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Reproductive Phenology and Seed Germination in Eight Tree Species From a Seasonally Dry Tropical Forest of Morelos, Mexico: Implications for Community-Oriented Restoration and Conservation

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Abstract

With the aim of providing information for ecological restoration programs, we studied reproductive phenology and seed germination of eight species from the tropical dry forest of Morelos, Mexico. With the participation of students from the local junior high school, we monitored monthly, over one year, the production of flowers and immature and mature fruits for each species. We estimated intensity, duration, seasonality, and synchrony for each fruiting phenophase and flowering duration. Germination tests were undertaken in a germination chamber (18°C–32°C) and under the environmental conditions at the local school. We applied specific pregermination treatments for each species. Two distinct peaks of mature fruit production were identified: one at the beginning and the other in the middle of the dry season. Fructification seasonality was significant in most cases. Germination was relatively high in three legumes and particularly low in two *Bursera* species. Four species responded to the germination environments, and differences among pregermination treatments were significant in most cases. Knowledge on fruiting patterns and seed viability and germination will allow adequate decision-making for seed collection and plant propagation of the study species. Student participation increased their interest and knowledge on local environmental problems and solutions.

Keywords

Burseraceae, environmental education, Leguminosae, propagation, social participation

Introduction

The transformation of seasonally dry tropical forests (SDTF) into crop fields or cattle pastures has proceeded at alarmingly high rates. It has been estimated that dry forests of Latin America experienced a loss of 12% of its area between 1980 and 2000 (Miles et al., 2006). Mexico hosts a significant share of the SDTF of the Americas (38%, ca. 197,446 km²; Portillo-Quintero & Sánchez-Azofeifa, 2010), mostly along the Southern Sierra Madre slopes facing the Pacific Ocean and the Balsas River Basin (Becerra, 2005; Rzedowski, 1978). Generally, when soil conditions become unfavorable, crop fields are abandoned and new pastures for cattle production are established, which usually have low yields (Gardner et al., 2009; Trejo & Dirzo, 2000).

In addition, much of the remaining old-growth forest is subjected to multiple disturbances and thus increasingly altered. This situation is aggravated by a poor

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representation of SDTF in natural protected areas (Meave, Flores-Rodríguez, Pérez-García, & Romero-Romero, 2012; Miles et al., 2006). In an attempt to face these problems, both government agencies, such as CONAFOR (the Mexican National Forest Commission), and nongovernmental organizations have fostered actions aimed at the recovery of SDTF by establishing rural nurseries and implementing reforestation programs. Regrettably, the diversity of species propagated in government-managed nurseries and used in reforestation programs is very low (Bonfil & Trejo, 2010; Guerrero, 2002). Moreover, inadequate species for the local conditions are often used, partly due to an insufficient knowledge of the native flora and its spatial and ecological distribution and the lack of efficient propagation methods. Thus, more complete information on the phenology and germination requirements of native species, along with sound criteria (both ecological and social) for their proper selection, may provide strong support to successful ecological restoration projects (Arteaga, 2007; Knowles & Parrotta, 1995), which improve the conservation value of transformed areas.

Phenology is defined as the study of vegetative and reproductive phases or periodic activities in the life cycle of plants, along with their temporal variation over the year (Nanda, Suresh, & Krishnamurthy, 2014; Williams-Linera & Meave, 2002). The systematic assessment of phenological events enables us to ascertain patterns in the production timing of plant structures. This information allows the development of fruit collecting strategies, which may increase both the amount and the quality of seeds for plant propagation in nurseries, and species diversity in forest plantations and restoration projects (Luna-Nieves, Meave, Cerdeira Morellato, & Ibarra-Manríquez, 2017; Ochoa-Gaona, Pérez Hernández, & De Jong, 2008).

Despite the relative scarcity of phenological knowledge for SDTF plants, the existing studies describe general patterns in these ecosystems and explore some factors that may act as the main triggers of phenological events. Given the strong rainfall seasonality, water availability is thought to be the most important driver of phenological behavior (Borchert, 1994; Lugo & Murphy, 1986). Most plants normally shed their leaves early in the dry season, whereas leaf flushing coincides mostly with the onset of the rains; moreover, many species flower and bear fruit in the dry season, which appears to be related to activity peaks of pollinators and dispersers (Bullock & Solís-Magallanes, 1990; Nunes, Da Luz, & De Lima Braga, 2012). However, water availability is not the only driver of phenological rhythms, as these may also be affected by other environmental factors such as temperature and photoperiod, and even by phylogeny (Bullock & Solís-Magallanes, 1990; Davies et al., 2013; Lobo et al., 2003).

The implementation of successful reforestation programs relies primarily on an adequate fruit and seed supply. To develop efficient fruit and seed collecting strategies, not only the investigation of the reproductive phenology of focal species is crucial, but also the recognition of the interest of local stakeholders in the propagation of native species adapted to their habitats (Buisson, Alvarado, Le Stradic, & Morellato, 2016; Luna-Nieves et al., 2017). Thus, the involvement of local inhabitants in knowledge acquisition processes should be encouraged, so that they are able to actively participate in managing their resources, rather than being mere spectators. In this context, environmental education represents an important tool to strengthen both the research and the implementation of conservation and restoration actions (Castillo, García-Ruvalcaba, & Martínez, 2002; Park, 1999). This kind of participatory research has already been implemented in some cases, notably in Bella Vista, Colombia, where young students joined a participative research program, in which the phenology, propagation, and regeneration of native tree species of local interest were studied (Calle, Murgueitio, Giraldo, Giraldo, & Giraldo, 2017).

The goal of this study was twofold. First, we aimed at advancing the knowledge on the reproductive phenology and seed germination patterns of eight SDTF tree species. Second, by engaging young students from a local junior high school in the study, through an environmental education program, we aimed at increasing their capabilities—in terms of data collection and analysis—to produce the necessary knowledge for a better management of their natural resources in the future.

