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Research

Reproductive Development and Yield Components of Bario Sederhana Rice in Response to Photoperiod

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ABSTRACT

A series of controlled environment treatments were conducted to quantify reproductive development and yield components of Bario Sederhana rice grown under five photoperiod regimes (8, 9, 10, 11, & 12 h). A 'broken-stick' linear regression of heading rate against photoperiod was used to determine the cardinal photoperiods for heading. The reproductive development towards photoperiod showed a delayed pattern in time to heading, anthesis, and maturity under lengthening photoperiod from 10 to 12 h. For example, under 10 h photoperiod the crops required 1680 °Cd (70.8 days) from emergence to heading but took an extended duration of 3147 °Cd (132.6 days) when they were sown at 12 h photoperiod. The prolonged time taken for reproductive development modified by photoperiod resulted in higher yield components. This is because the lengthening time from heading to maturity extended the duration of grain filling. The longest photoperiod of 12 h gave the highest percentage of filled spikelets (65.3%) thus consequently leading to the heaviest grain weight of 1.4 g per panicle. The base, optimum, and maximum photoperiod for heading were estimated to be 7.4 h, 10 h, and 14.8 h, respectively.

Key words: Day length, growing degree days, phenology, plant growth chamber, Sarawak traditional rice

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INTRODUCTION

The rice crop (*Oryza sativa* L.) is well adapted to a wide range of climatic variations from tropical to temperate. Several environmental factors, in addition to genetic factors, influence rice plant growth and development. Temperature is the most important determinant in crop development, however, it can be influenced by photoperiod (Vergara & Chang, 1985; Mapalana, 2017). Photoperiod also known as daylength, is defined as the duration from sunrise to sunset and includes civil twilight. Photoperiod influences crop development rate such as leaf production (Nemoto *et al*., 1995) and time to flowering (Jackson, 2009). Specifically, the modification in time taken to flowering caused by photoperiod variation can affect the growth performance and consequently affect the final yield production (Sonego, 2000; Nori *et al*., 2014).

In general, rice is classified as a short-day plant because it initiates panicle primordia in response to short photoperiods (Yoshida, 1981), which means it requires shorter exposure to daylight to transition from vegetative to reproductive phases. However, the degree of sensitivity to photoperiod varies widely among rice cultivars. It has been reported that traditional rice cultivars from tropical regions are photoperiod sensitive and require between 160-170 days to mature (Vergara & Chang,1985; Viraktamath, 2013; Nandini, 2020; Khotasena *et al*., 2022). Most of the studies on photoperiodism of traditional rice in the tropics are from Cambodia (Makara *et al*., 2001; Tsubo *et al*., 2009; Uch *et al*., 2023), Thailand (Cha-um & Kirdmanee, 2007; Boling *et al*., 2011; Sujariya *et al*., 2023), and Sri Lanka (Mapalana, 2017; Padukkage *et al*., 2017; Rathnathunga *et al*., 2019). The geographical locations of these countries are within 7.9 °N-15.9 °N latitude, thus experiencing different changes in day length throughout the year. In Malaysia, there was only one published work on the responses of rice toward photoperiod at the location of planting in the state of Melaka at the latitude of 2.1 °N (Dore, 1959). This study reported that 14 minutesdifference between day length in January and September resulted in a significant variation in time to flowering of rice plants. According to the study, rice plants sown in September took only 161 days to flower compared to 329 days for rice plants sown in January. This finding may apply to environmental conditions in Sarawak which is positioned at 1.5 °N near the equator. To date, the responses of Sarawak traditional rice toward photoperiod have not been studied.

Sarawak is renowned for its best-quality of traditional rice. In particular, Bario is the most famous traditional rice cultivar owing to its fine grains, exquisite taste, and high nutritive properties (Wong *et al*., 2009; Nicholas *et al*., 2014). This cultivar is registered as Malaysia Geographical Indication and marketed as premium rice with a price between MYR 16.00-18.50 per kilogram. The variety 'Bario Sederhana' is widely grown for commercialization. Traditional rice from Sarawak has been claimed to be photoperiodic sensitive because it possesses a longer growth duration and therefore can only be planted in one cropping season (Naeg, 2012; Morni, 2014). Nevertheless, questions related to what extent the photoperiod affects the growth and development of rice remained unanswered. Understanding the implication of photoperiod modification on rice physiology is important to improve existing farm decision-making for successful crop management. Given that the changes in photoperiod at the equatorial region are significantly small, controlled environment chambers can be used to grow rice plants within a range of photoperiod hour. Therefore, this study aimed to quantify the time to flowering and duration to grain maturity of Bario Sederhana landrace. The second aim was to quantify the growth of rice yield components.

