

Application of the thermal time model for different *Typha domingensis* populations

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Abstract

Background

Typha domingensis Pers. is a perennial emergent plant that in comparison to other *Typha* species, produces more biomass. This species is used in Green Floating Filters (GFFs), one of the most innovative systems of wastewater treatment to bioremediate eutrophic waters and produce biomass as biofuel feedstocks. The establishment of a GFF depends on the seed germination and plant responses under conditions of a new habitat. This study analysed the germination response of four different populations of *T. domingensis* through a thermal time model to determine which population would have the fastest germination for establishment in a GFF.

Results

Seeds from the Badajoz (Ba), Cuenca (Cu), Madrid (Ma) and Seville (Se) populations were exposed to different thermal regimes (constant and alternating temperatures between 15 and 30°C) and photoperiods (0, 3, 5, 7, 10 and 20 days in darkness) to determine the parameters of the thermal model. Regardless of other parameters, no germination occurred in total darkness (20 days). The mean value of the base temperature (T_b) was $16.4 \pm 0.2^\circ\text{C}$ in all treatments. The optimum temperature (T_o) values in **Ma** and **Ba** were 25°C , and those in **Cu** and **Se** were 22.5°C . The germination response decreased when the temperature approached T_b and increased when it was close to T_o . In comparison to temperatures with a $\Delta T = 5^\circ\text{C}$ or 10°C , those with a $\Delta T = 15^\circ\text{C}$ or $\Delta T = 0^\circ\text{C}$ had the highest germination response and lowest thermal time ($\theta_T(50)$). The photoperiod had a relationship with $\theta_T(50)$, but it was not proportional. The populations also affected germination; **Cu** had the highest values of T_o and germination response but had a lower $\theta_T(50)$, which coincides with the lowest mean ambient temperatures.

Conclusion

According to these results, the germination response of *T. domingensis* under optimal conditions was high in all populations but was affected to a greater or lesser extent depending on thermal regimes, photoperiods, and population. The thermal time model allowed us to determine that in comparison to other populations, **Cu** is the best population for establishment in a GFF due to its high germination response under the conditions tested.

Background

Typha is a perennial monocotyledon plant genus that is widely distributed(1) mainly in wetlands, marshlands and other aquatic habitats. *Typha domingensis* Pers. (commonly known as "cattail") is a species of this genus with an annual growth cycle and is widely distributed around the world(1). It is a warm temperate and pantropical species(2). This species is also often found in the Iberian Peninsula and the Balearic Islands(3). The reproduction of this species occurs by vegetative spread (rhizomes) and seed(4,5). Seed production is very high due to a single female spadix that can produce more than 600,000 small single-seeded fruits(1). Although considered an invasive plant, cattail provides different raw materials (weaving) and serves as food for humans and livestock (rhizomes). In recent years, cattail has been used in wastewater treatments and industrial-site remediation due to its great capacity to remove particle matter, nutrients and metals from eutrophic waters(6–8). For wastewater treatment, this species has been used to form green filters that use different types of biological elements (plants and microorganisms). Among the numerous existing green-filter systems, the innovative systems specially designed for small urban agglomerations are called green floating filters (GFFs) (9). In GFFs, different *Typha* plant species have been used, but *T. domingensis* presents an advantage compared to other species; it has the capacity to produce more biomass in deeper water(10,11) and quickly form a floating and filtering plant mat that improves the purification of wastewater in a GFF(12). Different studies have demonstrated that managed cattail constructed wetlands could provide beneficial ecosystem services (6,7) and sustainable biomass for biofuel feedstocks(13,14) and bioproducts(15).

Seed germination is an important biological process in plants. The success or failure in introducing a population in a new local habitat is closely related to seed germination ability. The dynamics of this process are complex and influenced by genetic changes or/and phenotypic variability in the different plant populations(16,17). An example of this complexity is the dormancy mechanism. It is an internal condition of seeds that prevents germination under correct water, thermal and gaseous conditions(18,19). This mechanism is very scarce in seed crops but common in weed populations and associated with weed dispersibility(20). Dormancy can be ended by one or more environmental factors such as temperature, water potential, light, and soil pH. However, different dormancy depends on the different environmental factors experienced during seed development(19), and seeds can incorporate the effects of these factors over time(21).

In the case of cattail, germination studies have focused on avoiding its invasion and negative impacts on natural systems. Previous studies have demonstrated that environmental requirements such as temperature, light, depth of water, salinity, pH, and O_2 concentrate could influence the seed germination of different species of *Typha*(5,16,22–24). One of the main factors required for seed germination is temperature(25). This factor has the greatest effect on dormancy and germination rate in the case of seeds that do not exhibit dormancy (26), and many studies have

been implemented using constant temperature(17,27,28) or/and alternating temperatures(29,30) on seed germination. Light exposure is another environmental factor related to seed germination (25,31). Among the environmental requirements related to cattail seed germination, one of the main factors is humidity. Germination of cattail seeds only occurs in wet or flooded environments(5,32,33) at low soil water potentials < 1 MPa (34).

Genetic determinants also influence the germination of cattail seeds(35,36). Sometimes, the origin of populations determine the germination conditions of the seeds regardless of whether they are of the same species (24,37). Moreover, the factors that determine the germination of the mother plant (temperature, light, humidity, and others) must be taken into account(38). Knowledge of the germination thresholds of each population can help us predict possible behaviours of the seeds that allow the establishment of GFF in different places or determine the germination capacity in a new habitat and have the opportunity to control its expansion(39).

There are different types of tools for studies on seed germination. In recent years, population-based models have been widely used in germination studies. There are two types of models: empirical and mechanistic models. The first is used for a specific objective, but the results are more difficult to apply(40,41). However, mechanistic models have been applied to explain the most successful seed germination in recent years(29,42,43). These models, called thermal time(44) or hydrothermal time(45), develop functions to explain seed germination in different plant species.

In this study, the thermal time model will be used to predict the occurrence of germination in seeds of different populations of *T. domingensis*. This model has been used successfully to predict the occurrence of seed germination under non-water-limiting conditions, thus explaining approximately 80% of the variation in the cumulative percentile(46).

This type of model studies the effect of temperature on germination within the seed population using the following mathematical parameters: thermal time $\theta_T(g)$ (degree-day/degree-hour) as the percentile of germination (g), T ($^{\circ}\text{C}$) as the mean temperature of incubation, T_b ($^{\circ}\text{C}$) as the base temperature, T_o as the optimum temperature for germination and t_g as the time to germination for a specific germination percentile, according to the following model presented by Garcia-Huidrobo et al. (1982)

$$\theta_T(g) = (T_o - T_b) t_g \quad (1)$$

Another parameter defined in this model is the germination rate (GR_g), which is the inverse of the time to radicle emergence of a specific percentile of the population defined by the Eq. 1.

$$GR_g = \frac{T - T_b}{\theta_T(g)} = \frac{1}{t_g} \quad (2)$$

There is a linear regression line between GR_g and T when the temperature is between T_b and T_o . Under these circumstances, the slope of this linear regression is equal to the reciprocal of thermal time $\theta_T(g)$. If the change in $\theta_T(g)$ within a seed population is a log-normal distribution, then the relation between GR_g and $\theta_T(g)$ can be described using the probit function(46).

$$\text{prob}_g = \left(\frac{1}{\sigma_{\theta_T}} \right) * \log(T - T_b) t_g - \frac{\log(\theta_T(50))}{\sigma_{\theta_T}} \quad (3)$$

In this function, prob_g is the probit transformation of the cumulative germination percentile g , $\theta_T(50)$ is the thermal time to 50% germination, and σ_{θ_T} is the standard deviation of θ_T for individual seeds in the population(47). An alternative way to the use of probit transformation is logistic transformation; when the sample size is not very large. In this case, the midpoint of the logit regression (logit = 0) is the same as that obtained with probit transformation and the slope (α) is related to the standard deviation of the normal distribution (σ) as defined(48) as:

$$\sigma = \pi * (\beta * \sqrt{3})$$

and the $\log \theta_T(50)$ as:

$$\log \theta_T(50) = -\frac{\beta}{\alpha}$$

This work proposes a thermal model for different populations of *T. domingensis*, Badajoz (Ba), Cuenca (Cu), Madrid (Ma) and Seville (Se), that allows us to understand and justify their behaviour, and know which would be the best for establishing a GFF and its ability to expand as a weed under a similar scenario with warmer temperatures in the Mediterranean zone. Different thermal regimes (level and amplitude of temperatures) and photoperiods (different times in darkness) were used to determine the T_b , T_o and $\theta_T(g)$ of each population.

