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Patterns of Root Dynamics in Mangrove Forests Along Environmental Gradients in the Florida Coastal Everglades, USA

Edward Castañeda-Moya,[1]* Robert R. Twilley,[1] Victor H. Rivera-Monroy,[1] Brian D. Marx,[2] Carlos Coronado-Molina,[3] and Sharon M. L. Ewe[4]

[1]*Department of Oceanography and Coastal Sciences, School of the Coast and Environment, Louisiana State University, Baton Rouge, Louisiana 70803, USA;* [2]*Department of Experimental Statistics, Louisiana State University, Baton Rouge, Louisiana 70803, USA;* [3]*Wetland Watershed Sciences Department, South Florida Water Management District, West Palm Beach, Florida 33416, USA;* [4]*Ecology and Environment, Inc., West Palm Beach, Florida 33401, USA*

Abstract

Patterns of mangrove vegetation in two distinct basins of Florida Coastal Everglades (FCE), Shark River estuary and Taylor River Slough, represent unique opportunities to test hypotheses that root dynamics respond to gradients of resources, regulators, and hydroperiod. We propose that soil total phosphorus (P) gradients in these two coastal basins of FCE cause specific patterns in belowground biomass allocation and net primary productivity that facilitate nutrient acquisition, but also minimize stress from regulators and hydroperiod in flooded soil conditions. Shark River basin has higher P and tidal hydrology with riverine mangroves, in contrast to scrub mangroves of Taylor basin with more permanent flooding and lower P across the coastal landscape. Belowground biomass (0–90 cm) of mangrove sites in Shark River and Taylor River basins ranged from 2317 to 4673 g m^{-2}, with the highest contribution (62–85%) of roots in the shallow root zone (0–45 cm) compared to the deeper root zone (45–90 cm). Total root productivity did not vary significantly among sites and ranged from 407 to 643 g m^{-2} y^{-1}. Root production in the shallow root zone accounted for 57–78% of total production. Root turnover rates ranged from 0.04 to 0.60 y^{-1} and consistently decreased as the root size class distribution increased from fine to coarse roots, indicating differences in root longevity. Fine root biomass was negatively correlated with soil P density and frequency of inundation, whereas fine root turnover decreased with increasing soil N:P ratios. Lower P availability in Taylor River basin relative to Shark River basin, along with higher regulator and hydroperiod stress, confirms our hypothesis that interactions of stress from resource limitation and long duration of hydroperiod account for higher fine root biomass along with lower fine root production and turnover. Because fine root production and organic matter accumulation are the primary processes controlling soil formation

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**Corresponding author; e-mail:* ecasta1@tigers.lsu.edu

and accretion in scrub mangrove forests, root dynamics in the P-limited carbonate ecosystem of south Florida have a major controlling role as to how mangroves respond to future impacts of sea-level rise.

Key words: root biomass; root productivity; root turnover rates; belowground allocation; P availability; mangroves; Florida Coastal Everglades.

Introduction

Plants allocate new biomass to acquire limiting resources that most strongly restrict growth of whole plant (Chapin and others 1987; Gleeson and Tilman 1992; Bazzaz 1997). Plants in nutrient-poor soils tend to allocate more biomass to roots, thereby maximizing efficiency for capturing the most strongly limiting resource and increasing root:shoot ratios that lead to a more favorable carbon:nutrient balance (Chapin 1980; Tilman 1985; Chapin and others 1987; Gleeson and Tilman 1992). Moreover, biomass allocation has a functional role in controlling ecological processes associated with carbon budgets of forest and wetland ecosystems (Nadelhoffer and others 1985; Jackson and others 1997; Chmura and others 2003; Bouillon and others 2008). For instance, biomass allocation is considered significant to soil formation and vertical accretion (Chen and Twilley 1999a; Turner and others 2004; McKee and others 2007), nutrient cycling (Nadelhoffer and others 1985), and nutrient uptake, transport, and storage (Eissenstat and others 2000). It is estimated that fine roots account for 10–30% of total forest tree biomass (Santantonio and others 1977) and from 30 to 50% of total net primary production in forest ecosystems (Jackson and others 1997). Thus, resource limitation of forested ecosystems may be significant in the ecological patterns of carbon storage and soil formation because plants respond differently to short- and long-term changes in soil nutrients according to species-specific evolutionary life history traits (Chapin and others 1987).

Mangroves are forested wetlands that are adapted to a variety of environmental settings characterized by stress gradients associated with interactions among resources (that is, nutrients), regulators (that is, soil salinity, sulfide), and hydroperiod (that is, frequency, duration, and depth of flooding; Twilley and Rivera-Monroy 2005). Mangrove species have the ability to adjust morphological and physiological traits in response to the interaction of these gradients as a mechanism that determines trajectories in ecosystem structure and function across the coastal landscape (Lugo and Snedaker 1974; Feller and others 2003a, b, 2007; Lovelock and others 2004; Twilley and Rivera-Monroy 2009). For example, simulation models of organic matter content and bulk density suggest that root production is a critical process in controlling organic matter accumulation and distribution in mangrove soils in the neotropics (Chen and Twilley 1999a). These models also predict that variations in root turnover have a more significant effect on these soil characteristics than variation in litterfall, as has been observed in a few empirical studies (McKee and Faulkner 2000; Middleton and McKee 2001).

Mangrove species are capable of allocating a large proportion (up to 40–60%) of their total biomass to belowground roots in response to nutrient limitation (Lugo 1990; Komiyama and others 2000; Khan and others 2007; Naidoo 2009). Recent studies of carbon allocation in mangrove wetlands around tropical and subtropical latitudes suggest that scrub forests allocate relatively more carbon to roots than do taller mangroves in response to low nutrient availability and anaerobic conditions (Lovelock 2008). The allocation of biomass among mangrove species also responds to changes in hydroperiod with distinct growth, productivity, and species zonation patterns along the intertidal zone (Twilley and others 1986; Castañeda-Moya and others 2006). Yet, there are few studies that have directly evaluated the influence of hydroperiod on mangrove root dynamics (Cardona-Olarte and others 2006; Krauss and others 2006; McKee and others 2007).

In this study, we investigate landscape patterns of belowground biomass and productivity of mangroves at sites along two Florida Coastal Everglades (FCE) basins, Shark River estuary and Taylor River Slough, to test the generality of biomass allocation models associated with distinct forest productivity gradients (Ewe and others 2006). These two basins have contrasting gradients in hydrology, regulators, and nutrients resulting in distinct riverine and scrub mangroves within an oligotrophic (that is, P-limited) carbonate platform (Chen and Twilley 1999b; Mancera-Pineda and others 2009; Castañeda-Moya and others 2010). Mangroves along Shark River basin are fertilized by sediment deposition associated with tropical cyclones, resulting in elevated aboveground productivity associated with

soil P availability that decreases with distance inland from the mouth of the estuary (Chen and Twilley 1999a, b; Krauss and others 2006; Castañeda-Moya and others 2010). Mangrove forests along Taylor River basin receive less inorganic sediments during storm events due to a geologic barrier called the ''Buttonwood Ridge'' that isolates these mangrove forests from storm P deposits from Florida Bay (Davis and others 2004; Castañeda-Moya and others 2010). Furthermore, mangroves along Shark River basin are tide-dominated, with higher frequency, duration, and depth of flooding in areas closer to the mouth of the estuary (Chen and Twilley 1999b; Krauss and others 2006; Castañeda 2010). In contrast, mangrove forests in southeastern Everglades, including Taylor River, are permanently flooded and have a negligible tidal frequency (Castañeda 2010).

We hypothesized that belowground root allocation will increase in response to both P limitation and permanently flooded conditions at the Taylor River sites compared to Shark River sites. We expected that mangrove forests along Taylor River basin would have greater root biomass allocation and lower root production due to increased root longevity as a result of lower root turnover rates. We also expected greater root biomass in the top 45 cm of the soil profile because roots tend to concentrate where soil nutrients are more abundant. We addressed the following questions: (1) Are the spatial and temporal patterns of belowground biomass and productivity consistent with expected trends associated with P-limited conditions of two basins in the FCE? (2) What is the relative change in root biomass and productivity with soil depth and root size distribution in response to nutrient, regulator and hydroperiod gradients of these two basins? (3) What is the relative change in root turnover with root size in response to gradients in soil nutrients, regulators, and hydroperiod? (4) What is the relative response of belowground biomass allocation, productivity, and root turnover across gradients in soil nutrients and hydroperiod? We focused only on sulfide as a regulator gradient because salinity did not explain the variation in community structure and function across our Florida mangrove sites (Mancera-Pineda and others 2009; Castañeda 2010).

