Amer. J. Bot. 75(9): 1352–1359. 1988.

REEXAMINATION OF PORE WATER SULFIDE CONCENTRATIONS AND REDOX POTENTIALS NEAR THE AERIAL ROOTS OF RHIZOPHORA MANGLE AND AVICENNIA GERMINANS[1]

KAREN L. MCKEE, IRVING A. MENDELSSOHN, AND MARK W. HESTER

Laboratory for Wetland Soils and Sediments, Center for Wetland Resources, Lousiana State University, Baton Rouge, Louisiana 70803

ABSTRACT

Soil redox potentials and pore water sulfide concentrations on a mangrove island in the Belizean barrier reef system were significantly correlated with the presence of the aerial roots of mangrove trees. Sulfide concentrations were three to five times lower near the prop roots of *Rhizophora mangle* (red mangrove) and the pneumatophores of *Avicennia germinans* (black mangrove) than in adjacent (≤1 meter away) unvegetated sediment. Soil redox potentials were also significantly higher near the aerial roots. A comparison of the two species revealed that sulfide concentrations in the rhizosphere of *R. mangle* were as low as that of *A. germinans.* However, sulfide concentrations in areas occupied by the black mangrove were variable and a function of pneumatophore density. The occurrence of an oxidized rhizosphere around the roots of both species suggests that the adult trees are equally capable of exploiting reduced sediments as long as their respective pathways for root aeration are functional.

RHIZOPHORA MANGLE L. and *Avicennia germinans* (L.) L. are dominant mangrove species of neotropical intertidal regions where they sometimes occur in monospecific zones. In the Caribbean region, *R. mangle* is typically found in regularly flooded intertidal areas and *A. germinans* in areas farther inland at higher elevations (Davis, 1940; Chapman, 1976). A number of hypotheses have been forwarded to explain mangrove species distribution. These explanations include 1) succession due to land building (Davis, 1940), 2) dispersal properties of propagules (Rabinowitz, 1978), 3) interspecific competition (Ball, 1980), 4) changes in abiotic factors along elevational gradients (Thom, 1967; Macnae, 1968), 5) physiological tolerance to flooding or salinity (Lugo and Snedaker, 1974; Walsh, 1974), and 6) predation of propagules (Smith, 1987).

Nickerson and Thibodeau (1985) and Thibodeau and Nickerson (1986) proposed that the distribution of *R. mangle* and *A. germinans* may be related to patterns of soil H_2S concentrations and the differential abilities of these two mangrove species to oxidize the anaerobic substrate. They found that the oxidized rhizospheres associated with the extensive network of negatively geotropic pneumatophores of *A. germinans* reduced pore water H_2S concentrations to much lower levels than that measured in adjacent unvegetated soil. In contrast, the oxidation state of the soil and pore water H_2S concentrations did not appear to be influenced by proximity to *R. mangle* prop roots. They further speculated that high concentrations of H_2S excluded *R. mangle,* but did not inhibit colonization by *A. germinans.*

The apparent differential effect reported by these investigators (Nickerson and Thibodeau, 1985; Thibodeau and Nickerson, 1986) contradicts previous work conducted with *R. mangle* and *A. germinans* which demonstrated the presence of a well-developed gas space system which provides an effective pathway for gas movement within the roots of both species, independent of the anaerobic substrate (Scholander, van Dam, and Scholander, 1955; Gill and Tomlinson, 1977). Scholander et al. (1955) demonstrated that oxygen enters the lenticels on the pneumatophores of *A. germinans* and moves by mass or bulk flow (driven by pressure changes resulting from the rise and fall of the tides) to the roots growing in the anaerobic sediment. A similar mechanism was demonstrated for *R. mangle* by which oxygen tensions in the roots were maintained by gas movement through the aerenchyma tissue in the prop (aerial) roots (Scholander et al., 1955). Oxygen

[1] Received for publication 31 August 1987; revision accepted 28 December 1987.

Contribution No. 232, Caribbean Coral Reef Ecosystems (CCRE) Program, Smithsonian Institution, partially supported by a grant from Exxon Corporation. We appreciate the comments of two anonymous reviewers.

