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ORIGINAL ARTICLE

Restoration implications of the germination ecology of six dry-forest woody Fabaceae species in Mexico

Citlali Aguirre-Salcedo[1] · **Susana Adriana Montaño-Arias**[2] · **Roland Jansson**[3]

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Abstract

Key message **Seed germination responses to variation in temperature and light differed among six dry forest species, results that will inform ecological restoration and climate change adaptation projects.**

Abstract In dry forests, where opportunities for plant establishment occur in a narrow window of opportunity, seeds must respond to cues to germinate when conditions for growth are suitable. Knowledge of the strategies and adaptations of seeds to the seasonal dry-forest ecosystems, being under constant threat, is needed to guide restoration and management actions in the face of climate change. We investigated the effects of scarification, temperature and light in germination percentage, germination time and synchrony of six woody Fabaceae species. The species have ecological potential for restoration and are of cultural or economic importance for the local people in the Tehuacán-Cuicatlán Valley, Mexico. We carried out a multifactorial germination experiment with five temperatures, two light regimes and two scarification conditions for *Mimosa luisana*, *M. polyantha*, *M. adenantheroides*, *M. lactiflua*, *Acaciella angustissima* and *Vachellia constricta*. All germinated in a wide range of temperatures (10–40 °C), and mechanical scarification highly increased the germination percentage. Higher temperature increased and speeded up germination in dark conditions for most of the species, but they exist heterogeneous responses in their germination synchrony. Studied species had high germination percentages in warm temperatures, but their recruitment in nature might be negatively affected by warmer and drier conditions, and by the loss of shade and seed dispersers due to deforestation and changes in land use. It is crucial to study not just germination percentage and time but also other aspects of the germination process such as the germination synchrony, since it might reveal useful information for management actions.

Keywords Restoration ecology · Climate change · Dry forest · Germination · Fabaceae

Introduction

Seed germination is the most audacious act in the unpredictability of nature's theater. Germination is a prerequisite for seedling establishment, plant recruitment and succession, and is hence a pivotal process that initiates the reestablishment and recovery of degraded ecosystems. Knowledge of germination is of immense importance in all types of nature management as germination kickstarts the revival and resilience of ecosystems, contributes to species diversity, and the plants recruited stabilizes soil, enhances nutrient cycling and aids in the overall development of populations, communities and ecosystems.

In tropical dry forests, where resilience battles adversity, germination emerges as the vital catalyst that breathes life into the dormant landscape. The pronounced seasonality of dry forests affects seed production, germination, and

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✉ Citlali Aguirre-Salcedo
cali.07matacaam@gmail.com

✉ Susana Adriana Montaño-Arias
sama@xanum.uam.mx

[1] Department of Ecology and Environmental Science, Umeå University, 90187 Umeå, Sweden

[2] Departamento de Biología, Universidad Autónoma Metropolitana-Iztapalapa, División de Ciencias Biológicas y de la Salud, Apdo, Postal 55-535 Ciudad de Mexico, México

[3] Department of Ecology and Environmental Science, Umeå University. SE-90187, Umeå, Sweden

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seedling development. Compared to other types of forest, establishment and growth of seedlings face challenging situations in dry forests, with just a narrow window of opportunity for germination: Germination, seedling establishment and growth of most of the species in tropical dry forests are restricted to the short rainy season with precipitation of 250–2000 mm, and high evapotranspiration (Hasnat and Hossain 2020).

Tropical dry forest is the second largest habitat type in the world (WWF 2016); they cover 42% of the tropical and subtropical forest areas globally (Hasnat and Hossain 2020). They are recognized for high level of endemism (Stoner and Timm 2004); about 40% of the woody plant species of dry forests are not found anywhere in the world (Hasnat and Hossain 2020). Moreover, these forests are more threatened and less protected than moist and wet forest (Miles et al. 2006; Rivas et al. 2020; Songer et al. 2009). Dry forests have faced a long history of disturbance as they are more attractive for human settlements than other forests (Hasnat and Hossain 2020). Therefore, they have been exposed to a variety of threats resulting from human activity: conversion to croplands and ranches, fire, habitat fragmentation, soil erosion and high human population density (Janzen 1988; Miles et al. 2006). In addition, climate change might be threatening the existence of some species, especially those with small geographic ranges. Hence, restoration of dry forest ecosystems is increasingly a priority.

Understanding germination is crucial for restoration of dry forests. Studies of germination at species and community levels are needed to investigate the effects of climate change and to identify endangered species. They can also help to detect beneficial and stressful conditions for recruitment, which might guide efforts of species introduction, reintroduction or augmentation of populations (Bhatt et al. 2019). Additionally, germination studies permit manipulation of biotic and abiotic components to increase the recruitment of desired species or to suppress undesirable species in ecological restoration (Ke and Li 2006).

Restoration efforts based on species with germination being sensitive to higher temperatures might result in restoration actions being unsuccessful under climate change. Including the temperature tolerance of germination as a criterion for selecting focal species to use in restoration might increase restoration success. In this study, the objectives were: (1) To unravel the effects of temperature, scarification and light on the germination percentage, time and synchrony of six woody Fabaceae species, i.e., *Mimosa luisana* Brandegee, *M. polyantha* Benth., *M. adenantheroides* (M.Martens & Galeotti) Benth, *M. lactiflua* Delile ex Benth, *Acaciella angustissima* (Mill.) Britton & Rose and *Vachellia constricta* (Benth.) Seigler & Ebinger. (2) To investigate whether the germination of these species is endangered by higher temperatures, and (3) to evaluate the tolerance of germination of these species at low temperatures, in order to explore their potential for assisted migration to higher altitudes, as a measure of climate-change adaptation of dry forests.

Methods

Study species

The Fabaceae family is one of the most important angiosperm families in terms of abundance, diversity, economic and ecological potential in the dry forests of tropical and subtropical regions (Appiah 2013; Gillespie et al. 2000; Thakur 2015; Gomes et al. 2018). In the Tehuacán-Cuicatlán Valley (TCV), Mexico, Fabaceae is a dominant family with high diversity and many endemic species (Dávila et al. 2002). The species of this family also provide local communities with cultural and economic services in the TCV (Camargo-Ricalde et al. 2001; Vallejo et al. 2015). The species used in this study were selected based on their economic and cultural importance for local populations, their potential for being used in ecosystem restoration, and their extinction risk based on small geographical range or endemism.

Mimosa luisana and *M. polyantha* are species endemic to the TCV. They form soil "resource islands" rich in nutrients and mycorrhizal propagules that improve soil conditions (Camargo-Ricalde and Dhillion 2003). *Mimosa luisana* provides suitable regeneration niches by facilitative interactions that allow coexistence of distantly related plant species (Flores-Martínez et al. 1994; Montesinos-Navarro et al. 2017), and has been shown to augment the survival of targeted species seedlings when used as a nurse species in restoration efforts (Badano et al. 2009). *Mimosa adenantheroides* and *M. lactiflua* are species endemic to Mexico, but their potential for restoration have not been explored. *Vachellia constricta* occurs in Mexico and United States. This species has mechanisms to keep ants separated from flowers, which help to reduce costs of reproduction, being an adaptation facilitating biotic interactions (Nicklen and Wagner 2006). *Acaciella angustissima* produces phenolic compounds that are used in ethnomedicine (Musara and Aladejana 2020).

