

Organic Matter Dynamics on the Forest Floor of a Micronesian Mangrove Forest: An Investigation of Species Composition Shifts¹

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ABSTRACT

Species composition shifts in mangrove forests may alter organic matter dynamics. The purpose of this study was to predict the effect of species replacements among mangrove trees on organic matter dynamics in a mangrove forest on the island of Kosrae, Federated States of Micronesia. We were particularly interested in elements of the carbon cycle that affect peat accumulation rates, organic matter exports to the estuary and coral reef systems, and soil microbiology. We compared organic matter production and decomposition rates among three mangrove species that commonly grow in similar hydrogeomorphic settings: *Rhizophora apiculata* BL, which is selectively harvested; *Bruguiera gymnorrhiza*, which may gradually replace *Rhizophora*; and *Sonneratia alba*, which is producing few mature fruits. *Sonneratia* had significantly higher rates of root production (estimated with ingrowth chambers) than *Bruguiera* or *Rhizophora*. *Sonneratia* foliage had significantly faster decomposition rates and significantly lower lignin:nitrogen ratios than *Bruguiera* foliage. Live root mass was positively correlated with ingrowth and soil carbon, although soil carbon and ingrowth were not significantly correlated with each other. Humic acid concentrations were significantly higher in *Sonneratia* rhizospheres than in either *Bruguiera* or *Rhizophora* rhizospheres and were positively correlated with root ingrowth. The species changes taking place on Kosrae are likely to result in lower rates of root production and foliage decomposition, and more refractory carbon pools in soil.

Key words: *Bruguiera gymnorrhiza*; *decomposition*; *Micronesia*; *organic matter*; *Rhizophora apiculata*; *root production*; *Sonneratia alba*; *species composition*.

ORGANIC MATTER FROM MANGROVE TREES is a primary carbon and energy source for micro- and macrofauna inhabiting mangroves (Robertson 1986) and, in many cases, adjacent estuaries (Cifuentes *et al.* 1996). Organic matter may accumulate as peat, be consumed and decomposed on or beneath the forest floor, or be exported to the marine ecosystem in particulate or dissolved forms. Production rate and chemical composition of organic matter need to be considered when assessing the ultimate fate of organic matter and the food chains that it supports (Brinson *et al.* 1980). Because different mangrove species are known to have distinct production (Duke *et al.* 1981) and decomposition (Robertson 1988) characteristics, species composition is likely to be an important factor influencing organic matter dynamics in mangrove forests. Production and decomposition processes were studied in mangrove forests on

the island of Kosrae, Federated States of Micronesia, to determine if organic matter dynamics are likely to change as a result of species composition shifts that are occurring there.

Eleven species of mangroves occur on Kosrae. The three most common species, *Sonneratia alba* J., *Bruguiera gymnorrhiza* (L.) Lamk., and *Rhizophora apiculata* BL, provide the focus for this study. *Sonneratia*, presently a dominant overstory species, shows very little natural regeneration and is gradually being replaced by *Rhizophora* and *Bruguiera* (Ewel, Bourgeois *et al.* 1998). Bats are believed to pollinate *Sonneratia* (Tomlinson 1986). The fruit bat *Pteropus marianus* is the only bat on Kosrae, but it is rare because it is hunted. The gradual decline in *Sonneratia* may be related to the decline in fruit bat numbers or may be the result of successional processes unrelated to fruit bat pollination. *Rhizophora* is the slowest growing and most often harvested (Devoe & Cole 1998). Continued harvesting pressure may result in the gradual replacement of *Rhizophora* by *Bruguiera* (Ewel, Zheng *et al.* 1998).

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Mangrove litter dynamics need to be considered when assessing the impacts of a major change in aboveground forest structure. The effects of litter production and quality on microfauna (Brinson *et al.* 1980, Carlson *et al.* 1983, Mall *et al.* 1991), macrofauna (Daniel & Robertson 1990, Alongi & Sasekumar 1992, Lee 1998), organic carbon accumulation (Megonigal & Day 1988, Boto *et al.* 1989, Lacerda *et al.* 1995, Chen & Twilley 1999), and oxidation–reduction potential (Carlson *et al.* 1983, Sherman *et al.* 1998) have been extensively documented. Crabs in particular have a large influence on the decomposition rate of mangrove litter and whether or not it is retained in the forest (Robertson 1986, Robertson & Daniel 1989, Lee 1998). In addition to direct effects on primary consumers and soil characteristics, litter production and decomposition are thought to be key processes influencing larger estuarine and wetland food chains (Odum & Heald 1975, Rodelli *et al.* 1984, Robertson *et al.* 1992).

