



Faculty of Resource Science & Technology

The Growth and Development of Sarawak Rice Towards Photoperiod

Putri Ainaa Afiqah Binti Hossen

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The Growth and Development of Sarawak Rice Towards Photoperiod

Putri Ainaa Afiqah Binti Hossen

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DECLARATION

I declare that the work in this thesis was carried out in accordance with the regulations of Universiti Malaysia Sarawak. Except where due acknowledgements have been made, the work is that of the author alone. The thesis has not been accepted for any degree and is not concurrently submitted in candidature of any other degree.



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Signature

Name: Putri Ainaa Afiqah Binti Hossen

Matric No.: 19020021

Faculty of Resource Science & Technology

Universiti Malaysia Sarawak

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ABSTRACT

A series of controlled environment treatments were conducted on Sarawak traditional rice, notably Bario Sederhana and Biris landraces, aimed to quantify the development and growth performance when sown at five photoperiod regimes (8, 9, 10, 11 and 12 hours). This study revealed that both landraces had a short basic vegetative phase, as crop sensitivity to photoperiod commenced after the appearance of fourth leaf for Bario Sederhana ($P < 0.001$) and third leaf ($P < 0.001$) for Biris. For Bario Sederhana landrace, phyllochron varied with different photoperiod regimes, except for rice plants that were sown at 11 and 12 hours photoperiod. Under these photoperiods, Bario Sederhana took a longer time to produce each successive main stem leaf at 12 hours photoperiod (215 °Cd/leaf, 8.5 day/leaf) compared with 11 hours photoperiod (135 °Cd/leaf, 5.6 day/leaf). Similar trend was seen in Biris landrace where the landrace sown at 12 hours photoperiod took an extended duration (213 °Cd/leaf, 8.4 day/leaf) to produce a new leaf than Biris sown at 11 hours photoperiod (117 °Cd/leaf, 4.9 day/leaf). Bario Sederhana produced a maximum number of 9.3 leaves on the mainstem with thermal time requirement between 1513-2903 °Cd and 64-122 calendar days to reach flag leaf development. In contrast, Biris failed to produce flag leaf under 8, 10, and 11 hours photoperiod and did not develop further. Nevertheless, Biris took 3667-3831 °Cd (152-160 days) to produce a maximum of 7.9 main stem leaves under both 9 and 12 hours photoperiod. The reproductive development towards photoperiod showed a delayed pattern in time to heading, anthesis and maturity for Bario Sederhana under lengthening photoperiod from 10 to 12 hours. For example, under 10 hours photoperiod the crop required 1680 °Cd (~71 days) from emergence to heading but took an extended duration of 3147 °Cd (~133 days) when it was sown at 12 hours photoperiod. Similarly, Biris took a longer time to heading ($P < 0.05$) at 12 hours photoperiod (4067 °Cd, 169 days) compared with 9 hours photoperiod (3800 °Cd,

158 days). The prolonged time taken for reproductive development modified by photoperiod resulted in higher yield components. This is because the extended time from heading to maturity means longer duration of grain filling. In both landraces, the longest photoperiod of 12 hours gave the highest percentage of filled spikelets, consequently the heaviest grain weight per panicle (1.4 g for Bario Sederhana, 3.5 g for Biris). Hence, under optimum photoperiod and proper farm management practices, the cultivation of the two Sarawak rice landraces will improve the socio-economics of local farmers.

Keywords: Daylength, growing degree days, phenology, plant growth chamber, traditional rice cultivar.

Tajuk: Pertumbuhan dan Perkembangan Padi Sarawak Terhadap Tempoh Pencahayaan

ABSTRAK

Sebuah siri eksperimen persekitaran terkawal telah dijalankan ke atas padi tradisional Sarawak, Bario Sederhana dan Biris, bertujuan bagi menyelidik pertumbuhan dan perkembangan padi tersebut apabila disemai di bawah tempoh pencahayaan yang berbeza (8 jam, 9 jam, 10 jam, 11 jam dan 12 jam). Kajian ini menunjukkan bahawa kedua-dua varieti padi tersebut mempunyai fasa juvana yang pendek. Hal ini demikian kerana tindak balas pokok padi terhadap tempoh pencahayaan bermula selepas kemunculan daun keempat bagi Bario Sederhana ($P < 0.001$), dan daun ketiga bagi Biris ($P < 0.001$). Bagi padi Bario Sederhana, kadar kemunculan daun adalah berbeza bergantung dengan tempoh pencahayaan, kecuali bagi pokok padi yang ditanam di bawah tempoh pencahayaan 11 dan 12 jam. Di bawah tempoh pencahayaan tersebut, pokok padi mengambil masa yang lebih lama untuk menghasilkan daun baharu pada batang utama pada tempoh pencahayaan 12 jam ($215\text{ }^{\circ}\text{Cd/daun}$, 8.5 hari/daun) berbanding tempoh pencahayaan 11 jam ($135\text{ }^{\circ}\text{Cd/daun}$, 5.6 hari/daun). Padi Biris turut menunjukkan trend yang sama apabila padi tersebut mengambil masa yang lebih lama untuk menghasilkan daun baharu pada batang utama di bawah tempoh pencahayaan 12 jam ($213\text{ }^{\circ}\text{Cd/daun}$, 8.4 hari/daun) berbanding tempoh pencahayaan 11 jam ($117\text{ }^{\circ}\text{Cd/daun}$, 4.9 hari/daun). Bilangan maksimum daun pada batang utama bagi Bario Sederhana adalah sebanyak 9.3 helai daun, dan keperluan masa terma antara $1513\text{--}2903\text{ }^{\circ}\text{Cd}$ dan 64-122 hari diperlukan untuk menghasilkan daun terakhir. Padi Biris yang disemai di bawah tempoh pencahayaan 8, 10 dan 11 jam gagal menghasilkan daun terakhir serta mengalami perkembangan yang terbantut. Walau bagaimanapun, padi Biris mengambil masa $152\text{--}160$ hari ($3667\text{--}3831\text{ }^{\circ}\text{Cd}$) untuk menghasilkan sebanyak 7.9 helai daun pada batang utama di bawah tempoh pencahayaan 9 jam dan 12 jam. Tindak balas perkembangan

reproduktif Bario Sederhana seperti tempoh kemunculan tangkai padi, tempoh berbunga dan kematangan padi terhadap tempoh pencahayaan tertunda apabila disemai di bawah tempoh pencahayaan 10 hingga 12 jam. Sebagai contoh, di bawah tempoh pencahayaan 10 jam Bario Sederhana memerlukan 1680 °Cd (~71 hari) dari perkecambahan benih ke tempoh kemunculan tangkai padi. Namun begitu, Bario Sederhana mengambil tempoh yang lebih lama 3147 °Cd (~133 hari) apabila padi tersebut ditanam di bawah tempoh pencahayaan 12 jam. Padi Biris turut mengambil masa yang lebih lama untuk mencapai tempoh kemunculan tangkai padi ($P < 0.05$) pada tempoh pencahayaan 12 jam (4067 °Cd, 169 hari) berbanding dengan tempoh pencahayaan 9 jam (3800 °Cd, 158 hari). Tempoh perkembangan reproduktif padi yang berpanjangan yang telah diubahsuai oleh tempoh pencahayaan telah menghasilkan hasil padi yang lebih tinggi. Hal ini demikian kerana pokok padi mempunyai tempoh pengisian bijian yang lebih lama akibat tempoh perkembangan reproduktif yang berpanjangan tersebut. Bagi Bario Sederhana dan Biris, tempoh pencahayaan 12 jam menghasilkan peratusan bijirin padi yang tertinggi, oleh itu ia turut menghasilkan bijirin yang paling berat bagi setiap tangkai (1.4 g untuk Bario Sederhana, 3.5 g untuk Biris). Oleh itu, di bawah tempoh pencahayaan yang optimum dan amalan pengurusan ladang yang betul, penanaman dua padi tradisional Sarawak tersebut mampu meningkatkan sosio-ekonomi pesawah.

Kata kunci: Tempoh pencahayaan, suhu pertumbuhan harian, fenologi, ruang pertumbuhan tumbuhan, padi tradisional.

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CHAPTER 1

INTRODUCTION

1.1 Study Background

Rice (*Oryza sativa* L.) is predominantly grown throughout Asia, as well as certain parts of Europe, America and Australia. This is because rice plant is well adapted to a wide range of climatic variation from tropical to temperate. Several environmental factors, in addition to genetic factors, influence rice plant growth and development. Temperature is the main driver of crop growth and development, but it can also be modified by photoperiod (Mapalana, 2017). Photoperiod also known as daylength is calculated as the duration from sunrise to sunset and includes civil twilight. Photoperiod influences crop development rate such as leaf production (Nemoto et al., 1995) and time to flowering (Jackson, 2009). Depending on whether the plant species exhibits a short-day or a long-day photoperiodic response, photoperiod can either shorten or delay crop development. This could have an influence on the yield production. For example, delayed development results in longer duration of phenophases, consequently leads to an increase in biomass accumulation (Debaeke & Aboudrare, 2004). However, the disadvantage is that it could increase the cost of crop management in relation to fertilizer input, pests and weed control.

In general, rice is classified under short-day plant because it initiates panicle primordia in response to short photoperiod (Yoshida, 1981), which means it requires shorter exposure to daylight in order to transition from vegetative to reproductive phases. However, the degree of sensitivity to photoperiod varies widely among rice cultivars. Vergara and Chang (1985) reported that tropical rice cultivars are more sensitive to photoperiod compared to temperate rice cultivars. A study done by Dore (1959) reported that 14 minutes

difference between day length in January and September in Melaka at latitude of 2 °N can result in a significant variation in time to flowering of rice plants. According to the study, rice plants sown in September took just 161 days to flower compared to 329 days for rice plants sown in January. In annual crop species, the modification in time taken to flowering caused by photoperiod variation can affect the growth performance and consequently affecting the final yield production (Sonego, 2000).

Sarawak is renowned for its vast range of traditional rice cultivars. Several examples of Sarawak traditional rice cultivars are Bario, Biris, Bajong, and Mamut. Farmers in Sarawak prefer to grow traditional rice because of its eating quality in terms of its exquisite taste, texture, and fragrant (Teo, 2007b). In addition, Sarawak traditional rice is well adapted to the undulating topography which makes it difficult to cultivate soil and construct an irrigation system in the rice fields. Therefore, the rice cultivation in Sarawak is mostly rainfed. In order to target grain ripening and harvesting activities in March when rainfall has drastically decreased, Sarawak traditional rice is often being planted on October. The rainy season allows the best vegetative development of the rice plants.

1.2 Problem Statement

It has been asserted that Sarawak traditional rice cultivars are photoperiodic sensitive, possessing longer growth duration, therefore can only being planted in one cropping season (Teo, 2007b). For example, the cultivation of Bario rice is a time-consuming process that takes six months of manual labour from sowing to grain harvesting (Naeg, 2012). Likewise, Biris rice matures within five to six months from the time of planting (Morni, 2014). However, there are still outstanding concerns regarding how photoperiod

affects the growth and development of Sarawak traditional rice. To date, there is no published study that investigates the developmental responses of Sarawak traditional rice towards photoperiod.

In general, traditional rice cultivars in the tropics are classified as photoperiod-sensitive, however most of the current knowledge regarding the photoperiodic sensitivity of traditional rice and its effect on growth and development are from Cambodia (Tsubo et al., 2009), Thailand (Cha-um & Kirdmanee, 2007; Boling et al., 2011), and Sri Lanka (Mapalana, 2017; Padukkage et al., 2017; Pushpakumari et al., 2017). The geographical locations of these countries are within 7.9 °N-15.9 °N latitude, thus experiencing different changes in daylength throughout the year compared to Sarawak which is positioned at 1.5 °N near the equator.

Therefore, these reports may not be directly applicable to the environmental conditions in Sarawak. Given that the changes in daylength at the equatorial region is significantly small, controlled environment chambers can be used to grow rice plants within a range of photoperiod hours. Observation of leaf appearance, time to flowering, and grain production could be used to establish the physiological characteristics of Sarawak traditional rice in relation to its sensitivity to photoperiod changes. Understanding the effects of photoperiod variation on rice physiology is important to understand the maximum yield potential of Bario Sederhana and Biris, consequently increasing the socio-economic status of local farmers through promoting the cultivation of high-yielding rice varieties. The hypotheses of this study were as followed:

Null hypothesis, H_0 : Photoperiod has no effect on the growth and development of Sarawak traditional rice.

Alternative hypothesis, H_a : Photoperiod affects the growth and development of Sarawak traditional rice.

1.3 Objectives

The aim of this study was to understand how photoperiod variation influences the growth and subsequent development of Sarawak traditional rice specifically Bario Sederhana and Biris landraces. To achieve this aim, a series of controlled environment experiments were conducted with the following objectives:

- i. To identify the commencement of photoperiod sensitivity in Bario Sederhana and Biris landraces.
- ii. To quantify duration of vegetative developmental stages i.e., leaf appearance rate and time to flag leaf.
- iii. To quantify duration of reproductive developmental stages i.e., time to flowering and duration to grain maturity.
- iv. To quantify growth in relation to rice yield components.

CHAPTER 2

LITERATURE REVIEW

2.1 Rice Cultivation in Sarawak

Rice plants are mainly being cultivated in the upland and lowland of Sarawak in three different ecologies; (i) rainfed upland; (ii) rainfed lowland; and (iii) irrigated lowland (Kendawang et al., 2005; Sang et al., 2018). The mountainous and hilly topography of Sarawak makes rice cultivation challenging (Hoki, 1977). Sarawak undulating terrain makes constructing an irrigation system and convey mechanisation aid to the upland rice cultivation difficult. Additionally, Sarawak lowland rice cultivation experiences frequent flooding, and proper irrigation is only feasible in limited lowland area due to topographical conditions. Hence, the main supply of water for the majority of the lowland rice fields from October to April is from natural rainfall (Teo, 2007b; Izzah et al., 2021). In 2019, the highest total rainfall recorded in Sarawak was between 3200 and 4600 mm (2019 Malaysian Meteorological Department Annual Report).

