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The Structure and Function of Dry Weather Mangroves on the Pacific Coast of Central America, with Emphasis on *Avicennia bicolor* Forests

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ABSTRACT: Mangrove forests along the Pacific Coast of Central America cover around 4,000 km². Most of this coast is occupied with tropical dry forest mangroves where basal areas range between 6 and 20 m² ha⁻¹ and canopy heights rarely exceed 20 m. Rainfall and runoff alter structure and floristic composition from site to site. Reproductive phenology and mortality appear to be related to soil water availability. *Avicennia bicolor* forests reach a density of 4,350 plants that are taller than 0.50 m ha⁻¹, with 769 trees above 5 cm diameter at breast height. A total basal area of 41 m² ha⁻¹ together with a canopy height of about 23 m place these forests among the most developed in the western hemisphere. Growth rate (0.38 m² ha⁻¹ yr⁻¹) is surprisingly high for mangrove forests under a seasonal dry climate.

Introduction

Covering over 4,000 km², mangrove forests are probably the most important coastal ecosystem along the Pacific Coast of Central America. This region contains highly diverse and structurally developed mangrove forests. This forest complexity is chiefly the result of the climatic and hydrological conditions occurring along the coast (Jiménez and Soto 1985) and the biogeographic history of the region (Gentry 1982; Jiménez 1984).

Studies dealing with the structure and function of mangrove forests in this particular area are limited. Most of the available information regarding structural characteristics is found in Golley et al. (1969), Pool et al. (1977), Godoy (1980), Soto and Jiménez (1982), Jiménez and Soto (1985), Jiménez (1988a), Jiménez (1988b), and the references included therein.

The most important mangrove sites on the Pacific Coast of Central America are shown in Fig. 1. The larger areas are found on protected coasts, where terrigenous sedimentation is very active and runoff provides, at least seasonally, abundant freshwater. The large tidal amplitude (2–5 m) along this coast enhances the semidiurnal inundation of the littoral zone, where six nuclear and over 40 associated species grow under three different life zones (*sensu* Holdridge 1982).

Mangrove coverage estimations for each country on the Pacific Coast of the isthmus are presented in Table 1. They have been obtained from the Forestry Divisions in each country. Among these sites, the larger structural development is observed in the southern section of the Pacific Coast of Costa Rica, and the extensive mangrove areas of the rainy Panamanian littoral zone. Basal area estimations for mangroves under high precipitation (over 1,800 mm yr⁻¹) vary between 20 and 30 m² ha⁻¹, with canopy heights exceeding 35 m in many areas (Jiménez and Soto 1985). Floristic composition attains the highest diversity in these rainy areas where *Pelliciera rhizophorae* Tr. & Pl. and *Rhizophora racemosa* Meyer are the most important species in terms of frequency and size (Jiménez 1987; Jiménez, 1988b).

North of the Gulf of Nicoya, in Costa Rica, lowland climates show a significant reduction in rainfall, with precipitation below 1,800 mm yr⁻¹, mostly distributed between May and November. As a result of this climatic pattern, soil salinities in the forest increase inland where the amount and frequency of tidal flooding are reduced and salt accumulation increases through evapotranspiration. These dry climate mangroves show, on the average, less structural development than mangrove forests in the rainy sections of the coast. Basal areas range from 4 to 30 m² ha⁻¹, with canopies rarely exceeding 20 m in height (Jiménez and Soto 1985).

One striking characteristic of dry climate mangroves is the high variability in structural and func-

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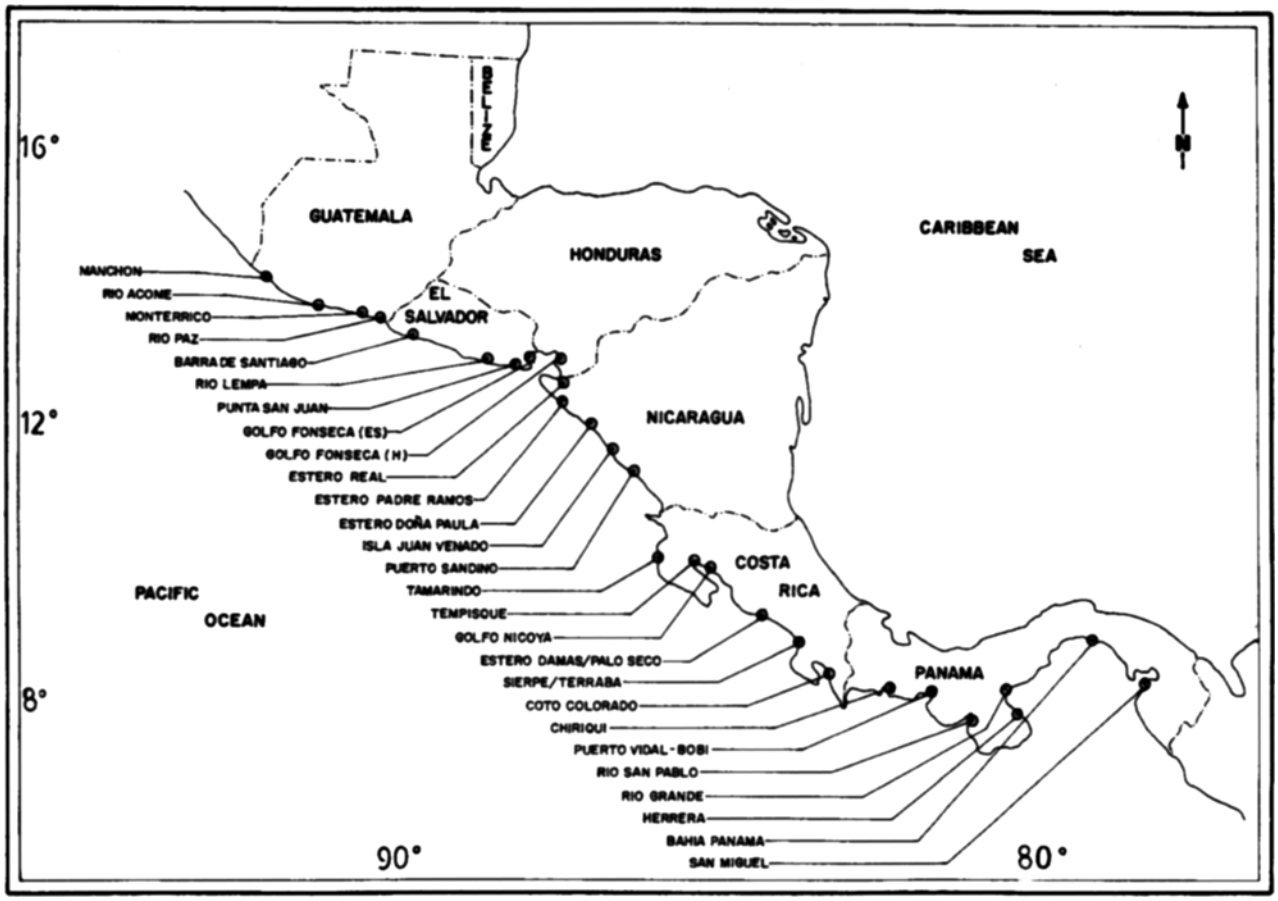


