

Changes in mass and nutrient content of wood during decomposition in a south Florida mangrove forest

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Summary

1 Large pools of dead wood in mangrove forests following disturbances such as hurricanes may influence nutrient fluxes. We hypothesized that decomposition of wood of mangroves from Florida, USA (*Avicennia germinans*, *Laguncularia racemosa* and *Rhizophora mangle*), and the consequent nutrient dynamics, would depend on species, location in the forest relative to freshwater and marine influences and whether the wood was standing, lying on the sediment surface or buried.

2 Wood disks (8–10 cm diameter, 1 cm thick) from each species were set to decompose at sites along the Shark River, either buried in the sediment, on the soil surface or in the air (above both the soil surface and high tide elevation).

3 A simple exponential model described the decay of wood in the air, and neither species nor site had any effect on the decay coefficient during the first 13 months of decomposition.

4 Over 28 months of decomposition, buried and surface disks decomposed following a two-component model, with labile and refractory components. *Avicennia germinans* had the largest labile component ($18 \pm 2\%$ of dry weight), while *Laguncularia racemosa* had the lowest ($10 \pm 2\%$). Labile components decayed at rates of 0.37 – 23.71% month⁻¹, while refractory components decayed at rates of 0.001 – 0.033% month⁻¹. Disks decomposing on the soil surface had higher decay rates than buried disks, but both were higher than disks in the air. All species had similar decay rates of the labile and refractory components, but *A. germinans* exhibited faster overall decay because of a higher proportion of labile components.

5 Nitrogen content generally increased in buried and surface disks, but there was little change in N content of disks in the air over the 2-year study. Between 17% and 68% of total phosphorus in wood leached out during the first 2 months of decomposition, with buried disks having the greater losses, P remaining constant or increasing slightly thereafter.

6 Newly deposited wood from living trees was a short-term source of N for the ecosystem but, by the end of 2 years, had become a net sink. Wood, however, remained a source of P for the ecosystem.

7 As in other forested ecosystems, coarse woody debris can have a significant impact on carbon and nutrient dynamics in mangrove forests. The prevalence of disturbances, such as hurricanes, that can deposit large amounts of wood on the forest floor accentuates the importance of downed wood in these forests.

Key-words: *Avicennia germinans*, decomposition, disturbance, Everglades National Park, hurricane effects, *Laguncularia racemosa*, mangroves, nutrients, *Rhizophora mangle*, wood

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Introduction

Despite considerable research interest in the ecology of mangrove forests, there is a surprising paucity of information concerning the role of wood in these systems. Smith (1992) indicated that, historically, researchers interested in mangrove forests had used paradigms developed from salt marshes, rather than from forests, to interpret ecosystem behaviour. Like other forest ecosystems, wood is the largest component of above-ground biomass in mangrove forests (Clough 1992) and this wood contains significant amounts of nitrogen and phosphorus (Robertson & Daniel 1989). The dynamics of N and P during wood decomposition in mangrove forests have been discussed in a single study for a single species in but a single location (Robertson & Daniel 1989). Variation in wood decomposition among species or between locations has never been described in mangrove ecosystems.

Coarse woody debris (CWD) represents a substantial amount of carbon and nutrients in forest ecosystems. The mass of CWD in forests with normal mortality generally varies from 15.9 Mg ha⁻¹ in a floodplain forest (Polit & Brown 1996) to more than 200 Mg ha⁻¹ in an old-growth *Sequoia* forest in California (Bingham & Sawyer 1988). Young and mature forest stands have relatively lower quantities of CWD than old-growth forests (Spies *et al.* 1988). Dead wood becomes the largest component of the litter pool, regardless of stand age, in forests that have been subjected to large-scale disturbances such as fire, flood and hurricanes (Everham & Brokaw 1996). These disturbance events play a substantial role in regulating the storage and turnover of carbon, nitrogen and phosphorus contained in woody biomass. Mangrove forests are routinely subjected to large-scale disturbances from hurricanes and typhoons (Craighead 1964; Smith 1992), which produce substantial pools of standing and downed dead wood. Following Hurricane Andrew, Smith *et al.* (1994) made estimates of 141 Mg ha⁻¹ of CWD in a coastal mangrove forest in south Florida. The dynamics of suddenly increasing the pool of wood debris in mangrove forests is unknown. Evidence from tropical forests indicates that large pulses of CWD can immobilize ecologically important nutrients, suppressing net primary production for decades (Zimmerman *et al.* 1995).

Coarse woody debris often consists of two distinct types: standing dead and downed wood, where decomposers of downed wood, unlike those of standing dead wood, can utilize nutrients from the soil by retranslocation of nutrients via fungal mycelia (Lambert *et al.* 1980). However, in tidal and irregularly flooded systems such as mangrove forests, there are sediment accretion processes, driven by input of allochthonous mineral sediments and autochthonous plant litter (Cahoon & Lynch 1997) so that downed wood decaying on the soil surface often becomes buried and thus subject to decomposition under different environmental conditions. In mangrove forests, therefore, standing dead

wood decomposes in a relatively dry environment, depending only on precipitation for moisture, whereas downed and buried boles are often flooded.

The chemical composition of the wood also controls the rates of microbial decomposition. Microbes decomposing litter of poor quality (i.e. low nutrient content) must utilize nutrients in the soil in order to raise the nitrogen content of the decomposing material to that of their own mass (Lambert *et al.* 1980; Zimmerman *et al.* 1995). Studies in various ecosystems have shown net accumulation of nitrogen during the decomposition of forest-derived litter. For example, Lambert *et al.* (1980) found that nitrogen concentrations of fir boles remained constant until the advanced stage of decay, at which point concentrations increased sharply. In contrast, nitrogen content in decaying *Rhizophora* boles increased fivefold (from 0.05% to 0.25%) during the first 2 months of decomposition (Robertson & Daniel 1989). Melillo *et al.* (1983) found that the nitrogen content of *Picea* and *Alnus* wood chips increased with decay, leveling off after 3–12 months depending on the species.

This relationship between nitrogen content and decay rate only applies for cases in which the physical removal of material is minimized, the nitrogen content of the litter material limits microbial activity, and in sites where there is a continuous external source of nitrogen to the decomposers (Aber & Melillo 1980). Consequently, nitrogen content alone or in combination with lignin content (i.e. lignin : N or C : N) is often used as a measure of litter quality and, thus, as a predictor of decomposition rates (Aber & Melillo 1980; Melillo *et al.* 1982; McLaugherty *et al.* 1985; Aber *et al.* 1990). The ratio of initial lignin to initial nitrogen is also highly correlated with decay rates in areas where exogenous nitrogen availability is low (Aber & Melillo 1982). The initial phosphorus content of plant litter has also been used as an index of litter quality in areas where plant growth is P-limited (Vitousek & Turner 1994). Some studies have reported that the phosphorus content of plant litter decreases during the initial phase of decay and increases slightly during the latter stages of decay (Lambert *et al.* 1980). In nutrient-poor environments such as the Everglades mangrove zone, the initial nutrient content of the CWD may be a valuable predictor of wood decay.

Climate and tidal variations are both important in determining the moisture and salinity content of mangrove forest soils (Wolanski *et al.* 1992). Tidal range determines the flooding period of the mangrove forest floor, and the tides, in conjunction with rainfall, evaporation and transpiration, control the porewater salinity in the upper levels of the soil (Wolanski *et al.* 1992). These factors are also important in regulating mangrove soil structure, composition and nutrient content along an estuarine gradient. In mangrove forests along the Shark River of south-west Florida, soil characteristics such as C, N and P content, bulk density and porewater salinity follow a gradient of tidal and upstream freshwater influence (Chen & Twilley 1999). Phosphorus

concentrations in the soil generally decrease from low estuarine (euhaline) to upper estuarine zones (oligohaline), while nitrogen content shows the opposite pattern (Chen & Twilley 1999). This results in a trend of increasing soil N : P from the mouth of this system to the upper estuary (Chen & Twilley 1999). Given the importance of tidal and upstream freshwater inputs in shaping mangrove soils, these factors should also have a considerable effect on the decomposition of CWD.

