Seed Priming Effects on Germination and Seedling Establishment of Useful Tropical Trees for Ecological Restoration

Authors: Peraza-Villarreal, Humberto, Sánchez-Coronado, María E., Lindig-Cisneros, Roberto, Tinoco-Ojanguren, Clara, Velázquez-Rosas, Noé, et al.

Source: Tropical Conservation Science, 11(1)

Published By: SAGE Publishing

URL: https://doi.org/10.1177/1940082918817886

Research Article

Tropical Conservation Science
Volume 11: 1–15

DOI: 10.1177/1940082918817886
journals.sagepub.com/home/trc
SAGE

Seed Priming Effects on Germination and Seedling Establishment of Useful Tropical Trees for Ecological Restoration

Humberto Peraza-Villarreal[1,2], María E . Sánchez-Coronado[1], Roberto Lindig-Cisneros[3], Clara Tinoco-Ojanguren[4], Noé Velázquez-Rosas[5], Luisa Cámara-Cabrales[6], and Alma Orozco-Segovia[1]

Abstract

We assessed the effects of seed priming and soil retainers on seed germination and early seedling performance of useful species in a tropical semideciduous forest in Veracruz, México. We determined mass and water and lipid content in the seeds of *Albizia saman*, *Cedrela odorata*, *Enterolobium cyclocarpum*, and *Swietenia macrophylla*. The seeds were exposed to hydropriming and natural priming (seed burial inside the soil) and germinated at 25°C and 25/35°C. The produced seedlings were grown in a shade house and planted in a plain terrain and a hillside (slope 75%). Seedling growth and survival were evaluated. *S. macrophylla* and *E. cyclocarpum* seeds had the lowest and highest water content, respectively. *S. macrophylla* and *C. odorata* had oil seeds. *A. saman* and *E. cyclocarpum* seeds had physical dormancy. Natural priming improved germination in *A. saman*, *C. odorata*, and *S. macrophylla* while hydropriming and 25/35°C enhanced germination in *E. cyclocarpum*. In the shade house, natural priming promoted seedling growth in all studied species and in the field survival of *A. saman* and *S. macrophylla*. In *E. cyclocarpum*, this effect was obtained with hydropriming in the plain terrain. In the hillside, hydropriming and natural priming and 25/35°C improved survival of *S. macrophylla* and *E. cyclocarpum*, respectively. Seed burial for 8 days improved germination, seedling performance, and survival. To bury seeds inside a pot placed in a shade house induced natural priming in *C. odorata*. We suggest natural priming for *A. saman*, *C. odorata*, and *S. macrophylla*, and hydropriming for *E. cyclocarpum* seeds. Germination pretreatments were inexpensive and easy tools potentially applicable in restoration and conservation programs.

Keywords

restoration ecology, seedling growth and survival, soil retainers, tropical semideciduous forest, useful timber species

Introduction

To maintain the biodiversity and functionality of the ecosystem, there is a great interest in restoring tropical and temperate forests with native species (Bozzano et al., 2014; Montagnini & Finney, 2011; Rogers & Montalvo, 2004). Nevertheless, the success of these projects relies heavily on the proper selection of native species. Criteria for selection ought to include native species that provide products or services required by local people (Vázquez-Yanes & Batis, 1996; Vázquez-Yanes, Batis, Alcocer, Gual, & Sánchez, 1999). Therefore, restoration practices based on native species are urgently required to face the effects of deforestation and climatic change, but there is

[1]Departamento de Ecología Funcional, Instituto de Ecología, Universidad Nacional Autónoma de México, México
[2]Posgrado en Ciencias Biológicas, Universidad Nacional Autónoma de México, México
[3]Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México, México
[4]Departamento de Ecología de la Biodiversidad, Instituto de Ecología, Universidad Nacional Autónoma de México, México
[5]Centro de Investigaciones Tropicales, Universidad Veracruzana, México
[6]Jefatura de Posgrado, División Académica de Ciencias Biológicas, Universidad Juárez Autónoma de Tabasco, México

Received 31 July 2018; Revised 13 November 2018; Accepted 17 November 2018

Corresponding Author:
Alma Orozco-Segovia, Departamento de Ecología Funcional, Instituto de Ecología, Universidad Nacional Autónoma de México, Av. Universidad 3000, Del. Coyoacán, C. P. 04510, México.
Email: aorozco@ecologia.unam.mx

limited knowledge about propagation requirements for most of the native species as well as methods to decrease seedling and sapling mortality in the field (Lamb, 2012). The use of locally valuable native species is also limited because of the lack of nurseries interested in their propagation; therefore, a limited number of native species are propagated worldwide, especially in the tropics (Schmidt, 2000).

To incorporate local people in restoration activities and make them part of the success of ecological restoration, it is necessary to study early stages of the plant life cycle, improve field survival, and generate inexpensive treatments which are easy to apply for any people. Performance of seeds and seedlings can be increased by applying pretreatment to seeds and seedlings before transplanting them to the field (Benítez-Rodríguez et al., 2014; Singh & Chaturvedi, 2018). Seed priming (hydration followed by dehydration, sensu Heydecker, Higgins, & Gulliver, 1973) has been successfully implemented to increase seed and seedling performance of agricultural plants and also for some native plants (Benech-Arnold & Sánchez, 2004; Pedrero-López, Rosete-Rodríguez, Sánchez-Coronado, Mendoza-Hernández, & Orozco-Segovia, 2016; A. Sánchez, Orta, & Muñoz, 2001; J. A. Sánchez et al., 2006; Schmidt, 2000). The priming treatments involve two steps: (a) seed hydration in water (hydropriming), osmotic solutions of NaCl (osmopriming), or other solutes; in a solid matrix as vermiculite (matrix priming); or it can occur naturally in the soil (natural priming; Benítez-Rodríguez et al., 2014; Gamboa de Buen et al., 2006; González-Zertuche et al., 2001; Lush, Kaye, & Groves, 1984), and (b) seed dehydration, in which all priming treatments ought to end before radicle protrusion; thus, after hydration, seeds are dehydrated up to their initial water content. During hydration, important advances in the germination process take place, such as mobilization of reserves, reparation of DNA, RNA, cell membranes, organelles, and others (Bray, 1995). Seeds maintain these changes during storage and, consequently, primed seeds germinate fast and synchronically. Hydropriming and natural priming have been applied successfully to orthodox seeds (long-lived; Orozco-Segovia et al., 2014). In the last few decades, it has been demonstrated that priming treatments can be an option to improve restoration practices (Benítez-Rodríguez et al., 2014; Orozco-Segovia et al., 2014; Pedrero-López et al., 2016; Singh & Chaturvedi, 2018).

In Veracruz, México, the tropical rainforest has a high biological diversity (Rodríguez-Luna et al., 2011). However, currently, this plant community occupies only 16% of its original coverage (Benítez, Pulido, & Equihua, 2004). Accelerate recovery of vegetation using restoration strategies takes a long time and is expensive; therefore, achieving this goal in a short time seems challenging (Benítez et al., 2004). However, in the tropics, cultivation and enrichment of yards around houses and agricultural lands with useful trees can be a strategy to increase plant cover and promote connectivity among forest fragments. In the vicinity of the Pre-Columbian archaeological site, El Tajín, the population (mainly indigenous Totonac) is impoverished. Vanilla cultivation (*Vanilla planifolia* Jacks. ex Andrews) is prevalent in the region. At present, climatic (high temperatures and low precipitation) and microclimatic changes (lack of tree shade) associated with deforestation are some of the causes which place traditional vanilla cultivation at risk (Borbolla-Pérez, Iglesias-Andreu, Luna-Rodríguez, & Octavio-Aguilar, 2016). To preserve vanilla cultivation, restoration of the native tree cover has become an urgent task (ZMAET, 2009). For increasing people's interest in restoration projects, we suggested to the community board of "San Antonio Ojital Nuevo" to start the restoration of native plant cover in the communal parcels adjacent to their homes with species useful for them. As a result, the communal assembly and the town council indicated to us that we could plant trees in the schoolyard and a commoner's yard. The purposes of our research were (a) to assess in the seeds of four native species, of the tropical semideciduous forest, the effect of priming treatments on seed germination and seedling growth, in a shade house, and in the field; (b) to generate an easy practice, which favors seed germination and seedling establishment of useful species; and (c) to show the community, how plant cover can be easily increased to provide shade to people, houses, cattle, vanilla culture, and to promote ecological tourism in near future. This last practice could be successful because this town is in the polygon of the archaeological site.

