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Association between pore water sulfide concentrations and the distribution of mangroves

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Abstract. At Humingbird Cay, Exuma, Bahamas, distributions of both *Rhizophora mangle* (red mangrove) and *Avicennia germinans* (black mangrove) are closely correlated with amounts of hydrogen sulfide (H_2S) in the soil. *R. mangle* is primarily distributed within large areas of low to moderate H_2S concentrations (mean = 40 mg/l). H_2S levels under *A. germinans* are lower (mean = 22 mg/l), but the area immediately beyond their root zone often has extremely high sulfide concentrations (mean = 120 mg/l). These results suggest that past attempts to explain mangrove distribution in terms of monotonic soil gradients, the dispersal characteristics of propagules, and interspecific competition are incomplete, and that it will be necessary to examine the link between soil sulfur chemistry and mangrove distribution more fully.

Introduction

Mangroves are the dominant vegetation in areas of low tidal energy along tropical coasts (McGill, 1959). In the central Bahama islands, where this study was performed, three species occur: red mangrove (*Rhizophora mangle*), black mangrove (*Avicennia germinans*), and to a lesser extent, white mangrove (*Laguncularia racemosa*).

Most mangrove communities seem to show patterns of monospecific zonation. In Florida, it is common to find *Rhizophora mangle* in regularly-flooded intertidal areas and *Avicennia germinans* behind it, at slightly higher elevations with inundation of less duration. Davis (1940) ascribed this patterning to succession based on land-building and the subsequent gradient of soil water salinity. Until recently, further studies (reviewed in Walsh, 1974; and Lugo and Snedaker, 1974) tended to support the broad hypothesis that spatial patterning is a result of individual plants' response to soil saturation or salinity. They also tended to reject Davis' original idea that this patterning is evidence of succession.

Rabinowitz (1976) challenged all these hypotheses by demonstrating that any of the four species of mangrove she examined in Panama, including the three found in the Bahamas, grows successfully in a zone predominantly inhabited by another. She suggested that tidal action sorts propagules by size, and therefore that zonation is independent of later physiological responses.

Ball (1980) has advanced yet another hypothesis. She confirmed that seedlings can root in any zone, but argued that interspecific competition for light becomes the dominant force determining species distribution in mature communities. This competition, she reasoned, forces species less competitive than *Rhizophora,* such as *Laguncularia,* into physiologically sub-optimal habitats.

Snedaker and Brown (1981) found significant anomalies between the patterns seen in the field and the results predicted by any of these models. None of them was satisfactory either in itself, or in combination, to explain the 'vigorous mangroves in poor environments', and 'mangroves showing severe growth restrictions in ostensibly optimum environments' which they observed.

All of the models reviewed above, as well as Snedaker and Brown's (1981) obections to them, assume that relevant geochemical parameters vary smoothly along a gradient perpendicular to the shoreline. However, the soils are a complex composed of varying layers of calcareous sand, mud, marl, shell, and mangrove peat. The latter is almost always anaerobic and therefore strongly reduced below a depth of a few centimeters (Odum et al., 1982). If soil parameters are variable with respect to a factor influencing species distribution within a single 'zone,' then all of these models need at least partial modification.

To the best of our knowledge, there has never been an investigation of sulfur cycling in mangrove ecosystems but, in temperate salt marsh, large standing stocks of reduced sulfur compounds may be present in the sediments (Howarth and Teal, 1979). While most of the reduced sulfur within the marsh was in the form of pyrite, hydrogen sulfide was also present (Howarth et al., 1983). Linthurst (1979) found that sulfide reduced the growth of the dominant plant species, *Spartina alterniflora,* and King et al. (1982) documented changes in both plant height and productivity associated with soil H_2S levels.

Data available on the chemistry of mangrove soils suggest that the role of reduced sulfur compounds may be fully as important in mangrove forests as it is in salt marshes. Hesse (1961b) demonstrated that reduced sulfur compounds are present under both *Rhizophora mangle* and *Avicennia germinans* and that such compounds occur in greater amounts in the muds under *R. mangle.* With anaerobic incubation, most of the sulfate in oxidized and re-reduced *Rhizophora* mud was converted to sulfide (Hesse 1961a). Dent (1980) showed that mangrove soils in New Zealand are 'always sulphidic' and that sulfide is associated with the fibrous roots of the one mangrove species of the area, *A. marina* var. *resinifera.* Carlson et al. (1983) quantified the amount of sulfide under both *R. mangle* and *A. germinans* in the field. They found *Rhizophora* sediments to have concentrations of H_2S between 0 and

1500 M and *Avicennia* soils to have concentrations of H_2S between 0 and 100 M. They also showed that concentrations were correlated with seasonal changes in flooding frequency and with depth into the soil.

