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LIFE SCIENCE AND BIOMEDICINE

NOVEL-RESULT

Genotypic variation in cardinal temperatures and thermal time for germination and seedling emergence of pigeonpea (*Cajanus cajan* [L.] Millsp.)

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Abstract

In this study, we define the cardinal temperatures and thermal time for germination and emergence of pigeonpea genotypes. Seeds of six genotypes were subjected to constant temperatures ranging between 5 and 50°C in petri dishes with filter paper (germination) and with media (emergence) were placed in a thermal gradient plate. A nonlinear bent-stick model fitted to the rate of development to germination and emergence resulted in parameters predicting cardinal temperatures including base (T_b), optimum (T_o), maximum (T_m), and thermal time. Estimated T_b for 50% germination and emergence were 8.4 and 10.8°C, respectively, with no significant differences between genotypes. Optimum temperatures were 33.8 and 37.9°C for germination and emergence, respectively, with genotypes differing significantly. Thermal time for 50% germination and emergence varied significantly among genotypes. The results suggest that genotypic responses to the temperature are typical for their tropical origin and hence their suitability for cropping in summer dominant rainfall regions insubtropical Australia.

Key words: base temperature; bent-stick model; thermal gradient plate

1. Introduction

Pigeonpea (*Cajanus cajan* [L.] Millsp.) is an important legume crop originating from India and grows well in tropical and subtropical environments extending between 30°N and 30°S latitude. Unlike other grain legumes, pigeonpea production is concentrated in developing countries, particularly in South/Southeast Asian and Eastern/Southern African countries (Sharma, 1980). Information on a crop's response to temperature and photoperiod is required to characterize the planting windows and assess the suitability of the crop to different growing environments. Estimation of cardinal temperatures provides the ability to predict most suitable temperatures for germination and emergence, and this information is crucial for understanding the seedling.

Seed germination and seedling emergence are biological processes dependent on the interaction of soil temperature and moisture that determine the successful establishment of the crop (Moot et al., 2000). Seed germination is driven by soil temperature and water potential, whereas emergence is mainly driven by soil temperature (Wang, 2005). The thermal time concept has been used to describe the effect of

temperature on germination and emergence in nonlimiting moisture conditions of several plant species (Grundy et al., 2000; Hardegree, 2006; Michele et al., 2009; Moot et al., 2000). The calculation of thermal time accumulation for germination and emergence requires the definition of the base (T_b), optimum (T_o), and maximum (T_m) temperatures. Cardinal temperatures are often determined by assessing the germination rates over a range of temperatures (Angus et al., 1981). The reported mean cardinal temperatures for pigeonpea germination were T_b of 9.9°C (range 6.7–12.4°C), T_o of 32.0°C (range 26.2–36.0°C), and T_m of 45.0°C (range 43.4–46.0°C) with a substantial genotypic variation (Carberry et al., 2001; de-Jabrun et al., 1980). Angus et al. (1981) examined six cultivars of pigeonpea under 16 sowing dates in field, reporting T_b for seedling emergence as 12.7–13.0°C and thermal time as 55.3–61.1°Cd. Moot et al. (2000) found that the T_b for germination and emergence of temperate herbage species were ≤4°C and thermal time (Tt) requirement for germination ranged from 40 to 160°Cd. The information about the germination and seedling emergence response to temperature is essential to characterize the planting windows and assessing suitability of crops to different growing environments (Covell et al., 1986). However, there is limited information on cardinal temperatures for Australian-bred pigeonpea genotypes. The objective of this study was to quantify the cardinal temperatures and thermal time requirements for germination and emergence of six selected pigeonpea genotypes under 10 different constant temperature conditions.

2. Methods

Laboratory experiments were conducted at the Gatton Campus, University of Queensland, Australia (Latitude 27.5571°S, 152.2770°E). Six genotypes selected for this study were Quest, Queensland pigeonpea line (QPL) 941, QPL 1001, ICRISAT pigeonpea line (ICPL) 88022, ICPL 88039, and ICP 14425. The genotypes Quest, QPL 941, and QPL 1001 were obtained from the Australian Grains Gene Bank. The genotypes ICPL 86022, ICPL 88039, and ICP 14425 were the advanced breeding lines introduced from the International Crop Research Institute for the Semi-Arid Tropics (ICRISAT), India.

