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DIURNAL VARIATION IN PHYSIOLOGICAL RESPONSES OF AEROBIC-ADAPTED RICE VARIETIES UNDER DIFFERENT MULCHING STRATEGIES

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Abstract

Rice consumes more water compared to other crops. Therefore, rice varieties that are able to adapt non-flooded (aerobic) condition could be an advantage to conserve water. Furthermore, the ground cover rice production system using mulching technique can be effectively reduced water stress for aerobic rice cultivation. In this study, the diurnal physiological responses of aerobic-adapted Malaysian rice (*Oryza sativa* L.) varieties MRQ74 and MR253 were investigated under different mulching strategies, i.e. plastic mulch (PM), rice straw mulch (SM), and no mulch (NM). Photosynthesis rate (A), transpiration rate (E), stomatal conductance (g_s), water use efficiency (WUE) and stomatal limitation (L_s) were measured at tillering and maturation stages of the rice plants. The latter stage have shown significant differences (ANOVA, $p \leq 0.05$) on the parameters studied, in which A was highest in PM (197 µmol m^{-2} s^{-1}) followed by SM (146 µmol m^{-2} s^{-1}) and NM (86 µmol m^{-2} s^{-1}) in MRQ74. Interestingly, the result showed a unimodal diurnal curve for A in both tillering and maturation stages, which indicates that the midday depression of A did not present. This suggests that the mechanism improves the ability of rice plant to adapt in aerobic condition. Furthermore, mulching treatments demonstrated an improved WUE on both MRQ74 and MR253 during maturation stage. At tillering stage, PM treatment increased WUE about 75% higher compared to NM during the midday. This study shows that mulching treatment such as PM and SM can be implemented to improve aerobic rice cultivation and subsequently sustaining rice production in water limited area.

Key words: *Oryza sativa,* Aerobic rice, Mulching technique, Physiological diurnal, Water use efficiency.

Introduction

Water is a crucial element for plant growth and development. Rice plant specifically is very susceptible to less water conditions as it consumes more water than any other crops (Zhi, 2015). Due to water scarcity, cultivated rice plant under non-flooded (aerobic) condition could be the best strategy to conserve water. Basically, aerobic cultivation in rice plants lead to water stress at different growth stages, e.g. germination, seedling, tillering, flowering and grain filling (Singh *et al.*, 2012). Rice genotypes with high water stress tolerance during tillering stage (vegetative stage) has superior survival rate. Studies reported that the crucial water stress during vegetative stage causes leaf senescence, reduction in photosynthesis, suppression of leaf expansion, stunted growth and consequently lower yield (Bita & Gerats, 2013; Zain *et al.*, 2014).

The physiological diurnal changes played an important interaction to regulate metabolism, cellular function, and growth of plant (McClung, 2006). This response exhibited dissymmetric behaviour on plants according to the severity of water stress (Olioso *et al.*, 1996; Shao *et al.*, 2008). Deng *et al.*, (2000) and Debabrata (2011) showed that diurnal depression of photosynthesis caused by drought environment reduces growth rate and yield production.

Water stresses in plants can be classified into two phases (Shao *et al.*, 2008): 1) the moderate water loss that causes stomatal closure and limitation of gas exchange; 2) the extensive water loss (desiccation) that leads to interference of cell structure, enzymatic reactions, and metabolism. The severe water stress finally resulted in plant death. The reduction in soil moisture decreases water content in the leaves, causing the guard cells to lose turgor pressure and subsequently stomatal closure (Lawson & Blat, 2014). In addition, an increased stomatal resistance may lead to the reduction of water transport in the leaves, thus decreasing stomatal conductance and transpiration. The prolonged in less water condition may cause plants to be dependent on the availability of essential soil water reserves in the root zone (Stiller *et al.*, 2003). The stomatal closure assists in sustaining high leaf water content and therefore increases leaf water potential. However, this may cause to a reduction in carbon assimilation activity (Singh *et al.*, 2012). Rice plant with higher capacities of CO_2 uptake provide great potential in the development of leaf-level photosynthesis with water stress tolerance and high productivity (Adachi *et al.*, 2010; Lauteri *et al.*, 2014).