Results

Final germination responses in the different treatments

In Table 1, the germination responses achieved in each treatment are shown. To simplify Table 1, the germination responses to each set of temperatures within the same population and photoperiod were summarized and are shown as lower and upper germination responses for constant (C) and alternating (A) thermal regimes.

Table 1
Final germination percentage in *T.domingensis* seeds. Line 150, page 7.

Photoperiod		0 days		3 days		5 days		7 days		10 days	
Population	Thermal regimen	Lower	Upper	Lower	Upper	Lower	Upper	Lower	Upper	Lower	Upper
Ba	C	91 ± 1.9 (17.5)	99 ± 1.3 (25)	59 ± 3.1 (17.5)	99 ± 1.6 (30)	65 ± 3.8 (17.5)	94 ± 2.0 (22.5)	69 ± 5.1 (17.5)	92 ± 1.8 (25)	58 ± 5.3 (17.5)	79 ± 4.7 (22.5)
	A	60 ± 4.5 (15/20)	99 ± 4.1 (20/25)	53 ± 5.2 (15/20)	98 ± 1.7 (15/30)	53 ± 4.5 (15/20)	94 ± 2.6 (15/30)	53 ± 6.1 (15/20)	93 ± 4.4 (15/30)	49 ± 7.6 (15/20)	91 ± 4.1 (15/30)
Cu	C	92 ± 1.2 (17.5)	99 ± 1.7 (22.5)	87 ± 2.7 (17.5)	99 ± 1.1 (22.5)	81 ± 2.9 (17.5)	98 ± 1.3 (22.5)	74 ± 3.6 (17.5)	99 ± 1.8 (22.5)	67 ± 4.2 (17.5)	94 ± 3.9 (22.5)
	A	61 ± 5.5 (15/20)	99 ± 3.2 (15/25)	55 ± 6.9 (15/20)	97 ± 4.6 (20/30)	54 ± 7.7 (15/20)	98 ± 1.3 (15/30)	49 ± 6.2 (15/20)	95 ± 2.7 (20/25)	51 ± 7.1 (15/20)	94 ± 1.5 (15/30)
Ma	C	89 ± 2.2 (17.5)	99 ± 2.1 (25)	72 ± 2.7 (17.5)	98 ± 2.8 (30)	73 ± 3.3 (17.5)	96 ± 2.0 (25)	65 ± 4.5 (17.5)	97 ± 2.2 (30)	48 ± 6.4 (17.5)	86 ± 1.6 (25)
	A	67 ± 6.2 (15/20)	97 ± 3.1 (15/30)	51 ± 4.3 (15/20)	99 ± 2.1 (20/30)	48 ± 6.7 (15/20)	98 ± 3.6 (20/30)	49 ± 7.9 (15/20)	94 ± 3.4 (30)	49 ± 8.4 (15/20)	93 ± 3.4 (15/30)
Se	C	86 ± 3.8 (17.5)	99 ± 4.6 (22.5)	92 ± 5.8 (17.5)	97 ± 4.5 (22.5)	75 ± 5.5 (17.5)	92 ± 4.2 (22.5)	66 ± 6.5 (17.5)	91 ± 4.9 (30)	53 ± 8.2 (17.5)	83 ± 4.4 (22.5)
	A	58 ± 4.5 (15/20)	95 ± 3.0 (15/25)	52 ± 6.8 (15/20)	92 ± 4.3 (15/25)	53 ± 6.6 (15/20)	84 ± 5.44 (15/30)	54 ± 7.2 (15/20)	85 ± 5.2 (25/30)	50 ± 6.3 (15/20)	79 ± 4.9 (15/30)

Maximum and minimum values ± SD of final germination percentage achieved according to different populations, thermal regimes and photoperiods in cattail seeds. The temperature at which these percentages were reached is shown between parentheses on the bottom line.

The results of the multifactor analysis of variance carried out with the data mentioned above are shown in Table 2. There were significant differences among the populations, photoperiods and thermal regimes when each of these factors was analysed separately at $p < 0.05$; however, the interaction between the two factors (AxB, BxC, AxC) and among the three factors (AxBxC) was not significant (Table 2).

Table 2

Multifactor analysis of variance and multiple range tests for different populations, photoperiods and thermal regimes. Line 159 page 8

Multifactorial ANOVA			Multiple Ranges test								
Factors	Fd	F	A	n	GR %	B	n	GR %	C	n	GR%
A	3	22.66 ^{***}	Ba	60	82.2 ^b	0d	48	91.4 ^b	17.5_0	20	74.0 ^d
B	4	30.77 ^{***}	Cu	60	88.2 ^a	3d	48	87.6 ^a	17.5_5	20	54.0 ^e
C	5	51.45 ^{***}	Ma	60	85.9 ^a	5d	48	82.3 ^a	20.0_0	20	83.0 ^{bc}
AxB	12	0.08	Se	60	76.6 ^c	7d	48	79.9 ^c	20.0_10	20	82.0 ^{bc}
AxC	9	0.68				10d	48	75.1 ^d	22.5_0	20	92.0 ^a
BxC	12	0.73							22.5_5	20	89.0 ^{ab}
AxBxC	36	0.15							22.5_15	20	93.0 ^a
									25.0_0	20	92.0 ^a
									25.0_10	20	87.0 ^{abc}
									27.5_0	20	88.0 ^{abc}
									27.5_5	20	82.0 ^c
									30.0_0	20	88.0 ^{abc}
Significant codes: *** 0.001, ** 0.01, * 0.05											
Different letters represent statistically significant differences between treatment of each population according to LSD test ($p < 0,05$).											

No germination was obtained in photoperiods that equalled 20 d so the data from these treatments have not been included in the study. These results suggest that the dormancy of cattail seeds was not interrupted independently of thermal treatment or population. In other photoperiods, different germination responses were reached according to the influence of the factors studied (Table 1), and there was an inverse relationship between the number of dark days and the germination response within the same population and thermal regime (Table 2). This difference was observed between the 0 d versus 10 d photoperiods.

Regarding the origin of the seeds, there were no significant differences between Cu and Ma, but differences did exist among Ba, Se and the two populations mentioned above (Table 2). Cu and Ma had the highest values, while Se had the lowest germination responses.

Thermal Model

The differences in the thermal regimes depended on the mean temperature of each regime. In Figs. 1 and 2, the relationship between GR_{50} and the cattail seeds of distinct populations, thermal regimes and photoperiods are shown. The mean value of T_b was 16.4 ± 0.2 °C with a minimum of 16.1 °C and a maximum of 16.7 °C. This value explains why no germination occurred in the thermal treatments lower than 17.5 °C and the lowest values of the germination responses occurred in the thermal treatments closest to T_b (Table 2).

