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TRENDS IN AQUATIC ECOLOGY

Fine root productivity varies along nitrogen and phosphorus gradients in high-rainfall mangrove forests of Micronesia

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Abstract Belowground biomass is thought to account for much of the total biomass in mangrove forests and may be related to soil fertility. The Yela River and the Sapwalap River, Federated States of Micronesia, contain a natural soil resource gradient defined by total phosphorus (P) density ranging from 0.05 to 0.42 mg cm^{-3} in different hydrogeomorphic settings. We used this fertility gradient to test the hypothesis that edaphic conditions constrain mangrove productivity through differential allocation of biomass to belowground roots. We removed sequential cores and implanted root ingrowth bags to measure *in situ* biomass and productivity, respectively. Belowground root biomass values ranged among sites from 0.448 ± 0.096 to 2.641 ± 0.534 kg m^{-2}. Root productivity (roots ≤20 mm) did not vary significantly along the gradient ($P = 0.3355$) or with P fertilization after 6 months ($P = 0.2968$). Fine root productivity (roots ≤2 mm), however, did vary significantly among sites ($P = 0.0363$) and ranged from 45.88 ± 21.37 to 118.66 ± 38.05 g m^{-2} $year^{-1}$. The distribution of total standing root biomass and fine root productivity followed patterns of N:P ratios as hypothesized, with larger root mass generally associated with lower relative P concentrations. Many of the processes of nutrient acquisition reported from nutrient-limited mangrove forests may also occur in forests of greater biomass and productivity when growing along soil nutrient gradients.

Keywords Carbon allocation · Roots · Nutrients · Productivity · Mangrove · Pacific high islands · Micronesia

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Introduction

Understanding root dynamics is an important part of elucidating structure and function of any ecosystem. However, the logistical difficulties of working in mangrove forests, which are tidal environments with substantial spatial variability, have been daunting. The emerging importance of these ecosystems in carbon sequestration (Twilley et al., 1992; McKee & Faulkner, 2000; Lovelock et al., 2006; Bouillon et al., 2008; Lovelock, 2008; Alongi, 2011; Donato et al., 2011; Mcleod et al., 2011) mandates that a better understanding of belowground structure and function be achieved. We know that mangrove forests are phenotypically plastic in their ability to exploit nutrients in response to environmental change (Feller, 1995; Feller et al., 2010; Reef et al., 2010) and that they can allocate 40–60% of their total biomass to belowground roots (Komiyama et al., 1987; Lugo, 1990; Snedaker et al., 1995; Khan et al., 2009). We also know that the phosphorus (P) limited scrub mangrove forests of Belize have slow root decomposition rates that can be accelerated experimentally with P fertilizers (Feller et al., 1999), as predicted by optimal foraging theory (Tilman, 1985; Gleeson & Tilman, 1992), and that greater efficiency of P use in P-deficient soils can be promoted through stimulated root growth in some settings (Castañeda-Moya et al., 2011). The current study was undertaken to determine whether such changes in belowground allocation patterns are likely to occur in mangrove forests on Pacific high islands with less severe nutrient limitation than those reported previously (Feller et al., 1999; Castañeda-Moya et al., 2011), as described below.

Biomass allocation in a plant is influenced not only by resource gradients, but also by regulator gradients (Huston, 1997). For mangrove ecosystems, regulators include abiotic stressors such as salt, hydrogen sulfide, and flooding (Twilley & Rivera-Monroy, 2005). The resource-ratio hypothesis suggests that plants optimize their exploitation of some limiting resource in exchange for a reduction in energy expenditure on other processes or non-limiting resource acquisition (Tilman, 1985). This hypothesis, however, does not account for the complex interaction of regulators on patterns of biomass allocation. Regulators affect survival, reproduction, and aboveground productivity of mangroves (Thom, 1967; Chapman, 1976; Tomlinson, 1986). Much attention has focused on the influence of hydrogen sulfide and flooding duration on patterns of aboveground forest structure and productivity in mangroves (McKee & Mendelssohn, 1987; McKee et al., 1988; McKee, 1993, 1995; Kryger & Lee, 1996; Pezeshki et al., 1997; Gleason & Ewel, 2002; Krauss et al., 2006). Regulator gradients may also affect patterns of root biomass and productivity (Reef et al., 2010), and thus shift the relative allocation of biomass in forests growing in estuaries, potentially against resource-ratio predictions (Castañeda-Moya et al., 2011).

A cohort model of soil biogeochemistry, in fact, demonstrated that soil organic matter content is controlled more by the capacity for root productivity than by litter fall in south Florida mangroves (Chen & Twilley, 1999), and empirical studies from Belizean mangroves support a similar hypothesis (Middleton & McKee, 2001, see also Krauss et al., 2014). Root data used in the south Florida model, however, were based on very few direct observations of mangrove biomass in relation to belowground nutrient concentrations, relying mostly on derived estimates of root:shoot ratios. Our understanding of mangroves is limited by the difficulties associated with measuring productivity, mortality, and longevity of complex root systems (Santantonio & Hermann, 1985; Cuevas & Medina, 1988; Majdi, 1996). Many studies that include belowground parameters assume that root dynamics can be estimated using common measures of aboveground forest productivity rather than measuring these compartments directly (Santantonio et al., 1977; Vogt & Persson, 1991; Vogt et al., 1995, 1996; Chen & Twilley, 1999; Ostertag, 2001; Komiyama et al., 2008; Jachowski et al., 2013). Yet, aboveground biomass distribution does not necessarily reflect the response of belowground components, because roots are exposed to different physicochemical conditions (Vogt et al., 1995).

We used a naturally occurring gradient in soil resources and regulators to test the hypothesis that less fertile sites corresponded to greater relative rates of belowground root productivity in mangroves. We compare these data with results from the other studies to seek similarities and differences in belowground processes in distinct mangrove habitats.

Materials and methods

Study sites

Soils in two watersheds, Yela on Kosrae and Sapwalap on Pohnpei, had different patterns of nutrient density between watersheds and among three hydrogeomorphic zones (Table 1). In Yela, nitrogen (N) density was similar in all three zones (about 0.71 mg N cm^{-3}) but higher in Sapwalap (1.63 mg N cm^{-3}). Total P, however, was higher in Yela (0.42 mg P cm^{-3}) than in Sapwalap (0.05 mg P cm^{-3}), probably due to difference in age of the islands. N:P ratios (atomic) were <10 for all sites in Yela, compared to 15–75 for Sapwalap; higher N:P ratios suggest nutrient limitation. This existing gradient provided the opportunity to determine the effect of soil fertility on biomass allocation in these mangrove forests.

Mean annual temperature on Pohnpei and Kosrae is 27°C, and annual rainfall is evenly distributed throughout the year, averaging 4,100–4,800 mm in the lowlands, with slightly more rainfall on Kosrae (Krauss et al., 2007). Tides on the islands are semidiurnal, with an average range of 0.79 m on Pohnpei and 0.98 m on Kosrae (Nautical Software, Inc., 1997). Groundwater and sheet flow from upland systems also provide fresh water input into coastal regions including the mangrove forests (Drexler & Ewel, 2001).

The mangrove forests of Kosrae and Pohnpei include eleven overstory species. Of these, *Rhizophora apiculata* Bl, *Bruguiera gymnorrhiza* (L.) Savigny, *Xylocarpus granatum* Koen., *Sonneratia alba* J.E. Smith, *Lumnitzera littorea* (Jack) Voigt, and *Heritiera littoralis* Aiton are common in and around the sites in Sapwalap (Fujimoto et al., 1995). On Kosrae, mangrove species composition is dominated by *S. alba*, *B. gymnorrhiza*, and *R. apiculata* (Ewel et al., 1998).

At Yela and Sapwalap, we used a five-point sampling design randomly located in the three hydrogeomorphic zones: fringe, riverine, and interior (sensu Ewel et al., 1998). The five-point sampling design consisted of four points, or replicates, located along N–S and E–W axes and within 50 m of a center (fifth) point. Each five-point sampling plot covers an area of approximately 1.9 ha in each zone.

Porewater and soil characteristics

Porewater samples for determination of sulfide, salinity, and temperature were collected at depths of 10 and 40 cm during low tide with procedures for sample extraction described by McKee et al. (1988). Hydrogen sulfide was measured with a Thermo Orion (Waltham, MA, USA) micro ion sulfide sensing electrode using optimum results solution A for determination of low levels of sulfide (<0.1 mM). Salinity, conductivity, and temperature were measured using a portable meter (Model 30, YSI Inc., Yellow Springs, OH, USA). Redox was measured with a multi-depth platinum electrode with sensors at 0, 10, and 40 cm below the soil surface (modified from Hargis & Twilley, 1994). Each electrode was inserted at random locations around each point and allowed to equilibrate for at least 15 min prior to recording values using a pH meter and calomel reference electrode. Redox readings were found to be very consistent after 15 min. Calibrations were made to adjust for the reference electrode; probes were periodically checked with quinhydrone and pH 4 solution (modified from Whitfield, 1969).

Soil cores for total nutrients, organic matter content, and labile P analysis were obtained using a 10.2-cm-diameter PVC core sampled to a depth of 45 cm. Subsamples were obtained from the 0–22.5 cm (top) and 22.5–45 cm (bottom) sections for the extraction process (Olsen & Sommers, 1982).

Root biomass

Root biomass was determined by collecting four, 10.2-cm-diameter cores from adjacent locations at each of the five points within a site to a depth of 45 cm. Root cores were collected in June–July 2000 and June–July 2001 using one of two techniques developed for tropical and temperate forest ecosystems (Vogt et al., 1998; Oliveira et al., 2000). The first approach used a longitudinally sectioned PVC pipe sealed together with duct tape, while the second approach used a soil auger of the same dimensions. Soil and root cores were sampled in increments of 0–22.5 cm (top) and 22.5–45 cm (bottom) at each sample point. When large roots, coral, or rock obstructed sampling, the sample was retaken as close to the original sampling location as permitted by soil conditions and aboveground roots.

