



## Soil redox conditions and plant–soil relationships in a micronesian mangrove forest

S.M. Gleason<sup>a,\*</sup>, K.C. Ewel<sup>b</sup>, N. Hue<sup>a</sup>

<sup>a</sup>Department of Tropical Plant and Soil Sciences, University of Hawaii, 1910 East-West Road, Honolulu, HI 96822, USA

<sup>b</sup>USDA Forest Service, Pacific Southwest Research Station, 1151 Punchbowl Street, Room 323, Honolulu, HI 96813, USA

Received 23 August 2001; received in revised form 1 May 2002; accepted 3 June 2002

### Abstract

We examined characteristics of the soil environment related to redox in the rhizospheres of three mangrove species that commonly grow in similar hydrogeomorphic settings: *Rhizophora apiculata* BL, *Bruguiera gymnorhiza* (L.) Lamk., and *Sonneratia alba* J. Redox potential (Eh) values and extractable P concentrations were significantly higher, whereas soluble reactive P (SRP) concentrations were significantly lower in *Bruguiera* plots than in either *Rhizophora* or *Sonneratia* plots. Correlations among Eh, SRP, pyrite and extractable P were significant only at plots with negative Eh values. *Sonneratia* and *Bruguiera* plots had significantly different soil redox conditions. *Bruguiera* plots were characterized by more oxidized soil conditions (ca. 80 mV), lower dissolved P concentrations in porewater (ca. 50%), and higher extractable P concentrations in soil (ca. 25%). Differences in Eh and P reflect real differences among species and appeared not to be associated with hydrology. Species-specific differences may be engendered by the trees themselves, or they may reflect microsite differences that have favored the germination, growth, and survival of particular mangrove species.

© 2003 Elsevier Science B.V. All rights reserved.

**Keywords:** species composition; redox potential; soluble reactive P; extractable P; Micronesia

### 1. Introduction

Previous studies suggest that mangrove species may alter sediment redox conditions through either rhizosphere oxidation (McKee, 1993; McKee, Mendelssohn, & Hester, 1988; Thibodeau & Nickerson, 1986) or nutrient cycling processes (Lacerda, Ittekkot, & Patchineelam, 1995; Sherman, Fahey, & Howarth, 1998). Other studies suggest that species distribution patterns depend on chemical and physical characteristics of soil and seawater (Alongi, Christofferson, & Tirendi, 1993). The question of whether or not mangroves can alter the chemistry of their rhizospheres significantly is important and needs to be resolved if scientists are to draw meaningful conclusions from correlative evidence linking species distribution patterns to plant and porewater chemistry.

We were particularly interested in plant–soil relationships in mangrove forests that are being selectively

harvested. If plants affect soil and porewater characteristics differently, altering species composition by harvesting is likely to affect edaphic conditions. On the other hand, if soil and/or porewater conditions are engendering a specific species composition, a closer examination of how seed germination, seedling survival, and growth rates are affected by microsite differences is needed. Regardless of whether edaphic conditions are altered by the plants or control plant compositions, if significant plant–soil relationships exist in mangrove forests, independent of broad-scale hydrologic influence, these relationships need to be quantified.

The objective of this study was to determine if species-specific redox variation existed in mangrove forests on the island of Kosrae, Federated States of Micronesia. Although Kosrae does have distinct tidal zones, species distribution patterns are more homogeneous than are found in many other mangrove forests throughout the world (Ewel, Bourgeois, Cole, & Zheng, 1998). Eleven species of mangroves occur on Kosrae. The three most common species, *Sonneratia alba* J., *Bruguiera gymnorhiza* (L.) Lamk., and *Rhizophora*

\* Corresponding author.

E-mail address: [gleasons@shafter.army.mil](mailto:gleasons@shafter.army.mil) (S.M. Gleason).

*apiculata* BL, provided the focus for this study. *Bruguiera* and *Rhizophora* belong to the family Rhizophoraceae whereas *Sonneratia* belongs to the family Sonneratiaceae. All three species have distinctly different types of above-ground root structures: pneumatophores (*Sonneratia*), knees (*Bruguiera*), and prop-roots (*Rhizophora*). *Sonneratia*, presently a dominant over-story species, shows very little natural regeneration and is gradually being replaced by *Rhizophora* and *Bruguiera* (Ewel et al., 1998). *Rhizophora* is the slowest growing and most often harvested species among these (Devoe & Cole, 1998). Continued harvesting pressure may result in the gradual replacement of *Rhizophora* by *Bruguiera*. If these three mangrove species are affecting soil redox chemistry differently, the species shifts described above could significantly alter broad-scale nutrient cycles. Previous studies attributed large differences in soil P and C to vegetation type (Lacerda et al., 1995; Sherman et al., 1998) and demonstrate the point that species composition shifts may result in large edaphic changes if strong plant–soil relationships exist. Our primary task was to quantify such plant–soil interactions separately from the effects of hydrology and salinity.

Species distribution patterns in mangrove forests are often constrained by salinity tolerance and tidal amplitude (Ball, 1998; Cardona & Botero, 1998; Lin & Sternberg, 1993; Naidoo, 1990; Wakushima, Kuraishi, & Sakurai, 1994). Hence, different species tend to favor specific hydrogeomorphic positions in the landscape (Smith, 1992). Isolating trends in porewater and edaphic variation that are associated with individual species, and are not affected by the hydrology unique to the sites that those species occupy, can be difficult (Alongi et al., 1993). By conducting species-specific studies in mixed-species mangrove forests, soil and porewater samples may be taken directly from the rhizospheres of different species occupying the same hydrogeomorphic position in the landscape. We assumed that edaphic differences found among the three species were caused by the species themselves or that microsite conditions had favored the growth and survival of specific mangrove species. We thought this assumption was reasonable considering the homogenous species distribution of the forest, the short distance between single-species plots (ca. 12 m), and the experimental design, which included species comparisons across a range of different hydrologic conditions.

We compared several redox variables in soil and porewater that are most likely to indicate a significant change in electron transfer potential (Eh), including soluble reactive P (SRP), extractable P, pyrite, and relative Eh. All of these variables are interrelated and serve as indicators of distinct soil redox processes. For example, the precipitation of reduced iron sulfide will bring about the release of iron-oxide-bound P (Krom & Berner, 1980) and thus increase the concentration of

SRP in soil solution. If several of these variables differ significantly among species and are correlated with one another, this would suggest that plant–soil relationships are strongly associated with redox chemistry. For a more complete review of Fe, P, and S dynamics in wetlands we suggest the following references: Berner (1970), Giblin (1988), Krom and Berner (1980), and Rhue and Harris (1999).

By studying redox variables at several sites in a mixed-species mangrove forest, we hoped that the effects of individual species could be separated and quantified independently of hydrologic effects. We wanted to evaluate the importance of species-specific effects relative to the effects of hydrology. We also hoped that the knowledge gained would assist mangrove ecologists in interpreting spatial patterns of forest and soil development within different hydrologic regimes.