Rice cultivation via non-flooded approach may lead to yield inconsistency. However, an alternative way of rice cultivation using mulching technique may reduce water stress effects in aerobic condition (Tao *et al.*, 2006; Mahmod *et al.*, 2014). The mulching technique could also prevent soil evaporation and reduce seepage (Zhang *et al.*, 2008). Moreover, this approach may increase soil temperature, improves soil moisture, prevents soil degradation, reduces soil erosion, and inhibits weed growth (Fan *et al.*, 2005; Zhi, 2015).

The information on physiological diurnal of cultivated rice to aerobic condition are remain unknown. Therefore, in this study, the diurnal temporal pattern of physiological aspects of aerobic-adapted Malaysian rice varieties grown under different mulching treatments was investigated. Furthermore, the water use efficiency (WUE) of the local aerobic-adapted rice varieties was evaluated.

Materials and Methods

Experimental design: The study was conducted at Malaysian Agriculture Research and Development Institute (MARDI), Seberang Perai, Pulau Pinang (5^0 32'N, 100^0 28'N). Two local rice varieties (MRQ74 and MR253) were obtained from MARDI. This experiment comprises of three treatments 1) soil covered by mulching rice straw (SM); 2) soil covered by a black plastic film (PM) and 3) uncovered soil (NM) (Fig. 1).

Seeds were sown in a tray nursery beds for 2 weeks. Subsequently, the seedlings were transplanted into the plots in completely randomized design (CRD) with three replications. Each plot was thinned to 25 seedlings (5 columns x 5 rows) per plot arranged by 15 cm apart. The treatments for PM and SM were performed according to Mahmod *et al.*, 2014. Green fertilizer (N15:P15:K15) was applied at 20 days and 40 days, while blue fertilizer (N12:P12:K17:MGO2) was applied at 65 days and 85 days after transplanting.

Diurnal physiological study: The study was conducted during tillering stage (30 DAT) and maturation stage (90 DAT) at 3 hours interval (0800 h to 1830 h). Photosynthetic rate (A), stomatal conductance (g_s) and transpiration rate (E) were determined using portable photosynthetic system (LI-6400XT Portable Photosynthesis System, Lincoln, Nebraska, USA) under normal ambient environmental conditions. Water use efficiency (WUE) was calculated as ratio of net photosynthesis rate and transpiration rate (A/E). Stomatal limitation value (Ls) was determined according to Berry & Downton (1982):

$$Ls = 1 - Ci/Ca$$

where Ci is the intercellular CO_2 concentration and Ca is atmospheric CO_2 concentration.

Statistical analysis

Data were analysed using analysis of variance (ANOVA) followed by LSD ($p \leq 0.05$) to test significant differences between means. Regression analysis was applied to explore relationship between WUE and g_s.

Results

The diurnal changes in physiological parameters at tillering and maturation stage: The photosynthetic active radiation (PAR) and air temperature measurements during tillering and maturation stages are shown in Fig. 2. The photosynthesis rate (A) curve showed a peak during midday in all treatments, varieties, and growth stages (Fig. 3a-d). In general, A started low in the early morning, increased rapidly until midday and then decreased by the evening. The pattern of A was parallel with the diurnal of air temperature and PAR indicating normal photosynthesis reaction of rice in the aerobic condition.

