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Degradation of mangrove tissues and implications for peat formation in Belizean island forests

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Summary

1 Macrofaunal leaf consumption and degradation of leaves, woody twigs and roots were studied in mangrove island forests on a Belizean island. Factors influencing accumulation of organic matter deposited both above and below ground in this oligotrophic, autochthonous system were assessed.

2 Leaf degradation rates of *Rhizophora mangle* (red mangrove), *Avicennia germinans* (black mangrove) and *Laguncularia racemosa* (white mangrove) measured in mesh bags, were much faster in the lower than the upper intertidal zone. Mass loss was most rapid in *A. germinans* but zonal effects were much larger than species differences.

3 Exposure to invertebrates such as crabs and amphipods tripled overall rates of leaf litter breakdown. In the lower intertidal, crabs completely consumed some unbagged leaves within 23 days. Crabs also had an effect on some upper intertidal sites, where degradation of leaves placed in artificial burrows was 2.4 times faster than when placed on the soil surface.

4 In contrast to leaves (27 ± 5% remaining after 230 days), roots and woody twigs were highly refractory (40 ± 2% and 51 ± 6% remaining after 584 and 540 days, respectively). Root degradation did not vary by soil depth, zone or species. Twigs of *R. mangle* and *A. germinans* degraded faster on the ground than in the canopy, whereas those of *L. racemosa* were highly resistant to decay regardless of position.

5 Peat formation at Twin Cays has occurred primarily through deposition and slow turnover of mangrove roots, rather than above-ground tissues that are either less abundant (woody twigs) or more readily removed (leaves).

Key-words: detritivores, leaf burying crabs, litter decomposition, litter processing, peat accumulation

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Introduction

Mangroves are assemblages of trees and shrubs that dominate the intertidal zone along coastlines, estuaries and islands in tropical and subtropical regions of the world. Work in Florida and tropical Australia has shown the importance of litter dynamics for the export of detritus to adjacent coastal ecosystems as well as to nutrient cycling (Robertson 1986; Twilley *et al.* 1986; Robertson & Daniel 1989a). Retention of organic matter is, however, important for vertical accretion and habitat stability in mangroves (Cahoon & Lynch 1997), particularly those that receive little allochthonous input of sediment, e.g. islands built on carbonate platforms that cannot otherwise keep pace with sea-level rise (Ellison & Stoddart 1991; Parkinson *et al.* 1994). For accumulation to occur, however, the rate of organic matter loss from the system must be slower than the rate of biomass production (Glaser 1987).

The processes leading to development of mangrove peat are not well understood, but its composition, i.e. the relative proportion of leaf, wood and root material, provides some insight. Some mangrove peats have extremely low ratios of aerial (shoot) to root debris (0.02–0.04), in contrast to freshwater swamp peats (1.50–1.86) (Spackman *et al.* 1966; Cohen & Spackman 1977), but although this supports other work suggesting roots are a major component of mangrove peat (Woodroffe 1983; Cameron & Palmer 1995; McKee & Faulkner 2000a), leaves (Lacerda *et al.* 1995) or wood (Robertson & Daniel 1989b) may also contribute to

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soil organic matter. These differences may be attributable to variation in the relative degradation rates of mangrove tissues within and among mangrove forests due to differences in biotic and abiotic factors. Thus, the overall goal of our work was to examine the degradation mechanisms controlling peat formation, since this information is essential to an understanding of mangrove forest development and habitat stability, particularly in the Caribbean region (Ellison & Stoddart 1991; Parkinson *et al.* 1994).

Mangrove-dominated islands occurring in Belize's Barrier Reef Complex provided an ideal setting for the study of litter degradation and the relative importance of organic matter accumulation to soil formation. Such island mangrove systems accumulate substrate more slowly than basin or riverine forests (1, 1–2 and > 2 mm/year, respectively; Twilley *et al.* 1992) and primarily through autochthonous processes (Ellison & Stoddart 1991; Parkinson *et al.* 1994; Cameron & Palmer 1995). Their remoteness from mainland sources of mineral sediments limits allochthonous inputs (Macintyre *et al.* 1995) and thus increases their vulnerability to submergence by rising sea level. Examination of soil cores reveals that the substrate is primarily peat and that organic matter contribution is key to the maintenance of these forests relative to sea-level rise (Cameron & Palmer 1995; Macintyre *et al.* 1995; Rützler & Feller 1996; McKee & Faulkner 2000a). The large amounts of peat underlying Belizean mangrove islands (Macintyre *et al.* 1995) further suggest that production rates are coupled with low rates of organic matter turnover. The relative isolation of these island systems has also prevented substantial human impacts that might alter rates of production or loss of organic matter. Our work was centred on a small archipelago called Twin Cays that has been the focus of numerous mangrove studies over the past 20 years (Rützler & Feller 1996).

