Degree-day requirement for heading and maturity of three most popular rice varieties in Sri Lanka as influenced by location and season

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**Highlights**

- Degree-days (DD) required for development of rice varied with location.
- DD required for development of rice correlated with seasonal temperature.
- Rice crop duration would not be lowered as expected under warming climates.
- DD requirement of rice is genotype and environment dependent.
Degree-day requirement for heading and maturity of three most popular rice varieties in Sri Lanka as influenced by location and season

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Abstract: Growing degree-days (DD- °C days) required to complete growth phases in plants is generally considered as a constant. However, this practice has recently been questioned. Therefore, we tested the DD requirement for the growth phases of three Sri Lankan rice varieties, Bg300, Bg352 and Bg358. These rice varieties are widely cultivated in Sri Lanka across years, seasons and locations. When averaged across seasons, years and locations, the DD required for heading and maturity of Bg300 were 1,051 and 1,545 °C days, while those of Bg352 were 1,098 and 1,627, and Bg358 were 1,203 and 1,698 °C days, respectively. Moreover, DD required for heading and maturity varied among locations. Number of days required for heading and ripening correlated negatively, i.e., reducing ripening duration by 8.4 h due to the delay in heading by one day. Further, DD required for heading and maturity were positively correlated with the mean seasonal minimum and maximum temperatures. Therefore, crop duration could not be lowered as expected under warming climates. Hence, genotype × environment dependent DD requirements of rice varieties need to be considered when making agronomic and policy decisions in both regional and seasonal scales, and increasing the precision of phenology predictions.

Keywords: development; growing degree-days; spatial variation; seasonal variation; thermal time.

INTRODUCTION

Average ambient temperature of the world is expected to increase by 1.5-4.5 °C by 2100 if the current emissions of greenhouse gas continue (IPCC, 2014). Agricultural productivity is under threat due to global warming as predicted by current and future climate change scenarios (Sanchez et al., 2014; Hatfield and Prueger, 2015). Under such circumstances, accurate quantification and prediction of development and growth processes of crops are crucial for better crop management and making policy decisions (Sanchez et al., 2014; van Oort et al., 2015).

Estimation and prediction of crop growth and development have been carried out through crop models. Crop models deviate significantly and increase uncertainty when simulating the impact of extreme temperatures on crop growth and development (Luo, 2011; van Oort et al., 2015; Wallach et al., 2017; Zhang and Tao, 2019). Moreover, acclimation of crop responses to changing climatic conditions has not been considered in crop models due to the lack of understanding. Therefore, the importance of improving crop model structures such as input parameters, both under optimal and extreme climatic conditions is crucial (Luo et al., 2011; Zhang and Tao, 2013; Li et al., 2015; van Oort et al., 2015, 2018; Hasegawa et al., 2017; Zhang et al., 2017).

Phenology simulation is one of the most important components of crop models in determining growth and yield (White et al., 1997; Streck et al., 2008; Amarasinha et al., 2015; Counce et al., 2015; Nissanka et al., 2015). As temperature is the most important driving force of crop development, a robust temperature response function is crucial to predict crop development and phenology (Counce et al., 2015; Zhang and Tao, 2019). Thermal time (TT) or growing degree-day (°C day) values are used to predict crop development (Yang et al., 1995; McMaster and Wilhelm, 1997), which usually integrate temperature values between thresholds on a daily basis. With increasing global temperatures, faster accumulation of degree-days and completion of phenological events are expected (Craufurd and Wheeler, 2009; Madan et al., 2012; van Oort and Zwart, 2018; Ahmed et al., 2019).

Rice (Oryza sativa L.) is widely grown in the tropics. Recently, many efforts have been undertaken to (i) estimate the productivity of rice under different management and environment conditions, (ii) predict the response of rice to possible climate change scenarios and propose adaptive mitigation strategies, and (iii) compare rice-based crop models and improve model predictability and reduce uncertainties (Hasegawa et al., 2017; Li et al., 2015; Rosenzweig et al., 2013; van Oort and Zwart, 2018; Wallach et al., 2017). Despite the progress made, uncertainties are still prevailing in models that simulate development of rice crops (Tebaldi and Knutti, 2007; van Oort et al., 2011, 2015; Zhang and Tao, 2013; Li et al., 2015; Hasegawa et al., 2017; Wallach et al., 2017; Zhang et al., 2017). For instance, most of these crop models, such
as APSIM (Meinke et al., 1997), CERES (Ritchie et al., 1998), and ORYZA2000 (Bouman et al., 2001) are driven by an implicit assumption that degree-day requirement to reach developmental events of crops would remain constant under various climatic conditions.

