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Belowground Decomposition of Mangrove Roots in Florida Coastal Everglades

Nicole Poret[1], Robert R. Twilley[2,*], Victor H. Rivera-Monroy[2], and Carlos Coronado-Molina[3]

[1] *Department of Biology, University of Louisiana at Lafayette, P. O. Box 42451, Lafayette, Louisiana 70504*

[2] *Wetland Biogeochemistry Institute, Department of Oceanography and Coastal Sciences, Louisiana State University, Baton Rouge, Louisiana 70803*

[3] *South Florida Water Management District, 3301 Gun Club Road, West Palm Beach, Florida 33406*

ABSTRACT: Mangrove root decomposition rates were measured by distributing mesh bags containing fine root material across six sites with different soil fertility and hydroperiod to compare ambient differences to substrate quality. Roots from a site with lower soil phosphorus concentration were used as a reference and compared to ambient roots at five other sites with increased phosphorus concentration. Four mesh bags of each root type (ambient versus reference), separated into four 10-cm replicate intervals, were buried up to 42 cm depth at each site and incubated for 250 d (initiation in May 2004). Mass loss of ambient mangrove roots was significant at all study sites and ranged from 17% to 54%; there was no significant difference with depth at any one site. Reference decomposition constants (−k) ranged from 0.0012 to 0.0018 d^{-1} among Taylor Slough sites compared to 0.0023–0.0028 d^{-1} among Shark River sites, indicating slower decomposition rates associated with lower soil phosphorous and longer flood duration. Reference roots had similar decomposition rates as ambient roots in four of the six sites, and there were no significant correlations between indices of root substrate quality and decomposition rates. Among these distinct landscape gradients of south Florida mangroves, soil environmental conditions have a greater effect on belowground root decomposition than root substrate quality.

Introduction

Several processes control soil formation in mangrove wetlands including aboveground and belowground organic matter production; organic matter export, decomposition, and burial; and allochthonous inorganic matter input (Chen and Twilley 1999a). Most mangrove decomposition studies have focused on aboveground components of litter fall (e.g., Twilley et al. 1986, 1997; Robertson 1988), but few studies have investigated belowground decomposition (e.g., Van der Valk and Attiwill 1984; Feller et al. 1999, 2002; McKee and Faulkner 2000; Middleton and McKee 2001). A large part of sedimentary organic matter in mangroves is derived from root organic matter (Alongi et al. 2001) and often roots can be the principle source of organic matter in many forest systems in the deeper soil layers (Ludovici et al. 2002). A cohort model (NUMAN) has shown that root production and the concentration of refractory organic matter in dead roots are important in controlling organic matter accumulation in mangrove soils (Chen and Twilley 1999a). Deposition and slow degradation of mangrove roots may contribute more to organic matter accumulation and vertical building of mangrove islands in Belize than total litter fall (Middleton and McKee 2001). In carbonate settings, like those of south Florida, belowground peat production is the primary control of sediment accretion (Lynch et al. 1989; Parkinson et al. 1994).

The objective of our study was to discern whether there are site differences in root decomposition, and if those differences follow patterns related to environmental conditions or substrate quality of root material described above. We hypothesized that: decomposition rates of mangrove roots will decrease with increasing depth at all study sites, decomposition rates will decrease at sites with lower soil fertility (measured as soil total phosphorus [P] concentration) and increased hydroperiod (duration), and differences in root substrate quality will have an effect on decomposition rates such that lower nitrogen (N) content and higher lignin will result in lower decay coefficients.

Materials and Methods

The southeast region of Everglades National Park, Florida, provides sites to test these hypotheses as part of the Florida Coastal Everglades Long Term Ecological Research (FCE-LTER) program (Fig. 1). FCE-LTER mangrove sites are located in an oligotrophic, carbonate setting where forest productivity differs along environmental gradients related to

*Corresponding author; tele: 225/578-6431; fax: 225/578-6423; e-mail: rtwilley@lsu.edu