We investigated: (i) relative rates of degradation among mangrove tissues (leaf, twig and root) as well as differences among species (*Rhizophora mangle* L. (red mangrove), *Avicennia germinans* (L.) Stearn. (black mangrove) and *Laguncularia racemosa* (L.) Gaertn. f. (white mangrove)); and (ii) spatial variation in degradation rates in response to biotic and abiotic factors that vary across the intertidal zone. In particular, effects of macrofaunal consumers on leaf litter degradation were examined at two intertidal positions. Vertical variation in decay rates was also determined in different forest strata by measuring degradation of leaves on the soil surface and buried in simulated crab burrows, of woody twigs in the canopy and on the ground, and of roots at different soil depths. This detailed study is the first to compare degradation rates of mangrove tissues in relation to the potential contribution of above- vs. below-ground litter to organic matter accumulation. The results provide insight into organic matter turnover rates and patterns and the processes controlling soil formation and vertical

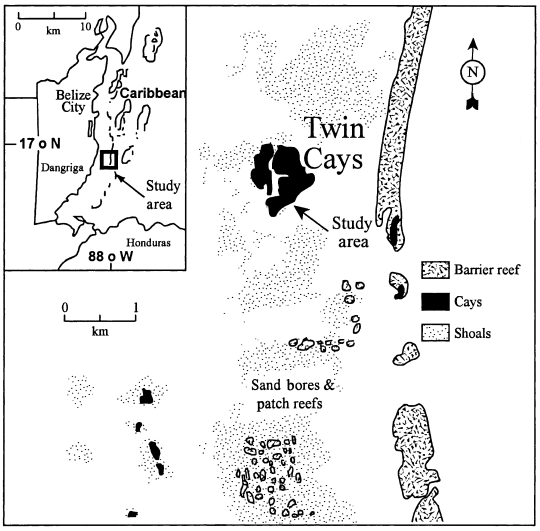

Fig. 1 Site map showing location of Belize and study site at Twin Cays (from Rützler & Macintyre 1982), Smithsonian, Washington, D.C., by permission.

accretion of mangrove islands in the Caribbean region (Ellison & Stoddart 1991; Parkinson *et al.* 1994), as well as other carbonate systems (Woodroffe 1992).

Study site

Belize contains about 78 000 ha of mangrove forest, 40% of which occurs on offshore islands in the Barrier Reef Complex that extends 257 km from Ambergris Cay to the Gulf of Honduras (Zisman 1992). The Twin Cays archipelago is 91.5 ha in area and is located 2.3 km west of the reef crest and about 12 km from the mainland (16°50′ N latitude, 88°06′ W longitude; Fig. 1). Based on corings and radiocarbon dates, these mangrove islands are underlain by several metres of peat atop a Pleistocene limestone platform and are about 7000 years old (Macintyre *et al.* 1995). The tides in this region are microtidal (range *c.* 20 cm) and of a mixed semidiurnal type (Kjerfve *et al.* 1982).

Belize's climate is subtropical, with an average minimum temperature of 20 °C in December and an average maximum temperature of 31 °C in August (Stoddart *et al.* 1982). Rainfall in Belize is highly variable, but in the vicinity of Twin Cays it varies seasonally from a maximum in November (monthly mean = 335 mm) to a minimum in March (monthly mean = 23 mm) (Rützler & Ferraris 1982).

The vegetative and edaphic conditions at Twin Cays (McKee 1995a) are typical of mangrove systems found elsewhere in the Caribbean. Floristically simple zones of vegetation occur along elevational gradients from the sea to the island interior. The dominant macrophyte overall is *R. mangle* and dense stands form fringes along the shoreline, with canopies averaging 3–7 m in height. At slightly higher landward elevations, stands are dominated by *A. germinans*, with *L. racemosa* and *R. mangle* often occurring as subdominants. The shoreline zone (hereafter referred to as lower intertidal)

was inundated twice daily (> 700 inundations per year), whereas the landward zone (hereafter referred to as upper intertidal) was generally only inundated during spring tides (< 100 inundations per year).

Materials and methods

HYDRO-EDAPHIC CONDITIONS

At the beginning of the study, measurements were made in each zone of water depth at high tide, redox potential (Eh) and temperature of the soil, and of salinity, pH and sulphide concentration as described in McKee *et al*. (1988) and McKee (1995a).

MACROFAUNAL CONSUMPTION

Macrofaunal consumption over a 23-day interval and leaf and root degradation experiments were conducted in five 10 × 10 m plots established along the shoreline in a fringing mangrove forest dominated by *R. mangle* and also in a further five in a zone 15–25 m from the shoreline dominated by *A. germinans*. Whole, senescent leaves were collected from trees of the three species on Twin Cays in January 1994, and individual leaves were deployed in mesh bags (1 mm^2 or < 0.01 mm^2 mesh size) or unbagged to differentially exclude macrofauna. Each leaf was numbered, measured (CID, Inc. leaf area meter) and tethered with monofilament attached either to the enclosing mesh bag or to the rachis (by threading it through tiny holes in the blade at the leaf base). Sets of bags were placed in each of the 10 plots. Five leaves per species per plot were removed at 0, 6, 11, 17 and 23 days, and leaf area was re-measured. Any unbagged leaves that completely disappeared were presumed to have come untied and were excluded from the analyses.

DEGRADATION EXPERIMENTS

Leaves and roots

Leaves of the three mangrove species were collected from Twin Cays, air-dried to a constant mass and 20 g (2–5 leaves) of each species separately placed in mesh bags (10 × 20 cm) with 1 mm^2 mesh and placed in the 10 plots in January 1993. An extra set of bags containing *R. mangle* leaves was also placed underground in an area (upper intertidal) containing burrows (2–5 burrows m^{-2}) of the herbivorous crab, *Ucides cordatus* L. Holes (5 cm diameter × 30 cm length) were cored to create artificial burrows and simulate conditions for leaves that are taken below ground by leaf-burying crabs. One bag was collected from each plot or the 'burrows' at intervals extending over 230 days.