Commonly used cardinal temperatures for rice are 8, 30 and 42 °C for the base (T_b) optimum (T_o) and maximum or ceiling (T_c) temperatures, respectively (Matthews et al., 1997; Bouman et al., 2001; Zhang et al., 2008; van Oort et al., 2015; Wallach et al., 2017), while cultivar specific values have also been reported (Keising et al., 1984; Counce et al., 2009; Luo, 2011; Dingkuhn et al., 2015; Rouan et al., 2018). Moreover, Sanchez et al. (2014) reviewed the cardinal temperatures for different developmental events of rice. Despite all these efforts, the validity of the commonly used default parameters was questioned mainly due to biasness in phenology simulation (Zhang et al., 2008; van Oort et al., 2011; Awan et al., 2014; Dingkuhn et al., 2015; Sharifi et al., 2017; Rouan et al., 2018). For example, number of days or degree-days required for leaf emergence and maturity increased with increasing growing seasonal temperature in the range of 20 to 33 °C (Ellis et al., 1993; Caton et al., 1998; Zhang et al., 2008). As a result, a crop model based on constant thermal time accumulation would significantly deviate from the observed growth and development trends in longer time scales or warmer regions, despite comparably accurate simulations of short periods or under near-optimal temperatures. Such deviations could result in misleading yield simulations. This casts serious doubts on the assumptions of constant thermal time accumulation made in previous modeling studies (Gao et al., 1987; Meinke et al., 1997; Caton et al., 1998; Ritchie et al., 1998; Bouman et al., 2001). Therefore, more studies on growth and development of rice on a broader spatial, temporal and temperature scales are warranted to establish the best relationships between the developmental response of rice and temperature (van Oort et al., 2011, 2015; Awan et al., 2014).

A range of rice varieties are grown in over 850,000 ha in Sri Lanka annually, representing wide climatic and soil conditions in two seasons (Yala and Maha) (Mapa et al., 1999; Punyawardhana, 2008). As highlighted above, despite its importance, cardinal temperatures for Sri Lankan rice varieties and the degree-day requirement for key developmental processes have not yet been estimated. Therefore, cardinal temperatures estimated for rice varieties grown in other countries have been used when estimating the productivity of rice under Sri Lankan context (Amarasingha et al., 2015, 2017; Wallach et al., 2017). Moreover, duration of the vegetative stage of rice varies with time required for maturity while the ripening duration is relatively less variable (Awan et al., 2014; Gaydon et al., 2017). However, the sensitivity of those vegetative and ripening durations of rice to changing seasonal mean temperature, and the relationship between vegetative and ripening durations are not known.

Accurate prediction of Sri Lankan rice crop productivity is of immense importance, because it is the major source of food and over 40% of the population is directly or indirectly involved in rice cultivation. Moreover, Sri Lanka has been identified as one of the most vulnerable countries to climate change, i.e. 2nd and 6th place in the globe among the most affected countries due to climate risks in 2017 and 2018, respectively (Eckstein et al., 2019). Therefore, the objectives of the present study were to ascertain the (i) degree-day requirement and time taken for heading (flowering), ripening and maturity, (ii) influence of location, year and season on degree day requirement and time taken for heading, ripening and maturity, and (iii) relationships between ripening and heading durations measured in terms of degree days and days, of the three rice varieties widely cultivated in Sri Lanka.

**MATERIALS AND METHODS**

As a part of the regular rice crop improvement and evaluation program, new breeding lines are being tested across 11 locations or research stations belonging to the Department of Agriculture in Sri Lanka representing diverse agro-climatic and soil conditions (Table 1) over two seasons annually (i.e. national coordinated rice variety testing-NCRVT). Those locations are namely Aralaganwila (Ar), Ambalanthota (At), Bathalagoda (Bg), Bentota (Bt), Bombuwala (Bw), Labuduwa (Ld), Mahailluppallama (Mi), Murunkan (Mu), Paranthan (Pa), Samanthurei (St), and Vavunia (Vv). Additionally, data from Ampara (Am) were also included although it is not a NCRVT site. According to the climate classification in Sri Lanka Am, Ar, At, Mi, Mu, Pa, St and Vv are situated in the Dry Zone, Bg in the Intermediate Zone and Bt, Bw and Ld in the Wet Zone (Punyawardhana, 2008) (Fig. S1). Soil types and fertility levels were largely varied among these locations (Table 1). The first cultivating season (i.e. Yala) coincides with the South-West monsoon, spans approximately mid-May to August and the second cultivating season (i.e. Maha) coincides with the North-East monsoon, spans approximately mid-November to February of the following year. The NCRVT were conducted as randomized complete block designs with four replicates at each site while the recommended varieties were used as standard checks along with other breeding lines to be tested. Already recommended improved rice varieties Bg300 and Bg352 representing short duration age-class (90-99 days of maturity) and Bg358 representing medium duration age-class (100 - 109 days of maturity) were used as standard checks in these studies. Standard plot size was 6 m × 3 m.