Root production in mangrove forests, although poorly understood, is likely to be an even more important soil carbon source than litterfall (Howarth & Teal 1980, Megonigal & Day 1988, Chen & Twilley 1999). Disparate soil carbon input and decomposition rates among mangrove species may affect microbial densities (Boto *et al.* 1989), oxidation–reduction potentials (Carlson *et al.* 1983, Sherman *et al.* 1998), and the chelation and adsorption of heavy metals (Lacerda *et al.* 1993, Cifuentes *et al.* 1996) and nutrients (Boto 1988, Alongi *et al.* 1992). Although no root production data for mangrove species have been published to date, different root production rates have been found among terrestrial tree species (Usman *et al.* 1999). Because of the importance of root production and turnover on soil carbon dynamics and soil chemistry, species-specific root production characteristics also need to be considered when predicting the impacts of changes in forest composition.

We compared root production rates, total soil carbon concentrations, and humic acid soil fractions among *Bruguiera*, *Rhizophora*, and *Sonneratia* rhizospheres. *Bruguiera* and *Sonneratia* leaf decomposition/leaching rates, as well as root and leaf lignin:N ratios, were also compared. *Rhizophora* foliage was not included in the decomposition experiment because litterfall rates of this species were insufficient to provide an adequate supply of leaves. Litterfall and sesarimid crab feeding characteristics were studied during the same time by others. These processes were examined to assess whether or not organic matter dynamics are likely to be substan-

tially altered as a result of the species-composition shifts occurring on Kosrae.

MATERIALS AND METHODS

SITE DESCRIPTION.—Kosrae, the easternmost island in the Federated States of Micronesia (5°19'N, 163°00'E), is a high volcanic island 109 km² in area and surrounded almost completely by a fringing reef. The average annual precipitation is 5000 mm (Merlin *et al.* 1993), the mean spring tide amplitude is 140 cm, and the average annual temperature is 27°C.

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 major watershed on the island's southern side; and Okat River basin, the major watershed on the island's northwestern side. The soils are classified as typic Sulfaquents (Soil Conservation Service 1984) and are generally saturated with brackish water throughout the day even at low tide. Mangrove soils cover an underlying coral sand substrate and range from *ca* 1.5 m deep at the mangrove fringe to *ca* 2.5 m deep in the interior (Fujimoto *et al.* 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 limited to selective firewood cutting; no major harvesting had occurred in any established plots associated with this study.

PLOT SELECTION AND EXPERIMENTAL DESIGN.—Two sites were chosen for analysis: one within Utwe River basin and one within Okat River basin. Both 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. Each of the three subplots contained aboveground 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 above ground biomass is likely to be correlated with root biomass and production, four measures of basal area were taken at all subplots.

Centered on each subplot, a 2, 4, and 8 m radius basal area measurement was recorded by summing the cumulative basal area of each stem within the plot. Basal area was measured at breast height with a diameter tape. 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, the analysis was repeated using each of the basal area measurements, one at a time, as a covariate. The covariate that generated the lowest *F*-value was chosen for hypothesis testing. All mean separations were performed by the LSD method using a significance level of 0.05.

FOLIAGE DECOMPOSITION.—Freshly fallen *Sonneratia* and *Bruguiera* foliage was collected on 4 and 11 August 1999. Fresh/dry weight conversion factors were calculated by oven-drying ten 40 g leaf sets for each species on both collection dates. Leaves were dried for three days in a gravity convection oven at 70°C. Each replicate consisted of *ca* 6 g (dry weight) of freshly fallen foliage sewed into a 20 x 20 cm nylon mesh bag. Forty mesh bags of each species were placed in the field on 5 August 1999, and 20 more were placed in the field on 12 August 1999. Mesh bags were distributed among the five Utwe River main plots so that each *Sonneratia* and *Bruguiera* subplot received 6 *Bruguiera* and 6 *Sonneratia* mesh bags.

