



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.

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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 the 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 SDTF 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 SDTF 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 (BS₀), 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).

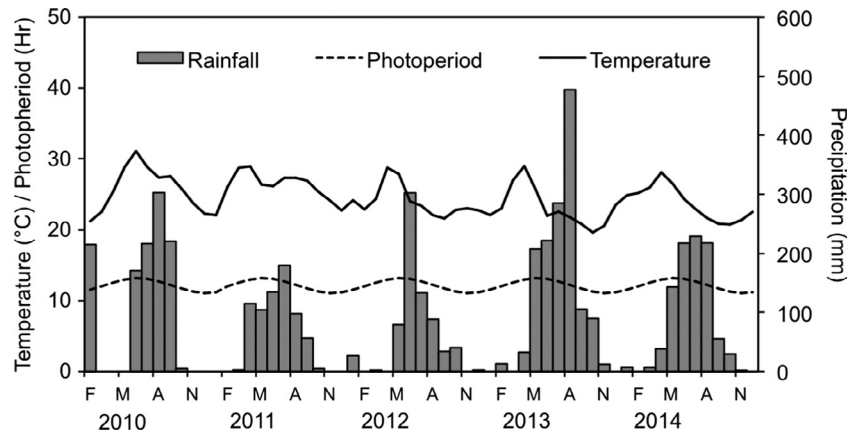


Fig. 1. Monthly rainfall, temperature and photoperiod in Churumuco, Michoacán state, Mexico, for the period of February 2010 to January 2015. Abbreviations: A (August), F (February), M (May), N (November).

Table 1

Tree species selected for phenological observations, along with vegetation type where they occur, number of individuals monitored, common names, reproductive systems, and traditional uses in the study region (Michoacán state, Mexico). Superscript numbers indicate selection criteria met by each species according to (1) interviews with local inhabitants, (2) interviews with officials of government agencies from the forestry sector, and (3) the list of endangered species reported in some threat category in the Mexican environmental law (SEMARNAT, 2010). Number of individuals observed for each species is indicated in parenthesis.

Family/Species	Common name	Sexual system	Uses
<i>Seasonally Dry Tropical Forest</i>			
Anacardiaceae			
<i>Amphipterygium adstringens</i> (Schltdl.) Standl. ^{1,2 (10)}	Chacualalate	Dioecious	Medicinal
Apocynaceae			
<i>Plumeria rubra</i> L. ^{2 (10)}	Parandazicua	Hermaphroditic	Ornamental
Bignoniaceae			
<i>Handroanthus impetiginosus</i> (Mart. ex DC.) Mattos ^{2,3 (10)}	Cañafístula	Hermaphroditic	Construction
Boraginaceae			
<i>Cordia elaeagnoides</i> DC. ^{2 (10)}	Cuerámo	Hermaphroditic	Construction, medicinal, poles
Leguminosae			
<i>Caesalpinia coriaria</i> (Jacq.) Willd. ^{1 (10)}	Cascalote	Hermaphroditic	Forage, commercial
<i>Caesalpinia platyloba</i> S. Watson ^{1,2 (10)}	Frijolillo	Dioecious	Construction, poles
<i>Eysenhardtia polystachya</i> (Ortega) Sarg. ^{1 (10)}	Palo dulce	Hermaphroditic	Medicinal, poles
<i>Gliricidia sepium</i> (Jacq.) Kunth ex Walp. ^{1 (10)}	Trébol	Hermaphroditic	Poles, forage
<i>Heteroflorum sclerocarpum</i> M. Sousa ^{1 (10)}	Ojo de perico	Dioecious	Forage
Malvaceae			
<i>Guazuma ulmifolia</i> Lam. ^{1,2 (10)}	Cahulote	Hermaphroditic	Forage, poles
<i>Semideciduous Tropical Dry Forest</i>			
Burseraceae			
<i>Bursera fragrantissima</i> Bullock ^{1 (20)}	Tecomaca	Dioecious	Medicinal
Chrysobalanaceae			
<i>Licania arborea</i> Seem. ^{2,3 (7)}	Cuirindal	Hermaphroditic	Forage
Meliaceae			
<i>Swietenia humilis</i> Zucc. ^{2 (7)}	Cóbano	Monoecious	Furniture, medicinal
Moraceae			
<i>Brosimum alicastrum</i> Sw. ^{1,2 (15)}	Uje	Monoecious	Forage, food

We characterized the distribution and abundance of the study species by recording every individual located within 50 m at each side of the line transect and logging their precise location with a GPS (Appendix A). Depending on their abundances, we then marked between 7 and 20 individuals of each species (149 trees in total), all of them having a minimum diameter at breast height of 10 cm, as trees of this size or bigger have a high probability of being reproductive (Bullock and Solís-Magallanes, 1990). The selected trees were separated by distances > 50 m to minimize genetic relatedness and space dependency of data.

We conducted monthly observations with binoculars in the last week of each of 60 months, from February 2010 to February 2014 (with the single exception of February 2011). The percent of the crown occupied by flowers in anthesis (flowering) and mature fruits (fruiting) in each marked individual was assessed by using Fournier's (1974) semi-quantitative scale of five categories (0–4) with an interval of 25% between each one.