A majority of the rice fields in Sarawak practised monoculture farming except for a few irrigation projects (Teo, 2007b). Monoculture rice cultivation in Sarawak is mostly performed by manual labor with minimum mechanisation aid (Hoki, 1977; Hanafi et al., 2009). Land preparation is often done in July and August after the *Gawai* festival in June. Most rice fields are neither ploughed nor harrowed before the transplantation of rice seedlings because farmers planted the crop traditionally without mechanisation aid. Herbicide is applied to remove herbaceous species and other vegetation on the land (Hoki, 1977; Kendawang et al., 2005).

Local farmers practice shifting cultivation that refers to a rotational farming technique in which land is cleared for upland rice cultivation and then left to regenerate after a few years (Kendawang et al., 2005; Echoh et al., 2017). According to Echoh et al. (2017), the high acidic soil of Sarawak makes it unsuitable for agricultural pursuits, hence shifting cultivation is preferred by the local farmers. This is due to the fact that the long fallow period of shifting cultivation could replenish soil fertility while minimising weed infestation (De Rouw, 1995). However, the present shifting cultivation system consists of continuous rice cropping for 2 years or more with a shorter fallow period of about 5 years (Kendawang et al., 2004). Various measures have been implemented to reduce shifting cultivation while encouraging permanent and sustainable agricultural systems (Kendawang et al., 2004; Hansen & Mertz, 2006). Subsidised fertilisers for upland rice are provided in order to prevent soil degradation while preserving the remnant tropical forests.

Although Sarawak traditional rice cultivars have a high commercialisation potential, the commercialisation is hindered by its lower grain yield when compared to modern rice cultivars. A study conducted by Shafiee et al. (2013) on MR 220 a local modern rice cultivar revealed that when SBAJA, a foliar-spray growth and yield enhancer is applied to the rice cultivar, the cultivar yielded 9660 kg ha⁻¹, compared to 7490 kg ha⁻¹ in a different planting ecosystem. In contrast, the average yield of Sarawak upland rice is low, ranging from 460 to 1184 kg ha⁻¹ with an average value of 738 kg ha⁻¹ (Hanafi et al., 2009). Low grain yields of upland rice are attributed to poor field management by farmers during rice cultivation period. In addition, inadequate water and fertiliser supplies could limit productivity and lead to a variety of problems that inevitably result in low yield production (Filzah et al., 2014).

In order to reduce input costs, farmers do not use excessive pesticides and fungicides during the cultivation of rice. Eventhough farmers received amorphous fertilisers (16% N and 48% P₂O₅) from the government as part of a fertiliser subsidy scheme, farmers are still reluctant to apply chemical fertiliser throughout rice cultivation period (Hanafi et al., 2009). Even so, government fertiliser subsidies are insufficient, and most farmers are unwilling to acquire additional fertilisers and pesticides at their own expense due to the increasing cost of these agricultural inputs (Fahmi et al., 2013). According to Hoki (1977), the lack of fertiliser is due to frequent flooding and unresolved field management problems in Sarawak that lead fertiliser to wash away when applied.

2.2 Sarawak Traditional Rice

Traditional rice cultivars, including pigmented and aromatic rice offer excellent eating qualities and health benefits (Nicholas et al., 2014). According to Bhat and Riar (2015), traditional rice cultivars possess low sugar content, higher amount of glutamic acid, fiber, and vitamins such as thiamine, iron, vitamin D, niacin, riboflavin, and calcium. Traditional rice cultivars that are pigmented and aromatic are also known to have high content of bioactive components. Pigmented and aromatic traditional rice cultivars besides having an excellent eating quality also possess an abundant content of anthocyanin such as Cyanidin-3-O- β -glucoside (Ryu et al., 1998). Such compound is associated with diverse functional properties such as anti-neurodegenerative activity (Kim et al., 2008), inhibition of glycogen phosphorylase (Jakobs et al., 2006), and possessing antioxidant (Tuncel & Yilmaz, 2011) and higher scavenging activity compared to modern and hybrid rice cultivars.

2.2.1 Bario Sederhana

Bario rice cultivar is cultivated by Kelabit farmers at the Kelabit Highlands in the northern region of Sarawak (4.2238 ° N, 114.3661 °E). The cultivar is mainly being cultivated in cool climates at altitudes more than 1200 meters (Kevin et al., 2007). Bario rice offers a wide range of cultivars, such as Bario Sederhana, Bario Chelum, Bario Halus, and Bario Banjar (Wong et al., 2009). The annual cultivation of Bario in July is done manually and traditionally by the farmers while the rice fields are irrigated by the clean mountain streams of the Kelabit Highlands (Kevin et al., 2007; Teo et al., 2008; Henrita et al., 2015). Therefore, it takes 170 to 175 days to mature from sowing for Bario rice to be harvested in January (Henrita et al., 2015). Due to the scarcity and the difficulty of transporting it to the Kelabit Highlands, pesticides and chemical fertilisers are not used in the cultivation of Bario rice.

Bario rice is considered one of the finest rice grains in the world due to its smooth texture, fine and elongated grains (Figure 2.1), and desirable eating qualities (Wong et al., 2009). Nicholas et al. (2014) reported that the ash contents in Bario rice were in the range of 1.07-1.46% making it useful in improving health due to the availability of minerals (Khalili et al., 2006). Besides that Nicholas et al. (2014) also reported that based on the Nutrient Reference Value in 18C Act, Table II Food Regulations of Malaysia, Bario rice is a good source of protein (> 5 g/ 100 g), low in fat content (< 3 g/100 g), contained higher crude fibre content (1.40-2.05%) than modern rice cultivar, MR 219 (0.90%) as well as lower carbohydrate content (73.96-76.76%) than that in MR 219 (78.45%). Hence, these numerous nutritional benefits proved that Bario rice cultivars have a high potential to be promoted as a healthy dietary ingredient. The cultivation of Bario rice may be sufficient for subsistence farming, but while the rice cultivar is in demand, the optimum yield has yet to be achieved.

On average, the yield of uphill rice in Sarawak is 0.46 to 1.1 tonnes per hectare (Sohrabi et al., 2012). Accordingly, if the rice cultivar is to be exported and sold as a specialty product outside of Sarawak, the existing farm management strategy may require improvements.



Figure 2.1: Bario Sederhana landrace grain.

2.2.2 Biris

Biris rice cultivar originated in Simunjan, Kota Samarahan (1.2406 °N, 110.6923 °E). Similar to Bario rice, the cultivation of Biris rice is done annually from September to October (Teo, 2007a). Biris rice can be harvested 5 to 6 months following the date of sowing (Morni, 2014). The cultivation required less input from farmers since it is done manually and with less fertiliser applications, while water availability is largely dependent on rainfall. Due to its significant economic potential in comparison to other Sarawak traditional rice cultivars such as Bario and Bajong, Biris was ranked among the top three rice cultivars in Sarawak by the Department of Agriculture Sarawak in the 1980s (Teo, 2007a; Sang et al., 2018).

Biris is regarded as a tall rice cultivar with long, slender grains (Figure 2.2) (7.8 ± 0.25 mm) and a thick stem (Libin et al., 2012; Ying, 2016). Nori et al. (2009) and (Libin et al., 2012) reported that Biris has a grain yield of 2190 kg/ha, with an average paddy spikelet count of 230 and a stem height ranging from 81.4-160 cm. Ying (2016) reported that the ash content of Biris is $1.5 \pm 0.02\%$, thus making the cultivar useful in improving health (Khalili et al., 2006). Biris is proven to be a good source of protein owing to its high crude protein content of $8.5 \pm 0.08\%$ and low carbohydrate content ($71.0 \pm 0.30\%$) when compared to modern rice cultivar MR 219 (78.45%). However, despite the health benefits of Biris rice, the cultivation of this cultivar is only sufficient for subsistence farming by smallholders.



Figure 2.2: Biris landrace grain.

2.3 Rice Plant Growth and Development

Plant growth is defined as the irreversible increase in plant or organ dimensions such as plant volume, mass, height, diameter, and leaf area expansion (Dambreville et al., 2015). It refers to the accumulation of dry matter as a result of light interception and partitioning of

photosynthetic assimilates. Ashraf and Harris (2013) reported that although physiological, biochemical, and molecular processes influence plant growth, photosynthesis is a crucial process that significantly affects plant growth and development. Energy conversion occurs during plant growth when incident light is converted into biomass through the process of photosynthesis.

The growth of plants is commonly depicted as a sigmoid curve with three successive phases; an early accelerating phase with exponential plant growth, a linear phase, and a plateau with growth tending toward zero when its final size is achieved (Dambreville et al., 2015). As plant matures, the accumulation of dry matter gradually decreases because the number of leaves is reduced by senescence, consequently photosynthesis is less efficient due to a significant drop in chlorophyll concentration (Monteith, 1965; Kura-Hotta et al., 1987).

Plant development is a series of sequential events that results in definite stages and leads to a qualitative or quantitative change in plant structure (Ritchie & Nesmith, 1991; Itoh et al., 2005). There are 3 distinct phases of rice morphological development (Figure 2.3); vegetative, reproductive, and ripening, and each stage of development reflects plant ontogenetic change (Counce et al., 2000; Nori, 2013). Germination and flowering are examples of qualitative changes in plants, whereas number of leaves and flowers are examples of quantitative changes in plants (Gatsuk et al., 1980; Bonhomme, 2000; Dambreville et al., 2015). Temperature and photoperiod are the two important environmental factors affecting rice growth and development (Vergara & Chang, 1985; Yin, 1996; Krishnan et al., 2011). Rice plants commence to photoperiod at photoperiod-sensitive phase during the vegetative phase. Understanding plant growth and developmental stages is crucial

in agronomy to identify the ideal time for pest management, fertiliser application, and to predict dates to flowering and harvest.

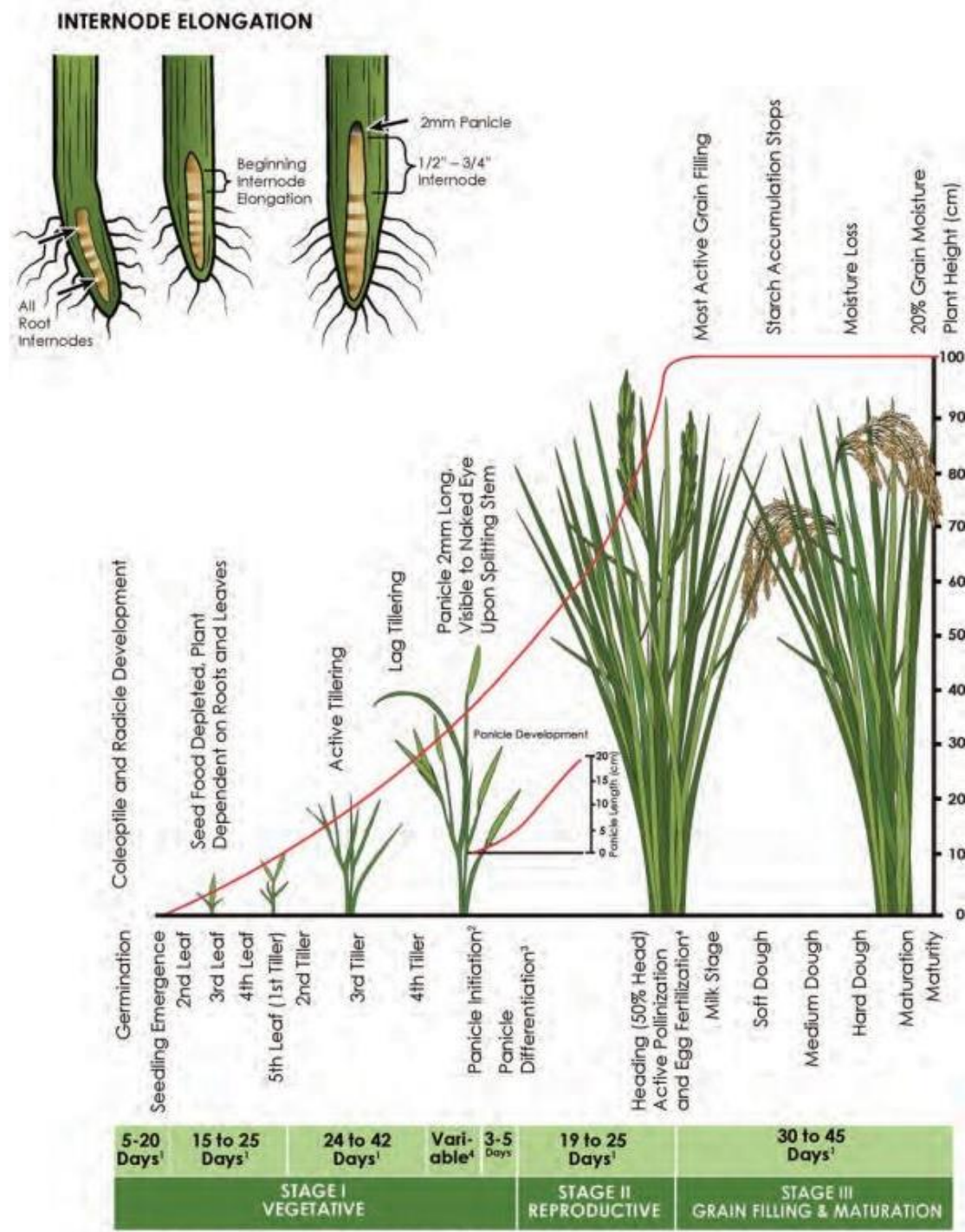


Figure 2.3: The growth and development stages of rice plant (Moldenhauer & Slaton, 2001).

2.3.1 Vegetative Phase

Vegetative phase is defined as the growth of rice plant from the germination of seed to the inception of panicle development inside the main stem (Vergara & Chang, 1985; Dunand & Saichuk, 2014). Moldenhauer and Slaton (2001) reported that the vegetative phase is a discrete phase that is frequently distinguished by the production of leaves at regular intervals, gradual increase in plant height, and active tillering. The growth duration of rice cultivars grown in a given environmental condition depends on the length of the vegetative phase, rice plant photosensitivity and thermo-sensitivity (Vergara et al., 1964). According to Dunand and Saichuk (2014), the vegetative phase of rice plant is further divided into four sub-phases; (i) seed germination and emergence, (ii) seedling development, (iii) tillering, and (iv) internode elongation.