There have been a number of studies on decomposition of fine litter in tidal marsh systems. However, research on the decomposition of wood in tidal systems is limited (Benner & Hodson 1985; Robertson & Daniel 1989; Mackey & Smail 1996). Furthermore, most studies of wood decomposition in mangroves and other forested ecosystems have been conducted over long time scales using chronosequence methods to age dead wood and to estimate biomass losses and nutrient dynamics (Christensen 1977; Lambert *et al.* 1980; Spies *et al.* 1988; Robertson & Daniel 1989; Frangi *et al.* 1997). This means that factors such as leaching, which influence initial mass and nutrient losses, have been mixed with the overall decay process. Thus, we conducted a 2-year study of mangrove wood decomposition along the SW coast of Florida to track short-term changes in wood mass and nutrient content. We recognized that hurricanes and other major disturbances could deposit huge amounts of CWD in a short period, and that this deposition could perhaps dominate the nutrient fluxes in the ecosystem for some period immediately follow-

ing the disturbance. First, we wanted to model biomass loss and nutrient dynamics in decomposing wood from the three dominant mangrove species in this region. Secondly, we sought to understand the variability in wood decomposition associated with vertical spatial condition (e.g. standing dead wood, downed wood and buried wood) in an estuarine mangrove system. As mangrove forests are located along a tidal range, and tidal influence could have a considerable effect on decomposition processes, we established sites along a tidal gradient to understand the spatial variability in wood decomposition rates and in the nutrient pool of decaying wood. Finally, we wanted to characterize the nutrient dynamics of nitrogen and phosphorus during decomposition.

Methods

DESCRIPTION OF SITES

The south-west coast of Florida has a continuous band of forested estuarine wetlands, extending from Naples southwards to Cape Sable and covering a total of 60 000 ha. Much of this is located within Everglades National Park (ENP). Three species of mangrove are found: *Rhizophora mangle* L., *Avicennia germinans* (L.) Stearn and *Laguncularia racemosa* (L.) Gaertn (Smith *et al.* 1994). Several large tidal rivers drain the Florida Everglades and enter the Gulf of Mexico (Craighead 1964) within ENP. We established four sites along a tidal gradient in one of these waterways, the Shark River (Fig. 1,

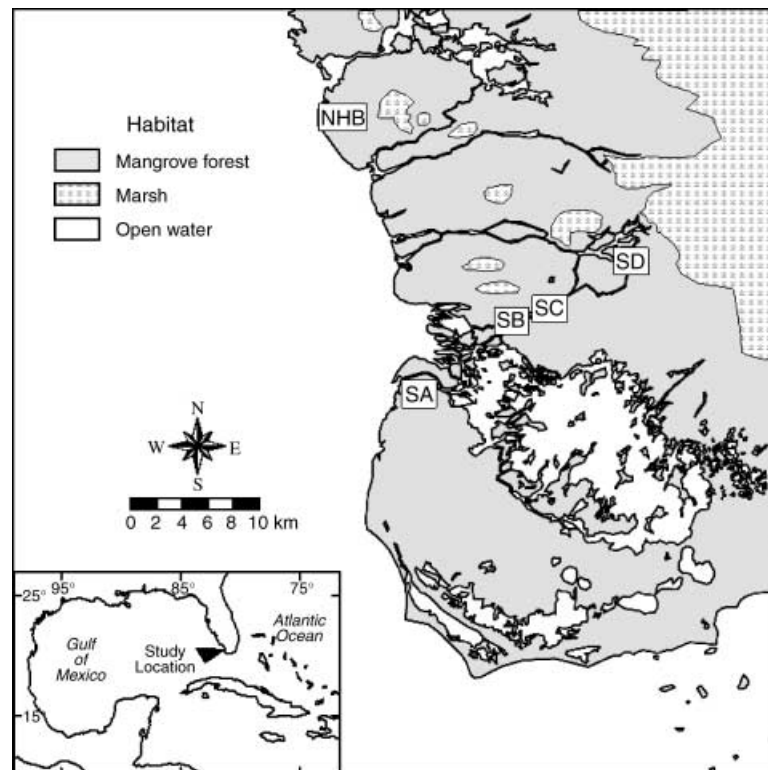


Fig. 1 Position within Florida of the south-west, estuarine coast of Everglades National Park. Four study sites were established along Shark River, with SA near the river mouth, following in alphabetical order to the furthest upstream site (SD). A fifth site was established behind a coastal shell dune at North Highland Beach (NHB). Open water, salt water marsh and mangrove forest habitats are indicated.

Table 1 List of sites in order of decreasing tidal influence. Other characteristics, including location, mean salinity and species composition, are also provided.

Site name	Latitude/longitude	Distance upstream from		
		Gulf of Mexico (km)	Mean salinity (‰)	Mangrove species present
Shark River A (SA)	25°19.38' N/81°08.28' W	0.5	36	<i>R. mangle</i> , <i>L. racemosa</i> , <i>A. germinans</i>
Shark River B (SB)	25°21.49' N/81°04.43' W	6	23	<i>R. mangle</i> , <i>L. racemosa</i> , <i>A. germinans</i>
Shark River C (SC)	25°22.73' N/81°01.84' W	11	3	<i>R. mangle</i> , <i>L. racemosa</i> , <i>A. germinans</i>
Shark River D (SD)	25°24.35' N/80°57.49' W	18	3.5	<i>R. mangle</i> , <i>L. racemosa</i>
North Highland Beach (NHB)	25°30.70' N/81°12.54' W	NA	25	<i>R. mangle</i> , <i>L. racemosa</i> , <i>A. germinans</i>

Table 1). Tides at these sites are semidiurnal, with depth of inundation varying from 0.75 m at SA to 0.10 m at SD. Site SD is most upstream and during the summer rainy season it may be inundated for periods much longer than a single tidal cycle. We established a fifth site at North Highland Beach (NHB; Fig. 1, Table 1) behind a beach ridge that acts as a barrier from tidal flushing. NHB remains flooded for extended periods of time due to local rainfall (L. M. Romero, T. J. Smith III & J. W. Fourqurean, personal observation). Because of the unique characteristics of NHB with respect to flooding regime, we thought it would allow us to estimate the effects of extended flooding events on wood decomposition.

Climate in this region is characterized by a pattern of alternating wet and dry seasons, and average annual precipitation in Everglades National Park ranges from 1190 to 1570 mm, approximately 60% of which falls from June through September (Duever *et al.* 1994). Air temperature at our sites ranged from a maximum of 33 °C to a minimum of 8 °C and soil temperature ranged from a maximum of 30 °C to a minimum of 12 °C.

EXPERIMENTAL DESIGN

Disks (1 cm thick) cut from live stems (10 cm d.b.h.) of the three mangrove species were used as substrate. Trees from which disks were cut were selected from a single mangrove forest stand located near Flamingo, ENP, to ensure the homogeneity in wood quality required to test the effect of location and condition on wood decomposition. After each disk was cut, it was immediately weighed, labelled and sewn into individual fibreglass litterbags of 1 mm mesh size. This mesh size was chosen to exclude macroinvertebrate shredders that might have confounded our estimations of microbial decomposition. Nine disks from each species were retained to derive fresh weight/dry weight conversion factors for the fresh wood disks placed in the field.

