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Recovery of a Mixed-Species Mangrove Forest in South Florida Following Canopy Removal

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ABSTRACT

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In October 1982, the upper structure and canopy of a 0.09 ha area of mixed species mangrove forest (654 trees) in southeast Florida was removed by tree trimmers. This represented a reduction in mean forest height from 7.1 to 4.8 m. In February 1983, recovery studies were initiated based in part on comparisons with a contiguous untouched mangrove forest. Of some 148 tall *Rhizophora mangle* trees with an original mean height of 9.0 m, 110 (74%) died within 3 years. Mortality of *R. mangle* was highest among tall single-boled trees with a concentration of foliage above 4.8 m. All individuals of *Avicennia germinans* and *Laguncularia racemosa* recovered quickly by releafing, coppicing, and initiating trunk sprouts. Based on comparative light transmission measurements, the time estimated for forest canopy reclosure was 50 months although it varied from 72 to 118 months in the *R. mangle* zone, to <1 to 24 months in the zone dominated by *L. racemosa*.

ADDITIONAL INDEX WORDS: *Canopy closure, light transmission, zonation, species mortality and recovery, reserve meristem.*

INTRODUCTION

Mangrove forests may be subjected to natural defoliation and/or canopy loss as a result of hurricanes, or freeze damage at their latitudinal range limits. Whereas hurricane damage frequently results in widespread mortality for reasons other than mere canopy loss (WADSWORTH and ENGLERTH, 1959; CRAIGHEAD and GILBERT, 1962), non-lethal freezing kills the terminal shoots and highest branches, but may leave the lower branches, trunk and root system largely unaffected (MACNAE, 1966; LOT-HELGUERAS *et al.*, 1975; LUGO and PATTERSON-ZUCCA, 1977). This differential effect is presumed to be due to the latent heat capacity of saturated sediment and water which protects the lower plant structures during short periods of freezing temperatures. When mortality does not occur, there is renewed growth that results in the recovery and eventual closure of the canopy. There is also a stimulation of the growth of mangrove seedlings, resulting from the increased light transmission through the opened canopy since the Florida species cannot develop in the full shade of a closed canopy.

There are also a number of studies that report the effects and subsequent responses of horticultural branch and foliage pruning of individual mangrove trees. With one exception, pruning stimulates net primary production as evidenced by an increase in height, branch development and production of new foliage (PULVER, 1976). The principal exception relates to the limited regrowth potential of *Rhizophora mangle* L. (see HAMILTON and SNEDAKER, 1984, for regrowth comparisons of the mangrove species). *R. mangle* lacks significant reserve meristem, and severed branches larger than about 2.5 cm in diameter (approximately equivalent to 2–3 years of recent growth) do not regenerate new foliage (GILL and TOMLINSON, 1971). In contrast, the removal of leaves without damage to branch structures does not affect the formation of new foliage (LUGO and SNEDAKER, 1974). The other dominant Florida mangrove species (*Avicennia germinans* (L.) Stearn and *Laguncularia racemosa* L. Gaertn. f.) have extensive reserve or secondary meristematic

