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Seed Longevity of Five Tropical Species From South-Eastern Mexico: Changes in Seed Germination During Storage

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Abstract

To design conservation strategies, the extent of plant richness of tropical forests needs to be characterized in terms of their seed longevity. In this study, we examined the potential seed longevity, that is, storage ex situ, of species from south-eastern Mexico: *Chamaedorea glaucifolia*, *Cymbopetalum baillonii*, *Magnolia mexicana*, *Nectandra coriacea*, and *Ternstroemia tepezapote*. Immediately after collection, seeds were stored at different temperatures ($\leq$23°C). We evaluated seed germination after different storage durations. Seed water content (WC) was determined for each period. Seed desiccation sensitivity was determined as WC_{50}, which is the WC at which the initial seed viability decreases to 50%; further, the time required to reach WC_{50} was also determined. Subsequently, we analyzed the relations between seed functional traits with other morphological and functional traits, along with the weather characteristics of their respective habitat. All of the studied species had short-lived seeds; they exhibited desiccation sensitivity after storage with differences across the species. Additionally, *C. baillonii* exhibited differences in seed desiccation sensitivity across 2 years of seed collection. Interaction was observed between storage time and storage temperature: Seeds exhibited less deterioration at 15°C in *C. glaucifolia* and *C. baillonii* and at 5°C in *M. mexicana* and *N. coriacea*. Seed storage behavior is discussed in this article. Finally, a relationship determined between germination traits, and seed WC, embryo size, endosperm amount, and rain and temperature patterns in the month of seed dispersal explained the limited longevity of the studied species.

Keywords

native plants, seed longevity, storage, seed desiccation sensitivity, tropical forest

Introduction

Plants with short-lived desiccation-sensitive seeds form an important biological group in tropical forests. They account for ~15% to 19% of global plant species richness (Wyse & Dickie, 2017). However, in tropical environments, they constitute ~50% (Tweddle, Dickie, Baskin, & Baskin, 2003). Generally, these seeds are large and have a low seed coat ratio (ratio of endocarp and seed coat mass to dispersal unit mass) and high water content (WC) at dispersal (Vázquez-Yanes & Orozco-Segovia, 1993; Hamilton, Offord, Cuneo, & Deseo, 2013). Further, they maintain a high metabolic rate even after their dispersal from the mother plant (Berjak & Pammenter, 2008), so they generally germinate at a fast rate. These reasons explain their short potential longevity (lifespan under optimal environment storage conditions;

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Vázquez-Yanes & Orozco-Segovia, 1993). Therefore, they are also classified as recalcitrant seeds, or they may be classified as intermediate seeds if they can survive considerable dehydration, but fail to survive conventional subfreezing storage temperature (Hong & Ellis, 1996). Storage difficulties coupled with potential environmental modifications due to climatic change and land use turnover make these species the central concern in terms of the conservation and restoration of tropical forests (O'Brien, Philipson, Tay, & Hector, 2013). Thus, it is necessary to evaluate the potential longevity and degree of seed desiccation sensitivity in tropical species as a first step toward defining their optimal ex situ management and susceptibility to habitat change.

Once short-lived desiccation-sensitive seeds are dispersed, their initial WC begins to decrease. At a certain point, the water deficit of the seeds triggers physiological, structural, and molecular damages at the cell level (Farrant, Berjak, & Pammenter, 1985; Obroucheva, Sinkevich, & Lityagina, 2016). These damages are reflected by a loss of vigor, which is a property that is expressed by the rate and the uniformity of seed germination (Rajjou et al., 2012). In this manner, the desiccation sensitivity of the seed can be identified with the determination of its "critical water content" or WC_{50} (King & Roberts, 1979) as well as the time elapsed to reach this value. The WC_{50} is the WC at which the initial seed viability decreases to 50% (Hill, Edwards, & Franks, 2012). Recalcitrant seeds have a WC_{50} in the range 25% to 20% and intermediate seeds ranged between 10% and 5% (Hong & Ellis, 1996). In comparison, orthodox seeds can reach a $WC < 5\%$ without a reduction of their initial viability (Hong & Ellis, 1996). Conversely, variability in WC_{50} is related to the morphological and physiological traits of seeds (Hill et al., 2012) and with the weather characteristics of the habitat (Dussert et al., 2000; Rodríguez, Orozco-Segovia, Sánchez-Coronado, & Vázquez-Yanes, 2000). Moreover, WC_{50} can vary according to the dehydration rate of seeds. A slow dehydration rate allows seeds to remain in a range of WC that allows germination metabolism to occur, but this causes an accumulation of metabolic and structural damage that increases desiccation sensitivity. Therefore, WC_{50} will be high during a fast dehydration rate (Farrant et al., 1985; Berjak & Pammenter, 2008). During storage, seed dehydration rate is slow compared with the fast dehydration techniques (e.g., using silica gel or an air fan). However, slow drying can provide us information regarding what occurs in the habitat and where slow drying conditions are present (Vázquez-Yanes & Orozco-Segovia, 1994).

The dehydration rate can be modified by external factors, such as relative humidity and temperature (Berjak & Pammenter, 2008). Reduction of the temperature slows down the metabolic activity, prevents germination, and reduces rate of water loss and cell damage of seeds (McDonald, 2004). Nevertheless, the high WC and metabolic activity of short-lived seeds render them sensitive to chilling damage even at temperatures above 0°C, that is, arrest of the enzymatic reactions and structural damage of cell membranes (Tommasi, Paciolla, Concetta de Pinto, & De Gara, 2006). Further, if the temperature drops to 0°C, freezing damage can occur (Hong & Ellis, 1996). Thus, the recommended temperature for storage of tropical recalcitrant seeds is between the optimum for germination and the temperature at which no chilling damage occurs ($\geq$10°C; Hong & Ellis, 1996). Additionally, these seeds can exhibit interannual variability in chilling sensitiveness (Berjak & Pammenter, 2008).

Mexico has tremendous plant diversity, but knowledge regarding the seed biology of most of the wild tropical species is extremely limited (Vázquez-Yanes, Batis-Muñoz, Alcocer-Silva, Gual-Díaz, & Sánchez-Dirzo, 2001). Determination of seed longevity and the desiccation sensitivity of wild species can increase the probability of tropical forest conservation (Hamilton et al., 2013; Wyse & Dickie, 2017) and being able to determine the effects of future climatic changes on the habitat of various species (O'Brien et al., 2013). In our research, we evaluated the seed longevity of five species from tropical forest in south-eastern Mexico. This research concentrates on the following questions: (a) What are the effects of storage time on seed germination? (b) What are the effects of storage temperature on seed longevity? (c) Does the desiccation sensitivity of seeds vary between years of collection? (d) What was the storage behavior of the studied species? (e) How are seed traits related to seed longevity, that is, WC_{50} and the time required to reach WC_{50} and other functional and morphological traits of seeds, in relation to the environmental factors of the habitat of the studied species?

Material and Methods

Seed Collection and Study Site

Fruit collection was done during the dispersal seasons of 2015 and 2016, in two localities with tropical forest, in south-eastern Mexico. One of them was the tropical rain forest at the UNAM Tropical Biology Station, localized in San Andrés Tuxtla (18°34′5″ N, 95°04′26″ W; 155 m asl). The second locality was the transition region between the tropical rain forest and the dry forest in Ocozocoautla, Chiapas, within the confluence area of the Central Depression of Chiapas and the North Mountains situated in this state (16°51′18″ N, 93°23′47″ W, 904 m asl). This site constitutes a part of the buffer area of the El Ocote Biosphere Reserve. The annual mean precipitation is 4,725 mm for Los Tuxtlas and 1,100 mm for El Ocote. The annual mean temperature is 24°C for

Los Tuxtlas and 23.4°C for El Ocote (Instituto Nacional de Estadística, Geografía e Informática, 2003; Soto & Gama, 1997; Gutiérrez-García & Ricker, 2011).

Study Species

The goals of this research were addressed with five subcanopy species: *Chamaedorea glaucifolia* H.Wendl. (Arecaceae), *Cymbopetalum baillonii* R.E.Fr. (Annonaceae), *Magnolia mexicana* DC. (Magnoliaceae), *Nectandra coriacea* (Sw.) Griseb (Lauraceae), and *Ternstroemia tepezapote* Cham. & Schltdl. (Pentaphylacaceae). The taxonomic status of these species is in accordance with The Plant List (2013). These species are shade tolerant and inhabit mature forests (Standley & Steyermark, 1946, 1949; Coates & Estrada, 1988; Becerra-Vázquez, Ramírez-Marcial, & Holz, 2011). Additionally, these species have local utility for the human settlements and potential economic value (Escobar-Ocampo & Ochoa-Gaona, 2007). All these species, except the understory palm *C. glaucifolia* that has a seed covered by the fruit pericarp (Corner, 1976) as its dispersal unit (henceforth, we will consider it as a seed), are trees. We collected seeds of *C. baillonii* in Los Tuxtlas, Veracruz, and seeds of *C. glaucifolia*, *M. mexicana*, *N. coriacea*, and *T. tepezapote* in El Ocote. Seeds characteristics and other biological and ecological traits of the studied species are presented in Figure 1 and Table 1.