Root degradation was also studied in the two zones, but only with *R. mangle* and *A. germinans*. Live, below-ground roots of these species were collected by excavation from monospecific stands in another area of Twin Cays. Live roots were distinguished by colour, turgidity and structural integrity and represented a range of size classes from fine (< 2 mm diameter) to coarse (> 10 mm diameter). The below-ground root material was separated from above-ground structures (e.g. prop roots) by severing at the soil line. Mesh bags divided into three sections at 10-cm intervals were filled with air-dried root material (4 g per section for a total of 12 g per bag). Roots representing both fine and coarse size classes were placed in each section of the bag. In January 1994 the bags were inserted vertically into the soil so that the tops of the bags were level with the soil surface and the bottoms were 30 cm deep, and soil was then carefully replaced to fill any space around the bags. Bags were collected from each plot at approximately 6-month intervals over 584 days.

Woody twigs

Fresh, small diameter (1–2 cm) branches of the three mangrove species were collected in January 1994 from trees at Twin Cays, divided into lengths of 12 cm and air-dried. Six twigs per species were tethered with monofilament either in the canopy or on the ground in the five plots in the lower intertidal zone only. The twigs were collected at approximately 6-month intervals over 548 days.

Processing of degraded material

After collection, the litter material in the leaf and root bags was cleaned with deionized water and extraneous material was removed. New roots had often grown into the root bags and immediate processing was necessary to allow accurate separation of ingrown from original root material. Unbagged stems were similarly washed and all material was then dried to a constant mass at 70 °C and weighed.

ANALYSIS

To assess differences in degradation rates that are relevant to peat formation, we calculated percentage loss day^{-1}. This approach was used instead of fitting the data to exponential models because we were more interested in the refractory material contributing to organic matter accumulation than the pattern of loss over time. Total percentage remaining (X) for leaves, stems and roots was calculated from the weight at the end of the study (X_t) and the initial biomass (X_o) as: $X = 100\ (X_t/X_o)$, and, for macrofaunal consumption, from changes in leaf area over time. Total percentage loss ($L = 100 - X$) was then divided by the number of days in the study.

One-, two- and three-way ANOVAS were used to analyse mean rates of percentage loss day^{-1} by using arcsine square root transformed data (SAS JMP 1998). Significance was determined at $P \leq 0.05$ (Sokal & Rohlf 1981). Single degree of freedom contrasts of interest were conducted to distinguish among three or more

Table 1 Comparison of hydro-edaphic conditions in the lower and upper intertidal zones at Twin Cays, where degradation and macrofaunal consumption rates were measured. Values are mean ± SE (n = 5); ***P < 0.001; **P < 0.01; *P < 0.05; NS = not significant

Variable	Lower intertidal	Upper intertidal	t-test
Eh (mV) at 1 cm	–19 ± 27	28 ± 1	1.74 NS
Eh (mV) at 15 cm	–86 ± 14	109 ± 8	12.5***
Soil temperature (°C)	25.9 ± 0.3	30.4 ± 0.3	13.0***
Water depth (cm)	9.9 ± 1.6	1.2 ± 0.1	5.32**
Salinity (‰)	35 ± 1	66 ± 3	10.4***
pH	6.4 ± 0.1	5.1 ± 0.03	14.7***
Sulphide (mM)	0.23 ± 0.07	< 0.01 ± 0.00	3.18*

levels of factors where ANOVA indicated a significant difference (SAS JMP 1998).

Results and discussion

HYDRO-EDAPHIC CONDITIONS

Hydro-edaphic conditions varied substantially across the intertidal zone and generated broad gradients in salinity and flooding, as reported previously (McKee 1995a). The lower intertidal zone, which was characterized by frequent tidal inundation and thus had a greater range of tidal fluctuation, also had lower Eh and higher sulphide and pH (Table 1). The upper intertidal zone, where the degree of soil flushing was diminished, experienced less frequent flooding over the soil surface and consequently exhibited higher soil Eh and lower sulphide concentrations (Table 1). Temperature and salinity were higher in the upper intertidal zone during this study (Table 1), similar to previous observations (McKee 1995a). Although average porewater salinity varied both spatially and temporally (between 30% and 80%) across Twin Cays, it tended to remain near sea strength year-round in the fringe forest (McKee 1995a). Conditions became hypersaline (> 50‰) in the less frequently inundated areas during the dry season (McKee 1995a).

LEAF DEGRADATION

Loss from mesh bags

Leaves in mesh bags degraded quickly in the lower intertidal zone, with little or no tissue remaining after 150 days (Fig. 2, Table 2). Rates of degradation were much slower in the upper intertidal zone, with between 50% and 75% of the original material remaining even after 230 days. Leaf degradation rates (0.20–0.43% loss day^{-1}) fell in the range reported for other tropical mangrove forests (0.20–0.55% loss day^{-1}; Heald 1971; Woodroffe 1982; van der Valk & Attiwill 1984; Twilley *et al.* 1986; Robertson 1988; Twilley *et al.* 1997) as well as for tropical lowland rain forests (0.15–0.58% day^{-1}; Anderson & Swift 1983).

