 1.0), 3rd walking legs evidently much longer then the others ............................ *Sesarma longipes*

36) - front/carapace width ratio <0.5 (Fig. 13a) ........................................ 37
- front/carapace width ratio >0.5, (Fig. 13b) carapace converging backwards ............ (Genus *Metopograpsus*) .......... 38

37) - carapace almost squarish, one teeth behind the antero-lateral one ...................................... *Grapsus fourmanoiri*
- 2-3 teeth behind the antero-lateral one, very small species .................................................... *Ilyograpsus paludicola*

*13a) Grapsus fourmanouri*

*13b) Metopograpsus thukuhar*

38) - one tooth behind the antero-lateral one .................. (fig. 14a) ........... *Metopograpsus oceanicus*
- no teeth behind the antero-lateral one (or only an accessory notch) ................................................................ 39

39) - carapace converging backwards, maximum carapace/posterior margin width ratio ~2 ............ (fig. 14b) ............ *Metopograpsus thukuhar*
- carapace strongly converging backwards, maximum carapace/posterior margin width ratio ~3 (fig. 14c) *Metopograpsus messor*

*14a) M. oceanicus*

*14b) M. thukuhar*

*14c) M. messor*

40) - walking legs flattened, propodus and dactylus
fringed by long dark hair .................................................... *Varuna litterata*
- walking legs not flattened, no or scarce
hair bordering the extremity ..................................................................... 41

41) - legs and carapace covered with small dark hair,
carapace almost squarish and flat with two teeth
behind the anterolateral one ............................................. *Utica barbimana*
- legs and carapace smooth and not hairy,
carapace slightly convex .................... (Genus *Pseudograpsus*) ............. 42

42) - two distinct teeth behind the antero-lateral one,
carapace converging backwards ......................... *Pseudograpsus elongatus*
- no or indistinct teeth behind the antero-lateral one,
carapace not converging backwards .......................... *Pseudograpsus albus*

43) - Whole carapace and legs covered with
grey long hair .......................................................... *Pilumnus vespertilio*
- carapace and legs not so ....................................................................... 44

44) - two well visible big spines on the upper internal
face of claw carpus ................................................................................ 45
- one visible spine on the upper internal face
of claw carpus ........................................................................................ 46

45) - five big teeth on the antero-lateral carapace margins,
carapace widely mottled (usually covered with mud).... *Epixanthus dentatus*
- no visible teeth on the carapace margins,
claw with dark fingers .................................................. *Pseudozius caystrus*

46) - four visible teeth on the frontal margin,
lower parts of the body red spotted, molariform
teeth on the fingers of the major claw .................................. *Ozius guttatus*
- a single central notch on the frontal margin,
fingers tips withish, carapace bright violet .......... *Eurycarcinus natalensis*

# APPENDIX 2 : EXPERTISE AND LIST OF VALORISED RESEARCH

Up-to-date version on http://www.vub.ac.be/APNA/staff/FDG/pub.html

## Home expertise and co-operation in the research framework presented

Since the 1980's, Belgian universities have acquired an internationally recognised leading expertise in the East-African mangrove research, and co-operated with various international institutes and universities. Under the VLIR/ABOS (Flemish Interuniversity Council / Belgian Development Cooperation Agency) funded Kenya-Belgium Project in Marine Sciences (KBP), each university performed research in its domain in co-operation with the Kenyan Marine and Fisheries Research Institute (KMFRI). The Free University of Brussels (VUB) concentrated on the functioning of the mangrove-ecosystem, trophic relations, oyster farming and mangrove regeneration and restoration, the University of Ghent (UG) on mangrove meiofauna and the Catholic University of Leuven (KUL) on mangrove fish assemblages.

The VUB spread its expertise by co-operating with the United Nations Environmental Program (UNEP), the Centre for Estuarine and Coastal Ecology of the Netherlands Institute of Ecology (NIOO-CEMO), the University of Nairobi (Kenya), the University of Dar-Es-Salaam (Tanzania), The Eduardo Mondlane University (Mozambique), the University of Lisbon (Portugal), the University of Stockholm (Sweden) and the University of Florence (Italy). Two projects funded by the European Commission (EC) also provided a basis for in-depth research on 'Interlinkages between Eastern-African coastal ecosystems' (Contract No. TS3*-CT92-0114) and 'Antropogenically induced changes in groundwater outflow and quality, and the functioning of Eastern African nearshore ecosystems' (Contract No. IC18-CT96-0065).

Also in the framework of research projects in India and Sri Lanka the research teams of the Mangrove Management Group of the VUB play a role and co-operate with the University of Andhra (India), the University of Ruhuna (Sri Lanka), the Small Fishers Federation of Lanka (SFFL), the Catholic University of Nijmegen (KUN), the University of Stockholm and the NIOO-CEMO. This research is also supported by an EC-funded project (Contract EBR IC18-CT98-0295) and on the level of scholarships by the Belgian National Science Foundation (FWO), the VUB and the Flemish Institute for the advancement of scientific-technological research in the industry (IWT), the latter in the framework of the doctoral research presented here.

Within the laboratory of General Botany and Nature Management (**A**lgemene **P**lantkunde en **NA**tuurbeheer) of the VUB both MSc and PhD theses have covered a wide series of mangrove issues such as remote sensing, vegetation structure and zonation of mangroves (De Bondt, 1995; Thomaes, 1996; Verheyden, 1997; Van Pottelbergh, 1999; Dahdouh-Guebas, 2001, this study), physico-chemical factors in the mangrove (Matthijs, 1995; Ladavid, 1996; Deschuytter, 2000), mangrove tree architecture (Atuke, 2000), mangrove regeneration and restoration (Verneirt, 1994; Bosire, 1999), mangrove conservation genetics (Abeysinghe, 1999), impacts of socio-economic nature on mangroves (Mathenge, 1998; Zetterström, 1998; Kajia, 2000; Stolk, 2000) and studies on mangrove fauna (Vrancken, 1999; Mwangi, 2000).