Table 1 Summary of physico-chemical variables from fringe, interior, and riverine hydrogeomorphic zones in mangrove forests along the Yela River (Kosrae) and Sapwalap River (Pohnpei), Federated States of Micronesia

Variable	Yela (Kosrae)			Sapwalap (Pohnpei)			*F* ratio	*P*
	Fringe	Interior	Riverine	Fringe	Interior	Riverine		
Bulk density (g cm^{-3})	0.334 ± 0.029^{a}	0.172 ± 0.010^{b}	0.188 ± 0.024^{b}	0.188 ± 0.006^{b}	0.186 ± 0.009^{b}	0.416 ± 0.033^{a}	15.15	<0.0001
Ash (% dry mass)	85.2 ± 0.6^{a}	78.0 ± 0.7^{b}	70.9 ± 1.0^{c}	43.3 ± 1.0^{d}	45.9 ± 2.3^{d}	$75.3 \pm 0.9^{b,c}$	277.84	<0.0001
Total C (mg cm^{-3})	19.15 ± 1.92^{a}	14.04 ± 2.03^{a}	19.22 ± 2.14^{a}	58.57 ± 1.92^{b}	52.32 ± 1.92^{b}	36.94 ± 1.92^{c}	92.30	<0.0001
Total N (mg cm^{-3})	0.71 ± 0.061^{a}	0.48 ± 0.065^{a}	0.71 ± 0.068^{a}	1.59 ± 0.061^{b}	1.63 ± 0.061^{b}	1.62 ± 0.061^{b}	74.86	<0.0001
Total P (mg cm^{-3})	0.38 ± 0.038^{a}	0.40 ± 0.025^{a}	0.42 ± 0.054^{a}	0.05 ± 0.002^{b}	0.09 ± 0.007^{c}	0.41 ± 0.032^{a}	87.94	<0.0001
C:N ratio (atomic)	$32.7 \pm 4.5^{a,b,c,d}$	$34.0 \pm 1.3^{a,c}$	$31.4 \pm 0.7^{a,d}$	43.0 ± 0.5^{b}	37.6 ± 1.1^{c}	27.1 ± 1.6^{d}	48.53	<0.0001
N:P ratio (atomic)	4.3 ± 0.3^{a}	2.5 ± 0.3^{b}	3.9 ± 0.2^{a}	70.3 ± 3.0^{c}	44.8 ± 2.4^{d}	9.2 ± 0.4^{e}	189.54	<0.0001
Org Matter (mg cm^{-3})	49.16 ± 4.09^{a}	37.99 ± 4.09^{a}	54.21 ± 4.58^{a}	106.64 ± 4.09^{b}	100.14 ± 4.09^{b}	101.33 ± 4.09^{b}	56.16	<0.0001
Inorg Matter (mg cm^{-3})	284.51 ± 29.59^{a}	133.73 ± 7.79^{b}	$133.35 \pm 18.07^{b,c}$	81.59 ± 3.09^{c}	86.10 ± 7.42^{c}	314.81 ± 27.96^{a}	42.46	<0.0001
Salinity (g kg^{-1})	34.2 ± 0.4^{a}	$15.1 \pm 2.5^{b,c}$	$17.1 \pm 1.8^{b,c}$	19.8 ± 1.0^{b}	18.0 ± 0.7^{b}	10.7 ± 0.9^{c}	187.70	<0.0001
Redox (mV)	$71 \pm 33^{a,b,c}$	117 ± 9^{b}	$120 \pm 19^{b,c}$	-13 ± 14^{a}	$44 \pm 8^{a,c}$	$105 \pm 17^{b,c}$	17.04	0.0005
Sulfide at 10 cm (mM)	0.01 ± 0.001^{a}	0.01 ± 0.001^{a}	$<0.01^{a}$	$6.11 \pm 1.75^{a,b}$	$2.07 \pm 1.08^{a,b}$	0.32 ± 0.028^{b}	32.24	0.0301
Sulfide at 45 cm (mM)	$<0.01^{a}$	0.01 ± 0.001^{a}	0.01 ± 0.001^{a}	6.15 ± 1.62^{b}	$6.33 \pm 2.29^{a,b}$	$1.19 \pm 0.90^{a,b}$	7.95	0.0050
pH at 1 cm	7.6	7.0	6.4	6.4	6.3	7.3		
Labile P (μg cm^{-3})	24.92 ± 2.24^{a}	9.38 ± 2.24^{b}	11.58 ± 2.70^{b}	0.45 ± 2.70^{b}	2.96 ± 2.37^{b}	65.42 ± 2.24^{c}	110.68	<0.0001

Values are the site mean ± SE ($n = 5$)

Means followed by the same letters (in superscript) are not significantly different at $\alpha = 0.05$

C carbon, *N* nitrogen, *P* phosphorus, *Exch P* exchangeable phosphorus

Root matter was separated by initially hand washing the samples over a 1-mm mesh sieve in seawater in the field. Soil-free samples were then sealed in airtight plastic bags for transport from remote field sites and stored at 4°C until live and dead roots could be separated. Prior to separation, roots were re-rinsed over 1-mm mesh sieves with deionized water to ensure complete removal of soil. All roots were separated into live (biomass) and dead (necromass) fractions within 4–6 weeks after collection using 17, 11, and 6% Ludox^{TM} solution, a colloidal silicate that separates live and dead roots based on density differences (Robertson & Dixon, 1993). Live root fractions were separated into diameter size classes of <1 mm, 1–2 mm, 2–5 mm, and >5 mm (>5–20 mm were considered medium-size-class roots). Large diameter coarse roots (>20 mm) were so infrequent that, while they were assayed in our experiment, they are not included in our results. All roots smaller than 2 mm diameter will be referred to here as fine roots. Root biomass in this text will refer to all live roots smaller than 20 mm collected in a sample. All live and dead roots were dried to a constant mass at 60°C and weighed.

Root productivity

Root productivity at each site was determined with root ingrowth techniques following established protocols (Raich et al., 1994; Majdi, 1996; Vogt et al., 1998; Oliveira et al., 2000), which have also been applied to mangroves (McKee et al., 2007; Castañeda-Moya et al., 2011). After cores for biomass sampling were removed in June–July 2000, ingrowth bags of equal dimension (10.2 cm × 45 cm) filled with sphagnum peat moss and soaked with local seawater replaced each soil core. Peat moss has been shown in past experiments to mimic mangrove soils in many characteristics (e.g., bulk density and organic matter content) and provides a standard substrate for making comparisons among watersheds, zones, and mangrove forests globally (see McKee et al., 2007). Ingrowth bags were made of synthetic mesh with expandable 1 mm apertures, sewn with 100% nylon thread, sealed with plastic ties (McKee et al., 2007), and marked with numbered aluminum tags to identify specific deployments and treatments.

Ingrowth bags were allowed to incubate in situ for 6 (January 2001 deployments) or 12 months (June 2001 deployments). Once extracted, excess exterior soil was removed, and roots were cut flush with the ingrowth bag to maintain the original volume. Samples were divided into 0–22.5 cm (top) and 22.5–45 cm (bottom) segments, sealed in plastic bags, transferred in ice and cold packs to the lab, and refrigerated at 4°C until further processing. Root productivity rates were determined using the amount of new fresh roots collected in the ingrowth bags during 6- and 12-month incubations. Roots from the ingrowth bags were processed in the same manner as roots from biomass cores. For productivity, however, we had to combine all roots <2 mm without further segregation because year-old decayed peat moss used to fill the ingrowth bags slightly obscured the <1 mm live root size class. Thus, flexible, white, live, <1 mm roots were hand picked from the separated samples and added to the <2 mm size class reported for productivity in order to include all new roots. Root size classes >2 mm were processed in the same manner as biomass samples for separation purposes.

Root productivity with P fertilization

Fine root productivity (roots <2 mm) in relation to P additions was investigated at the interior site in Sapwalap, where the P concentration was naturally low for Micronesian mangroves (Table 1). At each replicate point, two additional ingrowth bags were deployed, fertilized with P, and removed after 6 (January 2001 deployments) and 12 months (June 2001 deployments). Super-triple phosphate wrapped in organic coffee filter paper was added to the peat mixture at the top, center, and bottom of each ingrowth bag prior to deployment. Two P treatments included a lower fertilization that increased the background level of P to 1.5 times the concentration of total phosphorus at the interior site in Sapwalap (0.41 mg P cm^{-3}, treatment 1), and the higher fertilization increased phosphorus concentrations to triple that value (0.82 mg P cm^{-3}, treatment 2) to accentuate possible effects. Root matter in fertilized ingrowth cores was processed in the same manner as unfertilized ingrowth cores.

For the remainder of the manuscript, root productivity estimates derived from fertilized and unfertilized root ingrowth bags will be referred to as the 0.5 year incubation for bags removed after 6 months and the 1 year incubation for bags removed after

12 months. The volume of root material obtained from each of the cores is expressed per unit area to a depth of 0.45 m. Although we report root biomass in kg m^{-2} to facilitate comparison with the global literature, we report root productivity in g m^{-2} $year^{-1}$ because of the low amount of root material obtained using the ingrowth bag technique. Root turnover rates were calculated for each site using the equation

Turnover rate = root productivity/root biomass.

Statistical analyses

Soil nutrient and porewater data were analyzed for differences among sites and for correlations with fine root biomass and productivity. Soil nutrient and porewater data were first examined using mixed model procedures (PROC MIXED; SAS Institute, Inc. 1999–2000) and the Satterthwaite approximation for degrees of freedom to account for inherent variability among sites. Where significant differences among sample means were detected, Tukey's studentized range test ($\alpha = 0.05$) was used to determine significant groupings. Next, paired *t* test comparisons of root biomass for summer 2000 versus summer 2001 were conducted to determine whether standing crop root biomass data could be pooled for the 2 years. Coefficients of variation (CV) were examined for different subsets of root biomass and productivity data including: (1) within point, all 4 measures of replicates and length of incubation, $n = 4$; (2) within each year, across all points and replicates, $n = 10$; (3) within each site, across all points, replicates, and length of incubation, $n = 20$; (4) among points, $n = 5$; (5) between replicates within a year, $n = 2$; and (6) between years, mean of replicates, $n = 2$. When pooling was deemed appropriate, pooling by option (3) was statistically most appropriate based on CVs for root biomass data. A two-way, factorial ANOVA was then performed to determine the effects of site and depth on root biomass and root necromass. When pooling was inappropriate (root productivity), data were examined using mixed model procedures similar to those described above for soil nutrients and porewater data. This analysis also fit unequal variances by site for our data.