2.3.1.1 Seed Germination and Emergence

Germination and emergence are the two key phases of the life cycle of a plant since these stages determine how effectively plants utilise the nutrients and water resources at its disposal (Gan et al., 1996). Seed germinates when it is exposed to soil moisture, optimum soil pH, and temperature above 10 °C (Shaban, 2013; Dunand & Saichuk, 2014). Water imbibition triggers the germination process, which it causes the seed to swell, gain weight, convert carbohydrates to sugar, and activate the embryo. Meanwhile, the periodicity of seed germination is significantly influenced by temperature (Guan et al., 2009). The optimum temperature for the germination of Bario Sederhana and Biris rice seeds is 33.1 °C and 32.1 °C respectively (Luing. F.L., unpublished) (Table 3.3).

During seed germination, the radicle (first root) and coleoptile (protective layer enclosing the shoot) in the embryo develop and extend (Dunand & Saichuk, 2014). The coleoptile elongates until it comes into contact with light. The appearance of coleoptile on the soil surface heralds the emergence of the rice seeds. According to Counce et al. (2000), in dry-seeded conditions the coleoptile emerged before the radicle, while in water-seeded conditions the emergence of radicle might occur after the first complete leaf. Vergara (1991) reported that depending on the method of sowing, seedling germination could occur from 0 to 90 days.

2.3.1.2 Seedling Development

The emergence of a rudimentary (basic) leaf or prophyll after the coleoptile is exposed to light indicates the commencement of seedling development (Counce et al., 2000; Dunand & Saichuk, 2014). The prophyll elongates and acts as a protective covering for the first complete leaf with a blade and sheath. After the first leaf production, all subsequent leaves are complete leaves. In general, leaves produced on the main stem at an average of one leaf per week (Vergara, 1991), but environmental factors such as temperature, photoperiod, light intensity, and humidity could modify the leaf production rate (phyllochron) (Nemoto et al., 1995).

2.3.1.3 Leaf Appearance

The developmental time interval between the appearance of two successive leaves on the main stem is known as the phyllochron (Veeramani et al., 2012; Nori, 2013).

Generally, the leaf of rice plant emerges 4 to 5 days before the initiation of panicle primordia, and 7 to 8 days after panicle primordia initiation (Yoshida, 1981). In the grass family, the growth and development of plant is determined mainly by the leaf development in the shoot apex as well as the time of tillering and rooting of individual tillers relative to leaf development (Nemoto et al., 1995). This is because phyllochron is frequently observed to be constant regardless of planting time (Hotsonyame & Hunt, 1997; Slafer & Rawson, 1997). In general, the temperature at the growing point is the main factor influencing phyllochron of plants. As the temperature rises, the phyllochron increases (Miglietta, 1989). Jamieson et al. (1995) reported that, based on the location of the meristem apex, soil temperature is the best predictor of phyllochron in wheat (*Triticum aestivum* L.). This is due to the consistent results obtained when the phyllochron is evaluated using near-surface soil temperature. Besides temperature, other factors such as daylength (photoperiod), soil nutrition level, cultivar, seed age, and nursery method employed can also influence the phyllochron of plants (Cao & Moss, 1989; Veeramani et al., 2012).

Thermal time between the appearance of successive leaves for a particular genotype cultivated in the fields is not always constant, hence photoperiod and its rate of change can influence the rate of leaf appearance (Baker et al., 1980; Cao & Moss, 1989). For example, in long day plants as photoperiod increases, shorter growing degree days are required to produce a subsequent leaf, hence leaves are produced rapidly (Baker et al., 1980; Cao & Moss, 1989; Nori, 2013). However, Nemoto et al. (1995) reported that the effect of variations in photoperiod on rice phyllochron has been contested since photoperiod seems to have little effect on the phyllochron of the crop. Thus, in order to minimise the effects of other limiting factors and concentrate on the influence of photoperiod variation on rice phyllochron, this

study was conducted in a controlled environmental growth chamber with constant air temperature.

2.3.1.4 Tillering

During the pre-tillering phase, while the primary and secondary roots are still developing, the first to fourth main stem leaves are formed. The primary tiller appears on the main stem after 15 to 25 days of pre-tillering phase (Moldenhauer & Slaton, 2001). According to Dunand and Saichuk (2014), the primary tiller is the first tiller that emerges from the sheath on the first complete leaf before the fifth leaf. Subsequent tillers originating from the primary tiller are considered as secondary tillers. Tillers grow and develop in much the same manner as the main stem leaves. During active tillering phase, new leaves on the main stem will emerge every 3 to 5 days (Moldenhauer & Slaton, 2001).

Rice tillering ability is one of the factors affecting rice yield (Nuruzzaman et al., 2000). However, Yoshida and Hayakawa (1970) reported that in the same environment rice cultivars exhibit significant differences in tillering ability, thus it is regarded as a varietal characteristic. In comparison to low-tillering rice cultivars, high-tillering rice cultivars typically have more panicles, consequently producing a higher yield (Counce & Wells, 1990; Miller et al., 1991; Wu et al., 1998). This is because the final grain yield is determined by the quantity of panicles producing tillers per unit area (Patra & Haque, 2011).

Rice tillering progresses in a sigmoidal pattern until the maximum number of tillers is attained. No further effective tillers are produced after maximum tillering has achieved, and some late tillers perish due to competition. The primary factor contributing to tiller

mortality is competition for the carbohydrates produced and the nitrogen absorbed by each tiller (Nuruzzaman et al., 2000). According to Dunand and Saichuk (2014), tiller production ceases and tiller senescence begins during internode elongation. Internode elongation indicates the completion of rice vegetative phase.

2.3.1.5 Flag Leaf

The main stem ceases to produce leaves once internode elongation has taken place (Dunand & Saichuk, 2014). The flag leaf is the final leaf to emerge from the main stem, making it the uppermost leaf on the rice main stem. The total number of main stem leaves varies depending on the rice cultivar and its locality. According to Vergara (1991), high yielding tropical rice cultivars could produce 14 to 18 main stem leaves. Yoshida (1981) reported that the flag leaf has the greatest impact on grain yield. This is because the products of photosynthesis from the flag leaf are largely responsible for grain development (Dunand & Saichuk, 2014)), and yield and yield components (Ashrafuzzaman et al., 2009). During reproductive development stage, the flag leaf has the highest metabolic rate because it is the nearest source of sustenance for rice grains (Rahman et al., 2013). Thus, given the significance of flag leaf on grain yield, it is essential to study the physiological and morphological characteristics of functional leaves in order to increase grain yield in rice (Yue et al., 2006).

2.3.2 Reproductive Phase

Reproductive phase is the duration of the plant from the end of the vegetative phase to grain maturity. According to Counce et al. (2000), the reproductive phase of rice consists

of 10 growth stages based on discrete morphological traits; (i) panicle initiation, (ii) panicle differentiation, (iii) flag leaf collar formation, (iv) panicle exertion, (v) anthesis, (vi) grain length and width expansion, (vii) grain depth expansion, (viii) grain dry down, (ix) single grain maturity, and (x) complete panicle maturity.

The reproductive phase is distinguished by the emergence and development of panicle primordium (Vergara, 1991). Panicle initiation, also known as the green ring stage in rice is the process that occurs when cells in the growing point initially start actively dividing. Vergara (1991) asserted that panicle initiation for rice plants grown in the tropics occurs 70 to 75 days before maturity. However, during panicle initiation the panicle is not visible to the naked eye (Moldenhauer & Slaton, 2001). The young panicle is visible to the naked eye 10 to 13 days after panicle initiation. This phase is described as the time when the flag leaf sheath swells as a result of increasing panicle size as it ascends the leaf sheath. Therefore, the spikelets can be identified as the panicle develops. According to Vergara and Chang (1985), panicle initiation is the key factor to take into account when studying the effects of photoperiod on the flowering of rice plant since it signifies the actual transition from the vegetative to the reproductive phase.

2.3.2.1 Heading

Panicle heading is the extension of the panicle through the sheath of the flag leaf on the main stem (Dunand & Saichuk, 2014). From this point, the development phases are determined by the condition of the panicle outside of the rice stem. During heading, panicle alludes to the uppermost internode gradual and continuous elongation. Once it has finished elongating, the entire length of the panicle is visible above the collar of the flag leaf. As a

result, the stem is fully headed. The panicle emerges completely from the flag leaf sheath within 24 hours (Vergara, 1991). Panicle heading is measured in percentages, 50% heading stage occurs when 50% of the rice stems are heading or headed.

According to Yano et al. (2000), heading date is an important trait to consider when selecting a rice cultivar for a certain cultivation area and cropping season. Genotype, environment, and its interaction are often the determining factors of heading date (Chen et al., 2020). Photoperiodic response is an important genetic pathway that affects the heading date of rice plants (Gao et al., 2014). A long duration of low sunlight three weeks before and after the heading might cause poor exertion of the panicles hence leading to poor grain filling (Moldenhauer & Slaton, 2001).

2.3.2.2 Flowering of Rice Plant

The actions that take place between the opening and closing of the spikelet is referred to as the flowering of rice plant (anthesis). Anthesis begins as heading progresses or the following day, therefore, anthesis is frequently considered of as being synonymous with panicle heading. Depending on the temperature, humidity, and photoperiod (Moldenhauer & Slaton, 2001), it takes one day after panicle exertion for anthesis to occur and 7 days for all the spikelets to complete anthesis (Vergara, 1991). According to Moldenhauer and Slaton (2001), rice is a self-pollinating plant and there is a 1% chance that it will cross pollinate.

In rice plants, the time to flowering is crucial for ecological adaptability since it determines the crop duration (Andrés & Coupland, 2012). Temperature and photoperiod, which are frequently associated, are the key factors that affect the ability of rice plant to flower (Vergara & Chang, 1985). Since rice is sensitive to photoperiod and vary greatly in

the degree of sensitivity to photoperiod (Nandini et al., 2020), long-day conditions can inhibit or delay anthesis, hence rice plant is classified as short-day plants. According to Xu et al. (2014), early or late flowering in rice will reduce grain production due to inadequate growth of the vegetative organs or poor fertility. In contrast, temperature affects both photoperiod-sensitive and photoperiod-insensitive rice cultivars. High temperature accelerates meanwhile low temperature delays flowering (Vergara & Chang, 1985)

2.3.3 Grain Filling and Ripening

Florets on the panicle of the main stem develop into immature rice grains at the commencement of grain filling phase (Dunand & Saichuk, 2014). Moldenhauer and Slaton (2001) reported that grain development is a continuous process in which carbohydrates and sugars are translocated from the stem and leaf sheaths from which they have collected to the grain, hence resulting in an increase in grain size and weight. The accumulated weight of carbohydrate leads to the panicle to bend over at the end of grain filling phase, causing the panicle branches to be less compact around the panicle axis (Dunand & Saichuk, 2014).

Grain maturity can be identified when grain changes its colour from green to gold, the leaves of the rice plant begin to senesce, and the endosperm of the grains evenly hardens and turns translucent. Once the grain achieves grain maturity, carbohydrates are no longer translocated to the panicle. In the tropics, grain ripening may take 25 to 30 days or until more than 90% of the grains in the panicles are fully ripened (Yoshida & Hara, 1977; Vergara, 1991). Grain filling is predominantly influenced by photosynthesis (Yoshida, 1981; Murchie et al., 2002) and respiration losses, which are both temperature sensitive (Peng et al., 2004). Extremely high temperature can cause a significant decrease in photosynthesis, impacting

pollen formation and development, interfering with insemination, and inducing to spikelet sterility (Yoshida, 1981; Xiao et al., 2011).

2.4 Temperature

Temperature has a significant impact on the cultivation of rice plant in Malaysia (Krishnan et al., 2011; Ashraf & Harris, 2013; Alam et al., 2014). In general, the growth and development rate of rice plant increases with temperature. Rice cultivated in tropical climates is often regarded as being resistant to high temperature settings (Krishnan et al., 2011). However, extremely high or low temperatures above or below the optimal range can be detrimental to the growth and development of rice plant. In Malaysia, the actual farm yield of rice ranges from 2721.55 to 4535.92 kg/ha, when compared to its potential yield of 6531.73 kg/ha (Alam et al., 2014). The study reported that with the CO₂ levels in Malaysia, rice yield decreased by 4.6%-6.1% for every 1 °C increase in temperature.

Rice requires high temperatures throughout the growing season, but lower night temperatures during the grain filling phase for optimal growth and yield. Moldenhauer and Slaton (2001) reported that high night time temperatures during grain filling phase led to an increase in respiration, which causes the rice plant to absorb more carbohydrates. Consequently, there are fewer filled grains since photosynthesis is less effective during daytime. This will lead to a 50% reduction in grain yield due to the extreme temperature (39 °C and above) one day before or during grain-filling phase (Matsui & Omasa, 2002; Hu & Xiong, 2014). This is because photosynthesis contributes to 60-100% of the final grain carbon content in rice plants during the grain filling phase Yoshida (1981).

Since the response towards temperature varies by biotype, cultivar, and plant health prior to the extreme temperature, determining the optimum temperature for rice growth is challenging (Moldenhauer & Slaton, 2001). In addition, air temperature is frequently higher than the optimal range due to global warming. Thus, the probability of grain being exposed to prolonged periods of supra-optimal temperature (daily mean temperature > optimal temperature) during crop growth increased as a result of this phenomena (Krishnan et al., 2011). Given the afore mentioned information, it is important to control the range of temperatures in experiments conducted in controlled environmental chambers to minimise heat stress on plants in order to study the influence of photoperiod on the growth and development of rice plant.

2.4.1 Thermal time

The development of plant is reflected by the thermal units accumulated above a base temperature (T_b), whereas below the base temperature, plant development is insignificant or null (Schmidt et al., 2018). Plants require a certain temperature range to perform optimal physiological activities such as growth, development, and reproduction. Since temperature varies due to global warming, plants will not always require the same number of days to reach a certain developmental stage or complete its life cycle. Therefore, calculating the heat accumulated over time instead of counting calendar days provides a more accurate physiological prediction since counting calendar days might be inaccurate (McMaster & Smika, 1988), especially during the early phases of crop growth (Miller et al., 2001).