## 2. Materials and methods

### 2.1. Study site

Kosrae, the easternmost island in the Federated States of Micronesia (5°19' N and 163°00' E), is a high volcanic island 109 km<sup>2</sup> in area and surrounded almost completely by a fringing reef. Average annual precipitation for Kosrae is 5000 mm (Merlin, Taulung, & James, 1993), the mean spring tide amplitude is 140 cm, and the average annual temperature is 27°C. There are no well-defined wet or dry seasons.

Two mangrove forests located on opposite sides of Kosrae served as sites for this project. Each of these forests is located near the mouth of a river basin: Utwe River Basin, the largest watershed on the island's southern side; and Okat River Basin, the largest watershed on the island's northwestern side. Soils within Okat and Utwe River basins are aeric and typic Tropaquepts (Soil Conservation Service, 1984) and appear to be distributed homogeneously in both watersheds. The mangrove soils themselves are typic Sulfaquents (Soil Conservation Service, 1984) and are generally saturated with brackish water throughout the day even at low tide. Mangrove soil depths range from approximately 1.5 m deep at the mangrove fringe to about 2.5 m deep in the interior, and they cover an underlying coral sand substrate (Fujimoto, Miyagi, Kikuchi, & Kawana, 1996). Radiocarbon dating of mangrove soils in Utwe River Basin indicates that mangrove peat has been accumulating at these sites for at least 2000 years (Fujimoto et al., 1996). Anthropogenic disturbance is minimal at both sites and is limited to selective firewood cutting. No significant harvesting had occurred in any established plots associated with this study. Two homes are located on the banks of the Utwe River but are more than 400 m from the nearest

study plot. No homes are located on the banks of the Okat River or in the vicinity of study plots in the mangrove forest.

## 2.2. Plot selection and experimental design

Two sites within Utwe River Basin and one site within Okat River Basin were selected. All were located in either interior or riverine mangrove areas, although no effort was made to distinguish between the two mangrove types. Each site consisted of five 20-m-radius plots, each of which contained three smaller (2.5-m-radius) subplots (Fig. 1). Each of the three subplots contained above-ground biomass, root structures, and leaf area of only one species of mangrove. Subplots within plots were established so that all three major mangrove species (*Sonneratia*, *Rhizophora*, and *Bruguiera*) were equally represented. In this way species-specific effects could be compared without salinity or elevation gradients confounding the results of the experiment.

Because mangrove basal area is likely to be correlated with certain edaphic variables (Sherman et al., 1998), four measures of basal area were taken at all subplots. Within each subplot, a 2, 4, and 8-m-radius basal area measurement was recorded. Species-specific effects were compared using analysis of variance (ANOVA) with a randomized complete block (RCB) design combined across locations. When species-specific effects were found in the ANOVA, the analysis was repeated using each of the basal area measurements, one at a time, as a covariate. The covariate that generated the lowest species-specific *F* value was chosen for hypothesis testing.

ANOVA and analysis of covariance (ANCOVA) were performed for the complete data set, for each of the three sites, and for a data subset that included all plots that had negative Eh values ( $Eh < 0.0$  mV). This last data subset was analyzed to test the hypothesis that species-specific effects would be strongest at plots having significant rates of sulfate reduction. Because pyrite precipitation and

SRP solubility are partially dependent upon sulfate reduction, a soil Eh measurement of 0.0 mV (Bohn, McNeal, & O'Connor, 1985; Schulz, 2000) was chosen as the cutoff value to indicate conditions below which significant rates of sulfate reduction were likely to occur. Although sulfate reduction occurs when redox potentials are equal or less than  $-150$  mV in a pure sulfate/sulfide system, studies have shown that significant sulfate reduction occurs within microsites when soil redox potentials drop below 0 mV (Bohn et al., 1985; Gardner, Wolaver, & Mitchell, 1988; Schulz, 2000).

ANOVA was used to determine if edaphic variables differed significantly among the species. All mean separations were performed by the LSD method using a significance level of 0.05. Correlation analysis was used to examine the relationships among various edaphic and biologic measurements.

## 2.3. Soil redox potential

Soil redox potential (Eh) can be directly measured with an inert platinum electrode. However, because a mixture of redox pairs exists in soil, problems arise when using soil Eh measurements to generate thermodynamic predictions about iron or sulfate reduction. The assumption must be made that all redox pairs in the soil stratum respond immediately to shifts in electron potential and that these reactions are equally reversible. Such assumptions are likely invalid in soil systems (Bohn et al., 1985; Fiedler, 2000). However, Eh measurements have been shown to be a good indicator of relative redox states as long as the sediment composition is relatively constant over time and space (Ponnamperuma, 1972). Due to the uniform parent materials and sediment type found in Kosraean mangroves, we considered Eh measurements to be a reliable indicator of the relative redox environment.

Within a 24-cm radius from the center of each subplot, 10 platinum electrodes and a calomel reference

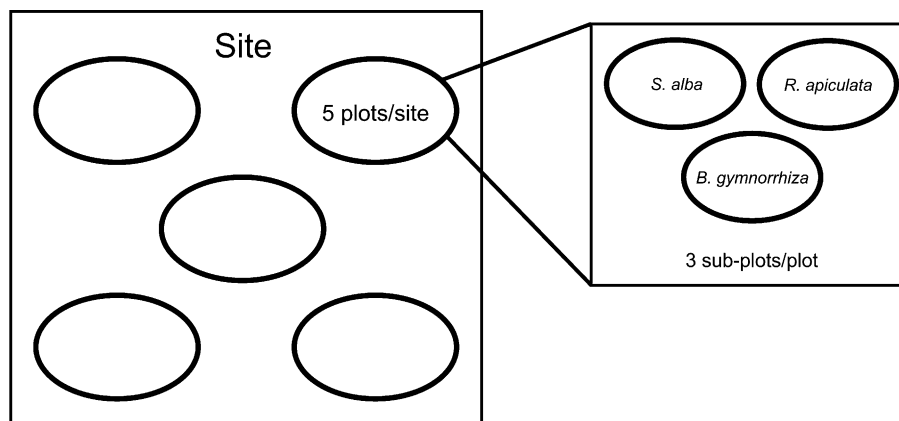


Fig. 1. Plot layout within sites: five plots (20-m radius), three subplots (2.5-m radius) within each main plot. Each subplot contained above-ground biomass, root structures, and leaf area of only one species of mangrove.

electrode were pushed 10 cm into the exposed substrate at low tide. If a tree was located directly in the center of the subplot, the electrode cluster was moved slightly off-center. The electrodes were allowed 45 min to equilibrate prior to recording Eh with a pH/Eh meter (250A series, Orion Research, Inc., Boston, MA). pH and temperature were recorded at the same time as Eh measurements. Eh values were corrected to account for temperature and the redox potential of the calomel reference electrode. Eh measurements were not corrected for hydrogen potentials because it was not known what redox reaction dominated the system. Because soil redox measurements are a mixed potential, it's inappropriate to apply a correction value to redox potentials taken in soil solutions (Bohn et al., 1985; Schulz, 2000). Electrodes were placed in each of the three subplots within one plot simultaneously, thus facilitating comparable Eh measurements. Elapsed time between subplot measurements rarely exceeded 3 min. After all three subplots were measured, the electrodes were removed from the soil, rinsed with distilled water, and placed in the next closest plot. After daily Eh measurements, the electrodes were cleaned with 'bath and tile cleaner' and tested to assure that redox measurements, in a standard quinhydrone solution, did not differ from one another by more than 10%. Eh was measured on three separate occasions between 28 June and 14 July, 1999.

