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 speciesdiverse 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 worldwide 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 km² 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

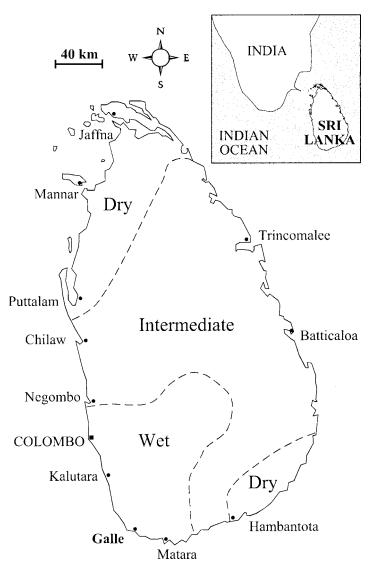


Figure 1. Map of Sri Lanka showing the climatic zones and some major cities along the coast, of which our study site Galle is printed bold. Climatic zones are after Mueller-Dombois (1968).

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

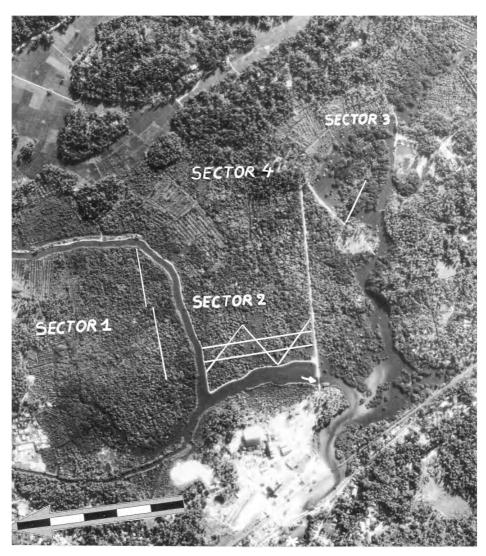


Figure 2. Aerial photograph of Galle showing the different sectors (please refer to the 'Results' section for detailed description of each sector). The white lines indicate the locations of the vegetation transects and the small white arrow beneath the transects in Sector 2 points to the dam (06°01'37.9"N, 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

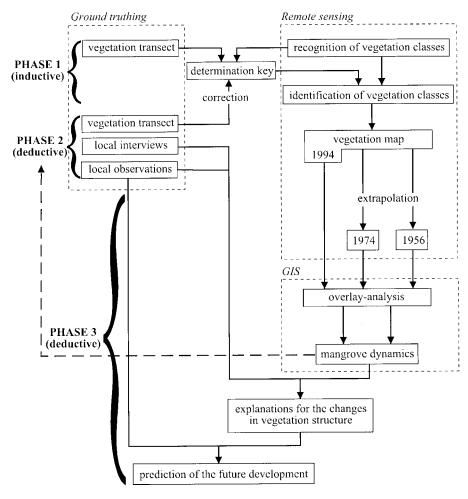


Figure 3. Scientific approach used in this study. In a first phase an inductive scientific approach was adopted to interpret aerial photographs based on a first field work mission (Verheyden et al., submitted). Different vegetation classes are recognized on aerial photographs, and with the help of a 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 $[D_r = (\text{number of individuals of species/total number of individuals}) \times 100]$, 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 three-fold 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

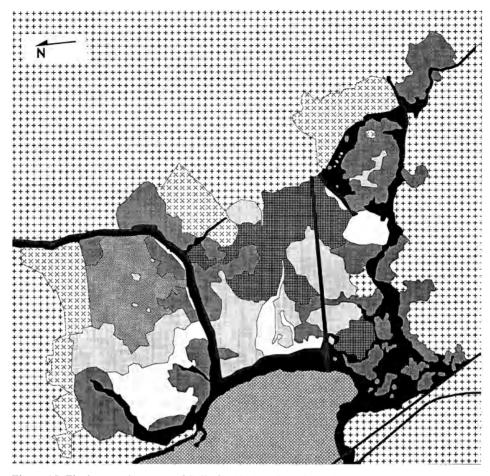


Figure 4C. Final vegetation maps of Galle for 1994. Refer to legend on page 746 and to Table 1 on page 750 for map conventions for Figures 4 and 5.