In Fig. 3, the relationship between GR_{50} and the mean temperatures of different populations with constant and alternating temperatures and photoperiods = 0 days are shown. In thermal regimes within constant temperatures (Fig. 2A), both Ma and Ba had a $T_o=25$ °C, while Cu and Se had a $T_o=22.5$ °C. In the regimes with alternating temperatures (Fig. 2B), only Ma had a $T_o=25$ °C, while the remaining populations had $T_o=22.5$ °C. The T_o was 22.5 °C, but a $\Delta T_o=2.5$ °C was found in the Ma population with constant and alternating temperatures and the Ba population at constant temperatures (Fig. 3).

The thermal regimes with mean temperatures and $\Delta T = 0$ °C close to T_b achieved the lowest germination responses of those in all the treatments, while the thermal regimes at temperatures close to T_o were the highest. The highest germination responses were observed in treatments with $\Delta T = 0$ °C. The germination responses in the thermal regimes with the same mean temperature but with $\Delta T = 5$ °C/10 °C were lower than $\Delta T = 0$ °C, while the germination in thermal regimes with $\Delta T = 15$ °C was much closer to the germination with $\Delta T = 0$ °C (Table 2).

The values of T_o with different photoperiods are the same as those at 0 d (Table 3). The highest values of GR_{50} (0.32) were reached within constant regimes close to T_o (22.5/25 °C) in all populations (Fig. 3A). In alternating regimes (Fig. 3B), these values are all approximately 0.23. The thermal treatments 15/30 °C and 20/25 °C showed different values of GR_{50} , although they had the same mean temperature; this difference could be related to the different ranges utilized in alternating temperatures (15 and 5 °C, respectively).

In Fig. 4, the relationship between accumulated germination and $\log(\theta T(50))$ in the different thermal regimes (C and A), populations and photoperiods 0 d, 5 d and 10 d are shown. The curves of the models within the same population were close, but not equal and slight differences were observed between different photoperiods and between thermal regimes with constant versus alternating temperatures. It seems that the curves of the regimes with alternating temperatures shift to the right when compared with those of constant temperatures. There are similar values of $\sigma\theta T$ in all treatments (Table 3) which means that final germination (50%) was reached in all treatments.

Table 3. Parameters of the thermal models for cattail seeds with constant (A) and alternating (B) temperatures.

A. Thermal regimes with constant temperatures

B. Thermal regimes with alternating temperatures

Code	Tb °C	Tm °C	log $\theta_T(50)$ (log°d)	$\sigma\theta T$ (log°d)	$\theta_T(50)$ (°d)	$\theta_T(50)$ (°h)	Code	Tb °C	Tm °C	log $\theta_T(50)$ (log°d)	$\sigma\theta T$ (log°d)	$\theta_T(50)$ (°d)	$\theta_T(50)$ (°h)
BaC0d	16 ± 0.3	25	2.72	0.5	15.33	368	BaC0d	16 ± 0.2	22.5	2.81	0.3	16.61	399
BaC3d	16 ± 0.3	25	2.81	0.5	16.61	399	BaC3d	16 ± 0.2	22.5	2.94	0.3	18.02	454
BaC5d	16 ± 0.3	25	2.87	0.5	17.64	423	BaC5d	16 ± 0.2	22.5	3.00	0.3	20.09	482
BaC7d	16 ± 0.3	25	2.96	0.5	19.21	461	BaC7d	16 ± 0.2	22.5	3.06	0.3	21.33	512
BaC10d	16 ± 0.3	25	3.06	0.5	21.27	510	BaC10d	16 ± 0.2	22.5	3.12	0.3	22.65	544
CuC0d	16 ± 0.2	22.5	2.41	0.4	11.13	267	CuC0d	16 ± 0.5	22.5	2.70	0.4	14.88	357
CuC3d	16 ± 0.2	22.5	2.50	0.4	12.18	292	CuC3d	16 ± 0.5	22.5	2.73	0.4	15.45	378
CuC5d	16 ± 0.2	22.5	2.63	0.4	13.87	333	CuC5d	16 ± 0.5	22.5	2.79	0.4	16.28	391
CuC7d	16 ± 0.2	22.5	2.71	0.4	15.03	361	CuC7d	16 ± 0.5	22.5	2.87	0.4	17.58	422
CuC10d	16 ± 0.2	22.5	2.84	0.4	17.11	411	CuC10d	16 ± 0.5	22.5	2.90	0.4	18.23	438
MaC0d	16 ± 0.5	25	2.57	0.5	13.06	314	MaC0d	16 ± 0.7	25	2.76	0.4	15.80	379
MaC3d	16 ± 0.5	25	2.70	0.5	14.92	358	MaC3d	16 ± 0.7	25	2.80	0.4	16.44	395
MaC5d	16 ± 0.5	25	2.80	0.5	16.44	395	MaC5d	16 ± 0.7	25	2.91	0.4	18.30	419
MaC7d	16 ± 0.5	25	2.90	0.5	18.17	436	MaC7d	16 ± 0.7	25	3.00	0.4	20.09	482
MaC10d	16 ± 0.5	25	3.01	0.5	20.29	487	MaC10d	16 ± 0.7	25	3.03	0.4	20.78	499
SeC0d	16 ± 0.1	22.5	2.75	0.4	15.70	377	SeC0d	16 ± 0.5	22.5	2.98	0.4	19.69	473
SeC3d	16 ± 0.1	22.5	2.80	0.4	16.44	395	SeC3d	16 ± 0.5	22.5	3.02	0.4	20.49	498
SeC5d	16 ± 0.1	22.5	2.89	0.4	17.99	432	SeC5d	16 ± 0.5	22.5	3.11	0.4	22.42	538

Tb = Base temperature, To = Optimum temperature; log $\theta_T(50)$ = log thermal time 50% germination in °d; $\sigma\theta T$ = standard deviation of the log thermal time distribution within the seed population; $\theta_T(50)$ = thermal time 50% germination in °d and °h, respectively.

Code	T _b °C	T _m °C	logθ _T (50) (log°d)	σθ _T (log°d)	θ _T (50) (°d)	θ _T (50) (°h)	Code	T _b °C	T _m °C	logθ _T (50) (log°d)	σθ _T (log°d)	θ _T (50) (°d)	θ _T (50) (°h)
SeC7d	16 ± 0.1	22.5	3.08	0.4	21.76	522	SeC7d	16 ± 0.5	22.5	3.21	0.4	24.78	595
SeC10d	16 ± 0.1	22.5	3.16	0.4	23.57	566	SeC10d	16 ± 0.5	22.5	3.24	0.4	25.53	613

T_b = Base temperature, T_o = Optimum temperature; logθ_T(50) = log thermal time 50% germination in °d; σθ_T = standard deviation of the log thermal time distribution within the seed population; θ_T(50) = thermal time 50% germination in °d and °h, respectively.

The treatments of the same population and photoperiod in regimes with constant temperatures show lower values of thermal time (Table 3) in comparison with regimes of alternating temperatures. The thermal time seemed to be influenced by the photoperiod treatments because when the number of days in which the seeds were kept in darkness increased, the thermal time also increased in all populations, levels, and amplitudes of temperatures. According to these results, there is a relationship between log(θ_T(50)) and the set of photoperiods (Table 4) characterized by an R² > 0.90. The σθ_T values obtained in the different treatments ranged from 0.3 to 0.5.

Table 4
Relationship between log(θ_T(50))
and photoperiods in treatments with
same population and amplitude of
temperature regime. Line 238 page
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Code	a	b	R ²
BaC	2.71	0.034	0.993
BaA	2.83	0.031	0.965
CuC	2.39	0.044	0.986
CuA	2.69	0.022	0.927
MaC	2.57	0.045	0.996
MaA	2.75	0.030	0.910
SeC	2.71	0.045	0.908
SeA	2.96	0.029	0.938
Log θ _T (50) = a + b* (photoperiod).			

