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**Salvador Sampayo-Maldonado**

UBIPRO, FES Iztacala, UNAM, Mexico State

**Daniel Cabrera-Santos**

UBIPRO, FES Iztacala, UNAM, Mexico State

**Patricia Dávila-Aranda**

UBIPRO, FES Iztacala, UNAM, Mexico State

**Norma Isela Rodríguez-Arévalo**

UBIPRO, FES Iztacala, UNAM, Mexico State

**Alma Orozco-Segovia**

UNAM

**Maraeva Gianella**

Royal Botanic Gardens

**Elizabeth Bell**

Royal Botanic Gardens

**Michael Way**

Royal Botanic Gardens

**Robert H. Manson**

Institute of Ecology AC, Mexico

**Gabina S. Quintas**

Veracruz University

**Cesar M. Flores-Ortíz**

[cmflores@unam.mx](mailto:cmflores@unam.mx)

UBIPRO, FES Iztacala, UNAM, Mexico State

**Tiziana Ulian**

Royal Botanic Gardens

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## Article

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# Using the cardinal temperature approach to determine the potential distribution of *Inga jinicuil* in Mexico under climate change scenarios

Salvador Sampayo-Maldonado<sup>1</sup>, Daniel Cabrera-Santos<sup>1</sup>, Patricia Dávila-Aranda<sup>2</sup>, Norma Isela Rodríguez-Arévalo<sup>2</sup>, Alma Orozco-Segovia<sup>3</sup>, Maraeva Gianella<sup>4</sup>, Elizabeth Bell<sup>4</sup>, Michael Way<sup>4</sup>, Robert H. Manson<sup>5</sup>, Gabina S. Quintas<sup>6</sup>, Cesar M. Flores-Ortíz<sup>1,\*</sup>, Tiziana Ulian<sup>4,7</sup>

<sup>1</sup>Plant Physiology Laboratory, UBIPRO, FES Iztacala, UNAM. Tlalnepantla 54090, Mexico State, Mexico.

<sup>2</sup>Natural Resources Laboratory, UBIPRO, FES Iztacala, UNAM. Tlalnepantla 54090, Mexico State, Mexico.

<sup>3</sup>Department of Functional Ecology, Institute of Ecology, UNAM. Av. Universidad 3000, C. P. 04510, CdMx, Mexico.

<sup>4</sup>Royal Botanic Gardens, Kew, Wellcome Trust Millennium Building, Ardingly, West Sussex RH17 6TN, UK.

<sup>5</sup>Functional Ecology Network, Institute of Ecology, A.C., Old Highway to Coatepec No. 351, El Haya C. P. 91073, Xalapa, Veracruz, Mexico.

<sup>6</sup>Faculty of Agricultural Sciences, Veracruz University. Lomas del Estadio S/N, Col. University Zone, 91000, Xalapa, Veracruz, Mexico.

<sup>7</sup>University of Turin, Turin, Italy.

\*Correspondence: cmflores@unam.mx; Tel. 1: +52-555-623-1137, Tel. 2: +52-552-922-2373

## ABSTRACT

*Inga jinicuil* is used extensively in shade coffee farms in Mexico, a diversified agroforestry system providing important environmental goods and services. However, its recalcitrant seeds represent an important barrier to its propagation. The objective of the study was to determine the cardinal germination temperatures for *I. jinicuil* using linear and non-linear models, as well as the species' potential distribution under contrasting climate change scenarios using the GISS-E2-1-G model. Seeds were placed in germination chambers at constant temperatures of  $5 \pm 2$  to  $40 \pm 2$  °C, and their thermal responses were then modelled using a thermal timing approach. Results indicated a good fit of models of *I. jinicuil* germination in response to temperature. Seeds germinated across a wide temperature range from 4.8 to 49.2 °C, with an optimal temperature between 29.58 and 33.02 °C. The suboptimal thermal time ( $\theta_1(50)$ ) for germination of 50% of the seed lot was  $117.164 \pm 0.636$  Cd, which under current climatic conditions is reached in 6.6 days. According to climate modeling, the distribution of *I. jinicuil* populations will decrease by up to 23% in the future relative to the current distribution. Results indicate that high temperatures have a negative effect on germination, which may be related to seed physiology. More research on seed germination and growth is needed to improve the management and conservation of this species and its continued use as a shade tree in coffee agroforestry systems.

**Keywords** Thermal time, Climate change, Seed germination, Niche models, Shade-grown coffee

## Introduction

Trees of the *Inga* genus belong to Fabaceae family, are native to the American tropics with a distribution extending from Mexico to Brazil<sup>1</sup>. In Mexico, *Inga jinicuil* Schltdl. & Cham. ex G.Don (common Spanish name: jinicuil) is distributed throughout the Gulf of Mexico, from Veracruz to Tabasco. In central México, this species is found in Puebla, Tlaxcala, Hidalgo, and Mexico State; and from Jalisco to Chiapas along the Pacific<sup>2</sup>. *I. jinicuil* forms part of the flora of deciduous tropical forest, gallery forests, and more commonly tropical montane cloud forest<sup>3,4</sup>. According to INEGI<sup>5</sup>, this latter forest occupies less than 1% of the country's terrestrial area, with remaining remnants isolated in agricultural matrices<sup>6</sup> including zones of shade-grown Arabic coffee farms (*Coffea arabica* L.)<sup>7</sup>.

*I. jinicuil* grows up to 30 m tall and, while it can be planted as an ornamental tree, is mainly used as shade in agroforestry systems with coffee (*C. arabica*), or to a lesser degree with cocoa (*Theobroma cacao* L.), and citrics (*Citrus* spp. L.)<sup>2</sup>. Jinicuil is a multipurpose species of great importance for the development of communities<sup>8</sup> providing food, fodder, nitrogen-fixation that can increase the fertility of soils<sup>2</sup>. Its seeds are edible and used for medicinal purposes<sup>9</sup>. Its pods are prized for their arils (cotton-like pulp), which are sweet<sup>10</sup>. *I. jinicuil* is a fast-growing species that can capture significant amounts of carbon<sup>11</sup> with wood used for the rural construction however, it is not reproduced via commercial plantations<sup>12</sup>. The species survives mainly through coffee cultivation under shade trees, which function as a biodiversity refuge and is considered a promising tree for the restoration of degraded areas and to counteract global warming<sup>13</sup>.

Seeds of *I. jinicuil* are dispersed by gravity in May and are sensitive to desiccation, rapidly losing their viability under standard seed banking conditions<sup>14</sup>. The species presents a precocious germination, so it can germinate 100% between 20 and 25 °C and they are also capable of germinating at low temperatures between 10 and 15 °C<sup>15-17</sup>. Germination at low temperatures depends on the environmental conditions (water and thermal) during maturation and seed dispersal<sup>18</sup>. However, information is limited on germination of the species under the higher temperatures expected with global climate change.

Most plants, including *Inga* spp., require seed production, emergence of seedlings to regenerate after germination<sup>19-21</sup>, a process that is sensitive to humidity and temperature signals and is therefore expected to be affected by climate change<sup>22</sup>. Increases in temperature and changes in rainfall patterns are predicted in various scenarios, threatening the diversity and functioning of ecosystems in coffee-growing regions of Mexico<sup>23</sup>. After humidity, the most important bioclimatic element is temperature, which shapes the speed and percentages of germination, thereby regulating plant growth<sup>24,25</sup>. To estimate cardinal temperatures, models that include linear and nonlinear functions are used<sup>26</sup>. Each species has a thermal niche for germination, which can vary depending on its ecological niche, which is defined by its geographic origin. The corresponding model should better explain the effect of temperature on germination and be species-specific<sup>27</sup>. Germination is essential for attracting individuals who are susceptible to temperature fluctuations because *I. jinicuil* has recalcitrant seeds that quickly lose their viability<sup>25</sup>. Such changes may be particularly important for species with fragmented distributions, small and dispersed populations, perhaps even making them vulnerable to extinction<sup>13</sup>. There are not any studies on thermal time or cardinal temperatures for germination of *I. jinicuil* despite the expected increase in temperatures due to climate change, and how this may affect its distribution and population size in the future. This study set out to produce models using a thermal time approach, calculate cardinal temperatures using linear and non-linear models, and forecast the possible effects of climate change on the germination and distribution of the species.

## Results

### Germination

The initial moisture content of the seeds was  $59.6 \pm 4.3\%$ , and 96% of them germinated. An average of 60% germination (with a range of 12 to 90%) was obtained in the temperature treatments, with significant differences between treatments ( $F_{7,32} 36.48$ ;  $p < 0.001$ ). The lowest germination was 12.5% at the lowest temperature (5 °C). There was a positive relation between temperature and germination up to 25 °C, however germination declined as temperature increases (Fig. 1).

