Restoration of Biogeochemical Function in Mangrove Forests

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Abstract

Forest structure of mangrove restoration sites (6 and 14 years old) at two locations (Henderson Creek [HC] and Windstar [WS]) in southwest Florida differed from that of mixed-basin forests (>50 years old) with which they were once contiguous. However, the younger site (HC) was typical of natural, developing forests, whereas the older site (WS) was less well developed with low structural complexity. More stressful physicochemical conditions resulting from incomplete tidal flushing (elevated salinity) and variable topography (waterlogging) apparently affected plant survival and growth at the WS restoration site. Lower leaf fall and root production rates at the WS restoration site, compared with that at HC were partly attributable to differences in hydroedaphic conditions and structural development. However, leaf and root inputs at each restoration site were not significantly different from that in reference forests within the same physiographic setting. Macrofaunal consumption of tethered leaves also did not differ with site history, but was dramatically higher at HC compared with WS, reflecting local variation in leaf litter processing rates, primarily by snails (*Melampus coffeus*). Degradation of leaves and roots in mesh bags was slow overall at restoration sites, however, particularly at WS where aerobic decomposition may have been more limited. These findings indicate that local or regional factors such as salinity regime act together with site history to control primary production and turnover rates of organic matter in restoration sites. Species differences in senescent leaf nitrogen content and degradation rates further suggest that restoration sites dominated by *Laguncularia racemosa* and *Rhizophora mangle* should exhibit slower recycling of nutrients compared with natural basin forests where *Avicennia germinans* is more abundant. Structural development and biogeochemical functioning of restored mangrove forests thus depend on a number of factors, but site-specific as well as regional or local differences in hydrology and concomitant factors such as salinity and soil waterlogging will have a strong influence over the outcome of restoration projects.

Key words: *Avicennia*, decomposition, detritivore, *Laguncularia*, leaf fall, litter dynamics, nitrogen recycling, root production, restoration, *Rhizophora*.

Introduction

An important type of tropical forest is the mangrove swamp, an intertidal plant community dominated by salt- and flood-tolerant trees and shrubs. Mangroves are widely valued for their ecological uniqueness and linkages to estuarine food webs in subtropical and tropical coastal regions (Twilley 1988; Baran & Hambrey 1998; Primavera 1998). Many mangrove areas have been destroyed or altered as a consequence of human activities or natural disturbance, however, and restoration efforts are being undertaken worldwide (Field 1996, 1998). Although conditions that allow replacement of dominant plant and animal species in a mangrove setting can be created and maintained, a constructed or restored system may or may not function like a natural system. Evaluation of function in a restored mangrove forest is often more difficult and time-consuming than assessment of its structural qualities. Also, the time available for restoration assessment is usually shorter than the time required for function to be restored in created wetlands (Simenstad & Thom 1996). Mangroves in particular may require many years to achieve structural maturity (Twilley et al. 1998). Evaluations, if they are conducted at all, have consequently focused on measurements of survival or structure (e.g., see Field 1996). However, the assumption that recreation of structure automatically leads to restoration of function may be false (Kusler & Kentula 1989).

The production of organic matter, establishment of food webs and movement of carbon and energy, and recycling of nutrients are all important functional aspects of mangrove ecosystems. Before a mangrove wetland can be considered to be "restored," it must not only resemble a "natural" forest in structure, but it must provide similar functions. This expectation does not mean

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that the restored system must function exactly as it did before alteration. In fact, replacement of a mangrove forest with an exact facsimile that functions in all respects like the original may be an unrealistic goal in some situations, e.g., where conditions under which the original forest developed no longer exist.

The overall objective of this study was to compare structural development and biogeochemical functioning of restored and natural mangrove forests to identify which factors are important in determining the outcome of restoration projects. Specifically, two restoration sites differing in age and site conditions were examined and compared with two mature forests within the same physiographic setting. The study was conducted on the southwest coast of Florida where mangrove forests are well developed but also where large areas have been lost to development (Patterson 1986). Although this research was site-specific, the results provide some valuable insights into how restored mangrove forests function. Such information can be used to establish procedures to evaluate other mangrove ecosystems and to set achievable endpoints for future restoration or rehabilitation projects.

Materials and Methods

Study Sites

Two locations in Southwest Florida were used. One mangrove area was located in south Naples, Florida along Naples Bay and immediately adjacent to the Windstar Golf Course and Multi-Family Community (30°23.326′ N, 91°8.645′ W). Dredge spoil from Naples Bay was deposited in mangrove forests along the eastern shore of the Bay, causing direct destruction of vegetation and alteration of natural hydrology. In 1982, the vegetation on three spoil mounds was cleared and chipped or burned. The sites were scraped down to an elevation of +0.45 m National Geodetic Vertical Datum (NGVD) to allow flooding at mean high tide. After the elevation was established, the sites were hand-planted with *Rhizophora mangle* L. (red mangrove) propagules in August 1982. The continued presence of a berm restricted tidal flushing of these sites, however, and variable topography yielded areas that were constantly flooded. The most accessible of the three restored areas at Windstar (WS), which was 1.3 ha in area, was used in this study. A reference site was established in the natural mangrove forest adjacent to the restoration site. The age of this forest was estimated to be in excess of 50 years, since it was not destroyed by Hurricane Donna in 1960 and is present in aerial photographs from the 1940s (Proffitt & Devlin 1991). The natural forest experiences seasonal flooding, similar to other basin forests in the region (Twilley et al. 1986).

The second study location was situated within the Rookery Bay National Estuarine Research Reserve (RBNERR) along Henderson Creek (HC) (30°23.326′ N, 91°8.645′ W). The site was originally altered by excavation of a 0.8 ha pond and deposition of the dredge material onto the surrounding area to raise elevations above mean high water. The site was rehabilitated by Collier County in two phases, each completed in December 1990 (Phase I) and January 1992 (Phase II). Phase I (~1 ha) of the restoration involved removal of exotic vegetation, reestablishment of the original elevations (+0.43 m NGVD) and excavation of flushing cuts through the area (to facilitate water movement), and planting of *R. mangle* seedlings. Phase II involved leveling of an additional 1.3 ha in 1992, and portions were planted with *R. mangle*, *Laguncularia racemosa* (L.) Gaertn. f. (white mangrove), and *Avicennia germinans* (L.) Stearn. (black mangrove) seedlings. Only the Phase I area was used in this study. The natural, reference forest, which was located adjacent to the restoration site, was comprised of red, black, and white mangroves. Historical, aerial photography indicated that this natural forest was once contiguous with the mitigation area and had been undisturbed for at least 60 years (T. Hopkins 1996, personal communication).

