Journal of Coastal Research	SI 39	1169 - 1174	ICS 2004 (Proceedings)	Brazil	ISSN 0749-0208

Structure and Litter Production of Mangrove Forests under Different Tidal Influences in Babitonga Bay, Santa Catarina, Southern Brazil

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ABSTRACT

CUNHA, S. R.; TOGNELLA-DE-ROSA, M. M. P. and COSTA, C. S. B., 2006. Structure and litter production of mangrove forests under different tidal influences in Babitonga Bay, Santa Catarina, southern Brazil. *Journal of Coastal Research*, SI 39 (Proceedings of the 8th International Coastal Symposium), 1169 - 1174. Itajaí, SC, Brazil, ISSN 0749-0208.

This work aimed to evaluate the influence of different flooding frequencies on structure and litter production of a mesohaline mangrove forest near to the southern limit of mangrove forest in South Atlantic. Tree sites with different flooding frequencies were selected. In each site 100m^2 plots were placed to evaluate species density, height, diameter and biomass, and 0.25m^2 litter traps were placed to evaluate monthly litter production from February 1998 to January 1999. Salinity, temperature and rainfall were recorded during the period. The structural data and specific litter fall were correlated with flooding frequency (FF). *Laguncularia racemosa* was the dominant species at the higher FF, presenting higher density (4000 trees ha^{-1}; 52%) tree biomass (25 tones ha^{-1}; 60%) and litter annual production (2.35 tones ha^{-1} year^{-1}; 70%) at site A. *Rhizophora mangle* was the dominant species at the lower FF, presenting higher density (4700 trees ha^{-1}; 65%) and litter annual production (2.36 tones ha^{-1} year^{-1}; 65%), at site C, but biomass was always low. *Avicennia schaueriana* presented low density and litter production in all sites. As *L. racemosa* and *R. mangle* presented this inverse pattern, total annual litter fall (3.8 tones ha^{-1} year^{-1}) was not correlated with the flooding frequency gradient.

ADDITIONAL INDEX WORDS: *Laguncularia racemosa; Avicennia schaueriana; Rhizophora mangle.*

INTRODUCTION

Mangrove forests are traditionally known as very productive ecosystems (ODUM and HELD, 1972; LUGO *et al*., 1988), because they are able to accumulate high values of carbon as trunks and roots biomass (CLOUGH, 1992; DAY JR., *et al*., 1996; CHEN and TWILLEY, 1999), and they also usually produce large amounts of litter fall, which might be used directly or indirectly by fauna, recycled internally, or exported to adjacent waters (ROBERTSON *et al*., 1992; DAY Jr. *et al*., 1996; RIVERA-MONROY *et al*., 1998).

The structural development of mangroves and the litter production present a close relation with environmental factors, and well developed forest usually occur in protected coasts of warmer places, with high rainfall and large tidal range (LUGO and SNEDAKER, 1974; CINTRON and SCHAEFFER-NOVELLY, 1985; SCHAEFFER-NOVELLY *et al*., 1990a; TWILLEY, 1995). These positive correlations usually result in high litter production in low latitudes (800 to 2000 g m^{-2} year^{-1}; TWILLEY *et al*., 1997; CLOUGH *et al*., 2000) and a decrease of production associated with high latitudes (200 to 1000 g m^{-2} year^{-1}; ADAIME, 1985; SESSEGOLO, 1997; SCHAEFFER-NOVELLY *et al*., 1990b). There is a large variability into each climatic zone, which indicates that local effects can limit the productivity in all latitudes (SCHAEFFER-NOVELLY *et al*., 1990a,b; TWILLEY, 1995; SHERMAN *et al*., 1998). These factors include topography, flooding frequency, hydrodynamics, salinity, fresh water and nutrients input, soil characteristics, interaction soil-plant and biological interactions. All these can affect mangrove structure and also litter production.

The flooding frequency can affect significantly carbon uptake of mangrove trees (LIN and STERNBERG, 1992). It can also affect the ratio of allocation of photosynthetic products to different compartments of trees, resulting in different rates of litter fall (CLOUGH, 1992; DAY JR., *et al*., 1996). The flooding frequency affects, sometimes in a complex way, the input of nutrients, the salinity, the soil pH, Eh and sulfites (LUGO *et al*., 1988; MCKEE, 1993, 1995; SHERMAN *et al*., 1998). So, to make good estimative of litter production is necessary to take in account the spatial heterogeneity induced by the gradient of flooding frequencies perpendicularly into the mangrove forest, from water edge to inland places.