#### 2.4. Total, soluble reactive, and organic P

A 100-ml porewater sample was taken 10 cm below the soil surface using a 20-cm length of perforated polyethylene tubing (see McKee et al., 1988) and a 60-ml syringe. Water samples were then passed through an acid-washed, 0.4  $\mu\text{m}$ , glass filter into an acid-washed, high density, polyethylene bottle. Water samples were placed on ice and transported back to the laboratory within 5 h where they were deep frozen at  $-15^\circ\text{C}$ . Samples were taken on three separate occasions from each of the three sites. Water samples were kept frozen in an ice chest for approximately 12 h during transport back to Hawaii where they were immediately placed back in frozen storage. SRP was analyzed using the Murphy–Riley technique modified for seawater analysis (Hansen & Koroleff, 1999). Total P was analyzed using inductively coupled plasma spectroscopy (ICP). Organic P was estimated by subtracting SRP from the total P determination. All porewater analysis took place within 2 months of water sample collection.

#### 2.5. Pyrite and reactive iron

One soil core was taken from each of the 45 subplots between 19 September and 22 September 1999. Soil cores were collected with a 10.2-cm-diameter PVC pipe

that was bisected lengthwise and held together with two metal-band fasteners. The corer was driven into the soil at least 30 cm deep. Soil was extracted from the corer by removing the fasteners; cores were then carefully sectioned into 0–15 cm and 15–30 cm segments. The soil sections were immediately sealed in airtight polyethylene bags and transported back to the lab within 6 h of collection, where they were placed in a refrigerator at  $4^\circ\text{C}$ . Soil cores were removed from the refrigerator after 4 days and sectioned lengthwise into two halves. One half of the 0–15 cm core was then oven-dried at  $70^\circ\text{C}$  for 3 days, sealed in an airtight polyethylene bag, and refrigerated until analysis.

The remaining soil core sections were set aside for root separation and analysis. The soil samples were kept cool in an ice chest for approximately 12 h during transport from Kosrae to the University of Hawaii, and were then placed back in refrigeration. In addition to the oven-dried soil, a 20-g sample was removed from the fresh core and frozen at  $-10^\circ\text{C}$ . These two soil preservation techniques were used in order to determine the effect of oven-drying on pyrite oxidation. Soil samples were analyzed within 1 month.

Pyrite and reactive iron were analyzed using a modified version of the technique used by Giblin (1988). The oven-dried soil samples were sifted through a 0.2-mm mesh sieve to remove root materials. A 0.5-g sample of the sifted soil was then digested overnight in 10 ml of 6 M HCl to remove iron oxides and exchangeable iron on silicate and organic colloids. This was considered to be iron available for pyrite formation. The soil solution was vacuum-extracted through a glass filter (GF/D, Whatman International, Ltd., Maidstone, England) and analyzed for iron using colorimetric techniques (Olsen & Ellis, 1982). The soil remaining in the filter was then digested overnight in Aqua Regia ( $2\text{HNO}_3:\text{HCl}$ ) at room temperature to remove iron bound in sulfide minerals, mainly FeS and FeS<sub>2</sub>. The soil solution was again vacuum-extracted through a glass filter and analyzed for iron using colorimetric techniques (Olsen & Ellis, 1982). Complete digestion of pyrite was verified by X-ray diffraction analysis.

#### 2.6. Extractable soil P

Extractable P was analyzed using both Olsen (Olsen & Summers, 1982) and Mehlich III (Mehlich, 1984) methods because of limited understanding concerning plant-available P extractions in mangrove soils. The Olsen method uses 0.5 M NaHCO<sub>3</sub> as the extracting solution. In alkaline soils high in Ca phosphates, Ca is precipitated as CaCO<sub>3</sub> in the presence of bicarbonate, thus releasing P. Mehlich III uses a combination of acetic acid and NH<sub>4</sub>F as the primary P extractants. Acetic acid reduces the pH below 3.0, increasing the activity of fluoride, which then displaces P held to

colloidal surfaces by anion exchange. By using two methods that operate on different extraction mechanisms, two separate plant-available P estimates could be compared. This comparison was thought necessary considering the limited information available regarding P availability at our sites.

Oven-dried soil samples were sifted through a 0.2-mm mesh sieve to remove roots. For the Olsen procedure, a 1.25 g sample was then shaken for 45 min in 25 ml of 0.5 M NaHCO<sub>3</sub> (adjusted to pH 8.5 with NaOH), filtered through a Whatman® 6S filter, and adjusted to pH 5.0 with H<sub>2</sub>SO<sub>4</sub>. For the Mehlich III procedure, a 2.0-g sample was shaken for 5 min in 25 ml of Mehlich III extractant, and filtered through a Whatman® 6S filter. The filtered solutions from both methods were then analyzed for inorganic P using colorimetric techniques (Olsen & Summers, 1982). Soil samples were dried prior to analysis because of logistical difficulties and in order to remove water from the samples quickly, thus preventing significant oxidation of pyrite and ferrous oxides. Although this procedure has been used successfully in other studies (Gardner et al., 1988; Giblin, 1988; Kaiserli, Voutsas, & Samara, 2002; Lord, 1981; Sherman et al., 1998), the possible effects of this procedure on extractable P will be covered in the discussion.

### 2.7. Salinity, pH, and relative elevation

We measured salinity, pH, and relative elevation to eliminate the possibility that 'species-specific' effects were coincidentally associated with species occupying different hydrologic microsites. A 50-ml porewater sample was taken 10-cm below the soil surface using a 20-cm length of perforated polyethylene tubing (see McKee et al., 1988) and a 60-ml syringe. Salinity was measured four times with a conductivity/salinity meter (model 30, YSI, Inc., Yellow Springs, Ohio). Salinity was measured using the Practical Salinity Scale. pH was measured in the field with a pH/Eh meter (250A series, Orion Research, Inc., Boston, MA). The relative elevation of each subplot within each site was determined by measuring the distance between the soil surface and the high water mark on a white, plastic pipe that had been driven into the sediment.