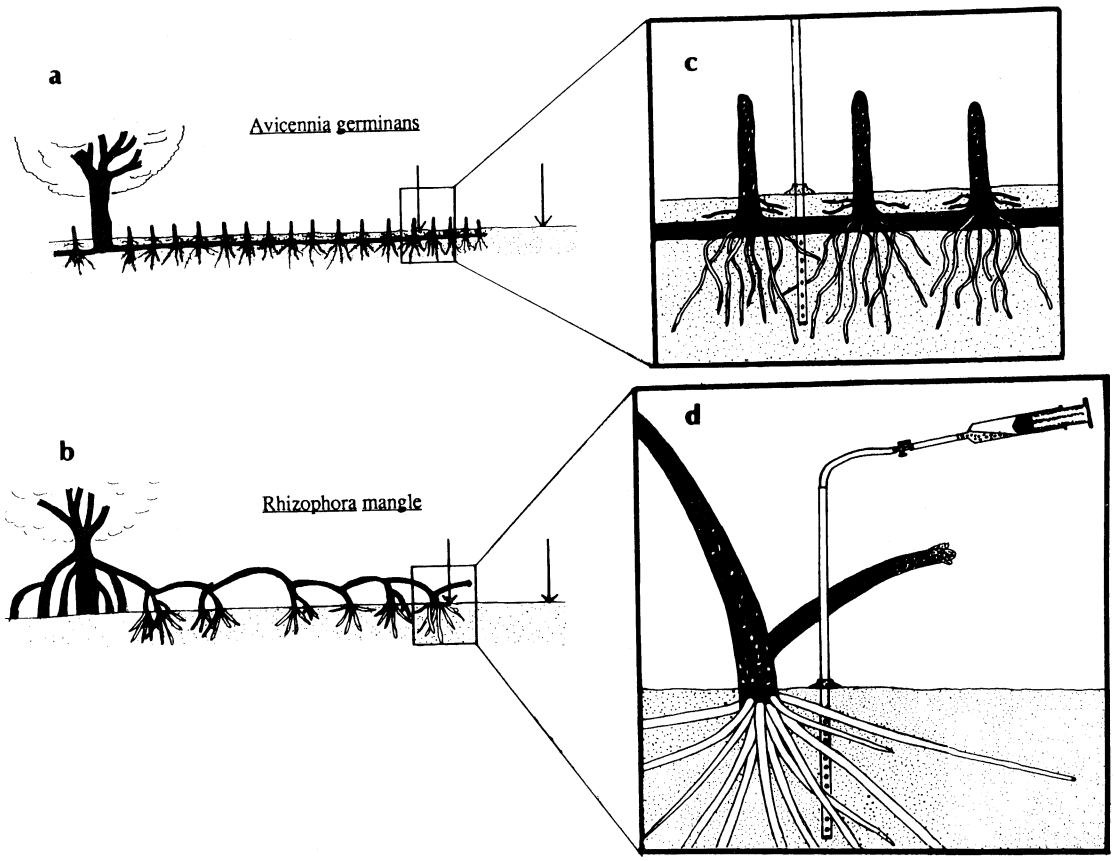

Fig. 1. Diagram showing the typical root system of *Avicennia germinans* (a) and *Rhizophora mangle* (b) and placement of interstitial water sampler (c & d) (after Scholander et al., 1955). Arrows to the right indicate the location of control sites relative to the aerial roots.

apparently enters a zone on the lower part of an aerial prop root where lenticel densities are highest, gas space volume is abundant, and the pathway for gas transport is at a minimum (Gill and Tomlinson, 1977). Thus, the potential exists for *R. mangle* to oxidize sulfide entering its roots or even to develop an oxidized rhizosphere similar to that described for *A. germinans* (Thibodeau and Nickerson, 1986). In an effort to resolve the apparent contradiction concerning the potential for sulfide oxidation between these two species (Nickerson and Thibodeau, 1985; Thibodeau and Nickerson, 1986), we reexamined pore water sulfide concentrations and soil redox potentials near the aerial roots of *R. mangle* and *A. germinans* growing on a mangrove island. The specific objectives of this study were to 1) determine whether soil redox potentials and interstitial water sulfide concentrations were significantly affected by proximity to mangrove aerating structures, i.e., prop roots for *R. mangle* and pneumatophores for *A. germinans* and 2) compare the relative effect of the presence of the two species' aerial roots on soil sulfide and redox potential.

