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Research

Cardinal Temperatures and Thermal Time for Germination of Sarawak Traditional Rice

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ABSTRACT

Germination of two rice landraces, namely Bario Sederhana and Biris, was determined from twelve temperatures (12.5 – 40 °C) in a series of incubation experiments. The cardinal temperatures and thermal time for germination were estimated from a 'broken-stick' linear model. Both landraces had a T_b of 10 °C, T_{opt} between 32 – 33 °C, and T_{max} of 43 °C. At the sub-optimal temperatures, the thermal time for germination was 62 °Cd for Bario Sederhana and 53 °Cd for Biris. Within the supra-optimal range (T_{opt} to T_{max}), both landraces required 27-29 °Cd for seed germination. The maximum final germination for Bario Sederhana was 93% at 30 °C while Biris had 100% seeds population germinated at 27.5 °C.

Key words: Development, growing degree days, linear model, *Oryza sativa*, paddy

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INTRODUCTION

In rural regions of Sarawak, East Malaysia, traditional rice remains a popular choice among rice growers because it is pest-resistant, resilient to unploughed land environments, and requires minimum farm input. Thus, cultivation of traditional rice is prevalent in Sarawak with an estimation of at least 300 rice varieties identified (Khazanah Research Institute, 2018). Many of these varieties are said to possess exceptional quality in terms of taste (Wong *et al*., 2009), texture (Chih, 2016), aroma (Libin *et al*., 2012), and nutritional properties (Ronie *et al*., 2022). These varieties are sold as specialty rice and they fetch a premium price between MYR 8.00 to 19.50 per kilogram in the retail market (Lai *et al*., 2017). Coupled with high consumer demand for specialty rice, the emphasis on the production of specialty, premium rice products could increase farmers' profits and improve rural development. Some varieties originate from specific locations, with the quality derived from the origin, and as such are registered as Malaysia Geographical Indication. Examples of such varieties include the Bario and Biris rice.

Bario rice originates from the Kelabit Highland in Bario, Sarawak. The varieties of Bario rice are renowned for its finest grain qualities such as aroma, soft texture, taste, palatability, and nutrition (Wong *et al*., 2009; Thomas *et al*., 2013; Nicholas *et al*., 2014; Ronie *et al*., 2022). Its moderate glycemic index suggests that Bario rice has the potential to control blood glucose levels and thus can be marketed as a healthy food (Nicholas *et al*., 2014). Specifically, a commercially grown variety 'Bario Sederhana' is classified as medium grain rice with high protein and low-fat content, low gelatinization temperature, and high gel consistency which indicates a soft texture of cooked grain (Chih, 2016). This variety is suitable for health-conscious consumers who at the same time prefer food with excellent taste. On the other hand, Biris rice originates from the rice farms of Simunjan, Kota Samarahan, Sarawak. This variety produced an average grain yield of 2.2 tonnes per hectare with a stem height of 0.81 m (Nori *et al*., 2009). Biris rice is popular for its strong aroma and the grain is classified as very long and slender with a low percentage of chalkiness (Chih, 2016). Similar to Bario varieties, the cooked grains of Biris have a soft texture and are high in protein content. In addition, extracts from seedlings of Biris rice were reported to contain antioxidant properties that may have the potential to complement anti-cancer drugs, i.e., doxorubicin (Brandon *et al*., 2019).

In Sarawak, the majority of rice is grown rainfed on upland and flat terrains. Early crop establishment relies on an adequate population of seedlings that emerge following sowing. To achieve this, decision-making on suitable seeding rate is essential and can be influenced by seed germination performance. Provided that soil moisture is adequate, seed germination rate and count are mainly driven by temperature (Shaban, 2013; Nori *et al*., 2014). In general, seed germination accelerates with increasing temperature up to an optimum value, and any extremes of temperature can inhibit the germination process. For example, Tilebeni *et al*. (2012) reported no germination was observed at temperatures below 12 ºC and above 40 ºC on 15 rice cultivars. Furthermore, the accumulated heat units during a specific growth period, known as thermal time (ºCd), are utilized to measure the time required for seeds to germinate.