A set of 10 mesh bags of each species was removed from the field after 0, 10, 20, 40, 80, and 149 days of decomposition. Upon removal, mesh bags were thoroughly washed free of sediment prior to opening, dried for 3 days at 70°C, and then weighed to the nearest 0.1 g. Oven-dried weight loss was calculated by applying the fresh/dry weight conversion factor to the original fresh weight measurement and subtracting the oven-dry weight after decomposition.

Data were recorded as percent oven-dry weight remaining after decomposition/leaching and were then arcsine transformed and tested for normality prior to analysis. An ANOVA with a split-plot design was used to test leaf (subplot treatment term) and site (main plot treatment term) decomposition characteristics of both species for each sampling date. Sampling dates were not combined in the ANOVA because variances among sampling dates were determined to be heterogeneous.

A single exponential model did not adequately fit our decomposition data, and so a double exponential model [$X_t/X_0 = Ae^{-k_1t} + (1 - A)e^{-k_2t}$], which is often used to provide a closer approxi-

mation of decay (Wieder & Lang 1982, Dierberg & Ewel 1984, Robertson 1988, Robertson *et al.* 1992), was applied. X_t/X_0 represents the change in dry-weight mass, and A and $(1 - A)$ represent labile and refractory substrate pools with their own decay constants (k_1 and k_2), respectively.

ROOT STANDING BIOMASS AND INGROWTH.—One root core was taken from each of the 30 subplots between 19 and 22 September 1999. Root 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 to a depth in excess of 30 cm. The soil was extracted from the corer and carefully sectioned into a 0–15 cm and a 15–30 cm segment. The sections were immediately sealed in air-tight polyethylene bags and transported within six hours of collection back to the lab and placed in a refrigerator at 4°C.

Soil cores were removed from the refrigerator after four days and sectioned lengthwise into two halves. One-half of each core was submitted for phosphate, pyrite, reactive iron, and organic carbon analysis. The other half of each core was submitted for root analysis using the procedure described below.

One-half of the 0–15 cm core was passed through a 2.0 and 0.5 mm mesh sieve under running water for one minute. Large roots (*ca* 4.0 mm) were removed and the remainder was sieved for another minute under running water to remove the rest of the sediment. Roots less than 4.0 mm but greater than 2.0 mm were defined as medium roots, while those less than 2.0 mm were defined as fine roots. Root size definitions were standard and based on the premise that medium roots (<4.0 and >2.0 mm) generally serve as transport conduits and support structures, whereas fine roots (<2.0 mm) serve as primary water and nutrient uptake structures (Persson 1988).

Roots were separated using previously established wet-sieving procedures (Fabiao *et al.* 1985, Persson & Ahlstrom 1994, Ruess *et al.* 1996). The root portions were then placed in labeled paper bags and put back in refrigeration. During transport from Kosrae to the University of Hawaii, the root samples were kept cool in an ice chest. In Hawaii, large woody debris (non-root, non-soil material) was removed from the root samples, and live/dead root separations were performed using a colloidal silica procedure (Robertson & Dixon 1993). Root samples were then oven-dried for three days at 70°C and weighed to within 0.01 g. Fine,

medium, large, and total root masses were calculated for each of the 0–15 and 15–30 cm root-core halves.

A 10.2 cm diameter, 30 cm long ingrowth chamber was placed into the opening that remained after the removal of the soil/root cores. In-growth chambers were constructed from rubber-coated iron mesh with 1 cm² apertures. These chambers were then filled with root-free sediment collected from each of the sites, and allowed to incubate for four months prior to removal. In-growth studies have been found to correlate well with sequential coring estimates of root production (Persson 1988), and we assumed that ingrowth accurately reflects production.