Fig. 1. Location of the most important mangrove sites along the Pacific Coast of Central America.

tional attributes within and between sites. As a result of strong salinity gradients (35–300‰), these forests exhibit large differences in structural development within the same forest region. The most obvious is a reduction in height and basal area with distance away from the channels. In many cases, the forest gives way to extensive salt flats which in some areas, as in the Gulf of Fonseca, extend over 13,000 ha. Drainage and seepage from nearby hills can play an important role in diminishing soil salinities in the salt flats. Areas exposed to this seepage usually show a narrow band of *Avicennia* and *Laguncularia* trees surrounding the inland margin of the salt flat.

Significant changes in structural development can also be observed between dry climate mangroves growing under different hydrological conditions. Dry climate forests under the influence of large, nonseasonal rivers that drain rainy basins, show structural characteristics very similar to those of mangroves growing in rainy areas. Inland sections, deprived of river flooding, show a more suppressed development unless abundant seepage occurs.

The main environmental differences among dry climate sites are observed in the inland section of the forests, where high evaporation or freshwater seepage can drastically influence growing conditions. Consequently, species composition and structural development in these inland areas can differ substantially from site to site. In forests where seepage or runoff seasonally reduces drought and high salinity conditions, *Avicennia germinans* (L) L. is clearly displaced by *Avicennia bicolor* Standl. which has a lower salt tolerance (Jiménez 1984). Where soil salinities during the dry season are below 50‰ *A. bicolor* forms almost pure stands and only isolated individuals of *A. germinans* are found. This pattern is reversed in sites where runoff and drainage are absent. Here, *A. germinans* becomes the dominant species.

The structural and functional attributes of dry climate mangroves along the Pacific Coast of Central America appear to differ significantly from those described for the Caribbean region (Cintrón et al. 1978).

The present study describes the structure and

TABLE 1. Mangrove coverage estimates (in hectares) for the Pacific Coast of Central America. Estimates are by regions of the country where tracks of mangrove forest occur, not by specific sites.

COSTA RICA	NICARAGUA	PANAMA
Tamarindo	Estero Real	Cocle
400	19,410	6,580
Tempisque	Padre Ramos	Chiriqui
2,340	4,590	43,050
Golfo de Nicoya	Corinto/Poneloya	Darién
10,671	10,700	28,225
Damas/Palo Seco	Peñitas/Juan Venado	Herrera
2,312	2,420	5,512
Sierpe/Terraba	Puerto Sandino	Los Santos
17,737	1,990	6,636
Coto Colorado	Other Areas	Panamá
875	200	107,925
Other Areas	Total	Veraguas
4,792	39,310	28,420
Total		Total
39,127		226,348
GUATEMALA	**EL SALVADOR**	**HONDURAS**
Manchón	Golfo de Fonseca	Golfo de Fonseca
10,850	4,657	46,869
Monterrico	Jiquilisco	Total
4,325	19,847	46,869
Other Areas	Jaltepeque	
911	5,385	
Total	Other Areas	
16,086	5,866	
	Total	Total for the Pacific Coast:
	35,755	403,495ha

dynamics of a pure *A. bicolor* stand on the Pacific Coast of Costa Rica. Emphasis is placed on aspects of dynamics related to the numeric changes occurring within the forest.

Avicennia bicolor is restricted to the dry sections of the Pacific Coast of Central America, from Chiapas, Mexico, to Panama. Like other mangrove types along the Pacific Coast, the *A. bicolor* stands have never been carefully studied. Jiménez (1981) reported relatively large basal areas (37 m^2 ha^{-1}) in a general description of one of these stands. Except for this study, only botanical descriptions of the species occur in the literature.

Study Site

The study area was located at the Tivives mangrove swamp (9°52″N, 84°42″W), at the mouth of the Jesus Maria River. In the 650-ha forest, *A. bicolor* forms an almost pure band of about 260 ha in the inland section (Fig. 2).

The site receives an average annual precipitation of 1,800 mm, falling mainly from May to November (Fig. 3). Between August and October precipitation is highest (129–195 mm per month) and maximum flooding levels are observed within the forest.

Mean tidal range in the site is 2.3 m with a mean spring tide range of 2.8 m and a mean neap tide range of 1.8 m (Voorhis et al. 1983). River discharge and seepage are seasonal, closely following rainfall. Higher river discharge and seepage between May and November account for more frequent flooding in the *A. bicolor* stand during this period. Brackish water seems to back up into the mangrove forest at this time.