A four-factor experimental design (species, site, condition and time) was employed to assign the 810 mangrove wood disks among the five sites. Three condition treatments were used, each representing a possible fate of coarse woody debris in these estuarine forests. To mimic dead wood that had been buried by sediment, a

third of the disks were placed about 5–10 cm below the soil surface to decompose ('buried'). Another third were placed on the surface of the soil to mimic fallen dead wood ('surface'). The litterbags containing these disks were tethered to nearby prop roots and pneumatophores to prevent removal via tidal action. Finally, to mimic standing dead wood, a third of the litterbags were hung on PVC poles approximately 1.5 m above mean high water ('air'). Because the litterbags excluded the macroinvertebrates that commonly attack standing dead wood, but not fallen or buried wood, we were able to examine leaching and microbial processes only. All disks were placed under a closed forest canopy at each site.

Each litterbag had colour-coded cable ties attached to facilitate species determinations in the field. Collections were made at each site at 2, 4, 7, 10, 13 and 28 months after deployment for the surface and buried treatments. For the air treatment, collections were made up to 13 months only because the winds from Hurricane Keith had removed many of these disks. During each sampling, 27 litterbags (3 species × 3 conditions × 3 replicates) were collected from each site. After collection, disks were brought to the laboratory and rinsed with freshwater over a 1-mm sieve to remove mud, algae, roots and other foreign particles. Some disks collected after 28 months had shells from shipworms (*Teredo* sp.), which were removed. After rinsing, samples were oven dried at 70 °C for 1 week to obtain dry weight. Dry weights were then subtracted from predicted initial dry weight, based on wet : dry weight ratios. Each disk was then sectioned into wedge-shaped pieces (like a piece of pie) in order to obtain proportional amounts of every part of the wood (bark, sapwood and heartwood). A randomly selected wedge from each disk was ground to a powder for nutrient analysis. Nitrogen content was determined using a Carlo Erba 1500-N CHN analyser. Total phosphorus was determined using the dry-oxidation, acid hydrolysis method (Solorzano & Sharp 1980).

DECAY MODEL

Both double and single exponential decay models were fit to the mass data for each site × species × condition

case. Based on the R^2 values for non-linear models ($1 - (\text{error mean square error}/\text{total mean square})$), the double exponential decay model described the data more effectively than a single component exponential model for most treatments. The double component model is a summation of a two single component models and assumes that the substrate is heterogeneous (Minderman 1968). Labile substrates (e.g. sugars, starches and proteins) will be rapidly utilized by decomposers, while recalcitrant materials (e.g. cellulose, fats, waxes, tannins and lignins) will be lost at relatively slower rates (Wieder & Lang 1982). Nonetheless, recalcitrance is a relative term. For instance, hemicellulose and cellulose decompose on the order of 0.0109 year^{-1} and lignin, decomposes on the order of 0.0039 year^{-1} (Means *et al.* 1985). Having this in mind, the decay model we used from Minderman (1968) is as follows:

$$\frac{W_t}{W_0} = \alpha e^{-k_1 t} + (1 - \alpha) e^{-k_2 t} \quad \text{eqn 1}$$

where: W_0 = initial dry mass, W_t = mass remaining at time t , α = the labile portion of initial material (fast decay component), $1 - \alpha$ = the refractory portion of initial material (slow decay component), k_1 = decay constant for the fast decay component, and k_2 = decay constant for the slow decay component. Units for k_1 and k_2 were time^{-1} ; for comparisons with literature values we converted our values with units of month^{-1} to year^{-1} by multiplying by 12.

The parameters k_1 , k_2 and α were estimated for each species, site and condition combination using an iterative least-squares non-linear regression technique (SPSS 8.0 for Windows). We used 13 months of data to calculate the decay parameters for the disks decomposing in the air and 28 months of data to calculate the parameters for buried disks and those on the soil surface. If the estimated value of the parameter α was not significantly different from zero, we interpreted this to mean that decay in those instances could be modelled as the decay of a homogeneous substrate, and a simpler single exponential model was fit to the data instead:

$$\frac{W_t}{W_0} = e^{-k_2 t} \quad \text{eqn 2}$$

NET CHANGES IN NUTRIENTS

To characterize the overall pattern of net mineralization or accumulation of N and P we calculated a nutrient accumulation index (NAI) for each wood disk (Harmon *et al.* 1986):

$$\text{NAI} = \frac{W_t X_t}{W_0 X_0} \quad \text{eqn 3}$$

where: W_t = the dry weight of the disk at time t , X_t = the nutrient concentration of the disk at time t , W_0 = initial dry weight of the disk, and X_0 = the initial concentration of nutrient in the disk. A NAI value of 1 indicates that the decomposed disk contained the same

mass of the element 'X' as when the disk was placed in the litterbag; $\text{NAI} < 1$ indicates net mineralization of the element from the decaying disk; and $\text{NAI} > 1$ indicates net accumulation of the element by the decaying disk. By collecting three disks of each species at each time, we could calculate the 95% confidence interval for NAI; if this confidence interval did not overlap 1, we interpreted it to mean there was net mineralization or accumulation.

STATISTICAL ANALYSES

We first described the shape of the decomposition time series using equations 1 and 2, then we used the parameters of the model fits (k_1 , k_2 and α) to assess whether the species of the wood, its location along the freshwater-to-marine gradient (site) and its position in the forest (reflected in its condition treatment) affect the rate of decay. We assessed these hypotheses using analyses of variance, with the model decay model parameters as response variables and species, site and condition as main effects. The loss of samples of wood decomposing in the air after 13 months led to a complication in the analyses. Decay rates in air were orders of magnitude slower than the buried and surface conditions. We used an analysis of variance to determine the effect of species (three species) and location (five sites) on the decay rates of air disks calculated with the first 13 months of data. To analyse for differences in decay of surface and buried disks over the 28 months, we limited the analysis to a test for the effects of the three species, location (five sites), and two conditions (buried and sediment surface). Three-way interactions and greater were not included in the ANOVAS. Furthermore, because later analyses revealed no significant two-way interactions, we re-ran the analysis of variance to include only main effects. Comparisons of treatment means for significant main effects were carried out using Scheffe's multiple comparison.

We hypothesized that CWD would increase in nutrient content through time as bacteria and fungi colonized the dead wood, and that the accumulation of nutrients would be a function of the species of wood, the location along the freshwater-to-marine gradient and the condition of wood within the forest. Simple linear regressions were used to estimate nutrient changes through time, and analyses of variance were performed to estimate the effects of site, species and condition on the slopes of the regressions.

Results

DECAY MODELS

The double exponential model was generally more efficient at describing decay patterns. However, for disks decomposing in the air, it was not significantly better than the single exponential model (Table 2). We attribute the comparatively poor fit of the single exponential

Table 2 Decay components for the single and two-component models for disks in air. Treatments with no data for α and k_1 indicate that a single exponential model was used and the results for these are listed under k_2 . Decay parameters were calculated for a 13-month period. Species: *A. germinans* (*Ag*), *L. racemosa* (*Lr*) and *R. mangle* (*Rm*)

Site	Spp	Air		
		$\alpha \pm SE$	$k_1 \pm SE$	$k_2 \pm SE$
SA	<i>Ag</i>	0.136 ± 0.035	0.580 ± 0.285	0.001 ± 0.004
	<i>Lr</i>			0.008 ± 0.001
	<i>Rm</i>	0.040 ± 0.000	10.890 ± 0.002	0.002 ± 0.015
SB	<i>Ag</i>	0.096 ± 0.023	0.928 ± 0.696	0.009 ± 0.004
	<i>Lr</i>			0.004 ± 0.001
	<i>Rm</i>			0.009 ± 0.001
SC	<i>Ag</i>			0.016 ± 0.002
	<i>Lr</i>			0.005 ± 0.001
	<i>Rm</i>			0.009 ± 0.001
SD	<i>Ag</i>	0.032 ± 0.000	10.295 ± 0.002	0.015 ± 0.018
	<i>Lr</i>	0.050 ± 0.018	0.604 ± 0.708	0.003 ± 0.001
	<i>Rm</i>			0.012 ± 0.001
NHB	<i>Ag</i>			0.014 ± 0.002
	<i>Lr</i>			0.006 ± 0.001
	<i>Rm</i>			0.009 ± 0.001

model to its lack of sensitivity to the initial relatively rapid (0–2 months) losses of wood mass, which is explicitly modelled in the double exponential model. The decay constants from the single exponential model and the decay constant from the slow decay component of the two-component model were comparable, with the former being slightly higher. For surface and buried disks, the decay constants of the labile portion, k_1 , ranged from 0.367 to 23.702 month⁻¹ and the decay constant of the more refractory components of the wood, k_2 , varied from 0.001 to 0.033 month⁻¹. The proportion of labile material, α , varied from 1.7 to 28.3% of total mass (Table 3).