Methods

Study Site and Species Selection

This study was conducted in Amatlán de Quetzalcóatl (hereafter Amatlán), Morelos State, southern Mexico (18°59'58.8"–18°55'33.61" N, 99°00'40.35"–99°03'21.75" W; Figure 1). This community's territory is ca. 2,600 ha and covers a broad elevational gradient, from 1,250 to 2,300 m asl, along which several vegetation types occur. Seasonally dry tropical forest is found at the foothills, where dominance corresponds to legumes of the genera *Lysiloma*, *Erythrina*, *Acacia*, and *Leucaena*, intermixed with individuals of *Bursera*, *Ipomoea*, *Ceiba*, *Ficus*, *Plumeria*, and *Dodonaea* (Vega-Guzmán, López-García, Delgado, & De Lourdes, 2008). At higher elevations, several temperate forests occur, mostly comprising oak, pine, and pine-oak forests.

We selected eight native tree species based on their local importance and people's preferences, obtained from interviews (Table 1). In January 2014, we marked between five and eight reproductive individuals of each

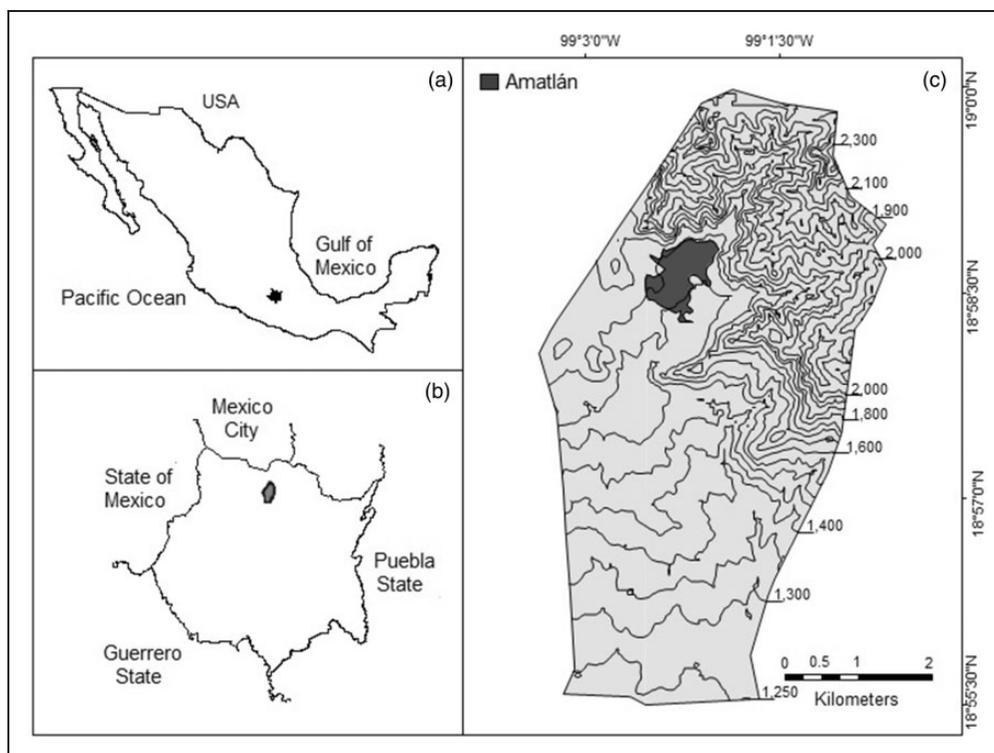


Figure 1. Study site: (a) Mexico, (b) Morelos state, and (c) territory of the community of Amatlán de Quetzalcóatl.

Table 1. Study Species of the Seasonally Dry Tropical Forest of Amatlán, Morelos, Mexico.

Family/species	Sexual system	N	Seed viability (%)	Environment	Ns	Germination (proportion)
Burseraceae						
<i>Bursera bipinnata</i> (DC.) Engl.	D	6	50.8	HS	60	0.01
				GC	60	0.01
<i>Bursera copallifera</i> (DC.) Bullock	D	8	94.8	HS	60	0.18
				GC	60	0.01
<i>Bursera fagaroides</i> var. <i>elongata</i> McVaugh & Rzed.	D	5	62.0	HS	24	0.06
				GC	38	0.38
<i>Bursera glabrifolia</i> (Kunth) Engl.	D	7	70.4	HS	60	0.01
				GC	60	0.01
Leguminosae						
<i>Eysenhardtia polystachya</i> (Ortega) Sarg.	H	5	82.7	HS	100	0.29
				GC	100	0.40
<i>Leucaena esculenta</i> Benth.	H	5	95.4	HS	60	0.50
				GC	80	0.47
<i>Leucaena macrophylla</i> Benth.	H	5	95.4	HS	60	0.54
				GC	80	0.49
Malvaceae						
<i>Guazuma ulmifolia</i> Lam.	H	5	92.0	HS	90	0.33
				GC	120	0.03

Note. D = dioecious; H = hermaphrodite; N = number of trees surveyed; Ns = number of seeds used in germination tests; HS = high school classroom; GC = germination chamber.

species, with a diameter at breast height ≥ 10 cm, based on their abundances. Selected trees had a healthy appearance and were separated at least by a distance of 50 m to minimize genetic relatedness (Fournier & Charpentier, 1975; Luna-Nieves et al., 2017).

Phenological Observations and Data Analysis

In the selected trees, the production of flowers and immature and mature fruits was monitored monthly over 1 year (Figure 2). Flowering was recorded as a binary variable (presence–absence), regardless of their developmental stage and abundances. In contrast, fruiting was recorded by counting the number of fruits present in one quarter of the tree's crown, which allowed estimating the total number of fruits in the entire crown by extrapolation. In counting fruits, we distinguished between immature and mature fruits, based on the changes in color, size, and texture.