Thermal time (T_t) has been widely used to quantify the growth and development of the grass family such as rice (Yin, 1996; Streck et al., 2011; Counce et al., 2015), wheat

(Addae & Pearson, 1992; Saiyed et al., 2009), and maize (*Zea mays* L.) (Kiniry, 1991; Tsimba et al., 2013). Thermal time is typically species dependent and unaffected by cultivar since it gives a uniform measurement of plant growth and development that can be utilised in a wide range of environmental setting. It can be calculated by subtracting the base temperature (T_b) below which no development happens from the mean daily temperature (T_{mean}) (Angus et al., 1981) (Equation 2.1), but a change in the use of soil temperature to air temperature is necessary at stem extension when plants enter different developmental phases (Jamieson et al., 1995).

$$\text{Thermal time (Tt)} = \Sigma(T_{mean} - T_b) \quad \text{Equation 2.1}$$

$$\text{Where, } T_{mean} = (T_{max} + T_{min})/2$$

2.5 Photoperiod

In addition to temperature, photoperiod is one of the environmental factors that controls rice plant growth and flowering (Cao & Moss, 1989; Hayama & Coupland, 2004). Photoperiod is defined as the length of a day or the amount of light throughout a 24 hours period. The response of a plant to photoperiod is known as photoperiodism. The discovery of photoperiodism by Garner and Allard (1923) revealed that plants flower in response to variations in photoperiod. Photoperiod is detected in plants by phytochrome, a class of red and far-red light photoreceptors in plants. Phytochrome monitors the quality of light and controls plant metabolism and growth accordingly (Holmes & Smith, 1977). Through distinct intracellular signaling pathways, photoreceptors detect, interpret, and convert light signals, and eventually results in adaptive changes in the cell and organism as a whole (Li et al., 2011).

Plants are then classified into three groups depending on its photoperiodic responses (Vergara & Chang, 1985): (i) short-day plant in which the response is triggered when the photoperiod is shorter than the critical daylength; (ii) long-day plant in which the response is triggered when the photoperiod exceeds the critical daylength; and (iii) day-neutral plant which are photoperiod-insensitive. According to Jackson (2009), the critical daylength (maximum photoperiod) varies among species and even among plants within the same species. Generally, rice is a short-day plant that initiates early flowering in short day conditions. According to Vergara and Chang (1985), the optimum photoperiod varies depending on the rice cultivars, however numerous studies have reported that the optimum photoperiod for rice is between 8 and 10 hours, meanwhile the maximum photoperiod reported for rice ranges from 12 to 14 hours. Therefore, studies on rice photoperiodism often employed photoperiods near to the optimum photoperiod (Yin, 1996).

Vergara and Chang (1985) reported that tropical rice cultivars are more sensitive to slight changes in photoperiod than temperate rice cultivars. Several studies have demonstrated that tropical rice cultivars have varied degrees of photoperiodic sensitivity (Shahidullah et al., 2009; Mapalana, 2017; Nandini et al., 2020; Khotasena et al., 2022). Although rice is often recognized as a short-day plant, rice plants have been developed through continuous domestication and breeding which triggers the reproductive transition to occur under different photoperiods (Izawa, 2007). The late reproductive phase may be extended without changing the anthesis date if the photoperiod sensitivity of particular developmental phases were altered. This would increase the assimilate available for spikelet growth, improving rice yield, and enable rice cultivation across a wide range of area (Slafer & Rawson, 1997). Thus, by understanding the photoperiod sensitivity of Sarawak traditional

rice, farmers and supporting agencies can implement proper farm management strategies to facilitate the needs of the rice plants in order to produce maximum yield.

2.5.1 Photoperiod Sensitive Phase

Rice only responds to photoperiod during the vegetative phase (Yin, 1996). The vegetative growth of rice is divided into two phases; (i) the basic vegetative phase, and (ii) the photoperiod sensitive phase. The rice plant must reach a certain growth threshold during the basic vegetative phase before transitioning into photoperiod sensitive phase. Photoperiod variation has little effect on the first few leaves of rice plants. Plants completed basic vegetative phase before responding to the photoperiodic stimulus for panicle initiation (Khotasena et al., 2022; Vergara & Chang, 1985). However, the duration of basic vegetative phase varies among rice cultivars. Even though it seems evident, identifying the basic vegetative phase of rice cultivar particularly in the study of rice photoperiodism is often disregarded.

The photoperiod sensitive phase is the growth stage that indicates the photoperiodic sensitivity of rice plant. Vergara and Chang (1985) stated that the photoperiod sensitive phase of photoperiod-insensitive rice cultivars lasts 0 to 30 days while that of sensitive cultivars lasts from 31 days or longer. Despite the photoperiod sensitive phase ended at panicle initiation, Collinson et al. (1992) found that rice continues to be photoperiod sensitive even after floral initiation is complete. Although classifying traditional rice cultivars as photoperiod sensitive or insensitive is essential for improving existing field management practices, it has received little attention in Malaysia. Sarawak traditional rice cultivars are generally recognized to be photoperiod sensitive (Teo, 2007b), but the extent

to which this sensitivity affects the growth and development of rice is unclear. Therefore, in order to study the photoperiodism of Sarawak traditional rice, determining the commencement of photoperiod sensitive phase in Bario Sederhana and Biris landraces is one of the objectives in this study.

CHAPTER 3

MATERIALS AND METHODS

3.1 Experimental Design and Treatments

Plastic pail containing 50 seeds of Bario Sederhana was prepared in four replicates to be germinated in a series of photoperiod treatments; 8, 9, 10, 11, and 12 hours. The same method was done using Biris landrace. Each photoperiod treatment was conducted in a controlled environmental chamber at one of five different photoperiod regimes. The plastic pails were arranged in a completely randomised design inside the controlled environmental chamber at plant growth laboratory in Universiti Malaysia Sarawak. The sowing dates of Bario Sederhana and Biris rice were shown in Table 3.1.

Table 3.1: Sowing dates of Bario Sederhana and Biris landraces sown at five photoperiod regimes inside a controlled environmental chamber at plant growth laboratory in Universiti Malaysia Sarawak.

Photoperiod (hr)	Sowing date
8	15/10/2020
9	23/9/2019
10	14/10/2020
11	14/10/2019
12	15/9/2020

3.1.1 Seed Source

Bario Sederhana seeds used in all photoperiod treatments and Biris seeds used in 9 and 11 hours photoperiod treatments were seeds harvested from Kampung Sungai Riset in Siburan, Serian. Meanwhile Biris seeds used in 8, 10, and 12 hours photoperiod treatments

were seeds harvested from Biris rice plants grown at post-harvest lab in Universiti Malaysia Sarawak in 2019.

3.1.2 Husbandry

Soil mixture was obtained using commercialised planting supplies due to time restrictions. The soil mixture consisted of organic soil, peatmoss and sand (2:1:1 by volume) were filled into a 15 L (32 cm length × 29 cm diameter) plastic pail. The soil mixture contained 1396 ppm of available phosphorus, 5.47 milliequivalent (meq)% of exchangeable potassium, 65.14 meq% of exchangeable calcium, 16.73 meq% of exchangeable magnesium, and 54.03 meq% of cation exchange capacity (C.E.C). In this study, potting mix was used instead of soil collected from the rice farm to prevent the possibility of weed infestation, as well as to minimise pest and diseases infestation. In each pail, 50 seeds of Bario Sederhana were sowed manually at a depth of 2 cm on the soil mixture, and the same method was done for Biris landrace. All plastic pails were flooded with tap water and the water level was maintained at ~5.0 mm above the soil level.

The photoperiod treatments were conducted in two controlled environmental chambers, i.e., Conviron S10H (Winnipeg, Canada) for photoperiod of 8, 9, 11, and 12 hours, and Percival Scientific E-75L1 (Perry, Iowa) for 10 hours photoperiod. In all controlled environmental chambers, the air temperature was programmed at 25/30 °C to simulate the natural field conditions in Sarawak. A mercury thermometer was placed at 10 mm below the soil surface to measure soil temperature during the minimum (25 °C) and maximum (30 °C) air temperature setting (Table 3.2). The soil temperatures were recorded every two weeks to determine the minimum and maximum values for thermal time calculations. A combination

of 16 fluorescent lights and 12 incandescent lights were used to lit Conviron S10H controlled environmental chamber, meanwhile a combination of 8 fluorescent lights and 6 incandescent lights were used to lit the Percival E-75L1 controlled environmental chamber. In all controlled environmental chambers, photosynthetic light above the rice canopies averaged $455 \pm 3.7 \mu\text{moles/m}^2/\text{s}$. The distribution of air temperature and intensity of light over a 24 hours period inside the controlled environmental chamber were shown in Figure 3.1.

Table 3.2: Mean soil temperature (°C) of the rice landraces inside the controlled environmental chamber as measured by laboratory thermometer during the minimum (25 °C) and maximum (30 °C) air temperatures.

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

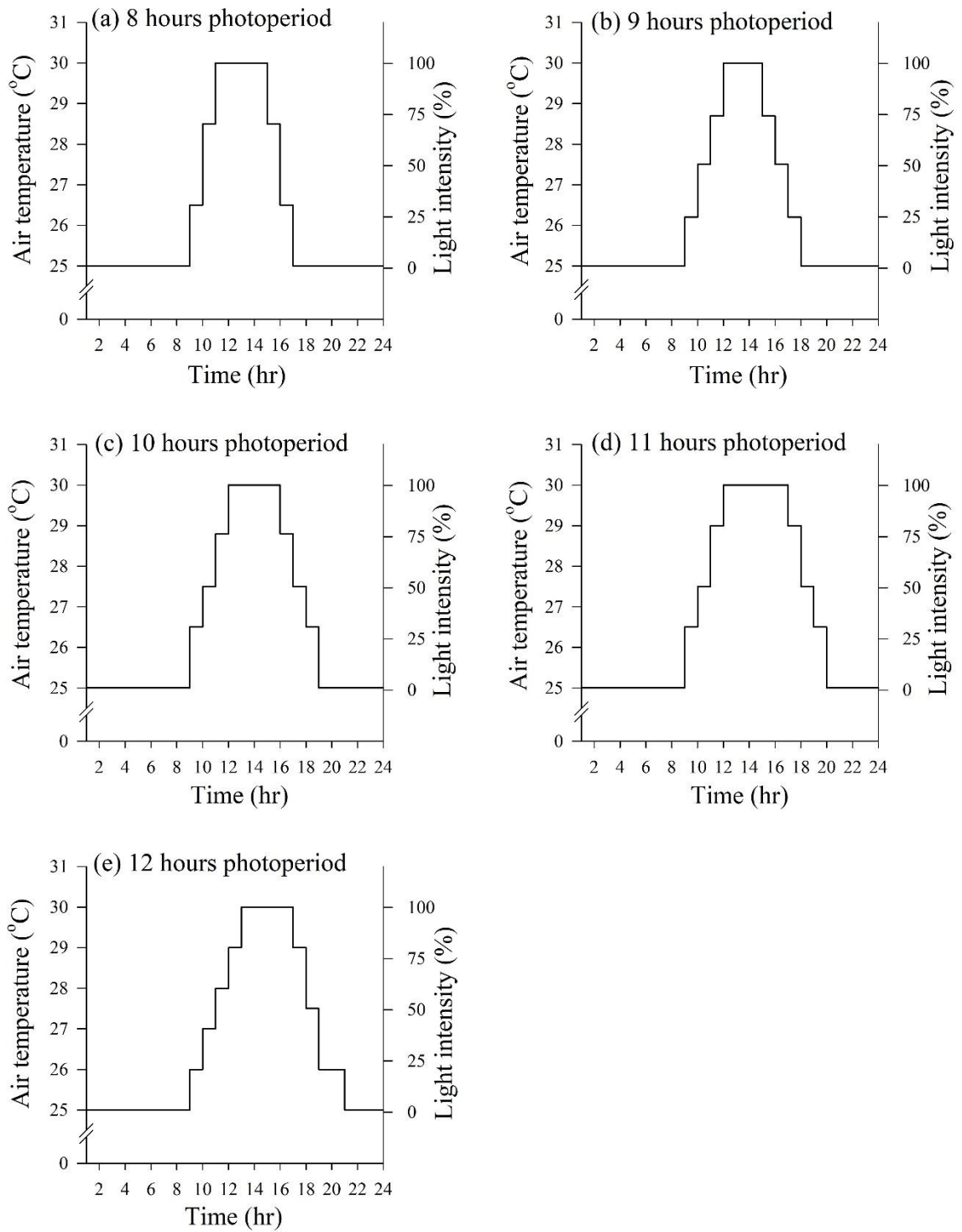


Figure 3.1: Air temperature (°C) and light intensity (%) over a 24 hours period inside the controlled environmental chambers programmed at (a) 8 hours photoperiod, (b) 9 hours photoperiod, (c) 10 hours photoperiod, (d) 11 hours photoperiod, and (e) 12 hours photoperiod at plant growth laboratory in Universiti Malaysia Sarawak.

Rice plants were thinned to reduce competition for nutrients and light after the development of the third leaf, which occurs 3 to 4 days after the sowing date. For each photoperiod treatment, only a total of 20 plants per rice landrace, with 5 plants per plastic pail were kept for detailed observation. The plastic pails were re-randomised once every 14 days to avoid chamber effect and bias data. A compound fertilizer containing 15% nitrogen (N), 15% phosphorus pentoxide (P₂O₅), 15% potassium oxide (K₂O) and 2% sulphur (S) was applied at 2.4 g/ pail during the third leaf appearance, induction of tillers, maximum tillering and panicle development stage.

3.2 Measurements

3.2.1 Emergence

After sowing, the number of emerged seedlings were counted daily until seedlings ceased to emerge. Emergence was considered to have occurred when the coleoptile was visible on the soil (Zhao et al., 2018). Cumulative seedling emergence in relation to time was described using a Gompertz function (Equation 3.1):

$$y = C \times e^{(-e^{(-B \times (t-M))})} \quad \text{Equation 3.1}$$

Where y was the cumulative percentage of seedling emerged at time 't' (days), C was the final emergence percentage, ln was natural logarithm, B and M were constants. The number of days after sowing to reach 50% of the final emergence was determined by rearranging the Equation 3.1 where y=50 as shown in Equation 3.2.

$$t_{50}=M- \ln [- \ln (\frac{50}{100})]/B \quad \text{Equation 3.2}$$

Thermal time requirement to reach 50% of the final emergence from the sowing date was analysed using soil temperature.