In this work we aimed to evaluate the structure and the litter production of a mangrove forest near to the southern limit of mangrove forest in South Atlantic. We also aimed to evaluate the influence of different flooding frequencies on structure and litter production of this mangrove forest.

METHODS

Study Site

This study was accomplished at Babitonga Bay (26°12'S-48°45'W), State of Santa Catarina, southern Brazil (Figure 1), near to southern limit of mangrove in Brazil (28°S). The bay area is about 167 Km^2, presenting 60 Km^2 of well preserved mangrove forests (IBAMA, 1998), occupied by *Rhizophora mangle*, *Avicennia schaueriana* and *Laguncularia racemosa.* Tidal regime is semidiurnal with tidal range about 1.2m. At the mesohaline mangrove forest three sites with contrasting conditions of tidal influence were selected along a transect: sites A (seaward), B (intermediate) and C (landward), with 90%, 70% and 50% flooding frequency, respectively. Flooding frequency was defined by the number of days (%), in a 1-year period, which tides reached the soil surface of each site. Each site had 100m parallel and 10m perpendiculars to river edge.

Data Sampling and Analysis

Water salinity and air temperature were measured daily. Soil salinity in each site was measured monthly. Meteorological data were obtained at CLIMERH/EPAGRI-SC.

To determinate the mangrove forest structure stands 100m^2 were placed at each site. Within the stands each tree was identified and tree heights were measured. The DBH (diameter

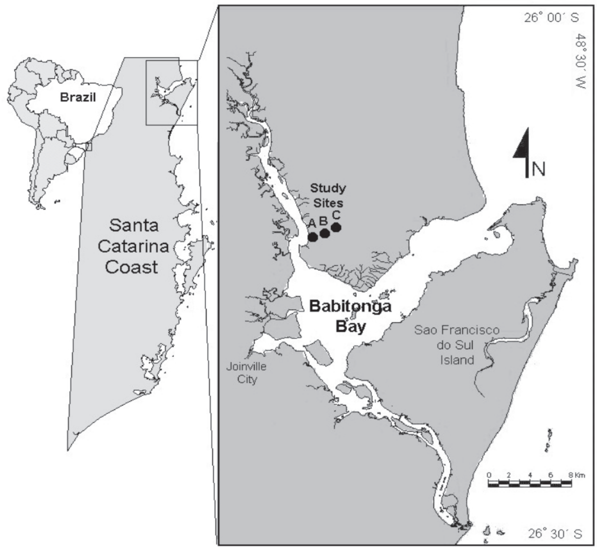

Figure 1. Study sites in Babitonga Bay, State of Santa Catarina, Brazil (Site marks are not in scale).

at breast-height) was measured for trees higher than 1.3m (adults), but not for trees with 1.3m high or lower (saplings). These data were used to estimate absolute and relative density, average tree height (adults), absolute and relative basal area and biomass. Allometric equations used to estimate biomass (g dry weight m^{-2} or ton dry weight ha^{-1}) was based on data from CINTRON and SCHAEFFER-NOVELLI, 1985.

Litter production was estimated using seven $0.25m^2$ litter traps (mesh baskets) placed randomly in each site (BROWN, 1984), 0.5m above high tide level. The baskets were emptied monthly from February 1998 to January 1999. Litter material was classified by leaves, stipules, flowers, fruits and wood, separate for the three species (*Laguncularia racemosa*, *Avicennia schaueriana*, *Rhizophora mangle*), dried and weighed (g dry weight m^{-2}). Litter production was expressed as monthly and annual production, for each species, for each site. Litter production rate was estimated using annual litter production as a percentage of species biomass (tree biomass).

After testing data normality, litter production was compared among species and among sites using analysis of variance and pos hoc Tukey HSD test. Pearson's correlations were tested between monthly litter production and abiotic data, and also between annual litter production and structural data.

