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ORIGINAL PAPER

Litterfall dynamics in carbonate and deltaic mangrove ecosystems in the Gulf of Mexico

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Abstract From 1996 to 2002, we measured litterfall, standing litter crop, and litter turnover rates in scrub, basin, fringe and riverine forests in two contrasting mangrove ecosystems: a carbonate-dominated system in the Southeastern Everglades and a terrigenous-dominated system in Laguna de Terminos (LT), Mexico. We hypothesized that litter dynamics is driven by latitude, geomorphology, hydrology, soil fertility and soil salinity stress. There were significant temporal patterns in LT with litterfall rates higher during the rainy season (2.4 g m^{-2} day^{-1}) than during the dry season (1.8 g m^{-2} day^{-1}). Total annual litterfall was significantly higher in the riverine forest (12.8 Mg ha^{-2} $year^{-1}$) than in the fringe and basin forests (9.7 and 5.2 Mg ha^{-2} $year^{-1}$, respectively). In Southeastern Everglades, total annual litterfall was also significantly higher during the rainy season than during the dry season. Spatially, the scrub forest had the lowest annual litterfall (2.5 Mg ha^{-2} $year^{-1}$), while the fringe and basin had the highest (9.1 and 6.5 Mg ha^{-2} $year^{-1}$, respectively). In LT, annual standing litter crop was 3.3 Mg ha^{-1} in the fringe and 2.2 Mg ha^{-1} in the basin. Litter turnover rates were significantly higher in the fringe mangrove forest (4.1 $year^{-1}$) relative to the basin forests (2.2 $year^{-1}$). At Southeastern Everglades there were significant differences in annual standing litter crop: 1.9, 3.3 and 4.5 Mg ha^{-1} at scrub, basin and fringe mangrove sites, respectively. Furthermore, turnover rates were similar at both basin and fringe mangrove types (2.1 and 2.0 $year^{-1}$, respectively) but significantly higher than scrub mangrove forest (1.3 $year^{-1}$). These findings suggest that litter export is important in regulating litter turnover rates in frequently flooded riverine and fringe forests, while in infrequently flooded basin forests, in situ litter decomposition controls litter turnover rates.

Keywords Litterfall · Turnover rate · Terminos Lagoon · Southeastern Everglades · Carbonate system · Terrigenous system

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Introduction

At the global level, temperature is the main factor affecting both mangrove distribution and productivity, including litterfall production that is generally higher near the equator (Saenger and Snedaker 1993). Similarly, regional geomorphology characteristics such as deltas, estuaries and carbonate environments also affect the structure and productivity of mangroves. In general, mangroves forests in deltaic environments have higher productivity than those located in carbonate environments (Twilley 1995). Furthermore, within any regional geomorphologic type, mangrove productivity is also determined by nutrient resources, soil type, and stressors such as salinity and sulfide (Twilley et al. 1996; Lugo and Snedaker 1974). Previous studies have demonstrated that these environmental factors control mangrove growth, production and zonation (Twilley et al. 1996; Day et al. 1987, 1996; Rivera-Monroy et al. 1995; McKee 1995; Feller et al. 1999).

There is high litterfall production variability among mangrove forest types, with scrub mangrove forests having the lowest production rates and riverine forests having the highest (Day et al. 1987; Pool et al. 1975), indicating that high litterfall rates characterize better-developed mangroves forests that are defined by short hydroperiods, high soil fertility, and low soil salinity. In contrast, low litterfall production sites characterize poor-developed sites that are defined by long hydroperiods, low soil fertility, and high soil salinity. Thus, litterfall measurements in mangrove forests represent a useful approach to not only describe ecosystem function but also testing hypotheses about mangrove production under a variety of environmental conditions (Lugo 1990). Furthermore, in mangrove ecosystems litterfall has been widely used as a measure of primary production due to its role as a primary source of energy for consumers and decomposers, its contribution to soil formation and its role on nutrient cycling and biogeochemical transformations (Twilley et al. 1996; Lugo 1990; Clough 1992; Clough and Attiwill 1982; Lugo and Snedaker 1974).

Production of leaves, fruits, and twigs in the canopy and subsequent fall to the ground surface describes litterfall production in mangrove ecosystems (Twilley et al. 1996). Furthermore, litterfall dynamics, which includes measurement of litterfall production, decomposition, consumption and export, can be estimated by measuring litterfall production and turnover rate by using the model $K = L/Xss$, where K is litter turnover rate, L is litterfall production rate, and Xss is the steady state value of litter on the forest floor (Nye 1961). This model assumes that the litter compartment is in steady state, in which litter production equals litter losses. In general, litter turnover rates in temperate forest have been estimated to be about 1 $year^{-1}$ compared to about 6–4 $year^{-1}$ for tropical forests where the influence of high temperature and soil moisture on the decomposition rate and consumption of litter on the forest floor promotes high litter turnover rates (Olson 1963). Additionally, in frequently flooded mangrove forests, another fate of the litterfall is tidal export to adjacent coastal waters, which enhances litter turnover rates in coastal forests. Previous results have shown that turnover rates in tidally influenced forests are higher than in inland basin forests where the frequency of inundation is lower (Twilley et al. 1986). For instance, litter turnover rates for frequently flooded mangrove forests are generally higher than 4 $year^{-1}$ with some values being as high as 12 $year^{-1}$ indicating the potential significance of litter export (Twilley 1995). In summary, litterfall production in basin forests is generally lower than in fringe and riverine sites, yet standing litter crop is much higher in this inland zone due to lower flushing.

Twilley (1998) integrated the factors affecting mangrove productivity into a hierarchical conceptual model. At the global level, temperature is the main factor affecting mangrove, distribution, forest structure and productivity. Within the tropics, geomorphological types such as deltas, estuaries and lagoons affect structure and productivity; however, mangroves in deltaic environments have the overall highest productivity. Furthermore, within any geomorphic type, the productivity ranking is riverine > fringe > basin > scrub (Day et al. 1996). Finally, within each habitat, nutrient resources, soil type, and stressors such as salinity and sulfides affect productivity (Twilley 1995). In this paper, we test this conceptual model using litterfall production data from carbonate and terrigenous environments bordering the Gulf of Mexico in southern Florida and southern Mexico.