Table 3 Decay components for the single and two-component models for the 'surface' and 'buried' conditions. Treatments with no data for α and k_1 indicate that a single exponential model was used and the results for these are listed under k_2 . Decay parameters were calculated for a 28-month period. Species abbreviations as in Table 2

Site	Spp	Surface			Buried		
		$\alpha \pm SE$	$k_1 \pm SE$	$k_2 \pm SE$	$\alpha \pm SE$	$k_1 \pm SE$	$k_2 \pm SE$
SA	<i>Ag</i>	0.128 ± 0.024	1.320 ± 1.571	0.021 ± 0.002	0.222 ± 0.026	0.517 ± 0.150	0.010 ± 0.002
	<i>Lr</i>	0.027 ± 0.000	9.860 ± 0.002	0.019 ± 0.025			0.015 ± 0.001
	<i>Rm</i>	0.017 ± 0.000	11.619 ± 0.004	0.033 ± 0.035	0.089 ± 0.016	1.558 ± 2.275	0.020 ± 0.002
SB	<i>Ag</i>	0.123 ± 0.022	2.500 ± 16.580	0.025 ± 0.002	0.193 ± 0.012	1.257 ± 0.509	0.010 ± 0.001
	<i>Lr</i>			0.024 ± 0.001	0.085 ± 0.000	11.757 ± 0.002	0.008 ± 0.018
	<i>Rm</i>	0.038 ± 0.000	15.521 ± 0.002	0.030 ± 0.018	0.150 ± 0.019	1.065 ± 0.666	0.014 ± 0.002
SC	<i>Ag</i>	0.123 ± 0.000	12.197 ± 0.001	0.027 ± 0.012	0.189 ± 0.025	0.436 ± 0.121	0.013 ± 0.002
	<i>Lr</i>	0.077 ± 0.015	0.662 ± 0.362	0.019 ± 0.001	0.043 ± 0.000	11.045 ± 0.002	0.014 ± 0.017
	<i>Rm</i>	0.087 ± 0.000	10.023 ± 0.002	0.019 ± 0.017	0.145 ± 0.013	0.719 ± 0.190	0.015 ± 0.001
SD	<i>Ag</i>	0.283 ± 0.104	0.367 ± 0.247	0.013 ± 0.009	0.223 ± 0.017	0.699 ± 0.182	0.005 ± 0.001
	<i>Lr</i>	0.067 ± 0.000	10.261 ± 0.003	0.029 ± 0.022	0.109 ± 0.013	1.478 ± 1.643	0.007 ± 0.001
	<i>Rm</i>	0.094 ± 0.035	0.406 ± 0.314	0.013 ± 0.002	0.165 ± 0.016	0.747 ± 0.247	0.009 ± 0.001
NHB	<i>Ag</i>	0.128 ± 0.000	13.150 ± 0.002	0.025 ± 0.018	0.159 ± 0.022	1.646 ± 2.082	0.014 ± 0.002
	<i>Lr</i>	0.063 ± 0.000	11.168 ± 0.002	0.018 ± 0.016	0.096 ± 0.027	0.413 ± 0.240	0.011 ± 0.002
	<i>Rm</i>	0.109 ± 0.000	23.702 ± 0.002	0.022 ± 0.014	0.109 ± 0.015	0.990 ± 0.656	0.018 ± 0.001

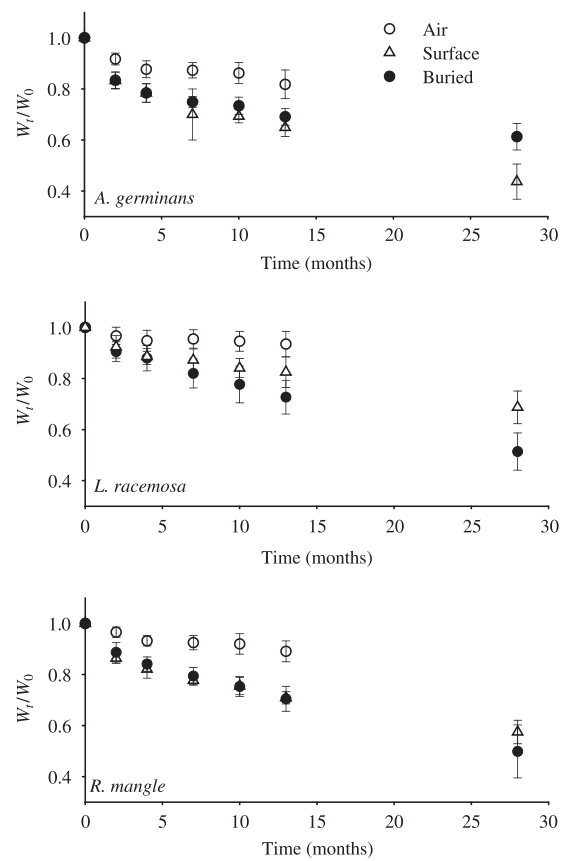


Fig. 2 Rates of mass loss from wood disks averaged across all sites. W_t = weight of disk (dry weight in g) at time t and W_0 = the initial weight of the disk. Data points indicate observed values; error bars are ± 1 SD.

Relative differences of the exponential decay rates among conditions are readily apparent (Fig. 2). Our hypotheses that decomposition would be affected by the species and condition of the CWD were consistent with the collected data. Condition and species both

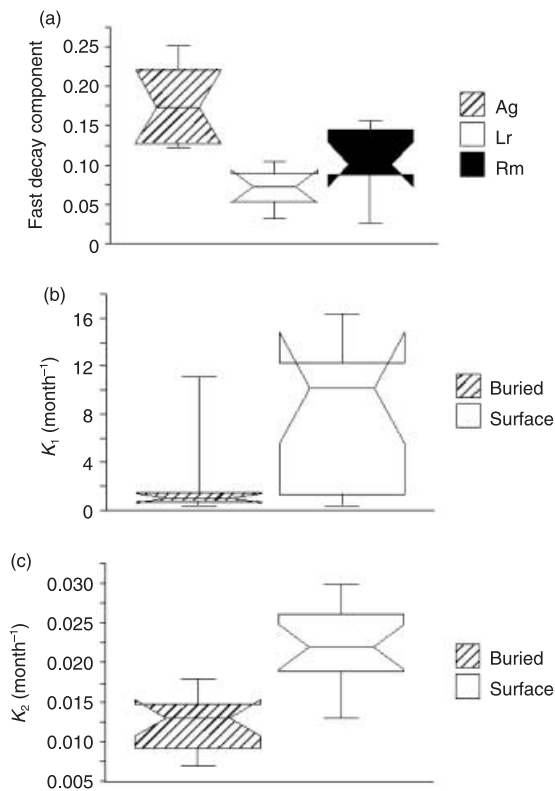


Fig. 3 Distribution of the parameter values of the decay models. (a) Boxplots of the fast decaying fraction (α) by species. (b) Boxplots of decay constant for the fast decaying fraction (k_1) averaged by condition. (c) Boxplots of the decay constant for the slow decaying fraction (k_2) averaged by condition.

had an effect on the decomposition model parameters. There was a species effect for α ($P < 0.005$), and a condition effect for both k_1 ($P < 0.005$) and k_2 ($P < 0.0001$). *Avicennia germinans* had the largest proportion in the

labile pool (0.18 ± 0.02) and *L. racemosa* had the least (0.10 ± 0.01 ; Fig. 3a). There were no significant differences between *L. racemosa* and *R. mangle* (Fig. 3a). Disks on the sediment surface had higher rates for k_1 ($8.51 \pm 1.74 \text{ month}^{-1}$) than buried disks ($2.29 \pm 0.96 \text{ month}^{-1}$; Fig. 3b). The latter was also true for the mineralization rates of the refractory pool (k_2). Decay constants (k_2) for surface and buried disks were $0.022 \pm 0.002 \text{ month}^{-1}$ and $0.012 \pm 0.001 \text{ month}^{-1}$, respectively (Fig. 3c).