Processing of Fruits and Seeds

We collected fruits of the studied species during the dispersal season of 2016 except for *C. glaucifolia* which seeds were collected in 2015. Additionally, in 2016, we collected seeds of *C. baillonii* and *M. mexicana* during the dispersal season of 2015. The dates of collection are shown in Table 1. We collected fruits directly from at least 10 mature trees. Immediately after collection, fruits were deposited in either plastic containers or black plastic bags and covered with a soil layer taken from the study area to avoid seed dehydration. After 2 days, fruits were taken from the recipients in a dark room (22 ± 0.9°C, 50 ± 3.2% RH). Seeds inside fleshy fruits were cleaned in the laboratory. Because fruits of *M. mexicana* are dry and woody, we placed them on a table in a dark room until fruit dehiscence occurred. Seeds with an aryl were cleaned by gentle rubbing on a fine steel mesh.

Morphological Traits of Seeds

We measured the length (L), width (W), and thickness (T) of recently collected seeds (RC-seeds, $n = 30$) with an electronic vernier caliper (accuracy = 0.01 mm). Subsequently, seed volume (V) was calculated with the formula for obtaining the volume of an ellipsoid (Cerdà & García-Fayos, 2002) as follows: $V = 1.333 \times \pi \times (L/2) \times (W/2) \times (T/2)$.

We measured the fresh weight of individual seeds (FW_{t1}) with an electronic analytical balance (model A-200DS, precision 0.001 g, Fisher Scientific, Fairlawn, NJ). Subsequently, individual seeds were dried in an oven (model 107801, Boekel Industries, Inc. Philadelphia, PA) at 80°C for 48 hr to avoid seed combustion, due to the low ignition point of seed lipids. Seeds were weighed again (DW_{t1}), and the initial water content (WC_{t1} of RC-seeds) was calculated. The seed WC was determined

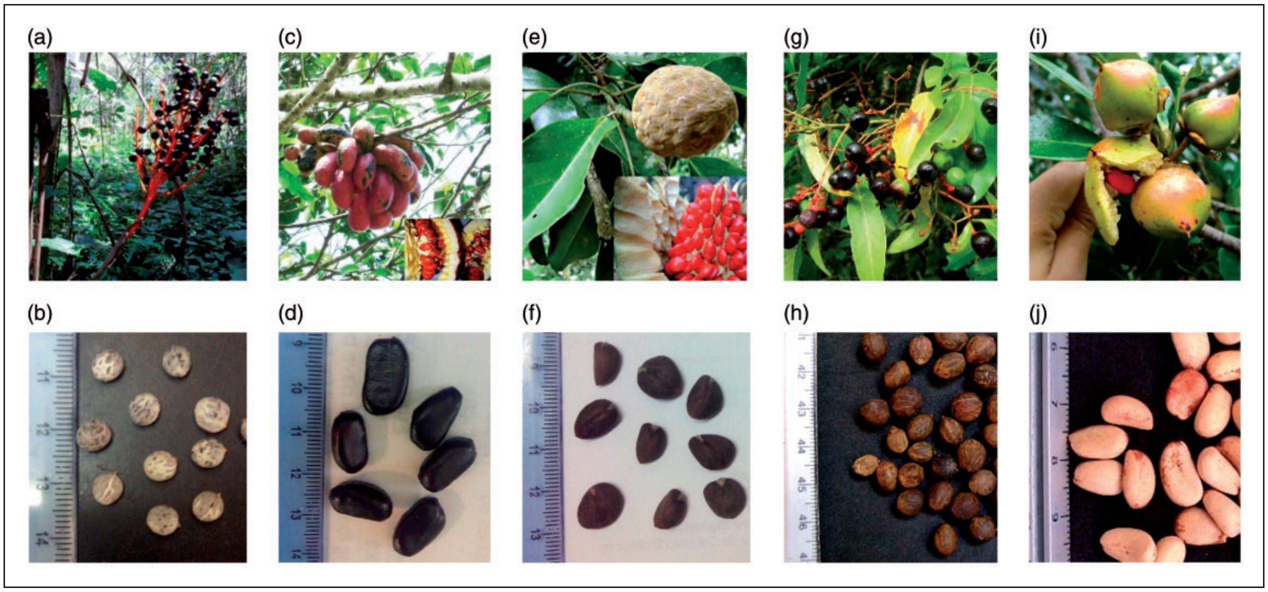

Figure 1. Fruits (upper row) and seeds (bottom row) of the studied species. (a and b) *Chamaedorea glaucifolia*, (c) and d) *Cymbopetalum baillonii*, (e and f) *Magnolia mexicana*, (g and h) *Nectandra coriacea*, and (i and j) *Ternstroemia tepezapote*. Image credit: A. G. Becerra-Vázquez.

Table 1. The Ecological Traits of the Studied Species, Environmental Traits of Their Habitat, and Seed Morphological Traits and Dates of Seed Collection and Season of Seed Dispersal.

Species	Seed collection date	Season of seed dispersal[a]	Precipitation[b] (mm)	Max. Temp.[b] (°C)	Embryo size[c]	Endosperm amount
Cg	October 2015	Late rainy season***	206.8	26.9	Small[4]	High[4]
Cb	April 2016	Late dry season**	20.8	28.8	Small[1,2]	High[1,2]
Mm	March 2016	Mid dry season*	0	27.1	Small[1,3]	High[1,3]
Nc	September 2016	Late rainy season*	104.4	27.8	Large[,2]	Absent[1,2]
Tt	January 2016	Early dry season*	10.7	25.7	Large[,2]	Low[1,2]

Note. Cg = *Chamaedorea glaucifolia*; Cb = *Cymbopetalum baillonii*; Mm = *Magnolia mexicana*; Nc = *Nectandra coriacea*; Tt = *Ternstroemia tepezapote*; Precipitation = total precipitation in the month of seed collection; Max. Temp. = maximum mean temperature in the month of seed collection; L, W, T = seed length, width, and thickness.

[a] Annual rain pattern in the collection sites (Instituto Nacional de Estadística, Geografía e Informática, 2003; Gutiérrez & Ricker, 2011). Dispersal dates from Becerra-Vázquez et al. (2011)*, Rodríguez et al. (2000)** and personal observations (A. G. Becerra Vázquez)*** in the study site.

[b] Total precipitation and mean of maximum temperature for the date of seed collections from Station 7319 and Torre CONAGUA-SMN – CONANP – IBUNAM (Comisión Nacional del Agua, 2017).

[c] Embryo and endosperm proportions are relative to seed size ([1]Corner, 1976; [2]Niembro-Rocas, 1989; [3]Alcántara-Flores, 2002; [4]Baskin & Baskin, 2014) and corroborated by personal observations (A. G. Becerra-Vázquez).

on dry basis (WC_{db}) as follows: $WC_{t1} = ((FW_{t1} - DW_{t1})/DW_{t1}) \times 100$ (Equation 1).

Seed Storage

Seeds were stored in closed glass jars with three replicates for each species. Germination of stored seeds (St-seeds) was evaluated after different storage times depending on the species (storage times, t2 ... tn). For *C. baillonii* and *M. mexicana*, we also evaluated the effect of the year of seed collection: 2015 (2015-S) and 2016 (2016-S) fruiting seasons. The jars were stored in laboratory conditions (23 ± 0.5°C, 50 ± 2.2% RH). To evaluate the effect of storage temperature, we maintained additional jars in growth chambers with controlled temperature (40 ± 5% RH, Labline Instruments Inc., Melrose Park, IL) at 15°C and at 5°C. In addition, *C. glaucifolia* and *C. baillonii* 2015-S were stored at 10°C. Seeds of *C. glaucifolia* were stored for 30, 101, and 426 days, seeds of *C. baillonii* for 30, 180, and 360 days (also 730 days for 2015 seeds), seeds of *M. mexicana* were stored for 25 and 210 days (and for 90 days only for 2015-S), seeds of *N coriacea* for 35, 90, and 180 days, and seeds of *T. tepezapote* for 16, 41, 251, and 365 days. All species differed in t2 ... tn, according to the seed collection dates and the number of collected seeds.

Prior to storage, seeds were treated with fungicide (Interguzan 30-30, pentachlorinenitrebenzene, and terametiltiuram disulphide). Subsequently, the jars were closed and sealed with a plastic film and placed in the storage site. The jars were reviewed and aerated periodically to prevent fungal contamination or avoid the increase in HR inside the jars due to the seed WC loss. After each storage time (t2 ... tn), a sample of seeds were sown on agar, and another sample ($n \geq 4$) was utilized to determine the WC ($WC_{t2 \ldots tn}$). For this purpose, Equation (1) was used, with the seed FW and DW data for each t2 ... tn ($FW_{t2 \ldots tn}$ and $DW_{t2 \ldots tn}$, respectively).

Seed Germination

Before (RC-seeds) and after storage (St-seeds), the seeds were sown on plates of 1% agar (10 g/L agar/water; Bioxon, Becton Dickinson de México S.A. de C.V., México). The agar medium was placed in transparent plastic boxes (12 × 16 × 5.5 cm). Before sowing, seeds were disinfected with a 1% sodium hypochlorite solution and, subsequently, with a 0.2% fungicide solution (Interguzan 30-30, pentachlorinenitrebenzene and terametiltiuram disulphide). All the sown boxes (30 seeds per box) were placed in growth chambers (25°C, 12/12 h photoperiod). Germination took place when the radicle protruded. Germination was registered every third day until no germination took place. Seeds that did not germinate were fully covered with fungal infection or were rotten. We used three replications for species for each germination essay.