The calculation of thermal time requires cardinal temperatures (base, optimum, & maximum) to be determined from the relationship between temperature and germination rate (Angus *et al*., 1981). The base temperature (T_b) is the lowest temperature below which no germination occurs. The optimum temperature (T_{opt}) is where the fastest rate of germination is achieved in the shortest amount of time and the maximum temperature (T_{max}) is the extreme point where germination can take place.

Linear regression analyses of germination rate against temperatures with the intersection of the regression lines are commonly used to estimate cardinal temperatures (Angus *et al*., 1981; Cave *et al*., 2011; Draper and Smith, 1998). Nevertheless, field environments can only provide a limited range of temperatures. Specifically, in the tropical region, temperatures in the field below 25 ºC are not achievable and this will result in inaccuracy to calculate T_b because of a considerable extrapolation of the regression line. It is important to note that the prediction of T_b from linear extrapolation is affected by the number of temperatures at the sub-optimal. Therefore, incubation experiments can extend the temperature range to obtain a more accurate value of T_b and thermal time requirements (Angus *et al*., 1981).

Linear equations have been used to quantify cardinal temperatures for the germination of cultivated rice (Ali *et al*., 2003; Tilebeni *et al*., 2012) and weedy rice (Puteh *et al*., 2010). For these studies, cardinal temperatures reported T_b between 10 and 13 ºC, T_{opt} between 30 and 33 ºC, and T_{max} between 38 and 48 ºC for cultivated rice. In contrast, T_b, $T_{opt,}$ and T_{max} for germination of weedy rice were 2-7, 28-37, and 42-43 ºC respectively. Typically, cardinal temperatures are species-dependent regardless of cultivars but the array of temperatures used was inadequate, and the thermal time (ºCd) requirement for germination was not quantified in the previous studies (Ali *et al*., 2003; Puteh *et al*., 2010; Tilebeni *et al*., 2012). Furthermore, the specific landraces of Bario Sederhana and Biris were not included in any of these previous studies. Therefore, the objectives of this study are to determine cardinal temperatures and thermal time for germination of Bario Sederhana and Biris rice from a series of incubator experiments.

MATERIALS AND METHODS

Source of seeds

The seeds of two traditional varieties of rice, namely Bario Sederhana and Biris were obtained from a farmer's field in Serian District, Sarawak. This planting location was outside of the historical origin of Bario Sederhana from Kelabit Highland in Bario and Biris from Simunjan District. Hence, the Bario Sederhana and Biris varieties used in this study are referred to as rice landraces because of their distinct identity, and adaption to local environments making them genetically diverse and associated with farmers' preferences (Villa *et al*., 2005).

Germination study

The experiment was conducted in three replicates with each consisting of 50 seeds of Bario Sederhana and Biris rice landraces. The seeds were put in disposable petri dishes containing wetted filter paper and were left to germinate in unlit incubators (Conviron G30 Model, Winnipeg, Canada) at twelve constant temperatures of 12.5 ºC, 15 ºC, 17.5 ºC, 20 ºC, 22.5 ºC, 25 ºC, 27.5 ºC, 30 ºC, 32.5 ºC, 35 ºC, 37.5 ºC, or 40 ºC. A mercury thermometer was placed inside the incubators to monitor the targeted temperature setting. Additional distilled water was added from time to time to ensure adequate moisture for the germination process. When the radicle protruded from the seed coat beyond 2 mm, the seeds were deemed as germinated. Seed germination was inspected twice per day during rapid germination times and regularly until the germination process ended (ISTA, 1993).

