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# Zonation in Mangrove and Salt Marsh Vegetation at Laguna de Mecoacán, México[1]

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## ABSTRACT

Plant zonation and distribution of two mangrove (*Avicennia germinans* and *Rhizophora mangle*) and three salt marsh species (*Batis maritima, Spartina spartinae,* and *Pithecellobium lanceolatum*) were studied along two transects with contrasting degrees of disturbance, but with corresponding landforms. In the first, undisturbed transect, soil samples were collected during the dry, low water level season and analyzed for physico-chemical characteristics. These changed continuously with relief, whereas the relation between cover and height of *A. germinans* and relief changed in a discrete manner. During the wet, high water level season, variation in salinity was unrelated to relief. In the second, disturbed transect, *B. maritima* occupies the mudflat from which *A. germinans* trees were removed by clear-cutting at least 16 years ago. Although a physiological response might account for the low *Avicennia* cover and height in the hinterland, *Batis* is probably excluded by *Avicennia* from the mudflat, the result being the observed zonation.

## RESUMEN

La zonación y la distribución de dos especies de manglar (*Avicennia germinans* y *Rhizophora mangle*) y tres de marisma (*Batis maritima, Spartina spartinae* y *Pithecellobium lanceolatum*) se estudiaron a lo largo de dos transectos con formas contrastantes de perturbación, pero correspondientes en geoformas. En el transecto no perturbado se colectaron muestras de suelo en la estación seca, de menor nivel de agua, y se analizaron sus características fisicoquímicas. Estas cambiaron de manera contínua con el relieve, en tanto que la relación entre la cobertura y la altura de *A. germinans* con el relieve cambió en forma discreta. En la estación de alto nivel de agua, la variación en la salinidad no se relacionó con el relieve. En el transecto perturbado, *B. maritima* ocupa la planicie lodosa de la que los árboles de *A. germinans* fueron removidos por aclareo hace al menos 16 años. En tanto que una respuesta fisiológica podría explicar la baja cobertura y altura de *Avicennia* en los suelos altos, esta especie probablemente excluye a *Batis* de la planicie lodosa, ocasionando la zonación observada.

PLANT ZONATION IN MANGROVES was interpreted by Davis (1940) as a consequence of ecological succession. This view was challenged by Thom (1967) on geomorphological grounds and by Chapman (1969), who argued that, under changing sedimentation conditions, some species will be displaced by others that are better adapted to the new conditions of the environment, even if this implies a regression towards "immature stages" in successional terms (Ball 1980, Lugo 1980). Most research on the zonation of halophytes has focused on the relation of plants to physical conditions of the environment and on interspecific relations. Hinde (1954) and Adams (1963) considered tidal fluctuation and microrelief to be the primary factors conditioning plant zonation. Eleuterius and Eleuterius (1979), however, alleged that the relation between plant zonation and water level is complex and involves other factors, such as soil conditions and biotic interactions. Stressing the importance of biotic relations in salt marsh vegetation, Vince and Snow (1984) argued that without adequate experimental evidence plant zonation cannot be attributed solely to physical factors.

Implicitly related to the zonation dilemma, recent work has analyzed the importance of plant responses to changes in salinity (Ball & Farquhar 1984a, b), salt resistance mechanisms (Mizrachi *et al.* 1980), and plant growth strategies (physiognomic by Ustin *et al.* 1982, phenologic by Nestler 1977, and morphometric by Seliskar 1985). Nutrient levels (P and N) have been experimentally studied under field conditions (Boto & Wellington 1984), and sulfide concentration and soil aeration have been identified as factors influencing plant productivity in salt marshes (King *et al.* 1982, Wiegert *et al.* 1983, Armstrong *et al.* 1985) and mangrove distribution (Nickerson & Thibodeau 1985). Selective exclusion by Silander and Antonovics (1982) and reciprocal transplants by Snow and Vince (1984) and Vince and Snow (1984) have shown that interspecific relations can play an important role in determining plant zonation in coastal environments.

This paper describes the relation between edaphic conditions and the distribution, abundance, and physiognomy of five halophylic species—two mangroves, *Avicennia germinans* L. and *Rhizophora mangle* L., and three salt marsh species, *Batis maritima* L., *Spartina spartinae* (Trin.) Merr, and *Pithecellobium lanceolatum* (H. et B.) Benth—along a transect near the inlet of the Mecoacán lagoon (Tabasco,