Seeds were soaked in water for one day and incubated for two days until germination begins and then the sprouted seeds were sown in the field at the rate of 180 g /plot (around 400 seeds m⁻²). Seedling emergence could be observed three days after broadcasting. All trials were kept free from weeds, pest and diseases. Water and nutrient management were practiced as recommended by the Department of Agriculture, Sri Lanka. Therefore, limitation of crop growth and development due to moisture and nutrient (i.e. nitrogen, phosphorus, potassium and zinc) deficiencies or pest and disease incidents were not observed. Heading date is normally defined as the date when 50% panicles of the plot are emerged. Date of harvesting coincides closely
with physiological maturity. Both the 50% flowering and physiological maturity were determined through visual observations. Dates of broadcasting of pre-germinated rice seeds, 50% heading, and physiological maturity of Bg300, Bg352 and Bg358 were obtained from the NCRVT records available at the Rice Research and Development Institute (RRDI) at Bathalagoda, Sri Lanka for all the sites. Durations from broadcasting to heading was defined as ‘heading’, heading to maturity as ‘ripening’ and broadcasting to maturity as ‘maturity’. Median value of four replicates at each site, season and year were recorded for the number of days taken for heading, ripening and maturity and were analyzed statistically. Crop data were available for 19 years (from 1997 to 2015) and 12 locations for Bg300, seven years (from 2007 to 2015) and 11 locations for Bg352 and 11 years (from 2004 to 2014) and 10 locations for Bg358 over two seasons annually with certain gaps in some locations and years (Table S1). Therefore, in total 192, 55 and 120 data points (i.e. sample size) were available for Bg300, Bg352 and Bg358, respectively.

Daily weather data collected from 12 locations for the experimental period were compiled at the Natural Resource Management Centre (NRMC) of the Department of Agriculture, Sri Lanka and thus weather data (i.e. daily-minimum and maximum temperatures) were accessed from the NRMC. The arithmetic average of daily-minimum and maximum temperatures was considered as the daily-mean temperature. The average of daily-minimum, mean and maximum temperatures over season were considered as the average seasonal-minimum, mean and maximum temperatures (T_{min}, T_{mean} and T_{max}, respectively). Thermal time (TT °C) requirement for heading, ripening and maturity were calculated as explained by Wallach et al., (2017) and as used in Agricultural Production Systems sIMulator (APSIM). First, hourly temperature (T_i) was calculated as

\[ T_i = \left( T_{\text{base}} + T_{\text{max}} - T_{\text{base}} \right) / 2 + \left( T_{\text{max}} - T_{\text{base}} \right) \times \cos \left( 0.2618 \times (i-1) \right) / 2 \]

for \( i = 1, \ldots, 24 \). This makes a sinusoidal interpolation between maximum and minimum temperatures. Then thermal time (TT) for the day was calculated as

\[ \text{TT} = \sum_{i=1}^{24} \frac{T_i}{24} \]

\[ \text{TT}_{i} = \left( T_i - T_{\text{base}} \right) \text{ if } T_{\text{base}} \leq T_i < T_{\text{opt}} \]

\[ \text{TT}_{i} = \left( T_{\text{opt}} - T_{\text{base}} \right) \left( T_{\text{opt}} - T_{\text{base}} \right) \left( T_{\text{opt}} - T_{\text{base}} \right) \text{ if } T_{\text{opt}} < T_i \leq T_{\text{ce}} \]

\[ \text{TT}_{i} = 0 \text{ if } T_i \leq T_{\text{base}} \text{ or } T_{\text{ce}} < T_i \]

The T_{base}, T_{opt} and T_{ce} for the shoot growth were considered as 8 °C, 30 °C and 42 °C, respectively (Zhang et al., 2008; Wallach et al., 2017).

