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Optimizing the establishment of bean and maize varieties in tropical environments

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Abstract. The successful establishment of any crop is the initial indication of its productivity. Optimizing the establishment of a crop implies ensuring generalized, fast and concentrated emergence. This work studies optimal temperature ranges, under non-limiting water conditions, for both germination and emergence of two bean (*Phaseolus vulgaris* L.) varieties (*catarina* and *ervilha*) and two maize (*Zea mays* L.) varieties (*matuba* and *sam3*).

Experiments used a thermogradient plate. Petri dishes were used for germination experiments. Emergence experiments were performed in aluminium containers filled with packed portions of a sandy loam clay textured soil. Size, speed and spread of both germination and emergence were measured at different temperatures by Cu-CuNi thermocouples.

Thermal ranges with optimal counts of both germination and emergence [T_{o1}^{sz} , T_{o2}^{sz}] were identified using a flattened bell curve function. Speed was maximized for either germination or emergence over thermal ranges [T_{o1}^{sp} , T_{o2}^{sp}] defined using the plateau model to relate either germination or emergence rates with temperature. Ranges along which the spread of both germination and emergence are nearly minimized [T_{o1}^{sd} , T_{o2}^{sd}] were identified with the aid of even-degree polynomials. The intersection of all three thermal ranges gave rise to optimal temperature ranges [T_{o1} , T_{o2}] for germination (OTR_G) of the four varieties in study and for emergence (OTR_E) of three of them. In general, the lower thermal limit of OTR_G was determined by speed ($T_{o1} = T_{o1}^{sp}$) and the upper thermal limit by size ($T_{o2} = T_{o2}^{sz}$). OTR_E begins at T_{o1}^{sp} for *ervilha* and *sam3* and at T_{o1}^{sd} for *catarina* and ends at T_{o2}^{sz} for *catarina* and at T_{o2}^{sd} for the others. The endpoints and length of both the OTR_G and OTR_E were also found to be crop-dependent. Thus, farmers can choose between crops and optimize their establishment. The identification of these parameters may also be useful in assessing weather forecasts and for warning systems and agro-climatic zoning. The influence of the substrate used in each experiment was also discussed.

Keywords: germination rate; emergence rate; germination size; emergence size; spread of germination; spread of emergence; optimal establishment; temperature; thermal time



1. Introduction

A successful establishment of a given crop is the initial indication of high productivity and requires firstly generalized, speedy and uniform germination. The success of both processes ensures a fast and early production of a closed canopy in its usual growing season. High percentages of emerged seedlings increase competitiveness for light [1] and protect against weeds [2]. Fast emergence improves competitiveness with weeds [3] and avoids the exposure of both seeds and seedlings to soil pathogens [4], especially at low temperatures [5], as well as to sudden soil-drying conditions, mainly at high temperatures [6]. Although germination of the seed population spread out across time may be a survival strategy [7], a more concentrated germination is required to ensure greater uniformity during post-germination development and for crop duration [8].

The establishment of a crop strongly depends on soil temperature and moisture. Knowing the thermal and water requirements of crops is therefore important in predicting both seed germination [9] and seedling emergence [10], thus providing information for choices between different crops or varieties (behaviour, compatibility between them) [11] or when deciding on sowing times [12] and depths [13]. They are also important for climate-dependent inventories of crops, which are crucial for agro-ecological zoning [14] and in defining agro-climatic zones [15] of a territory. Temperature is the key parameter in ensuring successful establishment, when crops are not confronted with limiting water and light conditions.

Optimization of both germination and emergence has been mainly associated with maximizing their speed (rate). The maximum rate and the temperature at which it occurs (optimal temperature) are the classic expression of this optimization in either linear or non-linear models for the rate of the processes as a function of temperature. The most frequently used models are the piecewise linear triangular model (e.g., [16, 17]) and the non-linear beta model (e.g., [18, 19, 20]). These optimizations have also been successfully modelled by thermal ranges over which the rate is maximized, using plateau-shaped piecewise-linear models (e.g., [21, 22]).

Piecewise linear models are useful in practice, since they allow the definition of thermal time, which is an important tool to assess the success and optimality of both processes [23]. For a given fraction of germinated seeds or emerged seedlings, thermal times for the sub-optimal intervals [24] should not be exceeded. Otherwise, other factors such as soil water levels may become limiting factors [25].

Garcia-Huidobro *et al.* [17] optimized the germination of pearl millet considering not only the optimal temperature estimated by using a triangular-shaped model to simulate its speed, but also a thermal range (included in the thermal-tolerance interval) for high germination (final counts). A broader concept of successful germination based on maximizing size and speed and minimizing dispersion was suggested by [26]. These authors optimized the germination temperatures of seven Mediterranean crops by overlapping three thermal bands along which high, fast and concentrated germinations are achieved.

Tropical agriculture is practiced in regions of climate types Aw (tropical wet-and-dry), Af (tropical rain forest), BS (semiarid) and Cw (subtropical highland) (Köppen Classification) [27]. Despite greater food production in recent years, sub-Saharan Africa remains the world's most food insecure region, with uneven progress in the eradication of hunger [28]. The less optimistic outlook for climate change in this part of the world compounds other problems, such as income growth rates and distribution and political and economic conditions for agricultural production. The Intergovernmental Panel on Climate Change (IPCC) reports predict larger temperature rises in these regions [29]. Warmer nights and longer and more frequent heat waves are predicted for regions between 15°S and 15°N [30]. For Africa, a drop in rainfall is foreseen, together with more and more severe droughts, negatively affecting crop productivity [31]. The IPCC's "high confidence" temperature and rainfall predictions highlight the importance of knowing the thermal [32] and water [33] needs of crops, adapting them to the predicted scenarios and/or mitigating the effects that such changes foreshadow [34].

The main purpose of this research was to optimize the establishment (in terms of both germination and emergence), in a controlled environment, of crops that are common in tropical agriculture. Specifically, two bean varieties and two maize varieties were studied. In non-limiting water conditions, thermal bands were delimited for each variety, over which high percentages of the seed and seedling

populations germinate or emerge (large size), as quickly as possible (maximum speed) and in as short a time span as possible (minimal spread). To achieve this goal, the size, speed and spread of both germination and emergence, as a function of temperature, were previously modelled. The research also sought to improve knowledge of the four crops thermal requirements.

2. Material and methods

2.1. Seeds

Seeds were used for germination and emergence experiments of two bean (*Phaseolus vulgaris* L.) varieties (*catarina* and *ervilha*) and two maize (*Zea mays* L.) varieties (*matuba* and *sam3*). These varieties are very common in sub-Saharan Africa and are important nutritionally, as well as from an economic and social point of view. They are the basic "cash crops" for many rural communities. The four selected varieties have high potential yields, despite having different characteristics in terms of rusticity and resistance to pests and disease.

One hundred seeds of *catarina* and *ervilha*, weighed $36.6 \pm 0.8\text{g}$ and $34.2 \pm 0.9\text{g}$, respectively; 100 seeds of *matuba* and *sam3* weighed $29.8 \pm 1.0\text{g}$ and $37.0 \pm 1.1\text{g}$, respectively. Each of these means \pm standard deviations were calculated from ten 100-seed samples. The seeds used were provided and certified by the Estação Experimental Agrícola of Chianga, Huambo, an appropriate authority in Angola. The seeds were selected by visual inspection after being immersed for 2 min in a sodium hypochlorite solution (1%) to minimize the risk of bacterial and fungal infection. They were then washed in distilled water.

2.2. Thermogradient plate

The germination and emergence experiments were carried out on a temperature-controlled thermogradient plate built in the Agrometeorology Laboratory of Instituto Superior de Agronomia, at the University of Lisbon, Portugal [35]. Uniform thermal gradients along an aluminum alloy plate were achieved by heating one end with electrical resistances connected in series and by cooling the other end with a coolant (ethylene glycol) pumped from a refrigeration unit. Changing the energy inputs and outputs on the plate endpoints provided different thermal ranges. Target temperature ranges were chosen based on the known thermal tolerance range of each crop in the substrate that was used. Type-T thermocouples in direct contact with the substrate for each experiment were used to measure temperatures in twelve transversal bands. Two additional ones measured the temperature at both ends. The plate had a stable behaviour once thermal equilibrium was achieved (Table 1). Details regarding materials, design, modus operandi, behavior, accuracy and reproducibility of the thermogradient plate have been described in [32].

Table 1. Examples of temperature means (T_{mean} , in $^{\circ}\text{C}$) and standard errors (SE, in $^{\circ}\text{C}$) on the thermogradient plate used in the germination (7°C - 40°C) and emergence (9°C - 42°C) experiments performed with *Zea mays* var. *matuba*. Letters A–L denote the transversal bands of the thermogradient plate; (A) and (L) are the cold and hot ends, respectively.

Experiment	Statistics ($^{\circ}\text{C}$)	Transversal bands													
		(A)	A	B	C	D	E	F	G	H	I	J	K	L	(L)
Germination	T_{mean}	7.30	8.7	11.9	14.2	16.8	18.5	21.0	23.2	25.5	27.9	31.0	33.8	37.5	40.4
	SE	0.03	0.03	0.02	0.02	0.02	0.03	0.04	0.04	0.05	0.06	0.04	0.16	0.01	0.03
Emergence	T_{mean}	8.7	11.5	13.6	15.9	19.2	20.9	23.1	26.1	28.3	30.4	32.7	35.1	36.3	41.5
	SE	0.06	0.10	0.13	0.16	0.51	0.32	0.30	0.45	0.39	0.43	0.51	0.58	0.61	0.82

2.3. Germination and emergence experiments

In germination experiments, seeds were placed on filter paper soaked in water, inside sixty (60) glass Petri dishes distributed across the plate as shown in Figure 1a (12 transverse bands \times 5 dishes per band). Twenty seeds per dish were placed, totalling 100 seeds for each temperature/band. First, a target basic

range of temperatures (7°C–40°C) was imposed for all the varieties under study. In a second step, another target range (25°C–42°C) was imposed twice to obtain additional information on germination at other temperatures, namely close to those where germination rates were found to be high and/or in the thermal range over which the final percentage of germinated seeds is tending to decrease.

Details on the characteristics of the filter paper and the plates used, on the procedures that kept the seeds permanently moistened (filter paper method), as well as on the criteria for germination and counting frequency were described in [36]. Total germination at each temperature was taken as percentage of the seeds sown and considered the corresponding final germination (G_f). Germination experiments will sometimes be denoted as G_{FP} mainly when the importance of the substrate used must be highlighted.

