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Structure, above-ground biomass and dynamics of mangrove ecosystems: new data from French Guiana

Abstract The article presents new results on the structure and the above-ground biomass of the various population types of mangroves in French Guiana. Nine mangrove stands were studied, each composed of three to ten adjoining plots with areas that varied depending on the density of the populations. Structural parameters and indices were calculated. Individuals representative of the three groups of taxa present were felled: *Avicennia germinans* (L) Stearn, *Rhizophora* spp., and *Laguncularia racemosa* (L) Gaertn. The trunks, branches and leaves were sorted and weighed separately. The biomass was obtained by determining the allometric relationships, the general equation selected being of the type $y = a_0 x^{a_1}$, where the diameter (x) is the predictive variable. The total above-ground biomass varied from 31 t ha^{-1} for the pioneer stages to 315 t ha^{-1} for mature coastal mangroves, but with large variations depending on the structural characteristics at each site. The results place the Guianese mangroves among those with high biomass, although lower than those reported for Asia. Based on the relationships between structural parameters and standing biomass, in particular with the use of the "self-thinning rule", population dynamics models are proposed.

Key words Mangroves · Structure · Biomass · Allometric relationships · Self-thinning rule

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Introduction

Between 25°N and 25°S, mangroves colonize almost 75% of the coastline (Day et al. 1987) although they only represent 1% (100 000 km^2) of the area of tropical forest. Their ecological importance in these areas is therefore considerable. Although the scientific studies devoted to them were for a long time descriptive, the trend over the last several years has been towards the study of how they function – the main outcome of these investigations being the demonstration of their high productivity and their role in supplying organic material to coastal marine ecosystems (Odum and Heald 1972; Lugo et al. 1980; Boto and Bunt 1981; Rojas-Beltran 1986; Hutching and Saenger 1987). The trophic relationships between mangroves and coastal marine ecosystems can be characterised by the biomass and the productivity of the mangroves, these data themselves being closely linked to the structure of the mangrove forests. In French Guiana (henceforth called Guiana), where mangroves stretch for 600 km^2, the rare studies concerning these environments have been restricted to the structure of the populations (Lescure 1977; Lescure and Tostain 1989). Similarly, in Brazil, where mangroves grow over about 25 000 km^2, descriptive studies are numerous (Schaeffer-Novelli et al. 1990), but no data have yet been reported on the primary productivity or the biomass.

In this study, new data concerning the structure of the Guianese mangrove forest are presented. Based on the analysis of the stages of development and the determination of the corresponding above-ground biomasses, the specific dynamics of the mangrove forest is discussed and a development model is proposed.

In this context, a major difficulty is insufficient field data, particularly concerning the ages of individuals and stands. Mangrove trees usually lack growth rings for age determination (Tomlinson 1986). In *Avicennia germinans*, growth rings are present but they are not correlated with the age of a given individual. The number of rings

in a given stem section is related to its diameter but varies within sections of the same age (Gill 1971; Zamski 1979). Nevertheless, rough indirect estimations of the age can be obtained from the analysis of the sediments on which they grow, considering that the age of *Avicennia* populations generally corresponds to that of the deposits on which they are found.

Materials and methods

The French Guiana mangrove forest

A. germinans (L) Stearn is the dominant species of mangrove in Guiana. It occurs in even-aged single-species formations, along the coast, reaching 30 m in height in adult stands. In pioneer stages *Laguncularia racemosa* (L) Gaert. accompanies *A. germinans* or even sometimes forms single-species populations of no higher than 6–8 m. Just inshore of the actual coast and in riverine environments, the genus *Rhizophora* appears (*R. mangle* L., *R. racemosa* Meyer), alone or mixed with *A. germinans*. It also occurs in swamp forests alongside species such as *Pterocarpus officinalis* Jacq., *Tabebuia insignis* Sandw. and the palm *Euterpe oleracea* Martius. The pantropical fern *Acrostichum aureum* L. and the liana *Rhabdadenia biflora* (Jcq.) Mull. are typical of mature mangroves. Other species such as *Machaerium lunatum* (L) Ducke, *Hibiscus tiliaceus* L. and *Montrichardia arborescens* Engler form dense bushy thickets adjacent to the mangrove. Among the other known mangrove species belonging to the Atlantic zone, although present in Brazil and in Guadeloupe, *Avicennia schaueriana* has not been recorded in Guiana, and *Conocarpus erectus* has been identified in one locality only.

As in the whole Atlantic area, the Guianese mangrove forest shows low diversity and it is on the structure and the dynamics of the stands that we based our typological study rather than on the floristic composition.

Study areas

The studies were carried out in three areas of mangrove chosen to be both representative and accessible: Cayenne (Marais Leblond: 52°19′W, 4°52′N), Sinnamary (Anse road and river banks: 52°50′ to 53°W, 5°23′ to 5°28′N), Iracoubo (Counamama river: 53°10′W, 5°30′N). In each area, one or several stands were chosen depending on the characteristics of the mangrove forest. Each stand consisted of one or several series of three to ten adjoining plots with a surface area fixed by the density of the populations: 3×3 m in pioneer mangrove and 30×30 m for mature stands.

Structure

In each plot, all the individuals were identified and their number, diameters (at 1.3 m for adults, at half-height for those under 2 m tall, and above the uppermost intersection of the prop roots for *Rhizophora*) and heights were noted. Structural indices established for rain forest and adapted to mangroves by various authors (Pool et al. 1977; Cintron and Schaeffer-Novelli 1984) were calculated: complexity index, I_c: number of species × density × basal area × mean height × 10^{-5}; and species importance value, I_v: relative density + relative frequency + relative dominance.

Above-ground biomass

This was determined from total clearance cutting for pioneer stages and the felling of representative trees for adult stages. The diameters (diameter at breast height, dbh) and the heights of all the trees cut were measured. Trunks, branches, leaves and, when appropriate, prop roots, were sorted and weighed on site (fresh weight). The dry weights were determined after oven drying (105°C) of subsamples. For the largest felled trees (20 cm < dbh < 45 cm), the procedure was different: the volumes of the trunks and large branches were calculated (diameter measured every 2 m) and the samples weighed before and after oven drying. The weight:volume ratios were calculated to obtain the total dry weights.

Each sampled individual was then described by its structural parameters and the partitioned (leaves, branches, trunk) and total biomass values. Correlations were sought between these parameters and the models established were then applied to all the individuals in the plots. The total biomass of a plot is equal to the sum of the individual masses expressed in tonnes dry weight per hectare.

Establishment of allometric relations

Methods using allometric relationships for the estimation of biomass are frequent in the literature, both for temperate (Rochow 1974; Rondeux 1993) and tropical forests (Lescure et al. 1983; Brown et al. 1989), with some data also available for mangroves (Cintron and Schaeffer-Novelli 1984; Saenger and Snedaker 1993). The most frequently used predictive variable is the dbh, i.e. at 1.30 m, either alone or associated with the height (h) and possibly, but rarely, with the diameter of the crown.

In this way, Suzuki and Tagawa (1983) established a regression of the type $y = b(dbh^2 \cdot h)^a$ for *Rhizophora mucronata* Lamk. ($n = 9$) and *Bruguiera gymnorrhiza* (L.) Lamk. ($n = 8$) in Japanese mangroves composed of small trees ($h = 6–8$ m and dbh < 16 cm, with n: number of individuals). Woodroffe (1985) reported the relationship $y^{-1/3} = a + bx$, where x is the diameter, the height of the trunk or the diameter of the crown (*Avicennia marina* (Forsk.) Vierh., New Zealand; $n = 12$, $h \leq 4$ m, dbh ≤ 10 cm). Putz and Chan (1986), found a relationship between dbh and biomass (*Rhizophora apiculata* BL., Malaysia) which was log $y = a$ log dbh $+ b$ ($n = 20$, 5 cm < dbh < 30 cm). Amarasinghe and Balasubramaniam (1992) established a relationship of the same type for a *R. mucronata* and *A. marina* mangroves in Sri Lanka ($n = 30$, dbh < 12 cm). Mackey (1993) used different regressions for a single population of Australian *A. marina*: linear, with circumference as the predictive variable ($n = 6$, 2 cm < dbh < 5 cm), and logarithmic, with height as the predictive variable ($n = 13$, $h < 2$ m). It appears from these data that, although the correlations obtained are good ($r^2 > 0.95$), the number of samples studied was often low and particularly took into account trees of small diameter. It can also be noted that most of the data published so far concern the mangrove forests of southeast Asia and Australia and the species native to those areas (*Bruguiera*, *R. mucronata*, *R. apiculata*, *A. marina*). Few data are available for western mangroves; we can however mention Golley et al. (1962) for Puerto Rico and Panama (Golley et al. 1975), Lugo and Snedaker (1974) for Florida, and Imbert and Rollet (1989) for Guadeloupe. Recently, some data on mangrove productivity were reported from Guyana (Chale 1996). Until now, however, no biomass data have been available for the South American continent.