The effect of intertidal position was similar to that reported for other locations. Twilley *et al.* (1986) found

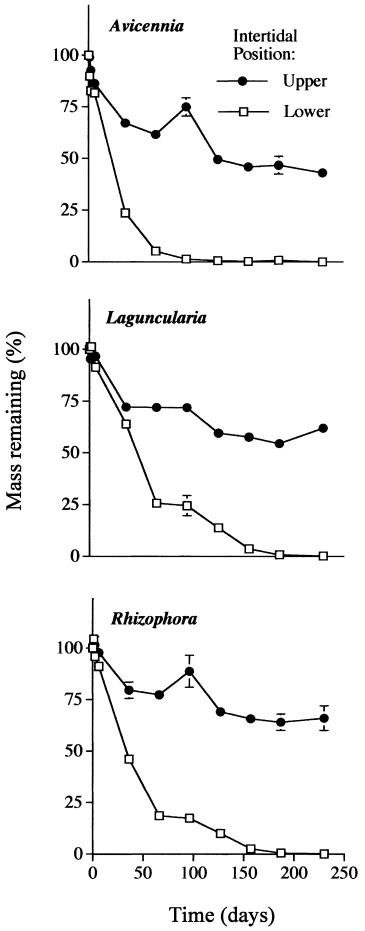

Fig. 2 Percentage of *Avicennia germinans*, *Laguncularia racemosa* and *Rhizophora mangle* leaf material remaining in mesh bags deployed in the upper and lower intertidal zones. Values are the mean ± 1 SE (n = 5).

that leaves of *R. mangle* and *A. germinans* degraded faster in a basin mangrove forest where 190 flooding tides occurred during the experimental period, compared with a site that had only 127 tides, and leaves tended to degrade two to three times faster in subtidal regions of mangrove systems than in the intertidal (reviewed in Robertson *et al.* 1992).

The initial rapid loss of mass was attributable to leaching of dissolved organic matter (Camilleri & Ribi 1986; Robertson 1988). Mass losses after the first 30 days were then mediated by microbial and fungal

Table 2 ANOVA comparison of percentage leaf loss day^{-1} for main effects and interaction between species (d.f. = 2, 29) and zone (d.f. = 1, 29) at Twin Cays, Belize: $^{**}P < 0.01$

Source	*F*	*P*	Mean (± 1 SE)
Species	27.2	**	
Avicennia germinans			0.341 ± 0.032
Laguncularia racemosa			0.300 ± 0.045
Rhizophora mangle			0.306 ± 0.043
Zone	1871	**	
Lower intertidal			0.434 ± 0.001
Upper intertidal			0.197 ± 0.011
Species × zone	26.8	**	

Table 3 ANOVA comparison of percentage leaf loss day^{-1} due to macrofaunal consumption by species, zone (d.f. = 1, 134) and bag type (d.f. = 2, 134) at Twin Cays, Belize: $^{**}P < 0.01$, NS = not significant

Source	*F*	*P*	Mean ± 1 SE
Species	2.1	NS	
Avicennia germinans			0.348 ± 0.204
Laguncularia racemosa			0.537 ± 0.247
Rhizophora mangle			0.175 ± 0.119
Zone	8.3	**	
Lower intertidal			0.699 ± 0.217
Upper intertidal			0.007 ± 0.007
Bag type	12.5	**	
No bag			0.989 ± 0.305
Coarse mesh			0.071 ± 0.071
Fine mesh			0.000 ± 0.000
Species × zone	0.4	NS	
Species × bag type	1.8	NS	
Zone × bag type	7.2	**	
Species × zone × bag type	0.4	NS	

populations, which develop rapidly on mangrove leaves (Benner *et al*. 1988). Frequent submergence (lower intertidal) probably both promoted leaching and maintained moisture and temperature conditions that were conducive to saprophytic decay (Reice *et al*. 1984) compared with limited moisture availability in the upper intertidal (Webster & Benfield 1986), where higher temperatures (Table 1) may also have exceeded optimum levels for decomposers, particularly on the soil surface. Overall, the stable conditions in the lower intertidal promoted degradation rates that were twice as fast as at upper intertidal sites (Table 2).

Differences in species also significantly affected leaf degradation rates, with *A. germinans* showing more rapid mass losses than *R. mangle* and *L. racemosa*, averaged over zone (Table 2), possibly due to its higher nitrogen and lower tannin concentrations (McKee 1995b, 1995c). Other workers have attributed the faster degradation of leaves of *Avicennia* spp. to differences in chemical composition (Cundell *et al*. 1979; Twilley *et al*. 1986; Robertson 1988). Intertidal zone, however, had a much greater effect than species (Table 2, Fig. 2), suggesting that external factors may be more important in determining overall degradation rates at Twin Cays.

Macrofaunal consumption or burial

Macrofauna can accelerate tissue breakdown of mangrove leaves by direct consumption and/or burial and mangrove leaves and other litter (e.g. propagules) may be removed by herbivorous crabs shortly after falling to the forest floor (Robertson & Daniel 1989a; Micheli *et al.* 1991; Steinke *et al.* 1993; McKee 1995c; Twilley *et al.* 1997). Mangrove tissues will degrade more rapidly following breakdown into smaller particles and passage through the macrofaunal gut (Camilleri 1992) and burrowing crabs may also carry leaves and leaf fragments below ground (Robertson 1986; Robertson & Daniel 1989a).