Because of the large number of soil variables analyzed (Table 1), principal components analysis (PCA) of all soil nutrient and porewater variables was conducted to determine which variables could be combined to form composite variables with greater statistical power. These composite variables were then analyzed among sites using an ANOVA model. Finally, multiple regression analysis, with a forward selection procedure, was performed to determine the effect of soil variables (again using the composite variables selected from PCA and depth on biomass). When necessary, data were log transformed before ANOVA or multiple regression analysis to achieve normality and variance homoscedasticity.

Results

Soil characteristics

Porewater salinities, sulfide concentrations, and redox potentials differed significantly among sites as well as with depth (Table 1). Salinity at Yela fringe (34.2 g kg^{-1}, Table 1) was significantly higher than at all other sites, where average salinity ranged from 10.7–19.8 g kg^{-1}. Salinity as low as 5 g kg^{-1} was recorded at Sapwalap riverine. Salinity increased with depth at all sites except Yela fringe, indicating more fresh water at the surface of the forest at Sapwalap, Yela riverine, and Yela interior during sampling periods.

Average redox potential ranged from −13 to +120 mV (Table 1), and readings generally decreased with depth. All mean values for redox potential were well below +300 mV, indicating that slightly to moderately reducing conditions predominated in the shallow mangrove soil horizons. Redox measurements near the soil surface did not vary greatly among sites, with only Sapwalap fringe (−13 mV) being lower than some sites (Table 1), but values among sites were significantly different at a depth of 45 cm ($F = 17.04$, $P = 0.0005$). pH ranged from 6.3 to 7.6 among sites. Porewater sulfide concentrations were significantly different among sites at both the 10 and 45 cm depth, varying by several orders of magnitude (Table 1). For example, at 45 cm depth, Sapwalap fringe had significantly higher sulfide concentrations (6.15 ± 1.62 mM) than all Yela sites (≤0.01 mM).

Labile P concentrations differed significantly among sites (Table 1). They were highest at Sapwalap riverine and Yela fringe (65.42 and 24.92 μg P cm^{-3},

Table 2 Summary of root biomass (live roots ≤20 mm), fine root biomass (live roots ≤2 mm), root necromass (dead roots ≤20 mm) and total root mass (biomass + necromass of roots ≤20 mm), root productivity (live roots ≤20 mm), and root turnover rate and turnover time for fringe, interior, and riverine hydrogeomorphic zones in mangrove forests along the Yela River (Kosrae) and Sapwalap River (Pohnpei), Federated States of Micronesia

Variable	Yela (Kosrae)			Sapwalap (Pohnpei)			*F* ratio	*P*
	Fringe	Interior	Riverine	Fringe	Interior	Riverine		
Root biomass (kg m^{-2})	$0.952 \pm 0.189^{b,c}$	1.191 ± 0.222^{b}	$1.425 \pm 0.219^{a,b}$	$1.368 \pm 0.170^{a,b}$	2.641 ± 0.534^{a}	0.448 ± 0.096^{c}	6.95	0.0004
Fine root biomass (kg m^{-2})	0.151 ± 0.021^{c}	$0.185 \pm 0.020^{b,c}$	$0.183 \pm 0.014^{b,c}$	0.292 ± 0.045^{b}	0.577 ± 0.080^{a}	0.170 ± 0.022^{c}	16.37	<0.0001
Root necromass (kg m^{-2})	6.362 ± 0.773^{d}	22.238 ± 1.424^{b}	15.266 ± 0.911^{c}	34.557 ± 3.254^{a}	$18.222 \pm 0.934^{b,c}$	12.804 ± 2.004^{c}	24.79	<0.0001
Total root mass (kg m^{-2})	7.830 ± 0.845^{d}	23.485 ± 1.476^{b}	$18.311 \pm 1.952^{b,c}$	36.921 ± 2.949^{a}	20.730 ± 1.209^{b}	$13.252 \pm 2.006^{c,d}$	27.30	<0.0001
Productivity								
0.5 year deployment (g m^{-2} 0.5 $year^{-1}$)	7.15 ± 3.83	24.42 ± 10.15	35.52 ± 16.50	9.87 ± 2.57	61.18 ± 19.74	23.19 ± 14.72	2.46	0.1393
1 year deployment (g m^{-2} $year^{-1}$)	45.88 ± 21.37	91.03 ± 53.58	100.40 ± 10.21	63.21 ± 30.24	118.66 ± 38.05	95.22 ± 14.54	1.35	0.3355
Turnover rate ($year^{-1}$)	0.039	0.063	0.075	0.044	0.054	0.193		
Turnover time (year)	25.87	15.92	13.27	22.56	18.49	5.18		

Biomass and necromass values are the site means of roots collected during June 2000 and June 2001 combined ($n = 20$). Values represent the treatment mean ± SE. Means followed by the same letters (in superscript) are not significantly different at $\alpha = 0.05$

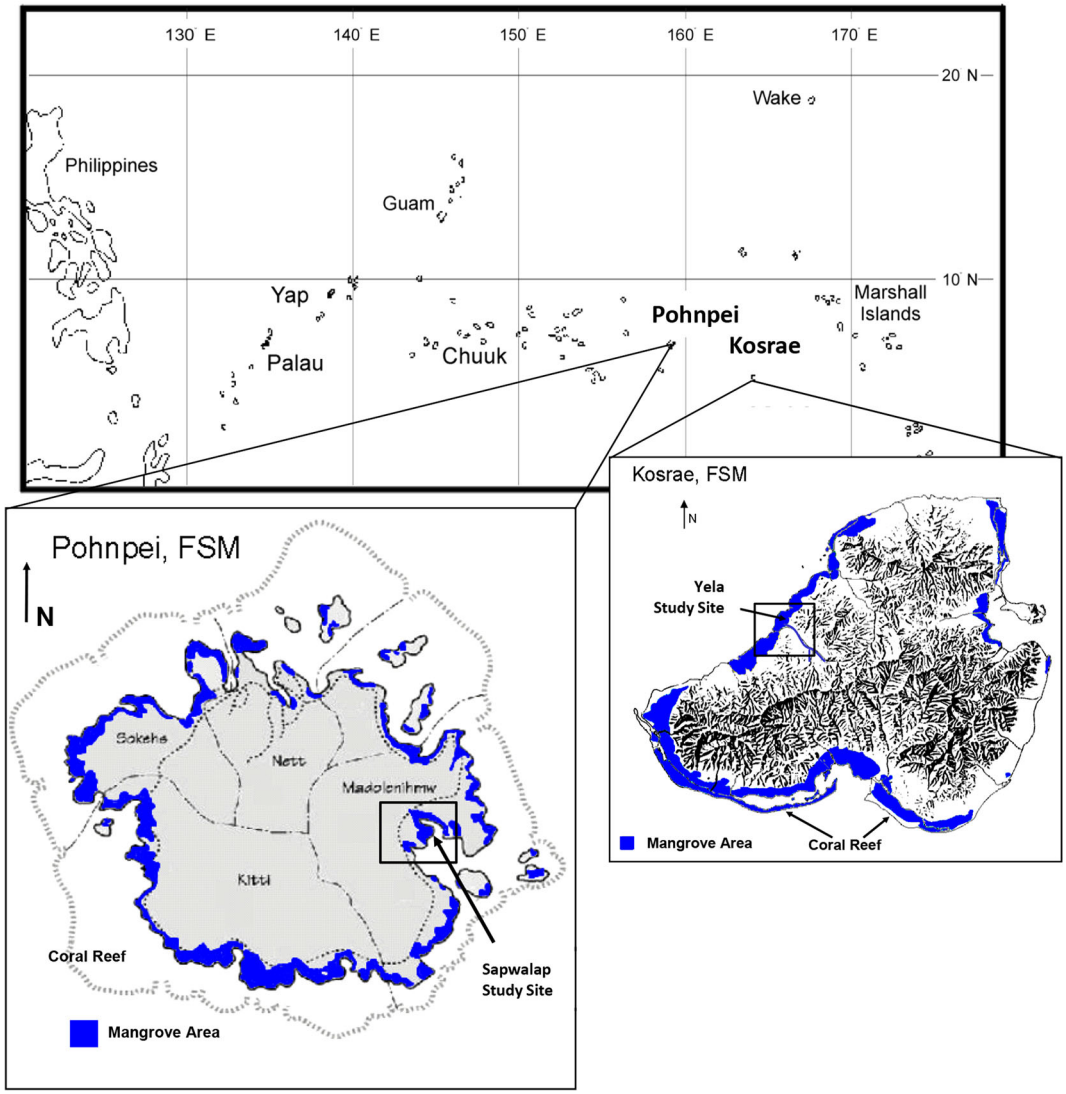

Fig. 1 Location of Kosrae and Pohnpei, Federated States of Micronesia

respectively), and total P concentrations (0.38–0.41 mg cm^{-3}) were among the highest at these sites also. Labile P concentrations were lowest at Sapwalap fringe (0.45 µg P cm^{-3}) and at interior sites on Pohnpei (2.96 µg P cm^{-3}), while Yela interior and riverine had the lowest labile P concentrations for Kosrae (9.38 and 11.58 µg P cm^{-3}, respectively). All three Yela sites were low in total N and high in total P, resulting in lower N:P ratios (2.5–4.3). Sapwalap riverine was the only site on Pohnpei with a low N:P ratio (9.2) due to relatively high concentrations of total P. N:P ratios for Sapwalap fringe (70) and riverine (45) sites were significantly higher than other sites (Table 1).

