

Can alternating temperatures be used to estimate base temperature for seed germination?

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Summary

Modelling weed seedling emergence pattern appears to be a promising approach in the development of effective weed management programmes based on the selection of optimal timing of control operations. Thermal and hydrothermal time models propose that seed germination rates are proportional to the amount by which temperature and water potential exceed threshold values for these environmental factors. Hence, base temperature for seed germination is a fundamental biological parameter for the prediction of weed emergence. A series of laboratory experiments were conducted to estimate base temperature in three weed species belonging to the Asteraceae family, predominant in conservation tillage fields in north-eastern Italy. The traditional method based on germination assays at constant temperatures was compared with a method based on assays at alternating temperatures. The latter might represent an alternative to the former

for those species which do not germinate or only poorly under constant temperatures. Base temperature was estimated by regressing the reciprocal of the median germination time on temperature comparing two functions, a broken-stick and an exponential-type model. Both models showed good fit to all data in the whole temperature range and in almost all cases provided similar estimates of base temperature. The main result is that, for the weed species examined in this study, the use of alternating temperatures for base temperature estimation appears to be possible. However, further research is required to test if the use of germination assays performed at alternating temperatures can be a suitable method to estimate base temperature of species that have too low germination at constant temperatures.

Keywords: threshold temperature, alternating temperatures regimes, weed modelling, *Senecio vulgaris*, *Sonchus oleraceus*, *Taraxacum officinale*.

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Introduction

Predictive models of weed emergence can be useful tools to suggest the best application timing for chemical weed control, optimising the treatments in terms of efficacy, cost and environmental impact. Various types of forecasting models have been developed to predict cumulative weed emergences and most are based on

the thermal or hydrothermal time concept (Gummeron, 1986; Forcella *et al.*, 2000; Alvarado & Bradford, 2002; Masin *et al.*, 2012; García *et al.*, 2013). In these forecasting models, seeds accumulate thermal or hydrothermal time according to environmental conditions, soil temperature only or soil temperature and water potential, and specific biological thresholds: base temperature and base water potential. Base

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temperature is defined as the temperature below and at which germination will not occur (Gummerson, 1986). Several base temperature estimation methods and approaches can be found in the literature. Early estimation methods were based on germination assays at suboptimal temperatures, and the most robust estimate was provided by the x -intercept of a linear regression of the reciprocal of median germination time on temperature (e.g. Holt & Orcutt, 1996). The single linear regression at suboptimal temperatures was then substituted by a linear model made up of two linear regressions, one in suboptimal and one in supra-optimal temperature range, with a maximum occurring at the intersection of the two straight lines (optimum temperature; Alvarado & Bradford, 2002). Rowse and Finch-Savage (2003) modified the equation for describing a curvilinear relationship between germination rate (GR) and temperature, near the optimum temperature level. Both methods assumed that the base water potential started increasing at supra-optimal temperature, causing a decrease in GR with temperature. Recently, Mesgaran *et al.* (2017) suggested a linear increase in base water potential across both suboptimal and supra-optimal temperature range, which results in a curvilinear GR response to temperature, described by a second-order polynomial equation (symmetric with respect to the vertical line through the vertex). Based on a thermal time approach, a non-linear (exponential-type) model was instead proposed by Catara *et al.* (2015), assuming a non-symmetric relationship between GR and temperature.

The most commonly used methods to evaluate threshold temperatures use germination assays performed at constant temperatures. However, some species need alternating temperatures to germinate, showing poor or no germination under isothermal conditions (Baskin & Baskin, 2001). Thompson and Grime (1983), studying the response to diurnal temperature fluctuation of 112 herbaceous species in Sheffield region (UK), found that some species required temperature fluctuation to germinate. In particular, they observed that species with very small seeds needed wider temperature fluctuation (i.e. *Chenopodium rubrum* L., *Epilobium adenocaulon* Hausskn. and *Epilobium hirsutum* L.), while species with the larger seeds were usually able to germinate at constant temperature. Liu *et al.* (2013), studying 445 species from the eastern Tibet plateau, found that the effect of temperature fluctuation on seed germination is species specific and that dicotyledons showed a positive germination response to fluctuating temperature, but monocotyledons did not. Thus, finding a method to estimate base temperature using germination assays performed at alternating temperatures is needed for those species

that germinate scarcely or not at all at constant temperature. Consequently, the aim of this research was to evaluate the possibility of using alternating temperature regimes to estimate base temperature for germination. In particular, the study focused on the estimation of the minimum temperature required for germination of three weed species very common in no-till fields of northern Italy, that is *Senecio vulgaris* L. (common groundsel), *Sonchus oleraceus* L. (annual sowthistle) and *Taraxacum officinale* W. (dandelion). They belong to the Asteraceae family and to the ecophysiological group of indifferent species (germinating in any season of the year), according to the classification of Montegut (1975). The objective of the research was to estimate base temperature for germination of these three weed species comparing the estimation obtained under constant and alternating temperature regimes using two estimation equations: broken-stick and exponential-type models. The latter model may be preferred because it describes a curved relationship between GR and temperature near to the optimal value, which might be more realistic from a biological point of view. Previous work (Catara *et al.*, 2015) suggests that an exponential model might be promising for base temperature estimation studies, and in this study, we compared it to the most widely used function, that is the broken-stick model, attractive for the simplicity of its linear segments (Andreucci *et al.*, 2016).

