



Thermal Time and Cardinal Temperatures for Germination of *Cedrela odorata* L.

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Received: 21 August 2019; Accepted: 24 September 2019; Published: 26 September 2019



Abstract: Thermal time models are useful to determine the thermal and temporal requirements for seed germination. This information may be used as a criterion for species distribution in projected scenarios of climate change, especially in threatened species like red cedar. The objectives of this work were to determine the cardinal temperatures and thermal time for seeds of Cedrela odorata and to predict the effect of increasing temperature in two scenarios of climate change. Seeds were placed in germination chambers at constant temperatures ranging from 5 ± 2 to 45 ± 2 °C. Germination rate was analyzed in order to calculate cardinal temperatures and thermal time. The time required for germination of 50% of population was estimated for the current climate, as well as under the A2 and B2 scenarios for the year 2050. The results showed that base, optimal and maximal temperatures were -0.5 ± 0.09 , 38 ± 1.6 and 53.3 ± 2.1 °C, respectively. Thermal time ($\theta_1(50)$) was 132.74 ± 2.60 °Cd, which in the current climate scenario accumulates after 5.5 days. Under the A2 scenario using the English model, this time is shortened to 4.5 days, while under scenario B2, the time is only 10 hours shorter than the current scenario. Under the German model, the accumulation of thermal time occurs 10 and 6.5 hours sooner than in the current climate under the A2 and B2 models, respectively. The seeds showed a wide range of temperatures for germination, and according to the climate change scenarios, the thermal time accumulates over a shorter period, accelerating the germination of seeds in the understory. This is the first report of a threshold model for C. odorata, one of the most important forest species in tropical environments.

Keywords: Cedrela odorata; seeds; germination; cardinal temperatures; thermal time; climate change

1. Introduction

Cedrela odorata L. is a tree of the Meliaceae family and is native to the American tropics [1]. According to Mendizábal-Hernández et al. [2], it is distributed in warm to subwarm climates in Mexico and requires fertile soil with good drainage; as such it is mainly found in the humid and subhumid tropics, associated with tropical deciduous forest, tropical semi-deciduous forest, and tropical rainforest, in addition to humid montane forest. According to Romo-Lozano et al. [3], *C. odorata* provides ecosystem services to mitigate the impacts of climate change, serving as a carbon sink that maintains the resilience



of ecosystems and as a source of genetic resources for medicinal and other uses in future environments. Navarro et al. [4] and Ramírez-García et al. [5] recognize its ecological importance as a pioneer species in tropical forests. It is important for reforestation of degraded areas and has potential for establishing plantations. According to Pérez-Salicrup and Esquivel [6] and Sampayo-Maldonado et al. [7], it is the most economically viable species for establishing commercial plantations, the most important for the forestry industry in Mexico, and preferred on the international market. It has a wide range of uses in construction, carpentry and cabinetmaking and therefore represents one of the most planted species in the country [8].

C. odorata is included in the Convention on International Trade in Endangered Species [9]. It is also included on the red list of threatened species in the category of vulnerable and is subject to special protection under the Mexican law Official Mexican Standard 059 (NOM-059-SEMARNAT) [10]. The distribution of plant communities is determined by several factors, but the main factor is climate. According to Gómez-Díaz et al. [11], the different models of climate change for Mexico, predict an increase in temperature and decrease in precipitation for the years 2050 and 2100. Hartmann et al. [12] mention that temperature is the most important factor in the adaptation of a species, considering its geographic origin. González [13] and Dewan et al. [14], state that temperature influences the physiological processes of seed germination including speed and germination percentage. Reduced germination time means higher economic efficiency in the production of a larger number of plants [15].

The germination response to temperature can be characterized through the germination rate and is defined by three cardinal or threshold temperatures: a base temperature (Tb) below which germination does not proceed; an optimal temperature (To) at which the rate of germination is highest; and a maximum or ceiling temperature (Tc) above which germination ceases [16]. The cardinal temperatures are the limits, while the optimum temperature is the one by which germination is fastest [17]. Thermal time is the thermal sum accumulated per day that is necessary for the germination of 50% of the seed lot [18]. Temperature is one of the most important bioclimatic elements in determining the response of seeds to changing environmental conditions [19].