We found no support for our hypothesis that decomposition rates would vary along the freshwater-to-marine gradient. There was no significant location effect on decay model parameters for the 28-month decomposition experiments on surface and buried disks. Neither species nor sites had any effect on the decay parameters for wood disks decomposing in the air.

NITROGEN DYNAMICS

We hypothesized that nitrogen content would increase through time as CWD decomposed; the data bore out this hypothesis. Nitrogen content in buried and surface disks increased for all species at all sites during 28 months of decomposition (Fig. 4a, Table 4). For *L. racemosa* and *R. mangle*, the nitrogen content tripled over the 28-month experiment for surface disks. Buried disks of all species had a twofold increase in N. The nitrogen content of *A. germinans* disks doubled in the buried and surface treatments. It is important to note that *A. germinans* had significantly higher initial nitrogen content (0.260% of dry weight $\pm 0.0159\%$) than *L. racemosa* ($0.157 \pm 0.0195\%$), but it was not significantly higher than *R. mangle* ($0.205 \pm 0.0139\%$). Unlike the trends for buried and surface disks, the nitrogen content of disks in the air remained unchanged throughout the study (Fig. 4a).

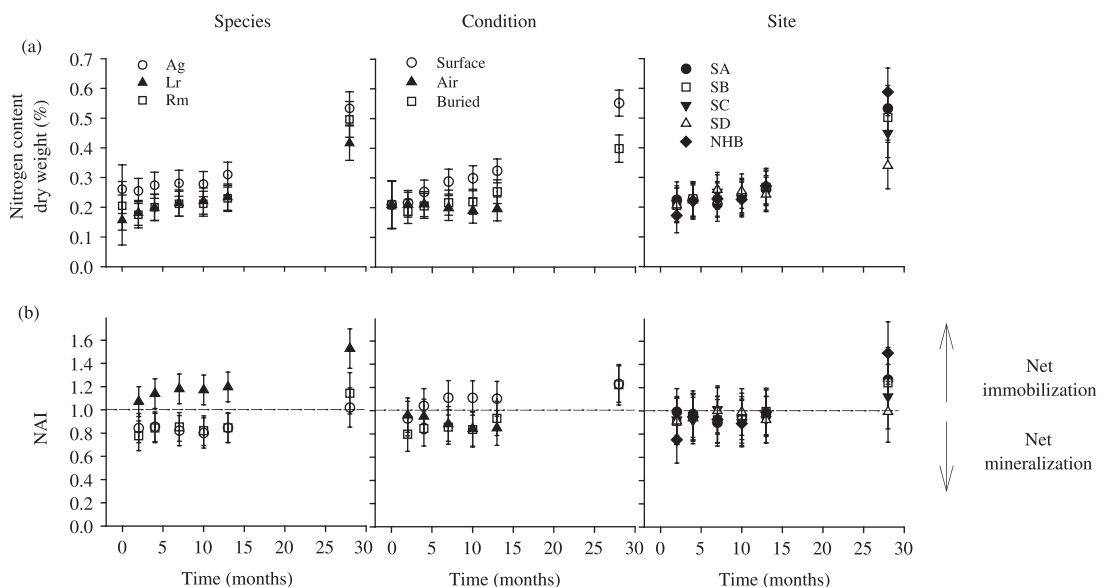


Fig. 4 Nitrogen content of decaying wood through time. (a) Changes in N content as a proportion of dry mass. (b) Changes in NAI. Both figures are averaged by species, condition and site. Error bars represent 95% CI.

Table 4 Slopes (%N mo⁻¹) of the significant linear regressions of nitrogen content as a function of time. * = slopes are significantly different from 0 at $P < 0.05$, ** = slopes are significantly different from 0 at $P < 0.005$, and *** = slopes are significantly different from 0 at $P < 0.0001$

Site Condition	Sp	13 months		28 months	
		N slope	r ²	N slope	r ²
SAair	Rm	-0.0040*	0.23		
SAsurface	Ag			0.010***	0.646
SAsurface	Lr	0.0090**	0.492	0.005***	0.521
SAsurface	Rm	0.009**	0.532	0.021***	0.866
SAburied	Ag	0.005*	0.222	0.009***	0.694
SAburied	Lr	0.005**	0.572	0.010***	0.783
SAburied	Rm	0.005*	0.261	0.009***	0.626
SBsurface	Ag	0.011***	0.592	0.014***	0.861
SBsurface	Lr	0.009***	0.622	0.012***	0.904
SBsurface	Rm	0.011***	0.601	0.018***	0.847
SBburied	Ag			0.008***	0.651
SBburied	Lr	0.005*	0.378	0.005***	0.668
SBburied	Rm	0.005*	0.261	0.007***	0.669
SCair	Rm	-0.003*	0.224		
SCsurface	Ag	0.008**	0.45	0.013***	0.843
SCsurface	Lr	0.010***	0.693	0.007***	0.755
SCsurface	Rm			0.008***	0.494
SCburied	Ag			0.006***	0.629
SCburied	Lr	0.005**	0.506	0.007***	0.835
SCburied	Rm			0.006***	0.575
SDsurface	Lr	0.021**	0.445	0.015**	0.505
SDsurface	Rm			0.003*	0.161
SDburied	Ag			0.003*	0.168
SDburied	Lr	0.004*	0.29	0.004***	0.682
NHBsurface	Ag	0.012**	0.466	0.019***	0.765
NHBsurface	Lr	0.011**	0.566	0.013***	0.865
NHBsurface	Rm	0.010**	0.465	0.018***	0.818
NHBburied	Ag	0.007*	0.3	0.010***	0.676
NHBburied	Lr	0.007**	0.522	0.100***	0.734
NHBburied	Rm			0.010***	0.619

Rates of increase for nitrogen in surface and buried disks varied from 0.005 to 0.019% dry weight month⁻¹ during the study. Condition did indeed have an effect on the rates of nitrogen accumulation. In the first 13 months of decomposition there were significant differences in the nitrogen accumulation rates between conditions ($P < 0.0001$) and among species ($P < 0.001$), but not sites. Nitrogen accumulation rates were higher in disks on the soil surface ($0.009 \pm 0.001\%$ dry weight month⁻¹) compared with buried disks ($0.004 \pm 0.001\%$ dry weight month⁻¹). Nitrogen accumulation rates were also different among species, increasing faster in *L. racemosa* ($0.006 \pm 0.001\%$ dry weight month⁻¹) than in *R. mangle* ($0.003 \pm 0.001\%$ dry weight month⁻¹). No significant differences between *R. mangle* and *A. germinans* were found. After 28 months of decomposition, there was no species effect on the absolute nitrogen accumulation in wood but there was a condition effect ($P < 0.05$). Nitrogen accumulation rates after 28 months remained higher for surface disks ($0.011 \pm 0.002\%$ dry weight month⁻¹) compared with buried disks ($0.007 \pm 0.001\%$ dry weight month⁻¹).