- Avicennia germinans mangal
- Disturbed Avicennia germinans mangal
- Halophytic community
- Crops with Cocos nucifera or Theobroma cacao
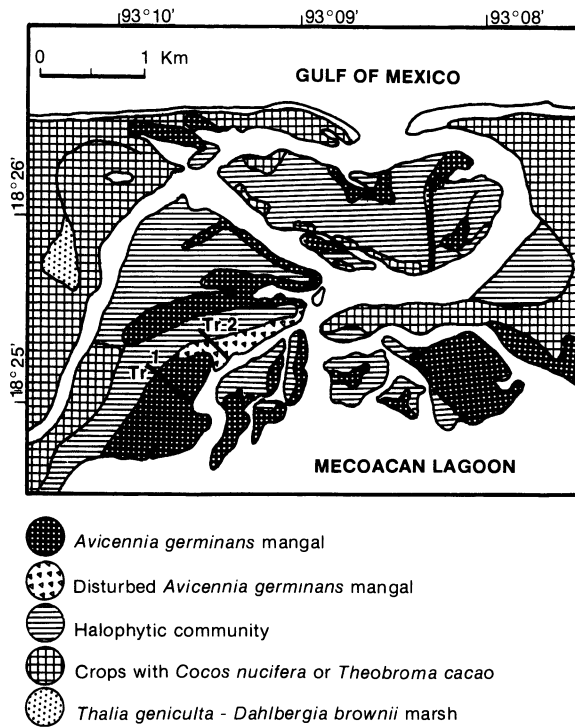- Thalia geniculta - Dahlbergia brownii marsh

FIGURE 1. Vegetation communities near the inlet of the Mecoacán lagoon indicating the location of transects 1 (tr1, undisturbed) and 2 (tr2, disturbed).

Mexico) that showed a marked, mostly unspecific banded zonation. We emphasize the possible interaction between *A. germinans* and *B. maritima,* from which complementary data belonging to disturbed areas is analyzed.

## METHODS

The study area is located NW of Laguna de Mecoacán (18°25′N, 93°10′W) in Tabasco, Mexico, near the inlet of the lagoon (Fig. 1). One transect was traced perpendicular to the lagoon fringe on a well preserved area and divided into 23 sampling stations 30 m apart from each other. Only station 3 showed some evidence of disturbance (sparse fallen trees).

Topographic level, soil oxygen, and temperature were measured directly in the field at each station. Twenty-five soil samples (belonging to the 23 stations, the immediate fringe, and the bottom of the lagoon) were collected on 28 June 1979 from 0 to 30 cm depth (where contribution of root biomass is most significant). They were dried at ambient temperature, homogenized, and sieved (2 mm mesh size) for subsequent analysis.

The methods used for the measurement of soil vari-ables were: (1) pH on a potentiometer using a mixture 1:2.5 soil : distilled water (for actual acidity, *sensu* Mengel & Kirkby 1982), and a mixture 1:2.5 soil : KCl solution 1 N, pH 7 (for potential acidity); (2) Cl by titration with silver nitrate; (3, 4) $Ca^{+2}$ and $Mg^{+2}$ by titration with EDTA; (5, 6) $Na^+$ and $K^+$ by flammometry; (7, 8) and $CO_3^{-2}$ and $HCO_3^{-}$ by titration with sulphuric acid (Richards 1974). Salt content was obtained by weight difference after evaporating 10 ml of the saturation extract, texture was obtained by the Bouyoucos (1963) method, and oxygen at ten cm (average root depth) was estimated by the Hoffer indirect method on two occasions (3 May 1979 and 14 April 1980) by evaluating the presence of ferrous (reduced) and ferric (oxidized) ions in the profile (Jackson 1976). Soil temperature was measured with a thermometer at two cm depth on a clear, hot, and sunny day (6 April 1979) between 1400 and 1500 h local time.

Electrical conductivity was measured by saturation extract on 28 June 1979 and by saturation paste on 14 April 1980. The purpose of this second measurement was to cover the range of variation in salinity through the annual cycle. As the determination of electrical conductivity differed on the two occasions, a selected number of the collected soil samples were simultaneously measured by saturated paste and saturation extract. A linear function that allowed the conversion of one measurement into the other was adjusted to the data ($r = .99$, $P < 0.05$, $N = 5$).

At every station, plant cover was measured in a 10 m × 10 m square by 50 random coordinates. In each point an optical vertical line was established with an automatically levelling pentaprism (Montaña & Ezcurra 1980), and interceptions by the foliage of different species were counted. Additionally, the height of the four dominant trees in each square was measured with a hand-held level. Average pneumatophore density was estimated from five random points within the sampling square, by counting in each point all the pneumatophores that fitted in a metal frame of 0.25 cm × 0.25 cm. Height was estimated from 20 randomly chosen pneumatophores per station.

A second transect approximately 500 m northeast of the first one was traced along 390 m (13 stations) in an area where the mudflat had been highly disturbed by the clear cutting of *Avicennia* trees about 16 years before (we do not know if more than one clearing has been made in this area during this period). Data corresponding to height and cover of *Avicennia* and *Batis* in the mudflat are presented here. Other data (relief, conductivity, and soil oxygen) are reported in López-Portillo (1982).