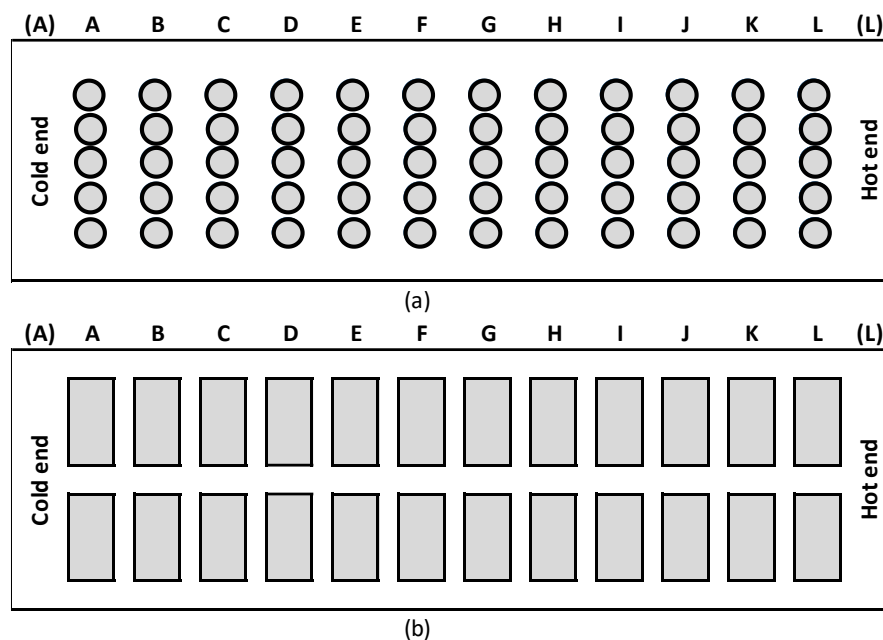


Figure 1. Experimental apparatus (thermogradient plate): (a) arrangement of Petri dishes \bigcirc used in the germination experiments with filter paper as substrate (five per band); (b) arrangement of aluminium containers \square used in the emergence experiments (two per band); Letters A–L stand for the transversal bands of the thermogradient plate (adapted from [36]).

Twenty-four (24) parallelepiped-shaped aluminium containers (257 mm long, 90 mm wide and 65 mm deep), filled with packed portions of soil (fine earth fraction), were distributed along the aluminium plate (12 transversal bands \times 2 containers per band) (Figure 1b). Ten seeds per container were placed at 2 cm depth about 2.5 cm apart, totalling 20 seeds for each temperature/band. Two target basic ranges of temperature (9°C–40°C for bean varieties and 9–42°C for maize varieties) were used considering the results obtained in the germination experiments. Here too, another thermal range (25°C–42°C) was imposed to obtain additional information about the emergence at other temperatures. Thermocouples were placed at sowing depth. Details regarding the type of soil used and corresponding characteristics (texture, bulk density, wilting point and field capacity), procedures that maintained optimal water conditions throughout the experiment and avoided damping off of seedlings (soil sterilization) as well as emergence and counting frequency criteria were described in [36].

Total emergence at each temperature was taken as percentage of the seeds sown and considered the corresponding final emergence (E_f). Emergence will sometimes be denoted as E_{soil} , especially when the importance of the substrate used must be highlighted.

2.4. Analytical procedures

The size, speed and dispersion of both germination and emergence were modelled separately, applying the models that were discussed in greater detail and successfully fitted to Mediterranean crops in [26]. The results will be discussed jointly, so as to highlight a successful establishment in terms of both germination or emergence.

Size (Sz)

Germination size (Sz_G) and emergence size (Sz_E) were measured at each temperature and denoted by G_f and E_f , respectively. High germination and/or high emergence are considered to occur whenever agronomically acceptable minimum (*a.a.m.*) values for G_f or E_f are achieved. This is a concept that varies depending on the crop [37]. As FAO Quality Declared Seed (QDS) [38] states that the percentage of seeds that germinate and develop should be at least 80% for maize and 70% for beans, these were the values of *a.a.m.* considered in this work.

High G_f and E_f values depend essentially on temperature, if water is not a limiting factor [16]. Values of G_f tend to be high and more or less constant along a fairly broad thermal range, but are significantly lower at both lower and higher extreme temperatures [17, 26, 39]. The variation of E_f with temperature follows a similar pattern to that of G_f [5, 40]. A kernel function of the type $f_k(x) = e^{-x^k}$ was proposed in [26] to model G_f as a function of temperature and was used here to model both Sz_G and Sz_E . The positive integer k is a shape parameter. When $k = 1$, a Gaussian (bell-shaped) curve is obtained. For $k > 1$, the curve becomes flatter at the top. Three additional parameters make this function more flexible: Sz_{max} (representing either G_{max} - maximum values of G_f , or E_{max} - maximum values of E_f), T_{max} (the midpoint of the plateau) and c_s (controlling the plateau width). The model equation to simulate either germination or emergence sizes (Sz), as a function of temperature (T), was therefore:

$$Sz(T) = Sz_{max} e^{-\left(\frac{T-T_{max}}{c_s}\right)^{2k}} \quad (\%) \quad (1)$$

Model (1) was fitted using a standard non-linear regression approach. Since k must be a positive integer (to ensure an appropriately shaped curve), different (small) fixed values of k were considered and the parameters were estimated by the least-squares approach. Goodness-of-fit was measured by the Residual Sum of Squares (RSS) and also Akaike's Information Criterion (AIC). By setting $Sz(T) = a.a.m.$ for each variety in Eq. (1), two temperatures are defined as the lower limit (T_{o1}^{sz}) and the upper limit (T_{o2}^{sz}) of a thermal range, across which the G_f or E_f are considered sufficiently high. For each variety, this thermal range $[T_{o1}^{sz}, T_{o2}^{sz}]$ optimizes the respective germination and emergence sizes.

Speed (Sp)

Germination and emergence speeds are often expressed by the reciprocal of the chronological time (t_G and t_E) necessary to achieve G_f or E_f (or some given fraction of them) and are denoted R_G and R_E .

The daily and annual thermal fluctuations make it more practical to identify a thermal range that maximizes either germination or emergence, rather than to calculate a single optimum temperature [32]. Furthermore, a model that gives more importance to the rate than to the optimum temperature and directly optimizes both germination and emergence (*i.e.*, without the need to subsequently resort to the prior imposition of a minimum rate) is consistent with farmers practical needs [26]. In this context, both germination and emergence speed were evaluated by using the Piper et al. model ([41]), successfully applied in the relationship between R_G [18, 32] or R_E [23, 42] (in day^{-1}) and temperature (T), which is a three-segment continuous piecewise-linear function. Specifically, this plateau-shaped broken-stick function is defined by equation (2) on the interval $[T_b, T_c]$ with an upward-sloping line segment that unites the points $(T_b, 0)$ and (T_{o1}, R_{max}) ; a horizontal line segment at height R_{max} , between the two temperatures T_{o1} and T_{o2} ; and finally a third, downward-sloping line segment uniting points (T_{o2}, R_{max}) and $(T_c, 0)$:

$$R(T) = \begin{cases} R_{\max} \frac{T-T_b}{T_{o1}-T_b} & , \text{ for } T_b < T < T_{o1} \\ R_{\max} & , \text{ for } T_{o1} \leq T \leq T_{o2} \\ R_{\max} \frac{T_c-T}{T_c-T_{o2}} & , \text{ for } T_{o2} < T < T_c \\ 0 & , \text{ elsewhere} \end{cases} \quad (\text{day}^{-1}) \quad (2)$$

The parameters T_b (base temperature), T_c (ceiling temperature) and T_{o1} and T_{o2} (optimal temperatures) are the cardinal temperatures, and parameter R_{\max} is the maximum rate. The interval $[T_{o1}, T_{o2}]$ provides an optimal range along which both germination and emergence rates are nearly maximum. The model generalizes the classic triangular model as parameterized by [43], which is a special case when $T_{o1} = T_{o2}$. In this work (optimizing germination or emergence speed), T_{o1} and T_{o2} will be denoted as T_{o1}^{sp} and T_{o2}^{sp} .

Standard linear regression techniques were used to fit both the ascending and descending segments (associated with the sub-optimal and supra-optimal ranges, respectively) and the horizontal segment (optimal range), by previously specifying a partition of the data points into groups corresponding to each interval. This rudimentary method always provides solutions, but it does not allow statistical inference for the cardinal temperatures and the maximum rate for either germination or emergence [32]. In order to overcome this drawback, the model (Eq. (2)) was also fitted with standard non-linear regression methods [44] using the full data set. However, the ‘broken-stick’ nature of the model, with points at which the function is not differentiable, means that sometimes optimal solutions cannot be found. The fitting algorithms only converge when the fitted values of T_{o1} and T_{o2} partition the same three groups of points used to fit each line segment. In such instances, standard nonlinear regression theory provides approximate confidence intervals for all model parameters. The initial values fed to the numerical algorithms used were the best estimates of the plateau-shaped (PS) model parameters obtained by the linear regression techniques proposed above for both germination and emergence. When convergence was not possible, no classical statistical inference is available. Whenever available, solutions that resulted from the nonlinear regression fitting algorithms were used. In all cases, the solutions chosen had the smallest value of RSS and the smallest difference between observed and estimated R_{\max} .

Goodness-of-fit was assessed by the global $R^2_{\text{glb}} = 1 - (\text{RSS}_{\text{glb}}/\text{TSS})$, where RSS_{glb} is the total sum of squared residuals (determined, for each point, in relation to the corresponding fitted line segment, as discussed in [32]) and TSS is the overall total sum of squares. In order to avoid the usual difficulties in fitting the initial part of the cumulative germination curve [45], the five parameters in Eq. (2) (T_{o1} , T_{o2} , T_b , T_c , and R_{\max}) were estimated for the 0.2 fraction of G_f . The parameters were also estimated for the fraction 0.8 G_f , which is an agronomically satisfactory final proportion for most crops, above which the number of germinated seeds per unit of time decreases considerably [7]. Frequent errors of observation associated with the small counts of initial and final germinations can also be avoided when considering these two percentiles of G_f [46]. Whenever no statistically significant differences are found between the values for both percentiles, the value of each cardinal temperature for either germination or emergence was taken to be their mean.