When testing the effects of location, season and year of cultivation on the number of days and degree days required for heading, ripening and maturity, analysis of variance (ANOVA) was used in SAS software using Proc GLM (SAS 2010). The explanatory variables used in the model were location, season, year and location × season interaction. Additionally, T_{min} and T_{max} were also included in the model to test whether there is a relationship between the number of days or degree days required for heading, ripening and maturity with T_{min} and T_{max}. Variability explained by each term in the model was determined using type I sum of squares. Means were compared using LSMEANS procedure. Relationships between variables were examined using regression (Proc REG) and Pearson’s linear correlation (Proc CORR) analyses. All significant differences were expressed at α=0.05. Grouping of sites with respect to standardized soil fertility characteristics was determined through hierarchical cluster analysis using the ‘complete linkage’ method.
RESULTS

Both the $T_{\text{min}}$ and $T_{\text{max}}$ across sites and seasons had a large range i.e. $T_{\text{min}}$ was in the range of 18.5 to 28.5 °C and $T_{\text{max}}$ was in the range of 25.9 to 36.9 °C (Fig. 1). Therefore, $T_{\text{mean}}$ also had a comparable range to those of $T_{\text{min}}$ and $T_{\text{max}}$. Apart from the temperature variation, soils in those study sites were largely varied on their fertility characteristics (Table 1). Moreover, soils from the sites located in northern Dry Zone grouped together while the rest grouped separately (Fig. S1).

The Yala season was characterized by higher mean $T_{\text{min}}$ and $T_{\text{max}}$ (i.e. warmer season) than those of Maha season (i.e. cooler season) across all the locations (Fig. 2). Labuduwa represented the coolest location during Yala season while Ampara and Paranthan represented the warmest locations. During Maha season Aralaganwila, Bathalgoda, Paranthan and Samanthurei represented the coolest locations while Ambalantota and Murunkan represented the warmest locations (Fig. 2). Labuduwa had the least difference between $T_{\text{min}}$ and $T_{\text{max}}$ (i.e. 3.5 and 3.4 °C during Yala and Maha, respectively) while

Figure 1: Frequency distributions of the average seasonal minimum, mean and maximum temperatures ($T_{\text{min}}$, $T_{\text{mean}}$ and $T_{\text{max}}$, respectively) across study locations, seasons and years.

Figure 2: Mean seasonal minimum, mean and maximum temperatures ($T_{\text{min}}$, $T_{\text{mean}}$ and $T_{\text{max}}$, respectively) of the study locations during the two cultivating seasons (Yala and Maha) across years. Note: Locations are denoted as Ampara (Am), Aralaganwila (Ar), Ambalanthota (At), Bathalgoda (Bg), Bentota (Bt), Bombuwala (Bw), Labuduwa (Ld), Mahailluppallama (Mi), Murunkan (Mu), Paranthan (Pa), Samanthurei (St), and Vavunia (Vu)
Aralaganwila and Samanthurei had the highest difference of the same (i.e. 12.2 and 9.9 °C during Yala and Maha seasons, respectively).

When averaged across locations, seasons and years, number of days required for heading, ripening and maturity of Bg300 were 66, 31 and 96 while those of Bg352 and Bg358 were 66, 32, 98 and 78, 30, 104, respectively (Fig. 3). Similarly, degree days required for heading, ripening and maturity of Bg300 were 1051, 491 and 1543 °C days while those of Bg352 and Bg358 were 1098, 529, 1627 and 1203, 496, 1698 °C days, respectively (Fig. 3). When averaged across locations and years and compare the two seasons, number of days and degree-days required for heading, ripening and maturity were similar between Yala and Maha seasons for the three rice varieties (p > 0.05, Fig. 3).

The number of days required for heading, ripening and maturity were largely affected by ‘location’ for all the rice varieties, except for maturity of Bg352 (Table 2). The ‘season’ effect was significant only to determine the heading and maturity durations of Bg352, and heading duration of Bg352. The effect of ‘year’ was not important to determine the number of days required for heading, ripening and maturity of any of the rice varieties. The two temperature terms, \( T_{\text{min}} \) and \( T_{\text{max}} \), were important to determine the number of days required for maturity and ripening of Bg300, respectively (Table 2). Therefore, selected sources of variability could explain 34-78% of the total variability (i.e. \( R^2 \)) in the number of days required for heading, ripening and maturity (Table 2).