2.4. Community-based phenology monitoring program

A community monitoring team conducted the quinquennial evaluation of the reproductive phenology on which this study is based. This team emerged as a strategy aimed to motivate the participation, organization and training of community members in the management of native trees species of forestry interest. During the first monitoring year, the coordinators of this project accompanied the monitoring team, which was formed for six peasants > 40 years old. In this way, the monitoring team received training on the identification of the different development stages of the reproductive structures of the study species, and on the use of the equipment needed for the evaluations. During the four following years the fieldwork was the exclusive responsibility of the community monitoring team. To increase the reliability of the results so gathered, we conducted four workshops during the first year of study to calibrate the phenological observations. In them,

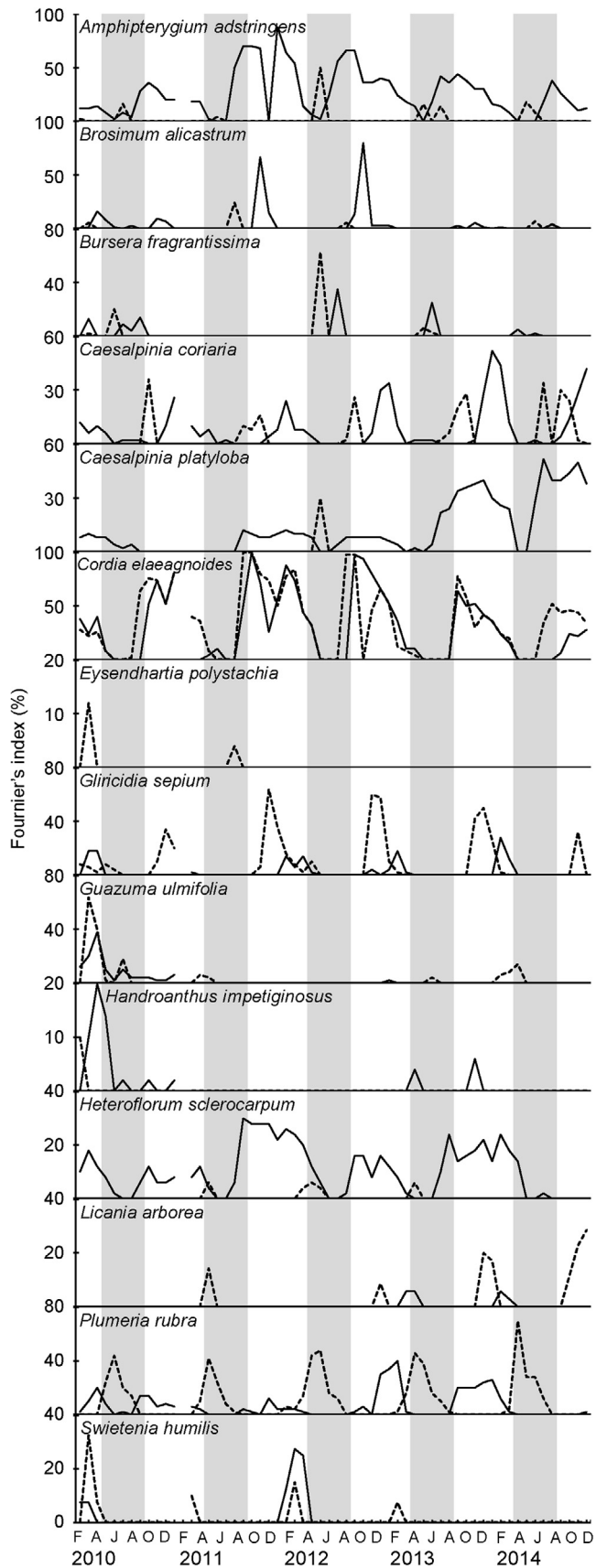


Fig. 2. Percent intensity index of flowering (dashed lines) and fruiting (solid lines) of 14 Seasonally Dry Tropical Forest tree species (Churumuco, Michoacán state, Mexico) from February 2010, to February 2015. Abbreviations: A (April or August), D (December), F (February), J (June), O (October). Gray bars indicate the rainy season.

each member of the monitoring group evaluated the presence of flowers and fruits independently. Then, we discussed together likely reasons for the discrepancies. In the last two workshops, the match between the different observers was approximately 95%.

2.5. Climatic data

We obtained daily minimum and maximum temperatures, and daily precipitation, from the closest meteorological station to our study area (National Water Commission, Las Cruces de Turicato, 19°3'55" N, 101°25'40" W, 800 m asl). Due to technical problems, we were only able to obtain climatic data for the 2010–2013 period. Information for 2014 was obtained through extrapolation, using an ARIMA model in forecast package in R (R Core Team, 2014) and taking into consideration the historical climate records of the region (Fig. 1). Daylight duration was obtained from the Astronomical Applications Department of the U.S. Naval Observatory (<http://www.usno.navy.mil>).

2.6. Data analysis

We calculated Fournier's (1974) intensity index to evaluate the proportion of flowering and fruiting in each species and month (values < 25% indicate a low intensity, those between 25 and 50% indicate a medium intensity; and those > 50% a high intensity). Additionally, we described the frequency of the phenophases (number of reproductive cycles by year) as annual if event occurred only once in the year, and supra-annual if the time elapsed between two phenological events was larger than one year, or if it was not consecutive over the five-year study period.

Synchrony was assessed through the index proposed by Freitas and Bolmgren (2008), which indicates whether the intensity peak of a given phenophase coincides completely (1) or not at all (0) among all individuals within a population (values < 0.25 signify that the species had an asynchronous reproductive event, values between 0.25 and 0.5 indicate that an event had low synchrony, and those values > 0.5 denoted a synchronic event).