The thermal time for a given vegetative process is also a useful indicator to measure speed [47]. For both germination and emergence in the suboptimal ranges, thermal time (θ) - the accumulated temperature (in °Cd) above the respective base temperatures (T_b) required by a given fraction of either G_f (to germinate) or E_f (to emerge) [24] - is assumed to be constant between T_b and T_{o1} and was estimated as the reciprocal of the slope in the ascending portion of model (Eq. (2)), that is,

$$\theta_1 = (T_{o1} - T_b) / R_{\max} \quad (^\circ\text{Cd}) \quad (3)$$

Equation (3) was also used to calculate the thermal time as a function of both t_G and t_E for temperatures T between T_{o1} and T_{o2} (the optimal range), where θ is no longer constant (it increases with temperature). This means that further increases in temperature in the optimal range made little difference for both germination and emergence processes [26]. Thermal times corresponding to 0.8 G_f and 0.8 E_f were, in this work, considered indicative of optimal germination and emergence, respectively.

Since both G_f and E_f are nearly constant over a relatively wide thermal range (see previous subsection) and the time course of cumulative percentage for either germination [39] or emergence [48] processes approximately follow a sigmoidal (S-shaped) curve regardless of temperature, both times t_G and t_E (in days) required for the germination or the emergence of a fraction of G_f or E_f , respectively were obtained by linear interpolations between observed germination or emergence percentiles [32].

Spread (Sd)

The three phases of S-shaped curves for both cumulative germination and emergence curves (lag phase, near-linear growth phase and the final asymptotic plateau phase) vary over the thermal tolerance range of any crop [16, 22, 49].

It is thus useful to know for each crop a temperature range that ensures minimum dispersion values or acceptable values from the farmer's point of view, rather than finding only a single temperature that minimizes dispersion. Also, in the case of dispersion, the relevance of this issue increases with both daily and annual variations in soil temperature [49].

Both germination and emergence dispersions (Sd_G and Sd_E , respectively) were assessed by the differences between the respective germination or emergence times necessary for $0.2G_f$ or $0.2E_f$ (t_{20}) and $0.8G_f$ or $0.8E_f$ (t_{80}) at each temperature tested [26, 49]. Reasons for using chronological time instead of thermal time can be found in [16] or [49]. The option for these two percentiles was largely justified in the previous subsection (speed). The difficulties arising from the use of TSG (Time Spread of Germination) should also be overcome by using them [50]. Thus, the dispersion analysis focuses on the fastest phase of each process. This means that, for each temperature, it will depend only on the slope of the line segments connecting the points $(t_{20}, 0.2G_f)$ and $(t_{80}, 0.8G_f)$, for the cumulative germination curves and $(t_{20}, 0.2E_f)$ and $(t_{80}, 0.8E_f)$ for the cumulative emergence curves. Steeper slopes are associated with less dispersion along time of either germination or emergence. Plots of germination or emergence times versus temperature [51, 52] suggested that, for all crops, both times were minimal along a fairly broad thermal range and increased toward the more extreme temperatures considered, regardless of the germination or emergence fraction. A polynomial function of even degree ($2k$, $k \in \mathbb{N}$) was proposed in [49] to model the relationship between Sd (either Sd_G or Sd_E , both expressed by $t_{80}-t_{20}$) and temperature (T):

$$Sd(T) = Sd_{\min} + \left(\frac{T - T_{\min}}{c_d} \right)^{2k} \quad (\text{hours}) \quad (4)$$

Here, the positive integer k controls the width of the interval where the function values are close to the minimum, Sd_{\min} is the minimum value of $t_{80}-t_{20}$ (minimum dispersion for either germination or emergence, in hours), T_{\min} (in °C) is the central (midpoint) value of temperatures in the range corresponding to the basin around Sd_{\min} and c_d (in °C) is a parameter associated with the basin width. For given values of k , this model was fitted using standard non-linear regression procedures, and estimates of Sd_{\min} , T_{\min} and c_d , were obtained. The solutions selected were those which, among the values of k considered, minimized RSS and AIC, which were again the measures of goodness of fit used. Unlike for size (both G_f and E_f), recommended admissible maximum values for the spread of both germination and emergence were not found in the literature. The value of $m.a.s. = 1.05Sd_{\min}$ was considered as the maximum acceptable spread [49]. Setting, in Eq. (4), $Sd(T) = m.a.s.$ for each variety, estimates for the lower and the upper endpoints of a thermal range $[T_{01}^{sd}, T_{02}^{sd}]$ across which the spread of both germination and emergence are minimal were obtained.

Optimal thermal range for both germination and emergence

The optimization of germination, based on the thermal conditions to which the seeds are exposed requires the identification of a thermal range that maximizes both size and speed, with minimal spread. For an optimal emergence, these same requirements must also be present in a thermal band that defines the conditions to which the seedlings are exposed while rising towards the soil surface.

Therefore, optimal thermal ranges for either germination (OTR_G) or emergence (OTR_E), ($[T_{01}, T_{02}]_G$ and $[T_{01}, T_{02}]_E$, respectively) can be obtained by intersecting the three ranges defined for speed, size and spread of each process, *i.e.*:

$$[T_{01}, T_{02}] = [T_{01}^{sz}, T_{02}^{sz}] \cap [T_{01}^{sp}, T_{02}^{sp}] \cap [T_{01}^{sd}, T_{02}^{sd}]$$

No optimal thermal range will be defined whenever the above intersection is an empty set. When $[T_{o1}^{sp}, T_{o2}^{sp}]$ varies with the percentile considered, two OTR_G and OTR_E were defined for each crop.

The R software [53] was used to fit the above models for size, speed and spread of germination. The statistical significance of differences between the estimates of the various parameters was assessed by possible overlaps of their 95% confidence intervals.

3. Results

G_{FP} below 10°C and above 35°C was not relevant for any of the studied varieties (Table 2). Only the germination of *sam3* was still noticeable at temperatures close to 40°C ($G_f = 46\%$ at 39°C). Thermal ranges along which E_{soil} occurred were narrower than those found for G_{FP} . Only *matuba* emerged at about 12°C (11.7°C) and residually ($E_f = 5\%$), whereas at about 37.5°C only maize varieties emerged (both with low E_f).

Table 2. Final germinations (G_f) and emergences (E_f) and corresponding standard errors (mean \pm SE, in%) at the mean temperatures (T) used to model their size, speed and spread for two bean varieties (*catarina* and *ervilha*) and two maize varieties (*matuba* and *sam3*).

Germination								Emergence							
<i>catarina</i>		<i>ervilha</i>		<i>matuba</i>		<i>sam3</i>		<i>catarina</i>		<i>ervilha</i>		<i>matuba</i>		<i>sam3</i>	
T (°C)	$G_f \pm SE$ (%)	T (°C)	$G_f \pm SE$ (%)	T (°C)	$G_f \pm SE$ (%)	T (°C)	$G_f \pm SE$ (%)	T (°C)	$E_f \pm SE$ (%)	T (°C)	$E_f \pm SE$ (%)	T (°C)	$E_f \pm SE$ (%)	T (°C)	$E_f \pm SE$ (%)
10.1	18 \pm 0.19	9.8	16 \pm 0.15	8.8	12 \pm 0.11	9.6	23 \pm 0.11	12.3	0 \pm 0	11.7	0 \pm 0	11.4	5 \pm 1.58	11.7	0 \pm 0
12.6	72 \pm 0.34	12.4	44 \pm 0.13	12.0	52 \pm 0.17	12.9	78 \pm 0.24	15.4	30 \pm 0	14.1	100 \pm 0	13.6	35 \pm 1.58	14.1	35 \pm 4.74
14.9	74 \pm 0.29	15.1	66 \pm 0.13	14.2	92 \pm 0.18	15.1	94 \pm 0.19	17.3	60 \pm 9.48	16.3	95 \pm 1.58	15.8	70 \pm 3.15	16.5	75 \pm 1.58
17.5	85 \pm 0.32	17.6	80 \pm 0.23	16.9	92 \pm 0.15	17.8	99 \pm 0.09	20.3	85 \pm 1.58	18.9	100 \pm 0	18.1	85 \pm 1.58	19.1	80 \pm 0
19.3	89 \pm 0.24	19.7	93 \pm 0.11	18.6	95 \pm 0.12	19.2	92 \pm 0.11	23.0	90 \pm 0	20.1	100 \pm 0	20.6	95 \pm 1.58	21.5	85 \pm 1.58
21.3	92 \pm 0.11	21.9	83 \pm 0.15	21.1	96 \pm 0.13	22.0	92 \pm 0.13	25.9	100 \pm 0	23.5	100 \pm 0	23.0	80 \pm 0	23.7	95 \pm 1.58
23.6	92 \pm 0.18	24.3	82 \pm 0.23	23.3	91 \pm 0.16	23.9	96 \pm 0.10	29.0	100 \pm 0	26.4	95 \pm 1.58	25.8	100 \pm 0	26.0	80 \pm 0
26.0	82 \pm 0.36	26.7	85 \pm 0.22	25.7	94 \pm 0.08	26.9	96 \pm 0.08	32.0	100 \pm 0	29.7	100 \pm 0	28.5	80 \pm 12.15	28.7	80 \pm 0
28.8	57 \pm 0.25	29.3	83 \pm 0.17	27.8	90 \pm 0.10	29.8	94 \pm 0.08	35.3	45 \pm 1.58	32.4	95 \pm 1.58	30.7	90 \pm 0	31.3	95 \pm 1.58
31.0	50 \pm 0.16	30.5	65 \pm 0.19	30.9	80 \pm 0.22	31.8	85 \pm 0.16	37.6	0 \pm 0	35.2	55 \pm 1.58	33.3	90 \pm 0	33.4	80 \pm 3.15
34.6	42 \pm 0.24	31.9	51 \pm 0.13	33.7	77 \pm 0.17	36.0	53 \pm 0.19			37.5	0 \pm 0	35.7	95 \pm 1.58	35.7	95 \pm 1.58
36.1	48 \pm 0.11	33.2	44 \pm 0.13	38.0	31 \pm 0.13	38.9	46 \pm 0.19					37.1	40 \pm 12.66	37.6	50 \pm 6.33
38.2	13 \pm 0.13	34.8	9 \pm 0.08			40.9	11 \pm 0.13							40.0	10 \pm 0
		39.3	2 \pm 0.05												

Variations in the values of S_z (S_{zG} or S_{zE}), R (R_G or R_E) and S_d (S_{dG} or S_{dE}) as a function of temperature (T) for both germination and emergence corroborate the assumptions that justified the use of the three proposed models: (a) both G_f and E_f were high (generally above the *a.a.m*) over a relatively wide thermal range, significantly decreasing for the highest and the lowest temperatures (Figure 2); (b) both the germination and the emergence speeds increased to a maximum value (R_{max}), remaining at this level over a more or less long interval, and then decreased to zero (Figure 3); (c) dispersions (D_G and D_E) were small over a broad thermal range and increased visibly toward the most extreme temperatures that were studied (Figure 4).