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	Identification
			(e.g. shape, shade, location)	
white	irregular	irregular	often clearly anthropogenic	infrastructure
				(tracks, constructions)
white	blurred	discontinuous canopy	star-shaped crown	Cocos nucifera (coconut)
			sparse and regular distribution	
white	blurred	irregular	no typical shape	Clerodendron inerme
			no shadow-side	
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	aggregating / often at water side	Rhizophora spp.
		separately visible crowns	wide horizontal spatial range	
dark grey / black	'cauliflower' texture	continuous canopy with no	aggregating / often at water side	Rhizophora spp.
		separately visible crowns	wide horizontal spatial range	
dark grey / black	coarse grain	discontinuous canopy	aggregating / often at water side	Rhizophora spp.
				wide horizontal spatial range
dark grey / black	plain or irregular	plain or irregular	'waves' may be present	water
		monad a few cases.	The state of the s	

N.B. A 'discontinuous canopy' implies that crowns are separately visible, but a 'continuous canopy' does not imply that separate crowns cannot be distinguished. N.B. The identification tag should always be considered as a vegetation assemblage dominated by a certain species, rather than as a pure stand.

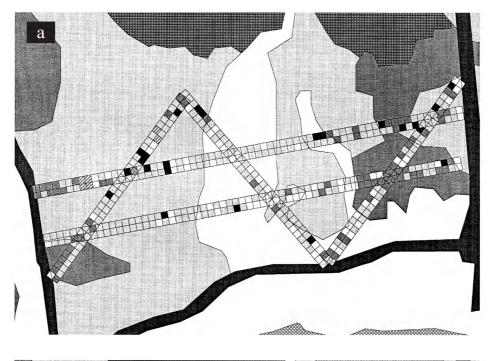
Table 2. Area covered by the various vegetation classes in 1956, 1974 and 1994 in Galle. The areas are expressed in hectares and as a percentage of the total mangrove cover (between brackets). The limits of the considered areas are real mangrove limits (the mangrove of Galle is completely covered by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

Vegetation class	Area in 1956	Area in 1974	Area in 1994
	(ha)	(ha)	(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.



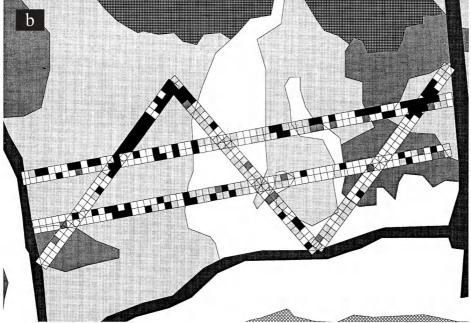


Figure 5. Overlay of the 1994 vegetation map (remote sensing) and the 1997 transect data (ground-truthing) for adult (a) and young (b) mangrove trees. Each block of four squares represents four PCQM quadrants with the PCQM sample point located in the centre. The pattern represents the tree nearest to 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		Sec	tor 3
Forest patch	B. spp. +	E. aga	R. api	E. aga	R. api	open	E. aga	R. api
	E. aga					space		
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	O	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	O
E. agallocha	2	5	0	1	2	2	0	O
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

 \overline{B} . = Bruguiera, \overline{E} . aga = Excoecaria agallocha, \overline{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. s	B. spp. $+ E. aga$	aga		E. aga			R. api	
	Adult		Young	Adult	ı	Young	Adult		Young
	Dr	I.V.	Dr	Dr	I.V.	Dr	Dr	L.V.	Dr
	(%)		(%)	(%)		(%)	(%)		(%)
Bruguiera spp.	41.0	2	93.3	24.5	2	72.7	23.3	3	100.0
E. agallocha	43.6	1	0	8.69	1	13.6	30.0	2	0
R. apiculata	15.4	ϵ	6.7	5.7	Э	13.6	46.7	1	0
B. = Bruguiera, E. aga = Excoecaria agallocha, R. api = Rhizophora apiculata.	a agallocha, R.	api = Rhiz	cophora apiculata.						
(b) Sector 2									
Forest patch		E. aga			R. api			open space	ė
	Adult		Young	Adult		Young	Adult		Young
	Dr	I.V.	Dr	Dr	I.V.	Ωr	Δ	I.V.	Οr
	(%)		(%)	(%)		(%)	(%)		(%)
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	1	,		1	1	,
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.	pi = Rhizophor	a apiculat	a, $-$ = not observed in	the respective fore	st patch.				
(c) Sector 3									
Forest patch		R. api							
	Adult		Young						
	Ωľ	I.V.	Dr						
	(%)		(%)						
Bruguiera spp.	2.4	3	-						
E. agallocha	7.1	2	,						
R. apiculata	90.5	1	,						
R. $api = Rhizophora\ apiculata$, $- = not\ calculated$.	not calculated.								

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

R. apiculata

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).

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 viability 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>.