Data analysis

Cumulative germination percentage, CG at a given period, t (days) was fitted using a Gompertz function:

$$CG = C \times e^{(-e^{(-Bx(t-M))})} \quad \text{– Equation 1}$$

Where C represents the final germination percentage, and B and M represent constants. The Gompertz equation was then rearranged into Equation 2 to determine the duration of 75% of the final germination (t_{75}), where CG =75:

$$t_{75} = M - ln\,[-\,ln\left(\frac{75}{100}\right)]/B \quad \text{– Equation 2}$$

The germination rate was calculated as the inverse of duration to 75% germination (1/days) about temperature (T). A broken-stick linear model was fitted to the germination rate in response to temperatures below and above the optimum for quantification of thermal time and cardinal temperatures. The broken-stick model was described as:

Germination rate = $a_1 + b_1T$ (for sub-optimal temperatures) – Equation 3

Germination rate = $a_2 + b_2T$ (for supra-optimal temperatures) – Equation 4

Where a represents the intercept for the y-axis, b represents the equation slope, and T represents the temperature ≤ T_{opt} (for sub-optimal range) and ≥ T_{opt} (for supra-optimal range). Calculations for T_b, T_{max}, $T_{opt,}$ and Tt can be obtained from the regression coefficients as:

$T_b = -a_1/b_1$ – Equation 5

$T_{max} = -a_2/b_2$ – Equation 6

$T_{opt} = (a_2-a_1)/(b_1-b_2)$ – Equation 7

$Tt_{sub} = 1/b_1$ – Equation 8

$Tt_{sup} = -1/b_2$ – Equation 9

Data points were omitted from the regression analysis should they show divergence from the model at temperature extremes as these were beyond the species' optimal thermal range (Angus *et al*., 1981). When 95% confidence intervals encompassed 10 ºC, a reanalysis of Tt was conducted with T_b =10 ºC to compare similarity across other rice landraces (Yoshida, 1981) and previously published works (Ali *et al*., 2003; Tilebeni *et al*., 2012).

The standard errors (S.E.) for T_b and Tt were determined as follows (Campbell *et al*., 1974):

$$S.E.T_b = \frac{\bar{y}}{b}\sqrt{\frac{s^2}{Ny^2} + \left[\frac{S.E.b}{b}\right]^2} \quad \text{– Equation 10}$$

$$S.E.Tt = \frac{S.E.b}{b^2} \quad \text{– Equation 11}$$

Where s^2 is the adjusted mean square error of the sample mean ($\bar{y}$) and y represents the germination rate. Gompertz curves were fitted using SigmaPlot 10.0 (Systat Software Inc. US) and least square regression analyses used Minitab 17.0 statistical software. For each parameter that was measured, the maximum standard error of the mean was recorded.

RESULTS

Total seed germination (%)

The accumulation of germinated seeds at a given time for Bario Sederhana and Biris was explained by the Gompertz functions (Figure 1). The germination pattern was described by a rapid linear increase before approaching a plateau where seed germination ceased. For most temperatures, seed populations took less than five days to attain their total germination. At 15 ºC and lower, the germination process was delayed. For Bario Sederhana and Biris landrace, total germination was above 80 and 90%, respectively. However, total germination was lesser at the near lower and upper end of the temperature range (Figure 2). For instance, the maximum germination percentage for Bario Sederhana was 73 - 91% at 17.5-35 ºC but then declined to less than 30% at temperatures ≤15 ºC and 40 ºC. In Biris, seeds barely germinated at temperatures ≤15 ºC.

Duration to 75% of total germination and germination rate

The time taken for seed populations to accomplish 75% of their total germination was shortened with every increment of temperature up to 32.5 ºC for Bario Sederhana and 27.5 ºC for Biris landrace (Figure 3). The germination time was then extended with further increments of temperature up to the maximum of 37.5 ºC. In particular, Biris took a similar time of 2.7 days to germinate at temperatures 27.5 – 35 ºC. The cardinal temperatures for each landrace were calculated using the reciprocals of these variables.

Broken-stick regression model described the germination rate in response to temperatures and enabled their cardinals to be estimated. From the base (T_b) to the optimum temperature (T_{opt}), the germination rate climbed linearly. It then declined until germination stopped at the maximum temperature (T_{max}) (Figure 4). The T_b was 11.6 ºC (±0.39) for Bario Sederhana and 9.5 ºC (±0.74) for Biris landrace. For both T_b estimates, the 95% confidence interval included 10 ºC (Table 1). The highest germination rate was achieved at T_{opt} of 32.1 – 33.1 ºC in both landraces while the germination process began to slow down with further increases in temperature until it stopped at an estimated T_{max} of 43.5 ºC.

