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Heat Unit–Based Prediction of Harvest Age in Rice under Different Planting Spacings and Genotypes

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ABSTRACT

Heat unit (HU) is widely used to describe crop thermal requirements; however, its application for determining rice harvest age across different planting spacings and genotypes remains limited. This study aimed to evaluate the effects of plant spacing and genotype on HU accumulation and to assess the usefulness of HU as a predictor of harvest age and yield-related traits in rice. The experiment was conducted in a greenhouse using a factorial randomized complete block design with three planting spacings (Jarwo 2:1, Tegel 25 cm × 25 cm, and transplanter-based spacing 35 cm × 15 cm) and four rice genotypes (PTP 01, Inpari 24, Jeliteng, and Pandan Wangi). Results showed that HU accumulation during the vegetative phase was uniform across all treatments, reaching approximately 776 °C·day, indicating a common thermal threshold for early growth. In contrast, significant differences emerged during the generative phase and at harvest. Plant spacing significantly affected HU accumulation and harvest timing, whereas genotype did not alter total HU requirement but strongly influenced yield expression. The Jarwo 2:1 system required the lowest total HU to reach physiological maturity (~1134 °C·day), followed by Tegel 25×25 cm (~1146 °C·day) and transplanter spacing (~1159 °C·day). Inpari 24 consistently exhibited superior plant height, grain filling, and grain weight per panicle, indicating higher efficiency in converting accumulated HU into yield. Heat unit–based thresholds provide a reliable tool for predicting rice harvest age and optimizing genotype–spacing combinations.

1. INTRODUCTION

Based on data from the Central Statistics Agency, the harvested area for rice in 2023 was recorded at 10.20 million hectares (BPS, 2023). In 2024, it is expected to decrease to 10.05 million hectares, representing a reduction of 167.25 thousand hectares (1.64%) compared to the previous year (Suparman *et al*., 2025). This decline in harvested area affects rice production, which reached 53.98 million tons of milled dry rice equivalent (MDRE) in 2023, but is projected to decrease to 52.66 million tons in 2024, representing a reduction of 1.32 million tons (2.45%). Rice production for food consumption is also experiencing a decline, from 31.10 million tons in 2023 to 30.34 million tons in 2024 (BPS, 2024). If this declining trend persists, it may pose a serious challenge to national food security (Jaya *et al*., 2025; 2023), highlighting the importance of optimizing rice production systems.

Various factors influence the harvesting age of rice, with harvest timing being a critical determinant of both yield and grain quality. Harvesting rice too early can result in incomplete grain filling (Qu *et al*., 2021), while delayed harvesting may increase losses and reduce quality (Putri *et al*., 2025). Therefore, accurate determination of optimal harvest age is essential to improve production efficiency and ensure stable rice supply (Dulbari *et al*., 2025).

Plant genotype plays a crucial role in determining harvest age and growth characteristics of rice plants (Oladosu *et al*., 2018). This is consistent with the research by Wang *et al*. (2017), which shows that genotype significantly affects plant height, harvesting age, and the number of tillers in rice plants. These genetic differences reflect variation in growth duration and developmental responses to environmental conditions (Hansen *et al*., 2012). In addition to genotype, planting systems or methods also influence rice growth and development (Uphoff *et al*., 2015). The use of appropriate planting methods aims to reduce competition for water, nutrients, and sunlight, thereby improving plant performance (Fan *et al*., 2025).

One method used to determine the harvest age of rice more accurately is the heat unit method. Heat units calculate daily thermal accumulation based on the difference between the average daily temperature and a base temperature specific to the crop (Fan *et al*., 2025; Majumder & Dhaliwal, 2024). This approach allows harvest age to be estimated based on actual thermal conditions rather than calendar days, enabling more precise prediction of plant growth rates and phenological stages (Brinkhoff *et al*., 2024; Ishimaru *et al*., 2022). Growing Degree Days (GDD) is the most widely used heat unit index to predict plant development stages and harvest time by accumulating daily temperature values throughout the growing period (Hachisuca *et al*., 2023; Liu *et al*., 2022).

However, studies that simultaneously evaluate different rice genotypes and planting methods using a heat unit approach remain limited. Therefore, this research aims to determine the amount of heat units required by several rice genotypes (*Oryza sativa* L.) at each growth phase and to analyze the relationship between heat unit accumulation, harvest age, and rice productivity under various plant spacing.

2. MATERIALS AND METHODS

2.1. Study Site

This research was conducted from September to December 2023 at the Polinela Organic Farm (POF) experimental field, Politeknik Negeri Lampung, Bandar Lampung, Indonesia (5°21′10″ S; 105°13′43″ E; 114 m above sea level) (Safrudin *et al*., 2024). The geographic location of the experimental site is presented in Figure 1.

2.2. Planting Materials

The planting materials consisted of four rice genotypes (*Oryza sativa* L.), namely PTP 01, Inpari 24, Jeliteng, and Pandan Wangi. PTP 01 is a rice breeding line developed by Politeknik Negeri Lampung (Safrudin *et al*., 2024), while Inpari 24, Jeliteng, and Pandan Wangi are nationally released varieties obtained from the Indonesian Rice Research Center (BB Padi).

