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A Synthesis of Existent and Potential Mangrove Vegetation Structure Dynamics from Kenyan, Sri Lankan and Mauritanian Case-Studies*

by

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KEYWORDS. — Mangrove ; Crab ; Ordination ; Remote Sensing ; Kenya ; Sri Lanka ; Mauritania.

SUMMARY. — Although the spatio-temporal changes in the mangrove stand extent, structure and composition, called mangrove vegetation structure dynamics, are rarely studied worldwide, the results produced by a few studies constitute a good basis to recognize various types of dynamics. Identifying these is important to provide information about the past, present and even future evolution of a mangrove forest, and to decide whether or not artificial regeneration is necessary. This contribution gives an overview of the theoretical types of mangrove vegetation structure dynamics and illustrates them with practical examples. At the same time it shows how such a study can be combined with research fields such as conservation genetics, mangrove restoration, stand characteristics and hydrology in order to generate an integrative idea of how the mangrove functions.

TREFWOORDEN. — Mangrove ; Krab ; Ordinatie ; Teledetectie ; Kenia ; Sri Lanka ; Mauretanië.

SAMENVATTING. — Alhoewel spatio-temporele veranderingen in de oppervlakte, in de structuur en in de samenstelling van mangroven, gedefinieerd als mangrovevegetatiestructuurdynamiek, wereldwijd weinig bestudeerd worden, vormen de resultaten die enkele studies hebben ontwikkeld een goede basis om verschillende dynamiek-typen te herkennen. Deze identificatie is belangrijk in het genereren van informatie met betrekking tot de verleden, de huidige en zelfs de toekomstige evolutie van een mangrovewoud, en in het beslissen of er al dan niet artificiële regeneratie noodzakelijk is. Deze bijdrage synthetiseert de theoretische typen mangrovevegetatiestructuurdynamiek en illustreert deze met praktische voorbeelden. Tegelijkertijd toont ze hoe zulk een studie gecombineerd kan worden met onderzoeksthema's zoals conservatiegenetica, mangroveherstel en -bestand-kenmerken, en hydrologie, teneinde een integratief beeld te vormen over hoe de mangrove functioneert.

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MOTS-CLES. — Mangrove ; Crabe ; Ordination ; Télédétection ; Kenya ; Sri Lanka ; Mauritanie.

RESUME. — *Synthèse de la dynamique existante et potentielle de la structure végétale de la mangrove à partir d'études de cas au Kenya, au Sri Lanka et en Mauritanie.* — Bien que les changements spatio-temporels dans la surface, la structure et la composition de la mangrove, définis comme la dynamique de la structure végétale de la mangrove, aient été peu étudiés à travers le monde, les résultats produits par quelques études forment une bonne base pour reconnaître différents types de dynamique. Cette identification est importante pour générer l'information sur le passé, le présent et même sur l'évolution future de la mangrove, et pour décider si une régénération artificielle est nécessaire. Cette contribution synthétise les types théoriques de dynamique de la structure végétale de la mangrove et les illustre d'exemples pratiques. En même temps elle expose comment ce type d'étude peut être combiné avec des thèmes de recherche comme la génétique de conservation, la restauration de la mangrove, les caractéristiques de son peuplement et l'hydrologie afin de se forger une idée du fonctionnement de la mangrove.

What Encompasses "Dynamics" ?

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 (CLARKE 1995, JIMENEZ & SAUTER 1991, FROMARD *et al.* 1998).

In a number of cases terms as "mangrove forest dynamics" (SMITH *et al.* 1991), "vegetation dynamics" (HEIL & VAN DEURSEN 1996, DAHDOUN-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". 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 "spatio-temporal changes in stand extent, structure and composition", as in the present paper.

Data Acquisition and Analysis in Studies on Vegetation Structure Dynamics

REMOTE SENSING

In the past two decades remote sensing technology prevailed for acquisition of full coverage data on vegetation (GANG & AGATSIVA 1992 ; COHEN *et al.* 1996 ; RAMACHANDRAN *et al.* 1998 ; DAHDOUNH-GUEBAS *et al.* 1999a, 2000a ; CHAUVAUD *et al.* 2001) 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 (REHDER & PATTERSON 1986, TASSAN 1987, ASCHBACHER *et al.* 1995, BLASCO *et al.* 1998, HOLMGREN & TURESSON 1998, HYYPPÄ *et al.* 2000, DAHDOUNH-GUEBAS 2002).

The integration of data on vegetation structure dynamics from different moments in time has become almost entirely dependent on remote sensing (HEIL & VAN DEURSEN 1996, MURALI *et al.* 1998, KADMON & HARARI-KREMER 1999, DAHDOUNH-GUEBAS *et al.* 2000a), which usually constitutes the only retrospective basis of long-term comparison to actual vegetation data (DAHDOUNH-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 (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 only hard 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 multispectral images with a 1 m to 4 m resolution. This type of resolution combined with the multispectral character of the imagery (including near-infra-red) may provide alternatives to the as yet unsolved inability of identification of mangroves on a species level (DAHDOUNH-GUEBAS 2001a, VERHEYDEN *et al.* 2002).