Materials and methods

Seeds of *S. vulgaris*, *S. oleraceus* and *T. officinale* were collected in summer 2011 from senescing plants at the Padova University Experimental Farm in the Po Valley, north-eastern Italy (45°21'N; 11°58'E; 6 m a.s.l.). Seeds were kept in paper bags in the dark at room temperature until the experiment began in spring 2012. The average weight of 100 seeds was 20 mg for *S. vulgaris*, 25 mg for *S. oleraceus* and 65 mg for *T. officinale*. Three replicates of 100 seeds of each species were placed on a single layer of filter paper in a 9 cm plastic Petri dish. The filter paper was moistened with 5 mL of distilled water. Before placing the seeds on the filter paper, they were sterilised with PPM™ (Plant Preservative Mixture, active ingredients: 5-chloro-2-methyl-3(2H)-isothiazolone and 2-methyl-3(2H)-isothiazolone) 2% v/v for 10 min to reduce fungal and bacterial contamination. Petri dishes were sealed with parafilm to avoid moisture loss, especially at high temperatures, and then placed in growth chambers at eight different constant temperatures (6, 9, 12, 15, 18, 21, 24 and 27°C) and eight regimes of alternating temperatures (T1/T2 day/night: 12.5/2.5, 15/5, 17.5/7.5, 20/10, 22.5/12.5, 25/15, 27.5/17.5 and 30/20°C). Photoperiod was

set at 12:12 h light:dark for both types of tests. Seeds were considered germinated when the radicle was visible and the number of germinated seeds was recorded every 24 h until no further germination occurred for 5 days.

Data analysis

Final germinated proportions were analysed using a generalised linear model with binomial errors and logit link (Sileshi, 2012). Back-transformed proportions were derived from model parameters, together with back-transformed standard errors (Bolker, 2008).

In order to comply with censoring (Onofri *et al.*, 2011), the observed germination times for each Petri dish were used to parameterise a time-to-event model (Ritz *et al.*, 2013) and to derive the median germination time (T50) for the whole seed lot (Bradford, 1995); median germination rates (GR50) for each Petri dish were obtained as the inverse of median germination times.

For assays performed at constant temperatures, the relationship between the observed GR50s and temperature for each species was described using several threshold thermal time models. The first one assumes a clearly defined optimum temperature at the convergence of two straight lines (broken-stick model):

$$\begin{cases} \text{GR50} = [1 - k(T_{D1} - T_o)] \frac{T_{D2} - T_b}{\theta_T} \\ T_{D1} = T(\text{if } T > T_o), T_o(\text{if } T < T_o), \\ T_{D2} = T(\text{if } T_o > T > T_b), T_o(\text{if } T > T_o), T_b(\text{if } T < T_b) \end{cases}, \quad (1)$$

where T is the environmental temperature, T_o is the optimum temperature, T_b is the base temperature, k describes the rate of decrease in GR50 beyond optimum temperature and θ_T is the thermal time constant, representing the germination time at $T = T_b + 1$. This model was derived by removing the effect of the environmental water potential from the equation in Bradford (2002).

This broken-stick equation cannot predict a curved relationship between T and GR50 around T_o , so an exponential model was also used, as follows:

$$\begin{cases} \text{GR50} = a(T - T_b)\{1 - \exp[b(T - T_c)]\} \\ \text{GR50} = 0 \text{ if } T < T_b \text{ or } T > T_c \end{cases}, \quad (2)$$

where T_c is the cut-off temperature, a and b are regression parameters, relating to the speed of increase in GR50 above T_b and the speed of decrease in GR50 above T_o respectively.

In the cases of assays at alternating temperature regimes, two fitting methods were attempted. First, the average germination rate (GR50_{alt}) was calculated as

the average of GRs at the two daily temperature values (T_1 and T_2 , the two temperatures of the interval), as shown by Garcia-Huidobro *et al.* (1982):

$$\text{GR50}_{\text{alt}} = \frac{h_{T1}}{24} \times \text{GR50}_{T1} + \frac{h_{T2}}{24} \times \text{GR50}_{T2}, \quad (3)$$

where GR50_{T1} and GR50_{T2} are germination rates, as predicted respectively at T_1 and T_2 , with either of the two above Eqns (1) or (2), while h_{T1} and h_{T2} represent the number of hours at T_1 and T_2 . Equation (3) was first used assuming that the daily progress to germination only depends on the prevailing temperature regime (i.e., the number of hours spent at each temperature), but not on the previous thermal sequence. Second, Eqns (1) and (2) were fitted to the observed GR50 using the average daily temperature (average of the two temperatures in the interval) as independent variable.