In this work, we present the biomass values established for *A. germinans*, *L. racemosa* and *Rhizophora* spp. (as the two species *R. mangle* and *R. racemosa* were difficult to distinguish in the absence of the inflorescence, they were considered together in the calculations). The predictive variable we used was the diameter. The reasons for this choice were the following:

1. This parameter can be measured for all the individuals in a population whereas the height can only be accurately determined in felled individuals. For standing trees, the height can only be estimated using a rangefinder, with an error estimated to lie between 10 and 15% (the various dendrometers intended for forestry applications are difficult to use in mangroves).

2. In *A. germinans* the tip of the tree often breaks off and apical growth is replaced by that of an axillary branch; the diameter/height correlation therefore no longer has the same biological significance.

Various forms of regression were tested. Depending on the statistical characteristics of the results (correlation coefficients, residuals distribution), the logarithmic model gave the best description of the relationships between biomass (y) and diameter (x) i.e.

$$y = a_0 x^{a_1}$$

Results

Stand structures

Four characteristic mangrove stages were distinguished, each occurring in one to three areas: sea edge pioneer and young mangroves (stands I–III); mature coastal mangroves or pure mangroves (stands IV and V); mature riverine mangroves or mixed mangroves (stands VI and VII); declining or dead mangroves (stand VIII) (Tables 1 and 2).

Pioneer and young mangroves (stands I, II: Cayenne, Marais Leblond; stand III: Sinnamary, Anse road)

Pioneer mangroves become established on the sea front after stabilisation of mud banks (stands I and II) or on the sandy offshore bar (stand III). They colonize the rather unstable marine clays that are regularly flooded by the tides. All these stands (Table 1) share a high density (reaching 41 111 trees ha^{-1}), limited height ($h < 8$ m) and a low average diameter (dbh < 5 cm).

Stand I has an almost single-species population of L. racemosa, with a few A. germinans. It presents a high level of structural homogeneity. The preponderance of a species gives rise to a high value of its importance value index ($I_v = 282$ for L. racemosa, Table 2). The high value of the complexity index ($I_c = 39$, Table 1) indicates especially the high density of the stand.

Stand II is situated 100 m inland from stand I. Its density is four-fold lower and the average diameter and height of the population are double those of stand I. L. racemosa remains dominant but A. germinans makes up 25% of the individuals and its relative dominance (34%) is considerably higher. This stand, less homogenous but still young (no large diameters), represents a further stage of maturation and precedes a formation in which A. germinans takes over from L. racemosa. Consequently, it must be considered as a young stand rather than a pioneer stand.

Stand III is dominated by A. germinans, still in association with L. racemosa. Isolated Rhizophora spp. individuals appear. The density is high and the diameters close to those of stand I. The five plots show greater structural diversity owing to the heterogeneity of the substrate where marine clays and coastal sands are interspersed.

The stands studied illustrate the two types of pioneer mangrove that are characteristic of Guiana, one of which is dominated by L. racemosa and the other by A. germinans. The process of establishment of each of these species seems to be the following. L. racemosa becomes rapidly established as soon as the muddy

Table 1 Structural characteristics of mangrove stages in French Guiana. Values are means $\pm$ SD for density (number of individuals per hectare), total basal area (sum of individual basal areas calculated per hectare) and stand height. Complexity index was calculated as follows: I_c: number of species $\times$ stand density $\times$ stand basal area $\times$ stand height $\times 10^{-5}$

Mangrove stages Type	Number (plot area)	Number of species	Density (n ha^{-1}) dbh < 10cm	Density (n ha^{-1}) dbh > 10cm	Total density (N ha^{-1})	Mean dbh (cm) dbh < 10cm	Total basal area (m^2 ha^{-1})	Mean dbh (cm) dbh > 10cm	Stand height (m)	Complexity index
Laguncularia pioneer stage	I 5 (3 m × 3 m)	2	41111	0	41111 ± 3928	2.1 ± 0.1	13.7 ± 0.5	–	3.5 ± 0.1	39
Laguncularia young stage	II 5 (3 m × 3 m)	2	11778	0	11944 ± 1064	4.7 ± 0.2	20.6 ± 2.8	–	7.7 ± 0.2	37
Avicennia pioneer stage	III 5 (3 × 3m)	3	31111	0	31111 ± 12669	2.4 ± 0.3	12.5 ± 4.2	–	2.8 ± 0.8	33
1 year regeneration	III'	3	281715	0	281715	–	–	–	0.4	–
Mature coastal mangrove (pure mangrove)	IV 3 (20 m × 20 m)	4	367	550	917 ± 29	6.2 ± 1.5	24.6 ± 1.3	23.6 ± 2.2	19.6 ± 1.4	18
	V 5 (20 m × 20 m)	3	338	450	780 ± 154	6.8 ± 0.8	33.6 ± 8.3	30.1 ± 0.3	22.7 ± 1.3	18
Adult riverine mangrove (mixed mangrove)	VI 5 (20 m × 20 m)	6	3090	220	3310 ± 1066	4.6 ± 0.6	24.0 ± 7.6	32.1 ± 0.8	23.0 ± 3.0	71
	VII 10 (15m × 10 m)	6	2667	380	3167 ± 2106	3.8 ± 1.0	17.8 ± 8.7	21.7 ± 0.6	19.1 ± 2.1	65
Senescent/dead mangrove ("cemetery")	VIII 3 (30 m × 30 m)	3	0	267	267 ± 64	0.0	18.5 ± 3.2	28.5 ± 0.3	–	–

Table 2 Structural characteristics of mangrove trees in French Guiana. The importance value (I_v) of a given species is the sum of the relative density, relative frequency and relative dominance of that species. These parameters were calculated using the standard methodology (Cintron and Schaeffer-Novelli 1984)

Mangrove stages		Specific density (n ha-1)	Relative density (%)	Relative frequency (%)	Relative dominance (%)	Importance value I_v
Types	Taxa					
Laguncularia pioneer stage	I					
	Laguncularia	40889	99.5	83.3	99.0	282
	Avicennia	222	0.5	16.7	1.0	18
Laguncularia young stage	II					
	Laguncularia	8889	75.5	55.6	66.1	197
	Avicennia	2889	24.5	44.4	33.9	103
Avicennia pioneer stage	III					
	Laguncularia	12667	40.7	41.7	29.3	112
	Avicennia	17333	55.7	41.7	68.8	166
	Rhizophora	1111	3.6	16.7	1.9	22
(Regeneration after clearcutting)	III′					
	Laguncularia	40278	14.1	36.4	–	–
	Avicennia	243333	85.4	36.4	–	–
	Rhizophora	1389	0.5	27.3	–	–
Mature coastal mangrove (pure mangrove)	IV					
	Laguncularia	125	13.6	18.2	0.6	32
	Avicennia	558	60.9	27.3	92.7	181
	Rhizophora	183	20.0	27.3	5.6	53
	Others	51	5.5	27.3	1.1	34
	V					
	Laguncularia	30	3.8	28.6	0.6	33
	Avicennia	115	14.7	35.7	73.5	124
	Rhizophora	635	81.4	35.7	25.9	143
Adult riverine mangrove (mixted mangrove)	VI					
	Laguncularia	1670	50.5	29.4	15.4	95
	Avicennia	1240	37.7	29.4	77.7	144
	Rhizophora	60	1.8	17.6	6.5	26
	Others	340	10.3	23.5	1.1	35
	VII					
	Avicennia	47	1.5	15.6	33.7	51
	Rhizophora	340	10.7	25.0	34.5	70
	Others	520	16.4	28.1	2.4	47
	Pterocarpus	2260	71.4	31.3	29.4	132
Senescent/dead mangrove ("cemetery")	VIII					
	Laguncularia	4	1.4	16.7	0.3	18
	Avicennia	218	81.7	50.0	98.4	230
	Rhizophora	15	5.6	16.7	1.3	24
	Acrostichum	30	11.2	16.7	–	–