Thus, for the improvement of seed germination and seedling establishment, we applied hydropriming and natural priming to the seeds of four important species for the San Antonio Ojital Nuevo inhabitants: *Albizia saman* (Jacq.) Merr., *Cedrela odorata*, *Enterolobium cyclocarpum* (Jacq.) Griseb., and *Swietenia macrophylla* King). In previous studies, it has been reported that scarified seeds of *A. saman* germinate in 80% after 35 days (Royal Botanic Gardens Kew [RBGK], 2017), the seeds of *C. odorata* germinate in 50% to 92% after 28 days, scarified seeds of *E. cyclocarpum* seeds germinate in 100% after 40 days (Vázquez-Yanes et al., 1999), and *S. macrophylla* germinate in 42% to 90% in a period from 40 to 128 days (Gullison, Panfil, Strouse, & Hubbell, 1996; Vázquez-Yanes et al., 1999).

Methods

Study Area

The semideciduous tropical forest in the community of San Antonio Ojital Nuevo is located in Papantla de

Olarte municipality, in the state of Veracruz, Mexico, at 20°27′38″N, 97°21′47″W, 240 m asl. The climate is warm subhumid extreme Ax(w)(e)w' (García, 1988), with annual average temperatures of 22°C, 18°C, and 29°C (mean, minimum, and maximum, respectively). Annual precipitation is 1,186 mm, concentrated from June to October (Servicio Meteorológico Nacional, 2014). The soils are thin layers of luvisols distributed among Neogenic upwelling limestone. The area was deforested and, consequently, the soils are deeply eroded, but small patches of old successional vegetation remain, with some valuable species from the original tropical forest, such as *C. odorata* L., *Bursera simaruba* (L.) Sarg., *Ceiba pentandra* (L.) Gaertn., and *Zwelania guidonia* (Sw.) Britton & Millsp. (ZMAET, 2009). In this town, the land use is communal. The community has a population of 390 individuals in a male:female ratio of 1.06 (adults = 64.08% and children = 35.92%), and 19% of the inhabitants are smallholder farmers or cattlemen. Subsistence agriculture and fruit culture (corn, bananas, and citrus) and livestock raising take place on the slopes of small limestone hills. These activities had increased notably in the last century with an increase in deforestation (ZMAET, 2009).

Studied Species

The selected tree species were two Fabaceae, *A. saman* and *E. cyclocarpum*; two species from the Meliaceae, *C. odorata* and *S. macrophylla* with orthodox and intermediate seeds, respectively (RBGK, 2017). The four species have high commercial and ecological values; they produce high-quality timber, have mellifluous flowers, forages for livestock, and some medicinal uses. The timber is also used to build part of the ceremonial "palo volador" (Durr, 2001; Flores, 2010; Trejo-González, 2012; Vázquez-Yanes et al., 1999). In addition, these species are used as shade trees for coffee and cacao crops and provide shade for cattle. *E. cyclocarpum* is frequently found in the disturbed tropical areas in Mexico (Pennington & Sarukhán, 2005). Fruits of *C. odorata, E. cyclocarpum*, and *S. macrophylla* were collected in February to March 2012, except *A. saman*, which did not produce fruits in 2012; thus, we used seeds collected in the same months, but in 2011. *A. saman* and *E. cyclocarpum* seeds were collected in Actopan, and *C. odorata* and *S. macrophylla* seeds were collected in Papantla. Fruits of all the species were collected directly from the trees, from at least 15 individuals per species. Per tree, we collected 30 fruits of *C. odorata* (contain 40–50 seeds per fruit) and *S. macrophylla* (~60 seeds per fruit), and 40 of *A. saman* (5–10 seeds per fruit) and *E.cyclocarpum* (8–16 seeds per fruit). Seeds were manually separated from the fruits.

Experimental Design

Fresh and dry seed mass, seed water content, and lipid content. Fresh and dry seed mass and seed water content were determined immediately after collection. Thirty seeds of each species were weighed with an analytical balance (A-200 Fisher Scientific, Fairlawn, NJ) to obtain fresh mass (FM). To allow dehydration, a cross slit was made in the seed coat of each *A. saman* and *E. cyclocarpum* seed. The seeds were dried in an oven at constant weight (Boekel Industries, Inc., Philadelphia, PA) at 80°C for 48 hours and weighed to obtain the dry mass (DM). The seed water content (WC) was calculated as a percentage of the DM ($WC_{db} = ((FM - DM)/DM) \times 100$) or as a percentage of the FM ($WC_{db} = ((FM - DM)/FM) \times 100$; Hong & Ellis, 1996). For each species, linear regression analysis between DM and FM was performed (Table Curve 2D, v.3, AISN Software, Chicago, IL, USA) to subsequently estimate the WC_{db}, without drying the seeds.

Lipid content (LC) was determined in 10 individual seeds (replicates). From each seed of *A. saman*, *E. cyclocaarpum*, and *S. macrophylla*, 0.1 g, 0.2 g, and 0.43 g of fresh seed tissue was taken, respectively. Previously, the seeds of *S. macrophylla* were deprived of the wing of spongy tissue, covering the seed (rafe-exostome; Corner, 1976). For *C. odorata*, the LC was determined in three replicates of 0.5 g, each one obtained from 30 seeds. The sample size of each species was determined by the availability of seeds. Lipid determinations were done according to Bligh & Dyer (1959). After that, the WC was calculated as an oil-free percentage (of) on a fresh basis ($WC_{offb} = (100 \times WC_{fb})/(100 - LC_{fb})$) and dry basis ($WC_{ofdb} = (100 \times WC_{db})/(100 - LC_{db})$), according to Caddick (2005). To determine WC_{ofdb}, DM of the tissue samples was calculated from the relationship between FW and DW of each species.

Effect of priming treatments on seed germination. For all following experiments and procedures, previous to be used, the seeds of *A. saman* and *E. cyclocarpum* were scarified (Sc) by immersing them in boiling water (96°C at 2,250 m asl.). The water was boiled inside a laboratory beaker and then retired from the stove; immediately, the seeds were introduced in the boiling water; after that, the water temperature was dropped to ~65°C and 8 minutes later, it reached ~25°C. Subsequently, seeds were recovered and air-dried. Before using the seeds of *S. macrophylla*, we cut the spongy wing of each seed. Controls were nontreated seeds (C).

For hydropriming treatment (HP), five replicates of 30 seeds of each species were placed in Petri dishes. To avoid oxygen deprivation, 75% of the surface of the seeds was covered with water for 48 h at 25°C (HP-25) and a 12/12-hour photoperiod inside environmental chambers (Lab-Line Instruments, Inc., 844, IL, USA) under fluorescent lamps. Simultaneously, HP was also applied at 25/35°C (16/8 hours; the highest temperature was applied at midday; HP-25/35). After hydration period, the seeds were taken out of the water and air-dried at environmental temperature (16–24°C, relative humidity (RH) 35–50%) in darkness for 48 hours.

Natural priming (NP) was applied by enclosing seeds in permeable nylon mesh bags (25×25 cm), five bags for species with 30 seeds in each one. The bags were buried in the semideciduous tropical forest at a depth of 5 cm in the soil of a forest gap. Based on the hydration curve, the seeds of *A. saman*, *E. cyclocarpum*, and *S. macrophylla* were unearthed after 7 days. As *C. odorata* germinated during burial, the seeds were buried 48 hours inside pots filled with soil of the study site, under shade house conditions (temperatures: mean 21.93 ± 2.6°C, minimum 12.77 ± 1.78°C, maximum 37.68 ± 5.49°C). The temperature inside the shade house was recorded with a datalogger (HOBO U12-013, Onset Computer Corporation, Bourne, MA, USA). After seed burial, pots were watered to field capacity. For seed recovery, the soil was covered with an aluminum foil to avoid seed exposure to light. After that, all the seeds were dried for 48 hours in darkness in laboratory conditions (16–24°C, RH 35–50%). Scarified seeds and nonscarified seeds of *E. cyclocarpum* and *A. saman* were subjected to NP. After that, NP seeds were germinated at 25°C (NP-25) and 25/35°C (NP-25/35). Particularly, the seeds with hydropriming at 25°C or 25/35°C were transferred to chambers with the same temperature. Scarified and nonscarified seeds (Sc-25, Sc-25/35, C-25, and C-25/35) were also germinated at both temperatures. All seeds were sown inside closed top plastic boxes ($22.5 \times 19 \times 8$ cm and $15 \times 13 \times 7.5$ cm, depending on seed size) on wet coarse sand as substrate. For germination, the boxes were placed randomly inside the environment chambers. The experimental design for *C. odorata* and *S. macrophylla* was 3 germination treatments (HP, NP, and C) $\times$ 5 replicates (each one of 30 seeds): 450 seeds per each species. The experimental design for *E. cyclocarpum* and *A. saman* was 4 germination treatments (HP, NP, Sc, and C) $\times$ 5 replicates (each one of 30 seeds): 600 seeds per each species.