## Biographical sketch

**Farid Dahdouh-Guebas** (°1972, Vilvoorde, BE) studied at the Vrije Universiteit Brussel (VUB) and at the Università degli Studi di Firenze (Italy), the latter within the ERASMUS program of the European Union, and obtained a degree in Biology at the VUB in 1994. His MSc thesis was on the feeding ecology and behavioural ecology of Kenyan mangrove crabs. In 1996 he finished a Master of Sciences in Advanced Studies in Human Ecology with a thesis on the remote sensing of seagrass beds along the Kenyan coast and their link with groundwater outflow (incl. a comparison with the situation in Florida, USA). In the same year he obtained a PhD fellowship from the Flemish Institute for the advancement of scientific-technological research in the industry (IWT) after defending his research proposal for a professional jury. Since then he travelled back and forth between Belgium, Kenya, Sri Lanka and Mauritania for his PhD research and spent many months in the mangrove. In the 7 years since his first acquaintance with the mangrove, he published 10 refereed papers, 7 special publications and 5 book reviews, he participated in 34 presentations on various national and international conferences, at which he was awarded twice for his research undertakings, and he was asked as a referee for a number of scientific journals and books. In his academic activities he guided 12 MSc students and gave seminars on mangrove ecosystems in universities and other academic institutions in Belgium, Sri Lanka and Mauritania. Currently he is lecturing in the MSc Program in Human Ecology and is part of the assisting academic personnel at the Unit of General Botany and Nature Management of the Free University of Brussels, where he also continues research and other academic activities related to mangrove ecosystems.

### Publications in scientific journals with referee system

1995 Cannicci, S., F. Dahdouh-Guebas, D. Anyona & M. Vannini. Homing in the mangrove swimming crab *Thalamita crenata* (Decapoda, Portunidae). *Ethology* 100: 242-252.

1996 Cannicci, S., F. Dahdouh-Guebas, D. Anyona & M. Vannini. Natural diet and feeding habits of *Thalamita crenata* (Decapoda, Portunidae). *Journal of Crustacean Biology* 16: 678-683.

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

1998 Dahdouh-Guebas, F., M. Verneirt & L. Triest. The importance of a hierarchic ecosystem classification in the biological evaluation and selection of least valuable sites. *Impact Assessment and Project Appraisal* 16(3): 185-194.

1998 Dahdouh-Guebas, F., M. Verneirt, J.F. Tack, D. Van Speybroeck & N. Koedam. Propagule predators in Kenyan mangroves and their possible effect on regeneration. *Marine and Freshwater Research* 49(4): 345-350.

1999 Dahdouh-Guebas, F., M. Giuggioli, A. Oluoch, M. Vannini & S. Cannicci. Feeding habits of non-ocypodid crabs from two mangrove forests of Kenya. *Bulletin of Marine Science* 64(2): 291-297.

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

2000 Dahdouh-Guebas, F., A. Verheyden, W. De Genst, S. Hettiarachchi & N. Koedam. Four decade vegetation dynamics in Sri Lankan mangroves as detected from sequential aerial photography : a case study in Galle. *Bulletin of Marine Science* 67(2): 741-759.

2000 Dahdouh-Guebas, F., C. Mathenge, J.G. Kairo & N. Koedam. Utilization of mangrove wood products around Mida Creek (Kenya) amongst subsistence and commercial users. *Economic Botany* 54(4). (in press).

200? Dahdouh-Guebas, F. & N. Koedam. Are the northernmost mangroves of West Africa viable ? - a case study in the Parc National du Banc d'Arguin, Mauritania - *Developments in Hydrobiology* (in press).

### Special publications and publications in books

1994 Giuggioli, M., F. Dahdouh-Guebas, A. Oluoch & S. Cannicci. Feeding specialization and activity in selected mangrove species. XVI th SIE Meeting, Parma, Italy. *Boll. Zool. Suppl.*: 41.

1994 Cannicci, S., D. Anyona & F. Dahdouh-Guebas. Homing in the mangrove swimming crab *Thalamita crenata*. XVI th SIE Meeting, Parma, Italy. *Boll. Zool. Suppl.*: 92.

1997 Cannicci, S., F. Dahdouh-Guebas & L. Montemagno. *Field keys for Kenyan Mangrove Crabs.* Museo Zoologico "La Specola" of the University of Florence, Firenze, Italy.

2000 Dahdouh-Guebas, F., T. Zetterström, P. Rönnbäck, M. Troell & N. Koedam. Conservation of mangroves vs. development of shrimp farming in Pambala - Chilaw lagoon, Sri Lanka. In : *Responsible Aquaculture in the New Millenium.* Rosa Flos and Leroy Creswell (comp.), European Aquaculture Society, Special Publication n° 28, Oostende, Belgium: 167.

2000 Wickramasinghe, A. & F. Dahdouh-Guebas. Eco-friendly rural aquaculture development in Sri Lanka. In : *Responsible Aquaculture in the New Millenium.* Rosa Flos and Leroy Creswell (comp.), European Aquaculture Society, Special Publication n° 28, Oostende, Belgium: 751.

2001 Dahdouh-Guebas, F. & N. Koedam. Mangroven, wandelende dijken. *Eos* (in press).

2001 Dahdouh-Guebas, F., S. Bouillon, J.F. Tack & N. Koedam. The Empire of Crabs. *Natuur en Techniek* (in press).

### Book reviews

1996 **Tropical Plant Science**, 1987, G. K. Berrie, A. Berrie and J. M. O. Eze, eds., Longman Group Ltd., Essex, UK: pp. 410. In : *International Journal of Environment and Pollution* 6 (2/3): 345-346.

1997 **Mangrove, the forgotten habitat**, 1996, Jeremy Stafford-Deitsch, ed., Immel Publishing Limited, London, UK: pp. 277. In : *Belgian Journal of Botany* 130: 118.

1998 **Biodiversity : a biology of numbers and difference**, 1996, K.J. Gaston, ed., Blackwell Science Ltd, Oxford, UK: pp. 396. In : *International Journal of Environment and Pollution* 9 (2/3): 316-317.

1998 **The Ecology of Tropical Forest Tree Seedlings**, 1996, M. D. Swaine, ed., Man and the Biosphere Series Vol. 18, The Parthenon Publishing Group, Carnforth, UK / UNESCO, Paris, France: pp. 340. In : *International Journal of Environment and Pollution* 9 (2/3): 329-331.

1999 **The Pantanal of Poconé : biota and ecology in the northern section of the world's largest pristine wetland**, 1998, C.W. Heckman, ed., Kluwer Academic Publishers, Dordrecht, The Netherlands: pp. 622. *International Journal of Environment and Pollution* 11(3): 405-406.

2001 **Remote Sensing Digital Image Analysis : an introduction**, 1999, J.A. Richard & X. Jia, eds., Springer-Verlag, Berlin, Germany: pp. 363. *International Journal of Environment and Pollution* (in prep.).