Duration (the time elapsed between the start and the end of a phenophase) was described by calculating the mean and the standard deviation of the number of months by year in which the two phenophases were observed. The presence of flowers and/or fruits in at least one individual was sufficient to indicate that a given species was flowering or fruiting in that month. Based on the mean number of months in which the phenophase occurred, the duration was classified as short (< 2 months), intermediate (2–5 months) or extended (> 5 months).

To assess phenophase seasonality we used circular statistics to test the null hypothesis that the presence of flowers and fruits was homogeneously distributed around the year as proposed by Morellato et al. (2000). We assigned to each month an angular value of 30° (February, 0°; March, 30°; April 60°; etc.), and calculated the mean angle α and the magnitude of the r vector; α indicates the time (month) of the year in which the largest number of individuals of a given species presented a phenophase, while r indicates the degree of dispersion or concentration of the observations (Zar, 1999). The r vector values range from 0 (indicating a totally homogeneous distribution of the data around the year) to 1 (indicating all data are concentrated in a single angle or data) and can be considered as a proxy of seasonality (Morellato et al., 2000, 2010). The significance of the mean angle α was tested through a Rayleigh's (z) test (Zar, 1999).

Finally, we analyzed the relationship between flowering and fruiting (monthly Fournier's intensity index for each phenophase) and climatic variables (mean monthly precipitation and photoperiod) through generalized linear models (GLM) with binomial error and a logit link function; this analysis was implemented in

Table 2
Phenological reproductive attributes of 14 tree species from Seasonally Dry Tropical Forest (Michoacán state, Mexico). The two first rows for each species show the flowering and fruiting, respectively. Synchrony was classified according to the index values as: asynchrony (< 0.25) = A, low synchrony ($0.25-5$) = L, and synchrony (> 0.5) = S. Duration was classified as: B = Brief (< 2 months), I = Intermediate ($2-5$ months), and E = Extended (> 5 months); in parentheses are the mean and the standard deviation, separated by a comma. Seasonality shows the results of circular statistic: the first and second values are the vector r , and the mean date or angle α , respectively. When the z-statistic was significant, $P \leq 0.05$ (*), the mean date is shown in parentheses. The symbol (–) indicates that the phenophase was not observed.

Species	Attribute	2010	2011	2012	2013	2014
<i>Amphipterygium adstringens</i>	Synchrony	L (0.5) A (0.14)	A (0) S (0.53)	L (0.29) L (0.32)	A (0.03) A (0.2)	A (0.04) A (0.12)
	Duration	B (0.5, 0.7) E (6, 4.5)	B (0.1, 0.3) E (6, 1.9)	B (0.7, 0.5) E (6.7, 4.3)	B (0.5, 0.8) E (7, 4.7)	B (0.4, 0.7) I (4, 3.2)
	Seasonality	0.6–140.9° (21 June) 0.2–38.2°	1–120° (1 June) 0.2–68.6° (9 April)	1–120° 0.2–69–6°	0.9–143.4° 0.2–83.6°	1–127.4° 0.3–61.1° (1 April)
<i>Brosimum alicastrum</i>	Synchrony	A (0.1) A (0)	A (0.21) L (0.45)	A (0) S (0.58)	A (0) A (0)	A (0.01) A (0)
	Duration	B (0.3, 0.5) B (1.7, 1.6)	B (0.9, 0.4) B (1.5, 0.5)	B (0.1, 0.4) B (1.1, 0.7)	– B (0.3, 0.5)	B (0.3, 0.5) B (0.1, 0.4)
	Seasonality	0.1–30° 0.1–6.2°	1–180° 1–79.7° (20 April)	1–150° (B–July) 0.9–88.6° (29 April)	– 0.9–88.6° (29 April)	0.9–160.9° 0
<i>Bursera fragrantissima</i>	Synchrony	A (0.12) A (0.08)	– –	A (0.47) A (0.14)	A (0) A (0.08)	– A (0)
	Duration	B (0.8, 0.6) B (1.1, 0.9)	– –	B (0.9, 0.4) B (0.5, 0.5)	B (0.2, 0.4) B (0.5, 0.5)	– B (0.1, 0.3)
	Seasonality	0.9–111.9° 0.2–62.6°	– –	1–120° 1–180° (31 July)	1–127.4° 1–150° (1 July)	– 0.9–120°
<i>Caesalpinia coraria</i>	Synchrony	A (0.22) A (0.11)	A (0.04) A (0)	A (0.08) A (0.09)	A (0.09) A (0.13)	A (0.18) A (0.19)
	Duration	B (0.8, 0.4) I (2.9, 2.6)	B (1, 1.2) B (1.7, 1.9)	B (0.6, 0.7) I (2.4, 2.5)	B (1.3, 1.4) B (1.9, 2.1)	B (1.9, 1.2) I (3, 2.4)
	Seasonality	1–120.2° 0.5–6.9° (6 February)	0.9–110.6° 0.5–29.2° (29 February)	1–125° 0.7–6.2° (5 February)	0.9–114.4° 0.7–4.4° (3 February)	0.8–125° 0.6–15° (14 February)
<i>Caesalpinia platyloba</i>	Synchrony	– A (0)	– A (0)	A (0.12) A (0)	– A (0.16)	– A (0.22)
	Duration	– I (2.1, 2.4)	– B (1.1, 1.9)	B (0.6, 0.5) B (1.8, 3.4)	– I (3.2, 3.3)	– E (5.2, 3.9)
	Seasonality	– 0.6–64.4° (4 April)	– 0.7–96.2° (7 May)	1–120° 0.4–15° (14 February)	– 0.5–91° (1 May)	– 0.2–82.6° (23 April)
<i>Cordia elaeagnoides</i>	Synchrony	L (0.46) L (0.42)	S (0.59) S (0.6)	S (0.64) S (0.66)	L (0.4) L (0.34)	L (0.28) A (0.23)
	Duration	E (8.4, 0.8) E (7.1, 0.9)	E (7.4, 0.5) I (4.2, 0.8)	E (7.4, 0.7) E (7.9, 0.3)	E (5.2, 1.5) E (6.6, 1.3)	E (8.1, 1.7) I (4.7, 0.9)
	Seasonality	0.4–42.7° 0.5–19.6° (19 February)	0.3–55.1° 0.7–87.3° (28 April)	0.3–2.1° 0.4–16.1° (15 February)	0.6–51.1° 0.5–31° (1 March)	0.3–49.3° 0.6–17° (16 February)
<i>Eysendhartia polystachya</i>	Synchrony	A (0.02) –	A (0) –	– –	– –	– –
	Duration	– B (0.3, 0.5)	– B (0.1, 0.3)	– –	– –	– –
	Seasonality	– 1–30°	– 1–180° (31 July)	– –	– –	– –
<i>Gliricidia sepium</i>	Synchrony	A (0.18) A (0.22)	L (0.43) A (0)	L (0.38) A (0.05)	L (0.33) A (0.08)	A (0.15) A (0.17)
	Duration	I (3.1, 1.7) B (1.8, 0.4)	I (2.1, 0.3) B (0.1, 0.3)	I (2.6, 1.2) B (1.1, 1.2)	I (2.2, 0.8) B (0.8, 0.6)	B (1.5, 1.1) B (1.3, 0.8)
	Seasonality	0.5–29.2° 1–45° (16 March)	1–47° 1–30° (29 February)	0.7–19.1° 0.8–29.1° (29 February)	0.9–31.8° 1–26.2° (26 February)	0.8–26.1° 1–41.5° (12 March)
<i>Guazuma ulmifolia</i>	Synchrony	L (0.37) A (0.18)	A (0.01) –	– –	A (0) A (0)	A (0.03) –
	Duration	I (2.8, 0.6) I (4.3, 3.3)	B (0.4, 0.7) –	– –	B (0.1, 0.3) B (0.1, 0.3)	B (0.7, 1.1) –
	Seasonality	0.7–67.2° 0.4–56.1° (27 March)	1–75° –	– –	1–150° (1 July) 1–0°	0.9–73.3° –
<i>Handroanthus impetiginosus</i>	Synchrony	A (0.06) A (0.08)	– –	– –	– A (0)	– –
	Duration	B (0.5, 0.5) B (1.8, 1.5)	– –	– –	– B (0.3, 0.5)	– –
	Seasonality	1–0° 0.7–62.2° (2 April)	– –	– –	– 0.4–36.2°	– –