All models were fitted using non-linear least squares and, to compensate for heteroscedasticity, a power-of-the-mean variance model was adopted, assuming a variance proportional to the square of the mean, as shown by preliminary inspection (Pinheiro & Bates, 2000). Model fit was performed using the `gls()` function of the `nlme` package (Pinheiro & Bates, 2000), within the R statistical environment (R Core Team, 2015). Model comparison was performed based on the Akaike's information criterion (AIC; Akaike, 1974), while T_b values were compared across models using heteroscedastic t -tests (Motulsky & Christopoulos, 2003).

Results

Final proportion of germinated seeds

With a few exceptions, seed germination in both constant and alternating temperatures regimes was more than 50% of the total seeds sown. Germination of *S. oleraceus* was generally favoured more at constant than alternating temperatures (Fig. 1), while germination of *S. vulgaris* seeds was better at alternating temperature regimes, except for the lower (12.5/2.5°C) and especially the higher (30/20°C) temperature regimes in which it dropped to 15%. For *T. officinale*, with the exception of the lowest constant temperature tested (6°C), final germination was around 70%–75% in both constant and alternating temperature regimes with high and low temperatures.

Constant temperatures

Considering the overall model fit, based on AIC (the lower, the better) (Table 1), the broken-stick model

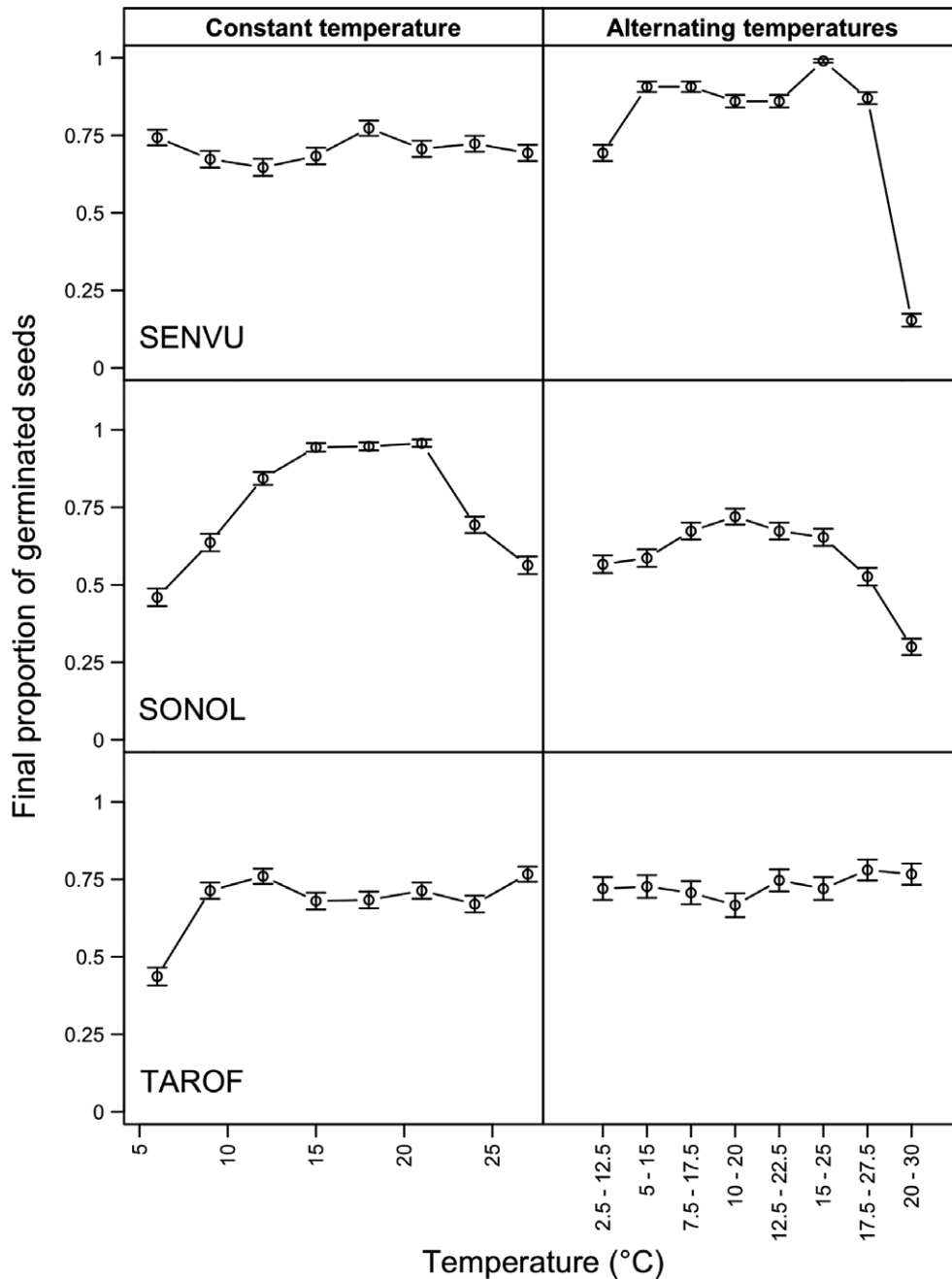


Fig. 1 Final proportion of germinated seeds (percentage of seeds sown that germinated) at constant and alternating temperature regimes for *S. vulgaris* (SENVU), *S. oleraceus* (SONOL) and *T. officinale* (TAROF). Each point represents the mean of three replications; error bars indicating twice the standard error are shown.

gave best performances with *S. oleraceus*, as it provided the best description of the observed GR50 near the optimal temperature level (Fig. 2). For *S. vulgaris* and *T. officinale*, the exponential model best described the curved relationship between temperature and GR50 (Fig. 2). In any case, differences between the two models were rather small for all species.

