

Comparison of different modeling approaches to estimate cardinal temperatures for germination of *Persicaria lapathifolia*, *Polygonum aviculare* and *Solanum nigrum*

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Citation: Loddo D., Carlesi S., Nikolic N., Masin R. (2025): Comparison of different modelling approaches to estimate cardinal temperatures for germination of *Persicaria lapathifolia*, *Polygonum aviculare* and *Solanum nigrum*. Plant Protect. Sci., 61: 378–386.

Abstract: Emergence predictive models can facilitate weed management, but estimating cardinal temperatures for germination of target species is necessary. Germination tests at a range of alternating temperatures from 12.5/2.5 °C to 35/25 °C were conducted to estimate cardinal temperatures of *Persicaria lapathifolia* (L.) Delarbre, *Polygonum aviculare* L. and *Solanum nigrum* L. Two statistical methodologies were tested: the Thermal time-to-event model (TTEM) and the Threshold limit model (TL). Germination of *P. aviculare* was maximum at low-mid temperatures, where its optimal range probably lies, and decreased at high temperatures. No differences were observed between the base (T_b) values estimated for this species with the two models (TTEM 3.5 °C, TL 4.1 °C), while a significantly higher ceiling (T_c) value was determined with TTEM (TTEM 41.5 °C, TL 33.6 °C). The Germination of *P. lapathifolia* and *S. nigrum* increased monotonically with the rise in temperature, indicating that their optimal temperature lies above the highest tested temperature. TTEM could not be applied to these species since it requires data from the supra-optimal thermal range. TL models could instead estimate T_b values (9.4 °C and 15.4 °C for *P. lapathifolia* and *S. nigrum*), while the lack of data in the supra-optimal thermal range impeded the estimation of T_c .

Keywords: emergence model; weed management; Thermal time-to-event model; Threshold limit model

To complete their life cycle, annual weeds need to concentrate germination flushes in the most favourable moments, defined by the seasonal fluctuations of environmental factors, including light, soil temperature and humidity, oxygen and nutrients (Benech-Arnold et al. 2000). Predicting the dynamic of weed germination and emergence can improve the timing for control operations or surveys. Temperature and water availability are key factors driv-

ing seed germination, and Gummerson (1986) proposed the concept of hydrothermal time. According to this concept, the germination dynamic is related to the difference between the temperature and water potential to which seeds are exposed and specific thresholds for germination. These thresholds are the cardinal temperatures, such as the base (T_b), the ceiling (T_c), the optimum (T_o) temperature, and the base water potential (Ψ_b). Once these threshold

parameters are estimated, normally by doing germination tests at a range of different temperatures and water potentials, models can be created to describe germination and emergence across a range of environmental conditions (Masin et al. 2014; Sousa-Ortega et al. 2020). The "x-intercept" method has been adopted to estimate the T_b of weeds (Masin et al. 2010; Guillemín et al. 2013) and implies a two-step procedure: firstly, germination data are analysed with non-linear regressions to estimate germination rate (GR) of each replicate, calculated as the inverse of the median germination time (t_{50}). Then, T_b is estimated as the x-intercept of the linear regression of GR versus incubation temperature. However, doubts about this approach's statistical correctness have been raised due to non-normality, autocorrelations and data censoring commonly observed in germination tests (Onofri et al. 2010). Alternative methodologies, such as Thermal time-to-event models (TTEM) (Bürger et al. 2020) and Threshold limit models (TL) (Onofri 2023), have been proposed to estimate cardinal temperatures for germination. TTEM models have the advantage of modelling the entire germination time course while accounting for censored data, e.g. the seeds that remained ungerminated at the end of the experiment. This allows proper uncertainty quantification in estimating T_b and T_c but requires larger datasets spanning from sub-optimal to supra-optimal temperatures, where a decrease in GR is normally observed. TL models are based solely on GR that can be parameterised with less calculation effort but do not quantify uncertainty rigorously as TTEM models. They can estimate T_b from germination data collected in the sub-optimal thermal range but cannot estimate T_c without data from the supra-optimal range. Ultimately, both modelling approaches provide more robust T_b and T_c estimates (Onofri et al. 2018).