2.1 Germination

Three replicates of 25 seeds of each genotype were placed in petri dishes of 9-cm diameter lined with a double filter paper, watered with 10 ml of deionized water, and incubated at constant temperatures 5 and 50°C (6.8, 11.5, 16.4, 20.8, 24.6, 28.9, 33.3, 37.4, 42.5, and 47.4°C) in a thermal gradient bar. Seeds were considered germinated when radicle length exceeded 2 mm.

2.2 Emergence

Three replicates of 25 seeds of each genotype were placed in a petri dish (9 cm of diameter × 2.5 cm of depth) incubated at constant temperatures between 10 and 45°C (12.4, 16.4, 19.6, 22.4, 25.2, 28.0, 30.9, 34.2, 38.4, and 43.3°C) at a thermal gradient bar. Topsoil (sandy loam with 20% clay)–peatmoss mix (2:3) was used as a germination media (Michele et al., 2009). Deionized water was added to the topsoil–peatmoss media, as required to ensure moisture was not limiting for emergence. The bottom of the petri dishes was wrapped with aluminum foil to create a dark environment to encourage the hypocotyl to grow upward. The visual appearance of the hypocotyl loop above the soil surface was considered as emergence.

The temperature was recorded at 1-hr intervals using "Tiny tag Ultra®" data loggers (TGU-1515, Gemini Data Loggers, Chichester, United Kingdom) with an accuracy of ±0.5°C and a range of −40 to 85°C. The germination and emergence were monitored daily at the same hour of the day and continued until no further germination or emergence occurred for three consecutive days.

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2.3 Statistical analysis

The inverse of the duration ($1/t^{50}$) for 50% of final germination and emergence represented the rate of development (Angus et al., 1981; Masin et al., 2017; Moot et al., 2000; Parmoon et al., 2015). Nonlinear bent-stick model (equation (1)) for the rate of development and temperature were fitted on aggregated data (over three replicates) using nonlinear least squares in *R studio*, version 4.1.0 (Faraway, 2009).

$$\mu = \beta_1 + \beta_2 X + \beta_3 (X - \delta) \times \zeta, \tag{1}$$

where $\zeta = 0$ when $X < \delta$; otherwise 1 (Michele et al., 2009).

In this equation, μ represents the germination or emergence rate, X is the temperature, δ is the breakpoint, β_1 is an intercept, β_2 is the slope of the first segment, and $\beta_2 + \beta_3$ is the slope of the second segment.

The germination and emergence rates ($1/t^{50}$) were calculated and plotted against temperature for each genotype, and the lines converge to an intercept on the x-axis whereas T_b (equation (2)). T_o was predicted from the breakpoint of the curve of the fitted model. The x-intercept at supraoptimal temperatures was provided as values of T_m (equation (3)).

$$T_b = -\beta_1/\beta_2, \tag{2}$$

$$T_{max} = (\beta_1 - \beta_3) * \delta/(\beta_2 + \beta_3), \tag{3}$$

$$Tt_{sub} = 1/\beta_2, \tag{4}$$

$$Tt_{sup} = -1/(\beta_2 + \beta_3). \tag{5}$$

Thermal times (°Cd) were calculated separately as the inverse slope of suboptimal and supoptimal regression equations (equations (4) and (5)). The above procedure was performed for individual genotypes and genotype groups (QPL and ICPL). A paired t-test was performed by combining QPLs and ICPLs into groups. All pairwise comparisons among genotypes and their significances were performed using least significant difference at $p < .05$ proposed by Piepho (2012). p-values were computed using permutation hypothesis test and compared with normal theory-based values derived by fitting replicated data (Faraway, 2009).

3. Results

The maximum germination and emergence percentage of each genotype differed across incubation temperatures. It was greater than 80% between the temperature ranges of 20.8–37.4°C for germination, whereas emergence was above 80% between 25.2 and 34.2°C for all the genotypes. There was no germination of any genotype below 6.8°C and above 47.4°C, and no emergence below 16.4°C and above 43.3°C were observed in all genotypes (Table 1).