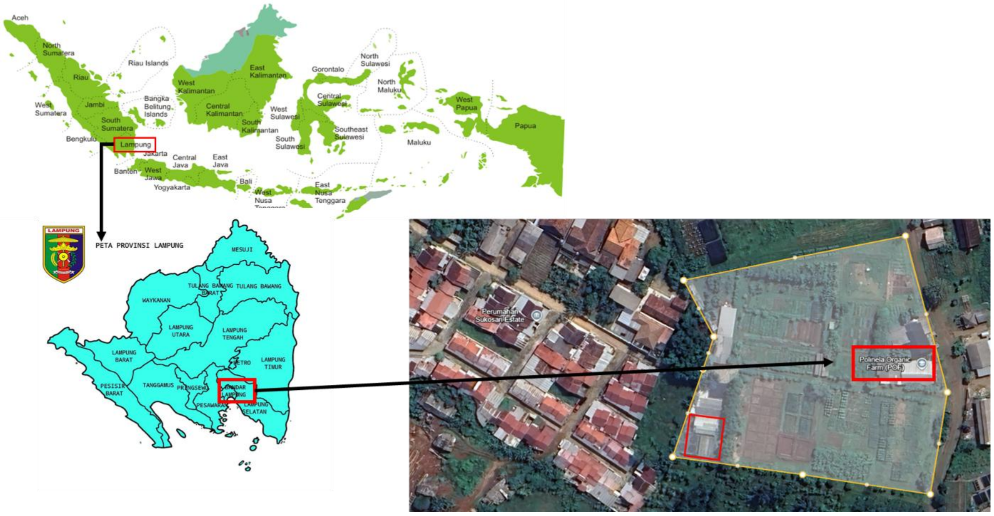


Figure 1. Location of the experimental site

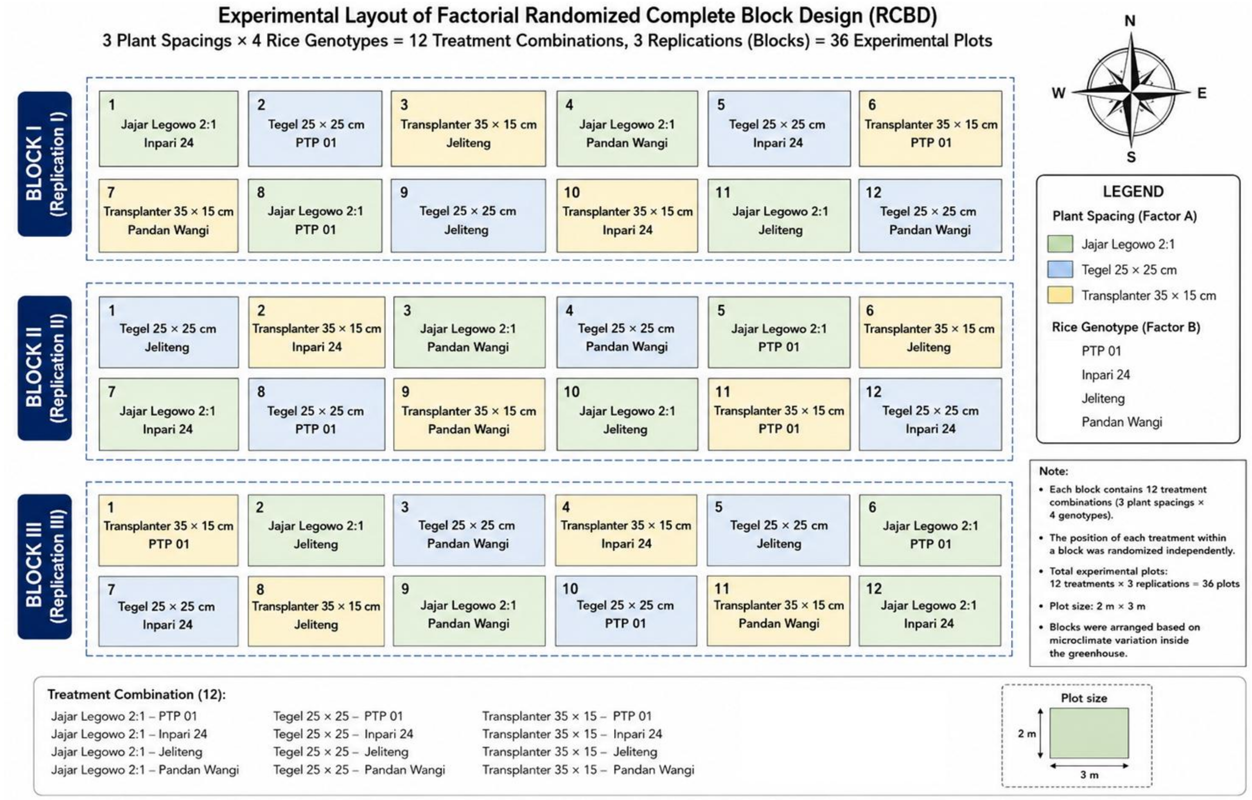
The experiment was conducted in a greenhouse with an approximate size of 10 m × 6 m. The experimental area was divided into six plots, each measuring 2 m × 3 m, providing sufficient space to accommodate all treatment combinations and ensure proper crop management. The greenhouse environment allowed uniform cultivation practices while maintaining field-relevant growing conditions for rice plants. Fertilization was applied using Urea (300 kg/ha), SP36 (200 kg/ha), and KCl (100 kg/ha) as sources of nitrogen (N), phosphorus (P), and potassium (K), respectively. Pest control was carried out using deltamethrin (25 EC) when necessary, following recommended application rates.

2.3. Experimental design

The experiment was arranged in a factorial Randomized Complete Block Design (RCBD) with two factors. The first factor was plant spacing, consisting of three levels: Jajar Legowo 2:1 (25 cm × 1.25 cm with one raw vacant every two rows), Tegel spacing of 25 cm × 25 cm, and Transplanter spacing of 35 cm × 15 cm. The term plant spacing (or planting pattern) was used because the treatments combined differences in row arrangement and intra-row spacing, particularly in the Jajar Legowo system. The second factor was rice genotype, consisting of four levels: PTP 01, Inpari 24, Jeliteng, and Pandan Wangi. The combination of both factors resulted in 12 treatment combinations (3 plant spacings × 4 genotypes), which replicated three times.

The experiment consisted of three blocks, which served as replications. Blocks were established based on spatial microclimate variation within the greenhouse, particularly differences in light exposure, air circulation, and temperature gradients along the greenhouse length. This blocking strategy was applied to minimize environmental heterogeneity that could influence heat unit accumulation and crop growth (Rahmat *et al*., 2023).

Within each block, the 12 treatment combinations were randomly assigned to experimental plots using a randomization procedure to avoid allocation bias (Figure 2). Each experimental plot measured 2m × 3m, and plots were



Experimental Layout of Factorial Randomized Complete Block Design (RCBD)

3 Plant Spacings × 4 Rice Genotypes = 12 Treatment Combinations, 3 Replications (Blocks) = 36 Experimental Plots

BLOCK I (Replication I)

1	2	3	4	5	6
Jajar Legowo 2:1 Inpari 24	Tegel 25 × 25 cm PTP 01	Transplanter 35 × 15 cm Jeliteng	Jajar Legowo 2:1 Pandan Wangi	Tegel 25 × 25 cm Inpari 24	Transplanter 35 × 15 cm PTP 01
7	**8**	**9**	**10**	**11**	**12**
Transplanter 35 × 15 cm Pandan Wangi	Jajar Legowo 2:1 PTP 01	Tegel 25 × 25 cm Jeliteng	Transplanter 35 × 15 cm Inpari 24	Jajar Legowo 2:1 Jeliteng	Tegel 25 × 25 cm Pandan Wangi

BLOCK II (Replication II)

1	2	3	4	5	6
Tegel 25 × 25 cm Jeliteng	Transplanter 35 × 15 cm Inpari 24	Jajar Legowo 2:1 Pandan Wangi	Tegel 25 × 25 cm Pandan Wangi	Jajar Legowo 2:1 PTP 01	Transplanter 35 × 15 cm Jeliteng
7	**8**	**9**	**10**	**11**	**12**
Jajar Legowo 2:1 Inpari 24	Tegel 25 × 25 cm PTP 01	Transplanter 35 × 15 cm Pandan Wangi	Jajar Legowo 2:1 Jeliteng	Transplanter 35 × 15 cm PTP 01	Tegel 25 × 25 cm Inpari 24

BLOCK III (Replication III)

1	2	3	4	5	6
Transplanter 35 × 15 cm PTP 01	Jajar Legowo 2:1 Jeliteng	Tegel 25 × 25 cm Pandan Wangi	Transplanter 35 × 15 cm Inpari 24	Tegel 25 × 25 cm Jeliteng	Jajar Legowo 2:1 PTP 01
7	**8**	**9**	**10**	**11**	**12**
Tegel 25 × 25 cm Inpari 24	Transplanter 35 × 15 cm Jeliteng	Jajar Legowo 2:1 Pandan Wangi	Tegel 25 × 25 cm PTP 01	Transplanter 35 × 15 cm Pandan Wangi	Jajar Legowo 2:1 Inpari 24

LEGEND

Plant Spacing (Factor A)
- 🟩 Jajar Legowo 2:1
- 🟦 Tegel 25 × 25 cm
- 🟨 Transplanter 35 × 15 cm

Rice Genotype (Factor B)
- PTP 01
- Inpari 24
- Jeliteng
- Pandan Wangi

Note:
- Each block contains 12 treatment combinations (3 plant spacings × 4 genotypes).
- The position of each treatment within a block was randomized independently.
- Total experimental plots: 12 treatments × 3 replications = 36 plots
- Plot size: 2 m × 3 m
- Blocks were arranged based on microclimate variation inside the greenhouse.