According to Calzada-López et al. [20], characterizing cardinal temperatures and thermal time is useful for finding the optimal temperature for fastest germination, as a criterion for species distribution under different climate change scenarios. Ruíz-Corral et al. [21] mention that cardinal temperatures are variable among species, among populations, and even within a species, as a direct effect of adaptation. Studies of the effect of temperature on germination are therefore needed, since this is a requisite step for forest conservation and sustainable management [22]. It is important to mention that there are no previous studies of cardinal temperatures and thermal time in *C. odorata*.

Seed germination is the most vulnerable and crucial stage in the life history of a tree [23]. According to Sánchez-Monsalvo et al. [24] and Castellanos-Acuña et al. [25], germplasm that is of known genetic origin and is adapted to environmental conditions in each region will be needed in studies to understand the impact of cardinal temperatures and thermal time during germination. Such studies are required to identify the effect of increased temperature on the species potential distribution under different climate change scenarios. However, there is currently no information on the optimal temperature or thermal time for germination in tropical trees of interest to forestry in Mexico. Thus, the objectives of this research were to determine the cardinal temperatures and thermal time of *C. odorata* seeds and to predict the effect of increasing temperature under two scenarios of climate change.

2. Materials and Methods

2.1. Seed Collection

The seeds of *C. odorata* are flat ovoid, with a brown-colored testa, provided with a dark wing contained in a woody dehiscent capsule. Each capsule has between 25 to 35 seeds. Each seed has two large and flat cotyledons; the endosperm is thin and attached to the white embryo. The embryo is axial, straight and spatulate, white to cream colour, it has a short radicle which protrudes laterally.

C. odorata seeds have a wide variation in morphometric characteristics, associated with environmental and genetic factors. One kg contains approximately $94,965 \pm 8108$ seeds [26].

Mature *C. odorata* capsules were collected in April 2018 (2 kg, 149,406 seeds) from 15 trees as a representative sample from a population in Zozocolco de Hidalgo. The brownest capsules were collected just before dehiscence by using pruners over a tarpaulin when capsules were low enough in the tree, but frequently it was necessary to climb the tree to obtain the most mature capsules. These were put in cotton bags and kept in the laboratory at ambient temperature. All capsules opened naturally in less than one week. The seeds were manually separated from plant debris and stored in paper bags at 15 °C until germination tests were carried out.

The municipality of Zozocolco de Hidalgo is in the state of Veracruz (649265.14 E, 2223834.28 N; 183 m a.s.l.), in the Totonacapan region. The climate at the site is warm and subhumid, with rains year-round ((Af) according to García [27]), with a mean annual precipitation of 2233 ± 33.93 mm and mean temperature of 23.4 ± 3.32 °C (Figure 1). The soils are Acrisol, deep with good drainage, with a sandy clay texture and pH of 5.7 [28].



Figure 1. Climate data from the area where seeds were collected. Historical monthly average of 1981–2010. Available in global climate data (http://es.climate-data.org/).

2.2. Disinfection

Following Sampayo-Maldonado et al. [29], the seeds were treated with powder soap and running water for 10 minutes, then rinsed three times with distilled water. They were soaked in Captan[®] (1 g L⁻¹) for 60 minutes, then rinsed three times with distilled water. Later, they were treated with 70% ethanol for 1 minute, rinsed three times with distilled water, and finally, soaked for one minute in 6% sodium hypochlorite and rinsed three times with distilled water.