In the study reported here we have demonstrated:

(1) That there is no clear zonation of mangroves parallel to the shore at Humingbird Cay,
(2) That pore water H_2S concentrations vary in a regular way among areas under *Avicennia, Rhizophora,* and in nearby unvegetated areas, and
(3) That the pattern of this variation suggests *Rhizophora* is primarily limited to pre-existing areas of low H_2S concentration while *Avicennia* decreases pore water sulfide.

Study area

Humingbird (Jewfish) Cay is an uninhabited island at 23.5°N 76°W, west of George Town, Great Exuma, in the central Bahama Islands. It is approximately 145 ha in area. Extensive growths of mangroves occur at three sites on the island, covering approximately 6000, 3500, and 200 m^2. All are 'fringe forests' by the classification of Lugo and Snedaker (1974) in that they occur along 'the fringes of protected shorelines' of the island and have 'low tidal velocities'.

All of these communities are exposed to diurnal rise and fall, and none is subject to any freshwater stream flow. At all sites, *Rhizophora mangle* and *Avicennia germinans* predominate. There are only a few scattered individuals of *Laguncularia racemosa.* None of the sites appears to have the strictly classic pattern of *R. mangle* in the lower tidal area and *A. germinans* at higher elevations, which all of the models cited above attempt to explain. In fact, we estimate that less than half of the mangrove communities in the central Bahamas follow this pattern.

At both of the larger mangrove forests which are examined in this study, there is a gradual rise in surface elevation without marked dips or rises. The soils at these sites are composed of layers of calcareous particles (oolites and peolites), finer muds, and mangrove peat. These layers vary substantially in pattern and thickness both within and among sites. Previous observations indicate that the depth to bedrock at both study sites is always less than 1 m, confining both roots and the following observations to the same vertical zone. Nickerson and Sullivan (1974) provided a more detailed description of near-shore soils on Hummingbird Cay.

Methods

In March, 1982, three transects at least 10 m apart were established in both of the large mangrove forests, which are on the west and north shores of the island. All transects ran perpendicular to the shore from the low-tide line to a point above the highest tide, beyond which no mangroves occurred. A total of 118 stations, each 1 m apart, was established along these transects.

At each station, two depth-integrated measurements of H_2S concentrations were taken in a well sealed from surface water. First, a piece of polyvinyl chloride pipe 5 cm in diameter was driven into the substrate approximately 10–15 cm, a depth sufficient to form a watertight seal with the underlying peat layer. A 30 cm core of material was then removed using a 1.25 inch diameter soil auger. Within approximately 15 seconds, the pipe would begin filling with pore water. Its H_2S content was determined immediately using the method described below. The water in the pipe was then drained using a hand pump, the well deepened to 45 cm, and the procedure repeated. At 22 of the 118 stations, it was impossible to drill to 45 cm without hitting the underlying rock, and therefore, some data from this depth are missing.

Measurements of H_2S concentration were made using an Orion Model 407A Portable Specific Ion meter with a Model #951600 hydrogen sulfide electrode. This electrode measures dissolved H_2S. It is insensitive to HS^- and $S^=$. The electrode was calibrated each day using freshly prepared 1, 10, and 100 mg/l solutions of Na_2S acidified with H_2SO_4 using the procedure developed by its manufacturer. In the field, the calibration was rechecked after each reading as recommended (Orion Research, unpublished operation manual) using a supersaturated solution of ZnS acidified with .5 m H_2SO_4, which produced a constant 10 mg/l of H_2S; it was seldom necessary to recalibrate the apparatus.

For statistical analysis, stations along a transect were assigned to one of five categories by surface condition: (1) under the prop roots of *Rhizophora mangle;* (2) unvegetated and 1 m or less from the prop roots; (3) within the pneumatophores of *Avicennia germinans;* (4) unvegetated and 1 m or more from pneumatophores; (5) unvegetated areas more than 1 but less than 3 m from any pneumatophores. Any station which has features of two or more categories was assigned by random number to one of them (e.g., a station within the prop roots of *R. mangle* where penumatophores were also present).

