

Knowledge product

Climate Resilience Evaluation Report

Cardinal temperatures of tree species used in agroforestry systems for coffee shade in Coatepec, Veracruz, Mexico

Abstract

The production of coffee under shade of trees is a diversified system that offers environmental goods and services, so it is a profitable and sustainable practice. The selection of the appropriate trees is of outmost importance. However, some are difficult to propagate and have recalcitrant seeds that lose their viability in a short time, which makes germination the key to their propagation. The objective of the study was to determine the cardinal temperatures and the thermal time for the germination of the seeds of four species of trees used in agroforestry systems with coffee and analyze the effect of the temperature on germination, according to the climate change scenarios. *C. odorata* presented the widest range of cardinal temperatures (-0.5 ± 0.09 to 53.3 ± 2.1 °C), followed by *I. jinicuil* (4.8 ± 1.3 to 49.2 ± 3.6 °C). In the case of *L. diversifolia* it was from 5.17 ± 2.43 to 39.45 ± 0.31 °C. While for *S. macrophylla* it was from 12.8 ± 2.4 to 52.7 ± 2.2 °C. The thermal time of *L. diversifolia* was 55.57 ± 2.85 °CD, which in the current scenario accumulates in 3.5 days. But with the increase in temperature in future scenarios, you will be able to accumulate the thermal time in less time. In the case of *I. jinicuil* it was 259.96 ± 0.93 °CD, which requires 14.7 days to accumulate. But in future scenarios it will need only 12.6 days. The thermal time of *C. odorata* was 132.74 ± 2.6 °CD, which accumulates in 6.3 days, but in the future, it will accumulate in 5.5 days. *S. macrophylla* requires 189.09 ± 4.23 °CD, which accumulates in 29.5 days, but in the future climate change will cause it to accumulate up to nine days earlier. *C. odorata* germinated in a wider germination range, followed by *I. jinicuil*. While *S. macrophylla* and *L. diversifolia*, their germination range was much lower. This represented a direct relationship with their respective cardinal temperatures for each species. Therefore, the increase in temperature as an effect of climate change, will have a positive effect on the speed and rate of germination in the species studied.

Introduction

Climate change is altering precipitation and temperature patterns in the subtropical and tropical regions of Mexico. A greater frequency of extreme climatic events will affect the coffee-growing regions of the country, affecting the phenology of the species, including flowering season and therefore germination (Anderson et al. 2012; Craufurd and Wheeler, 2009; Franks et al. 2007; Gaira et al. 2014; Iler et al. 2013; Wang et al. 2015), thus modifying the structure and composition of tree communities, and their geographic distribution (Iverson et al. 2005; Iverson and McKensie, 2013; Kelly and Goulden, 2007; McKenney et al. 2007; Parmesan and Yohe, 2003; Pautasso, 2013; Root et al. 2005; Thuiller et al. 2008). Among the factors that shape the distribution of species, seed dispersal and the environmental conditions for germination play an important role (Fernandez-Pascual et al. 2019; Kurpis et al. 2019; Walk et al. 2011).

Coffee (*Coffea arabica* L.) is the most important tropical crop in the world (Craparo et al. 2015; Torres-Castillo et al. 2022). However, climate change is impacting the reduction of areas suitable for its cultivation, in addition to the appearance of pests and diseases, which negatively impacts coffee production (Guerrero-Carrera et al. 2020). In addition, in Mexico there are other problems that have a negative impact on coffee production: such as high production costs, low prices in the international market, the decapitalization of the sector, the difficulty in accessing credit, the high costs of supplies and the rising labor costs (Avila-Victor et al. 2023; Robles-Berlanga, 2011). Therefore, to guarantee the sustainability of the crop in the future, it will be necessary to identify multipurpose species as an alternative to generate additional goods and services. Agroforestry systems have the potential to develop the coffee-growing areas of the country (Cassamo et al. 2023), so it will be necessary to develop research on the germination and establishment of shade trees for coffee.

The tropical regions are home to the greatest diversity in the country, which is why it is the basis for the development of the forestry and agricultural regions of Mexico. However, it is

a fragile ecosystem and highly vulnerable to climate change (Chong-Jing et al. 2019). According to Calvo et al. (2000), by the end of the last century, more than 60% of the original distribution of the tropical forest in the Americas had been lost. In the case of Mexico, only 24% of their natural populations have been conserved. The mechanism for its ecological regeneration and restoration is through seed production, but its success depends on the ability of these seeds to germinate (Walk et al. 2011) and resist climate change that threatens the function and diversity of agroecosystems. (Nunez et al. 2019).

During the last decades, many studies focused on proposing species in agroforestry systems with high potential to satisfy the demand for forest products and environmental benefits in rural areas, such as fruits, wood, firewood, seeds, livestock feed, improvement of the soil fertility, nitrogen fixation, carbon sequestration, wind and temperature moderation, in addition to increasing diversity in coffee plantations (Dagang and Nair, 2003; Pavlidis and Tsihrintzis, 2018;). The UK PACT project aims to rescue the knowledge and experiences of coffee growers, for the development of the coffee region of Veracruz. Therefore, workshops were held with the coffee producers. In the workshops, several tree species were identified as priorities for the region. The selection of the most appropriate species was based on the experiences, traditional and cultural uses that the producers give to each species. They were weighted according to the goods and services offered to coffee growers, taking into account the traditional use of forest vegetation by the communities of the coffee region of Veracruz. With which a socio-environmental algorithm was designed. However, it was not possible to evaluate some, due to the fact that the phenology did not coincide during the development of the project or the recalcitrance of its seeds. Therefore, the study of four tree species is presented, which are in the ranking of the 25 most important tree species for coffee growing in Mexico, according to the socio-environmental algorithm designed specifically for this evaluation.

Agroforestry systems are a method for the preservation of landscapes, agrobiodiversity and traditional knowledge (Santoro et al. 2020). They are also refuge areas for endangered species (Toledo-Aceves, 2017). But in addition, trees have been identified that have managed to increase the production of the crops in which they are associated. Among those that stand out, species of *Leucaena* spp. (Rosenstock et al. 2014), *Inga jinicuil* Schltdl. and cham. Ex

G. Don Schltdl. and cham. Ex G. Don (Toledo-Aceves, 2017), Spanish cedar (*Cedrela odorata* L.) (Calvé-Jarque et al. 2020) and mahogany (*Swietenia macrophylla* King) (Chinchilla-Mora et al. 2021). These species have been used mainly in agroforestry systems to shade coffee (*C. arabica*), cocoa (*Theobroma cacao* L.) and citrus (*Citrus* spp. L.) plantations (Vargas-Simón and Pire, 2017). These are promising tree species for restoring degraded areas and mitigating climate change.

The species considered in this study have a fragmented distribution in small and dispersed populations, which develop in a fragile ecosystem, making them vulnerable to extinction (IUCN, 2023). For its regeneration it depends on seed production and its ability to germinate and emerge (Rajjou and Debeaujon, 2008; Walk et al. 2011). Germination is the most important step for the propagation of trees (Bradford, 2002), it responds to humidity and temperature signals, which are expected to change in the context of climate change, affecting the physiological processes of the reproductive phenology of the species (Fernández-Pascual et al. 2019). Therefore, climate change is a threat to the function and diversity of the ecosystems of the coffee-growing regions of the country (Nunez et al. 2019). When humidity is not limiting, temperature is the most important bioclimatic element that regulates speed and maximum germination percentage, but also controls seedling growth (González, 1991; Sampayo-Maldonado et al. 2021). Each species has an optimal range of temperatures to germinate, which can vary due to its geographical origin (Sampayo-Maldonado et al. 2019). Some seeds lose their viability in a short time, which makes germination the key stage for the recruitment of individuals, which can be affected by temperature changes (Sampayo-Maldonado et al. 2021). However, there are no studies of cardinal temperatures or thermal time for the germination of the species considered in this study. Given the imminent scenario of temperature increase as a consequence of climate change, it will be unavoidable to carry out research to analyze the effect of temperature on the germination of species of agroforestry interest. The objective was to determine the cardinal temperatures and the thermal time for the germination of seeds of species that are used for coffee shade, as well as to analyze the impact of climate change on their germination and potential distribution.