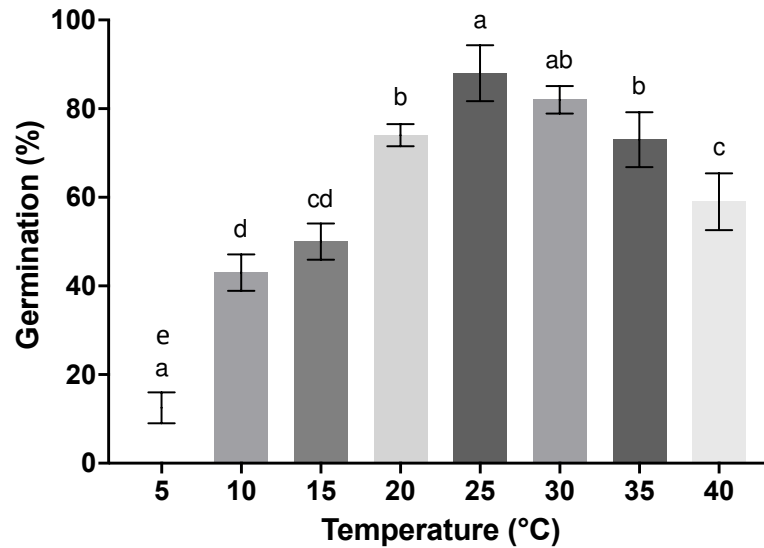


**Figure 1.** Percentages of germination at each temperature setting. The standard deviation is displayed by error bars. The means that have the same letter do not differ substantially ( $p \leq 0.001$ ).

*I. jinicuil* After two days, the seeds started to germinate at  $25$  to  $35 \pm 2$  °C. Germination started at 40 °C after 3 days, and at  $15$  and  $10 \pm 2$  °C, it started at 7 and 11 days, respectively. However, at  $5 \pm 2$  °C germination slowed considerably taking up to 16 days. There were significant differences between the temperature ranges in the amount of time that must pass before 50% of the seeds germinate ( $T_{50}$ ) ( $F_{4,28} 13.08$ ;  $p < 0.001$ ). After 7 days, at  $25 \pm 2$  °C, the  $T_{50}$  germination occurred at the fastest rate. Soon after, the  $T_{50}$  happened at 9 days, with temperatures between 30 and  $35 \pm 2$  °C. When the temperature was  $40 \pm 2$  °C,  $T_{50}$  happened after 11 and 12 days, respectively, but at  $15 \pm 2$  °C, it took longer than 17 days. Germination was always less than 50% at lower temperatures (Fig. 2).

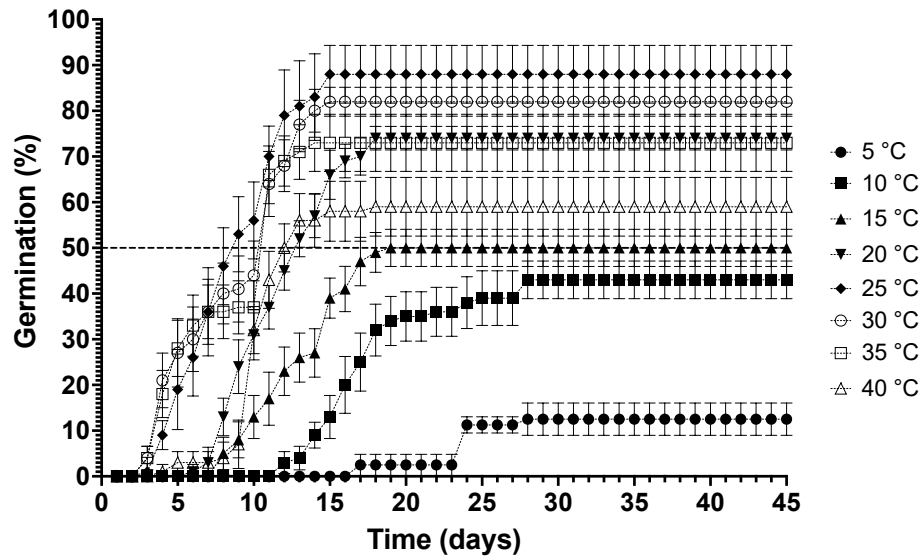


**Figure 2.** Cumulative percentages of seed germination and time to achieve 50% germination at each temperature. (Standard deviation is displayed by the SD bars).

Germination rates were significantly different between treatments ( $F_{7,32} 21.37$ ;  $p < 0.001$ ). At temperatures ranging from 25 to  $35 \pm 2$  °C, seven seeds germinated on average every day. On average, five seeds were observed to germinate in a single day at temperatures of  $20$  and  $40 \pm 2$  °C. Two seeds per day germinated at lower temperatures ( $10$  and  $15 \pm 2$  °C). However, a single seed took more than two days to germinate at the lowest temperature ( $5 \pm 2$  °C) (Fig. 3).

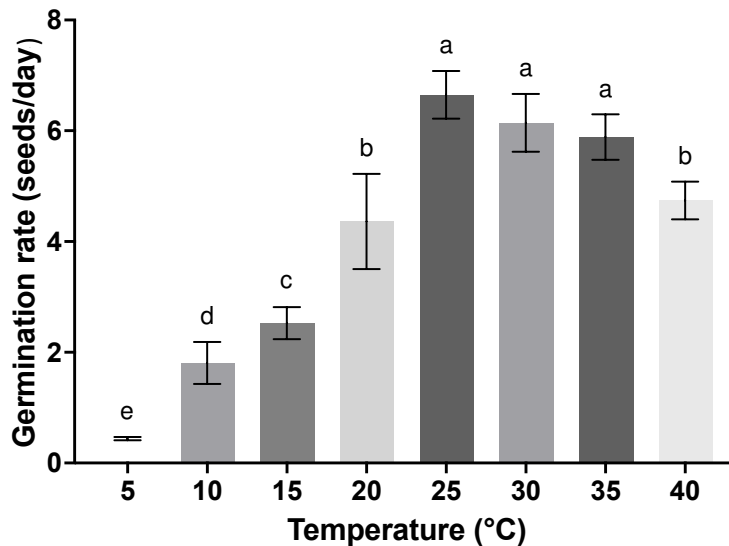


**Figure 3.** Rate of germination per day for every temperature setting. Standard deviation is displayed by error bars. Means that are similar in letter do not differ significantly ( $p \leq 0.001$ ).

### Cardinal temperatures

The cardinal temperatures defining the limits of the thermal niche for germination of *I. jinicuil* varied widely from 4.8 to 49.2 °C. The suboptimal and supraoptimal temperatures were explained in 76 and 92% for the

models, respectively. According to the models, the  $T_b$  for germination was in the range 4.8 to 9.45 °C (average of  $6.21 \pm 2.23$  °C) (Table 1). The germination rate rose with temperature until it reached its maximum rate at the  $T_o$  in the range of 29.58 to 33.02 °C (average of  $31.52 \pm 1.43$  °C). The germination rate drops as the temperature rises above  $T_o$ , reaching the  $T_c$ , in the range of 44.51 to 49.20 °C (average of  $47.6 \pm 2.73$  °C). The linear (SL1) and segmented model 1 (S1) and 2 (S2) most closely approximated the average value of the cardinal temperatures (Fig. 4). However, the Beta 1 (B1) and SL1 models had the best fittings according to the parameter analysis where low RMSE and better model estimation is indicated by  $R^2$  values near 1.

| Model            | $T_b$           | $T_o$            | $T_c$            | RMSE       | $R^2$  | Adjusted $R^2$ |
|------------------|-----------------|------------------|------------------|------------|--------|----------------|
| Linear (SL1)     | $4.80 \pm 1.33$ | $31.64 \pm 1.07$ | $49.20 \pm 3.64$ | 0.00212897 | 0.9500 | 0.9200         |
| Segmented 1 (S1) | $5.63 \pm 1.73$ | $33.02 \pm 6.33$ | $48.88 \pm 0.52$ | 0.00259518 | 0.9225 | 0.7675         |
| Segmented 2 (S2) | $4.97 \pm 2.24$ | $31.87 \pm 3.87$ | $48.18 \pm 1.24$ | 0.00259517 | 0.9225 | 0.7675         |
| Beta 1 (B1)      | $9.45 \pm 3.46$ | $29.58 \pm 1.05$ | $44.51 \pm 2.06$ | 0.00213562 | 0.9600 | 0.9200         |

$T_b$ : Base temperature;  $T_o$ : Optimum temperature;  $T_c$ : Ceiling temperature; RMSE: Root mean square of errors standard;  $R^2$ : regression coefficient; Adjusted  $R^2$ : adjusted regression coefficient.