Data Analysis

To compare the mean values for the different morphological traits of seeds (V, FW, DW, and WC), considering all the years of collection, we applied the Kruskal–Wallis test, because the assumptions required for analysis of variance (ANOVA) were not met with the available data. Tukey and Kramer's test constituted the post hoc comparison. These analyses were conducted with R software, version 3.2.3 (R Core Team, 2016).

For each species, we obtained the germination parameters relative to each germination test of RC-seeds and

St-seeds. First, the cumulative germination percentages were arcsine transformed and fitted to the exponential sigmoid curve $y = a\ /\ [1 + b^{(-cx)}]$ using the Table Curve 2D software, version 5.01 (AISN Software, Chicago, IL). All the fitted curves had $R^2 \geq 0.9$ and $p \leq .01$. From the fitted curve, we obtained the lag time (LT), maximum germination rate (MGR; i.e., maximum first derivative of the sigmoid curve), and mean germination time (MGT; i.e., time for maximum germination rate). These variables, along with the final germination (FG), were the germination parameters.

The mean values of the germination parameters of RC-seeds and St-seeds were compared, considering each storage time and each storage temperature (temperature). For this, we applied ANOVA tests, followed by the Tukey's test for post hoc comparisons. When the variance analysis assumptions were not met, the Kruskal–Wallis and post hoc Tukey and Kramer's tests were applied. To evaluate if there was any interaction between storage time and temperature, we employed a two-way ANOVA, and for *C. baillonii* and *M. mexicana*, a three-way ANOVA was conducted considering the year of seed collection. These analyses were conducted with *R*. Additionally, to determine the effect of temperature on seed germination (for 2015-S in *C. glaucifolia* and *M. mexicana* and for 2016-S in *N. coriacea* and *T. tepezapote* and for both years in *C. baillonii*), a multiple regression analysis with temperature and storage time as factors and the same intercept value (FG before storage or t1) was performed. We applied the square root or logarithm transformation to satisfy the assumptions of the regression analysis. Subsequently, ANOVA test was employed to determine the statistical significance of each slope values. This analysis was conducted with Statgraphics Centurion XVI version 16.1.03 (Statpoint Technologies, Inc.).

To evaluate seed longevity and desiccation sensitivity between species, we determined both WC_{50}, that is WC when the initial viability decreases to 50%, and the time required to reach WC_{50} (in days), respectively. To determine WC_{50}, the values of seed viability (FG) and seed WC for each storage time (t2 . . . tn) were fitted to the functions indicated in Appendix B. In the case of *C. glaucifolia*, we determined the WC_{50} from the fitted curve (FG vs. WC), because the seed FG achieved after 14 months of storage was higher than 50%. In addition, the time of storage at which seeds reach WC_{50} was calculated using a regression analysis (WC vs. storage time). All fittings were done with Table Curve 2D. To enable comparisons of WC_{50} and the time required to reach WC_{50} values between species, we selected the seeds from the same year and stored at the same temperature. For this, we considered 2016-S (2015-S in *C. glaucifolia*) stored in laboratory conditions (23 ± 0.5°C, 50 ± 2.2% RH, and only for *N. coriacea*, to avoid seed germination during storage, these seeds were stored at 15 ± 0.5°C, 40 ± 5% RH). The mean values of WC_{50} and the time required to reach WC_{50} were compared with ANOVA and followed for the Tukey's post hoc test. Also, we made comparisons between years of seed collection for both *C. baillonii* and *M. mexicana* (2015-S and 2016-S, respectively). Therefore, we applied the *t*-test or Wilcoxon rank sum test in cases of no normality and or homocestadicity of the data. Analyses were performed with *R*.

Finally, we performed a principal component analysis to explore the relationships between species in terms of (a) morphological traits, as seed DW, volume, initial WC, relative amount of endosperm, and embryo size, (b) functional traits, as seed WC_{50}, time required to reach WC_{50}, and initial values of LT, MGR, and MGT, and (c) ecological and environmental traits, as the season of seed dispersal and both mean maximum temperature and total precipitation for the month of seed collection (Table 1). Before the analysis, all variables were normalized. For this analysis, we included data for 2016-S of all species and 2015-S for *C. glaucifolia*. The analysis was also done with *R*.

Results

Morphological Traits of Seeds

The values for each morphological trait of the seeds of studied species are presented in Table 2. The volume ranged from 95.7 ± 17.0 to 386.9 ± 87.6 mm^3, FW from 0.16 ± 0.026 to 0.53 ± 0.101 g, and DW from 0.11 ± 0.019 g to 0.34 ± 0.075 g. *C. glaucifolia* had the smallest and lightest seeds, while *C. baillonii* had the largest and the heaviest seeds in terms of FW and DW. Seeds of *M. mexicana* had the lowest WC value (19.6 ± 5.63%). For the other species, WC was > 36%; seeds of *T. tepezapote* had the highest value (75.3 ± 13.81%). Seeds of *C. bailloni* collected in 2015-S were significantly heavier in FW than those from 2016-S (0.62 ± 0.057 and 0.53 ± 0.101 g, respectively).

Seed Storage

Before seed storage (t1), final germination (FG) ranged between 67% in *T. tepezapote* to 94% in *C. glaucifolia* (Table 3). The LT ranged from 8 days in *N. coriacea* to 26 days in *T. tepezapote* (Table 4). MGR ranged from 1.1% day^{-1} in *C. glaucifolia* to 5.4% day^{-1} in *C. baillonii* (2016-S; Table 3). MGT ranged from 22 days in *C. baillonii* (2016-S) to 89 days in the seeds of *C. glaucifolia* (Table 4).

After storage (St-seeds), both storage time and temperature exerted a significant effect on all germination parameters (FG, LT, MGR, and MGT) and in all species,

Table 2. Seed Morphological Traits ($n \geq 30$) of the Studied Species ($\bar{x} \pm SE$).

Species	Year	L × W × T (mm)	Volume (mm^3)	FW (g)	DW (g)	WC$_{db}$ (%)
Chamaedorea glaucifolia	2015	6.1, 5.5, 5.3 (±0.45, 0.30, 0.29)	95.7 ± 17.07e	0.16 ± 0.026e	0.11 ± 0.019d	36.3 ± 2.36c
Cymbopetalum baillonii	2015	15.4, 8.7, 5.5 (±1.27, 0.69, 0.65)	396.6 ± 64.57a	0.62 ± 0.057a	0.37 ± 0.057a	68.6 ± 14.51ab
	2016	14.9, 8.5, 5.7 (±1.27, 0.65, 0.75)	386.9 ± 87.69a	0.53 ± 0.101b	0.34 ± 0.075a	56.3 ± 16.26b
Magnolia mexicana	2015	10.4, 8.4, 4.5 (0.69, 1.37, 0.39)	211.6 ± 38.07c	0.20 ± 0.038d	0.16 ± 0.027c	21.9 ± 4.05d
	2016	10.5, 8.2, 4.6 (±0.74, 0.86, 0.53)	212.9 ± 42.05c	0.22 ± 0.039d	0.18 ± 0.030c	19.6 ± 5.63d
Nectandra coriacea	2016	9.0, 8.0, 7.8 (±0.82, 0.67, 0.63)	302.4 ± 73.02b	0.39 ± 0.098bc	0.25 ± 0.063b	56.5 ± 5.84b
Ternstroemia tepezapote	2016	10.6, 6.4, 4.7 (±0.95, 0.68, 0.77)	167.8 ± 26.6d	0.21 ± 0.04d	0.12 ± 0.021d	75.3 ± 13.81a
			$F_{(6,\ 224)} = 219.2$	$\chi^2 = 435.04$	$\chi^2 = 461.21$	$\chi^2 = 493.7$

Note. L = seed length; W = seed width; T = seed thickness; Volume = seed volume; FW = fresh weight; DW = dry weight; WC$_{db}$ = water content dry basis. Lowercase letters indicate statistical differences inside each column (Tukey's test or Tukey and Kramer's test, $p < .0001$). Year of seed collection for species is indicated.

except *C. glaucifolia* (Tables 3 to 6). As the storage time increased, both FG and MRG decreased, and LT and MGT increased. There was a negative relation between the duration of storage and seed viability of all species and all storage temperatures (Figure 2). In contrast, in *C. glaucifolia*, only storage time had a significant effect on the MGT and MGR (Table 6). In this species, the MGT of St-seeds decreased with time, and the MGR increased after 101 days of storage, but after 426 days, the MGR decreased.

Results of multiple linear regression showed that slopes of linear regression between FG and storage time differed significantly between temperatures for each species, as occurred in all species except in *T. tepezapote* (Figure 2). This means that the storage temperature had an effect in seed longevity: Lower slope values indicate less seed deterioration (Tables 3 and 4, Figure 2). The St-seeds at 15°C showed slower deterioration than at 23°C, 10°C, and 5°C in *C. glaucifolia*, $F(3,\ 4) = 7.04$, $p < .05$, and in *C. baillonii* for both years of seed collection, $F(2,\ 3) = 11.13$, $p < .05$ for 2015-S and $F(2,\ 3) = 28.54$, $p < .01$ for 2016-S. The St-seeds at 5°C showed slower deterioration than at 23°C and 15°C in *M. mexicana*, $F(2,\ 3) = 17.78$, $p < .01$, and at 15°C in *N. coriacea*, $F(1,\ 2) = 7.15$, $p < .05$. Although slopes did not differ significantly for *T. tepezapote*, $F(1,\ 3) = 1.99$, $p > .05$, after 251 days, germination only occurred in seeds stored at 5°C (Table 3). Summary of multiple regression analysis is shown in Appendix A.

