Oecologia (1997) 111:109–122

Robert R. Twilley · Mireya Pozo · Victor H. Garcia
Victor H. Rivera-Monroy · Ramon Zambrano
Alejandro Bodero

Litter dynamics in riverine mangrove forests in the Guayas River estuary, Ecuador

Received: 17 June 1996 / Accepted: 13 January 1997

Abstract The hypothesis that rates of litter turnover in mangroves are controlled by local geophysical processes such as tides has been studied at sites with mostly small tides (< 1 m) and minor crab consumption of leaf litter. Our study describes litter dynamics of three riverine mangrove sites (M1, M2, M3), inhabited by the mangrove crab *Ucides occidentalis*, located in a macrotidal (> 3 m) river-dominated tropical estuary in Ecuador (2.5°S latitude). There were statistical effects of site and depth on soil salinities, but all mean salinities were < 17 g kg^{-1}. Daily rates of leaf litter fall were higher in the rainy compared to the dry season, although no seasonal effects were observed for other components of litter fall. Annual total litter fall rates were significantly different among sites at 10.64, 6.47, and 7.87 Mg ha^{-1} year^{-1} for M1, M2, and M3, respectively. There were significant site (M3 > M2 > M1) and season (rainy > dry) effects on leaf degradation, and both effects were related to differences in the initial nitrogen content of senescent leaves. Mean leaf litter standing crop among the sites ranged from 1.53 to 9.18 g m^{-2}, but amounts were strongly seasonal with peak values during September in both years of our study (no significant year effect) at all three sites. Leaf turnover rates based on leaf fall estimates and litter standing crop were 10- to 20-fold higher than estimated from rates of leaf degradation, indicating the significant effect of leaf transport by tides and crabs. Field experiments demonstrated that the mangrove crab can remove daily additions of leaf material within 1 h at all three sites, except during August–October, when the crab is inactive on the forest floor. Even though there is seasonally elevated leaf accumulation on the forest floor during this time, leaf turnover rates are much higher than expected based on leaf degradation, demonstrating the importance of tidal export. This is the first description of how crabs influence litter dynamics in the New World tropics, and results are similar to higher rates of crab transport of leaf litter in the Old World tropics. Even in riverine mangroves with high geophysical energies, patterns of litter dynamics can be influenced by ecological processes such as crab transport.

Key words Crab transport · *Rhizophora* · Litter fall · *Ucides occidentalis* · Detritus export

Introduction

The dynamics of mangrove leaf litter, including productivity, decomposition, and export, can determine the coupling of mangroves to the secondary productivity and biogeochemistry of coastal ecosystems (Twilley 1988, 1995; Alongi et al. 1992; Robertson et al. 1992). Rates of leaf litter turnover may be specific among the different ecological types of mangrove wetlands such that riverine > fringe > basin, assuming that greater leaf litter export occurs in sites with increasing tidal inundation (Twilley et al. 1986). Variation in litter dynamics among mangrove wetlands may be explained by the different geophysical energies, such as tides, river flow, and winds, that are associated with distinct geomorphological types of coastal environments (Twilley 1995). Based on this hypothesis, mangrove sites with more frequent tides and river inundations are more productive, and higher proportions of leaf fall are exported to coastal waters. Studies are needed in diverse geomorphological settings to investigate if litter dynamics can be linked to specific types of geophysical

R. R. Twilley (✉) · V. H. Rivera-Monroy
Department of Biology, University of Southwestern Louisiana,
Lafayette, LA 70504, USA
Fax: 318 482 5834; e-mail: rtwilley@usl.edu

M. Pozo · V. H. Garcia
School of Natural Sciences, University of Guayaquil,
Guayaquil, Ecuador

R. Zambrano
Department of Forestry, Guayas District, Guayaquil, Ecuador

A. Bodero
Coastal Resource Management Project,
University of Rhode Island/Agency for
International Development, Guayaquil, Ecuador

processes of coastal environmental settings (Thom 1982, 1984; Twilley 1995).

Tests of the hypothesis that litter dynamics in mangrove ecosystems of the New World tropics are controlled by the geophysical processes of a coastal environment have been limited to lower-energy coasts of the Caribbean and Gulf of Mexico (Twilley 1995). Several studies in the Old World tropics in higher-energy coastal environments of Australia and Malaysia have emphasized the influence of crabs on the fate of mangrove leaf litter (Malley 1978; Leh and Sasekumar 1985; Robertson 1986; Lee 1989; Robertson and Daniel 1989; Camilleri 1992). In these coastal environments, a geophysical model of litter dynamics is inappropriate for mangrove sites where crabs consume 28–79% of the annual leaf fall (Robertson 1986, 1988; Robertson and Daniel 1989). These studies suggest that biological factors may influence leaf litter turnover more than the geophysical processes as suggested in Twilley et al. (1986) for New World tropical mangrove wetlands. Although there are references to the distribution of mangrove crabs in the Caribbean (Warner 1969; Jones 1984), there are no quantitative estimates demonstrating that crab consumption can influence the fate of mangrove leaf litter. It is not certain whether there is a difference between the tropical hemispheres in the relative influence of ecological and geophysical processes on the coupling of mangrove leaf litter to coastal waters (Robertson and Daniel 1989). However, resolving the differences between these two models of litter dynamics is important because sites dominated by geophysical energies may export more organic matter per unit of productivity than those dominated by ecological processes, where more leaf litter is retained within the mangrove wetland.

The Guayas River estuary provides a high-energy environmental setting to test the factors that control mangrove litter dynamics in low-latitude regions of the New World tropics. The river-dominated Guayas River estuary has a tidal range of 3 m compared to 0.25–0.5 m throughout the Caribbean and 1 m in sites of mangrove litter studies in Australia (Boto and Bunt 1981). The Guayas River is the largest estuarine ecosystem along the Pacific coast of South America with seasonal river discharge of nearly 1400 $m^3\ s^{-1}$ in the wet season with suspended sediment concentrations of 200–400 mg l^{-1} (Cárdenas 1995). The regional setting of the Guayas River estuary has an energy classification of II (allochthonous coasts with strong tidal currents) according to the scheme by Thom (1984) in comparison to a setting of IV (low-energy coasts dominated by winds with little effect of river and tides) for the sites of litter dynamics in south Florida (Twilley 1995).

The structure of mangrove forests in this river-dominated estuary indicates optimum growth conditions with tree heights from 25 to 40 m. However, this region maintains a species composition similar to other studies in Florida and Caribbean regions with low species richness usually in zones of monospecific forests. Based on this higher-energy coastal setting, the conceptual model by Twilley et al. (1986) predicts that the mangrove wetlands in Ecuador are very productive and export large quantities of organic matter to the estuary (> 500 g C m^{-2} $year^{-1}$). However, most of the mangrove forests along the Guayas River estuary are inhabited by the mangrove crab, *Ucides occidentalis*, which has been observed transporting leaf litter to its burrows. Therefore, these sites offer an opportunity to test the relative influence of geophysical and ecological factors on the fate of leaf litter in mangrove wetlands in the New World tropics.

Using litter dynamics to describe the function of mangroves is important in this coastal region of Ecuador given the exploitation of these forested wetlands for construction of shrimp ponds (Olsen and Arriaga 1989; Twilley et al. 1993). The contribution of mangroves to water and habitat quality, particularly the linkage of forest productivity to coastal waters, is key to understanding the ecological significance of mangrove loss in Ecuador. Massive losses of mangroves have occurred along the coast due to shrimp mariculture, where, in some extreme cases, more than 90% of mangroves, as in the Bahia de Caraquez, have been eliminated since 1977 (Twilley et al. 1993). The southern coastal provinces of Guayas and El Oro, in the vicinity of this study, have 79 396 ha or 89% of the total area of shrimp ponds in Ecuador, most of which have been constructed in the intertidal zone (CLIRSEN 1984). Conceptual models of litter dynamics in these mangrove environments are important for evaluating resource management plans in this coastal region.

Study site

The mangrove study sites are located in the Churute Ecological Preserve along the western shore of the Guayas River estuary which flows into the Gulf of Guayaquil in a southern coastal province of Ecuador (Fig. 1). Rainfall is seasonal with more than 95% of the precipitation occurring from December to May causing seasonal river discharge ranging from 200 $m^3\ s^{-1}$ during the dry season to 1400 $m^3\ s^{-1}$ in the wet season during an average year of precipitation (Stevenson 1981). Mean precipitation in the Guayas River drainage system north of Guayaquil is 885 mm $year^{-1}$, but ranged from 400 to 3800 mm $year^{-1}$ from 1978 to 1990 depending on the location of the dominant oceanographic currents off the coast of Ecuador (Cucalón 1984, 1986). Precipitation during our study in 1989 and 1990 was 1500 and 900 mm $year^{-1}$, respectively. Annual mean temperatures vary from 24 to 27°C along the coast, resulting in a potential evapotranspiration rate of about 1300 mm $year^{-1}$.