RESULTS

Annual rainfall during the study (3088 mm $year^{-1}$) was higher than historical values (2690 mm $year^{-1}$; Figure 2A). Air temperature ranged from 15 to 33°C (Figure 2B). There were no significant differences in soil salinity among sites or between soil and water salinity ($p>0.2$; Figure 2C). Salinity values (5.8 to 24) were inversely related ($r^2=0.79$; $p=0.003$) to rainfall (30 to 450 mm $month^{-1}$). Evapotranspiration rates were lower than precipitation, resulting in a water surplus in all months.

Mangrove Forest Structure

Some structural variables presented low variability among the sites with different flooding frequencies (Figure 3). Despite this, they all showed tendency of positive correlation with flooding frequency, except *Rhizophora mangle* density, which presented inverse correlation.

Total tree densities were quite similar among sites, with highest value at site B (A=7600; B=8100; C=7300 trees ha^{-1}), but relative densities largely varied from site A to C. *Laguncularia racemosa* comprised 52 % of total trees in site A, and about 26 % at sites B and C. Relative densities of *Rhizophora mangle* were 35, 60 and 65 % at sites A, B and C, respectively. Absolute and relative densities of *Avicennia schaueriana* were always low, ranging from 10 to 14 % (Figure 3).

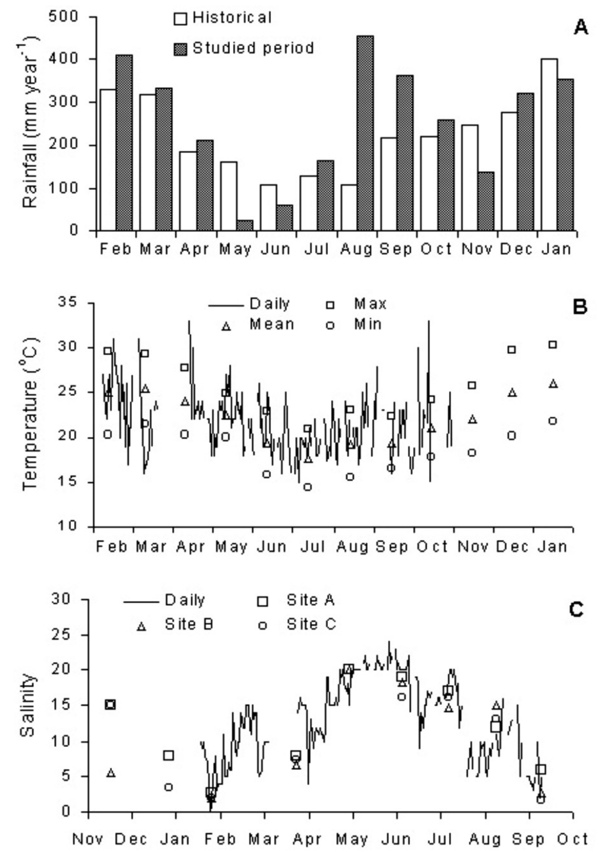

Figure 2. A) Precipitation from February 1998 to January 1999 and historical data (means from 1956 to 1977); B) Mean and maximum temperature; C) Daily water salinity and monthly soil salinity of each site.

Densities of *L. racemosa* saplings were similar among sites, ranging from 1600 to 1800 saplings ha^{-1}. There were few *A. schaueriana* saplings, with maximum of 500 saplings ha^{-1}. *R. mangle* saplings presented same density as *L. racemosa* at sites A and B, but at site C density was 11300 saplings ha^{-1}.

The mean diameters of *L. racemosa* were similar among sites (A=6.2 cm; B=6.0 cm; C=6.7 cm; Figure 3B), and tree height slightly decreased landward (A=3.8 m; B=3.2 m; C=3.1 m; Figure 3A). Despite the small differences of diameters and tree height among the sites, because of high density (Figure 3C), biomass was high at site A (25.0 ton ha^{-1}), compared to sites B (10.2 ton ha^{-1}) and C (11.4 ton ha^{-1}; Figure 3D).

The highest values of diameter (A=7.2 cm; B=7.0 cm; C=4.5 cm) and tree height (A=5.7 m; B=4.7 m; C=3.2 m) presented by *A. schaueriana* at sites A and B resulted in high values of biomass (11.4 and 10.8 ton ha^{-1}), even with low densities (Figures 3C and 3D). At site C biomass was very low (1.9 ton ha^{-1}).