The germination and emergence rates ($1/t^{50}$) were calculated and plotted against temperature for each genotype (Figures 1 and 2; Angus et al., 1981). The distribution of values of cardinal temperatures and thermal time requirements for the genotypes are reported in Tables 2 and 3.

Here, the mean T_b values for germination and emergence were 8.4 and 10.8°C, respectively. The mean T_m values for germination and emergence were 47 and 44°C, respectively. The T_b and T_m values for the 50th percentile showed no significant difference among genotypes in both experiments. The calculated T_b for emergence was higher than germination with lower T_o and T_m values (Table 2).

The mean value of T_o for germination (37.9°C) was greater than that of emergence (33.8°C). The genotypes varied significantly for T_o for germination and emergence (Table 2). Optimum temperatures

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Table 1. Maximum germination (G) and emergence (E) percentage under constant incubation temperature (T_1 – T_{10}) regimes for six pigeonpea genotypes. Within column values followed by different letters are significantly different at $p < .05$

	Quest		QPL 941		QPL 1001		ICPL 86022		ICPL 86039		ICP 14425	
Temperature	G (%)	E (%)	G (%)	E (%)	G (%)	E (%)	G (%)	E (%)	G (%)	E (%)	G (%)	E (%)
T_1	0	0	0	0	0	0	0	0	0	0	0	0
T_2	7^{d}	15^{d}	67^{c}	22^{d}	23^{c}	13^{e}	37^{b}	18^{e}	7^{c}	17^{de}	10^{ef}	25^{c}
T_3	23^{c}	65^{c}	97^{ab}	73^{b}	70^{b}	68^{b}	97^{a}	68^{c}	57^{b}	65^{c}	27^{de}	63^{b}
T_4	53^{b}	68^{c}	100^{a}	83^{b}	87^{ab}	70^{b}	97^{a}	68^{c}	93^{a}	78^{bc}	57^{bc}	73^{ab}
T_5	50^{b}	75^{bc}	97^{ab}	100^{a}	86^{ab}	92^{a}	93^{a}	87^{ab}	87^{a}	87^{ab}	63^{ab}	82^{a}
T_6	87^{a}	93^{a}	93^{ab}	100^{a}	100^{a}	93^{a}	97^{a}	93^{ab}	93^{a}	92^{ab}	83^{a}	83^{a}
T_7	80^{a}	88^{ab}	93^{ab}	100^{a}	90^{a}	100^{a}	90^{a}	97^{a}	90^{a}	97^{a}	83^{a}	80^{a}
T_8	50^{b}	73^{bc}	93^{ab}	100^{a}	70^{b}	92^{a}	90^{a}	82^{bc}	90^{a}	82^{abc}	87^{a}	70^{ab}
T_9	0	13^{d}	80^{bc}	55^{c}	13^{cd}	48^{c}	87^{a}	38^{d}	53^{b}	33^{d}	37^{cd}	30^{c}
T_{10}	0	0	0	0	0	0	0	0	0	0	0	0

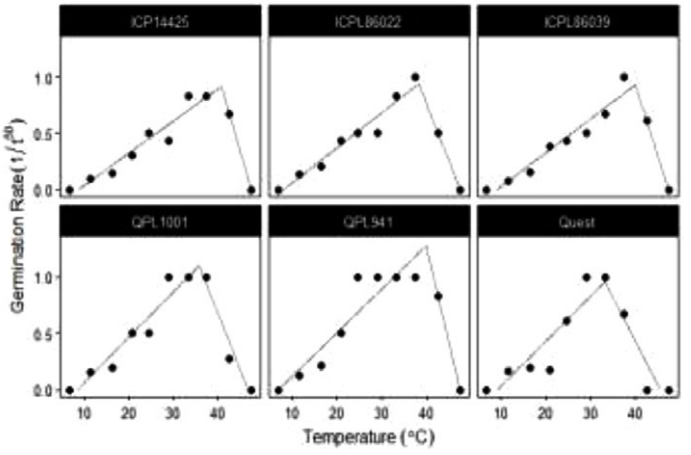

Figure 1. Fitting bent-stick nonlinear model for germination rate ($1/t^{50}$) as a function of incubation temperatures of 6.8, 11.5, 16.4, 20.8, 24.6, 28.9, 33.3, 37.4, 42.5, and 47.4°C for pigeonpea genotypes. $1/t^{50}$ is the rate of development to 50% of germination (d^{-1}).

for germination and emergence of genotype ICP 14425 were consistently higher (40.7 and 37.0°C, respectively).