deposits, even if they are still fluid, begin to emerge from the sea at low tide. Its system of growth by horizontal branching (Lescure 1977) enables it to cover the substrate efficiently. *A. germinans* seedlings, however, require a substratum that has already been consolidated by an overlaying deposit of sand or by the development of a *L. racemosa* pioneer stage. In the second case, the branching of *A. germinans* with its sub-apical growth units enables it to form an overstorey.

On stand III, a second structural study (III′) was carried out 1 year after the first total clearance-cut in order to estimate the biomass produced during that period. Observations showed that vegetation rapidly recolonized the site: density was high (282 000 trees ha^{-1}), due to sprouts and numerous seedlings. Mean height of the stand was low (0.4 m) and all diameters were smaller than 1 cm. The higher density of *Avicennia* compared to *Laguncularia* may be explained by a higher germination rate. Indeed, the environment protected by the neighbouring young mangrove provides unfavourable conditions for the development of heliophilous *Laguncularia* seedlings.

The Guianese coast has a particular sedimentary context owing to the transit of considerable masses of sediment coming from the Amazon (Guillobez 1980; Prost et al. 1994) which explains the large size of the banks formed often reaching widths of several hundred meters in build-up zones. In the portions of coast that are subject to erosion, the pioneer stages are absent and adult populations of *A. germinans* occupy the sea front directly.

Mature coastal mangroves or pure mangroves (stand IV: Sinnamary, Anse road; stand V: Cayenne, Marais Leblond)

This is the most frequent type of mangrove in Guiana. Its physiognomy is homogeneous and is dominated by

A. germinans. There are two strata in the stands studied: a high single-species stratum composed of *A. germinans* ($h = 20$ to 23 m) and a lower stratum of *A. germinans* and *Rhizophora* spp. ($h = 8–15$ m) in which *L. racemosa* and a few associated species (*Annona paludosa* Aubl., *Erythrina fusca* Lour.) are dispersed. Identical values of the complexity index ($I_c = 18$) indicate an overall homogeneous structure.

Stand V, further from the sea front, presents a higher basal area (33.6 m^2 ha^{-1}) and shows symptoms of *A. germinans* decline as it is an older mangrove stand than stand IV (24.6 m^2 ha^{-1}). It precedes evolution towards *Rhizophora* spp. domination, marking the preponderance of freshwater input (Cayenne river) over saltwater input. Dead standing *Laguncularia* individuals provide evidence of the previous pioneer stages of the mangrove stand.

Mature riverine mangroves or mixed mangroves (stand VI: Counamama river banks; stand VII: Sinnamary river banks)

On the banks of the rivers, the mangrove community becomes diversified on moving inland from the river mouth and the stands become richer in species that are linked to river dynamics rather than to tidal movement. Consequently, such stands can be considered as mixed mature mangroves. Two stands were studied in this environment: they presented a larger number of species (6) and a higher density than in the pure mangrove (> 3000 trees ha^{-1}) and a high complexity index (> 65).

Stand VI presented a low density of adult trees (220) and a high density of individuals with a small girth (3090). The latter develop in canopy openings with mainly *L. racemosa* (1670), *A. germinans* (1240) and *Muellera frutescens* Standl.. Here again, mangrove species are greatly predominant.

Stand VII is situated upstream on the river. *Pterocarpus officinalis* was the most abundant species (2260) and had a small diameter (81% had a diameter of < 5 cm). *Rhizophora* spp. (340) and *A. germinans* (47) were less frequent but occurred with larger diameters. The plots also presented numerous dead trunks of *A. germinans*. A tendency towards a marshy forest stand was very noticeable. This type of transition between a mangrove and a marshy forest can be found over the whole of the Guianese coastal plain, in particular along the larger rivers where the mangroves can become diversified with the occurrence of the palms *Euterpe oleracea* and *Mauritia flexuosa* L.

The declining and dead-standing mangrove forest or "cemetery stand" (stand VIII: Sinnamary Estuary)

In the sections of coastline subject to erosion, the mangroves disappear as the coast is pushed back. In areas of deposition, mangroves can also perish under the effect of over-sedimentation, the massive arrival of sediment suffocating the *A. germinans* pneumatophores in which gas exchanges can no longer take place (Blasco 1991; Fromard et al. 1996). The soil characteristics do not allow other species to become established except for a few *Rhizophora* spp. and the fern *Acrostichum aureum*. This trend towards dead mangroves, or "cemetery stand", is a characteristic feature of the Guianese coast, in particular near river mouths where sedimentation occurs most actively. The structural features of the cemetery stands are important for understanding the coastal dynamics. In the three plots described, all the *Avicennia* present were dead. Their mean diameters were relatively large (28.5 cm) and the density of the residual standing trees was low (267). Numerous uprooted and lying trunks were evidence of the on-going stand decay. No regeneration occurs in this environment.

Individual biomass values

The individual biomasses used to establish the regression laws (felled individuals) are reported in Table 3. The leaf mass varied from 1.4 to 18.7% of the total above-ground biomass depending on the species and the trunk diameter. The highest percentages were found in slender *Avicennia*. For *Laguncularia*, the proportion was between 10 and 14% for the small trunk diameters (dbh < 4 cm) and lower than 7% for the others. For *Rhizophora*, the values were about 10% leaf mass for small diameters and on average 2% for diameters greater than 20 cm.

Among the woody biomass, branches and trunks were considered separately:

1. In *A. germinans*, the distribution (of the proportions of branch mass) was homogeneous in the small-diameter plants (21–29% of the biomass as branches) and irregular for the larger diameters: note that breakage of tree crowns and branches is very frequent in adult *Avicennia*.

2. In *L. racemosa*, the proportions of branch mass in the total above-ground biomass were more regular (20–23% for the small diameters, 9–17% for diameters greater than 4 cm) illustrating the high degree of homogeneity of the stands composed of this species.

3. In *Rhizophora* spp. it can be seen, firstly, that the branch mass of a tree can be greater than its trunk mass and, secondly, that the mass of the prop roots can represent more than 30% of the total above-ground biomass of an individual.