4. Materials and Methods

4.1. Origin of the seeds

The natural distribution of *C. odorata*, *Leucaena diversifolia*, *I. jinicuil* and *S. macrophylla* in Mexico harbors a part of the state of Veracruz. For this reason, between the months of March, April and May, the ripe fruits of each species were collected, in coffee agroforestry systems with shade trees, in various locations in the Municipality of Coatepec, Veracruz. (718806.96 E and 2152610.24 N; 1189 m.a.s.l.), which is located in the central mountainous area of Veracruz. The climate at the site is humid temperate, with rainfall all year round (Cf) according to García (2004), with an average annual rainfall of 1761 mm, and an average temperature of 19.4 °C. Figure 1 shows the monthly average values of temperature and precipitation. The soils are humic andosol type of volcanic origin, with good drainage, have a clay-sandy texture and a pH of 6.5 (García-Franco et al., 2006).

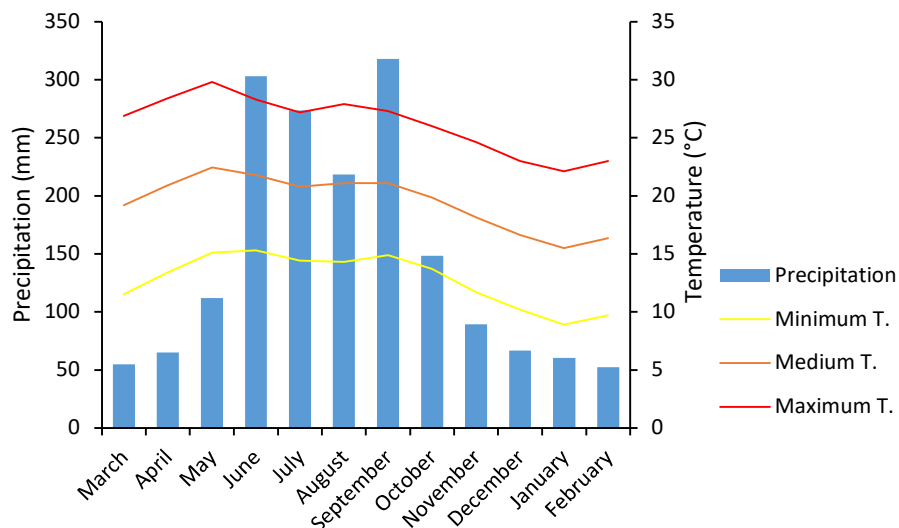


Figure 1. Climatic data of the area where seeds were collected in Coatepec, Veracruz. Historical monthly average of 1981–2010. Available in global climate data (<http://es.climate-data.org/>).

After making the collection in Coatepec, the fruits were sent to Tlalnepantla. Where the fruits were opened with tweezers. The seeds were manually separated from the plant debris and stored in paper bags (15 °C and 55-60% humidity) for one day. Subsequently, germination and moisture content tests were carried out. Then the experiment of cardinal temperatures was established. The protocol and the experiment were made in the facilities of the Plant

Physiology Laboratory, of the Biotechnology and Prototype Research Unit (Unidad de Biotecnología y Prototipos-UBIPRO), of the Iztacala Faculty of Higher Studies (Facultad de Estudios Superiores Iztacala-FESI), of the National Autonomous University of Mexico (Universidad Nacional Autónoma de México-UNAM), located in Tlalnepantla, State of Mexico.

4.2. Initial germination test

For the germination test, the seeds were placed in a medium with agar (10 g. L⁻¹) placed in Petri dishes (6 cm in diameter). A completely randomized design with ten replicates of 10 seeds was used for the *I. jinicuil* and *S. macrophylla* species. and four replicates of 25 seeds for the species of *C. odorata* and *L. diversifolia*. The Petri dishes were placed in a controlled environment chamber, at a temperature of 25 ± 2 °C and a relative humidity of 70%. A seed was considered germinated when the radicle measured ≥ 1 mm (ISTA, 2005; Parmoon et al., 2015; Peng et al., 2019).

4.3. Effect of temperature on germination

Seeding was carried out under aseptic conditions in a laminar flow hood. In the case of *I. jinicuil* and *S. macrophylla*, ten seeds were planted in agar medium (10 g. L⁻¹) in Petri dishes, with 10 replicates each, completely at random. For *C. odorata* and *L. diversifolia* it was five replicates with 25 seeds. Subsequently, they were sealed with Parafilm and placed in the sprouters at the following constant temperatures: 5 ± 2 , 10 ± 2 , 15 ± 2 , 20 ± 2 , 25 ± 2 , 30 ± 2 , 35 ± 2 , 40 ± 2 and 45 ± 2 °C, with a photoperiod of 12 hours of light and 12 hours of darkness, using halogen lamps with a light intensity of $28.05 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Quantum Meter Apogee Mod. QMSW-SS, Logan, UT, USA). The sowing was carried out on September 17, 2022. The germination record was carried out daily for 100 days. To evaluate the viability, at the end of the experiment the non-germinated seeds were cut. According to ISTA (2005), Parmoon et al. (2015) and Peng et al. (2019), a seed was considered germinated when the radicle measured ≥ 1 mm.

4.4. Evaluated variables

For total germination, the number of germinated seeds in each Petri dish was recorded for each temperature treatment. According to the following equation for germination percentage (G(%)) (1) (Sampayo-Maldonado et al., 2017):

$$G(\%) = \frac{n}{N} * 100 \quad (1)$$

Where: n is the number of germinated seeds and N is the total number of seeds.

The record of time when 50% of the seeds lot germinates (T_{50}) and the number of days elapsed from sowing the seeds until 50% germination was reached was made. According to Ordoñez-Salanueva et al. (2015), an adjustment was made to a sigmoid model, in which the value was obtained by interpolation in the graph of accumulated germination.

Germination speed(GS) is an estimate of the number of seeds germinated per day. According to the following equation (2) (Calzada-López et al., 2014):

$$GS = \frac{G_1}{N_1} + \frac{G_2}{N_2} + \dots + \frac{G_i}{N_i} + \dots + \frac{G_n}{N_n} = \sum_{i=1}^n \frac{G_i}{N_i} \quad (2)$$

Where: G_i is the number of germinated seeds and N_i is the number of days after the experiment started.

To calculate the base temperature (T_b), the time for germination was calculated in intervals of 10%, for all temperature treatments. Then their inverse were obtained and they were plotted in relation to the temperatures to observe the trend of the data, where the inflection point was located and the range of sub-optimal temperatures was determined, which is delimited by T_b and T_o (optimal temperature). According to Ellis et al. (1986), linear regression was determined to obtain the parameters for each germination percentage. Subsequently, the average value of (β_0) was obtained. With the average value, a second linear regression was performed for each germination percentage and the average value of (β_0) was calculated, which was the value of the base temperature.

To estimate the ceiling or maximum temperature (T_c), according to Hardegree (2006), the temperature range between T_o and T_c is defined as supra-optimal. The linear regression obtained was used to calculate T_c for germination in 10% intervals. The average value of

(β_0) was obtained, with which a second linear regression was performed and the average value of (β_0) was obtained again, which was the value of the maximum temperature.