Root biomass

There was no significant difference between years for root biomass among all sites ($P = 0.7571$), or within each site between the 2 years ($P > 0.16$ for all 6 sites). Hence, the two years of root biomass data were pooled for statistical analyses. Root biomass ranged from 0.448 ± 0.096 kg m^{-2} at Sapwalap riverine to 2.641 ± 0.534 kg m^{-2} at Sapwalap interior (Table 2) and differed significantly by site ($F_{5,24} = 6.95$, $P = 0.0004$). All other sites had intermediate values of root biomass, differing consistently by depth ($F_1 = 4.83$, $P = 0.0284$) and by the biomass present

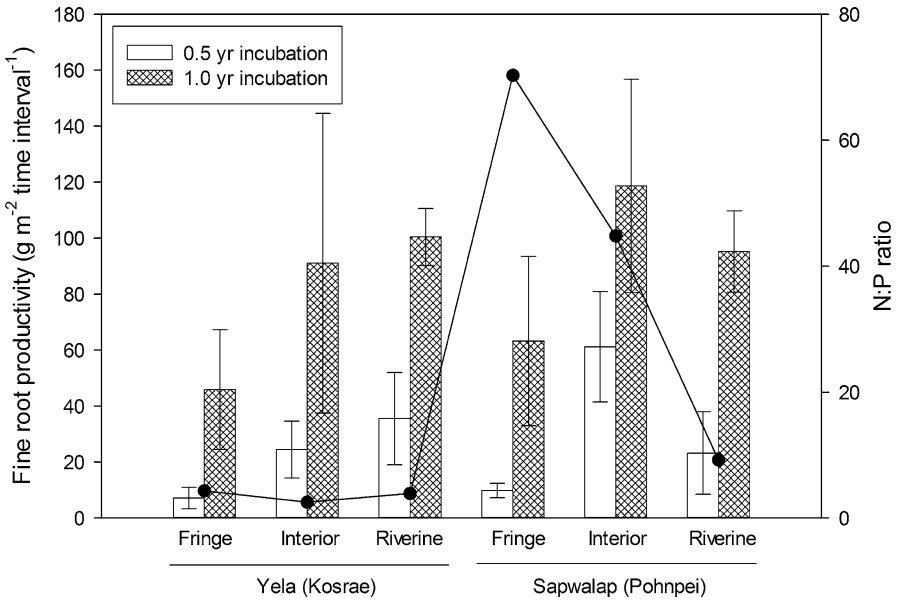

Fig. 2 Fine root productivity over 6 and 12 months versus N:P ratios in the fringe, interior, and riverine hydrogeomorphic zones in mangrove forests along the Yela River (Kosrae) and Sapwalap River (Pohnpei), Federated States of Micronesia. Error bars represent standard errors of the mean ($n = 5$)

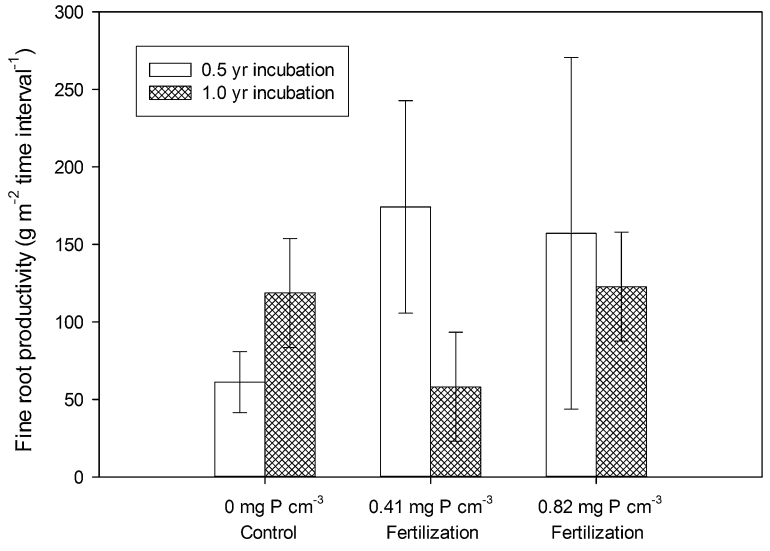

Fig. 3 Fine root productivity over 6 and 12 months with phosphorus fertilization in the interior hydrogeomorphic zone in a mangrove forest along the Sapwalap River (Pohnpei), Federated States of Micronesia. Treatments included fertilizations of 0 mg P cm^{-3} (control), 0.41 mg P cm^{-3}, and 0.82 mg P cm^{-3}. Error bars represent standard errors of the mean ($n = 5$)

as live versus dead ($F_1 = 613.15$, $P = 0.0001$). Root biomass averaged 0.776 kg m^{-2} from shallower and 0.550 kg m^{-2} from deeper sampling depths.

The distribution of fine root biomass ($\leq$2 mm size class) differed significantly among sites as well (Table 2). Sapwalap interior had significantly greater fine root biomass (0.577 $\pm$ 0.080 kg m^{-2}) than the other sites. At the Yela fringe and the Sapwalap riverine sites, for instance, fine root biomass ranged from 0.151 to 0.170 kg m^{-2}. This same trend was observed for total root mass (root biomass plus necromass, Table 2).

Live roots represented only 3–16% of total root mass among sites (Table 2). Although emphasis in this study was on live root biomass, it is important to note that root necromass (dead root material) was much greater than live root biomass for all sites. Total root mass (root biomass + root necromass) greatly increased when necromass was included, here surpassing 36 kg m^{-2} (Table 2). Total root mass was greatest for Sapwalap fringe (36.921 $\pm$ 2.949 kg m^{-2}) and lowest for Yela fringe (7.830 $\pm$ 0.845 kg m^{-2}), a pattern inconsistent with our live root biomass data. Sapwalap interior, which had one of the highest live root biomass measures

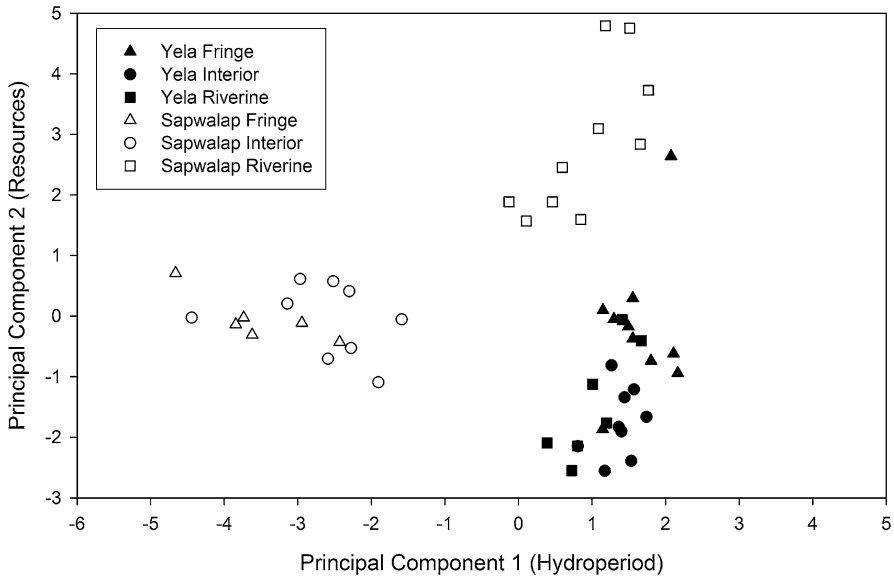

Fig. 4 Principal Component (PC) Analysis of porewater variables and soil nutrients showing PC1-hydroperiod, which incorporates variables associated with reducing soil conditions, and PC2-resources, which incorporates variables associated with soil texture and fertility. PC1-hydroperiod differed significantly among sites ($P < 0.0001$) and explained 47% of the variability in the analysis. PC2-resources also differed significantly among sites ($P < 0.0001$) and explained 26% of the variability in the analysis

among sites, had intermediate total root mass, while total root mass at Sapwalap riverine was low, similar to its live root biomass estimates. Yela interior also had high total root mass but only moderate live root biomass, in contrast with the Yela riverine site which had relatively high live root biomass but only moderate to low total root mass.

Root productivity

Root productivity after 1 year incubation ranged from 45.88 ± 21.37 g m^{-2} $year^{-1}$ at Yela fringe to 118.66 ± 38.05 g m^{-2} $year^{-1}$ at Sapwalap interior (Table 2). Although root productivity increased with increasing length of incubation, there were no significant differences among the six sites after either 0.5 or 1 year incubation because of high sample variability ($F_{5,6.76} = 2.46$, $P = 0.1393$ and $F_{5,7.92} = 1.35$, $P = 0.3355$; respectively) (Fig. 1).

For root size class >2 mm, there was no difference in productivity among sites. However, fine root productivity (≤2 mm) differed significantly with depth after 0.5 year incubation ($F_1 = 5.59$, $P = 0.0253$) and among sites after 1 year incubation ($F_1 = 3.10$, $P = 0.0363$). Differences in root size class did not occur with depth or P treatment of the ingrowth cores after 1 year incubation (data not shown). Fine root productivity was greatest at Sapwalap interior and least at the Yela sites as well as Sapwalap fringe, roughly equivalent with high and low N:P ratios, respectively (Fig. 2).

Root productivity response to P fertilization was inconclusive at the interior site in Sapwalap (Fig. 3). Absolute rates of total root ingrowth in bags fertilized with 0.41 mg P cm^{-3} (treatment 1) and 0.82 mg P cm^{-3} (treatment 2) doubled or tripled numerically relative to unfertilized ingrowth bags (control) after 0.5 year incubation; however, there were no statistically significant differences among sites ($F_{2,5.25} = 1.54$, $P = 0.2968$), even after 1 year of incubation with P fertilization ($F_{2,12} = 1.06$, $P = 0.3772$). Root productivity estimates after P fertilization, however, were significantly greater in the top section of the ingrowth bags for both the 0.5 year ($F_{1,12} = 8.81$, $P = 0.0118$) and 1 year ($F_{1,19.3} = 11.30$, $P = 0.0032$) incubations.