The leaves that were tethered, rather than bagged, lost 1.0 ± 0.3% day^{-1} of their original leaf area, averaged over species and zone (Table 3) and damage was attributable to herbivorous crabs, i.e. the leaf margins were either shredded, or large sections of the leaf lamina had been clipped off (Fig. 3). Of the two species of

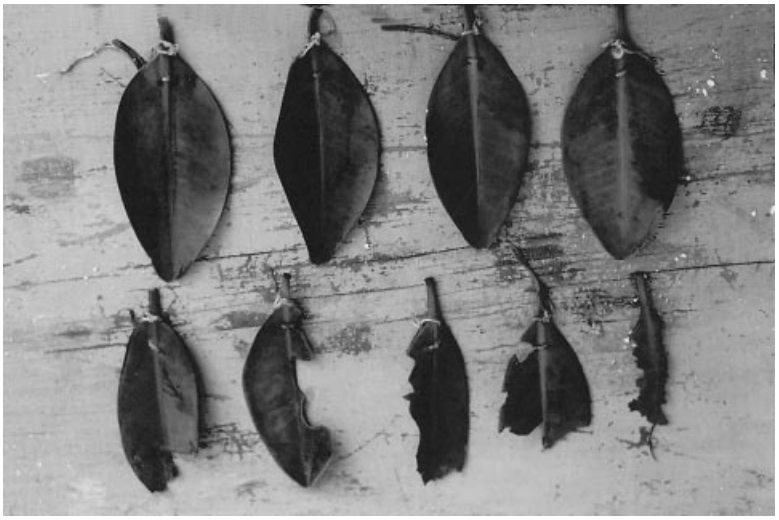

Fig. 3 *Rhizophora mangle* leaves (unbagged) that were tethered in the upper (top) and lower (bottom) intertidal zone at Twin Cays. Leaves placed in the lower intertidal position show characteristic damage by mangrove crabs.

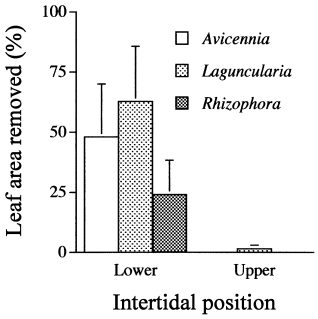

Fig. 4 Macrofaunal consumption as total percentage loss over a 23-day interval of *Avicennia germinans*, *Laguncularia racemosa* and *Rhizophora mangle* leaves (unbagged) in upper and lower intertidal positions. Values are the mean ± 1 SE (n = 5).

crab known to feed on mangrove leaves that were observed in the study area (*Goniopsis cruentata* Latreille and *U. cordatus*, McKee & Feller 1992; McKee 1995c), *G. cruentata* was observed picking up and tearing pieces from the tethered leaves during low tide, whereas leaves tethered near the burrows of *U. cordatus* were often missing large sections or were pulled underground. In contrast, only small amounts of tissue were removed from the coarse mesh bags, which excluded macrofauna (e.g. crabs) but allowed access to mesofauna (e.g. amphipods) (Table 3). Bags with damaged leaves often contained one or more amphipods (*Gammaridea*) that were apparently able to enter through the small (1 mm) holes in the mesh. No visible tissue damage occurred in fine mesh bags that excluded all meso- and macrofauna.

Although *R. mangle* leaves lost less tissue overall than *L. racemosa* and *A. germinans*, species differences were not significant (Table 3). A significant bag type by zone interaction (Table 3), reflected the fact that consumption of unbagged leaves differed across zones (Fig. 4) but bagged leaves did not (Table 2). Unbagged leaves were lost to macrofauna in the lower intertidal position ($1.96 \pm 0.50\%$ day^{-1}), whereas few leaves of those placed in the upper intertidal zone exhibited damage ($0.02 \pm 0.02\%$ day^{-1}; $t = -4.34$, $P < 0.0001$, 1 d.f. contrast). Bagged leaves disappeared to a similar small extent in both zones ($P > 0.05$, 1 d.f. contrast), showing that zonal effects are due to macrofauna, possibly reflecting spatial variation in relative abundance of herbivorous crabs. Jones (1984) found that the lower intertidal zone in a Jamaican mangrove forest was dominated by *G. cruentata* and *U. cordatus*, whereas higher elevations were characterized by *Uca* spp. that mainly feed on particulate material picked from the sediment.

Thus, a large percentage of the leaf material that is not lost to tidal export is rapidly processed in the lower intertidal zone. Macrofaunal consumption increased leaf degradation about three times over that of microbial decay but was less than that reported in Australian mangrove swamps where crabs increased turnover of leaf litter by as much as 75 times (Robertson & Daniel 1989a). Although some workers in south Florida have reported that little leaf litter is processed by mangrove crabs (McIvor & Smith 1995), others have reported high removal rates there by gastropods (60–80% leaf area removed in 42 days, Proffitt *et al*. 1993; McKee & Faulkner 2000b). Leaf consumption is also high (98–100%) in other New World forests where herbivorous crabs are abundant (Wiebe & Saucerman 1991; Twilley *et al*. 1997). Our work at Twin Cays further demonstrates that rates of leaf removal by macrofauna may vary substantially with intertidal position in New World forests.