2.3. Initial Germination Test

In order to know the quality of the seed lot, an initial germination test was performed. The seeds were placed randomly on agar medium (10 g L⁻¹) in Petri dishes (6 cm diameter), in a completely randomized design with four replicates, using 25 seeds each. The Petri dishes were placed in a climate-controlled chamber at a temperature of $25 \pm 2 \,^{\circ}$ C, and a photoperiod of 12 light hours and 12 dark hours. The test began on May 14, 2018. A seed was considered to have germinated when the size of the radicle reached $\geq 2 \,\text{mm}$ [30]. A cut test was undertaken at the end of the germination test on those seeds that did not germinate to check viability. Seeds with a filled, firm and white embryo were considered viable.

The seeds were tested for germination in the Plant Physiology Laboratory at the Biotechnology and Prototype Research Unit of the Faculty of Higher Education, Iztacala of the National Autonomous University of Mexico (Laboratorio de Fisiología vegetal, Unidad de Investigación de Biotecnología y Prototipos, Facultad de Estudios Superiores Iztacala, Universidad Nacional Autónoma de México) in Tlalnepantla, state of Mexico.

2.4. Effect of Temperature on Germination

Seeds were sown under sterile conditions in a laminar flow cabinet (Novatech, Mod. CF-13). A total of 30 seeds were placed in each Petri dish, with five replicates. The dishes were then sealed with parafilm and labeled. They were then placed in germination chambers at the following constant temperatures: 5 ± 2 , 10 ± 2 , 15 ± 2 , 20 ± 2 , 25 ± 2 , 30 ± 2 , 35 ± 2 , 40 ± 2 and $45 \pm 2 °C$, under a photoperiod of 12 hours light, 12 hours darkness, using halogen lamps at a light intensity of 28.05 µmol m⁻² s⁻¹ (Quantum Meter Apogee Mod. QMSW-SS). Seeds were sown on June 1, 2018; the seeds had three weeks of storage. Counts were conducted daily for the following 61 days in order to determine the proportion of germinated seeds. Following ISTA [30] and Parmoon et al. [31], a seed was considered to have germinated when its radicle reached ≥ 2 mm, measured with a stainless-steel Vernier ruler (Truper).

2.5. Variables Evaluated

2.5.1. Total Germination

The number of germinated seeds in each Petri dish of the five repetitions of each treatment was recorded, to obtain averages in each treatment. The proportion of germinated seeds was calculated using the following equation [29]:

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

where n is the number of seeds germinated and N the total number of seeds.

2.5.2. Median Germination Time (t_{50})

The total number of days between imbibition and 50% of the total germination was recorded. Following Ordoñez-Salanueva et al. [32] a sigmoid curve was fitted to the accumulated germination, allowing the median germination time to be determined by interpolation.

2.5.3. Germination Rate

This is an estimate of the number of germinated seeds per day, according to the following equation [20]:

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

where G_i is the number of germinated seeds and N_i is the number of days after the beginning of the experiment.

2.5.4. Base Temperature (Tb)

This represents the temperature in degrees Celsius below which germination does not occur; it was calculated in percentiles, in 10% intervals, for all temperature treatments. The inverse time to germination was then graphed as a function of temperature in order to observe data trends and locate the inflection point and determine sub-optimal temperatures. Following Ellis et al. [17] a linear regression was performed to obtain the parameters for each germination percentage. The mean value of x-intercept (β 0) was then calculated and used to generate a second linear regression for each germination percentage. The mean β 0 was the base temperature.

Following Hardegree [33], supra-optimal temperatures in degrees Celsius were determined for the upper threshold temperature, which were used to generate a linear regression to obtain the parameters for each germination percentage. The mean value of the x-intercept (β 0) was obtained and used to do a second linear regression. The mean β 0, again calculated from the second regression, represents the upper threshold temperature.

2.5.6. Optimal Temperature (To)

This represents the optimum germination temperature in degrees Celsius and was obtained by equating the straight-line equations of Tb and Tc at their intersection [33].

