

Estimation of base temperatures for nine weed species

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Abstract

Experiments were conducted to test several methods for estimating low temperature thresholds for seed germination. Temperature responses of nine weeds common in annual agroecosystems were assessed in temperature gradient experiments. Species included summer annuals (*Amaranthus albus*, *A. palmeri*, *Digitaria sanguinalis*, *Echinochloa crus-galli*, *Portulaca oleracea*, and *Setaria glauca*), winter annuals (*Hirschfeldia incana* and *Sonchus oleraceus*), and *Conyza canadensis*, which is classified as a summer or winter annual. The temperature below which development ceases (T_{base}) was estimated as the x -intercept of four conventional germination rate indices regressed on temperature, by repeated probit analysis, and by a mathematical approach. An overall T_{base} estimate for each species was the average across indices weighted by the reciprocal of the variance associated with the estimate. Germination rates increased linearly with temperature between 15 °C and 30 °C for all species. Consistent estimates of T_{base} were obtained for most species using several indices. The most statistically robust and biologically relevant method was the reciprocal time to median germination, which can also be used to estimate other biologically meaningful parameters. The mean T_{base} for summer annuals (13.8 °C) was higher than that for winter annuals (8.3 °C). The two germination response characteristics, T_{base} and slope (rate), influence a species' germination behaviour in the field since the germination inhibiting effects of a high T_{base} may be offset by the germination promoting effects of a rapid germination response to temperature. Estimates of T_{base} may be incorporated into predictive thermal time models to assist weed control practitioners in making management decisions.

Key words: Base temperature, germination, phenology, thermal time, weeds.

Introduction

Temperature is the single most important factor regulating germination of non-dormant seeds in irrigated, annual agroecosystems at the beginning of the growth season where light, nutrients, and moisture are typically not growth limiting (Garcia-Huidobro *et al.*, 1982). Consequently, the combination of temperature and time (i.e. degree-days) is a more appropriate unit of measure for predicting plant development than time alone (Ritchie and NeSmith, 1991). The degree-day approach has been implemented successfully in the prediction of agronomically important phenological stages for crop and weed species (Alm *et al.*, 1991).

A basic requirement for this approach is an estimate of the temperature below which phenological development ceases (T_{base}) for each species. Conventional approaches to estimating T_{base} involve regressing germination rate on sub-optimal temperatures and computing an x -intercept from the linear equation (Holt and Orcutt, 1996; Scott *et al.*, 1984; Wiese and Binning, 1987). Germination rate has been expressed in various ways, but no one way is universally superior in its linear relationship to temperature (Garcia-Huidobro *et al.*, 1982; Scott *et al.*, 1984).

Alternatively, other approaches rely on the sigmoidal shape that cumulative germination takes over time for most species (Scott *et al.*, 1984). For example, cumulative per cent germination is probit transformed and then paired with the temperature-time (i.e. $\ln[T - T_{\text{base}}] \times \text{time}$) at which the probit was observed (Dahal *et al.*, 1990). The probit minus five is equal to a normal equivalent deviate (NED) (Finney, 1971). The NEDs are in units of standard deviation and are defined by the standard

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normal cumulative density function (CDF). A straight line is fitted to the paired data, and T_{base} is varied until the mean square residual for the regression is minimized. This has been deemed the best estimate of T_{base} for several crop species (Covell *et al.*, 1986; Dahal *et al.*, 1990). The Weibull (Bridges *et al.*, 1989) and the logistic (Hsu *et al.*, 1984; Talbott Roché *et al.*, 1997) functions have also been fitted to cumulative per cent germination. A method by which T_{base} could be estimated according to least associated variation in degree-days or actual days would also be appropriate in the development of degree-day models. Several alternative methods have been developed based on several least variation criteria (Yang *et al.*, 1995), which estimate T_{base} from paired temperature and time to germination data.

A fundamental challenge in developing thermal time models has been deciding which method provides the most robust estimate of T_{base} . This can be especially problematic when each of the methods yields a different T_{base} estimate yet the mean square residuals, coefficients of determination (r^2), and coefficients of variation (CV) may not be significantly different among the methods. Combining the estimates from several different methods and weighting them by the reciprocal of the variation associated with each estimate provides a mathematical approach for estimating an overall T_{base} for a species. However, it is difficult to estimate the variance associated with the x -intercept, which is the negative ratio of the y -intercept and the slope of a linear equation. Additionally, a composite value for T_{base} is not necessarily biologically meaningful. Alternate methods are to choose the estimate that most closely matches observed germination thresholds obtained empirically or that also predicts the time-course of germination most accurately.

The primary objective of this research was to compare several conventional and alternative methods that have been used to estimate T_{base} for germination. Estimates of T_{base} were made for nine common weed species differing in taxonomic classification and life history. Statistical and biological criteria were employed to choose the most robust and realistic estimates for incorporation into predictive thermal time models.

Materials and methods

Seed collection

Seeds of nine weed species common to California agroecosystems were collected between August 1994 and May 1996 at the University of California Research Station at the Riverside campus (Table 1). The species were classified into two groups according to their life-history habits. Six species were summer annuals (*Amaranthus albus* L., *A. palmeri* S. Wats., *Portulaca oleracea* L., *Digitaria sanguinalis* (L.) Scop., *Echinochloa crus-galli* (L.) Beauv., and *Setaria glauca* (L.) Beauv.), which germinate in spring and flower in summer. Two species were winter annuals (*Hirschfeldia incana* (L.) Lagreze-Fossatt and

Sonchus oleraceus L.), which germinate in autumn and flower the following spring. *Conyza canadensis* L. Cronq. was classified as a winter-summer annual because it germinates in autumn or spring and grows as a rosette until it bolts and flowers in the late spring or summer (Whitson *et al.*, 1992). Seeds were stored in paper bags at room temperature ($\sim 25.3^\circ\text{C}$) and relative humidity ($< 15\%$).

Experimental design

The effect of temperature on germination response was assessed in experiments conducted between September 1995 and April 1997 on an insulated $45 \times 114 \times 3$ cm temperature gradient bar (Holt, 1987). The bar is a solid aluminium block with hot water running through one end and cold through the other resulting in a continuous temperature gradient along its length. The hot (37°C) and cold (-5°C) water was provided by two thermostatically controlled water baths (Lauda model RC-20 with B-2 circulator and model C-20 with B-1 circulator). The resulting average temperature range experienced by the seeds was 36°C to 9°C .

All seeds were germinated on moistened filter paper, which was placed in 53 mm diameter by 8 mm deep glass Petri dishes. A wick action method provided a continuous, uniform moisture supply for the seeds (Knudson and Tibbitts, 1973). Dishes were monitored daily for water loss and refilled with distilled water as necessary. For each species, 16 dishes were placed at about 2°C increments along the gradient bar in each experiment. Germination experiments were conducted twice, totalling 32 dishes with 20 seeds per dish for each species.

Fluctuations about the mean temperature in each dish ranged from $1\text{--}3^\circ\text{C}$ with the warmer temperatures occurring when room lights were on. Mean temperature of each dish was based on an integrated average. This was computed by measuring temperature of each dish hourly at the beginning of the experiment and every 6 h after it was apparent that temperatures did not fluctuate during the day or night hours. Temperature measurements were made with copper-constantan thermocouples (Omega Engineering, Inc., 1 Omega Drive, Box 4047, Stamford, Connecticut 06907 USA) and monitored on a CR5 Digital Recorder (Campbell Scientific, Inc., Box 551, Logan, Utah 84321 USA). The thermocouples were inserted through holes in plastic Petri dish lids and arranged so that the soldered tip was in direct contact with the moistened filter paper. Fluorescent and incandescent light banks provided at least $40 \mu\text{mol m}^{-2} \text{s}^{-1}$ for 24 h d^{-1} , which was sufficient to meet light requirements for germination of light-sensitive species.