As hypothesized, there was a site effect on the rate of change in nitrogen content ($0.10 > P > 0.05$). Disks at

NHB increased N content faster than disks decomposing at SD (0.013 ± 0.002 vs. $0.005 \pm 0.002\%$ dry weight month⁻¹).

Calculation of net changes in nitrogen (immobilization vs. mineralization) revealed differences among species, condition and sites (Fig. 4b). We found net mineralization of nitrogen in *A. germinans* and *R. mangle* for all three conditions and net immobilization of nitrogen for surface disks of *L. racemosa* during the first 13 months of decomposition. After 28 months, there was net immobilization of nitrogen in *L. racemosa* surface and buried disks. Averaged over condition and site, there were no net changes in *A. germinans* and *R. mangle* after 28 months. Averaged over species and condition, the sites located in more marine environments showed net immobilization of nitrogen (Fig. 4b).

PHOSPHORUS DYNAMICS

Initially, total phosphorus (TP) content was 0.037, 0.030 and 0.028% of dry weight for *L. racemosa*, *R. mangle* and *A. germinans*, respectively, with no significant differences among them. A large portion of the TP leached out during the first 2 months of decomposition for all species (Fig. 5a). Disks of *A. germinans* and *R. mangle* in the air treatment lost 17% and 24% of the initial TP in the first 2 months, respectively. *L. racemosa* air disks lost 42% after 2 months. TP losses for surface and buried disks, after 2 months, were even greater, varying from 50% to 68% for the three species, with highest losses occurring in buried disks. TP content in the air disks continued to decrease from 2 to 13 months until they had lost from 40% to 70% of the initial TP content for all three species (Fig. 5a). TP content for surface and buried disks increased slightly during the remaining months of decomposition (Fig. 5a).

Linear regressions of TP for all treatments as a function of time were performed without including the initial phosphorus contents. Had we included initial TP concentrations in the regression model, the small changes that occurred between 2 and 28 months would have been overshadowed by the large release of phosphorus that occurred over the first 2 months of decay. The only significant accumulation of TP through time (months 2–13) was for buried and surface disks at NHB (Table 5). For most disks in the air, there was a significant decrease in phosphorus content with time after 2 months (Table 5, Fig. 5a).

Site ($P < 0.0005$) and condition ($P < 0.0001$) had a significant effect on rates of phosphorus change during the first 13 months of wood decomposition, but species did not. The phosphorus content of wood decomposing at NHB increased at an average rate of $3.421 \times 10^{-4} \pm 2.902 \times 10^{-4}\%$ dry weight month⁻¹, whereas mean TP slopes of disks decomposing at all sites along Shark River were negative, indicating absolute losses of total phosphorus (Fig. 5a). These negative slopes resulted from greater losses of TP in disks decomposing in the air than TP gain in disks decomposing on the soil surface or those that were buried (Fig. 5a). As a consequence,

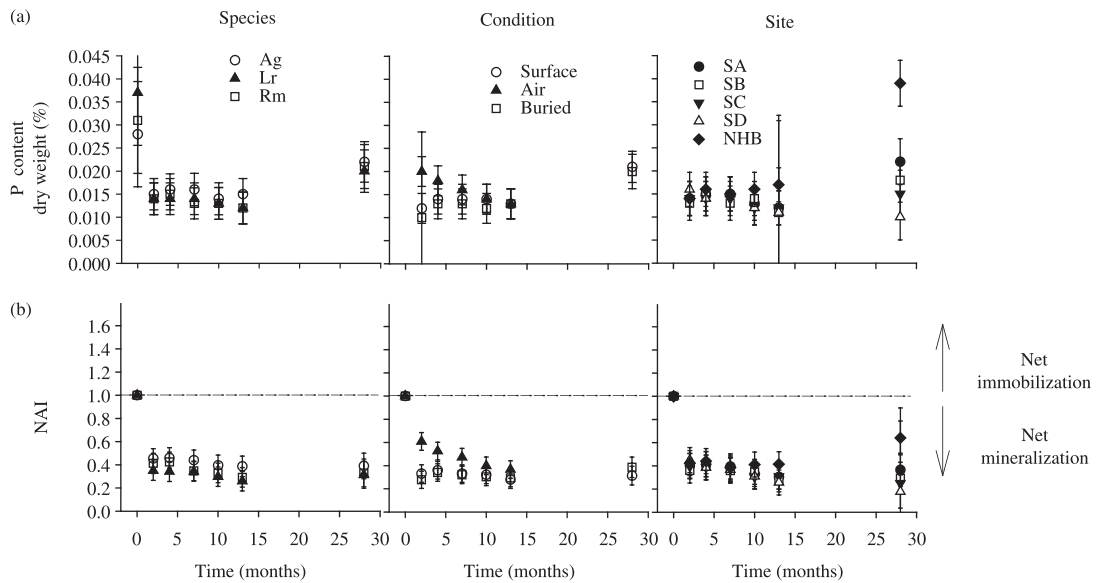


Fig. 5 Phosphorus content in decaying wood through time. (a) Changes in P content as a proportion of dry mass. (b) Changes in NAI. Both figures are averaged by species, condition and site. Error bars represent 95% CI.

Table 5 Slopes (%P mo⁻¹) of the significant linear regressions of phosphorus content as a function of time. * = slopes are significantly different from 0 at *P* < 0.05, ** = slopes are significantly different from 0 at *P* < 0.005, and *** = slopes are significantly different from 0 at *P* < 0.0001

Site	Condition	Sp	13 months		28 months	
			<i>P</i> slope	<i>r</i> ²	<i>P</i> slope	<i>r</i> ²
SA	air	<i>Ag</i>	-0.0005*	0.338		
SA	air	<i>Rm</i>	-0.0010*	0.311		
SA	surface	<i>Ag</i>			0.0003*	0.329
SA	surface	<i>Rm</i>			0.0005**	0.564
SA	buried	<i>Ag</i>			0.0010**	0.589
SA	buried	<i>Lr</i>			0.0010**	0.524
SA	buried	<i>Rm</i>			0.0005**	0.413
SB	air	<i>Lr</i>	-0.0010*	0.257		
SB	air	<i>Rm</i>	-0.0010*	0.274		
SB	surface	<i>Ag</i>			0.0003**	0.525
SB	buried	<i>Ag</i>			0.0002*	0.198
SC	air	<i>Ag</i>				
SC	air	<i>Lr</i>	-0.0004*	0.298		
SC	air	<i>Rm</i>	-0.0010*	0.276		
SC	surface	<i>Ag</i>			0.0002*	0.188
SC	buried	<i>Lr</i>			0.0003*	0.378
SD	air	<i>Ag</i>	-0.0010**	0.582		
SD	air	<i>Lr</i>	-0.0010**	0.497		
SD	air	<i>Rm</i>	-0.0010***	0.692		
SD	surface	<i>Rm</i>			-0.0002*	0.3
NHB	air	<i>Rm</i>	-0.0010**	0.517		
NHB	surface	<i>Ag</i>	0.0010**	0.532	0.0010***	0.684
NHB	surface	<i>Lr</i>			0.0010***	0.731
NHB	surface	<i>Rm</i>	0.0010*	0.265	0.0010***	0.831
NHB	buried	<i>Ag</i>	0.0010*	0.358	0.0010***	0.697
NHB	buried	<i>Lr</i>	0.0010*	0.42	0.0010***	0.793
NHB	buried	<i>Rm</i>			0.0010***	0.66

Phosphorus content of the wood disks increased from 2 to 28 months at all sites except at SD, the furthest site from the river mouth (Fig. 5a). The highest rate of TP increase was at NHB. TP increased at SA at a rate significantly higher than other Shark River sites, but significantly lower than at NHB ($0.001 \pm 1.498E-4$ vs. $0.001 \pm 0.000\%$ dry weight month⁻¹). The rate of *P* content change was significantly greater for buried disks than for surface disks ($4.200E-4 \pm 1.160E-4$ vs. $2.867E-4 \pm 1.073E-4\%$ dry weight month⁻¹). Although there was an absolute increase in TP in some treatments, there was no net gain of phosphorus during the period of this study due to large initial losses (Fig. 5b).