Methods

A 1-ha plot (50 × 200 m) was laid out within a monospecific *A. bicolor* stand. The plot was oriented perpendicularly to the flooding gradient and subdivided into 10 × 10 m subplots. Randomly distributed 1 × 1 m quadrats were located within subplots to assess seedling populations. The total number of 1 × 1 m quadrats located in the 1-ha plot (145) was determined after a pilot sampling and a minimum sample calculation were conducted.

The total number of seedlings in each 1 × 1 m quadrat was recorded during 24 months at irregular intervals. Distinctions were made between old seedlings and those that arrived since the last mea-

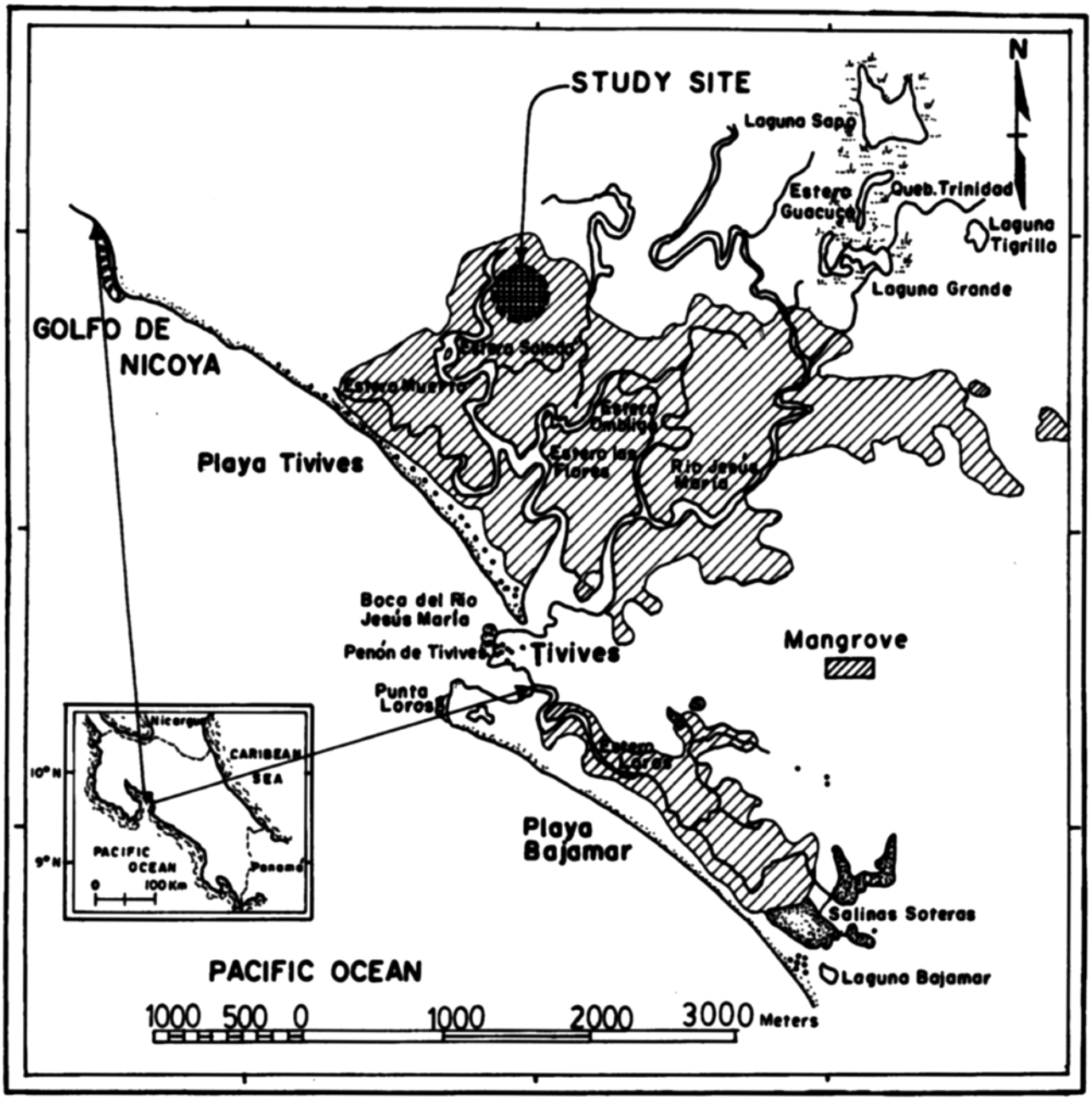


Fig. 2. The mangrove forest of Tivives, on the Pacific Coast of Costa Rica, showing the location of the study site.

surement. Recently established seedlings keep their cotyledons for over three months.

In all 10 × 10 m plots, all plants over 50 cm in height were measured. In addition to total height, diameter at breast height (DBH) was recorded for those plants with more than 3.5 cm DBH.

One section (80 × 40 m) of the plot was used to perform a spatial pattern analysis to estimate the pattern of the different size classes within the stand.

The size-class dispersion patterns were analyzed over a range of quadrat sizes from 25 m^2 to 3,200 m^2, using Morisita's index of dispersion (Morisita 1959). The measure of dispersion is given by:

$$I\delta = q \sum n_i(n_i - 1)/N(N - 1)$$

where n_i is the number of individuals of the size class in the i^{th} quadrat, q is the number of quadrats, and N is the total number of individuals in all the quadrats. The index equals 1.0 if the size class is