2.5.7. Thermal Time (θ , °C)

The inverse of the slope of the regression lines for each fraction were calculated separately to estimate the thermal time (θ , °Cd) in the sub-optimal (θ_1) and supra-optimal (θ_2) temperature range. The thermal time means the thermal requirements in temperature by time to reach the germination of each percentile in the population. Percentage data were transformed using Probit Analysis in Genstat (version 11.1.0.1504, International Ltd, Hemel Hempstead, Herts, England, UK). Linear regression for the sub- and supra-optimal temperature range for each species was used to express probit (G) as a function of θ .

To estimate the probability that a seed will germinate in a given time, the number of germinated seeds for the percentiles was calculated, at intervals of 10% for each of the temperature treatments. Then the inverse of the slope of the regression lines for each percentile was calculated and the percentage data were transformed into probits. For the sub-optimal temperature range, R^2 values were highest and residual variances were smallest when probit values were expressed as a function of θ_1 (sub-optimal thermal time). For the sub-optimal temperature range the following equation describes the form of cumulative germination response of seeds [34]:

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

where *K* is an intercept constant when thermal time is zero and σ is the standard deviation of the response to thermal time θ_1 . The same equation was used to determine the thermal time of germination of 50% ($\theta_1(50)$) of the population.

For the supra-optimal temperature range, R^2 values were highest and residual variances were smallest when probit values were expressed as a function of θ_2 the following equation describes the form of accumulative germination response of seeds [34]:

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

where *Ks* is an intercept constant, when thermal time is zero, $(T + \theta_2/t(G))$ is the maximum temperature (Tc), and σ is the standard deviation of the maximum temperature (Tc). The same equation was used to determine the thermal time required for germination of 50% $(\theta_2(50))$ of the population.

2.5.8. Climate Change Scenarios

Following Gutiérrez and Trejo [35], we used the projections of mean temperature proposed by two general circulation models—the German model (MPIECHAM5) and the English model (UKMOHADGEM1)—available from the Digital Climate Atlas of Mexico [36]. The projection for the year 2050 under the A2 (severe, or pessimistic scenario with high emissions of greenhouse gases) and the B2 (conservative or non-pessimistic model with low greenhouse gas emissions) were used. The area was located on the map and the mean temperature data for the A2 and B2 scenarios was obtained. The mean temperatures were projected for the month of April, since this is the period when *C. odorata* seed dispersal occurs [1].

Each scenario was used to predict the time in which seeds of *C. odorata* accumulate the thermal time necessary for germination of 50% of the seed bank in the understory. Following Flores-Magdaleno et al. [37], the analysis was performed using the mean temperature, so that the following formula was used [38]:

$$Thermal sum (^{\circ}Cd) = (Env T_m - T_b)t_m$$
(5)

where °Cd is the degrees days accumulated, T_b is the minimum germination temperature, T_m is the monthly mean temperature, and t_m is the number of days in the month.

2.6. Experimental Design and Analyses

We used a completely randomized design. All treatments were performed in similar conditions as can be seen in Figure 2. The data did not fulfill the assumptions of normality, so prior to the analysis of variance (ANOVA), percentage variables (Y) were transformed using the arcsine square root function (with the original value expressed as a proportion) [T = $\arcsin(\sqrt{Y})$] [39–41]. The ANOVAs were carried out in SAS statistical software (Cary, NC, USA) [42], and the Tukey test was performed for multiple comparisons to determine significant ($p \le 0.05$) differences between treatments. ($p \le 0.05$).



Figure 2. The experimental unit: (a) Petri dish with 30 seeds and (b) 5 replicates.

3. Results

The seeds did not show dormancy, so no pre-germination treatments were carried out. In the initial germination test, the seed lot used had a 98% germination rate at 25 ± 2 °C.

3.1. Germination

There was a significant effect of temperature on final percentage of germination ($F_{8,36}$ 49.82 p < 0.02). Seeds of *C. odorata* began to germinate after three days, and at the lowest temperature they began at 28 days after sowing. Mean germination was above 50%, and the highest frequency was 90% germination (Figure 3). The highest germination percentage was at 20 ± 2 °C and the lowest percentage was at the highest temperature.



Figure 3. Percentages of germination at each temperature. Error bars show standard deviation. Means that share a letter are not significantly different ($p \le 0.05$).