R. mangle presented the lower values of diameter (A=4.2 cm; B=3.3 cm; C=3.0 cm) and tree height (A=2.8 m; B=2.6 m; C=2.6 m) which resulted in low biomass values (A=5.6; B=5.9; C=4.6 ton ha^{-1}), even though the high densities at sites B and C (Figures 3C and 3D).

Litter Fall

Seasonal and spatial variations in litter production for all mangrove species and sites were evident, and higher values of litter fall usually occurred in summer wet months (Figure 4). There were a strong spatial heterogeneity of litter fall into each site, but it was smaller than differences among sites or months (Figures 3E and 4).

L. racemosa presented the highest value of monthly averaged litter fall at site A, which decreased from 21.6 19.9 g m^{-2} month^{-1} at site A, to 8.6 10.3 g m^{-2} month^{-1} at site C (Figure 4). *A. schaueriana* presented the lowest values of monthly averaged litter fall, and they ranged from 4.9 5,3 g m^{-2} month^{-1} (mean standard deviation) at site A, to 1.1 1.8 g m^{-2} month^{-1} at site C. (no significant differences between sites B and C for both species). *R. mangle* showed an inverse pattern. Its monthly averaged litter fall values were low at sites A and B (5.5 12.7 g m^{-2} month^{-1} and 7.5 23.3 g m^{-2} month^{-1}, respectively) and it was 18.7 5.5 12.7 g m^{-2} month^{-1} at site C (no significant differences between sites A and B).

Litter fall of all species showed significant positive correlations with maximum monthly temperature (*L. racemosa*: r^2=0.69; *R. mangle*: r^2=0.56; *A. schaueriana*: r^2=0.52). No significant correlation was observed among litter fall and salinity or rainfall. *L. racemosa* and *A. schaueriana* litter fall were positively correlated with flooding frequencies (r^2=0.88 and r^2=0.79, respectively), although *R. mangle* litter fall was negatively correlated with this variable (r^2=-0.88). Litter fall of mangrove forest (pooled data of three species) was not correlated with rainfall, salinity or flooding frequency, but it showed a significant positive correlation with maximum monthly temperature (r^2=0.66).

Leaves comprised 81 to 93% of litter fall for *L. racemosa* among sites, and propagules presented important contribution only at site A (19%). *A. schaueriana* leaves comprised 97 to 100% of its litter fall (Figure 4). Other structures were not significant to the litter production of these two species.

Fruits were more abundant in *R. mangle* litter at sites B and C. For these two sites, propagules represented about 40% of the litter fall for this species, while leaves and inflorescences comprised 45% and 10%, respectively. Seventy seven percent of *R. mangle* litter fall production of site A was composed of leaves and only 10% by propagules (Figure 4). Leaves, flowers, fruits, propagules and *R. mangle* stipules, presented a very similar seasonal pattern.

Annual litter fall (Figure 3E) was direct correlated with tree biomass of the sites for *L. racemosa* (r^2=0.92) and *A. schaueriana* (r^2=0.42). It was inversely correlated with tree biomass for *Rhizophora* (r^2=0.90). Because of the inverse productive pattern of *L. racemosa* (A=234.8; B=131.0; C=101.8 g m^{-2} year^{-1}) and *R mangle* (A=59.4; B=81.5; C=235.6 g m^{-2} year^{-1}), annual values of litter production at low and high intertidal zones were very similar (site A = 379.1 g m^{-2} year^{-1} and site C=360.5 g m^{-2} year^{-1}) and they were higher than annual litter Production at middle intertidal zone (site B=234.5 g m^{-2} year^{-1}; Figure 3E).