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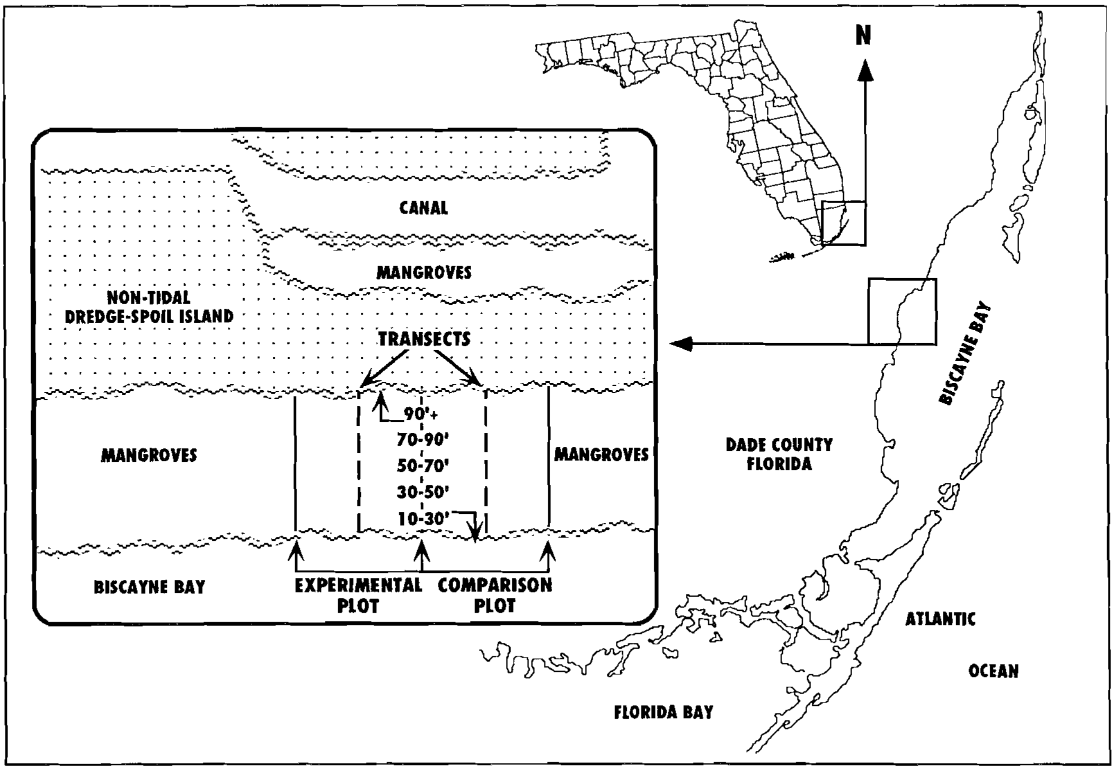

Figure 1. Map of study area showing location of transects in experimental and comparison mangrove forest plots.

tissues and can quickly regenerate by releafing, coppicing, and developing trunk sprouts.

In spite of limited branch regrowth, horticulturally pruned *R. mangle* can maintain a high incidence of fruiting when approximately 70 percent of the foliage is left intact on the tree (ESTEVEZ and EVANS, 1978). Also, their data suggest that the maximum pruning threshold limit for *R. mangle* may be around 50 percent of the branches and foliage. Because mangroves are not significantly different from most forest, fruit or ornamental trees in their responses to a variety of horticultural treatments, pruning of mangrove canopy foliage has been recommended as a useful horticultural practice in Florida (CARLTON, 1974; STEVELY and RABINOWITZ, 1982).

OBJECTIVES

In October 1982, the upper canopy of a 0.09 ha mangrove forest plot in southeast Florida was removed by novice tree trimmers which resulted in the loss of most of the upper canopy and foliage. The original pruning objective had been to reduce the forest height over a period of two years to approximately 6 m, after which it was to be maintained at that height. The trimming crew, in an effort to complete the work within budget, ignored the objective and uniformly removed portions of foliage from all trees on the plot including *R. mangle*. This *ad hoc* canopy removal experiment presented an opportunity to document mangrove forest community recovery, following the removal of a major part of the upper, above-ground, structure and foliage. The specific objectives were to: (1) determine the extent of canopy removal and the effects on the cut trees, and (2) determine the rate of canopy reclosure by measuring changes in subcanopy light levels. The field work was initiated in February 1983.

METHODS

Study Area

The mangrove study area (Figure 1) is located in southeast Dade County, Florida (Latitude

25°37′52″N and Longitude 80°17′30″W), adjacent to a housing development at 6200 S.W. 152nd Street in Miami. This mangrove forest developed along the intertidal slope on the south side of a dredge spoil bank opposite a canal which links the Florida Power & Light Company Old Cutler power generation facility to Biscayne Bay. The canal is reported to have been dredged in the 1940's, but it is not known when the subsequent mangrove colonization was initiated. The closed-canopy mangrove forest in the study area consists of mixed *R. mangle*, *A. germinans* and *L. racemosa*. All three species occur on the inland/upland side of the study area, but are reduced to a mono-specific stand of *R. mangle* at the shoreline.

Measurements and Calculations

Two contiguous study plots were identified to serve as experimental and comparison areas (Figure 1). All data measurements were made along 20 ft wide transects that were established perpendicular to the shoreline (Figure 1) in the experimental and comparison plots. The approximate 100 ft transects were subdivided into the 20 ft segments so as to take into acount the differences associated with the intertidal elevation gradient, and the observed zonation of the mangrove species.