The non-symmetrical broken-stick relationship between germination rate and temperatures, where data showed skewness required a separate thermal time for temperatures within the sub- and supra-optimal range (Figure 4, Table 1). For sub-optimal thermal responses, seed germination required 63 ºCd (±3.3) for Bario Sederhana and 53 ºCd (±4.7) for Biris at T_b=10 ºC. In contrast the Tt requirement for Bario Sederhana was 29 ºCd (±4.5) and 27 ºCd (±3.9) for Biris at temperatures beyond the optimum. A temperature of 40 ºC was not included in the quantification of Tt because it was outside of the regression model.

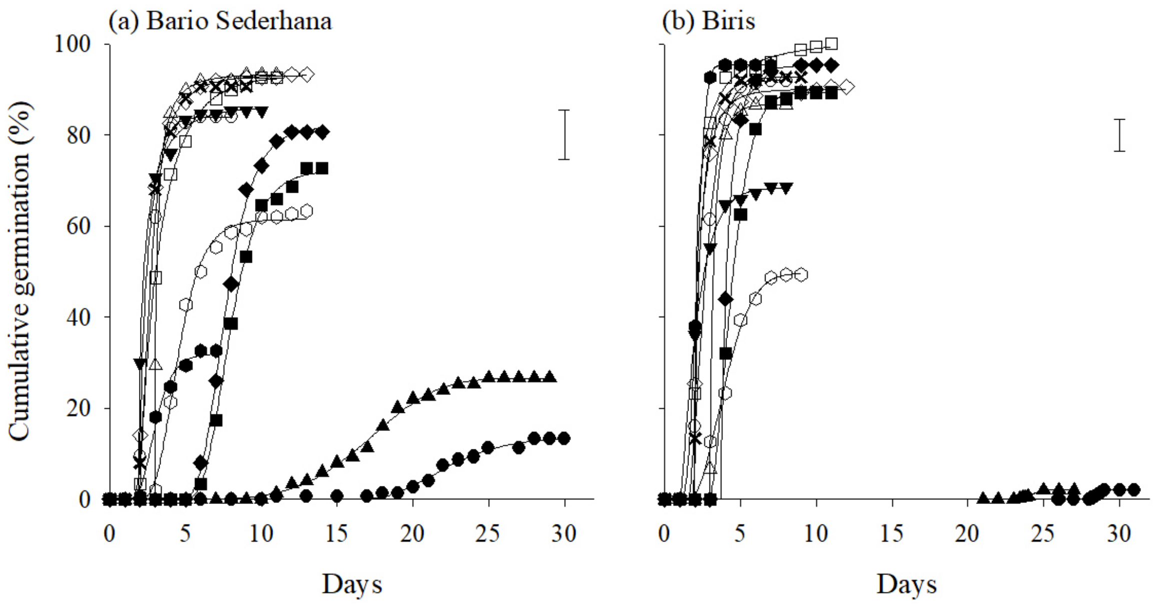

Fig. 1. Accumulated seed germination of (a) Bario Sederhana and (b) Biris rice landraces at (●) 12.5 ºC, (▲) 15 ºC, (■) 17.5 ºC, (◆) 20 ºC, (△) 22.5 ºC, (○) 25 ºC, (□) 27.5 ºC, (◇) 30 ºC, (▼) 32.5 ºC, (×) 35 ºC, (⬡) 37.5 ºC and (⬢) 40 ºC. Note: The error bars (I) show the total germination percentage's maximum standard error of the mean.