Materials and Methods

Study Site

This study was conducted in the southern region of Everglades National Park (ENP; Figure 1) in a zone referenced as the Florida Coastal Everglades (FCE). Mangrove forests are distributed along the coastal margin with an estimated total area of 144,447 ha (Simard and others 2006), which represents approximately two-thirds of all mangrove cover in south Florida (Lodge 2005; see Chen and Twilley (1999b) and Castañeda-Moya and others (2010) for a full site description). In 2000, three mangrove sites were established each along Shark River basin (SRS-4, SRS-5, and SRS-6) and Taylor River basin (TS/Ph-6, TS/Ph-7, and TS/Ph-8) as part of the FCE Long Term Ecological Research (LTER) program (Childers 2006; http://fcelter.fiu.edu/). In each site, two 20 × 20 m permanent plots (20 m apart) were established approximately between 30-50 m from the shoreline to monitor forest structural attributes and soil biogeochemical properties. Mangrove forests along Shark River basin are considered riverine consisting of *Rhizophora mangle* (L.), *Avicennia germinans* (L.), *Laguncularia racemosa* (L.) Gaertn.f., and *Conocarpus erectus* L. SRS-6 is located approximately 4.1 km from the mouth of the estuary, whereas SRS-5, and SRS-4 are approximately 9.9 and 18.2 km, respectively (Figure 1). Lower Shark River sites (SRS-5 and SRS-6) are tide-dominated, whereas SRS-4 is influenced by runoff although a tidal influence is observed, particularly in the dry season (Chen and Twilley 1999b; Castañeda 2010). Mangrove sites along Taylor River basin (TS/Ph-7 and TS/Ph-6) are located approximately 1.5 and 4 km inland from Florida Bay. Mangrove zones are dominated by *R. mangle* scrub forest (tree heights ≤ 2 m) with clusters of *C. erectus* and freshwater *Cladium jamaicense-Eleocharis* sp. TS/Ph-8 is located near Snook Creek, a tributary of Joe Bay, east of the Taylor River basin (Figure 1). This site supports a mixed community of *C. jamaicense* and mangroves, with mangrove tree heights about 3–4 m. *Rhizophora mangle* dominates fringe areas and tidal creeks, whereas *C. erectus* is found in the interior parts (Ewe and others 2006). Mangrove waterways of Taylor basin are non-tidal systems with flooded conditions (mainly TS/Ph-6 and TS/Ph-7; Castañeda 2010) compared to tidal conditions of Shark River basin. Flooded conditions of Taylor basin are determined by the interactions of seasonal precipitation, upland runoff, and wind (Sutula 1999).

Root Biomass

We performed two separate field experiments to estimate root biomass in all six mangrove sites of both coastal basins. For the first experiment, root cores were collected in December 2000 at the three Shark River sites (SRS 4–6) and one Taylor River site (TS/Ph-6); whereas the other two Taylor sites

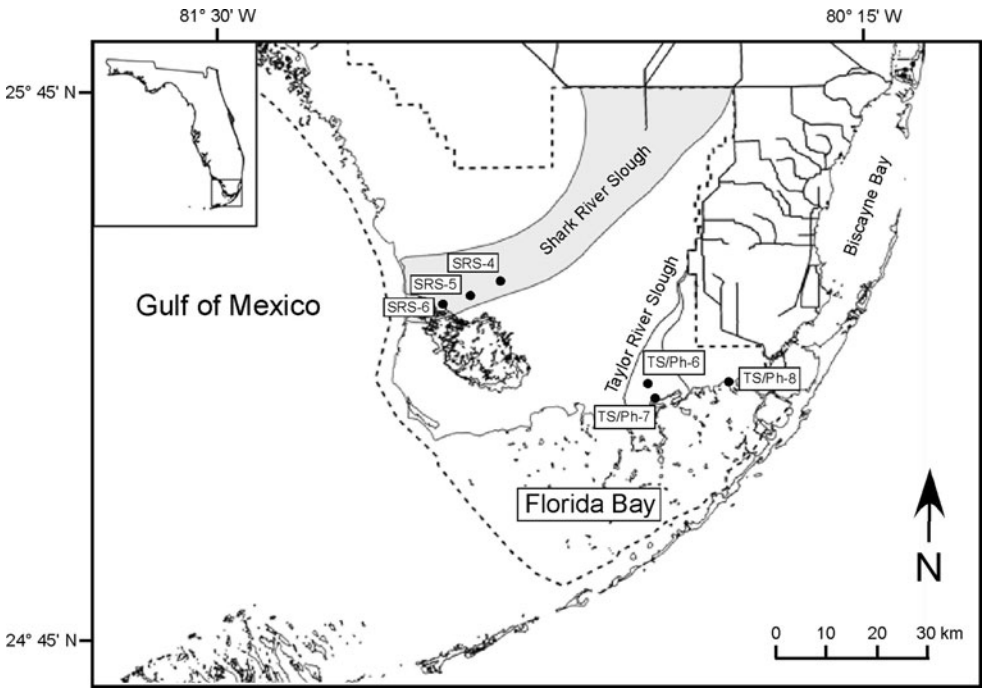

Figure 1. Location of the study sites in the Everglades National Park (ENP), south Florida, USA. SRS-4, SRS-5, and SRS-6 along Shark River estuary; TS/Ph-6, TS/Ph-7 along Taylor River Slough, and TS/Ph-8 in Joe Bay are part of the Florida Coastal Everglades Long-Term Ecological Research (FCE-LTER) program.

(TS/Ph-7 and TS/Ph-8) were sampled in May 2001. Five sampling points (replicates) were established in each site and treated as experimental units. Two sampling points were established in opposite corners of the two permanent plots, and the fifth sampling point was located in between the two plots. Due to the physiognomy of the forest (<2 m height) at two Taylor River sites (TS/Ph-6 and TS/Ph-7), five scrub mangrove islands (formed by 2–5 trees) of similar size were selected and treated as single sampling points; mangrove islands were selected in the same fashion around the plots as explained above. In each site, duplicate root cores (that is, sampling units; 0–45 cm depth; shallow root zone) were randomly collected as subreplicates at each sampling point, using a PVC coring device (10.2 cm diameter × 45 cm length); at TS/Ph-6 and TS/Ph-7 root cores were collected at the edge of each mangrove island. All root cores were stored separately in bags at 4°C and brought to the laboratory for further analyses. All root samples were processed separately and initially rinsed with water through 1-mm synthetic mesh screen to remove soil particles. Live roots were separated by hand picking those floating in fresh water, and sorted into diameter size classes of less than 2 mm, 2–5 mm, and greater than 5 mm (fine, small, and coarse roots, respectively). Coarse roots included size classes between 5 and 20 mm; roots greater than 20 mm in diameter were not included in this study due to sampling limitations. Each root sample was oven-dried at 60°C to a constant mass, and weighed. Preliminary tests of root separation techniques using fresh water and different concentrations (17, 11, and 6%) of a colloidal silica solution (Ludox™) that separate live and dead roots based on density differences (Robertson and Dixon 1993) indicated that using only fresh water to process our samples was the most cost-efficient technique for root separation.

For the second experiment, root cores were collected in December 2002 at two Taylor River sites (TS/Ph-7 and TS/Ph-8), and in May 2003 at the three Shark River sites and remaining Taylor River site (TS/Ph-6). In contrast to the first experiment, root biomass was estimated at two depths, 0–45 cm (shallow root zone) and 45–90 cm (deeper root zone) in all sites by using the same PVC coring device and sample processing as in the first experiment. In the Shark River sites, two sampling points (replicates) were established in opposite corners of the two permanent plots as in the first experiment. At each point, four cores (0–90 cm depth) were randomly collected as subreplicates and divided into 0–45 and 45–90 cm to estimate biomass at each of the root zones. At TS/Ph-6 and TS/Ph-7, mangrove islands of similar size were selected at the outside corners of the plots and treated as single sampling points as in the first experiment. In TS/Ph-6, five mangrove islands were selected and cores (0–90 cm depth) were collected in two habitats (inland and edge) of each island. Duplicate cores from each habitat were divided into 0–45 and 45–90 cm. In TS/Ph-7, one mangrove island was selected in the far left corner of each plot,

and four cores were collected at the inland and edge habitats of each island; only two cores per habitat (inland and edge) were saved and divided into 0–45 and 45–90 cm to estimate root biomass. In TS/Ph-8, five sampling points were established around the two permanent plots in the same fashion as in the first experiment. In each point, four root cores (0–90 cm depth) were collected but only two cores (subreplicates) were randomly selected, saved and divided into the two sampling depths. All samples were processed for root biomass as described above for the first experiment.

