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Litterfall dynamics and nutrient decomposition of arid mangroves in the Gulf of California: Their role sustaining ecosystem heterotrophy

R. Sánchez-Andrés [a,*], S. Sánchez-Carrillo [b], L.C. Alatorre [c], S. Cirujano [a], M. Álvarez-Cobelas [b]

[a] Royal Botanic Garden-CSIC, Pza de Murillo 2, E-28014-Madrid, Spain
[b] Institute of Natural Resources-CSIC, Serrano 115dpdo, E-28006-Madrid, Spain
[c] Pyrenean Institute of Ecology-CSIC, Avda. Montañana 1005, E-50080-Zaragoza, Spain

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ABSTRACT

This study shows results on litterfall dynamics and decay in mangrove stands of *Avicennia germinans* distributed along a latitudinal gradient (three forest sites) in the Gulf of California, in order to assess whether internal sources could support the observed mangrove ecosystem organic deficit in this arid tropic. Total mean annual litterfall production increased southward (712.6 ± 53.3, 1501.3 ± 145.1 and 1506.2 ± 280.5 g DW m^{-2} y^{-1}, in the Yaqui, Mayo and Fuerte areas respectively), leaves being the main component of litter in all locations during the entire year, followed by fruits. The wet season (June–September) showed the highest litterfall rates through fruits. The temporal trend of litterfall production was significantly explained through mean air temperature ($R^2 = 68\%$) whilst total annual litter production in the entire region showed a statistically significant relationship with total soil phosphorus, salinity, total nitrogen, organic matter and tree height ($R^2 = 0.67$). Throughout 117 days of the decomposition experiment, the litter lost 50% of its original dry weight in 5.8 days (average decay rate of 0.032 ± 0.04 g DW d^{-1}) and there were not significant differences in the remaining mass after 6 days. The percentage of both *C* and *P* released from the litter correlated significantly with the ratio of tidal inundated days to total experiment days ($R^2 = 0.62$, $p = 0.03$ and $R^2 = 0.67$, $p = 0.02$, respectively); however, the frequency of tidal inundation only showed a significant increase in *C* release from *Avicennia* litter after 6 and above 48 days of decomposition. Whereas the total *C* content of litter bags decreased linearly over the decomposition to (% Total $C = 5.52 - 0.46$ days, $R^2 = 0.81$, $p = 0.0005$), *N* content displayed an irregular pattern with a significant increase of decay between 48 and 76 days from the beginning of the experiment. The pattern for relative *P* content of litter revealed reductions of up to 99% of the original (%tot-$P = -9.77$ to 1.004 days, $R^2 = 0.72$, $p = 0.01$) although most of the *P* reduction occurred between 17 and 34 days after the experiment started . Soil *N* and *P* contents, which exhibited significant differences in the course of the decomposition experiment, appeared to show significant differences between sampling sites, although they were not related to tidal influence, nor by leaf and nutrient leaching. In a global basis, *C/N* litter ratios decreased linearly ($C/N = 32.86 - 0.1006$ days, $R^2 = 0.62$, $p = 0.02$), showing a strong and significant correlation with meteorological variables ($R^2 = 0.99$, $p = 0.01$). *C/P* ratios of litter increased through an exponential function ($C/P = 119.35e^{0.04\ \mathrm{day}}$, $R^2 = 0.89$, $p < 0.001$). Changes in the remaining percentage of litter mass during the experiment were significantly correlated with soil *C/N* ratio ($R^2 = 0.56$, $p = 0.03$) as well as with the soil *C/P* ratio ($R^2 = 0.98$, $p < 0.001$). Our results of litter decomposition dynamics in this mangrove support the fact of null net primary productivity of the arid mangrove wetlands: fast litter decomposition compensates the ecosystem organic deficit in order to sustain the mangrove productivity. Litter decomposition plays a key role in the ecosystem metabolism in mangroves of arid tropics.

1. Introduction

Mangrove forest dynamics have been cited to significantly contribute to the nutrient metabolism of subtropical coastal ecosystems (Ramos e Silva et al., 2007). Because the low aquatic primary productivity is inadequate to support community

* Corresponding author.
E-mail address: rsanchez@rjb.csic.es (R. Sánchez-Andrés).

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metabolism (Production/Respiration < 1), coastal lagoons depend mainly on nutrient flux provided by mangrove forests (Wafar et al., 1997). Because mobility of nutrients from or to mangrove forest is highly influenced by tidal hydrology (Sánchez-Carrillo et al., 2009), litter mineralization within the forest often appears to support further production (Imgraben and Dittmann, 2008). As tidal activity decreases, litter export declines and that *in situ* decomposition should, therefore, play a key role in ecosystem nutrient recycling (Twilley et al., 1986; Sánchez-Carrillo et al., 2009).

Litterfall has been cited to be influenced by mangrove species, geomorphology, salinity, weather, season and pollution (Day et al., 1996; Silva et al., 1998; Feller et al., 1999; Arreola-Lizárraga et al., 2004), the weight of each variable being highly variable between ecosystems, and early cited as independent of forest structure (Flores-Verdugo et al., 1987). Litterfall and the rate of *in situ* litter decomposition are often cited as key factors on nutrient export by mangroves to near-shore coastal ecosystems (Boulton and Boon, 1991): higher rates of decomposition within the mangrove forest is assumed to result in nutrient retention, whilst slow decomposition increases the chance of mangrove detritus to be exported (Imgraben and Dittmann, 2008). Furthermore, organic production and carbon turnover in mangroves tend to be higher near the equator and decrease towards temperate latitudes, being lowest in arid regions (Saenger and Snedaker, 1993). Thus, this suggests that heterotrophic mangroves, such as those in arid regions, should retain more nutrients in order to sustain its metabolism than those grown in tropical regions. However, there have been comparatively few studies on litter production and decomposition in arid mangroves, which might demonstrate very distinctive dynamics. Tidal inundation also appears to play a key role in decomposition, as litter submersion results in a rapid leaching of nutrients by microbial breakdown (Flores-Verdugo et al., 1987; Boulton and Boon, 1991). This would also suggest that mangroves in arid zones are spatially limited to develop in coastal areas where water is available, in order to allow for a quick nutrient recycling. Nevertheless, it has not yet been explored whether the effects of water on litter decomposition in heterotrophic arid mangroves appear to be determinant on ecosystem nutrient retention.

