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Effects of long-term inter-annual rainfall variation on the dynamics of regenerative communities during the old-field succession of a neotropical dry forest☆

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A B S T R A C T

Effects of long-term rainfall inter-annual variation on regeneration dynamics of tropical dry forests (TDF) are still poorly understood. Such understanding is particularly important to assess the regeneration potential of TDF in landscapes subjected to slash-and-burn farming management. Here, we studied from 2004 to 2016 the effects of inter-annual rainfall variation on the dynamics of regenerative communities of woody species during the old-field succession of a TDF in Western Mexico. Over the study period a severe drought, caused by an El Niño Southern Oscillation (ENSO) event in 2005, and two hurricanes (Jova, 2011, magnitude 2; Patricia, 2015, magnitude 4) were experienced. In 2004, we established a chronosequence of abandoned cattle pastures and old-growth forest sites, which were assigned to four successional categories, each one with three sites: Pasture (0–3 years fallow age), Early (3–5 years), Intermediate (8–12 years), and Old-Growth Forest (without any human disturbance). At each site, seedlings, saplings and resprouts 10–100 cm height of shrub and tree species were tagged, taxonomically identified, measured in height and monitored over 12 continuous year intervals. At each year, all new plants reaching 10 cm height were recorded and considered as recruits. Community rates (recruitment, relative growth rate in height, mortality, species gain and species loss) were calculated per year, considering all plants combined and separating shrub from tree species. All community rates varied notoriously in response to temporal rainfall variability, with almost null interaction with successional category. As expected, mortality and species loss rates declined as the amount of rainfall increased, especially when precipitation of the current and the previous year were taken into account; these rates peaked in the ENSO year and were still high in the following year. Unexpectedly, recruitment and species gain rates also declined with the increase in rainfall, especially with the amount of rainfall in the current year. Overall, community rates of tree species were more responsive than those of shrub species to temporal rainfall variation. The ENSO-related drought event produced a short and transient instability in the plant density and species density of regenerative communities. However, ENSO effects were smoothed out by subsequent rainy years, leading to a net increase in plant density and species density in all successional categories, especially in the younger one. Overall, our study shows that global (e.g. ENSO) and regional (e.g. storms, hurricanes) climate factors play a key role on forest succession, modulating the speed of the TDF regeneration dynamics. We conclude that low impact agricultural land use and the presence of good levels of remnant forest cover in the landscape confers a high potential for regeneration in abandoned agricultural fields, even under the impact of severe droughts and severe hurricanes.

1. Introduction

Rainfall temporal variation critically affects ecological attributes of tropical dry forests (TDF; Murphy and Lugo, 1986; Bullock et al., 1995; Dirzo et al., 2011). These forests are highly threatened due to their fast and extensive conversion to agriculture (Chazdon et al., 2011). However, farming fields are often abandoned giving place to secondary forests, which can play important roles in conservation of biodiversity

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and ecosystem functions and services in human modified landscapes (Chazdon, 2014; Poorter et al., 2016; Arroyo-Rodríguez et al., 2017). Thus, it is central to understand to what extent temporal rainfall variation affects the potential for TDF regeneration in abandoned fields. This is relevant as severe droughts (e.g. caused by El Niño Southern Oscillation, ENSO) and storms (e.g. hurricanes) are expected to increase in tropical dry regions due to global warming (Cai et al., 2014; Knutson et al., 2010).

Short-term studies have shown linkages between demographic rates of woody TDF plants at regenerative stages (seedlings, saplings, resprouts) and rainwater availability (e.g. Marod et al., 2002; Maza-Villalobos et al., 2013). Overall, growth and recruitment are highest during the rainy season and mortality during the dry season (Gerhardt et al., 1993; Lieberman and Li, 1992). Long-term studies are needed to assess the influences of inter-annual rainfall variation on forest regeneration dynamics, including lag-time effects. Some findings suggest, for example, that consecutive dry years may exacerbate mortality (Markesteijn et al., 2011; Pineda-García, et al., 2013), while growth and recruitment in a year may depend on rainfall from previous years (Bullock and Solís-Magallanes, 1990; Maza-Villalobos et al., 2013).

Besides inter-annual rainfall variation, successional changes in canopy openness affect water availability for TDF regenerative plants (Khurana and Singh, 2001). In open sites, high levels of evaporation reduce soil water availability (Lebrija-Trejos et al., 2011; Pineda-García et al., 2013), limiting growth or survival in seedlings (Schumacher et al., 2008). As succession advances and canopy closes, soil water availability increases (Kennard et al., 2002; Lebrija-Trejos et al., 2011) and so does the density of plants and species (Maza-Villalobos et al., 2011b), but light levels decrease in the understory, which may limit regeneration, especially that of light demanding species (e.g. Lebrija-Trejos et al., 2010, 2011). Also, in such shaded environments, activity of herbivores and pathogens may exacerbate in rainy years with negative demographic consequences for regenerative plants (Maza-Villalobos et al., 2013). Finally, the effects of rain may depend on whether regenerating plants belong to shrub or tree species. Overall, in dry environments shrub species tend to tolerate more than tree species the drought and high solar radiation conditions operating in open sites (e.g. Mooney and Dunn, 1970; DeLucia and Schilesinger, 1991; but see Pineda-García et al., 2013), so that the shrub species dominate early in TDF succession (e.g. Romero-Duque et al., 2007; Lebrija-Trejos et al., 2008). Therefore, regenerative rates of shrub species would be less sensitive to inter-annual rainfall variation than those of tree species, particularly early in succession.