At constant temperatures, T_b estimates with the two models were very similar, as demonstrated by

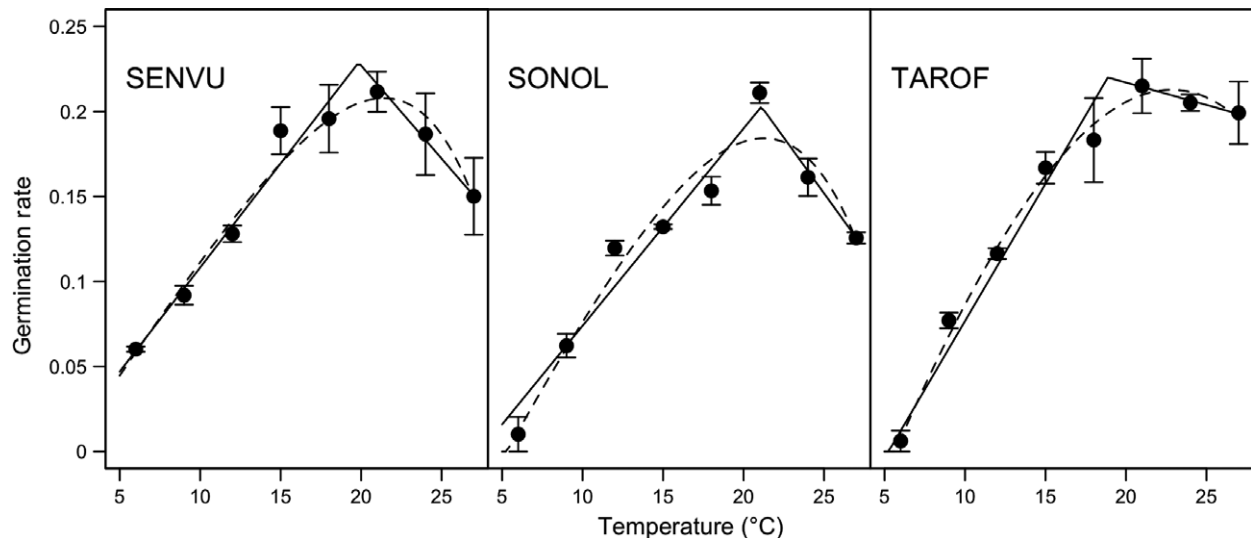
overlapping confidence intervals (Table 1). However, base temperature values for the broken-stick model were always lower and estimated with less accuracy with respect to the other model.

Alternating temperatures

For each species and model, we used Eqn (3) to predict the GRs at alternating temperatures, using the

Table 1 Akaike information criteria (AIC), root mean squared error (RMSE) and base threshold temperatures for the two regression models under comparison, fitted to the observed GR50 at constant temperature regimes, with standard errors and confidence intervals

Species	Model	AIC	RMSE	T_b	SE	95% Confidence interval	
<i>S. vulgaris</i>	Broken-stick	-87.5	0.4185	1.16	1.448	-1.68	4.00
	Exponential	-110.7	0.1519	1.79	0.970	-0.11	3.69
<i>S. oleraceus</i>	Broken-stick	-121.1	0.0101	3.63	0.848	1.97	5.29
	Exponential	-116.2	0.0265	5.29	0.495	4.32	6.26
<i>T. officinale</i>	Broken-stick	-107.6	0.0447	5.25	0.386	4.49	6.01
	Exponential	-115.2	0.0386	5.66	0.219	5.23	6.09

**Fig. 2** Germination rates (for the 50th percentile) at constant temperatures for *S. vulgaris* (SENVU), *S. oleraceus* (SONOL) and *T. officinale* (TAROF). Symbols are the observations; the solid line represents the broken-stick model (Eqn 1) and the dotted line the exponential model (Eqn 2). Vertical bars represent twice the SEs.

parameters estimated at constant temperatures. A good fit was never obtained as follows: an example with Eqn (2) is given in Fig. 3 (crosses and dotted lines), in which the root mean squared error (RMSE) was 0.054 for *S. vulgaris*, 0.071 for *S. oleraceus* and 0.045 for *T. officinale*. Clearly, germination behaviour did not just depend on the prevailing temperature and was not independent of the previous thermal sequence.