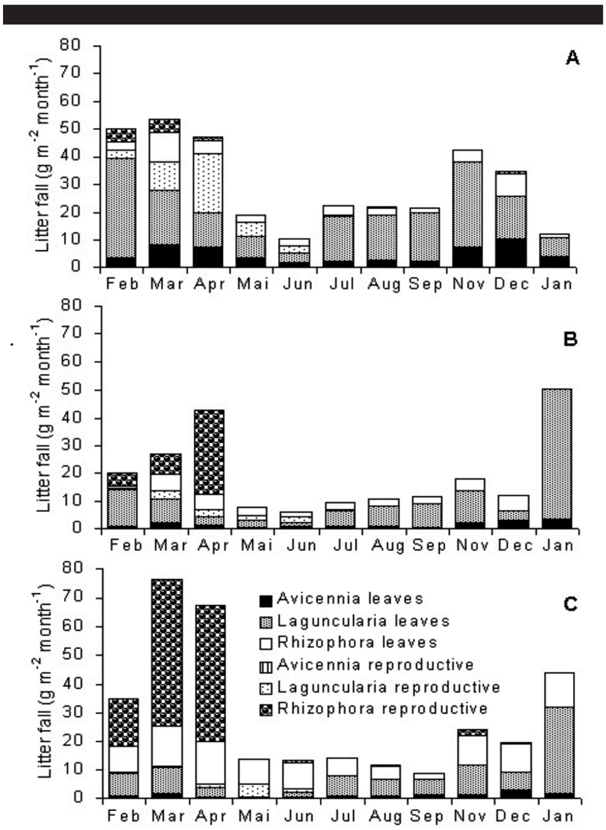

Figure 4. Monthly litter production (g m^{-2} month^{-1}) for leaves and reproductive structures of *A. schaueriana, L. racemosa* and *R. mangle* from February 1998 to March 1999 for: A) Site A; B) Site B; and C) Site C.

Litter fall presented tendencies of correlation with many structural variables of mangrove forests along sites. *L. racemosa* litter fall presented better positive correlation with biomass (r^2=0.92), tree densities (r^2=0.99) and tree height (r^2=0.81) than with mean diameter (r^2=0.53). *A. schaueriana* litter fall showed best correlation with tree height (r^2=0.72). *R. mangle* showed inverse correlations with biomass (r^2=0.90), mean diameter (r^2=0.63) and tree height (r^2=0.42).

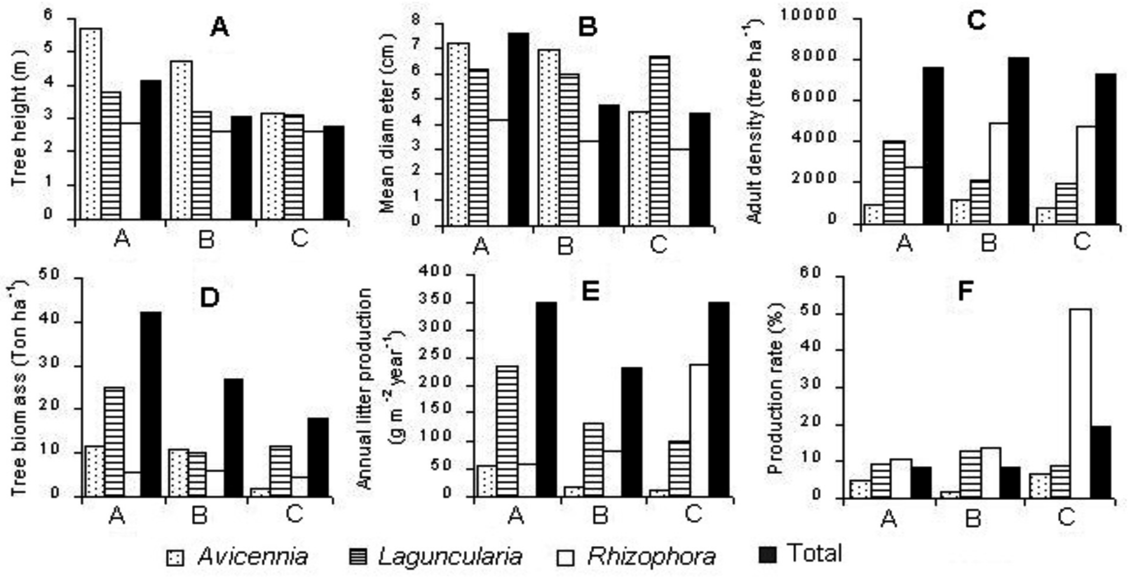

Figure 3. Structural and productive data of each species and also total data for each site: (a) Tree height (m); (b) Mean diameter (cm); (c) Tree density (adults, trees ha^{-1}); (d) tree biomass (ton ha^{-1}); (e) Litter production (g m^{-2}); (f) Production rate (ratio between litter production and tree biomass, %).