**Table 1.** Determination of cardinal temperature using linear and nonlinear regression model for *Inga jinicuil*.

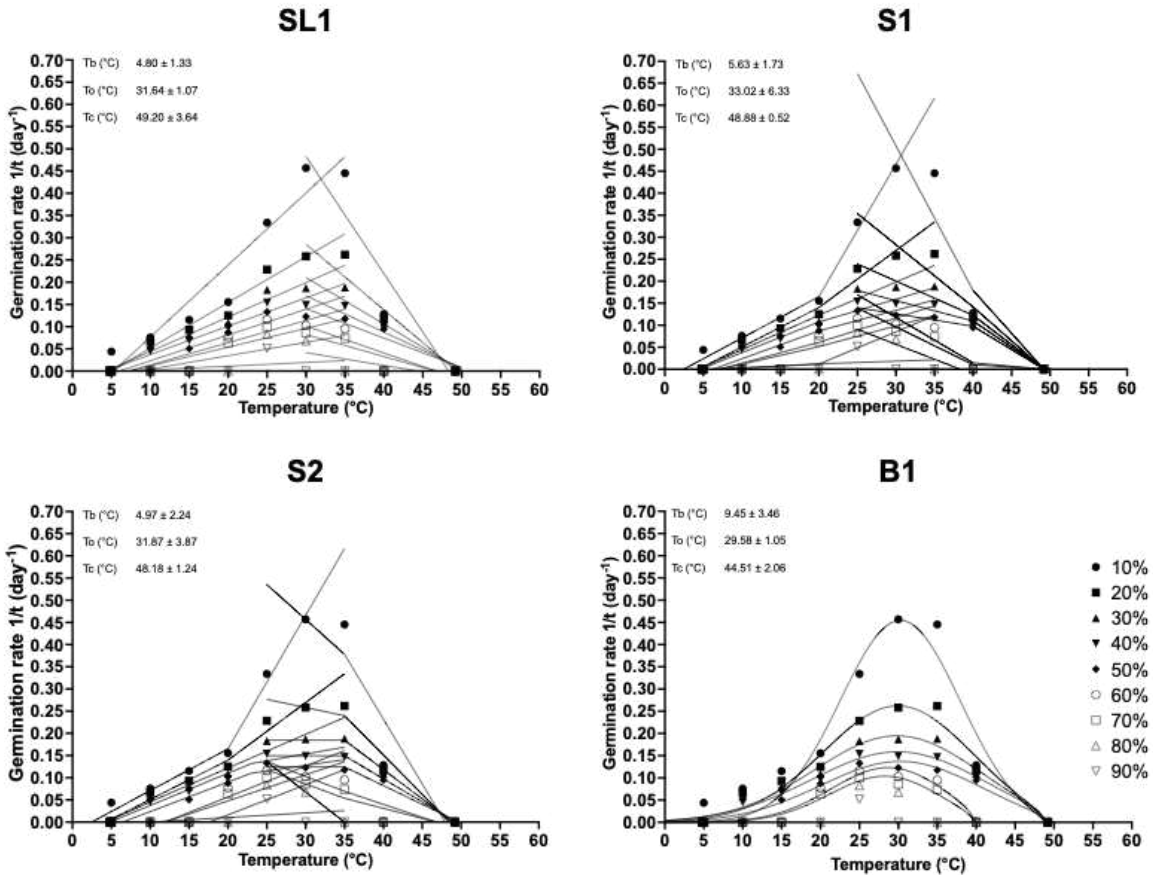


**Figure 4.** The cardinal temperature range is described by the germination rate for each percentile (the inverse of germination rate) for each temperature. The solid lines correspond to the values predicted by the model functions, and the symbols represent the experimental data: linear (SL1), segmented (S1-S2), and beta 1 (B1).

## Thermal time

The suboptimal temperature ( $\theta_1$  (50)) for 50% of a batch of seeds to germinate was  $117.164 \pm 0.636$  °C. The Probit model's fit percentage was higher than 91%. On the other hand, the average thermal time for the supraoptimal temperatures ( $\theta_2$  (50)) was  $51.327 \pm 0.523$  °Cd, and the model fit was greater than 60% (Table 2).

| Parameters    | Suboptimal          | Supraoptimal        |
|---------------|---------------------|---------------------|
| $R^2$         | 91.8                | 60.2                |
| K             | $-3.1873 \pm 0.14$  | $-0.9149 \pm 0.047$ |
| $\sigma$      | $0.0272 \pm 0.0013$ | $0.017 \pm 0.0011$  |
| $\theta$ (50) | $117.164 \pm 0.636$ | $51.327 \pm 0.523$  |

The values represent mean  $\pm$  standard deviation.  $R^2$ : regression coefficient; K: intercept constant;  $\sigma$ : standard deviation;  $\theta$  (50): thermal time.

**Table 2.** Probit analysis estimated thermal time parameters.

The likelihood of a higher percent germination increased as heat accumulation increased, as demonstrated by the thermal time in the suboptimal range (Fig. 5a). It is interpreted that when approaching the thermal sum of ( $\theta_1$  (50))  $117.164 \pm 0.636$  °Cd, it reaches higher germination percentages. Within the supraoptimal range (Fig. 5b), the accumulation of more heat negatively affects germination and percentages decrease. Therefore, the thermal time of the supraoptimal range is less. But with that value the germination of 50% of the batch of seeds is achieved.

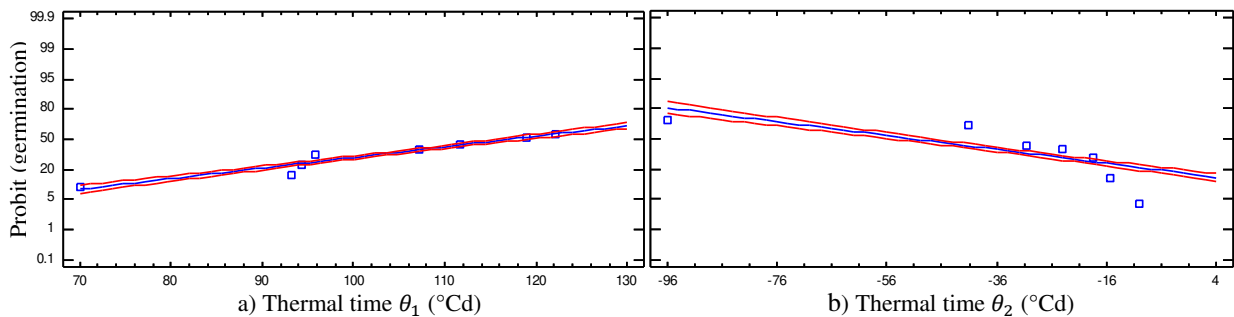


**Figure 5.** Probit scale germination as a function of thermal time for: (a) suboptimal range,  $\theta_1$ , (b) supraoptimal range,  $\theta_2$ , of temperatures. The red lines represent the germination confidence intervals. Estimated data is shown by the blue line. The points represent the experimental data's average.

## Germination under climate change scenarios

In the current scenario, *I. jinicuil* seed dispersal occurs in the month of May, with an average temperature of 22.4 °C. For germination to begin, the seeds need to accumulate the thermal sum of ( $\theta_1$  (50))  $117.164 \pm 0.636$  °Cd, which accumulates in 6.6 days. (Fig. 6). In the intermediate future (year 2050) and under the optimistic scenario (SSP1 2.6 Watts/m<sup>2</sup>), all models predict a temperature increase in May. Under the English model (HADGEM2-ES), an increase of 1.6 °C is predicted for this month, while average temperatures of 1.8, 2.1 and 2.5 °C are expected for the French (CNRMCM5), German (MPI-ESM-LR), and American (GFDL-CM3) models, respectively. Accordingly, germination start times are reduced, with thermal time accumulating in just 6.1, 6.0, 5.9, and 5.8 days for the English, French, German, and American models, respectively (Fig. 6).