2001 **Remote Sensing in Hydrology and Water Management**, 2000, G.A. Schultz & E.T. Engman, eds., Springer-Verlag, Berlin, Germany: pp. 483. *International Journal of Environment and Pollution* (in prep.).

### Publications of oral presentations at scientific meetings

1994 Dahdouh-Guebas, F. Walking behaviour and homing mechanisms in *Thalamita crenata* H. Milne-Edwards, 1834 (Portunoidea : Brachyura : Decapoda). First Benelux Congress of Zoology, November 4-5, Leuven, Belgium.

1996 Dahdouh-Guebas, F. Opening of the motion "Environmental Protection is Solely the Responsibility of the Government". Proceedings Addendum of VUB - British Council Seminar "Is Sustainable Development a Contradiction of Terms ?", October 9-13, Brussels, Belgium.

1996 Dahdouh-Guebas, F., M. Verneirt & N. Koedam. Propagule predators in mangrove forests and their possible effect on regeneration. Symposium on the Conservation of Mangal Ecosystems, December 15-17, Al-Ain, United Arab Emirates.

1997 Koedam, N., G. Ladavid, F. Dahdouh-Guebas, S. Matthijs, S. Hettiarachchi & D. Van Speybroeck. Can redox state in mangroves explain mangrove vegetation structure ? International Seminar on Mangroves, April, Andhra University, India.

1997 Koedam, N., F. Dahdouh-Guebas, R. De Bondt, K. Thomaes, J.G. Kairo, S. Hettiarachchi & D. Van Speybroeck. Mangrove vegetation dynamics : how to look into the past ? International Seminar on Mangroves, April, Andhra University, India.

1999 Dahdouh-Guebas, F. & N. Koedam. Are the northernmost mangroves of West Africa viable ? - a case study in the Parc National du Banc d'Arguin, Mauritania - Shallow Tropical Waters and Humans Conference, April 11-16, Naivasha, Kenya.

1999 Kairo, J.G., B. Kivyatu, J. Church, F. Dahdouh-Guebas, N. Koedam, G. Mwatha and R. Höft. Integrating needs of the local communities in the conservation and management of mangrove resources within Kiunga Marine National Reserve, Kenya. Shallow Tropical Waters and Humans Conference, April 11-16, Naivasha, Kenya.

1999 Bosire, J., F. Dahdouh-Guebas, J.G. Kairo & N. Koedam. Faunal and floral secondary succession in a restored mangrove system in Kenya. 15th Biennial International Conference of the Estuarine Research Federation "Where THE River Meets the Sea", September 25-30, New Orleans, U.S.A.

1999 Dahdouh-Guebas, F. & N. Koedam. Potential of mangrove dynamics and regeneration studies : on-going research in Kenya, Sri Lanka and Mauritania. "In the Hands of the Fishers" community based coastal resource management workshop, Mangrove Conservation and Demonstration Centre, Small Fishers Federation of Lanka (SFFL), December 8-15, Pambala-Kakkapalliya, Sri Lanka.

2000 Dahdouh-Guebas, F., T. Zetterström, P. Rönnbäck, M. Troell & N. Koedam. Conservation of mangroves vs. development of shrimp farming in Pambala - Chilaw lagoon, Sri Lanka. Responsible Aquaculture in the New Millenium, May 2-6, Nice, France.

2000 Dahdouh-Guebas, F. Propagule predation in Sri Lankan mangroves and its effect on vegetation structure dynamics. International Meeting on Mangrove Macrobenthos, September 7-11, Mombasa, Kenya.

2000 Bouillon, S., V. Raman, F. Dahdouh-Guebas & F. Dehairs. Importance of different primary producers for benthic invertebrates in an estuarine mangrove ecosystem (Andhra Pradesh, India) : results from carbon and nitrogen stable isotopes. International Meeting on Mangrove Macrobenthos, September 7-11, Mombasa, Kenya.

2000 Bosire, J.O., F. Dahdouh-Guebas, J.G. Kairo & N. Koedam. Macrofaunal recruitment into a reforested mangrove system in Kenya. International Meeting on Mangrove Macrobenthos, September 7-11, Mombasa, Kenya.

2000 Vannini, M., S. Cannicci, F. Dahdouh-Guebas, S. Fratini, F. Gherardi & F. Micheli. Homing e orientamento nei decapodi delle mangrovie : 13 anni di ricerche in Kenya. XIX Congress of the Italian Society of the Study of Animal Behaviour, October, S. Giuliano Terme, Italy.

### Publications of posters presented at scientific meetings

1993 Dahdouh-Guebas, F., M. Giuggioli, A. Oluoch & S. Cannicci. Feeding habits of magrove decapods from Kenya. International Senckenberg Symposium on Crustacea Decapoda, October 18-22, Frankfurt a.M., Germany.

1994 Cannicci, S., F. Dahdouh-Guebas, D. Anyona & R. Vezzosi. Feeding ecology of *Thalamita crenata* H. Milne-Edwards, 1834 (Portunoidea : Brachyura : Decapoda). First Benelux Congress of Zoology, November 4-5, Leuven, Belgium.

1994 Verneirt, M. & F. Dahdouh-Guebas. Food preferences in *Sesarma meinerti* de Man, 1887 (Decapoda : Grapsidoidea : Sesarmidae). First Benelux Congress of Zoology, November 4-5, Leuven, Belgium.

1997 Verheyden, A., F. Dahdouh-Guebas, K. Thomaes, S. Hettiarachchi & N. Koedam. Vegetation dynamics in Sri Lankan mangroves as detected from aerial photography. Symposium on Mangrove Ecosystems : Biodiversity, Functioning, Restoration and Management, July, Toulouse, France.

1997 Dahdouh-Guebas, F., A. Verheyden, S. Hettiarachchi & N. Koedam. Natural regeneration of mangroves in a disturbed site in Sri Lanka - a case study in Galle - Symposium on Mangrove Ecosystems : Biodiversity, Functioning, Restoration and Management, July, Toulouse, France.

1998 Zetterström, T., F. Dahdouh-Guebas & N. Koedam. Conservation of mangroves *vs.* development of shrimp farming : investigation of the recent evolution of Pambala (Sri Lanka) using remote sensing. Symposium on Recent Advances and Future Trends in Mangrove Research, July, Toulouse, France.

1998 Mathenge, C., F. Dahdouh-Guebas & N. Koedam. Exploitation of mangroves from a subsistence perspective : a case study in Mida Creek, Kenya. Symposium on Recent Advances and Future Trends in Mangrove Research, July, Toulouse, France.