The objective of this study was to describe litterfall production, standing litter crop, and litter turnover rates in scrub, basin, fringe and riverine forests in two contrasting mangrove ecosystems: a carbonate system located in the Southeastern Everglades and a deltaic system located in Terminos Lagoon, Campeche, Mexico. We were also interested in testing three particular hypotheses:

1. Overall, litterfall per unit area is higher in Terminos Lagoon than in Southeastern Everglades due to higher air temperatures, high frequency of inundation, high nutrient resources and low salinity stress.
2. Average litterfall per unit area is higher in Terminos Lagoon because a greater proportion of the mangrove area is composed by riverine and fringe mangrove types, while a greater proportion of the area in the Southeastern Everglades region dominated by scrub mangrove forests.
3. At the forest type level, fringe and basin sites in the Terminos Lagoon region have higher litterfall than similar forest types in the Southeastern Everglades region.

Study areas

Terminos Lagoon is coastal lagoon of approximately 1800 km^2, with a mean depth of 3.5 m, which borders the southern Gulf of Mexico in the State of Campeche, Mexico, at approximately 18.5 N and 91.2 W (Fig. 1). It is connected to the Gulf of Mexico through two inlets located on either end of Carmen Island. Soils at the Terminos sites are terrigenous due to strong riverine input by three rivers, Palizada, Candelaria and Chumpán, which drain into the lagoon. The highest freshwater discharge, which has a marked effect on the salinity and hydrology of the lagoon water, occurs during October and November. In this region there are three seasons, rainy, dry and "norte" or cold front (Yañez-Arancibia and Day 1982). Average annual precipitation (1,680 mm) is seasonal with low rainfall from February to May (dry season) and high rainfall from July to November (rainy season). Maximum

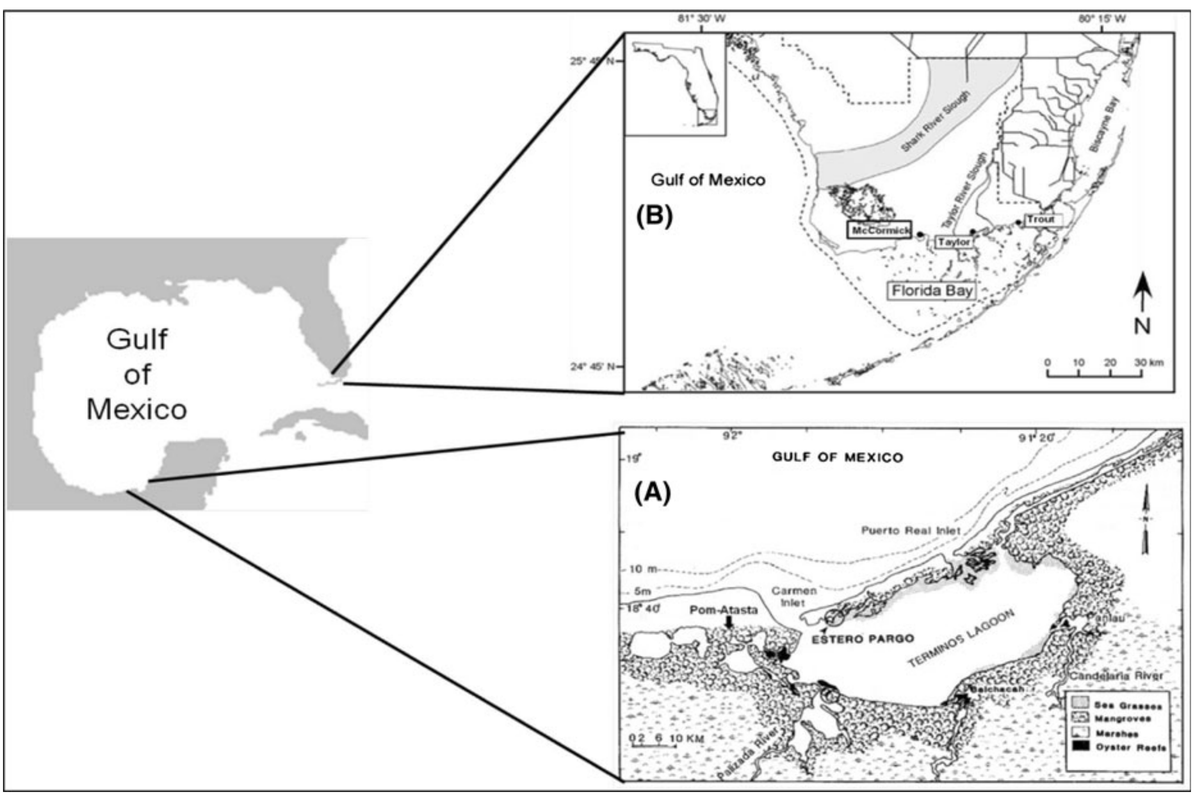

Fig. 1 (*A*) Terminos Lagoon region including Estero Pargo and Pom-Atasta the sites where fringe, basin, and riverine mangrove forests are located. (*B*) Southeastern Everglades region showing Taylor Slough and the location of fringe, basin and scrub mangrove forest sites

wind speeds occur during winter storm events locally known as "nortes" from December to February.

Terminos Lagoon is bordered almost completely by extensive mangrove forests that extend up the rivers and associated small lagoons to the limit of the tidal influence. Three mangrove species dominate: *Rhizophora mangle* L. (red mangrove), *Avicennia germinans* L. (black mangrove) and *Laguncularia racemosa* Gaertn f. (white mangrove). A fourth species, *Conocarpus erectus* L. (buttonwood), occurs only within the zones where tides rarely flood the mangrove forest, however, this species did not occur in the mangrove forest types we studied. Three mangrove forest types: Basin, Fringe and Riverine were selected to conduct litterfall production studies. Basin and fringe mangrove forests are located at Estero Pargo, a tidal channel 5.9 km long and averaging 8.5 m wide and located on the lagoon side of Carmen Island (Fig. 1). The fringe forest, which is adjacent to the channel and regularly inundated by tides, is about 40 m wide. In this zone, *R. mangle* and *A. germinans* dominate although *L. racemosa* also occurs. Behind the fringe forest, there is an extensive basin mangrove forest dominated almost completely by *A. germinans*. Pom-Atasta, a coastal lagoon system associated with Terminos Lagoon and surrounded by extensive mangrove forests, two mangrove types occur: riverine and fringe (Fig. 1).