To examine the hypothesis that the mangroves of Hummingbird Cay do not show the classic pattern of zonation, two chi-square goodness-of-fit tests were used. The null hypothesis for the first test was that the first mangrove species encountered in the intertidal zone was adequately predicted by the ratio of *Avicennia germinans* to *Rhizophora mangle* along the transects as a whole. Similarly, the null hypothesis for the second test was that the last mangrove before higher ground was adequately predicted by the frequencies of *A. germinans* and *R. mangle* along the transects.

To examine the association between H_2S concentration and species presence, three tests of similarity between H_2S concentration as a function of surface condition were performed using data pooled from the six transects and employing analysis of variance weighted for unequal sample sizes (SPSS 1979):

(A) under *Rhizophora mangle* prop roots compared to adjacent stations.
(B) within the pneumatophores of *Avicennia germinans* compared to their adjacent stations.
(C) stations 1 m or less from pneumatophores compared to ones 1–3 m from them.

The reasons for performing these three particular tests are explained below.

Results

There is no clear pattern of zonation by distance from open water along the transects. Chi-square goodness-of-fit tests failed to reject the hypotheses that the frequency of first and last plants are the same as their frequency along the transects as a whole ($n = 6$ and $p > 0.95$ in both cases). At Hummingbird Cay, both *Rhizophora mangle* and *Avicennia germinans* are each found throughout the range of the other species.

Hydrogen sulfide concentrations in the substrates examined varied from 0 to 148 mg/l. H_2S was found only in association with peat deposits capped by mud or calcareous sand, although not all capped peat deposits had high levels of H_2S as discussed below. Virtually all identifiable material in the peat deposits is decomposing *Rhizophora mangle* root. The lack of evidence of aboveground plant parts together with the lack of distinct calcareous layers within the peat suggests that the peat is formed primarily by *R. mangle* roots decomposing in place. Hesse (1960b) also found 'fibrous mud' in association with *R. mangle.* However, it is not clear whether he also observed *Avicennia germinans* plants in *R. mangle* peat as is the case at Hummingbird Cay. Odum et al. (1982) reviewed the evidence suggesting that most, if not all, mangrove peat is formed from *R. mangle* tissue.

The presence of both mangrove species is closely associated with H_2S concentration. At both test depths in the soil, the mean H_2S concentrations beneath the stands of *R. mangle* (40–50 mg/l) and in areas adjacent to them (35–50 mg/l) are low and not significantly different from one another (Table 1, part A). However, individual readings varied from 0 to 133 mg/l. While it would not be statistically valid to test repeatedly for significant differences at increasingly greater distances from the roots, inspection of the data did not suggest that there are marked increases in H_2S concentrations at any greater distance from *Rhizophora mangle* stands.

The distribution of *Rhizophora mangle* is centered at areas of low hydrogen sulfide concentrations, yet there is not reason to reject the hypothesis that plants are distributed *within* these areas independently of hydrogen sulfide concentration – unvegetated areas immediately adjacent to live stands of *R. mangle* are statistically similar to them.

In comparison, the mean H_2S concentration beneath *Avicennia germinans* pneumatophores is significantly lower than the concentration in areas only 1 m away, 18–22 mg/l compared to 132–120 mg/l (Table 1, part B). Again,

Table 1. Mean pore water H_2S concentration beneath five surface conditions at Hummingbird Cay, Exuma, Bahamas

		30 cm	45 cm
A)			
Under *Rhizophora mangle* prop roots	(1)	39.71 mg/l	48.19 mg/l
Unvegetated areas 1 m or less away	(2)	35.22 mg/l	50.13 mg/l
sample size		42	35
probability of similarity		0.735	0.903
B)			
Within *Avicennia Germinans* prop roots	(3)	21.88 mg/l	17.97 mg/l
Unvegetated areas 1 m or less away	(4)	119.98 mg/l	132.00 mg/l
sample size		65	38
probability of similarity		0.001	0.001
C)			
Unvegetated areas 1 m or less from *Avicennia germinans*	(4)	119.98 mg/l	132.00 mg/l
Unvegetated areas 1–3 m from *Avicennia germinans*	(5)	127.47 mg/l	129.45 mg/l
sample size		20	15
probability of similarity		0.632	0.796

individual readings varied substantially within groups. While the distribution of *A. germinans* is also centered on areas of low soil H_2S concentration, it is necessary to reject the hypothesis that these areas are part of larger areas with similar soil conditions. There is a greater than 6-fold difference in mean H_2S concentration between soils permeated with a network of pneumatophores and those soils without pneumatophores but within 1 m of them. In this study area peat deposits do not have the same boundaries as stands of *A. germinans* and deposits that are charged with H_2S outside the ring of pneumatophores have low or no H_2S within the areas covered by a black mangrove root system.