Root turnover was inversely related to root biomass, with low root turnover at the two fringe sites (Table 2). Root turnover rate was greatest at Sapwalap riverine at 0.193 $year^{-1}$, and lowest at Yela fringe at 0.039 $year^{-1}$ (Table 2). Overall, roots are expected to be replaced completely after 5–26 years on all sites,

Table 3 Belowground biomass data for mangrove ecosystems around the world

Species/association	Site	Belowground biomass (kg m^{-2}) total and (fine, ≤2 mm)	Reference
Mixed, lagoon	Celestun Lagoon, Mexico	0.9–3.0	Adame et al. (2014)
Avicennia marina	Lane Cove River, Australia	14.73	Briggs (1977)
Avicennia marina	Lane Cove River, Australia	16.03	Briggs (1977)
Mixed (SRS-4), riverine	Shark River, Florida (USA)	3.198 (0.587)	Castañeda-Moya et al. (2011)
Mixed (SRS-5), riverine	Shark River, Florida (USA)	4.389 (0.442)	Castañeda-Moya et al. (2011)
Mixed (SRS-6), riverine	Shark River, Florida (USA)	2.532 (0.353)	Castañeda-Moya et al. (2011)
Avicennia-Sonneratia zone	Trat River, Thailand	(0.089)	Chalermchatwilai et al. (2011)
Rhizophora zone	Trat River, Thailand	(0.075)	Chalermchatwilai et al. (2011)
Xylocarpus zone	Trat River, Thailand	(0.137)	Chalermchatwilai et al. (2011)
Mixed, fringe	Yela, Kosrae (FSM)	0.952 (0.151)	This study
Mixed, inland	Yela, Kosrae (FSM)	1.191 (0.185)	This study
Mixed, riverine	Yela, Kosrae (FSM)	1.425 (0.183)	This study
Mixed, fringe	Sapwalap, Pohnpei (FSM)	1.368 (0.292)	This study
Mixed, inland	Sapwalap, Pohnpei (FSM)	2.640 (0.577)	This study
Mixed, riverine	Sapwalap, Pohnpei (FSM)	0.448 (0.170)	This study
Rhizophora mangle	Cuba	1.705	Fiala & Hernandez (1993)
Avicennia germinans	Cuba	1.079	Fiala & Hernandez (1993)
Bruguiera zone	Utwe and Okat River, Kosrae (FSM)	0.72 (0.72)	Gleason & Ewel (2002)
Rhizophora zone	Utwe and Okat River, Kosrae (FSM)	0.69 (0.54)	Gleason & Ewel (2002)
Sonneratia zone	Utwe and Okat River, Kosrae (FSM)	0.87 (0.78)	Gleason & Ewel (2002)
Rhizophora mangle (dom.)	Puerto Rico	45.00[a]	Golley et al. (1962)
Rhizophora	Panama	18.97	Golley et al. (1975)
Rhizophora mucronata (12-year old)	Gazi Bay, Kenya	2.49	Kairo et al. (2008)
Kandelia obovata	Manko Wetland, Okinawa, Japan	7.33[b,c]	Khan et al. (2009)
Sonneratia zone	Thailand	15.59 (9.41)[c]	Komiyama et al. (1987)
Sonneratia- Bruguiera zone	Thailand	7.69 (5.11)[c]	Komiyama et al. (1987)
Bruguiera zone	Thailand	22.12 (12.47)[c]	Komiyama et al. (1987)
Rhizophora zone	Thailand	46.22 (21.45)[c]	Komiyama et al. (1987)
Sonneratia zone	Indonesia	3.85[c]	Komiyama et al. (1988)
Rhizophora zone	Indonesia	19.61[c]	Komiyama et al. (1988)
Bruguiera zone	Indonesia	11.08[c]	Komiyama et al. (1988)
Ceriops tagal	Thailand	8.75 (0.18)[c]	Komiyama et al. (2000)
Avicennia marina, mature	Brisbane, Australia	1.2	Mackey (1993)
Avicennia marina, regrowth	Brisbane, Australia	1.7	Mackey (1993)
Avicennia marina, thinned	Brisbane, Australia	2.3	Mackey (1993)
Inland estuary mangroves	Sapwalap, Pohnpei	2.685	Mori et al. (1997)
Outward estuary mangroves	Sapwalap, Pohnpei	3.479	Mori et al. (1997)
Coral reef mangroves	Sapwalap, Pohnpei	3.592	Mori et al. (1997)
Rhizophora apiculata (20-year old)	Malaysia	0.52[b]	Ong et al. (1995)

Table 3 continued

Species/association	Site	Belowground biomass (kg m^{-2}) total and (fine, ≤2 mm)	Reference
Avicennia marina	Hawkesbury River, Australia	14.50	Saintilan (1997)
Aegiceras corniculatum	Hawkesbury River, Australia	10.50	Saintilan (1997)
Rhizophora mangle and *Laguncularia racemosa*	Samaná Bay, Dominican Republic	6.78 (0.97)	Sherman et al. (2003)
Aegiceras corniculatum (dom.)	Shenzhen, China	3.40	Tam et al. (1995)
Rhizophora mucronata	Gazi Bay, Kenya	3.58	Tamooh et al. (2008)
Sonneratia alba	Gazi Bay, Kenya	4.84	Tamooh et al. (2008)
Avicennia marina	Gazi Bay, Kenya	3.91	Tamooh et al. (2008)

[a] Estimates include peat

[b] Estimated using calculations or computer simulated models

[c] Estimated first by trench method, then by root density distribution model for a given zone

Table 4 Belowground:aboveground ratios for mangrove ecosystems around the world

Species/association	Site	Root:shoot ratio	Reference
Mixed, fringe	Yela, Kosrae (FSM)	0.074[a]	This study; Devoe & Cole (1998)
Mixed, interior	Yela, Kosrae (FSM)	0.048[a]	This study; Devoe & Cole (1998)
Mixed, riverine	Yela, Kosrae (FSM)	0.053[a]	This study; Devoe & Cole (1998)
Mixed, fringe	Sapwalap, Pohnpei (FSM)	0.024	This study; Mori et al. (1997)
Mixed, interior	Sapwalap, Pohnpei (FSM)	0.046	This study; Mori et al. (1997)
Rhizophora mangle dominated	Puerto Rico	7.2[d]	Golley et al. (1962)
Rhizophora brevistyla	Panama	0.68	Golley et al. (1975)
Rhizophora mangle	Panama	0.79	Golley et al. (1975)
Rhizophora mucronata (12-year old)	Gazi Bay, Kenya	0.23	Kairo et al. (2008)
Kandelia obovata	Manko Wetland, Japan	0.91[b]	Khan et al. (2009)
Avicennia marina		0.005–0.91	Hutchings and Saenger (1987)
Sonneratia zone	Thailand, Indonesia	0.19[b,c]	Komiyama et al. (1987, 1988)
Bruguiera zone	Thailand, Indonesia	0.22–0.33[b,c]	Komiyama et al. (1987, 1988)
Rhizophora zone	Thailand, Indonesia	0.38–0.58[b,c]	Komiyama et al. (1987, 1988)
Ceriops tagal	Thailand	0.95[b]	Komiyama et al. (2000)
Laguncularia racemosa		1.00–1.75	Lugo and Snedaker (1974)
Avicennia marina	Brisbane, Australia	0.28	Mackey (1993)
Avicennia marina, mature	Brisbane, Australia	0.07	Mackey (1993)
Avicennia marina, regrowth	Brisbane, Australia	0.03	Mackey (1993)
Avicennia marina, thinned	Brisbane, Australia	0.11	Mackey (1993)
Rhizophora apiculata (20-year old)	Malaysia	0.05	Ong et al. (1995)
Avicennia marina, central-lower	Hawkesbury River, Australia	0.28–4.10	Saintilan (1997)
Avicennia marina, central-lower	Hawkesbury River, Australia	0.77	Saintilan (1997)
Aegiceras corniculatum	Hawkesbury River, Australia	0.40–1.90	Saintilan (1997)

Table 4 continued

Species/association	Site	Root:shoot ratio	Reference
Rhizophora mangle and *Laguncularia racemosa*	Dominican Republic	0.29	Sherman et al. (2003)
Aegiceras corniculatum (dom.)	Shenzhen, China	0.40	Tam et al. (1995)

[a] Aboveground biomass for Yela, Kosrae was converted using forest volume estimates published by Devoe & Cole (1998) and average wood density estimates for the mangrove species found at these sites

[b] Belowground estimated first by trench method, then by root density distribution model for a given zone

[c] Estimates include prop roots

[d] Estimates include peat

with faster root turnover associated with proximity to a river.

Constraints on root productivity

PCA of all soil variables yielded three principal components (PC1, PC2, PC3) with eigenvalues >1. Total P, total carbon, sulfur, and redox conditions defined PC1, suggesting this variable was associated with lower redox soil conditions (PC1-hydroperiod). Bulk density, labile P, total N, and organic and inorganic matter defined PC2, suggesting that this variable was associated with soil fertility or texture (PC2-resources). PC3 was predominantly defined by soil salinity (PC3-regulator). PC1-hydroperiod explained 47% of the variability, PC2-resources explained 26% of the variability, and PC3-regulator explained 16% of the variability in the overall PCA model (Fig. 4).

These principal component composite variables were then used in an analysis of variance of the 6 study sites. PC1-hydroperiod, the variable associated with reducing soil conditions, was composed of correlated variables that differed significantly among sites ($F_{5,21} = 89.96$, $P < 0.0001$). The three sites at Yela and Sapwalap riverine clustered together while Sapwalap fringe and interior were disparate. PC2-resources also differed significantly among sites ($F_{5,21} = 20.07$, $P < 0.0001$). Sapwalap fringe and interior as well as Yela fringe grouped together. Only Sapwalap riverine appeared to stand out. Sites segregated based on PC3-regulator as well. Under PC3-regulator, the two fringe sites with their high salinity were considered different from the other sites as well as from one another ($F_{5,21} = 21.54$, $P < 0.0001$).

The multiple regression model, comparing soil variables (principal components) and depth, was significant ($F_4 = 7.20$, $P < 0.0001$) and included all parameters of interest: depth, PC1-hydroperiod, PC2-resources, and PC3-regulator. Although the forward selection model kept depth and PC3-regulator in the model, the model did not explain much of the variance (low r^2) and was not significant. PC2-resources and PC1-hydroperiod, however, were significant additions to the regression model ($F = 13.12$, $P = 0.0005$ and $F = 11.38$, $P = 0.0011$; respectively), and suggested that any discussion of root biomass and productivity should include metrics related to flooding and soil fertility, particularly P dynamics, but perhaps not salinity on these Micronesian study sites. Depth, PC1-hydroperiod (reducing soil conditions), and PC2-resources all had a negative (or inverse) relationship with root biomass. PC3-regulator (salinity) had a positive, though slight, effect on root biomass.