Dishes were subjected to treatment temperatures on the bar for up to 21 d. Seeds were checked for germination four times a day at the beginning of each experiment while germination was rapid and once a day by the end of each experiment when germination had slowed. Germinated seeds were removed from the dish once the radicle or stem had extended more than 1 mm beyond the seed coat or caryopsis, respectively. All dishes were brought to room temperature for a 14 d post-treatment period following each 21 d treatment period in order to assess final germinability. It was assumed that 5 weeks was sufficient time for non-dormant seeds to germinate. A younger seed lot was used for subsequent experiments if germinability was less than 50% in any Petri dish following the post-treatment period. On the few occasions that germinability was below 50%, the data for that dish were not utilized in subsequent analyses.

Germination indices and analyses

Analyses using four conventional germination rate indices, a repeated probit analysis and a mathematical approach were

Table 1. List of species utilized in experiment

Life history classifies species as either summer annual (spring-germinating, summer flowering) or winter annual (autumn-germinating, spring-flowering). *Conyza canadensis* may be classified as either a winter or summer annual. Germinability was calculated over all temperature treatments as the average percentage of seeds that had germinated by the end of the 14 d post-treatment period at room temperature.

Species	Family	Life history	Common name	Germinability	
				Mean	SE
<i>Amaranthus albus</i>	Amaranthaceae	Summer	Tumble pigweed	83.3	0.2
<i>Amaranthus palmeri</i>	Amaranthaceae	Summer	Palmer amaranth	72.0	12.0
<i>Portulaca oleracea</i>	Portulacaceae	Summer	Common purslane	77.0	3.0
<i>Digitaria sanguinalis</i>	Poaceae	Summer	Large crabgrass	87.0	1.0
<i>Echinochloa crus-galli</i>	Poaceae	Summer	Barnyardgrass	95.0	3.0
<i>Setaria glauca</i>	Poaceae	Summer	Yellow foxtail	61.0	5.0
<i>Hirschfeldia incana</i>	Brassicaceae	Winter	Shortpod mustard	75.0	3.0
<i>Sonchus oleraceus</i>	Asteraceae	Winter	Annual sowthistle	81.5	13.5
<i>Conyza canadensis</i>	Asteraceae	Winter/summer	Horseweed	79.5	5.5

conducted with the data of each species, treating data from each dish separately. The optimum temperature was the temperature at which the highest germination rate was observed. The data utilized in calculating the indices were those from suboptimal temperatures. Suboptimal temperatures were those below the optimum temperature over which germination rate increased linearly according to visual inspection of the residuals. Total potential germinability of a species at any temperature along the gradient bar was assumed to be equivalent to that under optimal temperature, since there was no evidence for systematic differences in overall germinability that might be explained by temperature. In calculating the indices, total potential germinability was based on the total number of seeds that had germinated following the post-treatment period for each dish.

Index 1. Per cent germination: Average per cent germination per day was calculated at each temperature as:

$$\%Germination = \frac{100}{n} \sum_{i=0}^n \frac{G_i}{t_i G_n} \quad (1)$$

where $i=0$ is the beginning of imbibition, n is the last day (or its fraction) that any germination occurred during the 21 d treatment period, and G_i is the cumulative number of seeds germinated by time t_i . Index 1 is a variation of per cent germination per day (used by Wiese and Binning, 1987). Only data between 10–90% germination were utilized in the calculation of Index 1 since several seeds often germinated between inspections and the exact times for 10% or 90% germination could not be determined.

Index 2. Reciprocal time to median germination: The reciprocal time to median germination was assessed at each temperature for each species (Holt and Orcutt, 1996). In most cases, germination of the median seed was not observed directly so the PROBIT procedure in SAS was utilized to estimate the time that the median cohort germinated (SAS Institute, Inc., 1989, 1995). Cumulative per cent germination at a given temperature was transformed to probits and regressed against time (Finney, 1971) and the time to median (50%) germination was estimated from this function (Fig. 1). A Pearson Chi Square test ($\alpha=0.05$) was conducted to assess goodness of fit of the normal cumulative density function to per cent germination through time for each species at each suboptimal temperature (SAS Institute, Inc., 1995). Linearly interpolated values

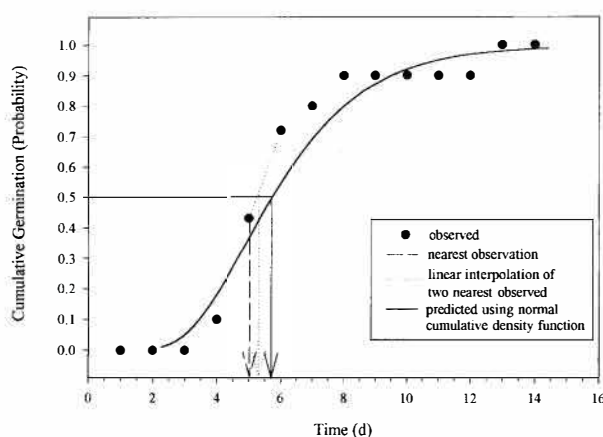


Fig. 1. Comparison of estimations of the time to median germination by the normal cumulative density function, the nearest observation, and the linear interpolation of the two nearest observations for *Portulaca oleracea* seeds exposed to an average temperature of 18 °C.

were utilized if the goodness of fit tests indicated significant divergence between predicted and observed times.

Index 3. Germination rate index (A): The Germination Rate Index (A) was calculated as:

$$GRI(A) = \frac{100 G_{tot}}{p} \sum_{i=0}^n \frac{g_i}{t_i} \quad (2)$$

where g_i is number of seeds that germinated between times t_{i-1} and t_i , p is the number of seeds incubated, and G_{tot} (germinability) is the total number of seeds that germinated in a dish by the end of the post-treatment period; all other terms are as defined for Index 1. $GRI(A)$ is equivalent to $GRI(1)$ in Holt and Orcutt (Holt and Orcutt, 1996).

Index 4. Germination rate index (B): The Germination Rate Index (B) was calculated as:

$$GRI(B) = \sum_{i=0}^n \frac{g_i}{t_i} \quad (3)$$

where all terms are as defined for Indices 1 and 2. $GRI(B)$ is

equivalent to *GRI(2)* in Holt and Orcutt (Holt and Orcutt, 1996).

Index 5. Repeated probit analysis: Cumulative germination as a per cent of germinable seeds at each time, i , was transformed to a normal equivalent deviate (NED) value using the NORMSINV function in Microsoft® EXCEL (Version 7), which returns the inverse of the standard normal cumulative density function with a reported accuracy within $3E^{-7}$. All cohorts of a given species were assumed to have a common base temperature (Ellis *et al.*, 1986). These NED values from all times and suboptimal temperatures were pooled and regressed against a function of time (t_i) and temperature (T) as:

$$NED(i) = a + b[\ln(T - T_{\text{base}})t_i] \quad (4)$$

where a and b are the intercept and slope coefficients, respectively (Dahal *et al.*, 1990; Ellis *et al.*, 1986). The intercept and slope were estimated by ordinary least squares methods and T_{base} was estimated by an iterative method (Dahal *et al.*, 1990). The iterative method involved varying T_{base} in equation (4) until the mean square residual term of the regression was minimized. The T_{base} producing the least residual was deemed the best estimate of base temperature according to this method (Dahal *et al.*, 1990; Ellis *et al.*, 1986).