MATERIALS AND METHODS—*Site description*—The study site was located on Twin Cays, an uninhabited mangrove island, located in the Belizian barrier reef system 2–3 km west of the reef crest (16°50′N, 88°06′W). The dominant species on this cay is red mangrove, *Rhizophora mangle,* which occurs primarily as a fringe around the periphery of the islands, although dwarf stands are also found in the interior. Also in the interior at higher elevations are extensive stands of black mangrove, *Avicennia germinans.* Some white mangrove, *Laguncularia racemosa* L., and buttonbush, *Conocarpus erectus* L., are scattered throughout the islands.

Several areas of unvegetated flats are present on Twin Cays, primarily in the interior of the islands. This study was conducted along the periphery of one of these unvegetated flats (0.01 km^2 in area) located on the easternmost island of Twin Cays.

Description of mangrove aerial roots—*Avicennia germinans* and *R. mangle* display adaptations in root morphology that are distinct for each species but which provide an efficient pathway for oxygen transport to the roots (Scholander et al., 1955). *A. germinans* produces horizontal (cable) roots which extend from the trunk base and radiate outward for several meters through the substrate just below the surface (Scholander et al., 1955; Gill and Tomlinson, 1977) (Fig. 1a, c). Negatively geotropic roots called pneumatophores, which are covered with lenticels, are produced from the horizontal roots and protrude from the substrate to a height of 10 to 30 cm (Fig. 1a, c). Shallow anchoring and absorbing roots are also produced along the horizontal root system. Aerenchyma tissue is abundant in the pneumatophores and cable roots (Scholander et al., 1955).

The aerial root system of *R. mangle* consists of roots which may be prop (which descend from the lower part of the stem) or drop (which descend from branches and the upper part of the stem) types (Gill and Tomlinson, 1977). The aerial root system extends outward from the main trunk through the formation of new above-ground laterals which have characteristics typical of aerial roots (Gill and Tomlinson, 1977) (Fig. 1b, d). The result is a succession of arches anchored at intervals to the substrate by aerial segments called columns (after Gill and Tomlinson, 1977). Abundant lenticels occur on the surface of the aerial roots, but are most dense near the sediment surface, particularly on the columns, which represent the primary pathway for oxygen movement to the substrate (see Fig. 1b; Gill and Tomlinson, 1977). Although the development of the subterranean root system is dependent upon the characteristics of the substrate (Gill and Tomlinson, 1977), the underground roots apparently can maintain high oxygen concentrations in anaerobic substrates (Scholander et al., 1955).

Description of sampling sites—Measurements for each species were taken in an area as close as possible to the primary aeration structures described above (Fig. 1c, d). For *A. germinans,* these sampling sites were located adjacent ($\leq$3 cm) to a pneumatophore and, by inference, a cable root (Fig. 1c). Depending upon the density, a site could be near one or more pneumatophores. The sampling sites for *R. mangle* were located near ($\leq$3 cm) a firmly rooted prop root (Fig. 1d). Samples were taken adjacent to the vertical portion, i.e., column of the terminal arch of a lateral root extending outward from the main trunk into the highly reduced sediment of the unvegetated flat (Fig. 1b). If the terminal segment was not well-rooted, the first subterminal column was chosen as depicted in Fig. 1b. In all cases, the diameter of the terminal arch was equal to or less than 3.2 cm. The length of the terminal columns was not measured, but estimated to be 5–10 cm on the average.

Sampling design—Three types of sites were chosen for this study. The first type consisted of sampling locations at an edge of the unvegetated flat where *R. mangle* had produced lateral extensions of the aerial root system into the unvegetated sediment and which were not associated with any other vegetative structures, i.e., *A. germinans* pneumatophores. At these sites, paired samples were taken adjacent (see description above) to a prop root and 0.5–1.0 m away in unvegetated sediment (Fig. 1b, d).

A second type of site was located in an area in which only pneumatophores of *A. germinans* occurred. These sampling sites were located at an edge of the unvegetated flat where the network of pneumatophores extended several meters into the flat (Fig. 1a, c). Samples were taken along transects oriented parallel to the unvegetated flat where pneumatophore density varied from 0 to ca. 700 m^{-2}.

