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Use of the Weibull Function to Calculate Cardinal Temperatures in Faba Bean

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ABSTRACT

The onset of germination of faba bean seeds at constant temperature was progressively delayed as that temperature diverged from an optimum of 25·5 °C. At temperatures below 10 °C, or above 28 °C, the maximum germination percentage fell to below 90%. There was no germination at 39 °C. Positive and negative linear relationships were established between the constant temperatures and the rates of progress of germination to different percentiles, at sub-optimal and supra-optimal temperatures, respectively. Like germination rates, base temperature (T_b) declined from 3·71 to −0·83 °C as the percentile value increased from 10% to 80%. Caution was urged in extrapolating beyond the experimental data set. Differences in the ceiling temperature (T_c) with percentile could not be discerned.

Cumulative germination progress curves at each temperature were modelled by the Weibull, logistic, and cumulative normal distribution functions. Cardinal temperatures (T_b and T_c) calculated from these data reasonably approximated the actual data. The Weibull function demonstrated a good approximation at all percentile levels, while the logistic and cumulative normal distribution functions, as a result of their inherent symmetry, deviated at the extreme percentiles. It was concluded that the Weibull function not only accurately modelled cumulative germination but could also be used in the calculation of cardinal temperatures.

Key words: Seed germination rate, cardinal temperatures, faba bean, Weibull function, probit and logit scales.

INTRODUCTION

Germination of seeds is affected by temperature. Nevertheless, the characterization and analysis of these effects is difficult. At a single temperature, germination progress curves are typically characterized by a lag phase, in which no germination occurs, an increasing, approximately linear phase, during which the rate of germination is constant, leading to a tailing off in germination rate as the maximum germination percentage is reached. Both maximum percentage and rate of germination increase as temperatures increase above a base temperature (T_b; at which time to germination is infinite) towards an optimum (T_o) and then both decline as temperatures increase beyond the optimum towards a ceiling temperature (T_c; at which time to germination is again infinite).

Comparison of these germination curves from different temperature regimes is problematic. Single indices of germination, which attempt to embrance all facets of the progress curve, have been proposed (Goodchild and Walker, 1971), but none appears satisfactory (Brown and Mayer, 1988*a*; Naylor, 1981; Bould and Abrol, 1981). Various standard functions (for example the logistic, Gompertz, and monomolecular; Tipton, 1984) have undoubtedly proved better models of germination than single indices. Nevertheless, as Hunter, Glasbey, and Naylor (1984) point out, these functions often erroneously assume that the cumulative germination data to successive times are independent and that the variances of the data are normally distributed. Such analytical difficulties may in part be overcome by an appropriate transformation of the time-scale. Unfortunately, no single transformation

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seems universally applicable (compare Hunter *et al.*, 1984 and Naylor, 1989) which must reduce the value of this procedure. The interpretation of the parameters of these standard functions may also prove difficult. However, both Bahler, Hill, and Byers (1989) and Brown and Mayer (1988*b*), building on the suggestion of Bonner and Dell (1976), have demonstrated that the Weibull function is superior to other indices or functions of germination and that it fulfils the role of accurately preserving the data of any single germination progress curve, while providing parameters with biological meaning which can be compared statistically with those from other curves.

An alternative to attempting to compare cumulative germination progress curves from different temperature regimes may be to define the cardinal temperatures (i.e. T_b, T_o, and T_c; Garcia-Huidobro, Monteith, and Squire, 1982*a*) and then to estimate the thermal time requirement for germination so that data from all temperatures fall on a single curve. Ellis, Covell, Roberts, and Summerfield (1986) have demonstrated that for a single seed population germination responses may be described by two cumulative normal distribution curves; one for sub-optimal temperatures and another for supra-optimal temperatures. However, the estimation of times to germination for different percentiles by interpolation from cumulative germination curves at different temperatures and the regression of these rates against temperature in order to obtain cardinal temperatures and thus thermal time requirement is laborious. In their proposed screening method, Ellis, Simon, and Covell (1987) have suggested estimating base temperature and, therefore, thermal time requirements and then repeating probit analyses until the residual variance is minimized. Although expedient in the light of current analytical procedures, this method appears unsatisfactory because it fails to utilize data from the original germination progress curves in the estimation of base temperatures. Clearly, the estimation of cardinal temperatures and thermal time requirements would be enhanced considerably if a suitable function (e.g. the Weibull function) could be fitted to the germination progress curves for each temperature such that it not only accurately preserved the characteristics of the data but also facilitated the calculation of cardinal temperatures and thus the estimate of thermal time requirement.