NUTRIENT RATIOS

Initial N : P molar ratios for mangrove wood were 22, 10 and 15 for *A. germinans*, *L. racemosa* and *R. mangle*, respectively. By the end of our study these had increased to 56, 43 and 47. Site, condition and species all had significant effects (all *P* < 0.0001) on the N : P ratios after 28 months of decay. *Avicennia germinans* had significantly higher N : P ratios than *L. racemosa* and *R. mangle* (Fig. 6a). N : P ratios increased from site SA (49) to SD (57), but there were not significant differences between sites SB and SC nor between SC and SD (Fig. 6b). Surface disks had significantly higher N : P ratios (53) than buried disks (45). Between sites, disks at NHB had lower ratios (38) compared with all Shark River sites (Fig. 6c).

Discussion

From our results, it is clear that there are two distinct phases in mass loss and nutrient dynamics that are likely to follow the deposition of CWD in mangrove forests. The first 2-month period is characterized by a

the mean slopes of the linear regressions for air disks were significantly different from the other conditions, and there were no significant differences between surface and buried disks.

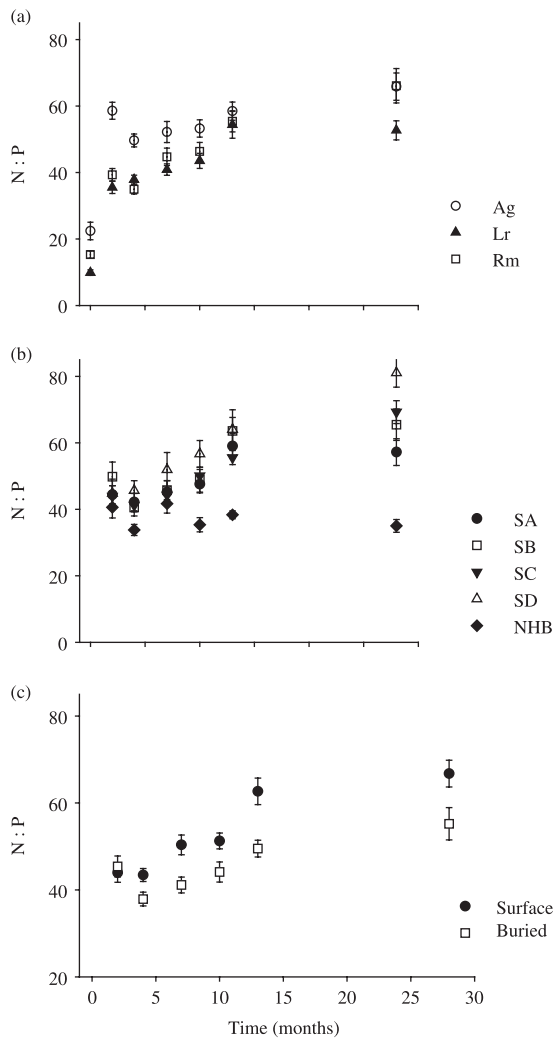


Fig. 6 N : P ratios through time averaged by species (a), site (b) and condition (c). Error bars represent standard errors.

rapid loss of mass and a net input of the nutrients N and P into the system as newly dead wood lost its most labile components. Mass loss from the downed wood would then slow down as bacteria and fungi decompose the more refractory components of the downed CWD and, during the next few years, the decomposing wood would serve as a minor sink for N and P in the forest. The relative importance of the initial phase would be dependent on the species composition of the forest, as we found that the relative proportion of labile to refractory components varied by species. We also found that the fate of the CWD (whether standing dead, lying on the sediment surface or buried in sediment) influenced the dynamics of wood decomposition and therefore the role that the CWD would play in ecosystem dynamics following a catastrophic deposition of CWD following a hurricane.

Unlike most long-term wood decomposition studies (e.g. Lambert *et al.* 1980; Spies *et al.* 1988), we used wood disks cut from living stems, which allowed us to do a more controlled comparison study in a shorter period of time. Thus, we were able to estimate the effects

of species, location and condition on wood decomposition, using a double exponential decay model to describe the two separate phases of mass loss. The observed length of the period of rapid mass loss is comparable with reported initial rapid losses of nutrients from wood in deciduous forest trees (France *et al.* 1997). We suspect that the early loss of mass in wood disks was attributed to abiotic leaching, as shown by others (Steinke *et al.* 1983; France *et al.* 1997). It was lowest for disks decomposing in the air and highest for disks decomposing on the soil surface, probably due to differences in water availability, as surface disks were subjected to regular tidal inundation at most of our sites, while disks decomposing in the air were dependent solely on the atmosphere for moisture. Little leaching would occur in air disks during the dry season, consistent with other studies that have suggested that leaching is enhanced in areas where there is strong flushing (Twilley *et al.* 1986; Currie & Aber 1997).

We suspect that difference in early mass loss between buried disks and those on the soil surface may have been a result of differences in both tidal flushing and oxygen availability for microbial decomposition. In most areas of Shark River, the soil surface is subjected to regular tidal flushing; however, areas beneath the soil surface may not be completely flushed after each tide. Tidal water trapped in the interstitial spaces of the soil can diminish the concentration gradient between water in disks and water of the surrounding environment, decreasing the advection potential of water-soluble components from buried disks. As microbial activity may have facilitated the initial rapid loss, anoxic conditions experienced by the buried disks could have depressed rates of mineralization. Other studies have demonstrated similar effects of oxygen availability on microbial degradation of tissue and leachate from *Rhizophora mangle* (Benner & Hodson 1985; Benner *et al.* 1986). However, Kristensen *et al.* (1995) suggested that fresh organic material is degraded at similar rates in the presence or absence of oxygen and that oxygen becomes more critical in the hydrolysis of some structurally complex and aromatic compounds.

We mimicked the composition of CWD deposited in the forest by extreme events, like hurricanes, by beginning our study with freshly harvested wood. The decay constant for the more refractory component of wood (k_2) in this study is analogous to the decay constants obtained from the single exponential model applied in other studies. Many studies on wood decomposition (Lambert *et al.* 1980; Lambert & Cromack 1982; Robertson & Daniel 1989; Polit & Brown 1996) use aged instead of freshly dead wood and do not therefore describe initial losses from the most labile components.

Due to the increased surface area: volume ratio of the disks used in this study, we estimated higher decay rates for mangrove wood (k_2) than reported for other types of wood in temperate forests. For instance, annual mass loss calculated for mangrove disks decomposing

on the soil surface (0.276 year^{-1}) occurred at rates three times higher than branches of *Quercus prinus* (0.092 year^{-1} ; Abbott & Crossley 1982) of similar diameter. However, mangrove wood decomposing in the air in our study, where moisture and presumably microbial activity was very low, had similar rates of mass loss (0.048 year^{-1}) to *Q. prinus* CWD decomposing in xeric conditions (0.0377 year^{-1} ; Abbott & Crossley 1982). The decay constant for *R. mangle* (0.288 year^{-1}) obtained in this study was also higher than that reported for large *Rhizophora* boles in Australia (0.083 year^{-1}), but similar to the decay constant obtained from branches (0.276 year^{-1}) in an Australian mangrove forest (Robertson & Daniel 1989). Unlike the decomposition of fine litter (e.g. leaves, flowers, stipules), the breakdown of woody tissue is largely influenced by the size of the CWD. Research has shown that, in general, decay coefficients decrease with increasing diameter of the bole (Christensen 1977; Abbott & Crossley 1982; Frangi *et al.* 1997).