Some other data of this type have been reported in the literature but are often incomplete as far as the structure of the stands is concerned. Golley et al. (1962) gave 12% dry leaf biomass for *R. mangle* ($h = 8$ m) and 1.3% for *R. brevistyla* ($h = 35$ m). Woodroffe (1985) reported different values for *A. marina* 20–58% of leaf biomass for young individuals ($h < 2.5$ m). Christensen (1978) showed that in a stand of *R. apiculata* in Malaysia, the prop roots constituted up to 39% of the total

Table 3 Characteristics of individual trees in biomass calculations. N_i is the number of individuals per diameter class. *Mean dbh* is the diameter at breast-height (or half-height for individuals under 2 m tall)

Species	N_i	Dbh (cm)	Actual above-ground biomass (kg dry wt)	Leaf biomass (% of total biomass)	Branch biomass (% of total biomass)
Avicennia	18	1.5 ± 0.2	0.5 ± 0.3	18.7	29.5
germinans	16	2.5 ± 0.3	1.2 ± 0.6	12.3	20.7
$1 < \text{dbh} < 4$	11	3.5 ± 0.2	2.8 ± 0.8	9.1	21.5
($n = 45$)					
Avicennia	8	4.5 ± 0.2	5.7 ± 2.1	10.3	23.6
germinans	3	5.5 ± 0.2	9.3 ± 3.2	9.7	14.7
dbh > 4	3	6.5 ± 0.2	11.3 ± 5.1	7.7	35.6
($n = 25$)	1	8.0	18.3	13.9	34.1
	1	9.0	40.9	9.8	24.7
	1	11.0	54.2	8.9	
	1	13.0	71.8	5.3	9.2
	1	15.5	87.6	3.1	14.7
	2	19.7	197.4 ± 8.7	4.6	20.3
	1	21.0	232.9	1.6	4.3
	1	25.4	411.0	5.2	20,0
	1	32.3	852.0	1.9	14.7
	1	42.0	1543.7	3.0	31.5
Laguncularia	25	1.5 ± 0.3	0.3 ± 0.1	13.8	23.2
racemosa	19	2.4 ± 0.3	0.9 ± 0.3	10.7	20.4
($n = 70$)	11	3.3 ± 0.3	1.9 ± 0.7	10.3	20.5
	6	4.5 ± 0.2	4.7 ± 0.8	7.3	14.0
	3	5.2 ± 0.2	7.3 ± 0.6	6.8	17.9
	2	6.3 ± 0.5	10.4 ± 0.9	4.6	8.8
	2	7.2 ± 0.3	17.1 ± 2.8	4.6	11.7
	1	8.1	22.1	4.6	16.7
	1	9.6	27.6	2.3	16.2
Rhizophora	4	1.3 ± 0.3	0.3 ± 0.2	9.7	51.1
spp.	1	3.1	0.5	11.2	43.9
($n = 9$)	1	4.8	9.8	7.6	11.8
	1	9.2	96.6	10.3	42.4
	1	23.3	466.9	3.4	25.5
	1	32.0	1036.6	1.4	38.1

above-ground biomass but that these percentages vary enormously with the type of mangrove considered.

Stand biomass values

Plots of individual biomass versus diameter for *A. germinans*, *L. racemosa* and *Rhizophora* spp. are shown in Fig. 1, with their respective regression lines and the corresponding regression equations. Stand biomass values are reported in Table 4.

For *A. germinans*, it appeared from the structural analysis that pioneer and adult individuals form distinct populations only occurring together as dead fallen trees in old mangrove stages. It can therefore be considered that they each belong to different "functional groups". Two separate regressions were then established depending on the diameters: smaller than 4 cm ($n = 45$) and greater than 4 cm ($n = 25$), this threshold value giving the best adjustments for our correlations.

For *L. racemosa*, all the data ($n = 70$) were considered together, the diameter classes represented in the sample belonging to the same stage (pioneer to young mang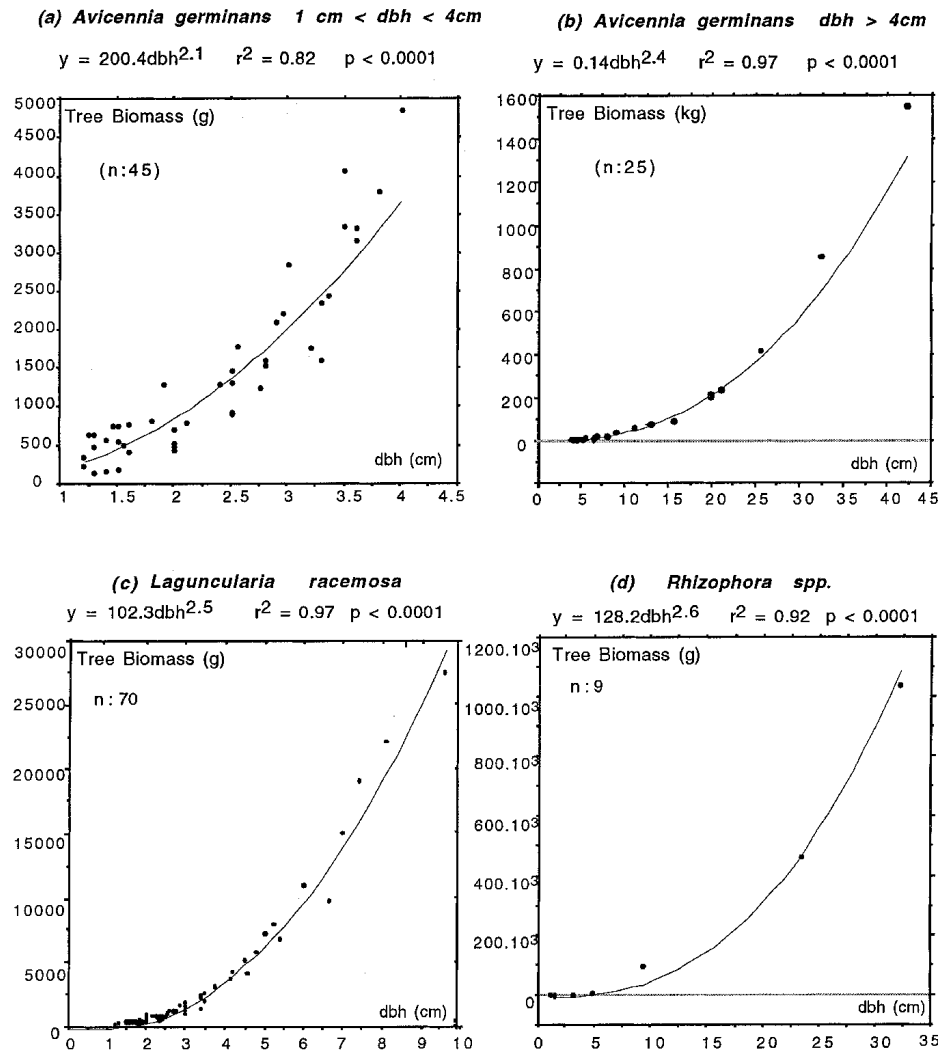rove). It was also checked that dividing the sample into two sub-groups did not cause any great modification of the adjustments.

For *Rhizophora*, the correlation that was established was based on nine individuals. A larger sample, in particular for trees of larger diameters, would be necessary for this relationship to be validated.

The pioneer and young stands (I, II, III)

The pioneer mangrove stands with *L. racemosa* (I) or *A. germinans* (III) dominating presented the lowest biomass values (31.5 ± 2.9 and 35.1 ± 14.5 t ha^{-1}). The greater heterogeneity in stand III can be attributed to the mixture of species (4–49% *L. racemosa*), whereas the five plots at stand I had only a single species. Stand II (young stand), with a basal area and a mean height twice that of stand I, also had double the biomass (71.9 ± 17.7 t ha^{-1}) and similar values for all plots. Compared to stand I we can also note the development of *A. germinans* (42.8% of the biomass) and the decrease of *L. racemosa* (57.2%) which is typical of the more mature character of the stand as already demonstrated by the structural study.

Fig. 1 Allometric relationships between diameter at breast height (dbh) and total above-ground biomass (y) according to the equation $y = a_0 \cdot dbh^{a_1}$ r^2 = square of correlation coefficient, P = level of significance, n = sample size

(a) Avicennia germinans   1 cm < dbh < 4cm

$y = 200.4dbh^{2.1}$ $r^2 = 0.82$ $p < 0.0001$

(b) Avicennia germinans   dbh > 4cm

$y = 0.14dbh^{2.4}$ $r^2 = 0.97$ $p < 0.0001$

(c) Laguncularia   racemosa

$y = 102.3dbh^{2.5}$ $r^2 = 0.97$ $p < 0.0001$

(d)   Rhizophora spp.

$y = 128.2dbh^{2.6}$ $r^2 = 0.92$ $p < 0.0001$

The leaf biomass represented between 6 and 10% of the total above-ground biomass. The distribution by species shows that *L. racemosa* contributed most to the biomass in stands I and II. *A. germinans* was the dominant element in stand III in terms of biomass, confirming the existence of two types of pioneer mangrove in Guiana.