Upon removal from the field, the ingrowth cores were placed into resealable plastic bags, brought to the laboratory, and wet-sieved. Roots and woody debris that had been removed from the chamber material were then placed in labeled paper bags and refrigerated. During shipment from Kosrae to the University of Hawaii, the root samples were kept cool in an ice chest for *ca* 12 hours during transport and then placed back in refrigeration. Each ingrowth core was spread out on a slide viewing table, and roots were removed from woody debris using a pair of tweezers. Roots were then dried for three days at 70°C and weighed to within 0.01 g. Fine, medium, coarse, and total root weights were calculated for each of the 0–15 and 15–30 cm root sections. ANOVA with an RCB design combined across locations was used to test species effects.

ROOT AND LEAF CHEMICAL ANALYSIS.—*Bruguiera* and *Sonneratia* leaf and root samples were analyzed for lignin, cellulose, and nitrogen concentrations at the Agricultural Diagnostic Service Center, Sherman Laboratory, University of Hawaii. Lignin contents were calculated by determining the weight loss from the acid detergent fiber (ADF) content of leaf and root samples after digestion with KMnO₄ (Van Soest & Wine 1968). Cellulose contents were calculated by determining the weight loss from the ADF residue upon ashing for four hours at 500°C (Van Soest & Wine 1968). Total nitrogen was analyzed with a Technicon® AAI autoanalyzer after block digestion (Schuman *et al.* 1973).

Species-specific root lignin, cellulose, and nitrogen concentrations were tested with a one-way ANOVA. Because leaf samples were collected from the forest floor, leaves from individual trees could not be separated, and true replications were not obtained. Approximately 100 leaves of each species

were collected within each river basin, and a mixed sample for each species was submitted for analysis. Lignin, cellulose, and nitrogen concentrations obtained from this analysis were then used for qualitative species comparisons.

SOIL ORGANIC CARBON.—Organic carbon was analyzed using a modified Walkley Black procedure (Nelson & Sommers 1982). Oven-dried soil samples were sifted through a 0.2 mm mesh sieve to remove root materials; 10 ml of 1/6 M potassium dichromate and 20 ml of H₂SO₄ were added to 0.3 g of oven-dried soil. The solution was shaken for 1 minute and then allowed to digest for 30 minutes at room temperature in a fume hood. The digested soil solution was then vacuum-filtered through a Whatman® GF/D glass filter and diluted to 125 ml. Cr³⁺ that had been reduced by the soil carbon in each sample was then measured with a spectrophotometer at 600 nm. To determine relative humic acid concentration, a 1.25 g sample was then shaken for 45 minutes in 25 ml of 0.5 M NaHCO₃, and filtered through a Whatman® 6S filter. The absorbance of the filtrate at 350 nm was recorded.

SALINITY AND ELEVATION.—We measured salinity and relative elevation to eliminate the possibility that “species-specific” effects were coincidentally associated with species occupying different hydrologic microsites. A 50 ml pore water sample was taken 10 cm below the soil surface using a 20 cm length of perforated polyethylene tubing (McKee *et al.* 1988) and a 60 ml syringe. Salinity was measured in the field with a YSI® model 30 conductivity/salinity meter. 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 PVC pipe that had been driven into the sediment.

RESULTS

LEAF DECOMPOSITION.—*Sonneratia* leaves decomposed significantly ($P < 0.05$) faster than *Bruguiera* leaves for three out of the five sampling periods (Fig. 1). *Sonneratia* and *Bruguiera* leaf weight losses were not significantly different at the 40-day sampling period, because 60 percent of our mesh bags were consumed by sesarmid crabs and had to be removed from the experiment. If any holes were observed in the nylon mesh, the bag was omitted from the analysis. Sesarmid crab interference effectively reduced the total degrees of freedom for the

TABLE 1. Double exponential decay parameters (A , k_1 , k_2), half-life decomposition values ($t_{0.05}$), and lignin:N ratios for *Bruguiera* and *Sonneratia* leaves. k values indicate percent original dry weight loss per day from labile (k_1) and recalcitrant pools (k_2). A = percent of dry weight present in labile pool.

	A (%)	k_1	k_2	$t_{0.5}$ (day)	Lignin: N
<i>Bruguiera</i>	74.5	0.044	0.001	26	30.6
<i>Sonneratia</i>	65.3	0.100	0.016	11	25.5

experiment from 120 to 104. Double exponential decay models accounted for 96 percent ($P < 0.05$) of the variation associated with both species.