### Table 2: Statistical significance of different sources of variability for the duration (days) and thermal time (degree days) required of different developmental stages of the three rice varieties.

| Cultivar | Sources of variability | \( df \) | \( T_{\text{min}} \) | \( T_{\text{max}} \) | Year | Location | Season | Location × Season | \( R^2 \) (%) | CV (%) |
|----------|------------------------|---------|----------------|-----------------|------|----------|--------|------------------|----------|--------|
| Bg300    | \( T_{\text{min}} \)  | 1       | ns             | ***             | ns   | ***      | **     | ***              | 45       | 8      |
|          | \( T_{\text{max}} \)  | 1       | ns             | ns              | ***  | ns       | ns     | ns               | 68       | 8      |
|          | Year                  | 1       | ns             | ns              | ns   | ns       | ns     | ns               | 51       | 12     |
|          | Location              | 11      | ***            | ***             | ***  | ***      | ***    | ***              | 61       | 13     |
|          | Location × Season     | 11      | ns             | *               | ns   | ***      | ns     | ns               | 41       | 5      |
|          | \( R^2 \) (%)         |         | 45             | 68              | 51   | 61       | 41     | 76               |
|          | CV (%)                |         | 8              | 8               | 12   | 13       | 5      | 5                |
| Bg352    | \( T_{\text{min}} \)  | 1       | ***            | ns              | ***  | ns       | ***    | ***              | 78       | 5      |
|          | \( T_{\text{max}} \)  | 1       | ns             | ns              | ns   | ns       | ns     | ns               | 81       | 5      |
|          | Year                  | 1       | ns             | ns              | ns   | ns       | ns     | ns               | 58       | 12     |
|          | Location              | 10      | ***            | ***             | **   | **       | ns     | ***              | 69       | 12     |
|          | Season                | 1       | *              | ***             | **   | ns       | ns     | *                | 59       | 5      |
|          | Location × Season     | 10      | ns             | **              | ***  | *        | ns     | ns               | 85       | 5      |
| Bg358    | \( T_{\text{min}} \)  | 1       | ***            | ns              | ***  | ns       | ***    | ***              | 50       | 5      |
|          | \( T_{\text{max}} \)  | 1       | ns             | ns              | ns   | *        | ns     | ns               | 84       | 5      |
|          | Year                  | 1       | ns             | ns              | ns   | ns       | ns     | ns               | 34       | 13     |
|          | Location              | 9       | ***            | *               | **   | **       | **    | *                | 55       | 13     |
|          | Season                | 1       | *              | ns              | ns   | ns       | ns     | ns               | 37       | 4      |
|          | Location × Season     | 9       | ns             | *               | ns   | ns       | ns     | ns               | 84       | 4      |

**Note:** n.s., no significant difference; *, P < 0.05; **, P < 0.01; ***, P < 0.001; Coefficient of determination (\( R^2 \)) value for the tested full model is given; \( CV \)- coefficient of variation; \( df \)- degree of freedom; \( T_{\text{min}} \) - mean seasonal minimum temperature; \( T_{\text{max}} \) - mean seasonal maximum temperature.
Degree-days required for heading, ripening and maturity were influenced by $T_{\text{min}}$, location and season for the three rice varieties while other variables were not important (Table 2). Moreover, $T_{\text{max}}$ was important to determine the degree-days required for ripening of Bg300 and Bg358. Therefore, selected sources of variability could explain 55-85% of the total variability (i.e., $R^2$) in the degree-days required for heading, ripening and maturity (Table 2).

The location × season effect was significant to determine the number of days required for ripening, and the degree days required for heading, ripening and maturity of Bg300 (Table 2, Fig. 4). The number of days required for heading, ripening and maturity of Bg300 ranged between 58-72, 24-36 and 91-102 days, respectively across seasons and locations (Fig. 4). Degree-days required for heading, ripening and maturity of Bg300 varied between 942-1214, 347-647 and 1307-1734 °C days, respectively across seasons and locations (Fig. 4).

The location × season effect was significant to determine the degree days required for heading of Bg358 (Table 2, Fig. 6). The number of days required for heading, ripening and maturity of Bg358 ranged between 68-83, 25-33 and 100-109 days, respectively across seasons and locations (Fig. 6). Degree-days required for heading, ripening and maturity ranged between 1035-1370, 370-564 and 1437-1831 °C days, respectively across seasons and locations (Fig. 6).

The statistical model with $T_{\text{min}}$, $T_{\text{max}}$, location, season, year and location × season interaction as explanatory variables could explain 68%, 61% and 76% of the total variability in the degree-day requirement for heading, ripening and maturity in Bg300, respectively (Fig. 7, Table 2). Similarly, the same for Bg352 were 81%, 69% and 85%, and for Bg358 were 84%, 55% and 84%, respectively. Irrespective of the development stage and variety, $T_{\text{min}}$ and location contributed to explain the variability of the degree days required for heading, ripening and maturity than other sources (Fig. 7).