The *Tt* for germination at suboptimal ($T < T_o$) and supraoptimal ($T > T_o$) ranges were lower than emergence (Table 3). A significant genotypic variation for *Tt* was observed in both germination and emergence experiments ($p < .05$). The *Tt* for 50% emergence at suboptimal and supraoptimal ranges were much higher than those of germination (Table 3).

Results of this study showed a well-defined trend between QPL and ICPL genotypes concerning the rate of germination. The QPL genotypes reached maximum germination rates at much lower temperatures than the ICPL lines and exhibited a much broader temp range at which rates of germination were at a maximum (Figure 3).

The results of the paired *t*-test revealed that the T_o for germination varied significantly ($p < .001$) between QPL (34.8°C) and ICPL (39.7°C) lines. However, two groups of pigeonpea lines (QPL and ICPL)

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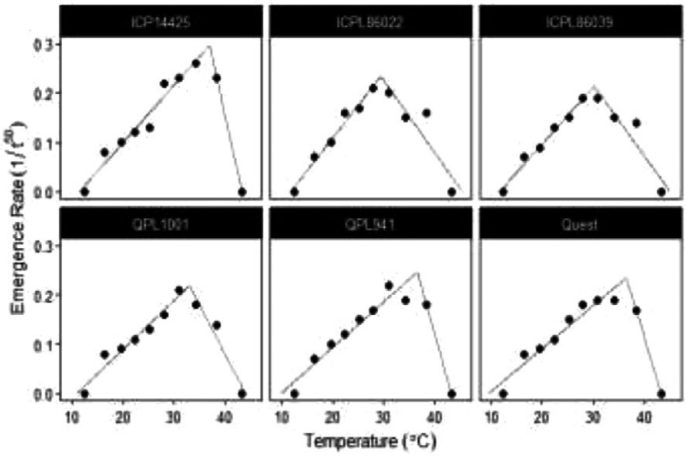

Figure 2. Fitting bent-stick nonlinear models for emergence rate ($1/t^{50}$) as a function of incubation temperatures of 12.4, 16.4, 119.6, 22.4, 25.2, 28.0, 30.9, 34.2, 38.4, and 43.3°C for the six pigeonpea genotypes. $1/t^{50}$ is the rate of development to 50% of emergence (d^{-1}).

Table 2. Cardinal temperatures for germination and emergence of pigeonpea genotypes. T_b is the base temperature, T_o is the optimum temperature, T_m is the maximum temperature, and s.e.m. - Standard error of the mean

	Germination			Emergence		
Genotype	T_b (°C)	T_o (°C)	T_m (°C)	T_b (°C)	T_o (°C)	T_m (°C)
Quest	9.2	33.1^{cd}	45.6	9.4	36.5^{a}	43.3
QPL 941	7.0	39.8^{a}	47.4	9.8	36.6^{a}	43.3
QPL 1001	8.5	35.7^{bc}	46.7	10.9	33.0^{bc}	44.0
ICPL 86022	7.9	38.2^{ab}	47.4	11.7	29.4^{b}	45.4
ICPL 88039	9.0	39.9^{a}	47.4	11.6	30.1^{b}	45.1
ICP 14425	8.7	40.7^{a}	47.4	11.4	37.0^{a}	43.3
Mean	8.4	37.9	47.0	10.8	33.8	44.1
s.e.m.	0.35	1.2	0.31	0.4	1.4	0.4
p-value	(0.065)	<0.05	(0.053)	(0.890)	<0.05	(0.753)

Note. Values followed by different letters differ significantly from one another ($p < .05$). Each cardinal temperature value was an average of three replications.

had similar response to different temperatures for emergence with the mean T_o of 36.3°C ($p = .034$; Figure 4).