To obtain the optimum temperature (T_o), once the base (T_b) and maximum (T_c) temperatures were obtained, according to Hardegree (2006), both equations were equal to zero. The value obtained was the optimum temperature.

Thermal time is the sum of the average temperature accumulated per day above the base temperature, which is necessary for the germination of 50% of the seed lot (Bradford, 2002). The number of germinated seeds was obtained in intervals every 10%, for all temperature treatments. To estimate the probability that a seed germinates in a given time, Probit analysis was used. For the range of suboptimal temperatures, the Probit values were expressed as a function of θ_1 . The following equation (3) was used, according to Covell et al. (1986):

$$Probit(G) = K + [\theta_1 / \sigma] \quad (3)$$

Where: K is an intercept constant when thermal time is zero and σ is the standard deviation of the thermal time response θ_1 . With the same equation, the thermal time required for the germination of 50% (θ_1 (50)) of the population was determined.

For the range of supra-optimal temperatures, the Probit values were expressed as a function of θ_2 . According to Covell et al. (1986), to describe the germination response, the following equation (4) was used:

$$Probit(G) = Ks + (T + \theta_2/t(G))/\sigma \quad (4)$$

Where: Ks is an intercept constant when thermal time is zero; $(T+\theta_2/t(G))$ is the maximum temperature (T_c) and σ is the standard deviation of the maximum temperature (T_c). With the same equation, the thermal time required for the germination of 50% (θ_2 (50)) of the population was determined.

4.5. Experimental design and analysis

A completely randomized design was used (the seeds had the same probability of being selected), with 9 temperature treatments and 10 repetitions, the experimental unit consisted

of a Petri dish with 10 seeds (*I. jinicuil* and *S. macrophylla*). For *C. odorata* and *L. diversifolia*, 5 replicates were used, the experimental unit consisted of a Petri dish with 25 seeds. The data did not meet the assumptions of normality; therefore, prior to the analysis of variance, the percentage variables (Y) were transformed with the arcsine function of the square root of the original value expressed as a decimal fraction [$T = \arcsin(\sqrt{Y})$] (Itoh et al., 2002; Syros et al., 2004). The variance analyses were carried out with the statistical program SAS (2004), applying post hoc Tukey's multiple comparisons ($p \leq 0.05$).

4.6. Germination in scenarios of climate change

According to Fernández-Eguiarte et al. (2015), the projections of the average temperature layers, proposed by the Global Circulation Models, were used; of the French model (CNRMCM5), American model (GFDL-CM3), English model (HADGEM2-ES) and German model (MPI-ESM-LR), available in the Digital Climate Atlas for Mexico (<http://atlasclimatico.unam.mx/AECC/servmaps/>). Which according to Manzanilla-Quíñonez et al. (2018), were generated from the Regional Models of the Phase 6 Coupled Models Intercomparison Project of the Intergovernmental Panel on Climate Change (IPCC), projected for the medium future horizon (2045-2069) and the distant future (2075-2099). With Shared Socioeconomic Pathways (SSP1) of 2.6 Watts/m² (constant CO₂ emissions), classified as a conservative scenario. With a monthly temporal and spatial resolution of 30" x 30" (approximately 926 * 926 m).

The areas where the seed collections were made were located, and the average temperature data was obtained for each Global Circulation Model (GCM), radiative forcing (SSP1) and each future projection (WorldClim, 2023). According to Cámara-Cabrales and Kelty (2009), mean temperatures were projected for the month in which seed dispersal begins. In the case of *S. macrophylla*, it starts in March, *C. odorata* and *L. diversifolia* in April, and *I. jinicuil* in May.

Each scenario was used to predict the time that the seeds of each species will accumulate the thermal time required for the germination of 50% of a seed bank in the understory. According to Flores-Magdaleno et al. (2014), the analysis was carried out by the mean temperature method, for which the following equation (5) was used according to Orrù et al. (2012):

$$\text{Suma térmica } (^{\circ}\text{Cd}) = (\text{Env } T_m - T_b)t_m \quad (5)$$

Where: °Cd are the accumulated degree days, T_b is the base germination temperature, T_m is the average temperature for the month (m) and t_m is the number of days in the month (m).

3. Results

3.1. Germination

The *I. jinicuil* seeds germinated in a range of 5 to 40 °C. The seeds presented an initial moisture content of $59.6 \pm 4.3\%$ and a germination of 96%. While in the treatments an average germination of 60% was obtained, in a range of 12 to 90%, these differences being significant in the statistical analysis ($F_{7,32} 36.48$; $p < 0.00001$). The lowest germination was 12.5% and was observed at the lowest temperature (5 °C), but as the temperature increased, germination also increased. This is valid up to 25 °C, where the greatest germination occurs. However, if the temperature increases, germination tends to decrease (Figure 2 a).

The seeds of *C. odorata* germinated in a range of 5 to 45 °C. There was a significant effect of temperature on the final percentage of germination ($F_{8,36} 49.82$; $p < 0.02$). The seeds began to germinate after three days, while at the lowest temperature they began 28 days after sowing. The average germination was above 50%, and the highest frequency was 90% germination (Figure 2 b). The highest percentage of germination was at 20 ± 2 °C and the lowest percentage was at the highest temperature.

The seeds of *S. macrophylla* germinated in a range of 15 to 45 °C. The germination average was above 70% and varied from 4 to 96% (Figure 2 c), these differences being statistically significant ($F_{6,28} 54.02$; $p < 0.00001$). The lowest germination percentage was at 15 °C, showing an abrupt decrease. It is important to point out that at low temperatures (5 and 10 °C) there was no germination (Figure 2 c). The highest germination rate was at 25 °C and

there was a tendency to decrease with increasing temperature, although there was no significant difference between the germination rates recorded between 20 and 35°C.

The seeds of *L. diversifolia* germinated in the range of 10 to 35 °C. Temperature significantly affected the proportion of germinated seeds, regardless of their rank ($F_{5, 20} 41.79$; $p < 0.0001$). The germination average in the temperature range was 90%, and the highest germination reached 98% at 20 and 25 °C, while the lowest germination was observed at 35 °C with 78% (Figure 2 d).