Treatment Combination (12):

Jajar Legowo 2:1 – PTP 01	Tegel 25 × 25 – PTP 01	Transplanter 35 × 15 – PTP 01
Jajar Legowo 2:1 – Inpari 24	Tegel 25 × 25 – Inpari 24	Transplanter 35 × 15 – Inpari 24
Jajar Legowo 2:1 – Jeliteng	Tegel 25 × 25 – Jeliteng	Transplanter 35 × 15 – Jeliteng
Jajar Legowo 2:1 – Pandan Wangi	Tegel 25 × 25 – Pandan Wangi	Transplanter 35 × 15 – Pandan Wangi

Figure 2. Experimental layout of the factorial randomized complete block design (RCBD) showing the arrangement of planting spacing treatments (Jajar Legowo 2:1,Tegel 25 cm × 25 cm, and Transplanter spacing 35 cm × 15 cm), rice genotypes, block structure (I–III), plot size (2 m × 3 m), and compass direction within the greenhouse

physically separated by plot boundaries and inspection paths to prevent interference among planting patterns. All treatment units were clearly labeled according to block, plant spacing, and genotype code to ensure accurate implementa-tion and data collection throughout the experiment.

2.4. Rice Cultivation Practices

Rice cultivation was conducted under greenhouse conditions following standard lowland rice management practices. Land preparation involved soil tillage to a depth of approximately 20–25 cm, followed by land leveling to ensure uniform water distribution. Experimental plots measuring 2 m × 3 m were established and clearly separated to prevent interference among treatments.

Seeds of each rice genotype were soaked in clean water for 24 h and incubated for 48 h to promote uniform germination. Seedlings were raised in trays and transplanted at 18–21 days after sowing, when plants reached the 2–3 leaf stage. All transplanting activities were performed manually according to the plant spacing treatments: Jajar Legowo 2:1, Tegel (25 cm × 25 cm), and Transplanter (35 cm × 15 cm). The spacing used in Transplanter was manually applied but adopted from the standard spacing configuration commonly used in rice transplanter systems, without the use of mechanical planting equipment.

Irrigation was managed to maintain a shallow water stand of approximately 2–5 cm during the vegetative stage, followed by intermittent irrigation during the reproductive stage. Fields were drained 10–14 days before harvest to support grain maturation. Fertilization was applied uniformly across all treatments using Urea (300 kg/ha), SP-36 (200 kg/ha), and KCl (100 kg/ha). Phosphorus and potassium fertilizers were applied as basal inputs, while nitrogen fertilizer was split-applied at 7, 21, and 42 days after transplanting (DAT).

Pest management was conducted based on field observations, with Deltamethrin (25 EC) applied when pest incidence exceeded acceptable levels. Weed control was carried out manually as needed. Harvesting was conducted at physiological maturity, indicated by grain yellowing and sufficient accumulation of heat unit or Growing Degree Days (GDD). Plants were harvested manually, followed by threshing, grain cleaning, and measurement of grain moisture content prior to yield analysis.

2.5. Observations and Measurements

2.5.1. Growth Parameters

Observations and measurements were conducted on growth, physiological, and yield-related parameters. Growth parameters included plant height (cm) and number of tillers that were recorded periodically at 14, 28, and 42 DAT. Plant height was measured from the soil surface to the tip of the tallest leaf, while tiller number was counted per hill.

2.5.2. Physiological Parameter (SPAD)

The chlorophyll index or SPAD (Soil Plant Analysis Development) was measured using a handheld chlorophyll meter. Measurements were taken on the middle portion of the fully expanded uppermost leaf, avoiding the midrib. Three readings per leaf were recorded and averaged to obtain a representative SPAD value. SPAD observations were conducted at the maximum vegetative stage (approximately 42 DAT) (Mubarok *et al*., 2024).

2.5.3. Yield Components

Yield-related parameters were measured at harvest including panicle length (cm), number of filled grains per panicle (grain), number of unfilled grains per panicle (grain), grain weight per panicle (g), and grain moisture content (%).

2.5.4. Thermal Time (HU or GDD)

Daily climate data in the form of maximum and minimum air temperatures were collected during the experiment and were supported by data obtained from the official website of the Meteorology, Climatology, and Geophysics Agency (BMKG). Based on these daily temperature data, the heat unit (HU) required for rice growth and harvesting was calculated, providing an overview of the optimal timing for rice harvest.

To determine the total heat requirement of rice plants at each stage of growth, the HU calculation method was employed. This method measures the accumulation of effective temperatures required for plant development until physiological maturity. In this study, HU is equivalent to Growing Degree Days (GDD), as both are calculated based on the difference between the average daily temperature. The HU or GDD was calculated as the following:

$$\text{HU or GDD} = \sum(T - To) \tag{1}$$

$$T = \frac{Tn+Tx}{2} \tag{2}$$

where HU is heat unit required by plants (°C·day), T is average daily temperature (°C), Tx is maximum temperature (°C), Tn is minimum temperature (°C), and To is base temperature for rice plants, which is 17 °C (Shofi *et al*., 2022).

The daily HU or GDD values were then cumulatively summed from planting until harvest to determine the total thermal requirement of each rice genotype and to estimate harvest age under different planting methods. This cumulative thermal time approach provides a reliable indicator of crop development and physiological maturity, enabling more accurate prediction of harvest time (Pullens *et al*., 2021). The total HU requirement was obtained by summing the HU accumulated during the vegetative and generative phases, representing the total thermal time required from transplanting to harvest for each planting method.

2.6. Statistical Analysis

The collected data were analyzed using the STAR application for the analysis of variance (ANOVA), employing an F-test (Budiarto *et al*., 2022). If ANOVA results indicate a significant difference, the analysis proceeds with the Honest Significant Difference (HSD) test at a 5% significance level to determine the actual differences among treatments.