Mature coastal mangroves (stands IV and V)

For the two stands analysed there are two very different values for the total biomass: 180 (stand IV) and 315 t ha^{-1} (stand V), with a fairly constant proportion of leaf mass (about 3% of the total).

Greater participation of *Rhizophora* in stand V (23% of the total biomass), and especially a higher total basal area than in stand IV (older stand), explains the large above-ground biomass in this stand: the largest of the whole study.

Mature riverine mangroves (stands VI and VII)

The biomass recorded was very similar in these two stands in spite of the different species composition: *A. germinans* made up 90% of the biomass in stand VI, whereas *Rhizophora* predominated (52%) in stand VII. It should be noted, however, that only mangrove trees (*Avicennia, Rhizophora, Laguncularia*) were taken into account in these calculations. The biomass of *Pterocarpus officinalis* was not evaluated, nor was that of the various other species in these stands.

The biomass values reported are thus clearly underestimated here, and, more than in the raw data, it is the great variability between the plots that is remarkable, illustrating the structural heterogeneity of this forest type.

Declining-to-dead mangrove (stand VIII)

The plots were inventoried on the basis of trunks still standing but most often dead. The regression used here

Table 4 Computed biomass of mangrove stages in French guiana according to the selected equations. Values are means ± SD for partial and total above-ground biomass

Mangrove	Pioneer and young stages			One-year-old regeneration	Mature coastal mangrove		Mature riverine mangrove		Senescent/dead mangrove
Biomass (t ha⁻¹ dry wt) Stands	I	II	III	III'	IV	V	VI	VII	VIII
Leaves	2.8±0.1	4.3±1.0	3.6±1.4	1.2±0.7	5.9±0.1	7.4±0.9	5.3±1.7	3.4±1.8	
Branches	5.4±0.3	10.8±3.4	7.0±2.8	3.0±2.2	30.0±0.9	58.4±4.7	29.7±13.0	28.3±16.2	
Trunks	23.7±2.3	53.9±12.1	24.0±9.8		142.2±5.8	249.2±40.8	157.0±68.4	81.0±63.2	
Total	**31.5±2.9**	**71.8±17.7**	**35.1±14.5**	**4.2±2.9**	**180.0±4.4**	**315.0±39.0**	**188.6±80.0**	**122.2±76.4**	**143.2±15.5**
Leaf biomass (as % of total biomass)	9.1	6.0	10.2	28.6	3.3	2.4	2.8	2.8	0.1
Specific biomass (as % of total biomass)									
A. germinans	1.2	42.8	74.6	83.2	96.6	76.0	90.7	47.9	98.2
L. racemosa	98.8	57.2	23.3	15.6	0.2	0.2	7.1	0.0	0.2
Rhizophora spp.	0.0	0.0	2.1	1.2	3.2	23.1	2.2	52.1	1.6

(a_0: 0.07 and a_1: 2.95) is that calculated from the biomass of the *Avicennia* trunks alone, the actual value being even lower if the high proportion of broken trunks is considered.

The declining-to-dead mangrove still represents a woody biomass of 143 t ha⁻¹ in the stands where it was studied. This biomass is either exported towards the ocean under the action of the tides or buried where it falls in sediment if the silting phase persists.

Discussion

The data presented in this study can be discussed following two complementary approaches:

1. The biomass values reported here are, to our knowledge, the first data ever published for South America. They can be discussed in comparison to similar data for other regions, complementing earlier reviews, particularly that of Saenger and Snedaker (1993).

2. The mangrove forest is certainly one of the most dynamic ecosystems among tropical forests. In the Guianese mangrove, particular sedimentary conditions (Prost 1990) causes coastal instability leading to fast changes in the associated coastal ecosystems It is therefore important to include the identified stages, with their structural features and biomass data, in any model of overall development and also to study the transformations between these stages.

Both these points will be discussed.

Biomass values

In agreement with the general model established for all terrestrial ecosystems, Saenger and Snedaker (1993) showed the occurrence, for mangroves, of a decrease in biomass values at high latitudes: in the absence of any particular ecological constraint, a mature stand of mangroves in an equatorial region develops a significantly greater biomass than at the northern or southern limits of its range.

Table 5 gathers the data from these authors concerning: firstly, the Asian and Australian mangrove populations (the data chosen are those that also give information on the structure of the stands studied); secondly, the Western mangrove populations (all the data reported for this region are gathered here).

It can be seen that the highest values for biomass occurred in Asia in mature stands of *Brugueria gymnorrhiza* (406.6 t ha⁻¹) and *Rhizophora apiculata* (436.4 to 460 t ha⁻¹; Komiyama et al. 1988; Putz and Chan 1986). The lowest values are for shrubby *R. mangle* (7.9 t ha⁻¹; Lugo and Snedaker 1974) and *A. marina* (6.8 t ha⁻¹; Woodroffe 1985) stands, young plantations of *B. gymnorrhiza* (5.8 t ha⁻¹, Choudhuri 1991) and pioneer *L. racemosa* stands.

In these data, large differences can be noted, even for populations that have a comparable floristic composi-

Table 5 Above-ground biomass in mangrove forests, bibliographic data. Latitude of studied sites, height, stand density and sampled areas are provided (major species are: *Av g. Avicennia germinans, Av. m. Av. marina, Br Bruguiera gymnorrhiza, C.t. Ceriops tagal, La. r. Laguncularia racemosa, Rh. a. Rhizophora apiculata, Rh. b. R. brevistyla, Rh. m. R. mangle, Rh.mu. R. mucronata, Rh. r. R. racemosa, So. Sonneratia spp.*)

Latitude (°)	Height (m)	Density (n ha^{-1})	Sampled area (m^2)	Major species	Locality	Total above-ground biomass (t ha^{-1})	Leaf biomass (t ha^{-1})	Leaf biomass (%)	Authors
Asian and Australian area									
1.2	21.3			*So*	Indonesia	356.8			Komiyama et al. 1988
1.2	22.3			*Rh. a.*	"	178.2			"
1.2	22.4			*Rh. a.*	"	436.4			"
1.2	15.5			*Rh. a.*	"	299.1			"
1.2	26.4			*Br*	"	406.6			"
4.5			4800	*Rh. a.*	Malaya	460.0			Putz & Chan 1986
5	15			*Rh. a.*	"	147.0			Ong et al. 1981
5	15			*Rh. a.*	"	314.0			"
8	11		25	*Rh. a.*	Thailand	159.1	7.4	4.7	Christensen 1978
8.2	3.9			*Rh*	Sri Lanka	71.0			Amarasinghe et al. 1992
8.2	7.2			*Rh*	"	240.0			"
8.2	10.3			*Rh*	"	193.0			"
12	12.5		500	*Rh.mu. & a.*	Andaman Isl.	124.0	6.6	5.3	Mall et al. 1991
12	22.5		500	*Br.g. & C.t.*	Andaman Isl.	214.0	10.3	4.8	"
21	5.2	13000	400	*Av. spp.*	India	101.9	11.0	10.8	Choudhuri 1991
21	5.4	10800	200	*Av. spp.*	"	118.7	6.03	5.1	"
21	1.2	12300	100	*Br.g.*	"	5.8	0.62	10.7	"
24	5.5		100	*Rh. mu.*	Japan	108.1	6.3	5.8	Suzuki et al. 1983
27.2	16.4			*Av. m.*	Australia	341.0			Mackey 1993
33.5	7	463		*Av. m.*	Australia	220.8	13.5	6.1	Briggs 1977
37	0.4	16000		*Av. m.*	New Zealand	6.8			Woodroffe 1985
37	2.7	3350		*Av. m.*	"	104.1			"
Atlantic area									
5	3.5	41000	45	*La. r.*	Fr. Guiana	31.5	2.9	9.1	This study (pioneer stage)
5	22.7	788	2000	*Av.g.*	Fr.Guiana	315.0	7.5	2.4	This study (mature stage)
8.5	38	712	2500	*Rh.b.*	Panama	279.2	3.6	1.3	Golley et al. 1975
14	10.6	3000	1200	*Rh.r.*	Senegal	60.0	6.7	11.2	Doyen 1986
16	13		3700	*Rh.m.*	Guadeloupe	98.6	6.0	6.1	Imbert & Rollet 1989
16			75	*Rh.m.*	"	152.3			"
16			500	*Av.g.*	"	52.8			"
18	7.5	1100		*Rh.m.*	Pto Rico	62.9	7.8	12,4	Golley et al. 1962
26	1			*Rh.m.*	Florida	7.9	0.7	9,0	Lugo and Snedaker 1974
26	6.3		25	*Rh.m.*	"	124.6	7.2	5,8	"
26	6.3		25	*La. r.*	"	8.2	2.2	27,1	"
27.3	7.4		"	*La. r.*	"	164.0			Lahmann 1988