The forest measurement and calculation procedures were adapted from standard forest mensuration practices that have been modified for use in mangrove forests (POOL *et al.*, 1977; see also CINTRON and SCHAEFFER-NOVELLI, 1984, for specific techniques). Because a high proportion of the *R. mangle* trees possessed two or more boles, diameter and height measurements were taken and recorded on both a tree and individual bole basis.

Mean forest height in each experimental transect segment was determined from regressions of bole height over bole DBH (diameter at breast height) for 236 trees in the comparison forest. Heights of all *A. germinans* were individually measured due to the small number of individuals (less than 0.05%) in the study area. The heights of individual tree boles of varying DBH for both *R. mangle* and *L. racemosa* were measured. Heights were determined with either a Hastings telescoping measuring rod or an optical distance measurer (Ranging 120 Opti-meter), where a clear line-of-sight was possible. The DBH of all boles >2.5 cm was measured at 1.3 m above the ground with a diameter tape. Correlation coefficients (r^2) for the best fit equation ($Y = a + bX$, where Y is height in meters and X is DBH in centimeters) ranged from 0.975 to 0.771 for *R. mangle*, and from 0.905 to 0.785 for *L. racemosa*. Based on the r^2 values, the algorithms were considered to be adequate for estimating both individual tree heights and mean forest height. The DBH-height algorithms were used to compute the original mean forest height in the experimental plot based on measurements of the DBH of individual trees.

Ambient and subcanopy light levels were determined with LI-COR quantum sensors (LI-190SR and LI-190SB) and photometric light meters (LI-185 and LI-1000). Although the LI-COR quantum sensors measure light in the photosynthetically-active region (PAR) of the radiation spectrum, the study emphasis was on percent light transmission through the forest canopies rather than on absolute light intensities. Close-to-synoptic readings were made in the open, and beneath the canopies along the transects at 1.3 m above ground level in both the experimental and comparison plots. Multiple light readings were made at 9 ($n = 10$), 13 ($n = 50$), 51 ($n = 20$), 71 ($n = 50$), 95 ($n = 50$), and 109 ($n = 50$) months following the canopy removal. Mean subcanopy light levels, expressed as a percent of ambient light, were calculated for each transect segment as an estimate of light transmission through the canopy.

RESULTS AND DISCUSSION

Structural Properties

Characteristics of the overall forest structure (basal area, density and forest height) and relative species dominance in each of the two plots are summarized in Table 1. Although there are structural differences in the experiment and comparison plots, the mean forest height (7.1 vs. 7.5 m) and the relative species dominance were considered to be sufficiently similar to allow for the comparisons of subcanopy light transmission.

Canopy Removal and Mortality

Following canopy removal in October 1982, it was determined that the majority of the 654 (actual count) mangrove trees in the experimental plot had lost varying amounts of foliage. Overall, the mean forest height (*i.e.*, mean height of all trees >2.5 cm DBH) in the experimental plot had been reduced from an original calculated height of 7.1 m (Table 1) to 4.8 m, representing an estimated vertical canopy loss of 2.3 m.

Table 1. *Characteristics of mangrove forest structure on 0.09 ha comparison and experimental plots based on tree diameters >2.5 cm DBH for red mangroves (*Rhizophora mangle*) and white mangroves (*Laguncularia racemosa*). Relative dominance computed as the percent contribution of each species to the total basal area, density and height.*

Distance from Shoreline (feet)	Basal Area (m^2/0.1 ha)			Density (number/0.1 ha)			Mean Height (m)			Relative/Dominance (%)	
	Total	Red	White	Total	Red	White	Total	Red	White	Red	White
Comparison											
10–30	3.70	3.70	—	431	431	—	8.2	8.2	—	100	0
30–50	2.67	2.67	—	646	646	–	8.7	8.7	—	100	0
50–70	5.60	1.62	3.98	1,669	727	942	8.1	7.4	8.7	40	60
70–90	3.00	0.19	2.81	1,049	269	780	6.8	4.2	7.8	22	78
90+	1.44	0.21	1.23	942	242	700	5.6	4.2	6.1	27	73
Experimental											
10–30	2.95	2.95	—	565	565	—	8.1	8.1	—	100	0
30–50	2.61	2.61	—	807	807	—	8.3	8.3	—	100	0
50–70	1.40	0.83	0.57	566	108	458	7.6	7.3	8.9	41	59
70 90	0.80	0.21	0.59	619	323	296	5.5	4.1	6.8	39	61
90+	1.21	0.52	0.69	619	215	404	5.9	4.9	7.8	39	61

The major contributor to the forest height reduction was attributed to 148 (actual count) tall *R. mangle* trees, the canopy dominants, that lost the majority of the uppermost branches and foliage. Based on the calculated mean height of 9.0 m for this subset of 148 trees, the height reduction to 4.8 m represented an estimated vertical canopy loss of 4.2 m.