3.2.2 Leaf Appearance

Main stem leaf appearance was counted after thinning has been done. The first leaf and successive leaves on the main stem of each rice plant were counted at 4 days interval until the flag leaf (final leaf) was produced. The leaf appearance rate (phyllochron) was calculated from least squares regression of time against the number of leaves. The phyllochron was determined in calendar days (days/leaf) and thermal time ($^{\circ}\text{Cd}/\text{leaf}$). Analysis of phyllochron used soil temperature because the shoot apical meristem of a rice plant during the vegetative development stage was located at the base of the plant near the soil surface.

3.2.3 Reproductive Development

The first sign of reproductive development of a rice plant was after flag leaf production. Time to heading (also known as flowering) was identified when the first panicle has emerged on 50% of the rice plant populations. Following heading, the anthesis was determined when the florets have opened, exposing the stamens. Physiological maturity was defined as the stage in seed development where the seeds have reached its final size and dry seed weight (Shaw & Loomis, 1950; Ansori & Abdul Rahman, 2021). Time to reproductive developments were quantified in both calendar days and thermal time using air temperature.

At these phenological stages, stem elongation has occurred thus raising the reproductive meristem apex above the soil surface. The relationship between heading and photoperiod was described using a ‘broken stick’ linear function (Equation 3.3 and Equation 3.4) as:

$$\begin{aligned} 1/\text{days to heading} &= a_1 + b_1P \\ (\text{For the positive linear portion}) \end{aligned} \quad \text{Equation 3.3}$$

$$\begin{aligned} 1/\text{days to heading} &= a_2 + b_2P \\ (\text{For the negative linear portion}) \end{aligned} \quad \text{Equation 3.4}$$

Where, 1/days to heading was the inverse of duration calculated from seed sowing, a_1 and b_1 was the y-axis intercept and the slope of the relationship for positive linear portion, a_2 and b_2 was the y-axis intercept and the slope of the relationship for negative linear portion, P was the photoperiod between the base and optimum (for the positive linear portion) and between the optimum and maximum (for the negative linear portion) photoperiod. The base (P_{base}) (Equation 3.5), optimum (P_{opt}) (Equation 3.6) and maximum (P_{max}) (Equation 3.7) photoperiods were calculated from the regression coefficients as:

$$P_{\text{base}} = -a_1/b_1 \quad \text{Equation 3.5}$$

$$P_{\text{opt}} = (a_2 - a_1)/(b_1 - b_2) \quad \text{Equation 3.6}$$

$$P_{\text{max}} = -a_2/b_2 \quad \text{Equation 3.7}$$

The base photoperiod (P_{base}) was the threshold photoperiod below which no heading occurs. The optimum photoperiod (P_{opt}) was the photoperiod where heading occurs within the shortest time. The maximum photoperiod (P_{max}) was the highest photoperiod at which heading will occur.

3.2.4 Yield Components

The number of panicles per plant was counted and panicle length was measured using a ruler from the pedicel to the tip of the panicle. The rice panicles were harvested following grain maturity and then air dried in the crop laboratory. For each panicle, total spikelets were quantified including empty and filled spikelets. Then, the weight of filled spikelets was determined using an electronic balance. The percentage of the filled spikelets per photoperiod treatments was calculated (Equation 3.8) as:

$$\text{Filled spikelets/ photoperiod (\%)} = \frac{\text{Weight of filled spikelets (g)}}{\text{Total weight of spikelets (g)}} \times 100 \quad \text{Equation 3.8}$$

3.3 Data Analyses

3.3.1 Thermal Time Calculation

Daily thermal time was calculated by incorporating the ‘broken stick’ model with cardinal temperatures (base, optimum and maximum) (Table 3.3) and using 8x3 hourly temperatures from a sinusoidal model (Carberry et al., 1989) derived from the daily maximum and minimum temperatures.

Table 3.3: Base (T_b), optimum (T_{opt}) and maximum (T_{max}) temperatures for seed germination of Bario Sederhana and Biris rice landraces. Source: Luing, F.L. (unpublished)

Rice landrace	T_b (°C)	T_{opt} (°C)	T_{max} (°C)
Bario Sederhana	11.6	33.1	43.5
Biris	9.5	32.1	43.5

3.3.2 Statistical Analyses

Gompertz curve fitting analysis and graphs were created using SigmaPlot 14.0 (Systat Software Inc., UK). Statistical analysis used Minitab 19.0 (Minitab, LLC). Parameters were analysed using analysis of variance (ANOVA) and treatment means were compared by Fisher's Least Significant Difference (LSD) whenever the ANOVA indicated that differences among treatments presented $P < 0.05$. Specifically, reproductive development and yield components of Biris landrace were analysed using unpaired t-test because only two photoperiod treatments were tested. For each measured parameter, coefficient of variance and pooled standard error of the mean were reported.

CHAPTER 4

RESULTS

4.1 Vegetative Development

4.1.1 Seedling Emergence

4.1.1.1 Final Emergence

The final seedling emergence percentage was between 41.0% to 89.5% for Bario Sederhana and 33.0% to 97.0% for Biris landrace (Table 4.1). Bario Sederhana showed a low percentage of final emergence (41.0%) when sown at 12 hours photoperiod whereas the lowest population of seedling emergence for Biris was at 33.0% when the seeds were sown at 8 hours photoperiod. Bario Sederhana (89.5%) and Biris (97.0%) appeared to have a high percentage of final emergence when the seeds were sown at 11 hours photoperiod.

Table 4.1: Final percentage of seedling emergence for Bario Sederhana and Biris rice landraces sown at five photoperiod regimes inside a controlled environmental chamber at plant growth laboratory in Universiti Malaysia Sarawak.

Photoperiod (hr)	Number of samples	Seedling emergence (%)	
		Bario Sederhana	Biris
8	200	63.0 ^{bc}	33.0 ^c
9	200	72.0 ^{ab}	95.5 ^a
10	200	42.0 ^{cd}	95.5 ^a
11	200	89.5 ^a	97.0 ^a
12	200	41.0 ^d	46.0 ^b
P-value		0.001	<0.001
CV (%)		36.87	40.23
S.E.M.		5.07	6.60

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

The cumulative seedling emergence over time of the two rice landraces were described by Gompertz models, ($R^2 > 99.3\%$) (Figure 4.1). Typically, there were distinct linear phases before the crop by photoperiod determined its final emergence percentage. For both landraces, seeds sown at 9 and 11 hours photoperiod took a short period of time (4-5 days) to reach final seedling emergence.

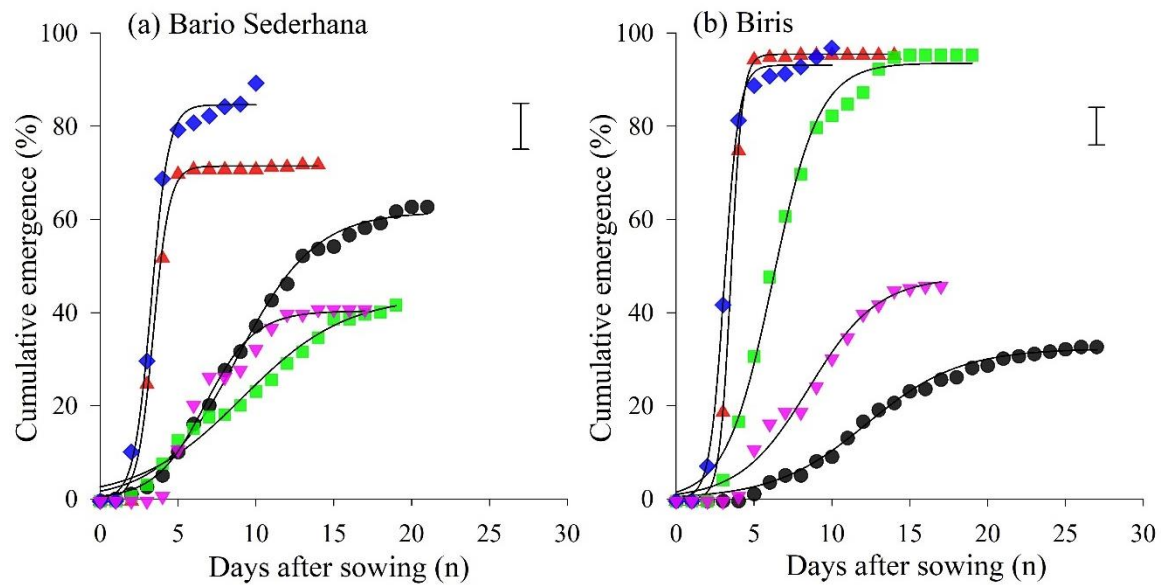


Figure 4.1: Cumulative emergence of (a) Bario Sederhana and (b) Biris rice landraces sown at 8 hours (●), 9 hours (▲), 10 hours (■), 11 hours (◆), and 12 hours (▼) photoperiod inside a controlled environmental chamber at plant growth laboratory in Universiti Malaysia Sarawak. Note: Error bars (I) represent the maximum standard error of mean for final emergence.

4.1.1.2 Time to 50% Emergence

The fitted Gompertz curves in Figure 4.1 enabled time to 50% of the final emergence to be calculated using Equation 3.2. In both landraces, thermal time requirement and number of days to reach 50% seedling emergence were affected ($P < 0.001$) by the duration of photoperiod (Table 4.2). Both rice landrace sown at 9 and 11 hours photoperiod took a shorter time to reach 50% seedling emergence. In contrast, seedling emergence was delayed at 8 hours photoperiod for both landraces (i.e., 227 °Cd/9.5 days for Bario Sederhana and 296 °Cd/12.3 days for Biris).

Table 4.2: The thermal time and number of days to reach 50% emergence for Bario Sederhana and Biris rice landraces sown at five photoperiod regimes inside a controlled environmental chamber at plant growth laboratory in Universiti Malaysia Sarawak.

Photoperiod (hr)	Bario Sederhana		Biris	
	Thermal time (°Cd)	Number of days (n)	Thermal time (°Cd)	Number of days (n)
8	227 ^a	9.5 ^a	296 ^a	12.3 ^a
9	78 ^c	3.3 ^c	84 ^d	3.4 ^c
10	209 ^a	8.9 ^a	151 ^c	6.2 ^b
11	72 ^c	3.2 ^c	78 ^d	3.2 ^c
12	143 ^b	6.1 ^b	199 ^b	7.3 ^b
P-value	<0.001	<0.001	<0.001	<0.001
CV (%)	49.6	49.2	52.4	55.2
S.E.M.	16.1	0.7	18.9	0.8

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

4.1.2 Appearance of 3rd to 7th Leaf

Photoperiod did not influence the time taken for the production of the first 3 main stem leaves (Table 4.3 &

Table 4.4) for Bario Sederhana landrace. Based on the result, photoperiod only began to change the duration of leaf production from the production of the 4th main stem leaf onwards ($P < 0.001$). On the contrary, leaf appearance of Biris was significantly different with photoperiod regimes starting from the formation of the 3rd main stem leaf ($P < 0.001$).

Table 4.3: Thermal time requirement for the production of 3rd until the 7th leaf of Bario Sederhana and Biris landraces sown at five photoperiod regimes inside a controlled environmental chamber at plant growth laboratory in Universiti Malaysia Sarawak.

Rice landrace	Photoperiod (hr)	Number of samples	Thermal time requirement (°Cd)				
			3 rd leaf	4 th leaf	5 th leaf	6 th leaf	7 th leaf
Bario Sederhana	8	20	275 ^a	489 ^b	608 ^b	799 ^b	990 ^{ab}
	9	20	227 ^a	471 ^b	591 ^b	734 ^b	853 ^b
	10	20	245 ^a	483 ^b	626 ^b	793 ^b	938 ^b
	11	20	233 ^a	358 ^c	453 ^c	549 ^c	668 ^c
	12	20	268 ^a	573 ^a	716 ^a	883 ^a	1145 ^a
	P-value		0.286	<0.001	<0.001	<0.001	0.001
	CV (%)		15.0	17.5	16.3	16.6	21.3
	S.E.M.		8.4	18.5	21.8	27.9	44.8
Biris	8	20	350 ^a	432 ^{bc}	799 ^a	853 ^a	1209 ^{ab}
	9	20	297 ^b	392 ^c	511 ^{ab}	677 ^b	819 ^c
	10	20	285 ^{bc}	540 ^a	704 ^{ab}	989 ^a	1272 ^a
	11	20	208 ^d	422 ^c	507 ^b	588 ^b	754 ^c
	12	20	273 ^c	511 ^{ab}	653 ^{ab}	891 ^a	1057 ^b
	P-value		<0.001	0.006	0.198	<0.001	0.001
	CV (%)		17.0	16.4	32.6	22.3	23.8
	S.E.M.		10.7	16.8	46.3	40.7	57.8

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

Table 4.4: Number of days required for the production of 3rd until 7th leaf of Bario Sederhana and Biris landraces sown at five photoperiod regimes inside a controlled environmental chamber at plant growth laboratory in Universiti Malaysia Sarawak.

Rice landrace	Photoperiod (hr)	Number of samples	Number of days (n)				
			3 rd leaf	4 th leaf	5 th leaf	6 th leaf	7 th leaf
Bario Sederhana	8	20	11.5 ^a	20.5 ^b	25.5 ^b	33.5 ^b	41.5 ^{ab}
	9	20	9.5 ^a	19.8 ^b	24.8 ^b	30.8 ^b	35.8 ^b
	10	20	10.3 ^a	20.3 ^b	26.3 ^b	33.3 ^b	39.3 ^b
	11	20	9.8 ^a	15.0 ^c	19.0 ^c	23.0 ^c	28.0 ^c
	12	20	11.3 ^a	24.0 ^a	30.0 ^a	37.0 ^a	48.0 ^a
	P-value		0.284	<0.001	<0.001	<0.001	0.001
	CV (%)		15.04	17.48	16.29	16.62	21.30
	S.E.M.		0.35	0.78	0.92	1.17	1.88
Biris	8	20	14.8 ^a	18.3 ^{bc}	33.8 ^a	36.0 ^a	51.0 ^{ab}
	9	20	12.5 ^b	16.5 ^c	21.5 ^b	28.5 ^b	34.5 ^c
	10	20	12.0 ^{bc}	22.8 ^a	29.8 ^{ab}	41.8 ^a	53.7 ^a
	11	20	8.8 ^d	17.8 ^c	21.3 ^b	24.8 ^b	31.8 ^c
	12	20	11.5 ^c	21.5 ^{ab}	27.5 ^{ab}	37.5 ^a	44.5 ^b
	P-value		<0.001	0.007	0.189	<0.001	0.001
	CV (%)		17.00	16.37	32.72	22.36	23.86
	S.E.M.		0.45	0.71	1.96	1.72	2.44

[CV] Coefficient of Variance. [S.E.M.] Standard error of the mean. Number of days was counted from time to 50% emergence. Within each column, means with the same letter are not significantly different at $\alpha=0.05$ according to Fisher's Least Significant Difference test.