1998 Szigetvari, C., F. Dahdouh-Guebas, G. Weyembergh & N. Koedam. A neglected strip of land between a cornfield and a bank of the Zenne river : a floristic treasure trove. Colloque sur la Faune et la Flore des Moissons, des Cultures et des Friches, Brussels, Belgium.

1999 Van Pottelbergh, I., F. Dahdouh-Guebas, J.G. Kairo & N. Koedam. Two decade vegetation dynamics in Kenyan mangroves as detected from sequential aerial photography : a case study in Gazi Bay. Shallow Tropical Waters and Humans Conference, April 11-16, Naivasha, Kenya.

1999 Mathenge, C., F. Dahdouh-Guebas & N. Koedam. Exploitation of mangroves from a subsistence perspective : a case study in Mida Creek, Kenya. Shallow Tropical Waters and Humans Conference, April 11-16, Naivasha, Kenya.

1999 Gichuki, J., F. Dahdouh-Guebas, J. Mugo & L. Triest. A gift from the lake : the ecology and utilization of macrophytes of lower Sondu Miriu, L. Victoria, Kenya. Shallow Tropical Waters and Humans Conference, April 11-16, Naivasha, Kenya.

1999 Kairo, J.G., F. Dahdouh-Guebas and J. Bosire. Bringing vanishing forests to life. Mangrove reforestation and ecological monitoring project (MAREMO). Shallow Tropical Waters and Humans Conference, April 11-16, Naivasha, Kenya.

1999 Dahdouh-Guebas, F., R. De Bondt, P. Abeysinghe, J.G. Kairo, L. Triest & N. Koedam. Ecologic-comparative study of the disjunct zonation pattern of *Avicennia marina* (Forsk.) Vierh. Gazi Bay (Kenya). 15th Biennial International Conference of the Estuarine Research Federation "Where THE River Meets the Sea", September 25-30, New Orleans, U.S.A.

1999 Dahdouh-Guebas, F. & N. Koedam. Is there a future for mangroves at their latitudinal limit ? Case-study : Banc d'Arguin National Park (Mauritania). 15th Biennial International Conference of the Estuarine Research Federation "Where THE River Meets the Sea", September 25-30, New Orleans, U.S.A.

1999 Kairo, J.G., B. Kivyatu, J. Chruch, F. Dahdouh-Guebas, N. Koedam & R. Höft. Management survey of mangrove forests within the marine protected area of Kiunga, Kenya. 15th Biennial International Conference of the Estuarine Research Federation "Where THE River Meets the Sea", September 25-30, New Orleans, U.S.A.

2000 Anuradha Wickramasinghe & Farid Dahdouh-Guebas. Eco-friendly rural aquaculture development in Sri Lanka. Responsible Aquaculture in the New Millenium, May 2-6, Nice, France.

2000 Dahdouh-Guebas, F., M. Verneirt, S. Cannicci, J.G. Kairo, J.F. Tack & N. Koedam. An explorative study on grapsid crab zonation in mangrove forests in Kenya. International Meeting on Mangrove Macrobenthos, September 7-11, Mombasa, Kenya.

2000 Vrancken, D., F. Dahdouh-Guebas & N. Koedam. On the possible impact of feral water buffaloes on the mangroves of the East-Godavari Delta (India). International Meeting on Mangrove Macrobenthos, September 7-11, Mombasa, Kenya.

2000 Stolk, M.E., S. Lahmani, F. Dahdouh-Guebas & N. Koedam. Patterns of mangroves use in Hoanh Bo District, Quang Ninh Province, Northern Vietnam. Symposium on Environment and development in Vietnam : an overview of relevant projects funded by the European Commission and Belgium, November 14, Brussels, Belgium.

2000 Jayatissa, L.P., F. Dahdouh-Guebas & N. Koedam. A revision of the floral diversity and distribution of mangroves in Sri Lanka : what are the effects of erroneous species lists ? Symposium on Biodiversity : from genes to landscapes, December 13-15, Louvain-La-Neuve, Belgium.

### Scientific awards

1994 Best Student Paper Award issued by the Royal Belgian Society of Zoology on the First Benelux Congress of Zoology, November 4-5, Leuven, Belgium.

2000 Golden Propagule Award issued at the international Meeting on Mangrove Macrobenthos, September 7-11, Mombasa, Kenya.

### Publications in progress

2000 Dahdouh-Guebas, F., T. Zetterström, P. Rönnbäck, M. Troell & N. Koedam. Conservation of mangroves *vs.* development of shrimp farming : investigation of the recent evolution of Pambala (Chilaw Lagoon, Sri Lanka) using remote sensing and GIS. (submitted).

2000 Bosire, J., F. Dahdouh-Guebas, J.G. Kairo & N. Koedam. Recovery process of a restored mangrove system in Kenya : a floral perspective. (submitted).

2000 Bosire, J., F. Dahdouh-Guebas, J.G. Kairo & N. Koedam. Macrofaunal recruitment in a restored mangrove system in Kenya. (submitted).

2000 Dahdouh-Guebas, F., I. Van Pottelbergh, J.G. Kairo & N. Koedam. Two decade vegetation dynamics in Kenyan mangroves as detected from sequential aerial photography : a case study in Gazi Bay. (submitted).

2000 Dahdouh-Guebas, F. & N. Koedam. Empirical estimate of the reliability of the use of the Point-Centred Quarter Method (PCQM) in mangrove forests. (submitted).

2000 Dahdouh-Guebas, F., J.G. Kairo, L.P. Jayatissa & N. Koedam. An ordination study to view past, present and future vegetation structure dynamics in disturbed and undisturbed mangroves forests in Kenya and Sri Lanka. (submitted)

2000 Dahdouh-Guebas, F. Propagule predation in Sri Lankan mangroves and its effect on vegetation structure dynamics. (submitted).

2000 Dahdouh-Guebas, F., M. Verneirt, S. Cannicci, J.G. Kairo, J.F. Tack & N. Koedam. An explorative study on grapsid crab zonation in mangrove forests in Kenya. (submitted).

2000 Verheyden, A., F. Dahdouh-Guebas, K. Thomaes, W. De Genst, S. Hettiarachchi & N. Koedam. High resolution vegetation data for mangrove research as obtained from aerial photography. (submitted).

2000 Dahdouh-Guebas, F., R. De Bondt, P.D. Abeysinghe, J.G. Kairo, L. Triest & N. Koedam. Ecologic-comparative study of the disjunct zonation pattern of the grey mangrove *Avicennia marina* (Forsk.) Vierh. in Gazi Bay (Kenya). (submitted).