The Churute Ecological Preserve was established in 1989 by the Dirección Nacional Forestal (DINAFOR) as one of the 14 forestry reserve areas in the country, and includes 30 000 ha of coastal and freshwater wetlands. There are 12 000 ha of mangrove wetlands classified into three groups according to tree height: M1 (trees > 15 m), M2 (trees 7–15 m), and M3 (trees < 7 m). Three mangrove study sites were established in the upper regions of the Churute River estuary representing each of these classifications (2°25′S, 79°40.5′W) (Fig. 1). All three mangrove sites in the Churute Preserve are dominated by *Rhizophora harrisonii* (Leachm) and *R. mangle* (L.). Sedimentation rates in the forest sites range from 4074 to 5151 g m^{-2} $year^{-1}$ with more than 75% of the total accumulation associated with inorganic sediments (Twilley et al. in review). The dry mass bulk density of sediments at all three sites was about 0.35 g cm^{-3} (Table 1). Total soil carbon and nitrogen concentrations are higher in M3 than in M1 and M2 sites (Table 1). The relatively lower concentrations of both carbon and nitrogen at M1 and M2 compared to M3 result in similar C:N ratios at all three sites (26–36). Total phosphorus concentrations were 0.71 mg g^{-1} at M1 compared to only 0.21 mg g^{-1} at M3. At M2, the 25-m-inland station had a total phosphorus concentration similar to M1, at 0.68 mg g^{-1}, whereas phosphorus concentrations at the 50-m-inland station were similar to M3, at 0.31 mg g^{-1} (Table 1). N:P ratios were 7.4 and 6.3 at the 25-and 50-m sites in M1, compared to ratios >29 at site M3. Thus the most striking difference in primary nutrients among the three stations is the lower phosphorus concentration relative to nitrogen at M3.

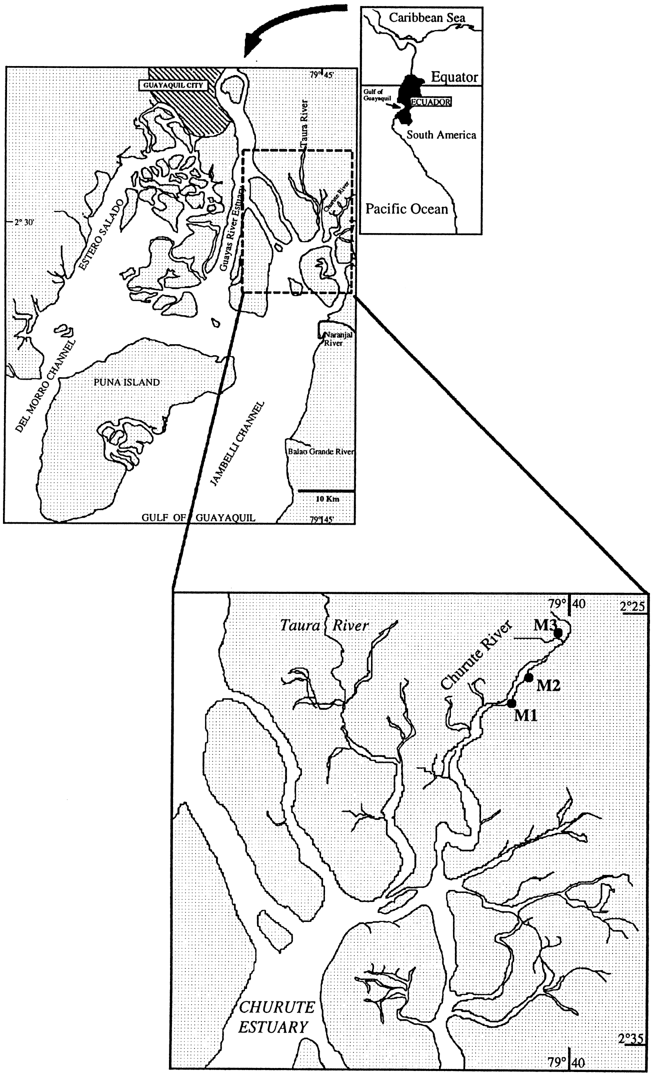


Fig. 1 Location of the three mangrove study sites (*M1*, *M2*, *M3*) in the Guayas River estuary, Ecuador

Materials and methods

A 100-m transect was established parallel to the shore 50 m inland within each of the three sites. Samples of litter dynamics and soil characteristics were randomly located along each transect. Litter fall was collected in 0.25-m^2 baskets supported approximately 1.8 m aboveground, and the bottom of each basket was constructed of fiberglass screening (1-mm mesh). Ten baskets were placed at random distances along the 100-m transect located 50 m inland from the shore. Collections were made from March 1989 to December 1990 at biweekly intervals during the rainy season and at monthly intervals during the dry season. Plant material within each basket was collected with gloves to prevent contamination, and dried for 48 h at 60°C. Material was separated into leaves, fruits, flowers, stipules, wood, and miscellaneous (which included frass), and weighed to the nearest 0.1 g. The number of leaves, fruits, flowers, and stipules was also recorded.

Litter standing crop was measured monthly at each of the three sites by collecting litter from the surface of the forest floor (L horizon) near each of the litter fall baskets. A 0.1-m^2 quadrat was placed 2 m from one of the four corners of the basket during each trip, and another corner was chosen during the subsequent trip. Litter was collected and processed in the same manner as litter fall samples. Field experiments were performed in May 1990 to measure the rate of leaf litter removed by crabs from the forest floor. In each site, ten leaves were placed in 4-m^2 areas near the vicinity of litter collection baskets and the fate of leaf litter was observed from a position in the canopy of the forest. Three observations were performed at each site during low tide, noting the number of leaves remaining after 2 h of observation.

Site and seasonal leaf degradation rates of *Rhizophora* were determined by measuring the loss of dry mass from fiberglass bags with 1-mm mesh. Senescent leaves were collected by shaking trees,

Table 1 Soil characteristics at two distances inland from the shore in three mangrove sites (*M1*, *M2*, *M3*) in the Guayas River estuary (*dm* dry mass)

Site	Units	M1		M2		M3	
		25 m	50 m	25 m	50 m	25 m	50 m
Bulk density	g cm^{-3}	0.51	0.50	0.34	0.26	0.39	0.45
Total carbon	mg g dm^{-1}	64.21	51.39	67.54	87.75	96.22	87.31
Total nitrogen	mg g dm^{-1}	2.24	2.01	3.03	3.59	3.32	2.80
Total phosphorus	mg g dm^{-1}	0.67	0.71	0.68	0.31	0.23	0.21
C:N		35.1	30.0	26.2	28.5	34.2	35.9
N:P		7.4	6.3	10.0	31.9	32.3	29.9

and 4–5 g of fresh leaves were placed in 20 × 20 cm bags. Seven bags were attached to each of three transects 1 m apart on the forest floor at 40 m along the 100-m transect. One bag was collected randomly from each transect monthly for 4 months beginning in February and August 1990 to represent degradation rates in the rainy and dry season, respectively. The plant material was rinsed, dried for 48 h at 60°C, and weighed to 0.1 g. Total carbon and nitrogen of the leaf litter were determined on a LECO CHN elemental analyzer standardized with acetonitrile and cross-calibrated with national standards (pine leaves).

Groundwater wells were placed at depths of 0.5, 1.0, and 2.0 m at 5, 35, 70, and 100 m along the 100-m transect. Wells were constructed of 2.5-cm-diameter PVC pipe, and water was sampled monthly from each well. Salinity was measured with a refractometer calibrated with freshwater.

A split-plot repeated-measures analysis of variance (univariate approach, Gurevitch and Chester 1986; Moser et al. 1990; von Ende 1993) was used to analyze salinity and litter fall. For the salinity data we included the factors site (M1, M2, M3) and depth (0, 0.5, 1.0, 2.0 m) and their interaction in the main plot; in the subplot we tested season (rainy and dry) and its interaction with site and depth (GLM; SAS 1993). Seasonal and site differences in total litter fall (g m^{-2} day^{-1}) and each of its individual components (leaves, stipules, wood, fruits, flowers, and frass) were also evaluated with a repeated-measure analysis by placing the factors site and season in the main plot and subplot, respectively. To test annual differences in litter fall among sites, annual rates (1990 only) were calculated for each experimental unit (basket) and a one-way analysis of variance was performed. Season and site factors were considered as fixed effects.

Leaf degradation rates, litter standing crop, and nitrogen content and C:N ratios in decomposing litter were analyzed using factorial analyses (Montgomery 1991). For the degradation rates and nutrient content data, area and season were considered the main factors, whereas year, season, and area were the main factors in the litter standing crop analysis. Degradation rates were the slope of the linear relationship between the natural logarithm of the mass loss and the sampling time for each area and season combination. C:N ratios were transformed (arcsine; Zar 1984) before analysis. After performing the several analyses of variance, linear contrasts (von Ende 1993) were used to evaluate differences among treatments.

Results and discussion

Soil salinity

The seasonal influence of freshwater discharge from the Guayas River to the Churute estuary was indicated by changes in salinity of mangrove surface waters at M3 (Fig. 2). Monthly measurements of salinity in the surface water within M3 varied from 1 to 22 g kg^{-1}, with peak salinity occurring in December 1989 and 1990, and minimum values in June and July (Fig. 2). Minimum salinities in the surface waters of this mangrove wetland occurred about 6 months after peak precipitation in the watershed (December; Cárdenas 1995). Soil salinity at a depth of 0.5 m within the mangrove site at M3 exhibited much less seasonal variation and mean monthly values ranged from 13 to 20 g kg^{-1} (Fig. 2).