3. RESULTS AND DISCUSSION

3.1. Daily Air Temperature Dynamics

Daily minimum and maximum air temperatures recorded during the experimental period showed relatively stable but fluctuating patterns (Figure 3). Minimum daily temperatures ranged from approximately 21.0 to 26.3 °C, while maximum daily temperatures varied between 31.4 and 38.3 °C. The highest maximum temperatures were observed in mid to late October, coinciding with the transition from the vegetative to the generative growth phase. Overall, the temperature regime during the study remained within the suitable range for rice growth, although several days experienced relatively high maximum temperatures (>36 °C). Such temperature fluctuations are critical because daily thermal conditions directly influence heat unit accumulation, which governs crop development rate and phenological progression (Guralnick *et al*., 2024; Zhu *et al*., 2021). The consistent pattern of minimum temperatures suggests stable nighttime conditions, while variability in maximum temperatures reflects diurnal heat stress that may accelerate physiological development (Shirdelmoghanloo *et al*., 2022). These temperature dynamics provide the climatic basis for interpreting heat unit (HU or GDD) accumulation across growth stages and planting methods.

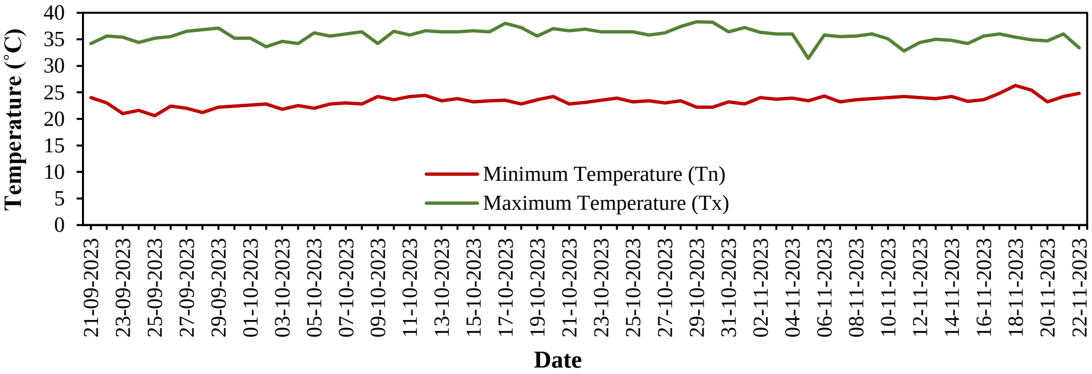


Figure 3. Daily minimum and maximum air temperatures recorded during the experiment (September–November 2023)

3.2. Heat Unit Accumulation during Vegetative and Generative Phases

Heat unit (HU) accumulation during the vegetative phase was remarkably similar across all rice genotypes and plant spacing, with values consistently 776.35 °C·day. This uniformity indicates that vegetative development reached a comparable thermal threshold regardless of genotype or plant spacing. Such consistency suggests that early growth processes, including tiller initiation and leaf expansion, are governed by intrinsic thermal requirements rather than planting configuration or genetic background under the environmental conditions of this study (Kefford *et al*., 2022).

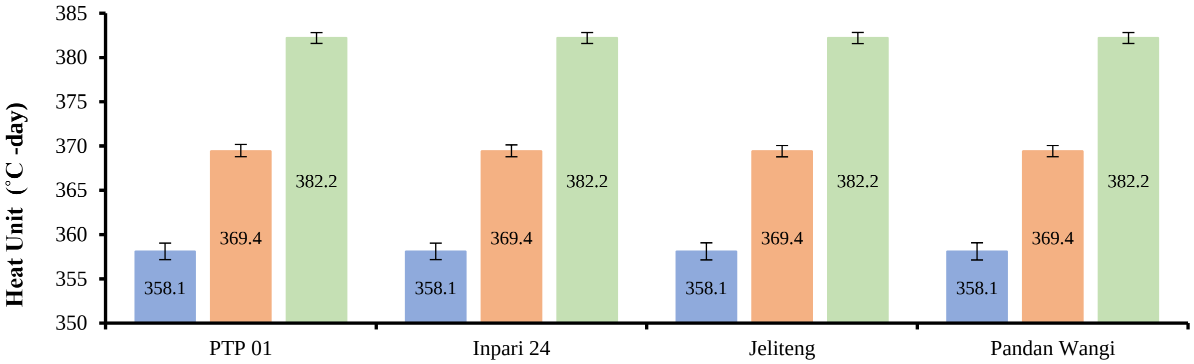


Figure 4. Cumulative heat unit (°C·day) during generative phases of four rice genotypes under different planting methods. Bars indicate SD of three replication (*n* = 3).

In contrast, clear differences in HU accumulation emerged during the generative phase (Figure 4b), indicating that reproductive development was more responsive to planting method. Rice plants grown under transplanter spacing (35 cm × 15 cm) required the highest thermal units to complete the generative phase (approximately 382.20 °C·day), followed by Tegel 25 cm × 25 cm (approximately 369.40 °C•day), while the Jarwo 2:1 system exhibited the lowest HU requirement (approximately 358.10 °C·day) across genotypes. These results demonstrate that although vegetative development terminated at a similar HU threshold, planting spacing significantly altered the thermal duration required for grain formation and physiological maturity.

The lower generative HU requirement under Jarwo 2:1 indicates a faster transition from flowering to maturity, suggesting earlier harvest potential. In contrast, the higher HU values observed under Tegel and transplanter spacing reflect a prolonged generative phase, which may support extended assimilate accumulation but delay harvest timing. This divergence highlights the role of planting configuration in modulating canopy microclimate, light distribution, and temperature exposure during the reproductive stage (Lambers & Oliveira, 2019; Guralnick *et al*., 2024).

These findings confirm that HU-based analysis effectively distinguishes vegetative thermal stability from generative thermal plasticity (Postma *et al*., 2021), with planting spacing acting as the primary driver of variation in generative HU accumulation and harvest readiness (Sanczuk *et al*., 2023).

3.3. Total Heat Unit Accumulation under Different Spacing Methods

The total heat unit (HU) accumulation differed among planting (spacing) methods, indicating variation in the thermal time required for rice plants to reach physiological maturity (Figure 5). Total HU represents the sum of thermal units accumulated during the vegetative and generative phases and reflects the overall temperature requirement from transplanting to harvest.

Among the spacing methods, rice cultivated under transplanter spacing (35 cm × 15 cm) exhibited the highest total HU accumulation (approximately 1159 °C·day), followed by Tegel 25 cm × 25 cm (approximately 1146 °C·day), whereas Jarwo 2:1 required the lowest total HU (approximately 1134 °C·day). These numerical differences clearly indicate that planting spacing significantly affected harvest timing, with Jarwo 2:1 accelerating crop maturity relative to Tegel and transplanter-derived spacing.