MATERIALS AND METHODS

Experimental design

Plastic pots containing 50 seeds of Bario Sederhana landrace were prepared in four replicates for a series of photoperiod treatments (8, 9, 10, 11, & 12 h). In each photoperiod treatment, the experiment was conducted inside a separate unit of a controlled environment chamber at the plant growth laboratory at Universiti Malaysia Sarawak. The plastic pots were arranged in a completely randomized design inside the controlled environment chamber.

Seed source

Bario Sederhana seeds used in this study were seeds harvested from a farmer's field in Kampung Sungai Riset in Serian Division, Sarawak, East Malaysia (1° 15'N, 110° 25'E, 9 m a.m.s.l.). The planting site extended beyond the origin of Bario Sederhana, which originally hailed from Kelabit Highland in Bario, Sarawak (3° 43'N, 115° 29'E 1296 m a.m.s.l.). Therefore, in the context of this study, Bario Sederhana was referred to as a rice landrace. Rice landraces represent lineages that have evolved through extensive artificial selection by farmers throughout the extended period of domestication (Ray *et al*., 2013).

Crop husbandry

The soil mixture consisted of organic soil, peat moss, and sand (2:1:1 by volume) were filled into a 15.0 L plastic pot. The soil mixture contained 1396 ppm of available phosphorus, 5.47 milliequivalent (mEq)% of exchangeable potassium, 65.14 mEq% of exchangeable calcium, 16.73 mEq% of exchangeable magnesium, and 54.03 mEq% of cation exchange capacity (C.E.C). In each pot, 50 seeds of Bario Sederhana rice were sown at a depth of 10 mm onto the soil mixture. All plastic pots were flooded with tap water and the water level was maintained at ~5.0 mm above the soil surface.

The experiment was conducted in Conviron S10H (Winnipeg, Canada) controlled environment chamber for photoperiod treatments of 8, 9, 11, and 12 h, and Percival Scientific E-75L1 (Perry, Iowa) controlled environment chamber for 10 h photoperiod treatment. In both controlled environment chambers, the air temperature was programmed at 25/30°C to simulate the natural field conditions in Sarawak. A mercury thermometer was placed at 10 mm below the soil surface to measure soil temperature during the minimum (25 °C) and maximum (30 °C) air temperature setting. The soil temperatures were recorded every two weeks to determine the minimum and maximum values for thermal time calculations (Table 1).

A combination of 16 fluorescent lights and 12 incandescent lights was used to light the Conviron S10H-controlled environmental chamber, meanwhile, a combination of 8 fluorescent and 6 incandescent lights was used to light the Percival E-75L1 controlled environment chamber. In all chambers, photosynthetic photon flux density (PPFD) above the rice canopies averaged 455 ± 3.7 µmoles/m^2/sec. Following the production of the third leaf, which was approximately 4 days after the seedling emergence, plants were thinned to minimize competition for light and nutrients as well as to optimize their growth performance. Only five healthy plants per pot were kept throughout this experiment for detailed observation. The pots were re-randomized every 14 days to avoid the chamber effect. A compound fertilizer containing 15% nitrogen (N), 15% phosphorus pentoxide (P_2O5), 15% potassium oxide (K_2O), and 2% sulfur (S) was applied at 2.4 g/pot during the third leaf appearance, induction of tillers, maximum tillering and panicle development stage.

Measurements

The first sign of reproductive development was after the production of a flag (final) leaf on the main stem of a rice plant. The total number of leaves on the main stem and the time taken for its production were quantified. Time to heading was identified when the first panicle emerged on 50% of the rice plant populations. Following the heading, anthesis was determined when the florets had opened, exposing the stamens. The number of panicles per plant was counted and panicle length was measured using a ruler from the pedicel to the tip of the panicle. Maturity was defined when the grains hardened and turned yellow. Following grain maturity, the panicles were harvested and then air-dried in the crop laboratory. For each panicle, total spikelets were quantified including empty and filled spikelets. Then, the weight of filled spikelets was determined using an electronic balance.