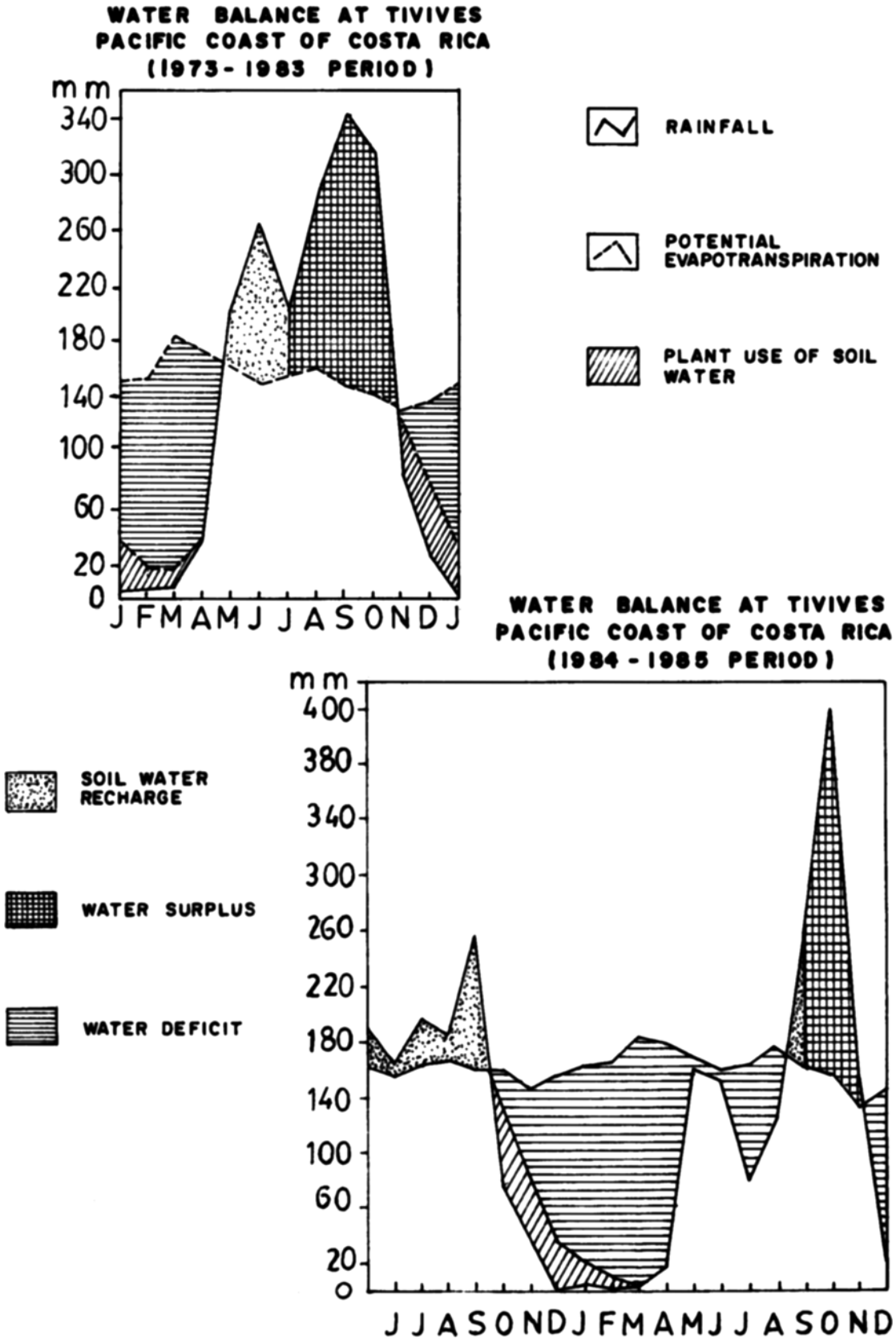


Fig. 3. Average water balance of the Tivives area for 1973–1983 and for June 1984 to December 1985.

TABLE 2. Height, diameter at breast height, and basal area mean increments per size class for *Avicennia bicolor* plants. n = number of plants used to estimate the mean, SD = standard deviation. Density of trees for each diameter size class within the one hectare plot is indicated.

Size class		Height Increments (m yr^{-1})	Diameter Increments (cm yr^{-1})	Basal Area Increments[a] (cm^2 yr^{-1})
Height (m)				
(0.5–1.4 m; n = 33)	mean	0.04	—	—
	SD	0.05	—	—
(1.5–2.4 m; n = 39)	mean	0.05	—	—
	SD	0.08	—	—
(2.5–4.4 m; n = 41)	mean	0.09	—	—
	SD	0.13	—	—
Diameter (cm)				
(3.5–5.9 cm; n = 22)	mean	—	0.06	0.43
trees ha^{-1} = 309	SD	—	0.05	1.25
(6.0–8.9 cm; n = 31)	mean	—	0.09	1.06
trees ha^{-1} = 191	SD	—	0.14	1.84
(9.0–14.9 cm; n = 38)	mean	—	0.13	2.43
trees ha^{-1} = 204	SD	—	0.15	3.04
(15.0–19.9 cm; n = 24)	mean	—	0.30	8.22
trees ha^{-1} = 83	SD	—	0.17	5.21
(20.0–24.9 cm; n = 11)	mean	—	0.33	11.36
trees ha^{-1} = 54	SD	—	0.19	6.0
(25.0–34.9 cm; n = 13)	mean	—	0.25	10.49
trees ha^{-1} = 52	SD	—	0.17	7.03
(35.0–55.0 cm; n = 17	mean	—	0.13	8.95
trees ha^{-1} = 52	SD	—	0.12	7.25
(>55.1 cm; n = 06)	mean	—	0.14	13.75
trees ha^{-1} = 53	SD	—	0.06	6.09

[a] Total basal area increment: 0.38 m^2 ha^{-1} yr^{-1}

randomly distributed, is <1.0 if the distribution is uniform, and is >1.0 if clumping occurs.

According to Morisita (1959), the significance of the departure from randomness of the studied distribution can be obtained using a calculated F value:

$$F = (I\delta(N - 1) + q - N)/q - 1$$

Fifty-two randomly selected 10 × 10 m plots were identified in the field and all plants above 50 cm in height were permanently marked. Tagged plants were grouped in size classes. Height growth for plants between 0.5 and 4.5 m in height and DBH increments for trees larger than 3.5 cm DBH were periodically measured over a 31-month period (December 1984 to July 1987). Height was measured with a marked pole. Diameter increments were measured with a diameter tape, on a band previously painted around the trunk. Mortality of the tagged plants was also recorded.