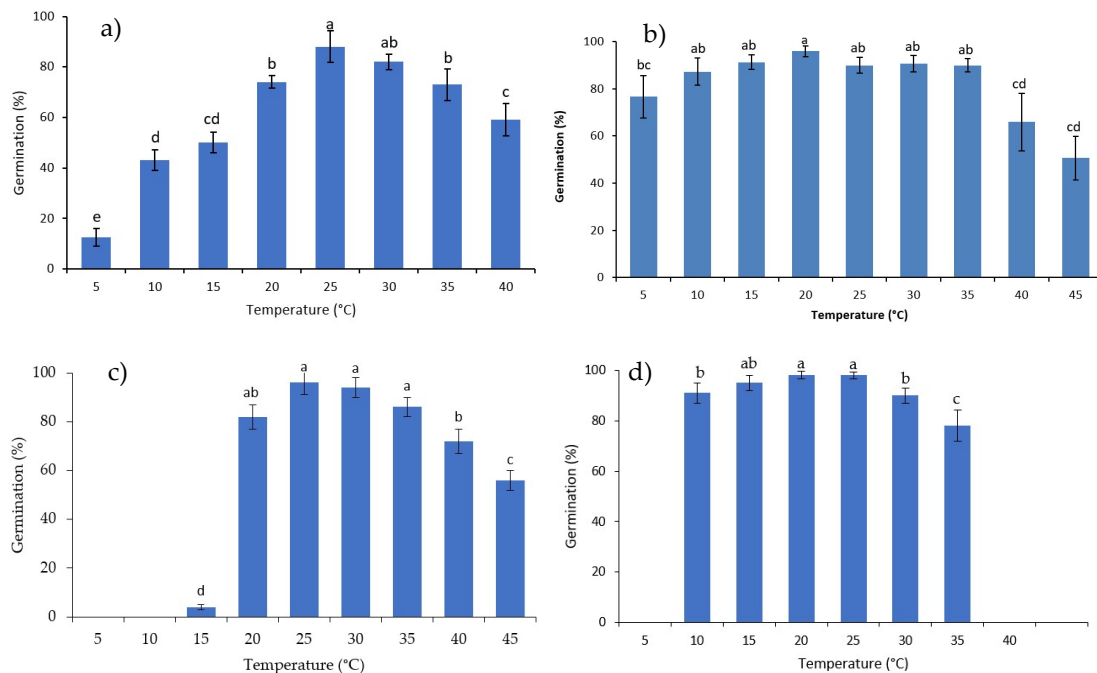


Figure 2. Germination percentages for each temperature treatment: a) *I. jinicuil*. b) *C. odorata*. c) *S. macrophylla*. d) *L. diversifolia*. Error bars show standard deviation. Means that share the same letter are not significantly different ($p \leq 0.05$).

For *I. jinicuil* seeds began to germinate after 2 days at temperatures of 25 to 35 ± 2 °C. At 40 °C, germination begins after 3 days. While at 15 and 10 ± 2 °C, germination begins at 7 and 11 days, respectively. But at 5 ± 2 °C germination occurs up to 16 days. The germination time of 50% of the seeds of each treatment (T50) showed significant differences between the temperature ranges ($F_{4,28}$ 13.08; $p < 0.0001$). The fastest germination of T50 occurred after 7 days at a temperature of 25 ± 2 °C. A short time later, at temperatures of 30 and 35 ± 2 °C, the T50 appears after 9 days. At temperatures of 40 and 20 ± 2 °C, T50 occurs at 11 and 12 days, respectively. While more than 17 days were required at the temperature of 15 ± 2 °C. At lower temperatures, germination was less than 50% (Figure 3 a).

The time required for 50% of the *C. odorata* seeds to germinate was significantly different between temperature treatments ($F_{8,36}$ 112.34; $p < 0.0001$). To reach 50%, three to five days were required at temperatures above 20 ± 2 °C, while at lower temperatures it took 18 to 47 days (15 ± 2 to 5 ± 2 °C respectively; Figure 3 b).

At temperatures from 30 to 45 ± 2 °C, seeds of *S. macrophylla* began to germinate after 6 days, while at temperatures of 20 and 25 ± 2 °C this occurred after 18 days. In the case of the 15 ± 2 °C temperature treatment, this was after 91 days (Figure 3). The time to germination of 50% of the seeds showed significant differences ($F_{5,24}$ 2.51; $p < 0.02$). At 35 ± 2 °C, 50% germination occurred at 9 days. At higher temperatures, less time was required than at lower temperatures; for example at 40 and 45 ± 2 °C, 50% germination was achieved in 10 days with 17 hours and 10 days with 3 hours, respectively. Meanwhile, at 30 ± 2 °C this occurred in 19 days, while more than 36 days were required at 25 ± 2 and 20 ± 2 °C (Figure 3 c).

For *L. diversifolia* seeds, the mean germination time (T50) was also significantly affected by temperature ($F_{5,20}$ 127.15; $p < 0.0001$). For 50% germination, the seeds needed less time at higher temperatures, e.g. 2 days at 30 °C, 3 days at 20 and 25 °C, 5 days at 35 °C but longer with lower temperatures, that is, 12 and 18 days at 15 and 10 °C, respectively.

b)

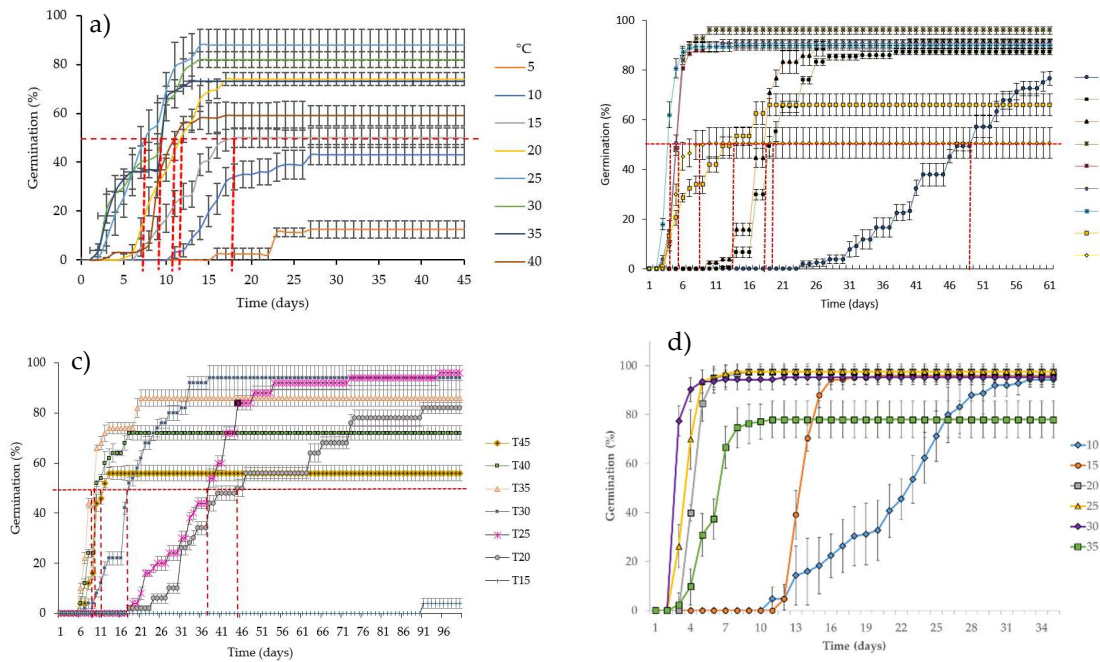


Figure 3. Cumulative seed germination percentages and time required for 50% germination at each temperature treatment (dashed vertical lines in red): a) *I. jinicuil*. b) *C. odorata*. c) *S. macrophylla*. d) *L. diversifolia*. The error bars show standard deviation.

The germination speed for *I. jinicuil* showed significant differences between the treatments ($F_{7,32} 21.37$; $p < 0.00001$). At temperatures of 25 to 35 ± 2 °C, an average of seven seeds germinated per day. While at 20 and 40 ± 2 °C the average germination of five seeds in one day was recorded. At lower temperatures (10 and 15 ± 2 °C), two seeds germinated per day. But at the lowest temperature (5 ± 2 °C), the seed took two days to germinate.

The germination speed for *C. odorata* differed significantly between temperatures ($F_{8,36} 28.13$; $p < 0.001$). Germination was fastest at 35 °C, where six seeds germinated per day, and the slowest was at 5 °C, with one seed every two days.

In *S. macrophylla* seeds, there were significant differences in germination speed ($F_{6,28} 32.61$; $p < 0.00001$). The highest germination speed occurred at 35 ± 2 °C, in which one seed germinated per day. As the temperature increased, the germination speed decreased and, at

45 ± 2 °C, one seed germinated every two days. At temperatures below 35 ± 2 °C, germination slowed down, requiring 100 days for a seed to germinate at 15 ± 2 °C.