The three weed species included in the present study are *Polygonum aviculare* L. (prostrate knotweed, POLAVI) and *Persicaria lapathifolia* (L.). Delarbre (pale smartweed, POLLA) and *Solanum nigrum* L. (black nightshade, SOLNI) are important weeds of spring-sown crops. These weeds form persistent seed banks with seasonal dormancy cycling (Kruk & Benech-Arnold 1998; Araki & Washitani 2000; Taab & Andersson 2009). Previous studies estimated cardinal temperatures for French and Spanish populations of *S. nigrum* (Del Monte & Tarquis 1997; Guillemín et al. 2013), for an Argentinian population of *P. aviculare* (Batlla & Benech-Arnold 2003) and a French population

of *P. lapathifolia* (Guillemín et al. 2013); however, adopting these values to create predictive models for other populations can lead to inaccurate predictions since inter-population differences were observed for several species, such as *Chenopodium album* L. and *Echinochloa crus-galli* (L.) P. Beauv (Bürger et al. 2020). The present study aims to estimate cardinal temperatures for germination of Italian populations of *P. aviculare*, *P. lapathifolia* and *S. nigrum*. with two distinct methodologies: TTEM and TL models.

MATERIAL AND METHODS

Seed collection and storage. Seeds were collected in autumn from at least 50 plants per species at the experimental farm of the University of Padova (Legnaro, 45°21'04" N 11°57'02" E, 8 m ASL, Italy). Seeds were cleaned and left to dry at room temperature (20 °C) for 2 weeks; afterwards, seeds were buried in the soil in metal mesh bags from November to February to expose seeds to winter conditions and reduce their dormancy. At the end of February, bags were exhumed, and seeds were left at room temperature for 1 week before the start of germination tests.

Germination Test. Seeds were placed in Petri dishes on filter paper imbibed with 3 mL of deionised water and incubated in germination chambers at 10 sets of alternating temperatures (12.5/2.5 °C, 15/5 °C, 17.5/7.5 °C, 20/10 °C, 22.5/12.5 °C, 25/15 °C, 27.5/17.5 °C, 30/20 °C, 32.5/22.5 °C, and 35–25 °C) and a 12 h light/12 h dark photoperiod. The different germination experiments were carried out almost simultaneously; thus, the duration of seed storage before the start of the experiment was essentially the same across all treatments. Temperature alternation had the same rhythm as the light cycle, with the highest temperature corresponding with the light period. Low germination was observed in preliminary tests with constant temperatures, so alternating incubation temperatures were chosen to promote germination (Taab & Andersson 2009). Four replicates, i.e., 4 Petri dishes with 50 seeds each, were included for each treatment. Petri dishes were arranged according to a complete randomised design. germination was monitored daily until no further germination was observed for 3 weeks. The viability of non-germinated seeds was assessed with an imbibed seed-crush test (Bor-

za et al. 2007), and nonviable seeds were excluded from data analyses.

Statistical analysis. Germination data were first fitted to a log-logistic distribution function to study the germination dynamics using a TTEM model (Onofri et al. 2018), obtaining for each treatment estimates of these key parameters: upper limit of germination (P_{MAX}), the slope at the inflexion point (b), and median germination time (t_{50}). The minimum germination parameter was set to 0 by default. The analysis was performed by applying models from the *drcSeedGerm* package for R (Onofri et al. 2018). Coefficient significance was tested using robust standard errors (Zeileis 2006). Variance-covariance matrix ($P \leq 0.05$) was used to identify significant differences between parameter values estimated for the different incubation temperatures using the sandwich package (Zeileis 2006). Two different methodologies were tested to estimate cardinal temperatures, using the mean temperature to represent each set of alternating temperatures, e.g. 20 °C for the 25/15 °C set, as already done in previous studies, such as Masin et al. (2017).

The first methodology (Method 1) was the single-step TTEM proposed by Onofri et al. (2018). Based on the following set of equations (Equations 1–3), this method can be applied when the tested temperature range extends to the supra-optimal range.

$$P(t, T) = \frac{P_{MAX}(T)}{1 + \exp\left\{b \left[\log(t) - \log(t_{50}(T)) \right] \right\}} \quad (1)$$

$$P_{MAX}(T) = G \left[1 - \exp \left(- \frac{T_c - T}{\sigma T_c} \right) \right] \quad (2)$$

$$\frac{1}{[t_{50}(T)]} = GR_{50}(T) = \frac{T - T_b}{\theta T} \left[1 - \frac{T - T_b}{T_c - T_b} \right] \quad (3)$$

where: P – the cumulative germination at temperature T and at time t ; $P_{MAX}(T)$ – the maximum germination at temperature T ; $t_{50}(T)$ – the median germination time at temperature T ; G – the germinable fraction of seed population, accounting for the fact that it may not reach 1, which would correspond to 100% of total seeds, in the case of dormant seeds; $GR_{50}(T)$ – the Germination Rate calculated as $1/t_{50}(T)$; T_c – the ceiling temperature; σT_c – the variability of T_c within the seed lot; T_b – the base temperature; θT – the thermal-time parameter; b – the slope of the curve at the inflection point