Experimental Design and Methods

The experimental design was a 2 × 2 factorial, with study location (HC and WS) and site history (restored [R] and natural [N]) as the main factors. Nine permanent sampling stations were established in each of the four forest sites in a stratified, random design to account for gradients in hydrology. All sampling, with the exception of forest structure characterization, was conducted at these nine permanent stations. Sampling was initiated in November 1996 and concluded in December 1997. Sampling frequency depended on the variable measured and is detailed below.

Forest Structure. Forest structure in the restored and natural sites at HC and WS locations was assessed once at the beginning of the study using the Point Centered Quarter Method (Cintrón & Novelli 1984). All stems ⩾2 m in height and ⩾2 cm in diameter were counted. Briefly, 21 points were used in each site to determine species composition, basal area, tree density and height, and species frequency. Structural indices were calculated according to Poole et al. (1977) and Cintrón and Novelli (1984).

Soil Condition. Physicochemical conditions were determined seasonally (November 1996, March 1997, July 1997, and November 1997) by measuring the following variables: soil redox potential (Eh), extractable nitrogen (NH_4^+), and extractable phosphorus (PO_4^{3-}); and porewater salinity, pH, sulfide, NH_4^+, and PO_4^{3-}. Soil Eh (15 cm

depth) was measured in situ with platinum electrodes (McKee et al. 1988). Porewater was collected with a sipper device and analyzed for salinity (refractometer, Cole-Parmer, Chicago, IL, USA), pH (Digi-Sense pH Meter), and concentration of total sulfides (Lazar Model IS-146 sulfide electrode, Lazar Research Laboratories, Los Angeles, CA) (McKee et al. 1988) and NH_4^+ and PO_4^{3-} (Parsons et al. 1984). Soil cores were collected once (November 1996) with a piston-type corer and analyzed for bulk density and organic matter content according to standard techniques. Ash content of soil was determined after combustion in a muffle furnace for 6 hr at 500°C, and organic matter content was calculated by subtraction.

Extractable NH_4^+ and PO_4^{3-} and total soil nitrogen and phosphorus were also measured seasonally using additional soil cores collected at each sample station. Soil samples were weighed in the field with a pocket balance and immediately transferred to centrifuge tubes containing either 2 M KCl or 0.5 M $NaHCO_3$ and refrigerated for determination of extractable NH_4^+ and PO_4^{3-}, respectively (Schoenau & Karamanos 1993; Mulvaney 1996). Soil extractions were completed in the laboratory by shaking for 1 hr, followed by centrifugation and assay of soil extracts according to Parsons et al. (Methods 1.4 and 1.6; 1984). The remainder of the soil sample was frozen and later oven-dried (65°C) for determination of water content and total carbon, nitrogen, and phosphorus (McGill & Figueiredo 1993; O'Halloran 1993).

Samples of green and senescent leaves for nutrient analysis were collected seasonally from all three species at each site ($n = 5$), frozen, and later freeze-dried in a Labconco (Kansas City, MO, USA) Freezedrier (LyphLock 6). Determination of carbon and nitrogen was conducted by direct combustion in a Perkin-Elmer CHN Analyzer (#2400 Series 2). Analytical procedures for plant tissues and soil were checked by concurrent analysis of standards of known composition (e.g., NIST Standard Reference Material #1575, Pine needles and #2704, Buffalo River sediment).

Leaf Fall and Root Production. Litter traps (0.25 m^2) were established at a 1 m height at each sampling station ($n = 9$ per site). Litter was removed at monthly intervals from all traps in a single day, separated into components, dried at 65°C, and weighed. Root production was determined with the implanted soil mass technique (Gallagher et al. 1984). Soil cores (7 cm diameter × 30 cm depth) were removed adjacent to each litter trap with a coring device, and the resultant holes filled with root-free sediment collected from mud flats at each site. The implant sites were marked with thin PVC caps (inside diameter 7 cm) and were recored after 12 months. In-grown root material was washed over a sieve (1 mm^2) to remove soil, dried, weighed, and analyzed for carbon content (see above description).

Leaf and Root Degradation in Litter Bags. Degradation of mangrove leaves and roots was measured using mesh bags (10 × 10 cm) constructed of 1-mm-mesh hardware cloth. Senescent leaves of the three species were collected from trees near each sampling station. Live roots of the three species were excavated from each study site, but well away from the sample stations to avoid disturbance to the area. The collected material was air-dried for several days at the field sites, and a known amount was enclosed in labeled litter bags. Leaf and root water content was measured on separate oven-dried samples and used to convert initial, air-dry mass to oven-dry mass. The leaf bags were laid on the soil surface, and replicate sets ($n = 9$ per species per site) were retrieved at 0, 1, 3, 6, 9, and 12 months. Root bags ($n = 9$ per species per site) were buried vertically and retrieved at 0, 3, 6, 9, and 12 months. After retrieval, the material was removed from bags, and gently rinsed over a sieve (mesh = 0.5 mm) with deionized water. Visible animals were removed, and the remaining material was dried (at 65°C) and weighed to determine mass loss. Degradation rate was the slope (k) of the linear relationship between the natural logarithm of the proportional mass remaining and the sampling interval for each species and site combination.

Leaf Consumption by Macrofauna. Consumption of mangrove leaves by macro-invertebrates (e.g., crabs and snails) at the study sites was assessed at 4-month intervals with tethered, unbagged leaves. Senescent, undamaged leaves of the three mangrove species were collected from each of the study sites. Triplicate sets of leaves were labeled, measured with a leaf area meter, tethered with fine monofilament, and placed on the ground at each sampling station (3 species × 3 leaves × 9 stations × 4 sites × 4 sample dates = 1,296 leaves). The total leaf mass deployed at each station (~2 g/m^2) was similar to that deposited daily in these forests. The leaves were retrieved after 3–4 weeks and remeasured to determine the leaf area removed.

Statistical Analyses. A fixed effects model was used to analyze the results, and statistical tests were performed with JMP® for the Macintosh® (SAS JMP, 1998). The data were analyzed by a two-way analysis of variance (ANOVA), where location and site history were grouping factors. Seasonal data were analyzed with a repeated measures ANOVA, and differences among means were tested with 1 df contrasts. Any data that did not meet the variance homogeneity or normality assumptions for ANOVA were transformed and retested prior to analysis. However, untransformed means ± 1 standard error (SE) are reported. A significance level of 5% was used in all cases.

Results

Forest Structure

The two reference forest sites were similar in species composition and typical of mixed-basin forests comprised of three species: *R. mangle*, *A. germinans*, and *L. racemosa* (Table 1). Stem diameter ranged from 2.0 to 41 cm, and some of the largest trees (*A. germinans*) occurred at HCN. Average tree density, average stand height, and total basal area were not significantly different between WSN and HCN (Table 2). Both reference forests were dominated by *R. mangle*, with *A. germinans* and *L. racemosa* occurring as subdominants (Table 1).