Secondly, we re-fitted Eqn (3) to the data observed at alternating temperatures, by replacing GR50T1 and GR50T2 with either Eqn (1) or Eqn (2), applied at the two temperatures T_1 and T_2 . In this way, we obtained a new set of parameters for both Eqn (1) and Eqn (2) that are specific to alternating temperatures, recognising that the previous thermal sequence may affect germination. However, model fit improved only slightly, as shown for example in Fig. 3 (open triangles and solid lines). In this case, the RMSE values decreased to 0.030 for *S. vulgaris*, 0.040 for *S. oleraceus* and 0.027 for *T. officinale*, but no signs of satisfactory fit could be observed. Clearly, in the case of alternating

daily temperatures, Eqn (3) did not provide a good description of the relationship between GR50 and temperature.

With this dataset, best results at alternating temperatures were obtained by fitting Eqns (1) and (2) to the observed data, using the average daily temperature as independent variable (Fig. 4). With alternating temperatures, the two models were almost equivalent in terms of AIC (Table 2), apart from the case of *S. vulgaris*, where the broken-stick model provided a better description of the GR50 at optimal temperature, as shown in Fig. 4. At alternating temperatures, T_b estimates with the two models were very similar with overlapping confidence intervals (Table 2).

Comparison between T_b estimated with constant and alternating temperatures

T_b values for *S. oleraceus* obtained with constant temperatures were not significantly different from those estimated for alternating temperatures by both models

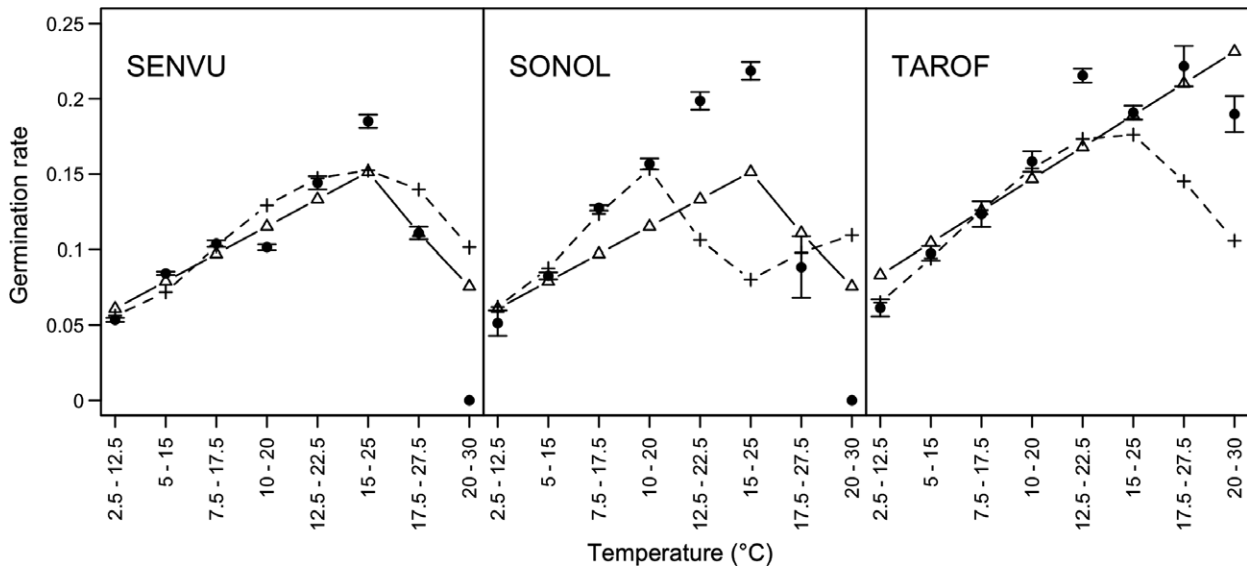


Fig. 3 Relationship between temperature and germination rates, as observed at daily alternating temperature regimes, for *S. vulgaris* (SENVU), *S. oleraceus* (SONOL) and *T. officinale* (TAROF). Closed circles represent the observed values with SE (vertical bars), crosses represent predictions made using Eqn (3), together with Eqn (2) (exponential model) and the parameters estimated at a constant temperature regime, for each species. Open triangles represent the results obtained by re-fitting Eqn (3), together with Eqn (2), to the data observed at alternating temperature (closed circles).