## 3. Results

Eh, SRP, extractable P, salinity, and basal area differed significantly among species for the combined analysis of all subplots (Table 1). Basal area was not significantly correlated with any of the redox variables. ANCOVA indicated that salinity differed significantly among the species but was associated with differences in basal area. A significant site by species interaction for salinity (Table 2) indicated that species trends were

Table 1  
Species comparisons of soil, porewater and basal area measurements for all subplots

Variable	<i>Bruguiera</i>	<i>Rhizophora</i>	<i>Sonneratia</i>
Eh (mV)	75.2 ± (27.8) <sup>a</sup>	20.5 ± (27.8) <sup>b</sup>	-4.8 ± (26.5) <sup>b</sup>
SRP (μmol l <sup>-1</sup> )	0.5 ± (0.2) <sup>a</sup>	0.7 ± (0.2) <sup>a</sup>	0.9 ± (0.8) <sup>b</sup>
Organic P (μmol l <sup>-1</sup> )	1.0 ± (0.7) <sup>a</sup>	0.3 ± (0.3) <sup>a</sup>	0.6 ± (0.2) <sup>a</sup>
Extractable P (mg kg <sup>-1</sup> )	28.4 ± (4.6) <sup>a</sup>	25.4 ± (3.7) <sup>ab</sup>	21.7 ± (3.3) <sup>b</sup>
Salinity	34.3 ± (2.1) <sup>a</sup>	33.5 ± (1.9) <sup>a</sup>	36.2 ± (1.4) <sup>b</sup>
Relative Elevation (mm)	349.0 ± (42.5) <sup>a</sup>	335.0 ± (40.0) <sup>a</sup>	349.0 ± (38.1) <sup>a</sup>
Basal area (m <sup>2</sup> ha <sup>-1</sup> )	32.5 ± (6.6) <sup>a</sup>	25.2 ± (8.3) <sup>a</sup>	61.0 ± (13.9) <sup>b</sup>

Mean (±SE, *n* = 15) separation performed using LSD method. SRP = soluble reactive P in porewater. Standard error of Eh values represents the variation among subplot averages (30 electrode measurements per subplot). Superscripts with different letters denote significant differences (*P* < 0.05). Extractable P values were obtained by the Olsen method (Olsen & Summers, 1982). Salinity was calculated using the Practical Salinity Scale.

strongly site dependent. ANCOVA indicated that differences in salinity and elevation among sites and within sites had little effect on edaphic and porewater comparisons among species (Table 2).

Eh, extractable P, salinity, and basal area were also significantly different among sites (Table 3). Non-significant site by species interactions for Eh, extractable P, and basal area (Table 2) indicated that species trends were similar among all sites. Although salinity differed significantly among species and sites, correlation analysis indicated that salinity was still strongly associated with relative elevation (Fig. 2). Examination of this relationship revealed that species were homogeneously distributed along salinity and elevation gradients, thus indicating that species-specific salinity differences were associated with microsite differences within subplot groups (blocks).

Relative elevation was correlated with Eh, extractable P, and SRP but never differed significantly among species. Salinity was correlated with Eh, extractable P, and SRP but differed significantly among species only without the basal area covariate. Olsen and Mehlich III P extraction data were correlated (*r* = 0.95) as were the two pyrite preservation techniques (*r* = 0.79) and resulted in the same conclusions after ANOVA regardless of which data sets were analyzed. Because of this, only Olsen extractable P and oven-dried pyrite data are shown.

Relationships among redox variables seemed to be strongest at the site with the most highly reduced soil conditions, Utwe River site #1 (Table 4). This is supported by the ANOVA for all plots that had an average Eh < 0.0 mV (Table 5), indicating strong species-specific effects for soil redox variables but not for salinity, relative elevation, or basal area. Figs. 2 and 3 show highly significant correlations between Eh, SRP,

Table 2

Values of  $P$  from ANOVA and ANCOVA for soil, porewater, and basal area measurements at all sites. Extractable P values were obtained by the Olsen method (Olsen & Summers, 1982)

Source	Eh	SRP	Extractable P	Salinity	Relative elevation	Basal area
ANOVA						
Species	0.000	0.004	0.044	0.013	0.351	0.002
River	0.000	0.134	0.000	0.014	0.138	0.018
River $\times$ Species	0.301	0.051	0.700	0.022	0.457	0.825
ANCOVA (salinity covariate)						
Species	0.000	0.003	0.019	–	0.664	0.024
River	0.010	0.245	0.000	–	0.096	0.012
River $\times$ Species	0.194	0.037	0.668	–	0.289	0.190
ANCOVA (relative elevation covariate)						
Species	0.000	0.097	0.047	0.018	–	0.003
River	0.000	0.218	0.001	0.000	–	0.022
River $\times$ Species	0.314	0.058	0.808	0.017	–	0.856

and extractable P only for subplots with Eh values  $<0.0$  mV.

The Okat River plots had the most oxidized soils ( $P < 0.01$ ). Eh and the other redox variables measured were not linearly correlated (Table 4) even though Eh was significantly different among species. Although there was no correlation between short-term redox indicators such as Eh and SRP, which may change within minutes as soils are flooded, long term indicators (pyrite and extractable P) remained strongly correlated (Table 4).

Utwe River site #1 had the most reduced soil conditions ( $P < 0.01$ ) and the strongest linear relationships among redox variables (Table 4). Although Eh differed among species and salinity did not, Eh and salinity were strongly correlated (Table 5). The strong correlations among Eh, SRP, and extractable P (Figs. 3

and 4) seemed to follow a similar trend as that observed in the comparison of highly reduced subplots (Table 5) and appeared not to be an autocorrelation induced by hydrology. Eh, SRP and extractable P all differed significantly among species within this site.

In Utwe River site #2, the short-term redox indicators (Eh and SRP) were not correlated with pyrite or extractable P, although pyrite and extractable P were negatively correlated with one another (Table 4). This was the only site in which no redox variables differed significantly among species. The pyritization index (reactive iron/{reactive + sulfide-bound iron}), a measure used to assess the limiting effect of reactive iron on pyrite formation (Berner, 1970), was also lower at this site than at the other two sites (Table 3). The pyritization index was not significantly different ( $P = 0.52$ ) among species.