The half-life of *Bruguiera* foliage was 26 days, whereas the half-life of *Sonneratia* foliage was only 11 days (Table 1). After 150 days in place, 24 percent of the original dry weight still remained in *Bruguiera* bags, whereas only 2 percent remained in the *Sonneratia* bags. *Sonneratia* leaves also had more negative k constants for both labile (k_1) and recalcitrant (k_2) substrate pools (Table 1). These results are supported by higher lignin:N ratios that were determined for *Bruguiera* leaves (Table 2). Decomposition rates at *Sonneratia* and *Bruguiera* subplots were neither significantly different nor had any significant leaf \times site interactions.

ROOT AND SOIL ANALYSIS.—Root ingrowth was significantly higher in *Sonneratia* subplots than in either *Bruguiera* or *Rhizophora* subplots (Table 2). Ingrowth:basal area and ingrowth:live-root mass ratios (Table 2) indicated that ingrowth was significantly higher in *Sonneratia* subplots than in either *Bruguiera* or *Rhizophora* subplots independent of significant structural differences among the species. Incorporating basal area as a covariate reduced the P -statistic slightly but did not eliminate significant ingrowth differences among the species ($\alpha = 0.05$). Ingrowth did not differ between the 0–15 cm and the 15–30 cm sections for any species.

Rhizophora had significantly more dead medium-root mass and significantly less dead fine-root mass than *Bruguiera* or *Sonneratia* (Table 3). *Bruguiera* had less live medium roots than did the other two species (Table 3). Unfortunately, the effectiveness of the dead/live root separations could not be statistically determined due to inconsistent fluorescence in live roots when stained with acridine orange (Henry & Deacon 1981). Live/dead root separation comparisons among species should therefore be interpreted with caution.

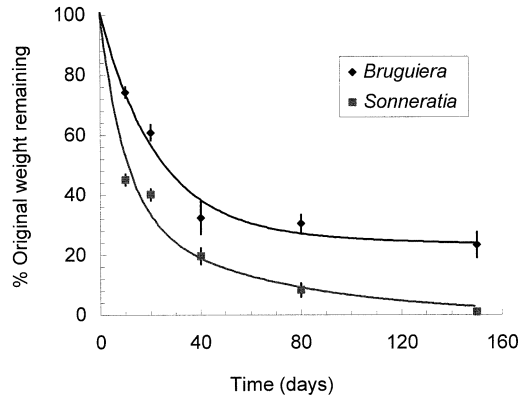


FIGURE 1. Dry weight loss of *Bruguiera* and *Sonneratia* leaves. Error bars represent ± 1 SE.

Standing live root mass was positively correlated with ingrowth ($P = 0.000$) and soil carbon ($P < 0.001$; Fig. 2), although soil carbon and ingrowth were not significantly ($P < 0.05$) correlated with each other. Relative humic acid fractions differed significantly among all the species ($P < 0.01$; Table 2) and were positively correlated with ingrowth ($r = 0.48$; $P = 0.008$). Total soil carbon was also positively correlated with salinity ($r = 0.55$; $P = 0.002$) and relative elevation ($r = 0.42$; $P = 0.020$).

DISCUSSION

LITTERFALL AND LEAF DECOMPOSITION.—Litter production, retention of leaves within the mangrove forest, and decomposition are important attributes of the carbon cycle that need to be considered when evaluating the effects of individual species. By examining the decomposition characteristics of leaves and utilizing litterfall and crab burial/retention data obtained in other studies, the likely impact of species composition shifts on organic matter dynamics can be predicted.

The large dry-weight loss of *Sonneratia* foliage during the first 10 days of the mesh bag study was most likely due to the leaching of soluble organic materials and probably not related to decomposition (Fell *et al.* 1975, Brinson *et al.* 1980, Twilley *et al.* 1986). Weight loss was most rapid in the first 20 days for both sets of leaves (Fig. 1). Leaching of soluble organics as well as microbial assimilation of labile substrates most likely account for this result and provide biological justification for use of the two compartment decay model; however, weight loss of *Sonneratia* leaves continued at a fast-

TABLE 2. Root, basal area, leaf lignin:N, and soil carbon comparisons among species. Ingrowth and live-root mass values represent roots in the top 15 cm of the soil horizon. Basal area indicates square meters of live tree area within an 8 m radius. Values followed by different letters are significantly different ($P < 0.05$).