There was a significant difference in soil salinities among the three mangrove sites, with the highest mean of 16.9 g kg^{-1} at M3 compared to 14.1 and 14.6 g kg^{-1} at M2 and M1, respectively (Table 2). There was no seasonal effect on soil salinity, with a mean of 14.9 and 15.6 g kg^{-1} in the rainy and dry season, respectively, for all three sites. This lack of seasonal variation was particularly evident in M3 where soil salinities were similar for nearly all samplings (Fig. 2). However, there was a significant difference in soil salinity with depth among the three sites. Mean salinity in surface waters was 13.2 g kg^{-1} and was significantly lower than salinities in soil waters (Table 2). Soil salinities at 0.5 and 1 m were

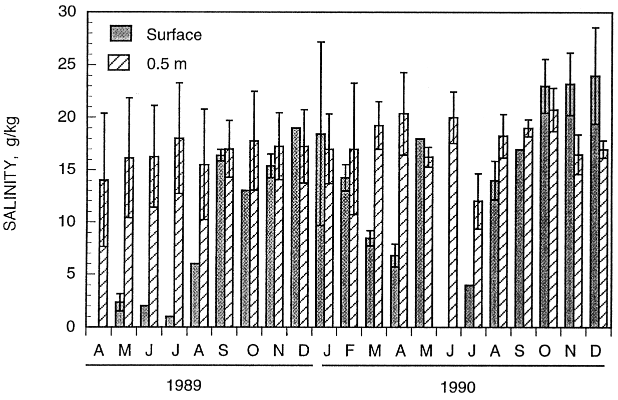


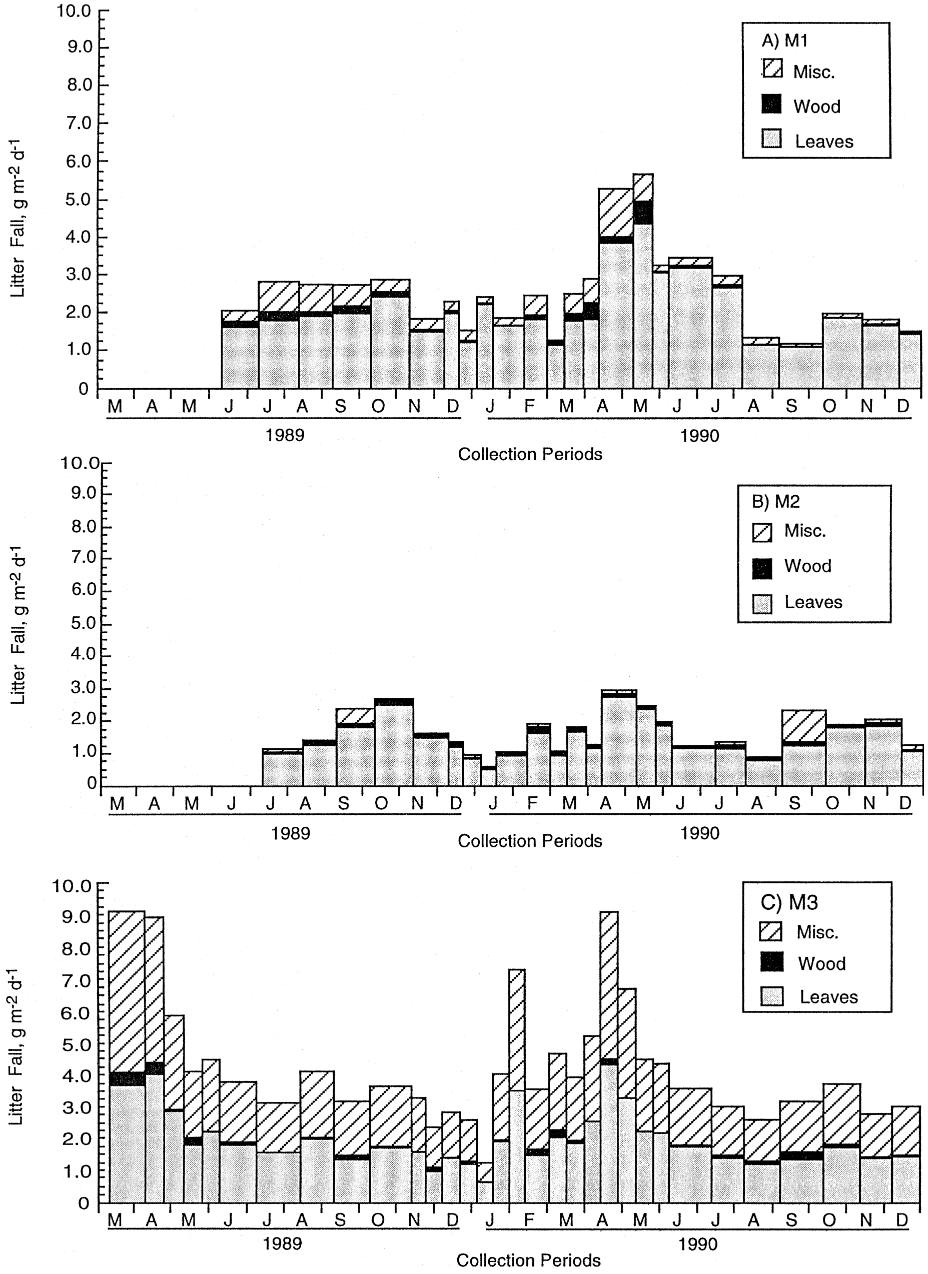
Fig. 2 Mean seasonal values (± SE) of salinity in surface waters and soil waters (0.5 m depth) at site *M3* in the Churute Ecological Preserve

Table 2 Statistical results of salinity measurements in the three mangrove sites during two seasons and at four depths with interactions. Means followed by a similar letter are not significantly different by alpha = 0.05

Source	*df*	MS	*F*	*P*	Mean	(±1 SE)
Area	2	845.433	33.548	***		
M1					14.6^a	(0.3)
M2					14.1^a	(0.3)
M3					16.9^b	(0.2)
Depth	3	565.786	22.451	***		
0.0 m					13.2^a	(0.3)
0.5 m					15.5^b	(0.3)
1.0 m					15.9^b	(0.3)
2.0 m					16.6^c	(0.3)
Area*depth	6	117.157	4.649	**		
Season	1	42.086	1.953	NS		
Rainy					14.9^a	(0.2)
Dry					15.6^a	(0.2)
Season*site	2	47.145	2.188	NS		
Season*depth	3	159.681	7.409	***		
Season*depth*site	6	13.686	0.635	NS		

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; NS not significant

Fig. 3A–C Daily rates of litter fall among three components for each individual sampling interval during the study at three mangroves sites in the Churute Ecological Preserve



similar at 15.5 and 15.9 g kg^{-1}, whereas soil salinity at 2 m was significantly greater at 16.6 g kg^{-1}. The small standard error for the annual mean of salinity at each depth indicates the absence of any seasonal variation. The statistically significant difference in salinity from 0.5 to 2 m is only 1.1 g kg^{-1}. Surface salinity values at M3 were similar to the other two mangrove sites, but soil salinities were higher at each of the other depths, with mean values of 19 g kg^{-1} at 2 m.

Litter fall

Average daily rates of litter fall in M1, M2, and M3 were determined for the periods of collection and distinctions were made among contributions from leaf, miscellaneous (stipules, reproductive structures, and frass) and wood components (Fig. 3). There were inconsistent seasonal patterns of litter fall among the three mangrove sites due to differences in the amount of reproductive structures contributing to this index of productivity (Fig. 3). The longest period of collection was for M3, which showed two distinct periods of higher litter fall in March–May in 1989 and 1990 (Fig. 3C). There was also an increase in litter fall in M1 during April and May 1990 (Fig. 3A), but litter production in M2 was nearly constant during the entire collection period at about 1.5 g m^{-2} day^{-1} (Fig. 3B). The miscellaneous component consisted mainly of reproductive structures, including propagules and flowers. The miscellaneous litter

Table 3 Statistical results for each component of daily litter fall in the three mangrove sites (*df* = 2) during two season (*df* = 1) with area * season interaction. Means (g m^{-2} day^{-1}) followed by a similar letter are not significantly different by alpha = 0.05

Variables	Source													
	Site						Season					Season*site		
	MS	*F*	*P*	Mean (±1 SE)			MS	*F*	*P*	Mean (±1 SE)		MS	*F*	*P*
				M1	M2	M3				Rainy	Dry			
Total	74.799	5.861	*	2.89^{a} (0.11)	1.75^{b} (0.11)	2.42^{c} (0.09)	8.916	3.262	NS	2.47^{a} (0.08)	2.24^{a} (0.09)	16.320	5.971	*
Leaves	22.00	3.20	**	2.04^{a} (0.08)	1.41^{b} (0.08)	2.00^{a} (0.07)	26.174	16.730	***	1.95^{a} (0.05)	1.58^{b} (0.07)	13.277	8.487	***
Stipules	2.53	8.54	**	0.40^{a} (0.01)	0.20^{b} (0.02)	0.25^{c} (0.01)	0.023	0.442	NS	0.28^{a} (0.01)	0.27^{a} (0.07)	0.002	0.053	NS
Wood	11.286	0.629	NS	0.12^{a} (0.26)	0.47^{a} (0.26)	0.09^{a} (0.23)	17.159	1.105	NS	0.37^{a} (0.18)	0.07^{a} (0.22)	12.220	0.787	NS
Fruits	0.174	0.385	NS	0.13^{a} (0.03)	0.07^{a} (0.03)	0.10^{a} (0.03)	0.120	0.651	NS	0.09^{a} (0.02)	0.12^{a} (0.02)	1.220	6.600	**
Flowers	1.600	10.916	***	0.17^{a} (0.01)	0.01^{b} (0.02)	0.08^{c} (0.01)	< 0.000	0.007	NS	0.09^{a} (0.01)	0.09^{a} (0.01)	0.340	6.664	**
Frass	0.574	6.540	**	0.05^{a} (0.01)	0.03^{a} (0.01)	0.13^{b} (0.01)	0.013	0.352	NS	0.07^{a} (0.01)	0.07^{a} (0.01)	0.074	2.014	NS