The second methodology (Method 2) was a two-step process, with the first step based on fitting a log-logistic function, which allows the calculation of GR for 19 quantiles (5–95th percentile) for each incubation temperature. GR is then restricted to the percentile of the population generated, and different TL models are applied to the GR , calculated and then compared. The models that best fit the three studied species according to the residual sum of squares (RSS) are presented hereafter.

The first TL model used in this study (Equation 4) was proposed by Masin et al. (2017).

$$GR = \frac{\max(T, T_b) - T_b}{\theta T} \left\{ \frac{1 - \exp \left[k \left(\min[T, T_c] - T_c \right) \right]}{1 - \exp \left[k (T_b - T_c) \right]} \right\} \quad (4)$$

where: T_b – the base temperature; T_c – the ceiling temperature (for each percentile of the population considered); k – the switch-off parameter (low k values mean that the negative effect on GR of temperature above T_o is more relevant); θT – the thermal-time (in degree days) for each percentile of the population considered

The second TL model (Equation 5) proposed by Mesgaran et al. (2017) consists of a symmetric model around the optimal temperatures; however, this model can also be applied to data from the sub-optimal temperatures alone.

$$GR = \frac{\max[T, T_b] - T_b}{\theta T} \left[1 - k \left[\min(T, T_c) - T_b \right] \right] \quad (5)$$

where: T_b – the base temperature, T_c – the ceiling temperature, k – the switch-off parameter described for Equation 4; θT – the thermal-time (in degree days) calculated for the whole population

The third TL model (Equation 6) tested was proposed by Garcia-Huidobro et al. (1982) to describe GR at sub-optimal temperatures.

$$GR = \frac{\max[T, T_b] - T_b}{\theta T} \quad (6)$$

where: T_b – the base temperature; θT – the thermal time (in degree days) calculated for the whole population

For those species that did not reach the T_o within the range of temperatures tested, and consequently, data from the supra-optimal range were unavailable, the TTEM model was not applied, and only TL models for sub-optimal temperatures were tested.

Table 1. Regression parameters estimated from the three-parameter log-logistic model (Equation 1) for germination of *Persicaria lapathifolia*, *Polygonum aviculare* and *Solanum nigrum*