Table 2 (continued)

Species	Attribute	2010	2011	2012	2013	2014
<i>Heteroeflorum sclerocarpum</i>	Synchrony	– A (0.08)	A (0.02) A (0.12)	A (0.02) A (0.09)	A (0.02) A (0.05)	– A (0)
	Duration	– I (3.7, 3.2)	B (0.3, 0.5) I (4, 3.4)	B (0.5, 0.5) I (4.3, 4.1)	B (0.3, 0.5) I (3.2, 3.6)	– B (1.6, 2.1)
	Seasonality	– 0.3–1.4° (30 January)	1–90° 0.4–76.8° (17 April)	0.9–90° 0.4–9.2° (8 February)	1–90° 0.4–60° (1 April)	– 0.7–45° (16 March)
	<i>Licania arborea</i>	Synchrony	– –	A (0) –	A (0) –	A (0.05) A (0.05)
Duration	– –	B (0.1, 0.3) –	B (0.1, 0.3) –	B (0.4, 0.5) B (0.4, 0.8)	I (2.3, 1.2) B (0.4, 0.5)	I (2.3, 1.2) B (0.4, 0.5)
Seasonality	– –	1–90° (30 April) –	1–30° (29 February) –	1–30° (29 February) –	1–30° 1–80.1°	0.9–39° 1–39.9°
<i>Plumeria rubra</i>	Synchrony	A (0.24) A (0.15)	A (0.22) A (0.07)	A (0.25) A (0.23)	A (0.23) A (0.24)	A (0.32) A (0.14)
	Duration	I (3.2, 0.8) I (4.2, 2)	I (2.7, 1.2) B (1.6, 1.4)	I (4, 1.1) B (1.7, 0.8)	I (3.6, 1.3) I (4.9, 1)	I (3.1, 0.9) B (1.3, 0.9)
	Seasonality	0.9–136° 0.2–0.3° (30 January)	0.9–106.3° 0.5–38.3° (9 March)	0.7–113.4° 0.8–21.9° (21 February)	0.8–122.1° 0.6–33.5° (4 March)	0.8–122.5° 1–15°
	<i>Swietenia humilis</i>	Synchrony	A (0.09) A (0)	A (0.01) –	A (0.02) A (0.1)	A (0) A (0)
Duration	B (0.8, 0.9) B (0.8, 0.9)	B (0.3, 0.5) –	B (0.3, 0.5) B (0.9, 1.2)	B (0.1, 0.4) –	– –	– –
Seasonality	1–39.9° 1–15° (14 February)	1–30° (29 February) –	1–30° (29 February) 0.9–38.8° (9 March)	1–30° (29 February) 0.1–6.2°	1–30° (29 February) –	– 0.9–88.6°

R (R Core Team, 2014). We calculated the coefficient of discrimination (D), a measure of the model's ability to discriminate failures and successes in a binary response variable (Tjur, 2009). Because of collinearity between temperature and photoperiod ($r = 0.64$), temperature data were excluded from further analyses.