Litter production rate (ratio between annual litterfall and forest biomass) presented large variation among sites and species (Figure 3F). *R. mangle* showed the highest values of litter production rate, and also the largest differences among sites (A=10.6; B=13.8; C=51.6 %). *L. racemosa* presented rates similar to *R. mangle* at sites A and B, but much lower than it at site C (A=9.4; B=12.8; C=8.9 %). *A. schaueriana* presented very low rates, especially at site B (A=4.8; B=1.6; C=6.6 %).

DISCUSSIONS

Seasonality

The strong influence of leaf fall on seasonal pattern of litter production at Babitonga Bay was a consequence of its high contribution to total litter, and also due its positive correlation with temperature. Stipules represent emergence of a new pair of leaves in genus *Rhizophora*, and its abundance along with senescent leaves indicates the seasonal turnover of leaves in the canopy (TOMLINSON, 1986). Assuming that, correlations between *R. mangle* stipules and leaves fall, and between stipules fall and temperature could be assumed as an evidence of coupling of emergence of new leaves and senescence of old ones. These patterns were also observed in mangroves of Equator (TWILLEY *et al*., 1997), but it was opposed to the observed in an Australia mangrove (Hinchinbrock Island, DUKE *et al*., 1981), where there was a lack of seasonal variation in fall of stipules, which were apparently independent of leaf fall. Other factors than temperature, as age of trees, could differently affect these two processes in some places (CLOUGH *et al*., 2000), but they appeared to be closely linked in Babitonga mangroves.

Despite the absence of correlation between rainfall and litterfall in Babitonga mangroves, in other studies litter production were usually well correlated with rainfall, since water availability increases, salinity decreases and runoff favors nutrient input (LEE, 1989; DAY JR. *et al*., 1987, 1996; TWILLEY *et al*., 1997; WAFAR *et al*., 1997). This absence of correlation in Babitonga Bay could be explained by the high ratio precipitation/evapotranspiration all months of year, which could avoid water stress. Another hypothesis could be used to explain it. In the summer, when temperature and rainfall were high in Babitonga Bay, leaf emergence was intense, as well as discharging of senescent leaves. But, during the period of this study, rainfall did not presented a seasonal pattern, with much higher values in August and September (end of winter) than the historical values. In these months of low temperature and high rainfall, the leaves produced in the last summer were not old enough to be discharged, so litterfall was not correlated with rainfall.

An important point to be considered is the fact of Babitonga Bay (about 26° S) is very close to southern limit of mangroves in South Atlantic (about 28° S). In this situation, the influence of temperature could be more important to determine the processes of leaf emergence and senescence, as well as production of reproductive structures, than in warmer places.

Spatial Pattern

Higher values of tree biomass, diameter, height and litter production in areas of higher flooding frequencies, as we observed for *L. racemosa* and *A. schaueriana* in Babitonga Bay, have been reported worldwide, especially when comparing fringe, riverine and basin mangroves (LUGO and SNEDAKER, 1974; TWILLEY *et al*., 1997; Day Jr. *et al*., 1987, 1996). There are higher photosynthetic rates (LIN and STERNBERG, 1992) and higher growth rates for trees (CHEN and TWILLEY, 1998, 1999) in more developed forests, near to water edge. These places are also less stressful to seedlings and saplings of mangrove trees (MCKEE, 1995; ELLISON and FARNSWORTH, 1996). These facts are largely attributed to the amelioration of soil conditions due to high turnover rate of water. Based on density, biomass and litter production, we can suppose that sites B and C (flooding frequencies lower than 70%) are much more stressful to *L. racemosa* and *A. schaueriana* than site A (flooding frequency about 90%), but salinity cannot be the reason for this, because it is low and it did not change among sites. Other soil characteristics should be studied to explain that.

The inverse pattern observed in Babitonga Bay for *R. mangle* (tree densities and litter production inversely correlated with flooding frequencies, absence of significant differences among diameter, tree height and tree biomass along sites with different flooding frequencies) were quite unusual, because *Rhizophora* is traditionally supposed to be better developed and productive seawards, not landwards. The structural differences between sites B and C were quite small, to explain the big differences of litter production between these two sites.