Germination trials

Pods were collected in the Tehuacán-Cuicatlán Valley, Mexico (Table 1), during November and December 2020, when the seeds were mature (Camargo-Ricalde et al. 2004). Pods were randomly collected from 10 to 15 adult individuals in an area of 10,000 m^2. Seeds were extracted from the pods; heathy seeds were selected with a stereo microscope and kept at room temperature (20–25 ℃) in paper bags until March 2021 when the experiment started. Seeds were washed with detergent solution (3 g/100 water ml/ 3 min) as

Table 1 Information of the seed collection sites. Location shows coordinates and the municipality. Vegetation type is based on Pérez-Valladares et al. (2019)

Species	Location	Vegetation type	Altitude
M. luisana	18°19′ 39.04′ N, 97°30′ 12.28″ W Zapotitlán Salinas, Puebla	Rosetophyllous desert scrub	1550 m asl
M. polyantha	17°55′ 24.89 N, 97°00′ 32.56′ W Santa Ma. Tecomavaca, Oaxaca	Succulent dominated scrub	587 m asl
M. adenantheroides	18°16′ 35.11″ N, 97°06′ 33.43″ W Coxcatlán, Puebla	Ecotone between tropical deciduous forest and oak forest	2022 m asl
M. lactiflua	17°36′ 16.05″ N, 96°57′ 02.52″ W Santiago Nacaltepec, Oaxaca	A glen in the tropical deciduous forest	1465 m asl
A. angustissima	17°53′ 11.46″ N, 97°05′ 30.46″ W Santa María Ixcatlán, Oaxaca	Ecotone between succulent dominated scrub and oak forest	1420 m asl
V. constricta	18°19′ 54.40″ N, 97°30′ 59.70′ W Zapotitlán Salinas, Puebla	Rosetophyllous desert scrub	1545 m asl

suggested by Camargo-Ricalde and Grether (1998), immediately before each experiment.

For each species, we tested germination under five temperatures, two light regimes (light and dark) and two scarification conditions (with and without scarification), a total of 20 treatments. Each treatment included four petri dishes with 25 seeds each, giving 100 seeds per treatment. The experiment was carried out in a WWR BOD incubator sequentially set at 3 ℃, 10 ℃, 20 ℃, 30 ℃ and 40℃ with light on, during 34 days per temperature. Seeds exposed to the dark regime were covered with aluminum foil to avoid the entrance of light. Scarification was made with a nail nipper on the opposite site to the hilum to avoid embryo damage immediately before the start of the experiment. Each petri dish contained 20 ml of bacteriological agar (1.5 g agar per 100 ml of distilled water) and was sealed with parafilm until the end of the experiment to keep humidity and avoid infection by microorganisms. Germination was considered to have occurred when the radicle was 1 mm and was recorded every day. After counting the germinated seeds each day, the petri dishes were placed back in the incubator in random order.

Statistical analysis

By species, the saturation rate (SR) and the germination rate (GR) were estimated (Montaño-Arias et al. 2015), which were analyzed with a Balanced Design Analysis of Variance to evaluate whether they differed between factors.

Germination percentage and uncertainty indices were obtained with the *germinationmetrics* package (Aravind et al. 2023). We eliminated the replicates with no germination, as the function for computing the indices does not work if there are zero values: two replicates of *V. constricta* from the 10 ℃-dark treatment; two replicates of *M. polyantha* from 10 ℃-dark and one from the 10 ℃-light treatment; and one replicate of *M. lactiflua* from the 10 ℃-dark treatment were thus removed. Cumulative germination was analyzed with nonparametric time-to-event models, using Kernel Density Estimator for each species using the *drcte* package (Onofri et al. 2022)**.**

Non-germinated seeds were considered as censored if germination did not occur during the duration of the experiment. As data censoring and late germination flushes are not accounted for in traditional statistical analysis (Onofri et al. 2010, 2022), we used semiparametric survival analysis (McNair et al. 2012). Thus, to quantify effects of temperature and light regime on mean time to germination we fitted a semiparametric Cox model for each species. Seeds were analyzed independently with Cox models using the coxph() function from the *survival* package (Therneau and Grambsch 2000). The proportional hazards assumption (i.e., that the explanatory variable only changed the chance of failure, not the timing of periods of high hazard) was explored graphically by plotting separate non-parametric Kaplan–Meier survivorship functions for temperatures and light regime and it was also explored with the cox.zph() function from the same package. As the assumption of proportional hazards was violated for all species, we corrected the Cox models with time splitting and stratification (Zhang et al. 2018; Therneau et al. 2023). The interaction term of temperature and light was maintained in the Cox model as it was significant for all species.

To assess germination synchrony, we used the uncertainty index (Ranal and Santana 2006). The effects of temperature and light on germination synchrony were analyzed with quadratic models for some species and linear models for others, as the data exhibited different relationships with temperature and light variables depending on species. The interaction term of temperature and light was kept in the models when it showed a significant effect. The results were considered as significant when $p < 0.05$. All

the analyses and graphics were done in Rstudio (R Core Team 2022).

Results

Seeds that were not scarified exhibited lower germination percentage (GP) than scarified seeds for all species and all treatments (Fig. 1). The highest GP of non-scarified seeds was reached at the temperature of 40 ℃ for all species. The non-scarified seeds of *M. luisana, M. adenantheroides*, *A. angustissima* and *V. constricta* showed a GP higher than 25% at 40 ℃, whilst the non-scarified seeds of *M. lactiflua* and *M. polyantha* exhibited a GP lower that 15% at 40 ℃ (Fig. 1). The analysis showed that GR depends on the light regime, the condition of the seed and the temperature to which it is exposed the seed (Table 2; Fig. 2), while the days that must pass to reach the final PG (SR) depend on all four factors (Table 2; Fig. 3). As the germination of non-scarified seeds was low for most of the treatments, the rest of the results are reported just for the scarified seeds.