Therefore, the major objective of this paper is to demonstrate not only that the Weibull function accurately models cumulative germination, but also that it can be used to calculate cardinal temperatures and thus thermal time requirement for the germination of seeds, in this case faba bean. Additionally, it seeks to compare these estimates of cardinal temperatures with those produced by fitting the cumulative germination progress curves to the logit and probit scales, the other established methods of modelling cumulative germination progress curves. All estimates of cardinal temperatures from fitted functions will be compared with those from the original data set.

MATERIALS AND METHODS

A single seed population of a spring sown faba bean (*Vicia faba* L.) cultivar Alfred was used in this study. The progress of germination was recorded at 13 constant temperatures, ranging from 6·2 to 39 °C, on a temperature gradient plate described by Garcia-Huidobro *et al.* (1982*a*). Three replicates of 20 seeds each were germinated on 10 g of moist sterile sand in 11 cm diameter Petri dishes placed across the gradient plate. The sand was sprayed with benomyl prior to germination to prevent fungal growth. Germination was defined as the protrusion of the radicle through the testa by 10 mm. Observations were initially made every 4 h for the first 2 d, thereafter observations were made every 6 h until 300 h had elapsed, when the experiment was concluded.

Estimation of cardinal temperatures from the original cumulative germination curve

At each temperature the data from the three replicates were bulked and a mean cumulative germination curve was plotted against time. From these curves estimates of the times to 10%, 50%, and 80% of the total germination achieved were obtained by interpolation (i.e. if total germination was only 80% of the seed present, then time to 50% germination would be when 40% of all the seed present had germinated). The 80th percentile was chosen since this represents a general minimum germination level acceptable for the commercial sale of seed. The other two percentiles were chosen to enable comparisons of the responses to temperature of the extremes of the seed population with that of the median values. The method of linearizing the data, adopted by Garcia-Huidobro *et al.* (1982*a*) was used rather than Arrhenius plots to enable comparisons with the results of Ellis *et al.* (1987). So, the rate of germination (i.e. the reciprocal of time to germination) for 10%, 50%, and 80% germination successively, was regressed against temperature, both for those temperatures below and those above the optimum temperature which was estimated by visual inspection from a plot of time to germination and temperature. The cardinal temperatures (T_b and T_c; Arnold, 1959) for each line are derived from the interception of each regression line with the abscissa, but this necessarily results in asymmetric confidence limits, the values of which can be calculated according to Feillers Theorem (Finney, 1978). T_o can be calculated from the intersection of these two regression lines. These values of T_b, T_o, and T_c were used to evaluate those estimated for fitted curves.

Fitted curves

Subsequently, the cumulative germination curves for each replicate at each temperature were modelled by one of three different functions;

Cumulative normal distribution,

$$y = M\frac{1}{\sqrt{2\pi}}\int_{-\alpha}^{t} e^{-1/2\mu^2}du$$

logistic function,

$$y = \frac{M}{1+e^{-(\alpha+Bt)}}$$

and the Weibull function,

$$y = M[1 - \exp(-k(t - z)^c)]$$

where y = cumulative germination at time t, M = maximum germination, k = rate of increase, z = lag in germination and c = shape parameter. Values of c around 3·6 suggest that the germination frequency distribution is symmetrical. Greater values indicate negative skewness, while lower values indicate a positively skewed distribution (Bahler *et al.*, 1989). Times to 10%, 50%, and 80% germination were obtained for each of the three replicates from each of these functions by calculation at each temperature. The regression of these rates of germination against temperature for each of the three percentiles allowed the calculation and comparison of cardinal temperatures derived by each method of analysis as previously described.

RESULTS

Estimation of cardinal temperatures from original data set

There was no germination of seed at 39 °C within 300 h and the maximum percentage germination within this time period was less than 50% at constant temperatures above 30 °C (Fig. 1). A similar, although less marked, decline in the maximum percentage germination achieved was seen at temperatures below 10 °C; these failed to reach 90% germination (Fig. 1). Ungerminated seed had fully imbibed.