However, for the present synthesis 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, providing correct mangrove tree species lists is essential (JAYATISSA *et al.* 2002a) and eventually fieldwork must be carried out as ground-truthing.

GROUND-TRUTHING

Fieldwork or ground-truthing, imperative in remote-sensing studies, has concentrated on the adult vegetation in many case studies (SPALDING *et al.* 1997), but

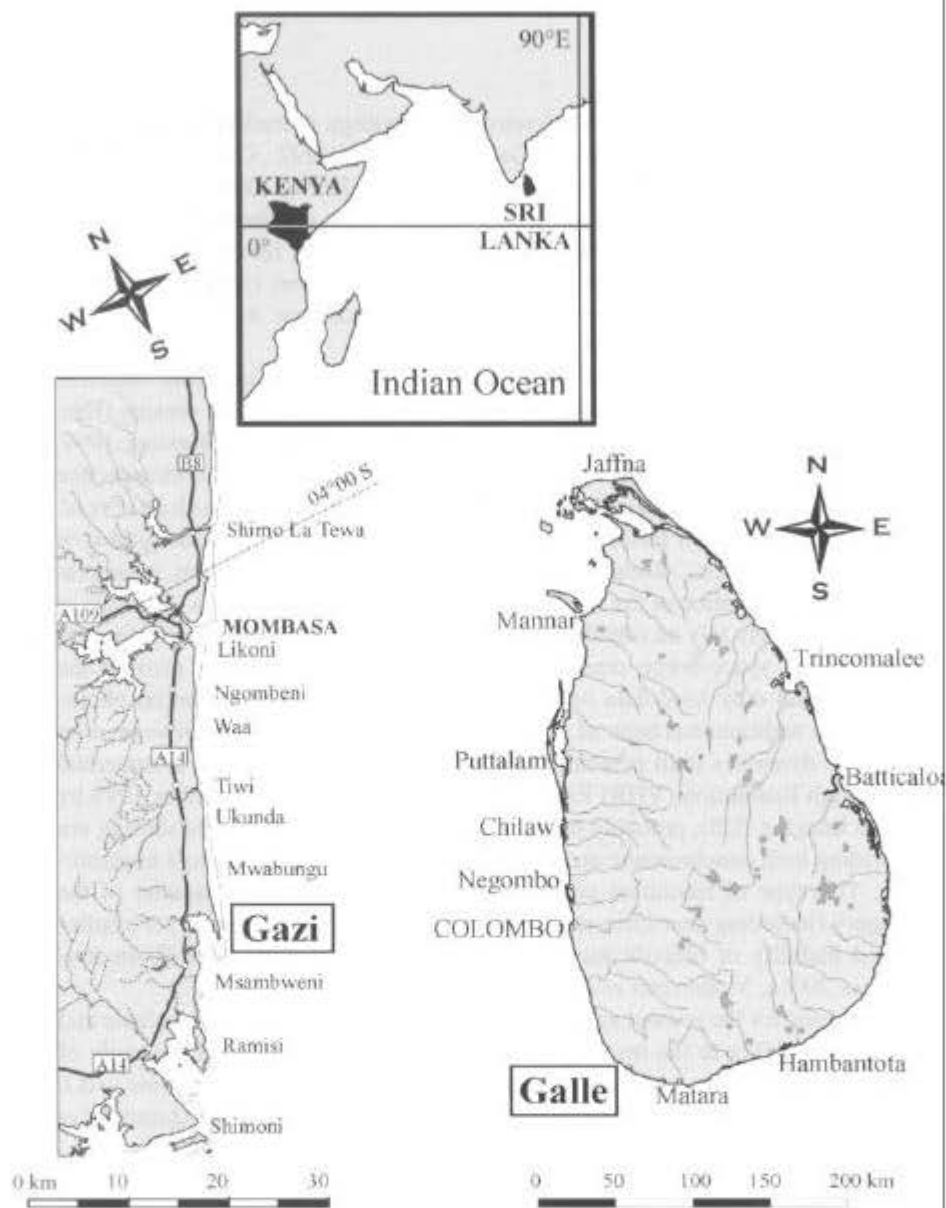


Fig. 1. — Western Indian Ocean (top) with indication of Kenya and Sri Lanka, two countries under focus. A map of the southern section of the Kenyan coast (bottom left) and one of Sri Lanka (bottom right) indicates major cities, rivers and our study sites, Gazi and Galle.

great benefit arises when combining these data with other vegetation layers (MURALI *et al.* 1998 ; DAHDOUNH-GUEBAS *et al.* 2000a, 2001b, 2002a). Below, the “adult” vegetation layer will be distinguished from the “young” and “juvenile” one. 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 (DAHDOUNH-GUEBAS *et al.* 2000a), 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 (DAHDOUNH-GUEBAS *et al.* 2000a, 2001b, 2002a).