3.1. Optimizing size

The relationships between either G_f or E_f and temperature, for the four varieties (Figure 2), were generally well described by Eq. (1). Thus, for all varieties a thermal plateau along which either G_f or E_f are high was identified. Goodness-of-fit measures (RSS and AIC) are generally good for all varieties, regardless of the stage of development considered (germination or emergence). The lowest values of RSS were obtained when the germination size of both *ervilha* and *matuba* varieties and the emergence size of bean varieties were modelled. AIC values were generally lower for emergence than for germination (the exception was *matuba*).

Best fits for germination size were obtained with different exponents than those found for emergence size (Table 3). The powers corresponding to the best fits depended on the variety used. In G_{FP}

experiments they ranged from $k=1$ for *catarina* to $k=3$ for *matuba* and *sam3*; for E_{soil} , they ranged from $k=3$ for *catarina* and *ervilha* to $k=9$ for *matuba*. Estimated values of G_{max} ranged from 86.5% to 93.5% (corresponding to a $T_{max} = 22.6^{\circ}\text{C}$ for *ervilha* and a $T_{max} = 24.4^{\circ}\text{C}$ for *sam3*, respectively) whereas E_{max} ranged from 86.1% to 100% (corresponding to a $T_{max} = 26.3^{\circ}\text{C}$ for *sam3* and a $T_{max} = 24.1^{\circ}\text{C}$ for *ervilha*, respectively). The 95% confidence intervals for both G_{max} and E_{max} values in the different varieties overlapped (that is, the values are therefore not significantly different). However, the values in the confidence intervals for T_{max} were always larger for E_{soil} than for G_{FP} . Furthermore, maize varieties had higher germination T_{max} than bean varieties, whereas no clear trend existed for emergence (T_{max} values remained significantly lower for *ervilha* only). T_{max} for G_{FP} ranged from 21.8°C (*catarina*) to 24.4°C (*sam3*) whereas T_{max} for E_{soil} ranged from 24.1°C (*ervilha*) to 26.3°C (*sam3*).

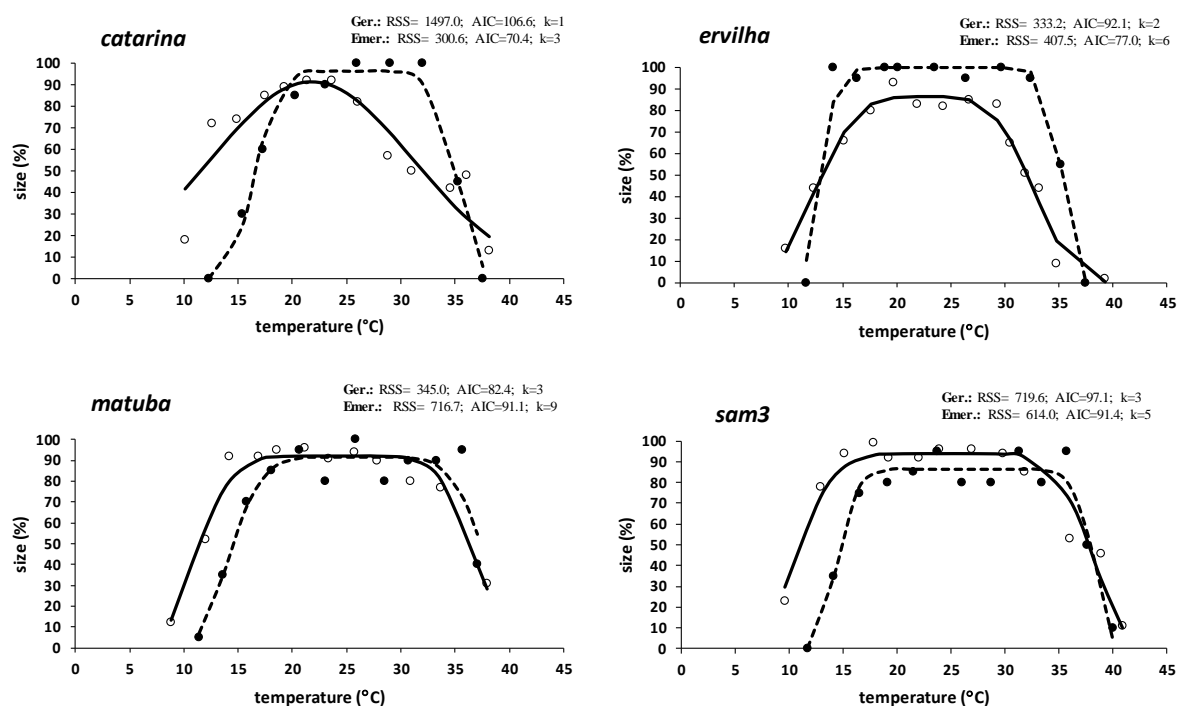


Figure 2. Final germinations (—○—) and emergences (---●---), both expressed in size (%), as a function of temperature (Eq. (1)), for two bean varieties (*catarina* and *ervilha*) and two maize varieties (*matuba* and *sam3*) and corresponding measures of "goodness-of-fit" (RSS and AIC). The values of G_{max} , T_{max} and c_s (model parameters) are shown in Table 3.

The width of the thermal plateau that ensures near-maximum levels of G_f or E_f (expressed by c_s) depends not only on the type of crop but also on the stage of development considered. Three of the varieties studied showed values of c_s for germination significantly greater than for emergence (only *ervilha* was an exception). Both for germination and for emergence, the c_s values were higher for maize varieties than for bean varieties.

Both the values of T_{01}^{sz} and T_{02}^{sz} and those of the length of the thermal plateau that guarantees either high G_f or E_f ($T_{02}^{sz} - T_{01}^{sz}$) differ with the stage of development considered. Furthermore, the values for each stage depend on the varieties studied. T_{01}^{sz} for germination were about $14-15^{\circ}\text{C}$ in all cases whereas for emergence they ranged from 13°C (*ervilha*) to 17.6°C (*catarina*). Values of T_{02}^{sz} for germination ranged from 28.7°C (*catarina*) to 35°C (*sam3*) whereas those for emergence ranged from 33.8°C (*matuba*) to 35.8°C (*sam3*). Maize varieties had longer interval lengths ($T_{02}^{sz} - T_{01}^{sz}$) for germination than for emergence, while the reverse was found for bean varieties. Differences between interval lengths ($T_{02}^{sz} - T_{01}^{sz}$) obtained for germination and emergence were greater for *ervilha* (about 7.1°C) than for the others (about $2-3^{\circ}\text{C}$).

Table 3. Parameters estimated by fitting Eq. (1) to final germination and final emergence for two bean varieties (*catarina* and *ervilha*) and two maize varieties (*matuba* and *sam3*) as a function of temperature: k is a (fixed) shape parameter; G_{\max} and E_{\max} are the maximum germination and emergence, respectively; T_{\max} is the plateau midpoint; c_s controls the plateau width; T_{01}^{sz} and T_{02}^{sz} are the lower and upper thermal limits for both high germination and emergence. Point estimates are given by *est.* and, when possible, the corresponding 95% confidence intervals are denoted by *conf. int.*

Experiment	Crop/ variety	k	G_{\max} (hours) or E_{\max} (hours)		T_{\max} (°C)		c (°C)		T_{01}^{sz}	T_{02}^{sz}
			est.	conf. int. (95%)	est.	conf. int. (95%)	est.	conf. int. (95%)		
Germination	<i>catarina</i>	1	91.8	[80.32, 103.24]	21.8	[20.30, 23.30]	13.2	[10.70, 15.67]	14.9	28.7
	<i>ervilha</i>	2	86.5	[82.03, 90.95]	22.6	[22.19, 23.00]	11.0	[10.53, 11.54]	15.2	30.3
	<i>matuba</i>	3	92.3	[87.98, 96.63]	24.0	[23.50, 24.51]	13.6	[13.07, 14.16]	14.2	33.8
	<i>sam3</i>	3	93.7	[87.83, 99.53]	24.4	[23.74, 25.04]	14.4	[13.73, 15.16]	13.8	35.0
Emergence	<i>catarina</i>	3	96.3	[90.41, 102.17]	25.8	[25.47, 26.19]	9.9	[9.51, 10.31]	17.6	34.0
	<i>ervilha</i>	6	100	-	24.1	[23.79, 24.38]	11.6	[11.27, 11.87]	13.0	35.2
	<i>matuba</i>	9	87.8	[81.94, 93.75]	25.7	[25.38, 25.94]	12.1	[11.80, 12.37]	17.5	33.8
	<i>sam3</i>	5	86.1	[80.97, 91.41]	26.3	[25.89, 26.73]	12.3	[11.84, 12.76]	16.8	35.8

3.2. Optimizing speed

Relationships between the rates of both germination and emergence and temperature for each of the four varieties in study were well-described by Eq. (2) irrespective of the percentile (20th and 80th) or the phase considered, germination or emergence (Figure 3). When using this plateau-shaped broken-stick, R^2_{glb} values exceeded 0.90 in all cases, and even 0.98 in most cases. Maximum rates (R_{\max}) and cardinal temperatures (T_b , T_{01}^{sp} , T_{02}^{sp} and T_c) varied with both the crop and the stage considered. Variations in cardinal temperatures with the fraction considered (20% or 80%) in each stage were generally small and without any defined trend model. Only in the case of T_{01} for germination of *catarina* and T_{02} for germination of *sam3* were there larger differences, of around 7-8°C, which could be considered statistically relevant because their confidence intervals did not overlap (Table 4). Thus, cardinal temperatures were taken as constant (a single temperature was considered for each variety/stage), except in those two cases where the values obtained for each of the two percentiles were considered for T_{01} and T_{02} (Table 5).