Therefore, these results suggested that Bario Sederhana landrace responded to photoperiod after the production of the 4th main stem leaf. Meanwhile, the commencement of photoperiod for Biris landrace happened after the 3rd main stem leaf appearance.

4.1.3 Phyllochron

The maximum number of leaves on the main stem for Bario Sederhana and Biris rice landraces varied with increasing photoperiod ($P < 0.01$) (Table 4.5). In particular, at increasing photoperiod from 10 to 12 hours, both landraces exhibited an increasing number of main stem leaves. The lowest number of main stem leaves for Bario Sederhana was at 10 hours photoperiod with 6.8 leaves, meanwhile 6 leaves for Biris landrace sown at 8 and 10 hours photoperiod. The maximum number of leaves on main stem with photoperiod variation showed that Bario Sederhana had the capacity to produce a maximum of 9.3 main stem leaves, while Biris could produce 7.9 main stem leaves before panicle heading (Table 4.5). The growth pattern of the main stem leaf for all photoperiod treatments can be observed in Figure 4.2.

Table 4.5: The maximum (total) number of leaves on main stem for Bario Sederhana and Biris rice landraces sown at five photoperiod regimes inside a controlled environmental chamber at plant growth laboratory in Universiti Malaysia Sarawak.

Photoperiod (hr)	Number of samples	Maximum (total) number of leaves on the main stem (n)	
		Bario Sederhana	Biris
8	20	7.8 ^{bc}	6.0 ^b
9	20	9.3 ^a	7.9 ^a
10	20	6.8 ^c	6.0 ^b
11	20	8.0 ^b	7.4 ^a
12	20	7.9 ^b	7.7 ^a
P-value		0.002	0.001
CV (%)		13.28	14.68
S.E.M.		0.24	0.30

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

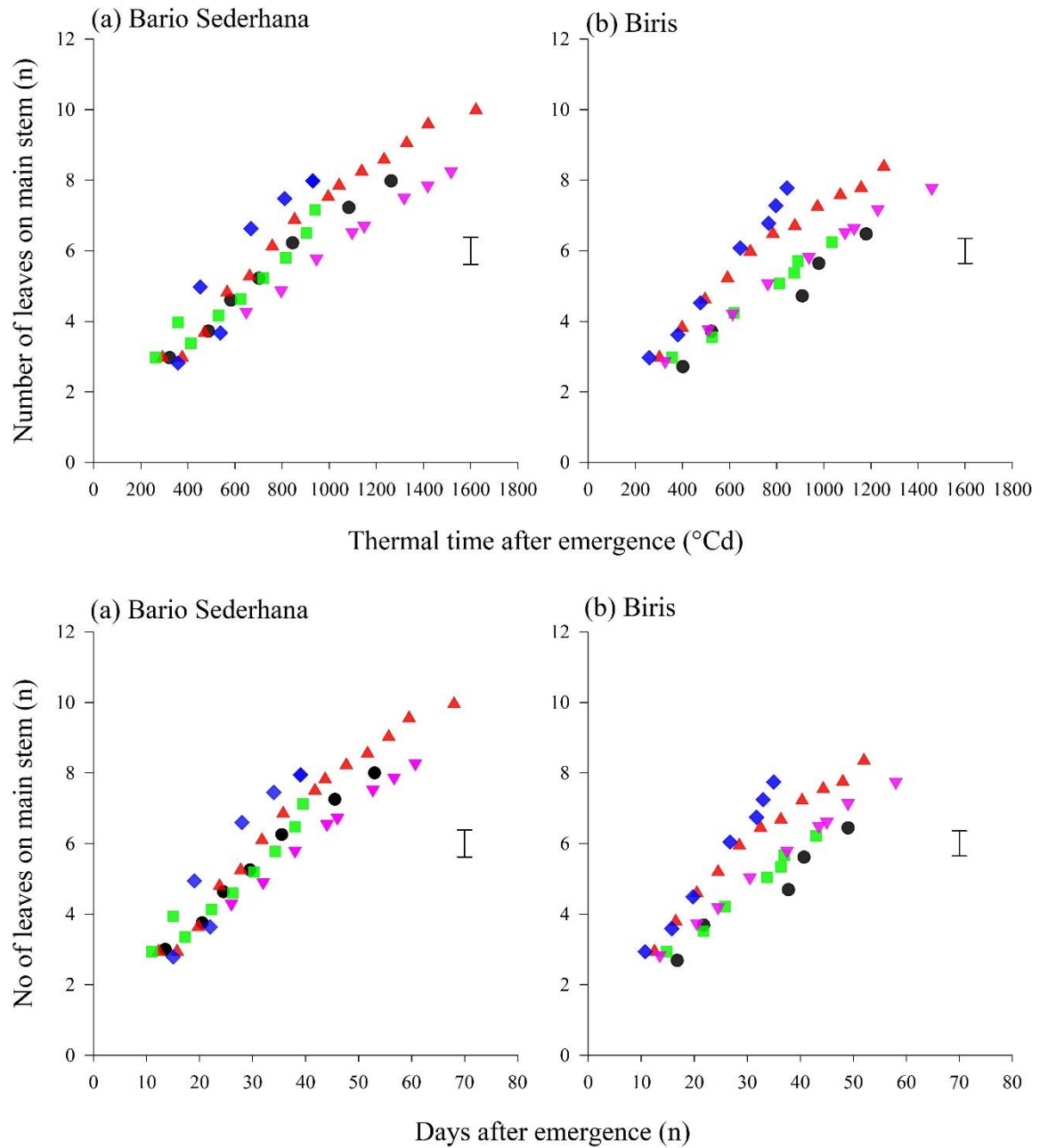


Figure 4.2: Number of leaves on the main stem of Bario Sederhana and Biris landraces sown at 8 hours (●), 9 hours (▲), 10 hours (■), 11 hours (◆), and 12 hours (▼) photoperiods inside a controlled environmental chamber against days (n) and thermal time (°Cd) after emergence at plant growth laboratory in Universiti Malaysia Sarawak.
 Note: Thermal time was calculated based on soil temperature. Number of days was counted from time to 50% emergence. Standard error bars (I) represent the maximum S.E.M.

Statistical analysis showed that thermal time and the number of days taken to produce a successive main stem leaf across increasing photoperiod for Bario Sederhana and Biris

landrace was inconsistent (Table 4.6). Both rice landraces under 11 hours photoperiod required the shortest thermal time (i.e., 135 °Cd/leaf for Bario Sederhana, 117 °Cd/leaf for Biris) and number of days (i.e., 5.6 days/leaf for Bario Sederhana, 4.9 days/leaf for Biris) to produce a successive main stem leaf. In contrast, at 12 hours (215 °Cd/leaf, 8.5 days/leaf) photoperiod Bario Sederhana required high thermal time and number of days to produce main stem leaf. Meanwhile Biris required a high thermal time and number of days to produce a successive main stem leaf at 10 hours (230 °Cd/leaf, 9.6 days/leaf) photoperiod.

Table 4.6: Phyllochron of Bario Sederhana and Biris landraces sown at five photoperiod regimes inside a controlled environmental chamber at plant growth laboratory in Universiti Malaysia Sarawak.

Rice landrace	Photoperiod (hr)	Phyllochron	
		Thermal time (°Cd/leaf)	Days (days/ leaf)
Bario Sederhana	8	193 ^{ab}	8.1 ^{ab}
	9	161 ^{bc}	6.7 ^{bc}
	10	175 ^b	7.4 ^{ab}
	11	135 ^c	5.6 ^c
	12	215 ^a	8.5 ^a
	P-value	0.002	0.005
	CV (%)	19.71	18.37
	S.E.M.	7.74	0.30
Biris	8	214 ^{ab}	8.9 ^{ab}
	9	177 ^b	7.4 ^b
	10	230 ^a	9.6 ^a
	11	117 ^c	4.9 ^c
	12	213 ^{ab}	8.4 ^{ab}
	P-value	0.004	0.004
	CV (%)	24.84	24.68
	S.E.M.	11.90	0.48

[CV] Coefficient of Variance. [S.E.M.] Standard error of the mean. Thermal time was calculated based on soil temperature. Number of days was counted from time to 50% emergence. Within each column, means with the same letter are not significantly different at $\alpha=0.05$ according to Fisher's Least Significant Difference test.

4.1.4 Time to Flag Leaf

The time taken to flag leaf production for Bario Sederhana and Biris landrace were inconsistent under increasing photoperiod regimes ($P < 0.05$) (Table 4.7). For Bario Sederhana landrace, the time to flag leaf production was delayed as photoperiod increased from 10 to 12 hours. Likewise, Biris landrace sown at 12 hours photoperiod took a longer time to produce flag leaf compared with the landrace sown at 9 hours photoperiod. Biris landrace sown at 8, 10, and 11 hours photoperiod showed no visible sign of flag leaf and reproductive development. Hence, the statistical analysis on Biris landrace was conducted only for rice plants sown at 9 and 12 hours photoperiod.

Table 4.7: Thermal time and number of days to flag leaf for Bario Sederhana and Biris landraces sown at five photoperiod regimes inside a controlled environmental chamber at plant growth laboratory in Universiti Malaysia Sarawak.

Rice landrace	Photoperiod (hr)	Time to flag leaf	
		Thermal time ($^{\circ}\text{Cd}$)	Number of days (n)
Bario Sederhana	8	1549 ^c	65.0 ^c
	9	2888 ^a	121.5 ^a
	10	1513 ^c	63.7 ^c
	11	2381 ^b	100.1 ^b
	12	2903 ^a	122.1 ^a
	P-value	<0.001	<0.001
	CV (%)	28.9	28.9
	S.E.M.	145.0	6.11
Biris	9	3667	152.4
	12	3831	159.5
	P-value	0.021	0.017
	CV (%)	2.9	3.0
	S.E.M.	38.5	1.65

[CV] Coefficient of Variance. [S.E.M.] Standard error of the mean. Thermal time was calculated based on soil temperature. Number of days was counted from date to 50% emergence. Within each column, means with the same letter are not significantly different at $\alpha = 0.05$ according to Fisher's Least Significant Difference test.

4.1.5 Number of Rice Plants Per Replicate Sown Under 8 Hours Photoperiod

Rice plants sown under 8 hours photoperiod treatment showed a high rate of mortality. Only 10 Bario Sederhana rice plants and 4 Biris rice plants survived for further observations (Figure 4.3). Consequently, data points for 8 hours photoperiod was excluded from further analysis due to the low number of plants per replicate thus, not representative of the whole population.

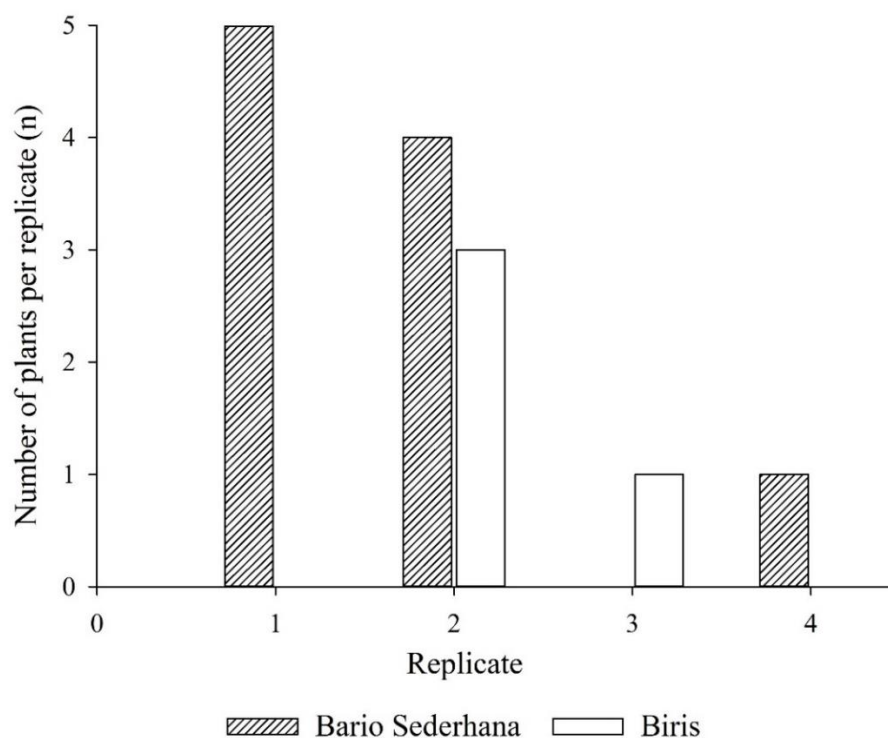


Figure 4.3: The number of Bario Sederhana and Biris plants per replicate survived when sown at 8 hours photoperiod inside a controlled environmental chamber at plant growth laboratory in Universiti Malaysia Sarawak.

4.2 Reproductive Development

Bario Sederhana landrace sown at 9 hours photoperiod required a higher thermal time and number of days to reach first heading, anthesis and grain maturity ($P < 0.001$) of that from the landrace sown at 8 hours photoperiod (Table 4.8 & Table 4.9). However, Bario

Sederhana took an extended time from emergence to become reproductive with each successive photoperiod from 10 to 12 hours photoperiod. For example, time to heading was shorter for rice plants sown at 10 hours photoperiod (1680 °Cd, 71 days) compared with 12 hours photoperiod (3147 °Cd, 133 days). Following heading, the plants required an average of 3.1 (± 0.45) days to reach anthesis across all photoperiod regimes. The rice landrace then required another 17.6 (± 2.19) days for grain filling to finally become mature.