Data analysis

Time to reproductive development was quantified in both calendar days and thermal time. Daily thermal time was calculated by incorporating a bi-linear model with cardinal temperatures (base, optimum, & maximum) (F.L.Luing, unpublished) and using 8x3 hourly temperatures from a sinusoidal model (Carberry *et al*., 1989) derived from the daily maximum and minimum air temperatures. The relationship between time to heading and photoperiod was described using a 'broken-stick' linear function (Equation 1 and Equation 2) as:

$$1/\text{days to heading} = a_1 + b_1P \quad \text{– Equation 1}$$

(for positive linear portion)

$$1/\text{days to heading} = a_2 + b_2P \quad \text{– Equation 2}$$

(for negative linear portion)

Where 1/days to heading was the inverse of duration calculated from seed sowing, a_1 was the y-axis intercept, b_1 was the slope of the relationship for the positive linear portion, a_2 was the y-axis intercept, b_2 was the slope of the relationship for negative linear portion, and P was the photoperiod between the base and optimum (for the positive linear portion) and between the optimum and maximum (for the negative linear portion). The base (P_{base}) (Equation 3), optimum (P_{opt}) (Equation 4), and maximum (P_{max}) (Equation 5) photoperiods were calculated from the regression coefficients as:

$$P_{base} = -a_1/b_1 \quad \text{– Equation 3}$$

$$P_{opt} = (a_2-a_1)/(b_1-b_2) \quad \text{– Equation 4}$$

$$P_{max} = -a_2/b_2 \quad \text{– Equation 5}$$

The base photoperiod (P_{base}) was the threshold photoperiod below which no heading occurs. The optimum photoperiod (P_{opt}) was the photoperiod where heading occurs within the shortest time. The maximum photoperiod (P_{max}) was the highest photoperiod at which the heading would occur. Statistical analysis used Minitab 19.0 (Minitab, LLC). Parameters were analyzed using analysis of variance (ANOVA) and treatment means were compared by Fisher's Least Significant Difference (LSD) whenever the ANOVA indicated that differences among treatments presented $P<0.05$.

Table 1. Mean soil temperatures (°C) inside the controlled environment chamber as measured by laboratory thermometer during the minimum (25 °C) and maximum (30 °C) air temperatures

Photoperiod (h)	Minimum soil temperature (°C)	Maximum soil temperature (°C)
8	24.5	30.5
9	25.0	31.0
10	24.5	30.5
11	25.0	30.0
12	25.0	31.0

RESULTS

Reproductive development

Crops grown under a photoperiod of 9 h required more thermal time and number of days to reach heading, anthesis, and grain maturity compared with those at 8 hours photoperiod (Table 2 & 3). However, the crops took an extended time from emergence to become reproductive with each successive photoperiod from 10 to 12 h. For example, time to heading was shorter for rice plants sown at 10 h photoperiod (1680 °Cd, 70.8 days) compared with 12 h (3147 °Cd, 132.6 days). Following the heading, the plants required an average of 3.1 (±0.45) days to reach anthesis across all photoperiod regimes. They then required another 17.6 (±2.19) days for grain filling to finally become mature.

Table 2. Thermal time from emergence to reproductive development for Bario Sederhana rice sown at five photoperiod regimes inside a controlled environment chamber at the plant growth laboratory in Universiti Malaysia Sarawak

Photoperiod (h)	Thermal time (°Cd) to reproductive development		
	Heading	Anthesis	Grain maturity
8	1722[c]	1799[c]	2044[d]
9	3007[a]	3061[a]	3437[b]
10	1680[c]	1745[c]	2234[d]
11	2500[b]	2566[b]	3019[c]
12	3147[a]	3266[a]	3796[a]
P-value	<0.001	<0.001	<0.001
CV (%)	27.3	26.8	24.5
S.E.M.	147.0	149.0	159.0

[CV] Coefficient of Variance. [S.E.M.] Standard error of the mean. Thermal time was calculated based on air temperature. Within each column, means with the same letter are not significantly different at α=0.05 according to Fisher's Least Significant Difference test.