There were also differences between θ_T(50) according to the populations (Table 3). The lowest θ_T(50) time (Table 3) corresponded to Cu, which coincided with the lowest yearly maximum, mean and minimum ambient temperatures (Table 5). Ma had θ_T(50) higher than of Cu with ambient temperatures slightly higher than those in Cu, while Se and Ba had the highest θ_T(g) (Table 3) and the highest ambient temperatures (Table 5).

Table 5

Codes, population name, geographic coordinates and temperatures of four locations where seeds were collected. Line 242 page 14

Code	Population	Latitude	Longitude	MAT _{o_{ax}} (°C)	MAT _o (°C)	MAT _{o_{in}} (°C)
Ba	Puebla de Alcocer, Badajoz	38°99'N	5°26'W	23,8	17,1	10,3
Cu	Olmedilla del campo, Cuenca	40°03'N	2°42'W	19,3	13,1	6,9
Ma	Ciudad Universitaria, Madrid	40°26'N	3°44'W	19,9	15,0	10,1
Se	Lantejuela, Seville	37°21'N	5°13'W	25,4	19,2	13,0

MAT_{o_{ax}} (yearly mean maximum temperature); MAT_o (yearly mean temperature) and MAT_{o_{in}} (yearly mean minimum temperature). Historical data obtained from The State Meteorological Agency of Spain (AEMET, 2019).

Discussion

The successful establishment of a plant species in a location is closely related to rapid germination. Different genotype and/or environmental factors can affect this process by increasing or decreasing it.

Light is a factor that does not prevent the germination of seeds if it acts as a signal(25) that could cause a change in the germination rate and final germination(31) and, therefore, in thermal time. This factor is necessary for the germination of many species(31), mainly in plants with small seeds(31,50), because large seeds can emerge from a much greater depth than light can penetrate(51). Light is one of the main determinants of the accumulation of a persistent soil seed bank of numerous weeds(52).

Exposure to light can be short, less than a minute, or long; short exposure is more common in small seed weeds than in large weeds(31). Light seems to influence the germination of different *Typha* species(5,53). This would explain why there was no germination in the treatments with photoperiods = 20 d (total darkness), even though cattail seeds absorbed water and began to swell; they did not break the coats for germination. In these circumstances, the dormancy of cattail seeds does not break. However, treatments with a photoperiod ≤ 10 d had a germination response greater than 50%, and this response increased when the number of days in darkness decreased (Table 1), with significant differences among different photoperiods (Table 2). These results seem to indicate that light is necessary for germination to occur in cattail seeds and that the longer the light period of the seeds is, the greater the germination response.

Treatments of the same population had an increase in θ_T (50) as the number of days in darkness increased. It seems that there was a relationship between θ_T (50) and photoperiod (Table 4). Initially, a linear increase in thermal time was expected as the number of days in darkness increased. Indeed, there was an increase, but was not proportional; for example, in the case of the population of Cu with constant temperatures, θ_T (50) at 0 d was 267 °h, and the value corresponding to 10 d is 411 °h, with a 10 day light period. This means a 50% increase in thermal time, not a 100% increase as expected. This modification would indicate that *T. domingensis* seeds accumulate hours of temperature and that when receiving light, the dormancy is broken, and the germination response occurs more quickly than expected. Dormancy broken in the presence of light has been studied(31) and is common in small seeds as cattails.

Water depth is another factor that seems to be related to the amount of light and the ease of germination of cattail seeds. Some authors have stated that flooded areas increase the germination of *Typha* species, and this increase in germination has a direct relation with depth(17,54). This seems to be caused by the decrease in the level of oxygen, not by the lower intensity of the light in these situations(33). However, there are other studies that show no relation between the increase in germination and depth(34,55). Some authors have established the limit of germination in *Typha* species in clear water deeper than 40 cm(2) or in sediment deeper than 1 cm(56). There is an extreme case where cattail seeds germinated under 80 cm water (survived 8 weeks)(57). Depth was not a factor in this study, but in our own experience, germination in cattail seeds is greater and faster when seeds are located on a saturated substrate than on a flooded substrate, although the depth used was small (< 0.4 cm). This seems to indicate a relationship between light and depth, but this relationship needs to be further examined.

The germination response in plants of distinct origins could be different(58). Differences related to the origin of a population are frequent in numerous species of plants, whether crops(59) or weeds(27,60). Successfully colonizing a new location is related to the greater adaptive capacity of these populations than other populations to harsher environmental conditions(61), allowing these populations to have greater flexibility and adaptability to different locations or future climate change scenarios(17).

The ambient temperatures of the different populations used (Fig. 5) show that the northern populations (Cu and Ma) have similar values but lower values than the southern populations (Ba and Se) (Table 5). The results of this study showed that in comparison to southern populations,

northern populations have a lower thermal time, and a higher germination response (Tables 2 and 3) despite similar temperatures and photoperiods.

These differences among populations are consistent with the results of other studies carried out with *Typha latifolia* L. in fifteen European populations(17) or USA populations(62); in both studies, in comparison to northern populations, southern populations germinated at a lower temperature. However, in our study, the opposite scenario occurred. Before providing conclusions, some points of these studies must be clarified. For example, in comparison to *T. latifolia*, *T. domingensis* is a species more adapted to warmer areas. In the European study, only two Mediterranean populations were used, and both populations germinated more rapidly than northern populations; the distances among the origins of the populations were greater than those in our study. Other authors mention that other factors, such as temperature or nutrient supply(63), seem to be more important than the origin of the seeds in the case of neighbouring populations(17).

In this study, the estimated mean T_b was 16.4 and no differences greater than 0.6 °C were observed regardless of origin, photoperiod, level or amplitude of temperatures. We could have considered that T_b was constant; however, other studies with crops(46) or weeds(64) estimated different T_b values for the different amplitudes of temperatures. There were significant differences in the germination responses both in terms of the level and amplitude of temperatures (Table 2). In comparison to treatments with other mean temperature, treatments with mean temperatures close to T_b achieved a lower germination response in all treatments (Table 2). No data were found for the calculated T_b for *Typha* species, but the estimated values of T_b for cattail seeds in this study were very similar to those obtained in other studies with summer weeds(29,65). Steinmaus (2000) established a relation between the slope of the line used to estimate T_b and germination rate; this rate will be greater with a higher slope. In our study, higher slopes occurred in Cu in thermal regimes with both constant and alternating temperatures and coincided with the lower θ_T (50) of all populations studied (Figs. 1 and 2).

Differences in T_o were obtained in the results of the multifactor analysis, mainly between the northern (Cu and Ma) and southern populations (Ba and Se) (Table 4). This difference in T_o is common with the results of other studies with different populations of weeds or with *T. latifolia* (17,22,23). The T_o for the Swedish populations of *T. latifolia* was approximately 20 °C(23) or 10–30 °C with alternating temperatures in Italian populations(22). Australian populations of the *Typha* genus germinate readily at high temperatures and decline when the mean temperature is lower than 20 °C (66).

Table 6 shows the results of different studies on the seed germination of *T. latifolia* and *T. domingensis*. There are few studies about the seed germination of *T. domingensis*. Lorenzen et al. (2000) stated that a T_o of 30 °C and 25/10 °C occurred in southeastern American populations of *T. domingensis* at constant and alternating temperatures, respectively. These T_o values are distinct from those obtained in our study (22.5–25 °C), but there are other studies with T_o values very similar to those obtained in this work (Table 6). These results showed different T_o values according to origins that were closely related to climate conditions at each location(17). Populations determine the conditions of germination, such as the temperature of the mother plants(38,67), regardless of whether the seeds were of the same species(24,37).