Discussion

Mangroves are touted as highly efficient carbon sinks in the wet tropics due to relatively high primary productivity and low rates of decomposition (Komiyama et al., 2008). The importance of the contributions of mangrove forests to global estimates of carbon sequestration above- and belowground reinforces the need for a better understanding of biomass allocation in these systems. It has been suggested that mangroves can allocate more carbon belowground than other forest species, especially under unfavorable conditions (Lovelock, 2008; Donato et al., 2011). Root productivity and belowground biomass accumulation also contribute to soil volume and consequently elevation change in mangroves (Cahoon et al., 2003; McKee et al., 2007; McKee, 2011). Terrigenous inputs as well as above- and belowground organic matter accumulation will affect elevation change and therefore affect the ability of a coastal forest to keep pace

with sea level rise (Krauss et al., 2014). Understanding the processes controlling biomass allocation and belowground productivity is key for management decisions focusing on carbon storage, surface elevation change, or sea level rise mitigation. Our current study adds to descriptions from mangroves developing in low-nutrient environments (e.g., Feller et al., 1999; Lovelock et al., 2004) and moderate nutrient environments (e.g., soil N:P ratios, 33–126; Castañeda-Moya et al., 2011) to suggest that even from nutrient-rich environments (soil N:P ratios, 3–70), root productivity is related to P dynamics such that greater root biomass might be expected as P becomes more limiting, thus possibly affecting the functional role of roots in many settings globally (e.g., maintenance of surface elevation gain, nutrient storage; see also Reef et al., 2010).

Root biomass distribution

Belowground biomass estimates in this study (Table 2) were generally lower than those reported for other mangrove forests (Table 3), but were similar to estimates from other Micronesian mangrove forests (Mori et al., 1997; Gleason & Ewel, 2002) and mangrove forests in Yucatan, Mexico with similar N:P ratios (Adame et al., 2014). Root biomass measurements in this study ranged from 0.448–2.640 kg m^{-2} (sampled to a depth of 45 cm) and were similar to values of 2.685–3.479 kg m^{-2} (sampled to a depth of 60 cm) measured near our interior site by Mori et al. (1997). Both studies reported high root biomass at Sapwalap interior, which corresponds with a high N:P ratio (although not the highest) as predicted by our hypotheses. Mori et al. (1997) also sampled roots >20 mm. Root biomass values as high as 10.95 kg m^{-2} were measured near our site when large live roots were included. Low root biomass at Sapwalap fringe, in spite of having the highest N:P ratio, is likely due to low redox and high sulfide levels (Table 1), also suggesting a potential role for sulfur.

Indeed, the high aboveground:belowground biomass allocation (Table 4) in our sites may be an overriding consequence of high rainfall and low frequency of major storms. High rainfall may also reduce salinities, especially between major tidal pulses, and promote flushing of phytotoxic porewater sulfides. Greater root zone flushing appears to be the case in Yela, with less sulfide apparently being flushed from Sapwalap fringe. High root mortality and low aboveground biomass accumulation result from high sulfide levels (Koch & Mendelssohn, 1989), which helps to explain greater root necromass (Table 2) and lower root:shoot ratios (Table 4) at Sapwalap fringe. In addition, this evidence supports our hypothesis that total root mass (live plus dead) can be high at sites where nutrients are relatively limiting even in non-stunted mangrove forests; Sapwalap fringe had among the lowest total and labile P concentrations, and high N:P ratios (Table 1).

Fine root biomass (<2 mm diameter) estimates reported in this study are lower than other estimates reported in the literature (Table 3) in all sites except at the Sapwalap interior. This may reflect greater overall fertility for Micronesian mangrove soils than other locations surveyed, as fewer fine roots may be necessary for nutrient foraging. Fine root biomass in our study, however, is similar to estimates from the Okat and Utwe Rivers on Kosrae (Gleason & Ewel, 2002) and mangrove forests in Thailand (Komiyama et al., 2000; Chalermchatwilai et al., 2011). High values have been reported elsewhere for forests dominated by *Rhizophora* and *Sonneratia* forests (Table 3), but all our sites contained a mix of these species and *Bruguiera*, so it is not likely that low root biomass in our stands is related strongly to species composition. Accordingly, root necromass ranged from 6.36 to 34.56 kg m^{-2} (sampled to a depth of 45 cm), which is also similar to root necromass values of 22–23 kg m^{-2} in the top 30 cm in the nearby Okat and Utwe mangroves on Kosrae (Gleason & Ewel, 2002). In contrast to fine root biomass, these estimates of root necromass are greater than those found in Gazi Bay, Kenya (1.03–3.26 kg m^{-2} in cores 0–60 cm; Tamooh et al., 2008) and in Thailand (1.5–13.3 kg m^{-2} in cores 0–30 cm; Chalermchatwilai et al., 2011), indicating a particularly strong capacity for carbon storage in Micronesian mangroves through root contributions. This would contribute to the high overall rates of soil carbon storage attributed to mangroves in places such as Yap, Federated States of Micronesia (Kauffman et al., 2011).

Low root biomass relative to other studies may also be due in part to differences in sample processing. Fluorescent microscopy suggests that the Ludox separation process can incorrectly assign live root material to the dead root category as often as 20% of the time (R.R. Twilley & B. Dame, unpubl.). Also, we did not test whether washing roots in the field, then later separating live from dead root material using the Ludox method, contributed to falsely identifying live roots. Water may move into root air spaces during an

initial seawater rinse which may affect root buoyancy and therefore contribute to an overabundance of "dead" roots. It is important to note that total root mass, which is live root biomass plus necromass, may therefore be a more appropriate metric for belowground biomass and productivity estimates, especially when making comparisons among studies and across techniques. Root necromass was much higher than root biomass at our sites; live roots accounted for only 3–15% of the total root mass (Table 2).

Root biomass did not decline with depth in the top 0.5 m in these Micronesian mangrove forests as reported in other mangroves (Tamooh et al., 2008; Chalermchatwilai et al., 2011) and many terrestrial forests (Santantonio et al., 1977; Laird, 1982, 1983; Jackson et al., 1996). An earlier study on Pohnpei also found no decline with depth in root biomass for 0–10 mm diameter roots to a depth of 60 cm, although roots ≥20 mm did decline with depth (Mori et al., 1997). Other studies have shown a concentration of live roots in the top 50 cm in mangroves (Komiyama et al., 1989; McKee, 2001; Castañeda-Moya et al., 2011). Roots of *R. stylosa* and *B. gymnorrhiza* extended to a depth of 50 cm in Japan, with fine and small roots reaching as far as 20–80 cm into the soil profile (Komiyama et al., 1989). In northern Australia, 80% of the root biomass was found in the top meter of mangrove soil (Boto & Wellington, 1984) and in south Florida, 62–85% of the root biomass was found in the top 45 cm (Castañeda-Moya et al., 2011).

Root productivity

Although the root ingrowth bag technique may underestimate root productivity slightly by restricting the number of roots or root growth into an introduced substrate, or by damaging in situ roots during implantation, it provides a relative comparison of root productivity among sites (McKee & Faulkner, 2000; Li et al., 2013). The slow turnover rates we estimated indicated that detection of dead roots would not be a problem in calculating productivity from root ingrowth bags. In addition, other direct measurements of fine root productivity in the mangrove literature are comparable to our range of 45.88 g m^{-2} $year^{-1}$ at the Yela fringe site on Kosrae to 118.66 g m^{-2} $year^{-1}$ at the Sapwalap interior site on Pohnpei (Table 2). Fine root productivity over 3 months in the top 30 cm at another interior site on Kosrae was 120 g m^{-2} $year^{-1}$ in plots dominated by *B. gymnorrhiza* and 750 g m^{-2} $year^{-1}$ in plots dominated by *S. alba* (Gleason & Ewel, 2002). Fine root growth ranged from 43–197 g m^{-2} $year^{-1}$ in Belizean mangroves (McKee et al., 2007), from 183–210 g m^{-2} $year^{-1}$ in the Florida Everglades, USA (Castañeda-Moya et al., 2011), and from 140–280 g m^{-2} $year^{-1}$ in restored mangrove sites near Rookery Bay, Florida, USA (McKee & Faulkner, 2000). Fine root productivity at the Sapwalap fringe was high, perhaps because of the high N:P ratio on that site, facilitating greater mining for locally scarce P. In fact, Sapwalap fringe, which had the highest total root mass (live plus dead), had, along with the Sapwalap interior site, the lowest soil fertility (highest N:P ratios) among the sites (Tables 1 and 2).

Fine roots increase nutrient cycling and availability within the soil environment through nutrient acquisition and rapid root turnover, facilitating nutrient release and recycling (Nadelhoffer et al., 1985; Meier et al., 1985; Ehrenfeld et al., 1997). Sites with significantly larger proportions of roots in <2 mm diameter size class, such as Sapwalap fringe and interior sites, may be more efficient at extracting limited resources from soil environments, even in environments such as Micronesian mangroves with relatively few resource limitations. Rapid turnover of fine roots is common (Hendrick & Pregitzer, 1993) and increases with nutrient availability (Nadelhoffer et al., 1985). Although root turnover should increase with root biomass (Vogt et al., 1986), root turnover rate (0.193 $year^{-1}$) was fastest at Sapwalap riverine, the site with the highest nutrient content, lowest live root biomass, low fine root biomass, and next to lowest root necromass (Table 2). This trend supports the theory that roots turn over faster where nutrient availability is higher, and in contrast have a propensity to turn over slowly, die, and build-up with reduced decomposition in soils with fewer nutrients (Feller et al., 1999). Belizean scrub mangroves fertilized with N and P responded with an increase in productivity of fine roots, but not coarse roots, in P-fertilized plots but not N-fertilized plots (McKee et al., 2007). At those sites, fine root productivity increased from 43 to 339 g m^{-2} $year^{-1}$ in interior zones and from 197 to 260 g m^{-2} $year^{-1}$ in fringe zones fertilized with P (McKee et al., 2007); mangroves are often forced to cope with similar P limitations globally (Feller, 1995; Feller et al., 1999; Reef et al., 2010).

On the other hand, we reject our hypothesis that root productivity at Sapwalap interior will be

stimulated with increased P fertilization. One explanation for this outcome may be because we did not reapply P during that time period; P can be quite mobile in mangrove soils and deplete rapidly (McKee et al., 2002; Krauss et al., 2006). The cores were only fertilized at the onset of the experiment, so P may have been lost with tidal or groundwater flushing or from uptake by surrounding root systems. Alternatively, the site may have already had an adequate supply of available P, since turnover rates of this nutrient were not measured. However, both total and labile P measured at this site were low in comparison to our other sites. Nutrient enrichment may have also stimulated microbial activity, which would decompose previously existing root necromass as well as new root material during the study (Nyman, 1999; Feller et al., 1999), resulting in reduced root productivity estimates.