The multiway ANOVA tests applied to the mean values of all parameters confirm in some cases an interaction between the factors year, storage time, and temperature (Tables 5 and 6). Individually, the year of seed collection exerted a significant effect on the St-MGT in *C. baillonii* (Table 5). In this species, RC-seeds collected in 2016 had a shorter MGT than RC-seeds collected in 2015, but in 2015-S seeds, the St-MGT was shorter compared with RC-seeds (Table 4). Conversely, in *C. baillonii*, we found a triple interaction between the collection year, storage time, and temperature (Table 5). That is, 2016-S seeds stored for 180 days at 23°C showed the longest St-MGT; whereas, 2015-S did not exhibit significant differences (Table 4). On the other hand, the collection year had a double interaction with both storage time and temperature for all germination parameters of *C. baillonii* seeds, except St-LG (Table 5). After 180 days of storage at 15°C, the FG of 2016-S decreased. Also, after 30 days of storage at 23°C for both years, the MGT decreased in 2015-S, but in 2016-S, it increased. Finally, only 2016-S showed differences in St-LT and St-MGR in terms of temperature of storage (Tables 3 and 4).

An interaction between storage time and temperature also was observed for St-FG, St-LT, and St-MGT in seeds of *N. coriacea* and *T. tepezapote* (Table 6). Seeds of *N. coriacea* stored for 180 days at 5°C had a higher FG and shorter LT and MGT than seeds stored at 15°C, while in *T. tepezapote*, germination occurred only in seeds stored for 251 days at 5°C (Tables 3 and 4).

We found significant differences in WC$_{50}$ values between species, ANOVA, $F(4,\ 10) = 329.1$, $p < .0001$. Seeds of *C. glaucifolia* had the lowest WC$_{50}$, $4.6 \pm 0.08\%$ (Figure 3). *C. baillonii* and *M. mexicana* showed no difference between them in WC$_{50}$, with

Table 3. Final Germination and Maximum Germination Rate of Seeds ($\bar{x} \pm SE$) After Different Storage Times or Durations (t2 . . . tn) in Different Storage Temperatures (°C) for Five Species From Tropical Forests of Mexico.

Storage time (days)	Final germination (%)				Maximum germination rate (% × day^{-1})			
	23°C	15°C	10°C	5°C	23°C	15°C	10°C	5°C
Chamaedorea glaucifolia (2015)								
	$F = 18.66$, $df = 11.13$, $p < .0001$				$F = 4.206$, $df = 11.23$, $p < .01$			
0 (t1)	94.4 ± 4.0a				1.1 ± 0.05c			
33	92.2 ± 2.23a	88.8 ± 2.22a	81.1 ± 1.11ab	95.5 ± 2.22a	2.2 ± 0.17abc	2.4 ± 0.07abc	2.1 ± .037abc	2.4 ± 0.04abc
101	74.4 ± 1.11abc	85.5 ± 1.11ab	62.2 ± 9.68bcd	NE	3.3 ± 0.23ab	3.9 ± 0.93a	2.7 ± 0.39abc	NE
426	54.4 ± 2.93cde	63.3 ± 5.77bcd	27.7 ± 8.01e	43.3 ± 5.77de	1.6 ± 0.32bc	2.4 ± 0.52abc	0.7 ± 0.21c	1.8 ± 0.42bc
Cymbopetalum baillonii (2015)								
	$F = 20.12$, $df = 7.16$, $p < .0001$				$F = 0.898$, $df = 6.13$, $p > .05$			
0 (t1)	84.2 ± 1.92a				4.4 ± 0.36			
30	64.4 ± 1.11ab	67.7 ± 2.93a	66.6 ± 8.81a	NE	4.7 ± 0.40	3.6 ± 0.38	3.0 ± 0.42	NE
180	12.2 ± 8.88c	63.3 ± 9.62ab	33.3 ± 8.38bc	NE	3.1 ± 0.63	8.0 ± 4.55	3.7 ± 0.84	NE
730	NG	5.5 ± 2.22c	NG	NE	NG	ND	NG	NE
Cymbopetalum baillonii (2016)								
	$F = 105.1$, $df = 8.18$, $p < .0001$				$F = 18.03$, $df = 6.14$, $p < .0001$			
0 (t1)	72.5 ± 7.40a				5.4 ± 0.41a			
30	82.2 ± 2.93a	85.5 ± 2.93a	NE	91.1 ± 4.00a	5.1 ± 0.15bc	4.6 ± 0.36c	NE	7.6 ± 0.69ab
180	9.9 ± 3.33cd	52.2 ± 7.77b	NE	22.2 ± 2.93c	2.5 ± 0.98cd	3.1 ± 0.18cd	NE	1.5 ± 0.21d
365	3.3 ± 1.92d	8.8 ± 1.11cd	NE	ND	ND	ND	NE	ND
Magnolia mexicana (2015)								
	$F = 22.72$, $df = 3.8$, $p < .001$				$F = 0.996$, $df = 3.8$, $p > .05$			
0 (t1)	88.8 ± 2.93a				1.92 ± 0.30			
25	18.0 ± 3.80b	35.0 ± 12.58b	NE	NE	0.8 ± 0.06	1.2 ± 0.47	NE	NE
90	NG	NG	NE	17.1 ± 4.36b	NG	NG	NE	1.0 ± 0.78
210	NG	NG	NE	NG	NG	NG	NE	NG
Magnolia mexicana (2016)								
	$F = 47.52$, $df = 3.8$, $p < .0001$				$F = 3.108$, $df = 2.6$, $p > .05$			
0 (t1)	77.7 ± 4.84a				1.9 ± 0.09			
25	2.2 ± 2.2c	40.0 ± 6.93b	NE	55.5 ± 2.93b	ND	1.4 ± 0.29	NE	2.6 ± 0.50
210	NG	NG	NE	NG	NG	NG	NE	NG
Nectandra coriacea (2016)								
	$F = 47.31$, $df = 6.14$, $p < .0001$				$F = 4.523$, $df = 6.14$, $p < .01$			
0 (t1)	82.2 ± 4.84abc				1.5 ± 0.16ab			
35	NE	100.0 ± 0.00a	NE	96.6 ± 3.33ab	NE	1.3 ± 0.08b	NE	1.4 ± 0.13ab
90	NE	64.4 ± 4.44c	NE	76.6 ± 5.09bc	NE	1.3 ± 1.16b	NE	2.4 ± 0.21a
180	NE	13.3 ± 1.92d	NE	64.4 ± 6.18c	NE	1.8 ± 0.38ab	NE	2.3 ± 0.26ab
Ternstroemia tepezapote (2016)								
	$F = 11.25$, $df = 5.12$, $p < .001$				$F = 7.23$, $df = 5.12$, $p < .01$			
0 (t1)	67.7 ± 5.55a				1.6 ± 0.11ab			
16	23.3 ± 3.84c	54.4 ± 11.11ab	NE	NE	0.7 ± 0.02bc	1.8 ± 0.37a	NE	NE
41	27.7 ± 1.11bc	53.3 ± 3.33ab	NE	NE	1.3 ± 0.15abc	1.7 ± 0.10a	NE	NE
251	NG	NG	NE	18.8 ± 5.87c	NG	NG	NE	0.6 ± 0.17c

Note. NG = no germination, ND: no determined; NE = no evaluated. Lowercase letters indicate statistical differences (Tukey's test after ANOVA, $p < .05$, or Tukey and Kramer's test after Kruskal-Wallis, $p < .05$). Comparisons were done individually for each germination parameter for each species and for each year of seed collection of *C. baillonii* and *M. mexicana*.

12.7 ± 1.25% and 11.7 ± 0.29%, respectively (Figure 3). Seeds of *N. coriacea* and *T. tepezapote* had the highest WC$_{50}$, with 37.9 ± 1.96% and 59.1 ± 1.87%, respectively (Figure 3). In addition, the time required to reach WC$_{50}$ varied with the species, ANOVA, $F(3, 8) = 272.8$, $p < .0001$. Seeds of *M. mexicana* required the shortest time, 9.1 ± 0.70 days, followed by *T. tepezapote* seeds that required 17.7 ± 1.46 days (Figure 3). Seeds of

Table 4. Lag Time and Mean Germination Time of Seeds ($\bar{x} \pm SE$) After Different Storage Times or Durations (t2 . . . tn) in Different Storage Temperatures (°C) for Five Species From Tropical Forests of Mexico.