The time required for 50% of the seeds to germinate was significantly different among 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 18 to 47 days were needed at lower temperatures (15 ± 2 to 5 ± 2 °C respectively; Figure 4).



Figure 4. Time required for 50% germination (t_{50}) at each temperature. (5 °C, 47.41 ± 3.1 t_{50} ; 10 °C, 19.76 ± 2.8 t_{50} ; 15 °C, 17.86 ± 2.2 t_{50} ; 20 °C, 5.02 ± 0.9 t_{50} ; 25 °C, 5.02 ± 0.7 t_{50} ; 30 °C, 4.83 ± 0.8 t_{50} ; 35 °C, 3.76 ± 1.2 t_{50} ; 40 °C, 5.34 ± 2.5 t_{50} ; 45 °C, 5.65 ± 0.9 t_{50}). Error bars show standard deviation.

The germination rate differed significantly among 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 (Figure 5).



Figure 5. Germination rate per day for each temperature treatment. Error bars show standard deviation. Means that share a letter are not significantly different ($p \le 0.05$).

3.2. Cardinal Temperatures

Figure 6 shows the germination rates for each temperature. For the sub-optimal temperatures, the model explained 86% of the variation in the germination rate, while for the supra-optimal temperatures the model explained 89% of the variation. With increasing temperature, the germination rate increased until reaching its optimal temperature (To) calculated according to the Hardegree cardinal temperature model [32] of 38 ± 1.6 °C, while decreasing the temperature, decreased the germination rate to zero at the base temperature calculated (Tb) of -0.5 ± 0.09 °C. As temperature increased above the optimal temperature (To), the germination rate decreased to its minimum at the upper threshold (Tc) temperature calculated at 53.3 ± 2.1 °C.



Figure 6. Germination rate in percentiles for each temperature in the range of cardinal temperatures (Tb: Base temperature; To: Optimal temperature; Tc: Upper threshold temperature).

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The base temperature was negative, given that more than 75% germination occurred at the lowest temperature tested, 5 ± 2 °C (Figure 3). The optimal temperature (38 ± 1.6 °C) was directly related to the temperature that had the highest germination rate (Figure 5). The upper threshold temperature was above 53 °C, and can be explained due to the fact that at 45 ± 2 °C, it took 5.6 days to germinate 50% of the seed lot (Figure 4). Although the germination percentages are similar in Tb, To and Tc, the significant differences between these calculated values can be observed in the germination rates as shown in Figure 5.

3.3. Thermal Time

According to the base temperature (Tb), in order to obtain 50% of seed germination in the lot, 132.74 ± 2.60 °Cd of thermal time must be accumulated ($\theta_1(50)$).. 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 thermal time was 0.125 ± 0.019 (Table 1). Using the upper threshold temperature (Tc) to obtain 50% of seed germination in the lot, 253.31 ± 4.73 °Cd of thermal time must be accumulated ($\theta_2(50)$), but the probit model explained only 82% of this.

Table 1. Estimated thermal time in seeds of *Cedrela odorata* (Tb = -0.5 °C) from probit regressions in the sub-optimal and supra-optimal temperatures range. θ_1 (50) and θ_2 (50) are shown in log and normal scale.

Parameters	Sub-Optimal	Supra-Optimal
R2	96.33	82.99
Κ	-4.91 ± 0.53	-2.02 ± 0.28
σ	0.125 ± 0.019	0.122 ± 0.012
$\log\theta$ (50)	2.12 ± 0.008	2.40 ± 0.001
θ (50)	132.74 ± 2.60	253.31 ± 4.73

The valor represent mean ± standard deviation)n.
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For the base temperature (Tb) in Figure 7a, it is evident that the increase in heat accumulation increases the probability of higher germination percentages because it approaches the thermal time $(\theta_1(50))$ of 132.74 ± 2.6, where 50% of the seed lot germinates. In the case of thermal time of the upper threshold temperature (Tc), it indicates that as more heat accumulates, there is an increase in the probability of lower germination percentages. This can be interpreted as movement away from the thermal time $(\theta_2(50))$ of 253.31 ± 4.73 °Cd (Figure 7b).



