Litter Fall of *Avicennia germinans* L. in a One-year Cycle in a Mudflat at the Laguna de Mecoacán, Tabasco, Mexico[1]

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ABSTRACT

The fall of four morphological components of *Avicennia germinans* L. was measured at monthly intervals along a transect in a monospecific mangrove near the inlet of the Laguna de Mecoacán, Tabasco, Mexico. Estimated mean total annual litter fall was 614.4 $g \cdot m^{-2} \cdot yr^{-1}$. Seasonal fluctuations of mean water level, insolation, temperature and evaporation were highly intercorrelated and were summarized in a principal component axis that explains 82 percent of their variability. The results suggest that litter fall in *A. germinans* responds to the environmental variables already mentioned but is statistically independent from local rainfall. Each litter component (leaves, flowers and reproductive parts, branches and woody parts, and propagules) shows a distinctive sequence, and significant correlations were obtained when comparing the principal component axis against leaf and propagule fall. Phenologic variation in litter fall as an adaptive response to environmental changes is discussed.

Descriptions of the phenology of mangal woody species have been done in Florida (Gill and Tomlinson 1971, Pool *et al.* 1975); Thailand (Christensen 1978, Wium-Andersen and Christensen 1978); Malaysia (Gong *et al.* 1980); Veracruz, Mexico (Rico 1979); and northeastern Australia (Williams *et al.* 1981). Emphasis, however, has been given in most cases to the whole community, or to species of *Rhizophora*. Recent reports have made clear that there are different species responses to the mangal environment and climate (*e.g.,* Wium-Andersen 1981, Williams *et al.* 1981, Snedaker and Brown 1982).

This paper describes the annual phenological variations in litter fall of *Avicennia germinans* L. in a mudflat environment and analyzes their relation to environmental parameters, such as temperature, insolation, water level, and rainfall.

THE STUDY AREA

The mangrove forest surrounding the Laguna de Mecoacán, Tabasco, Mexico (Fig. 1), has an area of about 40 km^2 and shows a gradient of vegetation types which goes from a mixed forest to a monospecific, banded forest, depending on the distance from the sea and the geomorphologic conditions. A description of the forests in this lagoon can be found in Thom (1967). At present, a report is being prepared which includes a quantitative analysis of the physiognomic variations of this mangal.

In this lagoon the mean tidal range is around 50 cm but can exceed 1 m during coastal fronts (*nortes*). The climate is humid tropical with a mean annual temperature of 25°C and annual precipitation of 1500 to 2000 mm. According to Thom (1967), two patterns of seasonality can be distinguished in Mecoacán: (a) a period of high temperatures (27–29°C) that coincides with low water input into the estuary (from spring to summer, the water level goes down and salinity increases in the lagoon); and (b) a period of low temperatures (15–20°C) in fall and winter, caused by a dense cloud cover in the months of June and September or by the entrance of up to 25 periodic *nortes* that can lower the temperature for a period of 5 days.

The study site is located in the northwest coast of Laguna de Mecoacán (18°25′N, 93°10′W). The mangrove forest is situated in a mudflat near the inlet of the lagoon (approximately 3 km). The trees contained within the study site occupy an area with no apparent disturbance and show a mean height of 8 m. Tree densities vary between 13 and 61 trees dam^{-2}, with an average value of 24.7 trees dam^{-2}. The soils are clayey, with 2–10 percent organic matter; pH is from 6 to 8, and water conditions range from saturation to excessive, which contributes to the anaerobic conditions of the soil. Soil salinity values measured along the transect on the soil saturation extract taken on 28 June 1979 range from 2.8 to 6.5 percent. (It is interesting to note that in other parts of Mecoacán where soil salinities are considerably lower, forests are mixed and can reach heights of up to 22 m.) The carpet of pneumatophores is homogeneous, with a mean density of 362 ± 63 per square meter.

METHODS

A transect was established normal to the beach and crossing the mudflat. Litter traps—at both sides of the line, two per sampling station, 10 m away from each other—were placed every 30 m along the transect. Each trap consisted of a basket with a 0.25 m^2 mouth section, made out of a 1 m^2 nylon mesh (opening width 1.5 mm) sewn

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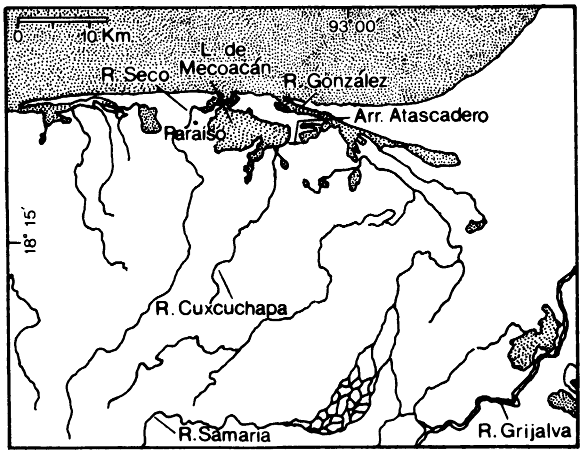

FIGURE 1. Section of the Grijalva-Mezcalapa deltaic system which contains the Laguna de Mecoacán (modified from Thom 1967).