Germination occurred most rapidly at about 25 °C and was progressively delayed as temperatures diverged from this assumed optimum (Fig. 2). Consequently, 23·8 °C was considered to be sub-optimal and 26·2 °C supra-optimal. The spread of germination was longer, i.e. the slope of the cumulative germination curve was shallower as temperatures became more extreme, especially at temperatures above the optimum (Fig. 2). The rates (i.e. the reciprocal of time to germination) at different percentile levels can be compared by regression analysis of rate against temperature. At both sub- and supra-optimal temperatures the regression coefficient was greater and, consequently, the thermal time requirement (°C days) was less at the lower percentiles than at the higher percentiles (Fig. 3). It may be noted also, that at sub-optimal temperatures the response to temperature was curvilinear, espe-

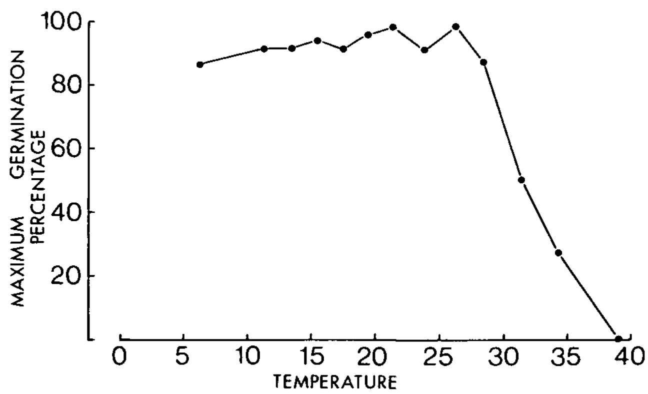

FIG. 1. The effect of constant temperatures (°C) on the maximum germination percentage after 300 h in faba bean.

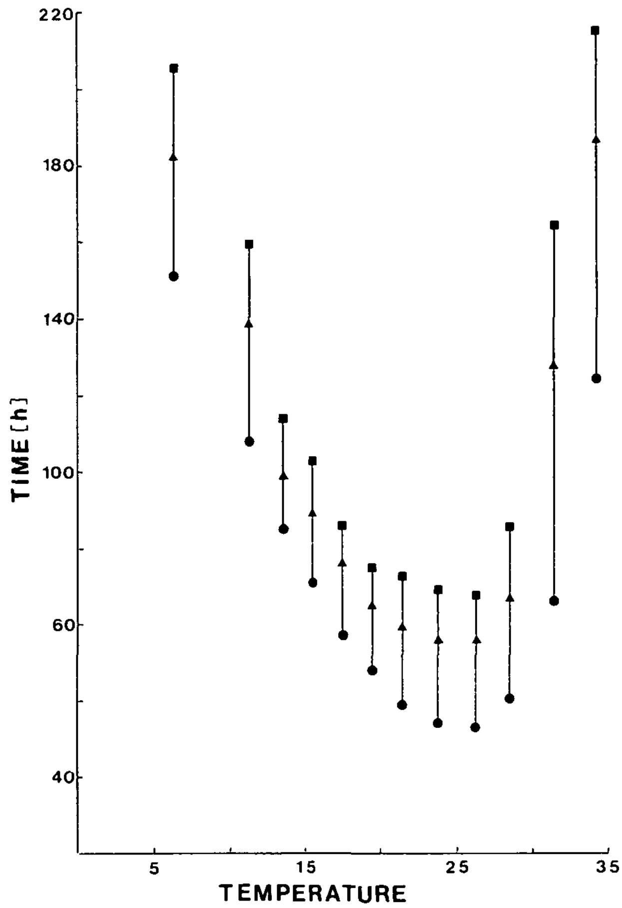

FIG. 2. Time to onset (h) and spread of germination (h) in faba bean in response to different constant temperatures (°C). Bar represents time to germination of percentiles of seed population which lie between 10% (●) and 80% (■); (▲) represents 50% germination.

TABLE 1. *Cardinal temperatures with their 95% confidence limits calculated according to Feillers theorem from the original data estimated for different percentiles from the regression of rate of germination of faba bean seeds against constant temperatures*

Percentile	T_b	Confidence limit		T_c	Confidence limit		T_o
		Lower	Upper		Lower	Upper	
t_{10}	3·71	1·43	6·31	36·94	26·48	52·26	26·19
t_{50}	0·40	−0·83	2·38	37·08	25·15	55·33	25·43
t_{80}	−0·83	−2·40	1·31	36·96	23·29	60·43	25·30