We estimated the following traits for each fruiting phenophase (i.e., mature and immature fruits): intensity, duration, seasonality, and synchrony. In turn, for flowering, we only estimated the duration. The calculation of intensity was based on the count of fruits in the crown of each individual at each observation. Upon completion of the study period, we identified which individual had the largest number of fruits in any given month, and set this number to represent a 100% intensity. We then calculated X_i values for each individual/observation

combination using the following categories: 0 (absent), 1 (1%–10%), 2 (11%–25%), 3 (26%–50%), 4 (51%–75%), and 5 (76%–100%; Herrerías-Diego, Quesada, & Lobo, 2006). Fruiting intensity was assessed for each species in each month using Fournier's Index (Fournier, 1974):

$$FI = \frac{\sum_i^n X_i(100)}{(m)(n)}$$

where X_i is the intensity category in a given period for the i th individual, m is the maximum value of the categorical intensity scale (5), and n is the number of trees tagged of each species (Table 1). Mean values of the index were transformed into one of the three categories: low ($\leq 20\%$), medium (20%–50%), or high ($> 50\%$) intensity.

Phenophase duration was assessed through the mean ($\pm SD$) of the number of months in which flowers or immature and mature fruits were observed. Mean duration was classified as short (< 2 months), intermediate (2–5 months), or extended (> 5 months) (Newstrom, Frankie, & Baker, 1994). In turn, assessment of seasonality required circular statistics, in order to test the null hypothesis that fruit production was evenly distributed around the year (Morellato, Alberti, & Hudson, 2010); this analysis was performed with Oriana software version 4.0 (Kovach, 2011).

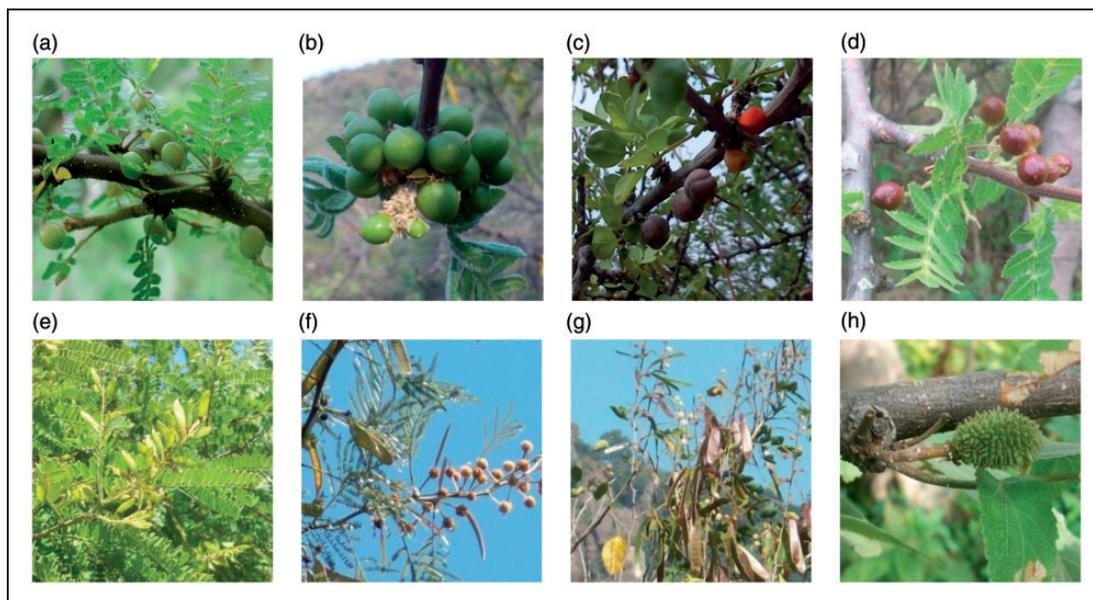


Figure 2. Reproductive structures of the study species: (a) *Bursera bipinnata*, (b) *Bursera copallifera*, (c) *Bursera fagaroides*, (d) *Bursera glabrifolia*, (e) *Eysenhardtia polystachya*, (f) *Leucaena esculenta*, (g) *Leucaena macrophylla*, and (h) *Guazuma ulmifolia*. Image credit: A. Núñez-Cruz and students.

Phenophase synchrony between conspecific individuals was assessed with the Synchrony Index (S) (Freitas & Bolmgren, 2008):

$$S = \sum \frac{d_i}{N}$$

and

$$d_i = \frac{1}{T_i} \frac{1}{N-1} \sum_{j=1}^N \sum_{t=1}^T \sqrt{f_{i,t} f_{j,t}}, \quad j \neq i$$

where d_i is the synchrony level of individual i in relation to the population of j sampled individuals, f is the relative value of the phenophase intensity (range: 0 to 1), T_i is the number of months in which the reproductive structure was observed in each individual, N is the total number of individuals studied in the population, t is a month of the year, and T is the number of months in which the reproductive structure was present in the population.

We conducted Pearson product-moment correlations to assess whether fruiting intensity of each species was related to two climatic variables (precipitation and temperature) obtained from the nearest meteorological station (Tepoztlán, Morelos).

Fruit and Seed Collection, Viability and Germination Tests

We collected mature fruits and extracted their seeds from 5 to 10 healthy trees per species (Cornelissen et al., 2003). Seeds of *Bursera* species are surrounded by their hard pericarps, and these propagules were used for the experiments. Preliminary viability tests for each species were based on the floatation method (Tsuyuzaki, 1991). Next, we conducted germination tests in two contrasting environments: (a) under controlled conditions, in a germination chamber with fluctuating temperature (18°C–32°C), which has been shown to increase germination (Bonfil-Sanders, Cajero-Lázaro, & Evans, 2008; Fenner & Thompson, 2005); and (b) under the environmental conditions naturally occurring at the site, in a classroom at the local junior high school (see later).

To maximize germination, we applied specific pregermination treatments to the seeds of each species, based on literature reports (Bonfil-Sanders et al., 2008; Cervantes, López, Salas, & Hernández, 2001; Cervantes & Sotelo, 2002; González & Camacho, 2000; González & Mendoza, 2008; Hernández-Cuevas, Santiago-Martínez, & Cuatlal-Cuahutencos, 2011; Muñoz, Sánchez, & Almaguer, 2004): (a) soaking in water during 24 hr, (b) soaking in water during 48 hr, (c) soaking in water during 48 hr with a subsequent 12-hr drying period at room temperature, (d) soaking in hot water for 2 min, (e) soaking in

hot water for 2 min with a subsequent 24-hr period of soaking at room temperature, (f) mechanical scarification (sanding the hard endocarp or seed coat), and (g) control (i.e., no treatment). Seeds were placed in PET transparent boxes filled with siliceous sand and rotated periodically in the germination spaces. The number of seeds used per species varied according to their availability (Table 1).