Storage time (days)	Lag time (days)				Mean germination time (days)			
	23°C	15°C	10°C	5°C	23°C	15°C	10°C	5°C
Chamaedorea glaucifolia (2015)								
	$F = 3.407$, $df = 11.23$, $p < .01$				$\chi^2 = 32.134$, $df = 11$, $p < .001$			
0 (t1)	22.6 ± 2.61ab				89.7 ± 2.71c			
33	22.3 ± 1.17ab	25.0 ± 1.79a	26.0 ± 4.52a	26.1 ± 0.65a	55.4 ± 0.67a	55.4 ± 0.67a	57.1 ± 1.91a	61.4 ± 2.61b
101	14.0 ± 1.80ab	18.2 ± 3.25ab	18.0 ± 2.31ab	NE	30.2 ± 0.52a	34.7 ± 0.53a	36.0 ± 0.64a	NE
426	11.9 ± 0.98b	18.7 ± 3.55ab	25.0 ± 8.02ab	23.3 ± 2.48ab	40.9 ± 4.29a	44.9 ± 0.56a	53.4 ± 6.56a	44.3 ± 0.98a
Cymbopetalum baillonii (2015)								
	$F = 1.964$, $df = 6.13$, $p > .05$				$F = 4.611$, $df = 6.13$, $p < .05$			
0 (t1)	19.6 ± 0.46				35.6 ± 0.93a			
30	16.4 ± 1.48	14.0 ± 1.40	11.4 ± 1.15	NE	27.1 ± 1.38b	28.7 ± 0.79ab	28.4 ± 0.70ab	NE
180	20.0 ± 3.27	23.0 ± 5.98	18.4 ± 0.71	NE	26.4 ± 1.00b	34.2 ± 2.69ab	26.7 ± 0.82b	NE
730	NG	ND	NG	NE	NG	ND	NG	NE
Cymbopetalum baillonii (2016)								
	$F = 12.7$, $df = 6.14$, $p < .0001$				$F = 10.96$, $df = 6.14$, $p < .001$			
0 (t1)	11.5 ± 0.71a				22.1 ± 1.45cd			
30	10.6 ± 0.93a	7.5 ± 1.29a	NE	9.8 ± 1.37a	23.0 ± 0.68bcd	22.0 ± 0.25bcd	NE	20.2 ± 0.44d
180	23.4 ± 2.50b	13.3 ± 0.25a	NE	11.8 ± 1.26a	30.1 ± 0.76a	26.6 ± 1.42ab	NE	25.4 ± 2.08abc
365	ND	ND	NE	ND	ND	ND	NE	ND
Magnolia mexicana (2015)								
	$F = 11.91$, $df = 3.8$, $p < .01$				$F = 2.815$, $df = 3.8$, $p > .05$			
0 (t1)	18.56 ± 5.78c				54.18 ± 3.13			
25	58.2 ± 5.34a	34.3 ± 3.07bc	NE	NE	71.6 ± 4.62	58.0 ± 2.20	NE	NE
90	NG	NG	NE	42.2 ± 4.47ab	NG	NG	NE	69.0 ± 8.06
210	NG	NG	NE	NG	NG	NG	NE	NG
Magnolia mexicana (2016)								
	$F = 9.396$, $df = 2.6$, $p < .05$				$F = 4.353$, $df = 2.6$, $p > .05$			
0 (t1)	25.5 ± 1.46a				57.2 ± 0.55			
25	ND	36.3 ± 2.27b	NE	34.1 ± 1.76b	ND	60.4 ± 1.20	NE	54.1 ± 2.23
210	NG	NG	NE	NG	NG	NG	NE	NG
Nectandra coriacea (2016)								
	$F = 107.5$, $df = 6.14$, $p < .0001$				$F = 7.603$, $df = 6.14$, $p < .001$			
0 (t1)	8.7 ± 0.83c				43.6 ± 1.45abc			
35	NE	7.1 ± 0.01c	NE	6.3 ± 0.79c	NE	56.9 ± 4.74a	NE	53.0 ± 8.37ab
90	NE	13.0 ± 2.16bc	NE	13.0 ± 1.63bc	NE	48.2 ± 0.81abc	NE	36.0 ± 0.81c
180	NE	52.8 ± 2.20a	NE	16.8 ± 1.94b	NE	60.9 ± 0.73a	NE	37.4 ± 2.20bc
Ternstroemia tepezapote (2016)								
	$F = 10.7$, $df = 5.12$, $p < .001$				$F = 8.85$, $df = 5.12$, $p < .01$			
0 (t1)	26.4 ± 1.13c				49.9 ± 1.65b			
16	15.5 ± 1.12c	16.8 ± 0.67bc	NE	NE	42.8 ± 2.25b	40.4 ± 2.33b	NE	NE
41	29.6 ± 1.82ab	18.4 ± 2.05bc	NE	NE	48.3 ± 0.69b	41.6 ± 1.36b	NE	NE
251	NG	NG	NE	38.1 ± 8.52a	NG	NG	NE	66.5 ± 7.50a

Note. NG = no germination; ND = no determined, NE = no evaluated. Lowercase letters indicate statistical differences (Tukey's test after ANOVA, $p < .05$, or Tukey and Kramer's test after Kruskal-Wallis, $p < .05$). Comparisons were done individually for each germination parameter, for each species and for each year of seed collection of *C. baillonii* and *M. mexicana*.

C. baillonii and *N. coriacea* required 88.4 ± 9.27 and 150.9 ± 3.78 days, respectively (Figure 3). After 426 days, the seeds of *C. glaucifolia* showed a reduction in their FG from 100% to 57%; thus, they had the longest WC_{50} (Figure 3). Functions used for the determination of WC_{50} and time to reach WC_{50} are shown in Appendix B.

We found significant differences in WC_{50} between the 2 years for *C. baillonii* ($t = -20.55$, $p < .0001$).

Table 5. Results of the Multiway ANOVA on Effects of Year (Y), Storage Time (Sti), and Storage Temperature (ST) on Germination of *C. baillonii* and *M. mexicana* Seeds.

	Cymbopetalum baillonii				*Magnolia mexicana*			
Source of Variation	MS	*F*	*p*	*df*	MS	*F*	*p*	*df*
Final germination (%)								
Y	2	0.024	.8774	1	101	0.945	.3456	1
Sti	11525	135.99	.0001	4	7053	65.822	.0001	2
ST	1121	13.223	.0001	3	2447	22.842	.0001	2
Y × Sti	892	10.526	**.001**	2	32	0.301	.5911	1
Y × ST	187	2.203	.1469	1	327	3.05	.0999	1
Sti × ST	849	10.023	**.0001**	4				
Y × ST × Sti	30	0.35	.5582	1				
Residuals	2881			34	107			16
Lag time (days)								
Y	259.84	17.55	.0002	1	44.5	1.135	.3015	1
Sti	201.93	13.639	.0001	2	1084.2	27.669	.0001	2
ST	53.28	3.598	.0262	3	595	15.186	.001	2
Y × Sti	9.7	0.655	.5275	2	12.5	0.318	.5799	1
Y × ST	62.87	4.246	.0490	1				
Sti × ST	18.4	1.243	.3136	3				
Y × ST × Sti	55.12	3.723	.0642	1				
Residuals	14.81			27	39.2			17
Mean germination time (days)								
Y	336.2	55.362	.0001	1	145.32	3.567	.0761	1
Sti	64.2	10.575	.001	2	146.51	3.596	.0498	2
ST	16.9	2.791	.0595	3	208.11	5.108	.0183	2
Y × Sti	88.7	14.609	**.0001**	2	2.44	0.06	.8096	1
Y × ST	64.7	10.658	**.0029**	1				
Sti × ST	7.8	1.29	.2980	3				
Y × ST × Sti	26	4.274	**.0484**	1				
Residuals	6.1			27	40.74			17
Maximum germination rate (% × day^{-1})								
Y	0.07	0.012	.9149	1	2.5731	5.522	.0311	1
Sti	21.46	3.725	.0372	2	0.5744	1.233	.3162	2
ST	3.74	0.648	.5908	3	1.7047	3.659	.0477	2
Y × Sti	34.08	5.915	**.0074**	2	0.0104	0.022	.8829	1
Y × ST	3.27	0.567	.4580	1				
Sti × ST	10.96	1.903	.1530	3				
Y × ST × Sti	8.3	1.44	.2405	1				
Residuals	5.76			27	0.4659			17

Note. Interactions that were statistically-significant (*p* values) are indicated with values in bold. MS = mean square; *df* = degrees of freedom.

The 2015-S seeds had lower WC_{50}, compared with 2016-S seeds, with $4.8 \pm 0.07\%$; but there was no difference in the time required to reach WC_{50} ($t = 1.3098$, $p > .05$). No differences were found in *M. mexicana* between 2015-S and 2016-S with respect to its WC_{50} ($t = 1.7132$, $p > .05$) and the time to reach WC_{50} ($W = 0.0$, $p > .05$).

Relationships Between Biological, Ecological, and Environmental Traits

The principal component analysis showed that Components 1, 2, and 3 accounted for 94% of the total variation (Figure 4, Appendix C). Component 1

Table 6. Results of the Two-Way ANOVA on Effects of Storage Time (Sti) and Storage Temperature (ST) on Germination of *C. glaucifolia*, *N. coriacea*, and *T. tepezapote* Seeds.