The restoration sites at WS and HC were vegetated with dense stands of mangroves (Table 1). Despite being planted initially with *R. mangle*, both sites were colonized naturally by *L. racemosa* and *A. germinans.* In general, the restoration forests were immature with a lower basal area and stand height and higher tree density compared with the reference forests (Table 2). The relative importance of *A. germinans* was low at both restoration sites and differed from that in the reference forests. Although *A. germinans* occurred at HCR, stems were rare and smaller than the minimum stature for inclusion. The WSR site contained some unvegetated or sparsely vegetated areas (stunted *A. germinans*).

Soil Condition

The restored soils at HC and WS, which reflected the presence of dredge spoil, were characterized as a very coarse to coarse mineral soil with deposits of limestone concretions, fossil shells, and sand present throughout the soil profile down to a depth of ~0.5 m. A thin organic layer (1–8 cm deep) occurred at the soil surface and was comprised of mangrove roots and aboveground litter. In contrast, the soil substrate at the reference forests was organic, unstratified, and did not contain limestone or shell fragments that would indicate deposition of dredge material. In comparison with natural soils, the restored soils, averaged over location, had a higher bulk density (0.68 ± 0.05 vs. 0.20 ± 0.01 g/cm^3) and a lower organic matter content (11 ± 2 vs. 47 ± 3%) (Table 3). Soil Eh ranged from +426 to −336 mV, indicating oxidized to strongly reducing conditions across sites. On average, Eh was 150 to 250 mV lower in the restoration sites. Porewater sulfide concentrations were also significantly higher at the restoration sites (Table 3). Porewater salinities varied spatially from 17 to 54% and seasonally from 30 to 39%, indicating brackish to slightly hypersaline conditions at the study sites (Table 3). Salinity was highest overall at WSR compared with the other sites (1 df contrast; $p \leq 0.001$) (Table 3). Soil saturation was significantly higher at HC compared with WS, but did

Table 1. Summary of forest structural characteristics at restored and natural sites at Windstar and Henderson Creek.

	Restored			*Natural*		
	Rhizophora mangle	*Avicennia germinans*	*Laguncularia racemosa*	*Rhizophora mangle*	*Avicennia germinans*	*Laguncularia racemosa*
Windstar						
Tree density (stems/ha)	2,927	651	3,252	1,040.0	609	482
Mean dbh (cm)						
<10 cm	2.4	2.7	2.1	7.4	4.6	9.5
≥10 cm	—	—	—	13.3	18.5	16.6
Basal area (m^2/ha)	1.47	0.43	1.28	10.6	6.9	10.7
Relative						
Density (%)	43	10	48	49	29	23
Dominance (%)	53	14	46	38	25	38
Frequency (%)	41	12	48	41	34	26
I_v	137	36	142	128	88	87
Henderson Creek						
Tree density (stems/ha)	2,968	—	24,732	1,621	88	131
Mean dbh (cm)						
<10 cm	2.2	—	2.7	6.3	—	5.1
≥10 cm	—	—	—	14.8	32.3	17.9
Basal area (m^2/ha)	1.3	—	17.1	15.7	7.4	3.3
Relative						
Density (%)	11	—	89	88	5	7
Dominance (%)	7	—	93	59	29	12
Frequency (%)	25	—	75	70	13	17
I_v	43	0	257	217	47	36

Diameter at breast height (dbh) was determined on all stems >2 cm in diameter and >2 m in height. The importance value (I_v) for each species as calculated as the sum of relative density, relative dominance, and relative frequency.

Table 2. Structural characteristics of restoration (R) and natural (N) mangrove forests at Henderson Creek (HC) and Windstar (WS) study areas in Florida compared with that of mature and young, natural forests and mangrove plantations (P) in various geographic regions.

Geographic Location	*Stand Type*	*Stand Age (Years)*	*Number of Species*	*Dominant Species*	*Total Density (Stems/ha)*	*Mean dbh (cm)*	*Total Basal Area (m^2/ha)*	*Stand Height (m)*	I_c	*Source*
Mexico	N	>50	2	Ag	3,120	24.7	15.2	9.0	9	Pool et al. (1977)
	N	>50	2–3	Lr	1,968	52.7	44.2	12.3	36	″
Costa Rica	N	>50	4	Lr	1,370	94.0	96.4	16.0	85	″
	N	>50	2	Rm	1,050	52.7	23.2	10.0	5	″
French Guiana	N	60–70	3	Rm	780	18.5	33.6	22.7	18	Fromard et al. (1998)
Florida/HC	N	>60	3	Rm	1,840	11.3	26.3	7.5	11	this study
Florida/WS	N	>50	3	Rm	2,131	11.4	28.2	7.4	13	this study
Malaysia	P	40	2	Ra	660	22.0	25.1	11.3	4	Chan (1996)
Puerto Rico	N	~20[a]	3	Lr	2,237	33.3	19.4	13.3	18	Pool et al. (1977)
Puerto Rico	N	~20[a]	3	Ag	1,380	39.2	16.9	16.0	11	Pool et al. (1977)
	N	~20[a]	2–3	Rm	3,875	27.9	22.8	11.8	24	″
Florida	N	~15[a]	3	Ag	5,900	20.8	20.3	6.5	23	″
	N	~15[a]	2	Rm	2,867	33.2	25.7	7.5	14	″
Malaysia	P	15	2	Ra	2,200	11.0	20.9	6.2	6	Chan (1996)
Vietnam	P	15	1	Ra	3,950	7.5	17.4	10.1	7	Hong (1996)
Cuba	P	15	1	Lr	3,500	8.4	19.4	8.7	6	Padron (1996)
Florida/WS	R	13	3	Lr/Rm	6,830	2.3	3.2	3.6	2	this study
Florida/HC	R	6	2	Lr	27,700	2.7	18.4	4.8	49	this study
Vietnam	P	6	1	Ra	14,349	3.0	10.1	4.6	7	Hong (1996)
French Guiana	N	5–6	2	Lr	11,944	4.7	20.6	7.7	37	Fromard et al. (1998)
Bangladesh	P	5	1	Sa	3,611	7.9	17.7	8.7	6	Siddiqi & Khan (1996)
Cuba	P	5	1	Rm	3,167	1.9	0.9	1.8	<1	Padron (1996)
French Guiana	N	3–4	2	Lr	41,111	2.1	13.7	3.5	39	Fromard et al. (1998)

Dominant species are indicated as: *Rhizophora mangle* (Rm), *R. apiculata* (Ra), *Avicennia germinans* (Ag), *Laguncularia racemosa* (Lr), and *Sonneratia apetala* (Sa). Complexity index (I_c) was calculated by multiplying the number of species × stand density × total basal area × stand height × 10^{-6}.
[a]Years since last hurricane.

not differ with site history (Table 3). Overall, porewater pH indicated neutral to slightly acidic conditions in the soils at the study sites and did not differ with site history (Table 3). Porewater concentrations of PO_4^{3-} were significantly higher at restoration sites, but NH_4^+ did not differ with site history (Table 3). Porewater nutrients also did not vary significantly with location or season. Soil temperature varied seasonally from 19.5°C (November 1996) to 26.6°C (July 1997), but there were no significant differences among sites.