A similar response was seen on Biris landrace with prolonged time taken to switch from emergence to reproductive development ($P < 0.05$) as plants emerged into an increasing photoperiod from 9 to 12 hours (Table 4.8 & Table 4.9). For Biris, planting at 9 hours photoperiod took 3800 °Cd (158 days) from emergence to the first heading. However, time of heading was delayed to 4067 °Cd (169 days) at 12 hours photoperiod. The time interval of subsequent phenopases were 3.5 (± 1.05) days from heading to anthesis and 25.2 (± 10.30) days from anthesis to grain maturity irrespective of photoperiodic condition.

Table 4.8: Thermal time from emergence to reproductive development for Bario Sederhana and Biris landraces sown at five photoperiod regimes inside a controlled environmental chamber at plant growth laboratory in Universiti Malaysia Sarawak.

Rice landrace	Thermal time (°Cd) to reproductive development			
	Photoperiod (hr)	Heading	Anthesis	Grain maturity
Bario Sederhana	8	1722 ^c	1799 ^c	2044 ^d
	9	3007 ^a	3061 ^a	3437 ^b
	10	1680 ^c	1745 ^c	2234 ^d
	11	2500 ^b	2566 ^b	3019 ^c
	12	3147 ^a	3266 ^a	3796 ^a
	P-value	<0.001	<0.001	<0.001
	CV (%)	27.3	26.8	24.5
	S.E.M.	147.0	149.0	159.0
Biris	9	3800	3866	4731
	12	4067	4175	4363
	P-value	0.05	0.02	0.46
	CV (%)	4.5	4.7	13.3
	S.E.M.	62.9	67.2	213

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

Table 4.9: Number of days from emergence to reproductive development for Bario Sederhana and Biris landraces sown at five photoperiod regimes inside a controlled environmental chamber at plant growth laboratory in Universiti Malaysia Sarawak.

Rice landrace	Number of days (n) to reproductive development			
	Photoperiod (hr)	Heading	Anthesis	Grain maturity
Bario Sederhana	8	72.5 ^c	75.9 ^c	86.0 ^d
	9	126.5 ^a	128.5 ^a	144.1 ^b
	10	70.8 ^c	73.6 ^c	94.2 ^d
	11	105.2 ^b	107.8 ^b	126.8 ^c
	12	132.6 ^a	137.3 ^a	159.9 ^a
	P-value	<0.001	<0.001	<0.001
	CV (%)	27.26	26.61	24.42
	S.E.M.	6.19	6.22	6.67
Biris	9	158.2	160.6	196.1
	12	169.1	173.6	188.5
	P-value	0.05	0.03	0.71
	CV (%)	4.41	4.82	12.67
	S.E.M.	2.55	2.85	8.61

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

4.2.1 Heading Rate in Relation to Photoperiod

For Bario Sederhana landrace, the heading rate showed a systematic variation with the changes of photoperiod (hours) (Figure 4.4). The rate to heading decreased linearly by 0.0047 hours per day as photoperiod decreased from the optimum photoperiod down to 7.4 hours photoperiod (Table 4.10). Further increases in photoperiod beyond 10 hours then decreases the heading rate by 0.0026 hours per day. The relationship between heading rate and photoperiod in Bario Sederhana enabled the cardinal photoperiods (P_{base} , P_{opt} , and P_{max}) to be defined in Table 4.10. The optimum photoperiod for panicle heading in Bario Sederhana is 10 hours.

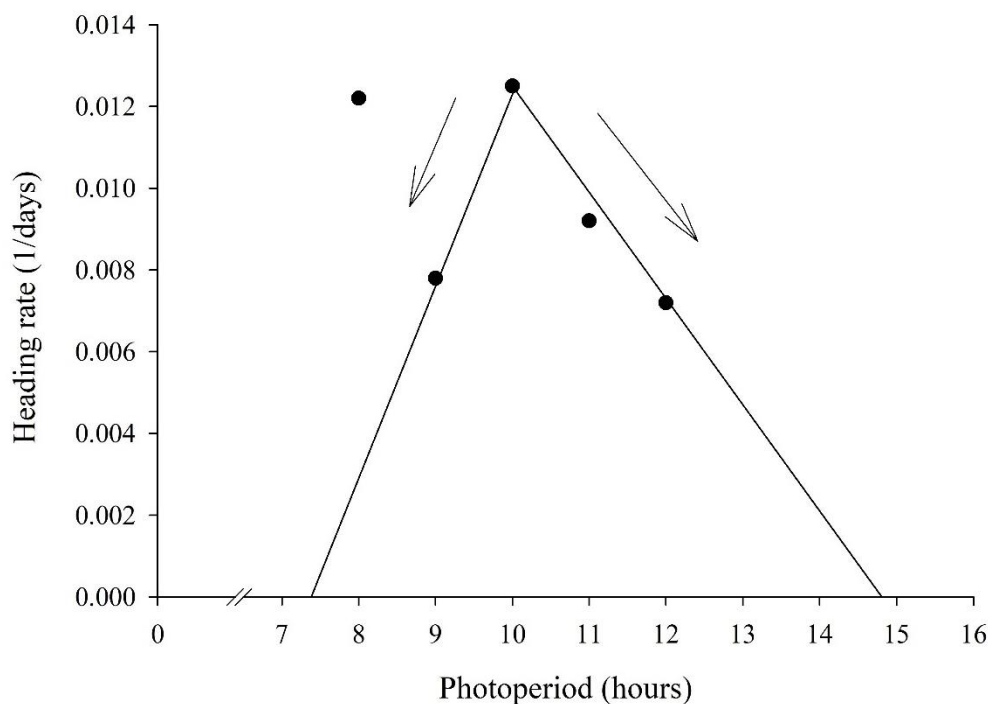


Figure 4.4: Heading rate (1/days) of Bario Sederhana landrace sown at five photoperiod regimes inside a controlled environmental chamber at plant growth laboratory in Universiti Malaysia Sarawak. Note: Arrows indicate direction towards increase and decrease in photoperiod in relation to heading. Time to heading was calculated from sowing date.

Table 4.10: Coefficient of fitted relationship between 1/days to heading and cardinal photoperiods of Bario Sederhana landrace sown at five photoperiod regimes inside a controlled environmental chamber at plant growth laboratory in Universiti Malaysia Sarawak.

Rice landrace	Direction of photoperiod	Relationship	R ² value (%)	Cardinal photoperiods (hr)		
				P _{base}	P _{opt}	P _{max}
Bario Sederhana	From 9 to 10 hours	$y = 0.0047x - 0.0347$	100			
	From 10 to 12 hours	$y = -0.0026x + 0.0385$	98	7.4	10	14.8

Note: R² refers to coefficient of determination.

4.3 Yield Components

The yield components of Bario Sederhana landrace showed variations in relation to photoperiod ($P < 0.05$) (Table 4.11). Bario Sederhana sown at 8 to 10 hours photoperiod had shorter panicle length (~14.2 cm averaged) and consequently produced lower number of spikelets per panicle (55 spikelets averaged) compared to the landrace sown at 11 and 12 hours photoperiod (~20.3 cm panicle length, ~117 spikelets/panicle). As photoperiod was extended from 9 to 12 hours, the percentage and weight of filled spikelets per panicle for Bario Sederhana exhibited an increasing trend.

Biris landrace sown at 9 and 12 hours photoperiod produced panicles that were 24.7-26.3 cm in length and had 205-217 spikelets per panicle (Table 4.11). However, the percentage of filled spikelets when the landrace was sown at 9 hours (42.8%) and 12 hours (70.1%) photoperiod showed a remarkable difference. This in return increased the weight of filled spikelets of Biris sown at 12 hours photoperiod.

Table 4.11: Yield components of Bario Sederhana and Biris landraces sown at five photoperiod regimes inside a controlled environmental chamber at plant growth laboratory in Universiti Malaysia Sarawak.

Rice landrace	Photoperiod (hr)	Yield components				
		No. of panicles/ plant	Panicle length (cm)	No. of spikelets/ panicle (n)	Filled spikelets (%)	Weight of filled spikelets/ panicle (g)
Bario Sederhana	8	2.0 ^c	13.8 ^b	61.3 ^b	68.7 ^a	1.0 ^{ab}
	9	2.4 ^{bc}	14.5 ^b	57.5 ^b	28.9 ^c	0.2 ^c
	10	4.9 ^{ab}	14.3 ^b	46.8 ^b	44.4 ^{bc}	0.4 ^c
	11	4.4 ^{abc}	20.5 ^a	113.5 ^a	33.5 ^c	0.6 ^{bc}
	12	6.2 ^a	20.0 ^a	120.9 ^a	65.3 ^{ab}	1.4 ^a
	P-value	0.014	0.001	0.002	0.008	<0.001
	CV (%)	55.26	22.45	48.83	45.36	68.23
	S.E.M.	0.49	0.83	8.73	4.88	0.11
Biris	9	14.3	24.7	205.3	42.8	1.8
	12	11.5	26.3	216.8	70.1	3.5
	P-value	0.33	0.23	0.68	0.01	0.02
	CV (%)	6.92	6.92	16.94	30.76	14.24
	S.E.M.	0.62	0.62	12.64	6.14	4.29

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

CHAPTER 5

DISCUSSION

5.1 Vegetative Development

In general, photoperiod does not affect the basic vegetative phase of rice plants. Abiotic factors such as temperature and moisture played an important role in determining the rate of emergence of rice plants. The variation in time to 50% seedling emergence in response to photoperiod (Table 4.2) was unexpected given that germinated seeds were buried beneath soil surface and unexposed to light, thus subsequent emergence was solely driven by the accumulation of temperature. The soil temperature was uniform across all treatments. Therefore, the significant difference in time to seedling emergence with photoperiod was merely a statistical value. In addition, the time to final seedlings emergence of Bario Sederhana and Biris was shown to be inconsistent across increasing photoperiod (Table 4.1).

It was assumed that this discrepancy was due to the loss of viability of the seeds throughout the quarantine period because photoperiod treatments for 8, 10, and 12 hours photoperiod for Bario Sederhana and Biris rice landraces were being halted for a year due to the global pandemic (Table 3.1). It was assumed that the low seedling emergence for Biris sown at 8 (33%) and 12 (46%) hours were due to post-harvest dormancy. In accordance with previous study, Krishnan et al. (2011) found that post-harvest dormancy, often referred to as exhibiting non-deep physiological dormancy, may cause a poor germination rate in freshly harvested rice seeds. Rice post-harvest dormancy can be reduced by exposing the rice seeds to 3 days of dry heat (50-55 °C) (Roberts, 1965). Therefore, future experiment is advised to test the viability of the seeds by conducting germination tests to avoid such problem.

Based on the statistical analysis, Bario Sederhana and Biris landraces were believed to have a short basic vegetative phase. The statistical analysis showed that the effect of photoperiod on thermal time could be seen after the appearance of the 4th leaf for Bario Sederhana and 3rd leaf for Biris landrace (Table 4.3). It was known that the first few leaves of rice plants does not respond to photoperiod (Vergara & Chang, 1985), thus this information was crucial to the study as it was an indicator of the inception of photoperiod-sensitive phases of Bario Sederhana and Biris landraces.

Variations in photoperiod influenced the phyllochron throughout the vegetative growing period. For example, the phyllochron of Bario Sederhana landrace ranged 135-175 °Cd/leaf at photoperiod of 9 to 11 hours, but were significantly higher at the lower (193 °Cd/leaf) and upper end (215 °Cd/leaf) of the photoperiod regime (Table 4.6). Biris landrace also had a similar phyllochron of 213 °Cd/leaf at both lower and upper end of photoperiod. In general, crop development is driven by the accumulation of temperature but can be modified by photoperiod at which the crop is grown. Specifically, in both landraces by photoperiod combination, the appearance of main stem leaves increased linearly with thermal time accumulation (Figure 4.2). The higher value of phyllochron for Bario Sederhana and Biris at 8 and 12 hours photoperiod were consistent with the generalized expectation that crop development rate decrease drastically at the lower and upper end of the extreme environmental conditions.

In contrast, other works on wheat (*Triticum aestivum* L.) reported that phyllochron was independent of photoperiod and sowing time and its quantification depends on the temperature perceived by the apical meristem (Miglietta, 1989; Hotsonyame & Hunt, 1997; Slafer & Rawson, 1997). The inconsistency of the phyllocron value with increasing

photoperiod from 9 to 11 hours could be attributed to the temperature used to quantify thermal time requirement for leaf appearance rate. In rice plants, the appearance of early leaves was more closely linked to soil temperature because the meristem apex was still below the ground, but when stem extension has begun, the apex was raised above the ground thus making subsequent leaf appearance responding to air temperature. In this study, the production of leaves until the flag leaf was observed in relation to thermal time accumulation based on soil temperature only, hence this may cause inaccuracy in predicting the slope of the relationship thus resulting in the unsystematic variation of the phyllochron with photoperiod.

5.2 Reproductive Development

Thermal time requirement to panicle heading of Bario Sederhana landrace was modified by the duration of photoperiod (Table 4.8). In particular, heading was delayed with lengthening photoperiod from 10 to 12 hours in Bario Sederhana and from 9 to 12 hours in Biris landrace. The use of a 'broken stick' linear model satisfactorily described the relationship between the development rate to heading (1/days) and photoperiod for Bario Sederhana landrace (Figure 4.4). It provided a statistical convenience to enable the cardinal photoperiods (base, optimum and maximum) to be estimated by using simple calculations. The response of development rate towards photoperiod using this linear function estimated a P_{base} of 7.4 hour, P_{opt} of 10.0 hour, and P_{max} of 14.8 hour for heading in Bario Sederhana landrace (Table 4.10).