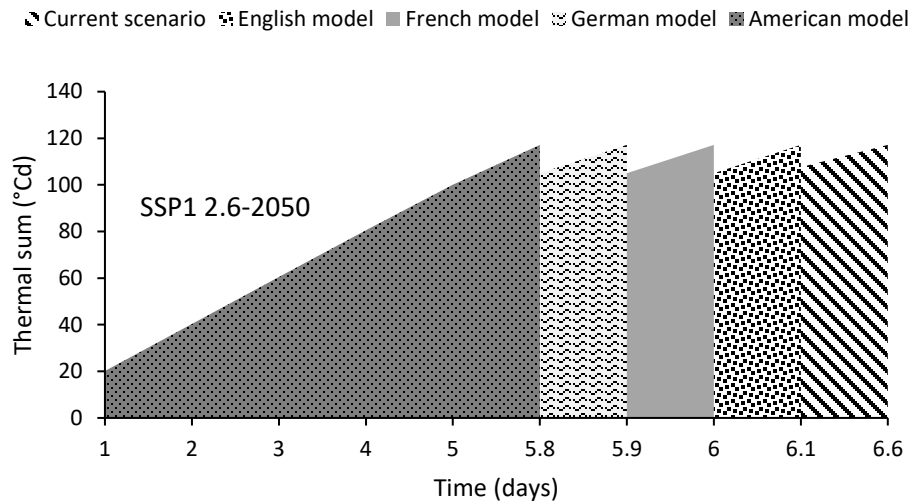


**Figure 6.** Time that during May, seeds accumulate their thermal sum ( $^{\circ}\text{Cd}$ ). In the intermediate future (year 2050), under the current circumstances and in the optimistic climate change scenario (SSP1 2.6 Watts/ $\text{m}^2$ ).

For the distant future (year 2090), under the optimistic climate change scenario (SSP1 2.6 Watts/ $\text{m}^2$ ), increases of 2.1, 2.3, 2.8, and 2.9  $^{\circ}\text{C}$  were predicted in May for the French (CNRMCM5), German (MPI-ESM-LR), English (HADGEM2-ES), and American (GFDL-CM3) models. This corresponds to a faster accumulation of the thermal sum ( $\theta_1$  (50)) of  $117.164 \pm 0.636$   $^{\circ}\text{Cd}$  required for germination, varying from 5.9 days for the French model and 5.7 days for the American model. Which is up to 20 hours earlier than the current scenario (Fig. 7).

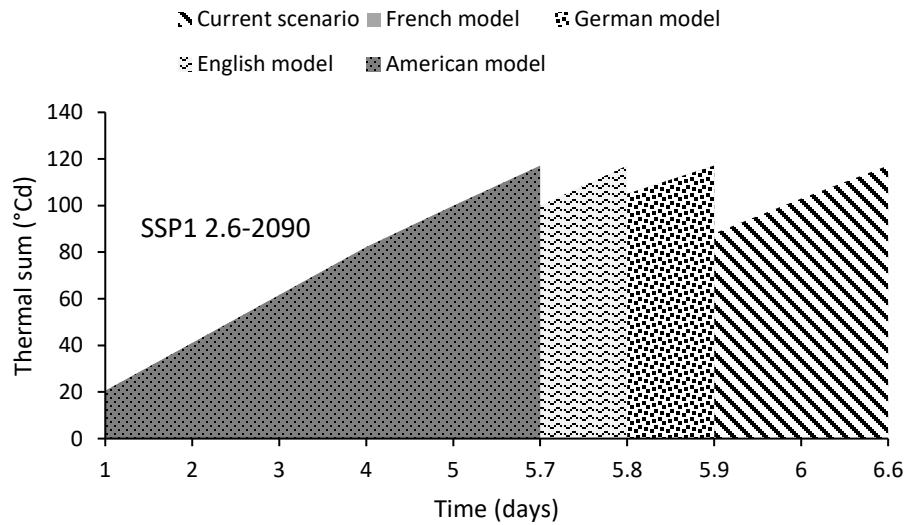


**Figure 7.** Time that during May, seeds accumulate their thermal sum ( $^{\circ}\text{Cd}$ ). For the distant future (year 2090). Assuming a conservative scenario (SSP1 2.6 Watts/ $\text{m}^2$ ).

### Potential distribution under climate change scenarios

In ecological niche modelling, if physiological variables such as optimal germination temperatures (OGT) are included, the resulting distributions are usually more restrictive (Sampayo-Maldonado et al. 2023). Table 3

shows how the inclusion of OGT typically reduced the predicted distribution of *I. jinicuil*. In theory, considering OGT results in more accurate models of a species' distribution, thus increasing the probability of finding *I. jinicuil* in predicted areas. According to the models, if the optimal temperatures for germination are included, models predict a decrease of 37.6% in the current distribution opposed to models without this variable. Under future scenarios the predicted reductions in species distributions with the addition of this variable are less pronounced (5.4 to 16%) and might result in a small increase in the species distribution (near future SSP5-8.5). Comparing predicted distribution changes under each climate change scenario versus the actual distribution reveals that losses in species distribution are expected under all climate change scenarios but these are more marked in models without the variable of optimal germination temperature (Table 3).

| Description                         | Consideration of optimal temperatures | Current (km <sup>2</sup> ) | 2050 (km <sup>2</sup> ) |                  | 2090 (km <sup>2</sup> ) |                  |
|-------------------------------------|---------------------------------------|----------------------------|-------------------------|------------------|-------------------------|------------------|
|                                     |                                       |                            | SSP1-2.6                | SSP5-8.5         | SSP1-2.6                | SSP5-8.5         |
| Suitability area (km <sup>2</sup> ) | No                                    | 28882.04                   | 18828<br>(34.8%)        | 16343<br>(43.4%) | 18135<br>(37.2%)        | 15593<br>(46.0%) |
| Suitability area (km <sup>2</sup> ) | Yes                                   | 18019                      | 17799<br>(1.2%)         | 17123<br>(5.0%)  | 15223<br>(15.5%)        | 13776<br>(23.5%) |
| Decline in area (km <sup>2</sup> )  |                                       | 10866                      | 1029                    | -780             | 2912                    | 1817             |
| Percentage decline (%)              |                                       | 37.6                       | 5.4                     | -4.7             | 16                      | 11.6             |

**Table 3.** Models of the distribution of *I. jinicuil* considering or not the effects of optimal temperatures for germination, across different temporal horizons and under optimistic (2.6) and pessimistic (8.5) climate change scenarios according to the GISS-E2-1-G model.

Results of the species distribution models, including cardinal temperatures, had AUC values of  $0.97 \pm 0.01$ ; indicating a good model fit to the data, with a greater than 50% probability of finding the species in predicted areas. According to the climate change scenarios of the GISS-E2-1-G model the distribution of *I. jinicuil* populations in the future will decrease between 34 and 46% of their current distribution (Fig. 8). Jackknife procedures identified annual precipitation (38.5%), type of soil (19.5%), precipitation during the driest period (13.4%), the altitude (8.2%), and average temperature of the driest month (5.1%) as the variables that most contributed to the construction of the MaxEnt model of the current species distribution.

In the near future (2050), under optimistic (2.6) and (8.5) pessimistic emissions scenarios a reduction of the species distribution by 1.21 and 4.96%, respectively, is expected as compared to the current distribution (Table 4). In the lower CO<sub>2</sub> emissions scenario (SSP1-2.6), a decrease of just over 1 percent of the current distribution is expected. Colima, Quintana Roo and Tamaulipas are expected to suffer reductions in the distribution of the study species, while increases are predicted in Jalisco (98.7%), Hidalgo (68.8%), Puebla (24.8%) and Chiapas (19%). The climatic variables that contributed the most to the model were: annual precipitation (29.9%), precipitation during the driest period (28.2%), soil type (15.4%) and altitude (8.1%). Under the higher CO<sub>2</sub> emissions scenario (SSP5-8.5), the distribution of the species decreases 3.75% more than in the scenario (SSP1-2.6). In general, spatial trends are similar to those reported for the lower CO<sub>2</sub> emissions scenario. The variables that contributed the most to the model were: precipitation during the driest period (33.3%), annual precipitation (22.6%), soil type (15.5%) and altitude (6.6%).