Table 3. Physico-chemical conditions at Windstar and Henderson Creek restoration and natural sites.

	Windstar		*Henderson Creek*	
	Natural	*Restored*	*Natural*	*Restored*
Soil				
Bulk density	0.23 ± 0.01	0.70 ± 0.07	0.17 ± 0.01	0.66 ± 0.04
S_r[a]	71 ± 2	67 ± 4	76 ± 2	80 ± 6
Organic matter	38 ± 3	12 ± 5	56 ± 3	10 ± 1
Eh	142 ± 14	−93 ± 17	85 ± 22	−99 ± 19
NH_4-N	4.2 ± 0.4	4.1 ± 1.0	4.3 ± 0.5	5.1 ± 0.7
PO_4-P	5.9 ± 0.7	3.8 ± 0.5	4.2 ± 0.3	5.1 ± 0.7
Porewater				
Salinity	34 ± 1	45 ± 1	28 ± 1	30 ± 1
pH	6.58 ± 0.04	6.75 ± 0.03	6.71 ± 0.05	6.82 ± 0.04
Sulfide	0.02 ± 0.01	0.68 ± 0.02	0.01 ± 0.01	0.63 ± 0.14
NH_4-N	3.73 ± 0.66	3.53 ± 0.87	2.92 ± 0.50	4.04 ± 0.93
PO_4-P	0.96 ± 0.15	1.76 ± 0.33	0.85 ± 0.14	2.08 ± 0.38

Soil redox potentials (Eh, mV), S_r (relative saturation, %), and extractable NH_4-N and PO_4-P concentrations (μg/cm^3); and porewater salinity (‰), pH, sulfide (mM) and soluble NH_4-N and PO_4-P concentrations (μM) were measured seasonally (n = 9). Soil bulk density (g/m^3) and organic matter content (%) were measured once in November 1996 (n = 9). Values are the mean ± SE.
[a]S_r was calculated by the formula: S_r = weight of water (g)/(V_t − [dry weight of soil/D_p]), where V_t = volume of soil core and D_p = soil particle density. D_p was calculated by the formula: $D_p = (1 + F)/[(F/1.55) + (1/2.65)]$, where F = (% organic matter)/(% ash).

Contents of total carbon and nitrogen were, respectively, greater overall in natural soils (21 and 1.2%) than in restored soils (6.7 and 0.3%) and were correlated with organic matter content (r = 0.97 and 0.98). Total phosphorus in mangrove sediment was lower in restored (0.52 ± 0.12 mg/g) than in natural (1.22 ± 0.08 mg/g) forests. Extractable NH_4-N and PO_4-P, respectively, were also higher at natural sites (23 ± 2 and 26 ± 2 μg/g dry mass) compared with restoration sites (8.1 ± 1 and 8.4 ± 2 μg/g dry mass). When compared on a soil volume basis (μg/cm^3), however, there were no significant differences in NH_4-N or PO_4-P with site history or location (Table 3).

Carbon Dynamics

Leaf Fall and Root Production. Leaves comprised 81% of litter at HCR and 46–65% at the other three sites. Daily leaf fall rates varied from 0.64 to 2.99 g/m^2/day across sites (average = 1.89 ± 0.09 g/m^2/day), and there was not a significant main effect of site history. However, daily leaf fall at HC (2.1 ± 0.1 g/m^2/day) was significantly higher than that at WS (1.7 ± 0.1 g/m^2/day), averaged over site history.

Root production varied from 0.05 to 3.14 g/m^2/day across sites (average = 1.38 g/m^2/d), and there was no difference between restored and natural sites. Similar to leaf fall, root production at HC (1.7 ± 0.2 g/m^2/day) was significantly higher than that at WS (1.1 ± 0.2 g/m^2/day).

The annual amount of carbon deposited in leaf fall or root production per unit area at the sites was calculated by multiplying the total mass of leaves or roots produced by an average carbon content (46 or 38%, respectively). Leaf carbon input varied from 332 to 471 g/m^2/year across sites, and was significantly higher at the HC location (Fig. 1). Root carbon input varied from 7 to 435 g/m^2/day and was also significantly higher at the HC location (Fig. 1). There was no difference, however, in total leaf or root carbon deposition between restored and natural forests within the same physiographic setting.

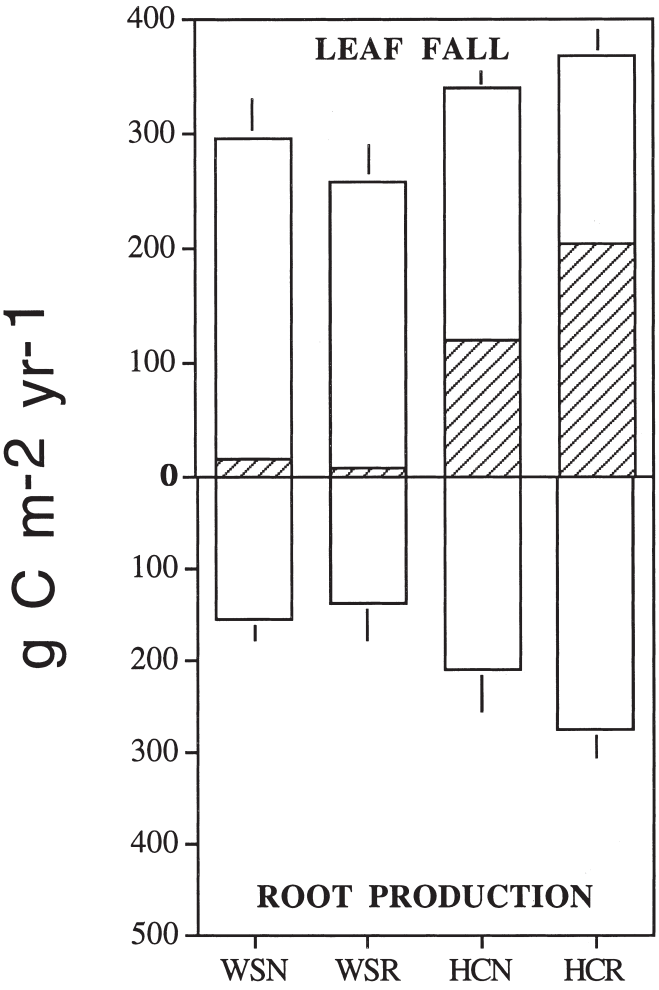

Figure 1. Annual leaf fall and root production rates at Windstar natural (WSN) and restored (WSR) and Henderson Creek natural (HCN) and restored (HCR) sites. Values are the mean ± 1 SE (n = 9). The amount of leaf material removed annually by macrofaunal consumption (patterned bar) was based on removal rates measured seasonally for three mangrove species (n = 112) and relative inputs of leaves during the same time interval.