Temperature (°C)	<i>b</i>			<i>P</i> _{MAX}			<i>t</i> ₅₀		
<i>Persicaria lapathifolia</i>									
12.5/2.5	2.0 ± 0.22	***	a	39.6 ± 3.70	***	a	16.5 ± 1.81	***	a
15.0/5.0	2.9 ± 0.35	***	a	32.8 ± 3.47	***	a	9.7 ± 0.64	***	b
17.5/7.5	11.3 ± 1.21	***	b	84.8 ± 3.74	***	b	5.9 ± 0.10	***	c
20.0/10.0	10.1 ± 0.75	***	c	96.0 ± 1.39	***	c	3.3 ± 0.05	***	d
22.5/12.5	11.5 ± 1.09	***	c	94.0 ± 1.68	***	c	2.8 ± 0.04	***	e
25.0/15.0	7.2 ± 0.70	***	c	93.0 ± 1.80	***	c	1.9 ± 0.04	***	f
27.5/17.5	18.3 ± 27.26	NS	—	91.5 ± 1.97	***	bc	1.8 ± 0.21	***	fg
30.0/20.0	10.5 ± 1.63	***	c	95.0 ± 1.54	***	c	1.8 ± 0.04	***	f
32.5/22.5	22.8 ± 66.85	NS	—	93.0 ± 2.77	***	c	1.7 ± 0.84	***	abcdefg
35.0/25.0	8.4 ± 0.55	***	bc	95.3 ± 1.62	***	c	1.5 ± 0.04	***	g
<i>Polygonum aviculare</i>									
12.5/2.5	5.5 ± 0.64	***	b	31.6 ± 3.37	***	a	9.6 ± 0.38	***	a
15.0/5.0	4.8 ± 0.49	***	bc	36.2 ± 3.43	***	a	10.6 ± 0.45	***	a
17.5/7.5	8.0 ± 0.90	***	a	33.2 ± 3.47	***	a	6.6 ± 0.19	***	b
20.0/10.0	3.6 ± 0.47	***	cd	22.5 ± 2.95	***	b	5.3 ± 0.38	***	c
22.5/12.5	4.6 ± 0.47	***	bc	35.5 ± 3.38	***	a	4.6 ± 0.22	***	cd
25.0/15.0	2.5 ± 0.43	***	de	13.6 ± 2.43	***	c	3.8 ± 0.52	***	de
27.5/17.5	4.1 ± 0.86	***	bcd	10.7 ± 2.21	***	cd	2.9 ± 0.29	***	e
30.0/20.0	2.2 ± 0.40	***	e	12.7 ± 2.37	***	cd	4.8 ± 0.78	***	cd
32.5/22.5	2.6 ± 0.62	***	de	7.1 ± 1.82	***	d	3.4 ± 0.61	*	de
35.0/25.0	2.4 ± 0.53	***	de	8.1 ± 1.94	***	cd	5.2 ± 0.97	***	bcd
<i>Solanum nigrum</i>									
12.5/2.5	23.9 ± 13.62	NS	—	3.0 ± 1.21	*	a	17.5 ± 0.71	***	b
15.0/5.0	11.0 ± 3.52	*	abc	2.1 ± 1.06	*	a	87.4 ± 12.03	***	a
17.5/7.5	2.7 ± 0.87	**	bc	4.1 ± 1.44	**	a	18.9 ± 4.68	***	bc
20.0/10.0	3.8 ± 0.48	***	bc	22.5 ± 2.96	***	b	11.8 ± 0.82	***	c
22.5/12.5	3.3 ± 0.47	***	bc	20.5 ± 2.86	***	b	5.9 ± 0.48	***	d
25.0/15.0	7.8 ± 0.74	***	a	69.5 ± 3.26	***	c	3.8 ± 0.12	***	e
27.5/17.5	4.4 ± 0.36	***	b	66.5 ± 3.34	***	c	3.6 ± 0.14	***	e
30.0/20.0	8.4 ± 0.67	***	a	86.0 ± 2.45	***	d	3.2 ± 0.05	***	f
32.5/22.5	2.6 ± 0.18	***	c	81.1 ± 2.78	***	d	2.8 ± 0.15	***	fg
35.0/25.0	2.8 ± 0.19	***	c	92.5 ± 1.86	***	e	2.5 ± 0.12	***	f

b – the slope of the curve at the inflexion point; P_{MAX} – the maximum germination % at a given temperature; t_{50} – the median germination time expressed in days (with standard errors); the significance of the difference between the parameters from zero is reported; parameters followed by different letters are significantly different at $P \leq 0.05$ according to the variance-covariance matrix

RESULTS

Effect of temperature on germination. The three species showed different germination responses. Overall, *P. lapathifolia* reached the highest average germination %, whereas *P. aviculare* showed

the lowest ($83.60 \pm 3.45\%$ and $22.50 \pm 2.04\%$, respectively). *S. nigrum* achieved an intermediate level ($44.80 \pm 5.83\%$) (Figure 1). The three species also showed different responses to temperature increases. *Polygonum aviculare* achieved germination % around 35–40% at the lowest temperatures until 22.5/12.5 °C,

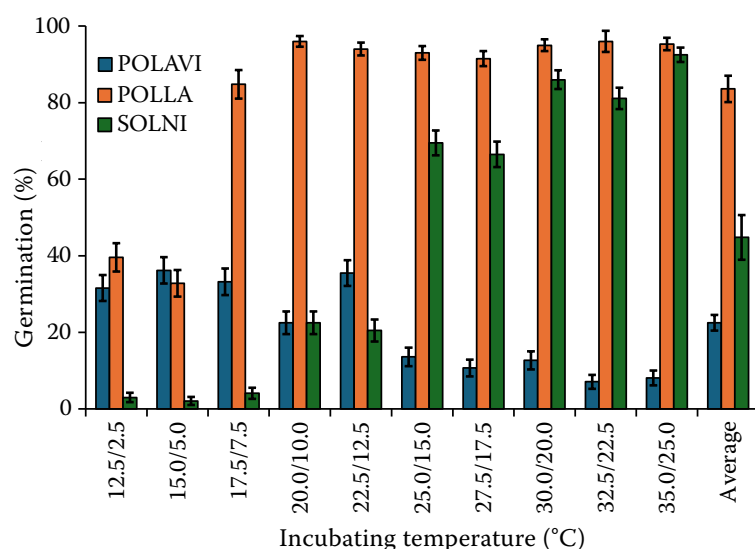


Figure 1. Mean germination % observed for *Polygonum aviculare* (POLAVI blue bar), *Persicaria lapathifolia* (POLLA red bar) and *Solanum nigrum* (SOLNI green bar) at the different incubation temperatures and on average.