## RESULTS

Based on plant distribution and landforms, the transect was divided into five bands (*cf.* Figs. 2 and 3a): the
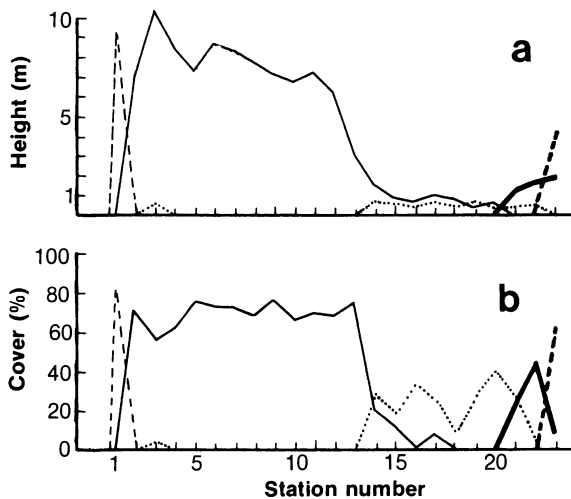
FIGURE 2. Height (a) and cover (b) of *Rhizophora mangle* (fine broken line), *Avicennia germinans* (fine line), *Batis maritima* (pointed line), *Spartina spartinae* (bold line), and *Pithecellobium lanceolatum* (bold broken line) along transect 1. Distance between stations is 30 m.
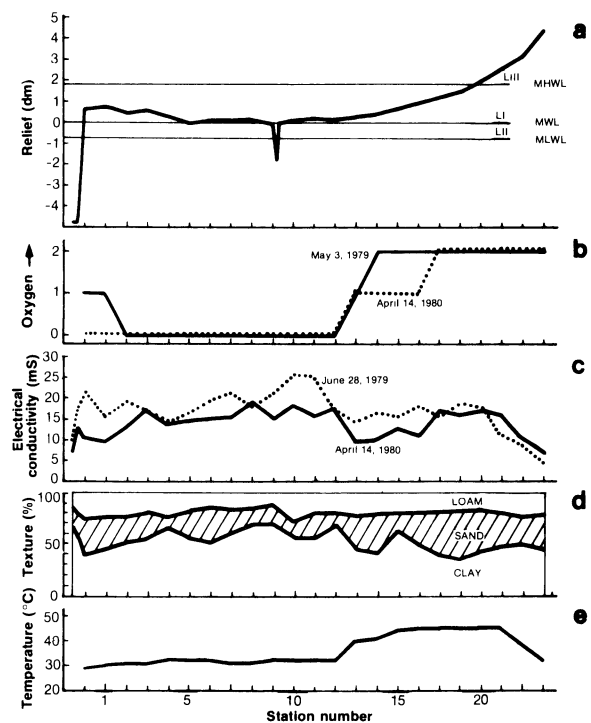


FIGURE 3. Environmental measurements along transect 1: (a) relief, (c) electrical conductivity, (b) oxygen level by Hoffer's colorimetric method, (e) soil temperature at 2 cm depth on 6 April 1979, and (d) texture (% sand. loam, and clay). For (a); LI, LII, and LIII are the water levels for 6 April, 28 June, and 9 October 1979; MLWL, MWL, and MHWL are the mean low, mean, and mean high water levels, respectively.

elevated *Rhizophora* fringe (station 1); the *Avicennia* mudflat (stations 2–13), which occupies the lowest reliefs in the transect; the low hinterland occupied by *Batis* and dwarfed *Avicennia* (stations 14–20); and the high hinterland (stations 21–23), occupied by *Spartina* and *Pithecellobium,* the latter being present only in the highest station of the transect. Relief correlated in a negative linear manner with *Avicennia* pneumatophore density and height ($P < 0.05$). The height and cover of *Avicennia* (Fig. 2) showed an abrupt change that is more evident when plotted against relief, although this effect was not apparent in *Batis* (Fig. 4a–d).

THE PHYSICO-CHEMICAL ENVIRONMENT.—Analyses of variance showed that most soil variables differ significantly between the three vegetation-landform bands (the fringe was not tested because of the lack of degrees of freedom). A Student-Newman-Keuls (SNK, Sokal & Rohlf 1981) test for different sample sizes was used to analyze the differences between the means in each environment (Table 1).

Mean low and high tidal water levels were calculated from a standard tide calendar as indicated in López-Portillo and Ezcurra (1985). Water level was measured directly in the lagoon on three occasions to provide fixed data lines that would allow adjusting the tide calendar to the specific levels of the lagoon (Fig. 3a). Soil oxygen in the fringe and low hinterland were low during the high water level season and acceptable during the dry season. Anaerobic

conditions prevailed in the mudflat at both sampling dates, but the high hinterland always showed good aeration (Fig. 3b).

The measurement of electrical conductivity was made on dates that represent the two contrasting seasons (Fig. 3c). Under high water level (14 April), conductivity along the transect was homogeneous; under low water level (28 June), conductivity was significantly higher in the mudflat and low hinterland (Table 1). Mean conductivity along the transect on 28 June was 3.5 mS higher than on 14 April. Similarly, salt concentration in June was higher in the lowest landform, the mudflat, which is always flooded or at least water-saturated. In the hinterland, lower soil moistures were indicated by polygonal cracking of the dried, clayey soils.

