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Reproductive phenology of a northeast Brazilian mangrove community: Environmental and biotic constraints

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ABSTRACT

Brazil has the third largest area of mangrove in the world, which is widely threatened by anthropogenic pressures. We carried out the first long-term phenological study investigating whether environment and competition for pollinators shape the reproduction of a western mangrove community in Brazil, and provide new information for mangrove conservation. We monitored monthly the flowering and fruiting of *Avicennia schaueriana*, *Conocarpus erectus*, *Laguncularia racemosa* and *Rhizophora mangle*, the only species composing this mangrove community. We applied circular statistics to detect seasonal trends, null models to test for aggregated, staggered or random flowering patterns, performed correlations between phenophases and climate, and calculated intra-specific phenological synchrony. Each species presented a different flowering pattern, from brief annual to continuous and from regular to irregular, resulting in a bimodal pattern at community level. Fruiting was annual or continuous and seasonally unimodal at community level. Precipitation showed the strongest correlation with reproduction for all species, except *L. racemosa*. Flowering was randomly distributed among species sharing pollinators and each species presented high intra-specific synchrony. The studied mangrove showed a diversity of flowering patterns despite the low number of species. Annual to sub-annual sequential flowering were prevalent, sustaining the pollinators of species all the year long, while the wind-pollinated species flowered continuously. We provide strong evidence that daylength, rainfall and temperature are driving the flowering and fruiting rhythm of these mangrove species.

Introduction

Phenology, the study of recurrent life cycle events, is fundamental for the understanding of climate influence on vegetation, future climatic change assessment, and for the analysis of interactions between plants and animals, such as pollination and seed dispersal (Bawa, 1983; Frankie et al., 1974; Morellato, 2003; Williams-Linera and Meave, 2002). Climate seasonality is the proximate factor shaping the timing of reproduction and growth of tropical plants, while biotic interactions such as competition for pollinators and seed dispersers can define the diversity of patterns in a community (Bawa, 1983; Boulter et al., 2006; Morellato, 2003; Morellato et al., 2000; Sakai, 2001; Wright, 1996). In tropical areas with well-defined dry and rainy seasons, precipitation is the main factor constraining the phenology of species (Machado et al., 1997; Morellato, 2003; Williams-Linera and Meave, 2002). Conversely, in tropical vegetation under low climatic seasonality, light (radiation and length of day) is recognised as the key climatic factor defining seasonal rhythms in growth and reproduction (Borchert et al., 2005; Morellato et al., 2000; Rivera and Borchert, 2001; Wright and Van Schaik, 1994).

Biotic interactions such as pollination and seed dispersal may also determine the time of flowering and fruiting (Bawa, 1983; Staggemeier et al., 2010; Wright, 1996). Competition for pollinators, for example, exerts a selective pressure that causes a staggered flowering pattern between species that share the same group of pollinators (Bawa, 1983; Boulter et al., 2006; Wright and Calderon, 1995). On the other hand, species sharing pollinators may show an aggregated flowering pattern, a phenomenon called facilitation, enhancing the attractiveness of flowers to the pollinators (Moeller, 2004; Staggemeier et al., 2010). In this case, the benefit of facilitation outnumbers the decline in reproductive success by the competition for pollinators (Boulter et al., 2006; Moeller, 2004).

Mangrove forests are tropical ecosystems occurring in the transition between terrestrial and marine environments, with their own characteristic vegetation, whose composition and biological processes are influenced by various abiotic factors such as

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tide amplitude and precipitation (Gilman et al., 2008; Hogarth, 2007; Tomlinson, 1994). Mangrove species are distributed in two main centres of diversity, the eastern group (Oceania, South and Southeast Asia and East Africa), with 43 species (17 genera and 15 families), and the western one (Tropical Americas and West Africa), with only eight species (four genera and four families); there are no common species in these two groups (Tomlinson, 1994). Rhizophoraceae, the family with the greatest number of species, and the genus *Avicennia* (Acanthaceae), occur in both centres (Tomlinson, 1994).

Brazil has the third largest area of mangrove in the world (more than 20,000 ha), which is an important, yet poorly known and under-valuated, carbon stock (Copertino, 2011). Mangroves are widely threatened by anthropogenic pressures and we are losing up to four times more mangrove areas than tropical forests yearly (Alongi, 2002; Copertino, 2011). Facing this situation, we examined plant phenological responses of this key ecosystem to climatic and biological factors and attempt to provide new basic knowledge for mangrove conservation.

Up to present, phenological studies have focused mainly on species from Rhizophoraceae (Gill and Tomlinson, 1971; Mehlig, 2006; Tyagi, 2004). Studies focusing a whole mangrove community are scarce, with only one in the eastern group (*sensu* Tomlinson, 1994) in Australia (Duke et al., 1984). For the western mangrove group (*sensu* Tomlinson, 1994) Fernandes (1999) addressed aspects of flowering and fruiting of mangrove species in northern Brazil, but his research concentrated upon the population phenology and was based on only one year of observations. More recently, Menezes et al. (2008) reviewed the research on mangroves from northern Brazil, compiling phenology data from different unpublished sources and localities data, together with some herbarium data, for five mangrove species, based on which they depicted an expected phenological scenario for northern Brazilian mangroves.