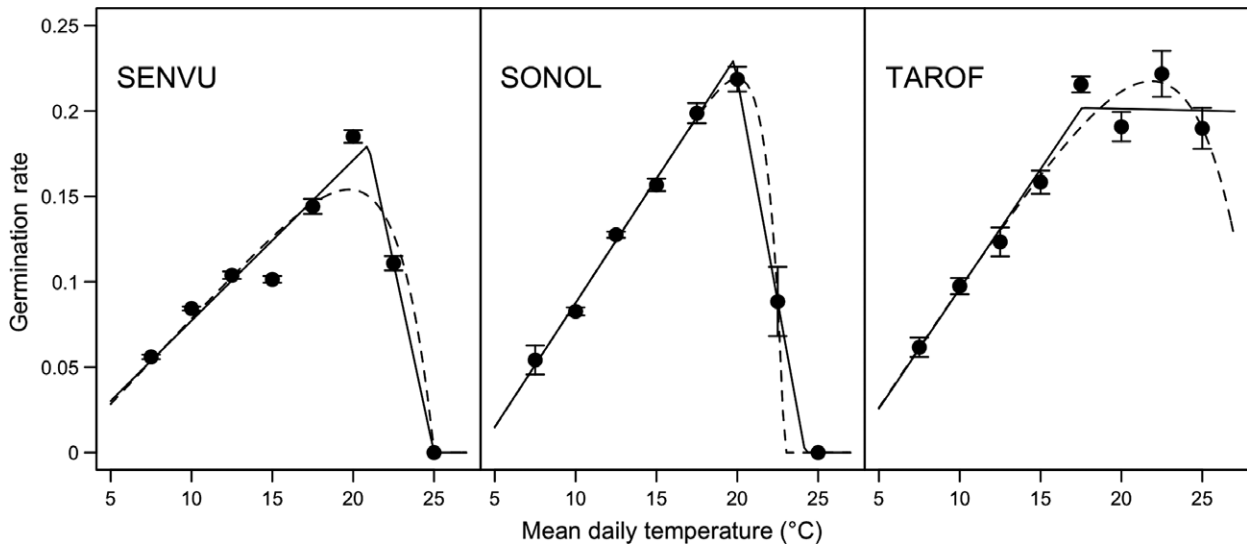


Fig. 4 Germination rates (for the 50th percentile) at alternating temperatures for *S. vulgaris* (SENVU), *S. oleraceus* (SONOL) and *T. officinale* (TAROF). Symbols are the observations; the solid line represents the broken-stick model (Eqn 1) and the dotted line the exponential model (Eqn 2), based on the average daily temperature. Vertical bars represent twice the SEs.

(Table 2). Conversely, base temperature of *T. officinale* always differed between the two thermal conditions, as indicated by a heteroscedastic *t*-test (Table 2). *Senecio vulgaris* showed no difference in terms of base temperatures between thermal regimes using either model. In short, the use of constant and alternating temperatures seemed to be equivalent for the estimation of T_b with the exponential and broken-stick models for *S. oleraceus* and *S. vulgaris*, while for *T. officinale* the use of

the two thermal regimes provided different results with both models.

Discussion

Determination of the temperature threshold for germination of *T. officinale* has, to our knowledge, never previously been attempted, even if it is a well-documented species in terms of its ecology, economic

Table 2 Akaike information criteria (AIC), root mean squared error (RMSE) and base threshold temperatures for the two regression models under comparison, fitted to the observed GR50 at alternating temperature regimes, using the average daily temperature as independent variable

Species	Model	AIC	RMSE	T_b	SE	95% Confidence interval		Difference*	<i>P</i> -value†
<i>S. vulgaris</i>	Broken-stick	-139.7	0.0117	1.78	0.876	0.06	3.50	-0.62	0.358
	Exponential	-122.4	0.0171	2.16	1.540	-0.86	5.18	-0.37	0.420
<i>S. oleraceus</i>	Broken-stick	-132.3	0.0137	3.96	0.635	2.72	5.21	-0.34	0.624
	Exponential	-132.2	0.0137	3.98	0.665	2.68	5.28	1.31	0.058
<i>T. officinale</i>	Broken-stick	-122.3	0.0855	3.16	0.532	2.12	4.20	2.09	0.001
	Exponential	-121.5	0.0964	3.13	0.758	1.65	4.62	2.53	0.001

*Difference between base temperature (T_b) levels at constant temperatures and alternating temperatures.