2000 Jayatissa, L.P., F. Dahdouh-Guebas & N. Koedam. A review of the floral composition and distribution of mangroves in Sri Lanka. (submitted).

2000 Dahdouh-Guebas, F., L.P. Jayatissa, A. Verheyden, D.W.N. Thisera, A. Wickramasinghe & N. Koedam. Mangrove species distribution and zonation in the Pambala - Chilaw Lagoon complex (Sri Lanka), an invaluable but threatened site. (in preparation).

2000 Dahdouh-Guebas, F., D.W.N. Thisera, A. Wickramasinghe & N. Koedam. Regeneration status of mangroves under natural and nursery conditions in Galle and Pambala, Sri Lanka. (in preparation).

2000 Dahdouh-Guebas, F., A. Verheyden, L.P Jayatissa & N. Koedam. A note on the identification of mangroves from aerial photography in Kenya and Sri Lanka. (in preparation)

2000 Dahdouh-Guebas, F. & N. Koedam. Mangrove vegetation structure dynamics : a review. (in preparation).

2000 Kairo, J.G., P.O. Gwada, F. Dahdouh-Guebas, N. Koedam, D. Van Speybroeck and C. Ochieng. Natural regeneration status of mangrove forests in Mida Creek, Kenya. (in preparation).

# Acknowledgements

The realisation of a research enterprise such as a Doctorate of Philosophy is never solely the result of hard work, but is aided by many discussions and good teamwork with scientists and local people. In this case more than 90 persons were involved on different levels. Since it is virtually impossible to thank and describe each person's contribution intensively I have chosen to thank only five key persons this way and then classify contributions in five categories in order of importance and proportion. Persons are thanked in a single category, but usually also contributed on other levels. Within each category names are mentioned in an alphabetical order.

First of all I would like to thank **Nico KOEDAM** for accepting the promotership of my PhD. I have extremely good memories on all the interactions we have had, from in-depth scientific discussions about my research up to escalating debates concerning culture and religion, from a coffee break in a local café in the vicinity of VUB up to the great lunches in the oyster bars of Bourbon Street, from a presentation on a local Benelux congress to an extra-ordinary scientific trip to an international conference and to the Everglades National Park, from marginal field work on the stinging nettle vegetation along the Zenne (Brussels) up to the great mangrove expedition to the Parc National du Banc d'Arguin (Mauritania). These are but a few of them that I will recall forever and which will make me remind that you are *l'uomo più colto* that I know (I find that this Italian term suits you best). Thank you for these precious moments.

I am also extremely grateful to **my parents** who have always supported me in my academic undertakings, and for that matter also to my entire family to whom this thesis is dedicated. I realise that my long fieldwork expeditions have not always been easy for you, and that I have put you through some difficult moments over the past few years. I hope you will forgive me for my mistakes and appreciate this piece of work as a result of personal and family input, and as a means to look forward to a bright future.

Finally, I am very thankful to **my wife** thanks to whom I had the unique experience not only to work but also to marry in the mangrove. Thank you for the trouble you went through shifting to a Belgian non-mangrove way-of-life, learning new local languages and giving birth to a beautiful **baby-girl**, whom I also thank for bringing so much joy into my life. Thank you both for your love.

Research financed by the European Community (Contract No. TS3*-CT92-0114, IC18-CT96-0065 and EBR IC18-CT98-0295), the Free University of Brussels (VUB), the Fund for Scientific Research (FWO), the Fund for Collective Fundamental Research (FKFO), the Foundation for the Promotion of Scientific Research in Africa and with a specialisation fellowship (961335) of the Flemish Institute for the advancement of scientific-technological research in the industry (IWT).

## Fieldwork

Fieldwork in Kenya, Sri Lanka and Mauritania formed the basis for this research. Therefore I am very grateful to all participants in the fieldwork expeditions on all levels, from mangrove vegetation transects to interviews with local people. Thanks to :

Samir ABUBAKR
Abdulbasit DAGHAR
Indunil D.W. DIVILEWATTAGE
Sanath HETTIARACHCHI
Loku Pulukkuttige JAYATISSA
Abdulhakim Abubakr Ali JILO
Omari Juma KISASI
Nico KOEDAM
Sall Alassane MAMADOU
Christine MATHENGE
Sandra MATTHIJS
Nassir MZEE
Saman NISHANTE
Fatuma M. SAIDI
Daglas THISERA
Katrien THOMAES
Neel G.W. TUSHIRA KUMARA
Ilse VAN POTTELBERGH
Anouk VERHEYDEN
Michael Y.L. VIJEDASA

## Deskwork / labwork

Computerised analysis of the data collected in the field and laboratory work are the next step in research, and all types of assistance is appreciated very much, from the complementary DNA research up to the preparation of conference presentations. Thanks to :

Pushpa D. ABEYSINGHE
Didier BIEN
Jean BOUE
Stefano CANNICCI
Frank CANTERS
William DE GENST
Georges DESTRE
Roland HAUSPIE
Edmond MAES
Ludwig TRIEST
Peter VAN ROSSEM
Tove ZETTERSTRÖM

The staff of the Department of Botany (University of Ruhuna, LK)

## Discussions, Advice & Support

Proportionally maybe ranked lower, but of very invaluable nature are scientific discussions and advice, from long and difficult conversations up to momentary suggestions, as well as administrative support. Thanks to :

S. AMARASINGHE
Mala AMARASINGHE
Joost BOGEMANS
Steven BOUILLON
Jared O. BOSIRE
Morley DE SILVA
Ruth DE BONDT
Karien DE CAUWER
Robert DE WULF
Frank DEHAIRS
Norman C. DUKE
Colin FIELD
Paul GOETGHEBEUR
Luc HENS
G. HATTI
James G. KAIRO
Kandasamy KATHIRESAN
Joe S.Y. LEE
Jean-Claude LEFEUVRE
Sunil LIYANAGE
Malawara Arachchige PEMADASA († 1997)
A. ROBYNS
Samuel C. SNEDAKER
Jean-Jacques SYMOENS
Marco VANNINI
Wim J. WOLFF

Anuradha WICKRAMASINGHE and the complete staff of the Small Fishers Federation of Lanka (SFFL, LK)

**Indirect (co-authors, local people)**

Some people made life easier by leading me to the right person, by helping to publish scientific results, by driving me around during fieldwork or just by being there and providing moral support. Thanks to :