Because of the limited regrowth potential of large *R. mangle* branches, it was hypothesized that essentially all of the 148 heavily damaged trees would eventually die. In February 1983 (four months after cutting), 92 of the heavily damaged *R. mangle* trees remained alive (Figure 2) as evidenced by the presence of green foliage, albeit minimal in many instances. Nine months following the pruning (July 1983), the number of living trees increased to 126, presumably due to the presence of limited reserve meristematic tissue, and also to better growth conditions attributable to warmer temperatures and higher precipitation during the spring and summer of 1983. However, in November 1983 (13 months after canopy removal), there were 69 dead *R. mangle* trees which increased to 110 in June 1985 (32 months later), and to 111 in January 1987 (51 months after canopy removal). In terms of the original population of 654 pruned trees, the final mortality of *R. mangle* was calculated to be 17 percent of the forest population in the experimental plot.

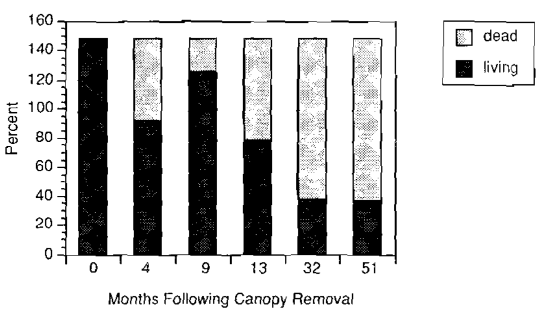

Figure 2. Change in percent of living and dead *R. mangle* trees (total 148 trees) in the experimental plot following canopy removal.

The spatial pattern of survival versus mortality was observed to be related to position relative to the shoreline, and growth form and height of *R. mangle*. Individuals of *R. mangle* within 20 ft of the shoreline exhibited a higher survival in spite of severe topping. This is attributed to the fact that the shoreline population consisted of multi-boled, multi-branched trees with a large proportion of foliage facing open water below the 4.8 m canopy removal height. In contrast, survival of *R. mangle* was lower in the interior (30 to 50 ft from the shoreline, Table 1) due to a greater density of tall, single-boled trees with minimal foliage below the cutting height.

Forest Canopy Reclosure

The forest canopy over the experimental plot is shown (Figure 3) to have essentially closed at approximately 50 months, although the transect

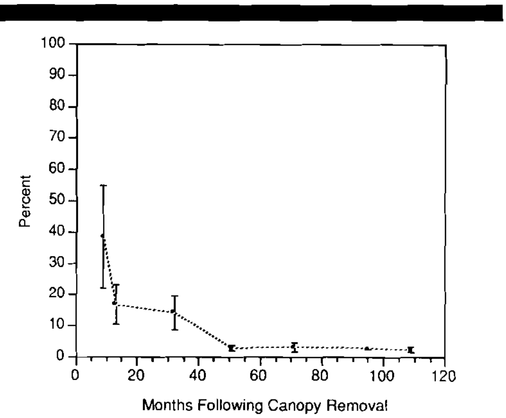

Figure 3. Change in subcanopy light transmission in the experimental plot expressed as a percent of ambient light (mean and standard error) in the open.

segments closed at variable rates. The differential rates of canopy reclosure were determined from regressions of light transmission over time for each transect segment based on the best-fit model $Y = aX^b$, where Y = percent light transmission and X = time in months following canopy removal (Table 2). Because the best-fit equations are exponential, the results are plotted along a logarithmic ($\log_{10}$) Y axis to emphasize the differences among the transect segments (Figure 4). To es-