Conclusions

The distribution of root biomass in Micronesian mangrove forests followed soil N:P ratios as hypothesized, with more root biomass generally associated with lower relative P concentrations (high N:P ratio). High variation in root productivity clouded cause and effect, which is further exacerbated by the interaction between nutrient limitation and soil physico-chemical variables. However, even in mangrove forests with lower apparent stress than many forests surveyed globally, roots turn over faster where P availability is locally higher, and have a propensity to turn over slowly, die, and build-up as necromass in relatively more nutrient-limited locations. Thus, many of the processes of nutrient resource acquisition reported from stunted, nutrient-limited mangrove forests are also apparent in forests of more stately structure and greater overall productivity.

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References

Alongi, D. M., 2011. Carbon payments for mangrove conservation: ecosystem constraints and uncertainties of sequestration potential. Environmental Science and Policy 14: 462–470.

Adame, M. F., C. Teutli, N. S. Santini, J. P. Caamal, A. Zaldívar-Jiménez, R. Hernández & J. A. Herrera-Silviera, 2014. Root biomass and production of mangroves surrounding a karstic oligotrophic coastal lagoon. Wetlands 34: 479–488.

Boto, K. G. & J. T. Wellington, 1984. Soil characteristics and nutrient status in a Northern Australian mangrove forest. Estuaries 7: 61–69.

Bouillon, S., A. V. Borges, E. Castañeda-Moya, K. Diele, T. Dittmar, N. C. Duke, E. Kristensen, S. Y. Lee, C. Marchand, J. J. Middelburg, V. H. Rivera-Monroy, T. J. Smith III & R. R. Twilley, 2008. Mangrove production and carbon sinks: a revision of global budget estimates. Global Biogeochemical Cycles 22: GB2013.

Briggs, S. V., 1977. Estimates of biomass in a temperate mangrove community. Australian Journal of Ecology 2: 369–373.

Cahoon, D. R., P. Hensel, J. Rybczyk, K. L. McKee, C. E. Profitt & B. C. Perez, 2003. Mass tree mortality leads to mangrove peat collapse at Bay Islands, Honduras after Hurricane Mitch. Journal of Ecology 91: 1093–1105.

Castañeda-Moya, E., R. R. Twilley, V. H. Rivera-Monroy, B. D. Marx, C. Coronado-Molina & S. M. L. Ewe, 2011. Patterns of root dynamics in mangrove forests along environmental gradients in the Florida Coastal Everglades, USA. Ecosystems 14: 1178–1195.

Chalermchatwilai, B., S. Poungparn & P. Patanaponpaiboon, 2011. Distribution of fine-root necromass in a secondary mangrove forest in Trat province, Eastern Thailand. ScienceAsia 37: 1–5.

Chapman, V. J., 1976. Mangrove Vegetation. J. Cramer, Valduz.

Chen, R. & R. R. Twilley, 1999. A simulation model of organic matter and nutrient accumulation in mangrove wetland soils. Biogeochemistry 44: 93–118.

Cuevas, E. & E. Medina, 1988. Nutrient dynamics within Amazonian forests. II. Fine root growth, availability and leaf litter decomposition. Oecologia 76: 222–235.

Devoe, N. N. & T. G. Cole, 1998. Growth and yield in mangrove forests of the Federated States of Micronesia. Forest Ecology and Management 103: 33–48.

Donato, D. C., J. B. Kauffman, D. Murdiyarso, S. Kurnianto, M. Stidham & M. Kanninen, 2011. Mangroves among the

most carbon-rich forests in the tropics. Nature Geoscience 4: 293–297.
Drexler, J. Z. & K. C. Ewel, 2001. Effect of the 1997-1998 ENSO-related drought on hydrology and salinity in a Micronesian wetland complex. Estuaries 24: 347–356.
Ehrenfeld, J. G., W. F. J. Parsons, X. Han, R. W. Parmelee & W. Zhu, 1997. Live and dead roots in forest soil horizons: contrasting effects on nitrogen dynamics. Ecology 78: 348–362.
Ewel, K. C., J. A. Bourgeois, T. G. Cole & S. Zheng, 1998. Variation in environmental characteristics and vegetation in high-rainfall mangrove forests, Kosrae, Micronesia. Global Ecology and Biogeography Letters 7: 49–56.
Feller, I. C., 1995. Effects of nutrient enrichment on growth and herbivory of dwarf red mangrove (*Rhizophora mangle*). Ecological Monographs 65: 477–505.
Feller, I. C., D. F. Whigham, J. P. O'Neill & K. L. McKee, 1999. Effects of nutrient enrichment on within-stand cycling in a mangrove forest. Ecology 80: 2193–2205.
Feller, I. C., C. E. Lovelock, U. Berger, K. L. McKee, S. B. Joye & M. C. Ball, 2010. Biocomplexity in mangrove ecosystems. Annual Review of Marine Science 2: 395–417.
Fiala, K. & L. Hernández, 1993. Root biomass of a mangrove forest in southwestern Cuba (Majana). Ekológia 12: 15–30.
Fujimoto, K., R. Tabuchi, T. Mori & T. Murofushi, 1995. Site environments and stand structure of the mangrove forests on Pohnpei Island, Micronesia. Japan Agricultural Research Quarterly 29: 275–284.
Gleason, S. M. & K. C. Ewel, 2002. Organic matter dynamics on the forest floor of a Micronesian mangrove forest: an investigation of species composition shifts. Biotropica 34: 190–198.
Gleeson, S. K. & D. Tilman, 1992. Plant allocation and the multiple limitation hypothesis. The American Naturalist 139: 1322–1343.
Golley, F. B., H. T. Odum & R. F. Wilson, 1962. The structure and metabolism of a Puerto Rico red mangrove forest in May. Ecology 43: 9–19.
Golley, F. B., J. T. Mcginnis, R. G. Clements, G. I. Child & M. J. Duever, 1975. Mineral Cycling in a Tropical Moist Forest Ecosystem. Georgia University Press, Athens.
Hargis, T. G. & R. R. Twilley, 1994. A multi-depth probe for measuring oxidation-reduction (redox) potential in wetland soils. Journal of Sedimentary Research A64: 684–685.
Hendrick, R. & K. Pregitzer, 1993. The dynamics of fine root length, biomass and nitrogen content in two northern hardwood ecosystems. Canadian Journal of Forest Research 23: 2507–2520.
Huston, M. A., 1997. Landscape patterns: gradients and zonation. In Huston, M. A. (ed.), Biological Diversity: The Coexistence of Species on Changing Landscape. Cambridge University Press, Cambridge: 271–299.
Hutchings, P. A., & P. Saenger, 1987. Ecology of mangroves. University of Queensland Press, St. Lucia.
Jachowski, N. R. A., M. S. Y. Quak, D. A. Friess, D. Duangnamon, E. L. Webb & A. D. Ziegler, 2013. Mangrove biomass estimation in Southwest Thailand using machine learning. Applied Geography 45: 311–321.
Jackson, R. B., J. Canadell, J. R. Ehleringer, H. A. Mooney, O. E. Sala & E. D. Schulze, 1996. A global analysis of root distributions for terrestrial biomes. Oecologia 108: 389–411.
Kairo, J. G., J. K. S. Lang'at, F. Dahdouh-Guebas, J. Bosire & M. Karachi, 2008. Structural development and productivity of replanted mangrove plantations in Kenya. Forest Ecology and Management 255: 2670–2677.
Khan, M. N. I., R. Suwa & A. Hagihara, 2009. Biomass and aboveground net primary production in a subtropical mangrove stand of *Kandelia obovata* (S., L.) Yong at Manko Wetland, Okinawa, Japan. Wetlands Ecology and Management 17: 585–599.
Koch, M. S. & I. A. Mendelssohn, 1989. Sulphide as a soil phytotoxin: differential responses in two marsh species. Journal of Ecology 77: 565–578.
Komiyama, A., K. Ogino, S. Aksornkoae & S. Sabhasri, 1987. Root biomass of a mangrove forest in southern Thailand. 1. Estimation by the trench method and the zonal structure of root biomass. Journal of Tropical Ecology 3: 97–108.
Komiyama, A., H. Moriya, S. Prawiroatmodjo, T. Toma & K. Ogino, 1988. Primary productivity of mangrove forest. In Ogino, K. & M. Chihara (eds), Biological system of mangroves. A report of east Indonesian mangrove expedition, 1986. Ehime University, Matsuyama: 97–117.
Komiyama, A., H. Moriya & K. Ogino, 1989. A quantitative analysis of root system of mangrove tree species in Iriomote Island, southern Japan. Galaxea 8: 89–96.
Komiyama, A., S. Havanond, W. Srisawatt, Y. Mochida, K. Fujimoto, T. Ohnishi, S. Ishihara & T. Miyagi, 2000. Top/root biomass ratio of a secondary mangrove (*Ceriops tagal* (Perr.) C.B. Rob.) forest. Forest Ecology and Management 139: 127–134.
Komiyama, A., J. E. Ong & S. Poungparn, 2008. Allometry, biomass, and productivity of mangrove forests: a review. Aquatic Botany 89: 128–137.
Krauss, K. W., T. W. Doyle, R. R. Twilley, V. H. Rivera-Monroy & J. K. Sullivan, 2006. Evaluating the relative contributions of hydroperiod and soil fertility on growth of south Florida mangroves. Hydrobiologia 569: 311–324.
Krauss, K. W., B. D. Keeland, J. A. Allen, K. C. Ewel & D. J. Johnson, 2007. Effects of season, rainfall, and hydrogeomorphic setting on mangrove tree growth in Micronesia. Biotropica 39: 161–170.
Krauss, K. W., K. L. McKee, C. E. Lovelock, D. R. Cahoon, N. Saintilan, R. Reef & L. Chen, 2014. How mangrove forests adjust to rising sea level. New Phytologist 202: 19–34.
Kryger, L. & S. K. Lee, 1996. Effects of mangrove soil ageing on the accumulation of hydrogen sulphide in root of *Avicennia* spp. Biogeochemistry 35: 367–375.
Kauffman, J. B., C. Heider, T. G. Cole, K. A. Dwire & D. C. Donato, 2011. Ecosystem carbon stocks of Micronesian mangrove forests. Wetlands 31: 343–352.
Laird, W. E., 1982. Soil Survey of Island of Ponape. Federated States of Micronesia. Soil Conservation Service. U.S. Department of Agriculture, Washington, DC: 81 pp.
Laird, W. E., 1983. Soil Survey of Island of Kosrae. Federated States of Micronesia. Soil Conservation Service. U.S. Department of Agriculture, Washington, DC: 67 pp.
Li, X., J. Zhu, H. Lange & S. Han, 2013. A modified ingrowth core method for measuring fine root production, mortality and decomposition in forests. Tree Physiology 33: 18–25.