Seedling growth in the shade house. Initially, seedlings of all species were grown in the shade house; however, the seedlings of *C. odorata* presented damping off and thus this species was excluded from this experiment. Coetaneous (2 days old) seedlings of *A. saman* (42 seedlings), *E. cyclocarpum* (42), and *S. macrophylla* (34) obtained from the priming treatments and Sc (identified with the seed treatment abbreviation) were transplanted to black plastic bags (12×25 cm), with small holes at the bottom and filled with soil of the study site. After 1.5 months, the plant height was measured from the stem base to the seedling tip (SH), the diameter at the base stem (DBS), and number of leaves (NL) per seedling was counted.

Seedling survival in the field. After 90 days in the shade house, seedlings were measured and then transferred to San Antonio Ojital Nuevo in September 2012; the seedlings were acclimatized for 7 days and then transplanted at two sites; one group of seedlings was planted in each one of the two sites with contrasting slope. The sites were in a schoolyard was $480\,m^2$ in size with a 1% slope (plain terrain) and the commoner yard was $100\,m^2$ in size with a 75% slope (hillside). In each site, at least 12 seedlings from each seed treatment of the three species were planted, randomly, in a quincunx pattern at a distance of 1.5 m between the plants. We deprived both sites of herbs and shrubby vegetation. Because of the sharp slope, during rains, many seedlings fell toward the base of the slope. Thus, after a new transplant, at the base of each seedling, facing the direction opposite to the slope (downside), we placed a retainer for trapping lixiviated soil and maintaining the soil and seedling in each place. The retainers (30×16 cm) were made with a sisal fabric mesh obtained from sacks used to pack grains. Each retainer was fixed to the soil by two wooden sticks (taken from debris of local vegetation), tied to both ends of the fabric and buried 15 cm in the soil.

Survival was recorded every 15 days from September 2012 to May 2013 in the plain terrain and to August 2013 in the hillside.

Data Analyses

In the recently collected seeds, a linear regression analysis between seed DM and FM was performed for each species (TableCurve 2D, ver. 3 (AISN, Software, Chicago IL, USA)). All percentages were arc-sin transformed. After hydration, the final WC_{db} values were compared for each species by analysis of variance (ANOVA) tests using Statgraphics Ver. 5.0 (Statistical Graphics Centurion XV v. 15.2. Corporation, Englewood Cliffs, NJ, USA).

To study the priming and temperature effects on seed germination, the cumulative germination percentages were arc-sin transformed and fitted to the exponential sigmoid model

$$y = a/[1 + b^{(-cx)}]$$

or the sigmoid model

$$y = a/[(1+bx^{c})]$$

Table 1. Seed Traits of Four Tropical Tree Species Growing in Papantla de Olarte Municipality, Veracruz, Mexico (mean ± *SD*, *n* = 30).

Species	Fresh mass (mg)	Dry mass (mg)	Length (mm)	Moisture content fresh basis (%)	Moisture content dry basis (%)	Lipid content dry basis (%)	Oil-free moisture content dry basis (%)
Albizia saman	0.28 ± 0.05	0.25 ± 0.04	12.87 ± 0.61	7.87 ± 1.46	8.56 ± 1.72	7.76 ± 2.1	9.29 ± 1.86
Cedrela odorata	0.019 ± 0.002	0.018 ± 0.02	28.17 ± 2.16	8.52 ± 2.51	9.3 ± 3.03	34 ± 4.8	14.24 ± 4.58
Enterolobium cyclocarpum	0.81 ± 0.12	0.71 ± 0.1	17.57 ± 0.95	12.26 ± 1.56	14 ± 2.06	4.06 ± 0.26	14.6 ± 2.15
Swietenia macrophylla	0.59 ± 0.09	0.56 ± 0.08	25.99 ± 2.14	4.95 ± 0.92	5.21 ± 1.04	53.33 ± 1.33	11.17 ± 2.22

Note. Seed length of *C. odorata* and *S. macrophylla* is reported for seeds without wings. *SD* = standard deviation.

From these fittings, the maximum germination rate (velocity, the maximum first derivative in these curves) and the lag time (time for the first seed germinates) were obtained. These parameters and final germination percentages were analyzed, individually for each species with two-way ANOVAs (three seed treatments × two temperature regimes), and post hoc comparisons were performed with Tukey's test to detect groups of homogeneous levels. The normality and homoscedasticity were determined by using Kolmogorov–Smirnov and Bartlett tests, respectively (Zar, 2010). The effect of the seeds' preconditioning treatments and germination temperatures on the seedling growth in the shade house was analyzed with two-way ANOVA test (treatments × temperature regimes) and post hoc comparisons were performed with Tukey's test to detect groups of homogeneous levels. Finally, probabilities of seedling survival in the field for each species were estimated with Logistic Regression using JMP software (v. 8, SAS Institute Inc. Cary, NC, USA). We used the Wald confidence intervals for the final seedling survival comparisons between seed priming treatments and germination temperatures (Correa & Sierra, 2003). In the Results section, only significant effects were reported.

Results

Fresh and Dry Seed Mass, Seed Water Content, and Lipids Content

The seed attributes of the four-studied species are shown in Table 1. Seed DM and FM were significantly related in the four species ($DM = a + (b \times FM)$, $R^2 \geq 95\%$, $p = .00001$).

The seeds of *C. odorata* had the lowest FM (0.019 ± 0.002 mg) and DM (0.018 ± 0.002 mg), at least an order lesser than in the other species. Seeds of *E. cyclocarpum* had the highest FM (0.81 ± 0.12 mg) and DM (0.71 ± 0.1 mg). On the other hand, the seeds of *S. macrophylla* showed the lowest WC_{fb} (4.95 ± 0.92%), WC_{db} (5.21 ± 1.04%), and the highest LC_{db} (53.33 ± 1.33%), contrasting with *E. cyclocarpum* with the highest WC_{fb} and WC_{db} and the lowest LC. The WC_{offb} among the species varied from 8.53 ± 1.58% to 14.61 ± 2.15% in *A. saman* and *E. cyclocarpum*, respectively, while the WC_{ofdb} varied from 9.28 ± 1.86% in *A. saman* to 14.24 ± 4.6% and 14.61 ± 2.5% in *C. odorata* and *E. cyclocarpum*, respectively.

Effect of Priming Treatments and Temperature on Seed Germination

Priming treatments and temperature differentially affected germination of the four studied species (Figure 1, Tables 2 and 3). Alternating temperature enhanced germination percentage in *A. saman* and *S. macrophylla*. In these species, germination rate was increased for NP, (Figure 1(a), (b), (g), and (h)). In *C. odorata*, HP reduced germination percentage and rate at 25/35°C (Figure 1(d)). HP increased germination rate in *E. cyclocarpum*. In this species, the germination percentage in C seeds was close to zero (Figure 1(e) and (f)).

Lag time was reduced in *A. saman* and *E. cyclocarpum* for both NP and HP (Figure 1(a), (b), (e), and (f)) and only NP reduced lag time in *S. macrophylla* (Figure 1(g) and (h)). In *C. odorata*, the lag time was reduced for 25/35°C in C and HP seeds (Figure 1(c) and (d)).

Seedling Growth in the Shade House

After 1.5 months in the shade house, some effects of the seed treatments were found in the growth variables of the three species (Table 4 and Figure 2). Most of the significant differences were associated with NP and alternating temperature. Only in *E. cyclocarpum*, the seedling height was improved for HP and 25°C during germination and the number of leaves in all treatments at this temperature.

Seedling Survival

The favorable effects of any of the priming treatments on the probabilities of seedling survival in the field were observed in the three species, even after 10 or 12 months in the field (Figure 3). In the plain terrain, seedling survival ranged from 0.52 to 0.93. In *A. saman*, NP regardless of temperature induced the highest probabilities of