The third type of site was located in areas in which *R. mangle* trees were growing in a field of *A. germinans* pneumatophores. Paired samples were taken, one adjacent to a *R. mangle* prop root (as described above; Fig. 1b, d) and another approximately 1 m away, but where pneumatophore density was not significantly less than that near the prop root (as in Fig. 1c). The pneumatophores at each of these sites were produced by *A. germinans* trees which were approximately 5–10 m from the *R. mangle* trees.

The *R. mangle* trees chosen for this study were usually isolated individuals, although some were associated with one or two other individuals. The height of the trees ranged from 0.7–2.2 m with a mean height of 1.5 m. The length of the lateral extension of the aerial root, i.e., distance of the sampling site from the main trunk, ranged from 1.5–2.5 m. In all cases, the paired sites were located within 1 m of each other to reduce the influence of hydrology on the parameters measured.

Surface elevation—Elevation of the soil surface was determined with a stadia rod referenced to water level at high tide at each sampling site to ensure that no large differences in elevation occurred between paired sampling locations.

Interstitial water sulfide—A simple apparatus consisting of a narrow diameter plastic tube connected to a 50 ml syringe was used to extract interstitial water from the soil (Fig. 1d). The rigid plastic tube (3 mm diameter and sealed at the lower end) was inserted into the soil to a 15 cm depth. The length of the inserted section (beginning 5 cm below the soil surface) was perforated by several small holes. A small (2 cm diameter) inverted plastic disc (commonly used to attach items to glass surfaces) was impaled on the plastic tube and pressed into the soil surface. This arrangement prevented the entry of surface water into the collecting tube. Suction was applied to the collection tube by a 50 ml-capacity syringe. A 3-way valve inserted between the syringe and collection tube allowed the expulsion of air and debris. This apparatus allowed the collection of 10 to 20 ml of relatively clear interstitial water from the mangrove substrate within a few seconds and without significant exposure to the atmosphere. The first 5 ml of each sample was discarded since it always contained some debris and sediment disturbed by the insertion of the collection tube. The subsequent interstitial water collected was invariably clear and relatively free of debris. We attribute the clearness of these samples to the low silt content of the mangrove substrate which was composed primarily of red mangrove peat. Although a comparison of the two sequential interstitial water aliquots could demonstrate no significant difference in sulfide concentration (data not shown), the first was routinely discarded (through the three-way valve) to prevent any volumetric error introduced by the presence of debris. An aliquot (5 ml) of the clear interstitial water collected in the syringe was transferred through the three-way valve to a graduated cylinder containing an equal volume of antioxidant buffer (Lazar operating instructions for Model IS-146 Sulfide Electrode). The antioxidant buffer prevented the oxidation of sulfide in the sample and converted H_2S and HS-forms of sulfur to S^{-2}. The samples were returned to the field station and analyzed for total sulfide with a Lazar (Model IS-146, Lazar Research Laboratories, Los Angeles, CA) sulfide electrode. A standard curve was constructed with a series of solutions of Na_2S prepared with the antioxidant buffer. An additional aliquot of interstitial water was collected in a separate container for the determination of pH (Digi-Sense pH Meter, Cole-Parmer Model 5985-80) and salinity (refractometer, American Optical).

Preliminary trials in the laboratory and the field demonstrated that surface water (when present) did not enter the collection tube to mix with the interstitial water when the collection tube was properly inserted into the substrate. At the mangrove field site, flocculant material in the overlying water acted as a marker that was easily spotted in the clear interstitial water and prevented any inadvertent collection of surface water. Any samples which were in doubt were discarded and repeated. A comparison with a method in which interstitial water was collected by centrifugation (in a nitrogen atmosphere) demonstrated that the direct collection of interstitial water with the collecting tube apparatus (Fig. 1d) did not allow significant oxidation of sulfide to occur and compared favorably with this other method (data not shown).

Soil redox potential—Soil redox potentials (Eh) at 1 and 10 cm depths were measured at each sampling site with brightened platinum electrodes which were allowed to equilibrate in situ for 1 hr prior to measurement. Each electrode was checked before use with quinhydrone in pH 4 and 7 buffers (mV reading for quinhydrone is 218 and 40.8, respectively, at 25 C). The potential of a calomel reference electrode (+ 244 mV) was added to each value to calculate Eh. Eh values were not corrected for pH, since differences between paired sites were negligible (mean pH = 6.73 ± 0.05 for all sites). A correction for temperature was also not calculated since Eh values change less than 1 mV for every °C.