Results were analyzed through two-way analyses of variance (ANOVAs) to assess the effects of germination environment (i.e., germination chamber vs. school classroom) and treatments (which varied depending on the species). The proportions of germinated seeds in each box (replicate) were arcsin transformed to fulfill ANOVA requirements. Post hoc comparisons were carried out with Tukey HSD tests (Zar, 2010). These analyses were made separately for each species with Statistica software version 8.0 (Statsoft, 2007).

Environmental Education

To encourage the interest of the local junior high school students in this research, we held 37 workshops in which all 22 registered students participated. The workshops provided ample opportunity to discuss various topics and to conduct activities that allowed the students to gather, through field work in collaboration with researchers, information on the reproductive phenology, and the propagation of SDTF native species. Finally, they also assisted in data analysis and generated their own final report.

Results

Reproductive Phenology

In species of *Bursera*, two phenological patterns were identified. Three species (*Bursera bipinnata*, *Bursera copallifera*, and *Bursera glabrifolia*) flowered in April to May, whereas fruit development started in early June, with mature fruits occurring in September and especially in October to November, when the intensity of this phenophase peaked (60%–80%; Figure 3(a), (b), and (d)). *Bursera fagaroides* departed notably from this pattern, as it flowered in March to April, but bore immature fruits throughout the year. Fruit maturity started in February, reaching its highest intensity in March (60%); therefore, in this species, the flowering and fruiting phenophases overlapped (Figure 3(c)).

Regarding the legumes, the two *Leucaena* species (*Leucaena macrophylla* and *Leucaena esculenta*) displayed a long flowering period, extending from August to as late as October to November (Figure 3(g) and (h)). Although immature fruits of these two species were already recorded in November, their intensity was highest in late December (almost 100%), while mature fruits were recorded in February and March, with 80% intensity

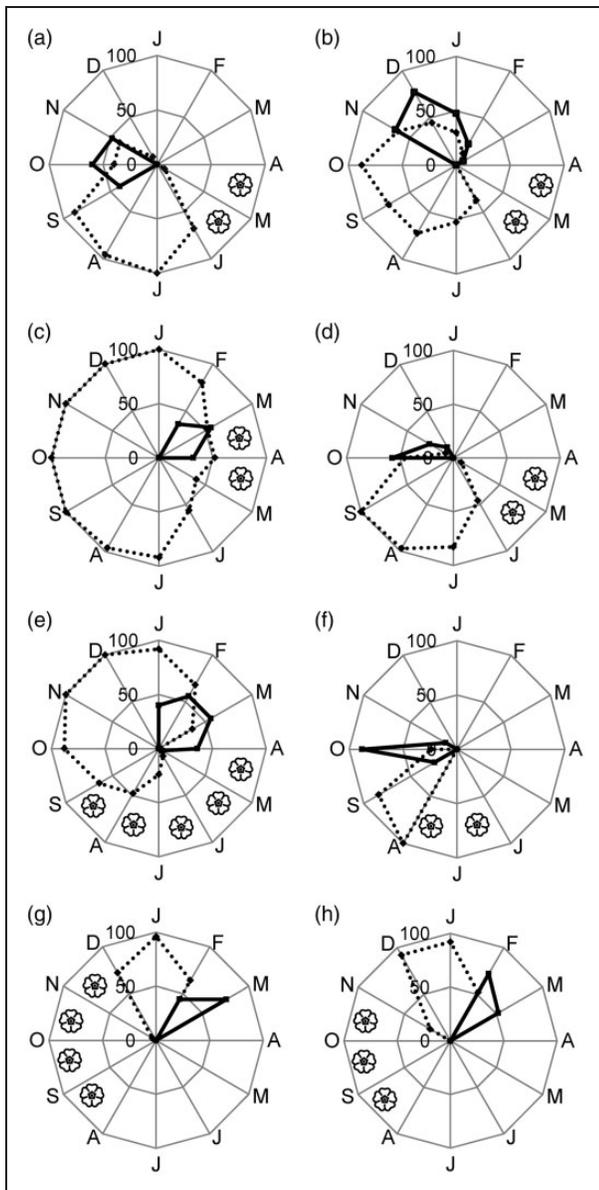


Figure 3. Presence of flowers (flower icon) and mean intensity, according to the Fournier index (percentage), of fruit production: immature (dotted line) and mature (solid line) of eight tree species of the seasonally dry forest of Amatlán, Tepoztlán, and Morelos. The rainy season started at the end of April and finished in early October.

in both months. Interestingly, the other legume, *Eysenhardtia polystachya*, had the shortest reproductive phenology: its flowering took place in June and July, immature fruit production started in August, and mature fruits were observed in September but peaked in October (90%; Figure 3(f)).

Reproductive phenology of *Guazuma ulmifolia* (Malvaceae) was distinct, as it had the longest flowering period (5 months, from April to August). Young fruits appeared in June but reached a high intensity between

October and January (>90%). There were mature fruits from January until the beginning of April, just before the following flowering period (Figure 3(e)).

The length of the flowering period was short in the four *Bursera* species as well as in *E. polystachya*; in the two *Leucaena*, it was intermediate (3–4 months), and in *G. ulmifolia*, it was the longest, as mentioned earlier (Figure 2). The length of the immature fruit phase was extended (>5 months) in the four *Bursera* species and *G. ulmifolia* but intermediate in the three legumes (2–5 months). Again, the four *Bursera* species and *G. ulmifolia* had a similar length of the mature fruit phase (intermediate), but in the legumes, this phenophase was short (Table 2).