At 3 ℃, no germination was observed for any species or light treatment (Figs. 2 and 3). However, imbibition took place in a few seeds of *M. luisana*, *M. adenantheroides, A. angustissima* and *M. lactiflua*. At higher temperatures, the germination response differed among species. At 10 ℃, *M.*

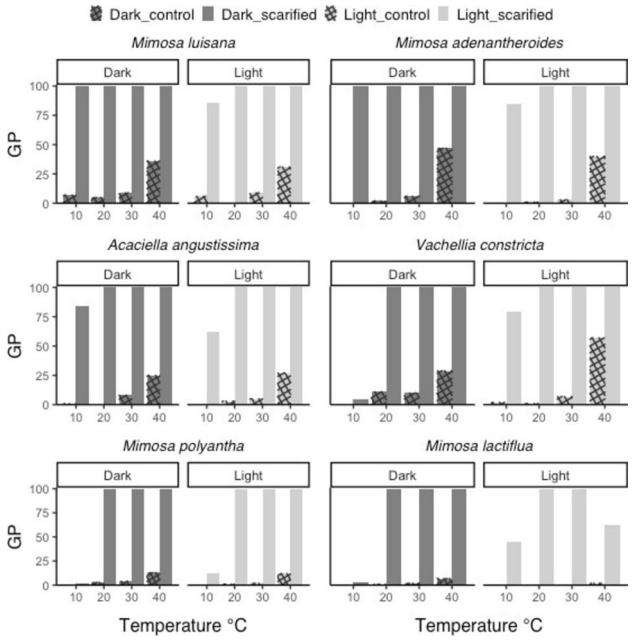

Fig. 1 Germination percentage (GP) of *M. luisana*, *M. adenantheroides*, *A. angustissima*, *V. constricta*, *M. polyantha* and *M. lactiflua* at each temperature treatment. For each species, the left panel shows the germination percentage for dark regime and the right for light regime. Control means non-scarified seeds and is indicated with a crosshatch pattern

Table 2 Balanced Design Analysis of Variance to analyze the effect of the species, temperature, light regimes, scarification condition on the percentage of seed germination of six species of Fabaceae. GR = Germination Rate; SR = Saturation Rate; ns = not significative; $^{*}p < 0.05$

	GR (seeds/days)		SR (days)
	DF	*F* Ratio	*F* Ratio
Species (S)	5	1.85 ^{ns}	53.14*
Regimen (R)	1	224.35*	131.67*
Condition (C)	1	632.37*	1366.74*
Temperature (T)	4	245.31*	394.91*
SxR	1	1.07	12.42*
SxC	5	1.01	26.25*
RxC	1	608.72*	98.19*
SxRxC	5	1.01	8.11*
SxT	20	1.15	34.02*
RxT	4	63.04*	30.77*
SxRxT	20	1.03	18.05*
CxT	4	159.05*	370.24*
SxCxT	20	1.05	39.72*
RxCxT	4	145.91*	15.43*
SxRxCxT	20	0.87	21.91*

luisana and *M. adenantheroides* reached 100% germination in dark conditions; in light conditions, their GP was 86% and 85%, respectively. Similarly, *A. angustissima* preferred darkness over light for germination at 10 ℃, having 84% and 62%, respectively. The rest of the species germinated better in light than in dark conditions at 10℃; *V. constricta* showed a GP of 79% in light and a 5% in darkness; *M. polyantha* a GP of 12% and 2% in light and darkness, respectively, while *M. lactiflua* had a GP of 45% in light and 3% in darkness at 10 ℃. At 20 ℃ and 30 ℃, all species achieved 100% of germination both in dark and light regime. At 40 ℃, *M. lactiflua* showed a GP of 62% in light, and a 100% of germination in darkness. The rest of the species reached the 100% of germination both in light and dark regime at 40 ℃ (Fig. 1).

Germination was faster at warmer than at colder temperatures for all species (Figs. 2, 3 and 4). At 10 ℃, only *M. luisana* and *M. adenantheroides* reached 100% germination in dark conditions during the 34 days of the experiment. The rest of the species did not complete germination at 10 ℃. At 20 ℃, *M. lactiflua* completed germination during the first 6 days of the experiment in both light and dark conditions; the rest of the species germinated during the first 6 days in darkness, and during the first 20 days in light regime at 20 ℃.

At 30℃, germination of all species started on the first or second day and finished during the first 10 days of the experiment. *M. luisana*, *M. polyantha*, *A. angustissima* and *V. constricta* reached 100% of germination in the first two

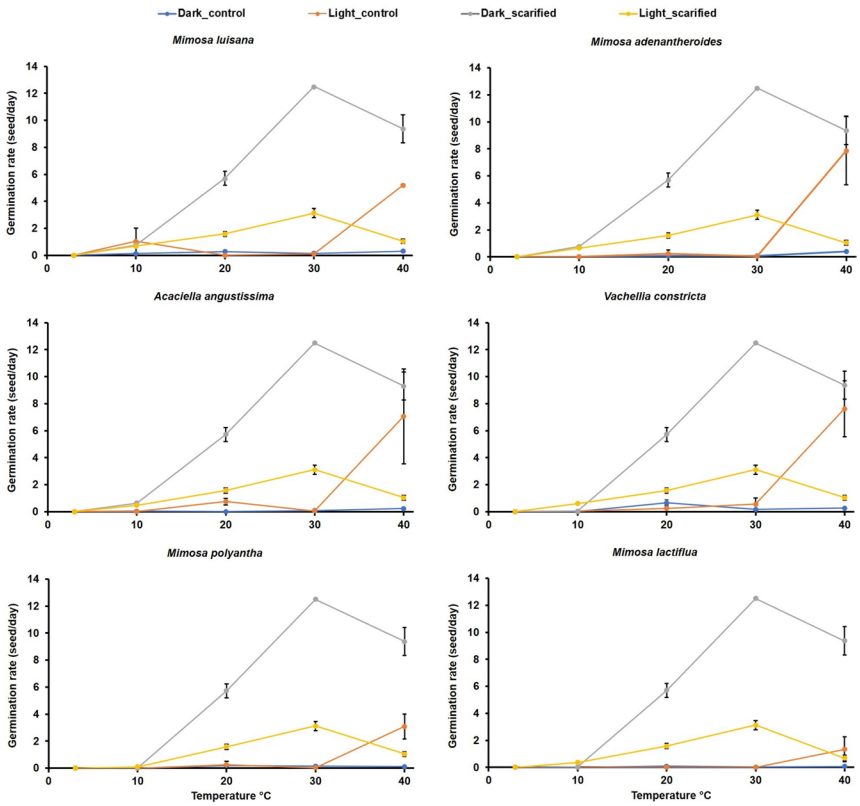

Fig. 2 Germination Rate (GR ± EE) of *M. luisana*, *M. adenantheroides*, *A. angustissima*, *V. constricta*, *M. polyantha* and *M. lactiflua* along a gradient temperature with two light regimes, and with or without scarification condition

