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Growth and mortality of mangrove seedlings in the wettest neotropical mangrove forests during ENSO: Implications for vulnerability to climate change

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ABSTRACT

Assessing factors affecting growth and mortality of mangrove seedlings, the critical transition between propagule dispersal and recruitment to the sapling state, is crucial to understand and predict the fate of mangrove forests in our changing climate. This work aimed to understand seedling's responses to contrasting temperature and precipitation regimes and analyze consequences for the persistence of these ecosystems under expected climate change scenarios. Growth rate and mortality of seedlings were monitored monthly in an array of mangrove forests located along a tidal and salinity gradient in the central Pacific coast of Colombia, one of the rainiest places on Earth. Seedlings were monitored from January to December 2016, coinciding with a major El Niño (EN) episode and the abrupt transition to La Niña (LN) conditions. Seedling growth rates were generally low and observed spatial patterns generally mirrored interspecific differences in the tolerance to stress induced by salinity and inundation levels. Seedlings in basin forests showed higher growth rates than those in riverine and fringe forests. Mortality was not different among species and unexpectedly low, considering the rates reported in the literature and the supposedly stressful conditions associated with the EN-LN cycle. According to our analyses the magnitude of local anomalies in air temperature and precipitation throughout the EN-LN cycle can be stronger than those expected locally for 2071–2100 in relation to global climate change. Current and expected shifts in precipitation regimes seem the main macroclimatic drivers of ecological changes in mangrove forests thriving in the Pacific coast of Colombia.

1. Introduction

Mangrove forests are comprised of a few specialized woody trees thriving in tropical and subtropical brackish intertidal wetlands. The seedling stage of mangrove trees represent the transition between water-borne dispersal and recruitment to the sapling stage making it the most critical life-stage (Krauss et al., 2008). Understanding the biotic and abiotic factors influencing this transition, particularly under different scenarios of climate change and variability is crucial. It is currently known that mangrove recruitment is spatially structured, because the mangrove forest is strongly influenced by environmental gradients (López-Hoffman et al., 2007). Canopy gaps control light incidence to the understory and therefore gap formation by climatic disturbances and biological processes strongly influence establishment, early development and persistence of seedlings (Clarke 2004; Krauss et al., 2008). Growth and mortality of seedlings leading to recruitment is also controlled by a set of climatic factors operating at global, regional and local scales (reviewed by Krauss et al., 2008). At local scales growth and mortality of seedlings varies among ecological or physiographic types of forest, because they differ in soil type, tide and salinity regimes and hydroperiod, which determine how seedlings move, settle and survive (Di Nitto et al., 2008; Krauss et al., 2008; Di Nitto et al., 2013).

El Niño-Southern Oscillation (ENSO) is the most important signal in the interannual variation of the ocean-atmosphere system, strongly affecting coastal ecosystems along the Tropical Eastern Pacific (Seeliger and Kjerfve, 2013). ENSO has changed its strength, frequency and characteristics over past decades and it is projected to change under different global warming scenarios (Wang et al., 1999; Timmermann et al., 1999; Yeh et al., 2009). In tropical areas of South America,

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climate anomalies associated with ENSO affect regional rainfall, river discharge and sediment transport to the ocean through teleconnections (Vörösmarty et al., 1996; Restrepo and Kjerfve, 2000; Riascos, 2006, Blanco, 2009). Such hydrological variability is probably the most important forcing function for tropical coastal marine ecosystems, particularly estuarine ecosystems, in Latin America, particularly along the Pacific coast (Kjerfve et al., 2001; Riascos et al., 2008). Therefore, climatic anomalies associated with El Niño and La Niña phases of ENSO seem to be important, particularly for reproduction, dispersion and recruitment in mangroves located in the Tropical Eastern Pacific (TEP; Ecuador, Colombia, Panamá and Costa Rica).

Despite the past warnings on the disappearance of mangroves due to growing anthropogenic pressures combined with climate change (Duke et al., 2007), Alongi (2015) predicted that climate change will generally have mild effects, with some negative effects for mangrove forest along arid coasts, subsiding river deltas and small islands. He based his prediction using the most recent global climatological forecasts of sea surface temperature, oceanic pH, CO_2 concentrations, sea level rise and precipitation and salinity by the Intergovernmental Panel on Climate Change toward the end of the century. However, little is known about the effects of sub-decadal variability associated with ENSO, which can be stronger than the expected long-term changes forecasted by the IPCC for tropical regions, given the strong influence on freshwater runoff. Recently, Banerjee et al. (2016) reported on the decline in the above-ground biomass of a mangrove species in India related to decadal-scale salinity alterations.

In 2015–2016 the TEP experienced one of the strongest El Niño on record; it was popularly depicted as the “Super El Niño” (Zhai et al., 2016; Ren et al., 2017). Globally, precipitation patterns changed, sea surface temperature exceeded historical records for 12 consecutive months and sea levels were driven ~7 millimeters higher as warming ocean water expanded.