Unlike most rice which displayed bimodal diurnal curve (Yang *et al.*, 2008; Debabrata, 2011; Zhi, 2015), MRQ74 and MR253 varieties adapted to aerobic condition showed unimodal curve of A in both growth stages (Fig. 3a-d). The highest level of A was detected during midday when the air temperature and PAR density were 33.8°C and 1500 mmol $m^{-2}s^{-1}$ at tillering stage and 31.2°C and 1400 mmol m^{-2} s^{-1} at maturation stage, respectively. At tillering stage, the level of An in MR253 was significantly higher than MRQ74 ($p \leq 0.05$). However, there is no significant difference if compared between the mulching treatments (Table 1). In contrast, the pattern of diurnal A for PM and SM treatment at maturation stage was about two fold higher in MRQ74 compared to MR253. The diurnal A was significantly different ($p \leq 0.05$) between treatments during maturation stage where PM showed the highest (196.6 µmol m^{-2} s^{-1}) followed by SM (145.7 µmol m^{-2} s^{-1}) and NM (86.4 µmol m^{-2} s^{-1}) (Fig. 3c).

The diurnal pattern in transpiration rate (E) and stomatal conductance (g_s) of tillering and maturation stage are shown in Fig. 3e-l. At tillering stage, both varieties demonstrated V-shaped pattern of diurnal in g_s and E (Fig. 3e-f and 3i-j). High E values were recorded in the early morning, then tremendously decreased during midday and increased again towards the late afternoon. There were similar diurnal changes of E and g_s because water transpired depending on stomata opening. A rapid decrease of g_s and E value at midday was due to its high sensitivity to water loss at high temperature and light intensity, therefore trigger the optimal stomata regulation.

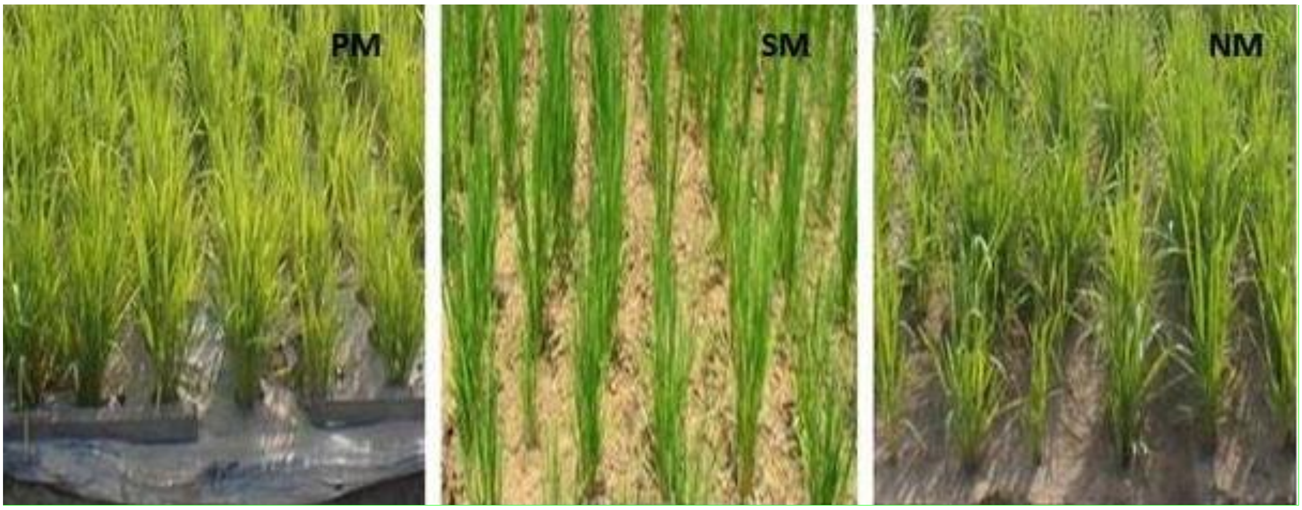

Fig. 1. Soil surface covered by plastic mulch (PM), rice straw mulch (SM) and no mulch (NM).