Root Productivity

We used the ingrowth core technique (Vogt and others 1998) to estimate root productivity only in the second experiment at all sites. Ingrowth cores (10.2 cm diameter × 45 cm length) made of flexible synthetic mesh material and filled with pre-sieved sphagnum peat moss were installed in each of the cored holes formed during sampling of root biomass. Commercial sphagnum peat moss had similar characteristics to mangrove peat in our sites, including bulk density (0.15 vs. 0.21 g cm^{-3}), organic matter content (AFDW: 97 vs. 75%), total C (470 vs. 330 mg g^{-1}), and total N (11 vs. 13 mg g^{-1}). Ingrowth cores were retrieved at 1- and 3-year intervals, and the subsequent root growth within the ingrowth core was used to estimate annual root production at two depths (0–45 and 45–90 cm) during both time intervals. Cores were harvested during December 2003 (1-year interval) and February 2006 (3-year interval) at TS/Ph-7 and TS/Ph-8, and during May 2004 (1-year interval) and February 2006 (3-year interval) at the Shark River sites and TS/Ph-6. During each time interval, two ingrowth cores (four in the case of TS/Ph-7) were retrieved as subreplicates from each depth at each sampling point in all sites. After each harvest, ingrowth cores were processed individually following the same protocol as in the root biomass section. Root turnover rate in the shallow root zone (0–45 cm depth) was calculated as root productivity divided by biomass (Eissenstat and Yanai 1997) of each root size class. Estimates of root turnover represent the average of root biomass cores and ingrowth cores for each sampling point within each site. Root longevity (turnover time) in the shallow root zone was calculated as the inverse of root turnover rate (y^{-1}) for each root size class.

Root Nutrient Content

We determined nutrient content of root biomass samples (0–45 cm depth) for the first experiment. Four oven-dried root core samples were randomly selected from each site and considered as replicates; the size classes of each root core were combined for further nutrient analyses. It was not possible to determine nutrient concentration of each root size class due to small sample volumes. Total N concentrations of root material were determined on two analytical replicates of each sample with an ECS 4010 elemental analyzer (Costech Analytical Technologies, Inc., Valencia, California). Total P was extracted on duplicate analytical replicates with 1 N HCl after combustion in a furnace at 550°C (Aspila and others 1976) and determined by colorimetric analysis using a segmented flow analysis Flow Solution IV autoanalyzer (OI Analytical, College Station, Texas). Root nutrient density was express on a volume basis (mg cm^{-3}) using the root density per volume of soil. The N:P atomic ratio of root tissue was used as an indicator of nutrient limitation (N or P-limited). An N:P atomic ratio less than 33 indicates N limitation, whereas N:P greater than 33 suggests P limitation (Koerselman and Meuleman 1996; Verhoeven and others 1996; Darby and Turner 2008a, b).

Statistical Analyses

All statistical analyses were performed with PROC MIXED (SAS Institute, Cary, North Carolina, USA). The variation in root biomass and productivity was not tested among size classes and estimates represent the sum of all size classes for each site. Root biomass was tested for differences among sites (first experiment) and sites and depth (second experiment) using a one- and two-way ANOVA, respectively. We used repeated measures ANOVA to test for differences in root productivity among sites, harvest, and depth (0–45 vs. 45–90 cm), with harvest as the repeated measure. Differences in total (0–90 cm) root biomass and productivity were tested between mangrove island habitats (inland vs. edge) and sites (TS/Ph-6 and TS/Ph-7) with a two-way ANOVA. Variation in shallow (0–45 cm) fine root biomass and productivity was tested independently with a one-way ANOVA to determine differences among sites and regions (Shark River vs. Taylor River). Root turnover in the shallow root zone was tested for differences among sites and size classes using a two-way ANOVA. For TS/Ph-6 and TS/Ph-7, we only used data collected in the inland habitat of these mangrove islands to examine the variation in shallow fine root biomass, productivity, and root turnover across all sites. This habitat represents more accurately patterns of root biomass accumulation and production as these mangrove islands grow in these two sites (see Fig-

ure 2 in Ewe and others 2007). Root nutrient content (total N and P) and N:P ratios of shallow root biomass samples were analyzed independently with one-way ANOVA to determine differences among sites.

All effects were considered fixed. Sampling points were nested within each site, considered random effects, and treated as experimental units. Sampling units (that is, root cores and ingrowth cores) were also nested with each site and considered random effects. The ANOVA design was unbalanced for most of the variables analyzed due to differences in the number of sampling points and total number of observations per point in each site. The Kenward–Roger procedure was used to adjust the degrees of freedom of the F test statistics when the design was unbalanced or when an unequal variance model was significant (SAS Institute, Cary, North Carolina, USA; Kenward and Roger 1997). Interaction effects were considered for all analyses. Pairwise comparisons were performed with Fisher's Least Significant Differences (LSD) when significant differences ($P < 0.05$) were observed within a main effect or interaction. The assumption of normality was tested using normal probability plots and ANOVA residuals. The assumption of homocedasticity was tested using the ''null model'' likelihood ratio test of the residual errors with a chi square distribution. All variables were log-transformed ($\ln(x + 1)$) prior to analysis to meet the ANOVA assumptions, except root turnover, root total N, and root N:P. Unless otherwise stated, data presented are means (± 1 SE) of untransformed data. Soil nutrient data (top 45 cm; Poret and others 2007; Castañeda 2010) in all six FCE mangrove sites were used for regression analyses with shallow fine root biomass, productivity, and turnover, and root nutrient content.

Results

Root Biomass

Shallow (0–45 cm depth) root biomass did not differ significantly (interaction site × experiment: $F_{5,132} = 1.95$, $P = 0.1$) between the two experiments (2000–2001 vs. 2002–2003) for any of the mangrove sites. Thus, root data for both samplings were pooled to obtain root estimates for the shallow root zone in each site. These data and the root data for the deeper (45–90 cm) root zone from the second experiment were used to estimate the variation in root biomass with depth at each of the six mangrove sites.

Root biomass was significantly different among sites and between depths, and there was a significant interaction between site and depth (Table 1). Shallow root biomass was greater in TS/Ph-8 (3302 ± 591 g m^{-2}) and SRS-5 (3176 ± 274 g m^{-2}) compared to SRS-6 (1973 ± 336 g m^{-2}). In the deeper root zone, TS/Ph-7 (1778 ± 575 g m^{-2}) had the highest root biomass and SRS-6 and TS/Ph-6 (560 ± 164 and 367 ± 60 g m^{-2}, respectively) showed the lowest estimates (Figure 2A). Overall, mean root biomass was significantly higher in the shallow root zone (2584 ± 249 g m^{-2}) compared to the deeper (45–90 cm) root zone (1008 ± 205 g m^{-2}) at all sites, except at TS/Ph-7 where root biomass was not significantly different between the two root zones (Table 1; Figure 2A).

Total (0–90 cm) root biomass ranged from 2317 ± 329 g m^{-2} (TS/Ph-6) to 4673 ± 401 g m^{-2} (TS/Ph-7), with the highest contribution (62–85%) of roots in the shallow root zone at all sites. Taylor River sites had both the high and low mean estimates of total biomass, with the general trend TS/Ph-7 > SRS-5 > TS/Ph-8 > SRS-4 > SRS-6 > TS/Ph-6. There were no significant differences ($F_{1,35} = 0.32$, $P = 0.6$) in mean total biomass

Table 1. Statistical Results of Belowground Root Biomass, Productivity, Turnover and Root Nutrient Content in Mangrove Forests of the Florida Coastal Everglades

Source of variation	df	F	P
Root biomass			
Site	5, 28.5	6.1	***
Depth	1, 73.6	119.4	***
Site × depth	5, 46.9	3.3	*
Fine root biomass			
Site	5, 99.6	2.7	*
Fine root productivity			
Site	5, 80	2.7	*
Root productivity			
Site	5, 17.9	1.5	ns
Harvest	1, 92	0.7	ns
Depth	1, 77.6	70.3	***
Site × harvest	5, 91.9	2.2	ns
Site × depth	5, 77.4	4.2	**
Harvest × depth	1, 93.5	0.1	ns
Site × harvest × depth	5, 93.3	1.2	ns
Root turnover			
Site	5, 47.7	7.0	***
Size	2, 45.9	54.2	***
Site × size	10, 45.9	4.4	***
Root nutrient content			
Total N (mg cm^{-3})	5, 18	6.4	**
Total P (mg cm^{-3})	5, 18	15.5	***
Atomic N:P	5, 18	94.2	***

*Significance levels are indicated by *P < 0.05, **P < 0.01, ***P < 0.001. ns = not significant.*