tion. Thus, for two stands of Indonesian *R. apiculata* of the same height (22 m), Komiyama et al. (1988) obtained biomass values of 178.2 and 436.4 t ha^{-1}. Likewise, Ong et al. (1981) reported, for two Malaysian populations of *R. apiculata* ($h = 15$ m), values of 147 and 314 t ha^{-1}. These results can be compared to those obtained in the present study for the mature coastal mangroves: for stands of similar height but different basal area, the calculated biomass values were 180 and 315 t ha^{-1}.

These observations clearly show that it is necessary to know all the structural characteristics of a stand to be able to compare the values of their corresponding biomasses, the basal area in particular seems to be the essential parameter to take into account. As for the structural indices used (I_v and I_c), they are not correlated with the biomass values obtained.

Certain, particularly low, biomass values can be viewed directly with respect to ecological factors that limit mangrove development:

1. The occurrence of hurricanes can explain the low biomass found for certain stands in Florida and Guadeloupe (Lugo and Snedaker 1974; Imbert and Rollet 1989), in which the mangroves rarely reach their maximum height.

2. The mangroves situated at higher latitudes, under the temperate climate of Japan (Suzuki and Tagawa 1983), New Zealand (Woodroffe 1985) and Australia (Briggs 1977) are among the low-biomass stands. Temperature (annual mean and range) is the limiting factor here. In other climatic regions, with low annual rainfall (800–1000 mm) and a well-marked dry season, the expansion of mangroves is also restricted and the biomass values are low (Senegalese *R. racemosa*, Doyen 1986).

3. When the overall climatic conditions are favourable, other features particular to one site can limit the growth of the mangroves, especially excess salinity. The biomass values of these shrubby stands are then very low.

If we consider the maximum values obtained here (stand V: 315 t ha^{-1}), the mature Guianese mangroves are included among the mangroves with a high biomass, lower however than the mangroves of Asia. These values indicate the absence of any ecological factor that would be limiting for their development (no climatic stress or hurricanes). Moreover, leaf biomass, expressed as a percentage of total biomass, is much lower in Guiana than elsewhere. The somewhat scruffy appearance of adult *Avicennia* with their often defoliated crowns could partly explain this result.

Lescure et al. (1983) established, for the Guianese rain forest, using a relationship of the same type as that used here for the mangrove forest, total biomass values of between 270 and 440 t ha^{-1}, also illustrating the variability of the results related to the "structural and architectural variability of the forest". Brown et al. (1989) gave, for various tropical forests, values falling between 205 (Sri Lanka) and 391 t ha^{-1} (Malaysia).

These data are comparable to the values found for the Guianese mangrove. In general, the data published are still too fragmented to allow precise correlations to be established for the production and primary productivity of mangroves. Moreover, sampling difficulties will not allow the multiplication of sampling sites (our own measurements correspond to the quantitative analysis of 1 ha of mangrove, i.e. 1.5/10 000 of the surface area of mangrove in Guiana).

Studies into the use of optical and radar satellite data are underway for the characterisation of the Guianese mangroves (Proisy et al. 1996; Mougin et al. in press); in the long term, they should make it possible to spread the biomass data over significant areas. Correlated with the productivity data which are in the process of being obtained at the same sites, the overall results should enable a quantification to be made of not only the total biomass of these stands, but also the exportable biomass (leaf biomass) potentially usable by the coastal marine environment.

Structure, biomass and evolution of stands

Correlation analyses between structural parameters and total biomass (Fig. 2) point out the arrangement of stages according to their degree of maturity and thus to the mean age of the individuals. Pioneer and young stages on the one hand and adult stages on the other hand correspond to two distinct groups of points.

Stands I and III show similar structural and biomass values, except for total densities, therefore their representative points overlap each other. Stand II (young stand) directly results from the maturation of stand I. It is characterized by an increase in all the values of structural parameters and biomass. The decline of the pioneer species (*L. racemosa*) and the concomitant development of a 'building' species (*A. germinans*) is also an indication of the dynamics of this stand.

Stand III′, 1-year-old regeneration, is not a natural pioneer stage. Analysis indicates that density is the most discriminating factor for the early development stages. It is clear that the one-year-old stand develops by decreasing the number of individuals (high mortality of seedlings), following a process not yet described. As well as intra- and inter- specific competition, seedling predators, particularly crabs, certainly play an important role in this process (MacGuiness 1997).

Our observations indicate that 2–3 years are probably sufficient for a pioneer mangrove to totally colonize a mudbank. Stands I and III, described above, can thus be considered of the same age, that is 3–4 years old. Stand II is probably 5–6 years old. However, additional observations are still necessary to estimate the rates of colonization processes.

Among the adult mangrove forests, stand V can be distinguished from the three others by all the parameters considered. This stand displays the largest diameters (*A. germinans*, 90 cm) and the tallest trees (30 m). Lo-

Fig. 2 a–e Relationships between total biomass and main structural parameters of mangrove stages
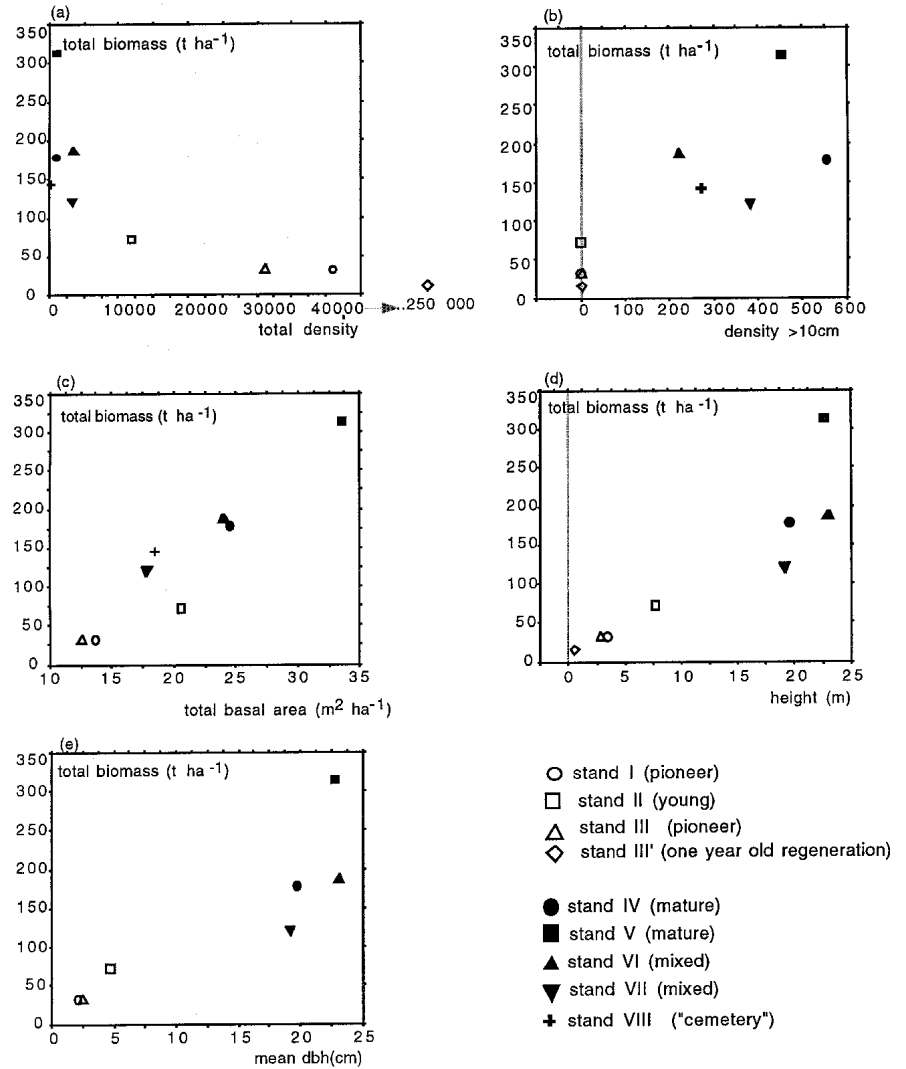
cated at a farther distance from the sea front, it probably corresponds to an older sedimentation phase.