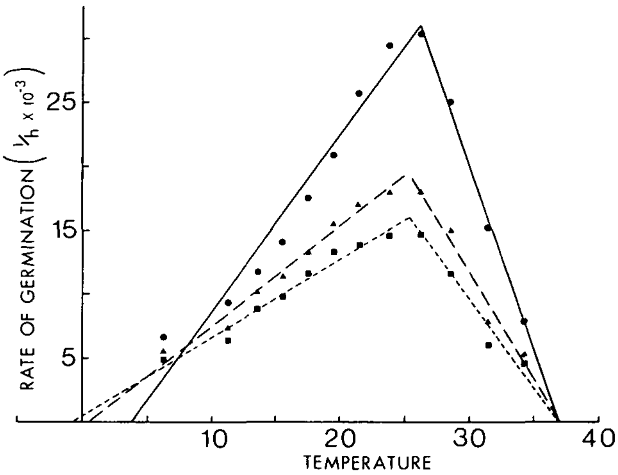

FIG. 3. The effect of germination percentile (10% ●——, 50% ▲——, 80% ■– – –) on the relationship between the rate of germination (h^{-1}) of faba bean seeds and constant temperature (°C) at both sub- and supra-optimal temperatures. (At sub-optimal temperatures $R^2 = 0.953$, at supra-optimal temperatures $R^2 = 0.951$.)

TABLE 2. *Constants describing the cumulative percentage germination* (M, k, z *and* c) *derived from the Weibull function at different constant temperatures*

M = Maximum percentage germination; k = rate of germination; z = lag phase; c = shape parameter.

Temperature (°C)	M (%)	k (1/h)	z (h)	c
6·2	85·6	0·015	122·9	2·413
11·3	91·9	0·015	80·8	2·617
13·6	91·7	0·027	67·6	2·827
15·4	93·5	0·026	53·7	2·743
17·5	91·7	0·024	35·9	3·520
19·4	96·7	0·027	30·6	3·000
21·5	98·3	0·020	14·6	3·160
23·8	91·9	0·020	9·8	3·147
26·2	98·3	0·017	0·0	4·067
28·5	78·5	0·023	30·2	1·487
31·4	50·0	0·008	67·0	3·097
34·2	28·3	0·008	70·0	2·725
s.e.d. (df = 24)	3·23	0·004	9·2	0·597

cially at the lower percentile levels, despite the large R^2 value. Base temperatures (T_b) were shown also to be different at the different percentile levels (Table 1). The base temperature was significantly greater at t_{10} than at t_{80} since their 95% confidence intervals failed to overlap, and so it seems that the base temperature declined as the particular percentile value increased. Ceiling temperatures (T_c) had wide confidence limits and so showed no significant variation with percentile (Table 1). Despite its consequently large error, the estimate of T_o, by the intersection of sub-optimal and supra-optimal rates vindicated the prior assumption of a T_o at approximately 25 °C (Table 1).

Estimation of cardinal temperature from fitted curves

The cumulative germination curves at each temperature were modelled by the Weibull function. Figure 4 demonstrates the complementarity of the function with the raw data even at extreme temperatures, especially at supra-optimal temperatures (Fig. 4B) where successive waves of germination with time provide evidence for sub-populations within the seed lot. Analysis of variance of the constants (k, z, and c) showed (Table 2) that the rate of germination (k) was reduced and the delay in onset of germination (z) increased at extreme temperatures. Analysis of deviance of M, assuming binomial errors, showed that the maximum germination percentage was reduced notably at supra-optimal temperatures (Table 2).

The cumulative germination curves were also transformed to both the logit and probit scales. From these fitted cumulative germination curves (fitted to the Weibull function, the logistic function, and cumulative normal distribution), time to germinate and, therefore, rates of germination of the t_{10}, t_{50}, and t_{80} percentiles could be calculated for the different temperatures (Fig. 5). Analysis of variance of these rates for sub-