In *L. diversifolia* seeds, the temperature range produced significant differences for germination speed ($F_{5,20}140.54$; $p < 0.0001$). The fastest germination occurred at 30 °C, in which 10 seeds germinated per day, but the germination rate decreased considerably when the temperature increased to 35 °C with four seeds per day. At 10-15 °C, the germination rate was slower with one seed per day, while at 20-25 °C the germination rate was medium with 4 and 3 seeds per day, respectively.

3.2. Cardinal temperatures

The cardinal temperatures of *I. jinicuil* showed a wide range (4.8 to 49.2 °C) of thermal niche for germination. The suboptimal temperatures were explained by the model in 95% and the supraoptimal temperatures in 92%. The base temperature (T_b) for the start of germination was 4.8 ± 1.3 °C. With the increase in temperature, the germination speed increased until it reached its maximum speed at 31.6 ± 2 °C, which was its optimum temperature (T_o). As the temperature increased above T_o , the germination rate resulted in the maximum or ceiling temperature (T_c), which was the maximum temperature for germination at 49.2 ± 3.6 °C. Table 1 shows the values of cardinal temperatures for the species.

The cardinal temperatures of *C. odorata*. For suboptimal temperatures, the model explained 89% of the variance in germination rate, while for supraoptimal temperatures, the model explained 97% of the variance. By increasing the temperature, the germination rate increased until reaching its optimum temperature (T_o) of 38 ± 1.6 °C, while decreasing the temperature will decrease the germination rate to zero at the base temperature (T_b) $-0, 5 \pm 0.09$ °C. As the temperature increased above the optimum temperature (T_o), the germination rate decreased to its minimum at the upper threshold temperature (T_c) at 53.3 ± 2.1 °C. The base temperature was negative, since there was a germination percentage higher than 75% at the lowest temperature tested, 5 ± 2 °C (Table 1). The optimal temperature (38 ± 1.6 °C) was directly related to the temperature that had the highest germination rate (Figure 1 b). The upper

temperature threshold was above 53 °C, and this can be explained because at 45 ± 2 °C it took 5.6 days for 50% of the seed lot to germinate (Figure 2 b).

Cardinal temperatures of *S. macrophylla* (Table 1). The suboptimal temperatures for the germination rate of this species were explained by the model by 86%, while the supraoptimal temperatures were explained by 91%. The calculation of the intercept of the slopes for each percentile indicated that the T_b for germination to occur was 12.8 ± 2.4 °C. As the temperature increased, the germination speed increased until it reached its maximum point with a T_o of 37.3 ± 1.3 °C. When the temperature increased above T_o , the germination rate decreased to a T_c of 52.7 ± 2.2 °C. As expected, the T_b of 12.8 ± 2.4 was below 15 ± 2 °C since the average germination rate was only 4% at this temperature after 100 days (Figure 2 c). The T_o (37.3 ± 1.3 °C) is directly related to the temperature that presented the highest germination speed, while the T_c was 52.7 ± 2.2 °C, and it is explained because at 45 ± 2 °C only 56% germinated. of the seeds and required 10 days and 3 hours for 50% of the seed lot to germinate.

The estimated mean cardinal temperatures for *L. diversifolia* (Table 1) were: 5.17 °C for T_b , 29.42 °C for T_o and 39.45 °C for T_c . For the model, the predicted T_c for 80% was 35 °C, affecting the average value (39.45 °C); this is due to the constriction of 35 °C for the inflection point, the temperature at which this percentage ceases to germinate. For the model in the suboptimal and supraoptimal, the RMSE tends to decrease from 10% to 70%, however, an increase in the RMSE value of 80% was observed. On the other hand, r^2 and adjusted r^2 tend to increase from 10% to 70%, while for 80% the values of r^2 decrease, indicating a lower adjustment for the 80% percentile.

Table 1. Cardinal temperatures and thermal time for seed germination, estimated for the species under study.

Species	T_b	T_o	T_c	Thermal time
<i>C. odorata</i>	-0.50 ± 0.09	38.00 ± 1.60	53.30 ± 2.10	132.74 ± 2.60
<i>I. jinicuil</i>	4.80 ± 1.30	31.60 ± 1.10	49.20 ± 3.60	259.96 ± 0.93
<i>L. diversifolia</i>	5.17 ± 2.43	29.42 ± 1.40	39.45 ± 0.31	55.57 ± 2.85

<i>S. macrophylla</i>	12.80 ± 2.40	37.30 ± 1.30	52.70 ± 2.20	189.09 ± 4.23
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Tb = base temperature, To = optimum temperature and Tc = ceiling temperature.

The thermal germination time of 50% of the *I. jinicuil* seed lot, at suboptimal temperatures (θ_1 (50)) was 259.969 ± 0.936 °Cd. The Probit model had a fit greater than 89% (Table 1). According to the base temperature (Tb), to obtain 50% germination of *C. odorata* seeds, 132.74 ± 2.60 °Cd of thermal time (θ_1 (50)) must be accumulated. The Probit model explained more than 96% of it. The intercept constant was -4.91 ± 0.53 , when the thermal time was zero, and the standard deviation of the thermal time was 0.125 ± 0.019 (Table 1). The thermal time for germination of 50% of the *S. macrophylla* seed lot for suboptimal temperatures (θ_1 (50)) was 189.091 ± 4.239 °Cd. The Probit model explained this with more than 92% (Table 1). For suboptimal temperatures (θ_1 (50)), the thermal time to reach 50% germination in *L. diversifolia* was 51.34 ± 2.89 °Cb according to the Probit model, in which the r^2 value was 75% (Table 1).

3.3. Germination under Climate Change Scenarios

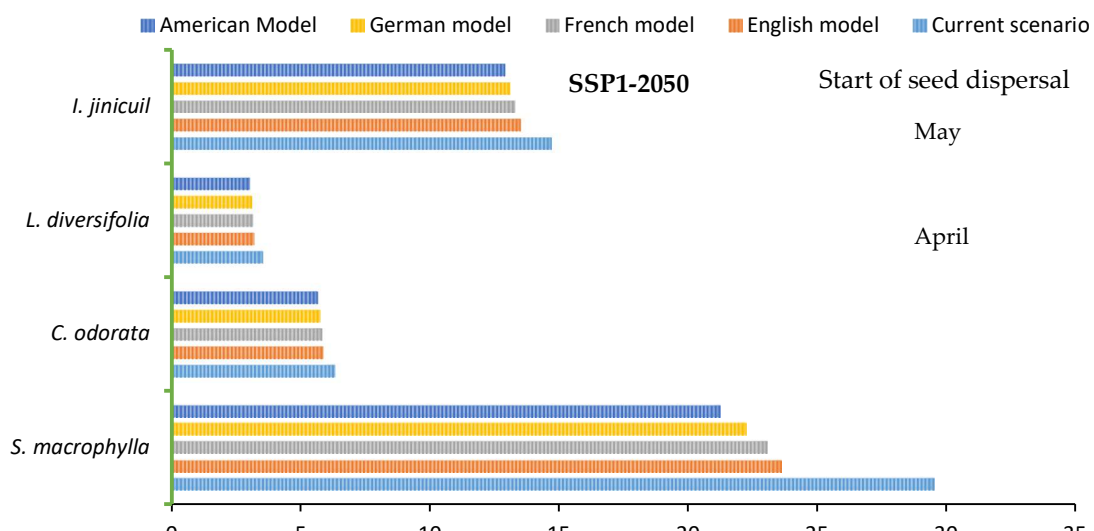
The seeds of *I. jinicuil* are dispersed in May, with an average temperature of 22.4 °C. in the current scenario, the thermal time (θ_1 (50) of $259,969 \pm 0.936$ °CD) accumulates in 14.7 days, when germination would begin (figure 4); For the intermediate future (2050), in the conservative scenario (SSP1 2.6 watts/m²), several models predict the increase in temperature. In the English model (Hadgem2-ES) an increase of 1.6 °C for the month of May is predicted. Similarly, in the French model (CNRMCM5), it will be 1.8 °C; For the German model (MPI-ESM-LR), 2.1 °C and for the American model (GFDL-CM3), the increase will be 2.5 °C. For the intermediate future, in the English model the thermal time accumulates at 13.5 days. For French and German models, they do it at 13.3 and 13.1 days, respectively. While in the American model it does in less than 13 days (Figure 4).