The crowns of tagged trees with DBH >3.5 cm were classified as suppressed, intermediate, codominant, and dominant, as defined by Smith (1962).

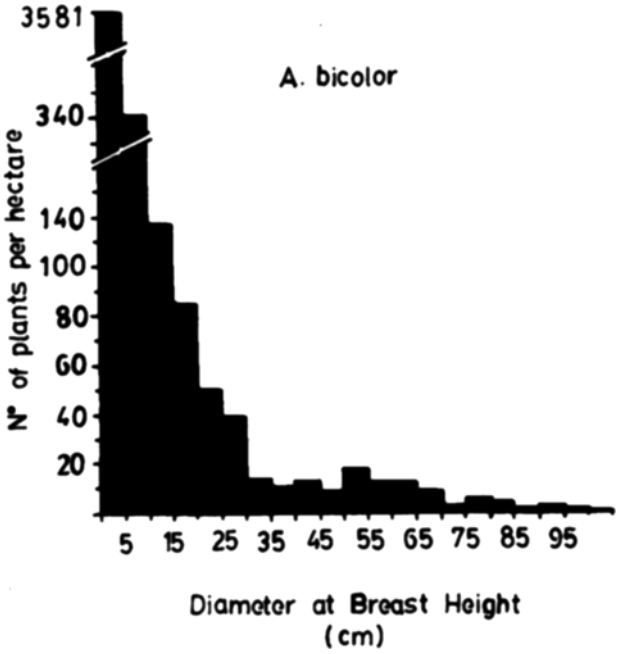


Fig. 4. Size class distribution of *Avicennia bicolor* plants taller than 50 cm growing in a monospecific stand.

Reproductive phenology of the trees in and around the 1-ha plot was observed monthly betweeen August 1983 and July 1987. Binoculars were used to note flower and fruit development.

Results and Discussion

Total plant density (plants above 50 cm in height) in the 1-ha plot was 4,350, with 769 trees above 5 cm DBH. This relatively low density results from the large tree sizes found in the forest. Total basal area is accordingly very high with 41.0 m^2 ha^{-1}, and, together with a canopy height of about 18 m, makes this one of the most structurally developed *Avicennia* forests reported in the literature. Size classes show the typical negative exponential distribution for plants taller than 50 cm (Fig. 4). There were 95 trees above 40 cm DBH in the 1-ha plot. The maximum DBH observed was 96.1 cm.

The dispersion patterns of the size classes showed a highly significant ($p < 0.01$) clumping at all quadrat sizes for plants smaller than 5 cm DBH (Fig. 5). These plants appear to be clumped at a light gap or a former light gap area. An analysis of the clump size ($1\delta(s)/I\delta(2s)$), as explained by Morisita (1959), shows that clumping in plants less than 5 cm DBH occurs in areas around 400 m^2. This seems to conform with the observed size of the light gaps in the forest. Plants above 5 cm DBH are already influenced by canopy competition processes, and their random distribution seems to result from the randomness of the processes that influence tree

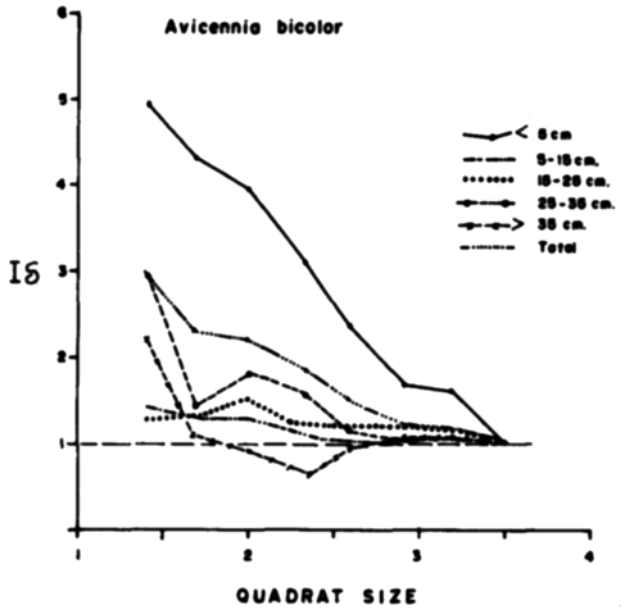


Fig. 5. Values of Morisita's index (I δ), at different quadrat sizes for *Avicennia bicolor* plants taller than 50 cm. Quadrat units are given in terms of log quadrat area.

survival of the medium and large size classes. The occurrence of light gaps seems to be a common phenomenon in the *A. bicolor* stand.

Height and DBH increments per size class are presented in Table 2. Height increments in the sapling layer range from 0.04 to 0.09 m yr^{-1}, a relative low rate which is probably a result of the low light intensities under the closed canopy. Under high light intensities in nearby light gaps, seedlings and saplings increased at a considerably faster rates.

DBH increments show a parabolic pattern with smaller increments in the smaller and bigger size classes. Trees over 15 cm DBH have already reached the canopy and their high DBH increments indicate a favorable reaction to the higher light regimes. Maximum diameter growth rates (0.25–0.33 cm yr^{-1}) were observed in trees between 15 and 35 cm in DBH. Trees over 35 cm DBH show lower DBH increments, a typical pattern for mature trees in a forest.