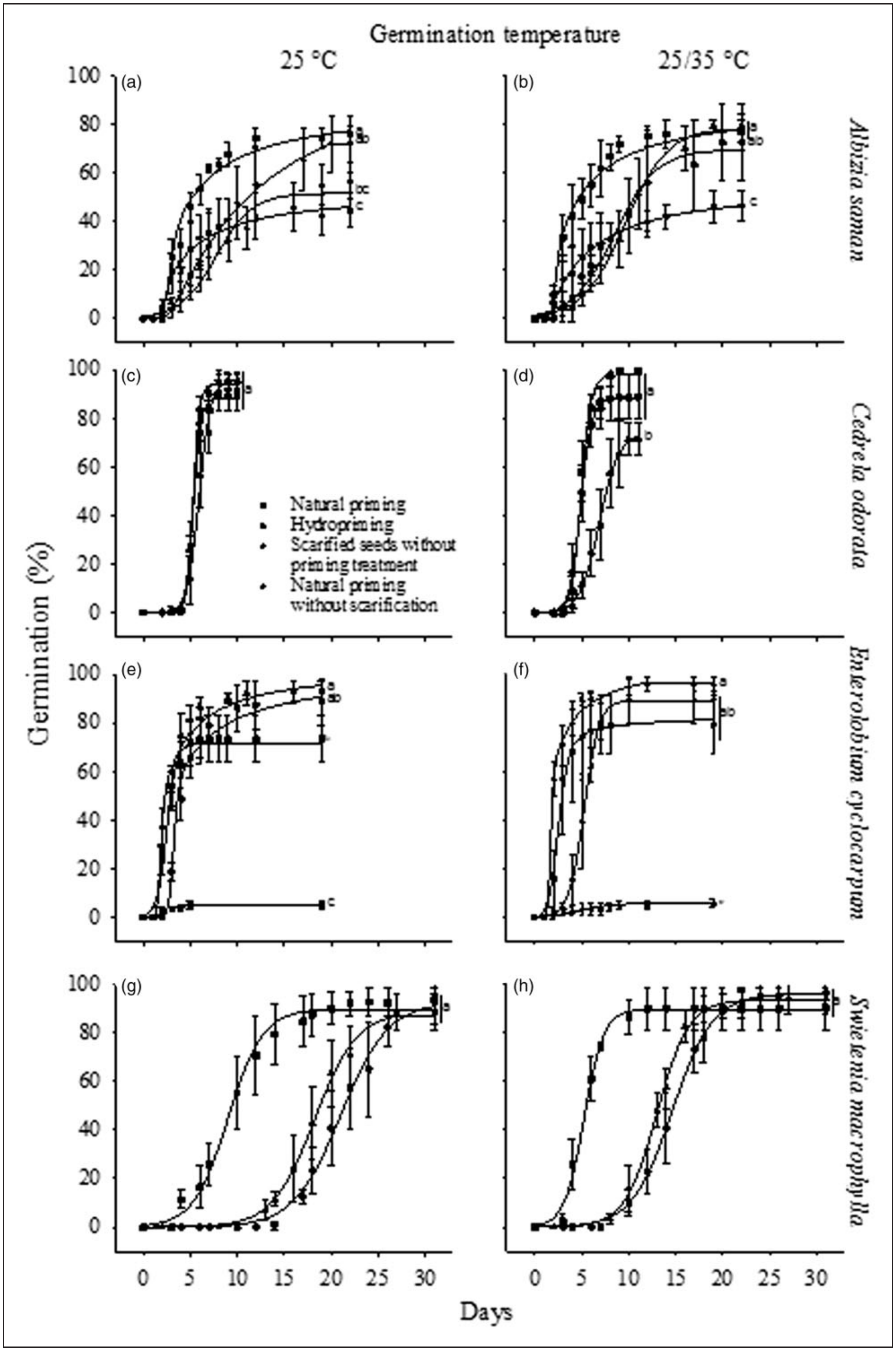

Figure 1. Cumulative germination (%) of the seeds of four tree species of the semideciduous tropical forest, in the community of San Antonio Ojital Nuevo, Papantla de Olarte municipality, Veracruz, Mexico, subjected to different priming treatments and germinated at two different temperature regimes. Before priming treatments seeds of *Albizia saman* and *Enterolobium cyclocarpum* seeds were scarified. Different letters indicate significant differences for the final germination percentages between treatments applied to the seeds. Bars indicate standard deviation.

Table 2. Germination Rate and Lag Time Values of the Seeds of Four Tree Species Treated With Hydropriming or Natural Priming and Germinated in 25°C or 25/35°C.

Species	Seed treatment	Germination rate (% d^{-1})	Lag time (days)
Albizia saman	Sc-25°C	6.64 ± 1.98 ab	1.01 ± 0.32 ab
	HP-25°C	5.45 ± 0.64 b	0.35 ± 0.22 b
	NP-25°C	13.87 ± 2.06 ab	0.88 ± 0.25 b
	NP-25°C US	13.04 ± 4.32 ab	1.06 ± 0.1 ab
	Sc-25/35°C	8.01 ± 4.32 ab	1.94 ± 1.21 a
	HP-25/35°C	6.44 ± 1.67 ab	0.59 ± 0.38 b
	NP-25/35°C	14.38 ± 3.06 a	0.46 ± 0.1 b
	NP-25/35°C US	10.32 ± 5.17 ab	0.60 ± 0.37 b
Cedrela odorata	Control-25°C	47.05 ± 8.67 a	3.35 ± 0.51 a
	HP-25°C	25.63 ± 3.4 bc	2.48 ± 0.51 abc
	NP-25°C	43.79 ± 13.83 ab	3.31 ± 0.34 ab
	Control-25/35°C	27.77 ± 8.67 abc	1.73 ± 1.09 c
	HP-25/35°C	13.39 ± 3.28 c	1.87 ± 1.02 c
	NP-25/35°C	34.56 ± 11.07 abc	1.94 ± 0.92 bc
Enterolobium cyclocarpum	Sc-25°C	21.06 ± 3.81 b	1.23 ± 0.21 a
	HP-25°C	25.01 ± 4.63 b	0.38 ± 0.13 c
	NP-25°C	27.35 ± 8.85 ab	0.50 ± 0.23 c
	Sc-25/35°C	21.77 ± 6.1 b	1.09 ± 0.95 ab
	HP-25/35°C	34.97 ± 4 a	0.04 ± 0.08 c
	NP-25/35°C	25.40 ± 6.53 b	0.55 ± 0.31 bc
Swietenia macrophylla	Control-25°C	5.82 ± 2.41 b	6.57 ± 2.21 a
	HP-25°C	6.75 ± 1.19 b	5.29 ± 1.31 b
	NP-25°C	6.78 ± 1.02 b	1.12 ± 0.61 c
	Control-25/35°C	7.01 ± 0.96 b	5.14 ± 1.01 b
	HP-25/35°C	8.42 ± 1.6 b	4.96 ± 0.89 b
	NP-25/35°C	15.69 ± 4.03 a	1.50 ± 0.28 c

Note. Different letters indicate significant differences ($p < .05$). HP = hydropriming; NP = Natural priming; Sc = scarified seeds without priming treatment; US = unscarified seeds.

Table 3. Results of a Two-Way ANOVA of the Effects of the Seed Treatments (Control, Hydropriming, and Natural Priming) and Germination Temperature (25 vs. 25/30°C) on the Germination Parameters of Four Species of the Semideciduous Tropical Forest of Veracruz, Mexico.

Species	Germination parameter	Factor	*F*	*df*	*p*
Albizia saman	Percentage	ST			*ns*
		GT	4.7	1.27	.04
		ST × GT	4.9	2.27	.01
	Rate	ST	25.1	2.27	.00001
		GT			*ns*
		ST × GT			*ns*
	Lag time	ST	8.3	2.27	.002
		GT			*ns*
		ST × GT			*ns*
Cedrela odorata	Percentage	ST	6.6	2.29	.005
		GT			*ns*
		ST × GT	18.1	2.29	.00001
	Rate	ST	15.3	2.29	.0001
		GT	17.9	1.29	.0003
		ST × GT			*ns*
	Lag time	ST			*ns*

(continued)

Table 3. Continued.

Species	Germination parameter	Factor	*F*	*df*	*p*
		GT	21.6	1.29	.0001
		ST × GT			*ns*
Enterolobium cyclocarpum	Percentage	ST			*ns*
		GT			*ns*
		ST × GT			*ns*
	Rate	ST	4.9	2.27	.017
		GT			*ns*
		ST × GT			*ns*
	Lag time	ST	11.10	2.27	.0005
		GT			*ns*
		ST × GT			*ns*
Swietenia macrophylla	Percentage	ST			*ns*
		GT	22.9	2.29	.0001
		ST × GT			*ns*
	Rate	ST	13.5	2.29	.0001
		GT	24.6	1.29	.00001
		ST × GT	9.9	2.29	.0007
	Lag time	ST	40.1	2.29	.00001
		GT			*ns*
		ST × GT			*ns*

Note. ST = seed treatment: GT = germination temperature; *df* = degrees of freedom; *ns* = not significant.

seedling survival (0.90–0.93, $\chi^2 = 5.12$, $df = 2$, $p = .05$). In *E. cyclocarpum*, alternating germination temperature produced the highest probability of seedling survival (0.91; $\chi^2 = 9.4$, $df = 2$, $p = .05$). In contrast, in *S. macrophylla*, HP induced the lowest survival probabilities (0.85; $\chi^2 = 6.75$, $df = 2$, $p = .03$).

In the hillside, seedling survival ranged from 0.08 to 0.79. For *A. saman*, there were no significant differences ($\chi^2 > 0.05$). In *E. cyclocarpum*, NP-25/35 induced the highest survival probabilities (0.79, $\chi^2 = 3.19$, $df = 1$, $p = .08$). In *S. macrophylla*, higher probabilities of seedling survival were found in the interaction between HP and 25/35 ($\chi^2 = 7.74$, $df = 2$, $p = .02$).