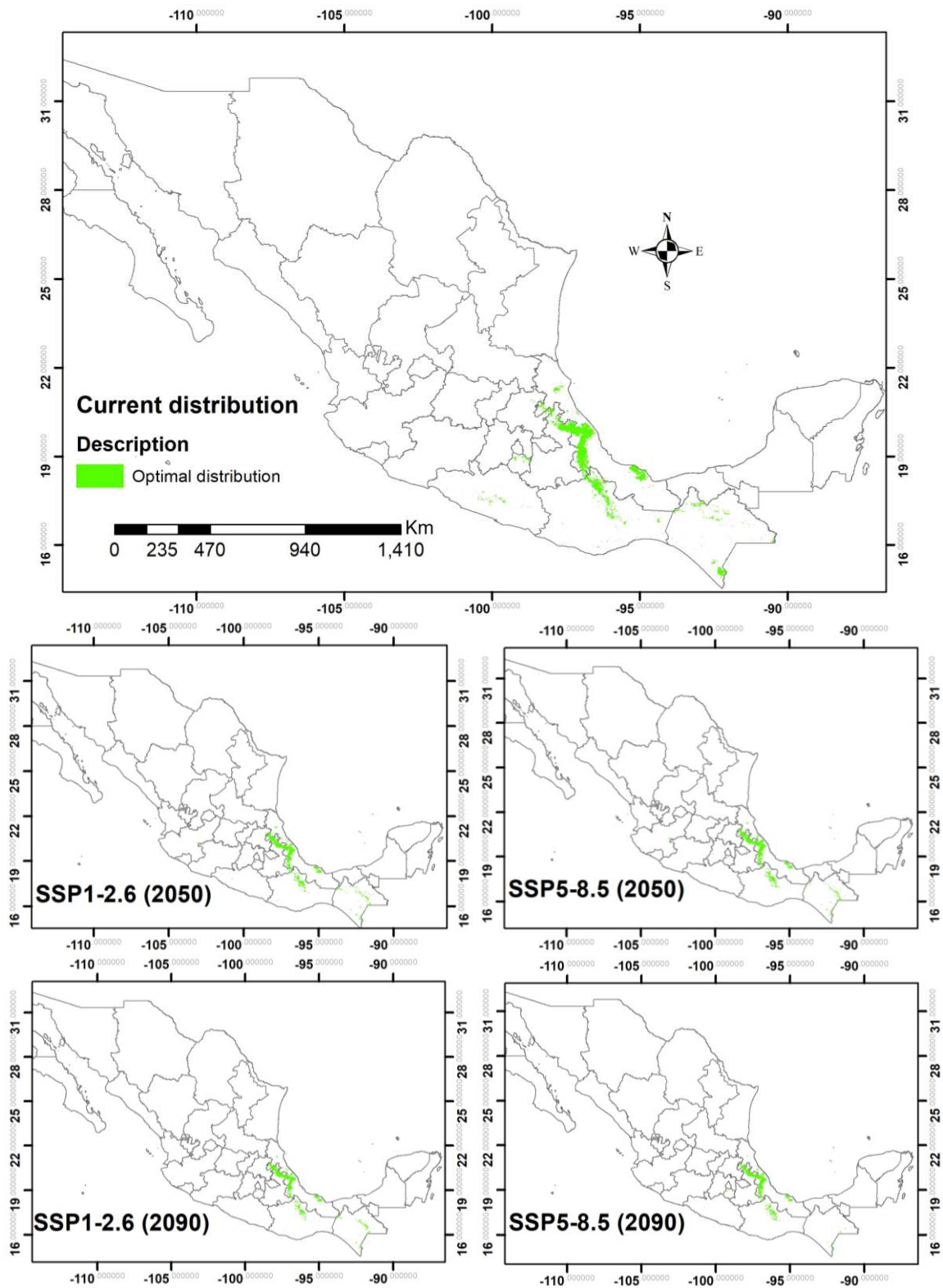


**Figure 8.** Predicted current and future (2050 and 2090) distribution of *I. jinicuil* under the SSP1-2.6 and SSP-8.5 scenarios in the GISS-E2-1-G model.

| State                               | Current<br>(km <sup>2</sup> ) | 2050 (km <sup>2</sup> ) |          | 2090 (km <sup>2</sup> ) |          |
|-------------------------------------|-------------------------------|-------------------------|----------|-------------------------|----------|
|                                     |                               | SSP1-2.6                | SSP5-8.5 | SSP1-2.6                | SSP5-8.5 |
| Chiapas                             | 2008.11                       | 2480.73                 | 2005.69  | 1964.47                 | 538.69   |
| Colima                              | 1.57                          | 0.00                    | 0.00     | 0.00                    | 0.00     |
| Guerrero                            | 452.09                        | 27.74                   | 15.36    | 13.58                   | 13.90    |
| Hidalgo                             | 220.35                        | 707.84                  | 576.86   | 608.81                  | 495.12   |
| Jalisco                             | 1.10                          | 87.35                   | 113.00   | 71.22                   | 0.00     |
| Mexico                              | 27.17                         | 24.95                   | 26.05    | 26.45                   | 13.17    |
| Michoacan                           | 13.28                         | 0.55                    | 0.55     | 0.55                    | 0.00     |
| Morelos                             | 274.47                        | 68.42                   | 71.54    | 64.65                   | 68.75    |
| Oaxaca                              | 3570.94                       | 3076.41                 | 3031.64  | 2387.35                 | 2604.90  |
| Puebla                              | 2528.21                       | 3365.28                 | 3295.90  | 3066.25                 | 2996.17  |
| Quintana Roo                        | 1.11                          | 0.00                    | 0.00     | 0.00                    | 0.00     |
| Tabasco                             | 29.28                         | 1.74                    | 0.44     | 0.63                    | 1.33     |
| Tamaulipas                          | 10.48                         | 0.00                    | 0.00     | 0.00                    | 0.00     |
| Veracruz                            | 8877.95                       | 7957.63                 | 7986.35  | 7018.91                 | 7043.92  |
| Suitability area (km <sup>2</sup> ) | 18016.11                      | 17798.64                | 17123.38 | 15222.88                | 13775.94 |
| Decrement area (km <sup>2</sup> )   |                               | 217.46                  | 892.73   | 2793.23                 | 4240.16  |
| Percentage of decrement (%)         |                               | 1.21                    | 4.96     | 15.50                   | 23.54    |

**Table 4.** The GISS-E2-1-G model estimates the current and projected area (km<sup>2</sup>) by state where populations of *I. jinicuil* might exist based on climate change scenarios.

In the distant future (2090), a reduction in the species' distribution between 15.5 and 23.5% is expected versus the current distribution (Table 3). In the SSP1-2.6 scenario, Colima, Quintana Roo and Tamaulipas lose all suitable area for the species. Tabasco (97.8%), Guerrero (97%), Michoacan (95.8%), Morelos (76.4%), Oaxaca (33.1%) and Veracruz (21%) will lose optimal area for the species, while Jalisco should add 71.22 km<sup>2</sup> of suitable area compared to the current scenario with 1.10 km<sup>2</sup>. In addition, Hidalgo will increase its surface area by 270% and Puebla should exhibit an increase of 21.3%. The variables that contributed the most to the construction of this model were: annual precipitation (32.6%), precipitation during the driest period (26.1%), soil type (14.3%) and altitude (6.6%). In the SSP5-8.5 scenario, an overall decrease 46% in the species distribution is predicted relative to the current distribution. The states of Colima, Jalisco, Michoacán, and Tamaulipas are expected to lose all suitable area for the species. The variables that contributed the most to the model construction were: precipitation during the driest period (39.1%), annual precipitation (19%), soil type (14.2%) and altitude (6.2%).

## Discussion

### Germination

Previous studies by Leão et al.<sup>15</sup>, Rodrigues et al.<sup>16</sup> and Barros-Guimarães et al.<sup>17</sup> reported that 20 to 25 °C was the ideal temperature range for *Inga* seed germination and suggest that the minimum temperature for germination could be in the range of 10 to 15 °C. Our study used a broader temperature gradient (5-40°C) for evaluating the germination of *I. jinicuil* resulting in a broader thermal niche than previously reported. According to the results, the highest germination percentages occurred at 25 ± 2 °C, which is in line with the studies of *Inga vera* Willd<sup>17</sup>. Nevertheless, this is below the ideal temperature (T<sub>o</sub>: 31.6 ± 1.1) and is consistent with findings for other tropical species such as *Cedrela odorata* L.<sup>27</sup> and *Swietenia macrophylla* King<sup>25</sup>.

Our findings support previous work indicating that optimal temperature is not always the site of maximum germination<sup>28</sup>. It is possible that recalcitrant tropical species seeds, which are susceptible to low temperatures

and lose viability at temperatures below 15 °C, are the reason why the lowest percentage of germination occurred in seeds exposed to the lowest temperatures ( $5 \pm 2$  °C)<sup>29</sup>. Low temperatures also cause germination processes' metabolic rates to decrease<sup>30</sup>. As a result, the conditions under which the seeds mature and disperse will determine whether germination takes place at low temperatures ( $\leq 10$  °C)<sup>18</sup>.