Leaf Degradation by Macrofauna. Unbagged, tethered leaves at the HC and WS sites were consumed at relatively high rates by meso- and macrofauna, and in some cases, leaves were completely skeletonized within 1 month. Qualitative observations indicated that the pulmonate snail, *Melampus coffeus* L. (Pulmonata: Ellobiidae) was the primary leaf processor at the study sites. Percent leaf area removed daily varied from 0 to 3.3%, but the annual average was ~2% per day. Although temporal and spatial variability was high, significant differences were found with site history and location. Averaged over species, daily rates of leaf loss were higher at natural sites (2.31 ± 0.25 %) compared with restoration sites (2.15 ± 0.32%). Rates were also higher at HC (3.92 ± 0.29%) compared with WS (0.18 ± 0.02%). Leaf consumption also varied over time with higher losses in March, July, and November of 1997 (2.5 ± 0.5%) compared with November 1996 (1.4 ± 0.2%). By species, *A. germinans* and *L. racemosa* leaves were consumed twice as fast as *R. mangle* leaves.

The measured consumption rates were used in combination with daily inputs of leaf litter by each species to calculate amounts of carbon processed by macrofauna at each site (Fig. 1). The values were not corrected for physical removal of leaves by tides before they could be consumed, since these basin forests are infrequently flooded. The annual amount consumed by macrofauna varied from 7.3 at WSR to 204 g of carbon/m^2/year at HCR (Fig. 1). Rates of annual losses to mac-

rofaunal consumption were higher overall at HC (162 ± 27 g of carbon/m^2/year) compared with WS (11 ± 2 g of carbon/m^2/year), but there was no difference with site history.

Leaf and Root Degradation in Bags. Leaf degradation in mesh bags was significantly slower at WSR compared with the other three sites (Fig. 2, Table 4). Patterns of leaf degradation differed by species, however. Degradation of *A. germinans* and *L. racemosa* leaves was rapid at both HC sites and at WSN, with most of the original mass lost after 9 months. Degradation of *R. mangle* leaves was also rapid and similar to the other two species at HC, but the leaves at both WS sites degraded more slowly (Fig. 2).

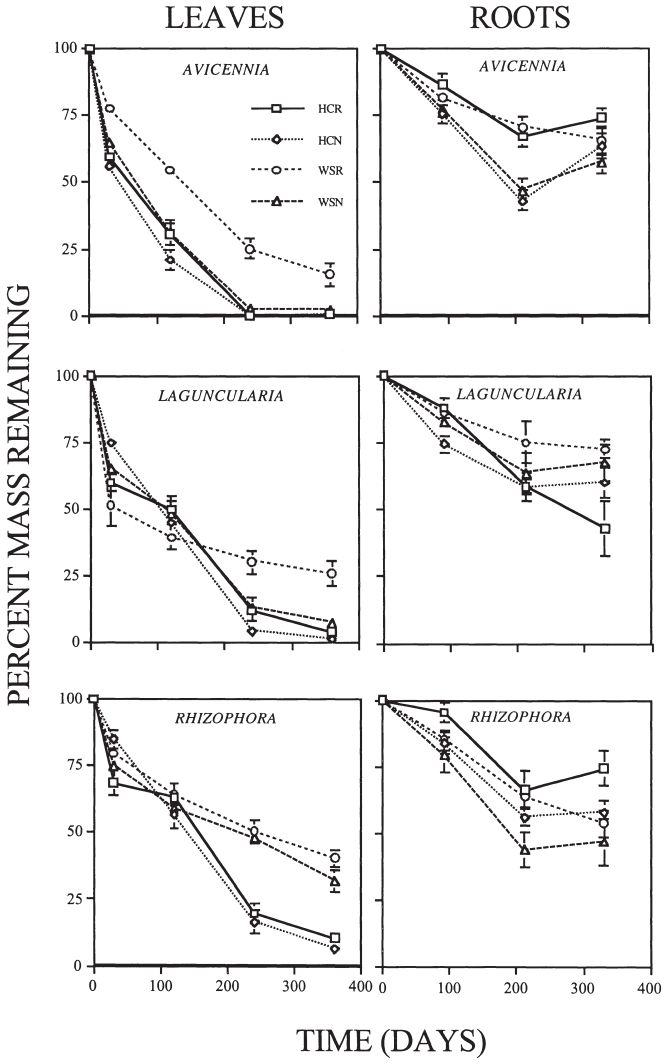

Figure 2. Percent leaf and root mass remaining in mesh bags deployed at Windstar natural (WSN) and restored (WSR) and Henderson Creek natural (HCN) and restored (HCR) sites. Leaf bags were placed on the soil surface, whereas root bags were buried. Values are the mean ± 1 SE (n = 9).

Root degradation belowground was considerably slower than leaves, with about 50% of the original mass remaining at the end of a year (Fig. 2). Root degradation was significantly slower overall at restoration sites compared with reference sites at both HC and WS (Table 4). *Laguncularia racemosa* roots decomposed more slowly than the other two species at WS, but faster at HC (Fig. 2).

Nitrogen Recycling

Nitrogen concentrations in senescent leaves were significantly higher at WS (7 ± 0.3 mg/g of dry mass) than at HC (6 ± 0.2 mg/g of dry mass) (Table 5), but did not differ with site history. Green and senescent leaf nitrogen concentrations varied significantly among species, respectively: *A. germinans* > *R. mangle* > *L. racemosa* (Table 5). Averaged over species, mangroves showed significantly higher resorption of nitrogen from senescing leaves at HC (61 ± 1%) compared with WS (53 ± 1 %) (Table 5), but there was no difference with site history. Percent resorption of nitrogen varied seasonally from 52 ± 1% (March 1997) to 60 ± 2% (November 1997).