Index 6 (a–d). Mathematical approach: Estimates of T_{base} were also made utilizing the mathematical formulae of Yang *et al.* (Yang *et al.*, 1995). These formulae reduce to single equations the T_{base} estimates for each species based on least standard deviation in degree-days (Index 6a), least standard deviation in days (Index 6b), least coefficient of variation in degree-days (Index 6c), and a regression coefficient method (Index 6d). These criteria are commonly utilized methods in the development of degree-day models. The T_{base} estimate based on least standard deviation in degree-days (Index 6a) was calculated as:

$$T_{\text{base}} = \frac{\sum_{i=1}^n T_i t_i \sum_{i=1}^n t_i - n \sum_{i=1}^n t_i^2 T_i}{\left(\sum_{i=1}^n t_i\right)^2 - n \sum_{i=1}^n t_i^2} \quad (5)$$

where T_i is the average temperature, t_i is the number of days to germination for each Petri dish i , and n is the total number of Petri dishes for each species. The T_{base} estimate based on least standard deviation in days (Index 6b) was calculated as:

$$T_{\text{base}} = T - \frac{\left(\sum_{i=1}^n D_i t_i\right)^2 - n \sum_{i=1}^n D_i^2 t_i^2}{n \sum_{i=1}^n t_i^2 D_i - n \sum_{i=1}^n D_i t_i \sum_{i=1}^n t_i} \quad (6)$$

where T is the overall mean temperature of all Petri dishes, D_i is the difference between T and T_i , and all other variables are the same as described for equation (5). The T_{base} estimate based on least coefficient of variation in degree-days (Index 6c) was calculated as:

$$T_{\text{base}} = \frac{\sum_{i=1}^n T_i t_i^2 \sum_{i=1}^n T_i t_i - \sum_{i=1}^n t_i \sum_{i=1}^n T_i^2 t_i^2}{\sum_{i=1}^n t_i^2 \sum_{i=1}^n T_i t_i - \sum_{i=1}^n t_i \sum_{i=1}^n T_i^2} \quad (7)$$

where all terms are as defined for equation (5). The T_{base} estimate based on a regression coefficient method (Index 6d)

was calculated as:

$$T_{\text{base}} = \frac{\sum_{i=1}^n T_i \sum_{i=1}^n t_i T_i - n \sum_{i=1}^n t_i T_i^2}{\sum_{i=1}^n t_i \sum_{i=1}^n T_i - n \sum_{i=1}^n t_i T_i} \quad (8)$$

where all terms are as defined for equation (5). Days to median germination in each Petri dish as determined for Index 2 were utilized in the estimates.

Linear regressions

Germination indices 1–4 were regressed against suboptimal temperatures for each species utilizing the regression procedure in SAS (SAS Institute, Inc., 1989). The x -intercept from each of these regressions was the estimated T_{base} , computed as $-a/b$, where a and b are the intercept and slope coefficients from each of the regressions. All comparisons among means, variances, coefficients of variation, and coefficients of determination were performed at the 5% significance level (Zar, 1984). The CV_y (coefficient of variation for the dependent variable) for Index 5 was computed after transforming NED values to probits to avoid division by zero.

Estimate of variance associated with x -intercept

The standard error associated with the x -intercept ($SE_{x\text{-int}}$) of indices 1–5 was estimated from the variance–covariance matrix generated with the OUTEST COVOUT options available with the regression procedure in SAS (SAS Institute, Inc., 1989). It was computed as:

$$SE_{x\text{-int}} = \sqrt{\frac{V_{aa}}{b^2} - \frac{2aV_{ab}}{b^3} + \frac{a^2V_{bb}}{b^4}} \quad (9)$$

where V_{ii} are the variances-covariances associated with a and b that were extracted from the covariance matrix. This estimate is based on a linear Taylor series approximation to the variance of the ratio $-a/b$ (Cox, 1990).

A weighted average (WAI) was computed utilizing the inverse of the standard error ($SE_{x\text{-int}}$) associated with the x -intercept (x_{int}) from each of the first four indices i as a weighting factor such that:

$$WAI = \frac{1}{n} \sum_{i=1}^n \left[\frac{x_{\text{int}}(i)}{SE_{x\text{-int}}(i)} \times \sum_{i=1}^n SE_{x\text{-int}}(i) \right] \quad (10)$$

where $n=4$. A second weighted average ($WA2$) was computed, including the T_{base} estimate from Index 5 (repeated probit analysis), utilizing the inverse of the relative variability associated with the x -intercept ($CV_{x\text{-int}}$) as a weight instead of $SE_{x\text{-int}}$ in equation (10) and $n=5$. The $CV_{x\text{-int}}$ was equivalent to $100 \times SE_{x\text{-int}}/x_{\text{int}}$. The variability associated with the x -intercept from the repeated probit analysis included both temperature and time sources of variation. The $CV_{x\text{-int}}$ for Index 5 was computed after taking the inverse logarithm of $SE_{x\text{-int}}$ and x_{int} .

Results

Seed germinability remained consistently high at $77.4 \pm 3.9\%$ averaged over all species (Table 1). Germinability neither increased nor decreased significantly throughout the entire experiment.

Germination rates for all species and indices increased with temperature within the range of 10°C to about 30°C

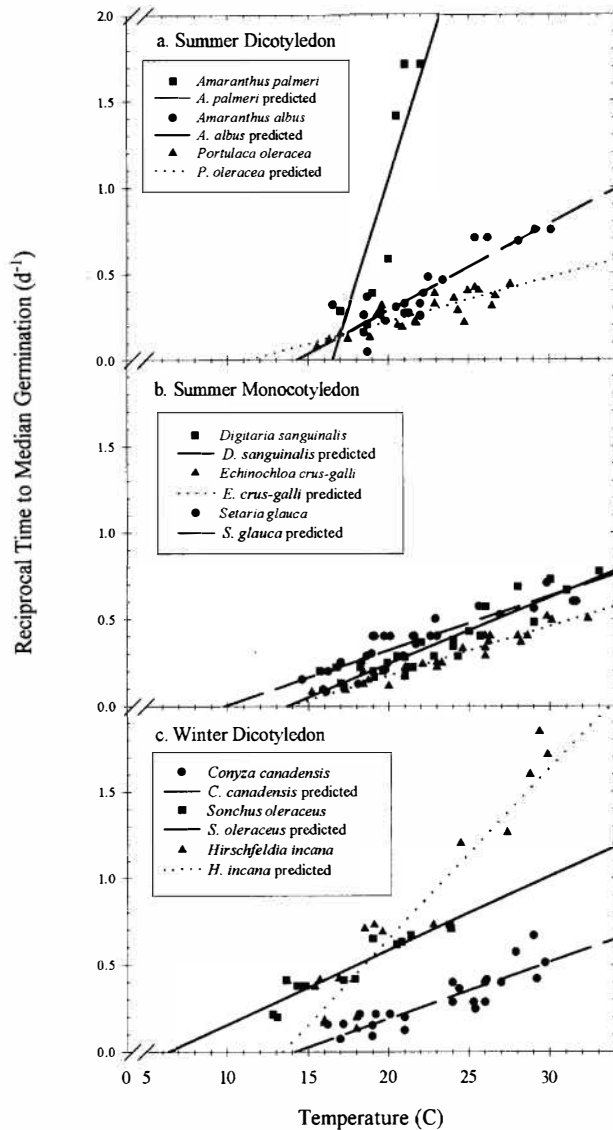


Fig. 2. Reciprocal time to median germination (Index 2) regressed on temperature for the (a) summer dicotyledons: *Amaranthus albus*, *A. palmeri*, and *Portulaca oleracea*; (b) summer monocotyledons: *Digitaria sanguinalis*, *Echinochloa crus-galli*, and *Setaria glauca*; and (c) winter dicotyledons: *Hirschfeldia incana*, *Sonchus oleraceus*, and *Conyza canadensis*. *C. canadensis* may be classified as either a winter or summer annual.

