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Reproductive phenology of useful Seasonally Dry Tropical Forest trees: Guiding patterns for seed collection and plant propagation in nurseries

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ABSTRACT

The propagation in nurseries of native plant species potentially useful for agroforestry, silvopastoral and restoration programs is hindered by an inadequate supply of high quality seed. Limitations in our knowledge on the phenological patterns of native species result in the lack of efficient collecting protocols. Here we analyze the reproductive phenology of 14 native tree species from Seasonally Dry Tropical Forest (SDTF) that are widely used in reforestation and restoration programs. We conducted monthly observations during five years through a community-based monitoring program in two conservation areas within the Zicuirán-Infiernillo Biosphere Reserve (West Mexico) to assess the flowering and fruiting phenology of 149 marked trees (7–20 trees per species). For each species we described the phenophase intensity, duration, seasonality, synchrony and frequency. We related the intensity of reproductive phenology to climatic variables (photoperiod, precipitation and temperature). We identified three main phenological strategies of SDTF species that differ in timing and climatic triggers: (1) flowering and fruiting exclusively in the rainy season; (2) flowering in the rainy season and fruiting in the dry season; and (3) flowering and fruiting exclusively in the dry season. For each phenological strategy we make recommendations of optimal collecting seeds schedules. The community-based monitoring program, which involves the participation of local social actors, guaranteed the success of long-term phenological monitoring. Our study provides valuable information on both the inter-annual and inter-specific variation of the phenological patterns of tree species of forestry interest, and demonstrates that qualitative descriptions of population-level phenological attributes is an essential input to develop adaptive management programs.

1. Introduction

A major hindrance faced by nurseries devoted to the propagation of native plant species used in agroforestry, silvopastoral or restoration programs, is the lack of a timely and permanent supply of high-quality seed (Böhringer et al., 2003; Botha et al., 2005, 2006). This situation reflects deficiencies in our knowledge on the reproductive biology of native species, in particular, their phenological patterns and the optimal times for plant reproduction when the best seeds are produced. Ultimately, the deficiency of phenological data results in the lack of efficient collecting protocols (Buisson et al., 2016; Fenner and Thompson, 2004; Kuaraksa et al., 2012).

Phenological studies seek to describe the timing of cyclic biological events and to identify their internal and external clues. In a plant's life cycle a distinction is made between two major reproductive phenophases, namely flowering and fruiting. The importance of accurate descriptions of reproductive phenological patterns for the design of conservation or management strategies and ecological restoration programs has recently been recognized (Morellato et al., 2016). The relevance relies in the need for phenological information to recognize specific times of the year with high flower, fruit and seed availability, to assess the duration, intensity, frequency and synchrony of their occurrence during the year, and to evaluate differences in phenological patterns between species, populations and communities (Miller-Rushing and Weltzin, 2009; Newstrom et al., 1994).

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In the context of Seasonally Dry Tropical Forests (SDTF), phenological information is of particular interest, since compared with temperate and tropical wet forest ecosystems, the diverse and complex phenological patterns of SDTF are still poorly explored and little is known for native species with forestry potential (Bonfil and Trejo, 2010). Most phenological studies conducted in SDTF have focused on the description of community-level patterns (Bullock and Solís-Magallanes, 1990; Cortés-Flores et al., 2017; Frankie et al., 1974; Justiniano and Fredericksen, 2000), while the assessment of such patterns at the population level has received less attention (Kuaraksa et al., 2012; Venter and Witkowski, 2011; Wallace and Painter, 2002).

The main drivers of the overall phenological patterns displayed by the SDTF tree community are precipitation seasonality and intensity, as the occurrence of the growth and reproduction largely depends on the variation of water availability throughout the year or the length of rainy season (Borchert, 1998; Borchert et al., 2002, 2004; Holbrook et al., 1995; McLaren and McDonald, 2005; Morellato et al., 2013). Therefore, in ecosystems with a marked dry season that lasts between four and eight months, phenological strategies have reflected the range of adaptations allowing plants to tolerate and survive the seasonal drought (Borchert et al., 2004; Morellato et al., 2013; Singh and Kushwaha, 2006). With respect to flowering, two major strategies have been identified (Singh and Kushwaha, 2006): species in which flower buds develop in response to increasing water availability during the rainy season, and species that flower in the dry season, either at the beginning (just after the end of the rainy season, in the fall), or at the end (several weeks before the onset of the rains, in the spring). For this latter group of species, changes in the photoperiod apparently trigger reproductive events in plants. According to Singh and Kushwaha (2005), the drier is a seasonal tropical forest, the larger is the number of species flowering during the dry season. In turn, fruit maturation concentrates almost exclusively in the dry period of the year, which is the season when seed dispersal by wind is favored, with the exception of fleshy fruits, which tend to mature in the rainy season, when environmental conditions favor maturation and seed dispersers are abundant (Bullock and Solís-Magallanes, 1990; Frankie et al., 1974; Justiniano and Fredericksen, 2000; Morellato et al., 2013; Singh and Kushwaha, 2005). Regardless of the timing of seed dispersal, most seeds of SDTF trees remain dormant until the beginning of the rainy season, when they germinate, an evolutionarily selected trait that may increase the probability for successful seedling establishment (Frankie et al., 1974; van Schaik et al., 1993).