	Chamaedorea glaucifolia				*Nectandra coriacea*				*Ternstroemia tepezapote*			
Source of variation	MS	*F*	*P*	*df*	MS	*F*	*p*	*df*	MS	*F*	*p*	*df*
Final germination (%)												
Sti	757.6	1.795	.185	2	3623	68.47	.0001	3	1215.2	11.25	.001	3
ST	440	1.043	.39	3	1867	35.29	.0001	2	2408.3	22.294	.001	1
Sti × ST	51	0.121	.887	2	1141	21.57	**.0001**	1	23.1	0.214	.6517	1
Residuals	422			27	53			14	108			12
Lag time (days)												
Sti	81.31	2.878	.0736	2	10.819	93.1	.0001	3	0.644	15.027	.001	3
ST	70.85	2.508	.0801	3	5.538	47.66	.0001	2	0.1218	2.841	.1176	1
Sti × ST	0.96	0.034	.9667	2	4.797	41.28	**.0001**	1	0.2379	5.551	**.0363**	1
Residuals	28.25			27	0.116			14	0.0429			12
Mean germination time (days)												
Sti	3579	75.362	.0001	2	0.0745	4.688	.0181	3	0.14816	13.581	.001	3
ST	47	0.992	.412	3	0.3809	23.959	.001	2	0.03263	2.991	.1093	1
Sti × ST	3	0.07	.933	2	0.0604	3.799	**.0480**	1	0.00582	0.533	.4793	1
Residuals	47			27	0.0159			14	0.01091			12
Maximum germination rate (% × day^{-1})												
Sti	7.56	14.571	.0001	2	0.5823	3.894	.0324	3	0.6616	6.298	.0082	3
ST	1.34	2.582	.0741	3	1.5822	10.58	.0057	2	1.4499	13.802	.0029	1
Sti × ST	0.124	0.238	.7897	2	0.3648	2.439	.1233	1	0.3679	3.502	.0858	1
Residuals	0.519			27	0.1496			14	0.1051			12

Note. Interactions that were statistically significant (*p* values) are indicated with values in bold. MS = mean square; *df* = degrees of freedom.

explained 38% of the variation and was represented for the positive loadings of seed DW, MGR, volume, and mean maximum temperature in the month of seed collection, followed by negative loadings of seed MGT and LT (Figure 4, Appendix C). Thus, large seeds germinate fast and are dispersed in the hottest months. Component 2 explained 34% of the variation and was represented for positive loadings in seed FG, the time required to reach WC_{50}, relative amount of endosperm, dispersal time, maximum mean temperature, and total precipitation in the month of seed collection, followed by negative loadings of seed WC, WC_{50}, and embryo size (Figure 4, Appendix C). Therefore, seeds with low WC, small embryos, and an abundance of endosperm tended to have less desiccation sensitivity, high viability (final germination), and were dispersed in wet months with high maximum temperatures. Component 3, which explained 21% of the variation, had positive loadings in seed LT and relative amount of endosperm, followed by negative loadings in seed WC, embryo size, dispersal time, and total precipitation in the month of seed collection (Figure 4, Appendix C). Thus, seeds with low WC, abundance of endosperm, small embryo, and those dispersed in dry seasons take more time to germinate.

Discussion

All species had short-lived desiccation-sensitive seeds, because their vigor and viability decreased after storage. These functional traits, along with morphological and physiological traits, were in accordance to those reported for tropical species with short-lived desiccation-sensitive seeds (Pritchard et al., 2004; Hamilton et al., 2013), but we found variation in seed longevity between them. Indeed, we found that seed longevity was related to other functional and ecological traits, along with the prevailing weather conditions at the time of seed dispersal. Seed WC and internal structure are related to longevity (Hong & Ellis, 1996; Hill, Edwards, & Franks, 2010). Moreover, the amount of precipitation and temperature influence the seed development (Finch-Savage & Farrant, 1997).

Seeds of both *T. tepezapote* and *N. coriacea* had $WC_{50} > 30\%$, which signifies that both species might be recalcitrant, but they differ greatly in terms of the time required to reach WC_{50} (17 and 150 days, respectively). However, WC_{50} was determined in *T. tepezapote* seeds stored at 23°C, as was done in the other species studied, while we pointed out that *N. coriacea* seeds were stored at

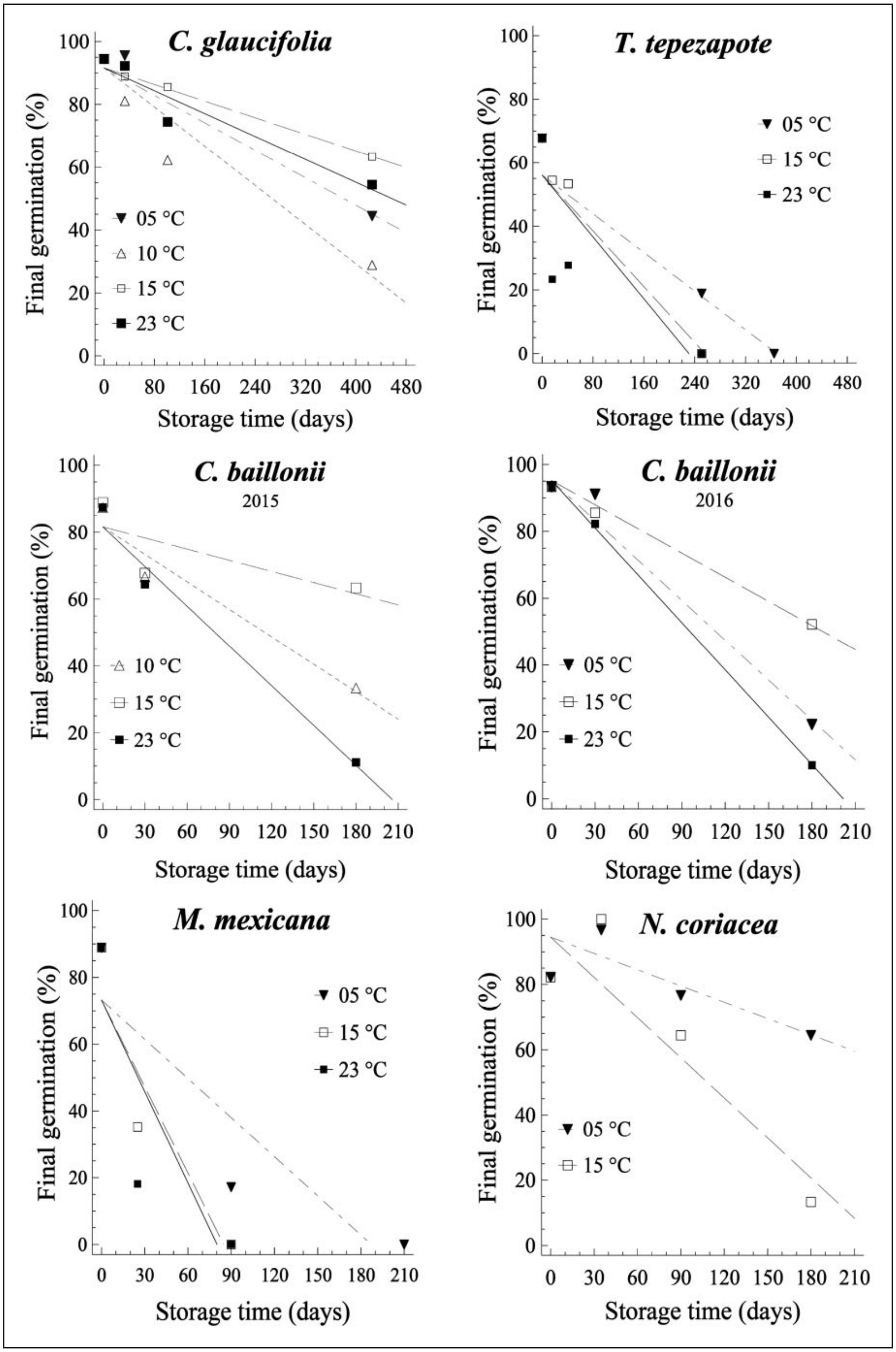

Figure 2. Final germination (%, x̄ ± SE, n = three replications) of seeds of the studied species after different storage times (t2 . . . tn) at different storage temperatures. The evaluation was done for seeds collected in 2015 (*Chamaedorea glaucifolia* and *Magnolia mexicana*), 2016 (*Nectandra coriacea* and *Ternstroemia tepezapote*), and those collected in both years, *Cymbopetalum baillonii*. Seeds were stored in closed glass jars at 23°C (room temperature, black square symbol), 15°C (white square), 10°C (up, white triangle), or 5°C (down, gray triangle). The values of multiple linear regression analysis are presented in Appendix A.