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; NS not significant

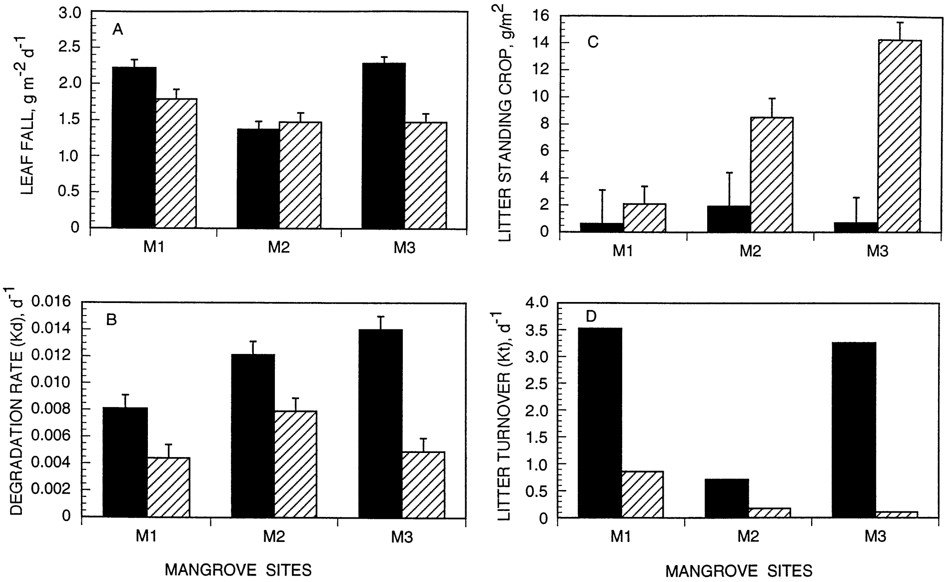


Fig. 4A–D Characteristics of leaf litter at each of three mangrove study sites averaged for the rainy (*solid bars*) and dry (*hatched bars*) seasons. **A** Leaf fall. **B** Leaf degradation. **C** Leaf litter standing crop. **D** Leaf litter turnover rates

fall component in M3 was larger than for M1 and M2, and contributed to the peak rates in April of both years. There was very little productivity of miscellaneous materials in M2.

There was a significant effect of site on daily rates of litter fall for the following components: total, leaf, stipules, flowers, and frass (Table 3). For total, stipules, and flowers the significance in rank of mean litter fall was M1 > M3 > M2. Mean rates of total litter fall were 2.89 (±0.11), 2.42 (±0.09), and 1.75 (±0.11) g m^{-2} day^{-1} for M1, M3, and M2, respectively. The rank in leaf fall rates among the three sites was similar to that for total litter fall, but mean rates for M1 and M3 were not significantly different; both however were > M2 (Table 3). There was no significant difference in wood and fruit accumulation in the litter baskets among the three mangrove sites. Wood fall had the highest standard error among the litter components at all three sites.

Data on daily litter production were grouped into dry (July–December) and rainy (January–June) seasons and compared among the three sites (Table 3). Seasonal effects of litter fall were only observed in the leaf component, with higher rates of 1.95 g m^{-2} day^{-1} in the rainy season compared to 1.58 g m^{-2} day^{-1} in the dry season (Table 3). No other litter components had significant seasonal effects. There was a strong significant interaction between site and season ($P = 0.0002$) for leaf fall, indicating that there may be some inconsistent seasonal effects among specific sites (Fig. 4A). Leaf fall was significantly higher during the rainy season in M1 and M3, while there was no significant difference between the two seasons in M2 (Fig. 4A). Leaf fall rates decreased from 2.21 to 1.79 and from 2.28 to 1.47 g m^{-2} day^{-1} in M1 and M3, respectively, from the rainy to the dry season. The daily litter production rates during the dry season were not significantly different among the three sites, but rates during the wet season were significantly different and the ranking was M1 > M3 > M2. Season * site interactions were also significant for total, fruit, and flower components of litter fall (Table 3).

Stipules represent the emergence of a new pair of leaves (Gill and Tomlinson 1971), and their abundance along with senescent leaves collected in the litter baskets indicates the seasonal turnover of leaves in the canopy. There was a significant effect of site ($P < 0.0001$) and of season ($P = 0.0261$) on the rate of new leaf production among the three sites (Table 3). The rank in daily production of new leaves was similar to results for litter fall: M1 (4.3 leaves m^{-2} day^{-1}) > M3 (2.9 leaves m^{-2} day^{-1}) > M2 (2.4 leaves m^{-2} day^{-1}). The average new-leaf production rates were 3.3 and 2.9 leaves m^{-2} day^{-1} for the rainy and dry season, respectively. The emergence of new leaves was slightly higher in M1 and M2 during the rainy compared to the dry season, but most of the seasonal effect was observed in M3 where rates increased from 2.4 to 3.1 leaves m^{-2} day^{-1}. The effect of season on new leaf production based on the number of stipules collected was not observed, based on the mass production of stipules between seasons as described above.

A seasonal periodicity in leaf fall has been observed for three species of *Rhizophora* (*R. lamarckii*, *R. apiculata*, *R. stylosa*) in Australia (18°S) that coincided with a 4-month lag in peak rainfall (Williams et al. 1981), and peak litter fall has been observed in other mangrove wetlands during the rainy season (Woodroffe 1982; Woodroffe et al. 1988). However, there are studies of litter fall that found no significant correlation with rainfall compared to other environmental factors (Sasekumar and Loi 1983; Woodroffe and Moss 1984; López-Portillo and Ezcurra 1985). The distinct rainy season in the southern coastal province of Ecuador begins in December, and the peak litter fall in April and May at M1 and M3 follows the trend observed in Australia. It is not certain why the M2 site exhibited no significant seasonal variation in leaf fall. Seasonality in leaf emergence is less clear, as Williams et al. (1981) did not observe a seasonal periodicity in stipule production based on the dry mass collected monthly at sites on Hinchinbrook Island (Duke et al. 1981). They concluded that the processes that influence leaf fall are apparently independent of those that control leaf emergence as indicated by lack of seasonal variation in the fall of stipules. Gill and Tomlinson (1971), however, found that leaf fall was closely linked with leaf expansion in south Florida (25.5°N), as was observed in our study in Ecuador (2.5°S). These differences may be related to the units of measurement used to compare leaf production and leaf fall, as indicated by the lack of seasonal effect in our study based on mass of stipule production, whereas the number of stipules as a measure of leaf production showed a significant seasonal effect.

Fruit and flower production showed no distinct seasonal variation between rainy and dry seasons, in contrast to phenology studies of other mangroves where there are distinct periods of floral production and propagule release from the canopy, usually linked to peak rainfall (Gill and Tomlinson 1971; Christensen and Wium-Anderson 1977; Wium-Anderson and Christensen 1978). However, Williams et al. (1981) noticed that strong seasonal patterns in litter fall of reproductive structures for *R. apiculata* and *R. stylosa* were not observed for *R. lamarckii*. Many distinct patterns in leaf emergence and reproductive ecology are observed in mangroves with strong seasonal patterns in soil salinity (Hutchings and Saenger 1987). The *Rhizophora* trees in all three sites in our study, while exhibiting significant spatial differences in leaf production and floral biology, lack significant seasonal variation in soil salinity associated with rainy and dry seasons of the region. This may be characteristic of riverine forested wetlands.

Daily litter fall rates for each component in each basket per site were multiplied by the number of days during each collection period and summed for the months of 1990, the most complete year of sampling (Fig. 3). These ten replicate estimates of annual litter fall were used to calculate a mean for each site for the various litter fall components (Table 4). There was a significant difference among the three sites in annual rates of total, leaf, and stipule litter fall; the first two components had a similar rank in means among the sites. Total litter fall was 10.64 (±1.31) at M1 compared to 7.87 (±0.47) and 6.47 (±1.53) Mg ha^{-1} $year^{-1}$ at M3

Table 4 Statistical results for each component of annual litter fall in the three mangrove sites ($df = 2,27$). Means (Mg ha^{-1} $year^{-1}$) followed by a similar letter are not significantly different by alpha = 0.05

Source	MS	*F*	*P*	Mean (±1 SE)		
				M1	M2	M3
Total	450 340	6.11	**	10.64^{a} (1.31)	6.47^{a} (1.53)	$7.87^{a, b}$ (0.47)
Leaves	156 337	3.59	*	7.67^{a} (0.90)	5.17^{b} (0.47)	$6.28^{a, b}$ (0.53)
Stipules	17 001.2	8.41	**	1.54^{a} (0.22)	0.76^{b} (0.07)	0.92^{b} (0.10)
Wood	782 310	0.82	NS	0.40^{a} (0.14)	1.85^{a} (1.69)	0.24^{a} (0.08)
Fruits	1 941.93	0.50	NS	0.55^{a} (0.31)	0.27^{a} (0.09)	0.42^{a} (0.11)
Flowers			*	$0.33^{a, b}$ (0.11)	0.05^{a} (0.03)	0.36^{b} (0.08)
Frass	672.26	2.07	NS	0.16^{a} (0.04)	0.17^{a} (0.05)	0.30^{a} (0.08)

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; NS not significant

and M2, respectively (Table 4). Site differences were also significant in mean annual rates of floral production; however, rates were much higher at M3 and M1 compared to M2. There was no significant effect of site on mean rates of wood, fruit, and frass components of annual litter fall. For all of the sites, mean leaf fall rates ranged from 5.17 to 7.67 Mg ha^{-1} year^{-1} and were 72–80% of total litter fall, with the higher percentages in M2 and M3 (Table 4). Stipules were the next most important contributor to total litter fall with rates ranging from 1.54 to 0.76 Mg ha^{-1} year^{-1}. An exception was M2 where wood fall was 1.85 Mg ha^{-1} year^{-1} compared to 0.76 Mg ha^{-1} year^{-1} for stipules; wood fall was much less at the other two sites with rates of 0.40 and 0.24 Mg ha^{-1} year^{-1}.