as indicated by significant *F*-tests for regression ($P < 0.05$) (Figs 2–5). Several data points for *Amaranthus palmeri* extended beyond the *y*-axes in Figs 2–5 and were not presented so that data of the other species could be interpreted more easily. In general, a straight line was adequate to describe the relationship of the different germination rate indices to suboptimal temperature for all species. Examination of the ellipses of concentration and the correlation coefficients ($\sqrt{r^2}$) revealed a strong linear relationship in most cases (Table 2). Additionally, residual

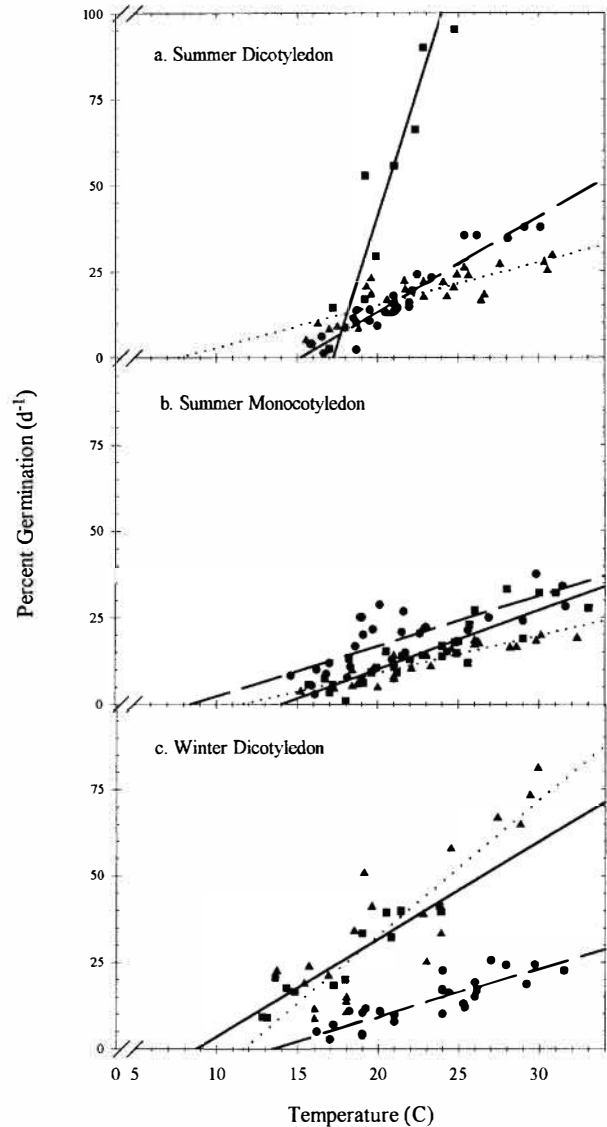


Fig. 3. Per cent germination (Index 1) regressed on temperature for the (a) summer dicotyledons, (b) summer monocotyledons, and (c) winter dicotyledons. See Fig. 2 legend for species list.

plots did not reveal any systematic deviation of observed values from predicted values, which would have suggested the use of an alternative model (data not presented).

The T_{base} estimates for a given species were not more than 3 °C different among all indices for *Amaranthus albus*, *A. palmeri*, *Conyza canadensis*, *Digitaria sanguinalis*, and *Echinochloa crus-galli* (Table 2). Differences in estimates among the indices for the remaining four species ranged from 5.6 °C for *Setaria glauca* to 8.2 °C for *Sonchus oleraceus*. The highest variability among estimates based on a pooled SE_{x-int} and CV_{x-int} was observed with *Portulaca oleracea* and *S. oleraceus* (Table 3). Estimates from Index 5 (repeated probit analysis) of T_{base} for the

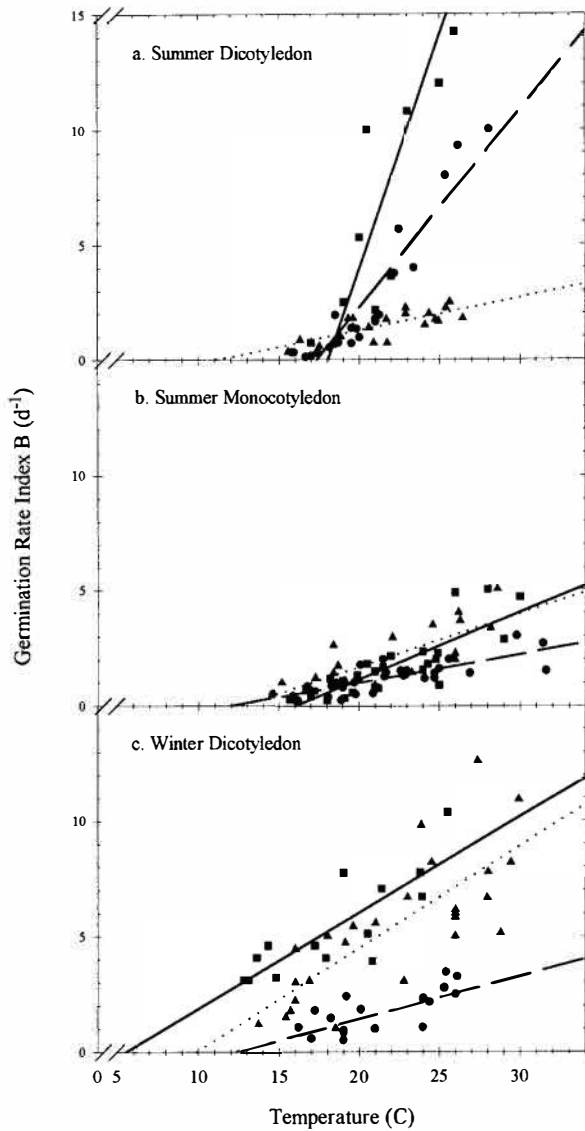


Fig. 4. Germination rate index B (Index 4) regressed on temperature for the (a) summer dicotyledons, (b) summer monocotyledons, and (c) winter dicotyledons. See Fig. 2 legend for species list.

two winter annuals, *Hirschfeldia incana* and *S. oleraceus*, were significantly lower than those of the other indices according to a standard t -test using the pooled SE_{x-int} over Indices 1–4 for each species (Tables 2, 3). Index 5 estimates for the other species were not significantly different from T_{base} estimates arithmetically averaged over the other indices.