Despite the generality of these findings, community phenological patterns may conceal a large diversity of phenological responses displayed by the tree species, which only emerges when patterns are assessed at the population level. When taking this approach, it becomes evident that plants' responses to changing climatic conditions throughout the year are no longer predictable, given the plethora of strategies that plants have evolved to face seasonal water limitations (Borchert et al., 2002; Singh and Kushwaha, 2005). Within this framework, we proposed the use of a community-based monitoring program involving the local inhabitants to conduct a five-year long phenology observation. We aimed to investigate the reproductive phenological patterns of STDF tree species with forestry potential, in order to provide essential information for the planning of seed collection schedules and their subsequent propagation in nurseries, while focusing on ecological restoration. We also evaluated the influence of climatic conditions on the onset of flowering and fruiting, and examined whether these STDF tree species differ in their reproductive strategies, reflecting divergent evolutionary responses to the dry season.

We hypothesized that in this highly seasonal environment, tree phenology responds primarily to rainfall seasonality, as this is the main constraining factor; consequently, inter-annual phenological variation should be mainly driven by rainfall variability. Alternatively, we hypothesized that phenological timing of species responds mainly to factors that are largely invariable among years, such as photoperiod, which would result in high predictability of the phenological patterns, regardless the inter-annual rainfall variation. If the amount of inter-annual variation (precipitation) overrides the regularity of within-year seasonal variation (photoperiod), this would result in greater phenological uncertainty among years. Clearly, in the context of a nursery-based plant propagation program it is important to discriminate between these contrasting hypotheses.

2. Materials and methods

2.1. Study site

The study was conducted in the lower portion of the Balsas river basin, Churumuco municipio (county), Michoacán state, Western Mexico (extreme coordinates 18°38′–18°44′N, 101°38′–101°41′ W). The area is part of the buffer zone of the Zicuirán-Infiernillo Biosphere Reserve and comprises of 892 ha, with an elevation range of 300–1200 m asl.

The regional climate is tropical dry with a summer rainfall regime (BS_0), with a mean annual temperature of 28 °C and a mean total annual precipitation of 650 mm, strongly concentrated between June and September (Fig. 1). The prevailing vegetation type is the SDTF, characterized by a large proportion (> 75%) of trees shedding all their leaves in the dry season, and a more or less continuous canopy with an average height of 8 m. In addition to the SDTF, in areas with higher soil moisture, such as ravines or close to water streams, the vegetation is a semi-evergreen tropical forest characterized by a smaller proportion of individuals shedding their leaves in the dry season (50–70%), and the presence of dominant trees with > 15 m height.

2.2. Species selection

The study species were selected according to three criteria: local, governmental and conservation status. Species with local interest were identified through 16 interviews with local people, who distinguish which species were the most preferred by the inhabitants of the region for different purposes (construction, fodder, food, medicine, ornament or poles). Governmental importance was identified through 10 interviews with officials from public institutions of the forestry sector, to identify species promoted by government agencies for propagation in reforestation and restoration programs, for which reason they have a high regional trade potential. Finally, we assessed conservation relevance based on the classification of species of interest for local inhabitants and government agencies in conservation or threat categories according to the Mexican environmental legislation (SEMARNAT, 2010). From 38 species mentioned by the two groups of interviewees we selected 14 that coincided in the selection criteria (Table 1).

2.3. Reproductive phenology

We established a 15 km line transect in the study region along an elevation gradient from 200 to 1000 m, which comprised three portions: (1) low (230–480 m, where prevailing physiography is slope foothills and prevailing vegetation is secondary SDTF), (2) medium (481–725 m, mostly medium slopes with moderate steepness, where SDTF is intermingled with old secondary stands), and (3) high (726 and 975, with SDTF and tropical semi-evergreen forest along a water stream).