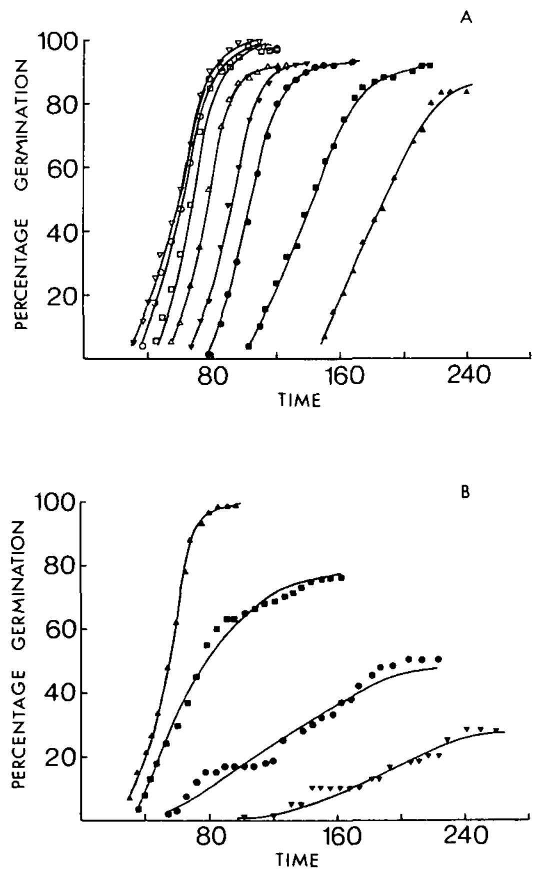

FIG. 4. A comparison of the cumulative germination percentage curves (symbols) with that predicted by the Weibull function (solid lines) for faba bean seed germinated at (A) sub- and (B) supra-optimal temperatures (°C). (▲ = 6·2, ■ = 11·3, ● = 13·6, ▼ = 15·4, △ = 17·5, □ = 19·4, ○ = 21·4, ▽ = 23·8, ▲ = 26·2, ■ = 28·3, ● = 31·2, ▼ = 34·2 °C).

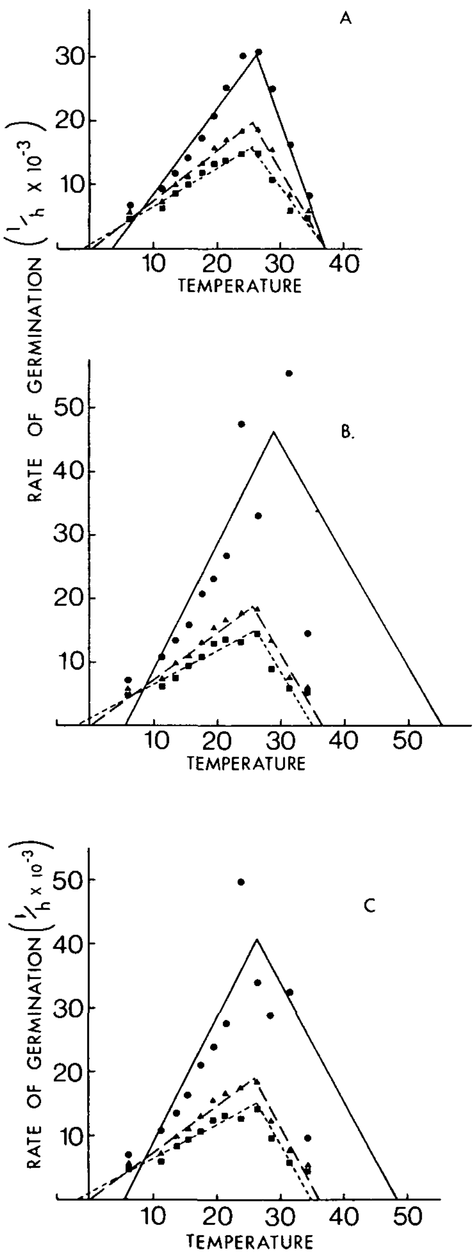

FIG. 5. The effect of different fitted functions (A) Weibull, (B) logit and (C) probit, and percentile (10% ●——, 50% ▲— —, 80% ■----) on the rate of germination (h^{-1}) of faba bean seed in response to constant temperatures (°C).

optimal temperatures showed a significant ($P < 0.001$) interaction between the function fitted and the percentile. Rates declined from the smallest percentile to the highest but less sharply with the Weibull function than with either the probit or logit analysis, which were similar. Greatest differences between methods in the calculation of the rates came at the extreme percentiles (especially t_{10}) while there was little difference at t_{50}. Not surprisingly, therefore, the accumulated thermal time (θ_1) requirement calculated from the reciprocal of the regression coefficient of the relationship between the rate and temperature differed for each percentile, increasing as the value of the percentile increased (Table 3). T_b also differed significantly for each percentile, decreasing as the percentile value increased. Table 3 shows that this was found within each method of analysis, and that the estimates of T_b and of θ_1, at each percentile showed greater similarity when the data were transformed to either the probit or logit scales than when the Weibull function was used. Despite this similarity the estimates of t_b and θ_1 were much more variable depending on the chosen percentile when either the logit or probit scales were used than when the Weibull function was used.