Discussion

Forest Structure and Soil Condition

The stand structure of the two reference forests was similar to that of mature, natural forests (same species composition) elsewhere in Florida and the neotropics (Table 2). Since natural stands of comparable age (5–15 years old) were not available in the study area, a comparison with young, natural forests, and plantations in other geographic regions was made to further assess structural development in the Florida restoration sites (Table 2). The structure of the HCR site was similar to that of natural, young forests dominated by *L. racemosa*, e.g., pioneer (3–4 years) or young (5–6 years) stands establishing on mud flats in French Guiana (Fromard et al. 1998). The WSR site was more similar to 15-year-old mangrove plantations, although total basal area, stand height and I_c at WSR were lower compared with HCR and plantations (Table 2). The restoration sites were thus structurally similar to other mangrove forests of comparable age, but site-specific conditions have led to differences between HCR and WSR in structural development.

Mangrove growth can be strongly affected by soil conditions such as soil texture, salinity, flooding, and nutrient availability. The problems that restoration substrates have can be divided into four categories and reflect the basic needs of plants: an appropriate physical structure and stability; adequate moisture (and in the case of mangroves, appropriate tidal fluctuation and concomitant effects on soil aeration); adequate nutrition

Table 4. Decomposition rate constants (k) ± 1 SE of mass loss and residence time for leaf and root material (averaged over species) at restored and natural sites at Windstar and Henderson Creek (n = 27).

	Leaf		*Root*	
	k (/d)	*Residence Time* (d)	k (/d)	*Residence Time* (d)
Windstar				
Natural	0.0082 ± 0.0009	122	0.0026 ± 0.0003	385
Restoration	0.0040 ± 0.0005	250	0.0017 ± 0.0002	588
Henderson Creek				
Natural	0.0132 ± 0.0008	76	0.0020 ± 0.0001	500
Restoration	0.0115 ± 0.0010	87	0.0018 ± 0.0002	556

Values for k were determined as the slope of the linear regression of ln(percent mass remaining) against time (d), and mean residence time was calculated as $1/k$.

(macro- and micronutrients); and lack of toxicity (pH, heavy metals, and in the case of mangroves, sufficiently high salinity to exclude other species, but not so high as to generate excessive stress). The restoration sites differed in soil condition from that of reference forests (Table 3), but this dissimilarity was expected due to differences in site history and forest maturity. The quality of the soil substrate at HCR and WSR reflected the restoration procedures, i.e., dredge and fill. Over time, however, the plants have contributed to the physical and chemical characteristics of the substrate through organic matter deposition as they shed leaves, stems, and roots.

Soil Eh, which was lower at the restored sites, may reflect greater flooding and less soil aeration due to lower elevations (McKee 1995*a*), a low soil porosity, or to less leakage of oxygen from mangrove roots (McKee et al. 1988; McKee 1993). The WSR site was impounded by a low berm that restricted tidal flushing and probably contributed to more reducing conditions there. The incomplete forest cover and low I_c at WSR may be attributable to impaired water movement, to the variable topography, and/or to poor soil texture that slowed mangrove establishment, survival, and growth. The HCR site was more open to tidal action due to a network of flushing channels, but also exhibited lower soil Eh than the reference forest. Despite the flushing cuts, the continued presence of dredge material may have altered drainage patterns, restricted percolation of water vertically, and promoted retention of water at HCR. Although soil Eh values in the restoration sites were significantly different from that in reference forests, they were within the range of values reported for mangrove forests in Florida (McKee 1993), Belize (McKee et al. 1988; McKee 1995*a*), Australia (Boto & Wellington 1984), and Malaysia (Alongi et al. 1998).

The lower Eh values at both restoration sites were also consistent with elevated sulfide concentrations. Sulfide may accumulate to high concentrations (2–3 mM) in some basin and scrub forests where soil drainage is restricted (McKee 1993; McKee 1995*a*) and can exert a negative effect on mangrove seedling growth (McKee 1993). The levels of sulfide, although elevated significantly above that of the reference forests, were not unusually high and similar to that reported for mature mangrove forests in Florida (McKee 1993) and Belize (McKee et al. 1988). The presence of sulfide in restoration sediments also indicates that sulfate reduction is an important anaerobic decomposition pathway at these 6- to 14-year-old sites (Table 3) and agrees with the findings of Alongi et al. (1998). Sulfate reduction was the dominant diagenetic pathway in 15- and 60-year-old plantations of *Rhizophora apiculata* in Malaysia (Alongi et al. 1998). In contrast, Mn reduction and denitrification-nitrification coupled with aerobic respiration accounted for most of the organic matter oxidation in a 2-year-old forest plantation.

The salinity and pH measured at the restoration sites were typical of basin mangrove forests elsewhere in Florida (Twilley et al. 1986; McKee 1993) as well as in other geographic regions (Boto & Wellington 1984; Mc-

Table 5. Green and senescent leaf nitrogen content (mg/g dry mass) and percent nitrogen resorption (%) measured in *Rhizophora mangle, Avicennia germinans,* and *Laguncularia racemosa* at Henderson Creek and Windstar (averaged over site history and season).

	Leaf Nitrogen Content		*Percent Resorption*
	Green	*Senescent*	
Avicennia			
Henderson Creek	21.0 ± 0.56	8.16 ± 0.38	60 ± 2
Windstar	20.1 ± 0.35	9.96 ± 0.48	51 ± 2
Overall	20.6 ± 0.33	9.06 ± 0.31	56 ± 2
Laguncularia			
Henderson Creek	10.4 ± 0.33	4.05 ± 0.16	61 ± 1
Windstar	10.1 ± 0.29	4.58 ± 0.22	55 ± 2
Overall	10.2 ± 0.22	4.32 ± 0.14	58 ± 1
Rhizophora			
Henderson Creek	15.3 ± 0.33	5.76 ± 0.17	61 ± 2
Windstar	13.5 ± 0.30	6.37 ± 0.22	53 ± 2
Overall	14.4 ± 0.24	5.98 ± 0.12	58 ± 1

Values are the mean ± 1 SE (n = 40).

Kee 1995*a*). However, porewater salinity at the WSR site was substantially higher than that at the other three sites (Table 3). Restricted tidal flushing may not only have promoted more reducing conditions and accumulation of sulfide there, but also led to accumulation of salts in the soil. Hypersaline conditions may have additionally contributed to slower growth of mangroves at WSR. However, a cause and effect relationship is difficult to establish due to the reciprocal effects of mangrove cover on evapo-transpiration rates. The higher porewater salinity observed at WSR may simply be a reflection of slower forest development, leading to greater solar radiation penetration and higher average soil temperatures in unvegetated areas or where the canopy was more open.