RESULTS—Sulfide concentrations measured at the experimental sites ranged from 0.03–3.70 mM. Values were highest (2.8 to 3.7 mM) in the center of the unvegetated flat approximately 50 m from the edge of the vegetated zone. Sulfide concentrations in bare sediment at the periphery of the unvegetated flat where the paired comparisons were conducted were generally lower—1.6 mM on the average (Table 1). Soil Eh varied from −168 to −204 mV (1 and 10 cm depths, respectively) in the unvegetated substrate and from −45 to −161 mV (1 and 10 cm depths, respectively) at vegetated sites. The lower sulfide levels at the outer edge of the unvegetated flat may have been partly due to a difference in elevation and drainage patterns since the center of the flat was always the last to be exposed at low tide. For this reason, the control sites were located at the periphery of the unvegetated flat in bare sediment and only a short distance (≤1 m) from the sites containing aerial roots (Fig. 1a, b).

Elevations between paired sampling locations usually did not differ more than 0.30 cm

TABLE 1. *Soil parameters measured near the aeration structures of* Rhizophora mangle *and* Avicennia germinans

Location	# Samples	Water depth at high tide (cm)	Sulfide (mM)	Eh (−1 cm) (mV)	Eh (−10 cm) (mV)
A. germinans pneumatophores[a]	13	9.5 ± 1.5	0.53 ± 0.09	−92 ± 39	−161 ± 10
Bare substrate (0.5–1 m away)	6	9.3 ± 1.9	1.44 ± 0.18	−172 ± 9	−202 ± 18
Probability of $>F$[b]		ns[c]	0.0001	ns	0.049
R. mangle prop roots (≤3 cm)	12	14.0 ± 2.1	0.33 ± 0.06	−90 ± 17	−115 ± 21
Bare substrate (0.5–1.0 m away)	12	15.8 ± 2.8	1.63 ± 0.22	−168 ± 8	−179 ± 18
Probability of $>t$[d]		ns	0.0002	0.003	0.035
R. mangle prop roots (≤3 cm) in field of pneumatophores[e]	6	5.1 ± 0.5	0.22 ± 0.04	−45 ± 40	−106 ± 31
Pneumatophores only (1 m away)[e]	6	5.9 ± 0.7	1.10 ± 0.15	−153 ± 19	−212 ± 33
Probability of $>t$[d]		ns	0.002	0.052	0.073

[a] Pneumatophore density ranged from 70 to 690 m^{-2}.
[b] Based on one-way ANOVA.
[c] Nonsignificant difference ($P > 0.10$).
[d] Based on paired t test.
[e] Pneumatophore density did not differ significantly between paired sites and averaged 351 ± 30 m^{-2}.

(mean elevational difference between paired sites = 0.91 cm ± 0.35; Table 1). Measurement of pH and salinity in the interstitial water showed no significant difference in these parameters between paired sampling locations and little variation among all sites (pH = 6.73 ± 0.05; salinity = 40.1 ± 0.7 ppt). Thus, the primary difference between the paired sites was the presence or absence of aerial roots.

A significant difference in interstitial water sulfide was found between areas with pneumatophores of *A. germinans* and those without (Table 1). Concentrations of sulfide, which were three times lower within the pneumatophore zone, ranged from 0.04–1.70 mM, depending upon the density of the pneumatophores (Fig. 2). A significant negative correlation ($r^2 = 0.42$) demonstrated the relationship between pneumatophore density and sulfide concentration (Fig. 2). Although soil Eh measured within the pneumatophore areas were higher than in nearby bare substrate, the difference was significant only at the 10 cm depth (Table 1).

Similar results were found for *R. mangle*. Sulfide concentrations were five times lower near a prop root than in bare sediment approximately 1 m away (Table 1). Soil Eh measured near prop roots was also significantly higher than at control sites (Table 1). In general, sulfide concentrations near prop roots were consistently low. A few dwarf *R. mangle* trees were observed growing in the center of the unvegetated flat in highly reduced substrate. Although the sulfide concentrations in this area were twice as high as those at the periphery of the flat, the levels near the prop roots of the dwarf trees (1.59 ± 0.16 mM) were significantly lower than those in the adjacent sediment (3.36 ± 0.27 mM).