Although herbivorous crabs were observed shredding leaves and other litter at Twin Cays in this and other studies (McKee & Feller 1992; McKee 1995c), some workers have reported that only a fraction of removed leaves was consumed immediately. In Australia and Africa, most of the leaves and leaf fragments were taken below ground and plastered along the walls of crab burrows (Giddins *et al*. 1986; Micheli *et al*. 1991). However, even if leaves are not consumed below ground, they may degrade more quickly than those placed on the soil surface, particularly in less frequently inundated areas. When *R. mangle* leaves were placed in simulated crab burrows, they degraded twice as fast as leaves placed on the soil surface in the upper intertidal zone (0.432 ± 0.002 vs. $0.178 \pm 0.009\%$ loss day^{-1}, $P < 0.0001$). Leaves in simulated burrows were probably subjected to periodic oxygenation and wetting, and these conditions may have enhanced degradation (Webster & Benfield 1986). More rapid leaching of leaf tannins below ground may also encourage faster saprophytic decay, as tannins may delay degradation by combining with internal enzymes of detritivores as well as the extracellular enzymes of microorganisms (Horner *et al*. 1988). Where leaf degradation is slow on the soil surface (e.g. upper intertidal), burial by crabs may thus increase degradation rates and decrease build-up of litter on the forest floor. However, such effects may be localized and dependent on crab densities and foraging patterns.

WOODY TWIG DEGRADATION

Mangrove twigs (whether remaining in the canopy or fallen) degraded extremely slowly at Twin Cays (Table 4, Fig. 5), as in other forest types (Harmon *et al*. 1986), and over time may build to large standing stocks in mature forests (Robertson & Daniel 1989b). The slow degradation of woody twigs has obvious consequences for long-term carbon turnover and soil formation in mangrove ecosystems, but few studies have provided estimates of decay rates. Dead twigs and small branches of *R. mangle* may persist in the mangrove canopy at Twin Cays for up to 1.5 years before falling into the litter (Feller & Mathis 1997) and 75 ± 3% persisted for 540 days in this study. Little is known about the factors affecting breakdown of standing dead wood in mangrove forests, although a

Table 4 ANOVA comparison of percentage woody twig loss day^{-1} for main effects and interaction species (d.f. = 2, 29) and position (d.f. = 1, 29) at Twin Cays, Belize: $^{**}P < 0.01$

Source	*F*	*P*	Mean ± 1 SE
Species	31.1	**	
Avicennia germinans			0.089 ± 0.010
Laguncularia racemosa			0.035 ± 0.005
Rhizophora mangle			0.083 ± 0.005
Position	40.5	**	
Canopy			0.047 ± 0.005
Ground			0.091 ± 0.011
Species × position	7.9	**	

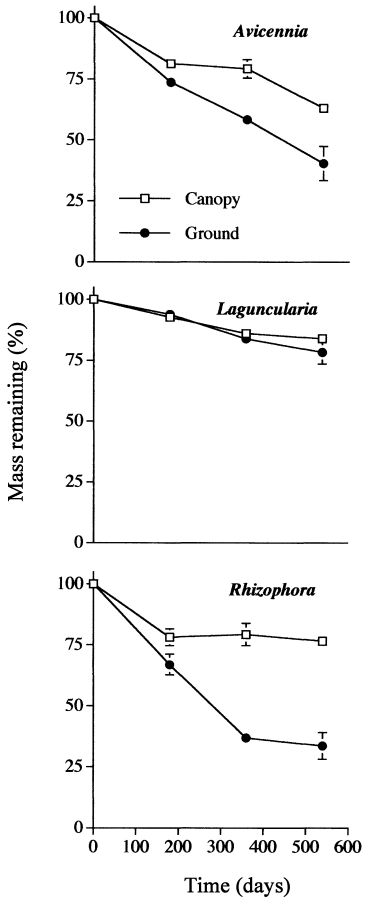

Fig. 5 Percentage of *Avicennia germinans*, *Laguncularia racemosa* and *Rhizophora mangle* woody twigs remaining in the canopy and on the ground. Values are the mean ± 1 SE (n = 5).

number of wood-boring insects and termites feed on it (Feller & Mathis 1997) and the numerous holes in some twigs suggested that wood-boring insects may have contributed to mass loss.

Deposition of *A. germinans* and *R. mangle* wood on the forest floor promoted more rapid mass loss (Fig. 5) but *L. racemosa* was as resistant to decay in the canopy (Fig. 5, Table 4). Overall, woody twigs placed on the ground at Twin Cays degraded at a comparable rate to that reported for Australian forests (Robertson & Daniel 1989b). Decay of fallen mangrove wood in other forests has been attributed mainly to marine

Table 5 ANOVA comparison of percentage root loss day^{-1} for main effects and interaction of species (d.f. = 1, 29), zone (d.f. = 1, 29) and depth (d.f. = 2, 29) at Twin Cays, Belize: NS = not significant

Source	*F*	*P*	Mean ± 1 SE
Species	0.8	NS	
Avicennia germinans			0.106 ± 0.004
Rhizophora mangle			0.100 ± 0.004
Zone	2.3	NS	
Lower intertidal			0.108 ± 0.004
Upper intertidal			0.098 ± 0.004
Depth	0.9	NS	
10 cm			0.105 ± 0.005
20 cm			0.098 ± 0.007
30 cm			0.106 ± 0.004
Species × zone	1.2	NS	
Species × depth	0.8	NS	
Zone × depth	0.3	NS	
Species × zone × depth	1.5	NS	

wood-boring organisms (e.g. teredinid molluscs) (Robertson & Daniel 1989b; Robertson *et al.* 1992). In contrast to mass loss in leaves, leaching and saprophytic decay are not important processes in wood degradation (Brinson *et al.* 1981). However, wood degradation may be similar to leaves in that it is greatly accelerated by wood-feeding meso- and macrofauna (Feller & Mathis 1997; Robertson & Daniel 1989b). Thus, standing and fallen wood will be processed at different rates and by different pathways depending on species composition of mangroves and wood-feeding organisms.