Measurements of annual litter fall in mangrove wetlands of the *N*ew World tropics have been dominated by sites located at $> 18°$ latitude (sensu Twilley et al. 1992; Saenger and Snedaker 1993), with the exception of one site on the Pacific coast of Colombia. The mean annual litter fall for three riverine mangroves sites in our study at 2.5°S latitude averaged 8.3 Mg ha^{-1} year^{-1}, which is lower than the mean rate of 13 Mg ha^{-1} year^{-1} for riverine mangrove wetlands reviewed by Twilley et al. (1986). The range of litter fall for riverine forests in this review was 9.1–23.4 Mg ha^{-1} year^{-1}, and two of the three riverine sites in Ecuador had litter fall rates below this range. Litter productivity in mangrove forests dominated by *R. mangle* at 25°N latitude in south Florida ranged from 10.7 to 11.7 Mg ha^{-1} year^{-1} (Pool et al. 1975). In forests dominated by *Rhizophora* spp. in Australia at 18°S latitude, litter fall ranged from 8.7 to 10.9 Mg ha^{-1} year^{-1} (Duke et al. 1981). Litter fall by *Rhizophora* spp. at lower latitudes in Malaysia (3–5°N) ranged from 10.7 to 15.8 Mg ha^{-1} year^{-1} (Ong et al. 1979, 1981, 1982; Sasekumar and Loi 1983; Putz and Chan 1986), exhibiting trends of higher potential litter fall at lower latitudes (Saenger and Snedaker 1993). However, mangroves along the Pacific coast of South America are limited in distribution to the northern coast of Peru at 4°S. Rates of annual litter fall for *Rhizophora* spp. in our study at 3°S latitude and within a fertile river-dominated estuary are lower than expected compared to results from other riverine mangrove sites. Litter fall rates in other low-latitude (12.3°S) macrotidal embayments (7.8 m tidal amplitude) also ranged (3.0–14.0 Mg ha^{-1} year^{-1}) below that expected given the fertile conditions of these sites (Woodroffe et al. 1988). Although litter fall is an important index of the potential carbon transport to coastal ecosystems, it is not representative of the net primary productivity of low-latitude mangrove wetlands where much of the organic production can be associated with the annual increment of forest structure (Saenger and Snedaker 1993).

Soil salinity at all three sites was nearly constant and less than 20 g kg^{-1} and thus not considered an important seasonal pulse regulating litter productivity in these mangrove wetlands. However, coastal oceanographic conditions in this region result in a fourfold range in interannual precipitation and river discharge, associated with the El Niño phenomenon (Stevenson 1981). The results of our study are for two normal-discharge years with peak discharge of Guayas River at 2397 m^3 s^{-1} in March 1989 compared to 1045 m^3 s^{-1} in February 1990. Thus the unexpectedly low rates in litter fall recorded at these three sites were not related to abnormally low discharge of the river. It is not known how extreme reductions in river discharge can influence mangrove productivity in this tropical estuary.

Leaf degradation

The percentage of original dry mass remaining in the mesh bags at specific time intervals was used to estimate rates of leaf degradation among the three sites during the rainy and dry seasons. We used leaf degradation rather than decomposition to describe the process of change in whole leaves to fragments less than the size of the mesh bags. A negative-exponential model was used to test the significant difference in rates of degradation by comparing the decay coefficient in the model:

$$M_t = M_o e^{-k_d t} \tag{1}$$

where M_t is the dry mass at time t, M_o is the original dry mass, k_d is the degradation coefficient (day^{-1}), and t is time (days). Coefficient of determination (r^2) of the model (ln dry mass vs time) for each replicate bag ranged from 0.70 to 0.99 and degradation coefficients varied from 0.003 to 0.016 day^{-1}. Triplicate decay coefficients were used to test for the effects of site and season on leaf degradation (Table 5).

Degradation rates were significantly different among sites, with higher rates at M3 and M2 at 0.010 day^{-1} ($\pm$ 0.001) compared to a significantly lower rate of 0.006 day^{-1} ($\pm$ 0.001) at M1 (Table 5). The mean rate for the rainy season (0.011 day^{-1}) was significantly higher than the rate during the dry season (0.006 day^{-1}, Table 6). There was a significant effect of the season*site interaction on rates of degradation. Leaf litter degradation rates increased from M1 to M3 during the rainy season, but during the dry season, rates of degradation at M3 were less than at M2 and not significantly different from M1 (Fig. 4B).

There were also significant effects of site and season on the initial nitrogen concentrations of leaf litter used in the degradation studies (Table 5). Nitrogen concentrations were significantly higher at M2 (9.31 mg g^{-1}) than at M3 (7.20 mg g^{-1}), while concentrations at M2 were similar to both sites. There was a much stronger effect of season on mean nitrogen concentrations with a mean of 9.28 mg g^{-1} in the rainy season compared to 5.31 mg g^{-1} in the dry season (Table 5). C:N (atomic) ratios of initial leaf litter among the three sites were significantly different and ranged from 43.3 to 57.7, with the same rank in means as nitrogen concentration (Table 5). Ratios of C:N in initial leaf litter were also

Table 5 Statistical results for each component of degradation including decay coefficients (k_d, day^{-1}), initial nitrogen concentration (mg g dm^{-1}), and carbon:nitrogen ratios (atomic) in the three mangrove sites and for two seasons. Means followed by a similar letter are not significantly different by alpha = 0.05

Source	MS	*F*	*P*	Mean (±1 SE)		
Site				M1	M2	M3
Degradation	< 0.001	6.180	*	$0.0062^{a, b}$ (0.0007)	0.0100^{a} (0.0007)	0.0095^{b} (0.0007)
Nitrogen	10.593	5.472	**	8.28^{a} (0.39)	9.31^{b} (0.40)	7.20^{a} (0.28)
C:N ratio	1219.049	3.342	*	$46.3^{a, b}$ (5.4)	43.3^{a} (5.5)	57.7^{b} (3.9)
Season				Rainy	Dry	
Degradation	< 0.001	29.121	***	0.0114^{a} (0.0012)	0.0057^{b} (0.0012)	
Nitrogen	165.749	85.607	***	9.28^{a} (0.22)	5.31^{b} (0.36)	
C:N ratio	2493.624	6.835	*	45.1^{a} (5.4)	62.8^{b} (5.5)	
Season*site						
Degradation	< 0.001	5.482	*			
Nitrogen	0.600	0.310	NS			
C:N ratio	896.05	2.456	NS			

$*P < 0.05$; $**P < 0.01$; $***P < 0.001$; NS not significant

Table 6 Statistical results of litter standing crop (g m^{-2}) in the three mangrove sites during two seasons for 2 years of study, with interactions. Means followed by a similar letter are not significantly different by alpha = 0.05

Source	*df*	MS	*F*	*P*	Mean (±1 SE)	
Area	2	1402.420	6.595	**		
M1					1.53^{a}	(1.41)
M2					$5.59^{a, b}$	(1.43)
M3					9.18^{b}	(1.12)
Year	1	308.422	1.450	NS		
1989					8.20^{a}	(1.34)
1990					3.92^{a}	(0.77)
Season	1	4205.805	19.779	***		
Rainy					1.11^{a}	(1.33)
Dry					8.26^{b}	(0.78)
Year*site	6	115.328	0.542	NS		
Season*site	2	1006.07	4.731	**		
Season*year	3	67.558	0.3177	NS		

$*P < 0.05$; $**P < 0.01$; $***P < 0.001$; NS not significant

significantly different at 45.1 during the rainy season compared to 62.8 during the dry season.

Degradation rates of *Rhizophora* leaves in Ecuador based on daily decay coefficients are among the upper rates reported for leaves of this genus compared to results from studies in other mangrove wetlands using similar techniques (Robertson 1988). Rates of *R. mangle* degradation in a basin mangrove forest in south Florida were 0.005 and 0.003 day^{-1} (Twilley et al. 1986). These degradation coefficients, both from Florida, are in microtidal sites, which may explain why they are lower than the rates observed in the macrotidal riverine forests of our study. Higher rates of leaf degradation in south Florida of 0.023 day^{-1} were associated with high densities of amphipods in bags submersed in the estuary (Heald 1969).