Mangrove ecosystems located in the Gulf of California represent the northern-most mangrove ecosystems in the Eastern Pacific. They can be considered as extreme mangrove forests growing under arid climate, not receiving river discharges and supporting high salinity (Glenn et al., 2006). Despite its huge extension along the coastal line (more than 75,000 ha, Glenn et al., 2006) and its positive influence on fishery yields of the Gulf of California (Aburto-Oropeza et al., 2008), very little is known about its ecosystem dynamics. Although these mangroves have been proven to be heterotrophic ecosystems (Sánchez-Carrillo et al., 2009), the role of litterfall and decomposition in sustaining the mangrove metabolism is yet unknown. Therefore, the aim of the present study was to investigate litterfall rates and decomposition dynamics of the arid mangroves in the Gulf of California in order to assess whether the internal sources could support the ecosystem organic deficit.

2. Material and methods

2.1. Study area

The study was carried out in the Northwestern area of the coast of the Gulf of California, in three areas covered by extensive mangroves (ca. 47,000 ha) that are linked to deltas of the Yaqui, Mayo and Fuerte Rivers (26°–28°N; Fig. 1). This area represents the largest continuous wetland extension of the Mexican Northwest. Climate in the area is warm and dry, with a mean annual air temperature of 24 °C (16–48 °C) and a rainfall of <300 mm yr^{-1}. Mangrove forests are mainly monospecific stands of *Avicennia germinans*, with *Rhizophora mangle* sometimes occurring at the shoreline fringe of lagoons. *Laguncularia racemosa* is sparsely distributed along the coast, shaping small forests and at some distance from tidal influence. Scattered small patches of pickleweeds (*Salicornia virginica* and *Batis maritima*) and small very shallow pools also appear within mangrove forests. Up to the 1940s, the region was still nearly pristine (Steinbeck and Ricketts, 1941) but since then the coastal zone has undergone rapid development and population growth, which, for example, in Sonora increased from 550,000 to 2.3 million during the period 1950–2000 (Almada-Bay, 2000). Shrimp farms, salt ponds, electricity generating plants and farming facilities have also been built along the coast, and villages have expanded into small cities (Almada-Bay, 2000). Because of this rapid development, the health of the marine ecosystem is threatened and the degradation of coastal habitats is already severe (Glenn et al., 2006), but little is known about its ecological functioning.

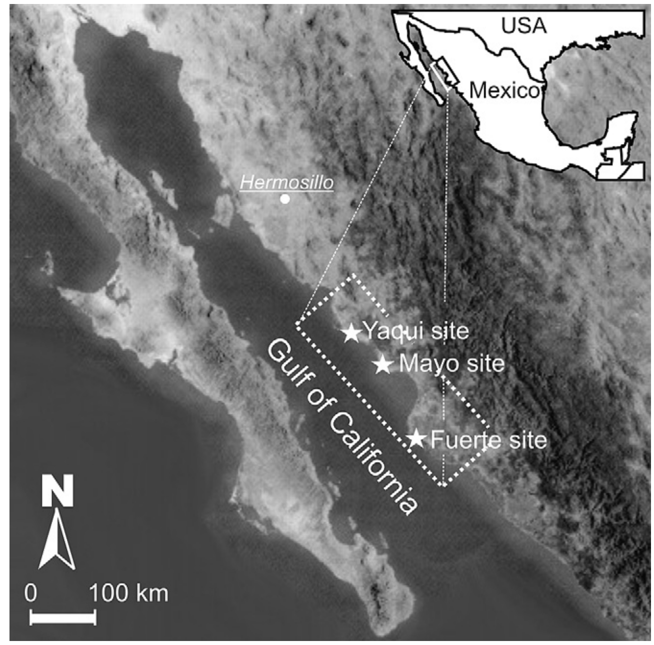

Fig. 1. Location of the mangrove forests studied along the Gulf of California. The decomposition experiment was performed at the Yaqui site.

2.2. Structure of the studied mangrove forest

The structure of mangrove forests was obtained using equidistant 10 m^2 quadrants around the experimental sites, in accordance with the criteria proposed by Cintron et al. (1978). The average *height*, *density* and *basal area* of mangrove trees were assessed following Holdridge et al. (1971). Triplicate soil samples were taken at each quadrant during May and October 2004 and April 2005 and analyzed for *organic matter* by means of Walkley–Black acid digestion (Walkley and Black, 1934), *total nitrogen* (using a Shimadzu high sensitivity CN analyzer model Sumigraph NC-80), *total phosphorus* (through high performance liquid chromatography using an Agilent 1100 HPLC), *salinity* (electrical conductivity converted to ppm), *bulk density* (paraffin clod method; Howard and Singer, 1981) and *grain size* (only once; Bouyoucos hydrometer method; Bouyoucos, 1962). Table 1 shows a summary of the mangrove forest stand structures at each studied site, as well as the main physical and chemical soil properties.