The Everglades study sites are located at the southeastern tip of the Florida peninsula bordering Florida Bay at approximately 25.5 N (Fig. 1). The climate of Florida Bay and the Everglades is characterized as sub-tropical savanna with conspicuous dry and rainy seasons (Jordan 1984). About 75% of the average annual rainfall occurs during the summer from May to October (Jordan 1984). The dry season (December–May) is characterized by mild temperatures and low precipitation. Tides in Florida Bay are semi-diurnal with amplitude of 30 cm in the western bay. However, due to restricted circulation between the eastern and western basins, the mean tide range within our mangrove study area, which includes eastern Florida Bay, is 5–10 cm (Wang et al. 1994). Fringe and basin forests, dominated by tall *R. mangle*, *A. germinans*, and *C. erectus*, are located in the salinity transition zone, which is the mangrove zone adjacent to Florida Bay. There are several creeks draining into Florida Bay from which three fringe and basin mangrove forests were chosen for study. A scrub red mangrove forest, located about 2 km north of the mouth of Taylor Creek, was also selected (Fig. 1).

Field methodology

Forest structure

At Terminos Lagoon, two 0.1 ha plots were randomly selected and established within the riverine, fringe and basin forests. Sites at Southeastern Everglades were established in a similar manner in fringe, basin, and scrub mangroves. Within each plot all trees with diameter at breast height (dbh) $\geq$2.5 cm were tagged and measured to determine species composition, basal area (m^{-2} ha^{-1}), tree density (stems ha^{-1}) and tree height (m). Forest structure is described by the complexity index, which is obtained by multiplying basal area $\times$ tree density $\times$ canopy height $\times$ number of species $\times$ 10^{-5} (Holdridge et al. 1971).

Litterfall and standing litter crop

At both study regions, five 0.25 m^2 litter traps with 1 mm screening were randomly deployed within each plot. At Terminos Lagoon, riverine, fringe and basin forests were monitored monthly from 1996 to 2002. Due to logistic constraints, the sites at Southeastern Everglades were sampled every 4–5 weeks at two different periods 1996–1998 and 2000–2002. Standing litter crop was measured by collecting litterfall accumulated on the surface of forest floor from twelve 0.1 m^2 randomly selected sites in the vicinity of the litterfall traps. At Terminos Lagoon, standing litter crop was collected monthly from 1996 to 2002 at fringe and basin mangrove forests only. At the Southeastern Everglades sites, standing litter was collected about every 4–5 weeks in 1996 and 1997. Litter from each trap was oven-dried to constant weight at 70°C for 72 h, sorted into leaves (by species), twigs, fruits, stipules and woody material, and weighed to within 0.01 g. Standing litter crop samples were sorted into leaves and miscellaneous and weighed to within 0.01 g.

Soil properties and interstitial salinity

At Southeastern Everglades and Terminos Lagoon sites, four soil samples were randomly taken within each plot (16 per site) using a 6 cm diameter by 40 cm long coring device. In the laboratory, samples were sectioned into 5 cm lengths. Fresh material was weighed to ±0.001 g, oven-dried at 60°C for 48 h and weighed to calculate bulk density and percent water. Samples were sieved through a 4 mm mesh and analyzed for carbon, nitrogen and phosphorus concentration. Carbon and nitrogen analyses were performed using a Fiston CHN Analyzer model NA 1500. Phosphorus analysis was performed following Solorzano and Sharp (1980), with a modification proposed by Fourqueran et al. (1992).

At the fringe and basin forests of Terminos Lagoon interstitial salinity was measured along three transects, with ten ground water piezometers each, that run perpendicular to the tidal channel. At the riverine forests, two transects, with five ground-water piezometers each, were installed at each study site. At the Everglades, two transects with six ground water piezometers each were set up for each study site. All transects were perpendicular to the tidal creeks and extended through all mangrove zones. Piezometers at Terminos Lagoon sites, spaced at 20 m intervals, were placed into the soil to a depth of 0.5 m. Piezometers at Southeastern Everglades were deployed at 1, 2, 4, 8, 16, and 32 m away from the tidal creek. Interstitial water salinity in each piezometer was measured during litter sampling using an optical refractometer.

Statistical analysis

Litterfall data expressed as g m^{-2} day^{-1} and standing litter data expressed as g m^{-2} were natural logarithm transformed and analyzed for testing significant differences ($p < 0.05$) among forest types and climatic seasons using a split-plot analysis. Plots were nested within each site, considered for random effects and treated as experimental units. Interaction effects were considered for all analyses. In the analysis, the main plot tested the effect of forest type (riverine, fringe and basin). The subplot tested the factor climatic seasons (dry and rainy) and the interactions forest type * season, and forest type * season * year. All effects were considered fixed for all analyses. Pairwise comparisons were performed with Tukey's Honestly Significant Difference (HSD) test when significant differences ($p < 0.05$) were observed within a main effect or interaction. The assumption of normality was tested using normal probability plots and ANOVA residuals. After performing the analysis, linear contrasts were used to assess differences between treatments. Statistical analyses were run with JMP® version 8.0.1 (SAS Institute 2009).

Results

Forest structure

The forest structural characteristics among the three mangrove forest types located at the Terminos Lagoon region were different in basal area, species dominance and complexity index (Table 1a). Basal area, tree height and complexity index increased from basin to riverine mangrove forests with *R. mangle* (red mangrove), *A. germinans* (black mangrove) and *L. racemosa* (white mangrove) dominating the riverine forest and *A. germinans* dominating both fringe and basin forests. At the Southeastern Everglades, mangrove forests were dominated by *R. mangle*, particularly in the fringe and scrub mangrove forests, where *R. mangle* relative importance was 69 and 99%, respectively (Table 1b). In contrast, the basin forest was dominated by *A. germinans* and *C. erectus* (buttonwood) that had the highest relative importance with 43%. Similarly, complexity index values were lowest at the scrub forest and highest at the fringe forest (Table 1b).