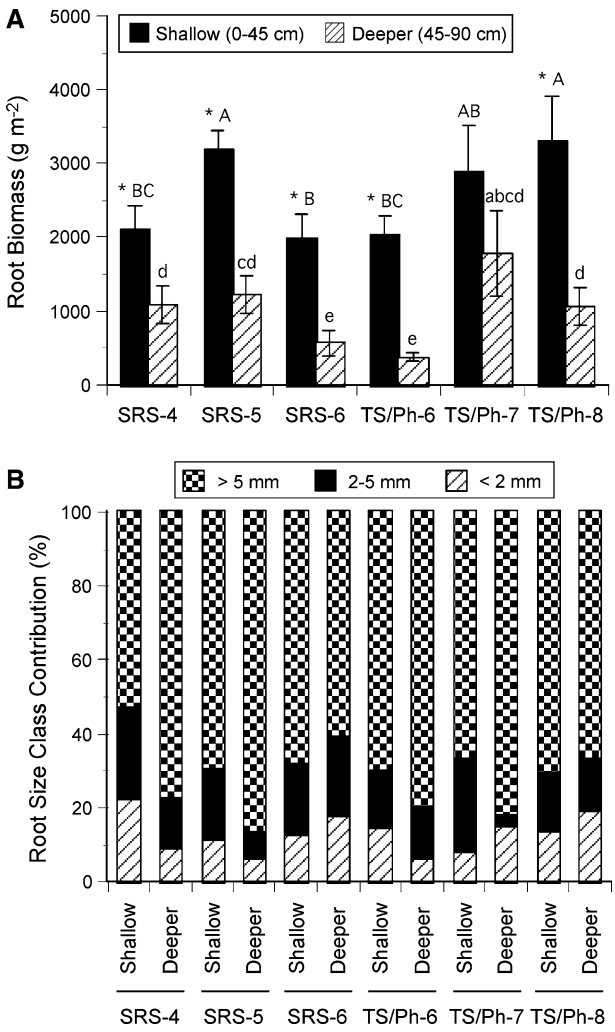

Figure 2. Total root biomass in the shallow (0–45 cm) and deeper (45–90 cm) root zones (**A**) and root size class distribution with depth (**B**) in mangrove forests of the Florida Everglades. *Asterisks* indicate significant differences ($P < 0.05$) within each site. Means (± 1 SE) with *different capital letters* are significantly different ($P < 0.05$) among sites in the shallow root zone. Means (± 1 SE) with *different small letters* are significantly different ($P < 0.05$) among sites in the deeper root zone.

between the Taylor River sites (3811 ± 710 g m^{-2}) and Shark River sites (3368 ± 544 g m^{-2}). Most of the root biomass was distributed in the larger size class for both root zones at all sites (Figure 2B). On average, the less than 2 mm and 2–5 mm size classes contributed 13 and 16% of the total live root biomass in each root zone at all sites, whereas the greater than 5 mm size class accounted for 71% of the total biomass.

Total (0–90 cm) root biomass allocation also varied between the inland and edge habitats of mangrove islands at two Taylor River sites with scrub mangrove forests (TS/Ph-6 and TS/Ph-7; Table 2). Overall, the inland habitat (4661 ± 576 g m^{-2}) of both sites had the highest root biomass compared to the edge habitat (2220 ± 372 g m^{-2}). The inland habitat (5975 ± 1333 g m^{-2}) of TS/Ph-7 had the highest root biomass, whereas the edge habitat (1059 ± 203 g m^{-2}) of TS/Ph-6 had the lowest (Table 2). In general, total (0–90 cm) root biomass was significantly greater in the mangrove islands of TS/Ph-7 (4677 ± 868 g m^{-2}) compared to TS/Ph-6 (2204 ± 356 g m^{-2}). There was no significant interaction between island habitats and sites indicating that the variation in root biomass between habitats is independent of site differences (Table 2).

Table 2. Statistical Results of Root Biomass and Productivity (Integrated to a Depth of 90 cm) in the Inland and Edge Habitats of Mangrove Islands at TS/Ph-6 and TS/Ph-7

Site	Island habitat	Biomass (g m^{-2})	Productivity (g m^{-2} y^{-1})
TS/Ph-6	Inland	3347 (408)^{b}	703 (150)^{a}
	Edge	1172 (203)^{c}	419 (30)^{b}
TS/Ph-7	Inland	5975 (1333)^{a}	491 (64)^{ab}
	Edge	3379 (638)^{b}	323 (18)^{b}
ANOVA source		Biomass	Productivity
Site		$F_{1,24}$ = 16.2 (***)	$F_{1,4.5}$ = 1.9 (ns)
Habitat		$F_{1,24}$ = 15.8 (***)	$F_{1,27.9}$ = 9.2 (*)
Site × habitat		$F_{1,24}$ = 0.1 (ns)	$F_{1,27.9}$ = 0.6 (ns)

*Means (± 1 SE) followed by different letters within each column are significantly different (Fisher's LSD post hoc test). ANOVA source with significance is indicated by *P < 0.05, **P < 0.01, ***P < 0.001. ns = not significant.*

Variation in shallow (top 45 cm of soils) fine (<2 mm) root biomass was also examined among sites, given that this root size class distribution accounts for most of nutrient uptake. Shallow fine root biomass varied significantly among mangrove sites and ranged from lowest value at a Shark River site (253 ± 38 g m^{-2}; SRS-6) to greatest value at Taylor River site (540 ± 102 g m^{-2}; TS/Ph-7; Table 1; Figure 3A). There was no significant difference in fine root biomass in five of the six sites; only the site at the mouth of Shark River (SRS-6) had significantly lower fine root biomass. Along Shark River basin, fine root biomass allocation in the shallow root zone increased from the mouth of the estuary with distance inland (Figure 3A). There were significant ($F_{1,105}$ = 5.1, $P < 0.05$) differences in mean shallow fine root biomass between Shark River (354 ± 26 g m^{-2}) and Taylor River basins (474 ± 53 g m^{-2}).

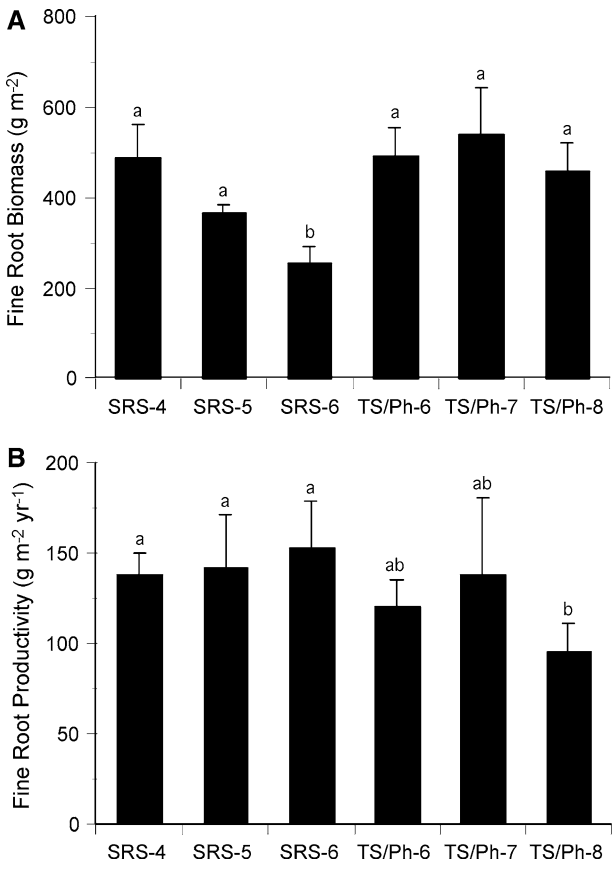

Figure 3. Mean (± 1 SE) fine root biomass (**A**) and fine root productivity (**B**) in the shallow (0–45 cm) root zone in mangrove forests of the Florida Everglades. *Different letters* indicate significant differences ($P < 0.05$) among sites.

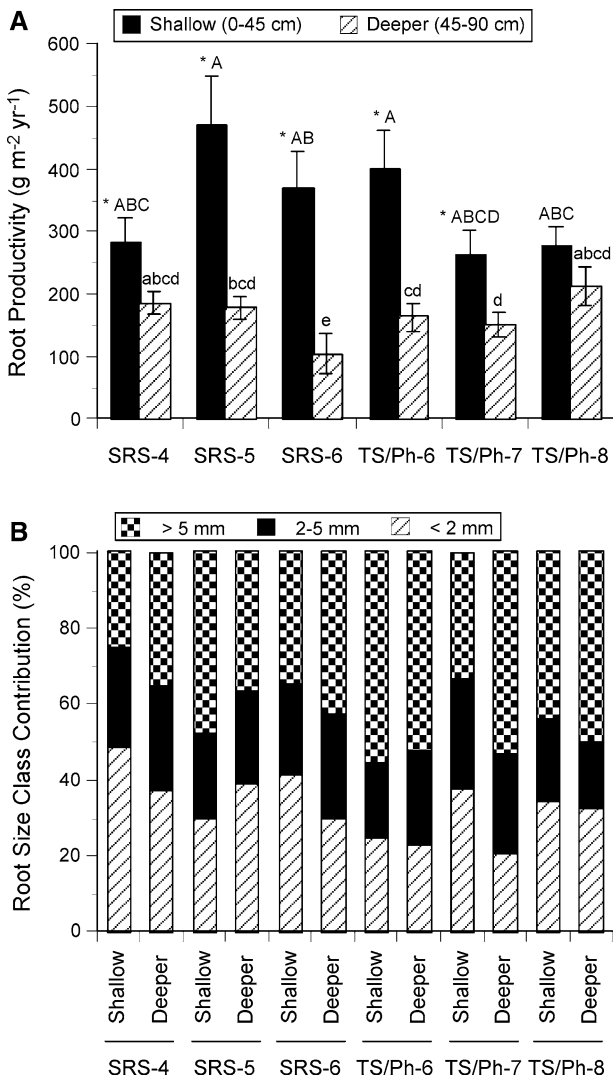

Figure 4. Total root productivity in the shallow (0–45 cm) and deeper (45–90 cm) root zones (**A**) and root size class distribution with depth (**B**) in mangrove forests of the Florida Everglades. *Asterisks* indicate significant differences ($P < 0.05$) within each site. Means (± 1 SE) with *different capital letters* are significantly different ($P < 0.05$) among sites in the shallow root zone. Means (± 1 SE) with *different small letters* are significantly different ($P < 0.05$) among sites in the deeper root zone.