Mean intensity of the presence of mature fruits was low in *E. polystachya* and *L. esculenta*. In *L. macrophylla* and three *Bursera* species, the intensity of this phenophase was medium, except for *B. fagaroides* and *G. ulmifolia*, whose respective intensities were high. In turn, the intensity of the occurrence of immature fruits was low in all species (Table 2).

Synchrony in the production of immature fruits was variable in the study species: synchronous events prevailed in five species, very synchronous events characterized two of them (*B. fagaroides* and *E. polystachya*), whereas only *B. copallifera* displayed low synchrony for this phenophase. Regarding mature fruits, low synchrony was the prevailing pattern, as it was observed in seven species, with only *L. macrophylla* producing mature fruits synchronically (Table 2).

Fructification seasonality varied notably among species, and it was significant in all cases but one. Most *Bursera* species and *E. polystachya* bore immature fruits mainly in the rainy season, whereas the two *Leucaena* species and *G. ulmifolia* produced them in the dry season; the only exception to this highly seasonal pattern was *B. fagaroides*, which produced fruits throughout the year. Again, mature fruit production was generally very seasonal: in three species (*B. bipinnata*, *B. glabrifolia*, and *E. polystachya*), they were recorded in the late rainy season, in four of them (the two *Leucaena* species, *G. ulmifolia*, and *B. fagaroides*) during the dry season, while mature fruit production in *B. copallifera* had an intermediate timing (Table 2).

Correlations between intensity of the production of mature and immature fruit and precipitation during the study period were significant and positive only for the mature fruits of *B. bipinnata* ($r=0.58$, $p=.046$) and significant and negative for *G. ulmifolia* ($r=-0.57$, $p=.048$). Correlations for the remaining six species and for all cases of immature fruits were not significant.

Seed Viability and Germination

Seed viability was high (80%) in five species: the two *Leucaena* species (*L. esculenta* and *L. macrophylla*),

Table 2. Duration (in Months, Mean \pm SD), Intensity (Annual Average of Fournier Index), Synchrony (Synchrony Index), and Seasonality in the Production of Immature and Mature Fruits of Eight Tree Species of the Seasonally Dry Tropical Forest of Amatlán, Morelos.

Species	Duration (months)	Intensity (%)	Synchrony	Seasonality		
				Mean angle (α)	(r)	Rayleigh (z)
<i>Bursera bipinnata</i>	E (6.4 \pm 0.9)	M (37.3)	S (0.61)	258° (mid RS)	0.57	10.69*
	I (3.0 \pm 0)	L (12.3)	L (0.43)	300° (late RS)	0.91	12.73*
<i>Bursera copallifera</i>	E (8.2 \pm 1.5)	M (40.0)	L (0.47)	297° (late RS)	0.32	7.03*
	I (4.1 \pm 0.8)	L (18.3)	L (0.48)	352° (early DS)	0.80	21.14*
<i>Bursera fagaroides</i>	E (12.0 \pm 0)	H (80.6)	HS (0.75)	–	–	–
	I (3.0 \pm 0)	L (10.3)	L (0.32)	90° (mid DS)	0.92	12.73*
<i>Bursera glabrifolia</i>	E (5.7 \pm 1.0)	M (32.4)	S (0.62)	257° (mid RS)	0.55	14.46*
	I (2.7 \pm 0.5)	L (7.8)	L (0.41)	324° (late RS)	0.93	14.64*
<i>Eysenhardtia polystachya</i>	I (2.4 \pm 0.5)	L (17.3)	HS (0.75)	262° (mid RS)	0.94	10.63*
	S (1.6 \pm 0.5)	L (10.3)	L (0.60)	291° (late RS)	0.98	6.77*
<i>Leucaena esculenta</i>	I (3.2 \pm 0.4)	L (19.6)	S (0.63)	26° (mid DS)	0.90	12.87*
	S (2.0 \pm 0)	L (10.0)	L (0.47)	79° (mid DS)	0.98	7.67*
<i>Leucaena macrophylla</i>	I (3.6 \pm 0.5)	M (21.5)	S (0.66)	10° (mid DS)	0.86	13.45*
	S (2.0 \pm 0)	L (10.3)	S (0.52)	75° (mid DS)	0.98	9.55*
<i>Guazuma ulmifolia</i>	E (8.0 \pm 0.7)	H (52.3)	S (0.67)	342° (early DS)	0.37	5.472*
	I (4.0 \pm 0.7)	L (16.0)	L (0.36)	76° (mid DS)	0.82	13.57*

Note. Values for immature fruits are shown in the first row and for mature fruits in the second row. Duration: S = short (≤ 2 months); I = intermediate (> 2 and ≤ 5 months); E = extended (> 5 months). Intensity: L = low ($\leq 20\%$); M = medium (20%–50%); H = high ($> 50\%$). Synchrony: L = low (0.25–0.49); S = synchronous (0.50–0.74); HS = highly synchronous (0.75–1). Seasonality: RS = rainy season; DS = dry season; mid RS (August); late RS (September and October); early DS (November–December); mid DS (January–March). A dash (–) indicates the presence of structures throughout the year; an asterisk (*) indicates significant seasonality ($p < .05$).

E. polystachya, *G. ulmifolia*, and *B. copallifera*. In contrast, viability was relatively lower in the remaining three *Bursera* species (*B. bipinnata*, *B. glabrifolia*, and *B. fagaroides*; Table 1). Likewise, germination was relatively high in the three legumes (Table 1), while *Bursera* species showed low germination, which was particularly low in *B. glabrifolia* and *B. bipinnata* (ca. 0.01; Table 1).

Four of the studied species showed different responses to the two germination environments, while the germination of the two *Leucaena* species was indifferent to them. Interestingly, those species with significant differences had contrasting behaviors. *B. copallifera* and *G. ulmifolia* had higher germination under natural conditions (i.e., the school classroom) than in the germination chamber, while in *B. fagaroides* and *E. polystachya*, the opposite was true (Table 3 and Figure 4). In turn, differences among pregermination treatments were significant in all species but one (*E. polystachya*, Table 3, Figure 4(d)). In two species (*B. fagaroides* and *G. ulmifolia*), the interaction between environment and treatment was also significant (Table 3). Germination was highest for the control and soaking treatments in *B. copallifera* and for the control treatment in the germination chamber in *B. fagaroides* (Figure 4(a) and (b)). Only previously soaked seeds of *G. ulmifolia* germinated, with germination being

much higher in the classroom than in the chamber (Figure 4(c)). Unexpectedly, once ungerminated seeds of this species were removed from the germination chamber (40 days after the start of the experiment) and kept under ambient conditions, most of them germinated, reaching a mean value similar to that recorded at the school (0.67). Sanding or soaking seeds increased germination in the two *Leucaena* species (Figure 4(e) and (f)).