3. Results

3.1. Reproductive phenological patterns

3.1.1. Intensity and frequency

Overall, reproductive phenophases occurred with mean low intensity (< 25%) in our study species (Fig. 2). The large variation between years and species makes it difficult to identify the moment of the year with flowering and fruiting peaks. Nevertheless, the reproductive period was strongly concentrated in the dry season (October–May). All species showed a considerable time lag between the presence of flowers and fruits, i.e., flowers were commonly recorded one to three months prior to the production of mature fruits, except in *Cordia elaeagnoides* and *Swietenia humilis*, for which there was a temporal overlap in the occurrence of the two phenophases (Fig. 2). In the case of *Caesalpinia platyloba*, in four of five years, fruits were observed without any previous record of flowering (missing observation probably related to very short – less than two weeks – flowering event), and the opposite happened with *Eysendhartia polystachya*, for which only two incipient flowering events were observed, but not a single fruiting event, during the entire study period.

The reproductive cycles of nine study species were annual, while the remaining five were classified as supra-annual (*E. polystachya*, *Guazuma ulmifolia*, *Handroanthus impetiginosus*, *Licania arborea* and *S. humilis*), as for these species flowers and fruits were not recorded in all consecutive years of the study. All nine annual species exhibited the same phenological pattern year after year, albeit with small variations in their timing and intensity (Fig. 2).

Regardless of reproductive frequency in our study species, three main phenological strategies were identified based on their flowering and fruiting time and intensity: (1) flowering and fruiting

exclusively during the rainy season (*Bursera fragrantissima*), (2) flowering in the rainy season and fruiting in the dry season (*Amphipterygium adstringens*, *Brosimum alicastrum*, *C. elaeagnoides* and *C. platyloba*), and (3) flowering and fruiting exclusively occurring during the dry season (*Caesalpinia coriaria*, *Gliricidia sepium*, *Heteroeflorum sclerocarpum*, *L. arborea*, *Plumeria rubra* and *S. humilis*). Three species could not be classified in any of these groups due to the erratic and incipient patterns in their reproductive phenology (*E. polystachya*, *G. ulmifolia* and *H. impetiginosus*).

3.1.2. Synchrony

Overall, flowering and fruiting of the study species were not synchronic (Table 2), with mean synchrony indices of 0.1 and 0.06, respectively. The analysis of the patterns between years and species revealed important differences. The only species that flowered and fruited synchronously during the five-year period was *C. elaeagnoides* (mean synchrony index of 0.5 for both phenophases). Other species showed some degree of synchrony in one phenophase but considerable asynchrony in the other. For example, flowering of *G. sepium* was moderately synchronic in three years, whereas its fruiting was always asynchronic, in contrast with *B. alicastrum*, in which flowering was asynchronic in all the years of study while fruiting was much more synchronic.

3.1.3. Duration

Reproductive structures generally remained on the trees less than two months (Table 2); generally, flowers had a shorter duration than fruits (means \pm SD: 1.2 ± 2 and 2.1 ± 1.4 months, respectively). When considering inter-annual and interspecific variation, *C. elaeagnoides* was the only species whose flowers and fruits were not only more synchronous in their appearance, but also fruits remained on the trees for over five months. In other species, the durations of the two phenophases were different. For example, flowers last longer than fruits in *G. sepium* and *P. rubra*, whilst in *A. adstringens*, *C. coriaria*, and *H. sclerocarpum*, the opposite was true, with a short flowering and an intermediate fruiting. All species classified as supra-annual retained their flowers and fruits for short periods (mean \pm SD: 0.5 ± 0.5 months).

Table 3
Results of generalized linear models constructed to assess the relationship of flowering and fruiting with climatic variables for 14 Seasonally Dry Tropical Forest tree species. Coefficients of discrimination (D) for the logistic regression models are given for each phenophase; β coefficients for precipitation and photoperiod are given in the upper and lower row of each model, respectively.