Root Productivity

Root productivity was not significantly different among sites for both shallow and deeper root zones. The shallow root zone ranged from 260 ± 40 g m^{-2} y^{-1} (TS/Ph-7) to 468 ± 78 g m^{-2} y^{-1} (SRS-5), compared to the lower range from 102 ± 32 g m^{-2} y^{-1} (SRS-6) to 210 ± 32 g m^{-2} y^{-1} (TS/Ph-8) in the deeper root zone (Table 1; Figure 4A). Estimates of root productivity among the six mangrove sites were similar (not significantly different) based on either 1-year (284 ± 23 g m^{-2} y^{-1}) or 3-year harvest intervals (231 ± 15 g m^{-2} y^{-1}) due, in part, to high sample variability (Table 1). However, there was a significant interaction between site and depth effects, with higher root productivity in the shallow root zone (341 ± 22 g m^{-2} y^{-1}) compared to the deeper root zone (166 ± 11 g m^{-2} y^{-1}) at all sites, except in TS/Ph-8 where root productivity estimates were not significantly different between the two root depths (Table 1; Figure 4A). Overall, total (0–90 cm) root productivity ranged from 407 ± 23 g m^{-2} y^{-1} (TS/Ph-7) to 643 ± 93 g m^{-2} y^{-1} (SRS-5) with the highest root production (57–78%) in the shallow root zone compared to the deeper root zone. Fine roots contributed 21–50% of the total root productivity in each root zone at all sites (Figure 4B). On average, the small (2–5 mm) and coarse (>5 mm) roots accounted for 24 and 41% of the total root production in each root zone at all sites, respectively.

Total (0–90 cm) root productivity varied between habitats (inland vs. edge) of mangrove islands at the two Taylor River scrub mangrove sites (TS/Ph-6 and TS/Ph-7; Table 2). Overall, total root productivity in the inland habitat (597 ± 106 g m^{-2} y^{-1}) was significantly higher compared to the edge habitat (371 ± 48 g m^{-2} y^{-1}) of mangrove islands. The inland habitat (703 ± 150 g m^{-2} y^{-1}) of TS/Ph-6 had the highest root productivity and the edge habitat (323 ± 18 g m^{-2} y^{-1}) of TS/Ph-7 the lowest. There were no significant differences in total root productivity among sites and no significant interaction between island habitats and sites (Table 2). The variation in shallow (0–45 cm depth) fine (<2 mm) root productivity was significant among mangrove sites, with the greatest root production in all Shark River sites (Table 1; Figure 3B). Mean shallow fine root production estimates were significantly higher in the Shark River basin (144 ± 5 g m^{-2} y^{-1}) compared to the Taylor River basin (111 ± 12 g m^{-2} y^{-1}; $F_{1,84}$ = 4.6, $P < 0.05$).

Root Turnover and Longevity

Root turnover in the shallow (0–45 cm) root zone differed significantly among sites and size class distribution (Table 1). Root turnover rates consistently decreased as the root size class increased from less than 2 mm to greater than 5 mm for all sites (Figure 5). Fine root turnover rates ranged from 0.23 ± 0.03 y^{-1} (TS/Ph-6) to 0.60 ± 0.07 y^{-1} (SRS-6), from 0.07 ± 0.01 y^{-1} (TS/Ph-7) to 0.24 ± 0.05 y^{-1} (TS/Ph-6) for small roots, and from 0.04 ± 0.01 y^{-1} (TS/Ph-7) to 0.15 ± 0.02 y^{-1} (TS/Ph-6) for coarse roots (Figure 5). There was a significant interaction between sites and root size classes (Table 1). Overall, mean turnover rates were higher at the Shark River sites compared to Taylor River sites for both fine (0.43 ± 0.09 and 0.24 ± 0.004 y^{-1}) and small roots (0.18 ± 0.01 and 0.14 ± 0.05 y^{-1}). In contrast, mean turnover rates of coarse roots were fairly similar for both Shark and Taylor River basins (0.09 ± 0.01 and 0.09 ± 0.03 y^{-1}, respectively). Root longevity estimates ranged from 1.7 to 4.4 years for fine roots, from 4.1 to 15.4 years for small roots, and from 6.6 to 24.8 years for coarse roots at all sites (Table 3).

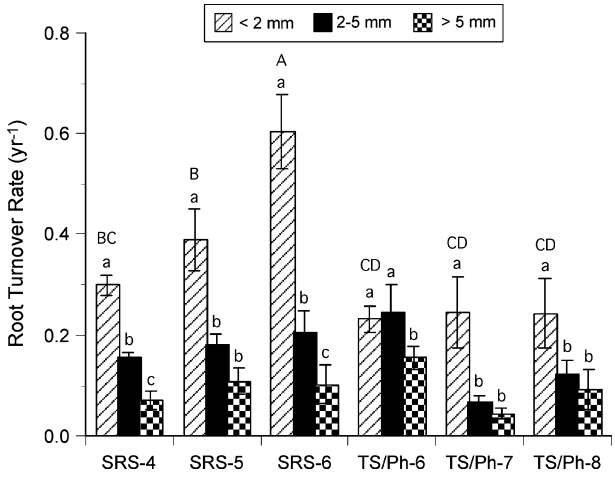

Figure 5. Mean (± 1 SE) turnover rates (to a depth of 45 cm) of root size classes in mangrove forests of the Florida Everglades. *Different small letters* indicate significant differences ($P < 0.05$) among root size classes within each site. *Different capital letters* indicate significant differences ($P < 0.05$) in fine root turnover among sites.

Root Nutrient Content

Root nutrient content of shallow root biomass differed significantly among sites (Table 3). Root N content was significantly higher at the Taylor River sites and SRS-6 compared to SRS-4 and SRS-5, and ranged from 0.016 ± 0.001 mg cm^{-3} (SRS-4) to 0.034 ± 0.006 mg cm^{-3} (TS/Ph-7; Table 3). Root P had the highest content at SRS-6 (1.74 ± 0.20 µg cm^{-3}) and differed significantly from all other sites (Table 3). Along Shark River basin, root P content decreased significantly with distance inland from the mouth of the estuary. The atomic N:P ratio of root tissue varied significantly from 33.3 ± 0.9 (SRS-6) to 125.6 ± 7.0 (TS/Ph-7) among sites, indicating P limitation at all sites, except at SRS-6 (Table 3).

Discussion

Total (0–90 cm) root biomass estimates are variable across our study sites (range: 2400–4700 g m^{-2}) and within the range of values reported for mangroves around the world (Table 4). Our estimates are similar to values reported for mangroves in Puerto Rico (Golley and others 1962), the Dominican Republic (Sherman and others 2003), and Kenya (Gazi Bay, Tamooh and others 2008) using similar techniques and sampling depths (Table 4). However, caution is needed when comparing global trends because varying results of belowground biomass can differ with methodological approaches (Vogt and others 1998; Clark and others 2001; Bouillon and others 2008). For instance, root estimates based on soil cores are similar across multiple mangrove regions, including our study site. But these estimates are considerably lower relative to soil pit and trench methods, which are the highest

Table 3. Root Longevity, Root Nutrient Content, and Root N:P Atomic Ratios in Mangrove Forests of the Florida Coastal Everglades

Sites	Root longevity (years)			Root nutrient content		
	Fine (<2 mm)	Small (2–5 mm)	Coarse (>5 mm)	Total N (mg cm^{-3})	Total P (μg cm^{-3})	Atomic N:P
SRS-4	3.4	6.5	15.0	0.016^{c} (0.001)	0.55^{c} (0.04)	63.1^{d} (1.2)
SRS-5	2.6	5.6	9.5	0.019^{c} (0.002)	0.80^{b} (0.07)	51.5^{e} (0.7)
SRS-6	1.7	4.9	10.1	0.026^{ab} (0.003)	1.74^{a} (0.20)	33.3^{f} (0.9)
TS/Ph-6	4.4	4.1	6.6	0.027^{ab} (0.002)	0.58^{c} (0.06)	102.8^{b} (4.3)
TS/Ph-7	4.1	15.4	24.8	0.034^{a} (0.006)	0.61^{c} (0.10)	125.6^{a} (7.0)
TS/Ph-8	4.2	8.3	11.3	0.029^{a} (0.001)	0.71^{b} (0.04)	89.5^{c} (2.3)

*Means (± 1 SE) followed by different letters within each column are significantly different (Fisher's LSD post hoc test). Significant levels are indicated by *P < 0.05, **P < 0.01, ***P < 0.001. ns = not significant.*

root estimates for mangroves (range: 18,970–50,950 g m^{-2}; Table 4). Some of these differences may be due to the larger size class (>20 mm) of roots included in these techniques and the more extensive sampling depth. In contrast, soil cores limit root size classes when sampling due to small (<10 cm in diameter) core dimensions. In addition, confounding variables such as forest age, species composition, history (planted vs. natural), and local climate variation could influence biomass allocation patterns resulting in observed differences (Kairo and others 2008; Tamooh and others 2008).