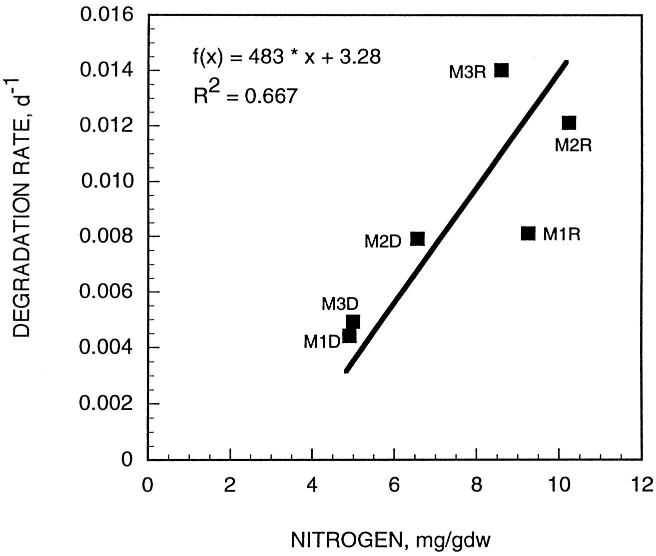


Fig. 5 Correlation of initial nitrogen content in leaves of *Rhizophora* spp. with measured rates of leaf degradation at each of three mangrove study sites (*M1*, *M2*, *M3*) during rainy (*R*) and dry (*D*) seasons

There was a strong seasonal difference in leaf degradation rates for *Rhizophora*, with higher values in the rainy season compared to the dry season. Higher rates of mangrove leaf degradation have been associated with more frequent tidal inundations (Twilley et al. 1986). However, in our study, the site with the higher degradation rate during the rainy season was M3, which has a slightly higher soil salinity indicating less frequent tidal inundations than the other sites. Leaf degradation rates among mangrove wetlands have also been linked to the chemical quality of leaf litter (Benner et al. 1986). The site and seasonal differences in rates of leaf degradation in our study did follow significant differences in the initial nitrogen content of the senescent leaves (Fig. 5). For each site, leaf degradation rates were higher in the rainy season when initial nitrogen concentrations in the leaf were higher than in the dry season (Fig. 5). For M1 and M2, differences in the degradation rate relative to seasonal concentrations of initial nitrogen were similar, while in M3 there was a greater effect of seasonal change in nitrogen concentration on leaf degradation rate. The slope of a regression line for these six points was significant ($r^2 = 0.667$) and is equivalent to a coefficient of 0.002 day^{-1} per mg g^{-1} of nitrogen (Fig. 5). In these three sites, the quality of leaf litter significantly influenced the seasonal and spatial patterns of leaf degradation.

Litter turnover

The production of litter from the canopy and subsequent storage on the forest floor describe the dynamics of litter in different types of mangrove wetlands (Twilley et al. 1986; Twilley 1995). Turnover rates of the leaf litter compartment can be evaluated using the equation:

$$k_t = L/\text{Xss} \tag{2}$$

where L is leaf litter fall (Table 3), Xss is the steady-state value of leaf litter on the forest floor (Table 6), and k_t is the leaf litter turnover rate (Nye 1961). This assumes that the leaf litter compartment is in a steady state, with leaf litter production equal to leaf litter losses. Leaf litter dry mass was generally < 5 g m^{-2} from January to June (rainy season) at all three sites (Fig. 6). In both 1989 and 1990, the peak standing crop of leaf litter occurred during the dry season from August to September in all three mangrove sites (Fig. 6). The peak value of leaf litter in M3 was 48 g m^{-2} in 1989 compared to 30 g m^{-2} in 1990, whereas peak values in M1 were only 5 g m^{-2} and 15 g m^{-2} in 1989 and 1990, respectively. Leaf litter on the forest floor in M2 during the dry season was between that in M1 and M3. The mean standing crop of leaf litter on the forest floor was significantly different among the three sites ($P = 0.0015$) and among seasons ($P < 0.0001$; Table 6). The mean standing crop of leaf litter was 1.53 g m^{-2} (± 1.41) at M1, 5.59 g m^{-2} (± 1.43) at M2, and 9.18 g m^{-2} (± 1.15) at M3. There was a strong difference in the amount of leaf litter in the dry and rainy seasons with a mean of 8.25 g m^{-2} (± 0.78) compared to 1.11 g m^{-2} (± 1.33), respectively; no significant effect of year indicates that these patterns were consistent (Table 6). In addition, there was no significant interaction of season*year or year*site, indicating that the trends for season and site were similar for both years (Fig. 4C). There was a significant interaction of season*site (Table 6). In all three sites, litter standing crop during the rainy season was less than in the dry season (Fig. 4C). However, litter standing crop increased during the dry season from M1 to M3, while in the rainy season values in M3 were similar to M1 and significantly less than M2.

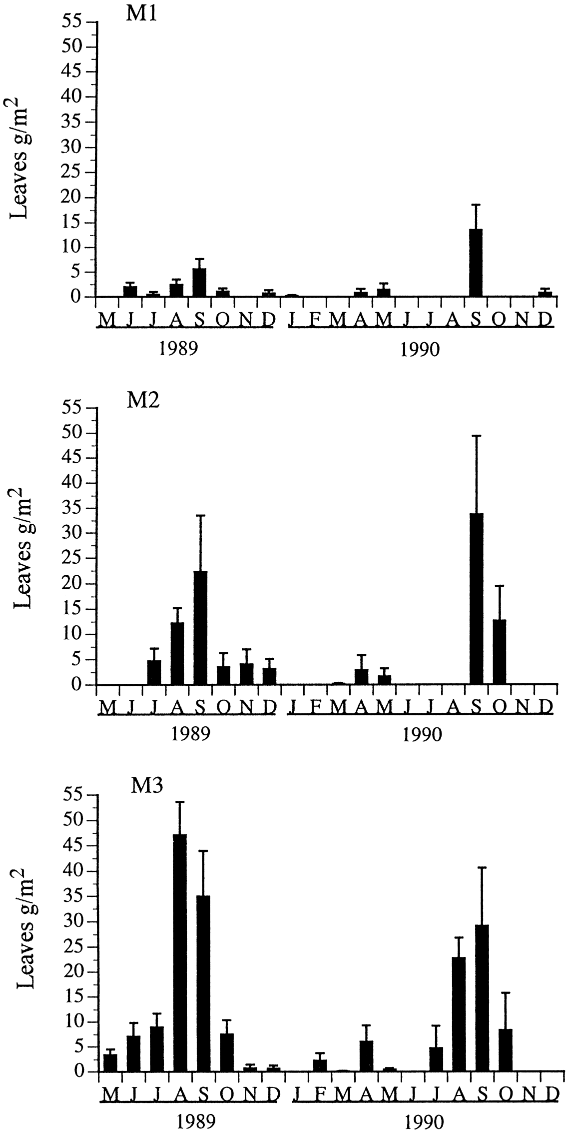


Fig. 6 Monthly mean values of leaf litter standing crop (± SE) at each of three study sites in the Churute Ecological Preserve

The turnover rate (k_t, Eq. 2), based on the relative measure of leaf fall and leaf litter at each of the three mangrove sites, can be compared to the coefficients of projected leaf litter turnover based on rates of leaf degradation (k_d, Eq. 1). Each coefficient represents a fraction of the leaf litter standing crop that is lost per day. Leaf litter turnover, k_t, integrates all of the ecological processes of leaf loss from the mangrove forest floor including degradation, tidal export, and crab consumption. Leaf degradation rates, k_d, indicate the disappearance of leaf material among sites and seasons associated with decomposition without the influence of tidal export or consumption by macroconsumers excluded by the mesh bags. The difference between these two coefficients of leaf litter turnover indicates the

Table 7 Estimates of leaf litter turnover (day^{-1}) based on degradation rates [$k_d = (\ln M_{t_0} - \ln M_{t_n})/(t_n - t_0)$; where M_{t_0} = dry mass in degradation bag at t_0, M_{t_n} = dry mass in degradation bag at t_n, $(t_n - t_0)$ = duration of degradation study (days)] compared to estimates based on leaf litter standing crop and leaf fall rates [k_t = LF/LSC; where LF = mean leaf litter fall rate (daily mean), LSC = mean leaf litter standing crop (annual mean)] ($T_{0.5} = 0.693\ \mathrm{k}^{-1}$)

Effect	k		$1/k$		$T_{0.5}$	
	k_d	k_t	$1/k_d$	$1/k_t$	k_d	k_t
Site						
M1	0.0062	1.3333	161	0.8	112	0.5
M2	0.0100	0.2522	100	4.0	70	2.8
M3	0.0095	0.2179	106	4.6	74	3.2
Season						
Rainy	0.0114	1.8108	88	0.6	61	0.4

relative contribution of these other pathways to leaf litter loss.

The actual residence times of leaf litter (Eq. 2) among the three sites were much shorter than the projected times based on leaf degradation rates (Eq. 1; Table 7). The projected residence time of leaf litter among the three sites based on k_d ranged from 100 days (M2) to 161 days (M1). In contrast, the actual residence times based on k_t were less than 1 day in M1, with slightly longer times of 4 and 5 days at M2 and M3, respectively. Based on leaf degradation studies, the longest residence time was expected in M1. But based on actual rates of leaf litter turnover, the residence time of leaves on the forest floor in M1 was much shorter than at the other two sites. Thus not only are the k_t rates much higher in all three sites than the k_d rates, but the relative differences in leaf litter turnover among sites were also different between the two methods (Table 7).

There was also a strong seasonal difference in leaf litter residence time based on both k_d and k_t estimates of leaf litter turnover (Table 7). The residence time of leaf litter based on k_d was 88 days during the rainy season compared to 175 days during the dry season. Using k_t rates, residence times were 0.6 and 5.3 days for rainy and dry seasons, respectively. As discussed above, this seasonal difference was associated with the quality of the leaf litter. These differences in residence times based on k_d and k_t also demonstrate that leaf litter turnover rates based on leaf fall and leaf litter standing crop are much higher than the leaf degradation studies. Leaf degradation rates at any one site were 1.5–2.8 times higher during the rainy season than during the dry season. However, the seasonal differences in k_t were from 3.5 to 22 times higher in the rainy season than in the dry season (Table 7). Thus not only are k_t rates of leaf turnover much higher than k_d rates based on degradation experiments, but the seasonal differences in leaf litter turnover for each site, particularly M1 and M3, are much greater than projections based on estimates of leaf degradation (Fig. 4B, D). The site and seasonal differences in k_d and k_t rates of leaf litter turnover suggest that there are mechanisms of litter loss other than leaf degradation that may control litter turnover in these riverine mangrove wetlands.