To analyze the importance of Na against K uptake, we used the sodicity ratio (Na/K) used before by Rains and Epstein (1967 in Rains 1972), Ball and Farquhar (1984a), and as K/Na by Downtown (1982). The concentration of all ions except $CO_3$ was positively correlated
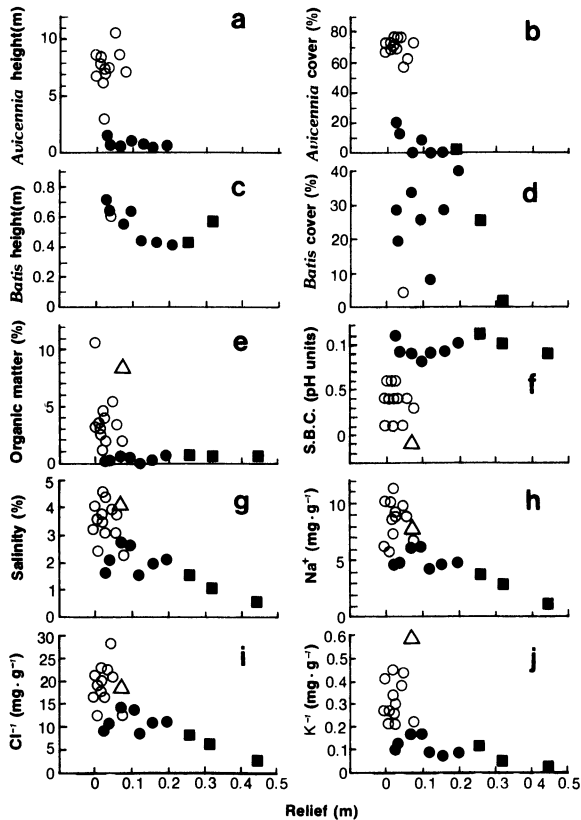
FIGURE 4. Height and cover of *Avicennia* and *Batis* (a–d) and soil characteristics plotted against relief (e–j) for transect 1. SBC = soil buffering capacity. Symbols represent the landform each station occupies: triangle, fringe; empty circles, mudflat; full circles, low hinterland; and squares, high hinterland. Note the discrete distribution of *Avicennia* height and cover against the continuous distribution of the other variables.

with salt content ($P < 0.05$ in all cases). In relation to landform and vegetation type, the results of the SNK test showed different groupings (Table 1): percent salts, Na, and Cl differed significantly in the three bands and increased towards the mudflat. The cations K and Ca and the Na/K ratio differed significantly between the mudflat and the hinterland. Carbonate and bicarbonate cations less clearly defined differences between bands. A two-dimensional ordination of the stations using Na/K and percent salinity clearly distinguished between the described environments (Fig. 5a), suggesting differences in the quality of salts.

Soil composition (Fig. 3d) was higher in sand content at the bottom and contiguous fringe of the lagoon. Sand content decreased in station 1 to give way to a clayey loam. The mudflat was clayey in texture. From station 13

onwards sand percent increased, giving way to a clayey loam in station 18 and a clayey-sandy loam in station 19 (this change in texture may indicate, as suggested by tide estimations, the mean water level limit), and subsequently decreased to a clayey texture in the rest of the sampling stations. The SNK test indicated differences only between the mudflat and the low hinterland.

SOIL CHARACTERISTICS INFLUENCED BY THE ESTABLISHMENT OF VEGETATION.—Observed soil temperature ranged from 25 to 40°C and differed significantly on the three bands, the highest temperature occurring on the hinterland (Fig. 3e). The soils covered by *Rhizophora* showed one of the highest organic matter contents (8%). The soils under *Avicennia* showed a comparably high content only in station 10 (10%), but the neutral pH indicates that it is qualitatively different. A waterway passes near this site, so the organic matter might be of allochthonous origin. The SNK test indicated that organic matter was significantly more abundant in the mudflat soils (range excluding station 10: 1.11–5.29%) than in the hinterland (0.12–0.69%).

Actual acidity (extracted with distilled water) fluctuated along the transect from 5.1 to 8.1, and potential acidity (extracted with KCl solution) from 5.2 to 7.3. The difference between both, which is an inverse measurement of the buffering capacity of the soil, was negatively correlated ($P < 0.05$) to organic matter content (Fig. 4e–f). This difference is minimal under the *Rhizophora* soils, where partially decomposed radicular fibres dominate and give the soil a high acidity. Under *Avicennia* the differences were higher, but were significantly lower than in the hinterland (Table 1). A two-dimensional ordination of stations, taking the soil buffering capacity and the organic matter content as axes, separates the mudflat from the hinterland (Fig. 5b).

TRANSECT 2.—This transect is similar to transect 1 in relief and soil oxygen (López-Portillo 1982), but the mudflat is dominated by *Batis*, growing abundantly between young *Avicennia* trees (mean height 1.86 m, SE 0.12 m) that had established after clear-cutting. Pooling together all the disturbed mudflat stations (station 3 from transect 1 and mudflat stations 1–6 from transect 2), a significant inverse correlation ($r = -.91$, $P < 0.005$) was found between the cover of *Avicennia* and the cover of *Batis* (Fig. 6). A major axis linear regression (Sokal & Rohlf 1981) between these two variables gave a slope coefficient (*b*) of 0.96.