Species	Phenophase	D	β	Z
<i>Amphipterygium adstringens</i>	Flowering	0.13	0.002 6.281	2.57** 11.25***
	Fruiting	0.06	0.001 -0.835	5.80*** -16.70***
<i>Brosimum alicastrum</i>	Flowering	0.03	0.006 0.364	10.21*** 2.26 ^{n.s.}
	Fruiting	0.04	-0.003 -1.406	-2.40** -9.70***
<i>Bursera fragrantissima</i>	Flowering	0.07	-0.004 2.048	-5.24*** 13.08***
	Fruiting	0.01	0.003 1.070	4.02*** 5.80***
<i>Caesalpinia coriaria</i>	Flowering	0.13	0.003 -0.922	7.33*** -12.13***
	Fruiting	0.06	-0.628 -0.010	-8.70*** -7.40***
<i>Caesalpinia platyloba</i>	Flowering	0.06	-0.011 2.859	-8.83*** 11.30***
	Fruiting	0.04	-0.003 0.977	-8.50*** 14.30***
<i>Cordia elaeagnoides</i>	Flowering	0.06	0.001 -1.246	26.30*** -4.67***
	Fruiting	0.05	0.006 -1.365	12.27*** -23.95***
<i>Eysendharthia polystachya</i>	Flowering	0.006	0.001 0.857	0.98 ^{n.s.} 4.50***
	Fruiting	-	- -	- -
<i>Gliricidia sepium</i>	Flowering	0.006	-0.019 -1.594	-6.70*** -6.40***
	Fruiting	0.03	-0.041 -0.825	-11.35*** -18.76***
<i>Guazuma ulmifolia</i>	Flowering	0.05	-0.009 1.520	-11.69*** 15.50***
	Fruiting	0.004	-0.004 0.541	-3.60*** 3.70***
<i>Handroanthus impetiginosus</i>	Flowering	0.006	0.005 -0.303	7.51*** -1.84 ^{n.s.}
	Fruiting	0.02	0.028 -1.375	-5.50*** 6.30***
<i>Heteroforum sclerocarpum</i>	Flowering	0.17	0.005 -0.303	-13.69*** 14.11***
	Fruiting	0.02	-0.028 1.375	-3.02** -7.20***
<i>Licania arborea</i>	Flowering	0.06	-0.005 1.984	-2.57** -9.64***
	Fruiting	0.007	-0.030 1.800	-3.40*** -4.30***
<i>Plumeria rubra</i>	Flowering	0.05	-0.009 3.404	-17.11*** 28.59***
	Fruiting	0.03	-0.006 -0.644	-6.20*** -6.90***
<i>Swietenia humilis</i>	Flowering	0.05	-0.130 0.745	-5.21*** 6.16***
	Fruiting	0.008	-0.011 0.403	-5.05*** 2.40**

n.s. - not significant.

** $P < 0.01$.

*** $P < 0.001$.

3.1.4. Seasonality

The reproductive events of the study species occurred mostly in the dry season; however, the statistical analysis of seasonality did not show significant results for the flowering of any species, even though some had a significant mean α in one year (Table 2). For example, *A. adstringens*, *B. alicastrum*, *G. ulmifolia* and *E. polystachya*

flowered in the rainy season, between June and August, while other species like *L. arborea* and *S. humilis* had flowers in the dry season (March-May).

Conversely, fruiting seasonality was significant in the five study years for *C. platyloba*, *C. coriaria*, *C. elaeagnoides* and *H. sclerocarpum*. For the former species, mean angle occurred between April

and May (one year in February), and for the latter three species it did so between February and April. Fruits of *G. sepium* and *P. rubra* were also observed in this latter period, but seasonality was significant in four out of five years (Table 2). As expected, those species that retained their reproductive structures for a long time did not present a significant seasonality, as exemplified by *C. elaeagnoides*.

3.2. Relation between reproductive phenology and climatic variables

The signs of the relationships between phenophases and environmental factors showed complex patterns across species (Table 3). In some species, flowering and fruiting showed a similar relationship (i.e. positive or negative) with precipitation, and the same was true for photoperiod. This situation is exemplified by *G. ulmifolia* and *S. humilis*, whose two phenophases were negatively related with precipitation, but positively with photoperiod (dry season, March to April), and by *G. sepium* and *L. arborea*, for which flowering and fruiting were negatively related with the two environmental factors. In other cases, one phenophase displayed contrasting relationships with precipitation and photoperiod, while the other showed similar relationships. For example, the flowering of *A. adstringens* was positively related both with rain and photoperiod (rainy season, May to July), whilst fruiting was positively related with the former factor but negatively with the latter. Also, the fruiting of *B. fragrantissima* was positively related with both environmental variables, whereas its flowering had contrasting relationships with them.

Finally, some species stood out from these patterns, as their flowering was significantly related with one environmental variable but not with the other. For example, in *B. alicastrum* and *H. impetiginosus* flowering was positively related with precipitation only, whereas in *E. polystachia*, a species for which no fruiting was observed throughout the five year monitoring period, flowering was unrelated with rainfall but positively related with photoperiod (Table 3).

4. Discussion

4.1. Reproductive phenological strategies and climatic clues

The flowering and fruiting of all species concentrated strongly either in the early (October–November) or the late (February–March) dry season. Overall, both phenophases had a low intensity (< 25%), a short duration (< 2 months), were asynchronous and had

an annual frequency. This general pattern largely coincides with reports for other SDTF species (e.g., Bullock and Solís-Magallanes, 1990; Borchert et al., 2004; Valdez-Hernández et al., 2010). Yet, the specific responses or phenological strategies to climatic seasonality during the year diverged, with the predominance of dry season phenological strategy, which includes the species reproducing exclusively during the dry season (Table 4; October–March). That strategy indicates a clear adaptation of those STDF trees to the strong precipitation seasonality, and it has been observed for other tropical dry forests (Singh and Kushwaha, 2005). Species presenting this strategy may remain dormant until leaf shedding occurs and the trunk rehydrates, allowing flower anthesis and fruit maturation (Borchert, 2000). Species in this study conforming to the above strategy (e.g., *A. adstringens*, *B. alicastrum*, *C. elaeagnoides* and *C. platyloba*) show a fruiting peak in the early dry season (October–November), but their fruits stayed on the trees for over five months, which resulted in the lack of statistically significant seasonality. The second most common phenological strategy grouped five species flowering in the rainy season (June–August) and fruiting in the dry season (September–November). Only one species presented the third phenological strategy, flowering and bearing fruits exclusively during the wet season (June–September), indicating a sensitivity to the dry season environmental constraints. Species with this latter strategy, in our study represented by *B. fragrantissima*, respond rapidly to increasing rainfall, usually have a single, short (< 2 months) flowering event each year; flower buds may mature quickly, and fruits are produced at the end of the same season, when dispersers abound (July–September; van Schaik et al., 1993). Therefore, phenological patterns of these STDF tree species are strongly related with precipitation seasonality, and thus deviations in the starting dates and intensity of the reproductive phenophases may be observed in response to large inter-annual variation in precipitation.