Figure 7. Germination as a function of thermal time for: (**a**) sub-optimal range and (**b**) supra-optimal range of temperatures. The red lines are confidence intervals of germination. The blue line is the estimated data. The points are experimental data.

3.4. Climate Change Scenarios

The current mean temperature for the month of April is 24.5 °C; for the same month in the year 2050, in the German model (MPIECHAM5) the A2 scenario projects a 2 °C and the B2 scenario projects a 1.3 °C increase in temperature. Under the English model (UKMOHADGEM1), scenario A2 projects a 3.1 °C and the B2 scenario projects a 2 °C increase in temperature.

Figure 8 shows the days of the thermal sum of the month of April (the month in which the dispersal of mature seeds begins), based on mean temperature and the increases in temperature under the different climate change scenarios. Under the current scenario, the thermal time is accumulated in 5.5 days. When the temperature increases by 2 °C based on the A2 scenario of the German model (MPIECHAM5), the thermal time accumulates 10 hours earlier than in the current climate. Under the B2 scenario, which projects a 1.3 °C temperature increase, the thermal time accumulates 6.5 hours earlier than the current scenario.



Figure 8. Time in which seeds accumulate the thermal sum (°Cd) during the month of April, for the current climate, and the year 2050 projections under the A2 and B2 scenarios of the German model. (Mt: Current mean temperature; Mt B2: Mean temperature under scenario B2; Mt A2: Mean temperature under scenario A2).

Figure 9 shows results for the English model (UKMOHADGEM1). In scenario A2, which projects a 3.1 °C increase in temperature, the accumulation of the thermal sum is accelerated, so that reaching the thermal time requires just over 4.5 days to germinate 50% of the bank of seeds scattered in the understory. This is 21.5 hours earlier than in the current scenario. For model B2, the thermal time is accumulated 10 hours earlier than in the current scenario.





Figure 9. Time in which seeds reach the thermal sum (°Cd) in the month of April, under the current climate scenario and under the 2050 projections for the A2 and B2 scenarios of the English model. (Mt: Current mean temperature; Mt B2: Mean temperature under the B2 scenario; Mt A2: Mean temperature under the A2 scenario).

4. Discussion

4.1. Germination

The highest germination percentage occurred below the theoretical optimal temperature calculated for this species, and does not necessarily occur at the optimal temperature [20]. The highest germination percentage at 20 °C coincides with reports of González et al. [43]. At the same time, the lowest germination percentage occurred in seeds exposed to the highest temperature (45 ± 2 °C), and was significantly lower than that of the lowest temperature tested in this study (5 ± 2 °C). This occurs because, according to Butler et al. [44] very high temperatures (>40 °C) can affect the metabolic processes of the seeds and even damage them, halting embryonic growth, which can inactivate and kill them.

At temperatures at or above 20 ± 2 °C, median germination time was three to five days, which is similar to the results shown by González et al. [43] in *C. odorata* L., and by Manjul and Metali [45] in *Acacia mangium* Wild, *Melastoma beccarianum* Cogn and *Melastoma malabathricum* L. According to Rajjou et al. [46], higher temperature accelerates the enzyme activity in biochemical reactions within the seeds following imbibition. This is true only to a point, after which a further increase in temperature inhibits germination. For this reason, Durán-Puga et al. [47] mention that shorter median germination times may confer a competitive advantage for colonization of fragmented habitats. In addition, Baskin and Baskin [48], suggest that selective pressure in extreme environments increases establishment success.