†*P*-values for the null hypothesis of no significant difference (heteroscedastic *t*-test).

importance as a medicinal plant and broad geographical distribution (Hoya *et al.*, 2004; Martinková *et al.*, 2011; Luo & Cardina, 2012). For *S. oleraceus*, Steinmaus *et al.* (2000) estimated base temperatures as varying from 5.3 to 6.8°C, according to the GR indices linearly regressed on temperature. These values are close to our results obtained using both thermal regimes (with maximum difference being 1.6°C at most). For *S. vulgaris*, only Guillemin *et al.* (2012) estimated a germination base temperature for this species in France using a linear regression method with several constant incubation temperatures. The value of T_b they estimated was $2.5 \pm 1.04^\circ\text{C}$, similar to the threshold parameter obtained in this study with all methods in both temperature regimes. These few comparisons with literature values showed a certain agreement with the results we obtained, which supports the robustness of our estimates. In general, including also temperatures as low as the expected T_b or even lower in the assays might be beneficial to obtain smaller standard errors. It should be noted that all the cited studies excluded the supra-optimal temperature range, to be able to estimate T_b using linear regression methods. In contrast, we favoured non-linear regression methods, which allowed us to describe also the reduction of GR at supra-optimal temperatures. This GR reduction could be important, in particular for those species with small seeds that emerge only from a shallow depth. When temperature is at the optimum, seeds at or near the soil surface need to germinate fast in order to rapidly utilise evaporating moisture, while the percentage of germinating seeds reduces when temperature rises above the optimum, and the risk of death by desiccation is higher (Watt & Bloomberg, 2012). The broken-stick and exponential models, thanks to their asymmetric shape, provide good fits to the data at supra-optimal temperatures. Unfortunately, we have no evidence to support one of the two models with respect to the other and a selection will have to be made empirically, according to the behaviour of the

data at hand. In all cases, the use of these two models estimated similar base temperature values with both constant and alternating temperatures in two of the studied species. This aspect deserves further study because there are many species whose germination is strongly affected by fluctuating temperatures (Liu *et al.*, 2013) and have low germination at constant temperatures, so may need the use of the alternating temperatures method.

Little is known about physiological and biochemical mechanisms involved in the responses of seeds to fluctuating temperatures. However, many authors agree that the enhancement of germination by fluctuating temperatures in some species is due to none of the single constant temperatures included in the fluctuating temperatures but to the fluctuation *per se* (Batlla *et al.*, 2003; Huarte & Benech-Arnold, 2005; Huarte, 2006). Moreover, it is also known that in some species, the rate of germination is accelerated by increasing the amplitude of fluctuation (Garcia-Huidobro *et al.*, 1982). In this paper, we used only a fixed interval of 10°C and the observed GR50 were fitted using the average temperatures of the intervals as the independent variable. There is no known physiological reason for using the average temperature of the interval, but we found in an empirical way that the average temperature provided better results than the use of the average of GRs. Further investigations are therefore needed. It would be especially interesting to investigate the influence of wider and narrower intervals of temperature fluctuations on germination response and base temperature estimation with alternating temperatures, in order to explore the possibility of providing a protocol for a general method of base temperature estimation.

In conclusion, for the weed species examined in this study, the use of alternating temperatures for base temperature estimation appears to be possible. However, further research is required with other species to test if the use of germination assays performed at alternating temperatures can be an alternative method to

estimate base temperature of species that have too low germination at constant temperatures. Only monitoring and modelling field emergence of species not germinating at constant temperatures could test the effectiveness of using the base temperatures estimated with the method of alternating temperatures in weed emergence prediction.