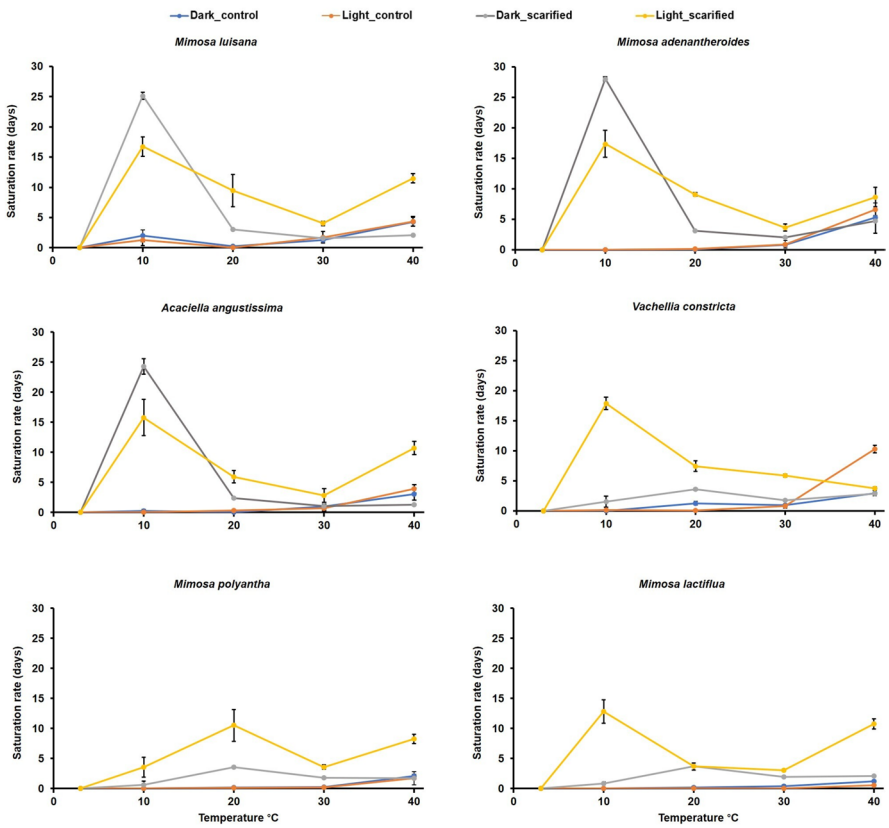

Fig. 3 Saturation Rate (SR ± EE) of *M. luisana*, *M. adenantheroides*, *A. angustissima*, *V. constricta*, *M. polyantha* and *M. lactiflua* along a gradient temperature with two light regimes, and with or without scarification condition

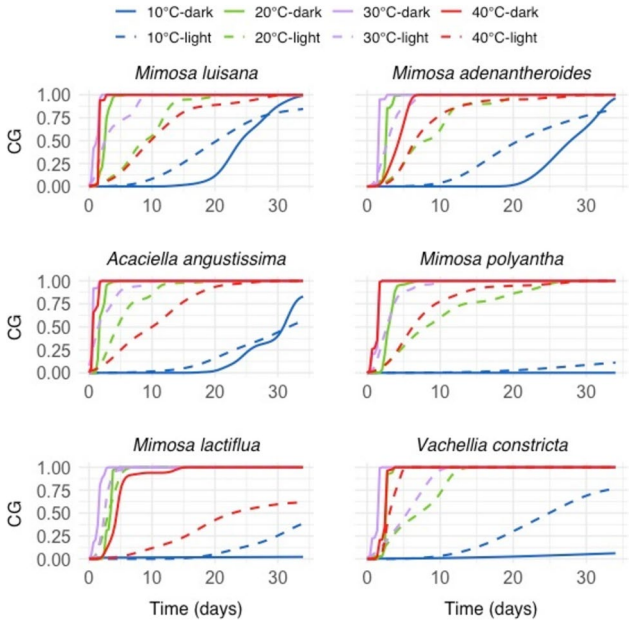

Fig. 4 Nonparametric time-to-event curves showing cumulative germination (CG) versus days of the experiment for the six species. Each color represents a temperature: blue is for 10 °C, purple for 20 °C, pink for 30 °C and red for 40 °C. Solid lines indicate light regime, and dotted lines dark regime for each temperature

days of the experiment in dark conditions, while their germination was up to 9 days longer with light. Complete germination of *M. lactiflua* and *M. adenantheroides* was reached during the first 5 days of the experiment in both dark and light conditions.

At 40℃, *M. luisana*, *M. polyantha* and *A. angustissima* completed germination in the first 3 days of the experiment in dark conditions, but their seeds exposed to light finished germination between day 20 and 25. Seeds of *V. constricta* completed germination during the first 5 days of the experiment in both light and dark conditions. *Mimosa adenantheroides* completed germination on day 6 in darkness and on day 17 in light regime. *Mimosa lactiflua* completed germination during the first 10 days in dark conditions; however, in the light regime *M. lactiflua* did not reach 100% of germination, the last germination occurred on day 28.

Temperature had a significant effect on the chance for germination of all species. As temperature increased, the chance for germination increased for all species (Fig. 5). For *M. luisana* and *M. adenantheroides*, the relationship between the chance for germination and temperature was best described by a linear relationship. The effect of light regime was dependent on the temperature for all species, as indicated by a significant interaction between light and temperature in the Cox models ($p < 0.05$). *Mimosa luisana*, and *M. adenantheroides* exhibited higher chance for germination in dark that in light conditions at 20 ℃, 30 ℃ and 40℃, whereas *A. angustissima* and *M. polyantha* showed higher chance for germination in dark than in light conditions for all temperatures. *Mimosa lactiflua* exhibited higher germination chance in light conditions at 10 ℃, but in dark regime at 40℃. *Vachellia constricta* showed a higher chance for germination in dark that in light regime at 10 ℃ and 20 ℃, while chances were slightly higher for light than darkness at 40 ℃.

As temperature increased, germination synchrony increased for *M. luisana*, *M. adenantheroides* and for *A. angustissima* in dark conditions (Fig. 6). In contrast, as temperature increases, the germination synchrony of *M. lactiflua* and *M. polyantha* decreased in both light and dark conditions. Temperature did not have a significant effect on germination synchrony of *V. constricta*; nevertheless, the interaction of light and temperature was significant ($t = -5.41$, $p < 0.05$); germination synchrony was significantly higher in darkness that in light condition at 10℃, 20℃ and 30℃ for this species.

There was a significant interaction between temperature and light regime for *M. luisana* ($t = 6.56$, $p < 0.5$), *A. angustissima* ($t = 5.03$, $p < 0.5$), and *V. constricta* ($t = -5.41$, $p < 0.5$), which indicates that the effect of the light regime on germination synchrony depends on temperature. The interaction of temperature and light was not statistically significant for *M. adenantheroides*, *M. lactiflua* and *M. polyantha*; therefore, the interaction term was removed from the model of those species.

Discussion

The experimental data on how germination respond to scarification, temperature and light provide information on seed adaptations to conditions for germination in dry forests, which is pivotal for guiding ecological restoration actions in response to anthropogenic disturbances and climate change. Thick seed coats are adaptations possessed by many species from arid and semi-arid regions as a strategy to protect their embryos from dehydration, which helps secure colonization under conditions of water scarcity and disturbance (Khurana and Singh 2001). Thick seed coats also make it unlikely that all seeds are scarified and germinate simultaneously, functioning as a risk spreading strategy (Childs et al. 2010). The six species we evaluated exhibit physical dormancy, and their germination was highly improved by mechanical scarification. However, temperatures as high as 40 °C can also help break physical dormancy, as shown by increased germination of un-scarified seeds at high temperatures (Fig. 1). Similar findings have been reported for other *Mimosa, Acacia* and *Vachellia* species (Orozco-Almanza et al. 2003; Silveira and Fernandes 2006; Chauhan and Johnson 2009; Aref 2011; Montaño-Arias et al. 2015; Maldonado-Arciniegas et al. 2018), suggesting that these species benefit from or