Here we describe the dynamics of growth and mortality of mangrove seedlings from Colombia’s Pacific pluvial and *meso*-tidal forests, considered among the most luxuriant forests in the world (West, 1956), during the latest El Niño warming episode. The aims of this study were (i) to analyze spatial-temporal differences in growth and mortality of mangrove species thriving in the study area, (ii) to estimate anomalies in precipitation and temperature in Bahía Málaga, their relationship with El Niño and La Niña episodes and compare the magnitude of these anomalies with the expected variations under climate change scenarios by 2071–2100; and (iii) to discuss the relevance of these findings for the long-term persistence of Colombia’s Pacific mangrove forest.

2. Materials and methods

2.1. Study area

The study was performed in the Uramba-Bahía Málaga National Park (hereafter Bahía Málaga), a south-facing bay located in the central region of the Colombian Pacific coast (Fig. 1). The bay is a tectonic estuarine system (Cantera et al., 2013) and it shows an array of coastal formations including soft substrates, mud or sand bottoms, cliffs and rocky shores. The Bay is located in a high rainfall area of the western hemisphere receiving between 7000–11,000 mm of precipitation annually (Restrepo et al., 2002). Because it is strongly influenced by the Inter-Tropical Convergence Zone (ITCZ) (the low-pressure belt of the ITCZ moves north and south between 10°N and 3°S) it passes over the Bay resulting in two rain periods: April-June and September-November. Water depth in the bay averages about 13 m, with a maximum depth of 40 m. Tides are semi diurnal, with a tidal range of 4.1 m, temperature varies between 25 and 30 °C and salinity between 19 and 28 in the mouth of the bay and 1.3 and 10 close to small rivers (Cantera et al., 1998; Lazarus and Cantera 2007).

2.2. Sampling design

Five ecological types of mangrove forests (*sensu* Twilley et al., 1998) distributed along a salinity gradient through the estuarine system were selected for this study: Basin, Riverine I and II, Fringe I and II (see Supplementary material 1 for details). These forests were monitored monthly between December 2015 and December 2016. Three replicated places were randomly chosen within each mangrove type, with at least 200 m distance among them (Fig. 1). In each place two 78.5 m^2 plots were established: a low-level water plot that was called “external” and a high-level water plot called “internal”, so 30 plots were monitored. Therefore, three sources of variability were considered in the sampling design: forest type, position in the intertidal and time, thus conforming a $5 \times 2 \times 12$ sampling design. There was, however, an important source of variability that could not be accounted for by the sampling design: the mangrove species composition, which differed among forest types, positions and plots. Therefore, spatial and temporal variability was analyzed separately for each species (*Mora oleifera*, *Pterocarpus officinalis*, *Rhizophora spp*., *Pelliciera rhizophorae* and *Avicennia germinans*).

In each plot, between five and ten mangrove seedlings were randomly selected, identified and tagged with a consecutive number using adhesive plastic tape. Growth rate and mortality of mangrove seedlings was monthly monitored. Mean growth rate (mm day^{-1}) was estimated by averaging differences in shoot length (from the top of the hypocotyl to the top of the plant) from the previous month in each plot. Any tagged seedlings which died were replaced by haphazardly selecting and tagging individuals from those remaining in the plot. There are not large gaps in the canopy of these forest that may influence growth and mortality. However, structure, age and development do vary among forest. Therefore, the Holdridge Complexity Index (HCI) was used as an estimator of spatial structure and development of the mangrove forest. The index was computed as:

$$HCI = \frac{sdbh}{1000}$$

where (s) is the number of mangrove species, (d) the stand density, (b) the basal area, and (h) mean height in each plot (see Blanco et al., 2001 for details and a discussion of this index). The ratio of sapling density (RSD) *i.e.*, the density of Trees 2.5–10 cm diameter at breast height with respect to the total tree density was estimated as an indicator of forest age or successional stage (Blanco et al., 2001). See supplementary material 1 for estimations of these indices.

2.3. Taxonomic issues

Two species of *Rhizophora (R. mangle* and *R. racemosa*) occur in the study area, with the former being much more abundant. They can be identified in the adult stage using mainly the morphology of the inflorescence, but these diagnostic characters are extremely plastic (see Cerón-Souza et al., 2010). A reliable identification at the seedling stage remains difficult, they are reported here as *Rhizophora* spp. *Pterocarpus officinalis* (Fabaceae) was abundant in the study area. It is not considered a true mangrove species, but was included in our study because it is tolerant to flooding and soil salinity, thus representing a transition between forested wetlands and tidal mangroves in the Pacific and Caribbean (Francis and Lowe, 2000; Medina et al., 2007). The consideration of *Mora oleifera* (Leguminosae) as a true mangrove tree remains controversial (*e.g.* Lacerda, 2002) but it was locally abundant and was included in our monitoring.

2.4. Environmental data sources

Regional climate change scenarios for mean temperature and precipitation to 2071–2100 were provided by IDEAM (Instituto de Hidrología, Meteorología y Estudios Ambientales, Colombia). These