4. Discussion

Information on cardinal temperatures is critical to predict germination time and seedling establishment in the field. The estimated mean values of cardinal temperatures for germination, T_b, T_o, and T_m, were 8.4°C ± 0.35 (range 7.0–9.2°C), 37.9°C ± 1.2 (range 33.1–40.7°C), and 47.0°C ± 0.31 (range 45.6–47.4°C), respectively. These values were consistent with the range reported for pigeonpea (Angus et al., 1981; Carberry et al., 2001; de-Jabrun et al., 1980). Carberry et al. (2001) reported that, mean values of cardinal temperatures for pigeonpea germination were, the T_b of 9.9°C (range 6.7–12.4°C) and the T_o of 32.0°C

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Table 3. Thermal time to 50% germination and 50% emergence of pigeonpea genotypes. Tt_{sub} is the thermal time at suboptimal temperatures, and Tt_{sup} is thermal time at supraoptimal temperatures

	Germination		Emergence	
Genotype	Tt_{sub} (°Cd) $[T_b - T_o]$	Tt_{sup} (°Cd) $[T_o - T_m]$	Tt_{sub} (°Cd) $[T_b - T_o]$	Tt_{sup} (°Cd) $[T_o - T_m]$
Quest	25.0^{b}	13.0^{ab}	114.9^{cd}	28.8^{d}
QPL 941	25.7^{b}	5.9^{c}	108.5^{cd}	27.2^{d}
QPL 1001	24.7^{b}	10.0^{ab}	100.9^{c}	49.9^{c}
ICPL 86022	32.1^{a}	9.8^{ab}	75.6^{b}	68.4^{b}
ICPL 88039	33.2^{a}	8.0^{a}	86.7^{a}	69.7^{b}
ICP 14425	34.8^{a}	7.3^{a}	85.9a	21.3^{a}
Mean	29.3	9.0	95.4	44.2
s.e.m.	1.88	1.01	6.2	8.8
p-value	<0.05	<0.05	<0.05	<0.05

Note. Values followed by different letters differ significantly from one another ($p < .05$). Each cardinal temperature value was an average of three replications.

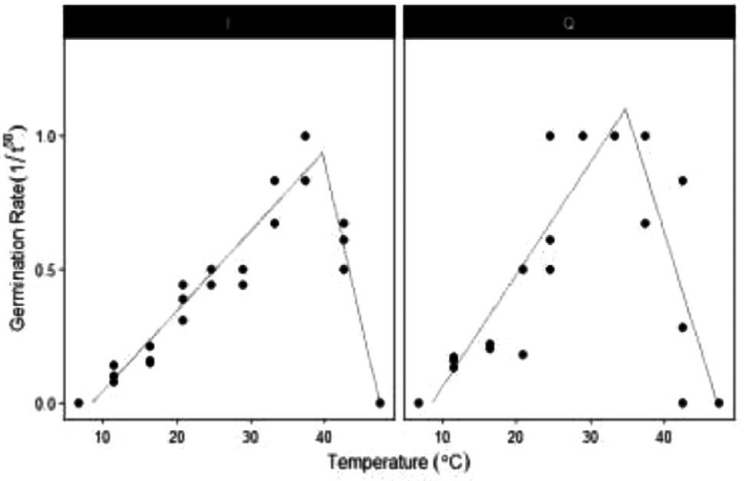

Figure 3. Fitting bent-stick nonlinear model for germination rate ($1/t^{50}$) as a function of incubation temperatures of 6.8, 11.5, 16.4, 20.8, 24.6, 28.9, 33.3, 37.4, 42.5, and 47.4°C for ICPL (I) and QPL (Q) pigeonpea lines. $1/t^{50}$ is the rate of development to 50% of germination (d^{-1}).

(range 26.2–36.0°C) and the T_m of 44.1°C (range 43.4–46.0°C) with a significant genotypic variation ($p < .05$). These figures were consistent with the cardinal temperatures reported by de-Jabrun et al. (1980), T_b of 7.1°C and T_o of 32.5°C (range 29.0–36.0°C) for germination.