Wikum
Saman ABEYSINGHE
Dickson M. ATUKE
Family BA'ALAWY *sensu lato*
Natalie BEENAERTS
Eric COPPEJANS
Nanette DARO
Raf DE SCHUTTER
Veerle DESCHUYTTER
Johnny ENGEL
Priyani FONSECA-HETTIARACHCHI
Irene GHITAIGA
Maddalena GIUGGIOLI
Abou GUEYE
Olivier HAMERLINCK
Katrien HAMELRYCK
Yusuph KAJIA
Rupasena KOSWATTAGE
Warnasena KOSWATTAGE
Michèle LE VOY
Agrey OLUOCH († 1998)
Tom PIETERS
Marc POLLET
Patrik RÖNNBÄCK
Glenn RONSSE
Yves SAMYN
Maria E. STOLK
Gamini K.T.
Jurgen F. TACK
Max TROELL
Dirk VAN SPEYBROECK
Marc VERNEIRT
Hilda VERWACHT
Family VIJEDASA
Ravindra R.G. INDRAJITH & Family
Deirdre VRANCKEN

The entire staff of the Kenya Marine and Research Institute (KMFRI, KE)
All the students and personnel of the Unit General Botany and Nature Management (APNA-VUB)
The staff and secretariat of the Department of Biology (DBIO-VUB) and the Faculty of Sciences (WE-VUB)

**Translations**

Particular gratitude goes to the people who took the difficult task to translate or to correct my findings in the official languages of the countries involved, a principle I enthousiastically support out of gratitude toward the local academic and non-academic people.

Michele LEVOY (English)
Nico KOEDAM (Dutch)
Fabienne VAN ROSSUM (French)
Heleen FERMON & Matthias WALTERT (German)
Melckzedeck "Kizzie" OSORE, James G. KAIRO & Fatuma M. SAIDI (Kiswahili)
Loku P. JAYATISSA, Sanath & Priyani HETTIARACHCHI (Sinhala)
K. ILANKOVAN (Tamil)

**Annex thesis / Bijstelling**

The formulation of the annex thesis was another task with many hindrances and fruitful discussions. However the subject has become extremely challenging and will be further studied. I would like to thank the following persons and institutions for their participation and support :

Nico KOEDAM
Fatuma M. SAIDI
Koen SMETS
Els TORREELE
Rita VAN MOLL
Sigrid VANDEPUT

Department for Research and Development (VUB)
Belgian Technical Cooperation (BTC)

# Index

This index is based on a selected number of keywords that are important in the general context of this work. All genus names have been included here. Keywords appearing in published manuscripts (CHAPTER II, VI and X) were not included.

A

abundance, 8, 33, 41, 42, 108, 109, 110, 111, 113, 125, 126, 127, 128, 129, 144, 145, 146, 148, 163, 170, 194, 280, 287
*Acanthus*, 37, 43, 44, 68, 82
*Acrostichum*, 32, 33, 39, 42, 43, 44, 68, 82, 275
*Aegiceras*, 42, 44, 48, 68, 80, 127, 129, 132, 135, 165, 189, 231
aerial photography, viii, 6, 9, 40, 49, 51, 52, 58, 59, 60, 73, 75, 76, 85, 105, 107, 108, 112, 113, 126, 169, 237, 254, 264, 270, 271, 277, 278, 287, 303, 305, 307
*Annona*, 33, 43
anthropogenic, viii, 5, 31, 107, 108, 113, 126, 127, 164, 165, 172, 173, 188, 189, 193, 231, 253
*Arthrocnemum*, 212, 213
assemblages, 51, 52, 54, 55, 56, 57, 58, 59, 60, 71, 75, 76, 141, 165, 169, 212, 223, 259, 301
*Avicennia*, 4, 34, 37, 38, 39, 40, 42, 44, 47, 48, 59, 68, 76, 78, 79, 80, 82, 83, 107, 108, 110, 111, 112, 113, 114, 117, 121, 127, 128, 129, 130, 132, 135, 141, 143, 146, 149, 163, 164, 169, 170, 174, 175, 180, 187, 189, 193, 196, 200, 209, 211, 212, 213, 214, 215, 216, 218, 222, 225, 231, 259, 264, 276, 277, 278, 279, 283, 284, 286, 288, 306, 307

B

*Barringtonia*, 43
basal area, viii, 9, 58, 109, 128, 132, 166, 190, 229, 230, 233, 235, 236, 237, 238, 239, 245, 249, 266, 273
biogeographical, viii, 4, 8, 31, 32, 39, 209, 210, 213, 215, 216, 264, 273
*Bruguiera*, 4, 34, 35, 36, 37, 40, 41, 42, 44, 48, 57, 58, 59, 67, 68, 81, 82, 83, 108, 110, 111, 112, 113, 121, 127, 129, 131, 132, 135, 141, 143, 146, 149, 163, 165, 167, 169, 174, 175, 180, 187, 189, 191, 192, 194, 195, 196, 200, 202, 231, 235, 265, 275, 279, 288

C

*Callinectes*, 212, 213, 214, 215
*Callophyllum*, 43
Canonical Correspondence Analysis. *See* CCA
canopy, 52, 54, 57, 77, 78, 79, 80, 81, 82, 83, 112, 169, 193, 230, 232, 254, 256, 281, 284
Cape Timiris, 209, 210, 211, 212, 216, 218, 219, 221, 222, 223, 224, 225
*Cardisoma*, 142
CCA, 6, 110, 111, 121, 125, 128, 129, 130, 134, 137, 258
*Cerbera*, 33, 43
*Ceriops*, 34, 38, 39, 42, 44, 45, 48, 68, 78, 79, 80, 83, 107, 108, 110, 111, 112, 113, 121, 127, 129, 130, 131, 132, 135, 141, 143, 145, 146, 149, 231, 283, 288
Chilaw, viii, ix, x, xi, 6, 33, 34, 35, 36, 38, 42, 48, 53, 75, 126, 164, 166, 187, 188, 190, 205, 231, 271, 277, 278, 288, 303, 304, 306, 307
*Chiromantes*, 167
*Clerodendron*, 43, 57, 67, 81
climatic, 33, 34, 42, 46, 53, 54, 65, 76, 287, 288
coconut, viii, 53, 56, 76, 77, 79, 81, 82, 232, 259
*Cocos*, 53, 67, 68, 76, 79, 80, 81, 82, 83
conservation, 31, 32, 40, 52, 107, 253, 254, 269, 275, 277, 280, 281, 287, 288, 301, 304
cover, ii, viii, 33, 52, 53, 108, 127, 128, 129, 136, 141, 166, 190, 192, 193, 194, 197, 213, 229, 231, 233, 269, 287
crabs, v, viii, 3, 113, 125, 128, 129, 130, 131, 136, 141, 142, 143, 144, 145, 148, 163, 166, 167, 169, 170, 171, 173, 190, 275, 276, 277, 278, 280, 284, 285, 286, 291, 302
crown, 54, 58, 60, 67, 68, 76, 79, 80, 81, 82, 83
*Cymodocea*, 213, 215
*Cynometra*, 35, 41, 43, 45