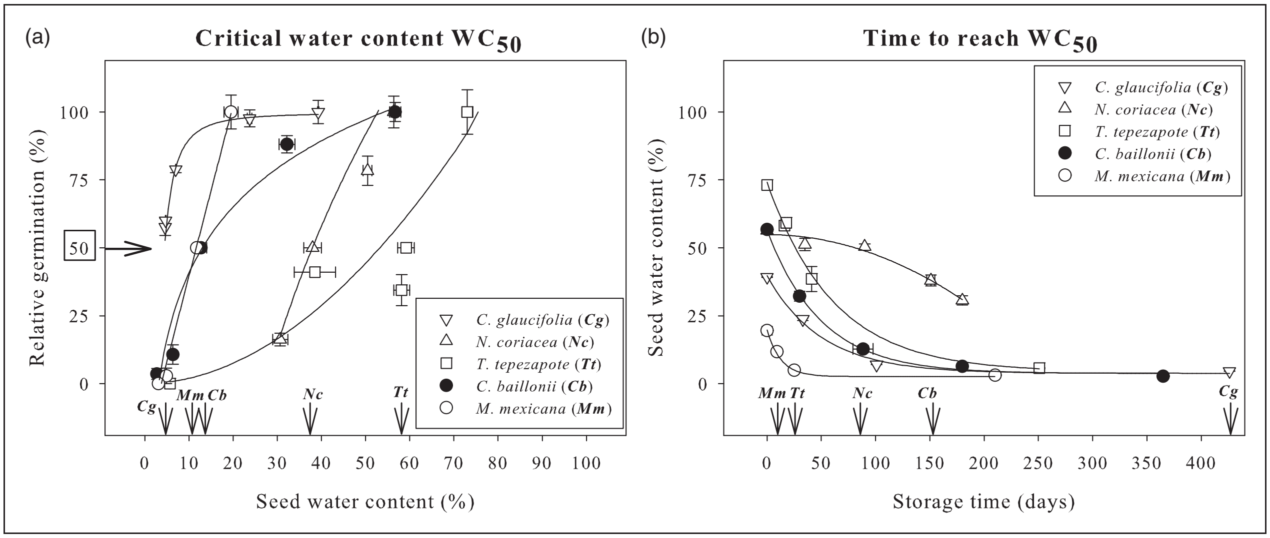

Figure 3. The determinations of the critical WC (WC_{50}, Panel A) and the time at which the seeds reached WC_{50} (B) for the seeds of the species studied. The final mean seed germination ($\bar{x} \pm SE$, n = three replications) was expressed as a relative percentage with respect to the initial seed germination before storage (germination at t1 = 100%). Seed water content was expressed in a dry weight basis. The arrow on the *x*-axis indicates the WC_{50} value of seeds (A) or the time required to reach WC_{50} (B) for each species (abbreviated names in bold and italicized letters).

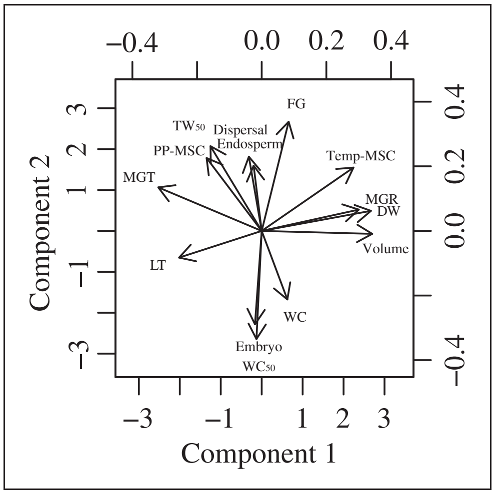

Figure 4. Relations between ecological, morphological, and functional, as well as environmental traits of the studied species, seeds, and habitat (tropical forest of Chiapas and Veracruz). Eigenvalues and eigenvectors are showed in Appendix C. FG = final germination; LT = lag time; MGR = mean germination rate; MGT = mean germination time; DW = seed dry weight; WC = seed water content dry basis; WC_{50} = WC at which viability decreased by 50% from the initial viability; TWC_{50} = time to reach WC_{50}; Endosperm = relative amount of endosperm in the seed; Embryo = embryo size; Volume = seed volume; PP-MSC = total precipitation in the month of seed collection; Temp-MSC = mean maximum temperature in the month of seed collection; Dispersal = season of seed dispersal.

15°C. This difference in storage temperature was because in 2014 seeds of *N. coriacea* with 78.8 ± 2.93% germination did not germinate after 90 days of storage at room environment (23 ± 0.5°C, 50 ± 2.2% RH; A. G. Becerra-Vázquez, personal observation, January, 2015). Thus, a storage temperature of 15°C may have entailed a longer time to reach WC_{50}. Therefore, the time required to reach WC_{50} for seeds of *N. coriacea* at 23°C might be less than 90 days, while at 15°C seeds of *N. coriacea* had a FG of 13% after 180 days. Regardless of this, the WC_{50} values of both species are consistent with those reported by Hong and Ellis (1996) for tropical recalcitrant seeds. In case of *T. tepezapote*, a closely related species *T. brasiliensis* has seeds with ecological longevity below 60 days (Pires, Cardoso, Joly, & Rodrigues, 2009). Inside the tropical forest, temperature could be almost constant above and beneath the litter (Vázquez-Yanes & Orozco-Segovia, 1994), closer to 23°C than to 15°C. Among the other *Nectandra* species, some are classified as recalcitrant (de Carvalho, Davide, Silva, & Carvalho, 2008).

Even though *M. mexicana* seeds had low WC_{50} (11.7%), the short longevity of its seeds might be related to the anatomical and functional traits of both seeds and fruits. A small embryo is a trait of the family Magnoliaceae (Niembro-Rocas, 1989), and morphological dormancy is reported for species of *Magnolia* (Royal Botanic Gardens Kew, 2017). Nevertheless, in our study, seeds of *M. mexicana* that did not germinate were rotten. Thus, its small embryos might be highly susceptible to dehydration, without entering into dormancy state, despite the large size of the surrounding endosperm (Alcántara-Flores, 2002). On the other hand, seeds of *M. mexicana* had lower WC_{50}, as in *C. glaucifolia* and *C. baillonii*, but *M. mexicana* seeds took shorter time to reach WC_{50} (9 days) compared with both species (> 80 days). Therefore, *M. mexicana* seeds might be classified as recalcitrant. Seeds of *M. ovata*, a species closely related to *M. mexicana* (Figlar & Nooteboom, 2004), loose water rapidly during dehydration in silica gel (~10% from initial 100%), and after this dehydration, the FG decrease from 84% to 19% (José, Da Silva, Davide, Melo, & Toorop, 2011). Pupim et al. (2009) found that *M. ovata* seeds have a relatively low WC ($WC_{db} = 30\%$ calculated from WC_{fb}, according to Caddick (2005)). This species has a dehiscent dry fruit that exposes seeds to drying before dispersal, thus rendering them highly susceptible to dehydration (José et al., 2011). This was observed in field in *M. mexicana*.

Seeds of *C. baillonii* had low WC_{50} (12%) and required 80 days to reach WC_{50}. Therefore, its seeds might be recalcitrant. Seeds of *C. baillonii* have been reported to be desiccation-sensitive (Rodríguez et al., 2000). As pointed out earlier, seeds of *M. mexicana* and *C. baillonii* exhibited no difference in their WC_{50}; but the fact that seeds of *C. baillonii* required a longer time to reach WC_{50} than *M. mexicana* is interesting. Both species have small embryos and abundant endosperm (Niembro-Rocas, 1989). However, they differ in seed anatomy, because the seed coat of *C. baillonii* has an inner tegument with multiple folds, and these folds extend into the fissures present in the endosperm tissue, that is, ruminate endosperm (Niembro-Rocas, 1989). Also, *C. baillonii* seeds were larger than those of *M. mexicana*. However, a single factor such as seed size cannot predict longevity in desiccation-sensitive seeds (Hill et al., 2012), influencing partially the dehydration rate of the seed, as it occurs in some tropical species (Hill et al., 2010). Large seeds have a great seed surface to mass volume ratio (Cleri, 2016); thus, they dehydrate at a slower rate than small seeds. Therefore, seed structure and size might explain the differences in seed longevity of *C. baillonii*.

We found annual variation in desiccation sensitivity in seeds of *C. baillonii*: 2015-S had the lowest WC_{50} compared with 2016-S. Weather conditions have influence on seed development. Indeed, RC-seeds from 2015 had higher FW than 2016. Seeds produced in different years can exhibit variation in their morphological and functional traits, as is the case of some tropical species (Sánchez-Coronado et al., 2007; Lamarca et al., 2016). Thus, weather conditions might have a similar effect during the development of the seeds of *C.baillonii*, because 2014 (the development year for seeds collected in 2015) had higher monthly mean maximum temperatures compared with 2015 (climatic data from Torre CONAGUA-SMN—CONANP—IBUNAM, Comisión Nacional del Agua, 2017). On the other hand, we found that seed vigor for *C. baillonii* increased after 30 days of storage for seeds collected in 2015 but not in 2016. This result agrees with that of Rodríguez et al. (2000), which found that a previous mild dehydration of the seeds of *C. baillonii* increased germination rate and final germination. The improving of germination velocity with the mild dehydration of seeds before germination is also found in other tropical species. (Eggers, Erdey, Pammenter, & Berjak, 2007; Rodríguez et al., 2000). During mild dehydration, seeds might end the seed maturation phase (maturation and dryness; Vertucci & Farrant, 1995) and maintain their active metabolism; so, if after this period they are placed in optimal germination conditions, seed germination rate might increase, as it occurs in recalcitrant seeds of *Avicennia marina* (Farrant et al., 1985).