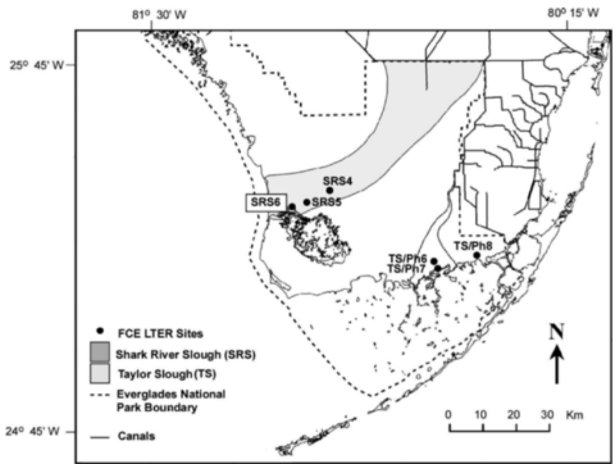

Fig. 1. Everglades National Park. SRS4, SRS5, and SRS6 indicate the sampling sites along the Shark River Slough. TS/Ph6 and TS/Ph7 indicate the sampling sites along the Taylor Slough and TS/Ph8 indicates the sampling site in Joe Bay.

hydroperiod and soil fertility (Koch 1996; Chen and Twilley 1999b; Ewe et al. 2006). Soil fertility, measured as P availability, decreases inland from the coast and is thought to be a major limiting factor to mangrove productivity in southwest and southeast Florida (Table 1; Chen and Twilley 1999b). Yet it has not been established if root decomposition follows these same patterns across these gradients in soil fertility.

Three mangrove sites have been established each along Shark River and Taylor Slough in FCE-LTER dominated by four mangroves species in the six sites: *Rhizophora mangle* L., *Avicennia germinans* (L.) Stearn, *Laguncularia racemosa* (L.) Gaertn., and *Conocarpus erectus* L (Chen and Twilley 1999b; Coronado-Molina 2004). Mangroves at the mouth of Shark River are considered riverine mangroves and those along the Taylor Slough sites are characterized as scrub mangrove forest types (Ewe et al. 2006). The Shark River sites (SRS4, SRS5, and SRS6) are influenced by a strong tidal regime and exhibit daily inundation. The Taylor Slough sites are located inland from Florida Bay (TS/Ph6 and TS/Ph7) and on the edge of Joe Bay (TS/Ph8). Soil fertility, as defined by soil P, is low at TS/Ph6 and TS/Ph7 compared to the other four sites, with SRS6 having the highest P concentration (84.2 g m^{-2}; Chen and Twilley 1999b; Table 1).

Root decomposition rates were compared among sites along these two FCE transects using the mesh bag approach (Hamond et al. 1999) by monitoring changes in the amount of root mass after 250 d of field incubation. Mesh bags of 10 × 40 cm dimensions and 1-mm^2 mesh were divided into four 10-cm sections, which were considered the experimental units. Each 10-cm section held 10.0 g of fresh root material with an equal mixture of three size classes: 1–4, 4–8, and 8–12 mm. Live, belowground roots were excavated by coring at each of the six treatment sites (SRS4, SRS5, SRS6, TS/Ph6, TS/Ph7, TS/Ph8), air dried to a constant mass, placed in bags, and buried. The use of ambient roots at each site measures the effect of plant substrate quality combined with environmental conditions on root decomposition (called ambient). To remove the effects of substrate quality, and determine the effect of environmental conditions (called reference) on decomposition, roots from TS/Ph6 (i.e., *R. mangle* roots) were buried at all six sites (Fig. 1). The bags were buried in May 2004 and retrieved after 250 d in the field. Seven bags were buried at each site, three with ambient roots (except for TS/Ph8 where four were buried) and four with roots from TS/Ph6. Two control bags with ambient roots from each site were inserted in the soil and removed one minute later to estimate initial mass and substrate quality indices.

Root material was cleaned with deionized water and oven dried at 60°C to a constant weight to determine dry mass. Live roots were considered those that were growing through the mesh and were white in color; these roots were not included in analyses. The mesh deterred the growth of any roots larger than 1 or 2 mm. Carbon (C) and N (mg g^{-1}) were determined on initial and final root material

TABLE 1. Porewater and soil characteristics of the six mangrove sites (SRS4, SRS5, SRS6, TS/Ph6, TS/Ph7, TS/Ph8) in the Florida Everglades National Park. (Modified from Chen and Twilley 1999b; Twilley and Rivera-Monroy unpublished data.)