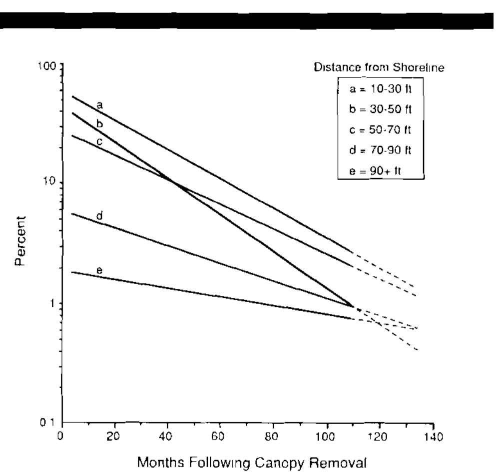

Figure 4. Estimated rates of mangrove forest canopy reclosure following canopy removal, as a function of distance from shoreline, based on regression equations in Table 2a. Dashed lines represent reclosure projections beyond the termination of the study at 109 months. Light transmission is expressed as a percent of subcanopy light in the comparison plot.

Table 2a. *Algorithm ($Y = aX^b$) for predicting rate of canopy re-closure along experimental transect where Y = percent light transmission through the canopy, and X = time in months following canopy removal.*

Distance from Shoreline (feet)	Algorithms for Predicting Rate of Canopy Re-closure	Correlation Coefficient (r^2)
10–30	$Y = (1{,}032.83)(X^{1.198})$	0.828
30–50	$Y = (1{,}390.97)(X^{1.460})$	0.960
50–70	$Y = (317.00)(X^{1.020})$	0.846
70–90	$Y = (26.28)(X^{0.658})$	0.533
90+	$Y = (4.83)(X^{0.389})$	0.194

timate the probable time required for canopy reclosure, the algorithms (Table 2a) were each solved for X (in months) using mean light transmission values for Y from the corresponding transect segments in the comparison plot (Table 2b).

The rate of regeneration of canopy foliage varied, mainly, according to species dominance along the segments of the transect (Table 1). In the zone with a high proportion of *L. racemosa* (50 to 90+ ft from the shoreline), there was a rapid regeneration of new foliage, and canopy closure occurred rapidly following canopy loss. In the *R. mangle* zone (0–50 ft), the production of new foliage was limited by the relatively slow growth of new branches by subcanopy saplings exposed to increased light. Because *R. mangle* produces only 5–11 leaves per branch tip, the rate of canopy closure is dependent upon the rate of appearance of new branches, and not to an increase in the number of new leaves on any existing branches.

Two distinct patterns of canopy reclosure in the experimental plot are apparent in the data (Table 2a and b, Figure 4). The calculated time for can-

Table 2b. *Estimates of numbers of months required for canopy re-closure along the experimental transect based on algorithms in Table 2a, and values for Y equal to the mean light transmission levels (percent of open) along the transect in the comparison forest plot.*

Distance from Shoreline (feet)	Mean Light Transmission in Comparison Forest (Y%)	Estimated Time Required for Canopy Re-closure (X months)
10–30	3.43	118
30–50	2.73	72
50–70	3.49	83
70–90	3.21	24
90+	5.44	<1

opy reclosure is estimated to be relatively long (72 to 118 months) in the shoreline zone (transect segments 10–30, 30–50 ft) where *R. mangle* is a mono-specific dominant, and in the 50–70 ft segment where it begins to share dominance with *L. racemosa*. In contrast, the time for canopy reclosure was relatively short (1 to 24 months) in the inland zone (transect segments 70–90, 90+ ft) where *L. racemosa* exhibits the highest relative dominance (Table 1). This apparent high rate of canopy reclosure is due to the rapid development of new foliage by *L. racemosa* (*cf.* WADSWORTH, 1959), most of which was observed to have formed prior to the initiation of the light transmission study nine months following canopy removal. The reason for the somewhat faster rate of reclosure in the 30–50 ft *R. mangle* segment was observed to be the result of the presence of a large number of viable branches below the 4.8 m cutting height. Although many of the shade leaves on these branches were sun scalded, or burned, by the exposure to high irradiance when the canopy was removed, this did not appear to have any subsequent affect on the production of new leaves on these branches.

CONCLUSIONS

The vertical loss of a major fraction of the canopy structure and foliage of a mixed-species mangrove forest resulted in two distinct patterns of recovery and canopy reclosure. Species (*L. racemosa* and *A. germinans*) with reserve or secondary meristems quickly produced new leaves and shoots in response to elevated light levels. In contrast, recovery of *R. mangle* was limited by the slow production of new branch structures because this species is unable to regenerate leaves on larger or older cut branches. Although there was an observed increase in seedling establishment following canopy removal, the effect was transitory as few of the seedlings were observed to grow taller than about 0.5 m during the study period. Consequently, canopy reclosure is shown to be the result of the growth of new foliage on the damaged but surviving mature trees.