Table 3

Site comparisons of soil, porewater and basal area measurements for all subplots

Variable	Utwe River site #1	Utwe River site #2	Okat River
Eh (mV)	$-61.3 \pm (25.1)^b$	$12.9 \pm (9.4)^b$	$139.4 \pm (17.2)^a$
SRP ( $\mu\text{mol l}^{-1}$ )	$0.72 \pm (0.2)^a$	$0.53 \pm (0.1)^a$	$2.3 \pm (0.8)^a$
Extractable P ( $\text{mg kg}^{-1}$ )	$19.2 \pm (1.5)^b$	$22.5 \pm (1.6)^b$	$41.9 \pm (4.6)^a$
Salinity	$40.6 \pm (0.7)^a$	$34.0 \pm (1.9)^{ab}$	$29.4 \pm (1.2)^b$
Relative elevation (mm)	$349.1 \pm (20.3)^a$	$437.6 \pm (49.0)^a$	$246.3 \pm (27.2)^a$
Basal area ( $\text{m}^2 \text{ha}^{-1}$ )	$40.0 \pm (8.8)^b$	$35.6 \pm (9.3)^b$	$81.1 \pm (12.0)^a$
Pyritization index (%)	$60.8 \pm (1.5)^b$	$80.1 \pm (1.0)^a$	$54.7 \pm (3.8)^c$

Mean ( $\pm$ SE,  $n = 15$ ) separation performed using LSD method. SRP = soluble reactive P in porewater. Standard error of Eh values represents the variation among subplot averages (30 electrode measurements per subplot). Superscripts with different letters denote significant differences ( $P < 0.05$ ). Extractable P values were obtained by the Olsen method (Olsen & Summers, 1982). Salinity was calculated using the Practical Salinity Scale.

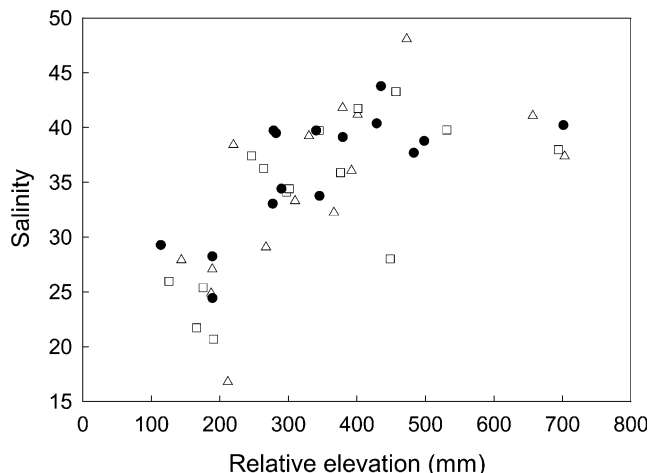


Fig. 2. Relationship between relative elevation and porewater salinity for *Bruguiera* (●), *Rhizophora* (□), and *Sonneratia* (△), subplots. Linear regression significant ( $P < 0.001$ ). Salinity was calculated using the Practical Salinity Scale.

Table 4  
Correlation coefficients among soil, porewater and site variables for subplots within sites

	Eh	Extractable P	SRP	Pyrite	Salinity	Relative elevation
<i>Okat River</i>						
Extractable P	0.03	–	–	–	–	–
SRP	–0.16	–0.24	–	–	–	–
Pyrite	–0.29	–0.86****	0.19	–	–	–
Salinity	–0.13	–0.24	0.32	0.45	–	–
Relative elevation	0.31	–0.38	–0.14	0.37	0.62*	–
Basal area	–0.34	0.28	–0.04	–0.37	0.29	–0.2
<i>Utwe River, site #1</i>						
Extractable P	0.91****	–	–	–	–	–
SRP	–0.80***	–0.82***	–	–	–	–
Pyrite	–0.58*	–0.69**	–0.68**	–	–	–
Salinity	0.82****	–0.75**	–0.75**	–0.28	–	–
Relative elevation	0.72**	0.73**	–0.74**	–0.2	0.86****	–
Basal area	–0.34	–0.34	0.18	0.31	0.03	–0.23
Organic P	0.31	0.32	–0.47	–0.48	0.2	–0.03
<i>Utwe River, site #2</i>						
Extractable P	0.32	–	–	–	–	–
SRP	0.19	0.12	–	–	–	–
Pyrite	–0.09	–0.71**	0.01	–	–	–
Salinity	0.00	–0.35	–0.69**	0.12	–	–
Relative elevation	0.09	–0.25	–0.43	–0.06	0.81****	–
Basal area	–0.21	0.02	0.18	0.27	–0.38	–0.51

SRP = soluble reactive P in porewater. Extractable P values were obtained by the Olsen method (Olsen & Summers, 1982). \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ , \*\*\*\* $P < 0.0001$ .

#### 4. Discussion

Our study revealed that large and statistically significant differences in Eh, SRP, and extractable P exist in the rhizospheres of different mangrove species on Kosrae. These differences appeared not to be associated with broad-scale hydrology but rather seemed to be engendered by the species themselves or caused by microsite edaphic and hydrologic differences that could have resulted in present species distributions.

A few studies have suggested that species distributions may be affected by nutrient concentrations (McKee, 1993; Ukpong, 1994), or salinity (Ball, 1998). There is a long history of correlative evidence associating species distribution patterns with salinity and elevation gradients (Ball, 1998; Duke, 1992; Watson, 1928). Greenhouse studies have demonstrated that

mangroves subjected to higher than optimum salinity levels or lower than optimum nutrient levels exhibit decreased growth (Lin & Sternberg, 1993; Naidoo, 1990; Smith, Yang, Kamiya, & Snedaker, 1996; Wakushima et al., 1994). A previous study found evidence for *Bruguiera gymnorrhiza* and *Sonneratia alba* zonation in Japan within similar ranges of salinity as those found on Kosrae (Wakushima et al., 1994). Although the differences in salinity among species found in Kosrae were relatively small, it may be possible that such small differences foster the development of microsite edaphic changes over the course of forest development. However, mangrove species on Kosrae did not appear to be distributed based on microsite differences in salinity or edaphic variation. Whereas salinity was significantly different among species, the magnitude of these differences (Table 1) was relatively small when compared to

Table 5  
Species comparisons of soil, porewater and basal area measurements for all subplots with Eh < 0.0 mV

Variable	<i>Bruguiera</i>	<i>Rhizophora</i>	<i>Sonneratia</i>	P statistic
Eh (mV)	–21.2 ± (27.8) <sup>a</sup>	–71.7 ± (27.8) <sup>b</sup>	–101 ± (26.5) <sup>b</sup>	0.011
SRP (μmol l <sup>–1</sup> )	0.3 ± (0.1) <sup>a</sup>	0.7 ± (0.3) <sup>b</sup>	0.6 ± (0.2) <sup>b</sup>	0.029
Extractable P (mg kg <sup>–1</sup> )	74.8 ± (2.3) <sup>a</sup>	55.6 ± (2.1) <sup>b</sup>	47.8 ± (2.5) <sup>b</sup>	0.022
Pyrite (mg Fe g <sup>–1</sup> )	17.0 ± (3.3) <sup>a</sup>	30.0 ± (7.3) <sup>a</sup>	32.7 ± (5.1) <sup>a</sup>	0.057
Salinity	39.2 ± (1.3) <sup>a</sup>	38.2 ± (1.1) <sup>a</sup>	38.5 ± (1.0) <sup>a</sup>	0.449
Relative Elevation (mm)	383.1 ± (60.6) <sup>a</sup>	348.6 ± (43.2) <sup>a</sup>	354.2 ± (33.0) <sup>a</sup>	0.414
Basal area (m <sup>2</sup> ha <sup>–1</sup> )	24.9 ± (10.1) <sup>a</sup>	20.3 ± (12.0) <sup>a</sup>	42.3 ± (19.7) <sup>a</sup>	0.225