The DBH increments are surprisingly high for a dry climate mangrove forest, where growth is likely to be restricted to the 6-month rainy season. Increments of 0.30 cm yr^{-1} are similar to those reported for trees in high rainfall areas (Putz and Chan 1986). Growth information for New World mangrove forests is scarce. Wadsworth (1959) reported average DBH increments of 0.13 cm yr^{-1} for large dominant saplings and 0.09 cm yr^{-1} for dominant poles of *Laguncularia racemosa*. Golley et al. (1969) reported DBH increments for *Rhizophora mangle* ranging between 0.0 and 0.58 cm yr^{-1}. Cintron and Schaeffer-Novelli (1984) reported DBH increments of 0.08–0.16 cm yr^{-1} for *R. mangle* trees, 0.23–0.86 cm yr^{-1} for *L. racemosa* stands, and 0.22–0.50 cm yr^{-1} for *A. germinans*. Lugo and Snedaker (1973) working in *R. mangle* forests in Florida, found DBH increments ranging from 0.12 to 0.22 cm yr^{-1}. Growth rates among mangrove forests vary considerably from site to site according to the climatological and hydrological conditions of the stand. Nevertheless, the growth rates of the *A. bicolor* stand appear to be high, especially for a stand growing under a severe seasonal drought. Unfortunately no comparable information is available for mangrove forests under tropical dry climate.

TABLE 3. Basal area mean increments (cm^2 yr^{-1}) per crown class (sensu Smith 1962) for *Avicennia bicolor* trees.

	Crown Class			
	Suppressed	Intermediate	Codominant	Dominant
Mean	0.92	4.30	10.28	11.02
SD	1.73	3.93	6.40	7.12
N	65	37	43	15

Basal area increments were above 8 cm^2 yr^{-1} for all size classes above 15 cm DBH. Maximum basal area increments (13.75 cm^2 yr^{-1}) were observed in the biggest size class (trees over 55 cm DBH). Growth expressed as basal area increments (Table 2) totaled 0.38 m^2 ha^{-1} yr^{-1}. This is significantly lower than the values reported for *Rhizophora mangle* stands (1.9 m^2 ha^{-1} yr^{-1}; Lugo and Snedaker 1973), and *Avicennia germinans* stands (1.8 m^2 ha^{-1} yr^{-1}; Lugo et al. 1980) in Florida. The seasonal dry climate, undoubtedly account for the comparatively low basal area increments of the Tivives stand but also the mature stage of this forest, and its location in a region not exposed to hurricanes must be considered.

Access to light is a major determinant of growth rate for this species. Basal area increments are clearly related to the tree crown position (Table 3). They become larger from suppressed to dominant trees and ranged from 0.92 cm^2 yr^{-1} at the suppressed class to 11.02 cm^2 yr^{-1} in the dominant class. Analyses of growth rates among different crown classes are very limited. Putz and Chan (1986) found an increasing diameter growth rate from suppressed to dominant crowns in a *Rhizophora apiculata* forest (0.09–0.35 cm yr^{-1}). No similar information is available for *Avicennia* species.

Mortality was higher in the small size classes, as expected (Table 4). This pattern agrees with descriptions of several Caribbean mangrove forests by Jiménez et al. (1985) and for Malayan forests

TABLE 4. Mortality per size class in an *Avicennia bicolor* stand. The number of living trees at the beginning of the sampling interval is followed in parentheses by the number of trees dying during that interval.

Size-Class	Time Intervals					Mortality (% yr^{-1})
	January 85 to May 85	May 85 to September 85	September 85 to January 86	January 86 to June 86	June 86 to June 87	
Height						
0.5–1.5 m	50 (11)	39 (0)	39 (0)	39 (8)	—	23.7
1.5–2.5 m	50 (3)	47 (1)	46 (1)	45 (7)	—	15.0
2.5–5.5 m	50 (5)	45 (0)	45 (1)	44 (4)	—	12.5
Diameter						
3.5–5.9 cm	30 (2)	28 (2)	26 (1)	25 (3)	22 (1)	11.1
6.0–8.9 cm	50 (3)	47 (0)	47 (0)	47 (15)	32 (1)	14.1
9.0–14.9 cm	40 (2)	38 (0)	38 (0)	38 (0)	38 (0)	01.8
15.0–19.9 cm	24 (0)	24 (0)	24 (0)	24 (0)	24 (0)	00.0
20.0–24.9 cm	11 (0)	11 (0)	11 (0)	11 (0)	11 (0)	00.0
25.0–34.9 cm	13 (0)	13 (0)	13 (0)	13 (0)	13 (0)	00.0
35.0–55.0 cm	18 (0)	18 (0)	18 (0)	18 (0)	18 (1)	02.0
>55.0 cm	06 (0)	06 (0)	06 (0)	06 (0)	06 (0)	00.0
Total	342 (26)	316 (3)	313 (3)	310 (37)	164 (3)	
Mortality (%)	7.60	0.95	0.96	11.90	1.83	