Our results reveal a significant decrease in total root biomass with soil depth across the FCE basins, with most of the roots distributed (62–85%) in the shallow root zone. This difference in root density with depth has been measured in other mangroves in the neotropics (Fiala and Hernandez 1993) and Asia (Komiyama and others 2000; Tamooh and others 2008). We also observed the highest root production (57–78%) in the shallow root zone that is comparable to other studies (Ruess and others 2003; Darby and Turner 2008b). Our root productivity estimates are also in agreement with the few direct estimates reported for neotropical mangroves (McKee and Faulkner 2000; Cahoon and others 2003; Giraldo 2005; McKee and others 2007; Table 4). Moreover, fine root production was a significant contributor (21–50%) to the total (0–90 cm) belowground allocation. This is consistent with previous studies suggesting that fine root production accounts for one-third of the total annual carbon allocation belowground in forest ecosystems (Nadelhoffer and Raich 1992). The higher biomass allocation to coarse roots (~70%) and substantial fine root production in all our FCE sites supports the hypothesis that belowground allocation is a significant contribution to soil carbon storage in mangrove forests (Chmura and others 2003; Khan and others 2007).

Canopies of plant communities respond to lower nutrient availability by increasing leaf longevity and reducing nutrient loss through leaf fall, which basically increases efficiency of intra-system recycling (Chapin 1980). It is assumed that root dynamics will exhibit similar intra-system recycling patterns with nutrient limitation (Chapin 1980; Ostertag 2001). We observed decreases in root P content with increasing soil N:P ratios across FCE basins, supporting the idea that root nutrient content can be used as an indicator of soil fertility in mangrove sites (Figure 6A). The gradient in root P storage for mangroves from west (SRS-6) to east (TS/Ph-8) across the Everglades mangrove ecotone region is similar to the pattern observed in foliar P of Florida Bay seagrasses (Fourqurean and others 1992). This P availability gradient was invoked as a variable controlling productivity and species composition of seagrass communities in this region (Herbert and Fourqurean 2009), as has been suggested for mangrove forests across FCE (Ewe and others 2006; Rivera-Monroy and others 2011). The N:P stoichiometry of root tissue across the two mangrove basins also supports that hypothesis.

Overall, total root biomass increased with lower P fertility across the two FCE basins, with the exception of TS/Ph-6 in Taylor basin, which had similar biomass allocation relative to the most fer-

Table 4. Summary of Belowground Biomass and Productivity of Worldwide Mangrove Forests

Location	Sampling method: Biomass	Sampling method: Productivity	Dominant species: Forest type	Belowground biomass (g m^{-2}) Total (fine: ≤ 2 mm)	Belowground productivity (g m^{-2} y^{-1}) Total (fine: ≤ 2 mm)	Reference
Shark River (SRS-4), Florida (USA)	Soil cores	Ingrowth cores	Rm, Lr, Ce—Riverine	3198 (587)[1]	465 (206)[1]	This study
Shark River (SRS-5), Florida (USA)	Soil cores	Ingrowth cores	Rm, Lr, Ag—Riverine	4389 (442)[1]	643 (210)[1]	This study
Shark River (SRS-6), Florida (USA)	Soil cores	Ingrowth cores	Rm, Lr, Ag—Riverine	2532 (353)[1]	469 (183)[1]	This study
Taylor River (TS/Ph-6), Florida (USA)	Soil cores	Ingrowth cores	Rm—Scrub	2404 (324)[1]	561 (137)[1]	This study
Taylor River (TS/Ph-7), Florida (USA)	Soil cores	Ingrowth cores	Rm – Scrub	4673 (508)[1]	407 (130)[1]	This study
Taylor River (TS/Ph-8), Florida (USA)	Soil cores	Ingrowth cores	Rm, Ce—Fringe	4358 (661)[1]	485 (164)[1]	This study
Utwe River, Micronesia	Soil cores	Ingrowth cores	Bg—Basin	720[2]	(120)[3]	Gleason and Ewel (2002)
Okat River, Micronesia	Soil cores	Ingrowth cores	Sa—Basin	870[2]	(750)[3]	Gleason and Ewel (2002)
Yela River, Micronesia	Soil cores	Ingrowth cores	Bg, Ra, Sa—Fringe	952 (151)[3]	(460)[3]	Cormier (2003)
Yela River, Micronesia	Soil cores	Ingrowth cores	Bg, Ra, Sa—Interior	1191 (185)[3]	(91)[3]	Cormier (2003)
Yela River, Micronesia	Soil cores	Ingrowth cores	Bg, Ra, Sa—Riverine	1424 (183)[3]	(100)[3]	Cormier (2003)
Sapwalap River, Micronesia	Soil cores	Ingrowth cores	Bg, Ra, Sa—Fringe	1368 (292)[3]	(63)[3]	Cormier (2003)
Sapwalap River, Micronesia	Soil cores	Ingrowth cores	Bg, Ra, Sa—Interior	2640 (577)[3]	(119)[c]	Cormier (2003)
Sapwalap River, Micronesia	Soil cores	Ingrowth cores	Bg, Ra, Sa—Riverine	449 (170)[3]	(95)[3]	Cormier (2003)
Rookery Bay and Naples Bay, Florida (USA)	Soil cores	Ingrowth cores	Rm—Fringe	15,395[3]	(352)[3]	Giraldo (2005)
Rookery and Naples Bays Florida (USA)	Soil cores	Ingrowth cores	Rm, Ag, Lr—Basin	6704[3]	(314–378)[3]	Giraldo (2005)
Rookery and Naples Bays Florida (USA)	Soil cores	Ingrowth cores	Rm—Scrub	6185[3]	(307)[3]	Giraldo (2005)
Windstar, Florida (USA)		Ingrowth cores	Lr, Ag, Rm—Basin		(140–150)[3]	McKee and Faulkner (2000)
Henderson Creek, Florida (USA)		Ingrowth cores	Lr, Ag, Rm—Basin		(220–280)[3]	McKee and Faulkner (2000)
Roatan Island, Honduras		Ingrowth cores	Rm—Fringe		265 (199)[3]	Cahoon and others (2003)
Roatan Island, Honduras		Ingrowth cores	Rm, Ag—Basin		302 (171)[3]	Cahoon and others (2003)
Twin Cays, Belize		Ingrowth cores	Rm—Fringe		525 (197)[3]	McKee and others (2007)
Twin Cays, Belize		Ingrowth cores	Rm—Transition		394 (189)[3]	McKee and others (2007)
Twin Cays, Belize		Ingrowth cores	Rm—Scrub		82 (43)[3]	McKee and others (2007)
Belize, Florida, Panama, Australia, New Zealand		Mass balance	Rm, Am, Ag—Fringe		337[5]	Lovelock (2008)
Belize, Florida Panama, Australia, New Zealand		Mass balance	Rm, Am, Ag—Scrub		476[5]	Lovelock (2008)
Mayaguez, Puerto Rico	Soil cores		Rm[6]	5000 (4000)[4]		Golley and others (1962)
Lane Cove River, Australia	Soil cores		Am[6]	14,730–16,030[2]		Briggs (1977)
Majana, Cuba	Soil cores		Rm—Fringe	1710 (818)[3]		Fiala and Hernandez (1993)
Majana, Cuba	Soil cores		Ag—Basin	1080 (614)[3]		Fiala and Hernandez (1993)
Brisbane River, Australia	Soil cores		Am[6]	10,900–12,700[2]		Mackey (1993)
Hawkesbury River, Australia	Soil cores		Am[6]	4500–16,600[2]		Saintilan (1997a)
Hawkesbury River, Australia	Soil cores		Ac[6]	3500–10,600[2]		Saintilan (1997a)
Mary River, Australia	Soil cores		Am[6]	1500–6000[2]		Saintilan (1997b)
Mary River, Australia	Soil cores		Ac[6]	2500–8000[2]		Saintilan (1997b)
Western Australia	Soil cores		Am[6]	(1790)[2]		Alongi and others (2000)