Discussion

Seasonality of Reproductive Phenology

The flowering patterns that we recorded are consistent with previous observations that have related phenological events in SDTF to water availability and photoperiod (Borchert, Meyer, Felger, & Porter-Bolland, 2004). Most *Bursera* species flowered very late in the dry season, when day length increases and the first rains occur; this is a common flowering pattern in other SDTF species (Borchert & Rivera, 2001; Bullock & Solís-Magallanes, 1990; Rivera et al., 2002; Singh & Kushwaha, 2006). Only *B. fagaroides* flowered earlier than its congeners. Leguminous species flowered in the rainy season, probably due to the hydration of

Table 3. Results of a Two-Way ANOVA of the Effects of Germination Environment (Germination Chamber vs. High School Classroom) and Pregermination Treatment (Depending on Species) on Seed Germination.

Species	Factor	df	SS	MS	F	p
<i>Bursera copallifera</i>	Environment (E)	1	0.634	0.634	75.124	<.0001
	Treatment (T)	2	0.139	0.069	8.220	.0056
	E × T	2	0.020	0.010	1.178	n.s.
<i>Bursera fagaroides</i>	Environment	1	0.241	0.241	193.210	.0002
	Treatment	1	1.026	1.026	824.329	<.0001
	E × T	1	0.241	0.241	193.210	.0002
<i>Eysenhardtia polystachya</i>	Environment	1	0.104	0.104	5.214	.0316
	Treatment	2	0.052	0.026	1.298	n.s.
	E × T	2	0.111	0.055	2.768	n.s.
<i>Leucaena esculenta</i>	Environment	1	0.007	0.007	0.575	n.s.
	Treatment	2	1.230	0.615	50.759	<.0001
	E × T	2	0.033	0.016	1.344	n.s.
<i>Leucaena macrophylla</i>	Environment	1	0.012	0.012	0.878	n.s.
	Treatment	2	1.281	0.640	45.446	<.0001
	E × T	2	0.019	0.010	0.678	n.s.
<i>Guazuma ulmifolia</i>	Environment	1	0.437	0.437	622.474	<.0001
	Treatment	1	1.229	1.229	1751.380	<.0001
	E × T	1	0.437	0.437	622.474	<.0001

Note. df = degrees of freedom; MS = mean square; n.s. = not significant; SS = sum of squares.

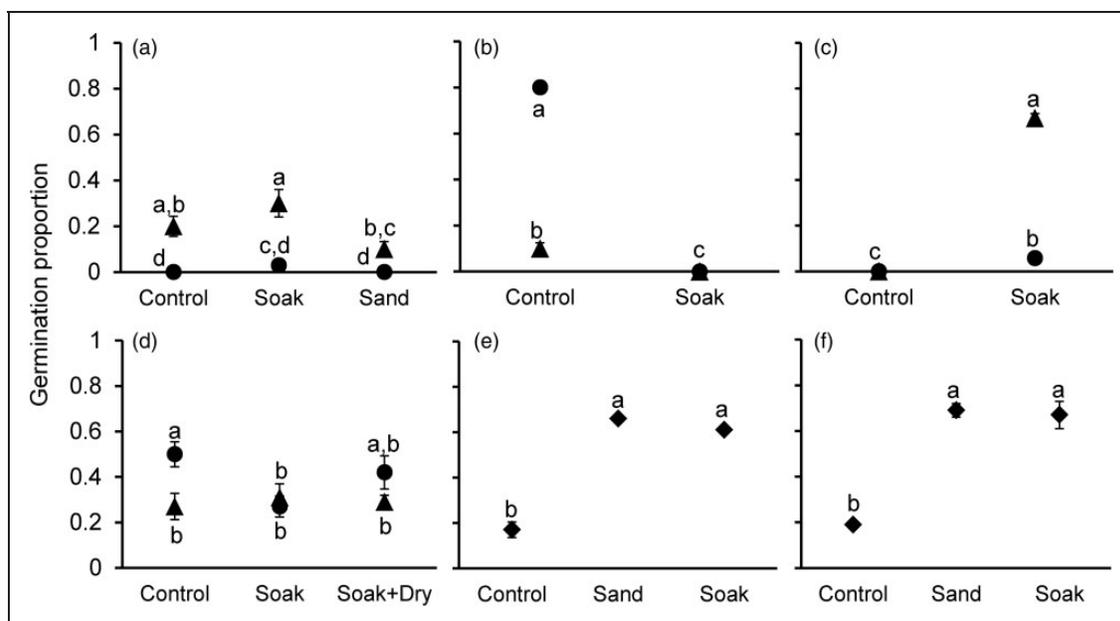


Figure 4. Germination proportions (mean ± SE) in two environments: junior high school classroom (triangles) and germination chamber (circles); diamonds depict mean germination (irrespective of environment) in the two *Leucaena* species. Each species had a specific soaking treatment: cold water for 24 hr (a and b), cold water for 48 hr (d), hot water for 2 min (e and f), hot water for 2 min with a subsequent 24-hr period at room temperature (c) and, 48 hr with a subsequent 12-hr drying period at room temperature (d). Different letters in each species indicate significant differences ($p < .05$). Soak, soaking treatment; Sand, sanding of hard endocarp or seed coat treatment; Control, no germination promoting treatment was applied.

apical meristems, which triggered leaf and flower bud development (Holbrook, Whitbeck, & Mooney, 1995). Regarding flowering length, *G. ulmifolia* stood out among the other study species due to its extended flowering period, which lasted since the first rains through most of the wet season (Figure 3e).