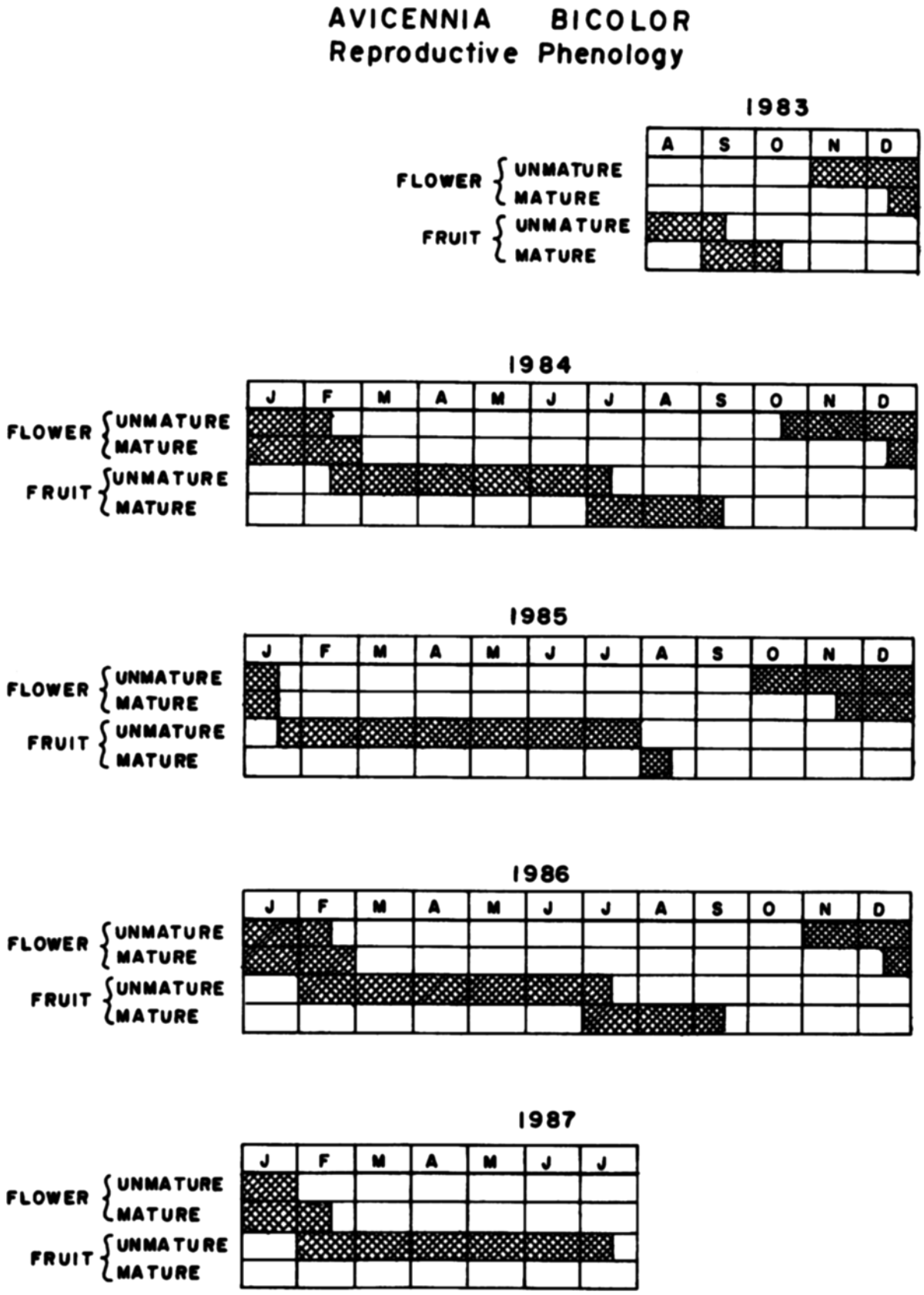
by Putz and Chan (1986). Intense competition during early stages coupled with a larger dependence on water availability significantly increase mortality in the smaller size classes. Smaller trees are more dependent on surface water because of shallow root systems, and are stressed by light deficiencies Mortality was seasonal, most likely as a result of the drought and higher soil salinities. During the dry months (December to May) mortality was >7% mainly due to trees <9.0 cm in DBH. During the rainy season mortality dropped to less than 1%. Larger trees were less seasonal in mortality, probably as a result of deeper roots that reach the water table.

Flowering was invariably observed at the beginning of the dry season (December—February, Fig. 6), as in many other dry forest species. Flowering peaks were observed early in the dry season, a tendency that could be related to a dependence of the flower development on groundwater availability. After January groundwater levels drop sharply and a severe water deficit occurs until the beginning of May (Fig. 3).

A small year-to-year variability in the reproductive events was observed in the forest. Most (90–95%) individuals above 15 cm DBH were observed bearing flowers each year within a period of 1 to 3.5 months which indicates a fair degree of synchrony. This pattern was constant within the population except during the peak of January 1985 when flowering activity was extremely low and restricted to the largest trees. This paucity in flowering activity was a generalized phenomenon throughout the forest except on the margins of the river, where flowering occurred in all trees above 15 cm DBH. The restriction of abundant flowering to high soil moisture levels suggested water stress as an important regulating factor. A subsequent analysis of the water balance at the site confirmed this suggestion. Using climatic data from the Puntarenas station (15 km away) a calculation of water deficits in the area indicated an anomalous weather pattern (Fig. 3). During October 1984 precipitation in the area was only 83 mm, sharply below the previous 10-yr average of 316 mm. The pronounced reduction in precipitation was followed by a water deficit lasting 10 months, in contrast to the usual 6-month period of water deficit.

This anomalous climatic pattern had a significant impact on flowering activity. Flower buds that normally started to develop in October were absent in most of the trees by the end of October 1984. Consequently, anthesis in January and fruit production in August 1985 were extraordinarily low. These observations suggest the necessity of high soil moisture levels in the forest prior to the development of flower primordia.

The fruiting peak always occurred in the middle of the rainy season (July–October). Development time between flower and propagule is therefore 7 to 8 months, higher than those reported for other species of the genus (Duke et al. 1984; Lopez-Portillo and Ezcurra 1985). Fruit development was very slow for most of the 7 to 8-month period. Increments in fruit size were only observed after June, when soil water was replenished. The release of propagules occurs when flooding levels in the forest are maximum (July–October). The timing of the propagule crop is very important for the establishment of the seedling. Besides assuring proper propagule dispersal, the seedlings that established before October have a deeper root sys-


AVICENNIA BICOLOR
Reproductive Phenology
1983
A S O N D
FLOWER UNMATURE
MATURE
FRUIT UNMATURE
MATURE
1984
J F M A M J J A S O N D
FLOWER UNMATURE
MATURE
FRUIT UNMATURE
MATURE
1985
J F M A M J J A S O N D
FLOWER UNMATURE
MATURE
FRUIT UNMATURE
MATURE
1986
J F M A M J J A S O N D
FLOWER UNMATURE
MATURE
FRUIT UNMATURE
MATURE
1987
J F M A M J J
FLOWER UNMATURE
MATURE
FRUIT UNMATURE
MATURE

tem and a better chance to withstand the upcoming dry season.