The interpretation of these data is discussed fully below, but it is necessary to note here that such abrupt changes in H_2S concentrations are not seen except in direct association with pneumatophores of *Avicennia germinans*. As a control, the mean H_2S concentration at stations 1 m removed from pneumatophores was compared to those 1–3 m removed (Table 1, part C). The mean concentrations of H_2S 2 m away were high (127–129 mg/l) and did not differ significantly from those 1 m away. Neither in these tests nor in any unvegetated areas more than 2 m away from any mangroves was it possible to find equally sudden discontinuities in H_2S concentration. Within the study area, such discontinuities are associated exclusively with the presence of pneumatophores.

Discussion

Past attempts to explain the distribution of mangrove species along tropical shores are of three types: those that associate distribution directly with monotonic changes in the abiotic environment, usually salinity or soil saturation (e.g., Macnae, 1969; Thom, 1967); those that associate it with propagule dispersal characteristics (e.g., Rabinowitz, 1975); and those that associate it with interspecific competition (e.g., Ball, 1980). All three types treat geo-chemical parameters as 'a collective influence, having a gradient roughly normal to the shore' (Ball, 1980). Both this study and Snedaker and brown (1981) found that the 'typical' pattern of somewhat monospecific zones parallel to the shore is only one of a number of possible distribution patterns, even within the classic fringe forests where much of the work on mangrove distribution has been done.

Rhizophora mangle shows a clear deviation from this pattern at Hummingbird Cay. It is found throughout the nearshore area and is as likely to be the last upland mangrove as it is to be the first in the low intertidal zone, although this latter distribution is documented at many other sites (Davis, 1940; Egler, 1952; Thom et al., 1975). Carlson et al. (1983) found levels of H_2S under *R. mangle* similar to those reported here. However, they did not report the sulfide levels in nearby unvegetated areas. Because contiguous unvegetated areas on Hummingbird Cay have similar H_2S concentrations, it would appear that *R. mangle* does not cause these areas of low H_2S, but rather establishes within them (Figure 1). The alternative hypothesis – that *R. mangle* lowers soil H_2S concentration – fails to account for the presence of similar H_2S concentrations nearby.

By contrast, *Avicennia germinans*, which is also found throughout the whole nearshore zone at this study site, appears to be able to lower soil H_2S concentrations. Again, our results for areas under *A. germinans* are comparable to those reported by Carlson et al. (1983). But in addition there are abrupt, statistically significant, discontinuities in H_2S levels between stations under *A. germinans* pneumatophores and those within 1 m of them, despite soil and elevation conditions that appear similar in all other respects. Such discontinuities occur only where *A. germinans* grows. Scholander et al. (1955) demonstrated that *A. germinans* is able to bring air to roots growing in anaerobic substrate through its root aerenchyma. While it has not been shown that sufficient air escapes the roots to oxygenate the surrounding substrate, it appears that this, or some other mechanism does exist to remove H_2S.

With the present data, it is impossible to reject totally a hypothesis that *Avicennia germinans* roots grow to the edge of already existing discontinuities and are then stopped by either the H_2S or by some other factor correlated with it. However, to support this hypothesis it would be necessary to explain why *A. germinans* is always more successful than *Rhizophora mangle* in areas of low H_2S concentration immediately surrounded by areas of much higher concentration. It would also be necessary to explain why *A. germinans* has managed to colonize every area of this type. And most importantly, it would be necessary to explain why these areas range in size and shape from exactly that of one circular *A. germinans* root system to that of an entire grove of *A.*