Stands IV, VI and VII, which have globally similar structures, are represented by close points on the different graphs. Stand VII nevertheless slightly differs from the others by a lower biomass. The presence of dead standing trunks of *Avicennia* and numerous *Pterocarpus officinalis* indicates a trend towards marshy forest in this mixed stand.

According to local accounts and to Lointier (1990), this latter stand is located on a site which was under the sea about 60 years ago. This gives an indication of the maximum age for this stand. Presently, we do not have any data allowing its age to be precisely determined. By analogy with similar stands in Guiana, the age of stand IV is roughly estimated to be about 50 years; stand V, noticeably older is considered to be 60–70 years old.

We have no indication for the "cemetery" stand (VIII) of either its age or the rate of its decline. In view of its geomorphological and structural features, it must be the oldest studied here and thus approximately 80 years old.

From the above considerations, it emerges that the most relevant parameters for describing the mangrove dynamics, as well as total standing biomass, are: (1) the distance between the seafront and the stands and (2) stand density. Figure 3 illustrates the correlation between biomass and distance and provides the bases of an evolutionary model:

1. Trajectory 1 corresponds to the simplest scenario: the pioneer stage (stands I or III) develops towards young (II) and mature (IV, V) stages. Progressively, the oldest stands undergo less influence from the tides with the successive sedimentation phases and the establishment of new mangrove stands at the seafront. In this way, a zonation in vegetation arises. The final stage, at the back of the mangrove, may be a savannah on which standing dead trunks of *A. germinans* can persist. However, the natural evolution is often disturbed by anthropic activities, as can be seen, for instance, in the areas around the cities of Kourou and Cayenne.

2. Trajectories 2 and 2′ illustrate the evolution from mangrove towards marshy forest that can be observed in
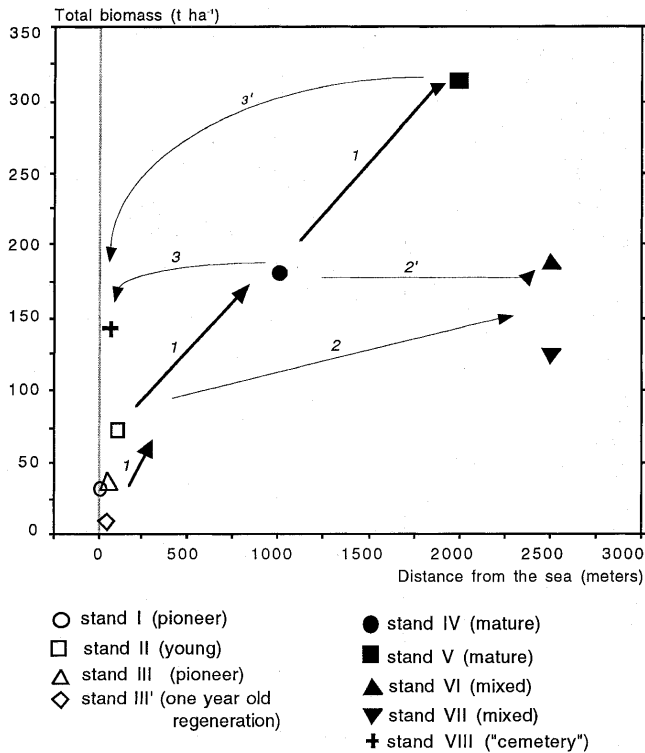
Fig. 3 Sketch of development for mangrove stages according to biomass and distance from the sea front

the vicinity of a large river when sedimentary conditions are favourable.

3. Trajectories 3 and 3′ correspond to an evolution towards "mangrove cemeteries", according to the process previously described. The cemeteries are, in Guiana, always located at the sea front.

Adding intermediate stages to our samples, particularly between young and mature phases, would improve the understanding of the overall mangrove dynamics. However, the data available allow us to test a model of vegetation dynamics that has never been used for a tropical ecosystem: the "self-thinning rule".

Originally developed by Tadaki and Shidei (1959) and Yoda et al. (1963) and recently modified by White (1981) and Westoby (1984), this model has been up to now applied to vegetation types in temperate and cold regions (Hara 1984; Schulze 1995). Under natural dynamics, this model states that stand biomass and stand density are related as:

$$\log (\text{biomass}) = \log C - 0.5 \log (\text{density})$$

where C is a constant. When the other parameters are expressed in grams and in number per square meter, the value of $\log C$ is between 3.5 and 4.4 for forest stands.

In this model, the parameters are not expressed as a function of time; hence, it can be used on different time scales, for herbaceous as well as woody stands. It can also be used when the age of stands is unknown, as in the present case. An other interesting point is that this model has been verified for numerous single species

stands as well as for mixed stands when they are considered as a whole (White 1981; Westoby 1984). Accordingly, it can be tested with mangrove data.

Results are given in Fig. 4a,b. Figure 4a shows the nine stands, whereas in Fig. 4b, two rather particular stands are removed: III′ (regeneration after clearcutting) and VIII (cemetery). In both cases (a and b), the equations derived are close to the theoretical one: experimental slopes are 0.53 and 0.54 respectively against 0.50 for the model. The values of $\log C$ are 3.74 and 3.85 respectively, within the predicted range (3.5–4.4). As expected, the correlation is better for the second case (r^2: 0.93).

Due to its structural simplicity, i.e. a few species and development through successive stages leading to even-age stands, the mangrove forest can be described by this model, and it is likely that this ecosystem is the only tropical forest to which the self-thinning rule can be applied.