Inter-annual rainfall variation has deemed to be critical in the successional dynamics of regenerative TDF communities (Maza-Villalobos et al., 2011a, 2013). Here, we assessed current and lag-time effects of the annual rainfall variation on rates of recruitment, growth, mortality, species gain, and species loss of regenerative plants (10–100 cm height) of shrub and tree species, during the old-field succession of a TDF. Our study covers 12-years (October 2004 to October 2016), including a severe drought ENSO event (in 2005) and two hurricanes (Jova, October 2011, magnitude 2; Patricia, October 2015, magnitude 4). We assessed the following hypothesis: (i) recruitment, growth, and species gain rates increase as annual rainfall increases, while mortality and species loss rates follow the opposite trend, (ii) recruitment, growth and species gain rates vary with the amount of rainfall in current years, whereas mortality and species loss rates are more responsive to variation in cumulative rainfall of current plus previous years, (iii) regenerative plants of shrub species exhibit lower mortality but higher growth and recruitment rates than those of tree species, especially early in succession, and (iv) effects of annual rainfall variation on regenerative community dynamics are higher at early than at late successional stages. Finally, to assess net effects of inter-annual rainfall variation on the potential for TDF regeneration in abandoned fields, we describe successional dynamical trajectories of plant density and species density along the 12 studied years.

2. Materials and methods

2.1. Study site

The study was carried out at the Chamela-Cuixmala Biosphere Reserve and surrounding rural areas, in the La Huerta municipality (19°30′N, 105°03′W), Western Mexico. Mean annual temperature is 22.1 °C and mean annual precipitation is 795.8 mm with a wide inter-annual (340–1329 mm) and seasonal variation (Maass et al., 2017). Almost 93% of the annual rainfall occurs from June to October, with a long dry season from November to end of May. The main vegetation type is a species rich TDF, with a canopy height of 5–10 m, with almost 95% of the plants dropping their leaves in the dry season (Durán et al., 2002; Lott and Atkinson, 2006). The human modified landscapes at La Huerta are dominated by pasture fields, crops, and managed forests (Burgos and Maass, 2004) and less than 30% is covered by TDF (Sánchez-Azofeifa et al., 2009).

2.2. Study system

In 2004, abandoned cattle pasture sites, with fallow ages ranging from 0 to 12 years, and old-growth forest sites (OGF, without any human disturbance) were selected for this study. Minimal distance between sites was 1.5 km (Maza-Villalobos et al., 2011a). Three sites were assigned to each one of following successional categories: Pasture (0–1 years since abandonment), Early (3–5 years), Intermediate (8–12 years) and OGF. At each site, an area of 120 × 90 m (1.08 ha) was delimited with metallic barbed wires to exclude cattle but no wild animals; in OGF only stakes were used to limit the study area. A permanent plot of 50 × 20 m (0.1 ha) was established at each site and 12 subplots (delimited in the corners with 0.5 m tall PVC poles) of 1-m^2 each were randomly established in the plot. In 2004, using satellite images, we estimated that percentage of forest cover in the matrix (in a radius of 500 m around each studied sites) increased from Pasture (range: 28–44%) to Early (47–61%) to Intermediate (63–80%) sites (details in Maza-Villalobos et al., 2011a). Some biophysical characteristics of the sites, such as terrain slope and aspect, were controlled. Maza-Villalobos et al. (2011a, 2011b) provide details of geographical location (including a map), biophysical characteristics, and land use history characteristics of the study sites.

In October 2004, at the end of the rainy season, in each subplot, all regenerative plants (seedlings, saplings and resprouts) with 10–100 cm height (measured from the ground level to the top of the plant canopy) of tree and shrub species were recorded, identified, measured in height and individually tagged. For all records, taxonomic identification and species classification in shrub or tree species follows the nomenclature provided by Lott (2002). To monitor the dynamics of studied communities, annual censuses were conducted over the next following twelve years every October. During these censuses new regenerative plants reaching a height of 10-cm or more (here after referred as recruits) were recorded, measured and identified while surviving plants were remeasured in height. Additionally, to assess possible microclimate effects on regeneration dynamics, in each study site and at each one of the 12 annual censuses, the percentage of canopy openness was recorded at 1.3 m aboveground as described in Maza-Villalobos et al. (2011a). Studies have shown that relative canopy openness is a good predictor of photosynthetic flux density (Lee, 1989; Anten and Ackerly, 2001), air and soil temperature, vapor pressure deficit, air relative humidity, and soil water content (Pineda-García et al., 2013).

Rainfall data used here are based on Maass et al. (2017). Because our annual vegetation censuses did not correspond to calendar years, annual rainfall for our studied years was adjusted to match our vegetation annual censuses (October 1 to September 31). This enabled us to relate the dynamics of regenerative communities with rainfall using same annual intervals.