Seeds germinated at temperatures below 15 ± 2 °C had lower germination rates, even slower than at the highest temperatures, such as 45 ± 2 °C. This coincides with the 15 °C reported by González et al. [43] for *C. odorata* in neotropical dry forest. This can be explained by the fact that, according to Adam et al. [49], lower temperatures decrease metabolic rates to the point that the processes that are essential to germination decrease. Furthermore, this species needs a higher temperature for its development due to its distribution in tropical climates. In addition, Caroca et al. [50] mention that at

high temperatures, chemical reactions are faster because water is absorbed more quickly into the seeds, causing the seeds to germinate faster.

4.2. Cardinal Temperatures

C. odorata presented a wide range of cardinal temperatures, from -0.5 °C to above 53 °C. According to Lindig-Cisneros [51], terrestrial vascular plants can tolerate a temperature range in terms of survival from -5 to 60 °C. As such, the ability to germinate at a wide range of temperatures is an adaptive strategy of the species, which gives it an advantage in terms of its potential distribution under different climate change scenarios. According to Parmoon et al. [31], with increasing temperature, there is a linear increase in germination percentage up to the optimal temperature. If temperature increases further, the germination will decrease to zero.

The optimal temperature was 38 ± 1.6 °C. This temperature is not registered in the study area, even in the warmest month, so these results suggest the physiological optimum in lab conditions, rather the ecological optimum temperature [52]. These findings are consistent with Caroca et al. [50], who showed that optimal temperature occurs at higher germination rate. In addition, Adam et al. [49] and Grey et al. [53] indicate that the germination rate increases with temperature, but when the temperatures are above the optimal temperature there is a decrease in the germination rate, specifically at the intersection where the optimal germination temperature is found.

The upper threshold temperature was above 53 °C, which could constitute a competitive advantage for the species when competing to colonize fragmented habitats, since according to Sánchez-Rendón et al. [54] the soil in forest clearings can reach temperatures above 45 °C. In addition, Cóbar-Carranza et al. [55] report germination percentages above 90% in *Pinus contorta* at temperatures between 60 °C and 80 °C.

The base temperature was -0.5 °C. This could be explained with a germination percentage above 75% at 5 ± 2 °C. According to Mendizábal-Hernández et al. [2], this species has a wide distribution due to its plasticity and adaptation to different environmental conditions. According to Calzada-López et al. [20], after imbibition, low temperatures decrease seed metabolism activity and protein synthesis, thus more days are needed to accumulate heat for the germination process. Parra-Coronado et al. [56] mention that below the base temperature, phenological development and metabolic processes stop. As such, according to Andreucci et al. [57] the base temperature predicts precisely the dates at which different stages in the phenological development occur in a species.

4.3. Thermal Time

The thermal time required for 50% germination of *C. odorata* seeds was 132.74 \pm 2.60 °Cd. This is consistent with findings obtained by Normand and Léchaudel [58] and Parra-Coronado et al. [56] in some tropical species, such as *Psidium* spp. and *Manguifera* spp., which require less time to reach the different phenological stages. According to Funes et al. [59], germination is accelerated by high temperatures in tropical climates, which maximizes individuals' establishment and survival. Furthermore, Asseng et al. [60] mention that in warm climates, phenological development is accelerated, leading to shorter growth periods, which is an adaptive competitive strategy for the species. According to Colauto-Stenzel et al. [61] and Parmoon et al. [31], thermal time is used to include the effect of temperature as the most important bioclimatic factor in regulating the germination process.

4.4. Climate Change Scenarios

Sánchez-Rendón et al. [54] and IPCC [62] consider that increasing temperature and decreasing precipitation will give rise to evolutionary changes and altitudinal and latitudinal migration among forest species. The A2 scenarios of the German and English models project a larger increase in temperature due to high emissions of greenhouse gases, which shortens the necessary time needed to accumulate the thermal sum (°Cd). This is consistent with results of Rajjou et al. [46], who indicate that at higher temperatures, the germination rate increases. According to Funes et al. [59], faster

germination assures the establishment of individuals that must compete for space. However, according to Grey et al. [53], very high temperatures decrease germination because they damage the embryo.