The reciprocal time to median germination (Index 2) provided the most robust T_{base} and best linear fit among indices across species as indicated by an average SE_{x-int} , CV_y , and r^2 of 0.99 °C, 20.5%, and 0.84, respectively (Table 2). Cumulative germination was described well by the normal cumulative density function (CDF) that was

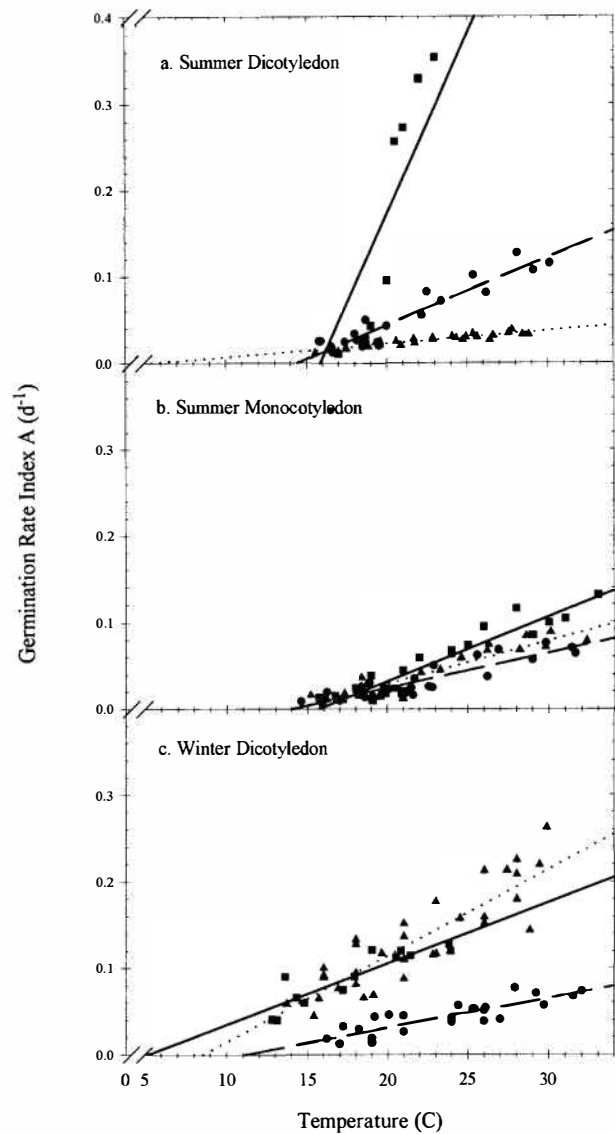


Fig. 5. Germination rate index A (Index 3) regressed on temperature for the (a) summer dicotyledons, (b) summer monocotyledons, and (c) winter dicotyledons. See Fig. 2 legend for species list.

used for Index 2, as Pearson Chi Square goodness of fit tests indicated no significant differences ($P > 0.10$) between observations and values predicted by the normal CDF (Fig. 1). Similar fits were achieved for the other species (data not presented). The data in Fig. 1 represent some of the largest differences among probit predicted, linearly interpolated, and nearest observed median values found for all species and temperatures. Time to median germination was often quite different between nearest observations and those estimated by Index 2. However, the times estimated by Index 2 were very similar (within a half day) to linearly interpolated values (Fig. 1).

By these same indicators, Index 4 (*GRIB*) provided the

Table 2. Seed germination characteristics for nine weedy species

Base temperatures (T_{base}) were estimated as the x -intercept for the linear regressions of germination rate (Indices 1–4) on temperature. Index 1 was per cent germination, Index 2 was reciprocal time to median germination, Index 3 was germination rate index A, Index 4 was germination rate index B, and Index 5 was repeated probit analysis. Estimates for Index 5 were based on the regression of NED on $\ln(\text{degree-days})$. Included are estimates for the intercept of the independent variable (T_{base}), slope (b), y -intercept (a), coefficient of variation for the dependent variable (CV_y), and coefficient of determination (r^2). The mean values for $SE_{x\text{-int}}$, CV_y , and r^2 represent averages across all species within an index.

Species	Coefficients	Index 1		Index 2		Index 3		Index 4		Index 5		
		Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	T_{base}	$\ln(\text{DD})$	SE $\ln(\text{DD})$
<i>Amaranthus albus</i>	T_{base}	15.20	0.41	14.32	0.87	14.41	0.54	17.36	0.36	16.00	1.18	0.02
	b	2.75	0.16	0.05	0.01	0.01	0.00	0.86	0.07		5.51	0.75
	a	-41.90	3.48	-0.72	0.12	-0.11	0.01	-14.90	1.47		-6.49	0.89
	CV_y	20.30		23.80		23.90		44.50			11.10	
	r^2	0.92		0.81		0.90		0.87			0.64	
<i>Amaranthus palmeri</i>	T_{base}	17.65	0.65	16.66	0.55	16.01	0.77	18.12	1.06	16.90	0.41	0.03
	b	15.46	1.23	0.31	0.02	0.04	0.00	2.06	0.28		2.28	0.16
	a	-272.90	30.55	-5.10	0.47	-0.68	0.08	-37.36	7.05		-0.93	0.11
	CV_y	19.70		13.30		16.10		36.70			7.20	
	r^2	0.93		0.96		0.93		0.82			0.82	
<i>Portulaca oleracea</i>	T_{base}	7.66	2.34	11.27	1.62	5.16	1.63	11.07	2.15	7.50	0.25	0.01
	b	1.23	0.18	0.03	0.00	0.00	0.00	0.14	0.03		5.94	0.60
	a	-9.41	4.22	-0.28	0.08	-0.01	0.00	-1.16	0.61		-1.47	0.19
	CV_y	21.10		22.60		10.20		28.00			8.60	
	r^2	0.66		0.69		0.83		0.58			0.67	
<i>Digitaria sanguinalis</i>	T_{base}	14.00	0.95	13.65	0.82	15.74	0.58	16.05	0.95	16.20	1.29	0.01
	b	1.69	0.16	0.04	0.00	0.01	0.00	0.29	0.04		3.88	0.35
	a	-23.71	3.79	-0.52	0.07	-0.12	0.01	-4.61	0.87		-5.02	0.47
	CV_y	26.80		21.10		25.70		45.90			7.30	
	r^2	0.79		0.86		0.90		0.68			0.70	
<i>Echinochloa crus-galli</i>	T_{base}	11.68	1.23	13.85	0.61	14.19	1.13	12.74	2.20	12.50	1.62	0.01
	b	1.08	0.11	0.03	0.00	0.00	0.00	0.23	0.05		4.67	0.40
	a	-12.55	2.53	-0.39	0.04	-0.07	0.01	-2.91	1.19		-7.55	0.66
	CV_y	18.20		12.80		26.20		36.90			8.30	
	r^2	0.82		0.92		0.82		0.55			0.64	
<i>Setaria glauca</i>	T_{base}	8.44	2.14	9.79	1.15	14.02	0.77	12.04	1.40	14.00	1.39	0.02
	b	1.45	0.23	0.03	0.00	0.00	0.00	0.12	0.02		3.34	0.35
	a	-12.22	4.94	-0.31	0.06	-0.06	0.01	-1.48	0.36		-4.65	0.50
	CV_y	30.00		19.80		29.40		34.50			7.50	
	r^2	0.61		0.82		0.83		0.65			0.65	
<i>Hirschfeldia incana</i>	T_{base}	11.67	1.33	13.45	0.86	8.57	1.36	9.91	2.23	6.50	1.27	0.02
	b	3.92	0.50	0.10	0.01	0.01	0.00	0.44	0.08		3.19	0.44
	a	-45.76	10.76	-1.33	0.21	-0.09	0.02	-4.39	1.70		-4.05	0.58
	CV_y	31.70		31.50		20.80		35.70			10.20	
	r^2	0.77		0.85		0.76		0.59			0.51	
<i>Sonchus oleraceus</i>	T_{base}	8.74	1.15	6.38	1.35	5.19	1.98	5.55	2.71	0.50	1.58	0.02
	b	2.82	0.33	0.04	0.00	0.01	0.00	0.42	0.08		3.26	0.42
	a	-24.68	5.99	-0.27	0.09	-0.04	0.02	-2.31	1.57		-5.16	0.67
	CV_y	17.40		13.20		16.10		24.10			9.40	
	r^2	0.87		0.88		0.80		0.68			0.55	
<i>Conyza canadensis</i>	T_{base}	13.41	1.23	14.18	1.07	11.14	1.58	12.35	2.23	11.50	1.56	0.01
	b	1.39	0.17	0.03	0.00	0.00	0.00	0.19	0.04		4.28	0.41
	a	-18.68	3.84	-0.46	0.08	-0.04	0.01	-2.29	0.92		-6.68	0.65
	CV_y	26.90		26.30		22.50		37.70			10.00	
	r^2	0.74		0.75		0.74		0.49			0.57	
	Mean $SE_{x\text{-int}}$	1.27		0.99		1.15		1.70		0.02		
	Mean CV_y^a	23.57		20.49		21.21		36.00		8.84		
	Mean r^2	0.79		0.84		0.83		0.66		0.64		