For those species that began to flower during the dry season, photoperiod may be the trigger of the reproductive activity, as they can either uptake soil water through a deep root system, or use water previously stored in low wood density trunks (Borchert and Rivera, 2001; Borchert et al., 2004; Rivera et al., 2002). Species displaying this dry season phenological strategy tend to flower briefly (< 2 months), two to three months after the end of the rains when photoperiod becomes shorter (Fall, November–December) like *G. sepium* and *C. coriaria*, or several weeks before the onset of the wet period, when photoperiod is longer (Spring, March–April), like *H. sclerocarpum*, *L. arborea*, *P. rubra* and *S. humilis*. When

Table 4

Monthly mean values of the intensity index of fruiting during a five year period, of 14 species from Seasonally Dry Tropical Forest with forestry potential (Michoacán state, Mexico). Bold values indicate the period in which it is recommended to collect their seeds according to their phenological patterns.

Phenological pattern/Species	January	February	March	April	May	June	July	August	September	October	November	December
<i>Flowering and fruiting in the rainy season</i>												
<i>Bursera fragrantissima</i>	0	0	2.6	0	1	0	7.2	7.8	2.8	0	0	0
<i>Flowering in rains, fruiting in drought</i>												
<i>Amphipterygium adstringens</i>	38	32.5	24.4	14.4	6	0.8	10	34	47.6	48.4	38	19.2
<i>Brosimum alicastrum</i>	0.8	0.7	0.5	3.2	1.6	0.3	0	0.5	0.8	3.2	31.2	5.9
<i>Cordia elaeagnoides</i>	54.8	53.5	31.6	22	10.8	2	0	0	10	64	62.8	46.4
<i>Caesalpinia platyloba</i>	19.2	14	10	8.4	3.6	0.8	6.8	16.4	16.8	18.4	19.2	20.8
<i>Flowering and fruiting in the dry season</i>												
<i>Gliricidia sepium</i>	0	4.5	14.4	9.2	0.4	0	0	0	0	0	0	0.8
<i>Caesalpinia coriaria</i>	26.8	30.5	15.6	6.8	4	0.4	1.6	0.4	0.4	0.8	2.8	10
<i>Heterofoflum sclerocarpum</i>	13.6	15.5	16.4	12.8	7.6	1.6	0	3.6	12.4	14	13.2	12
<i>Licania arborea</i>	0	0	1.1	1.7	1.1	0	0	0	0	0	0	0
<i>Plumeria rubra</i>	13.2	16.5	14.4	6	1.6	0	0.4	0	3.6	7.6	6.4	8
<i>Swietenia humilis</i>	0	5	7	5	0	0	0	0	0	0	0	0
<i>Uncertain pattern</i>												
<i>Eysendharthia polystachya</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Guazuma ulmifolia</i>	1.2	3.5	4	7.6	2	0.4	2	0.8	0.8	0.8	0.4	0.4
<i>Handroanthus impetiginosus</i>	0.4	0	2	4	3.6	0	0.4	0	0	0.4	0	1.2

flowering occurs in the middle of the dry season, fruit availability will peak shortly after (January–March). Conversely, if species bloom in the late dry season, they will initiate fruit production two–three months later, and fruits will remain in the trees for a variable time (3–9 months), which ensures that their seeds will be ready for dispersal just before the next rainy season (April–May). As photoperiod fluctuations are constant from year to year, the reproductive phenological patterns of these species should display small inter-annual variations.

Admittedly, the ability of the logistic models to efficiently discriminate failures and successes (i.e., presence or absence of reproductive structures) in our study species was modest. Although this result could imply that the environmental factors play a relatively minor role in the timing of phenological events, this is more likely due to the reduction of the observed phenological variability to a binary variable for this analysis. Yet, the importance of this result should not be disregarded, considering that the large majority of phenological studies comprising many species over long periods of time produce this kind of information.

4.2. Reproductive phenology asynchrony

Due to the large inter-annual variation in precipitation in the seasonally dry tropics, species with reproductive cycle responding to increasing water availability may have a more asynchronic phenology, compared with the constancy of species whose reproduction is triggered by photoperiod (Borchert et al., 2005; Singh and Kushwaha, 2006). Interestingly, our findings disagree with these generalizations: regardless of their phenological pattern, all species but one (*C. elaeagnoides*) were highly asynchronic in their flowering and fruiting. This suggests that despite strong environmental clues that may trigger their reproduction, morphological and physiological intra-specific variability may produce differential responses among individuals to micro environmental conditions (Holbrook et al., 1995; Singh and Kushwaha, 2005; van Schaik et al., 1993). The synchrony index used in this study takes into account both the degree of overlap between different phenophases and their intensity; thus, a high synchrony requires the phenophase peak in a given individual to coincide with the peaks of all its conspecifics (Freitas and Bolmgren, 2008). As the reproductive intensity recorded by us was generally low, this also resulted in low synchrony.