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. In our approach “juvenile”, “young” and “adult” merely represent stages in development, dispersion, establishment (*e.g.* beyond possibility of predation) and further development (see tab. 1 for definitions). Table 1 summarizes the possible combinations of vegetation layers and defines the type of vegetation structure dynamics that can form the basis for such combinations.

A mangrove forest, or a species within a forest, without adult individuals, has a pioneering or colonizing nature (colonization dynamic type, hereafter referred to as C-type or displaying C-dynamics). Examples of species with a colonizing nature belong to the genera *Avicennia* and *Sonneratia* (*e.g.* OSBORNE & BERJAK 1997). From a case study in Sri Lanka (DAHDOUNH-GUEBAS *et al.* 2000a) it is clear that in certain sectors *Rhizophora apiculata* Bl. must have had a colonizing nature in the past (*e.g.* island in the upper right section of figure 2 was coconut plantation in 1956 and 1974, but mangrove forest in 1994).

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 case study mentioned above (fig. 2), since no young or juvenile trees were found in that forest section during the recent fieldwork missions over several years (*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* (L.) Stearn trees usually do not show young or juvenile trees in their understory (DAHDOUNH-GUEBAS & KOEDAM 2001). A forest with adult trees and without either young or juvenile ones may be threatened with decline as well, unless there is only a transient lack of younger specimens and an accelerated growth subsequently. The latter can be very acute in forest areas where *Rhizophora mucronata* Lamk. dominates the canopy, *Ceriops tagal* (Perr.) C.B. Robinson dominates the young understory and a mix of both species dominate the juvenile understory. When canopy gap formation occurs due to the logging of *R. mucronata*, which is a highly preferred species by the local population in Mida Creek in Kenya (DAHDOUNH-GUEBAS *et al.* 2000b), *C. tagal* is actually the species that pre-empt the gap in the canopy (KAIRO 2001, KAIRO *et al.* 2002). What is preferred is logged, but what is logged is therefore not necessarily what will regenerate. Similar situations are reported

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 forest colonization	C-TYPE DYNAMICS
0	0	1		
0	1	1		
1	0	0	long-term lack of rejuvenation actual decline of forest	D-TYPE DYNAMICS
1	1	0	short-term lack of rejuvenation threatening decline of forest in the distant future, unless acute, transient decline	J-TYPE DYNAMICS
1	0	1	incipient rejuvenation or long rejuvenation cycle threatening decline of forest in the near future, unless growth is accelerated (e.g. canopy gaps in Kenya, KAIRO <i>et al.</i> 2002)	
1	1	1	COMPLETE VERTICAL VEGETATION STRUCTURE How has vertical vegetation structure changed in the past ? Static forest or dynamic forest (cf. table 2)	

0 or grey = absent ; 1 or black = present ; AT = adult trees (trees "larger" than YT and JT) ; YT = young trees (trees smaller than 1.3 m or with a $D_{1.3} < 2.5$ cm, but which had reached the sapling stage, a plant with more than 6 leaves) ; JT = juvenile trees (propagules or seeds up to the stage of sapling).