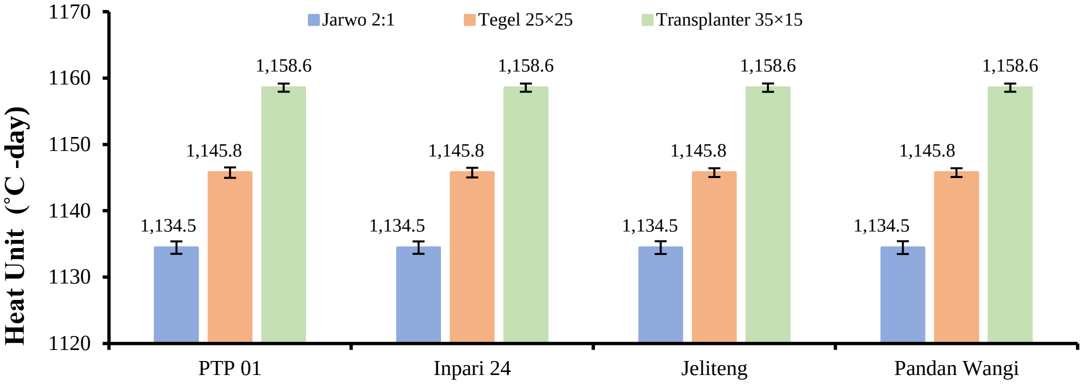


Figure 5. Total HU accumulation (°C·day) from transplanting to harvest under different rice spacing methods

The lower total HU requirement under the Jarwo 2:1 system suggests faster crop development and earlier physiological maturity, likely driven by improved light interception, enhanced air circulation, and more efficient canopy photosynthesis (Lambers & Oliveira, 2019), These conditions enhance assimilate production and promote more effective utilization of accumulated thermal energy, thereby reducing the total HU needed to reach harvest (Croce *et al*., 2024). In contrast, higher total HU accumulation under Tegel and transplanter spacing indicates delayed harvest age, reflecting a prolonged generative phase (Garcia *et al*., 2023). Although transplanter spacing was applied manually in this study, its uniform and denser planting geometry likely modified microclimatic conditions, extending the reproductive period and increasing thermal demand prior to maturity (Wang *et al*., 2020).

Although total HU accumulation was primarily influenced by planting spacing, slight differences in thermal responses among genotypes were still observed. Across all spacing methods, Inpari 24 tended to maintain superior growth and yield performance under similar total HU conditions compared with PTP 01, Jeliteng, and Pandan Wangi. This indicates that genotypic differences were not associated with major variation in total HU requirement itself, but rather with differences in the efficiency of converting accumulated thermal units into vegetative growth, assimilate production, and grain filling (Jan *et al*., 2025; Otero *et al*., 2021). Inpari 24 exhibited greater plant height, tiller production, and grain weight per panicle despite being exposed to comparable thermal conditions, suggesting higher thermal use efficiency and stronger sink capacity during reproductive development. In contrast, PTP 01, Jeliteng, and Pandan Wangi showed relatively more moderate responses, indicating lower physiological plasticity in utilizing accumulated HU for biomass and yield formation. These findings demonstrate that planting spacing determines the duration of thermal accumulation, whereas genotype regulates the biological efficiency of HU utilization under a given thermal regime (Cheng *et al*., 2025).

Taken together, these results demonstrate that plant spacing independently and significantly influences total HU accumulation and harvest age, whereas genotype primarily determines how effectively accumulated HU is converted into growth, grain filling, and yield components. From a practical perspective, this study shows that rice grown under Jarwo 2:1 can be harvested at around 1134 °C·day, while transplanter spacing delays harvest to around 1159 °C·day, providing a clear HU-based framework for predicting harvest time under different plant spacing (Wang *et al*., 2020).

3.4. Periodic Morphological and Physiological Responses of Rice Genotypes

Periodic observations showed clear differences in vegetative growth and physiological responses among rice genotypes during the early growth stages (Figure 6). Plant height increased progressively from 21 to 42 days after transplanting (DAT) in all genotypes (Figure 6a), indicating normal vegetative development under uniform environmental and management conditions (Egbuikwem *et al*., 2020). However, the rate of height increment differed among genotypes, with Inpari 24 consistently exhibiting the greatest plant height across all observation times. This response reflects stronger vegetative vigor and higher growth potential of Inpari 24 during the vegetative phase. In contrast, PTP 01, Jeliteng, and Pandan Wangi displayed more moderate and relatively similar growth patterns, suggesting genotype-dependent differences in growth efficiency and thermal responsiveness (Chaudhary *et al*., 2020).

The number of tillers per plant increased sharply between 21 and 35 DAT in all genotypes, followed by a slight decline or stabilization at 42 DAT (Figure 6b). This pattern indicates the transition from active tillering to internode elongation and early reproductive development (Mohapatra *et al*., 2025b). Inpari 24 and Pandan Wangi produced a higher number of tillers compared with PTP 01, particularly at 28 and 35 DAT, suggesting a greater capacity for vegetative branching and canopy establishment. The reduction in tiller number observed at 42 DAT likely reflects natural tiller senescence and assimilate redistribution as plants shift from vegetative growth toward reproductive development, which is a common physiological response in rice (Mohapatra *et al*., 2025a).

Physiological responses, as indicated by SPAD values, showed a declining trend from 28 to 42 DAT across all genotypes (Figure 6c). Higher SPAD values at earlier stages indicate active photosynthetic capacity and sufficient nitrogen availability during peak vegetative growth (Yue *et al*., 2019), while the gradual decrease toward 42 DAT suggests chlorophyll degradation and nutrient remobilization associated with plant maturation (Bhat *et al*., 2019).