The estimated cardinal temperatures for pigeonpea seedling emergence were 10.8°C ± 0.40 (range 9.4–11.7°C) for T_b, 33.8°C ± 1.4 (range 30.1–37.0°C) for T_o, and 44.1°C ± 0.41 (range 43.3–45.4°C) for T_m. According to Angus et al. (1981), the base temperature of pigeonpea grown in a field for emergence was 12.8°C ± 0.14°C. Among six genotypes tested, no significant differences were observed in the T_b for germination and emergence ($p > .05$), whereas a substantial genotypic variation was observed in the T_o for both germination and emergence ($p < .05$). The Tt for 50% germination and emergence varied significantly ($p < .05$) among genotypes (Table 3). The mean Tt for germination at sub- and supraoptimal

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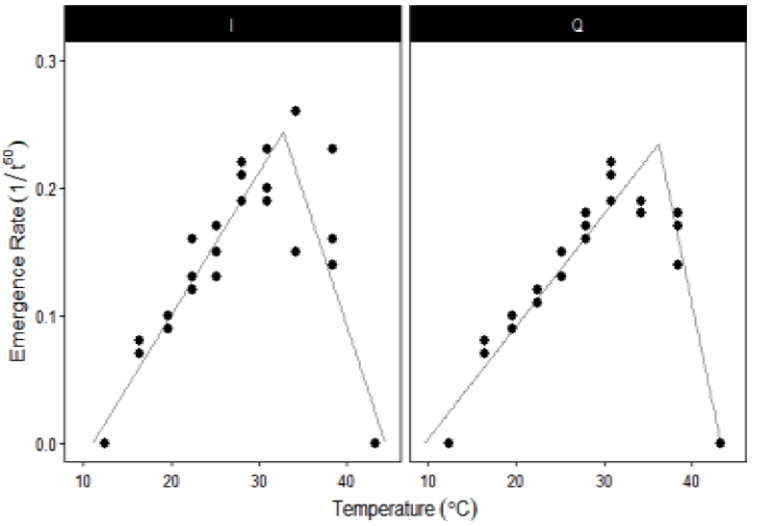

Figure 4. Fitting bent-stick nonlinear model for emergence rate ($1/t^{50}$) as a function of incubation temperatures of 12.4, 16.4, 119.6, 22.4, 25.2, 28.0, 30.9, 34.2, 38.4, and 43.3°C for ICPL (I) and QPL (Q) pigeonpea lines. $1/t^{50}$ is the rate of development to 50% of germination (d^{-1}).

temperature contrasts with the value of 58.2°Cd for thermal time requirement for emergence of pigeonpea presented by Angus et al. (1981). The authors used linear broken-stick model, which may fail to capture nonlinearity of the temperature response leading to this discrepancy. Moot et al. (2000) defined T_b and Tt for temperate pasture species found that a higher Tt for 50% field emergence for small seeded grass species (200–220°Cd).

The genotypic group analysis revealed that the germination and seedling emergence dynamics of the QPL genotypes were different from ICPL pigeonpea genotypes (Figure 4). The varying T_o among genotypes and between the two sets of pigeonpea genotypes might be attributed to the origin of these genotypes. For example, ICPL genotypes are adapted to the tropical environments of India and have a higher optimum growing temperature and not tolerant of cooler temperatures, whereas the QPL genotypes have broader optimum ranges.

The present study was conducted at constant temperatures, whereas, in field conditions, temperatures will have diurnal fluctuations. Furthermore, these cardinal temperatures are predictions only and may not indicate conditions that approximate the natural environment more closely.

Conclusion

The results of this study quantified the T_b for pigeonpea germination and emergence as 8.4 and 10.8°C, respectively. It also confirmed that no genotypic variation exists for the T_b and T_m temperatures ($p > .05$). However, the T_o for germination and emergence varied significantly among genotypes and between genotypic groups ranging from 33.1 to 40.7°C and 29.4 to 37.0°C, respectively ($p < .05$). The nonlinear broken-stick model also showed that there were significant differences in Tt requirements for germination and emergence between genotypes ($p < .05$). The results suggest that short duration pigeonpea genotypes exhibit germination and emergence responses to temperature and cardinal temperatures that are typical for their tropical origin. They are therefore broadly suited to cropping in the summer dominant rainfall regions of Australia, with soil temperature able to be used as guides to identify suitable sowing dates in different locations.