## DISCUSSION

VARIATION IN PHYSICO-CHEMICAL CHARACTERISTICS.—Although environmental variation is basically continuous, there seems to be a threshold after which *Avicennia* changes its life-form. The reasons for this drastic change may be

TABLE 1. *Average values of environmental variables in the different landforms along transect 1. Landforms are: stable fringe (station 1), mudflat (stations 2–13), low hinterland (stations 14–20), high hinterland (stations 21–23). Same letters indicate no significant differences (P > 0.05) from the SNK test. Except where indicated, soil variables were measured on samples taken on 28 June 1979. Soil parameters are ordered first as a decreasing function of their capacity to discriminate between environments through the SNK test, and second by the F values from the ANOVAs. Significances of the ANOVA are indicated by asterisks: \*\*\*, P < 0.005; \*\*, P < 0.01; \*, P < 0.05; n.s. not significant.*

| Environmental factor | Stations | | | | F | Significance |
|---|---|---|---|---|---|---|
| | 1 | 2–13 | 14–20 | 21–23 | | |
| % salts | 3.86 | 3.54a | 2.07b | 1.04c | 25.69 | \*\*\* |
| Na | 7.80 | 8.53a | 5.03b | 2.66c | 23.48 | \*\*\* |
| Cl | 18.64 | 19.29a | 11.10b | 5.51c | 21.11 | \*\*\* |
| Temperature | 29 | 32c | 44a | 39b | 53.69 | \*\*\* |
| K | 0.585 | 0.031a | 0.109b | 0.061b | 29.23 | \*\*\* |
| Ca | 2.52 | 2.52a | 1.231b | 0.678b | 22.92 | \*\*\* |
| Na/K | 13.3 | 28.5a | 48.3b | 46.6b | 18.92 | \*\*\* |
| Organic matter | 8.36 | 3.69a | 0.27b | 0.59c | 8.82 | \*\* |
| Soil buffering capacity | −1 | 0.37b | 0.93a | 1.0a | 38.47 | \*\*\* |
| Actual acidity | 5.1 | 7.3b | 7.6a | 7.9a | 3.64 | \* |
| Electrical conductivity | 21.7 | 19.4a | 16.6ab | 8.0b | 17.05 | \*\*\* |
| CO₃ | 0 | 0.419a | 0b | 0.726a | 3.25 | n.s. |
| HCO₃ | 0.229 | 0.349a | 0.192b | 0.207 | 3.64 | \* |
| Potential acidity | 5.2 | 7.0a | 6.6b | 6.9ab | 3.59 | \* |
| Clay | 40 | 59a | 45b | 48ab | 8.01 | \*\* |
| Sand | 40 | 21a | 35b | 30ab | 8.59 | \*\* |
| Mg | 0.396 | 0.199a | 0.135b | 0.148ab | 2.91 | n.s. |
| Electrical conductivity (14 April) | 10.5 | 15.3 | 13.3 | 10.8 | 2.90 | n.s. |

related to the effect on growth of lower water potentials (*i.e.*, the more distal buds have a higher probability of death) during the dry season, and to lower nutrient input (P and N) in the low hinterland caused by less frequent flooding through the annual cycle (*cf.* Boto & Wellington 1984).

Other factors probably involved are the higher concentration of Na and Cl in the hinterland, as well as the higher salinity. This means that the less abundant macronutrients (*e.g.*, K and Mg) must be incorporated selectively by the plant through a mechanism active for relatively low ion concentrations of the type suggested by Rains (1972), which increases metabolic expenditure and transpiration. For example, the proportion Na/K diminished from 40/1 in the environment to 7/1 in the leaves of *Avicennia marina* (Rains & Epstein 1967, cited by Rains 1972). Our own (average) values for this ratio are 29/1 in the mudflat soil against 48/1 in the hinterland soil, which indicate highly unfavorable conditions in the latter environment. Also, it is known that the physical and mechanical properties of the soil deteriorate when Na concentration increases (*e.g.*, Clarke & Hannon 1967), so the cost of producing below-ground biomass must also increase.

As the life-form of *Avicennia* changes from tree to shrub, *Batis* increases its presence. The relatively constant

height of *Batis* along the transect suggests that this species shows an ample tolerance range to environmental variation. The differences in *Batis* cover, which appear to be distributed bimodally, suggest that its establishment is inhibited by the mechanical effect of tidal overwash (Chapman 1964, Ranwell 1972) and the physical effect of higher sand content in the soil (McMillan 1975).

The high hinterland is flooded for a shorter period, and its salinity is lower. In this part of the transect infrequent anaerobiosis, higher relief, clayey texture, and decrease of salinity associated with the distance from the lagoon fringe combine to form a cline with progressively lower flooding levels toward station 23. This change is reflected in the species present. In higher reliefs, *Spartina* tends to dominate in height and cover, but by station 23 it is substituted by *Pithecellobium*.

Other characteristics that change with relief are the organic matter content and the buffering capacity of the soil, which were higher in the forested environments. Soil reduction is probably associated with flooding and the presence of plant species (Hesse 1961, Gledhill 1963, Dent 1980).