Fruiting in most SDTF species is known to strongly concentrate in the dry season (Bullock & Solís-Magallanes, 1990; Lobo et al., 2003; Luna-Nieves et al., 2017; Singh & Kushwaha, 2006; Valdez-Hernández, López-García, Delgado, & De Lourdes, 2010). We found a slightly different pattern, with two clearly distinct peaks of mature fruit production: one at the end of the rains and in the early dry season (*B. bipinnata*, *B. copalifera*, *B. glabrifolia*, and *E. polystachya*), and the other one in the mid-dry season (i.e., February–March; *B. fagaroides*, *G. ulmifolia*, *L. esculenta*, and *L. macrophylla*). The highly seasonal character of fruit production was evident for all species, with the single exception of *B. fagaroides* immature fruits.

In addition to the key role of climate seasonality, in seasonally dry environments, fruiting patterns are also frequently related to fruit type and dispersal syndrome (Griz & Machado, 2001; Hilje, Calvo-Alvarado, Jiménez-Rodríguez, & Sánchez-Azofeifa, 2015). Species bearing mature fruits during the rainy season usually have animal-dispersed fleshy fruits, which are typically present during a long period, in contrast with species producing mature fruits in the dry season, which tend to have wind-dispersed dry fruits and short fructification periods (Du, Mi, Liu, Chen, & Ma, 2009; Griz & Machado, 2001; Howe & Smallwood, 1982; Opler, Frankie, & Baker, 1980). Most of our findings agree with these patterns: three *Bursera* species—which have drupes with a fleshy pseudoaril that attracts dispersers (mainly birds and ants; Johnson, 1992; Ortiz-Pulido & Rico-Gray, 2006)—had intermediate mature fruit duration, concentrated at the end of the rainy season. These results agree with those of Cecon and Hernández (2009), who found that seed rain of *B. copalifera* in a nearby SDTF concentrates in December to February. In turn, two legumes had a short fructification period in the mid-dry season (Table 2), and the other legume, *E. polystachya*, had a short period of mature fruit production earlier in the year, during the rainy season (Figure 3f). *B. fagaroides* bore mature fruits in the mid-dry season, as did the dry-fruited *G. ulmifolia*. These latter three species exemplify the variability of reproductive phenological patterns among SDTF species.

Most study species had synchronic or even very synchronic patterns in the production of immature fruits. This may have important consequences, as similar patterns have been proposed to reduce the impact of pre-dispersal seed predation (Frankie, Baker, & Opler, 1974; Stiehl-Alves & Martins-Corder 2006), increasing

propagule survival (Augspurger, 1981, 1983; Poulin, Wright, Lefebvre, & Calderón, 1999). Interestingly, synchronicity in mature fruit production was low (Table 2), a pattern that likely acts as a mechanism to reduce competition among seed dispersers (Wheelwright, 1985). Seeds of *B. fagaroides*, *G. ulmifolia*, and the two *Leucaena* species, all of which are released during the dry season, have a shorter postdispersal permanence on the ground than the rest of the study species, thus reducing exposure to seed predators (García, Hobbs, Dos Santos, Flavio, & Rodrigues, 2014; Garwood, 1983; Wright, 1996).

The recognition of fruiting patterns is strategic for making adequate decisions regarding seed collection and native species propagation (Kuaraksa, Elliott, & Hossaert-Mckey, 2012; Luna-Nieves et al., 2017). The phenological indices that we used provided valuable information to identify optimal seed collection periods in this region, which ultimately translates into substantial savings of time and money. We could identify two favorable seed collection periods (when the intensity of mature fruits was >50%, Figure 3): one between October and December and the second in February to March. In this regard, the seasonality index is useful, as it allows identification of the period where mature fruit production concentrates. Besides, the length of the period with mature fruits (short for legumes and intermediate for the various *Bursera* and *G. ulmifolia*) can be used to decide whether it is possible to minimize the length of phenological surveys. It seems possible to concentrate seed collection efforts in legumes, as their mature fruit production is short and synchronous, but the overall low intensity and synchrony observed in the other five species indicates that few trees with many mature fruits may be found at any time, and thus the period for seed collection is longer.

Taxonomic Patterns in Reproductive Phenology

Phenological patterns have been explained mainly by abiotic and biotic factors, but the evolutionary history of a group can also influence the temporal distribution of biological activities (Williams-Linera & Meave, 2002). Some studies have reported similar flowering patterns among taxonomically related species, both at the genus and family levels (Davies et al., 2013; Johnson, 1993; Wright & Calderón, 1995). Such species have inherited common ancestral traits, and these can be either adaptive or not (Harvey & Pagel, 1991). Although we did not conduct a phylogenetic analysis of the study species, our results provide some insight into the relations between taxonomic relatedness and phenology. For one, the two species of *Leucaena* had similar flowering and fruiting patterns to those reported for congeneric species (*Leucaena leucocephala* and *Leucaena lanceolata*; Bullock & Solís-Magallanes, 1990; Chen, Chen, & Jump, 2012;

Ceccon, Sánchez, & Powers, 2015). Notably, *E. polystachya*, the other legume included in the study, displayed a different phenological behavior, with an earlier and shorter flowering period and mature fruit production. Such discrepancy could be related to the Eocene break-up of Fabaceae in three clades (39–59 Ma ago; Lavin, Herendeen, & Wojciechowski, 2005); the genus *Leucaena* is a member of the subfamily Mimosoideae, while *E. polystachya* is located in the subfamily Papilionoideae.