Seeds of *C. glaucifolia* had the lowest value of WC_{50} (4.6%) and required the longest time to WC_{50} (~426 days). This seems to be closely related to the values reported for intermediate seeds (Hong & Ellis, 1996), so *C. glaucifolia* might have this storage behavior. Seeds of *C. elegans* lost >50% of their initial viability when WC of seed reach 16%; while in the less sensitive *C. microspadix* seeds, the loss of >50% of initial viability occurs when seeds reach WC of 7% (Carpenter & Ostmark, 1994). Therefore, seeds of *C. glaucifolia* had a desiccation response similar to that of *C. microspadix*. Conversely, seeds of *C. glaucifolia* are the smallest compared with the other studied species; however, they might have a high dehydration rate corresponding to their high surface/volume ratio (Cleri, 2016). A structural trait in seed of *C. glaucifolia* might be related to its longer time required to reach WC_{50}. The fruit and seed tissues (endocarp and hard endosperm) that surround its embryo (Corner, 1976) isolate it more than the seed coat does in the other studied species. Internal differences in water distribution along with physical changes in seed structure might explain the unexpected desiccation patterns in seeds, as is the case with other rainforest species (Hill et al., 2010). Finally, morphophysiological dormancy is common in palms (Baskin & Baskin, 2014), such as *Chamaedorea* spp (Carpenter & Ostmark, 1994). The removal of dormancy might require a seed life span longer than in quiescent seeds that have a faster germination.

Effect of Temperature in Seed Longevity

The longevity of tropical desiccation-sensitive seeds can be extended by storage at ≥10°C (Hong & Ellis, 1996). In this study, longevity of *C. glaucifolia* and *C. baillonii* seeds was longer at 15°C than at 23°C, 10°C, and 5°C. Nevertheless, seeds of *M. mexicana*, *N. coriacea*, and *T. tepezapote* exhibited slower aging at 5°C than at $\geq$15°C. Seeds of these three species have lipid reserves (Niembro-Rocas, 1989), like temperate red oaks with seeds that have a high lipid content (17.54 ± 4.43%, $n = 26$ species; data included from Bonner & Vozzo, 1987; Xia, Seal, Chen, Zhou, & Pritchard, 2010) and relatively longer viability than white oaks. Tropical species that can also be found in subtropical and even temperate habitats, such as *Calophyllum brasiliense* and *Persea americana*, can prolong their longevity at temperatures below 10°C (Gálvez-Cendegui, Peñaloza, Oyanedel, & Castro, 2017; Nery, Prudente, Alvarenga, Paiva, & Nery, 2017). Moreover, differences in lipid composition in seeds are related to differences in the chilling sensitivity of several species of *Cuphea*, a tropical genus with intermediate seeds (Crane, Miller, Van Roekel, & Walters, 2003). Thus, to clarify this variation, further research must include a biochemical analysis of seeds that considers phylogenetic affinity and the geographic distribution of species.

Seeds of the studied species, except *C. glaucifolia*, are probably recalcitrant. Since we did not follow the protocol to determine seed storage behavior (e.g., Hong & Ellis, 1996), further research is needed that includes the storage of seeds dehydrated to a specific WC and placed at temperatures above and below freezing. Moreover, a detailed determination of the presence of seed dormancy is required, as in *C. glaucifolia*, because it demonstrated a reduction in MGT after storage, which could indicate dormancy removal. The presence of dormancy could mask the degree of desiccation sensitivity in tropical seeds (Rodríguez et al., 2000).

Implications for Conservation

The current deterioration of tropical forest requires the implementation of conservation strategies, but highly threatened species, such as those with desiccation sensitive seeds, clearly require special attention compared with other members of the plant community. Thus, knowledge about desiccation sensitivity in seeds is an essential step before designing in situ conservation and restoration programs for species with short-lived seeds (e.g., seedlings from seed in nurseries, direct seeding). In this study, we discovered that all species had short-lived desiccation-sensitive seeds. Therefore, this seed trait must be considered for conservation and restoration strategies of the species' habitat. In the same manner, the propagation and storage of seeds of these species must take into account their limited longevity and the temperatures with which the longevity can be extended.

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Appendices

Appendix A. Results of Multiple Linear Regressions Between Final Germination, Storage Time (Sti) and Storage Temperature (ST) for the Studied Species.

Species	Parameter	Estimate	Std. Error	t	p	ST	β
C. glaucifolia (2015)	Intercept (α)	9.973	0.127	78.51	.00001		
$R^2 = 0.959$	sqrt(Sti)	–0.151	0.0166	–9.07	.00001	5°C	–0.151
$F_{(4,14)} = 58.69$	sqrt(Sti) × ST = 10°C	–0.065	0.0202	–3.24	.0087	10°C	–0.216
$p = .00001$	sqrt(Sti) × ST = 15°C	0.058	0.0202	2.88	.0162	15°C	–0.092
	sqrt(Sti) × ST = 23°C	0.027	0.0202	1.36	.2022	23°C	–0.123
C. baillonii (2015)	Intercept (α)	81.607	3.4913	23.37	.00001		
$R^2 = 0.943$	Sti	–0.274	0.0482	–5.69	.0023	10°C	–0.274
$F_{(3,8)} = 28.06$	Sti × ST = 15°C	0.163	0.0606	2.68	.0433	15°C	–0.111
$p = .0015$	Sti × ST = 23°C	–0.122	0.0606	–2.01	.1003	23°C	–0.396
C. baillonii (2016)	Intercept (α)	95.185	1.7987	52.91	.00001		
$R^2 = 0.99$	Sti	–0.24	0.0248	–9.69	.0002	15°C	–0.24
$F_{(3,\ 8)} = 175.89$	Sti × ST = 23°C	–0.231	0.0312	–7.39	.0007	23°C	–0.472
$p = .00001$	Sti × ST = 5°C	–0.157	0.0312	–5.02	.004	5°C	–0.398

(continued)

Appendix A. Continued

Species	Parameter	Estimate	Std. Error	*t*	*p*	ST	β
M. mexicana (2015)	Intercept (α)	9.627	0.354	27.19	.00001		
$R^2 = 0.984$	sqrt(Sti)	–0.638	0.0472	−13.5	.00001	5°C	–0.638
$F_{(3,\ 8)} = 103.19$	sqrt(Sti) × ST = 15°C	–0.316	0.0737	–4.28	.0078	15°C	–0.954
$p = .0001$	sqrt(Sti) × ST = 23°C	–0.389	0.0737	–5.27	.0033	23°C	–1.027
N. coriacea (2016)	Intercept (α)	94.467	7.0043	13.48	.00001		
$R^2 = 0.832$	Sti	–0.41	0.0823	–4.97	.0042	15°C	–0.41
$F_{(2,\ 7)} = 12.40$	Sti × ST = 5°C	0.244	0.0912	2.67	.0441	5°C	–0.166
$p = .0115$							
T. tepezapote (2016)	Intercept (α)	8.56	0.6246	13.7	.00001		
$R^2 = 0.894$	sqrt(Sti)	–0.481	0.0926	–5.19	.0013	15°C	–0.481
$F_{(3,\ 10)} = 19.80$	sqrt(Sti) × ST = 23°C	–0.075	0.1072	–0.7	.5052	23°C	–0.557
$p = .0008$	sqrt(Sti) × ST = 5°C	.107	.0946	1.14	.2915	5°C	–.373

Note. Year of seed collection is indicated after species name. Slopes values (β) are indicated.

Appendix B. Functions Used for the Determination of WC_{50} and Time to Reach WC_{50}, Expressed as the Relation Between the Seed's Water Content (WC) and Seed Viability (FG) and WC and Storage Time (Sti).

Species	FG vs. WC		WC vs. Sti	
	Function	R^2	Function	R^2
C. glaucifolia	$y^{-1} = a + be^{-x}$	≥0.89	$y = a + b^{-x/c}$	≥0.98
C. baillonii	$y = a + b\ln x$	≥0.93	$y = a + b^{-x/c}$	≥0.99
M. mexicana	$y = a + bx$	≥0.90	$y^{-1} = a + bx^{0.5}$	≥0.93
N. coriacea	$y = a + b\ln x$	≥0.95	$y = a + bx^2$	≥0.91
T. tepezapote	$y = ax^b$	≥0.85	$y = a + b^{-x/c}$	≥0.98

Note. *p* values for all fittings were < 0.05.

Appendix C. Eigenvalues and Eigenvectors of Principal Component Analysis Done With Morphological and Functional Seed Traits Along With Ecological and Environmental Traits of the Habitat of the Studied Species.

	Component 1	Component 2	Component 3
Eigenvalue (%)	2.32	2.20	1.72
Percentage variation explained	0.38	0.35	0.21
Eigenvectors			
FG	0.10	0.42	−0.10045965
LT	−0.31932204	−0.10329617	0.36
MGR	0.38	0.08	0.17
MGT	−0.39985941	0.17	−0.02350418
DW	0.42	0.08	−0.0481389
WC	0.10	−0.26520745	−0.27745038
WC_{50}	−0.02027922	−0.41841439	−0.20356546
TWC_{50}	−0.19807148	0.33	−0.26254916
Endosperm	−0.03109828	0.25	0.45
Embryo	−0.02600443	−0.36145248	−0.3483421
Volume	0.43	−0.0113558	−0.04894734
PP_MSC	−0.21306285	0.28	−0.34563801
Temp_MSC	0.35	0.25	−0.06838661
Dispersal	−0.04966601	0.29	−0.43476992

Note. FG = final germination; LT = lag time; MGR = mean germination rate; MGT = mean germination time; DW = seed dry weight; WC = seed water content dry basis; WC_{50} = WC at which initial viability decreased by 50%; TWC_{50} = time to reach WC_{50}; Endosperm = relative amount of endosperm in the seed; Embryo = embryo size; Volume = seed volume; PP-MSC = total precipitation in the month of seed collection; Temp-MSC = mean maximum temperature in the month of seed collection; Dispersal = season of seed dispersal.