When analyzing successional patterns in mangroves, Ball (1980) suggested that each landform is characterized by a different set of physical conditions. This has been a constant claim in the work published by geomorphologists
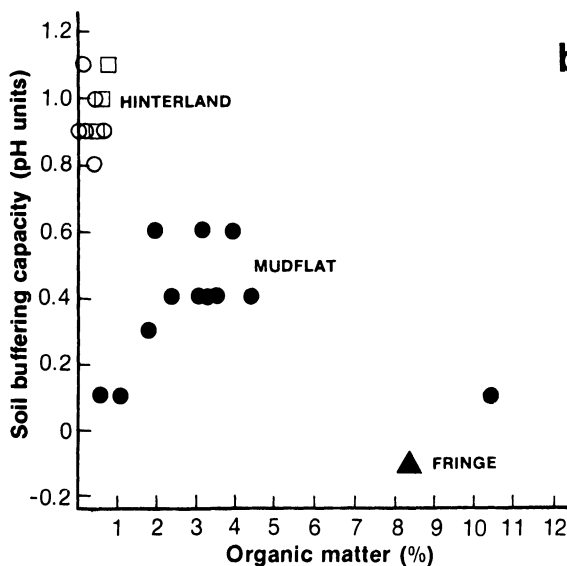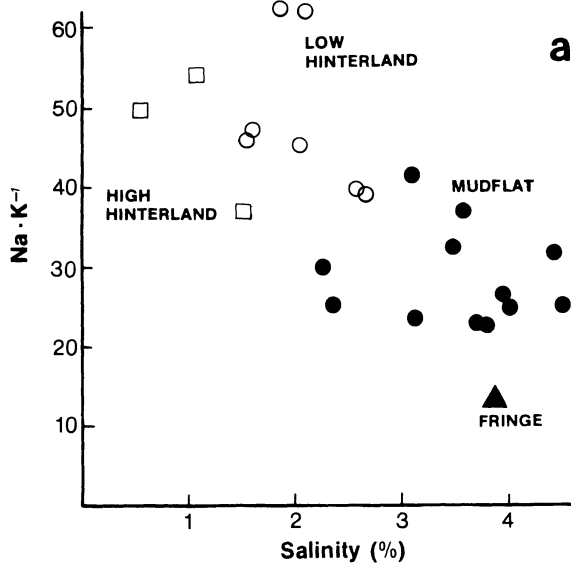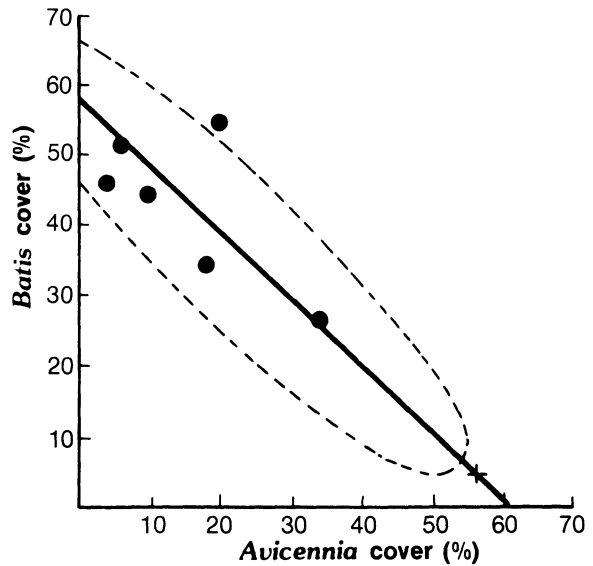
FIGURE 6. *Batis* cover against *Avicennia* cover on disturbed sites from transect 1 (full circle) and transect 2 (cross) ($r = -.91$, $P < 0.005$). The ellipse shows the 95 percent confidence limits for the normal bivariant distribution, the regression line ($y = 57.8 - 0.96x$) shows the principal axis of the sample cluster.

FIGURE 5. Bidimensional ordination of sampling stations along transect 1: (a) Na/K index vs percent salts, and (b) soil buffering capacity vs percent organic matter.

(*e.g.*, Thom 1967, Flood 1980, Semeniuk 1985). Our results point in a similar direction, since most characteristics measured in the dry season separated at least the mudflat from the hinterland environments. However, their individual change along relief is continuous. Even the plant-related physical characteristics measured did not show the same discrete distribution found in the height and cover of *Avicennia* along the transect. However, the synergistic

effect of different factors cannot be excluded as an explanation of differences in species distribution and physiognomic change, as noted in the relationship between the Na/K index and salinity.

SPECIES INTERACTIONS.—Taking into account the fact that *Batis* is physiologically capable of growing in the mudflat, it could be hypothesized that the nonoccurrence of this species in the mudflat is related to competitive exclusion. This is supported by the slope of the regression line in Figure 6, which was not significantly different from unity, indicating that for every unit of *Avicennia* cover that is removed from the mudflat's overstory, a similar amount of *Batis* will cover the understory. Furthermore, the degree of overlap measured as Colwell and Futuyma (1971) between *Avicennia* and *Batis* was 0.05 for transect 1, compared with 0.51 for the disturbed stations.