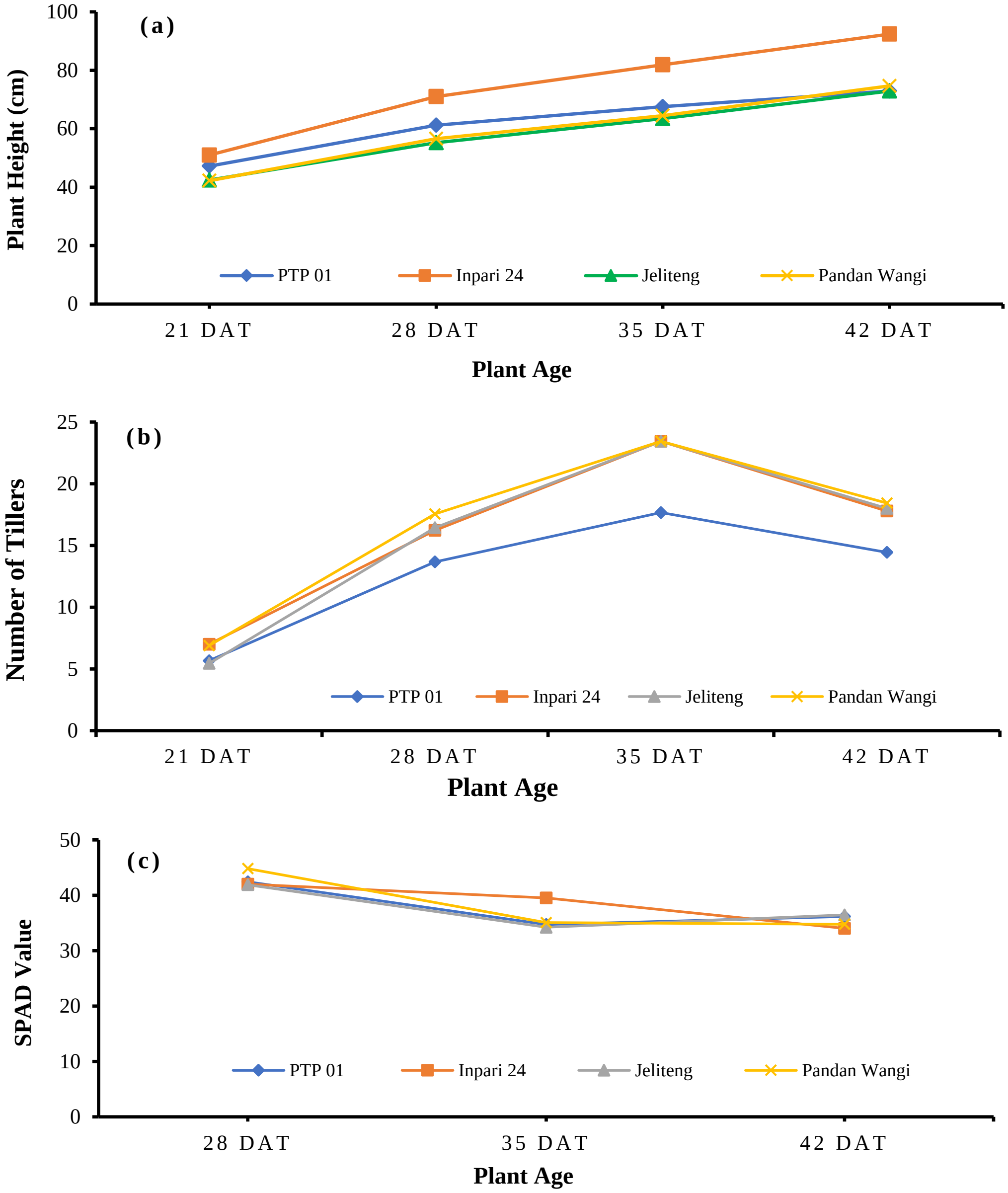


Figure 6. Periodic morphological and physiological responses of rice genotypes during the vegetative stage: (a) Plant height, (b) number of tillers, and (c) SPAD values measured at different days after transplanting (DAT)

Although Pandan Wangi exhibited slightly higher SPAD values at 28 DAT, differences among genotypes became less pronounced at later stages, indicating convergence of physiological status under similar growing conditions.

These periodic morphological and physiological responses indicate that genotypic differences in vegetative vigor, tiller production, and chlorophyll dynamics influence the efficiency with which accumulated heat units (HU) are utilized during early growth. Genotypes exhibiting faster height increment and higher tiller numbers during the vegetative phase, such as Inpari 24, are likely to convert available thermal time more effectively into biomass accumulation, leading to earlier canopy establishment and potentially altering the rate of subsequent HU accumulation toward the generative phase. Consequently, early vegetative performance provides a physiological basis for understanding genotype-specific differences in thermal efficiency, harvest timing, and yield formation observed under different planting systems (Li *et al*., 2020; Mwendwa *et al*., 2020).

3.5. Morphological and Physiological Responses of Rice to Different Plant Spacings and Genotypes

3.5.1. Plant Height Response at 42 DAT

Plant height at 42 days after transplanting (DAT) was significantly influenced by the interaction between plant spacing and rice genotype (Table 1). The response patterns indicate that plant height variation was not determined by genotype or spacing alone, but by their combined effects, highlighting differential adaptability of each genotype to specific planting configurations that modify thermal environments and heat unit accumulation during the vegetative phase.

Across all planting spacings, Inpari 24 consistently exhibited the tallest plants, reaching 104.87 cm under the transplanter spacing (35 cm × 15 cm), which was significantly higher than the other genotypes within the same spacing. This result reflects the strong vegetative vigor of Inpari 24 and its high responsiveness to closer plant spacing that potentially enhances light interception and promotes more efficient accumulation and utilization of heat units (HU) for internode elongation (Wang *et al*., 2020). Similarly, Inpari 24 maintained superior plant height under both Jarwo 2:1 (82.83 cm) and Tegel 25cm × 25 cm (89.47 cm), confirming its stable growth performance across different spacing arrangements under comparable thermal conditions.

In contrast, PTP 01, Jeliteng, and Pandan Wangi exhibited more moderate plant height, with values ranging from 62.70 to 81.37 cm, depending on planting spacing. These genotypes showed a significant reduction in plant height under the Tegel 25 cm × 25 cm spacing compared to Jarwo 2:1 and transplanter spacing, suggesting a lower competitive ability or reduced growth plasticity under wider spacing conditions where heat unit capture and canopy-level thermal efficiency may be less optimal. The relatively similar height responses among these three genotypes indicate comparable growth strategies and similar capacities to convert accumulated HU into vegetative biomass during the late vegetative stage.

From the perspective of planting spacing, transplanter spacing (35 cm × 15 cm) generally promoted greater plant height compared with Jarwo 2:1 and Tegel 25 cm × 25 cm, particularly for Inpari 24. Closer row spacing likely enhanced canopy microclimate conditions, reduced evaporative losses, and facilitated more efficient heat unit accumulation, thereby stimulating internode elongation (Sun *et al*., 2018). Conversely, the Tegel 25 cm × 25 cm spacing resulted in the lowest plant height across most genotypes, possibly due to reduced plant population density and less effective canopy closure, which may limit the effective use of available thermal time (Hou *et al*., 2019).

Table 1. Effect of plant spacing and genotype interaction on plant height (cm) of rice at 42 DAT

Plant Spacing	**Genotype**			
	PTP 01	**Inpari 24**	**Jeliteng**	**Pandan Wangi**
Jarwo 2:1	74.73 a A	82.83 b A	76.73 a A	77.27 ab A
Tegel 25×25	62.70 b B	89.47 b A	65.87 b B	67.87 b B
Transplanter 35×15	81.37 a B	104.87 a A	76.13 a B	78.87 a B

Note: Mean values followed by the same letter are not significantly different according to Tukey's HSD test at the 5% significance level. Lowercase letters indicate comparisons among genotypes within the same plant spacing (vertical comparison). Uppercase letters indicate comparisons among plant spacing within the same genotype (horizontal comparison).

The interaction effects observed in Table 1 demonstrate that genotypic growth potential and planting spacing must be considered simultaneously to optimize plant height development through their influence on heat unit accumulation and utilization. The superior performance of Inpari 24 under transplanter spacing indicates its suitability for intensive planting systems with higher thermal efficiency, while the more stable but moderate height of PTP 01, Jeliteng, and Pandan Wangi suggests their adaptability to less dense planting configurations. These morphological differences are expected to influence subsequent total HU requirements, canopy architecture, and yield formation, as discussed in the following sections (Hou *et al*., 2019; Lu *et al*., 2021).

3.5.2. Number of tillers at 42 DAT

The number of tillers at 42 days after transplanting (DAT) was significantly affected by plant spacing, while genotype did not show a significant effect on tiller number (Table 2). This indicates that tillering capacity at this growth stage was more strongly regulated by cultivation management than by genetic differences among the tested rice genotypes, particularly through differences in microclimate formation and heat unit accumulation during the vegetative phase.