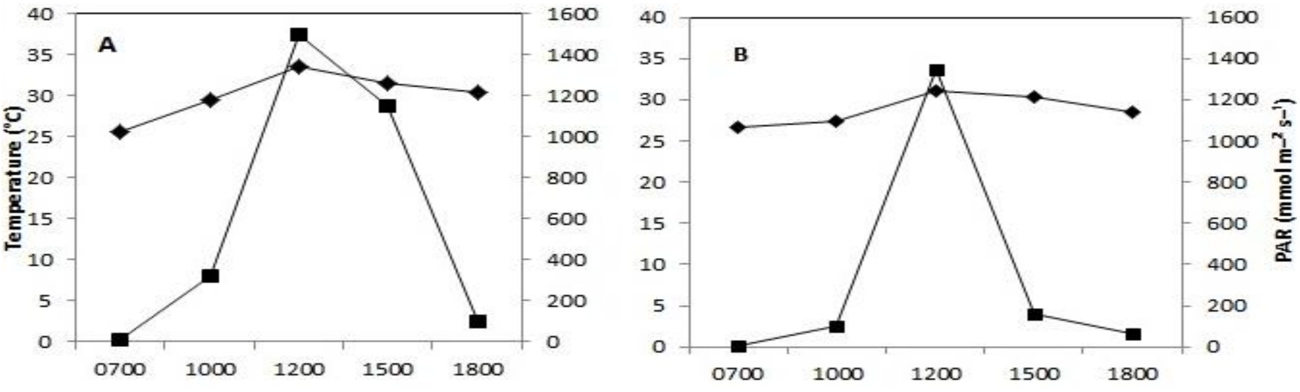

Fig. 2 Diurnal variations of net air temperature and photosynthetic active radiation at (A) tillering and (B) maturation stage. (♦ = Temperature, ■ = PAR).