The size of the thermal tolerance intervals ($T_c - T_b$) for germination were greater than for emergence (T_b for germination were always smaller than T_b for the emergence whereas T_c showed an inverse trend for three out of four varieties). Maize varieties tolerate wider thermal ranges than beans (the ranges for germination and emergence of maize varieties were greater than 40°C and 30°C, respectively, and smaller than those values for bean varieties). Variation in ranges throughout the population were only relevant (greater than 2-2.5°C) for the germination of the maize varieties. The values of T_b were larger for emergence than for germination whereas T_c values were larger for germination than for emergence (with statistic relevance in both cases). For germination, *sam3* had the largest T_b (9.0°C) and *matuba* the largest T_c (53.1°C) whereas the latter had the lowest T_b (3.8°C) and *ervilha* the lowest T_c (38.1°C). For emergence, differences between varieties were much smaller: T_b varied between about 10°C (*matuba*) and 12°C (*catarina*), whereas T_c were around 37.5°C for the bean varieties and 43-45°C for maize varieties.

The minimum time required (*i.e.* the reciprocal of the maximum rates estimated for the optimal thermal range) to upshoot 80% of G_f ranged from 30h (*ervilha*) to 46.2h (*sam3*). On the other hand, *catarina* and *ervilha* take longer to reach 0.8 E_f (82.8h and 58.2h, respectively) than *matuba* (55.8h) and *sam3* (48h). Differences either between 0.8 G_f and 0.8 E_f or 0.2 G_f and 0.2 E_f were more relevant for bean varieties than for maize varieties: the former ranged from 1.8h (*sam3*) to 42.4h (*catarina*) whereas the latter ranged from about 16-17h (maize varieties) to 46.8h (*catarina*).

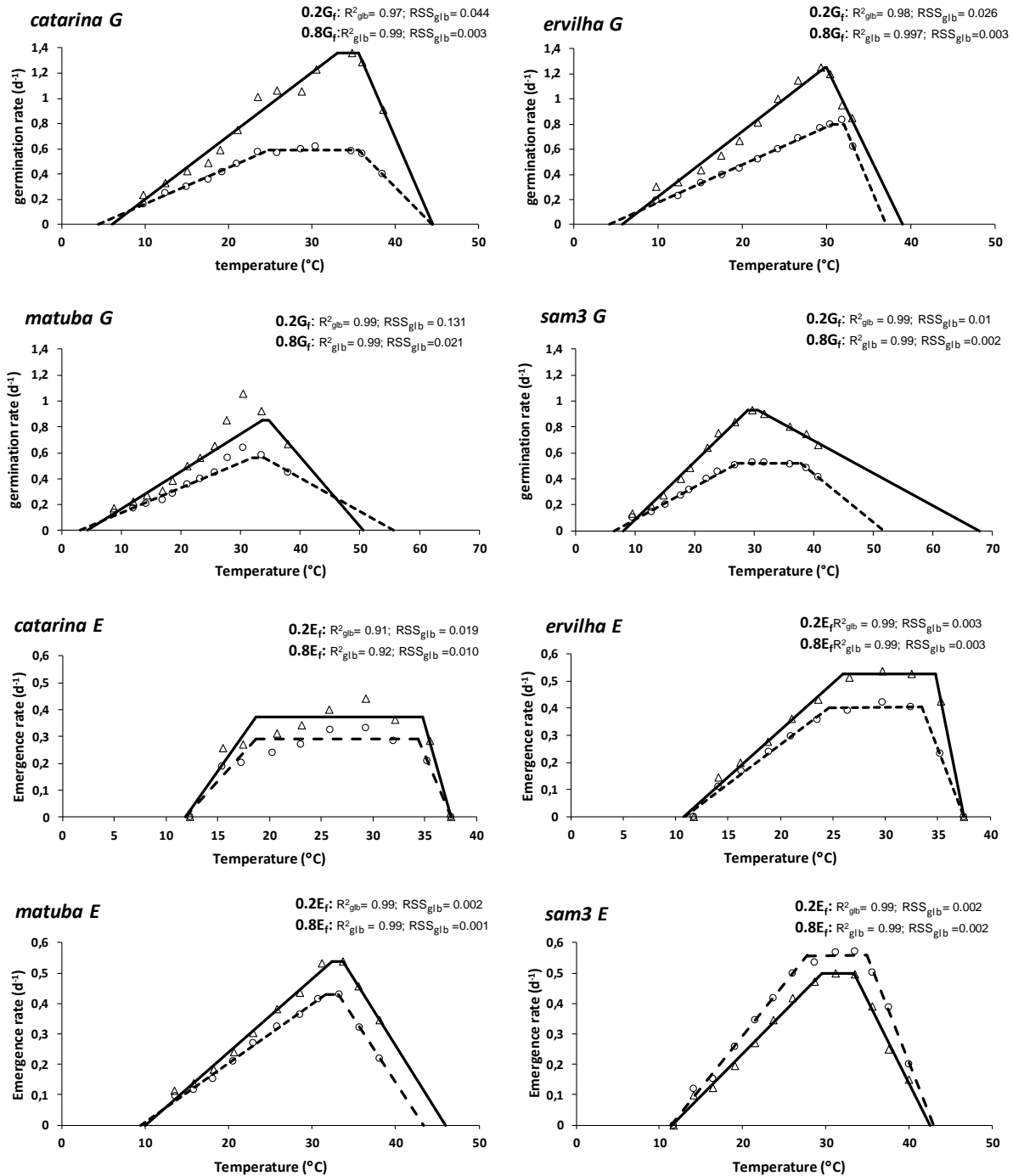


Figure 3. Germination (R_G) and emergence (R_G) rates as a function of temperature (T) for 0.2G_f or 0.2E_f (— Δ —) and 0.8G_f or 0.8E_f (--- \circ ---) and the corresponding measures of goodness-of-fit (R^2_{glb} and RSS_{glb}) for two bean varieties (*catarina* and *ervilha*) and two maize varieties (*matuba* and *sam3*), using the plateau-shaped model of Piper et al. [41] (Eq. (2)). G - germination; E – emergence.

Table 4. Coefficients estimated by applying Eq. (2) to the relationship between rate and temperature, cardinal temperatures (T_b - base temperature, T_{01} and T_{02} – optimal temperatures and T_c – ceiling temperature) and maximum rates (R_{max}) for two percentiles (20th and 80th) of both final germination and emergence of two bean varieties (*catarina* and *ervilha*) and two maize varieties (*matuba* and *sam3*), with the corresponding 95% confidence intervals (*conf. int.*) Exp.- Experiment; R – Regression techniques used (1- nonlinear; 0 – linear)

Exp.	variety	fraction (%)	Rt	coefficients				T_b		T_{01}		T_{02}		T_c		R_{max}	
				a1	b1	a3	b3	est.	conf. int. (95%)	est.	conf. int. (95%)	est.	conf. int. (95%)	est.	conf. int. (95%)	est.	conf. i (95%)
Germination	catarina	20	1	-0.305	0.050	6.761	-0.152	6.1	[3.88, 8.31]	33.2	[29.63, 36.72]	35.7	[34.16, 37.15]	44.6	[40.60, 48.59]	1.36	[1.21, 1.51]
		80	1	-0.128	0.029	2.983	-0.067	4.4	[2.94, 5.85]	24.8	[23.65, 26.01]	35.6	[34.88, 36.36]	44.5	[42.06, 46.87]	0.59	[0.57, 0.61]
	ervilha	20	0	-0.305	0.052	5.369	-0.137	5.8	-	29.8	-	30	-	39.1	-	1.25	-
		80	0	-0.13	0.03	5.937	-0.16	4.3	-	30.7	-	32.1	-	37.1	-	0.8	-
	matuba	20	0	-0.129	0.029	2.681	-0.053	4.4	-	33.6	-	34.6	-	50.6	-	0.85	-
		80	0	-0.06	0.019	1.434	-0.026	3.1	-	32	-	33.9	-	55.6	-	0.56	-
	sam3	20	1	-0.355	0.044	1.702	-0.025	8.0	[6.83, 9.17]	29	[27.10, 30.98]	30.7	[26.75, 34.60]	67.9	[55.48, 80.30]	0.93	[0.86, 1.00]
		80	1	-0.162	0.025	1.945	-0.038	6.5	[5.35, 7.60]	27.3	[26.17, 28.52]	37.9	[36.44, 39.39]	51.9	[44.40, 59.32]	0.52	[0.50, 0.54]
Emergence	catarina	20	1	-0.651	0.055	5.085	-0.135	11.9	[9.80, 13.95]	18.7	[16.27, 21.08]	34.8	[33.71, 35.99]	37.6	[36.79, 38.41]	0.37	[0.32, 0.42]
		80	1	-0.508	0.043	3.400	-0.090	11.9	[7.78, 13.94]	18.7	[18.10, 24.53]	34.4	[32.77, 35.74]	37.6	[36.68, 38.52]	0.29	[0.26, 0.32]
	ervilha	20	1	-0.374	0.035	7.227	-0.193	10.8	[9.86, 11.71]	26.0	[24.69, 27.25]	34.8	[34.08, 35.06]	37.5	[37.29, 37.71]	0.53	[0.50, 0.56]
		80	1	-0.32	0.029	3.766	-0.1	10.9	[10.04, 11.77]	24.7	[23.62, 25.84]	33.5	[32.83, 34.10]	37.5	[37.18, 37.82]	0.41	[0.39, 0.43]
	matuba	20	1	-0.24	0.024	2.022	-0.044	10.0	[8.81, 11.18]	32.4	[30.92, 33.85]	33.7	[32.15, 35.35]	46	[41.84, 50.08]	0.54	[0.51, 0.57]
		80	0	-0.183	0.019	1.823	-0.042	9.5	-	31.7	-	33.1	-	43.3	-	0.43	-
	sam3	20	1	-0.388	0.034	2.964	-0.069	11.4	[10.53, 12.16]	27.8	[26.76, 30.07]	34.9	[34.09, 35.53]	43.0	[42.13, 44.23]	0.56	[0.54, 0.58]
		80	1	-0.318	0.028	2.324	-0.055	11.5	[10.73, 12.26]	29.5	[28.10, 30.94]	33.4	[32.65, 34.20]	42.6	[41.78, 43.34]	0.5	[0.47, 0.53]

Table 5. Cardinal temperatures (mean values) for both germination and emergence of two bean varieties (*catarina* and *ervilha*) and two maize varieties (*matuba* and *sam3*), and thermal times at T_{01} (θ_{T01}) and T_{02} (θ_{T02}) for 0.8G_f and 0.8E_f.