^a CV_y for Index 5 is expressed in units of probit probit⁻¹ (where probit = NED + 5) to avoid dividing by zero.

poorest fit of the first four indices with an average $SE_{x\text{-int}}$, CV_y , and r^2 of 1.70 °C, 36.0%, and 0.66, respectively (Table 2). Index 3 (*GRIA*) was intermediate in its estimation of T_{base} and linear fit to temperature (Table 2). The germination cohorts from the 0–10% and 90–100% percentiles were omitted in the determination of Index 1 (per

cent germination) since their inclusion resulted in significantly lower r^2 and larger $SE_{x\text{-int}}$ values according to pairwise Z -tests and F -tests. Calculated in this way, the T_{base} estimate and linear fit of Index 1 to temperature, averaged across all species, were also intermediate in statistical robustness (Table 2).

Table 3. Seed germination characteristics for nine weedy species

The T_{base} averages across indices were the arithmetic average (*AA*), an average (*WAI*) weighted by the inverse of the standard error associated with the estimate ($SE_{x\text{-int}}$), and an average (*WA2*) weighted by the inverse of the coefficient of variation associated with the estimate ($CV_{x\text{-int}}$). The standard error and coefficient of variation for the intercept of the independent variable ($SE_{x\text{-int}}$ and $CV_{x\text{-int}}$), rank of the slope coefficients (b-rank) averaged across Indices 1–4, coefficient of determination (r^2), and coefficient of variation for the dependent variable (CV_y) averaged across all indices are also presented.

Species	T_{base} averages			$SE_{x\text{-int}}$ mean ^c	$CV_{x\text{-int}}$ ^a mean	b-rank mean ^c	r^2 mean	CV_y ^b mean
	<i>AA</i>	<i>WAI</i> ^c	<i>WA2</i>					
<i>Amaranthus albus</i>	15.46	15.63	15.74	0.54	9.17	3.00	0.83	24.72
<i>Amaranthus palmeri</i>	17.07	17.03	17.06	0.76	17.18	1.00	0.89	18.60
<i>Portulaca oleracea</i>	8.53	8.74	9.41	1.94	34.95	8.50	0.69	18.10
<i>Digitaria sanguinalis</i>	15.13	14.94	15.06	0.82	10.03	4.80	0.79	25.36
<i>Echinochloa crus-galli</i>	12.99	13.33	13.32	1.30	12.06	7.30	0.75	20.48
<i>Setaria glauca</i>	11.66	11.72	12.28	1.36	15.89	6.30	0.71	24.24
<i>Hirschfeldia incana</i>	10.02	11.35	11.22	1.45	16.99	2.30	0.70	25.98
<i>Sonchus oleraceus</i>	5.27	6.84	5.69	1.80	28.46	4.00	0.76	16.04
<i>Conyza canadensis</i>	12.52	12.99	12.91	1.53	14.06	7.00	0.66	24.68

^a $CV_{x\text{-int}}$ for Index 5 was computed after taking the inverse ln of SE ln(DD) and ln(DD).

^b CV_y for Index 5 is expressed in units of probit probit⁻¹ (where probit = NED + 5) to avoid dividing by zero.

^cMeans represent values pooled over Indices 1–4.

Index 5 (repeated probit analysis) cannot be compared with the other indices in the same manner because the independent variable was in different units (i.e. degree-days) and was also logarithmically transformed (Fig. 6). By one unitless measure, r^2 , Index 5 provided the poorest (0.64) fit of any index, yet by another measure, CV_y , it provided the best (8.8%) fit across species (Table 2). However, these indicators are only a partial reflection of how well the normal CDF fits the linear portion of the germination progression data because including cohorts from 0–10% and 90–100% percentiles in Index 5 resulted in significantly lower r^2 and higher $SE_{x\text{-int}}$ values, similar to Index 1.

The T_{base} estimates based on Index 6a–d (the mathematical approach; Yang *et al.*, 1995) tended to be 2–3 °C higher than those based on Indices 1–5 (Table 4). Index 6b (least standard deviation in days) produced estimates that were especially high. Index 6d (regression coefficient) consistently provided T_{base} estimates that were within 1 °C of the arithmetic or weighted averages for Indices 1–4.

The arithmetic (*AA*) and two weighted (*WAI*, *WA2*) averaging methods provided T_{base} estimates for each species that were within 1 °C of each other across all indices except for the two winter annuals, *Sonchus oleraceus* and *Hirschfeldia incana* (Table 3). Here, the arithmetic average T_{base} was not more than 1.5 °C lower than one or both of the weighted averages. The T_{base} estimates for the summer annual species tended to be higher than those for the winter annual species regardless of the averaging method (Table 3; Figs 2–5). Based on *WA2*, the estimated T_{base} for the summer species was 13.8 °C (\pm SD 2.7 °C), while it was 8.5 (\pm SD 3.9 °C) for the winter species (not including *Conyza canadensis*). Similar differences were observed with the other averaging

methods. The estimated T_{base} for *C. canadensis* appeared to be intermediate between summer and winter annuals, averaging close to 13 °C. The summer annual *Portulaca oleracea* was an exception to these trends, with an estimated T_{base} of about 9 °C. The only species with a lower estimated T_{base} was the winter annual, *S. oleraceus*, with a T_{base} of 5.7 °C. *Amaranthus albus*, *A. palmeri* and *Digitaria sanguinalis* had the highest T_{base} estimates of all species at 15.7, 17.0, and 15.1 °C, respectively, according to *WA2* (Table 3). There was no apparent difference in estimated T_{base} between the summer dicotyledon and summer monocotyledon groups primarily because of the variability introduced by *P. oleracea* and *A. palmeri* within the summer dicotyledons (Figs 2–5a, b).

In terms of the rate of germination response to temperature, *Amaranthus palmeri* and the winter annual *Hirschfeldia incana* ranked first and second highest according to their slope coefficients across Indices 1–4 (Table 3). *A. albus* and the other winter annual, *Sonchus oleraceus*, had the next two highest ranked slope coefficients. The average rank of the slope coefficients for *Portulaca oleracea* was lowest among all species at 8.5 across Indices 1–4.