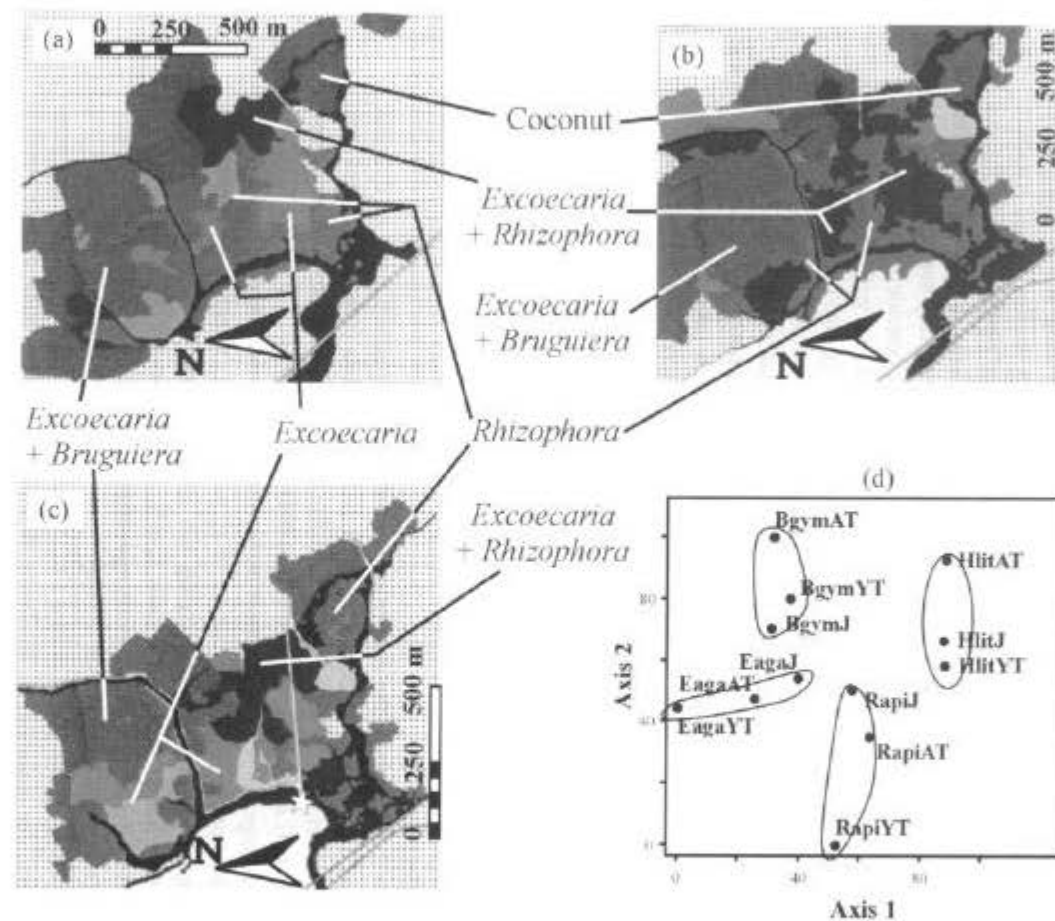


Fig. 2. — Example of past (a, b), present (c, d) and possible future dynamics (d) in Unawatuna-Galle (Sri Lanka) adapted from a remote-sensing study (DAHDOUN-GUEBAS *et al.* 2000a) and from an ordination study (DAHDOUN-GUEBAS *et al.* 2002a). Grey shades represent different mangrove assemblages, except "white" (= inhabited and terrestrial area), light grey (= human infrastructure) and "black" (water) and the northernmost and easternmost polygons (= coconut plantations). Some important assemblages discussed in the text are indicated. In (c), the white star indicates the position of 06°01'37.9"N 080°14'50.5"E with an accuracy of 7.0 m.

for *Sonneratia caseolaris* (L.) Engler replacing the more classical elements of the mangrove (e.g. members of the family of the Rhizophoraceae) due to inland hydrological works (JAYATISSA *et al.* 2002b).

A forest with adult, young and juvenile trees generally rejuvenates (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 is a significant shift in species composition from “mangrove species” towards “non-mangrove species” we will refer to “qualitative horizontal decline”. This should be taken *lato sensu* and applies in case of both shifts from strict or major mangrove components towards the minor mangrove components and shifts from mangrove species in general towards mangrove associates or non-mangrove species. A shift from major to minor mangrove components can be illustrated by the transition of a *Rhizophora apiculata* dominated forest to an *Excoecaria agallocha* L. in Sri Lanka (DAHDOUH-GUEBAS *et al.* 2000), whereas a shift from mangrove species towards non-mangrove species can be illustrated by the introgression of the herbaceous *Fimbristylis salbundia* (Nees) Kunth subsp. *pentaptera* (Nees) T. Koyama into the heart of mangrove sites in Sri Lanka (*loc. cit.*). Also the studies by KAIRO *et al.* (2002) and JAYATISSA *et al.* (2002b), discussed above, are examples of such qualitative horizontal declines.

Table 2 shows 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 the left section of the mangrove of Galle in figure 2, supports rejuvenation and other processes in its understorey (DAHDOUH-GUEBAS *et al.* 2000a).

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 and the vegetation patches themselves do not displace. In case of 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).

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 underlying steady-state mechanisms. The bullets represent exclusive options. Underlined examples for the respective situations have been taken from existing studies

		A C T U A L F I E L D D A T A				
		AT = YT = JT	AT = YT ≠ JT	AT = JT ≠ YT	AT ≠ YT = JT	AT ≠ YT ≠ JT
RETROSPECTIVE RESEARCH	Static forest	<ul style="list-style-type: none"> normal rejuvenating forest <p>(DAHDQJH-GUEBAS <i>et al.</i> 2001b, 2002a)</p>	<ul style="list-style-type: none"> rejuvenating forest, with elements of a dynamic forest nature, in which JT are spread over a wider area than where they can actually establish 	<ul style="list-style-type: none"> declining forest, in which YT fail to find areas appropriate to grow in and JT largely originate from AT, but possibly will be aborted (shift to dynamic nature) 	<ul style="list-style-type: none"> declining forest, in which YT fail to find areas appropriate to grow and JT largely originate from YT change in static nature (shift to dynamic nature) 	<ul style="list-style-type: none"> declining forest change in static nature (shift to dynamic nature)
	Dynamic forest	<ul style="list-style-type: none"> declining forest (shift to static nature) <p>DAHDQJH-GUEBAS <i>et al.</i> 2000a, 2001b)</p>	<ul style="list-style-type: none"> rejuvenating forest, with elements of a static forest nature, in which JT are spread over a wider area than where they can actually establish 	<ul style="list-style-type: none"> rejuvenating forest with elements of a static forest nature, in which JT largely originate from AT 	<ul style="list-style-type: none"> rejuvenating forest with elements of a static forest nature, in which JT largely originate from YT 	<ul style="list-style-type: none"> normal rejuvenating forest <p>DAHDQJH-GUEBAS <i>et al.</i> 2000a, 2001b)</p>

N.B. Juvenile trees can originate from either young or adult trees, which can however not be unequivocally established.