D

$D_{130}$, 54, 108, 127, 129, 131, 138, 232, 233, 240
DBH. *See* D130
DCA, 6, 111, 121, 125, 128, 130, 134, 137, 149, 258
density, viii, 9, 35, 54, 55, 56, 57, 58, 60, 109, 110, 112, 115, 116, 128, 132, 166, 170, 175, 177, 190, 192, 194, 197, 211, 212, 214, 215, 229, 230, 233, 234, 235, 236, 237, 239, 244, 245, 249, 266, 273
Detrended Correspondence Analysis. *See* DCA
development, iii, viii, 3, 4, 5, 60, 141, 165, 187, 189, 190, 191, 192, 193, 194, 195, 200, 212, 215, 216, 259, 264, 265, 269, 270, 271, 278, 280, 303, 304, 305, 306
diagnostic, 31, 33, 34, 37, 41

diameter at breast height. *See* DBH
distribution, viii, x, 4, 8, 9, 29, 31, 32, 34, 35, 36, 39, 40, 51, 65, 79, 81, 82, 110, 113, 126, 128, 129, 130, 141, 142, 143, 144, 145, 148, 164, 171, 188, 209, 229, 231, 233, 234, 236, 237, 254, 258, 264, 270, 271, 272, 275, 276, 277, 278, 281, 282, 284, 285, 286, 307
*Dolichandrone*, 33, 43, 45
dominance, 109, 115, 116, 145, 163, 164, 166, 169, 170, 171, 177, 188, 233, 235, 236, 244, 259, 263, 273, 283, 284, 286
dynamics, i, iii, viii, 4, 5, 6, 9, 51, 52, 53, 56, 59, 60, 75, 85, 105, 107, 108, 112, 114, 123, 125, 126, 128, 129, 130, 131, 166, 171, 193, 210, 215, 216, 231, 236, 253, 254, 255, 256, 258, 259, 260, 261, 262, 263, 264, 265, 266, 271, 273, 276, 277, 278, 279, 280, 281, 282, 283, 284, 285, 286, 287, 303, 304, 305, 307

E

environmental factors, 34, 76, 110, 111, 125, 127, 129, 130, 144, 145, 163, 168, 171, 182, 275
*Excoecaria*, 35, 40, 41, 42, 45, 48, 56, 57, 58, 59, 67, 68, 75, 76, 81, 82, 83, 127, 129, 130, 132, 135, 163, 164, 167, 174, 175, 188, 196, 229, 231, 236

F

*Fimbristylis*, 127, 130, 164, 188, 197
flooding, 130, 172, 173, 209, 281
floristic accretion, 259, 263
floristic composition, 6, 31, 59, 60, 107, 109, 110, 142, 164, 165, 188, 189, 253, 259
floristic dominance, 259
floristic extinction, 259
floristic invasion, 259, 263
Forest Department, 32, 37, 39, 54, 60, 283, 285
forest patches, 111, 163, 165, 166, 168, 169, 170, 171, 174, 175, 177, 180, 187, 188, 190, 191, 192, 193, 194, 196, 197, 200, 264, 273
frequency, 109, 115, 116, 129, 131, 138, 144, 146, 165, 166, 172, 177, 214, 233, 235, 237, 244, 247

G

Galle, viii, ix, x, xi, 6, 9, 33, 42, 48, 51, 53, 54, 55, 56, 57, 58, 59, 66, 67, 69, 71, 75, 76, 78, 85, 126, 127, 128, 129, 130, 132, 133, 135, 136, 163, 164, 165, 166, 167, 168, 169, 170, 172, 174, 175, 177, 180, 183, 185, 187, 188, 189, 190, 191, 193, 194, 196, 197, 200, 231, 232, 233, 234, 235, 236, 237, 239, 242, 244, 245, 247, 260, 271, 278, 303, 305, 307
Gazi, viii, ix, x, xi, xiii, xiv, 6, 9, 75, 77, 78, 105, 107, 108, 109, 112, 113, 114, 118, 120, 126, 127, 128, 129, 130, 132, 133, 135, 136, 141, 142, 143, 144, 145, 146, 147, 231, 232, 233, 234, 235, 236, 238, 239, 241, 242, 244, 245, 247, 261, 264, 271, 275, 278, 279, 280, 281, 282, 283, 286, 287, 305, 306, 307
Genetic, 216, 275, 279
geographic information systems. *See* GIS
GIS, iii, 6, 51, 52, 55, 75, 107, 108, 109, 125, 253, 255, 271, 273, 275, 276, 278, 284, 285, 287, 288, 306
growing mosaic, 259, 273
growing zones, 259, 273

H

*Heritiera*, 35, 42, 45, 48, 58, 108, 127, 129, 130, 132, 135, 138, 143, 149, 164, 189, 231
*Hibiscus*, 43

I

identification, 8, 9, 31, 33, 38, 41, 51, 52, 54, 55, 57, 59, 60, 73, 75, 76, 77, 78, 79, 80, 81, 82, 83, 108, 255, 270, 273, 277, 307
interpretation, viii, 31, 39, 51, 52, 53, 54, 55, 56, 57, 58, 59, 60, 75, 77, 108, 128, 135, 136, 149, 283
Interviews, 53
Iouik, 209, 210, 211, 213, 214, 216, 217, 225

K

*Kandelia*, 37, 39, 45

L

local, iii, viii, 3, 31, 34, 41, 51, 53, 77, 107, 109, 110, 112, 114, 119, 142, 145, 169, 188, 230, 231, 253, 269, 270, 273, 284, 304, 309, 310, 311
*Lumnitzera*, 4, 36, 41, 42, 45, 48, 59, 68, 80, 82, 108, 111, 127, 129, 132, 135, 163, 164, 174, 175, 189, 196, 231, 288