Long-term studies at species and community levels are fundamental for defining the phenological patterns of the western mangrove forests and for an understanding of the dynamics and ecological interactions in this ecosystem. In this context, the present study aimed to characterise, for the first time, the reproductive phenological pattern of a western mangrove forest community, located at the northeastern coast of Brazil, over four years of observations. The following questions were addressed: (1) Do the reproductive phenological patterns differ among the woody species component of the mangrove forest? Are the reproductive patterns of each species seasonal and related to abiotic factors? (2) In the mangrove forest studied, do the facilitation or competition hypotheses explain the flowering patterns of any species sharing pollinators? (3) Are the flowering and fruiting patterns of the mangrove forest seasonal? Do the patterns vary over the years?

Materials and methods

Study site

Field observations were carried out along the estuarine area of the north coast of the state of Pernambuco, north-eastern Brazil (7°39′32.4″S, 34°50′24.29″W), formed by the mouth of the river Itapessoca, in the municipality of Goiana, about 80 km north of Recife. The annual precipitation during the study period (June/2002 to May/2006) ranged from 1815 (June/2004 to May/2005) to 2256 mm (June/2003 to May/2004), with a rainy season from February to August and a dry season from September to January, when the average monthly rainfall was less than 100 mm. The average monthly temperature was 23.9 °C, with mean maximum and minimum temperatures of 30.4 °C and 20.4 °C, respectively, and the highest temperature was from November to May. The relative humidity was high, showing an annual average of 90% during the study period. The climatic data were collected at the Estação Experimental de Itapirema (7°38′39.12″S, 34°56′56.04″W), Empresa Pernambucana de Pesquisa Agropecuária (IPA) and supplied by the Laboratório de Meteorologia de Pernambuco (LAMEPE) of the Instituto de Tecnologia de Pernambuco (ITEP). Tidal amplitude data were obtained from the Banco Nacional de Dados Oceanográficos (BNDO) (http://www.mar.mil.br/dhn/chm/tabuas/index.htm), and monthly daylength is that in Goiana (7°39′32.4″S).

Studied species

In the study area the mangrove community is composed by three true mangrove species (*sensu* Tomlinson, 1994), *Rhizophora mangle* L. (Rhizophoraceae), *Avicennia schaueriana* Moldenke (Acanthaceae), and *Laguncularia racemosa* CF Gaertn. (Combretaceae), and one associate species (*sensu* Tomlinson, 1994), *Conocarpus erectus* L. (Combretaceae). The tree species *Rhizophora mangle* and the shrub *Laguncularia racemosa* are widely distributed in the western mangrove group, while *A. schaueriana* (tree) and *Conocarpus erectus* (shrub) have a more restricted distribution (Tomlinson, 1994).

Avicennia schaueriana, *L. racemosa* and *C. erectus* white flowers produce a small amount of accessible nectar, attributes that characterise them as a generalist pollination system (Nadia, 2009; Nadia et al., 2012). The three species are visited by the same group of pollinators, with a high proportion of common species, including flies (main pollinators), wasps and bees (Nadia, 2009). Detailed information on the pollination ecology of these plants and the pollinator species is provided by Nadia (2009) and Nadia et al. (2012). In contrast, *Rhizophora mangle* is pollinated by wind, and its hanging flowers present a high pollen–ovule ratio and no resources that would attract animal pollinators (Lemus-Jiménez and Ramírez, 2003; Menezes et al., 1997; Nadia, 2009; Tomlinson et al., 1979).

Reproductive phenology

The reproductive phenology (hereafter only 'phenology') of the four species was monitored monthly, from June 2002 to May 2006, by tagging 10 reproductive-aged plants in the mangrove forest – dry land transition, where all species co-occur. The sampled individuals presented similar high crown structure and ramification pattern (height of *C. erectus* and *L. racemosa*: 1.5–2.0 m tall, and *A. schaueriana* and *R. mangle*: 3.0–4.0 m tall). The intensity of each reproductive phenophase (hereafter only 'phenophase') in each individual was estimated using a semi-quantitative method, assigning the value 0 for the absence of this phenophase, and values from 1 to 4 at intervals of 25% (1 = 1–25%; 2 = 26–50%; 3 = 51–75%; 4 = 76–100% presence of phenophases), following the Fournier intensity index (Fournier, 1974).

The definition of the phenophases varied according to the species. *Rhizophora mangle*, *Laguncularia racemosa* and *Avicennia schaueriana* are viviparous, since their dispersal unit is the propagule, enclosing the developed seedling (Rabinowitz, 1978). In *R. mangle* the seedling is exposed before dispersal, while *A. schaueriana* and *L. racemosa* are crypto-viviparous, since germination occurs when the fruit is still attached to the mother plant, but the seedling remains inside the fruit during dispersal (Tomlinson, 1994). Thus, for *R. mangle* the stage in which the seedling is covered was considered as fruit, and the stage when seedling is exposed was denominated as 'propagule', whilst in the other species it was not possible to distinguish the latter two phases. Therefore, the phenophases observed in *R. mangle* were: flower bud, flower, fruit, and propagule (Fig. 1A–D). The phenophases observed for *A. shaueriana* and *L. racemosa* were flower bud, flower and propagule (Fig. 1E–J). The species *Conocarpus erectus* is not viviparous and the flowers are arranged in clusters, which subsequently forms a compound fruit (fruiting head, *sensu* Tomlinson, 1994), which becomes