Among *Bursera* species, *B. fagaroides* had a distinctly different phenological behavior, as it flowered earlier than its congeners, while it bore mature and immature fruits for 1 year thereafter. The evolutionary history of this genus may explain again, at least partially, such differences. Studies based on DNA sequencing suggest an old split of this group in two main clades, giving way to the sections *Bursera* and *Bullockia* some 50 Ma ago (De-Nova et al., 2012). Among other traits, the stems of plants belonging to either one of these two groups show important differences. In the case of *Bursera*, stems have a succulent, colored bark that peels off continuously, while plants in *Bullockia* have stems whose rough, grayish, or brownish bark does not peel off (Rzedowski & Kruse, 1979). The succulent stem of *B. fagaroides* stores water, which can trigger flower bud development in the mid-dry season. This flowering pattern has also been reported for *Bursera simaruba*, another member of section *Bursera* (Cortés-Flores, Hernández-Esquível, González-Rodríguez, & Ibarra-Manríquez, 2017; Singh & Kushwaha, 2005). The remaining three *Bursera* species, which flower later in the year, belong to section *Bullockia*, and thus they may depend more strongly on the first rains or on water from deeper soil layers to start flowering. Moreover, even though synchrony in mature fruit production was low in all *Bursera* species, it was higher in those of section *Bullockia* than in *B. fagaroides* (Table 2). This observation coincides with Rzedowski and Kruse (1979), who reported that in some species of *Bullockia* fruit maturation is more rapid and synchronous than in others of section *Bursera* (e.g., *B. fagaroides*, *Bursera longipes*, and *Bursera morelensis*), which bear fruits for longer periods and in any given day a tree has only a few mature fruits.

The examples provided by species belonging to these two families suggest a promissory avenue for future research aimed at establishing a sounder and broader relationship between differences in reproductive phenology and the evolutionary history of particular plant groups.

Seed Germination and Plant Propagation

Not surprisingly, in three *Bursera* species, seed germination was low, especially in *B. bipinnata* and *B. glabrifolia*, in agreement with previous reports on the poor germination success in species of this genus (Andrés-Hernández &

Espinoza-Organista, 2002; Bonfil-Sanders et al., 2008). Only seeds of *B. fagaroides* reached a high germination, but only in the germination chamber, not in the environment of the high school classroom. It is likely that the seeds of these species possess some kind of dormancy that is broken during the period elapsed between seed dispersal and the onset of the rainy season, when conditions are suitable for germination, as shown for other SDTF species (Frankie et al., 1974; Garwood, 1983; Venable & Lawlor, 1980). This period, which may be necessary for dormancy break up, is longer for *B. bipinnata* and *B. glabrifolia* (ca. 6 months), which have mature seeds earlier than for *B. fagaroides* (ca. 2 months). There are reports of both low (Ortiz-Pulido & Rico-Gray, 2006) and high (Suzán-Aspiri et al., 2017) germination in *B. fagaroides*, and this variation may be related to both the degree of embryo maturity/dormancy break up and the occurrence of suitable environmental conditions for germination.

Several pregermination treatments have been tested for a few *Bursera* species without any of them significantly increasing germination, except for cytokinin addition in the seeds of *B. copallifera* (Bonfil-Sanders et al., 2008). Regarding germination environment, however, temperature fluctuation has been shown to increase seed germination, as was the case of *B. fagaroides* but not of *B. copallifera* in this study. Experimental temperature fluctuation in the germination chamber probably simulates better natural field conditions, thus promoting germination in many species (Fenner & Thompson, 2005). Interestingly, in our study, this possibility also seems to apply to *E. polystachya*, the other non-*Bursera* species in our study with this response.

In three of the four species bearing mature fruits during the dry season (*G. ulmifolia*, *L. esculenta*, and *L. macrophylla*), seed germination increased with soaking or mechanical scarification. For the two *Leucaena* species, this finding was expected, since physical dormancy is a well-known phenomenon among legume species from a variety of habitats (Baskin & Baskin, 2014). Physical dormancy also occurred in *G. ulmifolia*, and it is probably broken when water input is sufficiently large to ensure prolonged soaking of the seeds under natural conditions.

Propagation of leguminous trees by seeds is relatively simple, and they have been widely used in soil conservation actions, silvopastoral systems, and ecological restoration of arid and semiarid regions (Hernández-Muciño, Sosa-Montes, & Ceccon, 2015; Murgueitio, Calle, Uribe, Calle, & Solorio, 2011). Similarly, *G. ulmifolia* is a multi-purpose species that thrives in dry habitats and can be used in silvopastoral systems (Wishnie et al., 2007).

Implications for Conservation

In the study area, SDTF is the most disturbed vegetation type, as most economic activities (agriculture and cattle

raising) take place on it. To reverse this situation, government agencies have funded rural nurseries for native tree species production, and these plants are later used in reforestation and restoration programs. In this study, we identified, through interviews with local people, the most relevant native tree species in terms of their local uses, such as edible, medicinal, resin production (copal), and as living fences. Successful management and conservation actions need, as a requisite, to consider the preferences of local stakeholders (Ezebilo, 2013; Moreno-Casasola & Paradowska, 2009). Moreover, the development of an environmental education program with the young students of the local high school allowed us to achieve significant goals. The phenological monitoring and germination trials increased their interest and knowledge on their territory and a variety of native tree species and also improved their abilities to gather and analyze data. They were also able to make a clear written report of their findings, in the form of a booklet that can be used for plant production in the local and nearby nurseries. Undoubtedly, all of these will have a strong positive impact in their future participation in programs related to the management of their natural resources and has increased the community social capital through training of its young members. In a similar study, Calle et al. (2017) found that participation in phenological surveys and restoration activities increased research capacities—such as posing research questions, designing experiments, gathering, analyzing and interpreting data—in young students and fostered values such as respect and appreciation for nature, concentration, and discipline.

Knowledge on propagation of both early and late-successional species is useful for reforestation programs, because plantations that combine them can catalyze natural succession and recover a variety of ecological functions (Knowles & Parrotta, 1995). Among our study plants, both *Leucaena* species are early successional, while *E. polystachya* and *G. ulmifolia* are mid-successional, and all *Bursera* species can be better regarded as late-successional species. The latter are useful for ecological restoration (Bonfil & Trejo, 2010; Gelviz-Gelvez, Pavón, Illoldi-Rangel, & Ballesteros-Barrera, 2015), because they act as resting and feeding places for frugivorous animals, promoting seed deposition and accelerating succession (Quesada et al., 2009). The use of the study species in these programs will make a significant contribution to the biodiversity and conservation value of transformed landscapes in this region.

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