	Ingrowth (mg/cm ³ /yr)	Ingrowth:basal area	Ingrowth:live- root mass	Lignin:N	Relative humic acid (absorbance)	Total soil carbon (mg/g)
<i>Bruguiera</i>	0.33b	0.01b	0.35b	66.5a	0.12c	308b
<i>Rhizophora</i>	0.29b	0.02b	0.44b	na	0.15b	354a
<i>Sonneratia</i>	2.78a	0.03a	1.68a	51.9b	0.19a	346ab
P-value	0.000	0.014	0.002	0.003	0.000	0.049

er rate than *Bruguiera* leaves throughout the duration of the study, indicating more rapid microbial colonization and degradation of nonsoluble organics as well. Larger decay constants for *Sonneratia* compared with *Bruguiera* foliage (Table 1) support the conclusion that both substrate compartments (A and 1 - A) for *Sonneratia* leaves decompose more rapidly and may be more easily assimilated into mangrove and benthic food chains.

Neither *Bruguiera* nor *Sonneratia* leaves are significantly favored by sesarmid crabs in Kosrae based on tethered leaf consumption/burial experiments (K. Amona, pers. comm.). Crab grazing directly on *Rhizophora* leaves within the canopy has been observed (K. Ewel, pers. obs.) and may result in an efficient within-mangrove carbon retention mechanism but it is not known if crabs graze on the other species too. *Bruguiera*, *Rhizophora*, and *Sonneratia* litterfall rates within Utwe River basin are not likely to differ significantly per unit basal area (R. Hauff, pers. comm.). Litterfall and crab consumption/burial characteristics are therefore not likely to result in significantly different soil carbon inputs as *Sonneratia* is replaced by *Bruguiera*.

The natural replacement of *Sonneratia* with *Bruguiera* is likely to result in lower rates of litter decomposition and higher rates of refractory organic matter accumulation in soil. Because previous studies have suggested that the effect of litterfall on soil organic carbon concentrations is of minimal

importance compared to root senescence (Howarth & Teal 1980, Megonigal & Day 1988, Chen & Twilley 1999), the impact of species composition shifts on total soil carbon concentrations via litterfall is likely to be small. A large change in litterfall production or decomposition characteristics, however, may be important to fungi, bacteria, and meiofauna populations associated with decomposing mangrove leaves (Fell *et al.* 1975) and to the development of mangrove forest structure and function (Mall *et al.* 1991). In marine wetlands, where up to 50 percent of organic matter mineralization is accounted for by sulfate-reducing bacteria (Jørgensen 1977), a change in substrate quality could also result in a major soil redox alteration.

Litterfall in Kosrae accounted for *ca* 8800 kg of organic matter/ha/yr (R. Hauff, pers. comm.), which exceeded root production estimates. The labile nature of this input and its importance to sesarmid crab populations suggest that any change in its retention within the mangrove system or in its decomposition characteristics is likely to have major effects on food chains and energy flows within the mangrove forest. The replacement of *Sonneratia* with *Bruguiera* is likely to result in a substantial change in litterfall recalcitrance and, thus, microbial and meiofauna populations. More investigation is needed to examine *Rhizophora* litterfall dynamics before the effects of its replacement with *Bruguiera* can be predicted with reasonable certainty.

ROOT PRODUCTION.—Research on root production in mangroves forests is almost completely lacking, although root production often exceeds above-ground production in wetland and terrestrial systems (Megonigal & Day 1988, Ruess *et al.* 1996) and is likely to influence soil carbon and nutrients to a greater extent than litterfall inputs (Edwards & Harris 1977). For this reason, production rates need to be examined to accurately evaluate the effects of individual species on soil organic matter dynamics.

TABLE 3. Live and dead standing root mass (mg/cm³) among species in the top 30 cm of the soil horizon.