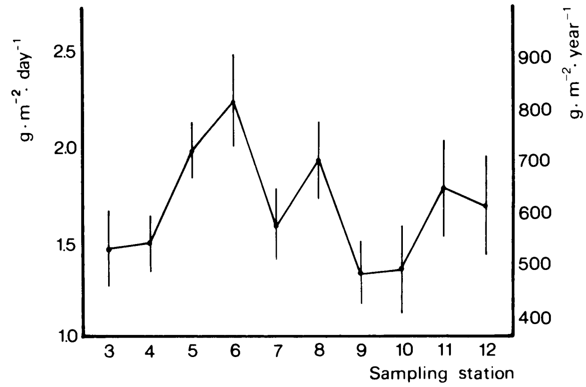

FIGURE 2. Estimated average daily litter fall per sampling station during the year cycle March 1979–March 1980. Vertical lines indicate the standard error. The scale on the right indicates the estimated average yearly litter fall.

into a square wire frame (0.5 × 0.5 m) and kept initially 0.7 m above the ground. After the October litter collection was lost due to an extremely high rise in the lagoon's water level, all the traps were raised 1.2 m above the ground. Fourteen stations were laid inside the mangrove forest, with station 1 corresponding to *Rhizophora mangle* fringe-forest and the rest to *A. germinans* pure stands. Because of frequent destruction of the extreme stations, only the data from the central ones (3–12) are presented.

Eleven litter collections were made at approximately 1-month intervals; flooding ruined the October collection. The collected material was classified into four different morphological components and dried at 80°C until constant weight was attained. The average litter production (dry weight per day per square meter) was assigned to the midpoint of each time interval. The morphological components considered are leaves, branches, aborted flowers and reproductive parts, and propagules. Under branches we grouped all parts of caulinar origin: stems, small branches, and (rarely) pieces of bark.

The meteorological data were obtained from the station in Paraíso, Tabasco, approximately 6 km SW from the study site. Mean water level was estimated as an average of the five lowest and five highest monthly water levels predicted in the 1980 tide calendar for Ciudad del Carmen, Campeche. Meteorological data were averaged in the same way as litter production.

RESULTS

Estimated average yearly litter fall for all stations was 614.45 $g \cdot m^{-2} \cdot yr^{-1}$. This value is within the range of values reported in the literature (Pool *et al.* 1975, Rico 1979, Duke *et al.* 1981, Snedaker and Brown 1982).

The average daily litter fall for the whole transect is shown in Figure 2. No significant correlation coefficients (r) were found between leaf fall in the different sampling stations and relief, nor between leaf fall per station and tree density. These results seem to suggest that leaf fall within the study area does not depend on these variables and that the environment inside the mudflat is relatively homogeneous. An analysis of variance, however, showed a highly significant variation in leaf fall with time and also a significant variation between sampling stations. A subsequent Student-Newman-Keuls test (Steel and Torrie 1980) separated station 6 (the station with the highest annual litter fall) from the rest of the set, which can be considered relatively homogeneous.[2] Hence, the rest of the analysis will refer to this homogeneous subset.

Relation between morphologic components.—The proportion by weight of fallen morphologic parts during the whole cycle was 83 percent for leaves, 9 percent for branches, 6 percent for aborted flowers and reproductive parts, and 2 percent for propagules. These results are similar to those reported by Duke *et al.* (1981) for *Avicennia marina* and Pool *et al.* (1975) for several mangrove sites in Florida and Puerto Rico. All the parts collected as branches were small—*i.e.,* in no cases were branches found that were thicker than 1.5 cm or longer than 20 cm.

Figure 3(G–J) shows the sequence of phenological

[2] Another subset, excluding only stations 9 and 10 (the stations with the lowest leaf fall), also was obtained in the same analysis. Since these subsets can be considered equally homogeneous, we chose the one with the highest number of stations.