Location of the wood within the forest at each site probably accounted for the overall pattern of decay throughout our study. Disks on the soil surface, which were exposed to tidal activity, precipitation and intermittent submergence in water, appeared to offer the best environment for microbial respiration. Disks in this treatment decomposed almost twice as fast as buried disks and five times as fast as disks decomposing in the air. When moisture in the substrate is below 30%, water is unavailable to microbial decomposers (Harmon *et al.* 1986). At each collection time, disks hanging in the air were always considerably dryer than disks from the other two conditions. In addition, after 7 months of decomposition, fungal mycelia were only present in the surface disks (L. M. Romero, T. J. Smith III & J. W. Fourqurean, personal observation).

We found that leaching and microbial decomposition prevailed during the initial 13 months for wood decomposing on the soil surface. However, by the second year of decomposition, disks lying on the soil surface in the more marine habitats had been colonized by shipworms. In a study of mangrove wood decomposition in Belize, shipworms were found to be the major decomposers (Kohlmeyer *et al.* 1995). Robertson & Daniel (1989) also found that shipworms were responsible for most of the weight loss from wood.

NITROGEN

Absolute nitrogen mass accumulation through time differed among conditions after 28 months of decay and was higher in disks decomposing on the soil surface compared with buried disks. Because lignin degradation is an oxidative process (Reid 1995), lignin-degrading fungi are probably not present in buried disks and it is possible that lower fungal activity may have contributed to their lower nitrogen accumulation rates in buried disks. During the first 13 months of decomposition in our study, nitrogen content increased by about 0.5–0.7%, and buried and soil surface wood disks lost

25–30% of their initial dry mass. Robertson *et al.* (1989) showed that 50% of the dry mass in *Rhizophora* branches was lost after about 2.5 years and that nitrogen content of the wood increased from 0.37% to 0.54%. Middleton & McKee (2001) found that small woody twigs lost from $49 \pm 6\%$ of their dry mass over 540 days. At our NHB site, which is characterized by much higher soil N concentrations than our other sites (Thomas J. Smith III, unpublished data), decomposing disks had the highest N accumulation rates. Unlike the Shark River sites, this site remains flooded for long periods of time after heavy rainfalls and is not tidally driven. The unique characteristics of this site may have contributed to this difference in nitrogen dynamics. In contrast to changes in nitrogen content of wood decomposing on or in the forest soil, the total nitrogen content of wood decomposing in the air remained essentially unchanged. Besides the low moisture for microbial colonization, dry precipitation and rainfall were the only sources of nitrogen.

The quality of litter was important during the initial 13 months of decomposition. Absolute nitrogen increased faster in *L. racemosa* than in the other two species. It has been shown in other studies that nitrogen accumulates faster when nitrogen content in litter is low enough to limit microbial activity (Aber & Melillo 1980). Although absolute nitrogen increased in all three species, only *L. racemosa* disks decomposing on the soil surface experienced net immobilization of nitrogen after 2 months of decomposition. Net nitrogen immobilization in *L. racemosa* buried disks only occurred at the end of this study. We can expect a large input of nitrogen to the forest soil in mangrove forest dominated by *A. germinans* and *R. mangle* during the initial stages of decomposition following a large-scale disturbance such as hurricanes when fallen dead trees is the largest pool of dead wood. However, these data suggest there may be later net immobilization of nitrogen in all three species and in wood that becomes buried with time. With time, wood becomes more recalcitrant as the labile components of wood are decomposed and nitrogen has been shown to increase during the lignin-controlled decomposition phase as this element is trapped in humic substances (Staaf & Berg 1982). This may be a mechanism to help explain measurements of nitrogen accumulation from surface waters within the wood-containing soils of mangrove forests (Rivera-Monroy & Twilley 1996).

PHOSPHORUS

The greatest loss of phosphorus occurred within the first 2 months of decomposition and greatly overshadowed any subsequent losses or gains over the next 2 years. Past decomposition studies on twigs and leaf litter would suggest that the bulk of this loss was due to leaching of soluble components from plant tissue (Steinke *et al.* 1983, 1992). We found that these initial P losses were greater in mangrove wood with higher

initial total phosphorus content. After the initial decrease, total phosphorus content in all treatment combinations stabilized at about 0.015% of the total dry mass. Between about 1 and 2 years of decomposition, there was a gross uptake of phosphorus, indicating bacterial translocation of P from the soil or other nearby sources. However, this was small in magnitude compared with the initial leaching losses, and was reflected in the calculation of net mineralization vs. net immobilization of TP in mangrove wood. Approximately 50–68% of the initial phosphorus was lost in the first 2 months for the buried and surface treatments. The gross TP gain during the last year of decomposition was not enough to regain the initial TP content in wood. Total phosphorus appears to be released more slowly during the first 13 months of decomposition from standing dead wood compared with downed and buried CWD, probably because of low microbial activity due to a lack of moisture in the substrate.

Total phosphorus accumulation rates decreased with distance from the mouth of the river except at SD where TP was continually released from the CWD over time. Concentrations of TP in the soil along the Shark River were shown to also decrease with distance from the mouth of the river (Chen & Twilley 1999). Therefore, the accumulation of phosphorus was lower in the most P-limited areas. A similar trend was shown by Sinsabaugh *et al.* (1993) with white birch sticks, where low P accumulation occurred in P-limited areas and high P accumulation occurred in areas least limited by P in a forested watershed in northern New York. Some studies in temperate systems have shown that following initial losses, phosphorus remains quite constant for a period of time and only increases when wood reaches an advanced state of decomposition (Lambert *et al.* 1980; Lambert & Cromack 1982). On the other hand, data from Sinsabaugh *et al.* (1993) showed that phosphorus increased linearly through time and that maximum TP concentrations were reached at approximately 80% mass loss.

The initial N : P molar ratios for mangrove wood were lower than or equal to the suggested optimum ratio of 20 for mineralization processes (Lambert *et al.* 1980). Compared with the initial N : P, this ratio increased twofold for *A. germinans*, fourfold for *L. racemosa* and threefold for *R. mangle* after 28 months of decay. The N : P ratios followed a similar trend of that for TP, where *A. germinans* has the lowest initial TP and the highest N : P ratio and the opposite was found for *L. racemosa*. However, N : P ratios for *L. racemosa* increased the most, but we attribute this to a larger increase in nitrogen compared with phosphorus. *A. germinans* had the lowest increase in N : P ratio during the 28 months of this study due to a lower rate of nitrogen increase.

Based on the numbers derived from the present study, and earlier reported estimates of dead wood biomass after Hurricane Andrew (Smith *et al.* 1994), we can estimate the ecosystem level impact of Andrew on

the coastal mangrove forest, although, for reasons previously described, our calculations may overestimate the amounts of nitrogen and phosphorus accumulated or released. The mangrove forests in south Florida are dominated by three species of trees, and our data show that there are species-level differences in nutrient dynamics of decaying wood. Importantly, our results allow us to predict patterns of nutrient dynamics at the species level, because Smith *et al.* (1994) provided data on the amount of CWD (branches and stems) from each species of mangrove (Krauss *et al.* 2005 report similar values for total CWD). Hurricane Andrew produced approximately 67 Mg ha⁻¹ of *A. germinans* wood, 47 Mg ha⁻¹ of *L. racemosa* and 46 Mg ha⁻¹ of *R. mangle* and our estimates of average change in nitrogen and phosphorus content in wood (averaged over condition and site) translate these figures into a release of 1.34 Mg N ha⁻¹ and 0.129 Mg P ha⁻¹ after only 2 months, summed over all three species. From months 2–13, the dead wood accumulated on average more than 9 Mg N ha⁻¹. Clearly, the large input of woody debris due to infrequent, large-scale events like Hurricane Andrew can have profound influences on nutrient dynamics in these forested, coastal systems. We have not attempted to estimate inputs from either root or leaf decomposition. Both of these plant tissues have higher concentrations of both nitrogen and phosphorus than does wood, so we would expect even greater releases of N and P in the first months following large-scale disturbances.

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