Plant-available concentrations of nutrients are also important in understanding and interpreting differences in plant growth and productivity at restored sites. Readily available concentrations of nutrients may be low in mature mangrove forests due to uptake by trees and rapid recycling by plants and microorganisms (Boto & Wellington 1984; Alongi et al. 1992). Alongi et al. (1998) found that porewater concentrations of NO_2^- + NO_3^-, NH_4^+, and PO_4^{3-} were similar in 15- and 60-year-old plantations of *R. apiculata* in Malaysia, but that NH_4^+ and PO_4^{3-} concentrations were significantly higher in 2-year-old plantations, presumably due to enhanced microbial activity and reduced uptake by plants. A similar pattern was seen at HC and WS, where the restored forests had higher porewater concentrations of PO_4^{3-}. Porewater concentrations of NH_4^+, however, did not differ with site history or location. On a mass basis, extractable NH_4-N (8.1 μg/g dry mass) and PO_4-P (8.4 μg/g dry mass) at HCR and WSR were within the range reported in an Australian mangrove forest (2–8 and 4–28 μg/g dry mass, respectively; Boto & Wellington 1984), but higher than that at HCN and WSN. Differences in soil bulk density, however, will influence comparisons made on a soil mass basis. When compared on a soil volume basis, extractable NH_4-N or PO_4-P at restoration sites were equivalent to that at the reference sites (Table 3). Thus, readily available nutrients in the porewater or loosely bound to soil particles at restoration sites were not substantially different from that measured in natural mangrove forests.

Stores of carbon and nutrients in soils reflect several ecosystem processes such as primary production and decomposition of organic matter as well as abiotic conditions (temperature, moisture, oxidation status, soil texture) and biotic activity (microbial and faunal). Soil organic matter is an important source of most nutrients, particularly nitrogen, and the pattern of higher total carbon and nitrogen in natural versus restored soils is consistent with site differences in organic matter content (Table 3). A similar pattern of increasing total organic carbon and nitrogen with stand age was found in sediments from 2-, 15-, and 60-year-old mangrove plantations in Malaysia (Alongi et al. 1998). Thus, as litter accumulates and is incorporated into the soil, the relative proportion of organic to inorganic soil constituents increases in restored forests. Total phosphorus at HC and WS was similar to that reported for the Shark River estuary in south Florida (Chen & Twilley 1999) and mangrove plantations in Malaysia (Alongi et al. 1998), but was not correlated with soil organic matter. However, phosphorus occurs in many different physicochemical forms, and phosphorus accumulation in mangrove soils may be more strongly correlated with inorganic sediment inputs (Twilley 1995).

Carbon Dynamics

Leaf Fall and Root Production. The leaf fall rates measured at HC and WS are comparable to that reported for basin mangrove forests elsewhere, e.g., 0.4–1.4 g/m^2/day in Florida (Twilley et al.1986) and 0.6–1.5 g/m^2/day in Mexico (Day et al. 1996). Although our study did not assess interannual variation in leaf fall rates and patterns, Day et al. (1996) reported that annual mean leaf fall rates during a 7-year observation period varied from 0.8 to 2.91 g/m^2/day in basin and mixed fringe forests in Mexico. Using our measured carbon content, the values reported for the Mexican mangrove forests would yield ~129 to 201 g of carbon/m^2/year from leaf fall in basin forests and ~183 to 489 g of carbon/m^2/year in mixed fringe forests. Based on this comparison, the annual leaf carbon input to the forest floor at the experimental sites (Fig. 1) fell within the range of annual values reported for other forests of similar composition and where long-term data sets do exist.

Leaf fall rates were significantly higher at HC compared with WS, regardless of site history. Differences in edaphic factors such as sulfide, Eh, nutrient availability, bulk density, and pH could not account for the different patterns of leaf litter production between HC and WS locations, since these variables were more similar between locations than between restored and natural forests (Table 3). The major difference was porewater salinity, which was inversely correlated with leaf fall rates across sites ($r = -0.85$), and S_r, which was positively correlated ($r = 0.99$). Twilley et al. (1986) also reported an inverse relationship between litter production among five basin mangrove sites and average soil salinity.

Root production may account for almost half of the carbon cycled annually in forest ecosystems (Vogt et al. 1996), but there are no published reports of belowground production rates in mangrove forests. This study provides the first direct field measurement of mangrove root production and suggests that carbon in-

put by roots is 60–70% of the aboveground carbon input through leaf fall in these basin forests (Fig. 1). However, because root growth into the ingrowth cores may differ from that in the undisturbed soil already occupied by roots, the absolute values may not provide accurate estimates of belowground production. Root growth into root-free soil may be faster than into occupied soil, or conversely may be retarded by disturbance of the root system during insertion of cores (Vogt et al. 1998). Nonetheless, the ingrowth core technique is effective in assessing relative growth rates of roots in different environments or in response to different treatments, particularly in ecosystems where root growth is rapid, e.g., wet tropical forests (Vogt et al. 1998). Root production across mangrove sites closely followed that of leaf fall rates (Fig. 1), and was also inversely correlated with salinity ($r = -0.74$) and positively correlated with S_r ($r = 0.98$). Thus, relative patterns of leaf and root carbon inputs were in agreement and indicated a greater similarity between reference and restoration sites than between HC and WS locations. Also, the WS restoration site, which was structurally immature with incomplete canopy closure, exhibited the lowest leaf fall and root production rates.

Leaf and Root Degradation. Decomposition is an important process controlling the flux of carbon and nutrients. Because decomposition processes integrate several factors such as litter quality, environmental conditions, and biotic activity, measurement of litter decay rates is extremely useful in the evaluation of biogeochemical function of restored wetlands. Since the mesh bag technique measures both microbial decomposition and fragmentation by mesofauna and physical factors, the term degradation is used here to describe the overall process.

Species, tissue type, and site differences in mangrove degradation rates may reflect differences in litter chemical composition and/or environmental conditions controlling microbial decomposition (Twilley et al. 1986; Robertson 1988). Leaves in mesh bags degraded more slowly at restoration sites, particularly at WSR (Fig. 2), which may be related to more waterlogged conditions there. The three mangrove species decomposed at significantly different rates, and the pattern suggested that litter dominated by *A. germinans* would degrade faster than leaf litter comprised primarily of *R. mangle* and *L. racemosa.* Degradation rates of *A. germinans* leaves in bags were faster than that reported by Twilley et al. (1986) for a basin forest at Rookery Bay, but similar to that in other basin sites in Florida (Cintrón et al. 1985) and to *A. marina* in Australia (Robertson 1986). Degradation rate for *R. mangle* leaves was generally similar to that reported at Rookery Bay (Twilley et al. 1986) and other basin forests in Florida (Cintrón et al. 1985), but somewhat greater than for *Rhizophora* spp. in Ecuador (Twilley et al. 1997).