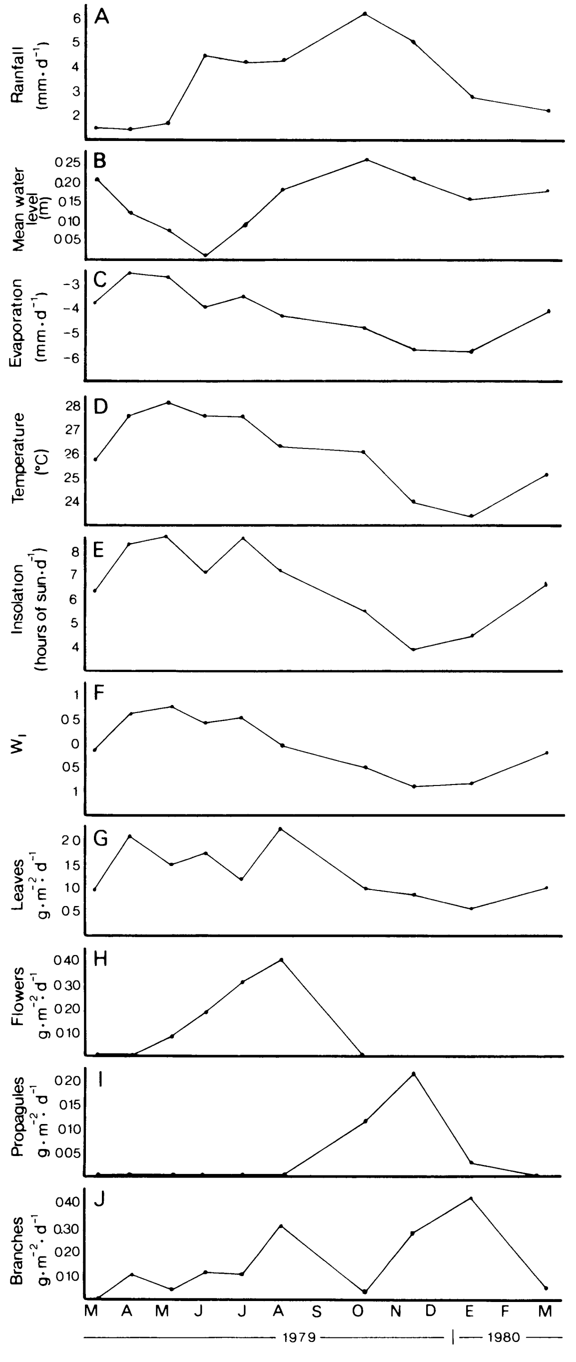

FIGURE 3. Progress of environmental factors averaged over collection interval: (A) rainfall, (B) mean water level, (C) evaporation, (D) temperature, (E) insolation, (F) principal component axis summarizing B, C, D, and E. Fall of morphologic parts averaged over collection interval: (G) leaves, (H) flowers and reproductive parts, (I) propagules, (J) branches and other woody parts.

events as evaluated through the fall of the different morphological components. There is significant variation in time for every component. Some branches seem to fall after the subtended part is shed (see Fig. 3). A multiple regression analysis showed that the fall of branches at month t is highly related to the fall of leaves and flowers during the same period and to the fall of seedlings in period $(t - 1)$ ($r^2 = 0.964$, $P < 0.0001$).

Relation with environmental factors.—A multiple correlation analysis also was calculated between daily fall of the different litter components, taken as the dependent variables, against a set of environmental variables which included local rainfall, estimated mean water level, evaportion, temperature, and insolation (Fig. 3A–E). It was found that, with the exception of local rainfall near the estuary, all the other variables were highly intercorrelated (Fig. 3B–E), making multiple regression unsuitable. To overcome this problem, the last four variables were reduced to one single axis (W) through principal component regression (Draper and Smith 1981). The new principal component values (W) can be considered as an index summarizing the four variables. The new axis (W), explaining 82 percent of the variability in the four original environmental variables, was obtained from the equation:

$$W(t) = -0.4194\, Z_1(t) - 0.5149\, Z_2(t) + 0.5227\, Z_3(t) + 0.5345\, Z_4(t)$$

where W represents the value of the principal axis at time (t) and $Z_1(t)$, $Z_2(t)$, $Z_3(t)$, and $Z_4(t)$ represent, respectively, the centered and standardized values of the variables water level, evaporation, temperature, and insolation at time t. The numerical coefficients represent the first eigenvector of the 4 × 4 correlation matrix, accounting for 82 percent of the trace. The correlation coefficients between each variable and the new axis are as follows ($N = 10$): $r = -0.76$ for water level, $r = -0.93$ for evaporation, $r = 0.95$ for temperature, and $r = 0.97$ for insolation (Fig. 3F).