### Cardinal temperatures

The three nonlinear models and the linear model developed for the study all showed good prediction, since realistic values were observed according to the experiment data. However, the lower RMSE values of B1 and the SL1 indicated they had the best fit to the empirical data. Due to the non-linear nature of the peak model was more flexible but also tended to underestimate the values of the maximum temperature similar to previous studies<sup>27</sup>.

To estimate the cardinal temperatures for germination of *I. jinicuil*, a wide temperature gradient (from 5 to 40 °C) was required. As a result, the models showed a good fit ( $>92\%$ )<sup>31</sup>. The studied species used a wide temperature interval, defining the thermal niche for germination of  $4.8 \pm 1.3$  to  $49.2 \pm 3.64$  °C between  $T_b$  and  $T_c$ , respectively. Given that all climate change scenarios predicted temperature increases, as a means of adapting to the rapid changes in climate, the ability to germinate across a broad temperature range might be considered<sup>27</sup>.

$T_o$  be attained in May, the hottest month, which coincides with the dispersal of seeds<sup>14</sup> and corresponds directly to the increased germination rates<sup>30</sup>. Daibes et al.<sup>32</sup> report a range of 20 to 40 °C, which includes the optimal temperatures for germination of tropical species in the western Brazilian Amazon. Therefore, a similar thermal range for *I. jinicuil* coincides with tropical species from Mexico such as *C. odorata*<sup>27</sup> and *S. macrophylla*<sup>25</sup>.

When optimum temperatures are surpassed germination rates decreases<sup>33</sup>. This may be due to affects in cell membranes initiating protein denaturation and can lead to embryo death<sup>34</sup> or, at the very least, a reduction in the germination metabolic processes<sup>35</sup>. At 40 °C, the species registered just over 60% germination on average, which coincides with the germination of *Astronium lecointel* Ducke, *Parkia nitida* Miq., *Schizolobium amazonicum* Ducke.<sup>32</sup>; in addition to *C. odorata*<sup>27</sup> and *S. macrophylla*<sup>25</sup> in the same thermal gradient.  $T_c$  for germination was close to 50 °C, which may offer a competitive advantage for germination in more open fragmented habitats where surface temperatures can reach or surpass 45 °C<sup>36,37</sup>. *I. jinicuil* had an average germination of 12.5% at 5 °C, which was the lowest percentage recorded in the study. Because seeds' metabolism is less active in colder temperatures, germination will take longer<sup>38</sup> and suggests that  $T_b$  accurately predicts the phenological stages of a species<sup>31</sup>.

### Thermal time

This study provides the first reports of thermal time for *I. jinicuil*, an important climatic parameter for analyzing how temperature impacts seeds metabolism, germination percentages, and rates<sup>39</sup>. In May, seeds are released ( $22.4$  °C  $T_m$ ), but germination occurs once a threshold thermal time has been obtained and germination can begin<sup>40</sup>. This was reached in 6.6 days on average under current conditions, when the emergence of seedlings maximized, thus affecting establishment success and the survival and regeneration of the species<sup>32</sup>. Using agroclimatic models, the accumulated temperature (°Cd) is used to characterize the phenological phases, such as germination, and has an impact on phenological variation<sup>41</sup> and thermodormancy. In terms of bioclimatic regulation of germination processes, temperature is the most significant factor<sup>42</sup>. Late successional species typically take longer than early successional species to reach phenological stages such as germination<sup>43</sup>. The thermal time ( $\theta_1$  (50)) for *I. jinicuil* of  $117.164 \pm 0.636$  °Cd was lower than that reported previously for *S. macrophylla* ( $189.091 \pm 4.239$  °Cd)<sup>25</sup>, *Cedrela fissilis* Vell. of ( $157 \pm 20$  °Cd)<sup>32</sup> and *C. odorata* ( $132.74 \pm 2.60$  °Cd)<sup>27</sup>.

### Germination under climate change scenarios

The impact of rising temperatures on flowering, fruiting, and germination periods (which in turn impact the functioning of tropical ecosystems) is typically assessed in studies on how climate change may affect tropical tree<sup>37</sup>. The models that forecast the impact of climate change on *I. jinicuil* germination in this study indicate a 1.6-2.9 °C increase. When compared to the current situation, this will reduce the amount of time required to

accumulate the thermal time (°Cd) for *I. jinicuil* seed germination. According to Funes et al.<sup>40</sup>, quicker germination confers an advantage in the competition for available spaces and guarantees the establishment of individuals. Thus, climate changes can affect the competitive capacity of a species, which in turn can affect its distribution and germination rate. The sustainability and smooth operation of forest ecosystems may be negatively impacted by such modifications, which may also result in a decrease in tree diversity<sup>44</sup>. Adaptation to new climatic conditions requires migrations in altitude and latitude that are not easy and can result in evolutionary changes including the colonization of new environmental niches<sup>45</sup>.

## Potential distribution under climate change scenarios

Based on the NASA GISS-E2-1-G model the optimal distribution of *I. jinicuil* is expected to decrease in the up to 23.5% due to climate change. The model's appropriate resolution for regional impact studies led to the decision to employ it<sup>46</sup>. Therefore, the projections had an excellent fit (AUC>0.96), depending on the area under the curve<sup>47</sup>. The two variables that had the greatest effects on the models used to create the distribution of the species under study were annual precipitation and precipitation during the driest period. The study species' geographic range may be further restricted by the combination of altered rainfall patterns and rising temperatures brought on by climate change, which will accelerate soil water evaporation, possibly prolong droughts, and exacerbate drought stress<sup>48</sup>. There are no previous studies on the potential biogeographic distribution for *I. jinicuil*, and providing such information for this species in Mexico was a central focus of this study. The findings imply that to preserve the genetic diversity of populations at risk from climate change, seeds should be collected in areas where suitable conditions for their distribution will be lost and in populations located at higher temperature levels<sup>25</sup>.

Since propagation by seeds is obligatory for this and most other tropical tree species, information on the responses of seeds to changing environmental conditions, it is essential to understand the physiological mechanisms underlying the growth and development of trees<sup>49</sup>. Effects on the hormone mechanisms involved in fruiting and flowering are additional effects that require additional research<sup>50</sup>, information on dispersal, competition, and establishment and resulting predictions of changes in species distributions<sup>51</sup>. Since the physiology of seeds is influenced by temperature from the maternal environment, changing seed maturation, seed research must therefore be conducted from the perspective of climate change<sup>52</sup>. Warmer-weathered fruits produce seeds with less moisture, increasing the likelihood that seeds susceptible to desiccation will not survive. This would eventually restrict the ability of seeds to proliferate and the range of species that can exist. As far as we are aware, this is the first investigation into cardinal temperatures, thermal time, and the impact of climate change on *I. jinicuil* germination and dispersal. This species is distributed in the remnants of the tropical montane cloud forest, a fragile ecosystem, making it a species vulnerable to extinction. The productivity and profitability of growing shade coffee, however, will be impacted by the decline in the range of this multipurpose tree, which is the species most commonly used as shade on coffee plantations. Given this scenario, farms are incorporating it more and more into agroforestry systems. Therefore, the study could be the basis for developing strategies for the management, conservation, and conservation of the tree biodiversity in the country's coffee-growing regions.

## Materials and Methods

### Origin of the seeds

Ripe fruits of *I. jinicuil* were collected in early May 2022, from a shade coffee farm in the town of Los Carriles, (718806.96 E and 2152610.24 N; 1189 m a.s.l.) placed in the Coatepec coffee region in central Veracruz state. The weather in this area is moist temperate, with year-round rainfall (Cf)<sup>53</sup>, usual annual precipitation of 1761 mm, and an average annual temperature of 19.4 °C. Fig. 9 graphs showing the average monthly temperature and precipitation. The volcanic soils are of the humic andosol type, with a pH of 6.5, good drainage, and a clay-sandy texture<sup>3</sup>.