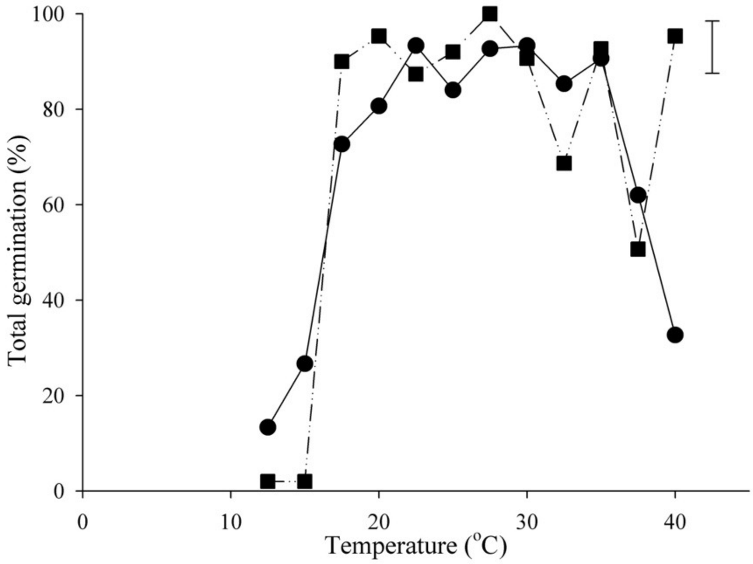

Fig. 2. Total germination versus temperature of Bario Sederhana (●) and Biris (■) rice. Note: The error bar (I) shows the total germination percentage's maximum standard error of the mean.

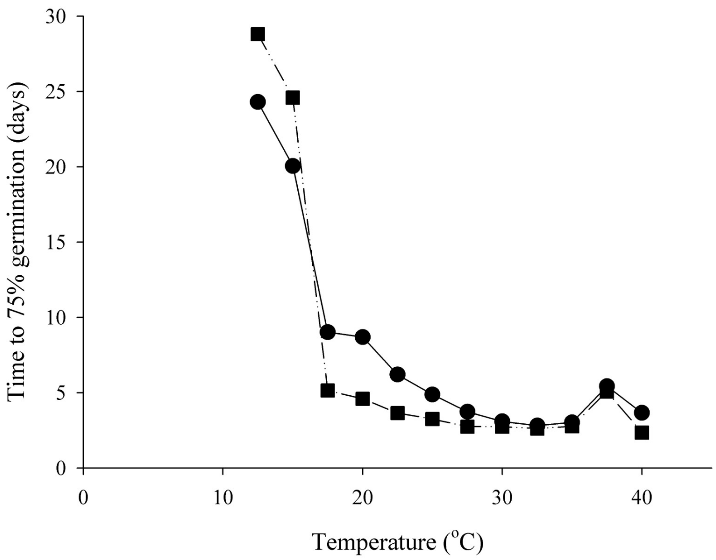

Fig. 3. Duration to 75% of total germination for Bario Sederhana (●) and Biris (■) rice at different constant temperatures.

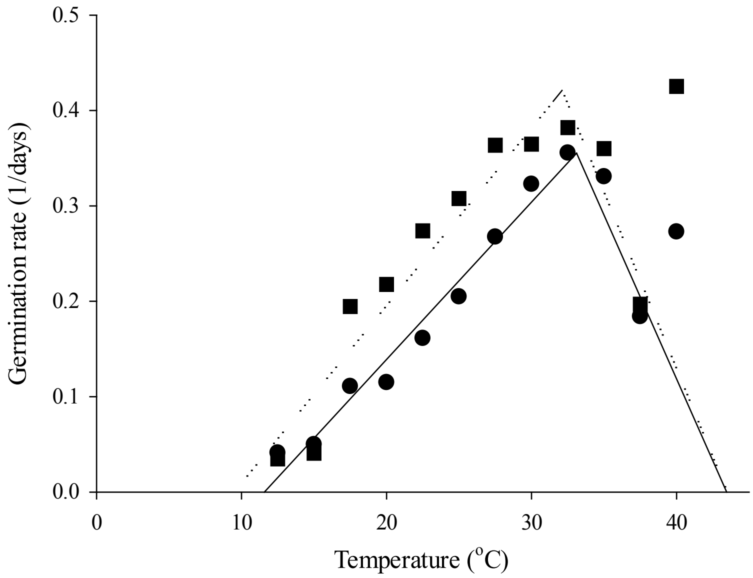

Fig. 4. Germination rate versus temperature of Bario Sederhana (●) and Biris (■) rice.