The relative effect of the presence of *R. mangle* and *A. germinans* aerial roots was further examined by measuring Eh and sulfide near individual *R. mangle* trees growing in fields of pneumatophores (mean density = 351 ± 30 m^{-2}). Pneumatophore density among the *R. mangle* prop roots at these sites was not significantly greater than that 1 m away from the prop roots. Sulfide concentrations were always significantly lower near the prop roots of *R. mangle* compared to adjacent areas (≤1 m) with similar densities of pneumatophores (Table 1). Soil Eh was also significantly higher near the prop roots (Table 1). Because sulfide concentrations differed significantly with pneumatophore density, values (0.05 ± 0.01 mM) measured at sites where pneumatophore density was high, i.e., ca. 700 m^{-2}, were lower than those near *R. mangle* prop roots (0.24 ± 0.03 mM, Table 1) associated with moderate pneumatophore densities, i.e., ca. 351 ± 30 m^{-2}. Thus, although sulfide concentrations associated with pneumatophores were variable, the minimum values observed among all *A. germinans* sites were comparable to those obtained near the prop roots of *R. mangle*.

DISCUSSION—Nickerson and Thibodeau (1985) previously demonstrated on a mangrove cay in the Bahama Islands that H_2S con-

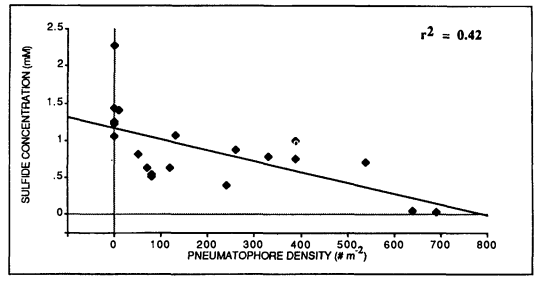

Fig. 2. Relationship between pneumatophore density and interstitial water sulfide concentration.

centrations were dramatically lower within areas of *A. germinans* pneumatophores than in nearby unvegetated sites. We also found similar results for this species (Table 1). These same investigators, however, could not demonstrate a significant difference in soil oxidation or sulfide concentration between areas occupied by prop roots of *R. mangle* and those without and concluded that this species was confined to areas of pre-existing low to moderate sulfide concentrations (Nickerson and Thibodeau, 1985; Thibodeau and Nickerson, 1986). Our results have shown that sulfide concentrations near *R. mangle* prop roots may be considerably lower (0.33 mM) than those in adjacent unvegetated sediment (1.63 mM) (Table 1). Even the soil substrate near dwarfed red mangrove trees growing in the center of the unvegetated flat was less reduced and had lower sulfide concentrations (1.59 ± 0.16 mM) compared to the surrounding sediment (3.36 ± 0.27 mM). The reason for the lack of agreement between these two studies with respect to *R. mangle* is not clear, but may be due to differences in sediment type and/or ecological plasticity of this species. Although further investigation is required to determine whether the effect observed in the current study is universal among red mangroves, our results demonstrated that more oxidized soil conditions near aerial roots are not unique to *A. germinans.*

The range of values obtained for interstitial water sulfide concentrations (0.24–3.36 mM) were comparable to that reported for mangrove substrates in Florida (Carlson et al., 1983) and in the Bahamas (Nickerson and Thibodeau, 1985). Carlson et al. (1983) reported values ranging from 0.01 to 1.50 mM sulfide in Florida mangrove substrates. Although the method of sulfide analysis used in the current study measured total soluble sulfide (H_2S, HS^-, S^{-2}), the pH of the mangrove substrate (mean pH = 6.73 ± 0.05) was such that the dominant soluble S forms present were probably H_2S and HS^-. Thus, the values for sulfide obtained in this study, although not directly comparable with the H_2S values reported by Nickerson and Thibodeau (1985), are within the range (0.68–4.1 mM) observed in Bahamian mangrove substrates.

The soil redox values measured at Twin Cays (Table 1) were somewhat higher than those reported by Thibodeau and Nickerson (1986) for the same depths in mangrove substrates. They found soil Eh to vary from −340 to −360 mV in unvegetated sediment and from −250 to −310 mV at sites with pneumatophores. However, since their values were uncorrected for the potential of the calomel reference electrode (+244 mV) (Nickerson, personal communication), a recalculation correcting for this factor brings their data into agreement with this study (Table 1) and studies conducted in other mangrove substrates, e.g., northern Australia (Boto and Wellington, 1984).