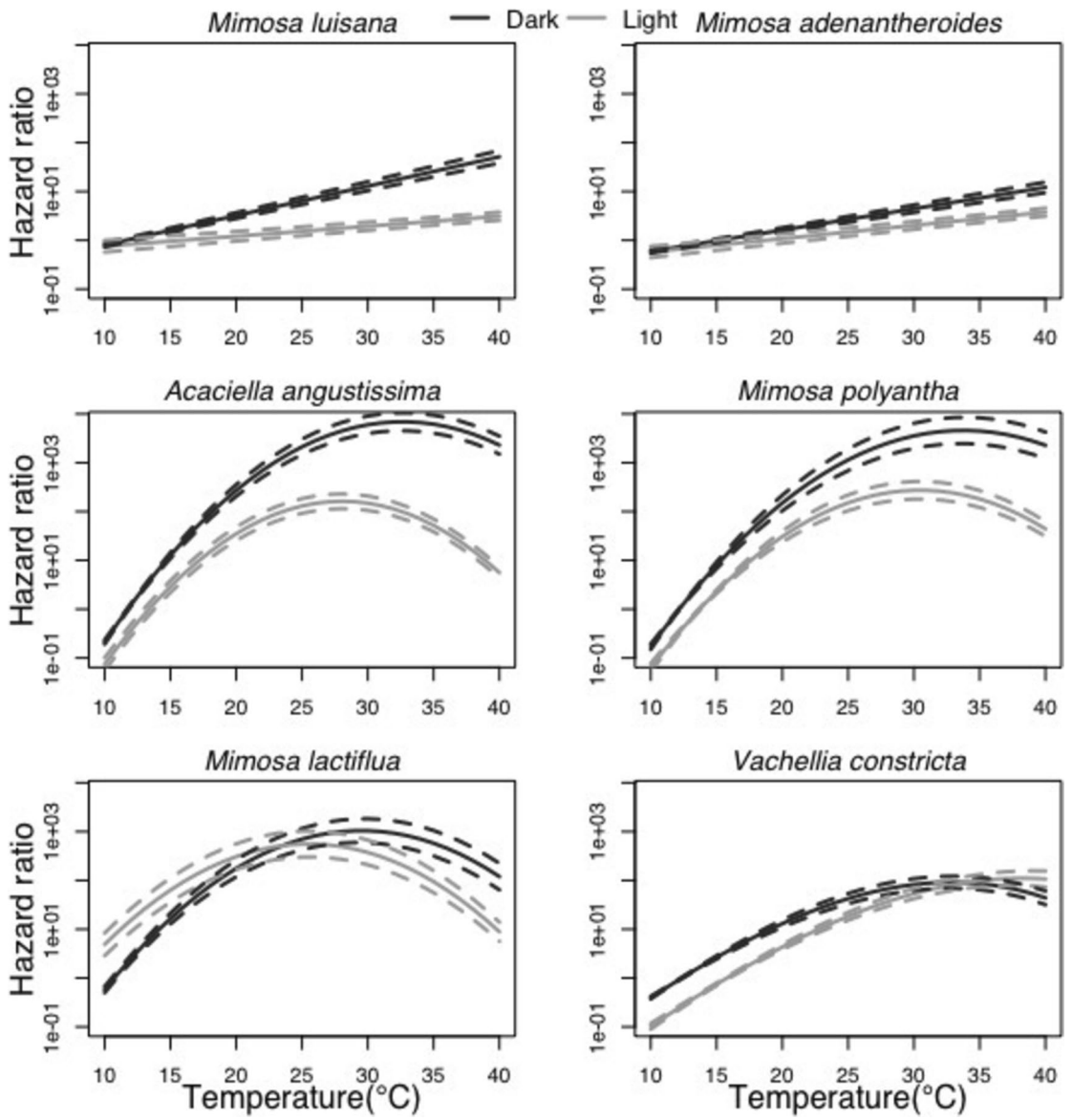

Fig. 5 Predictions of the Cox model chances for germination with relation to temperature (°C) for the six species. Hazard indicates the "risk" of an event happening at a particular time, thus increased hazard ratio indicates an increased chance for germination at a particular time. Orange solid line indicates the prediction for light, black line indicates the predictions in the dark regime. Dashed lines indicate the standard errors

need mechanical scarification for recruitment in nature. In the TCV, mechanical scarification is driven mainly by goats (Giordani et al. 2015). Alternatively, seed coats may also experience abrasion from rolling on the soil (Baskin et al. 1995).

The overall results show that seed germination response to light and temperature, and varied among species, as well as to the other aspects considered for the germination process. The six studied species were neutral photoblastic, meaning that they could germinate (germination percentages higher than 60%) both in presence or absence of light, at 20 °C, 30 °C and 40 °C, which coincides with what was reported by Camargo-Ricalde et al. (2004) and Montaño-Arias et al. (2015) for diverse species of the genus *Mimosa*.

On the other hand, the fact that the studied species are neutral photoblastic represents an advantage, since their seeds are able to germinate under the soil´s ground or on the soils´ surface under the canopy generated by other plants (i.e. *Neltuma* sp., *Parkinsonia* sp.), as it occurs in non-photoblastic seeds of other plant species (Pearson et al. 2002; Sánchez et al. 2017). Furthermore, considering that all species germinated faster in darkness than in light, at 20 °C, 30 °C and 40 °C, this is related to the formation of a seed bank, which is usually form in the first 2 cm depth of soil

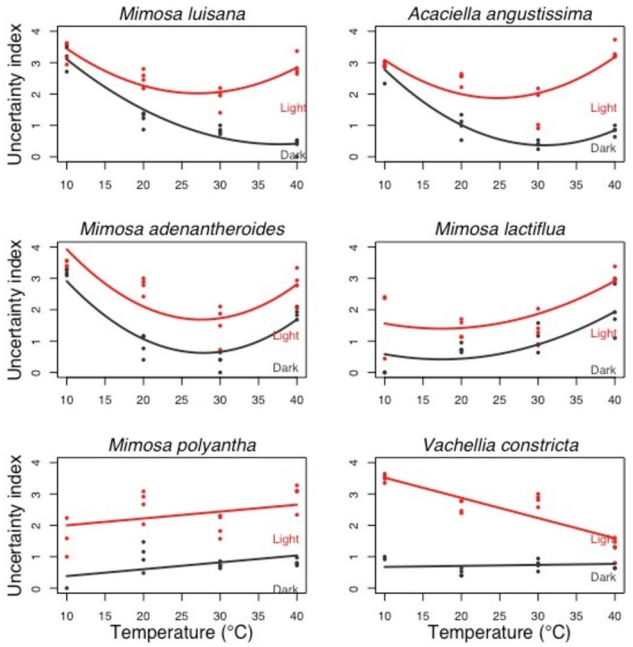

Fig. 6 Observations and predictions of uncertainty indices for the six species studied. Dots indicate the uncertainty index observed for petri dishes in dark (black) and light (red) regimes. Red line indicates the uncertainty index prediction for light and black for dark regimes. Lower values of the index indicate higher germination synchrony (Ranal and Santana 2006)

(Besnier-Romero 1989; Valbuena and Trabaud 2001), and to the brief window of opportunity that their seeds have to germinate and establish during the short rainy season (Ten Brink et al. 2013; Maleki et al. 2023).