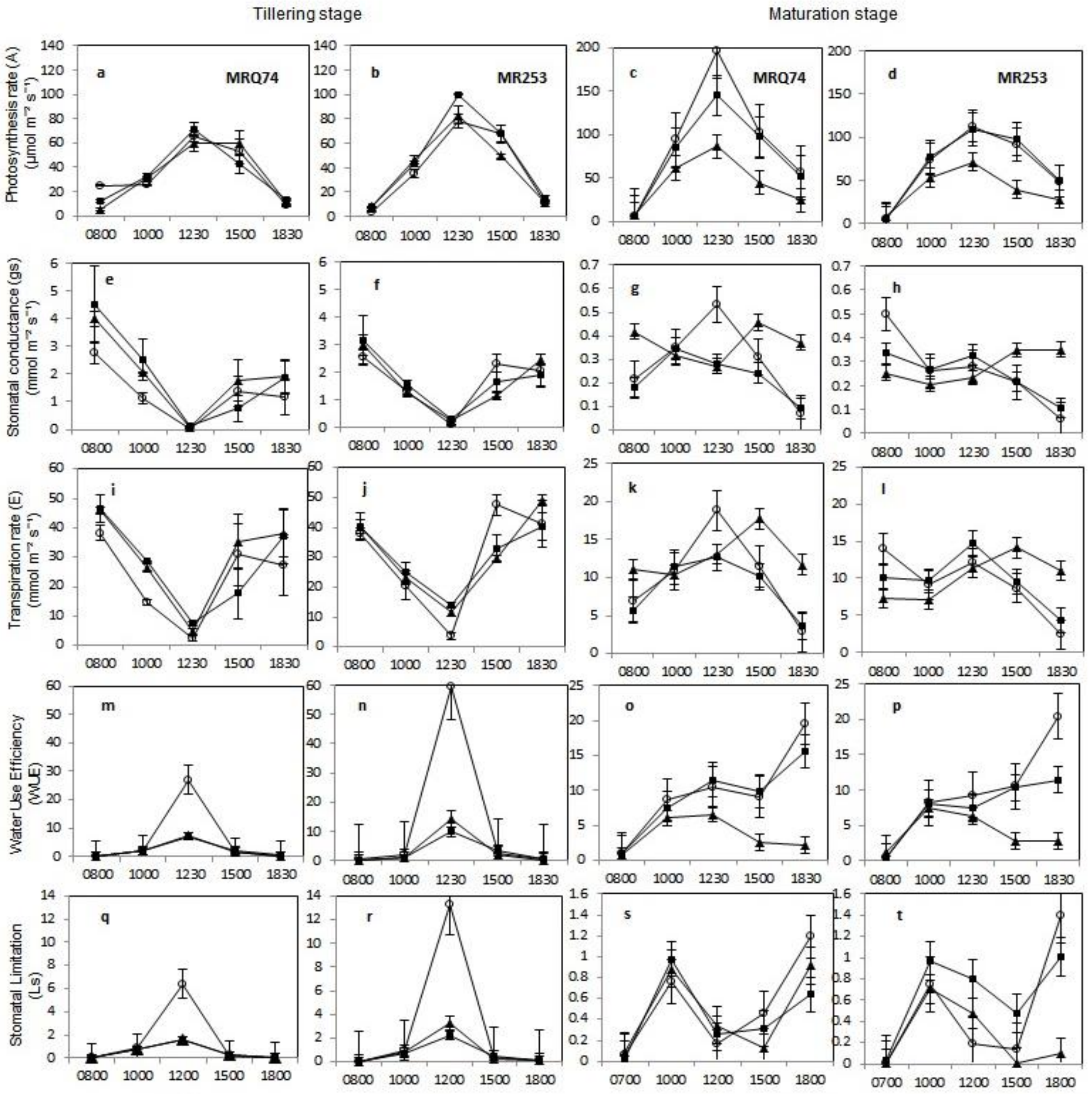

Fig. 3. Diurnal variations of photosynthesis rate (A), stomatal conductance (g_s), transpiration rate (E), water use efficiency (WUE) and stomatal limitation (Ls) for the rice plant varieties MRQ74 and MR253 at tillering stage and maturation stage upon different mulching treatments. Vertical bars represent standard error of the mean. ○: plastic mulching (PM), ■: rice straw mulching (SM), ▲: no mulching (NM).