Use of mesh bags, however, excludes some macrofauna that shred and consume mangrove leaves and can lead to an underestimate of degradation rates. Mangrove forests in several geographic regions show high litter consumption rates by invertebrates such as crabs and snails (20–100% of annual leaf fall; Robertson 1986; Robertson & Daniel 1989; Camilleri 1992; Proffitt et al. 1993; McIvor & Smith 1995; Twilley et al. 1997). Deployment of tethered leaves at HC and WS demonstrated that consumption by *M. coffeus* greatly accelerated degradation of mangrove leaves. Rates differed among mangrove species and with location, probably due to differences in tissue chemical composition, composition or abundance of the detritivore community, and/or environmental conditions affecting feeding behavior (Giddins et al. 1986; Camilleri 1989; McKee 1995*b*). Thus, the restoration sites were not only repopulated by important detritivores, but the proportion of leaf litter being processed through this pathway was similar to that in nearby, natural forests.

Degradation of roots belowground was considerably slower than that of leaves aboveground (Table 4, Fig. 2). Work with other mangrove species (*A. marina*) also showed slow degradation of roots, although this varied with root size class (van der Valk & Attiwill 1984) and depth (Albright 1976). Middelburg et al. (1996) found that sediment CO_2 efflux rates differed among mangrove forest sites in East Africa, suggesting site differences in decomposer activity, but could not distinguish between forest type or tidal elevation as causative factors. Other workers, however, have shown that benthic microbial activity is unaffected by mangrove forest type or stand age (Alongi et al. 1993, 1998). Alongi et al. (1993) concluded that site differences in benthic microbial activity among mangrove forest types in Papua, New Guinea were mainly a function of tidal elevation-inundation frequency. Similarly, the slow degradation (in mesh bags) of leaves and roots at WSR (Table 4) may be related to more waterlogged conditions, limiting aerobic pathways of decomposition.

Nitrogen Recycling

Nutrient recycling is an important process that determines whether a mangrove system functions as a nutrient sink or source to adjacent aquatic systems (Twilley 1988). Plant processes such as nutrient resorption from senescing leaves affect nutrient recycling in mangrove forests (Twilley et al. 1986; Feller et al. 1999). Twilley et al. (1986) found that resorption of nitrogen from *A. germinans* leaves (45%) was lower than from *R. mangle* leaves (55%). In our study, however, relative resorption efficiencies among species varied temporally. Only dur-

ing November 1996 was percent resorption of nitrogen from *A. germinans* leaves (51 ± 4%) lower than that of the other two species (62 ± 2%). During peak leaf fall (July 1997), percent resorption was higher from *A. germinans* (62 ± 2%) compared with *R. mangle* and *L. racemosa* (56 ± 2 %) leaves and was equal among species during March and November 1997. Resorption efficiency in mangroves may also vary with nutrient availability, either by artificial enrichment (Feller et al. 1999) or along natural fertility gradients (Steyer 1988). However, since nutrient availability was similar between HC and WS locations, site differences in nitrogen resorption efficiency may be attributable to some other factor such as salinity.

Litter quality also influences nutrient recycling through effects on rates of microbial decomposition (Horner et al. 1988) and macrofaunal consumption (Giddins et al. 1986; Camilleri 1989). The senescent leaf values are similar to that reported in a number of mangrove forests (range for *Avicennia* spp. = 5.1 to 14 mg/g dry mass; *Rhizophora* spp. = 2.9 to 6.8 mg/g dry mass; *Laguncularia* sp. = 6.4 mg/g dry mass; reviewed in Feller et al. 1999). The pattern of leaf nitrogen content does not precisely match that of microbial or macrofaunal degradation rates (*A. germinans* > *L. racemosa* > *R. mangle*), but other factors such as leaf concentrations of secondary compounds may influence decomposition (Horner et al. 1988) or macrofaunal consumption (Camilleri 1989).

Gong and Ong (1990) reported that turnover time of nitrogen, phosphorus, and potassium increased with stand age in *R. apiculata* plantations in Malaysia. In mixed forests, however, species differences in leaf nutrient concentrations and percent resorption, combined with relative species abundances, would ultimately determine nutrient recycling at a stand level. Our results suggest that forests dominated by *L. racemosa* and *R. mangle* (e.g., restorations sites) should exhibit slower recycling of nutrients compared with those where *A. germinans* is more abundant (e.g., reference sites), similar to the findings of Twilley et al. (1986). However, resorption of nutrients from other senescing plant parts (roots and woody stems) as well as exchange of gaseous nitrogen (nitrogen fixation and denitrification) must also be measured to fully assess recycling efficiency in restored and natural mangrove forests.

Conclusions

Assessment of biogeochemical functions in restored mangrove wetlands involves evaluation of complex processes controlling soil condition, movement of carbon, nutrient recycling, and other important interactions. Structural and functional development of two mangrove restoration sites varied due to differences in hydro-edaphic conditions that influenced soil development, plant growth, and faunal assemblages. The results illustrate the importance of hydrology and concomitant factors such as salinity and soil waterlogging, which in this study were influential in determining structural development and biogeochemical functioning of the two restoration sites. The younger site (HCR) was similar structurally to natural, developing forests, while the older site (WSR) was less complex and had incomplete plant cover. More stressful physico-chemical conditions resulting from incomplete tidal flushing and variable topography apparently affected plant survival and growth at the WSR site. These hydro-edaphic conditions resulted in lower overall leaf fall and root production rates at the WSR site, compared with the HCR site where they were 40 and 100% higher, respectively. Leaf and root inputs at each restoration site, however, were not significantly different from that in a mature (>50 years old) forest within the same physiographic setting, suggesting that local or regional environmental conditions were acting together with site history to control primary production. Consumption of leaf litter by macrofauna also varied between HC and WS locations due to differences in environmental conditions controlling relative abundance and activity of detritivores. Degradation of leaf and root material in mesh bags was slower overall at restoration sites, particularly at WSR where aerobic decomposition may have been more limited. Thus, litter turnover in these restored forests was not only influenced by reestablishment of microbial and detritivore populations but also by spatial and temporal variation in environmental conditions controlling relative abundance, species composition, and activity of these organisms.

These findings illustrate the importance of examining more than one reference forest when assessing restoration of function. The two reference forests differed significantly in leaf fall and root production rates, as well as in degradation rates of organic matter, reflecting local differences in hydro-edaphic conditions and other factors affecting plant growth and processes controlling turnover of organic matter. Consideration of the natural range for values used in assessing biogeochemical function is also important. Even where there were differences between restoration and reference forests, e.g., in soil Eh or sulfide, the restoration site values were within the range required for support of mangrove vegetation and indicated that soil diagenetic processes were qualitatively similar to that in developing, natural forests. Long-term measurements are, of course, necessary to fully assess functional status in these and other restored mangrove forests (Simenstad & Thom 1996). More information is also needed from different geographic regions, mangrove forest types and geomorphic settings before generalizations can be made. However, our work suggests that some sites can provide

important functions in the landscape as early as six years after restoration. Other restored sites may take longer, depending on restoration techniques and regional and local factors.

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