Germination of *Conyza canadensis* appeared to be the most variable compared to the other species as indicated by an r^2 value of 0.66 averaged across Indices 1–5 (Table 3). The r^2 values and the standard errors associated with the T_{base} estimates ($SE_{x\text{-int}}$) were negatively correlated ($r = -0.85$) for the first four indices. Consequently, variability was also high for this species as indicated by an $SE_{x\text{-int}}$ of 1.53 °C averaged across Indices 1–4. *Portulaca oleracea* and *Sonchus oleraceus* had $SE_{x\text{-int}}$ estimates that were higher at 1.94 °C and 1.80 °C, respectively (Table 3). The two *Amaranthus* spp. were least variable by these

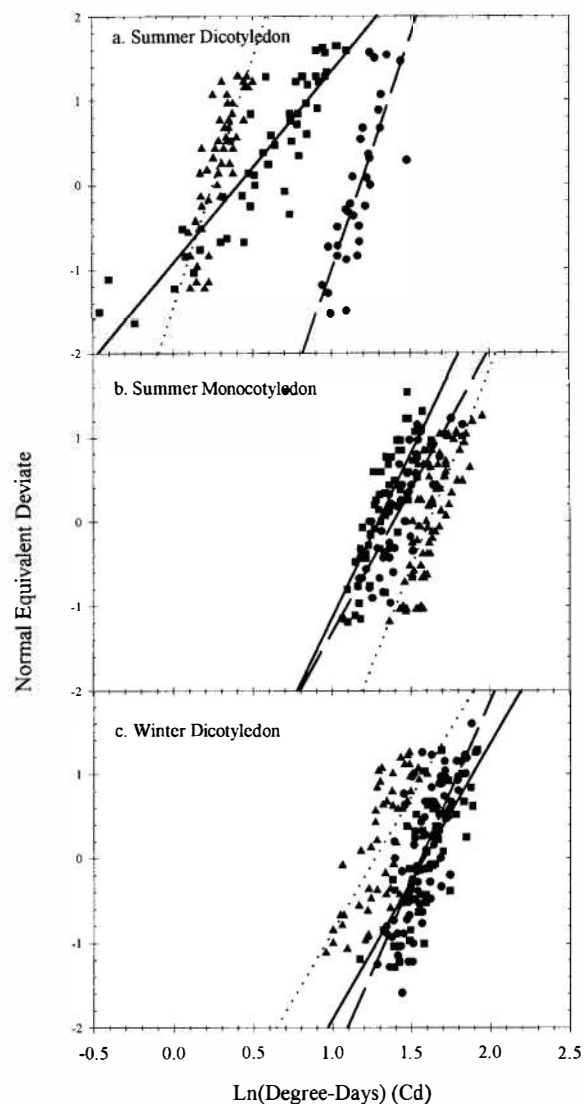


Fig. 6. Normal equivalent deviates (Index 5) regressed on ln(degree-days) for the (a) summer dicotyledons, (b) summer monocotyledons, and (c) winter dicotyledons. Degree-days = $(T - T_{\text{base}})t$ where T = average temperature, t = time and T_{base} = base temperature. See Fig. 2 legend for species list.

two indicators with an average r^2 of 0.86 and a pooled $SE_{x\text{-int}}$ of 0.65 °C compared with the 0.72 and 1.46 °C of all other species for the same indicators. *A. palmeri*, *P. oleracea* and *S. oleraceus* had less than 20% relative variability across all indices according to the coefficients of variation in germination rate (CV_y) while the CV_y for the other species ranged from 20.5 to 26.0% (Table 3).

Discussion

The indices utilized here represent transformations that linearize germination data with respect to suboptimal

Table 4. Base temperature estimates from formulae of Yang et al. (1995)

The four methods are the least standard deviation in degree-days (6a), least standard deviation in days (6b), least coefficient of variation in degree-days (6c), and a regression coefficient method (6d).

Species	Index			
	6a	6b	6c	6d
<i>Amaranthus albus</i>	17.9	20.5	17.5	16.2
<i>Amaranthus palmeri</i>	16.9	22.7	16.5	16.9
<i>Portulaca oleracea</i>	13.6	20.4	12.0	12.1
<i>Digitaria sanguinalis</i>	14.4	22.1	12.5	13.1
<i>Echinochloa crus-galli</i>	13.7	22.8	12.8	13.4
<i>Setaria glauca</i>	14.3	20.0	13.1	12.3
<i>Hirschfeldia incana</i>	16.2	20.2	13.0	13.9
<i>Sonchus oleraceus</i>	8.9	16.7	8.0	7.3
<i>Conyza canadensis</i>	16.1	21.9	14.2	14.0

temperature or the logarithm of thermal time. The transformations simplify parameter estimation and comparison. Several problems may arise with methods that rely on linear models, including lack of fit and an inflated error term due to the fact that T_{base} is extrapolated (Phelps and Finch-Savage, 1997). However, the indices used in this research provided transformations that were represented adequately by linear models. Consistent x -intercept estimates were obtained for most species using several different germination indices. Based upon residuals, parameter estimates did not suffer from non-linearity (as described in Marshall and Squire, 1996). This is partially due to the fact that few data points from very low or high temperatures (e.g. close to the estimated T_{base} or above optimal temperatures) were included in the analyses. Data within 2 °C of an estimated T_{base} were not included in the analyses because daily temperatures in the laboratory fluctuated several degrees. Including these data would underestimate T_{base} because, during periods when temperatures decreased below the true T_{base} for a species, the average daily temperature would decrease, but the average germination rate would remain constant (i.e. zero). Linear methods of estimating germination parameters are common, as in Angus et al., who compared linear and non-linear equations and found that linear models provided satisfactory estimates of thermal responses and T_{base} of emergence for 44 crop species (Angus et al., 1981). In that research, biologically meaningful T_{base} estimates were obtained by excluding both lower and upper tails of cumulative germination curves, as was done here (Angus et al., 1981).

Another concern regarding linear models is that they may not characterize seed populations accurately since seed lots may be comprised of subpopulations, each having a different T_{base} (Phelps and Finch-Savage, 1997). In this research it was assumed that seeds of each species were drawn from that population at random so that any effect of subpopulations would be minimized. The

relatively constant germinability across suboptimal temperatures observed here supports the assumption that subpopulations with different physiological responses to temperature either were not present or, if present, did not influence results. However, it is possible that such effects could occur undetected, for example, if slow germinating seeds also did not germinate at colder temperatures, such that T_{base} were overestimated.

Evaluating differences among indices was among the objectives of this investigation. However, statistical comparisons by conventional methods are not valid because the indices use much of the same data and therefore are not entirely independent. Data from different temperatures and species are independent as they come from different Petri dishes and completely randomized experiments. Approximations to $SE_{x\text{-int}}$ provided by Equation 9 allow direct comparisons of x -intercepts among species (Cox, 1990). The weighted averaging methods that utilize $SE_{x\text{-int}}$ provide a robust approach to combining estimates from different indices. The weighted average $WA2$, which utilizes the inverse of $CV_{x\text{-int}}$ as a weight, tends to be biased against Index 5 (repeated probit analysis) since in that index the variability associated with the x -intercept (thermal time) includes the variability associated with time to germination in addition to the variability associated with temperature. These composite estimates are useful for determining the variability among estimates derived from different calculation methods.

Investigators have utilized analyses of germination responses to temperature that do not rely heavily on the day that the first and last cohorts germinate because of the high variability associated with these cohorts compared with that of the median cohorts ($\sim 40\text{--}60\%$) (Dahal *et al.*, 1990, Hsu *et al.*, 1984). As cumulative germination values approach 0% and 100%, NED values approach negative and positive infinity, respectively. Therefore, a cumulative germination of 0% or 100% could not be utilized in Index 5 (repeated probit analysis). Significant reductions in r^2 values and increases in variability associated with the x -intercept were found when the 0–10% and 90–100% cohorts were included in Index 1 (per cent germination) and Index 5. For this reason, when estimating T_{base} it seems prudent to utilize indices that rely primarily on the observed or estimated median cohorts such as Indices 2 (reciprocal time to median germination) and 5. However, variability in the early and late cohorts is what makes weed germination so unpredictable, and thus, weed management so difficult. Thus, over- or underestimates in T_{base} that might occur from focusing on the majority germination response and omitting very early and late cohorts may need to be examined.