The seeds of *C. odorata* are dispersed in April, with an average temperature of 20.9 °C. in the present (current scenario), the thermal time (θ_1 (50) of 132.74 ± 2.60 °CD) accumulates in 6.3 days (figure 4). For the intermediate future (2050), on the conservative stage (SSP1 2.6 watts/m²). In the English model (Hadgem2-ES) an increase of 1.5 °C is predicted for the

month of April. Similarly, in the French model (CNRMCM5), it will be 1.73 °C; For the German model (MPI-ESM-LR), 2 °C and for the American model (GFDL-CM3), the increase will be 2.6 °C. For the intermediate future, in the English model the thermal time accumulates to 5.9 days. For French and German models, they do it in 5.8 and 5.7 days, respectively. While in the American model it does in 5.6 days (Figure 4).

The seeds of *L. diversifolia* are dispersed in April, with an average temperature of 20.9 °C. in the present (current scenario), the thermal time (θ_1 (50) of 55.57 ± 2.85 °CD) accumulates in 3.5 days (figure 4). For the intermediate future (2050), on the conservative stage (SSP1 2.6 watts/m²). In the English model (Hadgem2-ES) an increase of 1.5 °C is predicted for the month of April. Similarly, in the French model (CNRMCM5), it will be 1.73 °C; For the German model (MPI-ESM-LR), 2 °C and for the American model (GFDL-CM3), the increase will be 2.6 °C. For the intermediate future, in the English model the thermal time accumulates to 3.2 days. For French and German models, they do it at 3.15 and 3.1 days, respectively. While in the American model it does in 3 days (Figure 4).

The seeds of *S. macrophylla* are dispersed in March, with an average temperature of 19.2 °C. In the present (current scenario), the thermal time (θ_1 (50) of 189.09 ± 4.23 °CD) accumulates in 29.5 days (Figure 4). For the intermediate future (2050), on the conservative stage (SSP1 2.6 watts/m²). In the English model (Hadgem2-ES) an increase of 1.4 °C for the month of March is predicted. Similarly, in the French model (CNRMCM5), it will be 1.6 °C; For the German model (MPI-ESM-LR), 1.9 °C and for the American model (GFDL-CM3), the increase will be 2.4 °C. For the intermediate future, in the English model the thermal time will accumulate at 23.6 days. For French and German models, they do it in 23 and 22.2 days, respectively. While in the American model it does in 21 days (Figure 4).



April

March

Figure 4. Time in which the seeds accumulate the thermal sum ($^{\circ}\text{Cd}$) during the dispersal month for each species. For the intermediate future (2050), under a conservative scenario (SSP1 2.6 Watts/m²).

For the distant future (2070) of *I. jinicuil*, on the conservative stage (SSP1 2.6 watts/m²), the French model (CNRMCM5) predicts an increase of 2.1 $^{\circ}\text{C}$ for the month of May. The German model (MPI-ESM-LR), predicts an increase of 2.3 $^{\circ}\text{C}$ and the English model (Hadgem2-ES), 2.8 $^{\circ}\text{C}$. while in the American model (GFDL-CM3), the increase will be of 2.9 $^{\circ}\text{C}$. With the expected increase in temperature, thermal time (θ_1 (50) of $259,969 \pm 0.936$ $^{\circ}\text{CD}$) will accumulate in less time. It requires 13.1 days for the French model and 12.6 for the American model. Therefore, the accumulation of thermal time can occur up to two days before, compared to the current scenario (Figure 5).

For the distant future (2070) of *C. odorata*, on the conservative stage (SSP1 2.6 watts/m²), the French model (CNRMCM5) predicts an increase of 2.2 $^{\circ}\text{C}$ for the month of April. The GER-MAN (MPI-ESM-LR) model predicts an increase of 2.4 $^{\circ}\text{C}$ and the English model (Hadgem2-ES), 2.7 $^{\circ}\text{C}$. while in the American model (GFDL-CM3), the increase will be of 2.95 $^{\circ}\text{C}$. With the expected increase in temperature, thermal time (θ_1 (50) of 132.74 ± 2.6 $^{\circ}\text{CD}$) will accumulate in less time. It requires 5.7 days for the French model and 5.5 for the American model. Therefore, the accumulation of thermal time can occur up to one day before, compared to the current scenario (Figure 5).

For the distant future (2070) of *L. diversifolia*, in the conservative stage (SSP1 2.6 watts/m²), the French model (CNRMCM5) predicts an increase of 2.2 $^{\circ}\text{C}$ for the month of April. The

GER-MAN (MPI-ESM-LR) model predicts an increase of 2.4 °C and the English model (Hadgem2-ES), 2.7 °C. while in the American model (GFDL-CM3), the increase will be of 2.95 °C. With the expected increase in temperature, thermal time (θ_1 (50) of 55.57 ± 2.85 °CD) will accumulate in less time. It requires 3.1 days for the French model and 2.98 for the American model. Therefore, the accumulation of thermal time can occur until noon, compared to the current scenario (Figure 5).

For the distant future (2070) of *S. macrophylla*, on the conservative stage (SSP1 2.6 watts/m²), the French model (CNRMCM5) predicts a 2 °C increase for the month of March. The GER-MAN (MPI-ESM-LR) model predicts an increase of 2.2 °C and the English model (Hadgem2-ES), 2.6 °C. while in the American model (GFDL-CM3), the increase will be of 2.9 °C. With the expected increase in temperature, thermal time (θ_1 (50) of 189.09 ± 4.23 °CD) will accumulate in less time. It requires 22.2 days for the French model and 20.3 for the American model. Therefore, the accumulation of thermal time can occur up to nine days before, compared to the current scenario (Figure 5).

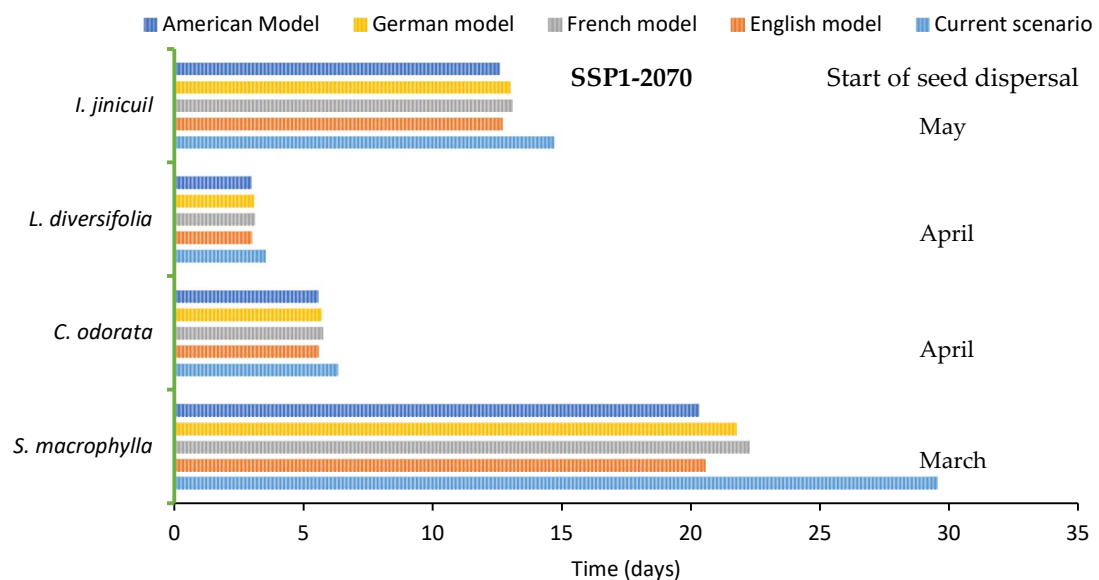


Figure 5. Time in which the seeds accumulate the thermal sum ($^{\circ}\text{Cd}$) during the dispersal month for each species. For the intermediate future (2070), under a conservative scenario (SSP1 2.6 Watts/m²).