Soil properties and interstitial salinity

Soil characteristics at the Terminos Lagoon mangrove forests indicate that nitrogen concentration (%) and mass (mg cm^{-3}) were highest at the basin forest and lowest at the riverine forest. In contrast, phosphorus values were relatively similar among the mangrove forest types; however, atomic N:P ratios were lowest (16) at the riverine forest and highest at the basin forest (51) suggesting phosphorus limitation in the basin forest (Table 2a). Soil characteristics at the Southeastern Everglades mangrove forests show that nitrogen concentration was highest at the scrub forest and similar at the fringe and basin forests. However, due to the lowest bulk density measured at the scrub forest (0.15 g cm^{-3}) nitrogen content was lowest at the scrub forest with similar values measured at the fringe and basin forests (Table 2b). In contrast, both phosphorous concentration (%) and content (mg cm^{-3})

Table 1 Structural characteristics by mangrove forest types at study sites

(a) Terminos Lagoon region			
Structure attributes	Basin	Fringe	Riverine
Basal area (m^2 ha^{-1})	8.6	33.2	79.9
Tree height (m)	5	10	12.5
Density (tree ha^{-1})	1,670	3,095	1,650
Complexity index	2.2	10.3	49.7
Relative importance (%)			
Rhizophora mangle	14	26	38
Avicennia germinans	85	60	32
Laguncularia racemosa	1	14	30

(b) Southeastern Everglades region			
Structure attributes	Scrub	Basin	Fringe
Basal area (m^2 ha^{-1})	4.4	12.9	16.9
Tree height (m)	1	4.7	5.2
Density (tree ha^{-1})	17,017	1,854	3,294
Complexity index	1.2	4.5	11.5
Relative importance (%)			
Rhizophora mangle	99	6	69
Avicennia germinans	0.5	33	11
Laguncularia racemosa	0.5	1	4
Conocarpus erectus		43	12
Non-mangrove species		17	4

values were similar among the mangrove forest types. However, atomic N:P ratios were relatively similar at fringe (49) and basin forests (53) and highest at the scrub forest with a N:P ratio of 70; those N:P values indicate that phosphorous is limiting at the Southeastern Everglades mangrove forests with the scrub forest showing the greatest P limitation (Table 2b).

At the Terminos Lagoon, annual average interstitial salinity was always lower in riverine (25 psu) and fringe mangroves (50 psu) than in the basin mangrove (70 psu). This pattern was consistent during the entire study period, with a coefficient of variation of only 4%, reflecting a relatively constant salinity gradient (Table 2a). Mean interstitial salinity values at the Southeastern Everglades sites were 12, 24, and 27 at the scrub, fringe and basin mangrove forests, respectively (Table 2b), reflecting freshwater input from the northern Everglades. Along the salinity transects, soil salinity values were highly variable, with coefficient of variations of 16, 21 and 6% at the scrub, fringe and basin mangrove types, respectively.

Litterfall production

At the Terminos Lagoon litterfall was highest at the riverine forest averaging 12.8 Mg ha^{-1} $year^{-1}$ during the study period, while at the fringe and basin mangrove forests litterfall averaged 9.7 and 5.3 Mg ha^{-1} $year^{-1}$, respectively. The spatial pattern observed at the riverine forest was driven by the leaf fall input by *L. racemosa*, *R. mangle* and *A. germinans* that was significantly higher relative to the other two mangrove forests ($p < 0.05$; Table 3a). Similarly, the riverine forest litterfall rates were highly seasonal with low litterfall rates observed during the dry season and high during the rainy season. The seasonal pattern observed at the riverine forest was consistent during the entire study period (Fig. 2a). Litterfall production at the fringe forest was significantly higher than at the basin forest ($p < 0.05$; Table 3a). The higher litterfall production at the fringe forest was driven by the leaf fall contribution by *R. mangle* and *A. germinans* while at the basin forest leaf fall was driven only by *A.*

Table 2 Soil physico-chemical properties

(a) Terminos Lagoon region

Soil Properties	Mangrove forest type		
	Riverine	Fringe[a]	Basin[a]
Soil C (%)	10.2	14.51	19.1
Soil N (%)	0.32	0.57	0.86
Soil P (%)	0.04	0.06	0.04
Bulk density (g cm^{-3})	0.41	0.29	0.31
Total C (mg cm^{-3})	42.1	41.7	58.7
Total N (mg cm^{-3})	1.30	1.62	3.40
Total P (mg cm^{-3})	0.18	0.17	0.15
Atomic C:N	37	30	26
Atomic N:P	16	22	51
Interstitial salinity (psu)	25	45	70

(b) Southeastern Everglades region

Soil properties	Mangrove forest type		
	Fringe	Basin	Scrub
Soil C (%)	12.5	13.6	25.1
Soil N (%)	0.85	0.86	1.38
Soil P (%)	0.04	0.04	0.04
Bulk density (g cm^{-3})	0.62	0.70	0.15
Total C (mg cm^{-3})	96.2	95.2	36.4
Total N (mg cm^{-3})	5.20	5.75	1.97
Total P (mg cm^{-3})	0.21	0.23	0.07
Atomic C:N	19	19	21
Atomic N:P	49	53	70
Interstitial salinity (psu)	24	27	12

[a] Soil data by Lynch 1989

Table 3 Spatial (a) and temporal (b) variability of litterfall rates by components (Mg ha^{-1} $year^{-1}$) at Terminos Lagoon

(a)

Forest type	*R. mangle*	*A. germinans*	*L. racemosa*	Twigs + fruits	Litterfall
Riverine	3.61 ± 0.37^a	3.92 ± 0.22^a	3.87 ± 0.29^a	1.40 ± 0.22^a	12.81 ± 0.79^a
Fringe	2.74 ± 0.15^b	5.26 ± 0.15^b	0.85 ± 0.11^b	0.88 ± 0.07^b	9.73 ± 0.79^b
Basin	0.04 ± 0.007^c	4.71 ± 0.15^c	0.11 ± 0.01^c	0.40 ± 0.04^c	5.26 ± 0.48^c

(b)

Seasons	*R. mangle*	*A. germinans*	*L. racemosa*	Twigs + fruits	Litterfall
Dry	1.31 ± 0.11^a	3.91 ± 0.11^a	0.88 ± 0.07^a	0.62 ± 0.04^a	6.72 ± 0.18^a
Rainy	1.79 ± 0.11^b	5.73 ± 0.15^b	0.69 ± 0.07^b	0.84 ± 0.07^b	9.05 ± 0.18^b

Different letters within each litterfall component among forest types and seasons are significantly different ($p < 0.05$)

germinans (Fig. 2b, c). Similarly, the fringe and basin forests litterfall production was highest during the rainy season (June–September) and lowest at the beginning of the dry season (December–January) (Fig. 2b, c). The temporal litterfall pattern observed among the three mangrove forests was significantly