Among planting spacings, the transplanter spacing produced the highest number of tillers (22.83 tillers per plant), which was significantly greater than both Jarwo 2:1 (13.75 tillers per plant) and Tegel spacing (14.92 tillers per plant), as indicated by different lowercase letters (Table 2). The higher tiller production under transplanter spacing suggests that closer and more uniform plant arrangement enhanced resource capture efficiency, particularly light interception and thermal time availability, thereby stimulating axillary bud development and tiller emergence. Increased HU accumulation under this spacing likely provided sufficient thermal energy to support prolonged tiller initiation during the vegetative phase (Chiluwal *et al*., 2018; Mohapatra *et al*., 2025b).

In contrast, Jarwo 2:1 and Tegel spacings resulted in significantly lower and statistically similar tiller numbers. This may be associated with differences in plant population structure and intra-specific competition, which can limit assimilate availability and reduce the effective utilization of accumulated heat units for tiller initiation during the late vegetative phase (Tausz-Posch *et al*., 2020). The reduced tillering under these spacings indicates that wider or less uniform spacing may constrain vegetative branching despite adequate nutrient supply, particularly when thermal conditions are not optimally translated into tiller formation (Hu *et al*., 2020).

Regarding genotypic effects, PTP 01, Inpari 24, Jeliteng, and Pandan Wangi exhibited comparable tiller numbers, ranging from 14.44 to 18.44 tillers per plant, with no significant differences detected among genotypes (Table 2). This suggests that, at 42 DAT, genetic variation in tillering potential was less pronounced than the influence of planting spacing, and that all genotypes had reached a similar physiological stage of tiller stabilization under comparable cumulative HU conditions (Chachar *et al*., 2025). The superior tiller production under transplanter spacing highlights its potential advantage for maximizing vegetative biomass and yield components through more efficient heat unit accumulation and utilization.

Table 2. Average number of tillers at 42 DAT

Genotype	**Plant Spacing**			**Average**
	Jarwo 2:1	**Tegel 25×25**	**Transplanter 35×15**	
PTP 01	13.67	11.33	18.33	14.44 a
Inpari 24	10.33	15.67	27.33	17.78 a
Jeliteng	14.00	17.33	22.67	18.00 a
Pandan Wangi	17.00	15.33	23.00	18.44 a
Average	13.75 b	14.92 b	22.83 a	

Note: Numbers followed by the same letter in the same column are not significantly different at the Tukey's HSD test α 0.05 significance level.

3.5.3. SPAD Response Response at 42 DAT

SPAD values at 42 days after transplanting (DAT) were significantly influenced by plant spacing, with additional variation observed among genotypes depending on the planting method (Table 3). SPAD measurements reflect relative chlorophyll content and are closely associated with leaf nitrogen status and photosynthetic capacity at the late vegetative stage (Safrudin *et al*., 2024) which are strongly affected by cumulative heat unit availability during vegetative growth.

Table 3. Effect of plant spacing and genotype interaction SPAD Value of rice at 42 days after transplanting (DAT).

Plant Spacing	**Genotype**			
	PTP 01	**Inpari 24**	**Jeliteng**	**Pandan Wangi**
Jarwo 2:1	34.23 b A	33.30 a A	34.03 b A	31.13 b A
Tegel 25×25	34.97 b A	35.33 a A	37.00 ab A	33.50 b A
Transplanter 35×15	39.30 a A	33.47 a B	38.33 a A	39.63 a A

Note: Mean values followed by the same letter are not significantly different according to Tukey's HSD test at the 5% significance level. Lowercase letters indicate comparisons among genotypes within the same plant spacing (vertical comparison). Uppercase letters indicate comparisons among plant spacing within the same genotype (horizontal comparison).

Across planting spacings, the transplanter spacing (35 cm × 15 cm) consistently produced the highest SPAD values, ranging from 38.33 to 39.63, which were significantly higher than those observed under Jarwo 2:1 and Tegel 25 cm × 25 cm for most genotypes (Table 3). This indicates that denser and more uniform plant spacing enhanced leaf chlorophyll retention, likely due to improved microclimatic conditions and more efficient utilization of accumulated HU, which support sustained nitrogen assimilation and chlorophyll synthesis during vegetative growth (Genesio *et al.*, 2021).

Under Jarwo 2:1, SPAD values were generally lower, particularly for Pandan Wangi (31.13), suggesting a more rapid decline in chlorophyll content as plants approached the transition to the generative phase. This pattern may be associated with less favorable thermal and canopy conditions, resulting in earlier chlorophyll degradation under lower effective HU utilization. Tegel spacing showed intermediate responses, with Jeliteng exhibiting relatively higher SPAD values (37.00) compared with other genotypes, indicating genotype-specific differences in chlorophyll maintenance under moderate spacing and thermal environments.

Genotypic effects were less pronounced than spacing effects, as reflected by the predominance of similar uppercase letters within each planting method (Table 3). However, under transplanter spacing, Pandan Wangi and PTP 01 showed the highest SPAD values, suggesting a stronger capacity for maintaining leaf nitrogen status and photosynthetic activity at 42 DAT under favorable spatial arrangement and optimal cumulative HU conditions. Overall, these results demonstrate that plant spacing plays a dominant role in regulating SPAD values through its influence on canopy microclimate and heat unit accumulation, while genotype contributes to differential chlorophyll retention under specific planting configurations (Berhe *et al.*, 2024). Higher SPAD values under transplanter spacing suggest delayed leaf senescence and sustained photosynthetic capacity, which may support greater assimilate availability for subsequent reproductive development and grain filling (Su *et al.*, 2025; Zhou & Yang, 2023).

3.6. Grain Filling Efficiency, Moisture Content, and Grain Weight of Rice

As shown in Table 4, planting method and genotype significantly influenced several yield-related traits at harvest, particularly grain filling characteristics and grain moisture content. Panicle length did not differ significantly among planting methods or genotypes, indicating that panicle elongation was relatively stable across treatments and less sensitive to planting arrangement or genetic background. This stability suggests that panicle length development was achieved under comparable cumulative heat unit (HU) conditions during the vegetative–early reproductive transition (Parida *et al.*, 2022).

In contrast, the number of filled grains responded more clearly to genotype than to planting method. Inpari 24 produced the highest number of filled grains (119.41 grains), which was significantly higher than those of PTP 01, Jeliteng, and Pandan Wangi. This result suggests that Inpari 24 possesses a stronger sink capacity and a higher efficiency in converting accumulated heat units into assimilate deposition during the grain filling period (Nasrudin *et al.*, 2023). Conversely, Pandan Wangi exhibited lowest number of filled grains, reflecting lower grain filling efficiency despite comparable panicle length, which indicated limitations in assimilate utilization under similar HU availability.

Table 4. Effects of plant spacing and genotype on rice grain characteristic at harvest

Treatment	**Panicle length**	**Filled Grains**	**Empty Grains**	**Moisture Content**
	(cm)	**(grain)**	**(grain)**	**(%)**
Plant Spacing				
Jarwo 2:1	25.26 a	104.28 a	21.86 a	27.27 a
Tegel 25×25	24.42 a	99.22 a	17.72 a	23.98 b
Transplanter 35×15	24.32 a	104.97 a	18.28 a	21.25 c
Genotype				
PTP 01	25.60 a	102.96 ab	18.04 ab	24.41 ab
Inpari 24	25.32 a	119.41 a	25.85 a	27.13 a
Jeliteng	23.88 a	97.56 b	27.07 a	22.25 b
Pandan Wangi	23.86 a	91.37 b	6.19 b	22.86 b

Note: Numbers followed by the same letter in the same column are not significantly different at the Tukey's HSD test α 0.05 significance level.