*Avicennia* can displace *Batis* in two ways, not mutually exclusive: by root competition for space or by overshadowing the *Batis* shrubs. In the low hinterland, where *Avicennia* is dwarfed and its cover is not comparable to that in the mudflat, the distance at which *Batis* appeared from the stem of *Avicennia* seemed to be related to the root cover of this species, and *Batis* is present in the mudflat of transect 1 only at the disturbed station.

One can conclude that, in these topographic gradients, the synergistic effect of some physico-chemical character-

istics coupled with water deficiency, the response of the species when coping with (and modifying) its environment, and the differential response to interspecific relations seem to be the factors that determine the observed plant zonation.

## ACKNOWLEDGMENTS

## LITERATURE CITED

ADAMS, D. A. 1963. Factors influencing vascular plant zonation in North Carolina salt marshes. Ecology 44(3): 445–456.

ARMSTRONG, W., E. J. WRIGHT, S. LYTHE, AND T. J. GAYNARD. 1985. Plant zonation and the effects of the spring-neap tidal cycle on soil aeration in a humber salt marsh. J. Ecol. 73: 323–339.

BALL, M. C. 1980. Patterns of secondary succession in a Mangrove forest of Southern Florida. Oecologia (Berl.) 44: 226–235.

————, AND G. D. FARQUHAR. 1984a. Photosynthetic and stomatal responses of two Mangrove species, *Aegiceras corniculatum* and *Avicennia marina*, to long-term salinity and humidity conditions. Plant Physiol. 74: 1–6.

————, AND ————. 1984b. Photosynthetic and stomatal responses of the Grey Mangrove, *Avicennia marina*, to transient salinity conditions. Plant Physiol. 74: 7–11.

BOTO, K. G., AND J. T. WELLINGTON. 1984. Soil characteristics and nutrient status in a northern Australian mangrove forest. Estuaries 71: 61–69.

BOUYOUCOS, G. J. 1963. Directions for making mechanical analysis of soil by hydrometer method. Soil Sci. 42: 25–30.

CHAPMAN, V. J. 1964. Coastal vegetation. The Commonwealth and International Library, Botany Division, Vol. 3. Pergamon Press, The Macmillan Company, U.K.

————. 1969. Lagoons and Mangrove vegetation. *In* A. Ayala-Castañares amd F. B. Phleger (Eds.). Lagunas costeras, un simposio, pp. 505–514. U.N.A.M.–U.N.E.S.C.O. No. 28–30, Mexico, D.F.

CLARKE, L. D., AND N. J. HANNON. 1967. The mangrove swamp and salt marsh communities of the Sydney district. I. Vegetation, soils and climate. J. Ecol. 55: 753–771.

COLWELL, R. K., AND D. J. FUTUYMA. 1971. On the measurement of niche breath and overlap. Ecology 52: 567–576.

DAVIS, J. H. 1940. The ecology and geologic role of mangroves in Florida. Pap. Tortugas Lab. 32. Publ. Carnegie Inst. 524: 113–195.

DENT, D. 1980. Acid sulphate soils: morphology and prediction. J. Soil Sci. 31(1): 87–100.

DOWNTOWN, W. J. S. 1982. Growth and osmotic relations of the Mangrove *Avicennia marina*, as influenced by salinity. Aust. J. Plant Physiol. 9: 519–528.

ELEUTERIUS, L. N., AND C. K. ELEUTERIUS. 1979. Tide levels and salt marsh zonation. Bull. Mar. Sci. 29: 394–400.

FLOOD, P. G. 1980. Tidal sedimentation along the shores of Deception Bay, Southeastern Queensland—a preliminary account. Proc. R. Soc. Queensl. 91: 77–84.

GLEDHILL, D. 1963. The ecology of the Aberdeen Creek mangrove swamp. J. Ecol. 51: 693–703.

HESSE, P. R. 1961. Some differences between the soils of *Rhizophora* and *Avicennia* mangrove swamps in Sierra Leone. Plant Soil 14(4): 335–346.

HINDE, H. P. 1954. The vertical distribution of salt marsh phanerogams in relation to tide levels. Ecol. Monogr. 24: 209–225.

JACKSON, M. J. 1976. Análisis químico de suelos, 3rd ed. Ediciones Omega, España.

KING, G. M., M. J. KLUG, R. G. WEIGERT, AND A. G. CHALMERS. 1982. Relation of soil water movement and sulfide concentration to *Spartina alterniflora* production in a Georgia salt marsh. Science 218: 61–63.

LÓPEZ-PORTILLO, J. 1982. Ecología de manglares y de otras comunidades de halófitas en la costa de la Laguna de Mecoacán, Tabasco. Tesis, Facultad de Ciencias, U.N.A.M. México.

————, AND E. EZCURRA. 1985. Litter fall of *Avicennia germinans* L. in a one-year cycle in a mudflat at the Laguna de Mecoacán, Tabasco, México. Biotropica 17: 186–190.