Table 6
Optimal temperature in *T. domingensis* and *T. latifolia* in different populations from various studies. Line 343 page 18

Plant species	Reference	C	A	Seed location
<i>Typha domingensis</i>	This study	22.5; 25 °C		Spain
	Lorenzen et al. (2000)	30 °C	25/10 °C	Florida, U.S.
	Royal Botanic Gardens (2002)	20 °C		Wakehurst, England
<i>Typha latifolia</i>	Sifton H.B (1959)	30 °C	20/30 °C	Ontario, Canada
	Bonnewell, V. et al (1983)	35 °C		Minnesota, U.S.
	Lombardi, T et al. (1997)		20/30 °C	Pisa, Italy
	Ekstam and Forseby (1999)	20 °C		Linköping, Sweden
	Heinz, S (2011)	25 °C	10/25 °C	Germany
	Meng, H. et al. (2016)		25/15 °C	Northeast of China.
C: constant temperature. A: alternating temperature				

In the *Typha* genus, temperature and amplitude were shown to be factors related to germination (23). The favourable effect of alternating temperatures on the germination response is well known in different weeds(22) because the effect enables a seed to understand when it is

buried and to prevent germination. In nature, seeds of the cattail are usually submerged. In this situation, fluctuations in the ambient temperature are rare; therefore, an increase in this fluctuation could indicate that seeds have reached land and germination could be increased. In this study, both thermal factors (level of and fluctuation in temperatures) influenced the final germination of cattail seeds. In the treatments within the same population and photoperiod, there was a greater germination response as the temperature approached T_o from values close to T_b , causing the existence of significant differences depending on the temperature level (Tables 1 and 2). An increase in the germination response is obtained with higher temperatures until T_o ; above this value germination begins to decrease. The same results occur in other studies with *Typha*(17,22,23,33) and weeds(27,29).

The use of different amplitudes of temperature in weeds is related to the loss of dormancy in weeds(29,69) or crops such as lentil(30). In the case of cattail seeds, the loss of dormancy is related to changes in germination responses. Treatments with $\Delta T=0^\circ\text{C}$ and 15°C had a higher germination response than those with $\Delta T=5^\circ\text{C}$ and 10°C (Table 1), so it seems that these last two amplitudes of temperature negatively affect germination. However, in studies with *T. latifolia*, the germination response in treatments with $\Delta T=0^\circ\text{C}$ had a lower germination response than that with $\Delta T=10^\circ\text{C}$ (17). On the other hand, $\theta_T(50)$ corresponds to treatments of the same population, and $\Delta T=0^\circ\text{C}$ is lower than treatments with $\Delta T \geq 0^\circ\text{C}$ (Figure 4), in contrast to *Solanum physalifolium*(29) whose thermal time is considerably reduced in an alternating regime (Table 3). These data are consistent with the germination rate (Figure 3) in which treatments with alternating temperatures reach lower values than those corresponding to constant temperatures. According to these results, the best season to germinate *T.domingensis* would be spring or autumn because these seasons have a regimen temperature of approximately $\Delta T=15^\circ\text{C}$ under natural conditions.

The thermal time value (Table 3) was substantially lower than that of other weeds, such as different species of *Solanum*(20,22) or tropical species such as *Pennisetum typhoides*(44,70). This indicates a rapid germination response compared with those of other plant species. There were also differences between populations, with **Cu** being the one with the lowest thermal time, both in $\Delta T=0$ and $\Delta T>0$ treatments. Although **Cu** and **Ma** obtained similar germination values (Table 2), $\theta_T(50)$ was the highest in **Ma**.

Therefore, **Cu** seems to be the population that presented the most vigour during this process because this population had the fastest germination under the conditions tested. The final germination percentages were very similar in all populations. It would be necessary to carry out new tests to determine whether the development in other stages of plant growth would also be fast in this population.

In comparison to other species of the genus, such as *T. angustifolia*, *T. domingensis* is a plant species more adapted to warm temperatures. In Spain, it has been observed that *T. domingensis* has been colonizing places where *T. angustifolia* once stood (3). If this capacity occurs with an increase in temperatures due to climate change, then it is possible to consider that *T. domingensis* increases its expansion to the detriment of other *Typha* species such as *T. angustifolia*.

Conclusions

Although there are differences among the different populations, the T_b was the same in the four populations. On the other hand, T_o was also the same except for that of **Ma**, for which T_o was higher.

The thermal time model for the different populations of *T. domingensis* allows an understanding of the germination response of each population established in the GFF. The germination response of *T. domingensis* was affected by thermal regimes, photoperiods, and populations. These factors could determine the success of seed germination for *T. domingensis* in a new habitat.

Among the different populations of *T. domingensis*, the best population for use in the GFF system is one that can tolerate a vast range of temperatures of a new local habitat. In this study, **Cu** had the highest germination rates and the highest germination percentage; therefore, this population could be applied in a GFF system to produce bioethanol. If growth chambers are used to proceed with the germination of *T. domingensis* seeds, then the most appropriate temperature treatment will be a constant temperature of 22.5°C . Under natural conditions, the best time for seed germination occurs when there is a thermal period of approximately 15°C , which only occurs in the springtime.

Methods

Plant material

The plant material used for this study was obtained and subsequently identified by experts of the Botany Unit of the Department of Agrarian Production (UPM). The Botanical key used was: Flora Iberica, Vol. XVIII, Gen. *Typha*(3). *T. domingensis* is a species widely distributed throughout Spain. For this reason, no specimens were taken to be included in any Herbarium. According the International Union for Conservation of Nature and Natural Resources (IUCN) Red List Categories, *T. domingensis* does not qualify for critically endangered, endangered, vulnerable or near threatened(72) so permissions were no necessary to collect samples.

The seed material for this study came from natural *T. domingensis* stand growth at four different locations in Spain (Fig. 5). Mature spadices were collected from Puebla de Alcocer (Ba); Olmedilla del Campo (Cu) and; Lantejuela (Se). The plants of these populations were located in naturally flooded areas (ponds, lagoons, and marshes) in late summer or early autumn and this study is titled as Ba, Cu and Se for plant populations from Badajoz, Cuenca and Seville (Table 5). Ma location was the fourth population. The seeds of this population were obtained from macrophyte nursery in the experimental fields of GA, Madrid, whose initial source was the Manzanares River, which is very close to these facilities.

According to the classification of Köppen-Geiger, the four locations are classified as having temperate climates with dry and hot summers. The geographic coordinates and temperatures of the different locations are shown in Table 5(49).

In the laboratory, the seeds were removed from the female spadices by agitating the fruits in water. Only seeds settling to the bottom of the container were selected as viable seeds for the germination test. Then, the selected seeds were dried on filter paper and stored in a refrigerator (5 °C) until they were used in the germination test. Previous experiments had been carried out to verify that most of the seeds were viable. Shortly before the experiment, the seeds were treated with 1% sodium hypochlorite to prevent infection during the assay(73), washed with sterile distilled water to eliminate any residue and dried rapidly at room temperature.

Germination Tests

Germination tests were carried out in three identical growth chambers. Different photoperiods and thermal regimes on four seed cattail populations (Ba, Cu, Ma, Se) were studied as factors that could alter the final germination and the result of the germination model. The relationship among thermal time, temperature and darkness for the cattail seeds was studied. For this reason, different photoperiods of 0, 3, 5, 7 10 and 20 d in darkness (24 h) before the normal cycle (12 h light/dark) were included in this study (Table 7). The longest number of days was the same (20 days) for the seeds, so the number of days with 12 h light/dark cycles was reduced successively. In the treatment 20 d, the seeds were incubated in total darkness for the entire time.