As in other reports, the reciprocal time to median germination (Index 2) provided the best estimate of T_{base} in this research. The robustness of the probit analysis utilized for Index 2 likely occurred because the first and

last cohorts carry little weight in probit analysis (Finney, 1971) and the entire germination progression was utilized in the estimate of median time rather than one or a few data points. Similar observations have been made by other authors (Hsu *et al.*, 1984; Talbott Roché *et al.*, 1997), who utilized a logistic function to estimate median times, which is similar to the normal CDF. The PROBIT procedure in SAS allows for logistic and Gompertz functions to be utilized as CDFs in the analysis, but these provided worse fits than the normal CDF according to the lack of fit tests. The degree to which germination progression follows a normal CDF is indicative of the robustness of the approach, but this CDF may not always provide the best fit to germination (Oryokot *et al.*, 1997).

Index 4 (*GRIB*) tended to provide the poorest fit among indices for all species, possibly because this index included both early (0–10%) and late (90–100%) cohorts. Index 3 (*GRIA*) also included these same cohorts yet was less affected by their variability since dividing by the total per cent germination of seeds in the Petri dish had a stabilizing effect. Germination rate and per cent germination are often combined into one term to estimate T_{base} ; however, there are objections to this approach since it confounds the effect of response time and per cent germination (Heydecker, 1973; Scott *et al.*, 1984).

Estimates made by the regression coefficient method (Index 6d; Yang *et al.*, 1995) appeared to correspond fairly well with Indices 1–4 for all species. Minimizing the standard deviation in days (Index 6b) has been used as a criterion to validate degree-day models (Wilén *et al.*, 1996). However, this formula (Yang *et al.*, 1995) provided T_{base} estimates that were consistently higher than those provided by any other method utilized in this research. From a statistical standpoint, Indices 5 (repeated probit analysis) and 6 (mathematical formulae) are attractive methods because they do not rely on extrapolation to obtain the T_{base} estimate.

Ecological significance of T_{base} estimates

For most species, similar T_{base} estimates were obtained regardless of the calculation method, although methods differed in statistical robustness and goodness of fit. However, Index 2 (reciprocal time to median germination), the most statistically robust index tested, is also expected to be the most biologically relevant index since parameter estimates are obtained from an analysis that utilizes the progression of cumulative germination over time (Angus *et al.*, 1981; Hsu *et al.*, 1984). Such an analysis may be used to estimate other biologically meaningful parameters in addition to T_{base} , such as time to onset of germination, maximum germination rate, and germination response to various factors (Hsu *et al.*, 1984). Thus, the validity of Index 2 for estimating T_{base} is strengthened by its broader applicability for predicting

the time-course of germination in the field. In addition, T_{base} estimates from Index 2 were consistent with observations of seed germination during experiments; that is, no seeds germinated below the estimated values.

The two winter annuals (*Hirschfeldia incana* and *Sonchus oleraceus*) appear well adapted for germination in cooler temperatures as they had relatively low T_{base} estimates compared to the summer annual species. *Conyza canadensis* had T_{base} estimates intermediate to those of the winter and summer annuals. Therefore, its classification as either winter or summer annual seems appropriate (Whitson *et al.*, 1992). The greatest variability in T_{base} estimates among indices was found for the summer annual, *Portulaca oleracea*, which had a T_{base} close to the values for winter annual species. In other research, *P. oleracea* seeds were dormant upon dispersal and had greater germination under alternating than constant temperatures, although sensitivity to temperature fluctuations disappeared as dormancy was broken by seed storage for several months at room temperature (Kruk and Benech-Arnold, 1998). These authors also estimated a low T_{base} for *P. oleracea* (7 °C), consistent with our findings. Since seed age and physiological status are known to influence germination responses to temperature (Probert, 1992), seed dormancy status and sensitivity to alternating temperatures should be determined prior to conducting experiments such as those reported here.

In the field, a species with a relatively high T_{base} would experience little germination in early spring when temperatures would frequently drop below its T_{base} . However, a rapid germination response to an increase in temperature (i.e. large slope) could offset the low early germination caused by the high T_{base} . For example, *Amaranthus palmeri* had the highest estimated T_{base} (17 °C), but also the highest ranked slope of all species studied. A large percentage of the germinable seeds of this species would likely germinate rapidly after the first hours that temperatures exceeded 17 °C in the field. Therefore, even though its T_{base} was high relative to other species, *A. palmeri* may not be underrepresented in the early season weed population because of its high response rate. *A. palmeri* is native to the hot, dry, high light conditions of the Sonoran desert in the south-western United States where moisture is limiting; therefore, germinating quickly following imbibition is an adaptive characteristic of this species (Percy and Ehleringer, 1984).

Portulaca oleracea had the lowest T_{base} of the summer annuals, but also the lowest slope of the species studied. With a small germination response to an increase in temperature, only a small percentage of the germinable seeds of *P. oleracea* would likely germinate over a given period of time. However, due to a low T_{base} , the duration of germination by this species would likely be much longer than for *A. palmeri*. Thus, it appears that each of the summer annuals could be equally represented in the

early spring weed population due to these offsetting characteristics. A pattern of decreasing thermal time to germination with increasing T_{base} was also observed for 44 crop species and attributed to selection for early competitive advantage (Angus *et al.*, 1981).

The differences in T_{base} and slope estimates observed for the two *Amaranthus* species is not unusual for this genus. Different estimates were also found for two *Amaranthus* species (*A. powellii* S. Wats. and *A. retroflexus* L.) (Oryokot *et al.*, 1997). As with these results, they found that the species with the higher T_{base} also had the higher estimated slope. Base temperature estimates have been reported by others for the species studied here, including *Digitaria sanguinalis* (Alm *et al.*, 1988), *Echinochloa crus-galli* (Wiese and Binning, 1987), and *Portulaca oleracea* (Kruk and Benech-Arnold, 1998). Different estimates among published reports are expected, however, due to selection of local ecotypes.

Supra-optimal temperatures

Temperatures above which germination does not occur were not estimated here. Direct temperature measurements at the University of California, Riverside Research Station at 1–5 cm depths in soil with adequate moisture levels for germination indicated that maximum temperatures were between 5–10 °C cooler than maximum air temperatures (unpublished data). The year 1996 was unusually warm in southern California, having eight days that were 40 °C or higher (University of California Statewide Integrated Pest Management Program, www.ipm.ucdavis.edu). The germination rates of *Hirschfeldia incana*, *Sonchus oleraceus* and *Conyza canadensis* had just begun to plateau or decline slightly at 35 °C on the gradient bar. Germination rates of all the other species were still increasing albeit not linearly at 35 °C. Therefore, it appears that maximum air temperatures are not likely to limit germination in soil with non-limiting moisture levels. Estimating an upper temperature threshold for germination for these species is probably unnecessary for thermal time models. While maximum summer temperatures may inhibit growth of the winter annual species, this would likely occur only following emergence.

Conclusions

Several of the methods tested for quantifying temperature responses of germination provided consistent estimates of T_{base} and were statistically robust. However, the reciprocal time to median germination method was the best choice based on both statistical criteria and biological relevance. This method distinguished summer annual species with relatively high T_{base} values from winter annual species with lower values. However, differences were found within each life history type, among related taxa, and between

these results and reports in the literature for the same species. Thus, estimates of germination response are not valid for all members of a species, but should be derived for locally adapted ecotypes. Data from this research provided reasonable estimates of a parameter needed for predictive thermal time models of plant development, which have utility in making weed management decisions. These initial estimates should be further validated with observations made under field conditions.

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