Table 3. Number of days from emergence to reproductive development for Bario Sederhana rice sown at five photoperiod regimes inside a controlled environment chamber at the plant growth laboratory in Universiti Malaysia Sarawak

Photoperiod (h)	Number of days (n) to reproductive development		
	Heading	Anthesis	Grain maturity
8	72.5[c]	75.9[c]	86.0[d]
9	126.5[a]	128.5[a]	144.1[b]
10	70.8[c]	73.6[c]	94.2[d]
11	105.2[b]	107.8[b]	126.8[c]
12	132.6[a]	137.3[a]	159.9[a]
P-value	<0.001	<0.001	<0.001
CV (%)	27.26	26.61	24.42
S.E.M.	6.19	6.22	6.67

[CV] Coefficient of Variance. [S.E.M.] Standard error of the mean. Several days were counted from the date of emergence. Within each column, means with the same letter are not significantly different at α=0.05 according to Fisher's Least Significant Difference test.

Heading rate about photoperiod

The heading rate showed a systematic variation with the changes in photoperiod (h) (Figure 1). The rate of heading decreased linearly by 0.0047 h per day as the photoperiod decreased from the optimum photoperiod down to 7.4 h photoperiod (Table 4). Further increases in photoperiod beyond 10 h then decreased the heading rate by 0.0026 h per day. The 'broken-stick' linear model which described the relationship between heading rate and photoperiod in Bario Sederhana rice enabled the cardinal photoperiods (P_{base}, P_{opt}, & P_{max}) to be estimated in Table 4. From this model, the optimum photoperiod for panicle heading for Bario Sederhana rice was 10 h.

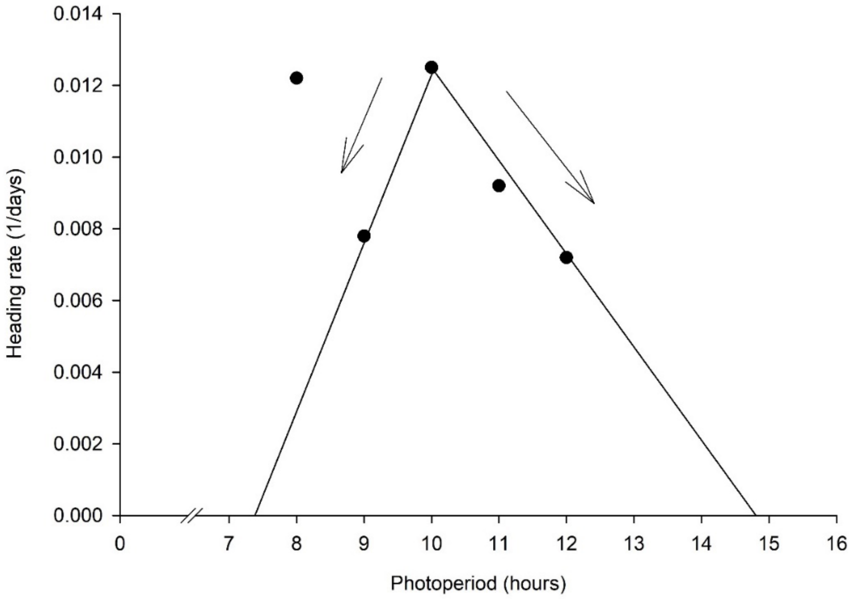

Fig. 1. Heading rate (1/days) of Bario Sederhana rice in response to photoperiod settings inside a controlled environment chamber at plant growth laboratory in Universiti Malaysia Sarawak. Note: Arrows indicate direction towards decrease and increase in photoperiod. Time to heading was calculated from sowing.

Yield components

The yield components showed variations in photoperiod (*P*<0.05) (Table 5). Crops grown at photoperiods between 8 and 10 h had shorter panicles (~14.2 cm averaged) and consequently produced a lower number of spikelets per panicle (55 spikelets averaged) compared with those at 11 and 12 h photoperiod (~20.3 cm panicle length, ~117 spikelets/panicle). As the photoperiod was extended from 9 to 12 h, the weight of filled spikelets per panicle for Bario Sederhana exhibited an increasing trend.