Lovelock, C. E., 2008. Soil respiration and belowground carbon allocation in mangrove forests. Ecosystems 11: 342–354.

Lovelock, C. E., I. C. Feller, K. L. McKee, B. M. Engelbrecht & M. C. Ball, 2004. The effect of nutrient enrichment on growth, photosynthesis and hydraulic conductance of dwarf mangroves in Panama. Functional Ecology 18: 24–33.

Lovelock, C. E., R. W. Ruess & I. C. Feller, 2006. Fine root respiration in the mangrove *Rhizophora mangle* over variation in forest stature and nutrient availability. Tree Physiology 26: 1601–1606.

Lugo, A. E., 1990. Fringe wetlands. In Lugo, A. E., M. Brinson & S. Brown (eds), Ecosystems of the World, 15, Forested Wetlands. Elsevier, Amsterdam: 143–169.

Lugo, A. E., & S. C. Snedaker, 1974. The ecology of mangroves. Annual Review of Ecology and Systematics 5: 39–64.

Mackey, A. P., 1993. Biomass of the mangrove Avicennia marina (Forsk.) Vierh. near Brisbane, South-eastern Queensland. Australian Journal of Marine and Freshwater Research 44: 721–725.

Majdi, H., 1996. Root sampling methods-applications and limitations of the minirhizotron technique. Plant and Soil 185: 255–258.

Mcleod, E., G. L. Chmura, S. Bouillon, R. Salm, M. Björk, C. M. Duarte, C. E. Lovelock, W. H. Schlesinger & B. R. Silliman, 2011. A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO_2. Frontiers in Ecology and the Environment 9: 552–560.

McKee, K. L., 1993. Soil physicochemical patterns and mangrove species distribution-reciprocal effects? Journal of Ecology 81: 477–487.

McKee, K. L., 1995. Seedling recruitment patterns in a Belizean mangrove forest: effects of establishment ability and physic-chemical factors. Oecologia 101: 448–460.

McKee, K. L., 2001. Root proliferation in decaying roots and old root channels: a nutrient conservation mechanism in oligotrophic mangrove forests? Journal of Ecology 89: 876–887.

McKee, K. L., 2011. Biophysical controls on accretion and elevation change in Caribbean mangrove ecosystems. Estuarine, Coastal and Shelf Science 91: 475–483.

McKee, K. L. & P. L. Faulkner, 2000. Restoration of biogeochemical function in mangrove forests. Restoration Ecology 8: 247–259.

McKee, K. L. & I. A. Mendelssohn, 1987. Root metabolism in the black mangrove (*Avicennia germinans* (L.)): response to hypoxia. Environmental and Experimental Botany 27: 147–156.

McKee, K. L., I. A. Mendelssohn & M. W. Hester, 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.

McKee, K. L., I. C. Feller, M. Popp & W. Wanek, 2002. Mangrove isotopic ($\delta^{15}N$ and $\delta^{13}C$) fractionation across nitrogen and phosphorus limitation gradients. Ecology 83: 1065–1075.

McKee, K. L., D. R. Cahoon & I. C. Feller, 2007. Caribbean mangroves adjust to rising sea level through biotic controls on change in soil elevation. Global Ecology and Biogeography 16: 545–556.

Meier, C. E., C. C. Grier & D. W. Cole, 1985. Below- and aboveground N and P use by *Abies amabilis* stands. Ecology 66: 1928–1942.

Middleton, B. A. & K. L. McKee, 2001. Degradation of mangrove tissues and implications for peat formation in Belizean island forests. Journal of Ecology 89: 818–828.

Mori, T., R. Tabuchi, K. Fujimoto, H. Utsugi, S. Kuramoto, M. Hiraide & A. Imaya, 1997. US-Japan joint research for conservation and management of mangrove forests in the South Pacific Islands – dynamics and production of mangrove forests in Pohnpei Island. Report of the Bilateral International Joint Research, Forestry and Forest Products Research Institute, Japan.

Nadelhoffer, K. J., J. D. Aber & J. M. Melillo, 1985. Fine roots, net primary production, and soil nitrogen availability: a new hypothesis. Ecology 66: 1377–1390.

Nautical Software, Inc., 1997. Tides and Currents Pro for Windows, Version 2.51. Nautical Software, Inc, Beaverton, OR.

Nyman, J. A., 1999. Effects of crude oil and chemical additives on metabolic activity of mixed microbial populations in fresh marsh soils. Microbial Ecology 37: 152–162.

Oliveira, M. G., M. Van Noordwijk, S. R. Gaze, G. Brouwer, S. Bona, G. Mosca & K. Hairiah, 2000. Auger sampling, ingrowth cores and pinboard methods. In Smit, A. L., A. G. Bengough, C. Engels, M. van Noordwijk, S. Pellerin & S. C. van de Geijn (eds), Root Methods: A Handbook. Springer, New York: 176–210.

Olsen, S. E. & L. E. Sommers, 1982. Phosphorus. In Page, A. L., R. H. Miller & D. R. Keeney (eds), Methods of Soil Analysis. Part II. American Society of Agronomy, Madison: 403–448.

Ong, J. E., W. K. Gong & B. F. Clough, 1995. Structure and productivity of a 20-year old stand of *Rhizophora apiculata* Bl. mangrove forest. Journal of Biogeography 55: 417–424.

Ostertag, R., 2001. Effects of nitrogen and phosphorus availability on fine-root dynamics in Hawaiian montane forests. Ecology 82: 485–499.

Pezeshki, S. R., R. D. DeLaune & J. F. Meeder, 1997. Carbon assimilation and biomass partitioning in *Avicennia germinans* and *Rhizophora mangle* seedlings in response to soil redox conditions. Environmental and Experimental Botany 37: 161–171.

Raich, J. W., R. H. Riley & P. M. Vitousek, 1994. Use of root-ingrowth cores to assess nutrient limitation in forest ecosystems. Canadian Journal of Forest Research 24: 2135–2138.

Reef, R., I. C. Feller & C. E. Lovelock, 2010. Nutrition of mangroves. Tree Physiology 30: 1148–1160.

Robertson, A. I. & P. Dixon, 1993. Separating live and dead fine roots using colloidal silica: an example from mangrove forests. Plant and Soil 157: 151–154.

Saintilan, N., 1997. Above- and below-ground biomasses of two species of mangrove on the Hawkesbury River estuary, New South Wales. Marine and Freshwater Research 48: 147–152.

Santantonio, D. & R. K. Hermann, 1985. Standing crop, production, and turnover of fine roots on dry, moderate, and

wet sites of mature Douglas-fir in western Oregon. Annals of Forest Science 42: 113–142.
Santantonio, D., R. K. Hermann & W. S. Overton, 1977. Root biomass studies in forest ecosystems. Pedobiologia 17: 1–31.
SAS Institute Inc., 1999. SAS/STAT User's Guide (version 8). SAS Institute Inc., Cary, NC.
Sherman, R. E., T. J. Fahey & P. Martinez, 2003. Spatial patterns of biomass and aboveground net primary productivity in a mangrove ecosystem in the Dominican Republic. Ecosystems 6: 384–398.
Snedaker, S. C., S. J. Baquer, P. J. Behr & S. I. Ahmed, 1995. Biomass distribution in *Avicennia marina* plants in the Indus River Delta, Pakistan. In Thompson, M. & N. M. Tirmizi (eds), The Arabian Sea: Living Marine Resources and the Environment. Vanguard Books Ltd., Lahore: 389–394.
Tam, N. F. Y., Y. S. Wong, C. Y. Lan & G. Z. Chen, 1995. Community structure and standing crop biomass of amangrove forest in Futian Nature-Reserve, Shenzhen, China. Hydrobiologia 295: 193–201.
Tamooh, F., M. Huxham, M. Karachi, M. Mencuccini, J. G. Kairo & B. Kirui, 2008. Below-ground root yield and distribution in natural and replanted mangrove forests at Gazi bay, Kenya. Forest Ecology and Management 256: 1290–1297.
Thom, B. G., 1967. Mangrove ecology and deltaic geomorphology: Tabasco, Mexico. Journal of Ecology 55: 301–343.
Tilman, D., 1985. The resource-ratio hypothesis of plant succession. The American Naturalist 125: 827–852.
Tomlinson, P. B., 1986. The Botany of Mangroves. Cambridge University Press, New York.
Twilley, R. R., R. H. Chen & T. Hargis, 1992. Carbon sinks in mangroves and their implications to carbon budget of tropical coastal ecosystems. Water, Air and Soil Pollution 64: 265–288.
Twilley, R. R. & V. Rivera-Monroy, 2005. Developing performance measures of mangrove wetlands using simulation models of hydrology, nutrient biogeochemistry, and community dynamics. Journal of Coastal Research 40: 79–93.
Vogt, K. A., C. C. Grier & D. J. Vogt, 1986. Production, turnover and nutrient dynamics of above- and belowground detritus of world forests. Advances in Ecological Research 15: 303–378.
Vogt, K. A. & H. Persson, 1991. Measuring growth and development of roots. In Lassoie, J. P. & T. M. Hinckley (eds), Techniques and Approaches in Forest Tree Ecophysiology. CRC Press, Boca Raton: 477–501.
Vogt, K. A., D. J. Vogt, H. Asbjornsen & R. A. Dahlgren, 1995. Roots, nutrients and their relationship to spatial patterns. Plant and Soil 168–169: 113–123.
Vogt, K. A., D. J. Vogt, P. A. Palmiotto, P. Boon, J. O'Hara & H. Asbjornsen, 1996. Review of root dynamics in forest ecosystems grouped by climate, climatic forest type and species. Plant and Soil 187: 159–219.
Vogt, K. A., D. J. Vogt & J. Bloomfield, 1998. Analysis of some direct and indirect methods for estimating root biomass and production of forests at an ecosystem level. Plant and Soil 200: 71–89.
Whitfield, M., 1969. Eh as an operational parameter in estuarine studies. Limnology and Oceanography 14: 547–558.