ROOT DEGRADATION

Roots degraded at a similar rate in the two zones, and there was little difference between the two species tested or with burial depth (Table 5); an average was therefore plotted in Fig. 6. Other workers have documented a similar slow decay of mangrove roots belowground. Roots of *Avicennia marina* (*c.* 1 mm diameter) degraded slowly in New Zealand (30% in 154 days; Albright 1976) and Australia (15% and 60% loss in 270 days for small and large diameter roots, respectively; van der Valk & Attiwill 1984). At Twin Cays, about half of a coarse and fine root mixture was lost in 300 days, but little of the original mass was lost thereafter (Fig. 6). Although some of the remaining material could perhaps be attributed to roots that had grown into the bags and then died, the original material was meticulously separated from extraneous roots. Also, most of the refractory material was identified as the lignified epidermis of large roots (> 1 cm diameter) that could not have grown into the bag through the 1-mm mesh material. Even allowing for a 10% overestimation of remaining material, about 30–40% of the root mass deposited below ground degraded extremely slowly, indicating a high potential for accumulation over time.

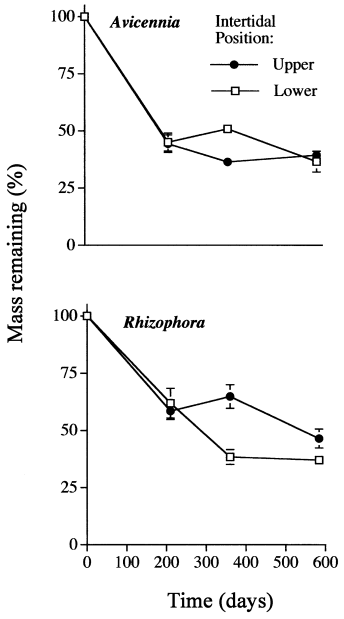

Fig. 6 Percentage of *Rhizophora mangle* and *Avicennia germinans* roots remaining in mesh bags (averaged over depth) deployed in the upper and lower intertidal zones. Values are the mean ± 1 SE (n = 5).

IMPLICATIONS FOR PEAT FORMATION AND HABITAT STABILITY

Peat deposits are found beneath many tropical mangrove forests (Ellison & Stoddart 1991; Parkinson *et al*. 1994; Fujimoto *et al*. 1996; Fujimoto *et al*. 1999), except in deltaic environments where mineral sediment makes a large contribution to soil formation (Woodroffe 1983). Island forests such as Twin Cays that receive little terrigenous sediment depend upon organic matter deposition to maintain soil surface elevations and for nutrient regeneration. Sediment cores up to 10-m deep in the Tobacco Range (*c*. 5 km north of Twin Cays) document some of the thickest Holocene peat deposits ever recorded (Cameron & Palmer 1995; Macintyre *et al*. 1995). Analyses of these peat cores indicate average organic matter contents ranging from 50% to 90% and dominance by mangrove-derived plant fibres (Cameron & Palmer 1995; McKee & Faulkner 2000a).

The amount of organic matter accumulated in mangrove ecosystems generally depends on litter production and degradation processes, in combination with physical processes such as tidal export. Although organic matter and/or carbon accumulation has been quantified in some mangrove wetlands (e.g. Fujimoto *et al*. 1999), there is little understanding of the specific mechanisms controlling this process, particularly below ground. Some information exists for other peat-forming systems, however. The accumulation of peat in tropical wetland systems occurs under conditions of low oxygen and low concentrations of nutrients, in combination with refractory plant material (e.g. lignin-rich tissues) (Kivinen & Pakarinen 1981). Wetland sediments are characterized by little or no oxygen and degradation of plant material in anaerobic environments is generally slower than under aerobic conditions (Brinson *et al*. 1981). In addition, low concentrations of alternate, high-energy oxidants (e.g. nitrate), in combination with a paucity of fungi, limit degradation of lignin-rich, vascular plant material in anaerobic environments (Valiela 1995). Thus, refractory plant material produced or deposited in anaerobic, oligotrophic environments degrades very slowly and, over time, can accumulate in large quantities.

The role of degradation, however, can not be evaluated without knowledge of the inputs of mangrove tissues capable of peat formation. Rates of mangrove leaf fall are higher along the shoreline of Twin Cays (lower intertidal zone in this study; 700 g m^{-2} $year^{-1}$) than in the *A. germinans*-dominated mixed stands (upper intertidal zone in this study; 450 g m^{-2} $year^{-1}$) or in the dwarf *R. mangle* stands in the island interior (280 g m^{-2} $year^{-1}$) (Koltes *et al*. 1998). However, leaves in the lower inertidal may be removed quickly by tidal action, consumption by fauna and rapid microbial decay (Tables 1–3, Figs 2–4), and leaf litter may therefore contribute to peat formation, mainly in areas lacking macrofaunal consumers and/or with less frequent tidal inundation, e.g. at higher intertidal locations at Twin Cays (Tables 2 and 3 and Figs 2–4, this study) and basin forests at Rookery Bay (Cahoon & Lynch 1997).