The number of empty grains further highlighted genotype-dependent differences in reproductive efficiency. Inpari 24 and Jeliteng showed the highest numbers of empty grains, indicating that although these genotypes formed more spikelets, not all were successfully filled. This pattern suggests a potential imbalance between sink size and assimilate supply during the late reproductive stage, particularly when cumulative HU availability is insufficient to fully support spikelet filling (Smith *et al*., 2018). In contrast, Pandan Wangi had the lowest number of empty grains, indicating more efficient grain filling, albeit with a smaller total sink size (Yagioka *et al*., 2021).

Grain moisture content at harvest was significantly affected by planting method. Jarwo 2:1 resulted in the highest grain moisture content, while both Tegel 25 cm × 25 cm and transplanter spacing (35 cm × 15 cm) produced significantly lower moisture levels. Lower grain moisture under wider or more uniform spacing suggests improved canopy aeration and microclimatic conditions that enhance heat dissipation and accelerate physiological maturity, thereby improving the efficiency of heat unit utilization during the final grain maturation phase (Chen *et al*., 2025). Genotypically, Inpari 24 exhibited the highest moisture content, consistent with its larger sink size, prolonged grain filling duration, and higher total HU requirement to reach full maturity (Biswas *et al*., 2023). These results indicate that genotype primarily determines grain filling capacity, while plant spacing plays a more prominent role in regulating grain moisture dynamics at harvest through its influence on microclimate and HU effectiveness (Fernando *et al*., 2025; Tu *et al*., 2025).

While grain filling characteristics and moisture content reflect the efficiency of assimilate utilization during reproductive development, grain weight per panicle provides an integrative measure of how these processes, together with accumulated heat unit (HU) availability, ultimately translate into final yield formation. Therefore, the interaction effects of planting spacing and genotype on grain weight per panicle at harvest were evaluated. Grain weight per panicle at harvest was significantly influenced by the interaction between planting spacing and genotype (Table 5), indicating that final yield formation is determined by both genetic potential and spatial crop arrangement through their combined effects on microclimate and HU utilization. With Jarwo 2:1 spacing, most genotypes exhibited relatively comparable grain weight per panicle, except for Pandan Wangi, which was significantly lower. This suggests that although Jarwo 2:1 enhances plant population and light interception, its effectiveness in increasing assimilate accumulation and converting accumulated HU into grain biomass may be genotype dependent (Chen *et al*., 2022).

Table 5. Effect of plant spacing and genotype interaction on grain weight per panicle (g) of rice at harvest

Plant Spacing	**Genotype**			
	PTP 01	**Inpari 24**	**Jeliteng**	**Pandan Wangi**
Jarwo 2:1	3.76 a	3.47 a	3.47 a	2.62 b
	A	A	A	A
Tegel 25×25	3.12 a	4.42 a	2.22 a	4.66 a
	BC	AB	C	A
Transplanter 35×15	3.06 a	3.95 a	3.15 a	2.66 b
	A	A	A	A

Note: Mean values followed by the same letter are not significantly different according to Tukey's HSD test at the 5% significance level. Lowercase letters indicate comparisons among genotypes within the same plant spacing (vertical comparison). Uppercase letters indicate comparisons among plant spacing within the same genotype (horizontal comparison).

Under the Tegel 25 cm × 25 cm spacing, clear genotypic differentiation was observed. Inpari 24 and Pandan Wangi produced the highest grain weight per panicle, while Jeliteng showed the lowest value. The wider and more uniform spacing in this system likely reduced inter-plant competition, allowing genotypes with higher sink capacity to optimize assimilate allocation and more efficiently translate cumulative HU into grain filling (Tokatlidis, 2022). This result is consistent with the higher number of filled grains previously observed for Inpari 24, reinforcing its superior yield potential under spacing conditions that support optimal HU effectiveness.

In contrast, the transplanter spacing (35 cm × 15 cm), although applied manually in this study, resulted in relatively uniform grain weight per panicle across genotypes, with no significant differences detected. This indicates that denser within-row spacing may limit individual panicle sink development due to increased competition for assimilates (Zhong *et al*., 2024; C. Zhou *et al*., 2019), thereby constraining the allocation of accumulated HU at the panicle level and reducing the expression of genotypic yield differences (Anand & Dhaliwal, 2024).

4. CONCLUSIONS

This study was conducted to evaluate the effects of plant spacing and rice genotype on heat unit (HU/GDD) accumulation and to assess the usefulness of HU as a predictor of harvest age and yield-related traits. The results clearly demonstrate that HU accumulation is an effective and quantitative indicator for explaining growth progression, harvest timing, and yield expression under different planting systems. Vegetative growth across all genotypes and planting spacings reached a similar thermal threshold of approximately 776 °C•day, indicating that early growth stages are governed by a stable intrinsic thermal requirement. However, during the generative phase and at harvest, HU accumulation differed significantly among planting spacings. The Jarwo 2:1 system required the lowest total HU to reach physiological maturity (≈ 1134 °C•day), indicating faster crop development and earlier harvest potential. In contrast, Tegel 25 cm × 25 cm and transplanter-derived spacing required higher total HU (≈ 1146 and ≈ 1159 °C•day, respectively), reflecting prolonged generative development and delayed maturity.

Plant spacing had a significant independent effect on HU accumulation and harvest age, whereas genotype did not significantly alter total HU requirement. However, genotype strongly influenced how accumulated HU was converted into growth and yield components. Inpari 24 consistently showed superior plant height, grain filling, and grain weight per panicle, indicating higher efficiency in utilizing accumulated thermal time for biomass and yield formation. Other genotypes exhibited more moderate responses, suggesting lower plasticity in HU utilization.

Overall, this study confirms that plant spacing determines thermal duration and harvest timing, while genotype determines yield performance under a given HU regime. These findings support the use of HU-based thresholds as a practical tool for optimizing planting systems, predicting harvest age, and selecting suitable genotype–spacing combinations for improved rice production.

AUTHOR CONTRIBUTION STATEMENT

Author	C	M	So	Va	Fo	I	R	D	O	E	Vi	Su	P	Fu
YKS			✓	✓	✓			✓	✓	✓	✓			
Dul	✓	✓				✓	✓		✓	✓		✓	✓	✓
JSM		✓				✓	✓					✓		
MHISJ	✓		✓	✓	✓				✓	✓	✓			

C: Conceptualization
M: Methodology
So: Software
Va: Validation
Fo: Formal Analysis
I: Investigation
D: Data Curation
R: Resources
O: Writing - Original Draft
E: Writing - Review & Editing
Vi: Visualization
Su: Supervision
Fu: Funding Acquisition
P: Project Administration

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