One hypothesis to explain the higher density of *R. mangle* in the most stressful site, could be its larger tolerance to low concentration of nutrients (especially phosphate) when in low salinity. Better performance of *Rhizophora* in nutrient poor places, compared to *Laguncularia* and *Avicennia,* have been reported by MCKEE (1993, 1995), SHERMAN *et al*. (1998, 2000), CHEN and TWILLEY (1998) and others, using experimental approaches with seedlings/sapling or comparing forest structure along environmental gradients.

The high production rate (ratio between litter production and tree biomass), and consequently the high annual litter production of *R. mangle* at site C (flooding frequency about 50 %), in comparison to site B (flooding frequency about 70 %), were unexpected, since density, mean diameter and biomass at site C were lower than these variables at site C. One hypothesis to explain that could include differences of allocation rates and leaf lifespan between these two sites. Site B could be less stressful to *R. mangle*, so a representative part of photosynthetic production could be allocated to trunk and roots growth, and just a small part could be allocated to production of leaves and reproductive structures. At site C, the high level of stress could be accelerating the leaves turnover, so a big part of photosynthetic production could be allocated to leaves, and less could be allocated to trunk and roots growth.

To test these hypotheses in Babitonga Bay, additional work must include measurement of soil dynamics (as Eh, iron, sulfur, and phosphorus), together with long-term projects to evaluate seedling recruitment and development, tree growth, nutrient content at different parts of trees, photosynthetic rates in each site.

Comparisons with Other Mangroves

The annual production of litter fall in Babitonga Bay (25°S) was low (234 to 379 g m^{-2} year^{-1}), compared with some mangrove forests that can produce from 500 to more than 10000 g m^{-2} year^{-1} (TWILLEY *et al*., 1997; DAWES a *et al*., 1999; COUGH *et al*., 2000). But Babitonga Bay litter production was similar to some mangrove forests in Brazilian States of Paraná (25°S; SESSEGOLO, 1997) and São Paulo (24°S; SCHAEFFER-NOVELLI *et al*., 1990b). It was also similar to some mangrove forests in New Zealand (WOODROFFE, 1982), Australia (COUGH and ATTIWILL, 1975, *apud* WOODROFFE, 1982), Mexico (TOVILLA-HERNANDEZ *et al*., 1994; Day Jr. *et al*., 1996), and Sri Lanka (AMARASHINGE and BALASUBRAMANIAM, 1992).

Since Babitonga Bay showed an annual fresh water surplus (high ratio rainfall/evapotranspiration) and maximum salinities usually below 30, low productivity cannot be attributed to soil hypersalinity. Despite the proximity of southern limit of mangroves in South Atlantic, the winter temperatures seem not to be responsible for such low annual productivity, once higher litter production (865 g m^{-2} year^{-1}) was observed at mangrove forests southernmost of Babitonga Bay (27°30'S; PANITZ, 1986). Local factors might be responsible for spatial changes in forest structure, and also in annual litter production, resulting in the low observed values. Large variability in forest structure and litter production were observed for Paranaguá Bay, where SESSEGOLO (1997) found forests with different soil conditions and hydrodynamics presenting different structure and annual litter production (317 and 640 g m^{-2} year^{-1}). As mangrove forests in Babitonga Bay occur along strong hydrodynamic and salinity gradients, forest structure also presents large variability along these gradients (CUNHA *et al*, 2004), it is possible to find places with higher and even lower litter production than were observed at the studied sites in mesohaline area of Babitonga Bay. Additional studies must be done to check out this possibility.

CONCLUSIONS

The flooding frequencies presented strong influence on mangrove structure and litter productivity, especially when the focus was on each species. The observed spatial variability cannot be attributed to salinity because it was the same in all sites. Long term studies including larger spatial scale into the bay, soil characteristic, recruitment and growth, as well as photosynthetic production must be done to elucidate the causes of the observed patterns.

ACKNOWLEDGEMENTS

We thank to Maria Cristina Moreira da Silva, Robson Santos and Valdenir Ines for their help in fieldwork. We thank to FUNDEMA (Fundação do Meio Ambiente de Joinville) and to Joinville Iate Clube for provided cars, boats and sailormen to fieldwork.

First author was partially supported by a Ph.D. fellowship from CAPES.

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