4. Species considerations

4.1. Germination

A range of temperatures (20 to 25 $^{\circ}\text{C}$) suitable for the germination of ingas had been reported, and another range that indicated the low temperatures in which it could germinate (10 to 15 $^{\circ}\text{C}$). However, a broader temperature gradient in germination (5 to 40 $^{\circ}\text{C}$) of *I. jinicuil* had not been tested. The results showed that the species germinates in a larger thermal niche. The highest germination percentages occurred at 25 ± 2 $^{\circ}\text{C}$, which coincides with Leão et al. (2012) and Rodrigues et al. (2007) who mention that the genus *Inga* presents good germination between 20 and 25 $^{\circ}\text{C}$. However, it is below the optimum temperature (T_o : 31.6 ± 1.1), which coincides with the results reported for other tropical species, such as: *C. odorata* (T_o : 38 ± 1.6) and *S. macrophylla* (T_o : 37.3 ± 1.3). Therefore, the highest germination does not always occur at the optimum temperature (Calzada-López et al., 2014). While the lowest percentage of germination occurred in the seeds exposed to the lowest temperature (5 ± 2 $^{\circ}\text{C}$), which may be due to the fact that the recalcitrant seeds of tropical species are sensitive to low temperatures and lose viability at temperatures below 15 $^{\circ}\text{C}$ (Magnitskiy and Plaza, 2007). In addition, low temperatures reduce the metabolic rates of germination processes (Caroca et al., 2016). Therefore, the germination occurred at low temperatures (≤ 10 $^{\circ}\text{C}$), will depend on the thermal conditions during the maturation and dispersal of the seeds (Lamarca et al., 2013).

The highest germination percentage for *C. odorata* occurred below the theoretical optimum temperature calculated for this species, sometimes the highest germination percentage does not necessarily occur at the optimum temperature (Calzada-López et al., 2014). The highest germination percentage was at 20 $^{\circ}\text{C}$ and coincides with that reported by González-Rivas et al. (2009) for the same species. At the same time, the lowest germination percentage occurred

in the seeds exposed to the highest temperature ($45 \pm 2 \text{ }^{\circ}\text{C}$), and it was significantly lower than that of the lowest temperature tested in this study ($5 \pm 2 \text{ }^{\circ}\text{C}$).). This occurs because, according to Butler et al. (2014) very high temperatures ($>40 \text{ }^{\circ}\text{C}$) can affect the metabolic processes of the seeds and even damage them, stopping the growth of the embryo, which can inactivate and kill them. According to Rajjou et al. (2012), temperature affects enzymatic activity in biochemical reactions inside seeds after imbibition, accelerating them at higher temperatures. This is true only up to a point, after which further increases in temperature inhibit germination. For this reason, Durán-Puga et al. (2011) mention that shorter mean germination times may confer a competitive advantage to colonize fragmented habitats. According to Baskin and Baskin (2005), selection pressure increases establishment success in increasingly uncertain environments.

Seeds germinated at temperatures below $15 \pm 2 \text{ }^{\circ}\text{C}$ had lower germination rates, their speed was slower than the highest temperatures, such as $45 \pm 2 \text{ }^{\circ}\text{C}$, which coincides with what was reported by González-Rivas et al. (2009) for *C. odorata* at $15 \text{ }^{\circ}\text{C}$ in the Neotropical dry forest. This can be explained by the fact that, according to Adam et al. (2007), lower temperatures decrease metabolic rates to the point that processes that are essential for germination decrease. In addition, this species needs a higher temperature for its development due to its distribution in tropical climates. Furthermore, Caroca et al. (2016) mention that at high temperatures, chemical reactions are faster because water is absorbed more quickly in the seeds and they germinate faster. The highest germination percentage for *C. odorata* occurred below the theoretical optimum temperature calculated for this species, sometimes the highest germination percentage does not necessarily occur at the optimum temperature (Calzada-López et al., 2014). The highest germination percentage was at $20 \text{ }^{\circ}\text{C}$ and coincides with that reported by González-Rivas et al. (2009) for the same species. At the same time, the lowest germination percentage occurred in the seeds exposed to the highest temperature ($45 \pm 2 \text{ }^{\circ}\text{C}$), and it was significantly lower than that of the lowest temperature tested in this study ($5 \pm 2 \text{ }^{\circ}\text{C}$).). This occurs because, according to Butler et al. (2014) very high temperatures ($>40 \text{ }^{\circ}\text{C}$) can affect the metabolic processes of the seeds and even damage them, stopping the growth of the embryo, which can inactivate and kill them.

The highest germination percentage of *S. macrophylla* was recorded in the range of 25-35 °C, which coincides with Sol-Sánchez et al. (2016), who obtained 100% germination in seeds of this species at 30 °C. The highest germination percentages occurred below the optimal temperature (suboptimal range), which coincides with the results for *C. odorata*. Calzada et al. (2014) mentioned that the temperature at which the germination percentage is higher does not always coincide with the temperature at which the highest germination speed occurs (optimal temperature). Thus, the wide range of temperatures in which the best germination percentage occurs, according to Casillas-Álvarez et al. (2018), it can constitute an adaptive mechanism against climate change, which benefits the survival and distribution of species.

The germination performance of *L. diversifolia* under a temperature range was unknown before this investigation, and the influence of this variable had only been recorded for 28 °C (Ordoñez-Salanueva et al., 2018). Germination responses over a range of temperatures have only been reported in other species of the same genus, e.g. *L. leucocephala* (Lam.) de Wit (20 to 70 °C) (Pan et al., 2022). The highest germination recorded at 25 and 30 °C (98 and 95%, respectively) was higher than the study reported by (de Souza et al., 2007), which found 82% germination at 26 days. We also found a higher germination percentage than the one reported by (Pan et al., 2022), which reported 60% at 40 °C for *L. leucocephala*, but a similar percentage (91% at 20 °C and more than 95% at 24-2 °C) with the trials of (McDonald, 2002). Based on the results, a higher germination was reached at 25-35 °C because it is possible that in this range the physiological processes occur better. The ability to germinate in a wide range of temperatures indicates that the species is well adapted to the different conditions of the country.

4.2. Cardinal temperatures

To estimate the cardinal temperatures for germination, a wide temperature gradient was evaluated (5 to 45 °C). Therefore, the models showed a good fit and a good precision of the results was obtained (>92%) (Andreucci et al., 2016). Therefore, the ability to germinate in a wide range is an adaptive strategy in the face of temperature increases in different climate change scenarios (Sampayo-Maldonado et al, 2021).