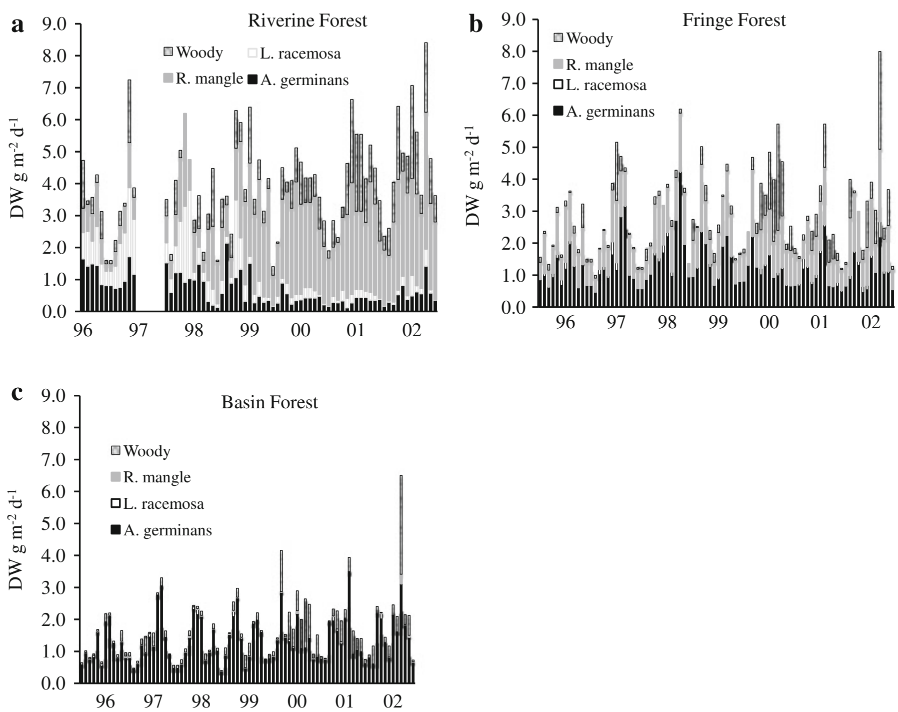

Fig. 2 Spatial and temporal pattern of litterfall at the mangrove forests located in the Terminos Lagoon region. **a** Riverine forest, **b** fringe forest, and **c** basin forest

different ($p < 0.001$; Table 3b). The observed spatial and seasonal variability among the three mangrove forests was relatively constant during the study period, which suggests that this tropical region environmental condition remained relatively constant.

At the Southeastern Everglades litterfall was highest in the fringe forest averaging 9.1 Mg ha^{-1} year^{-1} during both study periods, while at the basin and scrub mangrove forests litterfall averaged 6.5 and 2.4 Mg ha^{-1} year^{-1}, respectively (Table 4a). The spatial litterfall pattern observed at the three mangrove forests was significantly different ($p < 0.05$) with fringe > basin > scrub (Table 4a). At the three mangrove forests, leaf fall made up 80% of the total litterfall with *R. mangle* contributing more than 85% of the total leaf fall in the scrub forest, while at the fringe and basin forests its contribution was 38 and 4%, respectively (Table 4a). The contribution of *A. germinans* was highest in the basin forest (22%) and lowest in the dwarf mangrove (0.3%). *L. racemosa* contribution was highest in the fringe forest (2.4%) and lowest in the basin forest (0.05%). *C. erectus* occurred only in the fringe and basin forests where its contribution was relatively high (25 and 47%, respectively; Table 4a). Leaf fall pattern contribution by species reflects the dominance that each mangrove species has at each study site. Temporally, litterfall rates at the fringe and basin forests were seasonal with high litterfall rates observed at the end of the dry season and beginning of the rainy season (May–July) (Fig. 3a, b). In contrast, litterfall rates at the scrub forest were higher during the rainy season with *R. mangle* contributing with 95% of the total litterfall (Table 4b; Fig. 3c). The interannual spatial and seasonal litterfall pattern among the three mangrove forests was highly variable during the study period suggesting that environmental conditions in this subtropical region were affected by natural disturbances such as drought and hurricanes.

Standing litter crop and turnover rates

In Terminos Lagoon, the average standing litter crop in the fringe (3.8 Mg ha^{-1}) was significantly higher than the basin forest (3.5 Mg ha^{-1}) ($p < 0.05$; Table 5a). Similarly, litterfall turnover rates were significantly higher in the fringe mangrove forest (4.1 year^{-1}) relative to the basin forest (2.2 year^{-1}) (Table 5a). This result indicates that litterfall remains a shorter time in the fringe forest than in the basin forest (3 and 6 months, respectively). Furthermore, differences in litterfall residence time between fringe

Table 4 Spatial (a) and temporal (b) variability of litterfall rates by components (Mg ha^{-1} year^{-1}) at Southeastern Everglades region

(a)

Forest type	*R. mangle*	*A. germinans*	*L. racemosa*	*C. erectus*	Twigs + fruits	Stipules	Total litterfall
Fringe	3.43 ± 0.15^{a}	0.69 ± 0.11^{a}	0.22 ± 0.07^{a}	2.29 ± 0.18^{a}	1.87 ± 0.19^{a}	0.37 ± 0.02^{a}	9.12 ± 0.68^{a}
Basin	0.26 ± 0.11^{b}	1.46 ± 0.11^{b}	0.004 ± 0.07^{a}	3.07 ± 0.18^{b}	1.09 ± 0.22^{b}	0.04 ± 0.01^{b}	6.47 ± 0.41^{b}
Scrub	2.15 ± 0.22^{c}	0.007 ± .01^{c}	0.007 ± 0.09^{a}	–	0.11 ± 0.20^{c}	0.18 ± 0.02^{c}	2.45 ± 0.18^{c}

(b)

Seasons	*R. mangle*	*A. germinans*	*L. racemosa*	*C. erectus*	Twigs + fruits	Stipules	Total litterfall
Dry	1.49 ± 0.15^{a}	0.69 ± 0.11^{a}	0.04 ± 0.07^{a}	2.77 ± 0.22^{a}	0.62 ± 0.19^{a}	0.15 ± 0.01^{a}	6.05 ± 0.33^{a}
Rainy	3.30 ± 0.15^{b}	2.06 ± 0.07^{b}	0.18 ± 0.07^{a}	0.18 ± 0.18^{b}	1.84 ± 0.15^{b}	0.26 ± 0.01^{b}	8.14 ± 0.30^{b}