Values are the mean of four replicates; bars represent standard error

then germination significantly decreased to a minimum of about 8% at the two highest temperatures. *Persicaria lapathifolia* instead achieved intermediate germination % at the two lowest temperatures; then, from 17.5/7.5 °C, germination significantly increased to above 90%. Finally, the germination % of *S. nigrum* was minimal at the lowest temperatures, then it slightly improved to about 20% at 20/10 °C and 22.5/12.5 °C, followed by a steep increase to above 90% at the highest temperatures. Both parameters (b and t_{50}) related to germination rate differed across the temperatures tested for each species (Table 1). For *P. lapathifolia* and *S. nigrum*, values for b and t_{50} decreased monotonically with temperature, suggesting that the highest temperature tested (35/25 °C) did not overcome their T_c . Given the low germination % obtained for *S. nigrum* at the lowest temperatures,

high standard errors were estimated for both b and t_{50} parameters. This does not enable a proper statistical comparison across all treatments. Values of b and t_{50} for *P. aviculare* reached their minimum at 25/15 °C and 27.5/17.5 °C; then, they progressively increased at the highest temperatures.

Estimation of cardinal temperatures. *Polygonum aviculare* data allowed the TTEM to be run, as depicted by Equations 2–3, that estimated a T_b of 3.50 ± 0.39 °C and a T_c of 41.40 ± 1.98 °C (Table 2). As highlighted by the σT_c value and the relative standard error, the standard deviation of T_c was higher than expected, showing a high data variability. Indeed, as shown by Figure 2, the model underestimates germination % at 17.5/7.5 °C and 22.5/12.5 °C and overestimates at 25/15 °C, 27.5/17.5 °C and 32.5/22.5 °C. Germination data of *P. aviculare* were

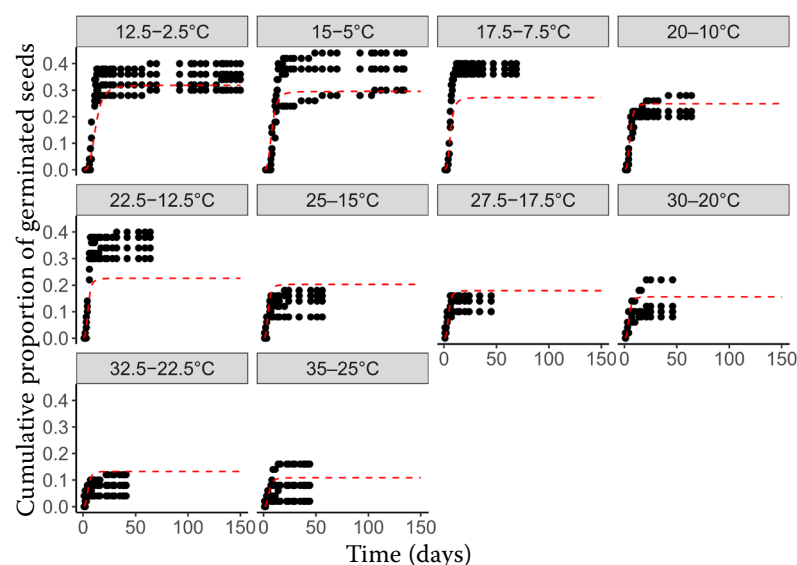


Figure 2. Effect of temperature on germination dynamics in *Polygonum aviculare*. A cumulative proportion of germinated seeds equal to 1 means that 100% germinated; black dots represent the observed data expressed as the mean of four replicates; the dashed red lines represent the TTEM model fits (Equations 1–3)

Table 2. Parameter estimates and standard errors for the TTEM (Equation 1), fitted to the *Polygonum aviculare* data

Parameter	Estimate	Standard error
G	7.9	8.32
T_c	41.4	1.98
σT_c	821.3	871.12
T_b	3.5	0.39
θT	42.2	2.54
b	3.6	0.16