Table 1. The cardinal temperatures and thermal time for germination of Bario Sederhana and Biris rice

Rice landrace	T_b (ºC)	T_{op} (ºC)	T_{max} (ºC)	Tt_{sub} (ºCd)	Tt_{sup} (ºCd)	[1]Tt (T_b=10ºC) (ºCd)	[2]Excluded temperature
Bario Sederhana	11.6	33.1	43.5	61	29	63	40
Biris	9.5	32.1	43.5	54	27	53	40
Maximum S.E.	0.74	1.25	0.30	6.0	4.5	4.7	
95% C.I.	1.8, 15.2	26.6, 39.1	40.0, 49.2				

[1]Analysis assumes a base temperature of 10 ºC; [2]Excluded temperature because germination rate diverged from the regression line; Tt_{sub}, temperatures ≤ T_{opt}; Tt_{sup}, temperatures ≥ T_{opt}; S.E., Standard Error; C.I., Confidence Interval.

DISCUSSION

The germination response to temperature was described using a broken-stick regression model (Figure 4). The rate of seed germination accelerated with every increasing temperature until it reached an optimum. It then began to decline as temperature shifted further from the species-specific optimum with minimal differences between the landraces. Regression analyses estimated T_b of 9.5-11.6 ºC, T_{opt} of 32-33 ºC, and T_{max} of 43.5 ºC for Bario Sederhana and Biris rice landraces (Table 1). These findings were compatible with previous reports for other rice cultivars (Ali *et* al., 2003; Tilebeni *et* al., 2012). The Tt requirements for germination of Bario Sederhana and Biris were 54-61 ºCd at sub-optimal and 27-29 ºCd at supra-optimal temperatures. In both landraces, the germination rate at 40 ºC diverged from the linear range and was therefore excluded from analysis. Such an extreme temperature was beyond their thermal optima which approached toward the upper end of the critical temperature. This means that seeds either germinated quickly or died, thus resulting in an overestimation of germination rate from a small population of survived seeds. For example, Bario Sederhana took three days to germinate at 40 ºC (Figure 3) but the seed population that successfully germinated was below 35% (Figure 2). An exception was observed in Biris which had 95% of its seed populations that germinated within two days at 40 ºC. The ability of the Biris landrace to endure thermal extremes may be attributed to its origin from the lowlands of Simunjan where air temperatures frequently surpass 36 ºC resulting in elevated soil surface temperatures. Similarly, 13-27% of Bario Sederhana seed populations were able to germinate at lower temperatures between 12.5 and 15 ºC (Figure 2) despite a longer time requirement (Figure 1a) because of the cultivar's origin from the Kelabit Highlands of Bario, Sarawak where the average air temperature is around 19-22 ºC.