Discussion

Fresh and Dry Seed Mass, Water, and Lipid Content

Seed biochemical, morphological, and storage behavior information is relevant to design conservation, propagation and restoration strategies. Based on the seed LC, *S. macrophylla* (53.3%) and *C. odorata* (34%) were lipid species because they had >17% of lipids, as in soya, canola (Caddick, 2002), and *Brassica napus* seeds (33.5%; RBGK, 2017). It has been previously reported that *S. macrophylla* and *C. odorata* seeds (34%) have low LC, 40.4% and 21.4% (for *S. macrophylla* and *C. odorata*, respectively; RBGK, 2017). The storage behavior of *S. macrophylla* has been reported as intermediate because of viability being no longer than 1 year, while *C. odorata* has been reported as an orthodox species (RBGK, 2017). However, storage behavior of *S. macrophylla* is under discussion, because of some authors reporting 2 years of viability in dry storage at relatively low temperatures (3–5°C; Orwa, Mutua, Kindt, Jamnadass, & Simons, 2009). In addition, seeds of *S. macrophylla* stored under suboptimal conditions (*sensu* Vázquez-Yanes & Orozco-Segovia, 1993), in glass jars, maintained viability up to 3 years (~80%, H. Peraza-Villarreal, personal observations).

Species with intermediate storage behavior had high LC, as *Carica papaya* (29.6%, Malacrida, Kimura, & Jorge, 2011; RBGK, 2017), *Citrus limon* (41.9%, Reazai. Mohammadpourfard, Nazmara, Jahanbakhsh, & Shiri, 2014; RBGK, 2017), and *Elaeis guineensis* (49.03%, RBGK, 2017). The seed WC for these species has been reported on a fresh basis; based on these data, we calculated that their WC_{offb} might be between 34.8 and 84.36%. In contrast, *S. macrophylla* had a lower WC_{offb} (11.17 ± 2.2%) than *C. papaya*, *C. limon,* and *E. guineensis,* but *S. macrophylla* LC (53.33%) is higher than that in these three species. Because of the variability in published results, it is necessary to accurately assess the storage behavior of *S. macrophylla*. Usually, LC is related to rapid aging because of lipid peroxidation under suboptimal storage (Sung & Jeng, 1994); however, it is relevant to determine the relation between the relative content of specific fatty acid and lifespan of seeds that explains the storage behavior of some tropical species (*Caesalpinia echinata*, *Erythrina*

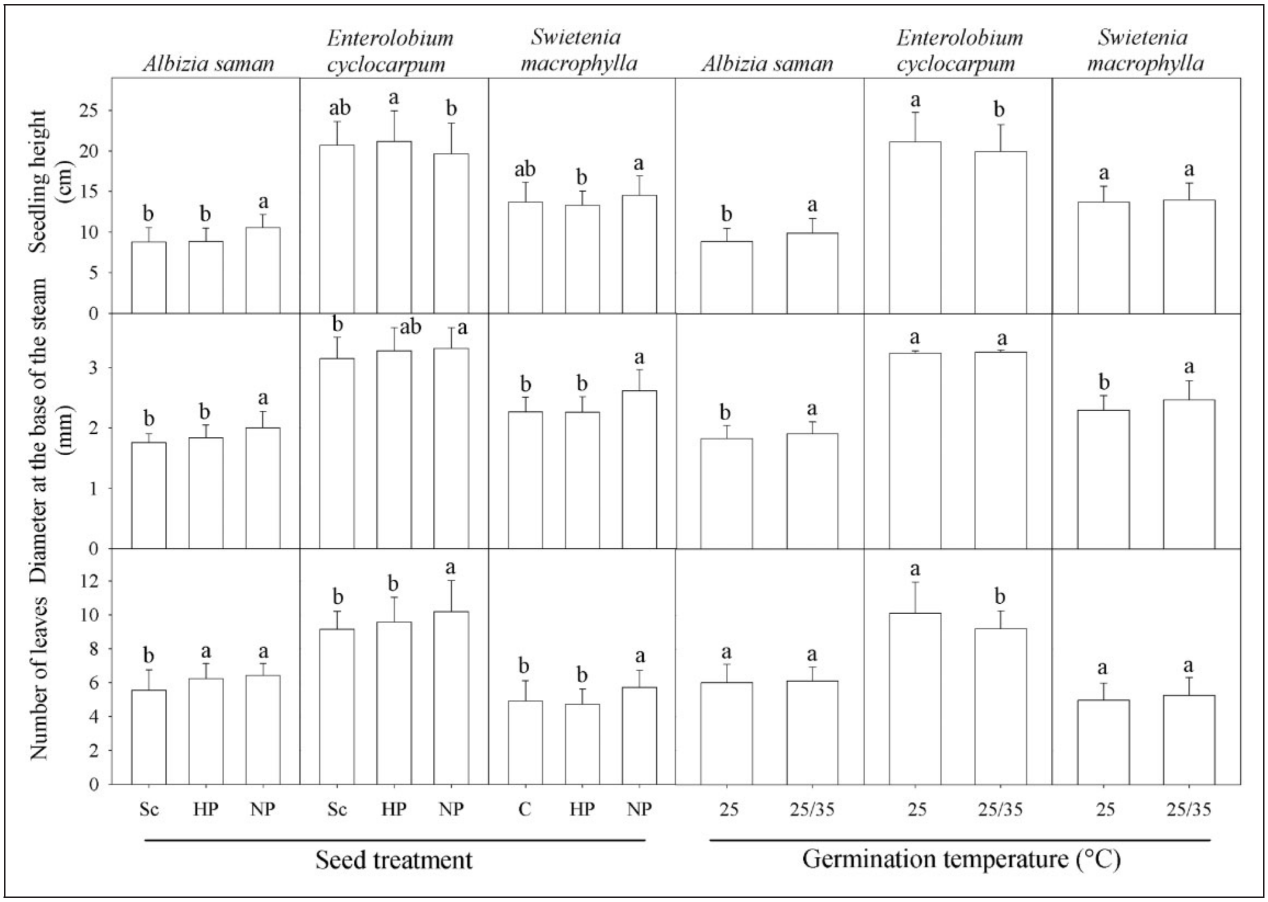

Figure 2. Growth variables of the seedlings of three tree species, of the semideciduous tropical forest, in the community of San Antonio Ojital Nuevo, Papantla de Olarte municipality, Veracruz, Mexico, growing in a shade house. The seedlings were obtained from seeds subjected to different priming treatments and germinated at two different temperature regimes. Bars indicate mean values, and error bars standard deviation. Different letters indicate significant differences for the final value of each growth variable between treatments applied to the seeds.

speciosa, *Eugenia uniflora*, and *Inga vera*; Mello, Barbedo, Salatino, & Figueiredo-Ribeiro, 2010). The two other studied species, *A. saman* and *E. cyclocarpum* had no lipid seeds and their WC_{offb} were low (8.53 and 12.77%, respectively); these are values expected for orthodox seeds of the Fabaceae family and in seed species with physical dormancy (Baskin & Baskin, 2000; RBGK, 2017). We suggest to store seeds of *S. macrophylla* in a fresh and dry environment or at 5°C (in a home refrigerator) that may be available even in rural conditions.

Effects of Temperature and Priming Treatments on Seed Germination

The effect of temperature on germination was limited to *C. odorata*; it could be related to the environmental information that the seeds of tropical species require sense to germinate in response to the environment (Vázquez-Yanes & Orozco-Segovia, 1994). The clearest effect of alternating temperature was the reduction of lag time in *C. odorata*. In natural conditions, the survival of the fast-growing seedlings of this species is higher in sunny than in shady microenvironments (Burns & Honkala, 1990); thus, the alternating temperature during germination could be acting as an environmental cue, at the beginning of the rainy season, outside of a plant cover.

Any seed priming treatment (hydric, osmotic, matric, and drum priming) may improve germination parameters, such as germination rate and synchrony. However, germination percentage can increase or decrease after priming (Bray, 1995). In this study, priming treatments did not have the same effects among studied species, but at least one priming treatment reduced the lag time, increased germination percentage, and the germination rate, which might be a competitive advantage for seedling establishment and growth. In *E. cyclocarpum*, *S. macrophylla*, and *A. saman*, germination percentage was not modified by priming pretreatments, only in

Table 4. Results of a Two-Way ANOVA of the Effects of the Seed Treatments (Control, Hydropriming, and Natural Priming) and Germination Temperature (25 vs. 25/35°C) on the Growth, in a Shade House, of the Seedlings of Three Species of the Semideciduous Tropical Forest of Veracruz, Mexico.