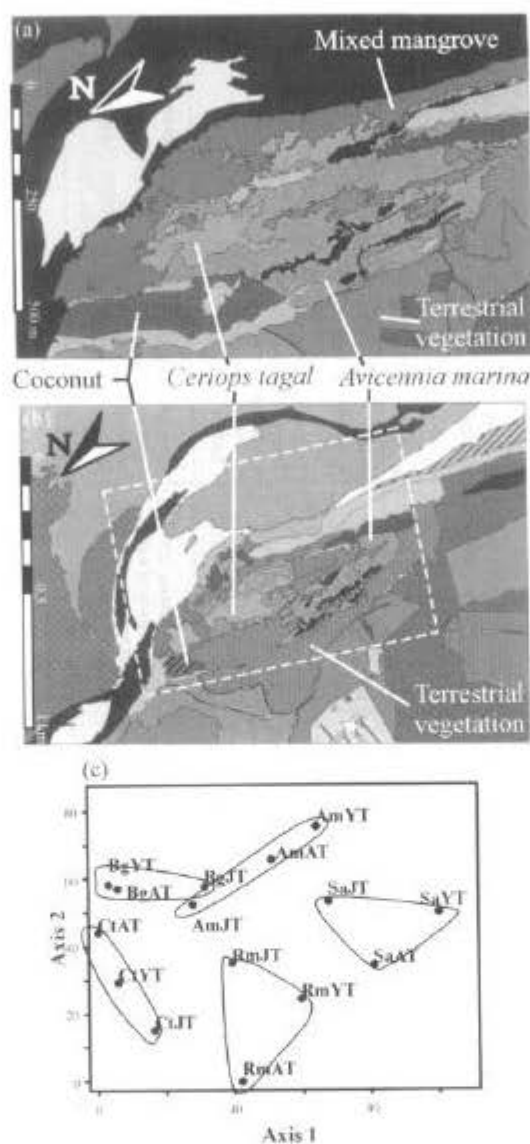


Fig. 3. — Example of past (a), present (b,c) and possible future dynamics (c) in Gazi Bay (Kenya) adapted from a remote-sensing study (DAHDOUH-GUEBAS *et al.* 2001b) and from an ordination study (DAHDOUH-GUEBAS *et al.* 2002a). Grey shades represent different mangrove assemblages, except "white" and "light grey" (= tidal and non-tidal sand banks), grey (= human infrastructure), the dotted polygons (terrestrial vegetation) and the complex of polygons in the lower right corners of the images (= coconut plantations and terrestrial vegetation). The polygons starting in the upper right corners as well as "black" polygons represent water. Some important assemblages discussed in the text are indicated. In (b), the dashed rectangle indicates the approximate position of the map in (a), whereas the white star indicates the position of $04^{\circ}25'27.4''$ S, $039^{\circ}30'22.1''$ E with an accuracy of 10.5 m.

This type of analysis, the results of which can be shown using a clear and highly qualitative graphical design based on image analysis and GIS, can be supported by a statistical analysis that is based on the same type of data and generates quantitative results (figs. 2 and 3). Detrended correspondence analysis (DCA), canonical correspondence analysis (CCA) and non-linear multidimensional 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, DAHDOUNH-GUEBAS *et al.* 2001b, 2002a).

Types of Vegetation Structure Dynamics in Mangroves

Basically, the vegetation structure of mangroves can be typified as “zoned” in several places (*e.g.* in the Kenyan sites), with a vegetation “zone” defined as a long band-like patch of vegetation, or as “non-zoned” elsewhere, which then displays a mosaic pattern of monospecific or assemblage “vegetation patches”, 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 (GALLIN *et al.* 1989). However, Walter & Steiner’s hypothesis that the height above datum is the determining factor in mangrove zonation, or that tree species composition can be predicted based on a topographic gradient (WATSON 1928), has been rejected (DAHDOUNH-GUEBAS *et al.* 2002b).