Experiment	variety	T_b	T_{01}^{SP}	T_{02}^{SP}	T_c	θ	
						θ_{T01}	θ_{T02}
Germination	<i>catarina</i>	5.2	33.2 ¹ /24.8 ²	35.6	41.0	33.2	51.6
	<i>ervilha</i>	5.1	30.3	31.1	38.1	31.5	32.5
	<i>matuba</i>	3.8	32.8	34.3	53.1	51.9	54.5
	<i>sam3</i>	7.3	27.6	30.7 ¹ /37.9 ²	47.5	35.8	55.7
Emergence	<i>catarina</i>	11.9	18.7	34.6	37.6	23.4	78.3
	<i>ervilha</i>	10.8	25.3	34.1	37.5	35.4	56.8
	<i>matuba</i>	9.8	32.1	33.4	44.7	51.9	55.0
	<i>sam3</i>	11.5	28.7	34.2	42.8	34.4	45.4

¹Value referring to 0.2G_f; ²Value referring to 0.8G_f

The differences between the values of T_{01}^{SP} or T_{02}^{SP} for germination and for emergence were not relevant in four cases (differences did not exceed 1°C for T_{01}^{SP} in the case of maize varieties and for T_{02}^{SP} in the cases of *matuba* and *catarina* varieties) (Table 5). On the contrary, the T_{01}^{SP} of the bean varieties were noticeably larger for germination than for the emergence (the differences reached almost 15°C when the value of the 20th percentile for the germination of the *catarina* was compared with the respective value obtained for the emergence) whereas the T_{02}^{SP} for *ervilha* and *sam3* showed a different trend (in any case, the differences were around 3-4°C).

Hence, the length ($T_{02}^{SP} - T_{01}^{SP}$) of the optimal ranges [T_{01}^{SP} , T_{02}^{SP}] varied with both the variety used and its stage (germination or emergence) and, in two cases (*catarina* and *sam3* germinations), with G_f fractions (Table 5). *Catarina* and *sam3* (the varieties with the heaviest seeds) presented the most extensive optimal ranges for germination (10.8°C and 10.6°C for the 80th percentile, respectively, and both about 2.5°C for 20th percentile) whereas *ervilha* and *matuba* had much narrower optimal ranges (about 1-1.5°C in extension). As a rule, the range lengths found for emergence were greater than for germination (*sam3* is the exception when the optimal range for 0.8G_f was considered). These differences seem to be clear for the bean varieties (higher by at least 5°C) but irrelevant for the *matuba* variety. This trend was also evident for the 20th percentile of *sam3*, but not for the 80th percentile.

Germination speed was optimized at lower temperatures for *catarina* (24.8°C, when 0.2G_f is considered) than for *sam3* (27.6°), *ervilha* (30.3°C) or *matuba* (32.8°C). The emergence of bean varieties

was optimized at lower temperatures (18.7°C in case of *catarina* and 25.3°C for *ervilha*) than in maize varieties (32.1°C for *matuba* and 28.7°C in the case of *sam3*).

The accumulated temperature above $T_b(\theta_1)$ was constant up to T_{o1} . For G_{FP} , *catarina*, *ervilha* and *sam3* needed at least 33.2°Cd, 31.5°Cd and 35.8°Cd to complete 0.8 G_f , respectively, whereas *matuba* needed much more (51.9°Cd). To complete 0.8 E_f in soil *matuba* also needed to accumulate more temperature (*catarina*, *ervilha* and *sam3* required 23.4°Cd, 35.4°Cd and 34.4°Cd, respectively) (Table 5). Above the optimum range $[T_{o1}^{sp}, T_{o2}^{sp}]$ defined for germination, the accumulated temperature increased by 18°Cd for *catarina* and 20°Cd for *sam3*, but only about 1-3°Cd for *ervilha* and *matuba*. On the other hand, the increase over the interval $[T_{o1}^{sp}, T_{o2}^{sp}]$ defined for emergence was greater for the bean varieties (54.9°Cd and 21.4°Cd for *catarina* and *ervilha*, respectively) than for maize (3.1°Cd and 11°Cd for *matuba* and *sam3*, respectively).

3.3. Optimizing spread

Given the observed U-shaped pattern in the relation between dispersion of either G_{FP} or E_{soil} and temperature, the success of the application of the model expressed in Eq.4 was not surprising. This shape means that the dispersion ($t_{80}-t_{20}$) is minimal along a fairly wide thermal range and increases noticeably toward the most extreme temperatures (Figure 4). The increases observed in the thermal extremes for the three varieties (*ervilha*, *matuba* and *sam3*) seem to be more visible in emergence than in germination, and for germination, more evident in the coldest than in the warmest thermal range.

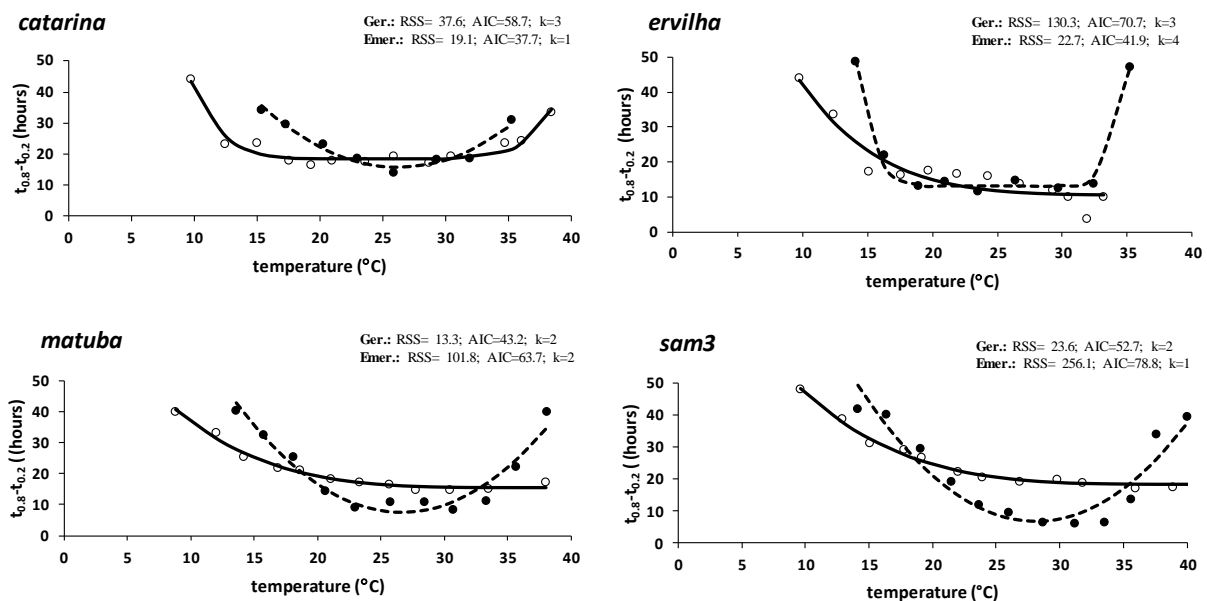


Figure 4. Dispersion of both germination (—○—) and emergences (---●---), expressed by $t_{80}-t_{20}$, (in hours) vs. temperature (Eq. (5)), for two bean varieties (*catarina* and *ervilha*) and two maize varieties (*matuba* and *sam3*). Also shown are the corresponding measures of "goodness-of-fit" (RSS and AIC). The values of D_{min} , T_{min} and c_d (model parameters) are given in Table 5.

Measures of goodness-of-fit (RSS and AIC) are generally good for all crops. They are better for emergence than for germination in the case of bean varieties and worse in the case of maize. For germination they were obtained with polynomials of degree $2k=6$ for bean varieties and $2k=4$ for maize varieties, whereas for emergence they were obtained with lower k values for three varieties ($2k=2$) and with a greater value ($2k=8$) for *ervilha*. Values of D_{min} , and T_{min} , and c were both crop and stage-dependent (Table 6). Maize varieties had significantly greater D_{min} , T_{min} and c values for germination than for emergence. The same trend was found for c values of both bean varieties, for D_{min} of *catarina* and for T_{min} of *ervilha*. Statistical significance was also found for differences in the c values of both varieties and in the T_{min} values for the *catarina* (reverse trend, in this case). *Ervilha* and *matuba* varieties

had the lowest D_{\min} values for germination (10.5 and 15.4 hours, respectively) whereas the maize varieties had the lowest values for emergence (about 7 hours). In both stages (germination and emergence), differences for the other varieties were relevant. The estimated T_{\min} value for the germination of *catarina* was significantly lower (24.7°C) than those found for other varieties, which ranged from 38.2°C to 45.8°C. Also, the T_{\min} value for the emergence of *ervilha* (24.7°C) was significantly lower than those of other varieties, whose values ranged from 26.3°C to 28.1°C. The 95% confidence intervals of T_{\min} for the emergence of *catarina* and *sam3* also did not overlap.

The intersection of each even-degree polynomial function (Eq. (4)) with horizontal lines representing $1.05D_{\min}$ delimited a thermal band along which the dispersion is nearly minimal [T_{01}^{sd} , T_{02}^{sd}]. Both the interval sizes ($T_{02}^{sd} - T_{01}^{sd}$) and their thermal endpoints were crop-dependent. For any variety, the range was always larger for germination than for emergence (Table 6). Differences in ranges for both stages were less relevant for *catarina* (12.5°C) than for other varieties (always greater than 20°C). *Ervilha* had the widest interval for both germination and emergence. Maize varieties had very similar ranges, both for germination (about 26-27°C) and for emergence (about 4°C).

Table 6. Parameters estimated by applying Eq. (4) to simulate dispersion of both germination and emergence for two bean varieties (*catarina* and *ervilha*) and two maize varieties (*matuba* and *sam3*) as a function of temperature (k- shape parameter; D_{\min} - minimal dispersion; T_{\min} - the plateau midpoint; c- extent of the plateau), with the corresponding 95% confidence intervals (*conf. int.*), and the lower (T_{01}^{sd}) and upper (T_{02}^{sd}), thermal limits of optimal thermal ranges that ensure minimal dispersions [T_{01}^{sd} , T_{02}^{sd}] when a maximum dispersion of $1.05 D_{\min}$ was accepted.