Besides, in dry deciduous forests, shade at the soil surface is restricted to the rainy season; most of the woody species within the TCV are caducifolious and lose their leaves during the dry season, leading to sun exposure of understory plants and soil. However, the annual herbs die when the rainy season is over, forming a mulch that creates shade and moist microenvironments that remain a few weeks into the dry season (Khurana and Singh 2001). This mulch might provide a short opportunity for germinating to the species that produce their seeds at the end of the rainy season, as the ones we studied here. Additionally, it has been reported that, in dry areas, there are biological soil crusts, which favor the establishment and development of divers' plant species (Havrilla et al. 2019; Sosa-Quintero et al. 2022).

At 10 °C, germination was faster in darkness for all species, except *M. lactiflua*, suggesting that the seeds of five of the studied species are naturally located below the soil surface (Escobar-Escobar and Cardoso 2015; González-Vélez et al. 2020), and that only the seeds of *M. lactiflua* locate above the soil, promoting its establishment in exposed sites (Wulff et al. 1994). However, according to Taiz et al. (2010) and Bewley et al. (2013), different aspects have to be considered, such as the type of seed, the plant species and the quantity and quality of light received by the seeds.

The preference for darkness was also true for the germination synchrony of *M. luisana*, *M. adenantheroides*, and *A. angustissima*. The synchrony of these species increased with temperature, which might indicate that these species produce enough viable seeds to germinate in a wide range of temperatures and they germinate quickly when they experience optimal conditions (Escobar-Escobar and Cardoso 2015). The synchrony of *V. constricta* was not affected by temperature alone, but the interaction of temperature and light: the germination synchrony of this species is high in dark conditions from 10 to 40 °C, indicates that detection of seasonal changes in soil temperature would synchronize germination seeds, while light detection, in addition to avoiding the germination in gaps, in the Rosetophyllous desert scrub (Wulff et al. 1994; Escobar-Escobar and Cardoso 2015). In contrast, seeds of *M. lactiflua* may not have experienced selection to synchronize their germination; the germination synchrony of its seeds decreased with temperature, indicating that this *Mimosa* species has developed a seed germination strategy by not overlapping, to avoid the competition with other seed plants (Ranal and Santana 2006; Londoño-Lemos et al. 2024).

Mimosa luisana, *M. lactiflua*, *M. adenantheroides, A. angustissima,* and *V. constricta* exhibited a wider tolerance of temperature (10–40 °C) than *M. polyantha* (20–40 °C). Montaño-Arias et al. (2015) also found a broad temperature tolerance of *M. luisana* and *M. aculeaticarpa*. These results suggest that the germination of *M. luisana*, *A. angustissima*, *M. adenantheroides* and *M. polyantha* might not be threatened by the warming predicted for Mexico with climate change in the short and medium term (Sáenz-Romero et al. 2010). However, the recruitment of *M. lactiflua* might face trouble at temperatures higher than 30 °C in stressful environmental conditions in the present and short-term future.

None of the studied species showed any germination at 3 °C during the duration of the study. However, imbibition took place in some seeds of *M. luisana*, *M. adenantheroides* and *A. angustissima,* suggesting that low temperatures do not completely hinder but delay germination in these species (Figueroa et al. 2024), which is consistent with the findings of Montaño-Arias et al. (2015) for the germination of *M. luisana* at 5 °C. The wide temperature tolerance of *M. luisana*, *M. adenantheroides, M. lactiflua*, *A. angustissima* and *V. constricta* support the potential use of these species in climate change adaptation projects such as assisted migration to higher altitudes. *Mimosa lactiflua* might need assistance in its recruitment when the climate becomes warmer.

For ecological restoration efforts using the species we studied, we suggest the germination to take place between 20 and 40 °C, which coincides with the optimal germination temperatures of several Fabaceae (Camargo-Ricalde et al.

2004; Cruz-Medina and Orozco-Almanza 2010; Montaño-Arias et al. 2015). Although some of the species we studied serve as nurse plants, they might also benefit from germinating in darkness resulting from burial or shadow. Mechanical scarification is a reliable method for breaking physical seed dormancy, increasing germination up to 100% for all the species we studied. Additionally, a careful selection of healthy seeds is needed to increase the germination in restoration or conservation actions, given that all the species we studied are highly infected by bruchids, and the eggs and early traces of infection are hard to detect at first sight.

This study shows the potential of laboratory experiments to provide important insights into the ecology of seed germination and inform ecological actions. By experimentally varying scarification, temperature, and light, being conditions of central importance for germination in dry forests, and by using modern statistical methods, allowing modelling the time-dependent chance for germination (Fig. 5) and germination synchrony (Fig. 6) as a function of temperature and light, we were able to extract considerably more information than by employing classic germination indices only.

Finally, it is important to highlight that we did not study the effects of drought on germination. Water is a limiting resource for species in dry caducifolious forests and is an indispensable resource for their germination. Despite the species we studied can tolerate high temperatures, they might be threatened by the decreasing precipitation projected for the future (Sáenz-Romero et al. 2010). Additionally, their recruitment might also be affected by alterations of conditions for shade caused by land use changes or deforestation, and by the lack or decrease of seed dispersers that naturally assist the germination of these species by breaking their physical dormancy.

The overall results show that these species present a high germination percentages when their seeds are scarified, regardless of the presence or absence of light, which is a strategy to respond according to the environmental conditions; however, other factors must be considered (i.e. precipitation, seed size).

The information generated in this study is a contribution to understand the seed germination processes of the studied species; as well as the location of their seeds in their natural habitats. This information is necessary to propose safe sites for their seed germination and seedlings establishment. We highly encourage conservation and restoration actions with the Fabaceae species we have studied here.

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Data availability Data generated and analyzed in this study are included in this published article.

Declarations

Conflict of interest The authors of this study have no conflict of interest.

References

Appiah M (2013) Tree population inventory, diversity and degradation analysis of a tropical dry deciduous forest in Afram Plains, Ghana. For Ecol Manag 295:145–154. https://doi.org/10.1016/j.foreco.2013.01.023

Aravind J, Vimala Devi S, Radhamani J, Jacob SR, Kalyani Srinivasan (2023) Germinationmetrics: Seed germination indices and curve fitting. R package version 0.1.8 https://aravind-j.github.io/germinationmetrics/ https://CRAN.R-project.org/package=germinationmetrics.