Establishment of *A. bicolor* propagules was restricted to the months between August and early December (Fig. 7). Surface drainage patterns and microtopography play an important role in the establishment process. Branches, trunks, or elevation gradients on the floor, prevent further dispersal of the propagules and allow anchoring after a few days of stranding. The number of propagules established changed from year to year. After the 1984 crop, a total of 83.2 propagules m^{-2} became established in the forest floor. In 1985 only 0.4 propagules m^{-2} were established due to a very severe drought in the preceding 10 months that reduced flowering and crop size to unusually small amounts.

Approximately 380 propagules m^{-2} were produced in this stand from the 1986 crop (Jiménez 1988b). About 58% of the crop (219 propagules m^{-2}) established in the site. This amount was more than double the number of propagules established in 1984, a climatically average year. Crop size is clearly a major factor determining the number of established propagules.

No information is available regarding establishment rates in other *Avicennia* forests. The values found in this study are likely higher than in any forest of *A. germinans*. *Avicennia bicolor* seems to be highly prolific compared to that species. This higher reproductive capacity probably is responsible for the displacement of *A. germinans* by *A. bicolor* and consequent dominance of the latter in areas influenced by seasonal seepage and runoff.

Seedling mortality also showed a clear seasonal pattern (Fig. 7). A peak in seedling mortality was evident during the dry seasons. During the dry season in early 1985, the number of seedlings dying was particularly high (23 dead propagules m^{-2} $month^{-1}$), most likely as a result of the severe drought that also affected other size classes in the forest. Although mortality, in absolute numbers, was lower in the 1986 dry season, this was due to low recruitment in late 1985. Expressing results as monthly percentage mortality resulted in comparable values (Fig. 7). During the 1985 dry season, monthly mortality was up to 38.6% and in the 1986 dry season those values reached 30.3%. The seasonality in seedling mortality is clearly dependent on severe droughts.

Mortality did not show any relationship with total seedling density in the quadrats. Intensity of drought and soil salinities seem to override any effect density could have on the seedling mortality pattern of the site.

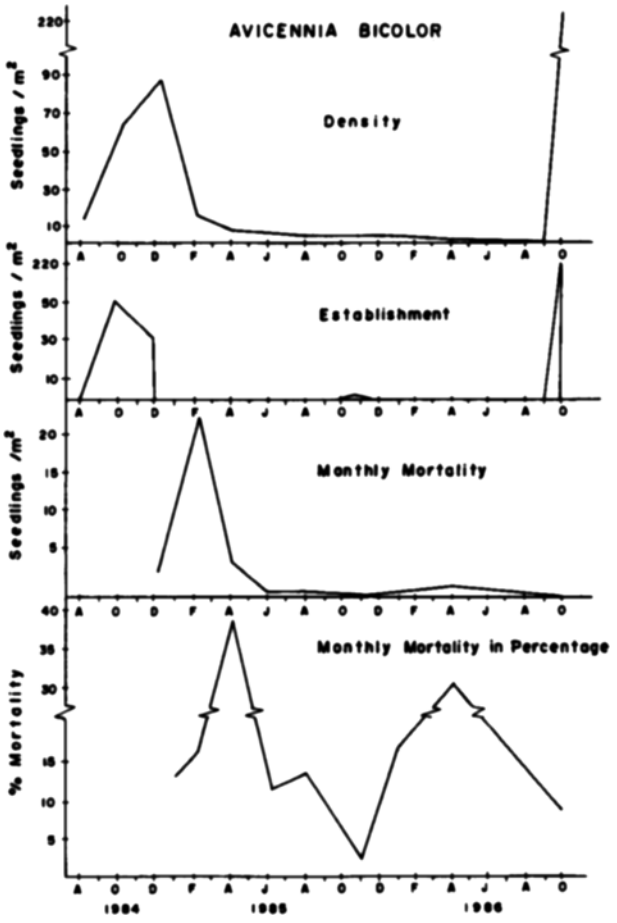


Fig. 7. Density, establishment, and mortality of *Avicennia bicolor* seedlings in the Tivives mangrove forest from August 1984 to October 1986.

Seedling density on the forest floor closely follows the establishment and mortality patterns previously described. Seedling density is high after crop release and is drastically reduced during the dry seasons. The small 1985 crop was insufficient to affect seedling density appreciably (Fig. 7). Density values after the 1986 crop (220 seedlings m^{-2}) more than double the density observed after the 1984 crop (89 seedlings m^{-2}).

These values are considerably higher than those reported in other *Avicennia* forests. Lugo et al. (1980) reported densities ranging from 0 to 0.17 seedlings m^{-2} in *A. germinans* forests. Burns and

←

Fig. 6. Reproductive phenology of *Avicennia bicolor* trees at the Tivives mangrove site. Observations started in August 1983.

Ogden (1985) reported 18.4 seedlings m^{-2} in an *A. marina* forest.

Conclusions

In *Avicennia bicolor* forests growing under dry seasonal climates, freshwater availability regulates mortality, growth, and phenological events. The close correlation of aspects of life history in these forests with rainfall and seepage patterns clearly points out that in many sections of a mangrove forest tides are not always the major hydrological factor. This probably also applies to other types of dry climate mangrove forests.

The relatively high basal area increments observed in this forest indicate the favorable conditions that seasonal runoff and seepage can provide to mangrove forests in dry climate environments. Alterations of these hydrological processes are likely to result in drastic changes in the structural and functional attributes of the forest.

The high seedling and sapling density in these forests seems to be the result of a large reproductive capacity of the population. High mortality in these small size classes, likely due to the combined effect of drought and shade, play an important role in determining the low tree density values observed in this site. The magnitude of the variations in seedling density throughout the study period indicates that sporadic density counts in the seedling layer of mangrove forests are meaningless. At least in seasonal mangrove forests, seedling stocks seem to be a function of the year and the season.

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