Different letters within each leaf component among forest types and seasons are significantly different ($p < 0.05$)

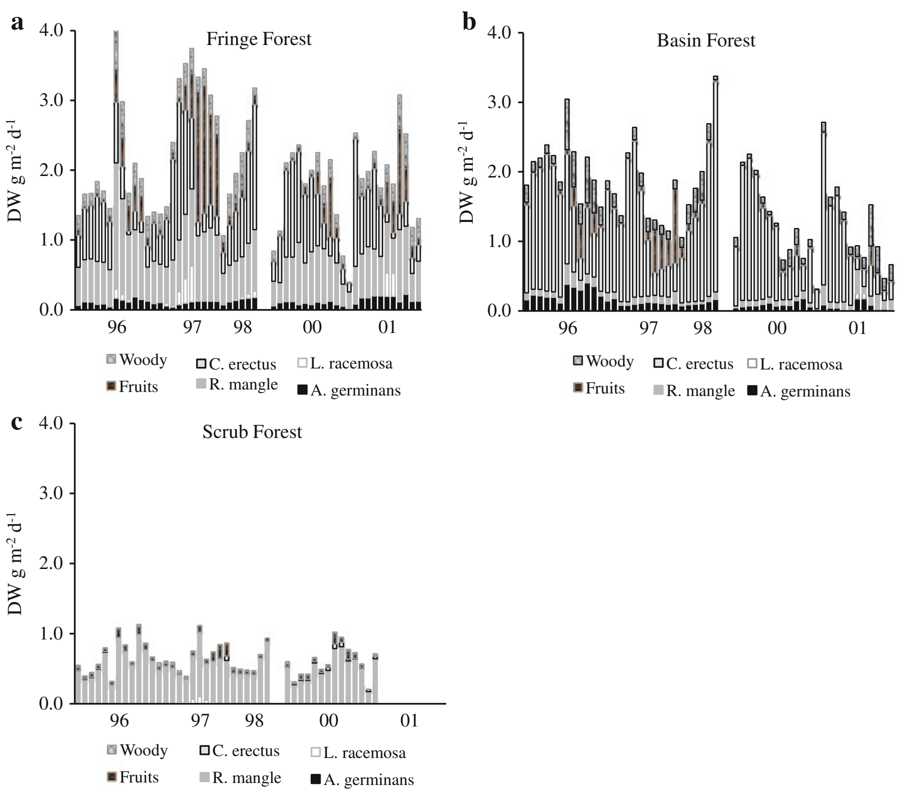

Fig. 3 Spatial and temporal pattern of litterfall at the mangrove forests located in the Southeastern Everglades region. **a** Fringe forest, **b** basin forest, and **c** scrub forest

and basin forests are related to differences in hydrology, with fringe forest being flushed more frequently than the basin forest. At Southeastern Everglades mangrove forests, the average litter standing crop was 1.9, 3.3 and 4.5 Mg ha^{-1} at scrub, basin and fringe mangrove forests, respectively (Table 5b); spatial standing crop differences were significant among the three mangrove forest types ($p < 0.05$). Similarly, turnover rates were significantly higher at both basin and fringe mangrove types (2.1 and 2.0 year^{-1}, respectively) than at the scrub mangrove forest (1.6 year^{-1}) (Table 5b), indicating that litterfall

Table 5 Standing litter and turnover rates at (a) Terminos Lagoon region and (b) Southeastern Everglades region

(a)

Zone	Standing litter (Mg ha^{-1})			Turnover rate (year^{-1})		
	Leaf litter	Woody	Standing litterfall	Leaf litter	Woody	Litterfall
Fringe	2.4 ± 0.11[a]	1.4 ± 0.09[a]	3.8 ± 0.31[a]	6.2[a]	0.38[a]	4.1[a]
Basin	2.2 ± 0.08[b]	1.3 ± 0.08[a]	3.5 ± 0.11[b]	4.8[b]	0.35[b]	2.2[b]

(b)

Site	Standing litter (Mg ha^{-1}) ± SE			Turnover rate (year^{-1})		
	Leaf litter	Woody	Litterfall	Leaf litter	Woody	Litterfall
Scrub forest	1.4 ± 0.08[a]	0.52 ± 0.05[a]	1.9 ± 0.12[a]	1.6[a]	0.62[a]	1.3[a]
Basin forest	2.5 ± 0.26[b]	0.75 ± 0.06[b]	3.3 ± 0.30[b]	2.2[b]	1.4[b]	2.0[b]
Fringe forest	3.5 ± 0.18[c]	1.1 ± 0.08[b]	4.5 ± 0.26[c]	2.1[b]	2.1[b]	2.1[b]

Different letters within each component among forest types are significantly different ($p < 0.05$)

remains longer in the scrub mangrove forest than in fringe or basin forest types (9 and 6 months, respectively).

Discussion

Litterfall production

Geomorphological landforms such as deltas, estuaries, lagoons and carbonate environments affect mangrove structure and productivity. In general, in deltaic environments mangroves have higher productivity when compared to carbonate environments (Twilley 1995). Furthermore, within a geomorphological landform, the litterfall of riverine, fringe, basin and scrub mangrove ecological types is affected by factors such as hydrology and topography. Within each mangrove forest type, nutrient resources and stressors such as soil salinity and sulfide along the inundation gradient affect mangrove productivity (Lugo and Snedaker 1974). In terms of nutrients, P limits mangrove productivity in carbonate environments, while there seems to be a mixture of P and N limitation in deltaic environments (Alongi et al. 1992; Feller 1995; Feller et al. 1999; Twilley et al. 1996). Furthermore, it has been shown that forest structure and productivity are highest in riverine forests and lowest in scrub forests (Pool et al. 1975; Brown and Lugo 1982; Twilley 1995). In our study sites, basal area, which is a property of forest structure, varied along nutrient gradients with basal area values steadily decreasing with increasing soil N:P ratios (Tables 1, 2). This pattern underlines the importance of soil resources in affecting mangrove forest structure along a nutrient gradient with the highest basal area values associated with riverine forest, lowest with scrub mangrove forest, and basin and fringe forest falling in between.