Table 7
Characteristics of the photoperiod regimes. Line 442 page 22

Photoperiod	Titled	Description
0 + 20	0d	20 days 12 h/light and 12 h darkness
3 + 17	3d	3 days darkness and 17 days 12 h light/12 h darkness
5 + 15	5d	5 days darkness and 15 days 12 h light/12 h darkness
7 + 13	7d	7 days darkness and 13 days 12 h light/12 h darkness
10 + 10 20 + 0	10d 20d	10 days darkness and 10 days 12 h light/12 h darkness 20 days 24 h darkness

Different thermal regimes were included in this study. These regimes include different levels of constant or alternating temperatures as explained below. The constant temperatures ($\Delta T = 0$ °C) used were: 17.5, 20, 22.5, 25, 27.5 and 30 °C; the alternating temperatures ($\Delta T > 5$ °C) used were: 15/20, 15/25, 15/30, 20/25, 20/30, and 25/30 °C. In the alternating regimes, higher temperatures coincide with light periods and lower temperatures with the dark period of each photoperiod regime used. The mean value of both temperatures was used to calculate the model. No temperatures greater than 30 °C were used because *T. domingensis* is a plant species whose germination season coincides with middle spring, so it would be very odd if mean temperature above 30°C was reached at that time in the study area.

The treatment name was composed of the name of the population, mean temperature value, letter of the temperature regime C/A with a number that indicated the difference in the temperature between the dark and light period (0, 5, 10 or 15 °C) and photoperiod (Table 7), for example Ba25C5d and Ba25A103d.

The experimental design was completely randomized. A total of 240 treatments were carried out and three replicates of 33 seeds each were used for each treatment. The germination test was conducted in a filter paper-lined Petri dish, filled with 15 ml of distilled water. To prevent evaporation losses, the edges of the Petri dishes were closed using laboratory film. HOBO U12 (Onset Computer Corporation, Pocasset, MA, USA) data loggers were used to monitor the temperature inside the growth chambers. Data from the chamber were accepted if the temperature registered showed a difference of less than ± 0.5 °C. All treatments were set up at 9:00 hours. Germinated seeds were counted daily for 20 days. A seed was considered to have germinated when the coleoptile broke the pericarp(22).

Data analysis for the thermal time model

Data from the different temperature regimes were normalized following the concept of thermal time basis (Covell et al., 1986) where $\theta_T(50)$ is the mean thermal time to 50% germination used for the log thermal time distribution that was estimated from the equation:

$$\theta T_{(50)} = \frac{(T_m - T_b)}{GR_{50}}$$

The different variables to solve this equation were obtained as follows:

The Eq. $(1 \cdot t_{50}^{-1})$ was used to calculate GR_{50} for the different treatments. In each treatment, the results of GR_{50} were used to calculate a linear regression whose x-intercept represented the estimated value of $T_b(46,64)$. The T_o was obtained from the relationship between GR_{50} and the mean temperatures of each thermal regime (C or A) with the same type of photoperiod where T_o was the point on the x-axis that coincided with the maximum GR_{50} of the above relationship. The estimated $\theta T_{(50)}$ was used to obtain the σ of the log thermal time in the different treatments, and using the logit model(29), the median germination time was estimated using the values to logit = 0 as was mentioned above. Only $GR\%$ values less than 95% from T_b to T_o were included in the logit regression(28).

The multifactor analysis of variance with final germination response as a percentage was carried out with the software package Statgraphics Centurion XVI (Starpoint Technologies ©, 2011) to determine the relationships among origin, thermal conditions and photoperiod treatments of cattail seeds. Germination responses were transformed to meet the assumption of the ANOVA. In this case, the transformation used was arcsine ($\sqrt{\text{final germination \%}}$). A multiple range test was also performed to determine which variables were significantly different from the others. The method to make the comparisons was LSD (Least Significance Difference). Statistical differences were defined as $p < 0.05$.

Abbreviations

A
Alternating
ANOVA
Analysis of variance
Ba
Badajoz
C
Constant
Cu
Cuenca
GA
Agroenergy Group
GFF
Green floating filter
IUCN
International Union for Conservation of Nature and Natural Resources
LSD
Least Significance Difference
Ma
Madrid
Se
Seville
USA
United States of America

Declarations

Availability of data and materials: All data generated or analyzed and its supplementary information files during this study are included in this published article.

Ethics approval and consent to participate: Not applicable.

Consent for publication: Not applicable

Availability of data and materials: All data generated or analyzed and its supplementary information files during this study are included in this published article.

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Authors' contributions: MC performed and analyzed the seed germination test. PLA interpreted and proceeded with the data analyzed. MCM and MTC review and improved the thermal time model. MC and PLA conceived the study, planned experiments, and draft the manuscript. All authors read and approved the final manuscript.

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Figures

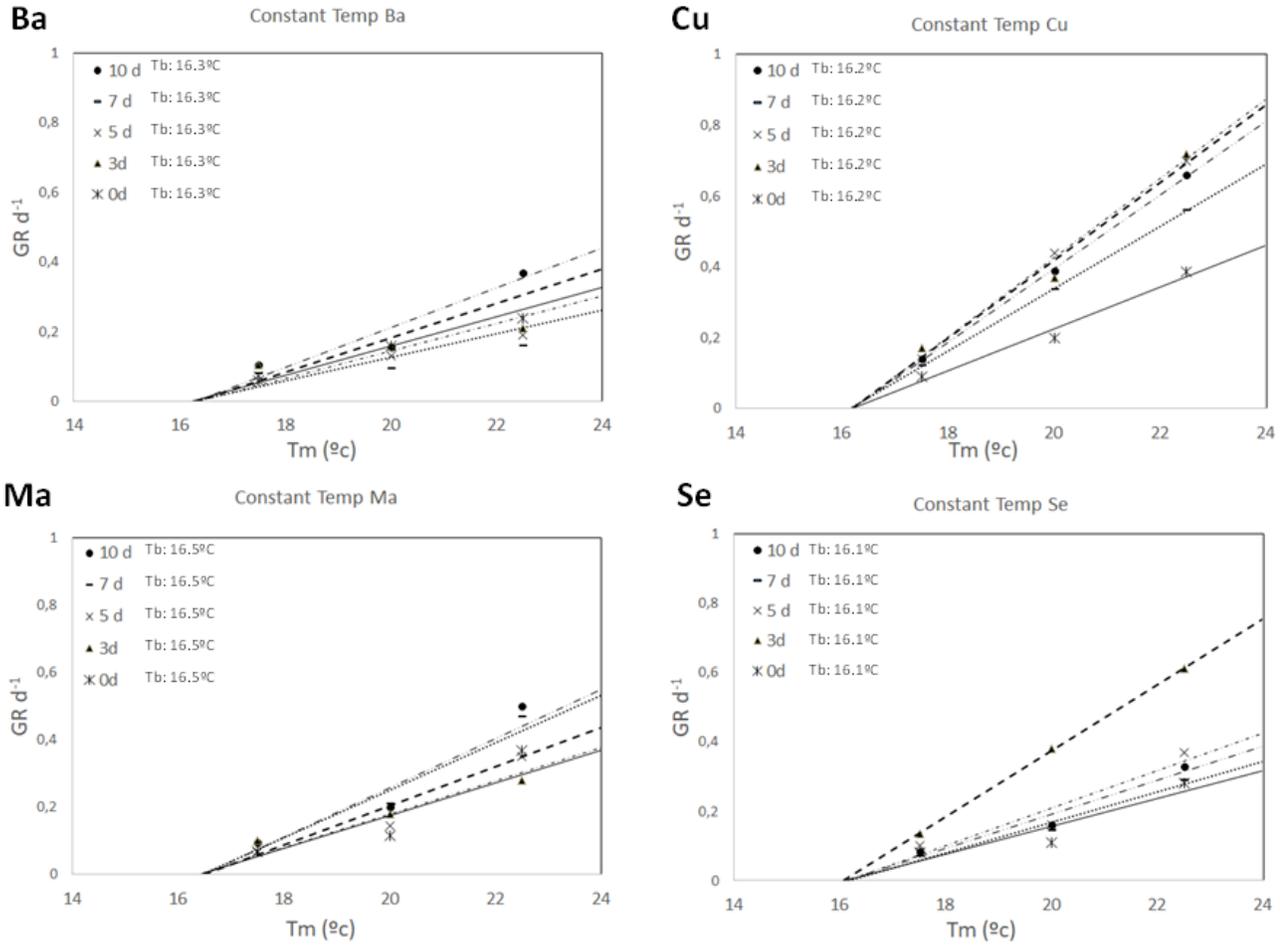


Figure 1

Relationship between GR(50) and Tm of cattail seeds from different populations with $\Delta T=0^{\circ}\text{C}$ and different photoperiods. Line 184, page 9.