The absence of leaf litter on the forest floor at all three sites during the rainy months in contrast to increased standing crop during the dry months was significant for both years of this study. According to the conceptual model of Twilley et al. (1986), this reduction in leaf litter during the rainy season may be associated with greater export owing to the effect of tides on the transport of leaf litter from the forest. Yet observations in all three mangroves sites suggested that most of the leaf litter on the forest floor was harvested by the mangrove crab, *U. occidentalis*, and transported to sediment burrows. Field observations of areas enriched with leaf litter demonstrated that crabs completely removed all the leaves from the forest floor within an hour of leaf deployment. The average dry mass of a leaf is approximately 1 g, and based on ten leaves, the rate of artificial leaf fall in these deployment studies was about 2.5 g m^{-2} day^{-1}, slightly higher than the measured rates in each of the three sites (Table 3). Thus, crabs were able to remove the daily equivalent of leaf fall within 1 h in all three sites.

Leaf deployment studies were not performed each month, but based on studies of the population dynamics of this crab in other mangrove sites along the coast of Ecuador, the activity of *Ucides* is very seasonal, due to a specific period of ecdysis (Muñiz and Peralta 1983). Early signs of molting are observed in the population in July, and by September more than 90% of the crabs sampled have a soft carapace and remain inactive within their burrows. *Ucides* is a very important local fishcrop (Barragán 1993), and the harvesting of crabs during this molting season is restricted during August and September since their physiological condition causes sickness to human consumers. The seasonal period of decreased crab activity on the forest floor in September has been documented at several mangrove sites along the coast of Ecuador (Muñiz and Peralta 1983), and coincides with the increase in standing crop of leaf litter at all three sites in our study. Estimates of crab hole densities vary from 2–5 m^{-2} at each of the three sites. The molting season of *Ucides* coincides with the July–December period designated as dry season in our analysis of leaf litter standing crop. The lack of leaf litter on the forest floor during the rainy season from January to June can be largely attributed to the transport of surface leaf litter by crabs.

The fate of leaf litter in the three mangrove wetlands in our study depends on the relative effects of tides and crabs. If a leaf falls from the canopy when there is no tide within the forest and crabs are seasonally active, then the leaf will be transported to crab burrows and remain within the forest soil. However, if the wetland is inundated by a tide, regardless of whether crabs are active or not, a leaf falling from the canopy will most likely be transported to the estuary. The ecological significance of crab transport can be estimated by com-

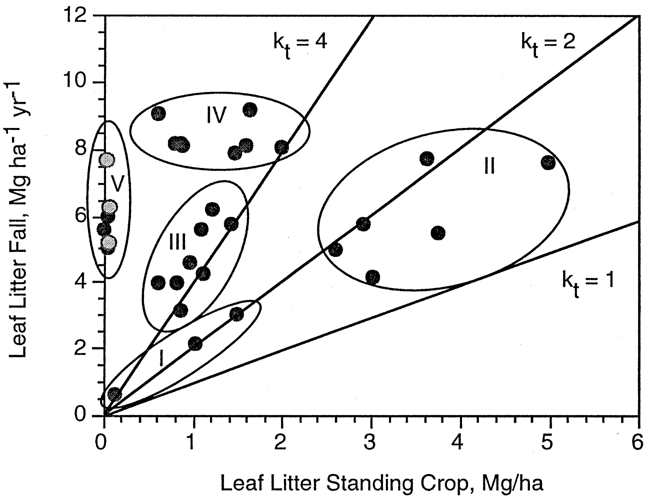


Fig. 7 Plots of leaf litter fall (LF) and leaf litter standing crop (SC) in mangrove wetlands around the world. *Diagonal lines* represent leaf turnover rates based on k_t (k_t = LF/SC) and groups are based on cluster analysis of data for each site. Results from sites in Ecuador are designated with *hatched circles*

paring k_t values when crabs are inactive (September) to average annual values (Table 7). During September, k_t ranged from 0.047 to 0.204 day^{-1} among the three sites with half-lives ranging from 3 to 15 days. These values of k_t are about one-fifth the turnover rates when crabs are active at the sites. However, litter turnover rates with limited influence of crab transport from August to October (see Fig. 6) have k_t values that are five times higher than k_d (Table 7). Thus even with the absence of crabs, geophysical processes have a strong influence on the fate of leaf litter export in these mangrove wetlands.

This is the first report of the potential influence of crab transport on litter dynamics of mangrove wetlands in the New World tropics and indicates that this ecological process contributes to the extremely high litter turnover rates of these sites. The first quantitative estimates of litter consumption by crabs was in northeastern Australia and ranged from 22 to 42% of the daily leaf fall (mean of 28%) depending on the time of year (Robertson 1986). The effect of sesarmides on consumption of leaf litter (reported as percentage of leaf fall) has been documented throughout the eastern hemisphere: 44% of *Avicennia marina* leaf fall by *Sesarma meinerti* in southern Africa (Emmerson and McGwynne 1992), 71% and 79% of *Ceriops tagal* and *Bruguiera exaristata* annual litter fall, respectively, in Australia (Robertson and Daniel 1989), with reduced rates in Malaysia at about 9% of *Rhizophora* leaf fall in mid intertidal and up to 20–30% of leaf fall in high intertidal forests by *Chiromanthes onychophorum* and *Chiromanthes eumolupe* (Leh and Sasekumar 1985). Lee (1990) estimated that 40% of particulate organic matter produced by the mangrove *Kandelia candel* and the reed *Phragmites communis* was consumed by crabs, while crabs from the genus *Chiromanthes* were capable of consuming $>57\%$ of the litter produced by the mangrove *K. candel* in a tidal shrimp pond (Lee 1989).

The relative effects of ecological and geophysical processes on litter dynamics can be evaluated by comparing global patterns of leaf fall relative to leaf litter standing crop among mangrove wetlands in different environmental settings (Fig. 7). Results for these mangrove sites were subjected to a cluster analysis that included the variables leaf productivity, leaf standing crop, turnover rate, and turnover time. Five distinct groups of mangrove wetlands were determined based on characteristics of leaf litter production and dynamics. All mangrove sites have turnover rates >1, and 23 of the 34 sites have turnover rates ≥ 4. Groups I, II, and III are dominated by basin (inland) and fringe mangroves in the New World tropics, while group IV includes mainly riverine and overwash island mangrove wetlands from Florida and Malaysia. Sites in groups II, III, and IV from Florida, Mexico, and Puerto Rico are representative of the mangrove wetlands used to develop the conceptual model of leaf litter dynamics by Twilley et al. (1986). Their model suggested that the geophysical energies such as tides and river discharge that influence the structural attributes of mangrove ecological types (e.g., riverine, fringe, and basin, sensu Lugo and Snedaker 1974) can also control the fate of leaf litter in mangroves. However, studies of leaf litter turnover in several Old World mangrove wetlands associated with crab transport have the highest litter turnover rates reported in the literature and are represented by cluster group V (Fig. 7). The three sites in our study also fall in this group, representing mangrove wetlands in the New World tropics that have similar processes as those in the Old World tropics. All of the sites in this group have leaf litter standing crop <0.1 Mg ha^{-1}, and turnover rates >50, which clearly distinguishes them from the other mangrove wetlands that are influenced mainly by geophysical processes.

The distinction in ecological and geophysical processes on litter dynamics in mangroves can be evaluated among the sites in Fig. 7. One of the sites in cluster group III is the *Avicennia* forest studied by Robertson and Daniel (1989) where crabs removed 24% of leaves, compared to removing 82% of the leaves in two of the sites in group V. This gives some idea of the relative effect of crab transport required to differentiate these clusters of leaf litter turnover in mangroves. Distinctions among litter turnover rates in groups I–IV are a combination of species-specific degradation rates, hydrology (tidal frequency), and soil fertility that influence the rates of litter dynamics as discussed by Twilley et al. (1986). Our study, together with those in the Old World tropics, indicates that crab transport of leaf litter in New World mangroves with crabs such as *U. occidentalis* can have effects similar to those observed in the Old World tropics. However, even with the absence of crab activity during certain months of the year in the Guayas River estuary, geophysical processes of riverine mangroves result in litter turnover rates higher than those expected on the basis of leaf degradation alone. There are diverse global patterns of litter dynamics in mangrove wetlands, and conceptual models in any region must consider the ecological and geophysical processes that control the fate of leaf litter in these coastal ecosystems.

Acknowledgements This project was funded by the Agency for International Development through the Science and Technology Committee by grant no. DPE-5542-G-SS-8011-00. Additional support was provided by the Coastal Resource Management Project, Dr. Luis Arriaga, Director. We thank Mr. Lino Delgado, former Chief of Guayas District Forestry Office for site logistics and permission to work in Churute Ecological Preserve. Assistance with site logistics was provided by Gladys de Tazán, University of Guayaquil, and Gilberto Cintrón, Puerto Rico Department of Natural Resources. Field help was provided by Niki Gaibor and Krugel Loor. Kathy Ewel, Ariel Lugo, and two anonymous reviewers provided important comments on this manuscript.