Species	Growth variable	Factor	*F*	*df*	*p*
Albizia saman	Seedling height	ST	24.60	2.195	.00001
		GT	21.89	1.195	.00001
		ST × GT	4.95	2.195	.008
	Diameter at the base of the steam	ST	22.31	2.195	.00001
		GT	8.32	1.195	.004
		ST × GT	0.76	2.195	.46
	Number of leaves	ST	15.85	2.195	.00001
		GT	0.58	1.195	.44
		ST × GT	4.33	2.195	.01
Enterolobium cyclocarpum	Seedling height	ST	3.99	2.244	.01
		GT	7.03	1.244	.008
		ST × GT	2.45	2.244	.08
	Diameter at the base of the steam	ST	4.58	2.244	.01
		GT	0.31	1.244	.57
		ST × GT	7.56	2.244	.0007
	Number of leaves	ST	8.86	2.244	.0002
		GT	20.52	1.244	.00001
		ST × GT	5.80	2.244	.0035
Swietenia macrophyla	Seedling height	ST	3.05	2.132	.059
		GT	0.33	1.132	.56
		ST × GT	1.57	2.132	.21
	Diameter at the base of the steam	ST	18.46	2.132	.00001
		GT	9.55	1.132	.002
		ST × GT	4.28	2.132	.01
	Number of leaves	ST	7.94	2.132	.0006
		GT	1.71	1.132	.19
		ST × GT	3.47	2.132	.03

Note. ST = seed treatment; GT = germination temperature; *df* = degrees of freedom; ANOVA = analysis of variance.

C. odorata, the HP-25/35 germination percentage decreased. All the other germination parameters were improved significantly; NP was more effective than HP for *A. saman*, *C. odorata*, and *S. macrophylla*; however, for *C. odorata*, it mainly occurred in seeds germinated at 25/35°C. In contrast, in *E. cyclocarpum* HP-25/35 shortened lag time and increased germination rate. Some of the differences obtained with priming treatments were marginal, but if germination rate and lag time were faster and shorter, respectively, such as in *S. macrophylla*, these advantages turn relevant for the nursery practices (Schmidt, 2000), because even small changes in the germination parameters might shorten permanence of seedlings in the seedbed and greenhouse or shade house.

Differences among species in seed response to treatments might be the result of the microclimate in the collection sites (Cendán, 2013; Vázquez-Yanes & Orozco-Segovia, 1982). For example, *S. macrophylla* and *C. odorata* grow in the tropical rainforest, tropical dry forest, and disturbed areas (Pennington & Sarukhán, 2005; Vázquez-Yanes & Batis, 1996). However, for this study, seed collection sites for each species differ in the precipitation regime. Seeds of *S. macrophylla* were collected in Papantla; in this site, the mean annual precipitation is 1,186 mm, the seeds are dispersed in the dry season (January to March), and trees also grow in soils with drainage problems. In contrast, *C. odorata* seeds were collected in Actopan, where mean annual precipitation is 883 mm (Servicio Meteorológico Nacional, 2014) and seeds are dispersed close to the rainy season (April to May). Therefore, *S. macrophylla* remains in the soil for at least 2 months until the following rainy season. In contrast, *C. odorata* germinates fast in the soil; in May, when the mean monthly temperature is one of the highest in the year and the rains begin. Probably, because of that, NP occurred in the seeds exposed a short time to similar conditions in the pots placed in the shade house.

In general, NP improved most of the germination variables in all the species except in *E. cyclocarpum*, in which HP enhanced germination, suggesting that the boiling water treatment did not weaken the seed coat sufficiently to be hydrated in the soil during the short

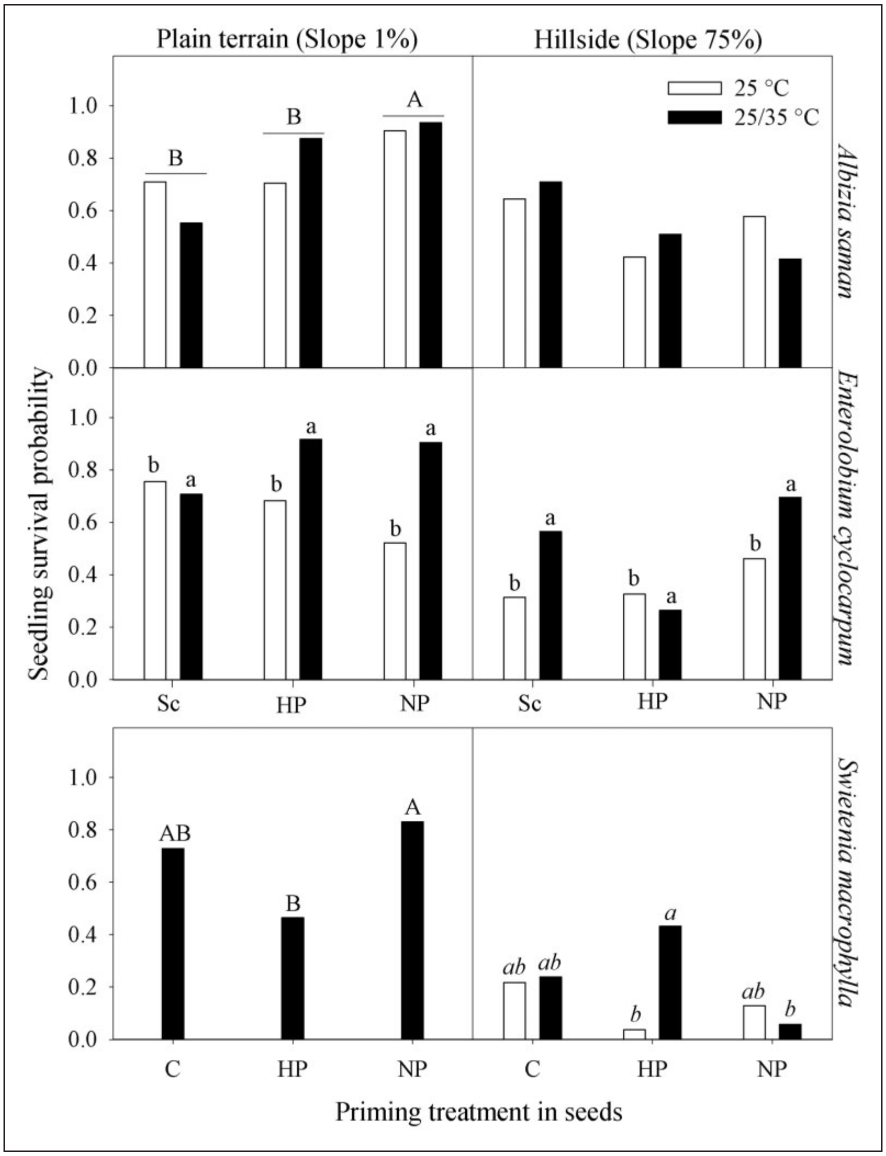

Figure 3. Final survival probability for seedlings of three tree species of the semideciduous tropical forest growing in the field in two sites with different slope. Different letters indicate significant differences: Capital letters between seed priming treatments, lowercase letters between germination temperature regimes and italicized letters indicate significant interaction between both factors. Before priming treatments seeds of *Albizia saman* and *Enterolobium cyclocarpum* were scarified to remove physical dormancy. C = control seeds, Sc = scarified seeds without priming, HP = Hydropriming, NP = Natural Priming.

burial time because soil has a lower water potential than pure water (as in HP; Taiz & Zeiger, 2006). In contrast, results obtained in *A. saman* with NP suggest that physical dormancy may be lost during burial, as in *Dodonaea viscosa* (Benítez-Rodríguez et al., 2014).

Seedling Growth in the Shade House and Survival in the Field

The enhancing effect of NP and alternating temperature on the seedling growth of *A. saman* and *S. macrophylla* may reflect the maintaining of preparation acquired by the seed's embryos to endure moisture and temperature fluctuations in the field (González-Zertuche et al., 2011). Temperature fluctuation in the shade house might also improve seedling success. The favorable effect of HP and constant temperature during germination on seedling growth of *E. cyclocarpum* is consistent in both germination and growth, which suggests that the seeds of relatively high seed size of this species require constant availability of moisture for hydration during germination pretreatments. Seedling survival in the field suggests that effects of priming on the seeds might remain in seedlings. In *D. viscosa,* it can be observed even a year after germination (Pedrero-López et al., 2016). We only planted in the field three species, *A. saman*, *E. cyclocarpum*, and *S. macrophylla*. The *C. odorata* seedlings died in the shade house because of damping off, although it has been reported that priming induces resistance to seedling diseases (Mondal & Bose, 2014). Species' distribution and diversity in the tropical forests can be related to their tolerance to high or low soil water potential (Born et al., 2015). This might explain why the seedlings of *C. odorata* survive in relatively dry soils (H. Peraza-Villarreal, personal observations). In *A. saman* and *S. macrophylla*, NP also enhanced seedling survival in the plain terrain and in *E. cyclocarpum* HP-25/35 did it. In the slope (hillside), the soil is dryer and shallower in relation to the plain terrain.