At supra-optimal temperatures, rates of germination were greater for lower percentiles (Fig. 5). The confidence limits around T_c were large, suggesting that T_c is poorly defined, although it too seems to decline with increasing percentile level (Table 4). Separate analyses of the rate of germination, for the three different percentiles derived from each fitted function, against temperature showed that for the probit and logit analyses, three parallel lines described the data (i.e. θ_2 was identical for the different percentiles but T_c differed (Table 4)). By contrast, the data for the three percentiles from the Weibull function fitted the independent lines (i.e. θ_2 as well as T_c differed; Table 3), more closely matching the actual data (Table 1).

DISCUSSION

Covell, Ellis, Roberts, and Summerfield (1986) and Ellis *et al.* (1986) have demonstrated that for a number of species of grain legume the cardinal temperatures for germination, particularly T_b and T_o, match the temperature environment for the geographical locations in which the different species or cultivars naturally occur. *Vicia faba* L. is no exception (Ellis *et al.*, 1987). Seeds of the cultivar Alfred had a temperature optimum of about 25·5 °C, which compares with that for the cultivar Sutton, which had a similar geographical range (Ellis *et al.*, 1987). However, the estimates of T_b for these two cultivars differed markedly. T_b for the cultivar Sutton was estimated at −3·0 °C, and was unaffected by the germination percentile. By contrast, the estimate of T_b for the cultivar Alfred varied with the germination percentile, declining as the percentile increased. Nonetheless, the estimate for T_b from even the largest percentile did not reach a value of −3·0 °C, but only −0·9 °C. T_b estimated when 50% of the seeds had germinated was 0·4 °C, identical to the value estimated by Bierhuizen and Wagenvoort (1974) for broad bean.

The significant decline in T_b as germination percentile increased suggests that seeds at the higher percentile should germinate before those of lower percentiles, assuming of course that each percentile makes an identical response to each unit increase in thermal time. If this assumption were correct, then the results present a biologically impossible situation. Alternatively, this assumption

TABLE 3. *Effect of model of cumulative percentage germination and percentile on the estimate of accumulated thermal time requirement (ϕ_1 °Cd) and base temperature* T_b *(including 95% confidence limits) at sub-optimal temperature for faba bean seed germinated at constant temperatures*

Percentile	Model								
	Weibull			Logit			Probit		
	θ_1	T_b		θ_1	T_b		θ_1	T_b	
t_{10}	31·2	3·59	(1·43 −6·31)	21·0	5·50	(1·50 −11·66)	21·0	5·50	(1·27 −12·37)
t_{50}	52·8	0·64	(−0·83 −2·38)	54·7	0·39	(−1·17 −2·29)	54·8	0·43	(−1·17 −2·37)
t_{80}	68·1	−0·75	(−2·40 −1·31)	76·2	−1·79	(−3·48 −0·37)	77·0	−1·72	(−3·49 −0·55)
R^2	0·947			0·866			0·847		

TABLE 4. *As for Table 3, but at supra-optimal temperatures, including an estimate of ceiling temperature* T_c

Percentile	Model								
	Weibull			Logit			Probit		
	θ_1	T_c		θ_1	T_c		θ_1	T_c	
t_{10}	15·1	37·0	(26 5 −52·3)	24·1	55·6[a]		22·3	48·2[a]	
t_{50}	24·6	37·0	(25·2 −55·3)	24·1	36·5	(24·6 −55·5)	22·3	36·2	(24·5 −55·9)
t_{80}	32·3	37·1	(23·3 −60·4)	24·1	34·9	(23·4 −59·3)	22·3	34·5	(23·8 −59·9)
R^2	0·932			0·350			0·507		

[a] Variances and covariance, at least 100-fold, greater due to lack of fit of regression line (see Fig 5B and 5C). Therefore no confidence limits are presented.