The validity and the biological significance of this model have been discussed by many authors (see White 1981; Westoby 1984) and will not be detailed in the present study, but a more complete analysis will be given in a forthcoming paper. The "self-thinning rule", relating tree density and stand biomass, describes how a homogeneous stand is regulated by mortality on the basis of a given threshold of overcrowding. This regulation takes into account phenomena both related to population dynamics (e.g. mortality, competition) and ecosystem functioning (e.g. biomass increase, growth, nutrient cycles).
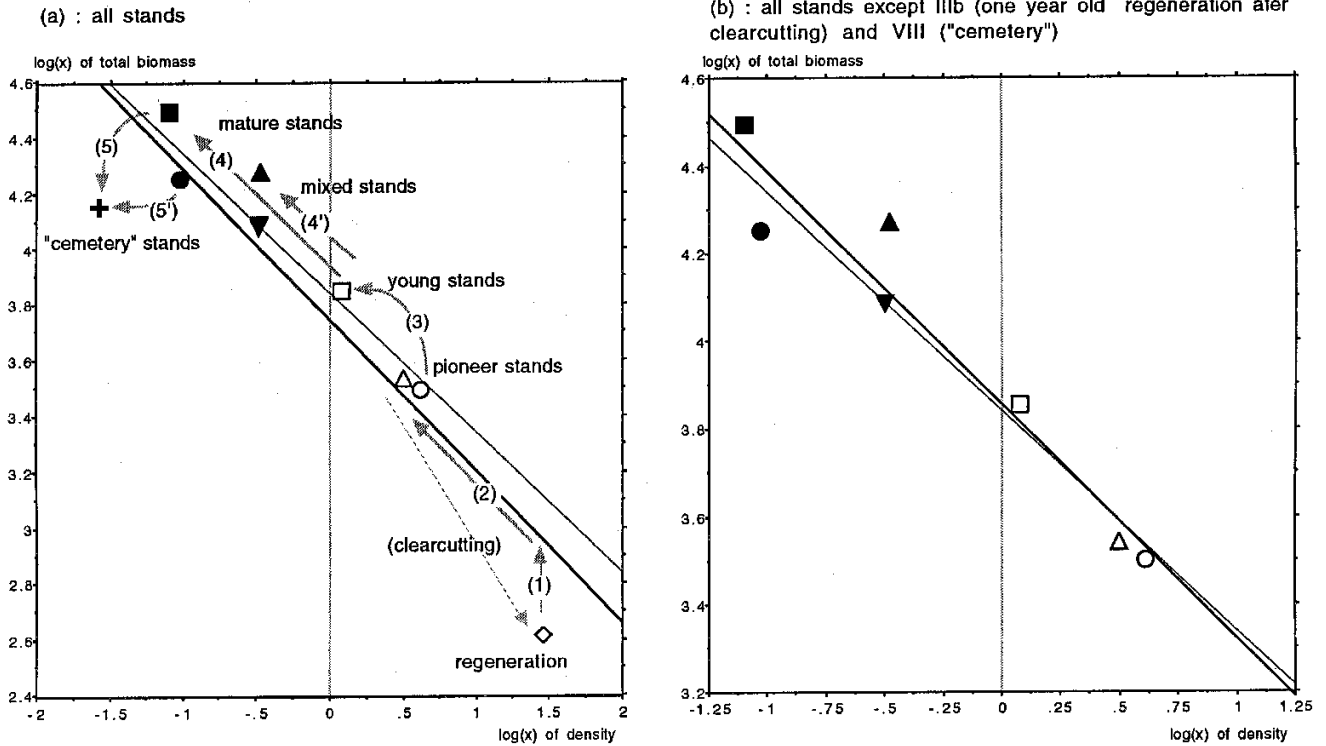
Here, the good fit of our data to the model confirms that the stands studied can be considered as different stages of the same ecosystem and also that the density level reached by each of them corresponds to an equilibrium state from the trophic and structural points of view. The two points which depart slightly from the model (Fig. 4a) represent two stands which are not in equilibrium:

1. Stand III′ (1-year-old regeneration after clearcutting): its position suggests a phase of increasing biomass (growth of existing individuals) up to a level given by the model (trajectory 1), followed by a decrease of density (through mortality) and a slower increase of the standing biomass (development of remaining individuals) up to a type close to the pioneer stage (trajectory 2). Then, there is a return to the natural development described previously (trajectory 3): the pioneer stage (I or III) evolves towards a young stage (II) through both a decrease in density (death of young individuals by competition) and an increase in biomass of the remaining individuals (growth in height and diameter).

2. Stand VIII ("cemetery"): it can derive from any adult mangrove stand described (trajectory 5 or 5′), by a decrease in density (death of individuals) and in standing biomass (broken trees, without foliage and twigs).

The model also indicates how a young stand develops to a pure or mixed adult stand (trajectories 4 and 4′).

Theoretically, homogeneous stands cannot be located above the line given by the model: for a given density,

(a) : all stands

log(x) of total biomass

mature stands

(5) (4)

mixed stands

(5')

"cemetery" stands

young stands

(3)

pioneer stands

(2)

(clearcutting)

(1)

regeneration

log(x) of density

log(biomass) = -0.54 log(density) + 3.74

r^2 = 0.83   p = 0.0006   n = 9

(b) : all stands except IIIb (one year old regeneration afer clearcutting) and VIII ("cemetery")

log(x) of total biomass

log(x) of density

log(biomass) = -0.53 log(density) + 3.85

r^2 = 0.93   p = 0.0004   n = 7

○ stand I (pioneer)   □ stand II (young)
△ stand III (pioneer)   ◇ stand III' (one year old regeneration)
● stand IV (mature)   ■ stand V (mature)
▲ stand VI (mixed)   ▼ stand VII (mixed)
✚ stand VIII ("cemetery")

linear regressions (experimental points)

theoretical thinning rule (from Westoby, 1984):
log(biomass) = - 0.5 log(density) + logC

arrows indicate the   trajectories
that stands can follow

Fig. 4 Logarithmic relationships between total above-ground biomass (gm^{-2}) and stand density (number m^{-2}). Experimental linear regressions and theoretical self-thinning rule (from Westoby 1984)

any point on the line corresponds to a given biomass value. Nevertheless, this density can be exceeded, particularly when regeneration occurs under an adult stand, leading to an increase in density without any significant increase in biomass (Westoby 1984). This is the case of stand VI, located slightly above the theoretical line: a new population of individuals with small diameters (see Table 1) occurs in the understorey of the adult forest. Conversely, the occurrence of gaps in an adult stand would lead to a sudden decrease in biomass. Such a stand would be located under the theoretical line.

Jimenez and Lugo (1985) proposed a general evolutionary model for mangrove forests relating age and stand density. This model is displayed in Fig. 5, together with the location of stands studied based on actual densities and estimated ages. Overall, there is a good

agreement between our data and the four stages identified by the authors:

1. The initial colonization phase occurring on a mudbank is not reported here. However, stand III' is close to this type. Its density is high but less than that reported by Jimenez and Lugo (140–330 individuals per square meter for *A. germinans*). This first phase occurs rapidly and is favoured by the arrival of large numbers of propagules carried by the tides.

2. During the early development stage, competition is high as is growth in diameter and height. In agreement with Lugo et al. (1980), the mortality recorded for an increase of 1 cm in diameter is much higher during the early stage than in the following stages. The self-thinning process plays an important role here. In Guiana competition between *Laguncularia* and *Avicennia* occurs during this stage, leading to the removal of the pioneer species in adult stands.

3. The mature phase corresponds to a decrease in competition, growth, and mortality. At this stage, the
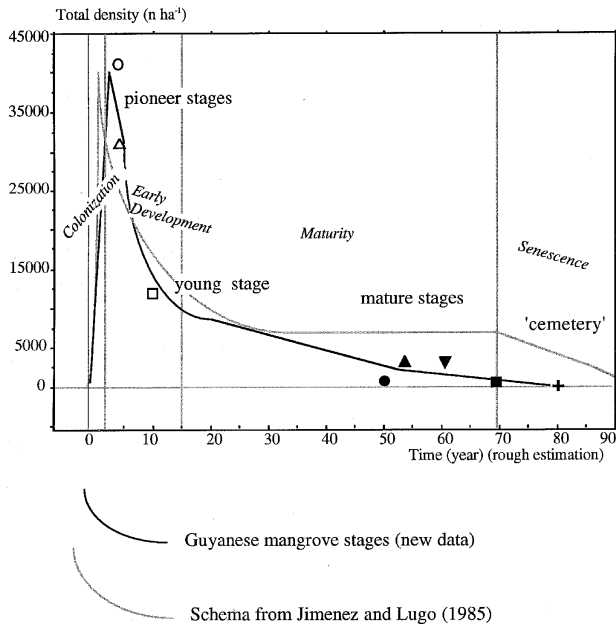
Fig. 5 Schematic correlation between time and stem density from pioneer to senescent mangrove stages (from Jimenez and Lugo 1985)

mangrove can develop in different ways depending on the geomorphological characteristics. For instance, the mangrove forest can evolve towards a marshy forest.

4. Finally, the senescence phase corresponds to the drying of the tops of *Avicennia*, an increase in gap occurrence and the development of species like the fern *Acrostichum aureum* and various epiphytes (*Bromeliaceae, Araceae*). The appearance of "cemeteries" is due to a high mortality in adult stands due to massive arrival of fresh sediment. At this stage, new and fast colonization can occur when the conditions become favourable again. A pioneer mangrove stand (*Laguncularia racemosa*) then develops around standing dead trees, the two extreme stages being encountered at the same time.

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