It was found that this new axis was significantly correlated with leaf fall ($r = 0.65$, $P < 0.05$) and with propagule fall ($r = -0.68$, $P < 0.05$). Correlation between total litter fall, and the fall of individual morphological components, against local rainfall in the estuary was nonsignificant.

DISCUSSION AND CONCLUSIONS

Progression of phenologic events.—Although leaves fall all the year round, there is an evident temporal variation in the shedding intensity. From April to September, leaf fall tends to be higher than during the rest of the year. Flowering, as indicated by the shedding of aborted flowers and flower parts, has a peak in July, August, and September. Seedlings are shed 3–4 months later and show a peak in December. The fall of branches is highly correlated with the shedding of the parts they subtend—*i.e.*, leaves, flowers, and propagules. There is a high peak in branch shedding approximately 45 days after propagules have fallen. This probably occurs because no living buds are present on the stems which supported the inflorescences; once all the seedlings fall, these stems have no functional value and consequently are shed.

The timing of the flower and leaf fall resembles that reported by Rico (1979) for *A. germinans* in Veracruz, Mexico, but is different from that reported by Wium-Andersen and Christensen (1978) for a Southern Thailand forest occupied by *A. marina* (with a flowering period from April to June and high leaf fall from August to January) and by Williams *et al.* (1981) for *Avicennia* species (most likely *A. marina*) in northeastern Australia, with heavier leaf fall in Autumn (February to April).

It is interesting to note that, during this study, an increase in leaf fall was registered when the intensity of flower fall was highest. This coincides with the reports by Rico (1979) and Williams *et al.* (1981) but differs from the pattern reported by Wium-Andersen and Christensen (1978), who found a depression in leaf-shedding rates when production of flowers was at a maximum.

Environmental influence on litter fall.—Three points of interest emerge from the statistical study of litter fall in relation to environmental data: (a) estimated mean water level, evaporation, temperature, and insolation are highly intercorrelated variables which can be summarized in one principal axis that describes the general conditions of the estuary; (b) local rainfall has little influence on these general conditions (*i.e.*, it is statistically independent); and (c) litter fall is strongly associated with the general conditions of the estuary (described by water level, evaporation, temperature, and insolation) but shows no statistical relation to local rainfall. On this basis, two different seasons can be described in the Mecoacán system under study: (a) a drier and hotter season with low water levels, intense evaporation, and high substrate salinity from April to September; and (b) a wetter and colder season with higher water levels and lower substrate salinity induced by lower evaporation and higher continental rainfall runoff, from October to March.

Although rainfall has proved to be an important environmental factor in the phenology of some *Rhizophora* species (Christensen and Wium-Andersen 1977, Williams *et al.* 1981), lack of correlation between local rainfall and the growth pattern of *A. marina* has been reported (Wium-Andersen and Christensen 1978). These different responses of the two main mangrove genera possibly are associated with the characteristic geomorphic environment *Avicennia* species occupy: mainly mudflats, or basins in the upper intertidal zone (Wium-Andersen and Christensen 1978, Duke *et al.* 1981). In the Mecoacán lagoon, which is part of the Grijalva-Mezcalapa large deltaic system occupying the Tabasco lowlands (Fig. 1), the salinity and water level of these mudflats may be much more related to the total continental runoff than to the direct impact of local rainfall. Continental runoff in Tabasco is mostly a product of rains in the Sierra Madre de Chiapas, and there is a time lag of around 2 months for continental rains to affect water levels and salinities in the estuaries.

Other authors mention general wet or dry periods (Pool *et al.* 1975) and drought conditions (Lugo and Snedaker 1975) as the possible causal factor in the sequence of phenological events in mangrove communities. These explanations are consistent with our results, although there is a contradiction between our data and the results reported by Pool *et al.* (1975), since we found a higher leaf fall during the dry season (April to September).

The high correlation between environmental variation and the shedding of leaves and seedlings suggests that the change in time in the shedding pattern is of adaptive value. Rabinowitz (1978) has shown that extrapolated median lifetime of *Avicennia* propagules is longer in fresh than in salt water, and an adequate water level is essential for their dispersal (see also Steinke 1975). Salinities in Mecoacán are at a minimum in late fall. Mean water salinity values, measured for 22 sampling stations distributed around the lagoon, were 3.7 for December 1979, 9.4 for February 1980, and 13.0 mmhos·cm^{-1} for May 1980, showing a tendency to increase during the months of low water levels and high evaporation. Hence, the shedding of flowers and branches appears to be a consequence of the general strategy of the species: it tends to lose more leaves (possibly decreasing leaf cover) during high water-stress periods, while it tends to drop seedlings during periods of high water level and milder salinity conditions.

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