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. The term “moving mosaic” (figs. 2 and 4) was introduced by DAHDOUNH-GUEBAS *et al.* (2000a) for the type of vegetation structure dynamics 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 dynamics 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”. DAHDOUNH-GUEBAS *et al.* (2000a) suggested that a moving mosaic vegetation structure dynamic may

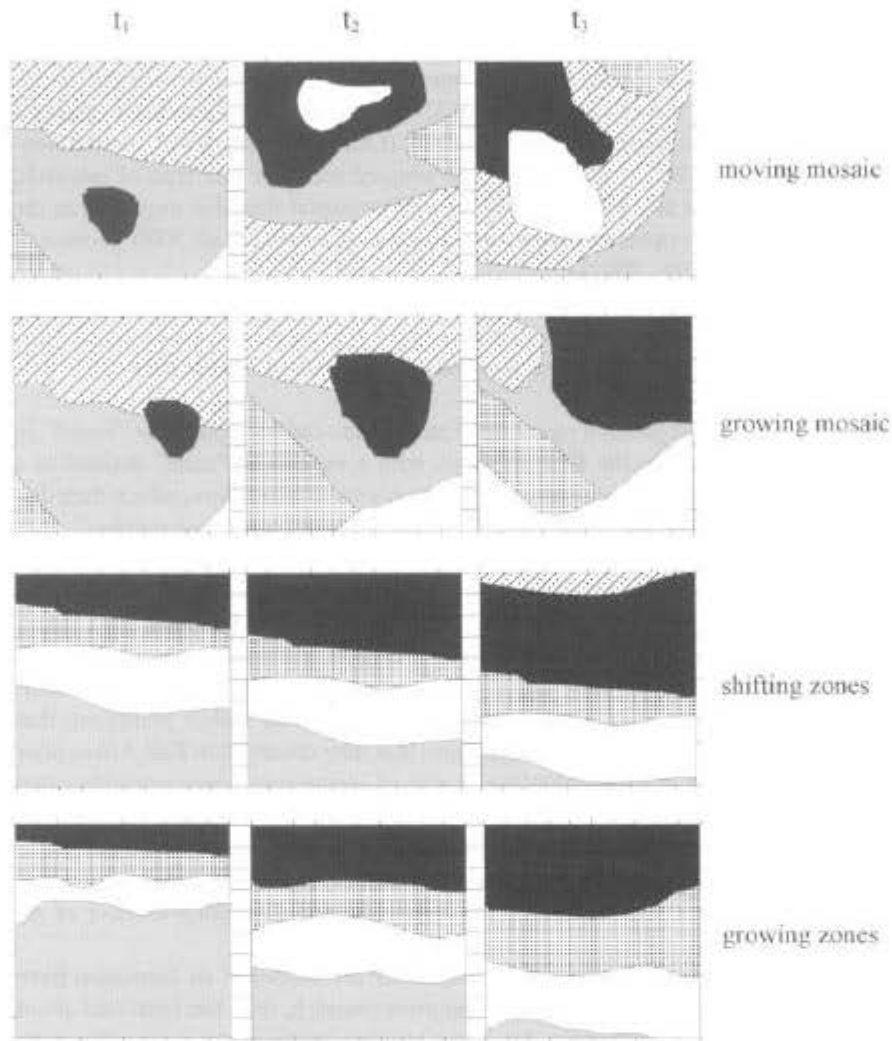


Fig. 4. — Types of spatio-temporal vegetation structure dynamics. Each row represents a forest area on three different and chronologically ordered moments in time (t_1 , t_2 and t_3). The shades represent different mangrove tree species.

be typical for mangroves that are characterized 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 (DAHDJUH-GUEBAS *et al.* 2001b). The vegetation structure dynamics that occur under these circumstances can be typified as “shifting zones” (fig. 4), if the zones are displaced entirely, or as “growing zones” (figs. 3

and 4) if the zones become larger (positive growth, *e.g.* seaward patches in Gazi that have fragmented the mixed mangrove zone into several assemblages, fig. 3) or smaller (negative growth, *e.g.* landward *Avicennia* patches in Gazi, fig. 3). 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, 2002a ; KAIRO 2001, *et al.* 2002), to sea-level change or to altered tidal hydrodynamics (WOODROFFE 1990, 1995, 1999 ; SAINTILAN & WILLIAMS 1999), and to natural events (STEVENS & MONTAGUE 1999, SAINTILAN & WILLIAMS 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 with succession, particularly in a situation in which a naked or denuded habitat is colonized and further develops. We recognize three categories : floristic accretion, floristic invasion and floristic dominance/extinction (fig. 5). “Floristic accretion” occurs when a first pioneering species is in part responsible for the development of new