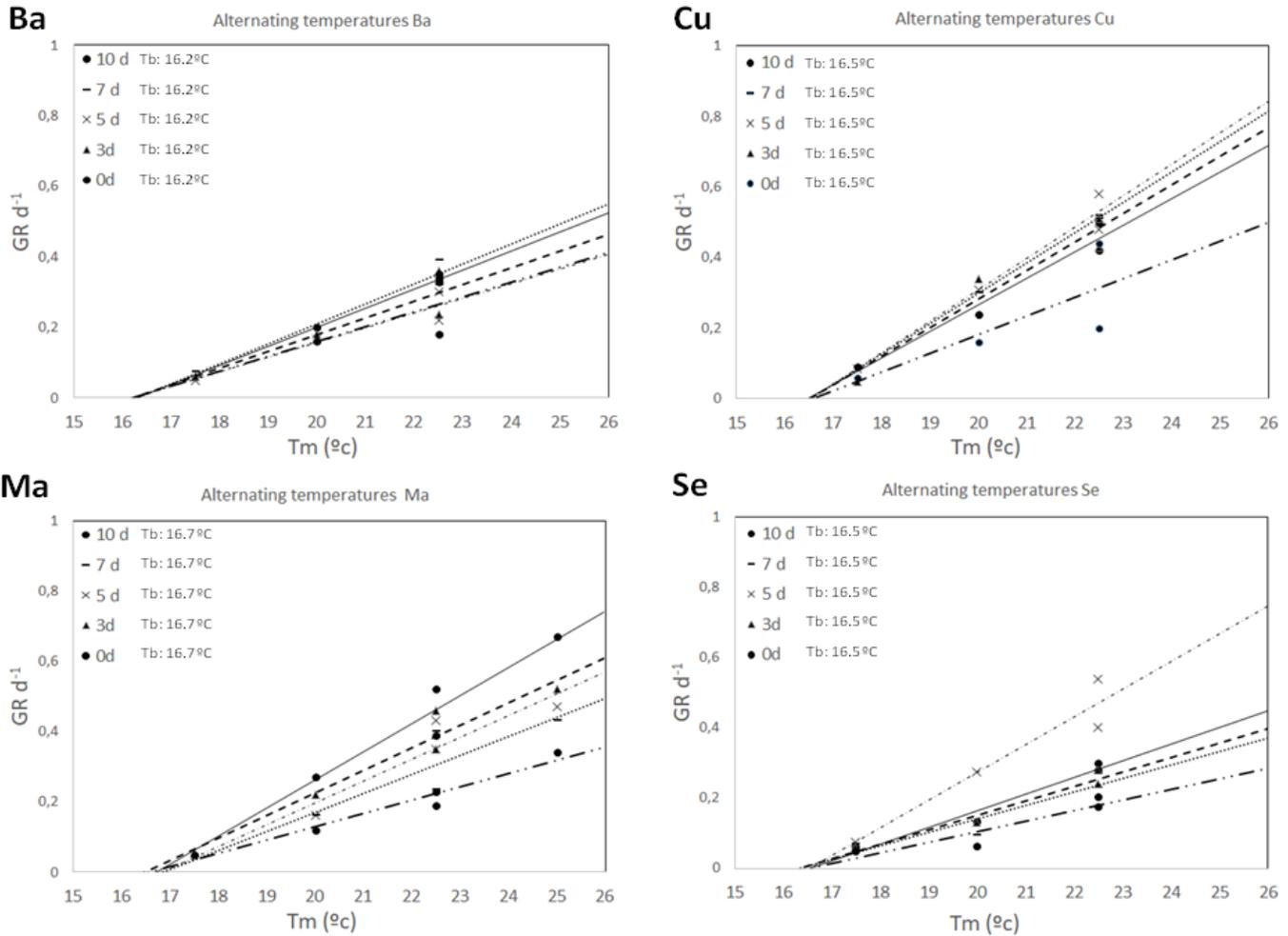


Figure 2

Relationship between GR(50) and Tm of cattail seeds from different populations with $\Delta T \geq 0^\circ\text{C}$ and different photoperiods. Line 186 page 10

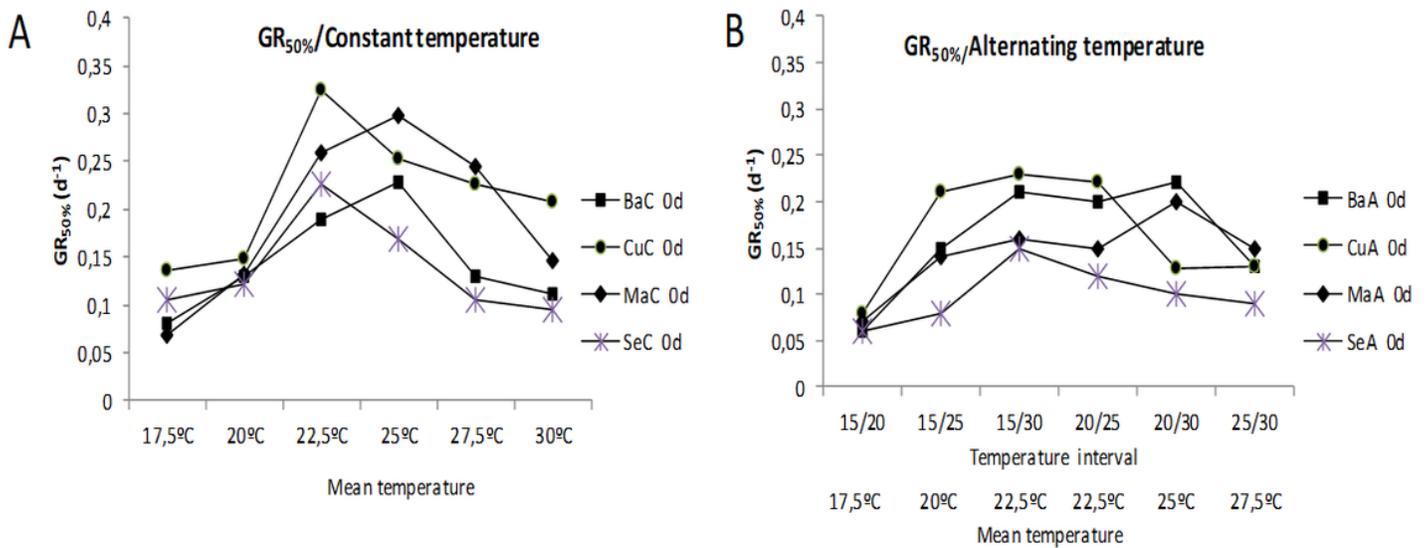


Figure 3

Relationship between GR(50) and mean temperatures in treatments within constant and alternating temperatures and photoperiod=0d. Line 203 page 11