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Conflicts of interest. The authors of this study declare none.

Authorship contributions. S.M., R.C.N.R., M.C., and Y.S. conceived and designed the study and contributed to writing. S.M. conducted data gathering. S.M. and V.M. performed statistical analysis.

Data availability statement. The data that support the findings of this study are available from the corresponding author (S.M.) upon reasonable request.

Supplementary Materials. To view supplementary material for this article, please visit http://dx.doi.org/10.1017/exp.2021.31.

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Peer Reviews

Reviewing editor: Dr. Richard Erickson

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This article has been accepted because it is deemed to be scientifically sound, has the correct controls, has appropriate methodology and is statistically valid, and has been sent for additional statistical evaluation and met required revisions.

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Review 1: Genotypic variation in cardinal temperatures and thermal time for germination and seedling emergence of pigeonpea [Cajanus cajan (L.) Millsp.]

Reviewer: Mr. Carlos Sousa-Ortega

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Conflict of interest statement. "Reviewer declares none"

Comments to the Author: L93: Check the equation. I think it is = (3 — 1) ∗ / (2 + 3)

L98: How did you get these equation?, I think you should cite the articles that used these equations.

L100-101: If you did a regression using the aggregated data, you would have one data of Tb, To, Tm, Ttsub and Ttsup by biotype. So how did you perform the ANOVA without replicates for tables 2 and 3?

L102: "paired t-test" or "t-test".

L179-182: I do not know where the "34.8ºC" and "36.3ºC" come from. According to the methods (L102), you conducted a t-test comparing the QPL and ICPL lines. So, the average of the data presented in table 2 and 3 for each line must match, but it does not.

The second option is that you conducted another regression combining the QPL and ICPL lines, and then, these parameters were compared with a t-test. If you did this second option, you should clarified at the method section.

L205: In my point of view, you did not conduct a cluster analysis, you got the differences between lines with a t-test. Although, I think the information of this paragraph is interesting and I could fit better at L199 after "germination and emergence ($P<0.05$)."

L220-222: "The results ... tropical origin". This conclusion is good; however, you did not discuss it at previous section. I think that you should compare your results with the results of Moot et al., (2000). It would fit at L204.

Score Card

Presentation

Is the article written in clear and proper English? (30%)	5/5
Is the data presented in the most useful manner? (40%)	4/5
Does the paper cite relevant and related articles appropriately? (30%)	2/5

Context

Does the title suitably represent the article? (25%)	5/5
Does the abstract correctly embody the content of the article? (25%)	5/5
Does the introduction give appropriate context? (25%)	4/5
Is the objective of the experiment clearly defined? (25%)	4/5

Analysis

Does the discussion adequately interpret the results presented? (40%)	3/5
Is the conclusion consistent with the results and discussion? (40%)	3/5
Are the limitations of the experiment as well as the contributions of the experiment clearly outlined? (20%)	4/5

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Review 2: Genotypic variation in cardinal temperatures and thermal time for germination and seedling emergence of pigeonpea [Cajanus cajan (L.) Millsp.]

Reviewer: Dr. Richard Erickson

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Date of review: 21 September 2021

Conflict of interest statement. None

Comment

Comments to the Author: Please see my comments in the attached file.

Score Card

Presentation

3.6 /5

Is the article written in clear and proper English? (30%)	5/5
Is the data presented in the most useful manner? (40%)	3/5
Does the paper cite relevant and related articles appropriately? (30%)	3/5

Context

4.0 /5

Does the title suitably represent the article? (25%)	4/5
Does the abstract correctly embody the content of the article? (25%)	4/5
Does the introduction give appropriate context? (25%)	4/5
Is the objective of the experiment clearly defined? (25%)	4/5

Analysis

4.0 /5

Does the discussion adequately interpret the results presented? (40%)	4/5
Is the conclusion consistent with the results and discussion? (40%)	4/5
Are the limitations of the experiment as well as the contributions of the experiment clearly outlined? (20%)	4/5