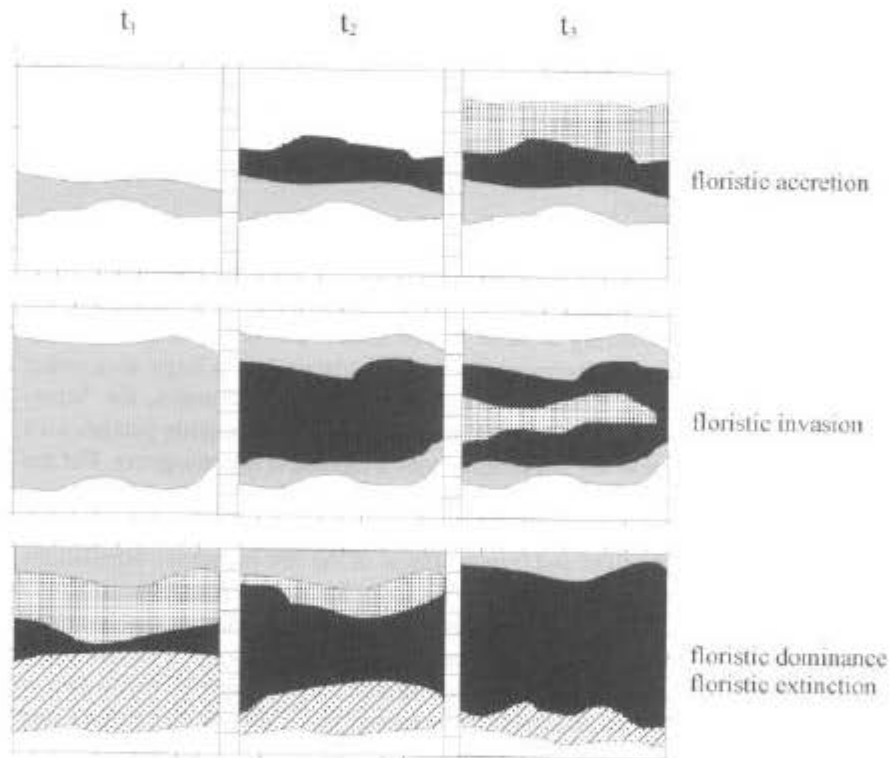


Fig. 5. — Types of spatio-temporal floristic succession in vegetation structure dynamics : floristic accretion, floristic invasion and floristic dominance/extinction. Legend as in figure 4.

adjacent zones, mostly located more landward. This is the case for several species of the pioneering mangrove genera *Avicennia* or *Sonneratia* (OSBORNE & BERJAK 1997). "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. 3). This may be the process underlying the double zonation often observed in *Avicennia marina* (Forsk.) Vierh. (DAHDOUH-GUEBAS *et al.*, in press). 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. 2). 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 cases floristic invasion and floristic dominance may be difficult to distinguish, or an interaction between both may exist (*cf.* fig. 2). The ease with which these processes 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 (including 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 (*ca.* 19°-20° N), *Avicennia germinans* is the sole mangrove-tree species that constitutes the mangrove ecosystem in a very discontinuous formation (DAHDOUH-GUEBAS & KOEDAM 2001).

"Vegetation structure dynamics", as defined above (*i.e.* spatio-temporal 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 (DAHDOUH-GUEBAS & KOEDAM 2001). The only possible case would be for the sebkha formation to evolve into a shrub formation. In the PNBA, the lack of

success of *Avicennia germinans* North of the very last tree (that still produces numerous propagules) could be of a climatic nature (frost frequency) as reported for this species along the North-American west coast (STEVENS & MONTAGUE 1999).

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 ground-water fluxes (TACK & POLK 1999), mangrove forests are adversely affected both quantitatively and qualitatively all around the globe (PERNETTA 1993a, b ; RUTZLER & FELLER 1996). Research groups are trying to quantify this decline from different angles using remote sensing. However, it is as 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 species or at the patterns of succession, both of which could 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 an optimal level, must thus 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 (LEE *et al.* 1996, CALOZ & COLLET 1997). DAHDOUNH-GUEBAS *et al.* (2000a) emphasized that there is a need for a methodology that allows to make reliable predictions about the state of mangroves using a relatively small input from vegetation field work, and to decide whether a mangrove stand of a certain location has the potential to successfully renew and rejuvenate or 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 (DAHDOUNH-GUEBAS 2002). 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 (fig. 5). 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 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

(HOLMGREN *et al.* 1997, HOLMGREN & THURESSON 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 biocomplexity data (biologic, hydrologic, physico-chemical, geographic,...), socio-geographic or socio-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 (fig. 5).

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 recognized : mangrove in a virtually pristine condition (Kiunga and Lamu, north Kenyan coast), 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 2001). 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 vegetation structure dynamics in sites disturbed by man probably requires human interference to rehabilitate the mangrove (DAHDOUH-GUEBAS *et al.* 2000a, 2001b, 2002a). A prediction following from combination with investigations on the distribution of young and juvenile trees confirms this (*loc. cit.*). The above studies therefore lead 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 & HUSTON 1989 ; MCKEE 1995 ; MCGUINNESS 1997 ; DAHDOUN-GUEBAS *et al.* 1997, 1998 ; DAHDOUN-GUEBAS 2001c). 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). DAHDOUN-GUEBAS *et al.* (1999b), BALLERINI *et al.* (2000), CANNICCI *et al.* (2000), DAHDOUN-GUEBAS *et al.* (2001c) and DAHDOUN-GUEBAS *et al.* (2002b) 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 SMITH & HUSTON (1989), OSBORNE & SMITH (1990), MCKEE (1995), MCGUINNESS (1997), DAHDOUN-GUEBAS *et al.* (1997, 1998), STEELE *et al.* (1999), DAHDOUN-GUEBAS (2001c) and ALLEN *et al.* (2003). The results found for