G – the germinable fraction; T_c – the ceiling temperature; σT_c – the variability of T_c within the seed population; T_b – the base temperature; θT – the thermal-time parameter; b – the scale parameter for the log-logistic distribution

also studied with the TL models, and the best was represented by Equation 4. Model estimates are presented in Figure 3. In contrast, model parameters are reported in Table 3. TL model estimated a T_b of 4.10 ± 1.21 °C while T_c varied from 33.60 ± 1.19 °C and 31.40 ± 0.73 °C for $T_c:g$ 1% and $T_c:g$ 5% (T_c for the 1st and 5th percentile of seed population) to values slightly above 20 °C for $T_c:g$ 15%, $T_c:g$ 25% and $T_c:g$ 35% (T_c for the 15th, 25th and 35th percentile of seed population).

Germination data of *P. lapathifolia* did not enable the calculation of the TTEM due to the lack of information about the supra-optimal thermal range. For this reason, we could only calculate a TL model, described by Equation 5, based on the GR estimated on a log-logistic three-parameter model. Model parameters are reported in Table 4, while the results of model estimates are presented in Figure 4. The TL model calculated this species' T_b of 9.40 ± 0.42 °C.

For the same reason already explained for *P. lapathifolia*, the germination data of *S. nigrum* did not allow the creation of a TTEM model.

Table 3. Parameter estimates and standard errors for the TL model (Equation 4) fitted to the *Polygonum aviculare* data

Parameter	Estimated parameter	Standard error
k	0.15	0.06
T_b	4.10	1.21
$T_c:g$ 1%	33.60	1.19
$T_c:g$ 5%	31.40	0.73
$T_c:g$ 15%	20.60	0.79
$T_c:g$ 25%	20.60	1.33
$T_c:g$ 35%	22.60	4.38
$\theta T:g$ 1%	24.00	3.98
$\theta T:g$ 5%	40.90	8.56
$\theta T:g$ 15%	36.90	10.68
$\theta T:g$ 25%	62.20	22.98
$\theta T:g$ 35%	271.00	279.83

T_b – the base temperature, and k is the switch-off parameter; different estimated parameters for T_c (ceiling temperature) and θT (thermal-time in degree days) are reported for the 1st, 5th, 15th, 25th and 35th percentiles for the whole population

As a result, we could only calculate a TL model using GR estimated on a log-logistic three-parameter model. The best TL model to represent the effect of temperature on *S. nigrum* germination was based on Equation 6, with model parameters reported in Table 5. In contrast, the results of model estimates are presented in Figure 5. The TL model estimated a T_b of 15.40 ± 1.35 °C for this species.

DISCUSSION

Taking into account both germination % and GR observed across the different alternating temperatures,

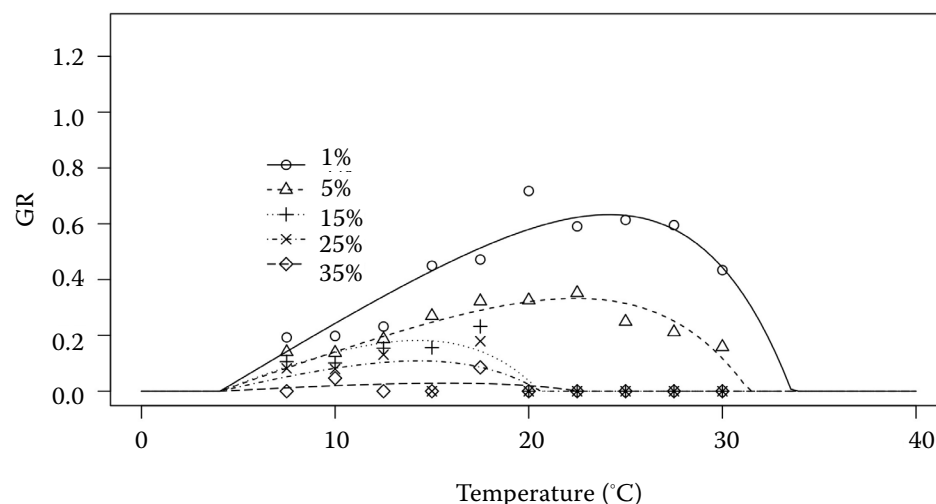


Figure 3. Effect of temperature on the Germination Rate (GR) for the 1st, 5th, 15th, 25th and 35th percentiles for the whole population of *Polygonum aviculare*