Experiment	variety	k	D_{\min} (hours)		T_{\min} (°C)		c (°C)		T_{01}^{sd}	T_{02}^{sd}
			est.	conf. int. (95%)	est.	conf. int. (95%)	est.	conf. int. (95%)		
Germination	<i>catarina</i>	3	18.3	[17.10. 19.59]	24.7	[24.37. 25.00]	8.7	[8.47. 8.92]	16.1	33.3
	<i>ervilha</i>	3	10.5	[6.84. 14.16]	45.8	[29.33. 62.30]	20.1	[10.80. 29.41]	26.0	65.6
	<i>matuba</i>	2	15.4	[14.00. 16.74]	38.2	[33.17. 44.44]	13.1	[10.83. 15.97]	25.3	51.0
	<i>sam3</i>	2	18.6	[17.14. 19.98]	41.7	[36.11. 47.35]	13.8	[11.29. 16.25]	28.3	55.2
Emergence	<i>catarina</i>	1	15.8	[13.68. 17.87]	26.3	[25.62. 26.94]	2.5	[2.18. 2.73]	23.9	28.6
	<i>ervilha</i>	4	13.2	[11.75. 14.74]	24.7	[24.59. 24.79]	-6.8	[6.69. 6.84]	18.0	31.4
	<i>matuba</i>	2	7.4	[4.17. 10.63]	26.6	[25.97. 27.29]	-2.2	[1.98. 2.40]	24.5	28.8
	<i>sam3</i>	1	6.9	[2.36. 11.50]	28.1	[27.21. 28.99]	2.2	[1.89. 2.41]	26.0	30.2

3.4. Optimizing establishment

T_{01}^{sz} values were always lower than either T_{01}^{sp} or T_{01}^{sd} , irrespective of the stage. T_{02}^{sp} values were greater than both T_{02}^{sd} and T_{02}^{sz} for E_{soil} of the four varieties and in two out of the six cases for G_{FP} (in the other cases, T_{02}^{sd} was lower than T_{02}^{sp}). The range for low spread [T_{01}^{sd} , T_{02}^{sd}] was the largest for the germination of the four varieties ($(T_{02}^{sd}-T_{01}^{sd})/(T_c-T_b) \geq 0.44$), whereas the maximum speed interval [T_{01}^{sp} , T_{02}^{sp}] was the narrowest ($(T_{02}^{sp}-T_{01}^{sp})/(T_c-T_b) \leq 0.28$). Thermal ranges that maximize the final emergence counts [T_{01}^{sz} , T_{02}^{sz}] were larger ($0.47 \leq (T_{02}^{sz}-T_{01}^{sz})/(T_c-T_b) \leq 0.83$) than those that ensure the fastest emergence ($0.04 \leq (T_{02}^{sp}-T_{01}^{sp})/(T_c-T_b) \leq 0.62$) or minimize dispersion ($0.12 \leq (T_{02}^{sd}-T_{01}^{sd})/(T_c-T_b) \leq 0.50$). The near-minimum dispersion range for emergence was generally larger than the maximum speed range [T_{01}^{sp} , T_{02}^{sp}] (*catarina* was the exception). Thermal ranges that maximize either germination or emergence rates are often the narrowest in most cases (only intervals for the speed of emergence in *catarina* and *sam3* [T_{01}^{sd} , T_{02}^{sd}] are narrower).

Table 7 contains optimal thermal ranges ($[T_{01}, T_{02}]$, thermal bands that combine high, fast and sparsely dispersed germinations or emergences) for both G_{FP} (OTR_G) and E_{soil} (OTR_E), estimated for the four varieties and for a level of $m.a.s. = 1.05D_{\min}$. In most cases, it was possible to calculate them. Only OTR_E of *matuba* and OTR_G for the 20th percentile of *catarina* were empty sets. In the former case, the intersection would only be possible if the required G_f falls to an unacceptable level (*a.a.m.*, below 50%).

In the second case, the maximum acceptable value for the dispersion would have to double (*m.a.s.* = $2D_{\min}$). In cases where it was possible to compare OTR_G with OTR_E , they overlapped to a greater or lesser extent.

Table 7. Ideal thermal range for germination ($OTR_G = [T_{o1}, T_{o2}]_G$) and emergence ($OTR_E = [T_{o1}, T_{o2}]_E$) that guarantees minimum dispersions $[T_{o1}^{sd}, T_{o2}^{sd}]$, maximum speeds $[T_{o1}^{sp}, T_{o2}^{sp}]$ and high final percentages $[T_{o1}^{sz}, T_{o2}^{sz}]$, for *catarina*, *ervilha*, *matuba* and *sam3*. NOTES: (1) $[T_{o1}, T_{o2}]$ were estimated for both 20th and 80th percentiles of *catarina* and *sam3* germinations; (2) maximum acceptable spread (*m.a.s.*) considered = $1.05D_{\min}$.

Experiment	varieties	T_{o1}	T_{o2}
		(°C)	
Germination	<i>catarina</i> (0.2G _f)	-	-
	<i>catarina</i> (0.8G _f)	24.8	28.7
	<i>ervilha</i>	30.3	30.3
	<i>matuba</i>	32.8	33.8
	<i>sam3</i> (0.2G _f)	28.3	30.7
	<i>sam3</i> (0.8G _f)	28.6	35.1
Emergence	<i>catarina</i>	23.9	28.6
	<i>ervilha</i>	25.3	31.4
	<i>matuba</i>	-	-
	<i>sam3</i>	28.7	30.2

In general, the lower thermal limit of OTR_G was determined by speed ($T_{o1} = T_{o1}^{sp}$) and the upper limit by size ($T_{o2} = T_{o2}^{sz}$). The OTR_G for *sam3* was the exception in both cases ($T_{o1} = T_{o1}^{sd}$ and $T_{o2} = T_{o2}^{sp}$), but only for the 20th percentile. The lower limits of OTR_G (T_{o1}) were around 28.5°Cd for *sam3* (both percentiles), 33°Cd for *matuba*, 30°Cd for *ervilha* and about 25°Cd for *catarina* (80th percentile). *Sam3* and *catarina* had the largest OTR_G (from 2.4°C for the 20th percentile of *sam3* to 6.4°C for its 80th) whereas *matuba* presented the narrowest (1°Cd). OTR_G for *ervilha* was reduced to a single temperature (=30.3°C, corresponding to both T_{o1}^{sp} and T_{o2}^{sz}). The lower and the upper thermal limits of OTR_E for both *ervilha* and *sam3* were determined by speed ($T_{o1} = T_{o1}^{sp}$) and by dispersion ($T_{o2} = T_{o2}^{sd}$), respectively whereas those for *catarina* were determined by dispersion ($T_{o1} = T_{o1}^{sd}$) and by size ($T_{o2} = T_{o2}^{sz}$), respectively. The lower thermal limits of OTR_E were about 24-25°C for *bean* varieties and about 29°C for *sam3*. *Bean* varieties had the largest OTR_E (about 5-6°C) whereas *sam3* had the narrowest (1.5°C). In these intervals, optimal chronological durations are therefore expected for 0.8G_f or 0.8E_f corresponding to the estimated R_{\max} for the respective percentile.

Table 8 contains thermal times for the 80th percentile at the lower (θ_1 at T_{o1}) and upper (θ_1 at T_{o2}) thermal limits of both OTR_G and OTR_E for the four varieties. To optimize germination, bean varieties needed to accumulate less temperature (above the base temperature) than maize varieties. *Catarina* needed to accumulate 33.2°Cd at least (at T_{o1}) for 0.8G_f to be reached, whereas *ervilha* needed 31.6°Cd; maize varieties always need more than 40°Cd (at least 41.1°Cd for *sam3* and 51.9°Cd for *matuba*). The range of thermal times that optimize germination is narrower for *matuba* (1.8°Cd) than for *catarina* (6.6°Cd) and *sam3* (12.5°Cd).

Bean varieties needed to accumulate more temperature above T_b to reach 0.8E_f in soil than to guarantee the same percentage of seeds germinated on filter paper, regardless of the thermal limit considered (T_{o1} or T_{o2}). This was not, however, the case with *sam3* (no results were obtained for *matuba*), which makes the substrate used an issue to be discussed in future work. *Catarina* and *ervilha* needed, at least (T_{o1}), around 8°Cd and 3.7°Cd more to emerge in optimal conditions, whereas *sam3* needed 6.6°Cd less for this. These trends were accentuated over their optimal ranges (more than 18°Cd for bean varieties and less than 16.1°C for *sam3*, at T_{o2}). *Ervilha* and *sam3* needed to accumulated about 35°Cd to emerge 0.8 E_f, and *catarina* needed 41.4°Cd. $\theta_1(T_{o2}) - \theta_1(T_{o1})$ were about 15-16°Cd for bean varieties and 3°Cd for *sam3*.

Table 8. Thermal times corresponding to the lower (T_{o1}) and the upper (T_{o2}) thermal limits for the Optimal Thermal Ranges (OTR_G) of four varieties (*catarina*, *ervilha*, *matuba* and *sam3*) obtained, verified at both $0.8G_f$ and $0.8E_f$, for a maximum acceptable spread ($m.a.s.$) = $1.05D_{min}$.