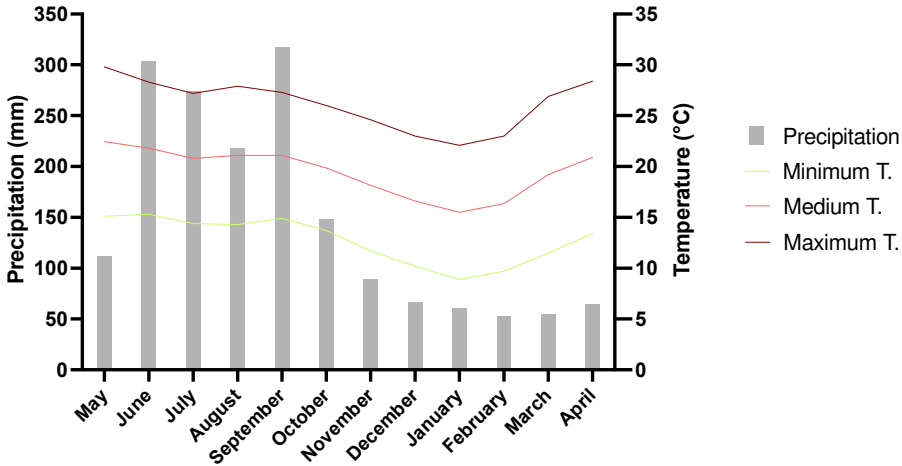


**Figure 9.** Temperature and precipitation information for the Coatepec, Veracruz, area where *I. jinicuil* seeds were collected. Historical monthly averages are reported for the period 1981-2010. Data obtained from a global climate database (<http://es.climate-data.org/>). T.= temperature.

Fruits pods were placed in breathable cloth bags and sent immediately to a laboratory in Tlalnepantla, state of Mexico. The pods were opened with tweezers in the Plant Physiology Laboratory of FESI, UNAM. After manually removing the seeds from their pods, they were placed in paper bags (15 °C and 55-60% humidity) for 24 hours prior to tests of germination and moisture content including the experiment of cardinal temperatures.

### Plant authentication

The collection of fruits and herbario specimens was carried out by the PRONATURA team in accordance with the standards established by the Kew Millennium Seed Bank Partnership. The authentication of the plant material, of fruits and seeds, was carried out by Biol. Armando Ponce Vargas. The herbarium specimen was deposited in the internal collection of the FESI-UNAM Seed Bank, with folio number BSMAMG50. It is available to the general public for educational and research purposes.

### Initial germination test

Germination test consisted of placing 10 seeds on agar medium (10 g L<sup>-1</sup>) in Petri dishes (6 cm diameter), using ten replicates of a random design. The Petri dishes were kept in a controlled environment chamber with a relative humidity of 70% and a temperature of 25 ± 2 °C. A seed was considered germinated when the radicle measured ≥ 1 mm<sup>54-56</sup>. Non-germinated seeds were subjected to a cutting test at the conclusion of the experiment to determine viability.

### Effect of temperature on germination

The methodology described by Sampayo et al.<sup>26</sup> was applied in order to evaluate the effect of temperature on germination. In Petri dishes, 10 seeds were planted in 10 replicates using a completely randomized design on agar medium (10 g. L<sup>-1</sup>). Using halogen lamps with a light intensity of 28.05 μmol m<sup>-2</sup> s<sup>-1</sup> (Quantum Meter Apogee Mod. QMSW-SS, Logan, UT, USA), petri dishes were placed in germinators with a thermal gradient of

5 to 40 °C and a 12-hour photoperiod of light. Germination was recorded daily for 45 days. Non-germinated seeds were subjected to a cutting test at the conclusion of the experiment to determine viability.

Evaluated variables

The following formula was used to determine the total germination for each temperature treatment: (1)<sup>57,58</sup>:

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

where n is the number of germinated seeds in each Petri dish and N is the total number of seeds.

The following equation (2)<sup>59</sup> was used to calculate the germination rate, which was an estimate of the quantity of seeds that germinated each day:

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

where  $G_i$  is the quantity of seeds that germinate, and  $N_i$  is the number of days that the experiment began.

### Determination of cardinal temperature using nonlinear regression models.

The approach suggested by Cabrera-Santos et al.<sup>25</sup> was used to measure the cardinal temperatures of *I. jinicuil* and analyze the impact of temperature on germination speed. was used, so linear and nonlinear regression models were used. In addition, the effectiveness and adjustment of each models was determined<sup>30</sup>.

The two segmented models used to determine cardinal temperatures were a pair of two-segment linear regressions, each for suboptimal and supraoptimal ranges, respectively. The x-intercept of each regression line and, consequently, the base temperature ( $T_b$ ) were estimated using the first segment of the regression in the suboptimal range. The second regression segment was utilized to estimate the x-intercept and, consequently, the ceiling temperature ( $T_c$ ) for the supraoptimal range<sup>60</sup>. Calculating the  $T_b$  and  $T_c$  involved averaging the x-intercept of fractions in the suboptimal and supraoptimal temperature range<sup>61</sup>. The optimum temperature ( $T_o$ ) be determined as the point where the second and first segments of the suboptimal and supra-optimal range regression lines, respectively, intersect<sup>62</sup>.

Segmented models (S1 and S2) were built with two segments of the linear regression in the suboptimal range, where X = any value of X and  $X_0$  = the X coordinate value at the intersection of the two segments. The first segment's condition was  $X < X_0$ , and the second segment's condition was  $X > X_0$ <sup>25</sup>. According to the empirical data, this was observed where there were statistically different changes in the slope of the 1/VG in function of temperature at 20 °C in the suboptimal range and between 35-40 °C in the supraoptimal range; consequently,  $X_0$  for S1 were restricted at 20 °C and 35 °C for sub- and supraoptimal ranges; while  $X_0$  for S2 were restricted to 20 °C and 40 °C, respectively. Segmented models were run for 10-80% of the seed population.

The non-linear curvilinear Asymmetric Peak Function was run for 10-70% of the seed population with the following equation (3)<sup>25,63</sup>:

$$Y = \left( a^x \left( \exp \left( (-b^x (x/c)^{-1})^2 + 1/(x-d) \right) \right) \right) \quad (3)$$

where  $a$  is the maximal germination rate in each curve,  $b$  is  $1/\sigma^2$  of the asymmetric Peak Function,  $c$  is the temperature where the germination rate is highest, and  $d$  is the interception between the abscise axis and temperature in the descending extreme of the Peak Function.  $T_b$  and  $T_c$  temperatures were defined as the temperatures in the intersection between the tangent at the inflection points of the Peak Function and the abscise axis. The thermal time was defined as the reciprocal of the slope of the tangent at the inflection points of the function<sup>64</sup>.

In each case, the best goodness-of-fit parameters (RMSE,  $R^2$  and, adjusted  $R^2$ ) of the models (4) were used, according to:

$$RMSE = \sqrt{\left(\frac{1}{n}\right) \sum (Y_{obs} - Y_{pred})^2} \quad (4)$$

where  $Y_{obs}$  presents the measured value,  $Y_{pred}$  estimated amount, and  $n$  the quantity of samples<sup>65</sup>, and with the regression coefficient ( $R^2$ ) determining the models' goodness of fit:

$$R^2 = SSR/SST \quad (5)$$

where  $SSR$  indicates the sum of squares ( $SS$ ) for regression ( $\sum_{i=1}^n (\hat{Y} - \bar{Y})$ ) and  $SST$  the total  $SS$  ( $\sum_{i=1}^n (Y_i - \bar{Y})$ ). The observed value is  $Y_i$ , and the corresponding estimated value is  $\hat{Y}$ .

## Determination of cardinal temperature using linear regression model

Following the methodology of Cabrera-santos et al.<sup>25</sup>,  $T_b$  was calculated by computing the time for germination in percentiles. Their inverse was then calculated and plotted against temperature to see how the data was trending, locate the inflection point, and identify the range of suboptimal temperatures that  $T_b$  and  $T_o$  define. In accordance with Ellis et al.<sup>61</sup>, linear regression was used to determine the parameters for each germination percentage. The base temperature was then determined by calculating the average value of  $(\theta_0)$ . The temperature range between  $T_o$  and  $T_c$  is defined as supraoptimal by Hardegree<sup>62</sup>, which can be used to estimate the  $T_c$ .  $T_c$  for germination was determined using linear regression and expressed in percentiles. The  $T_c$  value was the average value of  $(\theta_0)$  that was obtained. In the end,  $T_o$  was determined as the intersection of the first and second segments of the supraoptimal and suboptimal range regression lines, respectively.

## Thermal time

Thermal time, as defined by Sampayo-Maldonado et al.<sup>26</sup>, is the daily temperature accumulation needed for 50% of the seed lot to germinate<sup>18</sup>. For each temperature treatment, the number of germinations was measured in percentiles. The likelihood that a seed will germinate in a specific amount of time was calculated using Probit analysis. The following equation (6) represents the range of suboptimal temperatures for which probit values were expressed as a function of  $\theta_1$ <sup>66</sup>:

$$Probit (G) = K + [\theta_1 / \sigma] \quad (6)$$

where: When thermal time is zero,  $K$  is the intercept constant, and  $\sigma$  is the standard deviation of the  $\theta_1$  thermal time response. Using the same equation, the thermal time needed for 50% ( $\theta_1$  (50)) of the population to germinate was calculated.