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□ RESUMEN □

Durante el mes de Octubre de 1982, al sudeste de Florida en un manglar compuesto de especies variadas (654 árboles), y sobre una superficie de 0.09 hectareas, se podaron las estructuras superiores y las copas de los árboles del bosque. Esto representaba un disminución en la altura media del bosque de 7.1 m a 4.8 m. En Febrero de 1983, se iniciaron estudios de recuperación, parcialmente basados en la comparación con un bosque de manglares conntiguo y sin podar. De los 148 árboles altos (*Rhizophora mangle*) con una altura original media de 9 m, el 74% (110) murieron dentro de los 3 años. La mortalidad de los *R. mangle* fue mayor entre los troncos altos con concentración de follaje superior a los 4.8 m. Todos los individuos de *Avicennia germinans* y *Laguncularia racemosa* fueron rápidamente recubiertos por el follaje, y la maleza e iniciaron retoños de troncos. Basados en mediciones de transmisión de la luz, el tiempo estimado para el cierre de las copas del bosque fue de 50 meses aunque varió de 72 a 118 meses en la zona de los *R. mangle* y desde <1 a 24 meses en la zona dominada por *L. racemosa.—Néstor W. Lanfredi, CIC-UNLP, La Plata, Argentina.*

□ ZUSAMMENFASSUNG □

Im Oktober 1982 wurde der obere Bereich und das Laubdach einer 0.09 ha großen Fläche eines Mangrove Misch-Waldes (654 Bäume) in Südost-Florida durch Baumbeschneider entfernt. Dieses ergab eine mittlere Reduzierung der Waldhöhe von 7.1 m auf 4.8 m. Im Februar 1983 begannen Untersuchungen zur Wiederbegrünung im Vergleich zu benachbarten Mangrove Wäldern. Von 148 *Rhizophora mangle* Bäumen mit einer Ursprungshöhe von 9 m starben 110 (74%) innerhalb von 3 Jahren ab. Die Sterblichkeit von *Rhizophora mangle* war die Höchste von allen stammbildenden Bäumen, deren Laubkonzentration oberhalb von 4.8 m lag. Alle Individuen von *Avicennia germinans* und *Laguncularia racemosa* erholten sich schnell durch Wiederbelebung, Unterholzbildung und Austrieb von Stammauswüchsen. Gestützt auf Vergleichsuntersuchungen zur Lichtdurchdringung wurde die Zeitspanne zur vollständigen Etablierung des Laubdaches auf 50 Monate geschätzt, schwankt aber zwischen 72 und 118 Monaten in der Zone der *Rhizophora mangle* und weniger als einem bis zu 24 Monaten in der Zone, wo *Languncularia racemosa* dominiert.—*Dieter Kelletat, Essen, Germany.*

□ RÉSUMÉ □

En octobre 1982, au SW de la Floride, environ 0.09 ha de mangrove mixte (654 arbres) ont été émondés mécaniquement (structure supérieure et feuillage). La hauteur moyenne de la forêt s'est ainsi trouvée réduite de 7.1 m à 4.8 m. En février 1983, on a commencé une étude de la restauration par comparaison avec une forêt à mangrove contigue non touchée. Des 148 hauts arbres de *Rhizophora mangle* dont la hauteur originelle était de 9 m, 110 sont morts (74%) dans les 3 ans. La mortalité de *R. mangle* était plus grande parmi les grands arbres à un seul tronc dont la concentration du feuillage est située au dessus de 4.8 m. Tous les individus de *Avicennia germinans* et *Laguncularia racemosa* se sont rapidement restaurés par refoliation, création de taillis et bourgeonnement des troncs. On a estimé en comparant les mesures qu'il faudrait 50 mois pour que le couvert végétal se reforme totalement, bien que ce ce temps variait de 72 à 118 mois dans zone à *R. mangle,* à <1 à 24 mois dans la zone dominée par *L. racemosa.—Catherine Bousquet-Bressolier, Géomorphologie E.P.H.E., Montrouge, France.*