Table 5. Yield components of Bario Sederhana rice grown at five photoperiod regimes inside a controlled environment chamber at a plant growth laboratory in Universiti Malaysia Sarawak

Photoperiod (h)	Yield components				
	No. of panicles/ plant	Panicle length (cm)	No. of spikelets/ panicle (n)	Filled spikelets (%)	Weight of filled spikelets/ panicle (g)
8	2.0^{c}	13.8^{b}	61.3^{b}	68.7^{a}	1.0^{ab}
9	2.4^{bc}	14.5^{b}	57.5^{b}	28.9^{c}	0.2^{c}
10	4.9^{ab}	14.3^{b}	46.8^{b}	44.4^{bc}	0.4^{c}
11	4.4^{abc}	20.5^{a}	113.5^{a}	33.5^{c}	0.6^{bc}
12	6.2^{a}	20.0^{a}	120.9^{a}	65.3^{ab}	1.4^{a}
P-value	0.014	0.001	0.002	0.008	<0.001
CV (%)	55.26	22.45	48.83	45.36	68.23
S.E.M.	0.49	0.83	8.73	4.88	0.11

[CV] Coefficient of Variance. [S.E.M.] Standard error of the mean. Within each column, means with the same letter are not significantly different at α=0.05 according to Fisher's Least Significant Difference test.

DISCUSSION

The thermal time requirement for panicle heading was modified by the duration of the photoperiod (Table 2). In particular, heading was delayed with lengthening photoperiod from 10 to 12 h. The use of a 'broken-stick' linear model satisfactorily described the relationship between the development rate to heading (1/days) and photoperiod. It provided a statistical convenience to enable the cardinal photoperiods (base, optimum, & maximum) to be estimated by using simple calculations. The response of development rate towards photoperiod using this linear function estimated a P_{base} of 7.4 h, P_{opt} of 10.0 h, and P_{max} of 14.8 h for heading time in Bario Sederhana rice (Table 4).

Table 4. Coefficient of the fitted relationship between heading rate (1/days) and photoperiod (P) in Bario Sederhana rice

Direction of photoperiod	Relationship	R^2 (%)	Cardinal photoperiods (h)		
From 9 to 10 h	1/days = -0.0347 + 0.0047P	100	P_{base}	P_{opt}	P_{max}
From 10 to 12 h	1/days = 0.0385 - 0.0026P	98	7.4	10	14.8

R^2, coefficient of determination

The bi-linear response of development rate over the range of photoperiod between 9 and 12 h per day was non-symmetrical. The relationship showed that when the duration of the photoperiod decreased below the optimum photoperiod at the sub-optimal (when the length of the photoperiod was shorter), the heading was delayed, thus making Bario Sederhana rice behave like a long-day plant. In contrast, the rice crops showed characteristics of a short-day plant by delaying heading with prolonged photoperiod above the optimum value at the supra-optimal. These long and short-day responses of rice were consistent with the literature reviewed by Best (1960), Horie (1994), and Vergara and Chang (1985). The long-day response in the sub-optimal photoperiod can be explained by an insufficient supply of energy for growth and development under short photoperiods (Horie, 1994) despite uniform temperature and the amount of radiation received by plants across all photoperiod regimes. For example, crops grown at a photoperiod of 8 h had a high mortality rate during early establishment. Only 5 out of 20 plant populations survived to reach the reproductive development phase, thus representing a survival rate of 25% Consequently, data point at 8 h photoperiod was excluded from the analysis for two reasons: (1) low number of plants per replicate thus, not representative of the whole population, and (2) it deviated from the linear model. The development rate deviated because at the lowest photoperiod of 8 h, plants either flowered quickly or died and the heading rate was over-estimated based on the 25% of the plant populations that survived. Although excluded from the analysis, the data point was retained as it still yielded significant findings and was noteworthy. The short-day response of time to heading at photoperiods in the supra-optimal range was expected because these were natural photoperiods in rice-growing regions (Vergara & Chang, 1985). Hence, it can be concluded that photoperiod has a significant influence on the time to heading of Bario Sederhana rice.

On a different note, crops grown at 11 and 12 h of photoperiod took different times (2381 °Cd versus 2903 °Cd) to produce a similar total of 8 leaves on the main stem (Table 6). However, at 12 h of photoperiod, the extra time of 522 °Cd was used by the rice plants to produce more secondary leaves on the tiller development which then yielded 6.2 panicles/plant. In contrast, 11 hours photoperiod rice plants that had a shorter time to complete leaves on the main stem did not produce many secondary leaves on tiller production and thus only gained 4.4 panicles/plant. Note that the number of tillers determined the panicle yield. Increased photoperiod from 9 to 12 h extended the duration of grain filling and resulted in a higher percentage of filled spikelets (Figure 2). Consequently, this resulted in a higher weight of filled spikelets per panicle with increasing photoperiod.