The thermal time method offers a consistent way to quantify crop phenology because it summarizes each temperature response within the linear range into a single coefficient that can be used in a broad context of environments. For instance, the thermal time estimated for germination of Biris landrace was 54 ºCd for temperatures below 32 ºC (Table 1), hence at soil temperature of 27 ºC, the seed germination can be predicted to occur within two days (54 ºCd ÷ 27 ºC = 2 d) compared with 3 days at 18 ºC (54 ºCd ÷ 18 ºC = 3 d). The linear model gave a satisfactory cardinal estimate based on the extrapolation of the regression line between germination rate and temperature. It gave a simple calculation of the development rate as a function of temperature. However, particular attention needs to be addressed when using the linear method in estimating T_b because a regression line can only fit a limited set of temperature data. Commonly, the response of the development rate toward temperature begins with a slow curve at lower temperatures near the minimum threshold (Bonhomme, 2000). When linear extrapolation was made to intercept the x-axis, it excluded thermal responses at the slow curve, resulting in a higher estimation of T_b (Nori *et al*., 2014). It is therefore important to understand that the estimated T_b based on regression analysis is merely a statistical value. In reality, the observed value of T_b is much lower than the calculated value. For example, the T_b from linear extrapolation was 11.6 ºC for Bario Sederhana but at 12.5 ºC there was still about 13% of seeds germinated which suggests that there is a probability for the slightest germination activity at the estimated T_b. Given this limitation, the confidence interval at 95% level was used to decide if the range of estimated T_b encompassed 10 ºC. The rationale for adopting 10 ºC as a benchmark for the lowest temperature threshold was based on numerous works reported on tropical crops which include rice (Yoshida, 1981; Angus *et al*., 1981; Schultink *et al*., 1987; Bonhomme *et al*., 1994; Weikay & Hunt, 1999). It is plausible to accept that at temperatures below 10 ºC, there is no development occurring in tropical crops. As expected, the base temperature's confidence interval for Bario Sederhana and Biris included 10 ºC (Table 1) thus allowing re-analysis of Tt with T_b = 10 ºC for comparability with rice cultivars and other tropical crop species.

The findings of this study highlighted the effect of temperature as the main driver of development and its implication on rice establishment. For example, the final germination percentage of Bario Sederhana rice was 93% inside an incubator at 22.5 ºC (Figure 2). This is also the average soil temperature in the Kelabit Highlands of Bario, Sarawak during rice planting season in September. Accordingly, the seeding rate can be increased by 7% to maximize plant population for optimum yield. The cardinal temperatures for germination of Bario Sederhana and Biris landraces were found to overlap with the thermal range of common weed species in Malaysian rice fields such as *Echinochloa crus-galli* (Guillemin *et al*., 2013), *Echinochloa colona* (Elahifard & Mijani, 2014), *Leptochloa chinensis* (Benvenuti *et al*., 2004) and *Fimbristylis miliacea* (Begum *et al*., 2008). Their similarity in thermal response means that these will most likely induce problems associated with weed infestation, hence justify the need for pre-emergence weed control in the rice field. Essentially, high-temperature values in the supra-optimal can limit crop productivity by delaying phenology, reducing growth, and causing organ damage. Nevertheless, crop responses to high temperatures vary with the phenological stage. In rice, the leaf production rate increased with temperature up to an optimum of 33 ºC, but as the crop progressed throughout reproductive development, temperatures above 25 ºC decreased grain formation and yield (Baker *et al*., 1995; Matsushima *et al*., 1964). The most temperature-sensitive phase in rice crops is during anthesis (Farrell *et* al., 2006; Satake and Yoshida, 1978). Specifically, temperatures above 33 ºC at anthesis reduced pollen viability until there was no more viability at the maximum temperature of 40 ºC (Kim *et al*., 1996). This can cause a high percentage of spikelet sterility and consequently lead to empty grain. Understanding the impact of temperature on rice phenology and productivity can facilitate decision-making in choosing the right time for seed sowing based on meteorological data of the planting location. Therefore, in wet-and-dry climatic conditions of Sarawak, it is recommended to sow traditional rice between late September and early October for optimum seedling emergence and subsequent crop establishment during the rainy season. Given that traditional rice varieties require about five months to mature, the grains can be harvested in March when rainfall significantly starts to decrease and mean air temperature is around 31 ºC. This could avoid crop flowering during hot weather in May (~33 ºC) and thus prevent empty grain.

CONCLUSION

The application of the broken stick regression model to establish cardinal temperatures and growing degree days for plant development was appropriate while considering the interference of non-linearity to some degree. The cardinal temperatures were rather species-dependent and unaffected by landraces. Above a T_b of 10 ºC, seed germination of Bario Sederhana required a larger thermal time (63 ºCd) in comparison to Biris (53 ºCd) landrace. Less than 30% of Bario Sederhana seed populations germinated at temperatures of 15 ºC and below.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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