In general, the effect on survival was observed for variable periods, such as in *A. saman*, up to 9 months after being transplanted to the field and 6 months in *E. cyclocarpum*. Although seedlings were only 2 to 3 months old on being transplanted to the field, survival probabilities were from 0.45 to 0.9 in the plain terrain and from 0.2 to 0.7 in the hillside. Shade house temperature conditions might also have induced the stress memory, which contributed to the initial survival (Walter, Jentsch, Beierkuhnlein, & Kreyling, 2013). In the plain terrain, mortality was related to herbivory, trampling by people and loading animals, and the use of herbicides. However, survival was significantly higher in seedlings coming from pretreated seeds, as in *A. saman* and *S. macrophylla*. In the hillside, the main mortality factors were herbivory, branches and rocks rolling down the slope, and high heterogeneity in soil and shade distribution in the plot. In spite of that, the hillside survival was successful, because of the use of inexpensive soil retainers, which both maintained the soil and supported the seedlings on the sharp slope. Without the retainers, it might not have been possible to achieve seedling establishment at this stressful site.

Two years after this study, in the plain terrain, the school teacher (nonnative from Papantla) cut 70% of the trees to make a football field. In contrast, in the hillside the farmer cut several trees (1.5 m in height) to clear the area and then he used the remaining trees as support and shade for vanilla culture, which requires ~50% of shade. After 3 years, these trees were around 2 m in height (H. Peraza-Villarreal, personal observations).

Conclusions

Our results suggest that for three of the studied species, seed burial for 7 days in the native soil gave seeds with traits which provided advantages against environmental stress by way of improving germination and increasing seedlings' or saplings' performance. Particularly, because of *A. saman* and *E. cyclocarpum* seed coat being impermeable to water, we recommend NP after water boiling scarification and longer times of burial. The burial time ought to be related to the period seeds remain in the soil from dispersal to the rainy season. For *C. odorata*, the short time between seed dispersal and field germination and fast seed germination made seed burial difficult in the field. However, seed burial in simulated soil conditions (inside a pot placed in a shade house) was enough to induce priming in *C. odorata*, because the way the seeds take water from the substrate determines seed response (Gibson & Bachelard, 1986; Wuest, 2007). We can therefore suggest applying NP in the field for *A. saman*, *C. odorata*, and *S. macrophylla* and HP for the *E. cyclocarpum* seeds. Despite the agreements made with the inhabitants of San Antonio, Ojital Nuevo, those related to the private property only were fulfilled. At difference, in the school yard (municipal property) the teacher took a personal decision that truncated the effort made.

Implications for Conservation

Our research proposes inexpensive germination pretreatments (hydropriming and natural priming), easy to put into practice, and potentially applicable to many other species and forest types. To maintain the biodiversity and functionality of tropical forests, it is necessary to generate conservation and restoration strategies using native species useful for people (Bozzano et al., 2014). Thus, the success of these projects relies heavily on the proper selection of native species, increase in the knowledge about plant propagation and establishment, and making these activities easy to apply in the daily life of rural communities. Finally, the continuity of this restoration effort was defined by the type of the land property regime: private or common. Thus, it is necessary to take in account this aspect.

Acknowledgments

The authors are grateful to León Pasiano Martínez from the San Antonio Ojital Nuevo population for providing field support during this research. The authors also thank Sandra Alvarado López, Alejandro González Ponce, Gerardo Rodríguez Tapia, Irma Acosta Calixto, Luz Palestina Llamas Guzmán, Miguel Baltazar Gálvez, Pedro Eloy Mendoza-Hernández, and Jimena Rey for their technical and field support. The authors also thank Adolfo Vergara, Jesús Trejo González, and Judith Alva from the Instituto Nacional de Antropología e Historia for their logistic support.

Declaration of Conflicting Interests

The author(s) declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

Funding

The author(s) received no financial support for the research, authorship, and/or publication of this article.

ORCID iD

Alma Orozco-Segovia http://orcid.org/0000-0003-0143-6343

References

Baskin, J. M., Baskin, C. C., & Li, X. (2000). Taxonomy, anatomy and evolution of physical dormancy in seeds. *Plant Species Biology*, *15*, 39–152.

Benech-Arnold, R. L., & Sánchez, R. A. (2004). *Handbook of seed physiology: Applications to agriculture*. New York, NY: The Haworth Press.

Benítez, G., Pulido, M., & Equihua, M. (2004). *Árboles multiusos nativos de Veracruz para reforestación, restauración y plantaciones [Multipurpose trees native to Veracruz for reforestation, restoration and plantations]*. Xalapa, México: Instituto de Ecología-Sigolfo-Conafor.

Benítez-Rodríguez, L., Gamboa-deBuen, A., Sánchez-Coronado, M. E., Alvarado-López, S., Soriano, D., Méndez, I., ... Orozco-Segovia, A. (2014). Effects of seed burial on germination, protein mobilization and seedling survival in *Dodonaea viscosa*. *Plant Biology*, *16*, 732–739.

Bligh, E. G., & Dyer, W. J. (1959). A rapid method of total lipid extraction and purification. *Canadian Journal of Biochemistry and Physiology*, *37*, 911–917.

Borbolla-Pérez, V., Iglesias-Andreu, L. G., Luna-Rodríguez, M., & Octavio-Aguilar, P. (2016). Perceptions regarding the challenges and constraints faced by smallholder farmers of vanilla in Mexico. *Environment Development and Sustainability*, *19*, 2421–2441.

Born, J., Bagchi, R., Burslem, D., Nilus, R., Tellenbach, C., Pluess, A. R., & Ghazoul, J. (2015). Differential responses of dipterocarp seedlings to soil moisture and microtopography. *Biotropica*, *47*, 49–58.

Bozzano, M., Jalonen, R., Thomas, E., Boshier, D., Gallo, L., Cavers, S., . . . Smith, P., L. J. (2014). *Genetic considerations in ecosystem restoration using native tree species. State of the World's Forest Genetic Resources—Thematic Study*. Rome, Italy: FAO and Biodiversity International.

Bray, C. M. (1995). Biochemical processes during osmopriming of seeds. Water relations in seed germination. In: J. Kigel (Ed.), *Seed development and germination* (pp. 767–789). New York, NY: Marcel Dekker.

Burns, R. M., & Honkala, B. H. (1990). *Silvics of North America* (*Vol.2*). Washington, DC: Forest Service United States Department of Agriculture.

Caddick, L. (2002). Store canola cool and dry to enhance oil quality. *Farming Ahead*, *132*, 19–21.

Caddick, L. (2005). *Moisture isotherms and conversion of indices used to describe moisture relations in stored grain*. Retrieved from http://sgrl.csiro.au/storage/moisture/conversion.html

Cendán, C., Sampedro, L., & Zas, R. (2013). The maternal environment determines the timing of germination in *Pinus pinaster*. *Environmental and Experimental Botany*, *94*, 66––72.

Corner, E. J. H. (1976). *The seeds of dicotyledons* (Vol. 1). Cambridge, England: Cambridge University Press.

Correa, J. C., & Sierra, E. (2003). Intervalos de confianza para la comparación de dos proporciones [Confidence intervals for the comparison of two proportions]. *Revista Colombiana de Estadística*, *26*, 61–75.

Durr, P. A. (2001). The biology, ecology and agroforestry potential of the raintree, *Samanea saman* (jacq) Merr. *Agroforestry Systems*, *1*, 223–237.

Flores, E. M. (2010). *Samanea saman (Jacq.) Merr. Manual de semillas de árboles tropicales [Seed manual of tropical trees]*. New Orleans, LO: Departamento de Agricultura de los Estados Unidos, Servicio Forestal.

Gamboa de Buen, A., Cruz-Ortega, R., Martínez-Barajas, E., Sánchez-Coronado, M. E., & Orozco-Segovia, A. (2006). Natural priming as an important metabolic event in the life story of *Wigandia urens* (Hydrophyllaceae) seeds. *Physiologia Plantarum*, *128*, 520–530.

García, E. (1988). *Modificaciones al sistema de clasificación climática de Köppen (para adaptarlo a las condiciones de la República Mexicana)* [Modifications to the climate classification system of Köppen (to adapt it to the conditions of the Mexican Republic)]. México D. F., México: Instituto Nacional de Estadística y Geografía.

Gibson, A., & Bachelard, E. P. (1986). Germination of *Eucalyptus sieberi*, L. Johnson seeds. I. Response to substrate and atmospheric moisture. *Tree Physiology*, *1*, 57–65.

González-Zertuche, L., Vázquez-Yanes, C., Gamboa, A., Sánchez-Coronado, M. E., Aguilera, P., & Orozco-Segovia, A. (2001). Natural priming of *Wigandia urens* seeds during burial: Effects on germination, growth and protein expression. *Seed Science Research*, *11*, 27–34.

Gullison, R. E., Panfil, S. N., Strouse, J. J., & Hubbell, S. P. (1996). Ecology and management of mahogany (*Swietenia macrophylla* King) in the Chimanes Forest, Beni, Bolivia. *Botanical Journal of the Linnean Society*, *122*, 9–34.

Heydecker, W., Higgins, J., & Gulliver, R. J. (1973). Accelerated germination by osmotic seed treatment. *Nature*, *246*, 42–44.

