Forest Ecology and Management 417 (2018) 110–121

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Regeneration responses to climate and land-use change of four subtropical tree species of the southern Central Andes

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ARTICLE INFO

Keywords:
Climate change
Land use change
Elevation gradient
Subtropical forest tree species
Drought
Shading

ABSTRACT

Land-use and climate change are impacting species and ecosystems around the world. The reproductive phase of plants is especially vulnerable to environmental change. Global environmental changes normally act collectively with nonlinearities and synergistic interactions being reported. Here we combined two techniques (i.e. a space-for-time substitution approach and a full factorial experiment) to assess the combined effects of climate and land-use change on the regeneration (seed production, seed germination and seedling survival and growth) of four subtropical forest tree species of the southern Central Andes (Yungas forest) in Argentina. We focus on temperature and precipitation changes and on decreased shading at the forest floor, a likely impact of changing land-use and management. We detected species-specific and phase-specific responses. Seed mass and quality was influenced by elevation (here used as a proxy for temperature change) while germination, seedling survival and growth were mainly affected by changes in the seedbed conditions (i.e. changes in shading and in moisture related to precipitation change). Despite the influence of environmental conditions on all the phases of plant regeneration studied here, we show that the major bottleneck of the regeneration phase of these species is germination. Interactive effects between the elevation of the seeds' provenance, precipitation and shading underpin the importance of studying the effects of different environmental changes collectively on plant regeneration to better forecast the effects of climate and land-use change on the Yungas forest.

1. Introduction

Terrestrial ecosystems and their associated biodiversity are strongly threatened by several human-induced changes in the environment. Land-use change was underpinned as the driver that has the largest global impact on biodiversity due to its devastating effects on habitat availability and species extinction (Sala et al., 2000). Climate change is the second most important driver of biodiversity change, mainly as a result of the expected warming of the climate system (Sala et al., 2000). These environmental changes normally do not act individually. Ecosystems are frequently under the pressure of more than one of these drivers and nonlinearities and synergistic interactions are expected (Feddema et al., 2005; Matsui et al., 2011; Perring et al., 2016; Pielke, 2005; Sala et al., 2000). However, the impacts of these interactions represent one of the biggest uncertainties in projections of future biodiversity (Feddema et al., 2005; Perring et al., 2016; Pielke, 2005; Sala et al., 2000).

Between 1990 and 2005, 66.4 million ha (or 1.7%) of the global forests were converted to other land uses (FAO and Jrc, 2012). In South America, this conversion resulted in a loss of 2.8 and 4.3 million ha of forest per year between 1990 and 2000 and between 2000 and 2005, respectively (FAO and Jrc, 2012). Moreover, models indicate that most land-use change will continue in tropical and temperate forests of South America, mainly due to urbanization, agriculture and the increasing demand for woody biomass and biofuel (Matsui et al., 2011). Therefore, larger areas dominated by croplands and more, and larger, gaps in the forest canopy and forest edge habitats are expected in the future. Due to the significant influence of the canopy cover on the forest floor (e.g. by influencing microclimatic temperature, light and humidity), changes in land use and forest management can strongly influence the performance of species occurring in the understory.

Climate change is considered the second most important driver of biodiversity change. Global mean temperatures increased by 0.8 °C during the 20th century (IPPC, 2014), and increases of up to 5 °C are predicted to occur over the next century (IPPC, 2014). As a result of warming, precipitation amount and frequency will likely be modified (Chaoyang et al., 2012; IPCC, 2013). Moreover, the impacts of contemporary climate change have already been documented in several

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https://doi.org/10.1016/j.foreco.2018.02.006
Received 24 October 2017; Received in revised form 4 February 2018; Accepted 6 February 2018

organisms and ecosystems around the world (e.g. Dillon et al., 2010; Pereira et al., 2010a; Bellard et al., 2012; Fronzek et al., 2012; Ceballos et al., 2017).

Sexual reproduction has been highlighted as one of the most sensitive phases of a plant species' life cycle. Responses of reproduction are often used as indicators of the species' sensitivity to climate and other environmental changes (Lescop-sinclair and Payette, 2016; Walck et al., 2011; Wang et al., 2006; Zhang et al., 2014). The impacts of climate change on plant species' reproduction include impacts on seed production, dormancy break, germination, and seedling establishment and performance (Gibson and Bachelard, 1986; Daws et al., 2004; Graae et al., 2009; Milbau et al., 2009; Shevtsova et al., 2009; De Frenne et al., 2011a, 2012; Mok et al., 2012; Sun et al., 2012; Carón et al., 2014). The environmental conditions, especially the temperature, experienced by the mother plant during seed production can influence seed quality by modifying morphological, chemical and physiological aspects that later determine the seeds' responses to changes in the local environmental conditions under which seeds are germinating (i.e. seedbed conditions; De Frenne et al., 2011b; Sun et al., 2012; Carón et al., 2014). Therefore, the study of seed characteristics developed under contrasting temperatures with a space-for-time substitution approach (Fukami and Wardle, 2005) can provide important information about the impacts of environmental change on seed production. Moreover, dormancy break, seed germination and seedling establishment are influenced by seedbed conditions (Hermann and Chicote, 1965; Gibson and Bachelard, 1986; Robson et al., 2009; González-rodríguez et al., 2012; Carón et al., 2014). Particularly, changes in precipitation and light (incident radiation) of the seedbed have been shown to strongly affect the success of the regeneration of tree species (González-Rodríguez et al., 2012; Quero et al., 2007; Robson et al., 2009). However, future seedbed conditions are difficult to predict and will probably be the result of a combination of the influence of climate and local forest management practices.