Carlson et al. (1983) found spatial patterns of sulfide under *R. mangle* and *A. germinans* in Florida similar to those reported by Nickerson and Thibodeau (1985). Carlson's interpretation of this pattern differed from that of Nickerson and Thibodeau (1985), however. Carlson et al. (1983) concluded that it was not clear from their data whether the mangrove species had different effects on soil chemistry or whether the mangroves were responding to differences in soil chemistry resulting from physical factors. Because of elevational differences between *A. germinans* and *R. mangle* sites (20 cm), Carlson et al. (1983) were unable to differentiate between abiotic and biotic factors affecting the soil oxidation patterns they observed. In the current study, the comparison of paired sites at equivalent elevations and over short distances (≤1 m) eliminated these potentially confounding abiotic factors and produced evidence that the more oxidized zones were primarily associated with the presence of the aerial roots and not to any differences in physical parameters which might have influenced soil chemistry.

The explanation that the mangroves were simply exploiting areas of preexisting low sulfide concentration does not seem reasonable since the pattern of low sulfide appeared to closely conform to the spatial distribution of the aerial root systems. In fact, many of the control (unvegetated) sites were located between lateral extensions of aerial roots which were separated by a distance of only 1–2 m; sulfide concentrations were always significantly higher between laterals compared to those near an aerial root. Furthermore, the significant correlation between pneumatophore density and sulfide concentration strongly indicates that it was the occurrence of aerial roots which influenced the soil oxidation and not the reverse. The significantly lower sulfide concentrations measured near the prop roots of *R. mangle* growing in fields of pneumatophores compared to nearby areas (≤1 m) with only pneumatophores (Table 1) further substantiates this conclusion. The possibility that the prop roots entered the soil in the precise location among the pneumatophores where the soil was most oxidized is highly unlikely.

The apparent oxidizing effect of the aerial roots on the sediment could have occurred by several mechanisms: 1) oxygen diffusion through the aerenchyma to the belowground roots and into the rhizosphere, 2) a drawdown

of oxygen during a tidal cycle along the external surface of the aerial roots, or 3) an inhibition of sulfate-reducing bacteria in the root zone. Although our results cannot differentiate among these possibilities, evidence from other work suggests that the most likely explanation is oxygen leakage from the roots. Scholander et al. (1955) demonstrated that the pneumatophores of *A. germinans* and the prop roots of *R. mangle* serve as conduits for oxygen flow from the atmosphere to the roots growing in the anaerobic substrate. Work with other wetland plant species has demonstrated oxygen diffusion from roots (Armstrong, 1964, 1967; Wium-Andersen and Andersen, 1972; Thursby, 1984). Radial oxygen diffusion from the roots of a floodplain/swamp tree species, *Nyssa sylvatica* var. *biflora,* has also been observed (Keeley, 1979). Since the passive diffusion of oxygen from the atmosphere through the plant and into the surrounding substrate is largely a function of aerenchyma tissue (Armstrong, 1967) and because the mangrove roots contain abundant aerenchyma (Scholander et al., 1955; Gill and Tomlinson, 1977), it is possible that the lower sulfide concentration near the mangrove roots was the result of oxygen leakage into the rhizosphere. Boto and Wellington (1984) working in an Australian mangrove community found that the soil at sites with less plant biomass tended to be more reduced and that the highest Eh values at each site coincided with periods of increased plant growth. Their results, although only correlative, support the suggestion that mangroves may transport oxygen to the root zone. The most compelling evidence for this mechanism in mangroves was presented by Thibodeau and Nickerson (1986), who showed that blockage of air movement through the pneumatophores of *A. germinans* decreased the Eh in the soil surrounding the pneumatophores. However, since evapotranspiration would also have been reduced by their method, they could not eliminate the possibility that the observed chemical changes in the soil were due to some factor other than decreased oxygen diffusion from the roots. The exact nature of the effect of mangroves on soil oxidation remains unclear and requires further investigation.