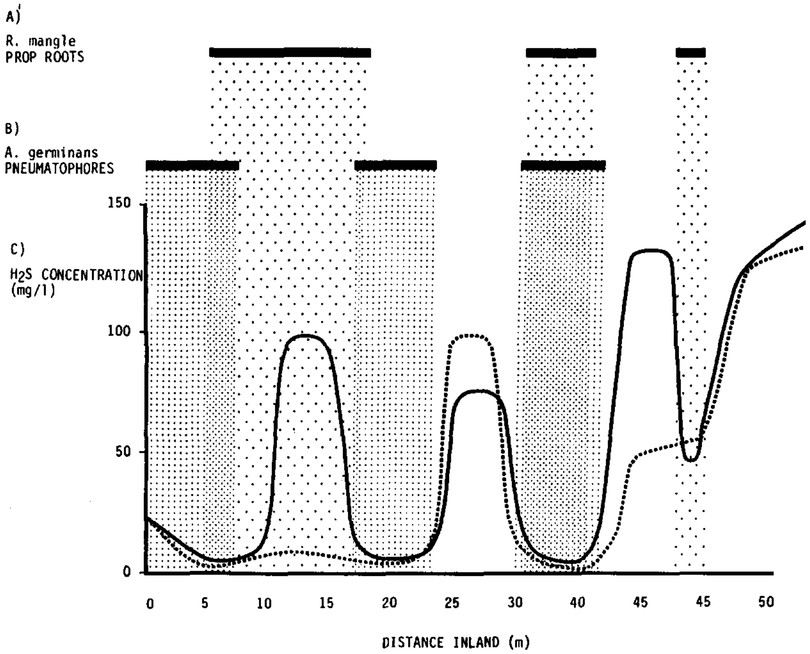

Figure 1. The association between (A) *Rhizophora mangle* and (B) *Avicennia germinans*, both shown by horizontal heavy lines and dotted shading, and (C) hydrogen sulfide concentrations, shown at 30 cm into the substrate by the solid curve and at 45 cm by the dashed curve.

germinans. Because *A. germinans* appears to maintain low H_2S levels near its root zone, there is no reason to suspect that high levels of H_2S limit distribution. In fact, because the presence of such high levels largely excludes *R. mangle*, high H_2S levels may provide unoccupied and otherwise suitable habitat for *A. germinans*.

These data suggest that it will be necessary to re-examine current hypotheses regarding the distribution patterns of mangroves. The distribution appears to be tied strongly to the sulfur cycle through a previously unknown feedback system. It may be that the usual pattern of *Rhizophora mangle* in the low intertidal and *Avicennia germinans* at higher elevations is primarily an expression of a common, but not universal, physical pattern caused by the interaction between mangroves and the sulfur cycle. This hypothesis does not exclude the effects of other parameters such as soil saturation, the sorting of propagules, or later competition for light within areas of low sulfide concentration, but it does modify them substantially.

Conclusions

Most previous explanations of mangrove distribution rely on the assumption that soil parameters vary smoothly from the low intertidal to the highest inundated areas. From this assumption, they proceed to examine the effect of both these gradients and other physical parameters. However, at least some mangrove habitat does not have these characteristics.

The mangroves along the shore of Hummingbird Cay do not grow in clearly defined bands parallel to the shore. Instead, their distribution appears to correlate most strongly with the pattern of H_2S concentration.

To the best of our knowledge, soil H_2S has never been shown to be a factor influencing, or influenced by, the growth of mangroves, although Carlson et al. (1983) and others have shown that there are lesser amounts of H_2S under *Avicennia* than under *Rhizophora.* At Hummingbird Cay, soil H_2S varied from 0 to 144 mg/l along transects perpendicular to the shore in a manner clearly associated with the mangrove species present. The occurrence of both *R. mangle* and *A. germinans* was clearly linked to these changes in H_2S concentration, but the full pattern of variation was only interpretable in relation to H_2S concentrations in nearby unvegetated areas. With present data it is not possible to document fully the nature of the relationship between mangroves and pore water sulfur, but it is clear that such a link does exist and that it should be examined more closely.

Rhizophora mangle does not tolerate conditions where high H_2S levels are found, but yet its decomposing root tissues are the primary substrate for sulfate reduction. *Avicennia germinans* appears most successful where it is surrounded by areas of high sulfide concentration, i.e., areas where *R. mangle* once grew but now cannot. These data suggest a slow, semi-cyclic succession of the two species, mediated, in part, by sulfide levels. It will be necessary to examine the effect of sulfide levels on interspecific competition to test this hypothesis. Further, it will be necessary to determine whether and how H_2S limits the growth of *R. mangle,* or whether some factor strongly associated with it is the causal factor. And, it will be necessary to examine the relationship between *A. germinans* root systems and soil chemistry. While none of these data are yet available, the distribution patterns documented above suggest a strong feedback relationship between mangroves and soil sulfur chemistry which has not been documented previously.

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