CONCLUSION

The 'broken-stick' linear model used in describing the relationship between development rate to heading and photoperiod estimated the base, optimum, and maximum photoperiod for heading in Bario Sederhana as 7.4 h, 10 h, and 14.8 h, respectively. This model showed that rice responded as a long-day plant at the sub-optimal photoperiod, meaning that heading was delayed as the photoperiod decreased below the optimum. In contrast, rice behaved like a short-day plant when the photoperiod exceeded the optimum at the supra-optimal range. Reproductive development was delayed with prolonged photoperiod from 10 to 12 h and gave positive attributes to the yield components through the extension of vegetative growth and duration of grain filling. Understanding the impact of photoperiodism on rice phenology and productivity can facilitate on-farm decision making. Therefore, in the Sarawak tropical environment where the photoperiod is 12 h all year round, growing Bario Sederhana traditional rice requires around five months to harvest. This means that more farm inputs about fertilizer and weed, pests, and disease control would be required to sustain this long-maturity rice.

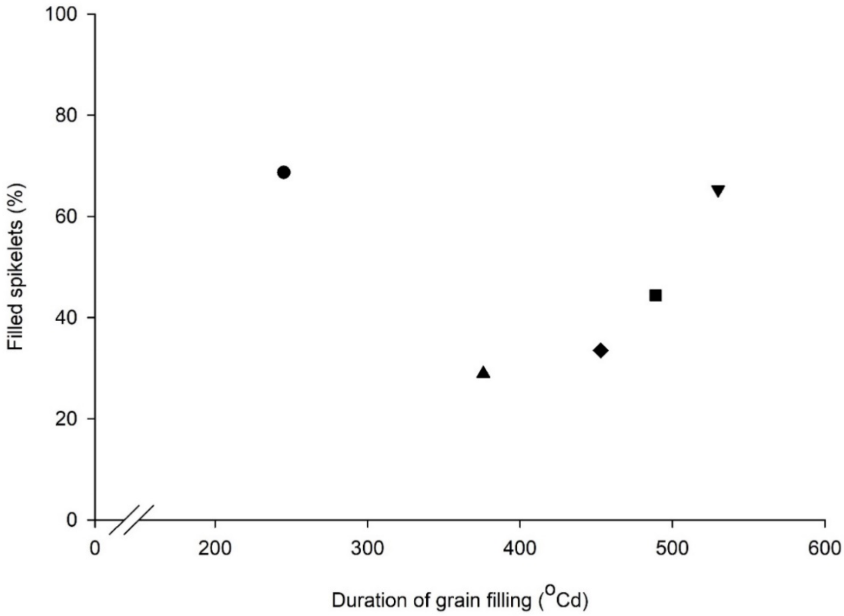

Fig. 2. Filled spikelets percentage (%) against the duration of grain filling (°Cd) of Bario Sederhana rice grown at a photoperiod of (●) 8 h, (▲) 9 h, (■) 10 h, (♦) 11 h, and (▼)12 h inside a controlled environment chamber at plant growth laboratory in Universiti Malaysia Sarawak.

Table 6. Summary of the vegetative and reproductive development of Bario Sederhana rice grown at five photoperiod regimes inside a controlled environmental chamber at the plant growth laboratory in Universiti Malaysia Sarawak

Photoperiod (h)	Total leaves on main stem (n)	Total time taken to total leaves (°Cd)	Total time taken to heading (°Cd)	Number of panicles/ plant (n)
8	7.8[bc]	1549[c]	1722[c]	2.0[c]
9	9.3[a]	2888[a]	3007[a]	2.4[bc]
10	6.8[c]	1513[c]	1680[c]	4.9[ab]
11	8.0[b]	2381[b]	2500[b]	4.4[abc]
12	7.9[b]	2903[a]	3147[a]	6.2[a]
P-value	0.002	<0.001	<0.001	0.014
CV (%)	13.28	28.9	27.3	55.26
S.E.M.	0.24	145.0	147.0	0.49

[CV] Coefficient of Variance. [S.E.M.] Standard error of the mean. Thermal time was calculated based on soil temperature. Within each column, means with the same letter are not significantly different at α=0.05 according to Fisher's Least Significant Difference test.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

ETHICAL STATEMENT

Not available.

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