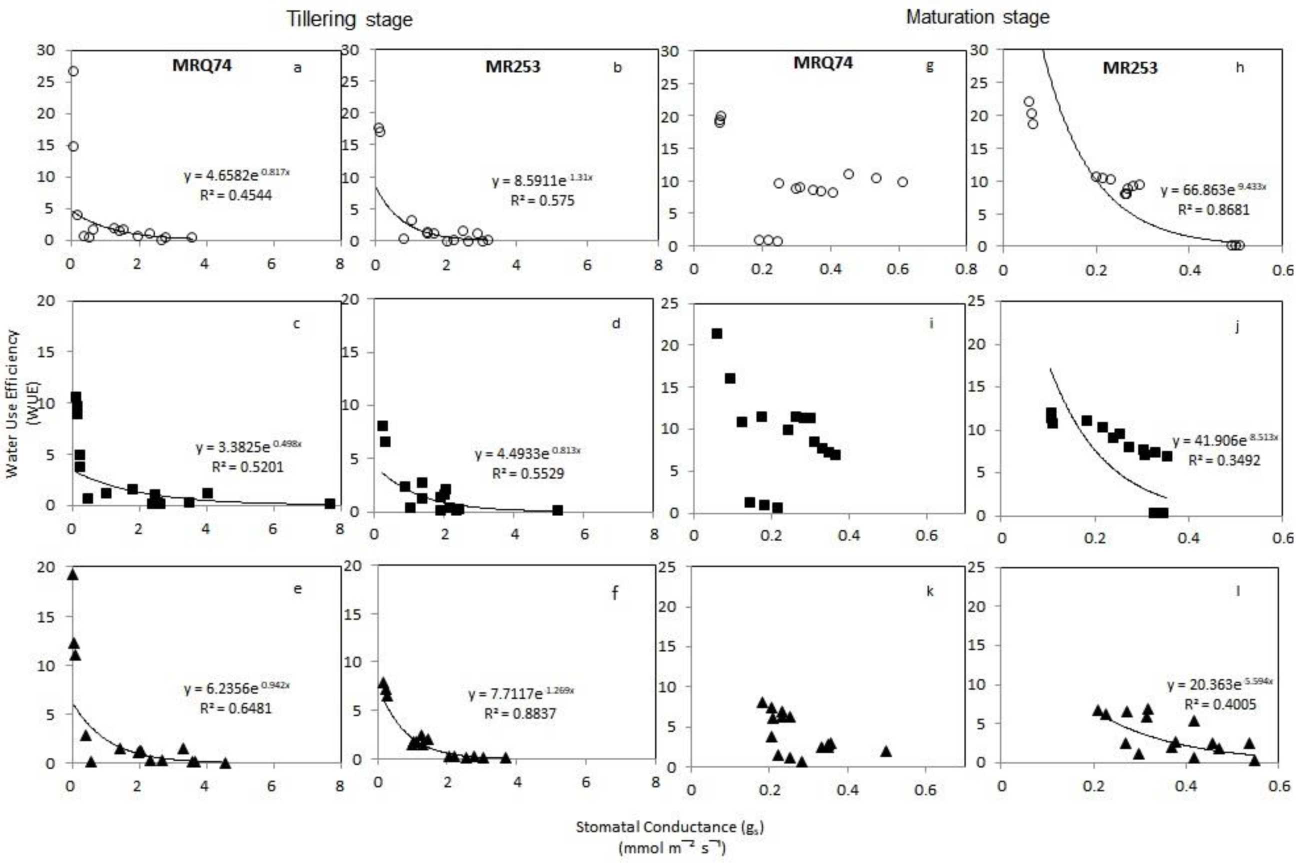

Fig. 4. Relationship between water use efficiency (WUE) and stomatal conductance (g_s) at tillering and maturation stages in all treatments and varieties. ○: plastic mulching (PM), ■: rice straw mulching (SM), ▲: no mulching (NM).

Table 1. Analysis of variance for diurnal of photosynthesis rate (A), stomatal conductance (gs), transpiration rate (E), water use efficiency (WUE) and stomatal limitation (Ls) among varieties, treatments and hours at tillering and maturation stages.

Source of variation	df	Tillering					Maturation				
		A	gs	E	WUE	Ls	A	gs	E	WUE	Ls
Variety	1	1374.73**	0	386.3	168.38	8.33**	3582.54**	0.04**	29.30**	3.36	0.04
Treatment (Soil Cover)	2	129.46	0.98	126.1	453.43	25.30**	11768.0**	0.06**	47.59**	288.91**	0.14
Time (Hour)	4	13727.7**	23.1**	3449.18 **	1396.44 **	71.85**	29744.3**	0.06**	162.98**	271.61**	8.13**
Variety x Treatment	2	134.11	1.15	93.63	94.71	3.69*	893.03**	0.02*	17.67**	9.16**	0.38*
Variety x Time	4	422.58**	0.98	111.62	182.51	8.13**	1550.58**	0.01	10.89*	5.20**	0.12
Treatment x Time	8	140.67	0.76	146.56	459.34 **	22.83**	1557.17**	0.05**	45.65**	81.53**	0.31**
Variety x Treatment x Time	7	190.86*	0.39	73.03	87.94	3.59**	347.13**	0.02**	14.44**	3.07*	0.11
Error	61	76.78	0.90	99.24	159.57	0.93	35.53	0.00	2.99	1.39	0.06

*, ** Represent significance at the $p \leq 0.05$ and $p \leq 0.01$, respectively