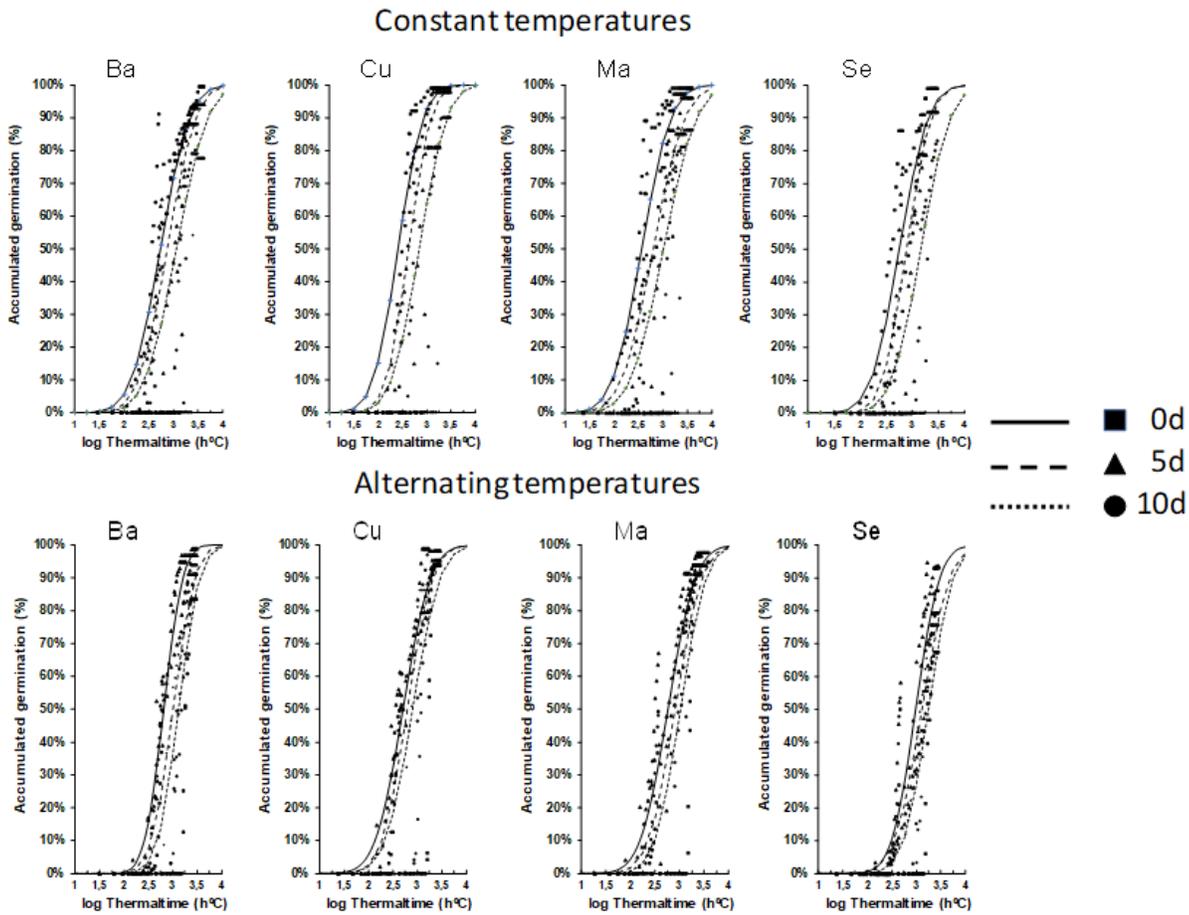


Figure 4

Relationship between accumulated germination and $\log(\Sigma T(g))$ in different populations with temperatures and photoperiods. Photoperiods: 0d, 5d and 10d. Temperatures: (C) constant and (A) alternating. Line 223 page 13

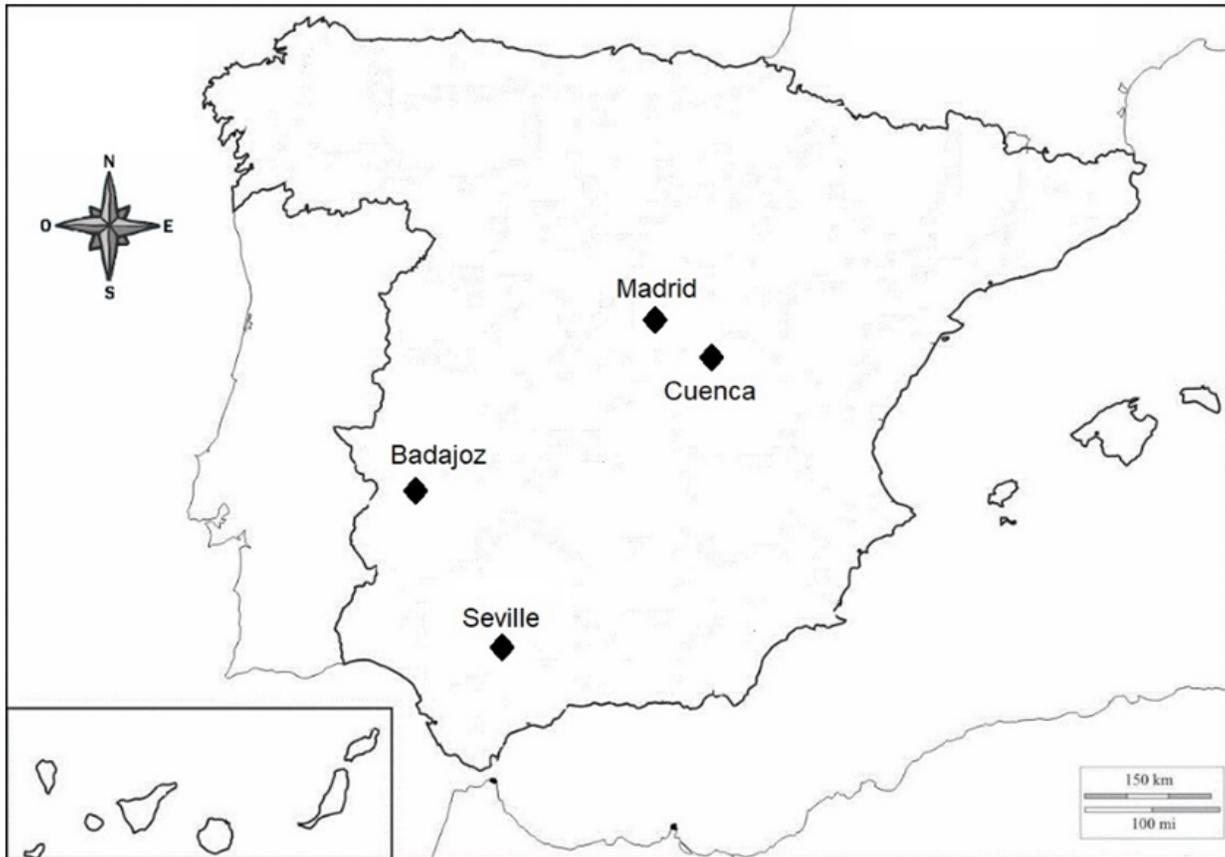


Figure 5

Origin of the populations of *T. domingensis* used in this work. Source: self-made. Puebla de Alcocer, Badajoz (Ba); Olmedilla del Campo, Cuenca (Cu); Lantejuela, Seville (Se), and the macrophytes nursery of GA, Madrid (Ma). Line 310 page 17.

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