References

Alongi DM, Boto KG, Robertson AI (1992) Nitrogen and phosphorous cycles. In: Robertson AI, Alongi DM (eds) Tropical mangrove ecosystems. American Geophysical Union, Washington, DC, pp 251–292

Barragán J (1993) Biología del cangrejo de manglar, *Ucides occidentalis*, Ortmann, (Crustacea: Decapoda: Gecarcinidae). Rev Cienc Mar Limnol 3: 135–149

Benner R, Peele ER, Hodson RE (1986) Microbial utilization of dissolved organic matter from leaves of the red mangrove, *Rhizophora mangle*, in the Fresh Creek estuary, Bahamas. Estuarine Coast Shelf Sci 23: 607–619

Boto KG, Bunt JS (1981) Tidal export of particulate organic matter from a northern Australian mangrove system. Estuarine Coast Shelf Sci 13: 247–255

Camilleri JC (1992) Leaf-litter processing by invertebrates in a mangrove forest in Queensland. Mar Biol 114: 139–145

Cárdenas W (1995) Patterns of phytoplankton distribution related to physical and chemical characteristics of the Guayas River estuary, Ecuador. Thesis, University of Southwestern Louisiana, Lafayette, La

Christensen B, Wium-Anderson S (1977) Seasonal growth of mangrove trees in southern Thailand. I. The phenology of *Rhizophora apiculata* Bl. Aquat Bot 3: 281–286

CLIRSEN (1984) Aplicación de sensores remotos en el estudio del levantamientos integrados de recursos naturales por sensores remotos. Center for Remote Sensing, Technical Report, Quito, Ecuador.

Cucalón E (1984) Temperature, salinity and water mass distribution off Ecuador during an El Niño event in 1976. Rev Cienc Mar Limnol 2: 1–25

Cucalón E (1986) Oceanographic characteristics off the coast of Ecuador. In: Olsen S, Arriaga L (eds) Establishing a sustainable shrimp mariculture industry in Ecuador. University of Rhode Island, Technical Report Series TR-E-6, pp 185–194

Duke NC, Bunt JS, Williams WT (1981) Mangrove litter fall in N.E. Australia. I. Annual totals by component in selected species. Aust J Bot 29: 547–553

Emmerson WD, McGwynne LE (1992) Feeding and assimilation of mangrove leaves by the crab *Sesarma meinerti* in relation to leaf-litter production in Mgazana, a warm-temperate southern African mangrove swamp. J Exp Mar Biol Ecol 157: 41–53

Ende CN von (1993) Repeated-measures analysis: growth and other time-dependent measures. Chapman and Hall, New York

Gill AM, Tomlinson PB (1971) Studies on the growth of red mangrove (*Rhizophora mangle* L.) 3. Phenology of the shoot. Biotropica 3: 109–124

Gurevitch J, Chester ST (1986) Analysis of repeated measures experiments. Ecology 67: 251–255

Heald EJ (1969) The production of organic detritus in a south Florida estuary. Dissertation, University of Miami, Coral Gables, Fla

Hutchings P, Saenger P (1987) Ecology of mangroves. University of Queensland Press, St Lucia

Jones DA (1984) Crabs of the mangal ecosystem. In: Por FD, Dor I (eds) Hydrobiology of the Mangal. Junk, The Hague, pp 89–109

Lee SY (1989) The importance of sesarminae crabs *Chiromanthes* spp. and inundation frequency on mangrove (*Kandelia candel* (L.) Druce) leaf litter turnover in a Hong Kong tidal shrimp pond. J Exp Mar Biol Ecol 131: 23–43

Lee SY (1990) Net aerial primary productivity, litter production and decomposition of the reed *Phragmites communis* in a nature reserve in Hong Kong: management implications. Mar Ecol Prog Ser 66: 161–173

Leh CMU, Sasekumar A (1985) The food of sesarmid crabs in Malaysian mangrove forests. Malay Nat J 39: 135–145

López-Portillo J, Ezcurra E (1985) Litter fall of *Avicennia germinans* L. in a one-year cycle in a mudflat at the Laguna de Mecoacan, Tabasco, Mexico. Biotropica 17: 186–190

Lugo AE, Snedaker SC (1974) The ecology of mangroves. Annu Rev Ecol Syst 5: 39–64

Malley DF (1978) Degradation of mangrove leaf litter by the tropical sesarmid crab *Chiromanthes onychophorum*. Mar Biol 49: 377–386

Montgomery DC (1991) Design and analysis of experiments. Wiley, New York

Moser EB, Saxton AM, Pezeshki SR (1990) Repeated measures analysis of variance: application to tree research. Can J For Res 20: 524–535

Muñiz L, Peralta B (1983) Aspectos biometricos de *Ucides occidentalis* Ortmann. Rev Cienc Mar Limnol 2: 151–170

Nye PH (1961) Organic matter and nutrient cycles under moist tropical forests. Plant Soil 13: 333–346

Olsen S, Arriaga L (1989) Establishing a sustainable shrimp mariculture industry in Ecuador. University of Rhode Island, Technical Report Series TR-E-6.

Ong JE, Khoon GW, Hoong WC, Dhanarajan G (1979) Productivity of a managed mangrove forest in west Malaysia. In: Trends in Applied Biology in S.E. Asia, University Sains Malaysia, Penang pp 1–10

Ong JE, Gong WK, Wong CH (1981) Ecological monitoring of the Sungai Merbok estuarine mangrove ecosystem. Penang, Malaysia, School of Biological Sciences, University Seins Malaysia

Ong JE, Khoon GW, Hoong WC (1982) Productivity and nutrient status of litter in a managed mangrove forest. In: Symposium on Mangrove Forest Ecosystem Productivity. Bogor, Indonesia, pp 1–21

Pool DJ, Lugo AE, Snedaker SC (1975) Litter production in mangrove forests of southern Florida and Puerto Rico. In: Walsh G, Snedaker S, Teas H (eds) Proceedings of the International Symposium on the Biology and Management of Mangroves. Institute of Food and Agricultural Sciences, University of Florida, Gainesville, Fla, pp 213–237

Putz FE, Chan HT (1986) Tree growth, dynamics, and productivity in a mature mangrove forest in Malaysia. For Ecol Manage 17: 211–230

Robertson AI (1986) Leaf-burying crabs: their influence on energy flow and export from mixed mangrove forests (*Rhizophora* spp) in northeastern Australia. J Exp Mar Biol Ecol 102: 237–248

Robertson AI (1988) Decomposition of mangrove leaf litter in tropical Australia. J Exp Mar Biol Ecol 116: 235–247

Robertson AI, Daniel PA (1989) The influence of crabs on litter processing in high intertidal mangrove forests in tropical Australia. Oecologia 78: 191–198

Robertson AI, Alongi DM, Boto KG (1992) Food chains and carbon fluxes. In: Robertson AI, Alongi DM (eds) Tropical mangrove ecosystems. American Geophysical Union, Washington, DC, pp 293–326

Saenger P, Snedaker SC (1993) Pantropical trends in mangrove above-ground biomass and annual litterfall. Oecologia 96: 293–299

SAS (1993) SAS/STATR user's guide, 4th edn. SAS Institute, Cary, NC

Sasekumar A, Loi JJ (1983) Litter production in three mangrove forest zones in the Malay Peninsula. Aquat Bot 17: 283–290

Stevenson MR (1981) Seasonal variations in the Gulf of Guayaquil, a tropical estuary. Bol Cient Tec Inst Nac Pesca 4: 1–133

Thom BG (1982) Mangrove ecology – a geomorphological perspective. In: Clough BF (ed) Mangrove ecosystems in Australia. Australian National University Press, Canberra, pp 3–17

Thom BG (1984). Coastal landforms and geomorphic processes. In: Snedaker SC, Snedaker JG (eds) The mangrove ecosystem: research methods. UNESCO, Paris pp 3–17

Twilley RR (1988) Coupling of mangroves to the productivity of estuarine and coastal waters. In: Jansson BO (ed) Coastal-offshore ecosystem interactions. Springer, Berlin Heidelberg New York, pp 155–180

Twilley RR (1995) Properties of mangrove ecosystems related to the energy signature of coastal environments. In: Hall CAS (ed) Maximum power: the ideas and applications of H.T. Odum. University Press of Colorado, Niwot, pp 43–62

Twilley RR, Lugo AE, Patterson-Zucca C (1986) Production, standing crop, and decomposition of litter in basin mangrove forests in southwest Florida. Ecology 67: 670–683

Twilley RR, Chen RH, Hargis T (1992) Carbon sinks in mangroves and their implications to carbon budget of tropical coastal ecosystems. Water Air Soil Pollut 64: 265–288

Twilley RR, Bodero A, Robadue D (1993) Mangrove ecosystem biodiversity and conservation: case study of mangrove resources in Ecuador. In: Potter CS, Cohen JI, Janczewski D (eds) Perspectives on biodiversity: case studies of genetic resource conservation and development. AAAS, Washington, DC, pp 105–127

Warner GF (1969) The occurrence and distribution of crabs in a Jamaican mangrove swamp. J Anim Ecol 38: 379–389

Williams WT, Bunt JS, Duke NC (1981) Mangrove litter fall in north-eastern Australia. II. Periodicity. Aust J Bot 29: 555–563

Wium-Andersen S, Christensen B (1978) Seasonal growth of mangrove trees in southern Thailand. II. Phenology of *Bruguiera cylindrica*, *Ceriops tagal*, *Lumnitzera littorea* and *Avicennia marina*. Aquat Bot 5: 383–390

Woodroffe CD (1982) Litter production and decomposition in the New Zealand mangrove, *Avicennia marina* var. *resinifera*. NZ J Mar Freshwater Res 16: 179–188

Woodroffe CD, Moss TJ (1984) Litter fall beneath *Rhizophora stylosa* Griff., Vaitupu, Tuvalu, South Pacific. Aquat Bot 18: 249–255

Woodroffe CD, Bardsley KN, Ward PJ, Hanley JR (1988) Production of mangrove litter in a macrotidal embayment, Darwin Harbour, N.T., Australia. Estuarine Coast Shelf Sci 26: 581–598

Zar JH (1984) Biostatistical analysis. Prentice-Hall, Englewood Cliffs, NJ