The $T_{\text{min}}$, $T_{\text{mean}}$ and $T_{\text{max}}$ had significant correlations with the degree-days required for heading, ripening and maturity of all the rice varieties (Table 3). As the daily mean temperature was calculated using daily-minimum and maximum temperatures, only the daily-minimum and maximum temperatures, and there by $T_{\text{min}}$ and $T_{\text{max}}$ were independent. Both $T_{\text{min}}$ and $T_{\text{max}}$ had significant positive correlations with the degree-days required for heading, ripening and maturity of all the rice varieties.
Figure 4: Number of days and degree days required for heading, ripening and maturity of Bg300 at different locations and seasons (Yala and Maha). Note: location names are given in Figure 2.

Figure 5: Number of days and degree days required for heading, ripening and maturity of Bg352 at different locations and seasons (Yala and Maha). Note: location names are given in Figure 2.
Figure 6: Number of days and degree days required for heading, ripening and maturity of Bg358 at different locations and seasons (Yala and Maha). Note: location names are given in Figure 2.

Figure 7: Fraction of the total variability in degree days required for heading, ripening and maturity of the three rice varieties explained by the explanatory variables used in the statistical model.

Table 3: Correlation coefficients ($r$) of seasonal mean minimum ($T_{\text{min}}$), mean ($T_{\text{mean}}$) and maximum ($T_{\text{max}}$) temperatures with degree day requirement for heading, ripening and maturity of the three rice varieties. $p<0.0001$ in each cell, $n=202, 55$ and $120$ for Bg300, Bg352 and Bg358, respectively.

| Variety | Heading stage | Ripening stage | Until maturity |
|---------|---------------|----------------|---------------|
|         | $T_{\text{min}}$ | $T_{\text{mean}}$ | $T_{\text{max}}$ | $T_{\text{min}}$ | $T_{\text{mean}}$ | $T_{\text{max}}$ | $T_{\text{min}}$ | $T_{\text{mean}}$ | $T_{\text{max}}$ |
| Bg300   | 0.762         | 0.668          | 0.502         | 0.948         | 0.918          | 0.844          | 0.975         | 0.968          | 0.947          |
| Bg352   | 0.942         | 0.903          | 0.835         | 0.938         | 0.882          | 0.763          | 0.979         | 0.949          | 0.959          |
| Bg358   | 0.700         | 0.585          | 0.421         | 0.950         | 0.916          | 0.834          | 0.981         | 0.976          | 0.961          |
Significant negative relationships were observed between the number of days required for heading and the number of days required for ripening for all the rice varieties (Fig. 8). Moreover, slopes of the relationships were in the range of -0.3 to -0.4, i.e. shortening the ripening duration by 7.2 to 9.6 h when the heading was delayed by one day. However, such relationships were not observed between the degree-day requirements for heading and ripening phases. It was also observed that the relationships between time (i.e. year of cultivation) and $T_{\text{min}}$ or $T_{\text{max}}$ were not significant at tested locations ($p>0.05$) (data not shown).

**DISCUSSION**

Rice is more sensitive to temperature during vegetative period and immediately preceding anthesis (Chaudhary and Ghildyal, 1970; Satake and Yoshida, 1978; Prasad et al., 2006; Jagadish et al., 2007; De Costa, 2010; Luo, 2011; Sanchez et al., 2014). To date the relationships between temperature and phenology of rice have mostly been established using the data collected from pot experiments conducted under controlled environmental conditions or crops grown in one location for several seasons (Ellis et al., 1993; Caton et al., 1998; Awan et al., 2014; Counce et al., 2015; Rouan et al., 2018). However, we used a more generic approach using the data collected from field grown plants of different varieties across locations, seasons and years to derive temperature and phenology relationships for Sri Lankan improved rice varieties, which would have wider applications than previous approaches.

**Growing season temperatures of Sri Lankan rice**

Data collected from 12 locations representing diverse agro-climatic conditions in Sri Lanka over a decadal time scale covered a reasonable range of temperatures to study the development of rice under actual field conditions. The $T_{\text{opt}}$ values reported in the literature vary from 27 to 35 °C (Matthews et al., 1995, 1997; Bouman et al., 2001; Sanchez et al., 2014; van Oort et al., 2015; Wallach et al., 2017), and the $T_{\text{opt}}$ used in the present study was 30 °C as used previously for Sri Lankan rice (Wallach et al., 2017). The $T_{\text{mean}}$ of most of the rice cultivating locations in Sri Lanka ranged from 24 to 31 °C, and $T_{\text{max}}$ reached up to 36.9 °C (Fig. 1). This may cause negative implications for Sri Lankan rice production in the near future. Because, it could be postulated that climate change would cause more locations and/or seasons to be in supra-optimal range of temperatures for rice in the immediate future. Under such circumstances yield losses due to spikelet sterility, higher rates of respiration and extended crop duration have been predicted (De Costa, 2010). The expected negative impacts on phenology and productivity of rice would immediately be visible in warmer Yala season than that in cooler Maha season. As a result, much attention is needed when determining cropping calendars, variety selection and prioritizing research and policy decisions in regional, provincial or seasonal scales in the country (De Costa, 2010; Amarasingha et al., 2015). Moreover, as an adaptive strategy, it is also important to seek heat tolerant rice varieties either through screening local rice germplasm or