4.3. Seed collection strategies and phenological patterns

In SDTFs, plant propagation in rustic nurseries is confined to the rainy season. The relevance of a good seed collection schedule for the proper functioning of the nurseries resides thereby, as it ensures a timely seed supply (Blakesley et al., 2002; Böhringer et al., 2003). Seed collection planning requires precise knowledge of phenological patterns, as this allows deciding the time of the year when it is more likely to find mature fruits for the focal species, and helps understand the close relationship between reproductive cycles of plants and the typically changing climatic conditions in dry forest regions (Buisson et al., 2016; Morellato et al., 2016). Regrettably, phenology-informed seed collecting agendas are often constructed based on short-term studies in which different phenological attributes are not evaluated quantitatively (Buisson et al., 2016). A major drawback of this approach is that it results in inflexible collecting schemes that prevent adapting to the intrinsic inter-annual phenological variability. Our study exemplifies this situation: in the first monitoring year a high-intensity, three day-long rainfall event took place in the middle of February, a typically dry month, which strongly modified the usual reproductive pattern of species that respond rapidly to water inputs. Consequently, in that year flowering began early and it was

followed by flower bud abortion due to insufficient water in subsequent months. Our approach provided essential elements to translate the observed phenological patterns into adaptive management plans.

For species that concentrate their reproductive cycle in the rainy season one may be confident that fruit availability will be high in July and August. However, because flowering and fruiting in these species tend to be very short (usually < 1 month), frequent monitoring of their trees (at least fortnightly) will increase the probability to find fruits for seed collection. The trade-offs related to frequency of observation and sample sizes have been discussed by Morellato et al. (2010) and support our findings. In our study, *B. fragrantissima* was the only species in this situation: in 2011 we failed to record flowers and fruits, probably due to an insufficient temporal resolution in the monitoring schedule rather than because of a supra-annual pattern in its reproductive cycle. Species that flower in the rainy season represent a contrasting situation; many of them bore immature fruits already in September, and they became mature one or two months later, in the early dry season. For these species it would be advisable to collect their seeds at this time, regardless of how long their fruits stay on the trees, given the considerable reductions in seed viability reported after this period (Fenner and Thompson, 2004).

The flowering and fruiting of any individual plant are not independent events: the onset of the flowering largely determines the timing of fruiting (Primack, 1987; Singh and Kushwaha, 2005). For those species that display any of the first two phenological strategies described here, recording flower initiation in any given year is very relevant, as one may forecast one or two months ahead of time when seeds will be available. Likewise, for species flowering and fruiting exclusively in the dry season, either because their reproductive cycle responds to a decreasing or increasing photoperiod, we recommend to collect their seeds in February and March (Table 4).

When planning seed collection one must consider other relevant issues in addition to the time schedule of this activity. For example, it is also necessary to know the sexual system of target species; for dioecious species one should select individuals to be monitored carefully to prevent the inclusion of male trees only. Information on the spatial distribution and abundance patterns of focal species is also important: collecting seeds of rare species that are widely spread spatially will have very different logistic requirements compared to abundant species or those having clumped spatial patterns (Buisson et al., 2016; Morellato et al., 2016).

To close, we emphasize that the success of a long-term phenological study, like the one presented here, largely depends on the coordinated participation of the various social actors involved in seed management of native species, including local communities, government agencies, private initiatives and the academia. In our experience, the implementation of the community-based monitoring (CBM) program allowed local stakeholders to become familiar with the underlying causes of the large variability in the observed phenological patterns, and to acquire basic abilities that will allow them to conduct an adaptive management of seeds of native species in this highly dynamic system. The CBM represents a prime example of the citizen science approach (Burgos et al., 2013; Dickinson et al., 2010; Kobori et al., 2016), which will allow the community to use wisely and in a more sustainable way the natural resources they have traditionally extracted from the STDF (Balvanera et al., 2011). Ideally, our study will serve to stimulate citizen science in the tropics, as this approach would offer important avenues for future studies in phenology and conservation science, as well as in education and management programs (Buisson et al., 2016; Mayer, 2010; Morellato et al., 2016; Scheffinger and Templ, 2016).

5. Conclusions

Long-term phenological studies that include qualitative descriptions of population-level phenological attributes provide valuable information needed to understand both the inter-annual and interspecific variation implicit in the phenological patterns of tree species. Understanding this variation is critical for the design of flexible seed collection strategies that can adapt to the intrinsic variations of plants' life cycles, and thus to ensure a timely and permanent provision of seed to multiple programs aimed at the propagation of native species of forestry interest.

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Appendix A

See Table A1.

Table A1

Total number of individuals of 14 tree species recorded within the study area in Churumuco, Michoacán state, Mexico. Sites (m): Low (230–478), Medium (479–726) and High (727–974).

Species	Low	Medium	High	Total
<i>Amphipterygium adstringens</i>	3	38	45	86
<i>Brosimum alicastrum</i>	–	16	12	28
<i>Bursera fragrantissima</i>	–	–	50	50
<i>Caesalpinia coriaria</i>	10	1	–	11
<i>Caesalpinia platyloba</i>	8	32	–	40
<i>Cordia elaeagnoides</i>	42	49	20	111
<i>Eysenhardtia polystachya</i>	–	–	28	28
<i>Gliricidia sepium</i>	40	19	2	61
<i>Guazuma ulmifolia</i>	2	5	56	63
<i>Handroanthus impetiginosus</i>	19	32	4	55
<i>Heteroeflorum sclerocarpum</i>	18	31	–	49
<i>Licania arborea</i>	2	3	–	5
<i>Plumeria rubra</i>	–	37	–	37
<i>Swietenia humilis</i>	–	1	10	11
Total	144	264	227	635

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