Mean (±SE,  $n = 8$ ) separation performed using LSD method. SRP = soluble reactive P in porewater. Standard error of Eh values represents the variation among subplot averages (30 electrode measurements per subplot). Superscripts with different letters denote significant differences ( $P < 0.05$ ). Extractable P values were obtained by the Olsen method (Olsen & Summers, 1982). Salinity was calculated using the Practical Salinity Scale.

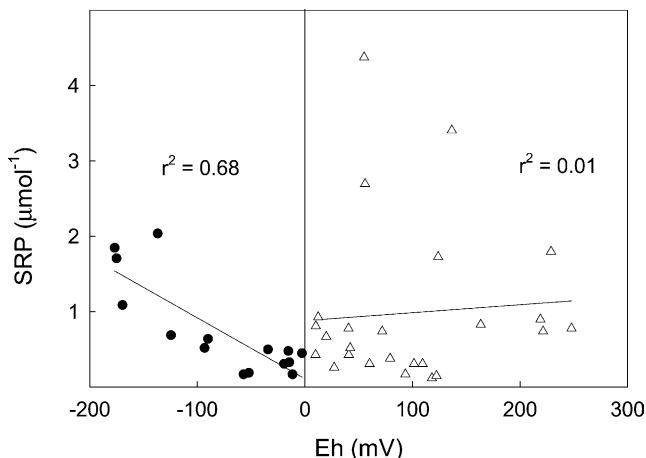


Fig. 3. Relationship between soil Eh and soluble reactive P for subplots with Eh < 0.0 mV (●) and subplots with Eh > 0.0 mV (△).

differences among sites (Table 3). The small differences in salinity among species reflect real differences in the rhizospheres of trees growing in close proximity (<20 m) yet all three species of mangroves were found in relatively homogenous distribution throughout a fairly large hydrologic range (Fig. 2). ANCOVA (Table 2) also supports the conclusion that the experimental design utilized in this study successfully removed the effects of salinity and elevation from species comparisons. If species comparisons were confounded by salinity and/or elevation, ANCOVA would have significantly altered species comparison P statistics. Similar salinity differences between *Rhizophora mangle* and *Avicennia germinans* rhizospheres in another study were attributed to the partial exclusion of salts from water taken up by transpiration (Carlson, Yarbrow, Zimmerman, & Montgomery, 1983).

Considerable evidence gathered over the past two decades suggests that mangroves are able to oxidize their rhizospheres by translocating oxygen absorbed through lenticels on above-ground root structures to below-ground roots, where it then presumably diffuses into the surrounding soil (McKee, 1993; McKee et al., 1988; Thibodeau & Nickerson, 1986). Because the three species of mangroves examined in this study have distinctly different types of above-ground root structures, these species may not be equally able to oxidize their rhizospheres. Further study is needed to test this hypothesis directly.

Decomposition and mineralization of organically bound P may have been partially responsible for the redox/P relationships found on Kosrae. A study of an overwash mangrove island in Florida revealed that microbial communities and organic matter fractions can vary greatly among mangrove species (Carlson et al., 1983). There is direct evidence that different types of decomposing organic matter can have different effects on Fe and Mn dynamics in wetlands (Nagarajah, Neue, &

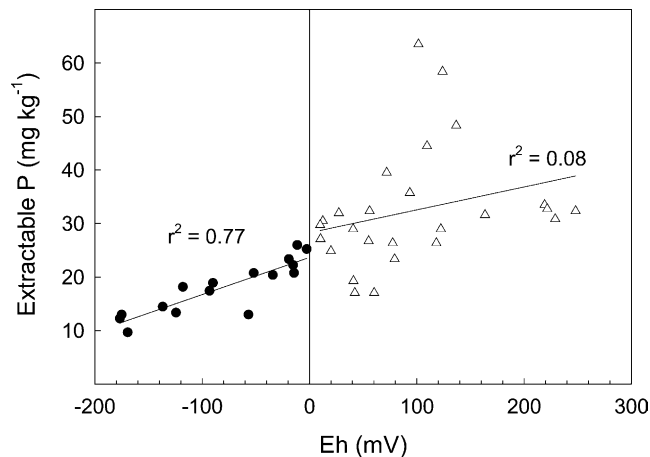


Fig. 4. Relationship between soil Eh and extractable P for subplots with Eh < 0.0 mV (●) and subplots with Eh > 0.0 mV (△). Extractable P values were obtained by the Olsen method (Olsen & Summers, 1982).

Alberto, 1989; Yodkeaw & De Datta, 1989). Microbes themselves can alter the concentrations of P, Fe, Mn (Das, Mandal, & Mandal, 1991; Saha & Mandal, 1979) and micro-nutrient chelates (Kerby, Niven, Rowell, & Stewart, 1987) in porewater. If organic matter inputs, decomposition rates, and microbial communities differ significantly among species, it is possible that differences in Eh, extractable P, and SRP, similar to those found on Kosrae, could result. A study of above- and below-ground organic matter turnover and decomposition in Kosrae revealed that there were significant differences in humic acid concentration and root production among species but that these differences were not correlated with P dynamics (Gleason and Ewel, unpublished data). Also, organic P concentrations in porewater did not follow inorganic P trends (Table 1). This would have been expected if there was a close relationship between Eh and organic P mineralization.

SRP and extractable P differed significantly among species only under highly reducing conditions. Because SRP, pyrite, and extractable P were all highly correlated at subplots that had Eh values < 0.0 mV, the species-specific nature of these redox variables may be most significant at reduced sites. There may be a strong sulfide/reactive iron dependency controlling P solubility under reduced conditions, a hypothesis supported by studies of sulfur, iron, and phosphorus dynamics in other wetlands (Boto, Bunt, & Wellington, 1984; Krom & Berner, 1980; Ponnampereuma, 1972; Rhue & Harris, 1999). A portion of P sorbed to ferric oxide minerals is released into solution as ferric ( $\text{Fe}^{3+}$ ) iron is reduced to ferrous ( $\text{Fe}^{2+}$ ) iron (Rhue & Harris, 1999). The remaining P is then released into solution as ferrous oxides are precipitated as iron sulfide (Rhue & Harris, 1999). The extent of this reaction depends upon the availability of sulfide, reactive iron, sulfate reducing bacteria, and carbon source. If soil conditions are too

oxidized to favor the reduction of sulfate or if reactive iron concentrations are very low, the precipitation of iron sulfide (including pyrite) and the subsequent release of SRP into solution will be limited. This mechanism would be affected by direct oxidation from mangrove roots as well as nutrient cycling, plant uptake, and mineralization processes.