The base temperature (T_b) is the minimum temperature where the species germinates; with increasing temperature the germination rate has a linear increase up to the optimum temperature (T_o), if the temperature continues to increase germination will drop to zero at the ceiling temperature (T_c), which is the maximum temperature at which they can germinate (Parmoon et al., 2015). The cardinal temperature gradient for germination of the evaluated species is in the range (0 to 60 °C) that vascular plants tolerate to survive (Lindig-Cisneros, 2017).

The optimum temperature was high, but it is reached in the warmest season recorded in the region; which is synchronized with the dispersal of the seeds (Kew, 2022) and is directly related to the higher germination speed (Caroca et al., 2016). What is in the range between 20 and 40 °C, which is where the optimum temperature of tropical trees can be found (Daibes et al., 2019).

When temperatures are above optimum temperatures, the germination rate decreases (Adam et al., 2007). This may be due to the fact that the temperature above the optimal temperature affects the cell membrane, initiating the denaturation of the proteins and can cause the death of the embryo (Durán-Puga et al., 2011). What inhibits the metabolic processes of germination (Grey et al., 2011). At 40 °C, *I. jinicuil*, *C. odorata* and *S. macrophylla* registered more than 60% average germination, which coincides with the germination of *Astronium lecointel* Ducke, *Parkia nitida* Miq., *Schizolobium amazonicum* Ducke, (Daibes et al. 2019), in the same thermal gradient. The maximum temperature to germinate was close to 50 °C for *I. jiniuil* and was higher for *C. odorata* and *S. macrophylla*, which can be a competitive advantage to germinate in fragmented habitats, which can reach temperatures above 45 °C. C (Sánchez-Rendón et al., 2011).

Germination in the 5 °C gradient was very good for *C. odorata* and low for *I. jinicuil*. While *S. macrophylla* and *L. diversifolia* did not germinate. This is because low temperatures decrease the activity of seed metabolism and protein synthesis; with which they will need more time to germinate (Calzada-López et al., 2014). Therefore, the base temperature (T_b)

accurately predicts the phenological stages of a species (Andreucci et al., 2016). But below the base temperature, the metabolic processes of the seeds stop (Parra-Coronado et al., 2015).

The determination of the thermal time for the forest species is important to analyze how the temperature determines the metabolism of the seeds, with significant effects on the percentages and rates of germination (Fallahi et al., 2015). Seeds are dispersed in spring (March to May), but germination occurs when thermal weather accumulates. Therefore, the thermal time specifies the beginning of germination (Funes et al., 2009), which in the current scenario accumulates in 3.5 days for *L. diversifolia* and up to 29.5 days in *S. macrophylla*. What maximizes the emergence of seedlings, and can explain the success in the establishment and survival of the regeneration of the species. The accumulated temperature ($^{\circ}\text{Cd}$) influences the phenological variation; Therefore, it is used to describe the phenological phases such as germination, with the development of agroclimatic models (Parra-Coronado et al., 2015). Therefore, temperature is the most important bioclimatic factor for the regulation of germination processes (Stenzel-Colauto et al., 2006). For climax species such as the species under study, longer times are required to reach phenological stages such as germination than those necessary for late successional species (Normand and Léchaudel, 2006). The thermal time ($\theta_1(50)$) for *I. jinicuil* was 259.969 ± 0.936 $^{\circ}\text{Cd}$, which is higher than that reported for *S. macrophylla* (189.091 ± 4.239 $^{\circ}\text{Cd}$), *C. fissilis* Vell. of (157 ± 2.0 $^{\circ}\text{Cd}$) and *C. odorata* (132.74 ± 2.60 $^{\circ}\text{Cd}$) and *L. diversifolia* (55.57 ± 2.85 $^{\circ}\text{CD}$).

4.3. Germination under Climate Change Scenarios

Research on the effect of climate change on forest species (Sánchez-Rendón et al., 2011), consider that the increase in temperature will affect the periods of flowering, fruiting and germination; which will affect the function of tropical ecosystems. Models to predict the effect of climate change on germination project a temperature increase of 1.6 to 2.9 $^{\circ}\text{C}$ for shade-grown coffee production areas. This increase in temperature will be due to the increase in greenhouse gas emissions, which will shorten the time necessary to accumulate the thermal sum ($^{\circ}\text{Cd}$). What in the future is predicted that the seeds will germinate in less time. According to Funes et al. (2009), a faster germination, is an advantage to compete for spaces

and ensure the establishment of individuals. Therefore, climate change can alter the distribution and abundance of species. This will impact the diversity of ecosystems, with negative effects on the sustainability of the coffee-growing regions of the country (Gutiérrez and Trejo, 2014). To adapt to the new climatic conditions, the populations will have to face migrations in altitude and latitude; which can cause evolutionary changes to colonize new environmental niches (IPCC, 2013).

In the workshops held with coffee producers in the Coatepec Veracruz region, the analysis showed that the trees were an important part of coffee plantations. The coffee cultivation that takes place in the area is mainly under the shadow of fruit, forestry and bananas trees. So this agroforestry system serves to recover the vegetation that was eliminated in the change in land use from forest to agricultural. Producers prefer tree species that provide multiple uses (Bernal-Ramírez et al., 2019), among which stand out:

- a) Food: at least a part of the tree (seeds and fruits) is ingested either raw, cooked, such as infusion or condiment without another purpose than obtaining nutrients.
- b) Environmental: carbon capture, essential for rain infiltration, soil formators, wildlife refuge.
- c) Artisanal: Crafts, toys, rustic tools, kitchen utensils.
- d) Ceremonial: parts of the trees are part of magical-religious events such as traditional rituals or patronal festivities, or in psychosomatic treatment (clean).
- e) Construction: Armed and formation of structures that function as houses, warehouses, pens and for fences.
- f) Fuels: dendroenergy (such as coal, ocote, firewood and pellets) and biofuels.
- g) Scenic: forests are important as part of the landscape and is the main component of ecotourism.
- h) Industrial: products from resins extracted from trees, wooden pulp for paper.
- i) timber: processed as tables and to make furniture or sale of wooden wood.
- j) Medicinal: at least part of the trees or their derivatives (resins) is used to cure, treat or combat diseases.
- k) Ornamental: Some species are used to decorate and as gardens parts.

- 1) Veterinarian: At least a part of the tree is used to cure, treat or combat conditions in animals.

5. Conclusions

Of the species, *C. odorata* and *I. jinicuil* had a wide germination range, the highest germination percentages occurred in 20 and 25 °C respectively. *L. diversifolia* germinated in a range of 10 to 35 °C, registering the largest germination in 20 and 25 °C. While *S. macrophylla* germinated 15 to 45 °C, with a range of 25 to 35 °C recorded the greatest germination. For *I. jinicuil*, germination occurred at 2 days in temperatures of 25 to 35 °C, but for the lowest temperature it required 16 days to start germination. For *L. diversifolia* germinated at 3 days at 30 °C, but needed 18 days to germinate in 10 °C. In the case of *C. odorata*, 5 days were required to germinate at 20 °C and 47 days to germinate in 5 °C. While *S. macrophylla* needed 6 days to germinate at 20 °C and 91 days to germinate in 15 °C. *C. odorata* presented a wide range of cardinal temperatures. While the lowest rank of cardinal temperatures was for *L. diversifolia*. He also needed the shortest thermal time to germinate, which accumulates it in 3.5 days. In the case of *S. macrophylla* requires the most thermal time to germinate, which in the current scenario accumulates in 29.5 days. That in the distant future will accumulate it nine days before. According to climate change scenarios, the temperature will have a positive effect on the germination rate. So the species with the shortest thermal time will be the first to germinate.

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