	TS/Ph6	TS/Ph7	TS/Ph8	SRS4	SRS5	SRS6
Porewater characteristics						
Redox (45 cm)	−80.57	−81.83	−100.87	64.13	−16.1	39.19
Salinity (g kg^{-1})	16.79	20.00	20.24	4.56	20.78	26.99
pH	7.67	7.82	7.84	7.21	7.80	7.78
Soil characteristics						
Bulk density (g cm^{-3})	0.55	0.15	0.21	0.12	0.18	0.21
Total nitrogen (g m^{-2}) (to 40 cm depth)	586.7	1075.2	1104.3	967.4	1014.9	1153.8
Total phosphorous (g m^{-2}) (to 40 cm depth)	13.8	25.0	45.2	21.8	50.7	93.2
N:P ratios	42.6	42.1	24.4	44.3	20.0	12.4
C:N ratios	34.9	19.9	21.0	18.1	22.4	16.2

TABLE 2. Statistical results for each component of mass loss including depth, reference roots, and ambient roots (decay coefficient, k_d). The last row shows a comparison of k_d for reference roots versus ambient roots within each site using Least Squares Means Contrast. Decrease the number of decimal places from <0.0001 to <0.001.

Source	df	SS	F	p
Depth	3	0.0441	0.11	0.9547
Treatment (site)	11	15.32	10.33	<0.001
Depth × treatment	33	2.30	0.52	0.9858
Treatment: Reference roots	5	0.00	38.26	<0.001
Treatment: Ambient roots	5	0.00	5.18	0.004
Reference roots versus ambient roots	34	0.000003	2.94	0.02

using a NC 2500 Elemental Analyzer (CE Elantech, Lakewood, New Jersey). Lignin analysis on selected control samples used the Van Soest Acid Detergent Fiber and Lignin Procedure (Soil and Forage Analysis Laboratory at the University of Wisconsin), which reports percent dry mass of root material that is lignin (Van Soest 1963).

Mass loss was tested with depth along the vertical gradient and among treatment sites using two-way analysis of variance (ANOVA). Mass losses and decomposition rate values at the treatment sites were analyzed using one-way ANOVA followed by Student's *t*-test or Least Squares Contrast test (SAS JMP 2004). Decomposition rate was determined by the relationship between the natural logarithm of dry mass remaining and the sampling period (Twilley et al. 1997). Nutrient data (indices) were analyzed using one-way ANOVA followed by Student's *t*-test. All data met the assumptions of normality and homoscedasticity and no transformations were necessary. Relationships between initial nutrient data and decomposition rate values were examined by regression analysis (SAS JMP 2004).

Results

There was no significant difference in mass loss with depth ($p = 0.96$) or with the interaction of depth and treatments ($p = 0.99$; Table 2), so depth was removed from further analyses. Decomposition rates of ambient roots were significantly different among the FCE-LTER sites ($p < 0.001$; Fig. 2 and Table 2). The highest losses among the ambient roots occurred along the Shark River transect in SRS5 (50% loss), SRS4 (45% loss), and SRS6 (43% loss). The lowest losses occurred along the Taylor Slough transect in TS/Ph7 (35% loss), TS/Ph8 (31% loss), and TS/Ph6 (25% loss). Decay rates of ambient roots in Shark River estuary were also similar among the three sites from 0.0023 to 0.0028 d^{-1}. The high rate in Taylor Slough (TS/Ph7) was significantly different from the high rate in Shark River (SRS5), but similar to the lower rates

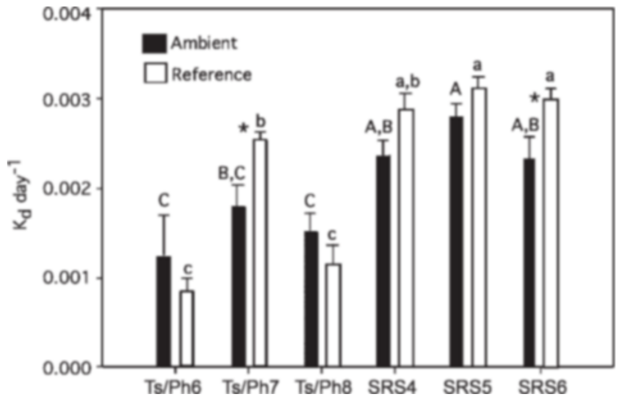

Fig. 2. Decay constants for both ambient (solid bars) and reference (open bars) roots compared across sites (capital letters are for ambient, small letters for reference) and within each site (asterisk).

in Shark River (SRS4 and SRS6). The lower rates in Taylor Slough (TS/Ph6 and TS/Ph8) were significantly lower than all the sites in Shark River (Fig. 2). Ambient decay rates were lower among Taylor Slough sites than in the Shark River sites, with the exception of TS/Ph7.