As a function of  $\theta_2$ , Probit values were expressed for the range of supra-optimal temperatures. Equation (7) was employed to explain the germination response, in accordance with Covell et al.<sup>66</sup>:

$$Probit (G) = Ks + (T + \theta_2/t(G))/\sigma \quad (7)$$

where:  $\sigma$  is the standard deviation of the maximum temperature  $T_c$ ,  $(T + \theta_2/t(G))$  is the maximum temperature  $T_c$ , and  $Ks$  is an intercept constant when the thermal time is zero. The thermal time needed for 50% germination ( $\theta_2$  (50)) of the population was calculated.

## Experimental design and statistical analysis

Since the percentage germination results did not meet the normalcy assumptions, the analysis of variance was performed using Kruskal-Wallis, and the multiple comparisons were performed using Dunn's post hoc test. For the analysis of regression models, the effectiveness and adjustment were determined through the analysis of RMSE,  $R^2$  and adjusted  $R^2$ .

## Potential effects of climate change on germination

Sampayo-Maldonado et al.<sup>24</sup> methodology was followed in this analysis, which made use of maps of the combined projections<sup>67</sup> of the global circulation models' average temperature layers from the Digital Climate Atlas for Mexico, which were available for the French (CNRMC5), American (GFDL-CM3), English (HADGEM2-

ES), and German (MPI-ESM-LR) models (<http://atlasclimatico.unam.mx/AECC/servmaps/>). These models were developed using the Regional Models of Phase 6 for the Intergovernmental Panel on Climate Change's Coupled Model Intercomparison Project (IPCC), with projections for the medium future (2045-2069) and the distant future horizon (2075-2099). The assumptions for CO<sub>2</sub> emissions and associated radiative forcing were 2.6 and 8.5 (SSP5) Watts/m<sup>2</sup>, respectively<sup>68</sup>. We were able to predict the average temperatures for May, which is when seed dispersal starts, using these maps<sup>69</sup>.

The time it will take for *I. jinicuil* seeds to accumulate the thermal time needed for 50% of a seed bank in the understory to germinate was predicted for each scenario. Analysis was performed using the mean temperature method<sup>70,71</sup>:

$$\text{Thermal sum } (^{\circ}\text{Cd}) = (\text{Env } T_m - T_b)t_m \quad (8)$$

Where: the average base germination temperature ( $T_b$ ), the average temperature for the month ( $T_m$ ), the number of days in the month ( $t_m$ ), and the accumulated degree days ( $^{\circ}\text{Cd}$ ) are all given.

## Modelling potential distributions under climate change scenarios

The maps of the various climate change scenarios were created using the methodology described in Sampayo et al.<sup>72</sup>. Specimens of *I. jinicuil* collected in the nation were georeferenced in a database from the Global Biodiversity Information Facility (GBIF) platform (<https://www.gbif.org/>), which was one of the data sources used in distributional modeling. For distribution modeling, a subset of people in the ideal germination temperature range (average value of  $T_o \pm 2^{\circ}\text{C}$  standard deviations) was then found, resulting in an ideal range of 29.5 to 33.5  $^{\circ}\text{C}$ , which includes 93% of the population<sup>24</sup>; 2) Data from 1970 to 2000 were used to parameterize 19 climatic variables from BioClim (v2.0), using 1 km<sup>2</sup> pixels<sup>73,74</sup>; and 3) land use and cover maps from the National Commission for the Knowledge and Use of Biodiversity<sup>75</sup>.

Program MaxEnt 3.3.3 was used to run the current distribution models. Georeferenced sites reporting the presence of *I. jinicuil* within its ideal germination temperature range were used to parameterize the models. The relative contribution of each Bioclim climatic variable to the model was calculated using the Jackknife method<sup>76</sup>. The program was run again to produce maps of the expected current species distribution in ideal climatic habitat after these crucial climate variables were determined. The number of pixels was obtained and converted to km<sup>2</sup> using the ArcMap 9.3<sup>®</sup> tool<sup>24</sup>. Lastly, maps showing the species' distribution in the current climatic conditions were produced with a probability higher than 50%.

To obtain the surface with optimal climatic habitat for future distribution, BioClim (v2.0) was used together with MaxEnt 3.3.3 software<sup>76</sup>. We downloaded the climatic layers of the General Circulation Model (GCM) of the Goddard Institute for Space Studies (GISS) of the National Aeronautics and Space Administration (NASA) of the United States of America (GISS-E2-1-G). These layers were produced from the Regional Models of the Coupled Models Intercomparison Project Phase 6 of the Intergovernmental Panel on Climate Change (IPCC), with projections for 2050 as a medium future horizon (average for 2041-2060) and 2090 as a distant future horizon (average for 2081-2100). Given two Shared Socioeconomic Pathways (SSP1) with radiative forcing of 2.6 and 8.5 (SSP5) Watts/m<sup>2</sup> (respectively, decreasing and increasing CO<sub>2</sub> emissions)<sup>77</sup>. The sites were georeferenced and contained populations of the species, spread across the ideal temperature range for germination (29.5 to 33.5  $^{\circ}\text{C}$ ). The climatic factors that made the biggest contributions to the distribution model were assessed using the Jackknife method. Counting the pixels and converting them to square kilometers using the ArcMap 9.3<sup>®</sup> tool. Ultimately, maps showing the species' distribution in projected future climates were produced, with a probability higher than 50%.

To examine if the environmental variables were multicollinearity, Pearson correlation coefficients were employed<sup>78</sup>. The type of response to the environmental variable, being uncorrelated ( $r \leq 0.8$ ) with the normal distribution, and having the highest contribution as indicated by the Jackknife test were the three criteria used to select the predictive variables. Furthermore, areas that present barriers to the species' dispersal were eliminated, thereby restricting the results of biogeographical regions.

## Conclusions

The study's findings showed that both the linear and non-linear models examined fit the empirical data on *I. jinicuil* germination in response to temperature reasonably well. The linear and beta models, on the other hand, fit the data better than the segmented ones and both precisely define the cardinal temperatures for the species. Temperature had an impact on *I. jinicuil*'s ability to germinate. Wide range were observed in the cardinal temperatures for germination (4.8 to 49.2 °C). The optimum temperature was in the range of 29.58 to 33.02 °C. At 25 °C, the percentage of germination reached its maximum, and at 31.6 ± 1.1 °C, the rate of germination was fastest. The calculated thermal time ( $(\theta_1 (50))$  117.164 ± 0.636 °Cd) takes 6.6 days to reach under the current climate conditions. Temperature rises are predicted by climate change models, which will reduce the amount of time it takes for seeds to reach the temperature required for germination. The Goddard Institute for Space Studies (GISS) of NASA's GISS-E2-1-G model predicts that, in comparison to its current distribution, the future distribution of *I. jinicuil* populations will decline by 1.2 to 23.5%. In areas where the climate will no longer be ideal, it is advised to collect seeds and conduct provenance tests in accordance with models of the species' potential distribution in order to preserve valuable genotypes for future environments. It is also possible to create commercial plantations of the species and acquire seeds of exceptional genetic quality by planting seed orchards. Distribution modeling of *I. jinicuil* led to the identification of locations where temperature will maximize establishment and adaptation under various climate change scenarios by positively influencing seed germination.

## Data Availability Statement

The datasets used and/or analysed during the current study available from the corresponding author on reasonable request.

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## Author Contributions

Conceived the idea and designed the experiment C.M.F.O. and T.U. Performed the experiments S.S.M. and D.C.S. They carried out the seed collections N.I.R.A. and G.S.Q. Verified the analytical methods T.U., M.W., M.G. and E.B. Supervised the development of this work and analysed the data P.D.D.A., A.D.O.S. and R.H.M. Wrote the article S.S.M., D.C.S. and C.M.F.O. All authors interpreted the results and contributed to the final manuscript. All authors read and approved the final manuscript.

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### **Competing of Interest**

The authors declare that they have no competing of interest.

### **Additional information**

The corresponding permits and licenses were obtained to collect seeds and specimens for herbarium, as well as permits for their transfer and final disposal in the FESI-UNAM seed bank. License for scientific collection for teaching purposes on wildlife, document number SGPA/DGVS/02141/22. Granted by the Wildlife Directorate of the Secretariat of Environment and Natural Resources (SEMARNAT), Mexico.