![Figure 8: Relationships between the ripening and heading durations (in terms of days and degree days) of the three rice varieties.](image-url)
importing promising lines to be used in breeding programs with the aim of developing heat tolerant rice varieties for future.

The cardinal temperatures of Sri Lankan rice varieties are not yet known and the values reported in literature from other countries with different genetic make-ups may not be appropriate for Sri Lankan rice varieties. The range of temperatures experienced in this study (i.e. 23.9-31.1 °C) was inadequate to extrapolate and predict \( T_{\text{min}} \) and \( T_{\text{max}} \) for Sri Lankan rice varieties. Therefore, experiments need to be conducted under control environment conditions with broad range of temperatures to estimate cardinal temperatures for different developmental events of major rice varieties grown in Sri Lanka. It is also reported that a definite \( T_{\text{c}} \) may not exist because of an asymptotic slowing of physiological processes at low-temperatures (Parent et al., 2010). Furthermore, genotypic differences in acclimation may also exist (Shimono et al., 2011) and even acquired adaptation by epigenetics may play a role (Koumoto et al., 2014). Ultimately, the use of variety-dependent cardinal temperatures will enhance the predictive power of simulation models under current and future climatic conditions (Rouan et al., 2018).

Degree-day requirement for heading

Degree-day requirement for heading, ripening and maturity were not unique or constant for the three rice varieties. Out of the sources used in this experiment, variability of the degree-day required for heading, ripening and maturity were explained in the order of \( T_{\text{min}} \) > location > year > location × season > season > \( T_{\text{max}} \) (Fig. 8). Therefore, the degree-day required for heading, ripening and maturity differed largely among locations and affected by \( T_{\text{min}} \). As reported in literature, soil characteristics such as fertility and moisture availability may also contribute to determine the timing of developmental events (Sahrawat et al., 1995; Franks, 2011; Mayamulla et al., 2017). However, the sensitivity of crop development to location-specific soil characteristics was largely ignored when calculating degree days. It is reported that, development events may either be advanced or delayed depending on the limitation in soil e.g., early heading was observed when nitrogen or moisture limitations were occurred (Kleining and Noble, 1967; Franks, 2011; Minh-Thu et al., 2018; Ye et al., 2019), whereas development events were delayed under phosporus deficiency (Sahrawat et al., 1995; Mayamulla et al., 2017). Thus, the potential impact of soil in determining the timing of development events such as heading cannot be ignored for field grown crops. This was confirmed by the significant ‘location’ effect in the ANOVA (Table 2). Even though the degree-day requirement for the initiation of development events was considered as constant across varieties, environments and management in most of the previous modeling exercises (Amarasingha et al., 2015; Nissanka et al., 2015; Wallach et al., 2017), our observations from the field studies did not support this concept. Similar results have also been reported recently (Counce et al., 2015; Dingkuhn et al., 2015). Therefore, genotype × environment-dependent degree-day requirements need to be considered to enhance the precision of phenology predictions across spatial and temporal scales.

Sri Lanka experiences 44 minutes variation of day length each year. However, the effects of season and location × season interaction on determining the degree days required for heading and maturity of rice were not prominent as those effects were significant only in few instances (Table 2). This would be due to the lack of sensitivity of improved Sri Lankan rice varieties to photoperiod.

Relationships between crop developmental events and growing season temperatures

As the time required for heading extended, the ripening durations of all three rice varieties were shortened, i.e. 8.4 h reduction in ripening duration for the delay in heading by one day. This can be considered as an efficient physiological adaptation strategy for survival. It is known that up to 40% of the photosynthates stored in rice grains is contributed by pre-anthesis photosynthates (Ntanos and Koutrobas, 2002). Therefore, delayed heading may have allowed rice plants to store more photosynthates in vegetative tissues and rapidly re-translocate that to filling grains (i.e., higher rate of grain filling), thereby reducing the time required for grain filling.