The experimental design assumed that decomposition rates between reference and ambient roots at TS/Ph6 would be similar and lower compared to the other five sites. At each of the other sites, the differences in decomposition of ambient and reference roots would detect the relative influence of environment versus substrate factors on root decomposition, since root substrate is held constant using reference roots at each site. Decay rates of reference and ambient roots were similar at TS/Ph6 (0.00085 and 0.0012 d^{-1}) and there were significant differences in decay rates of reference roots at the other five sites compared to TS/Ph6 (Fig. 2). Root decomposition rates for TS/Ph6 and TS/Ph8 were similar at 0.001 d^{-1} and significantly lower than decomposition of reference roots at TS/Ph7 (0.0025 d^{-1}). Reference roots had similar decomposition rates in all three Shark River sites (ranging from 0.0029 to 0.0031 d^{-1}), and decay at SRS4 was similar to TS/Ph7. In four of the six sites, the reference and ambient roots were not significantly different in decay rates (Fig. 2). The two exceptions were reference and ambient roots at TS/Ph7 and SRS6, where in both cases the reference roots had higher decomposition rates than ambient roots. Based on reference roots, there is significant difference in decomposition at TS/Ph7 compared to TS/Ph6 and TS/Ph8; in Shark River, sites near the mouth of the estuary have higher rates than in the upper estuary.

The initial substrate quality characteristics of roots show significant differences in root N (mg

TABLE 3. Statistical results for initial nitrogen content (mg g^{-1}), initial C:N ratio, and initial lignin (% dry mass) in roots from the six sites. Means (± 1 SE) followed by a similar letter in each row are not significantly different ($p > 0.05$).

					Mean					
Source	df	SS	F	p	TS/Ph6	TS/Ph7	TS/Ph8	SRS4	SRS5	SRS6
Initial N	5	5.980	17.40	<0.001	3.24^{b} (0.09)	2.91^{c} (0.09)	$3.03^{b,c}$ (0.09)	2.96^{c} (0.09)	2.54^{d} (0.09)	3.70^{a} (0.09)
Initial C:N	5	16314	37.37	<0.001	104^{c} (3.3)	120^{b} (3.3)	117^{b} (3.3)	147^{a} (3.3)	148^{a} (3.3)	103^{c} (3.3)
Initial lignin	5	134.9	6.197	0.002	18.5^{c} (1.04)	$22.9^{a,b}$ (1.04)	$23.4^{a,b}$ (1.04)	24.5^{a} (1.04)	$20.5^{b,c}$ (1.04)	25.5^{a} (1.04)
Lignin:N					5.7	7.9	7.7	8.3	8.1	6.9

g^{-1}), C:N ratios, and lignin among the six sites (Table 3). The high N content of SRS6 roots differed significantly from all other sites; the low N content in SRS5 roots also differed significantly from all other sites ($p < 0.05$). The high C:N ratios of SRS4 (147) and SRS5 (148) differ significantly from the other four sites. The lowest C:N ratios were from sites TS/Ph6 (104) and SRS6 (103); these ratios were similar and differed significantly from the other four sites. Root lignin content from TS/Ph6 (18.5%) was significantly lower than the other sites. The values of root lignin content from SRS6 (25.5%) and SRS4 (24.5%) were significantly higher than the other sites. Regressions of decomposition constants, k_d, as a function of N content, C:N ratios, lignin, lignin:N ratios, and change in N content showed no clear relationships for any of the indices related to k_d (data not shown). The strongest relationships were lignin content and lignin:N ratios, yet they were opposite of what was expected based on the hypotheses described above.

Discussion

Our study found no difference in mass loss with depth from 2 to 42 cm below the soil surface. Although differences in root decomposition with depth (to 20 and 30 cm) have been found in salt marshes (Hackney and De La Cruz 1980; Buth 1987), of the few mangrove root decomposition studies only Middleton and McKee (2001) tested depth and they found no difference in rates to depth of 30 cm. There was significant loss of original mass in bags from all the study sites with decomposition rates varying threefold between TS/Ph6 and SRS5 for both reference and ambient roots. The Shark River sites consistently had significantly higher decomposition rates than TS/Ph6 and TS/Ph8. Roots from TS/Ph6 had one of the highest N contents, the lowest C:N ratio, and initial lignin content, yet had the lowest rates of mass loss for both ambient and reference roots. When the TS/Ph6 roots were buried in SRS4 and SRS5, whose own roots had low N content, high C:N ratios, and high lignin content, rates of decomposition were higher and similar to ambient roots. Decay rates of reference roots compared across the six sites indicate a substantial effect of environmental conditions on the patterns of root decomposition.