Although woody twigs degrade extremely slowly with 51 ± 6% remaining after 1.5 years, they constitute a much smaller fraction (< 10%) of above-ground litterfall in mangrove ecosystems as compared with leaves (> 70%) (Day *et al*. 1996; Twilley *et al*. 1997). It is thought that most of the processed wood remains in the mangrove system (Boto & Bunt 1981) and that the small particles of wood detritus are incorporated into the sediments (Robertson & Daniel 1989b).

Roots, however, have a much greater potential to contribute to peat build-up at Twin Cays, particularly at low intertidal positions (Fig. 6), where 40 ± 2% of roots remained after 1.5 years but most leaf material disappeared within 1 year (Fig. 2). Information about below-ground production in mangrove forests is almost entirely lacking but work in south-west Florida indicates that root inputs may be as high as 50–60% of leaf fall values (McKee & Faulkner 2000b). In addition, roots generally degrade where they are produced (reduced loss) and the absence of spatial variation in degradation may reflect more homogeneous conditions below ground. Slow degradation of mangrove roots, in combination with high biomass production, would thus promote high accumulation rates and agrees with observations that mangrove peat in Belize is comprised predominately of root material (Cameron & Palmer 1995; McKee & Faulkner 2000a). Higher degradation rates for leaves than roots or wood are consistent with other studies (Table 6), although more information is needed about wood and root degradation in a variety of locations to confirm the generality of these findings.

Table 6 Mangrove tissue degradation rates at various world locations. The means ± 1 standard error are given for each tissue type by intertidal position

	Percentage loss day^{-1}							
	Leaves		Roots		Wood			
Species	Low/ Middle	Upper	Low/ Middle	Upper	Low/ Middle	Upper	Location	Citation
Aegiceras corniculatum	0.971						China	Tam *et al*. 1998
Avicennia germinans	0.435	0.247	0.108	0.104	0.111		Belize	This study
Avicennia germinans	0.568						Florida, USA	Twilley *et al*. 1986
Avicennia marina	0.324						Australia	van der Valk & Attiwill 1984
Avicennia marina	0.540	0.455			0.167	0.10	Australia	Mackey & Smail 1996
Avicennia marina			0.133				Australia	van der Valk & Attiwill 1984
Avicennia marina	0.404						New Zealand	Woodroffe 1982
Avicennia schaueriana	0.274						Brazil	Sessegolo & Lana 1991
Kandelia candel	1.286						China	Tam *et al*. 1998
Kandelia candel	0.530	0.540					Hong Kong	Lee 1989
Laguncularia racemosa	0.434	0.166			0.040		Belize	This study
Rhizophora apiculata					0.074		Australia	Robertson and Daniel 1989b
Rhizophora apiculata	1.070						Malaysia	Ashton *et al*. 1999
Rhizophora mangle	0.434	0.178	0.108	0.092	0.123		Belize	This study
Rhizophora mangle	0.298						Florida, USA	Twilley *et al*. 1986
Rhizophora mangle	0.283						Brazil	Sessegolo & Lana 1991
Rhizophora mucronata	1.527						Kenya	Woitchik *et al*. 1997
Rhizophora mucronata	1.250						Malaysia	Ashton *et al*. 1999
Rhizophora spp.	0.320						Ecuador	Twilley *et al*. 1997
Mean	0.644	0.317	0.116	0.098	0.103	0.10		
SE	0.109	0.076	0.008	0.006	0.022			

Peat formation at Twin Cays has thus occurred primarily through deposition and slow turnover of mangrove roots, with above-ground components either contributing less to total litterfall (woody twigs) or being subject to more rapid microbial decay, consumption by macrofauna and/or tidal export (leaves). A recent simulation model of organic matter accumulation in mangrove swamps also indicates that organic matter accumulation is primarily the result of below-ground production–degradation processes (Chen & Twilley 1999). Their simulation results suggest that rates of root production and deposition of refractory dead roots are critical processes controlling accumulation and vertical distribution of organic matter in mangrove soils. Our study provides the first empirical analysis linking above- vs. below-ground degradation rates to peat formation in mangrove wetlands and emphasizes the importance of below-ground processes in controlling soil formation and vertical building of mangrove islands in the Belizean Barrier Reef Complex. Furthermore, this work illustrates the importance of detritivores in accelerating litter degradation and that their relative influence on organic matter degradation varies spatially within mangrove forests.

Our findings have implications for understanding and predicting patterns of accumulation and distribution of organic matter in mangrove wetlands. Knowledge of the mechanisms controlling organic matter provides insight into carbon storage potential (Fujimoto *et al*. 1999), biogeochemical cycles of nutrients (Chen & Twilley 1999) and maintenance of soil surface elevations in relation to sea-level rise (Cahoon & Lynch 1997). The latter process is critical to habitat stability of mangroves. Slight differences in degradation rates may thus make a tremendous difference in mangrove capacity to counterbalance eustatic sea-level rise and other factors affecting habitat stability. Although global sea level is predicted to rise *c.* 50 cm over the next century (Watson *et al*. 1996), the potential for submergence of mangroves and other coastal wetlands is primarily determined by local factors of relative sea-level rise (interaction of eustatic sea-level rise and land subsidence), coastal geomorphology, sediment supply and frequency of major storms (Gornitz 1995). An account of biogenic contributions to vertical accretion will not only result in more accurate models to predict mangrove response to global change, but will also promote an understanding of the full suite of factors potentially affecting habitat stability. Accurate estimates of the potential for submergence of mangroves are essential to predicting the future extent of mangrove forests world-wide and for developing sound management plans to protect them.

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