The idea that *R. mangle* is more sensitive to sulfide than *A. germinans* and is limited to sites where sulfide concentrations are relatively low (Nickerson and Thibodeau, 1985) does not appear to be tenable for two reasons. First, the aeration of subterranean roots of *R. mangle* has been shown to be similar to that of *A. germinans* (Scholander et al., 1955) and along a pathway analogous to that created by pneumatophores (Gill and Tomlinson, 1977). Thus, any sulfide entering the roots of either species could potentially be oxidized. Second, the data presented in this study (Table 1) demonstrated that sulfide concentrations in the rhizosphere of *R. mangle* were just as low as those of *A. germinans* and significantly different from those in unvegetated sediment. However, the results of this study do not exclude the possibility of differential oxidation due to a differential blockage of air flow through the aerial roots during a tidal cycle. Sulfide or soil Eh may also have a differential effect on the establishment of propagules of *R. mangle* and *A. germinans.*

While soil reduction and sulfide accumulation may have some effect on the growth of mangroves, the data suggest that *R. mangle* and *A. germinans* are capable of exploiting reduced sediments as long as their respective pathways for root aeration are functional. Sulfide concentrations, which often reached relatively high levels in the anaerobic sediment, were significantly lower wherever the aerial roots of either mangrove species occurred. Regardless of the mechanism responsible, this effect could be as important to the survival of mangroves as is the transport of oxygen to the roots for aerobic metabolism.

LITERATURE CITED

ARMSTRONG, W. 1964. Oxygen diffusion from the roots of some British bog plants. Nature 204: 801–802.

———. 1967. The oxidizing activity of roots in waterlogged soils. Physiol. Pl. 23: 623–630.

BALL, M. C. 1980. Patterns of secondary succession in a mangrove forest of southern Florida. Oecologia 44: 226–235.

BOTO, K. G., AND J. T. WELLINGTON. 1984. Soil characteristics and nutrient status in a northern Australian mangrove forest. Estuaries 7: 61–69.

CARLSON, P. R., L. A. YARBRO, C. F. ZIMMERMAN, AND J. R. MONTGOMERY. 1983. Pore water chemistry of an overwash mangrove island. Florida Sci. 46: 239–249.

CHAPMAN, V. J. 1976. Coastal vegetation. Pergamon, Oxford.

DAVIS, J. H. 1940. The ecology and geologic role of mangroves in Florida. Publ. Carnegie Inst. Wash., Publ. 517, Washington, DC.

GILL, A. M., AND P. B. TOMLINSON. 1977. Studies on the growth of red mangrove (*Rhizophora mangle* L.) 4. The adult root system. Biotropica 9: 145–155.

KEELEY, J. E. 1979. Population differentiation along a flood frequency gradient: physiological adaptations to flooding in *Nyssa sylvatica.* Ecol. Monogr. 49: 89–108.

LUGO, A. E., AND S. C. SNEDAKER. 1974. The ecology of mangroves. *In* R. F. Johnston, P. W. Frank, and C. D. Michener [eds.], Annual review of ecology and systematics, 39–64. Annual Reviews, Palo Alto, CA.

MACNAE, W. 1968. A general account of the flora and fauna of mangrove swamps in the Indio-West Pacific region. Advances Mar. Biol. 6: 73–270.

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

RABINOWITZ, D. 1978. Dispersal properties of mangrove propagules. Biotropica 10: 47–57.

SCHOLANDER, P. F., L. VAN DAM, AND S. I. SCHOLANDER. 1955. Gas exchange in the roots of mangroves. Amer. J. Bot. 42: 92–98.

SMITH, T. J. 1987. Seed predation in relation to tree dominance and distribution in mangrove forests. Ecology 68: 266–273.

THIBODEAU, F. R., AND N. H. NICKERSON. 1986. Differential oxidation of mangrove substrate by *Avicennia germinans* and *Rhizophora mangle*. Amer. J. Bot. 73: 512–516.

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

THURSBY, G. B. 1984. Root-exuded oxygen in the aquatic angiosperm *Ruppia maritima*. Mar. Ecol. Prog. Ser. 16: 303–305.

WALSH, G. E. 1974. Mangroves: a review. *In* R. Reimold and W. Queen [eds.], Ecology of haplophytes, 51–174. Academic Press, New York.

WIUM-ANDERSEN, S., AND J. M. ANDERSEN. 1972. The influence of vegetation on the redox potential of the sediment of Grane Langso, A Danish Lobelia lake. Limnol. Oceanogr. 17: 948–952.