	Live fine	Live medium	Dead fine	Dead medium	Total live
<i>Bruguiera</i>	2.4a	0.08b	43.6a	34.5b	2.4a
<i>Rhizophora</i>	1.8a	0.51a	32.8b	40.2a	2.3a
<i>Sonneratia</i>	2.6a	0.33a	44.1a	31.9b	2.9a
P-value	0.419	0.005	0.002	0.019	0.606

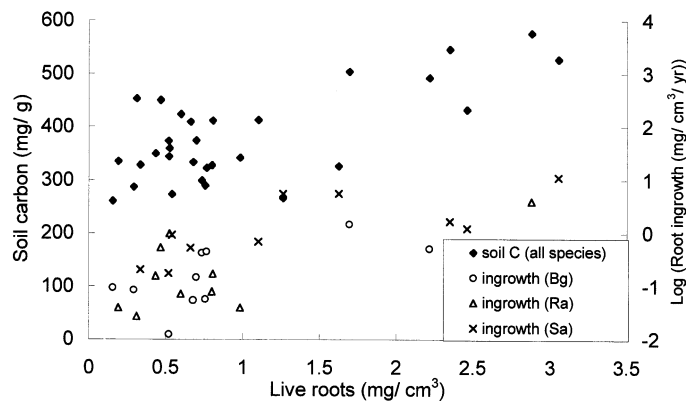


FIGURE 2. Relationship among live-root mass, soil carbon, and root ingrowth. Root and ingrowth values indicate roots existing in the top 15 cm of the soil horizon.

Higher rates of root ingrowth associated with *Sonneratia* subplots suggest that root production may be another organic matter input that will be substantially altered as a result of species composition shifts. Such a change in belowground organic matter production will likely affect soil microbial communities, redox potentials, and possibly peat accumulation rates.

How a decrease in root production will affect soil carbon concentrations is more difficult to predict. Soil carbon was significantly correlated with relative elevation and salinity, which suggests that hydrologic factors may confound ingrowth and soil carbon relationships. Organic carbon concentrations in *Sonneratia* subplots did not reflect the accelerated rates of root production measured there (Table 2). This discrepancy may be explained in part by the lower lignin:N ratio of *Sonneratia* roots (22% lower than *Bruguiera* roots; Table 2). The lignin:N ratio for *Sonneratia* leaves was 17 percent lower than for *Bruguiera* leaves, whereas the half-life of *Sonneratia* leaves was 58 percent that of *Bruguiera* leaves (Table 1). If root decomposition follows a similar pattern, the lower lignin:N ratio for *Sonneratia* roots may result in much faster rates of decomposition and offset the effect that higher rates of root production may have on soil carbon concentrations. Higher humic acid concentrations in *Sonneratia* plots (Table 2) suggest that higher rates of root production and decomposition may be resulting in a more refractory soil carbon pool.

Although no published root production estimates for mangrove forests exist, root production in other ecosystems ranges from *ca* 2500 kg/ha/yr in Himalayan pine forests (Usman *et al.* 1999) to *ca* 22,600 kg/ha/yr in cypress wetlands (Megonigal &

Day 1988). Root production on Kosrae averaged 1200 kg/ha/yr in *Bruguiera* plots to 7500 kg/ha/yr in *Sonneratia* plots, which is at the lower end of this range, but total root production estimates on Kosrae are likely to be conservative owing to the shallow depth sampled (upper 30 cm). Root production did not decrease significantly in the 15–30 cm cores compared to the 0–15 cm cores, which suggests that root production continues much deeper in the sediment than 30 cm. Because root production was not measured below 30 cm, comparisons of total carbon inputs between belowground and aboveground sources were not possible. Comparisons of belowground and aboveground carbon inputs were also difficult because the percentage of leaf litter that was exported to the estuary during the tidal cycle was not known. This is particularly important because leaf export rates can vary widely among mangrove forests (Robertson 1986).

Significantly higher root production rates in *Sonneratia* rhizospheres suggest that its replacement by *Bruguiera* will result in reduced soil organic matter inputs. *Bruguiera* and *Rhizophora* root production rates were similar, and therefore unlikely to result in significantly different soil organic matter inputs via root senescence. Decreased soil organic matter inputs from root production can be expected as a result of species composition shifts occurring on Kosrae. The effect that this will have on soil microbiology, redox potentials, nutrient availability, and food chain structure is likely to be substantial.

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