Over the past three decades, considerable data on mangrove productivity has been generated. From this information, some general trends have emerged on the spatial patterns of mangrove productivity and the environmental factors affecting litterfall production (Lugo and Snedaker 1974; Pool et al. 1975; Brown and Lugo 1982; Twilley et al. 1986; Alongi et al. 1992; Feller 1995; Day et al. 1996). For instance, reported mean annual litterfall ranges from 12.8 to 17.0 Mg ha^{-1} year^{-1} for riverine forests, from 4.3 to 10.8 Mg ha^{-1} year^{-1} for fringe forests, from 2.5 to 9.7 Mg ha^{-1} year^{-1} for basin forests and from 1.2 to 2.5 Mg ha^{-1} year^{-1} for scrub forests (Pool et al. 1975; Ong et al. 1982; Twilley 1995; Day et al. 1996). Our study sites in Mexico and Florida span the range of all of these mangrove forest types and allowed us to test our hypotheses on how different environmental factors interact to drive productivity at different levels of organization. Results from this study indicate that litterfall was highest in the riverine forest (12.8 Mg ha^{-1} year^{-1}) followed by the fringe forests (9.7 and 9.1 Mg ha^{-1} year^{-1} at Terminos and Southeastern Everglades, respectively), basin forests (6.5 and 5.2 Mg ha^{-1} year^{-1} at Southeastern Everglades and Terminos, respectively) and scrub forest (2.5 Mg ha^{-1} $year^{-1}$). The value for the riverine site in Terminos Lagoon is similar to that of Boca Chica (12.1 Mg ha^{-1} $year^{-1}$), another riverine forest located in Terminos Lagoon (Day et al. 1987). Furthermore, results from this study demonstrate that litterfall in Terminos and Southeastern Everglades followed the ranking riverine > fringe > basin > scrub that has been observed in the Churute River, Ecuador (Twilley et al. 1997), Shark River, Florida (Castañeda-Moya 2010) and Celestum, Mexico (Zaldivar Jimenez et al. 2004), as well as other areas.

Results from this study show how interactions among soil salinity and soil nutrients influence litterfall at particular sites. Particularly, it has been shown that interstitial salinity affects spatial patterns of litterfall (Pool et al. 1975; Day et al. 1996). At the Terminos Lagoon study sites, litterfall was inversely related to interstitial salinity, as it has been shown in previous studies in this region where salinity explained 77% of litterfall variability (Day et al. 1996). Twilley et al. (1986) also reported an inverse relationship between litter production and soil salinity at Rookery Bay, Florida. Our results along with those of Twilley et al. (1986) demonstrate that soil salinity negatively affects litterfall, especially at those sites that are infrequently flushed by tides, such as the basin forest located at Terminos Lagoon. The spatial pattern of soil salinity at the Terminos Lagoon mangrove forests, lowest at the riverine forest (mean = 25), low at the fringe forest (mean = 45) and highest at the basin forest (mean = 70), follows the zonation of *R. mangle*, *L. racemosa*, and *A. germinans* (Table 2a). Interstitial salinity at the Southeastern Everglades sites ranged from 12 to 27, with the scrub forest having the lowest values and both basin and fringe forests having the highest salinity values (Table 2b). Because interstitial salinity values at Southeastern Everglades were relatively low, it explained only 12% of litterfall variability and litterfall rates were not negatively associated with soil salinity. These results suggest that at Southeastern Everglades environmental factors other than soil salinity affects spatial patterns of litterfall.

These results further emphasize the importance of soil salinity as an environmental factor constraining litterfall production. However, soil resources, such as nitrogen and phosphorous, control also litterfall production. For instance, at the study sites in Southeastern Everglades and Terminos Lagoon, a N:P soil nutrient gradient was strongly related with spatial patterns of litterfall production with highest litterfall rates observed in riverine forest where N:P ratio was the lowest. Similarly, lowest litterfall rates were observed in scrub forest where N:P ratio was the highest with basin and fringe forests falling between riverine and scrub end members (Fig. 4). The importance of soil resources has been also shown in other mangrove forests (Twilley et al. 1997; Castañeda-Moya 2010) where litterfall production is highest where soil resources are not limited (Fig. 4). This spatial pattern is important because better predictions can be made concerning the influence of stressors and soil resources on litterfall production in mangrove ecosystems, regardless of the environmental setting.

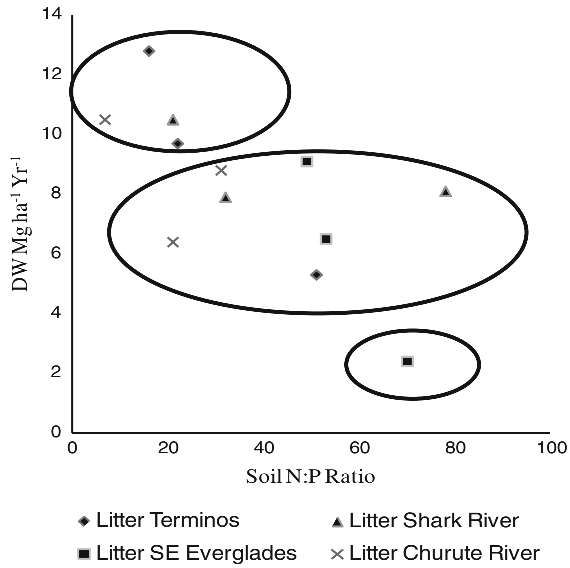

Fig. 4 Spatial pattern of litterfall production (Mg ha^{-1} $year^{-1}$) along a soil N:P ratio nutrient gradient. Data from Shark River by Castañeda-Moya, E. 2010. Data from Churute River by Twilley et al. (1997)