Symbols denote the calculated GR values, and lines show the TL model fit (Equation 4); each set of alternating temperatures is reported as its mean temperature

Table 4. Parameter estimates and standard errors for the TL model (Equation 5) fitted to the *Persicaria lapathifolia* data

Parameter	Estimated parameter	Standard error
k	0.02	0.003
T_b	9.40	0.420
θT	17.50	1.360

T_b – the base temperature; k – the switch-off parameter as described; θT – the thermal time (in degree-days) calculated for the whole population

T_o of the studied *P. aviculare* population is probably in the 22.5/12.5 °C range, as reported in previous studies (Kruk & Benech-Arnold 1998; Batlla & Benech-Arnold 2003). No significant difference was observed between the estimated values of T_b with the TTEM and the TL model. In contrast, a significantly higher value of T_c was determined with the TTEM model in comparison even with the highest T_c value estimated with TL (TTEM T_c 41.50 ± 1.98 °C, TL T_c :g 1% 33.6 ± 1.19 °C). Experimental observations seem

Table 5. Parameter estimates and standard errors for the TL model (Equation 6) fitted to the *Solanum nigrum* data

Parameter	Estimated parameter	Standard error
T_b	15.4	1.35
θT	35.6	5.14

T_b – the base temperature; θT – the thermal time (in degree days) calculated for the whole population

to agree with the lowest value of T_c given the limited germination (7–8%) achieved at the highest temperatures. Moreover, the T_c calculated with the TL model was closer to the value (30 °C) proposed by Batlla and Benech-Arnold (2003). The same authors reported a significantly lower T_b (0 °C); however, this can be derived from methodological differences and intra-specific variability cannot be excluded. The germination % and GR of the studied *P. lapathifolia* and *S. nigrum* populations increased monotonically with the incubation temperature. This suggests that their T_o probably lies above the highest temperature tested. Previous studies confirmed this behaviour for both species

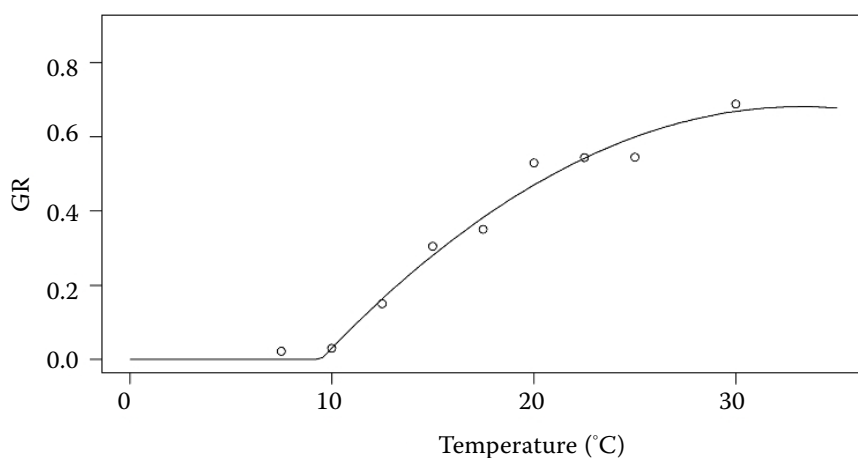


Figure 4. Effect of temperature on the Germination Rate (GR) of *Persicaria lapathifolia*. Symbols denote the calculated GR values for the population, and lines show the TL model fit (Equation 5); each set of alternating temperatures is reported as its mean temperature

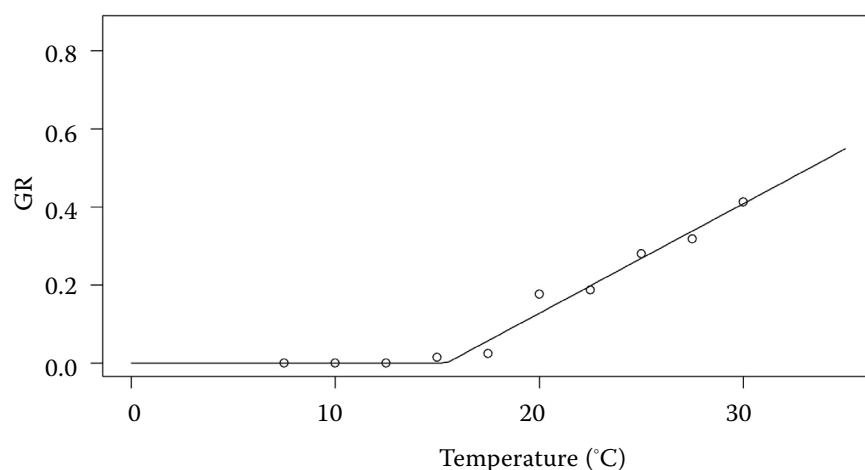


Figure 5. Effect of temperature on the Germination Rate (GR) for the whole population of *Solanum nigrum*. Symbols denote the calculated GR values for the population, and the line shows the TL model fit (Equation 6); each set of alternating temperatures is reported as its mean temperature