The bi-linear response of development rate over the range of photoperiod between 9 and 12 hours per day was non-symmetrical. The relationship showed that when the duration

of photoperiod decreased below the optimum photoperiod at the positive linear portion (sub-optimal), heading was delayed, thus making Bario Sederhana behaved like a long-day plant. In contrast, Bario Sederhana showed characteristics of a short-day plant by delaying heading with prolonged photoperiod above the optimum value at the negative linear portion (supra-optimal). These long and short day responses of rice were consistent with the literatures reviewed by Best (1961), Vergara and Chang (1985), and Horie (1994).

The long day response in the sub-optimal photoperiod can be explained by insufficient supply of energy for growth and development under short photoperiod (Horie, 1994) despite uniform temperature and amount of radiation received by plants across all photoperiod regimes. For example, both landraces sown at 8 hours photoperiod had high mortality rate during the vegetative growth stage (Figure 4.3). Only 25% of Bario Sederhana plants and 10% of Biris plants survived to reach reproductive development phase.

Consequently, data point at 8 hours photoperiod was excluded from the analysis for two reasons: (1) low number of plants per replicate thus, not representative of the whole population, and (2) it deviated from the linear model (Figure 4.4). The short day response of time to heading at photoperiods in the supra-optimal range was expected because these were natural photoperiods in rice growing regions (Vergara & Chang, 1985). Hence, it can be concluded that photoperiod has a significant influence on the time to heading of Bario Sederhana landrace.

For Biris landrace, rice plants sown at 8, 10, and 11 hours photoperiod showed no further development after its 7th leaf. It was unclear whether the result was related to the source of seed however, non-photoperiodic factors such as light intensity, humidity, oxygen and carbon dioxide content within the controlled environmental chamber could have

influenced the growth and development of Biris landrace. In support of the results, there were reports that rice remained in vegetative stage for several years under non-inductive photoperiods (Vergara & Chang, 1985). Hence, Biris landrace was assumed to be sensitive to an artificial setting.

5.3 Yield Components

Bario Sederhana sown at 11 and 12 hours photoperiod took different time (2381 °Cd versus 2903 °Cd) to produce a similar total of 8 leaves on the main stem (Table 5.1). However, at 12 hours photoperiod, the extra time of 522 °Cd was used by the rice plants to produce more secondary leaves on the tiller development which then yielded 6.2 panicles/plant. In contrast, 11 hours photoperiod rice plants that had shorter time to complete leaves on the main stem did not produce much secondary leaves on tiller production and thus only gained 4.4 panicles/plant. Note that the number of active tillers determined the rice yield (Mu et al., 2021). Increased photoperiod from 9 to 12 hours extended the duration of grain filling and resulted in higher percentage of filled spikelets (Figure 5.1). Consequently, this resulted in a higher weight of filled spikelets per panicle with increasing photoperiod.

Table 5.1: Summary of the vegetative and reproductive development of Bario Sederhana landrace sown at five photoperiod regimes inside a controlled environmental chamber at Universiti Malaysia Sarawak.

Rice landrace	Photoperiod (hr)	Total leaves on main stem (n)	Total time taken to total leaves ($^{\circ}\text{Cd}$)	Total time taken to heading ($^{\circ}\text{Cd}$)	Number of panicles/plant
Bario Sederhana	8	7.8	1549	1722	2.0
	9	9.3	2888	3007	2.4
	10	6.8	1513	1680	4.9
	11	8.0	2381	2500	4.4
	12	7.9	2903	3147	6.2

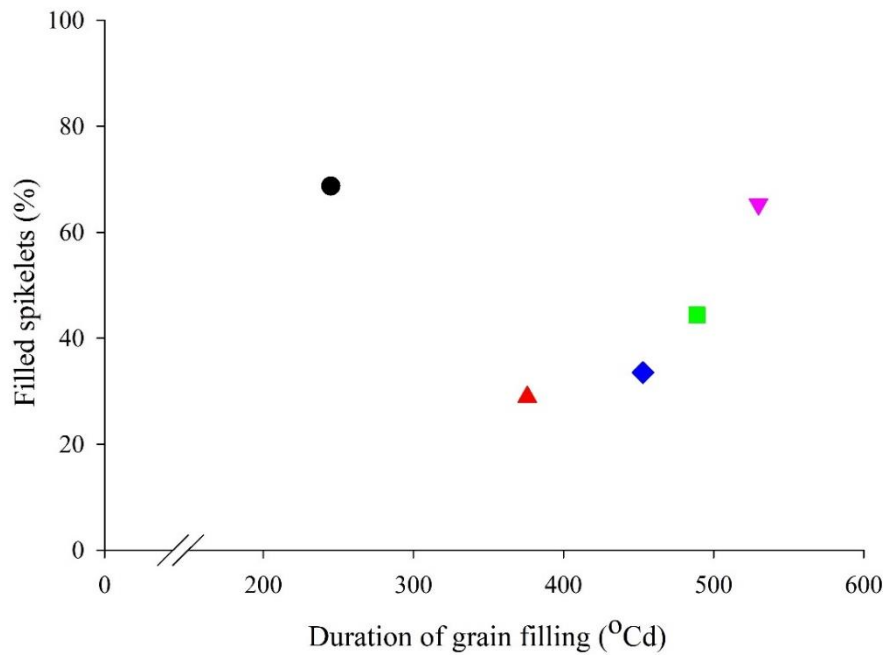


Figure 5.1: Filled spikelets percentage (%) against the duration of grain filling ($^{\circ}\text{Cd}$) of Bario Sederhana landrace sown at 8 hours (●), 9 hours (▲), 10 hours (■), 11 hours (◆), and 12 hours (▼) photoperiod inside a controlled environmental chamber at Universiti Malaysia Sarawak.

In general, Akhter et al. (2007) reported that the yield, spikelet weight, and percentage of filled spikelets were independent by the rice plant sensitivity to photoperiod.

The high percentage of filled spikelet at 12 hours photoperiod treatment for Bario Sederhana (65.3%) and Biris (70.1%) were assumed to be influenced by the condition of the leaves. According to Lee and Masclaux-Daubresse (2021), under unfavorable environmental conditions, premature senescence or yellowing of leaves can reduce grain yield. Erect and healthy rice leaves increased light capture for photosynthesis thus served as nitrogen reservoirs for grain filling and allowing denser plantings with higher leaf area index subsequently increasing the rice yield, consequently increasing grain yield (Sakamoto et al., 2006). Thus, despite having higher number of panicles (14.4 panicles/plant) at 9 hours photoperiod in comparison with 11.5 panicles/plant at 12 hours photoperiod, there was a drastic difference in the weight and percentage of filled spikelets for Biris rice plants (Table 4.11).

5.4 Limitations of a Controlled Environmental Chamber Study

Controlled environmental chamber provided controlled environments needed to produce reliable observations related to plant physiology. Environmental factors such as temperature, photoperiod, and relative humidity can have a significant impact on plant growth and development. Therefore, a controlled environmental chamber was commonly used to simulate, control and extend the range of settings, especially when a field experiment only offers a limited array of climatic conditions. The two controlled environmental chambers used in this study were Conviron S10H (Winnipeg, Canada) and Percival Scientific E-75L1 (Perry, Iowa). However, the controlled environmental chambers only featured basic settings for temperature and light, without control for carbon dioxide, which was an important factor in photosynthesis activity. In addition, the maximum light intensity

within the controlled environmental chambers at 12 p.m. ranged between 650 to 700 $\mu\text{moles/m}^2/\text{s}$ at plant canopy level. In contrast, light intensity in a field condition at mid-day could reach up to 2000 to 2200 $\mu\text{moles/m}^2/\text{s}$ (Hay & Walker, 1989).

As a consequence, the rice leaves were thin and short (Figure 5.2) despite sufficient supply of nutrients from fertilizer and water. This affected the growth and development of rice plants growing inside the controlled environmental chamber. The size and health condition of leaf determined the capacity of photosynthesis which manufacture carbohydrates for distribution to the rice grain following anthesis. According to Yoshida (1981), the optimum leaf area index of erect leaves was higher than that of rice with horizontal leaves, thus improving the yield production (Sakamoto et al., 2006). Hence, the low amount of carbohydrates produced by the poor photosynthetic activity due to the thin and droopy leaves of Bario Sederhana and Biris landrace inside the controlled environmental chamber produced grains of lower weight.

Despite being widely used in studies, there were limitations of using controlled environmental chamber. Potvin and Tardif (1988) reported that even the most sophisticated controlled environment chamber cannot ensure that environmental fluctuations within the chamber will not occur during plant growth and development. Long-term experiments could modify the environmental parameters inside the environmental chamber. Consequently, it caused spatial variations in the physiology of plants as a result of the decaying of light due to light bulb age, humidity fluctuations, varying temperature and atmospheric CO_2 concentration (Porter et al., 2015). Thus, due to the lack of control for atmospheric CO_2 concentration, fluctuating CO_2 concentration within the controlled environmental chamber

used in this study may have an impact on photosynthesis and consequently influenced rice plant growth and development (Edwards et al., 2009).

Therefore, it is suggested that Conviron S10H (Winnipeg, Canada) and Percival Scientific E-75L1 (Perry, Iowa) growth chambers are best suited for short-term experiments (<6 months) with smaller plants. Given that traditional rice matures at a maximum of 6 months, degradation of light quality may have led to a skewed result. In the future, the use of a walk-in controlled experimental chamber that has more control on the environmental settings may be a better alternative in conducting studies on the photoperiodism of Sarawak traditional rice.

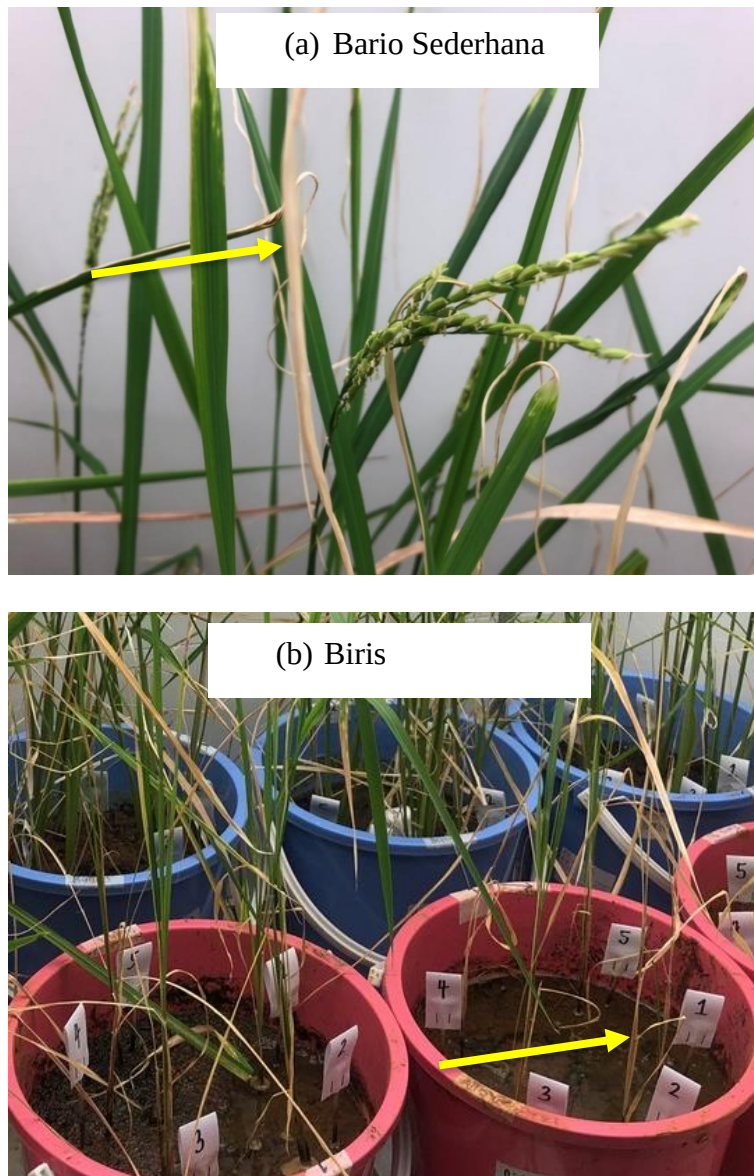


Figure 5.2: The (a) thin and brown tip of Bario Sederhana leaves; and (b) thin leaves of Biris landrace (pink pails) sown at 8 hours photoperiod inside a controlled environmental chamber at Universiti Malaysia Sarawak. Note: Arrows indicate the (a) thin and brown tip of Bario Sederhana leaves; and (b) thin leaves of Biris landrace.

CHAPTER 6

CONCLUSION

The study presented in this thesis has demonstrated the development and growth responses of two Sarawak traditional rice landraces, i.e., Bario Sederhana and Biris toward photoperiod. The results seemed to indicate that Bario Sederhana and Biris landraces had a short basic vegetative phase. The photoperiod sensitive phase of Bario Sederhana commenced at the fourth leaf, whereas the photoperiod sensitive phase of Biris landrace commenced at the third leaf. The phyllochron of Bario Sederhana and Biris was affected by photoperiod with slow development rate at the lower and higher end of the photoperiod range.

The linear model used in describing relationship between development rate to heading and photoperiod estimated the base, optimum, and maximum photoperiod for heading in Bario Sederhana as 7.4 hours, 10 hours, and 14.8 hours, respectively. The linear model showed that Bario Sederhana responded as a long day plant at the sub-optimal photoperiod, meaning that heading was delayed as photoperiod decreased below the optimum. In contrast, this landrace behaved like a short-day plant when photoperiod exceeded above the optimum at the supra-optimal range. Biris landrace grown under 8, 10, and 11 hours photoperiods remained dormant in the vegetative phase and did not develop further. Hence, Biris landrace was assumed to be sensitive to an artificial setting.

In both landraces, rice plants sown at 12 hours photoperiod turned reproductive later by having a longer period of vegetative growth. This extended time was used to produce more tillers which led to production of more panicles per plant. The lengthening photoperiod following anthesis prolonged the duration of grain filling, thus resulted in high grain weight

per panicle. Therefore, Sarawak tropical environment where photoperiod is 12 hours throughout the year provides an optimum photoperiod for the rice landraces to produce high yield. Hence, farmers need to incorporate more agricultural inputs such as controlling weeds and pest using modern agricultural techniques, proper use of fertilizers, and upgrading the mechanisation and infrastructure of the farm in order to facilitate high yield production.

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