Here, we study the regeneration from seed of four Yungas forest tree species; *Anadenanthera colubrina*, *Enterolobium contortisiliquum*, *Jacaranda mimosifolia* and *Handroanthus impetiginosus* from populations with contrasting temperatures along an elevational gradient. The Yungas' forest is a highly biodiverse mountain forest distributed between Venezuela in the north and Argentina in the south (Brown and Kappelle, 2001a). We test for the effects of contrasting seedbed conditions (i.e. contrasting levels of precipitation and light) and specifically addressed the following aspects: (i) the variation of morphological and physiological fruit and seed traits (i.e. number of seeds per fruit, mean seed weight and seeds' viability) of trees growing under contrasting temperatures along an elevation-climatic gradient, (ii) the germination, survival and early growth of these species under different seedbed conditions (i.e. contrasting levels of light and precipitation), (iii) the presence of an interactive effect of precipitation and light and the link between the response to the changes in seedbed conditions with the temperature experienced by the mother tree. We expect that seed traits will vary with the elevation of the provenance of origin. A general increase of the seed mass with elevation is expected due to the prevalent colder conditions at higher elevations that might allow the seed to ripen more slowly with a longer filling period allowing a greater total assimilation (Fenner and Thompson, 2005). Additionally, we expect that the different phases of plant regeneration will be differently impacted by the factors analyzed here with the germination as the most sensitive phase of plant regeneration. Finally, we expect that germination, seedling survival and growth of seedlings from seeds produced at higher elevations will be more sensitive to reduced precipitation and light due to the predominant lower tree densities and higher precipitation at higher elevations. However, if heavier seeds are produced at higher elevations, the seeds and seedlings from higher elevations might have a better performance under elevated drought and shade (Fenner and Thompson, 2005).

2. Material and methods

2.1. Study area

The Yungas' forest is a highly biodiverse forest type in South America, distributed between Venezuela in the north and Argentina in the south (Brown and Kappelle, 2001a). Even though this forest type is one of the most biodiverse ecosystems of the continent (Brown and Kappelle, 2001b), it is strongly affected by forest loss, degradation and fragmentation mainly due to a strong pressure for agriculture and cattle raising during the 20th century (Brown and Pacheco, 2006; Grau and Brown, 2000; Volante et al., 2012). Nevertheless, the remaining area is extremely important for provisioning essential ecosystem services including wood production, watershed protection, and recreational benefits (Brown, 1995).

In Argentina, the Yungas cover approximately 56,000 km^2, are distributed between 22° and 28° latitude south, and between 400 and 3000 m a.s.l. (Malizia et al., 2012). The climate in the region is subtropical humid with a dry season. The mean temperature is 22 °C, while the precipitation fluctuates between 900 and 2000 mm annually varying with the elevation and the exposure of the slopes being, in general, higher in the slopes facing east. This forest contains three contrasting vegetation types associated to the elevation; Premontane Forest (*Selva Pedemontana*), Montane Humid Forest (*Selva Montana*) and Montane Forest (*Bosque Montano*; Malizia et al., 2012).

The populations considered for this study belong to the Premontane and Montane Humid Forest types and are located along an elevational-climatic gradient that extends between 23°11′ and 25°4′ latitude South and 64°41″ and 65°32″ longitude West (Table N 1), covering an elevational-climatic gradient of almost 500 m with an average difference of mean annual temperature of 3.24 °C and 286 mm of difference in annual precipitation between populations (Table 1).

2.2. Species studied

Four characteristic tree species of the Premontane and Montane Humid Forest were selected for this study: two Fabaceae species namely *Anadenanthera colubrina* (Vell.) Brenan. *var. cebil* (Griseb.) Altschul. and *Enterolobium contortisiliquum* (Vell.) Morong and two Bignoniaceae species namely *Handroanthus impetiginosus* (Mart. ex DC.) Mattos and *Jacaranda mimosifolia* D.Don. These species are distributed in the Yungas along an elevational gradient from 400 till 2000 m a.s.l (Digilio and Legname, 1966). The selected species are economically important since their wood is used for furniture and house carpentry in general (*Jacaranda mimosifolia*), for lumber to make flooring and decking (*Handroanthus impetiginosus*), for beams, frames, sleepers, posts, rods (*Anadenanthera colubrina*), for roofs, containers, shipbuilding and beehives and interior and exterior furniture (*Entherolobium contortisiliquum*). In addition, these species are frequently used in urban landscaping due to their conspicuous and colorful flowers. In terms of ecological relevance, the two Fabaceae species (*Anadenanthera* and *Entherolobium*) are important due to their capacity to fix nitrogen. Finally, flowers of all species are pollinated by insects (mostly by bees) and are frequent and conspicuous elements of the forest and the transitions to other vegetation types such as Chaco and Monte (Digilio and Legname, 1966).

2.3. Fruit and climatic data collection

Along an elevational-climatic gradient, five populations of each species were selected for fruit collection. In each population, fruits from at least ten dominant and randomly selected individuals were collected at seed maturity during their natural dispersion period between September and November of 2015.

Climatic data of the populations where the seeds were collected were extracted from Worldclim (Hijmans et al., 2005) due to the lack of