LUGO, A. E. 1980. Mangrove ecosystems: successional or steady state? Biotropica 12: 67–72.

McMILLAN, C. 1975. Interaction of soil texture with salinity tolerances of *Avicennia germinans* L. and *Laguncularia racemosa* (L.) Gaertn. f. from North America. *In* G. E. Walsh, S. C. Snedaker, and H. J. Teas (Eds.). Proc. int. symp. biol. and management of mangroves, pp. 561–566. Inst. Food Agric. Sci., Univ. Florida, Gainesville, Florida.

MENGEL, K., AND E. A. KIRKBY. 1982. Principles of plant nutrition, 3rd edition. International Potash Institute, Bern, Switzerland.

MIZRACHI, D., R. PANNIER, AND F. PANNIER. 1980. Assessment of salt resistance mechanisms as determinant physio-ecological parameters of zonal distribution of Mangrove species. I. Effect of salinity stress on nitrogen metabolism balance and protein synthesis in the Mangrove species *Rhizophora mangle* and *Avicennia nitida*. Bot. Mar. 23: 289–296.

MONTAÑA, C., AND E. EZCURRA. 1980. Simple instrument for quick measurement of crown projections. J. For. 178: 699.

NESTLER, J. 1977. Intersticial salinity as a cause of ecophenic variation in *Spartina alterniflora*. Estuarine Coastal Mar. Sci. 5: 707–714.

NICKERSON, N. H., AND F. R. THIBODEAU. 1985. Association between pore water sulfide concentrations and the distribution of mangroves. Biogeochemistry 1: 183–192.

RAINS, D. W. 1972. Salt transport by plants in relation to salinity. Annu. Rev. Plant Physiol. 23: 367–388.

RANWELL, D. S. 1972. Ecology of salt marshes and sand dunes. Chapman and Hall, London.

RICHARDS, L. A. 1974. Suelos salinos y sódicos. Limusa, México.

SELISKAR, D. M. 1985. Morphometric variations of five tidal marsh halophytes along environmental gradients. Am. J. Bot. 72(9): 1340–1352.

SEMENIUK, V. 1985. Development of mangrove habitats along ria shorelines in north and northwestern tropical Australia. Vegetatio 60: 3–23.

SILANDER, J. A., AND J. ANTONOVICS. 1982. Analysis of interspecific interactions in a coastal plant community—a perturbation approach. Nature 298: 557–560.

SNOW, A. A., AND S. W. VINCE. 1984. Plant zonation in an Alaskan salt marsh. II. An experimental study of the role of edaphic conditions. J. Ecol. 72: 669–684.

SOKAL, R., AND F. J. ROHLF. 1981. Biometry. W. H. Freeman and Company, San Francisco.

THOM, B. G. 1967. Mangrove ecology and deltaic geomorphology: Tabasco, Mexico. J. Ecol. 55: 301–343.

USTIN, S. L., R. W. PEARCY, AND D. E. BAYER. 1982. Plant-water relations in a San Francisco Bay salt marsh. Bot. Gaz. 143: 368–373.

VINCE, S. W., AND A. A. SNOW. 1984. Plant zonation in an Alaskan salt marsh. I. Distribution, abundance and environmental factors. J. Ecol. 72: 651–667.

WIEGERT, R. G., A. G. CHALMERS, AND P. F. RANDERSON. 1983. Productivity gradients in salt marshes: the response of *Spartina alterniflora* to experimentally manipulated soil water movement. Oikos 41: 1–6.

## Announcement: Flora of the Philippines Project

The Flora of the Philippines Project is designed to evaluate the status of flowering plants in the Philippine Archipelago within ten years. It will provide, as quickly as possible, information on the endangered, threatened, and vulnerable plants of the Philippines; information that need not await the completion of the entire flora. Urgency is required because most of the information being provided to conservation planners within the country is based on work accomplished in the very early part of the century.

The project will be carried out at three centers: the National Museum in Manila, the University of the Philippines at Los Baños, and the Bishop Museum in Honolulu. The three functional parts of the project are: Plant Inventory, Collections Management, and Writing/Documentation. The first two will take place in Manila, the latter in Los Baños. The Bishop Museum will serve an overall coordinating role, provide oversight, and will loan members of its staff to the project as needed.

Merrill, in his *Enumeration of Philippine Flowering Plants* (1923–1926), believed that 75% of the 8000–12,000 species in the Philippine Archipelago were endemic. This statistic is probably high, but the endemicity would be significant in any case. With the progressive loss of so much of the forest it is feared that a significant number of species have already become extinct. For this reason the project will attempt to coordinate its activities with botanical gardens and arboreta inside and outside the Philippines to try to bring particularly endangered species into cultivation.

Inquiries are welcomed. Please write to Dr. S. H. Sohmer, Bishop Museum, P.O. Box 19000-A, Honolulu, Hawai'i 96817-0916, U.S.A. Dr. Sohmer is maintaining a list of potential collaborators for the project and will respond to all inquiries. He will send upon request information concerning the organization, format, and goals of the project.