Remarkably, the diurnal curve of g_s and E at maturation stage (Figs. 3g-h & 3k-l) exhibited dissimilar pattern than the tillering stage (Fig. 3e-f and 3i-j). At maturation stage, g_s and E were responded higher during midday compared to tillering stage where g_s almost reached zero values. However, the diurnal range of E at maturation stage was found lower (≤ 20 mmol $m^{-2}s^{-1}$) than tillering stage (≤ 50 mmol $m^{-2}s^{-1}$). It showed that E was decreased from tillering to maturation stage as comparable with g_s. The diurnal range of g_s at maturation was less than 1 mmol $m^{-2}s^{-1}$ whereas wide range was observed at tillering stage (0-5 mmol $m^{-2}s^{-1}$). Furthermore, there were significant differences ($p \leq 0.05$) between the rice varieties as well as between the soil cover treatments in both g_s and E at maturation stage (Table 1). In terms of mulching treatments, each variety performed differently in response to diurnal E and g_s. For MRQ74, PM and SM transpired the most at midday (18.8 mmol m^{-2} s^{-1} and 12.7 mmol m^{-2} s^{-1}), while NM (17.7 mmol m^{-2} s^{-1}) at late afternoon, whereas for MR253, PM exhibited the highest E value at early morning (13.0 mmol m^{-2} s^{-1}), SM at midday (14.7 mmol m^{-2} s^{-1}) and NM (14.1 mmol m^{-2} s^{-1}) at late afternoon.

The diurnal changes in water use efficiency (WUE) and stomatal limitation (Ls): The diurnals of WUE were not significantly different between treatments and varieties at tillering stage but showed differences (*p≤0.05*) at maturation stage (Table 1). In general, WUE at tillering stage showed a concave response where it was low in the morning, increased in midday and then decreased towards evening (Fig. 3m-n). Apparently, PM showed the highest

WUE during midday in both varieties. At maturation stage, PM and NM monotonically increased throughout a day whereas NM started to decrease at late afternoon (Fig. 3o-p). WUE reached maximum values at late afternoon (1800 h), where PM was the highest for both varieties (19.6 in MRQ74, 20.4 in MR253) followed by SM (15.6 in MRQ74, 11.5 in MR253) and NM (2.2 in MRQ74, 2.8 in MR253). Although A was found low during late afternoon (Fig. 3c-d), E saved the most (Fig. 3k-l) and generates highest WUE (Fig. 3o-p). Furthermore, the results exhibited a 20% reduction of WUE at maturation stage compared to tillering stage. NM was recorded the lowest WUE in all conditions in response to water loss.

It was found that the stomatal conductance was negatively correlated to WUE at tillering stage in MRQ74 and MR253 (Fig. 4a-f). At maturation stage, only MR253 retained the correlation (Figs. 4h, 4j, 4l) but MRQ74 displayed no correlation between WUE and g_s (Figs. 4g, 4i, 4k). The relationship at tillering stage displayed a decreasing trend line of WUE before becoming constant. Manzoni *et al.*, (2011) elaborates the optimal stomata behaviour when A/E (WUE) is constant. This theory forecasts that WUE did an alteration in time when the constraint to the optimization (water availability) changes depending on the variable control which is stomatal conductance (g_s). Therefore, the optimal stomata started at the turning points of constant where MRQ74 were at 1.4 mmol $m^{-2}s^{-1}$ (PM) (Fig. 4a), 2.2 mmol $m^{-2}s^{-1}$ (SM) (Fig. 4c) and 1.6 mmol $m^{-2}s^{-1}$ (NM) (Fig. 4e), while MR253 were at 1.2 mmol $m^{-2}s^{-1}$ (PM) (Fig. 4b), 2.4 mmol $m^{-2}s^{-1}$ (SM) (Fig. 4d) and 1.5 mmol $m^{-2}s^{-1}$ (NM) (Fig. 4f). The highest g_s at the turning points were SM, followed by NM and PM in both varieties. However, the trends at maturation stage showed a decrement throughout the day and did not reach constant.