Table 3

A synthesis of the findings on propagule predation in Kenya and Sri Lanka (DAHDOUNH-GUEBAS *et al.* 1997, 1998 ; Dahdouh-Guebas, 2001c)

KENYA	SRI LANKA
differential predation among forest <u>zones</u> : more predation in landward and <i>Rhizophora</i> dominated zones	differential predation among forest <u>patches</u> : more predation in <i>Excoecaria</i> dominated patches
no differential predation among mangrove <u>propagules</u> : all species are predated	differential predation among mangrove <u>propagules</u> : <i>Avicennia</i> predated more than <i>Bruguiera</i> , which in turn is predated more than <i>Rhizophora</i>
differential predation among mangrove <u>crabs</u> : more predation by <i>Neosarmatium</i> spp. and <i>Sesarma</i> spp.	differential predation among mangrove <u>crabs</u> : more predation by <i>Episesarma</i> spp. and <i>Chiromanthes</i> spp.

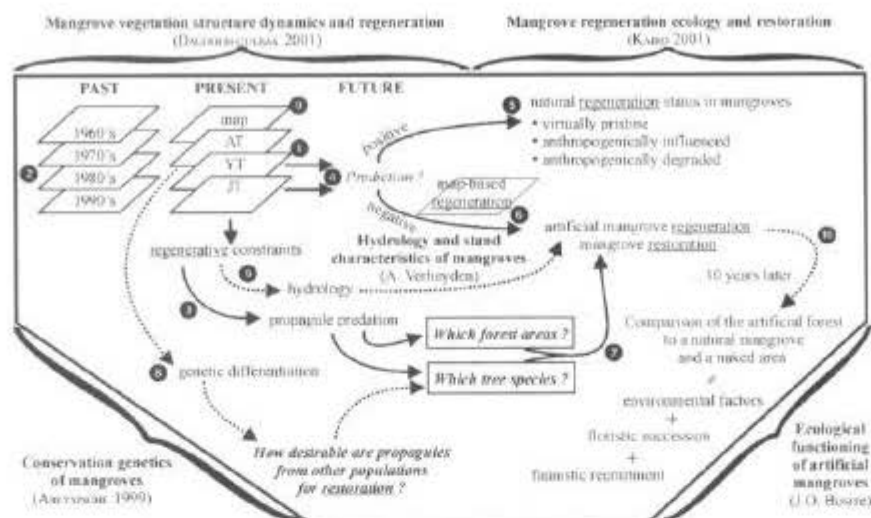


Fig. 6. — Example of the research framework in Kenya and Sri Lanka involving vegetation structure and its dynamics, natural and artificial regeneration including issues of regenerative constraints, conservation genetics, restoration and monitoring. The study starts with the mapping of the present vegetation structure through airborne remote sensing. ① 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. ② Retrospective investigation of the same area is done through sequential aerial photography from the past. ③ These three first steps constitute the basis of the Ph.D. research that was awarded by the Royal Academy of Overseas Sciences (DAHDOUN-GUEBAS 2001). The juvenile vegetation layer is subjected to regenerative constraints, amongst which propagule predation is investigated in-depth. ④ 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. ⑤ 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. ⑥ This is part of the research framework which is only in part covered here and is predominantly investigated by the Ph.D. framework of J.G. KAIRO (2001), awarded the Development Cooperation Prize of the Belgian Directorate-General for Development Cooperation. In case of a negative prediction, artificial regeneration and restoration may be necessary. ⑦ 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 ? ⑧ The study on propagule predation contributes to the answer on both questions. The steps introduced so far are part of research on mangrove vegetation structure dynamics and regeneration (DAHDOUN-GUEBAS 2001, KAIRO 2001). The links with other research frameworks are given in dotted lines. 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). ⑨ The investigation of hydrology in general or as a regenerative constraint in particular provides information to the rehabilitation of mangroves (carried out by A. Verheyden). ⑩ The questions that have often been forgotten by mangrove researchers and for which we designed a separate framework (carried out by J.O. Bosire) 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. ⑪ This research framework fits into a larger framework on mangroves and nearby ecosystems (not shown).

Kenya and Sri Lanka are summarized in table 3. In Mauritania no evidence for propagule predation has been found (DAHDOUH-GUEBAS & KOEDAM 2001).

It has also been shown how propagule predation and vegetation structure dynamics may be interlinked through anthropogenic hydrological factors : 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 lead to a particular mangrove vegetation structure or zonation (DAHDOUH-GUEBAS 2001c). The integrated research framework that explores this and other relationships amongst others, is introduced in figure 6. Vegetation structure dynamics imply changes, which in turn may imply instability. For instance, for faunal communities the association between fauna and specific mangrove tree species is often obscured. However, mangroves behaving as units of varying scale (lagoon, estuary) with constant gradual change in moving mosaic or shifting zones, but with a persistence of all mangrove species or assemblages, may prove ecologically very stable over time. Future research may throw light on whether mangrove forests must be seen as spatially heterogeneous but ecologically coherent formations.

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