Because the soils in this experiment were oven-dried there is a chance that ferrous oxide-bound P may have co-precipitated with ferric oxides during the drying process. Depending on the efficacy of NaHCO<sub>3</sub> (Olsen method) and NH<sub>4</sub>F (Mehlich method) to extract this iron-bound P, an exaggerated, positive correlation between Eh and extractable P may have resulted. Mehlich (1978) found that NH<sub>4</sub>F extracted nearly 100% of the Fe and Al bound P in a wide range of upland soils. Both Olsen and Mehlich extractions were highly correlated ( $r = 0.91$ ) and were found to extract P adequately from mangrove soils high in Al and Fe bound P (Mongia & Bandyopadhyay, 1996). Also, the strong correlations among extractable P, SRP, and pyrite at the most reduced site suggest that the relationship between Eh and extractable P was not an artifact. Boto et al. (1984) found a similar relationship for Australian mangrove forests.

Plant uptake may also result in strong differences in porewater P and soil P concentrations among temporal and spatially discrete measurements (Boto et al., 1984; Boto & Wellington, 1988; Wolaver & Spurrier, 1988). Extractable P was positively correlated with above-ground biomass in Australian mangroves (Boto et al., 1984), and total dissolved P was positively correlated with basal area in mangrove forests of the Dominican Republic (Sherman et al., 1998). However, in this study neither basal area nor live root mass (Gleason and Ewel, unpublished data) were correlated with porewater P or extractable P. Plant uptake, while possibly being inhibited by reducing conditions (Koch & Snedaker, 1997; Naidoo, 1990), could not account for the strong relationships found among Eh, SRP, and pyrite in this study.

Regardless of whether the species-specific differences found in this study were engendered by the species themselves or by existing microsite differences, the implications of such disparate edaphic conditions among species are significant. If microsite differences, developed over the course of forest development, have resulted in the present species composition, then scientists need to take a much closer look at how edaphic conditions affect the establishment, growth, and survival of mangroves. If the mangroves themselves are altering the redox chemistry of their rhizospheres, any natural or anthropogenic disturbance that affects species composition is likely to affect P and organic matter dynamics significantly. In order for mangrove ecologists to develop useful conceptual models and make sound management decisions that concern mangrove species composition

and forest community development, the importance of plant–soil interactions must be determined.

### Acknowledgements

This research was supported by the USDA Forest Service. We thank the Kosrae Development Review Commission for assistance with this study. Appreciation is also extended to Robert Hauff, Kaliko Amona, Jason Jack, Moses Palik, and Erick Waguk for their technical assistance in the field. We thank James Silva and James Baldwin for helping with the experimental design and statistical analysis. We also thank Kenneth Krauss, Brian Fry, and Mark Walbridge for helpful comments on the manuscript.

### References

- Alongi, D. M., Christofferson, P., & Tirendi, F. (1993). The influence of forest type on microbial-nutrient relationships in tropical mangrove sediments. *Journal of Experimental Marine Biology and Ecology* 171, 201–223.
- Ball, M. C. (1998). Mangrove species richness in relation to salinity and waterlogging: a case study along the Adelaide River floodplain, northern Australia. *Global Ecology and Biogeography Letters* 7, 73–82.
- Berner, R. A. (1970). Sedimentary pyrite formation. *American Journal of Science* 268, 1–23.
- Bohn, H. L., McNeal, B. L., & O'Connor, G. A. (1985). *Soil Chemistry* (2nd ed.). New York, NY: Wiley.
- Boto, K. G., Bunt, J. S., & Wellington, J. T. (1984). Variations in mangrove forest productivity in Northern Australia and Papua New Guinea. *Estuarine, Coastal and Shelf Science* 19, 321–329.
- Boto, K. G., & Wellington, J. T. (1988). Seasonal variations in concentrations and fluxes of dissolved organic and inorganic materials in a tropical, tidally-dominated, mangrove waterway. *Marine Ecology Progress Series* 50, 151–160.
- Cardona, P. L., & Botero, L. B. (1998). Soil characteristics and vegetation structure in a heavily deteriorated mangrove forest in the Caribbean coast of Colombia. *Biotropica* 30, 24–34.
- Carlson, P. R., Yarbrow, L. A., Zimmerman, C. F., & Montgomery, J. R. (1983). Pore water chemistry of an overwash mangrove island. *Florida Scientist* 3, 239–249.
- Das, S. C., Mandal, B., & Mandal, L. N. (1991). Effect of growth and subsequent decomposition of blue-green algae on the transformation of iron and manganese in submerged soils. *Plant and Soil* 138, 75–84.
- Devoe, N. N., & Cole, T. G. (1998). Growth and yield in mangrove forests of the Federated States of Micronesia. *Forest Ecology and Management* 103, 33–48.
- Duke, N. C. (1992). Mangrove floristics and biogeography. In A. I. Alongi, & D. M. Alongi (Eds.), *Tropical mangrove ecosystems, coastal and estuarine studies series* (pp. 63–100). Washington, DC: American Geophysical Union.
- Ewel, K. C., Bourgeois, J. A., Cole, T. C., & Zheng, S. (1998). Variation in environmental characteristics and vegetation in high-rainfall mangrove forests, Kosrae, Micronesia. *Global Ecology and Biogeography Letters* 7, 49–56.
- Fiedler, S. (2000). In situ long-term-measurement of redox potential in redoximorphic soils. In J. Schuring, H. D. Schulz, W. R. Fischer,