may perhaps be incorrect, suggesting not only that the T_b of a physiological process for any particular seed or plant population may not be an invariate character but also that physiological responses to temperature may not always be linear, although the use of Arrhenius plots may help to resolve this. Nevertheless, within the range of observed values (i.e. between 6·2 and 34·2 °C) the regression lines have an acceptable fit ($R^2 > 0·95$) to the data. Anderson, Smith, and McWilliam (1978) comment on the variation in T_b arising from extrapolation of data beyond the range of experimental temperatures and, therefore, it is clear that these values too, ought to be treated with circumspection. For in this case the lowest experimental temperature was 6·2 °C, and although the lowest temperature used by workers at the University of Reading was 0 °C, no germination was seen at this temperature after 28 d (Ellis *et al.*, 1987). Indeed, none has been seen after 800 h (approximately 33 d) at 3 °C (Kantar and Pilbeam, unpublished data) with other cultivars of faba bean. In the field, this failure to germinate at low temperatures would undoubtedly increase the likelihood of attack by fungal pathogens and other pests, and it is perhaps necessary to question the physiological importance of base temperatures for germination which are beyond those temperatures with obvious practical relevance. However, Arnold (1959) cautioned against rejecting base temperatures which seem physiologically too extreme. A suitable compromise has been suggested by Wagenvoort and Bierhuizen (1977) who propose the adoption of a practical minimum temperature which, because it is greater than the base temperature, gives rapid germination of a high percentage.

It is also important to note than these experiments were conducted at constant temperatures whereas environmental temperatures will show diurnal fluctuations superimposed on seasonal trends. Consequently, these estimated base temperatures, because they are derived from data obtained from artifical conditions, may give no indication of base temperature in conditions which approximate the natural environment more closely. Germination rates are more rapid, especially at extreme temperatures, if the seed experiences variations in temperature rather than a constant temperature (Garcia-Huidobro, Monteith, and Squire, 1982*b*; Thompson, Grime, and Mason, 1977). This may allow for the possibility of T_b beyond the experimental range of temperatures, but does not suggest that the estimate from constant temperatures accurately indicates the actual base temperature. At supra-optimal temperatures germination failed at 39 °C and was reduced to 50% or less at temperatures above 31·4 °C for the cultivar Alfred, a similar response to that for the cultivar Sutton (Ellis *et al.*, 1987). Nevertheless, T_c was estimated to lie between 36·9 °C and 37·1 °C depending on the percentile.

Germination may be modelled by a binomial distribution, or if sufficient samples were taken, by a normal distribution. However, these distributions which describe germination events do not account for the frequently skewed nature of germination or for bimodal distributions arising from differential dormancy of particular subsets of the seed population (Bould and Abrol, 1981) and in evidence here (Fig. 4B). Nevertheless, germination progress curves have been quantified by standardized normal distributions (Janssen, 1973) or by the logistic function (Schimpf, Flint, and Palmblad, 1977; Hsu, Nelson, and Chow, 1984). But probit or logit analyses, in attempting to linearize the data introduce distortions at the extreme percentiles. For this reason Ellis *et al.* (1987) omitted the extreme observations (i.e those observations where germination was less than 6% or within 6% of maximum germination at each temperature) for their analysis of the faba bean data. The Weibull function, however, while having no particular form has sufficient parameters to provide an accurate model of the germination progress curve data (Brown, 1987; Fig. 4). If any of these functions fails to preserve the form of the germination curves then the estimates of the cardinal temperatures for the different percentiles from any of these functions will differ from the actual value to a degree which matches the distortion. The data presented here show that the greatest divergence between methods in the estimation of cardinal temperature (T_b and T_c especially) occurred at the extreme percentiles. It also shows that this response was more pronounced with the probit and logit analyses than with the Weibull function, which more closely approximated to the values calculated from the actual data. Evidently any error in the calculation of T_b or T_c must also affect the estimates of θ_1 and θ_2 (thermal time requirements for germination at sub- and supra-optimal temperatures, respectively. However, the results from each of the methods were statistically indistinguishable suggesting that each of the three methods is acceptable, a conclusion supported by Bahler *et al.* (1989).

The Weibull function accurately fits the germination progress curve data (see Fig. 4 and the confidence limits of Tables 1, 3 and 4) and allows the calculation of cardinal temperatures. Estimates of these values are closer to those values calculated from the original data when the Weibull function is used to model the progress of germination than when the logit or probit analyses are used. Consequently, it might be supposed that the screen proposed by Ellis *et al.* (1987) could be improved by fitting the Weibull function rather than probits to the plot of cumulative germination against thermal time for sub-optimal temperatures and against T_c for supra-optimal temperatures, assuming still an iterative method for estimating T_b and θ_2.

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