Time required for heading was longer in warmer locations as those sites were in supra-optimal range. Moreover, the degree-day required for heading, ripening and maturity of all the rice varieties were significantly and positively correlated with the seasonal \( T_{\text{min}} \) and \( T_{\text{max}} \) (Table 3). This indicates that an increase in \( T_{\text{min}} \) (e.g., an increase in night-time temperature) and \( T_{\text{max}} \) (e.g., an increase in day-time temperature) increases the degree-days required to complete development events. Therefore, the predicted global warming will have adverse impacts on the phenology of rice as it may require additional time, in terms of degree-days to complete developmental events. As authors are aware, this is the first time to explore such relationships.

There is a general agreement that increase in environmental temperature will reduce the duration (days) of most cereal crops by hastening their phenological development (De Costa, 2010). However, our results revealed that, due to the positive correlation between \( T_{\text{min}} \), \( T_{\text{mean}} \) and \( T_{\text{max}} \) with degree-days required to complete developmental events, crop duration (days) would not be lowered as expected under warming climates. Thus, the crops would remain in the field for a longer duration than the duration expected earlier under climate change (i.e. crop duration would not be shorten as expected). These relationships need to be explored and validated further for other crops grown in different environments and management conditions before making generic conclusions across species and varieties.

CONCLUSIONS

Phenology of rice was not studied widely using field grown crops. Therefore, the relevance and validity of phenology
estimations made using crops grown under controlled environments or with limited field observations were recently questioned. Our data provided an opportunity to answer those uncertainties raised. The $T_{\text{min}}$ for heading of Sri Lankan rice varieties and the $T_{\text{max}}$ of most of the rice growing regions in Sri Lanka were mostly similar. Therefore, the predicted increase in global temperature due to climate change would alter the phenology of Sri Lankan rice varieties.

Though the degree-days required for heading and maturity were largely explained by the growing season temperature, the contribution from location specific characteristics such as water availability and fertility status cannot be ignored for field grown rice varieties. Therefore, genotype × environment-dependent degree-day requirements need to be considered to enhance the precision of phenology predictions. It has also been found that the increase in $T_{\text{min}}$ and $T_{\text{max}}$ extended the degree-day requirement for heading and maturity. Therefore, rice crops would not shorten their growth durations under warming climates as expected before. This increase in the degree-day requirement could be mainly due to the delayed heading, despite the reduced duration of ripening.

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DECLARATION OF CONFLICT OF INTEREST

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this manuscript.

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Table S1. Data collected years, seasons and locations for the three varieties.

| Bg300 | 1997 | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 | 2007 | 2008 | 2009 | 2010 | 2011 | 2012 | 2013 | 2014 | 2015 |
|-------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|
| Y     | M    | Y    | M    | Y    | M    | Y    | M    | Y    | M    | Y    | M    | Y    | M    | Y    | M    | Y    | M    | Y    | M    |
| Am    |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| Ar    |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| At    |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| Bg    |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| Bt    |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| Bw    |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| Ld    |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| Mi    |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| Mu    |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| Pa    |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| St    |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| Vu    |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |

| Bg352 | 1997 | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 | 2007 | 2008 | 2009 | 2010 | 2011 | 2012 | 2013 | 2014 | 2015 |
|-------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|
| Y     | M    | Y    | M    | Y    | M    | Y    | M    | Y    | M    | Y    | M    | Y    | M    | Y    | M    | Y    | M    | Y    | M    |
| Ar    |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| At    |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| Bg    |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| Bt    |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| Bw    |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| Ld    |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| Mi    |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| Mu    |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| Pa    |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| St    |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| Vu    |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |

SUPPORTING INFORMATION
| Bg358 | 1997 | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 | 2007 | 2008 | 2009 | 2010 | 2011 | 2012 | 2013 | 2014 | 2015 |
|-------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|
| Y     | M    | Y    | M    | Y    | M    | Y    | M    | Y    | M    | Y    | M    | Y    | M    | Y    | M    | Y    | M    | Y    | M    |
| Ar    |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| At    |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| Bg    |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| Bt    |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| Bw    |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| Ld    |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| Mi    |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| Mu    |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| Pa    |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| St    |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |

Note: Yala season (Y), Maha season (M), Ampara (Am), Aralaganwila (Ar), Ambalanthota (At), Bathalagoda (Bg), Bentota (Bt), Bombuwala (Bw), Labuduwa (Ld), Mahailluppallama (Mi), Murunkan (Mu), Paranthan (Pa), Samanthurei (St), and Vavunia (Vu).
Figure S1: Sites used to conduct national coordinated rice variety testing (NCRVT) trials in Sri Lanka (A) and the grouping of those sites based on the soil characteristics stated in Table 1 (B).