- J. Alongi, & W. H. M. Duijnsveld (Eds.), *Redox: Fundamentals, processes and applications* (pp. 81–93). Berlin: Springer.
- Fujimoto, K., Miyagi, T., Kikuchi, T., & Kawana, T. (1996). Mangrove habitat formation and response to holocene sea-level changes on Kosrae Island, Micronesia. *Mangroves and Salt Marshes 1*, 47–57.
- Gardner, L. R., Wolaver, T. G., & Mitchell, M. (1988). Spatial variations in the sulfur chemistry of salt marsh sediments at North Islet, South Carolina. *Journal of Marine Research 46*, 815–836.
- Giblin, A. E. (1988). Pyrite formation in marshes during early diagenesis. *Geomicrobiology Journal 6*, 77–97.
- Hansen, H. P., & Koroleff, F. (1999). Determination of nutrients. In K. Grasshoff, K. Kremling, & M. Ehrhardt (Eds.), *Methods of seawater analysis* (pp. 170–173). Weinheim: Verlag Chemie.
- Kaiserli, A., Voutsas, D., & Samara, C. (2002). Phosphorus fractionation in lake sediments—Lakes Volvi and Koronea, N. Greece. *Chemosphere 46*, 1147–1155.
- Kerby, N. W., Niven, G. W., Rowell, P., & Stewart, W. D. P. (1987). Ammonia and amino acid production by cyanobacteria. In T. Stadler (Ed.), *Algal biotechnology* (pp. 170–173). London: Elsevier.
- Koch, M., & Snedaker, S. C. (1997). Factors influencing *Rhizophora mangle* L. seedling development in Everglades carbonate soils. *Aquatic Botany 59*, 87–98.
- Krom, M. D., & Berner, R. A. (1980). Adsorption of phosphate in anoxic marine sediments. *Limnology and Oceanography 25*, 797–806.
- Lacerda, D. L., Ittekkot, V., & Patchineelam, S. R. (1995). Biogeochemistry of mangrove soil organic matter: a comparison between *Rhizophora* and *Avicennia* soils in south-eastern Brazil. *Estuarine, Coastal and Shelf Science 40*, 713–720.
- Lin, G., & Sternberg, L. (1993). Effects of salinity fluctuation on photosynthetic gas exchange and plant growth of the red mangrove (*Rhizophora mangle* L.). *Journal of Experimental Botany 44*, 9–16.
- Lord, C. J. (1981). A selective and précis method for pyrite determination in sedimentary materials. *Journal of Sediment Petrology 51*, 664–666.
- McKee, K. L. (1993). Soil physicochemical patterns and mangrove species distribution—reciprocal effects? *Journal of Ecology 81*, 477–487.
- McKee, K. L., Mendelssohn, I. A., & Hester, M. W. (1988). Reexamination of pore water sulfide concentrations and redox potentials near the aerial roots of *Rhizophora mangle* and *Avicennia germinans*. *American Journal of Botany 75*, 1352–1359.
- Mehlich, A. (1978). Influence of fluoride, sulfate and acidity on extractable phosphorus, calcium, magnesium and potassium. *Communications in Soil Science and Plant Analysis 9*, 455–476.
- Mehlich, A. (1984). Mehlich 3 soil test extractant: a modification of Mehlich 2 extractant. *Communications in Soil Science and Plant Analysis 15*, 1409–1416.
- Merlin, M., Taulung, R., & James, J. (1993). *Plants and environments of Kosrae*. East-West Center, Honolulu, HI.
- Mongia, A. P., & Bandyopadhyay, A. K. (1996). Phosphate fractions and their relation to available phosphorus indices in soils of tropical deciduous and mangrove forests of Adamans. *Journal of the Indian Society of Soil Science 44*, 514–516.
- Nagarajah, S., Neue, N. V., & Alberto, M. C. R. (1989). Effect of Sesbana, Azolla, and rice straw incorporation on the kinetics of NH<sub>4</sub>, K, Fe, Mn, Zn and P in some flooded rice soils. *Plant and Soil 116*, 37–48.
- Naidoo, G. (1990). Effects of nitrate, ammonium and salinity on growth of the mangrove *Bruguiera gymnorrhiza* (L.) Lam. *Aquatic Botany 38*, 209–219.
- Olsen, R. V., & Ellis, R. (1982). Iron. In A. L. Page, & D. R. Keeney (Eds.), *Methods of soil analysis* (pp. 303–305). Madison, WI: Soil Science Society of America, Inc.
- Olsen, S. R., & Summers, L. E. (1982). Phosphorus. In A. L. Page, & D. R. Keeney (Eds.), *Methods of soil analysis* (pp. 421–422). Madison, WI: Soil Science Society of America, Inc.
- Ponnamperuma, F. N. (1972). The chemistry of submerged soils. *Advances in Agronomy 234*, 29–96.
- Rhue, R. D., & Harris, W. G. (1999). Phosphorus sorption/desorption reactions in soils and sediments. In K. R. Reddy, G. A. O'Connor, & C. L. Schelske (Eds.), *Phosphorus biogeochemistry in subtropical ecosystems* (pp. 187–206). Boca Raton, FL: Lewis Publishers.
- Saha, K. C., & Mandal, L. N. (1979). Effect of algal growth on the availability of P, Fe and Mn in rice soils. *Plant and Soil 52*, 139–149.
- Schulz, H. D. (2000). Redox measurements in marine sediments. In J. Schuring, H. D. Schulz, W. R. Fischer, J. Bottcher, & W. H. M. Duijnsveld (Eds.), *Redox: Fundamentals, processes and applications* (pp. 81–93). Berlin: Springer.
- Sherman, R. E., Fahey, T. J., & Howarth, R. W. (1998). Soil–plant interactions in a neotropical mangrove forest: iron, phosphorus and sulfur dynamics. *Oecologia 115*, 553–563.
- Smith, T. J., III. (1992). Forest structure. In A. I. Robertson, & D. M. Alongi (Eds.), *Tropical mangrove ecosystems, coastal and estuarine studies series* (pp. 101–136). Washington, DC: American Geophysical Union.
- Smith, S. M., Yang, Y. Y., Kamiya, Y., & Snedaker, S. C. (1996). Effect of environment and gibberellins on the early growth and development of the red mangrove, *Rhizophora mangle* L. *Plant Growth Regulation 20*, 215–223.
- Soil Conservation Service. (1984). Soil survey of the island of Kosrae, Federated States of Micronesia. United States Department of Agriculture, Washington, DC.
- Thibodeau, F. R., & Nickerson, N. H. (1986). Differential oxidation of mangrove substrate by *Avicennia germinans* and *Rhizophoramangle*. *American Journal of Botany 73*, 512–516.
- Ukpong, I. E. (1994). Soil-vegetation interrelationships of mangrove swamps as revealed by multivariate analysis. *Geoderma 64*, 167–181.
- Wakushima, S., Kuraishi, S., & Sakurai, N. (1994). Soil salinity and pH in Japanese mangrove forests and growth of cultivated mangrove plants in different soil conditions. *Journal of Plant Research 107*, 39–46.
- Walbridge, M. R. (1991). Phosphorus availability in acid organic soils of the lower North Carolina Coastal Plain. *Ecology 72*, 2083–2100.
- Watson, J. G. (1928). Mangrove forests of the Malay Peninsula. *Malayan Forest Records 6*, 1–275.
- Wolaver, T. G., & Spurrier, J. D. (1988). The exchange of phosphorus between a euhaline vegetated marsh and the adjacent tidal creek. *Estuarine, Coastal and Shelf Science 26*, 203–214.
- Yodkeaw, M., & De Datta, S. K. (1989). Effects of organic matter and water regime on the kinetics of iron and manganese in two high pH rice soils. *Soil Science and Plant Nutrition 35*, 323–335.