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References

- AKAIKE H (1974) A new look at the statistical model identification. *IEEE Transactions on Automatic Control* **19**, 716–723.
- ALVARADO V & BRADFORD KJ (2002) A hydrothermal time model explains the cardinal temperatures for seed germination. *Plant Cell and Environment* **25**, 1061–1069.
- ANDREUCCI MP, MOOT DJ, BLACK AD & SEDCOLE R (2016) A comparison of cardinal temperatures estimated by linear and nonlinear models for germination and bulb growth of forage brassicas. *European Journal of Agronomy* **81**, 52–63.
- BASKIN CC & BASKIN JM (2001) *Seed: Ecology, Biogeography, and Evolution of Dormancy and Germination*. Academic Press, San Diego, CA, USA.
- BATLLA D, VERGES V & BENECH-ARNOLD RL (2003) A quantitative analysis of seed responses to cycle – doses of fluctuating temperatures in relation to dormancy: development of a thermal time model for *Polygonum aviculare* L. seeds. *Seed Science Research* **13**, 197–207.
- BOLKER BM (2008) *Ecological Models and Data in R*. Princeton University Press, Princeton, NJ, USA.
- BRADFORD KJ (1995) Water relations in seed germination. In: *Seed Development and Germination* (eds J KIGEL & G GALILI), 351–396, Marcel Dekker Inc., New York, NY, USA.
- BRADFORD KJ (2002) Applications of hydrothermal time to quantifying and modeling seed germination and dormancy. *Weed Science* **50**, 248–260.
- CATARA S, CRISTAUDO A, GUALTIERI A, GALES R, IMPELLUSO C & ONOFRI A (2015) Threshold temperatures for seed germination in nine species of *Verbascum* (Scrophulariaceae). *Seed Science Research* **26**, 30–46.
- FORCELLA F, BENECH ARNOLD L, SANCHEZ R & GHERSA CM (2000) Modeling seedling emergence. *Field Crop Research* **67**, 123–139.
- GARCÍA AL, RECASENS J, FORCELLA F, TORRA J & ROYO-ESNAL A (2013) Hydrothermal emergence model for rigput brome (*Bromus diandrus*). *Weed Science* **61**, 146–153.
- GARCIA-HUIDOBRO J, MONTEITH JL & SQUIRE R (1982) Time, temperature and germination of pearl millet (*Pennisetum typhoides* S & H.). 2. Alternating temperatures. *Journal of Experimental Botany* **33**, 297–300.
- GUILLEMIN JP, GARDARIN A, GRANGE S, REIBEL C, MUNIER-JOLAIN N & COLBACH N (2012) Assessing potential germination period of weeds with base temperatures and base water potentials. *Weed Research* **53**, 76–87.
- GUMMERSON RJ (1986) The effect of constant temperature and osmotic potential on the germination of sugar beet. *Journal of Experimental Botany* **37**, 729–741.
- HOLT JS & ORCUTT DR (1996) Temperature thresholds for bud sprouting in perennial weeds and seed germination in cotton. *Weed Science* **44**, 523–533.
- HOYA A, SHIBAKE H, MORITA T & ITO M (2004) Germination and seedling survivorship characteristics of hybrids between native and alien species of dandelion (*Taraxacum*). *Plant Species Biology* **19**, 81–90.
- HUARTE HR (2006) Hydrotime analysis of the effect of fluctuating temperatures on seed germination in several non-cultivated species. *Seed Science and Technology* **34**, 555–569.
- HUARTE HR & BENECH-ARNOLD RL (2005) Incubation under fluctuating temperatures reduces mean base water potential for seed germination in several non-cultivated species. *Seed Science Research* **15**, 89–97.
- LIU K, BASKIN JM, BASKIN CC, BU H, DU G & MA M (2013) Effect of diurnal fluctuating versus constant temperatures on germination of 445 species from the Eastern Tibet Plateau. *PLoS One* **8**, e69364.
- LUO J & CARDINA J (2012) Germination patterns and implications for invasiveness in three *Taraxacum* (Asteraceae) species. *Weed Research* **52**, 112–121.
- MARTINKOVÁ Z, HONĚK A & LUKAS J (2011) Viability of *Taraxacum officinale* seeds after anthesis. *Weed Research* **51**, 508–515.
- MASIN R, LODDO D, BENVENUTI S, OTTO S & ZANIN G (2012) Modelling weed emergence in Italian maize fields. *Weed Science* **60**, 254–259.
- MESGARAN M, ONOFRI A & COUSENS RD (2017) Water availability shifts the optimal temperatures for seed germination. *Ecological Modelling* **351**, 87–95.
- MONTEGUT J (1975) Ecologie de la germination des mauvaises herbes. In: *Germination des Semences* (eds R CHAUSSAT & Y LE DEUNFF), 191–217. Gauthier-Villars, Paris, France.
- MOTULSKY H & CHRISTOPOULUS A (2003) *Fitting Models to Biological Data Using Linear and Nonlinear Regression: A Practical Guide to Curve Fitting*. GraphPad Software Inc., San Diego, CA, USA.
- ONOFRI A, MESGARAN MB, TEI F & COUSENS RD (2011) The cure model: an improved way to describe seed germination? *Weed Research* **51**, 516–524.
- PINHEIRO JC & BATES DM (2000) *Mixed-Effects Models in S and S-Plus*. Springer-Verlag Inc., New York, NY, USA.
- R Core Team (2015) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- RITZ C, PIPPER CB & STREIBIG JC (2013) Analysis of germination data from agricultural experiments. *European Journal of Agronomy* **45**, 1–6.
- ROWSE H & FINCH-SAVAGE W (2003) Hydrothermal threshold models can describe the germination response of carrot (*Daucus carota*) and onion (*Allium cepa*) seed populations across both sub- and supra-optimal temperatures. *New Phytologist* **158**, 101–108.

- SILESHI GW (2012) A critique of current trends in the statistical analysis of seed germination and viability data. *Seed Science Research* **22**, 145–159.
- STEINMAUS SJ, PRATHER TS & HOLT JS (2000) Estimation of base temperature for nine weed species. *Journal of Experimental Botany* **51**, 275–286.

- THOMPSON K & GRIME JP (1983) A comparative study of germination response to diurnally fluctuating temperatures. *Journal of Applied Ecology* **20**, 141–156.
- WATT MS & BLOOMBERG M (2012) Key features of the seed germination response to high temperatures. *New Phytologist* **196**, 332–336.