Mangrove forests tend to be widely distributed in tropical deltas because of the broad flat areas characteristic of these environments, which is the case in the southern parts of Terminos Lagoon. Furthermore, as we have shown, mangrove forests are also more productive in deltas where soil salinity is low and input of freshwater and nutrients are high, which environmental parameters that stimulate litterfall production. Thus more productive mangrove forests are more common in deltas when compared to mangrove forests located in carbonate environments. For instance, we estimate that riverine mangrove forests cover about 50% of total mangrove area in Terminos Lagoon region, with fringe and basin forests contributing 30 and 20%, respectively. At the other end of the geomorphological scale, riverine and fringe mangrove forests tend to be less widely distributed in carbonate environments, where large areas of scrub mangroves cover more than 60% of the total mangrove area. Using above estimations, the average litterfall production in the Terminos Lagoon region is about 9.0 Mg ha^{-1} $year^{-1}$ compared to about 4.5 Mg ha^{-1} $year^{-1}$ in the Southeastern Everglades region. These results underline the importance of how geomorphological setting affects overall litterfall productivity. However, this is not because similar habitats (i.e., fringe and basin forests) differ in productivity but rather the relative proportion of different vegetation types (i.e., riverine vs scrub). In summary, the spatial pattern of litterfall production is similar at both study regions where litterfall was significantly higher in the fringe than in the basin forest. Similarly, in the riverine mangrove forest, litterfall was the highest among all the mangrove types with the scrub forest having the lowest production. Based on these results, the litterfall production spatial pattern Riverine > Fringe > Basin > Scrub was directly related to both the hydrological and environmental conditions found in each forest type. For instance, low soil N:P ratios, low soil salinity and short hydroperiods characterized the highly productive riverine forest while high soil N:P and long hydroperiods characterized the low productive scrub forest.

The Terminos Lagoon region is fully tropical (18.5 N) while the Southeastern Everglades region is located near the northern limit of mangrove distribution (25.5 N) and are, therefore, affected by colder temperatures and occasional frosts. Since the Terminos Lagoon region is seven degrees further south than the Southeastern Everglades (18.5 N vs 25.5 N) and never experiences frosts, we hypothesized that due to the effect of warmer temperatures similar mangrove types would have higher productivity at the Terminos Lagoon region than at the Southeastern Everglades region. However, there were no significant differences in litterfall production between similar mangrove forests type located at either region. In fact, fringe mangrove forests were slightly more productive in the Southeastern Everglades (Tables 3, 4). The higher litterfall production observed in fringe mangrove forests located at Southeastern Everglades was due to the contribution of *C. erectus*, an associated mangrove species that is not found at any of the mangrove forest types in the Terminos Lagoon region. Thus, based on these results we conclude that differences in latitude between Southeastern Everglades and Terminos Lagoon play a small role in driving litterfall production between the two regions. However, long-term studies are needed to clearly establish the effect of climate variability on litterfall production between these two regions.

Standing litter crop and turnover rates

Four processes influence litter dynamics in mangrove forests: litterfall production, litter decomposition, litter consumption and litter export. The relative importance of each of these processes determines the fate of litter on the forest floor (Steyer 1988; Twilley et al. 1997). Litter export is high in mangrove environments that are tidally dominated, relative to environments where tidal influence is minimal. Similarly, litter accumulation on the forest floor is lower in highly productive tropical forests and higher in relatively low productivity temperate forests (Olson 1963; Scott et al. 1992). A major reason for this pattern is due to the high rates at which organic matter decomposes and is incorporated into the soils at tropical forests. Thus, warm, highly productive tropical forests have higher litter decomposition rates relative to cool, low productive temperate forests (Scott et al. 1992). Litter turnover, which is the litterfall: standing litter crop ratio, is an indirect measurement of litter decomposition and/or litter export within a forest (Olson 1963; Twilley et al. 1986). Research has shown litter turnover rates in fringe and riverine forests are much higher than litter turnover rates in basin forests (Steyer 1988; Lee 1989; Twilley et al. 1986). For instance, low litter turnover rates (1.1 $year^{-1}$) have been reported for Mai Po, Hong Kong, which is a mangrove forest characterized with little tide influence (Lee 1989). In contrast, very high turnover rates have been found at riverine mangrove forests of Ecuador where litter turnover rates were higher than 50 $year^{-1}$, which is the result of not only high tidal export, but also due to very high leaf consumption by crabs such as *Ucides occidentalis* (Twilley et al. 1997). Similarly, litter turnover rates in riverine and fringe forests at Fort Myers, FL and Rookery Bay, FL ranged from 4 to 6 $year^{-1}$ (Steyer 1988; Twilley et al. 1986) indicating that both riverine and fringe mangrove forests are more frequently flushed than mangrove forests at Southeastern Everglades where litter turnover rates were relatively low, with an average value of less than 2.5 $year^{-1}$. This low turnover rate suggests that in Southeastern Everglades mangroves where tidal flushing is minimal, there is very little litter export. In addition to low litter export, crab consumption has little impact in this area (Smith et al. 1989). Thus, in situ decomposition seems to control the fate of leaves on the forest floor.

At Terminos Lagoon, leaf litter turnover rates in the fringe forest were similar to that of fringe forest at Fort Myers (average 6 $year^{-1}$) while turnover rate in the basin forest was similar to that of basin and fringe forests at Southeastern Everglades (2.5 $year^{-1}$). Tides in Terminos Lagoon frequently inundate the fringe forests (Rivera-Monroy et al. 1995), while the basin forest is flooded only during very high tides associated with storms resulting in a higher turnover rates in the fringe forest relative to the basin forest. Thus, higher turnover rates suggest that in situ litter decomposition is less important in determining litter turnover rates in fringe forests at the Terminos Lagoon region. It also suggests that fringe forests have a more open biogeochemical cycle, exchanging nutrients and organic matter with the adjacent tidal channel (Rivera-Monroy et al. 1995). In contrast, the basin forest, with low tidal influence and low litter export has a higher accumulation of organic matter in the forest floor. This result is consistent with results of Lynch (1989) who found that organic matter content in the basin forest was higher (0.130 g cm^{-3}) than at the fringe forest (0.093 g cm^{-3}). Our results suggest that in the basin forest there is a different mechanism to cope with low nutrient input by tides, in which in situ litter decomposition plays an important role in recycling nutrients on the forest floor (Rivera-Monroy et al. 1995). Davis et al. (2003) reported that N and P accumulated in decomposing leaves in our study sites, indicating a long-term accumulation of these nutrients into soil detritus. Since lower turnover rates were measured in the fringe, basin, and scrub forests in the Southeastern Everglades, a similar mechanism to cope with low nutrient inputs may also occur at those forests. Thus, results from this study indicate that litter dynamics at the Southeastern Everglades sites are mainly controlled by in situ litter decomposition. In contrast, at Terminos Lagoon, tides play a major role on litter turnover in the fringe and riverine forests; therefore, litter decomposition plays a minor role in controlling litterfall dynamics, while in situ litter decomposition plays an important role controlling litterfall dynamics in the basin forest.

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