Experiment	varieties	θ_1 at T_{o1} and T_{o2}	
		(°Cd)	
Germination	<i>catarina</i>	33.2	39.8
	<i>ervilha</i>	31.6	31.6
	<i>matuba</i>	51.9	53.7
	<i>sam3</i>	41.1	53.6
Emergence	<i>catarina</i>	41.4	57.6
	<i>ervilha</i>	35.3	50.1
	<i>matuba</i>	-	-
	<i>sam3</i>	34.5	37.5

4. Discussion

The size, speed and spread of both germination and emergence in two varieties of beans (*catarina* and *ervilha*) and two varieties of maize (*matuba* and *sam3*) were plotted against temperature of the substrate used (filter paper for germination and soil for emergence). The successful use of a plateau-shaped piecewise-linear function to simulate speed (expressed as rates) as a function of temperature was consistent with the results obtained by [21, 32] and [42]. Both a flat Gaussian-type function to simulate size and an even degree polynomial function to simulate dispersion (expressed as t_{80} - t_{20}) were effective, thus validating results in [26] and [49], respectively. These results suggest that these models may be promising also for other crops, under similar conditions. The good fits identify three thermal intervals along which size, speed and spread were optimized: $[T_{o1}^{sz}, T_{o2}^{sz}]$, $[T_{o1}^{sp}, T_{o2}^{sp}]$ and $[T_{o1}^{sd}, T_{o2}^{sd}]$, respectively. Nevertheless, the definition of each interval is not automatic. Only Eq. (2) defines, for a given fraction of G_f or E_f , a thermal range associated with the maximum speed of each of the stages. With both the flat Gaussian model (Eq. (1)) and the even-degree polynomial model (Eq. (4)) it is necessary to specify minimum requirements for successful percentages of final germination and emergence (*a.a.m.*) and maximum acceptable spreads (*m.a.s.*), respectively. These requirements depend on the crop or variety used, on local climate and local agronomic criteria [37, 54].

The ranges that minimized the dispersion $[T_{o1}^{sd}, T_{o2}^{sd}]$ for germination were larger than those that maximize size and speed ($[T_{o1}^{sz}, T_{o2}^{sz}]$ and $[T_{o1}^{sp}, T_{o2}^{sp}]$). These results differed not only from those obtained for E_{soil} but also from those found in [26] (G_{FP} of Mediterranean crops). In all cases (G_{FP} , E_{soil} and [26]) the thermal intervals that maximized size, $[T_{o1}^{sz}, T_{o2}^{sz}]$, were the largest. The tropical varieties used in this study thus seem to guarantee minimum Sd_G at temperatures close to the ceiling temperatures (*i.e.*, maximizing the germination growth rate is still possible at the greatest tolerated temperatures) which may represent a relevant adaptive value. This issue deserves further investigation, not least because the results regarding the emergence of the same varieties in clayey soil did not reflect the same trend.

As found in [26] for the germination of seven Mediterranean crops, it was in most cases possible (emergence of *matuba* was the exception) to define thermal ranges that optimized both germination and emergence, *i.e.*, along which G_f or E_f were high, R_G or R_E maximum and Sd_G or Sd_E minimum. However, the upper and lower limits of either OTR_G or OTR_E were not often determined by the same parameters that defined the OTR_G of the crops studied in [26]. The best-defined difference concerns the parameter that determines the upper limit of OTR_G . In fact, $[T_{o1}^{sd}, T_{o2}^{sd}]$ found for tropical varieties was large enough that the upper limit of OTR_G is dependent on size ($T_{o2} = T_{o2}^{sz}$) and not on dispersion ($T_{o2} = T_{o2}^{sd}$), as in the case of Mediterranean crops.

The results obtained in the germination and emergence experiments for each variety are not concordant in most cases, either in the corresponding OTR thermal limits (and the limits for the thermal time associated to each of them) and respective ranges or in the parameters (size, speed and spread) that guide such ranges. In fact, results regarding size (k , G_{max} , T_{min} , c), speed (cardinal temperatures, t_{o2}^{sp} -

t_{01}^{sp}) and dispersion (k , D_{min} , T_{min} , c) parameters for the germination of each variety were not the same as for the subsequent emergence. In many cases the differences were even relevant (e.g., only for *catarina*, the OTR_G and OTR_E are they similar).

There are factors that affect one process but not the other. For example, hypocotyl/coleoptile elongation (cell multiplication that depends essentially on temperature) and cell growth (which depends mainly on water) as the seedling moves towards the soil surface can influence the different results obtained, with possible repercussions in the greater or lesser extent of the thermal range that optimizes speed [T_{01}^{sp} , T_{02}^{sp}], especially in bean varieties. On the other hand, several factors affect germination and emergence to a different degree, namely oscillations in both soil temperature and soil moisture [6,10,13] and the residence time of seeds or seedlings in the soil [4, 55], and can to a large extent explain those differences. The increasing thermal amplitudes to which the seedling is exposed as it moves towards the surface [56] and the influence that temperature has on the circulation of water in the soil, thus influencing emergence more than the germination, are an example of such factors. The excessive residence time of seeds and seedlings in the soil, usually due to more extreme temperatures, exposes them to soil pathogens, slowing or even preventing not only germination but also the upward trajectory towards the soil surface of the seedlings constituted in the meantime [4, 55]. The larger this residence time, the greater the chances that soil pathogens will limit the survival of seeds and seedlings. The combined action of these two factors clearly increases the likelihood that not only will E_f be less than G_f but also that the difference between E_f and G_f will grow with lower temperatures. It may even imply that the base temperature for emergence is greater than T_b for germination, as [57] and [55] have already suggested, although without data to back up the claim.

As the substrate used in the germination and emergence experiments was different, its nature can become an important factor to consider when discussing the observed differences. The results obtained seem to corroborate the importance of such influence (e.g., final germination with filter paper was sometimes lower than final emergence in the soil, thermal times for emergence were sometimes lower than those for germination), but debating the influence of the substrate used is not an easy task because the methodology used did not include the study of germination in the soil. Even so, the results obtained in [58], where seed losses of the varieties studied here were evaluated as a function of temperature and the substrate used, may help to discuss E_f - G_f values. Those authors showed that, for lower temperatures, germination in soil is more limited than on water-soaked filter paper (G_{FP}), and suggested that this may be due to the different levels of contact between water and seeds and/or to the interaction between temperature, moisture and permeability from soil to air, that is, the conditions that affect the rate of oxygen diffusion in the soil [58]). Discussion on crop-dependent differences between germination and emergence regarding speed (e.g., R_G - R_E) and dispersion (Sd_G vs. Sd_E) are limited due to the different types of substrate used.

Considering the base temperature in both processes (always greater in E_{soil} than in G_{FP}) the thermal times tended to be close for any of the varieties. There were cases in which the thermal times were even greater for G_{soil} than for E_{soil} (*catarina* and *sam3* for temperatures that optimize speed and *sam3* for temperatures that optimize the respective processes), which reinforces the potential influence of the type of substrate.

Not surprisingly, the results showed relevant differences between the behavior of the crops studied (and even between varieties of the same species), allowing for clearer choices depending on the agroclimatic conditions present (options between crops to be installed, sowing time or even sowing depth). The consistency of the options should be based mainly on the differences between the parameters of OTR_G and/or OTR_E (limits and lengths) found for each crop or variety. Thermal ranges that optimize either germination or emergence allow agroclimatic zoning in tropical areas depending on the altitude. On the other hand, their corresponding lengths can highlight the role of proximity to the sea as an influential climatic factor in that zoning. Differences between OTR_G and OTR_E (more visible for *ervilha* and *matuba* than for *catarina* and *sam3*) may also indicate different levels of adaptability of each variety to the substrate used, thus suggesting future work on germination and emergence in soils with different textures.

Results for *sam3* only converge when OTR_G for $0.8G_f$ is considered, for *ervilha* they converge in T_{o2} but have completely different extensions, whereas for *catarina* T_{o1} and T_{o2} they are almost coincident. *Catarina* (and *ervilha* if only the results obtained for the emergency are considered) seem to adapt better to tropical climates of medium-altitude than maize varieties. Although the lengths of both OTR_E and OTR_G are relatively small (never exceeding 6°C), the establishment of *catarina* still seems to be more favoured in regions further from the sea than the other varieties (the greater the thermal interval length ($T_{o2} - T_{o1}$) of a crop, the greater its adaptability to regions further away from the coast). When the results for the germination of *ervilha* can be compared with those for emergence, we find apparently contradictory results with regard to the adaptability of this variety, both for more inland and highland zones (those for emergence suggest greater adaptability to areas further away from the coast and/or greater altitudes, whereas those of germination suggests the opposite), which again indicates the influence of the substrate used. *Sam 3* will be favoured in warmer areas but is more sensitive to large thermal variations, that is, more inland regions.

Although no OTR_E has been defined for *matuba* (no comparison with OTR_G is possible), it is possible to predict sub-optimal thermal conditions for its establishment between 28.8°C (T_{o2}^{sd}) and 32.1°C (T_{o1}^{sp}). With an assured high percentage of seedlings emerged ($E_f \gg a.a.m.$), the closer the temperature is to 28.8°C , the lower the dispersion over time, the closer to 32.1°C (temperature very close to T_{o1} for germination) the faster the emergence will be. Considering this sub-optimized range and the estimated OTR_G , *matuba* may be more suitable for warmer areas and with less thermal amplitudes. These results to some extent counter suggested guidelines from studies based only on the size parameter for the same varieties [27].

5. Conclusions

Thermal ranges for two varieties of beans (*catarina* and *ervilha*) and two varieties of maize (*matuba* and *sam3*) were defined by fitting functions relating germination or emergence counts with temperature (a flatter version of a Gaussian curve), germination or emergence rates with temperature (plateau-shaped piecewise-linear function) and germination or emergence dispersions with temperature (even degree polynomial). Across these thermal ranges, both germination and emergence are high ($[T_{o1}^{sz}, T_{o2}^{sz}]$), their speeds are maximal ($[T_{o1}^{sp}, T_{o2}^{sp}]$) and their dispersions are minimal ($[T_{o1}^{sz}, T_{o2}^{sz}]$), respectively.

The intersection of these three temperature intervals usually resulted in an interval of optimal temperature ranges $[T_{o1}, T_{o2}]$ for germination (OTR_G) and emergence (OTR_E). For most OTR_G , speed determined the lower thermal limit ($T_{o1} = T_{o1}^{sp}$) and size the upper limit ($T_{o2} = T_{o2}^{sz}$). For OTR_E , this trend was not so clear. The endpoints (T_{o1} and T_{o2}) and lengths of both OTR_G and OTR_E are crop-dependent. For the varieties that were considered, OTR_G and OTR_E do not always coincide. Differences found between values of the germination and emergence parameters suggested not only that different factors act differently in both processes, but also that the type of substrate used in the experiments may need to be taken into account for its interpretation.

This three-interval approach can provide farmers with an important tool to increase the chances of establishment success under favourable soil water conditions. This approach allows decisions regarding either the crops or varieties to be installed, or the sowing times of a particular crop or variety, to be made with a view to optimizing their establishment. Farm weather forecasts, warning systems of various kinds and agro-climatic zoning can also benefit from the knowledge of the parameters obtained.

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