Table 4. continued

Location	Sampling method: Biomass	Sampling method: Productivity	Dominant species: Forest type	Belowground biomass (g m^{-2}) Total (fine: ≤ 2 mm)	Belowground productivity (g m^{-2} y^{-1}) Total (fine: ≤ 2 mm)	Reference
Western Australia	Soil cores		Rs[6]	(5030)[2]		Alongi and others (2000)
Samana Bay, Dominican Republic	Soil cores		Rm, Lr[6]	6600 (790)[3]		Sherman and others (2003)
Gazi Bay, Kenya	Soil cores		Rmu[6]	2490[2]		Kairo and others (2008)
Gazi Bay, Kenya	Soil cores		Am[6]	3910[4]		Tamooh and others (2008)
Gazi Bay, Kenya	Soil cores		Rmu[6]	3580[4]		Tamooh and others (2008)
Gazi Bay, Kenya	Soil cores		Sa[6]	4840[4]		Tamooh and others (2008)
Panama, Pacific coast	Soil pit		Rb[6]	18,970[2]		Golley and others (1975)
Hatsaikhao, Thailand	Trench and root density model		Sa[6]	17,180 (10,370)[4]		Komiyama and others (1987)
Hatsaikhao, Thailand	Trench and root density model		Sa–Bg[6]	8480 (5630)[4]		Komiyama and others (1987)
Hatsaikhao, Thailand	Trench and root density model		Bg[6]	24,380 (1375)[4]		Komiyama and others (1987)
Hatsaikhao, Thailand	Trench and root density model		Ra[6]	50,950 (23,640)[4]		Komiyama and others (1987)
Thailand	Trench and root density model		Ct[6]	8750[4]		Komiyama and others (2000)
Indonesia	Trench		Sa[6]	3850[2]		Komiyama and others (1988)
Indonesia	Trench		Bg[6]	19,610[2]		Komiyama and others (1988)
Indonesia	Trench		Ra[6]	11,080[2]		Komiyama and others (1988)

Ag, Avicennia germinans; Am, Avicennia marina; Ac, Aegiceras corniculatum; Bg, Bruguiera gymnorrhiza; Ce, Conocarpus erectus; Ct, Ceriops tagal; Lr, Laguncularia racemosa; Ra, Rhizophora apiculata; Rb, Rhizophora brevistyla; Rm, Rhizophora mangle; Rs, Rhizophora stylosa; Sa, Sonneratia alba

[1]*Root production or biomass estimates for size classes <2 to <20 mm in diameter (to a depth of 90 cm).*

[2]*Root size class was not reported. Estimates for root biomass are reported for the top 30–60 cm of mangrove soils.*

[3]*Root production or biomass estimates for size classes <2 to <20 mm in diameter (to a depth of 30–50 cm).*

[4]*Root biomass estimates for size classes <40–50 mm in diameter (to a depth of 60 cm).*

[5]*Root production (not direct estimates) was calculated by using the mass balance approach of Raich and Nadelhoffer (1989).*

[6]*Forest type was not reported.*

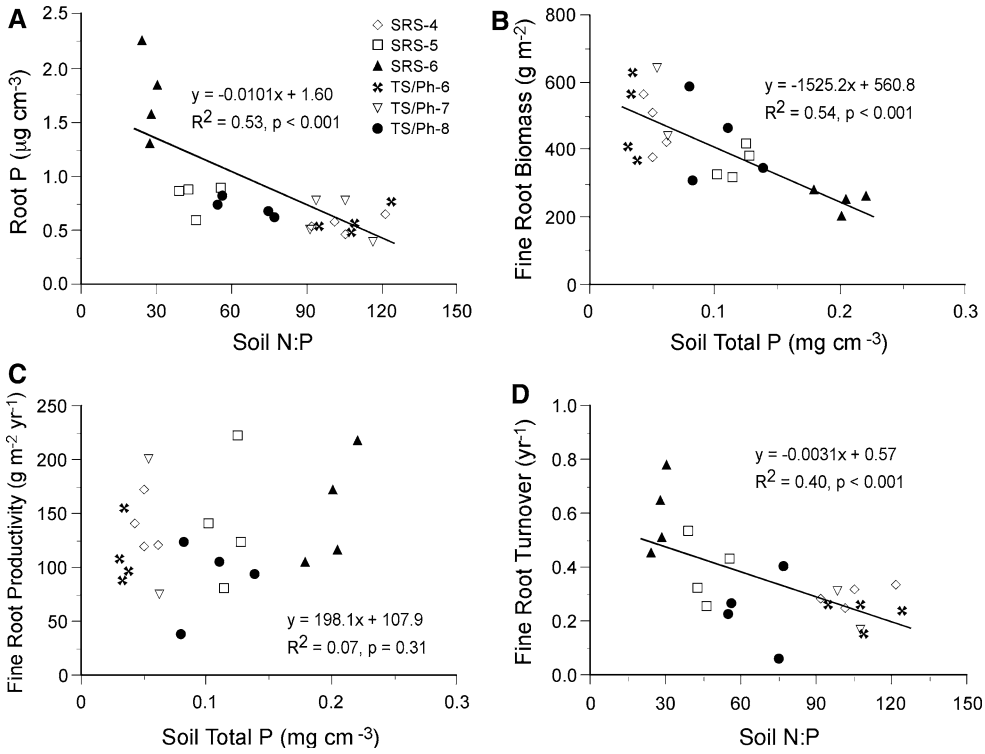

Figure 6. Variation in root P content with soil N:P ratios (**A**), shallow fine root biomass (**B**) and shallow fine root productivity (**C**) with soil P density, and fine root turnover (**D**) with soil N:P ratios in mangrove forests of the Florida Everglades. Standard parameters of the linear regression models are included.

Table 5. Comparison of Forest Structure (2001–2004), Aboveground Net Primary Productivity (ANPP:Litterfall + Wood Production; 2001–2004), Hydroperiod (2001–2006), and Soil Nutrients (to a depth of 45 cm; 2000–2002) in Everglades Mangrove Forests

Sites	Structure and productivity		Hydroperiod		Soil nutrients		
	Basal area (m^2 ha^{-1})	ANPP (g m^{-2} y^{-1})	Flooding duration (h y^{-1})	Frequency of inundation (# tides y^{-1})	Total N (mg cm^{-3})	Total P (mg cm^{-3})	Atomic N:P
SRS-4	21.1[1] (1.3)	1091[1] (70)	3965 (163)	217 (16)	2.3 (0.12)	0.05 (0.004)	105 (6.2)
SRS-5	23.8[1] (1.6)	973[1] (66)	4716 (168)	165 (7)	2.4 (0.10)	0.12 (0.006)	46 (3.5)
SRS-6	38.3[1] (1.8)	1398[1] (54)	5592 (433)	395 (70)	2.5 (0.30)	0.20 (0.009)	28 (1.3)
TS/Ph-6	–	322[2]	8566 (144)	12 (1)	1.7 (0.13)	0.03 (0.001)	109 (5.9)
TS/Ph-7	–	378[2]	8653 (150)	6 (2)	2.5 (0.19)	0.06 (0.004)	102 (5.8)
TS/Ph-8	1.2[1] (0.3)	333[1] (24)	3541 (50)	48 (10)	2.4 (0.10)	0.10 (0.014)	66 (5.9)

Values are the mean (± 1 SE).
[1]Data from Castañeda (2010).
[2]Data from Ewe and others (2006).
– Basal area was not calculated because mangrove tree heights < 1.5 m.

tile site in Shark River basin (SRS-6). Mangrove forests in TS/Ph-6, in the more inland region of Taylor basin, have the lowest forest productivity and are the most P-limited (N:P = 109; Table 5) compared to all other FCE sites (Castañeda 2010). It was expected that root biomass allocation at this site would be comparable to other Taylor River sites. Yet, TS/Ph-6 had the lowest total root biomass values compared to the other Taylor basin sites (TS/Ph-7 and TS/Ph-8). Mangroves in TS/Ph-6 are young forests that recently colonized this region and encroached inland approximately 1.5 km from Florida Bay during the past 50 years (Ross and others 2000). This encroachment transformed previous freshwater wetlands dominated by *C. jamaicense*- to brackish *R. mangle*-dominated community. This mangrove succession in the upper mangrove region of Taylor basin (TS/Ph-6) was

triggered by reductions in freshwater drainage into this region along with a gradual increase in sea level (Ross and others 2000). As a result, the mangrove peat overlying marl at TS/Ph-6 is less than 0.5 m depth, in contrast to peat depths greater than 1 m at TS/Ph-7 and TS/Ph-8 (Ewe and others 2006). Hence, it appears that the age of soil formation in this scrub forest growing in a P-limited environment may be an additional variable in comparing root biomass allocation among these sites.

Fine root dynamics show a more consistent trend that belowground biomass allocation will increase with limited P availability (Figure 6B). Mangroves across the two FCE basins have a significant negative relationship between fine root biomass and soil P density, doubling the amount of root allocation in sites with soil N:P ratios greater than 50. Along Shark River basin, fine root biomass decreased from upstream (SRS-4) to downstream (SRS-6) mangrove areas, in contrast to the pattern for aboveground biomass along this estuarine gradient (Chen and Twilley 1999a, b). Our findings are consistent with those reported along a soil fertility gradient in Micronesia mangrove forests (Cormier 2003) and with a long-term fertilization study in an *A. marina*-scrub mangrove in South Africa (Naidoo 2009). Similar patterns were observed in a Louisiana salt marsh, where belowground root biomass of *Spartina alterniflora* decreased by 40–60% in response to P and P–Fe additions relative to control plots (Darby and Turner 2008a).