Patterns in mangrove leaf decomposition have been related to initial substrate quality such that high N and P content, low C:N ratio, and low lignin content result in higher decomposition rates (Twilley et al. 1986; Robertson 1988), as has been found for other wetland ecosystems (Brinson et al. 1981; Mellilo et al. 1982; Aber et al. 1990). Apparently root decomposition may not follow such a predictable pattern since C:N ratios and lignin content do not correlate to root degradation rates (McClaugherty et al. 1982, 1984; Richert et al. 2000; Scheffer and Aerts 2000) as was found in our study. Instead, indices of total nonstructural carbohydrate and lignin:N ratios correlate more accurately with patterns of root decomposition (McClaugherty et al. 1982, 1984). Yet lignin:N ratios showed no relationship to spatial patterns in our study of mangrove roots.

The two main differentiating environmental factors between Shark River and Taylor River sites are soil fertility and hydroperiod (Table 1). Cotton strip assays found that belowground decomposition increased with increasing nutrient availability (Feller et al. 1999), and P fertilization caused a dramatic increase in belowground decomposition (Feller et al. 2002). Total P in the soil varies greatly among our six study sites from 12.9 g m^{-2} in TS/Ph6 to 84.2 g m^{-2} in SRS6 (Table 1), yet there was no general model that correlated ambient root decomposition to soil P fertility in our study. The three SRS sites increase in soil P from SRS4 (21.6 g m^{-2}) to SRS6 (84.2 g m^{-2}), yet the decomposition rates of ambient roots at these three sites were not significantly different from one another. Decay rates for reference roots are significantly higher in SRS6 and SRS5 compared to SRS4. Soil total P in TS/Ph8 is comparable to concentrations in SRS5, but both ambient and reference roots at TS/Ph8 had significantly lower decomposition rates than SRS5, by a factor of more than 2. Roots degraded faster in TS/Ph7 than TS/Ph8, although TS/Ph7 has half the soil P content and nearly double the N:P ratio.

One additional factor could be the differential effects of hydroperiod among these sites (Krauss et al. 2006). The Shark River sites are influenced by semidiurnal tides, whereas the Taylor Slough sites are seasonally inundated, with flooding during the rainy season (from May through October). More frequent tidal inundation, which prevents hypersaline conditions (Wolanski and Gardner 1981; Twilley and Chen 1998), has been correlated with higher rates of mangrove leaf litter decomposition (Twilley et al. 1986; Robertson 1988; Mackey and Smail 1996; Woitchik et al. 1997; Feller et al. 2002). Tidal processes also flush out toxins such as sulfides and tannins that may accumulate in soil and slow decomposition rates (Howarth and Hobbie 1982; Robertson 1988). Microbial population densities and respiration also increase during rewetting in habitats experiencing wet-dry cycles (Sorensen 1974; Brinson et al. 1981). These conditions best fit the Shark River sites, which have more positive redox values and a wet-dry regime in contrast to the more permanently flooded sites in Taylor Slough.

Studies on production, turnover, and decomposition of mangrove roots have lagged far behind similar studies on aboveground components of mangrove wetlands, limiting our understanding of how root dynamics contribute to nutrient cycling and soil accretion in mangrove ecosystems. The range of values for this study (0.00085 and 0.00031 d^{-1}) is within the lowest and highest recorded for mangroves (0.0007 and 0.0039 d^{-1}respectively). Several studies have found that decay of belowground material is slower than leaf litter (Hackney and de la Cruz 1980; Van der Valk and Attiwill 1984; McKee and Faulkner 2000; Middleton and McKee 2001). Others have found that mangrove roots are a major portion of soil organic matter (Alongi et al. 2004) and are critical to accretion rates and peat formation (Cahoon and Lynch 1997; Middleton and McKee 2001). Model simulations suggest that root production and dead root refractory components are critical to soil accumulation (Chen and Twilley 1999a). Our results point to greater control of belowground processes by the particular environmental setting of each site rather than the chemical components of the roots. This suggests that differences in hydroperiod, soil fertility, tidal regime, topography, and other microscale changes in sites could have a greater effect on decomposition than the plant material itself in the short term dynamics in which this study was conducted.

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