The climate change scenarios, according to Sánchez-Rendón et al. [54], in the medium term will present increased temperature and decreased precipitation. However, they also predict extreme events such as droughts and floods, which will impact the function of tropical ecosystems, affecting flowering, fruiting, germination, and establishment periods of forest species. With the increase in temperature, it is expected that the dispersion of *C. odorata* seeds will be in a shorter period, likely with shorter time spans for the accumulation of thermal time necessary for the phenological stages of the species.

Gutiérrez and Trejo [35] state that climate change will alter the distribution and abundance of species because they will be forced to migrate, altering the sustainability of the region. This is consistent with projections for *C. odorata*; according to Romo-Lozano et al. [3] the timber stocks of this species in Mexico will be valued at \$5,282,183,403 Mexican Pesos, and 68% of the stock will be found in the Gulf of Mexico region. However, according to the results of the present work, these projections need to be reanalyzed, since the wide range between Tb and Tc temperatures implies significant changes in their distribution, and in the potential forest areas. In addition, Hernández-Ramos et al. [63], predict that by the year 2050 a reduction in the current area reported for *C. odorata* in Tabasco and the Yucatan Peninsula, as well as the southern part of Veracruz and Chiapas, will occur. However, there is a high probability that it will be distributed in the southern part of the Yucatan Peninsula, northern Chiapas and the coastal plain of the Gulf of Mexico in Veracruz. Furthermore, Gómez-Díaz et al. [11] mention that they expect a reduction in the species' distribution in the state of Hidalgo, due to the increase in temperature and decrease in precipitation. However, the species is also expected to adapt to the new limited precipitation conditions with possible altitudinal and latitudinal migration [25].

To our knowledge, this is the first study of cardinal temperatures and thermal time in seeds of *C. odorata*, which is one of the most important forest species in tropical environments, since its wood is highly valuable in carpentry and cabinetmaking. Additionally, the study will be the basis for the generation of bioclimatic models that can be used to predict the potential distribution of the species, under extreme ecological conditions, in order to develop conservation strategies for fragile ecosystems, and restore fragmented habitats.

5. Conclusions

C. odorata presented a wide range of cardinal temperatures; the base temperature was half a degree below zero and the maximum threshold temperature of 53.3 °C. while the optimum temperature for germination was 38 °C. With results obtained, a thermal time (θ_1 (50)) of 132.74 °Cd could be calculated for the germination stage, which in the current scenario accumulates in 5.4 days. Thus, as the temperature increases according to the climate change scenarios MS-2050 and MS-2100, the germination of the soil seed bank in the undergrowth will accelerate. Because of these findings, it is advisable to evaluate the cardinal temperatures in this work in successive developmental stages such as establishment and growth to understand predicted reduction in its distribution.

Author Contributions: Conceptualization: S.S-M., C.A.O.-S., P.D.D.-A., R.L.-S., O.T.-V., and C.M.F.-O. Data curation: N.I.R.-A. Formal analysis: S.S.-M., C.A.O.-S., R.L.-S., O.T.-V., and C.M.F.-O. Funding acquisition: T.U., M.W., and P.D.D.-A. Investigation: S.S.-M., T.U., and C.M.F.-O. Methodology: C.A.O.-S., and N.I.R.-A. Project administration: T.U., P.D.D.-A., and N.I.R.-A. Resources: M.W., and N.I.R.-A. Writing—original draft: S.S.M., and C.M.F.-O. Writing—review & editing: C.A.O.-S., E.M., T.U., M.W., E.C.-L., P.D.D.-A., R.L-S., and O.T.-V.

Funding: This study has been funded by the Garfield Weston Foundation, as part of the Global Tree Seed Bank Project, managed by the Royal Botanic Gardens, Kew.

Acknowledgments: We thank the Postdoctoral Fellowship Program at the UNAM, of the General Direction of Academic Personnel Affairs. This study has been funded by the Garfield Weston Foundation, as part of the Global Tree Seed Bank Project, managed by the Royal Botanic Gardens, Kew.

Conflicts of Interest: The authors declare that they have no conflict of interest.

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