Hong, T. D., & Ellis, R. H. (1996). *A protocol to determine seed storage behaviour*. *IPGRI Technology Bulletin No. 1*. Rome, Italy: International Plant Genetic Resources Institute.

Lamb, D. (2012). Forest restoration—The third big silvicultural challenge. *Journal of Tropical Forest Science*, *24*, 295–299.

Lush, W. M., Kaye, P. E., & Groves, R. H. (1984). Germination of *Clematis microphylla* seeds following weathering and other treatments. *Australian Journal of Botany*, *32*, 121–129.

Malacrida, C. R., Kimura, M., & Jorge, N. (2011). Characterization of a high oleic oil extracted from papaya (*Carica papaya* L.) seeds. *Food Science Technology*, *31*, 929–934.

Mello, J. I. D. O., Barbedo, C. J., Salatino, A., & Figueiredo-Ribeiro, R. D. C. L. (2010). Reserve carbohydrates and lipids from the seeds of four tropical tree species with different sensitivity to desiccation. *Brazilian Archives of Biology and Technology*, *53*, 889–899.

Mondal, S., & Bose, B. (2014). An impact of seed priming on disease resistance: A review. In R. N. Kharwar, R. Upadhyay, N. Dubey, & R. Raghuwanshi (Eds.), *Microbial diversity and biotechnology in food security* (pp. 193–203). New Delhi, India: Springer India.

Montagnini, F., & Finney, C. (2011). *Restoring degraded landscapes with native species in Latin America*. New York, NY: Nova Science Publishers, Hauppauge.

Orozco-Segovia, A., Sánchez-Coronado, M. E., Martínez-Villegas, J. A., Pedrero-López, L. V., Becerra-Vázquez, A., Rosete-Rodríguez, A., & Peraza-Villarreal, H. (2014). Ecofisiología de semillas de plantas tropicales: El acondicionamiento mátrico una herramienta útil para germinar especies nativas, útiles para la restauración y conservación de especies [Ecophysiology of seeds of tropical plants: The matric conditioning a useful tool to germinate native species, useful for the restoration and conservation of species]. In T. R. dos Santos Silva, C. W. do Nascimento Moura, L. C. Lima e Lima, & F. A. Ribeiro dos Santos (Eds.), *Botânica na America Latina: Conhecimento, interação e difusão. Memorias del LXV Congresso Latinoamericano de Botânica* (pp. 194–203). Salvador, B. A., Brazil: Sociedad Latinoamericana de Botánica.

Orwa, C., Mutua, A., Kindt, R., Jamnadass, R., & Simons, A. (2009). *Agroforestree database: A tree species reference and selection guide* (Version 4.0). Nairobi, Kenya: World Agroforestry Centre ICRAF. Retrieved from http://www.worldagroforestry.org/treedb2/speciesprofile.php?Spid=1566

Pedrero-López, L. V., Rosete-Rodríguez, A., Sánchez-Coronado, M. E., Mendoza-Hernández, P. E., & Orozco-Segovia, A. (2016). Effects of hydropriming treatments on the invigoration of aged *Dodonaea viscosa* seeds and water-holding polymer on the improvement of seedling growth in a lava field. *Restoration Ecology*, *24*, 61–70.

Pennington, T. D., & Sarukhán, J. (2005). *Árboles tropicales de México: Manual para la identificación de las principales especies [Tropical trees of Mexico: Manual for the identification of the main species]*. México, D. F., México: UNAM-Fondo de Cultura Económica.

Reazai, M., Mohammadpourfard, I., Nazmara, S., Jahanbakhsh, M., & Shiri, L. (2014). Physicochemical characteristics of citrus seed oils from Kerman, Iran. *Journal of Lipids*, *2014*, 1–3. doi: 10.1155/2014/174954

Rodríguez-Luna, E., Gómez-Pompa, A., López-Acosta, J. C., Velázquez-Rosas, N., Aguilar- Domínguez, Y., & Vázquez-Torres, M. (2011). *Atlas de los espacios naturales protegidos de Veracruz [Atlas of the protected natural areas of Veracruz]*. Veracruz, México: Gobierno del Estado de Veracruz, Secretaría de Educación del Estado de Veracruz, Universidad Veracruzana, Centro de Investigaciones Tropicales.

Royal Botanic Gardens Kew. (2017). *Seed Information Database* (Version 7.1). Retrieved from http://data.kew.org/sid/

Rogers, D. L., & Montalvo, A. M. (2004). *Genetically appropriate choices for plant materials to maintain biological diversity*. Report to the USDA Forest Service, Rocky Mountain Region, Lakewood, CO, USA. University of California, Berkeley. Retrieved from http://www.fs.usda.gov/Internet/FSE_DOCUMENTS/fsbdev3_039080.pdf

Sánchez, A., Orta, R., & Muñoz, B. C. (2001). Pretratamientos pregerminativos de hidratación-deshidratación de las semillas y sus efectos en plantas de interés agrícola [Pregerminative pretreatments of hydration-dehydration of the seeds and their effects in plants of agricultural interest]. *Agronomía Costarricense*, *25*, 67–91.

Sánchez, J. A., Muñoz, B. C., Hernández, L., Montejo, L., Suárez, A. G., & Torres-Arias, Y. (2006). Pretratamientos robustecedores de semillas para mejorar la emergencia y el crecimiento de *Trichospermum mexicanum*, árbol tropical pionero [Robust seed pretreatments to improve the emergence and growth of *Trichospermum mexicanum*, a pioneer tropical tree]. *Agronomía Costarricense*, *30*, 7–26.

Schmidt, L. H. (2000). *Guide to handling of tropical and subtropical forest seed*. Copenhagen, Denmark: University of Copenhagen, Danida Forest Seed Centre.

Servicio Meteorológico Nacional. (2014). Comisión Nacional del Agua, normales climatológicas, NORM-51-10 [National Water Commission, climatological normal, NORM-51-10]. Retrieved from http://smn.cna.gob.mx/es/informacion-climatologica-ver-estado?estado=ver

Singh, J. S., & Chaturvedi, R. K. (2018). *Tropical dry deciduous forest: Research trends and emerging features*. Singapore: Springer Nature Singapore.

Sung, J. M., & Jeng, T. L. (1994). Lipid peroxidation and peroxide scavenging enzymes associated with accelerated aging of peanut seed. *Physiologia Plantarum*, *91*, 51–55.

Taiz, L., & Zeiger, E. (2002). *Plant physiology*. Sunderland, MA: Sinauer Associates.

Trejo-González, J. (2012). *Los que siguen volando: La danza de los voladores entre los totonacos de Papantla*. [Those who keep flying: The dance of the fliers among the Totonacs of Papantla] (Bachelor's Thesis). Ciudad de México, México: Universidad Autónoma Metropolitana-Iztapalapa.

Vázquez-Yanes, C., & Batis, A. I. (1996). La restauración de la vegetación, árboles exóticos vs árboles nativos [The restoration of vegetation, exotic trees vs. native trees]. *Ciencias*, *43*, 16–23.

Vázquez-Yanes, C., Batis, A. I., Alcocer, M., Gual, M., & Sánchez, C. (1999). *Árboles y arbustos nativos potencialmente valiosos para la restauración ecológica y la reforestación [Native trees and shrubs potentially valuable for ecological restoration and reforestation]*. México, D. F., México: Instituto de Ecología, UNAM–CONABIO.

Vázquez-Yanes, C., & Orozco-Segovia, A. (1982). Seed germination of a tropical rain forest pioneer tree (Heliocarpus donnell-smithii) in response to diurnal fluctuation of temperature. *Physiologia Plantarum*, *56*, 295–298.

Vázquez-Yanes, C., & Orozco-Segovia, A. (1993). Patterns of seed longevity and germination in the tropical rainforest. *Annual Review of Ecology and Systemantics*, *24*, 69–87.

Vázquez-Yanes, C., & Orozco-Segovia, A. (1994). Signals for seeds to sense and respond to gaps. In M. Caldwell & R. Pearcy (Eds.), *Exploitation of environmental heterogeneity* *by plants: Ecophysiological processes above and below ground* (pp. 209–236). New York, NY: Academic Press.

Walter, J., Jentsch, A., Beierkuhnlein, C., & Kreyling, J. (2013). Ecological stress memory and cross stress tolerance in plants in the face of climate extremes. *Environmental and Experimental Botany*, *94*, 3–8.

Wuest, S. (2007). Vapour is the principal source of water imbibed by seeds in unsaturated soils. *Seed Science Research*, *17*, 3–9.

Zar, J. H. (2010). *Biostatistical analysis*. Englewood Cliffs, NJ: Prentice Hall.

ZMAET. (2009). *Plan de manejo para la zona de monumentos arqueológicos El Tajín. [Management plan for the area of archaeological monuments El Tajín]*. México, D. F. México: Instituto Nacional de Antropología e Historia.