M

mangrove associates, 31, 32, 33, 41, 42, 43, 127, 258
marsh, 32, 52, 277, 284
*Metopograpsus*, 141, 142, 143, 144, 148
Mida, viii, ix, x, xi, xiii, xiv, 6, 9, 11, 75, 78, 112, 126, 127, 128, 129, 130, 131, 132, 133, 135, 136, 141, 142, 143, 144, 145, 146, 147, 264, 270, 271, 276, 278, 280, 281, 282, 283, 303, 305, 307
monitoring, viii, ix, x, 8, 51, 114, 131, 171, 188, 190, 195, 253, 264, 266, 271, 285, 287, 306
mosaic, 129, 170, 231, 258, 259, 273
moving mosaic, 259, 273

N

Negombo, 33, 34, 36, 38, 48
*Neosarmatium*, 113, 141, 143, 148, 167, 170, 271, 278, 302
Nouâmghâr, 210, 211, 217
*Nypa*, 42, 45, 48

P

Pambala. *See* Chilaw
Parc National du Banc d'Arguin. *See* PNBA
PCQM, iii, viii, ix, x, xi, xv, 9, 54, 55, 57, 58, 108, 109, 111, 177, 227, 229, 230, 231, 232, 233, 234, 235, 236, 237, 238, 242, 244, 245, 247, 249, 273, 277, 307
*Pemphis*, 41, 43, 45, 48
*Phoenix*, 37, 43, 45
PNBA, 209, 210, 214, 215, 216, 217, 284
point-centred-quarter method. *See* PCQM
*Premna*, 43
propagule predation
  predated, iii, viii, 5, 40, 130, 163, 164, 166, 169, 171, 173, 187, 211, 264, 265, 271, 273, 284
Propagule predation, 9, 161, 163, 271, 277, 304, 307
Puttalam, 33, 34, 35, 36, 38, 40, 42, 48, 280, 282

R

regeneration, i, iii, viii, 4, 5, 8, 9, 51, 52, 107, 112, 114, 142, 151, 163, 187, 188, 189, 190, 193, 194, 209, 210, 211, 212, 214, 215, 216, 253, 264, 265, 266, 270, 271, 273, 277, 278, 281, 282, 301, 302, 304, 305, 307
Rekawa, 33, 35, 38, 42, 48, 51, 53, 54, 55, 56, 59, 66, 67, 68, 69, 75, 76, 78
remote sensing, iii, 8, 31, 32, 40, 51, 60, 75, 76, 125, 253, 254, 255, 260, 261, 271, 273, 275, 276, 277, 278, 279, 280, 281, 282, 283, 285, 286, 301, 302, 305, 306
resolution, 9, 49, 51, 52, 60, 232, 255, 270, 276, 283, 287, 307
restoration, viii, 4, 52, 107, 253, 265, 266, 270, 271, 281, 283, 287, 301
*Rhizophora*, 4, 36, 43, 45, 48, 57, 58, 59, 67, 68, 77, 78, 79, 80, 81, 82, 83, 107, 108, 110, 112, 113, 114, 117, 121, 127, 128, 129, 130, 131, 132, 135, 141, 143, 144, 145, 146, 149, 163, 164, 166, 167, 168, 169, 170, 171, 174, 175, 177, 178, 180, 187, 188, 189, 190, 191, 192, 193, 194, 195, 196, 197, 200, 202, 229, 230, 231, 233, 234, 235, 236, 238, 240, 241, 265, 275, 276, 277, 279, 280, 282, 284, 285, 286, 288
rooting, v, 8, 131, 165, 187, 188, 189, 190, 191, 192, 193, 196, 216, 218, 273

S

*Salicornia*, 212
sampling point, 109, 127
Satellite imagery, 51, 52
*Scyphiphora*, 36, 41, 43, 45, 48, 288
sebkha, viii, ix, x, 215, 264, 273
*Sesarma*, 141, 143, 144, 148, 276, 284, 287, 305
*Sesuvium*, 212, 213
shifting zones, 259, 273
shrimp aquaculture, 269
shrimp farming, 126, 165, 189, 231, 271, 278, 303, 304, 305, 306
*Sonneratia*, 4, 36, 38, 39, 41, 43, 45, 47, 48, 79, 107, 108, 110, 111, 112, 113, 114, 117, 121, 127, 128, 132, 135, 141, 143, 146, 149, 231, 279
*Spartina*, 213
species composition, 5, 31, 33, 34, 37, 40, 41, 44, 56, 57, 58, 59, 60, 76, 110, 131, 145, 195, 210, 258, 259, 273, 283
species richness, 31, 32, 34, 41, 51, 57, 60
*Sphaeranthus*, 43
structure, i, iii, viii, x, 4, 5, 6, 8, 9, 31, 51, 54, 56, 57, 58, 59, 60, 75, 76, 107, 108, 114, 123, 125, 126, 128, 129, 130, 141, 145, 161, 163, 164, 166, 169, 172, 173, 182, 187, 188, 189, 190, 193, 210, 211, 229, 230, 231, 232, 233, 234, 235, 236, 237, 246, 253, 254, 255, 256, 258, 259, 262, 263, 264, 265, 266, 271, 273, 275, 276, 277, 278, 279, 280, 284, 285, 286, 287, 301, 304, 307
*Suaeda*, 212, 213
succession, 114, 130, 145, 173, 253, 259, 263, 266, 275, 276, 304

T

*Tamarix*, 43
*Terebralia*, 128, 166, 170, 175, 190, 265, 284, 286
texture, 34, 51, 54, 57, 58, 59, 60, 75, 76, 77, 79, 80, 81, 83, 108, 131
*Thalassina*, 77, 127, 167, 170
*Thespesia*, 43
tidal amplitude, 127, 164, 188, 191, 231, 236, 273
Tidra, 210, 215
tonality, 40, 75, 76, 77, 108
typology, 52, 53, 54

U

*Uca*, 145, 212, 213, 214, 215, 218, 277, 280, 281
Unawatuna. *See* Galle

X

*Xylocarpus*, 4, 35, 41, 43, 45, 48, 68, 82, 108, 127, 129, 132, 135, 136, 143, 146, 164, 189, 231

Z

zonation, viii, x, 9, 57, 59, 76, 107, 108, 109, 110, 111, 113, 114, 127, 130, 139, 141, 142, 143, 144, 145, 163, 165, 172, 188, 259, 264, 270, 277, 278, 283, 285, 301, 302, 306, 307

*Zostera*, 213, 215

*Zygophyllum*, 212