Aref (2011) Effects of seed pretreatment and seed source on germination of five *Acacia* spp. Afr J Biotechnol. https://doi.org/10.5897/AJB11.1763

Badano EI, Pérez D, Vergara CH (2009) Love of nurse plants is not enough for restoring oak forests in a seasonally dry tropical environment. Restor Ecol 17(5):571–576. https://doi.org/10.1111/j.1526-100X.2009.00530.x

Baskin CC, Baskin JM, Chester EW (1995) Role of temperature in the germination ecology of the summer annual Bidens polylepis Blake (Asteraceae). Bull Torrey Bot Club 122:275–281

Besnier-Romero F (1989) Semillas. Ediciones MundiPrensa, Biología y Tecnología, p 637

Bhatt A, Bhat NR, Lozano-Isla F, Gallacher D, Santo A, Batista-Silva W, Fernandes D, Pompelli MF (2019) Germination asynchrony is increased by dual seed bank presence in two desert perennial halophytes. Botany 97(11):639–649. https://doi.org/10.1139/cjb-2019-0071

Camargo-Ricalde SL, Dhillion SS (2003) Endemic *Mimosa* species can serve as mycorrhizal "resource islands" within semiarid communities of the Tehuacán-Cuicatlán Valley. Mexico Mycorrhiza 13(3):129–136. https://doi.org/10.1007/s00572-002-0206-5

Camargo-Ricalde SL, Grether R (1998) Germinación, dispersión y establecimiento de plántulas de *Mimosa tenuiflora* (Leguminosae) en México. Rev Biol Trop 46(3):543–554

Camargo-Ricalde SL, Grether R, Martínez-Bernal A, García-García V, Barrios-del-Rosal S (2001) Useful species of the genus *Mimosa* (Fabaceae-Mimosoideae) in Mexico. Bot Sci 68:33–44. https://doi.org/10.17129/botsci.1634

Camargo-Ricalde SL, Dhillion SS, Garcia-García V (2004) Phenology, and seed production and germination of seven endemic *Mimosa* species (Fabaceae-Mimosoideae) of the Tehuacán-Cuicatlán Valley. Mexico J Arid Environ 58(4):423–437

Chauhan BS, Johnson DE (2009) Germination, emergence, and dormancy of *Mimosa pudica*. Weed Biol Manag 9(1):38–45. https://doi.org/10.1111/j.1445-6664.2008.00316.x

Childs DZ, Metcalf CJE, Rees M (2010) Evolutionary bet-hedging in the real world: empirical evidence and challenges revealed by plants. Proc Royal Soc B 277(1697):3055–3064. https://doi.org/10.1098/rspb.2010.0707

Cruz-Medina D, Orozco-Almanza S (2010) Germinación de ocho especies de la familia Fabaceae, bajo diferentes regímenes de temperatura. Universidad de Sonora, Hermosillo, Sonora, México Trabajo en extenso, VII Simposio Internacional sobre la flora silvestre en zonas áridas, pp 197–215

Dávila P, Arizmendi MDC, Valiente-Banuet A, Villaseñor JL, Casas A, Lira R (2002) Biological diversity in the Tehuacán-Cuicatlán valley, Mexico. Biodivers 11:421–442

Escobar-Escobar DF, Cardoso VJ (2015) Seed germination and dormancy of *Miconia chartacea* (Melastomataceae) in response to light, temperature and plant hormones. Rev Biol Trop 63(4):1169–1184

Figueroa JA, Donoso C, Fernández F, Reyes M (2024) Estrategias de germinación de semillas de 10 plantas herbáceas nativas del matorral esclerófilo de Chile central. Gayana Bot 81(1):43–54

Flores-Martínez A, Ezcurra E, Sánchez-Colón S (1994) Effect of *Neobuxbaumia tetetzo* on growth and fecundity of its nurse plant *Mimosa luisana*. J Ecol 82(2):325–330. https://doi.org/10.2307/2261300

Gillespie TW, Grijalva A, Farris CN (2000) Diversity, composition, and structure of tropical dry forests in Central America. Plant Ecol 147(1):37–47. https://doi.org/10.1023/A:1009848525399

Giordani L, Baraza E, Camargo-Ricalde SL, Moe SR (2015) The domestic goat as a potential seed disperser of *Mimosa luisana* (Leguminosae, Mimosoideae) in the Tehuacán-Cuicatlán Valley. Mexico J Trop Ecol 31(1):91–94. https://doi.org/10.1017/S0266467414000510

Gomes G, Silva G, Silva D, Oliveira R, Conceição G (2018) Botanical composition of Fabaceae family in the Brazilian Northeast, Maranhão. Brazil Asian J Environ Ecol 6(4):1–10. https://doi.org/10.9734/AJEE/2018/41207

González-Vélez G, Andrés-Hernández AR, Valdez-Eleuterio G, Álvarez-Quiroz N, Martínez-Moreno D, Rivas-Arancibia SP (2020) Germinación de semillas de seis especies arbóreas maderables de una selva baja caducifolia en Puebla. México Agrociencia 54(2):227–240

Hasnat GN, Hossain M (2020) Global overview of tropical dry forests. In: Bhadouria R, Tripathi S, Srivastava P, Singh P (eds) Handbook of research on the conservation and restoration of tropical dry forests. IGI Global, Pennsylvania, pp 1–23

Havrilla CA, Chaudhary VB, Ferrenberg S, Antoninka AJ, Belnap J, Bowker MA, Eldridge DJ, Faist AM, Huber-Sannwald E, Leslie AD, Rodríguez-Caballero E, Zhang Y, Barger NN (2019) Towards a predictive framework for biocrust mediation of plant performance: a meta-analysis. J Ecol 107:2789–2807

Janzen DH (1988) Management of habitat fragments in a tropical dry forest: growth. Ann Mo Bot Gard 75(1):105. https://doi.org/10.2307/2399468

Ke X, Li W (2006) Germination requirement of *Vallisneria natans* seeds: implications for restoration in Chinese lakes. Hydrobiologia 559(1):357–362. https://doi.org/10.1007/s10750-005-1276-0

Khurana E, Singh JS (2001) Ecology of seed and seedling growth for conservation and restoration of tropical dry forest: a review. Environ Conserv 28(1):39–52. https://doi.org/10.1017/S0376892901000042

Londoño-Lemos V, Torres-Gonzáles AM, Madriñán S (2024) Linking seed traits and germination responses in Caribbean seasonally dry tropical forest species. Plants 13:1318. https://doi.org/10.3390/plants13101318

Maldonado-Arciniegas F, Ruales C, Caviedes M, Ramírez DX, Leon-Reyes A (2018) An evaluation of physical and mechanical scarification methods on seed germination of Vachellia macracantha (Humb. & Bonpl. Ex Willd.) Seigler & Ebinger. Acta Agron 67(1):122–127. https://doi.org/10.15446/acag.v67n1.60696

Maleki K, Maleki K, Soltani E, Oveisi M, Gonzalez-Andujar JL (2023) A model for changes in germination synchrony and its implements to study weed population dynamics: a case study of Brassicaceae. Plants 12(2):233. https://doi.org/10.3390/plants12020233

McNair JN, Sunkara A, Frobish D (2012) How to analyze seed germination data using statistical time-to-event analysis: non-parametric and semi-parametric methods. Seed Sci Res 22(2):77–95. https://doi.org/10.1017/S0960258511000547