Fine root productivity did not show any significant trend with increasing P density (Figure 6C). This finding is in contrast with observations in oceanic islands of Belize where P additions dramatically increased production rates of fine (2 to 8 times) and coarse roots in nutrient-limited scrub mangroves sites (McKee and others 2007). In addition, fine root production in tall fringe mangroves in the same sites was 5 times greater compared to the interior scrub forest under natural conditions (McKee and others 2007). Although fine root productivity was 1.2 times greater in the Shark River sites compared to Taylor River sites, rates do not change proportional to nutrient gradients. Yet, our results show a significant decrease in fine root turnover with increasing N:P ratios (Figure 6D), indicating the potential interaction with other soil processes such as decomposition. Because root productivity was similar across both FCE basins, we hypothesize that fine root longevity is more a function of decomposition rather than productivity. Indeed, previous root decomposition rates at the Shark River sites were not significantly different from each other, but were significantly higher compared to Taylor River sites, except for TS/Ph-7 (Poret and others 2007). This result indicates that soil P and hydroperiod may play a major role in root decomposition. Apparently, high P availability may promote greater annual fine root turnover rates, which correlate with greater belowground carbon allocation and fine root production.

The variation in root turnover among the two FCE basins suggests a strong coupling between P availability and carbon allocation to fine root production. There is evidence that fine root turnover increases with increasing nutrient availability in forest ecosystems (Aber and others 1985; Nadelhoffer and others 1985; Nadelhoffer 2000), and that nutrient availability controls the timing and duration of root growth (Nadelhoffer and others 1985). Similar results have been reported for mangrove forests in Micronesia, with the highest fine root

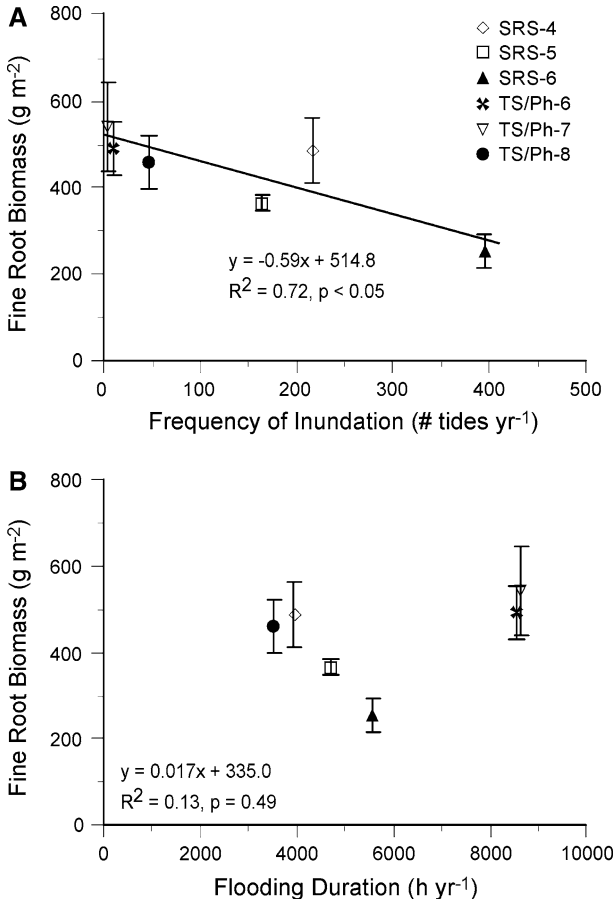

Figure 7. Relationship between shallow fine root biomass and frequency of inundation (**A**) and flooding duration (**B**) in mangrove forests of the Florida Everglades. Standard parameters of the linear regression models are included.

turnover in the most fertile (soil N:P < 15) site, and the lowest rates at the nutrient limiting sites with soil N:P greater than 45 (Cormier 2003). Thus, the greater longevity of fine roots in the lower fertility sites could reflect a physiological adaptation of mangroves to nutrient-poor environments (Nadelhoffer and others 1985).

Turnover rates of coarse roots in our mangrove sites are lower compared to those of fine roots, indicating that root longevity increases with larger size class distribution, as in the case of terrestrial forests (Table 3; Gill and Jackson 2000). Coarse roots function as storage and structural support (Eissenstat and Yanai 1997). In contrast, fine roots have lower longevity due to their greater metabolic activity (that is, respiration, high nutrient content) and higher energy requirements (Eissenstat and Yanai 1997; Norby and Jackson 2000). Turnover rates of fine roots (0.23–0.60 y^{-1}) observed in our study are higher than those reported for mangrove forests in Micronesia (Cormier 2003) and Florida (Giraldo 2005), and considerably lower than rates (range: 0.5–1.2 y^{-1}) measured in terrestrial forests (Burton and others 2000; Gill and Jackson 2000). Because our study is the first to report contemporary turnover and longevity rates for both small and coarse roots, it is difficult to extrapolate the contributing role of these size classes in total root productivity patterns in other mangrove regions. Nonetheless, this information will certainly help to determine the relative importance and interaction of biological and environmental variables when assessing soil carbon storage in neotropical mangrove forests.

Few studies have documented the effect of hydroperiod on changes in biomass allocation in mangroves (Krauss and others 2008). Our results show that shallow fine root biomass correlated negatively with frequency of inundation (Figure 7A), suggesting that higher tidal frequency at the Shark River sites decreases root biomass allocation due to less soil reducing conditions and higher supply of P with tidal input (Krauss and others 2006; Castañeda 2010). In fact, sulfide concentrations in the Taylor River sites were significantly higher (range: 0.86–1.6 mM) compared to Shark River sites (range: 0.01–0.14 mM; Mancera-Pineda and others 2009; Castañeda 2010), underscoring the regulatory effect of hydroperiod on root biomass allocation patterns (Krauss and others 2006). Sulfide concentrations have also been considered an important factor in determining carbon isotope discrimination between Shark River and Taylor River mangrove sites (Mancera-Pineda and others 2009). In addition, a previous study in our mangrove sites suggests that root:shoot ratios increase with increasing sulfide concentrations ($r^2 = 0.73$, $P < 0.05$; Castañeda 2010), and that most of the variation (38–49%) in forest structure (that is, basal area and wood biomass) and productivity (that is, wood and litterfall production) can be explained by changes in sulfide concentrations (Castañeda 2010). Accordingly, the interaction between hydroperiod and P availability explains the higher fine root biomass and lower fine root production of scrub mangroves in the Everglades and in other neotropical scrub forests, as a result of higher soil stress conditions (McKee 2001; McKee and others 2007).

Although fine root biomass was not correlated with flood duration in our study (Figure 7B), patterns in root biomass allocation can be associated with the competitive ability of mangrove species and their tolerance limit to flooding (Ball 1996; Cardona-Olarte and others 2006; Krauss and others 2006). The lower P fertility (N:P = 102 to 109; Table 5) and permanent flooding (~8600 h y^{-1}; Table 5) conditions in Taylor River basin (TS/Ph-6 and TS/Ph-7) compared to Shark River basin may explain why *R. mangle* is the dominant species (Koch 1997). Due to higher flooding tolerance, this species out-competes *L. racemosa* and *A. germinans,* which are generally restricted to flooding duration regimes less than 50% of the year (Koch 1996; Cardona-Olarte and others 2006). In contrast, moderate hydroperiods (range: 4000–5600 h y^{-1}; Table 5) in Shark River sites allow the co-existence of all three mangrove species, where *L. racemosa* is the dominant species in the more fertile site (SRS-6) and *R. mangle* dominates in the upstream P-limited sites (SRS-4 and SRS-5; Chen and Twilley 1998, 1999b; Krauss and others 2006). Thus, the lack of correlation between fine root biomass and flood duration is not surprising because the competitive ability of mangrove species and the morphological adaptations to cope with soil stress conditions determine species-specific biomass allocation and spatial distribution patterns (Krauss and others 2006).

Our findings provide evidence that stress conditions coupled to mangrove species site-specific life history traits are predictably related to habitat stability and productivity, and determine the degree of plasticity in belowground allocation (Schlichting 1986). Thus, we conclude that mangroves in nutrient-poor sites with long duration of flooding and restricted tidal influence produce roots with greater longevity as a mechanism to enhance nutrient conservation. In contrast, sites with higher nutrient content and tidal regimes produce short-

lived roots with high nutrient uptake, rapid growth rates, and higher turnover. These tradeoffs are indicative of the strong link between belowground processes and the phenotypic plasticity of mangrove roots in response to the interactions among gradients in nutrients, regulators, and hydroperiod across the FCE landscape. These belowground allocation patterns are ecologically significant given that fine root production and organic matter accumulation are the primary processes controlling soil formation in scrub mangrove forests [for example, Belize, McKee and others (2007)]. Thus, the feedback of environmental gradients on mangrove root dynamics in south Florida could have tremendous implications as to how soil formation and accretion serve as adaptations of mangroves to future impacts from sea-level rise throughout the Gulf of Mexico and the Caribbean region.

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