(Del Monte & Tarquis 1997; Taab & Andersson 2009; Guillemín et al. 2013; Dong et al. 2020; Ma et al. 2021). T_c for *S. nigrum* germination was estimated in those studies in the 35–40 °C range, shortly above the T_o range. Temperatures higher than 35/25 °C were not tested since soil temperatures above 35 °C are hardly observed in the study area even during full summer, so seeds of *P. lapathifolia* and *S. nigrum* are normally exposed only to sub-optimal temperatures during their germination period. However, this situation did not enable the application of the TTEM model.

In contrast, TL models could be run to estimate T_b values for both species, even if the lack of data in the supra-optimal thermal range impeded a correct estimation of T_c . Regarding *P. lapathifolia*, the TL model estimated a T_b of 9.4 °C; however, some inconsistencies with the experimental observations must be pointed out. Relevant germination (about 40%) was also observed at 12.5/2.5 °C, corresponding to an average temperature of 7.5 °C. It can be supposed that germination advanced at that treatment only during the daily period (12 h) when the temperature was above the 9.4 °C threshold. The significantly longer t_{50} observed at this temperature seems to support this theory. Anyhow, TL models aim at estimating cardinal temperatures that are representative of the whole seed population; thus, treatments with low germination have a lower weight in the estimation. The only value of T_b reported for *P. lapathifolia* (5.8 °C, Guillemín et al. 2013) was instead estimated using the "x-intercept" method that assigns for the estimation of T_b the same weight to the different treatments regardless of their final germination %. This could lead to an over-representation of the small sub-populations of seeds germinating at low temperatures. Thus, TL models seem more appropriate for estimating T_b values that are representative of the average behaviour of the whole seed population.

Regarding *S. nigrum*, the TL model estimated a T_b of 15.4 °C, even if limited germination was observed also at the lowest temperature. However, 80% of total seeds did not germinate at 22.5/12.5 °C or lower, confirming a behaviour described in previous studies (Dong et al. 2020; Ma et al. 2021). Therefore, a T_b value of 15.4 °C could be a reasonable representation of the average behaviour of the whole seed population, even if it is significantly higher than those previously reported for Spanish and Chinese populations (Del Monte & Tarquis 1997; Ma et al. 2021). As stated above for *P. lapathifolia*, dissimilarities between parameters reported in different studies can be ascribed to the different statistical procedures adopted and to intra-

specific variability caused by progressive adaptation of local populations to the local environmental conditions (Del Monte & Tarquis 1997). Estimating specific T_b values for populations from different areas seems recommended to create reliable models for other species (Sousa-Ortega et al. 2020).

CONCLUSION

The germination response of *P. aviculare* was maximum at 22.5/12.5 °C, where its optimal range probably lies, and started to decrease from 25/15 °C. On the contrary, *P. lapathifolia* and *S. nigrum* reached the maximum germination at 35/25 °C, indicating that all tested incubation temperatures were in the sub-optimal range for germination of those species. The availability of data in the supra-optimal thermal range for *P. aviculare* enabled the estimation of the T_b and T_c with both TTEM and TL. Conversely, only TL models could be applied for *P. lapathifolia* and *S. nigrum*, enabling the estimation of the sole T_b values. Anyhow, given that soil temperatures above 35 °C are improbable in Italy even in full summer, *P. lapathifolia* and *S. nigrum* seeds are normally exposed only to sub-optimal temperatures. Thus, T_b is the only relevant thermal parameter for creating robust models for field seedling emergence for these two species. The creation of these models for the studied species will enable the prediction at the local level of seedling emergence and consequently adjust the timing of control operations, even with erratic or contrasting weather trends observed in recent years due to the ongoing climate change.

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Received: September 17, 2024

Accepted: April 28, 2025

Published online: July 23, 2025