Miles L, Newton AC, DeFries RS, Ravilious C, May I, Blyth S, Kapos V, Gordon JE (2006) A global overview of the conservation status of tropical dry forests. J Biogeogr 33(3):491–505. https://doi.org/10.1111/j.1365-2699.2005.01424.x

Montaño-Arias SA, Camargo-Ricalde SL, Grether R, Díaz-Pontones D (2015) Effect of scarification and temperature on seed germination of two Mexican species of *Mimosa* (Leguminosae-Mimosoideae). Bot Sci 93(3):649–659. https://doi.org/10.17129/botsci.185

Montesinos-Navarro A, Verdú M, Querejeta JI, Valiente-Banuet A (2017) Nurse plants transfer more nitrogen to distantly related species. Ecology 98(5):1300–1310. https://doi.org/10.1002/ecy.1771

Musara C, Aladejana EB (2020) *Acaciella angustissima* (Mill.) Brit. & Rose: Botanical features, distribution, medicinal and pharmacological properties. J Pharm Nutr Sci 10:325–330

Nicklen EF, Wagner D (2006) Conflict resolution in an ant–plant interaction: *Acacia constricta* traits reduce ant costs to reproduction. Oecologia 148(1):81–87. https://doi.org/10.1007/s00442-006-0359-6

Onofri A, Gresta F, Tei F (2010) A new method for the analysis of germination and emergence data of weed species. Weed Res 50(3):187–198. https://doi.org/10.1111/j.1365-3180.2010.00776.x

Onofri A, Mesgaran MB, Ritz C (2022) A unified framework for the analysis of germination, emergence, and other time-to-event data in weed science. Weed Sci 70(3):259–271. https://doi.org/10.1017/wsc.2022.8

Orozco-Almanza MS, De Leon-Garcia LP, Grether R, Garcia-Moya E (2003) Germination of four species of the genus *Mimosa* (leguminosae) in a semi-arid zone of Central Mexico. J Arid Environ 55(1):75–92. https://doi.org/10.1016/S0140-1963(02)00265-3

Pearson TRH, Burslem DFRP, Mullis CE, Dalling JW (2002) Germination ecology of neotropical pioneers: interacting effects of environmental conditions and seed size. Ecology 83:2798–2807

Pérez-Valladares CX, Velázquez A, Moreno-Calles AI, Mas JF, Torres-García I, Casas A, Rangel-Landa S, Blancas J, Vallejo M, Téllez-Valdés (2019) An expert knowledge approach for

mapping vegetation cover based upon free access cartographic data: the Tehuacán-Cuicatlán Valley. Central Mexico Biodivers 28(6):1361–1388

Ranal MA, Santana DG (2006) How and why to measure the germination process? Rev Bras Bot 29(1):1–11. https://doi.org/10.1590/S0100-84042006000100002

Rivas CA, Navarro-Cerillo RM, Johnston JC, Guerrero-Casado J (2020) Dry forest is more threatened but less protected than evergreen forest in Ecuador's coastal region. Environ Conserv 47(2):79–83. https://doi.org/10.1017/S0376892920000077

Sáenz-Romero C, Rehfeldt GE, Crookston NL, Duval P, St-Amant R, Beaulieu J, Richardson BA (2010) Spline models of contemporary, 2030, 2060 and 2090 climates for Mexico and their use in understanding climate-change impacts on the vegetation. Clim Change 102(3–4):595–623. https://doi.org/10.1007/s10584-009-9753-5

Sánchez JA, Martínez J, Pernús M (2017) Efecto de la temperatura y la iluminación sobre la germinación de semillas no dormantes de *Guazuma ulmifolia* (Malvaceae). Acta Bot Cub 216(2):55–60

Silveira FAO, Fernandes GW (2006) Effect of light, temperature and scarification on the germination of *Mimosa foliolosa* (Leguminosae) seeds. Seed Sci Techno 34(3):585–592. https://doi.org/10.15258/sst.2006.34.3.05

Songer M, Aung M, Senior B, DeFries R, Leimgruber P (2009) Spatial and temporal deforestation dynamics in protected and unprotected dry forests: a case study from Myanmar (Burma). Biodivers 18(4):1001–1018. https://doi.org/10.1007/s10531-008-9490-5

Sosa-Quintero J, Godínez-Álvarez H, Camargo-Ricalde SL, Gutiérrez-Gutiérrez M, Huber-Sannwald E, Jiménez-Aguilar A, Maya-Delgado Y, Mendoza-Aguilar D, Montaño NM, Pando-Moreno M, Rivera-Aguilar V (2022) Biocrusts in Mexican deserts and semideserts: a review of their species composition, ecology, and ecosystem function. J Arid Environ 199:104712. https://doi.org/10.1016/j.jaridenv.2022.104712

Stoner KE, Timm RM (2004) Tropical dry-forest mammals of palo verde. In: Frankie GW, Mata A, Vinson SB (eds) Biodiversity conservation in Costa Rica Learning the lessons in the seasonal dry forest. University of California Press, pp 48–66

Taiz L, Zeiger E, Moller IM, Murphy A (2010) Plant physiology and development, 6a edn. Sinauer Associates Inc, p 700

Ten Brink DJ, Hendriksma HP, Bruun HH (2013) Habitat specialization through germination cueing: a comparative study of herbs from forests and open habitats. Ann Bot 111(2):283–292. https://doi.org/10.1093/aob/mcs253

Thakur AS (2015) Floristic composition, life-forms and biological spectrum of tropical dry deciduous forest in Sagar District, Madhya Pradesh. India Trop Plant Res 2(2):112–119

Therneau TM, Grambsch PM (2000) Testing proportional hazards. Modeling survival data: Extending the Cox model Statistics for Biology and Health. Springer, New York

Therneau T, Crowson C, & Atkinson E (2023) Using time dependent covariates and time dependent coefficients in the Cox model.http://stat.ethz.ch/R-manual/R-patched/library/survival/doc/timedep.pdf. Accessed 16 Mar 2023

Valbuena L, Trabaud L (2001) Contribution of the soil seed bank to post-fire recovery of a heathland. Plant Ecol 152:175–183

Vallejo M, Casas A, Pérez-Negrón E, Moreno-Calles AI, Hernández-Ordoñez O, Tellez O, Dávila P (2015) Agroforestry systems of the lowland alluvial valleys of the Tehuacán-Cuicatlán Biosphere Reserve: an evaluation of their biocultural capacity. J Ethnobiol Ethnomedicine 11(1):8. https://doi.org/10.1186/1746-4269-11-8

Wulff RD, Caceres A, Schmitt J (1994) Seed and seedling responses to maternal and offspring environments in *Plantago lanceolata*. Funct Ecol 8(6):763–769

WWF (2016) Major habitat types. WWF Global. https://web.archive.org/web/20161017075416/http:// wwf.panda.org/about_our_earth/ecoregions/about/habitat_types/. Accessed 23 Jun 2023

Zhang Z, Reinikainen J, Adeleke KA, Pieterse ME, Groothuis-Oudshoorn CGM (2018) Time-varying covariates and coefficients in Cox regression models. Ann Transl Med 6(7):121. https://doi.org/10.21037/atm.2018.02.12