The trend of diurnal variation in Ls was observed similar with WUE specifically at tillering stage (Fig. 3q-r). Ls showed significantly difference between treatments whereas no different at maturation stage (Table 1). Generally, Ls also showed a concave response (bell shape) at tillering stage throughout a day. At maturation stage, the response of Ls showed fluctuations throughout a day where it started low at the early morning, increased at mid-morning, decreased at midday, and recovered afterward (Fig. 3s-t). In comparison between treatments, PM performed the highest Ls at tillering stage particularly during midday however it decreased at maturation stage.

Discussion

In C3 plants, the activities of photosynthesis will be inhibited when the intensity of light go beyond the threshold value for photosynthesis (Yang *et al.*, 2008). Midday depression of photosynthesis may appear at the light saturation point by temporal decreasing of carbon assimilation rate. Interestingly, in this study, all the mulching treatments and rice varieties showed a unimodal curve of photosynthesis compared to other findings of rice diurnal which demonstrated a bimodal curve (Yang *et al.*, 2008; Zhi, 2015). No midday depression of photosynthesis is inferred due to the ability of aerobic rice plants to save water from transpirations and utilize it for regulating assimilation process, and thus increase photosynthesis rate (A) at the light saturation point. This hypothesis is supported by other studies in maize and soybean (C3 plant species) that exhibited unimodal curve due to water stress (Liu *et al.*, 2017) and different light treatment (Zheng *et al.*, 2017).

In general, water stress is the most sensitive condition for rice plant. The declining in physiological performance of rice such as producing low photosynthesis is the sign of water stress condition (Zhang *et al.*, 2008; Cha-Um *et al.*, 2010; Sikuku *et al.*, 2010). However, MRQ74 and MR253 rice varieties were adapted well to aerobic condition which make these varieties suitable for non-flooded (aerobic) cultivation. This in agreement with some reports that showed MRQ74 and MR253 demonstrated higher physiological performance compared to other Southeast Asia rice varieties under drought condition and nutrient deficiency (Herman *et al.*, 2015; Shamsudin *et al.*, 2016). A higher photosynthesis rate in MRQ74 and MR253 with mulching treatment indicated a lower susceptibility to oxidative stress under dry condition.

Photosynthesis rate varies due to several factors including light, temperature, and soil moisture. Moreover, evaporative demand of the atmosphere in midday tends to reduce the photosynthesis (midday depression). However, in this circumstance, mulching treatment could minimize the evaporation rate resulted in high moisture content in the soil. In this study, plastic mulch (PM) exhibited higher photosynthesis rate compared to rice straw mulch (SM) and no mulch (NM) treatment. Furthermore, genetic characteristic of rice varieties may also contribute to the variation of physiological changes.

Photosynthesis correlates to stomatal conductance and consequently with water stress (Deng *et al.*, 2000; Yang *et al.*, 2008). Stomata are the gateway of water loss and CO_2 intake; it is conceivable that stomatal closure is the initial response to water stress. We observed that photosynthesis rate increased at midday along with decreasing of stomatal conductance at tillering stage (Fig. 3a-b and 3e-f). Different pattern was shown at maturation stage (Fig. 3c-d and 3g-h) which suggested an adaptation mechanisms at this stage to alter stomatal conductance even at very low level. This indicates that the aerobic rice could conserve water by reducing water loss via stomata. The regulation of stoma is associated to transpiration rate and thus the pattern for both are similar as found in this study.

Water use efficiency (WUE) is a trait associated with drought avoidance mechanism. Plant genotypes with improved drought resistance have desirable WUE (Liu & Hsiao, 2004; Songsri *et al.*, 2013) and that rice with high WUE has great potential to be grown in drought environment. In this study, PM shows greater WUE at the midday during tillering stage (Fig. 3m-n), while both PM and SM provide better WUE value compared to NM at maturation stage (Fig. 3o-p). Gilbert *et al.*, (2011) reported that breeding plants with low water use during a mild drought could increase plant photosynthetic capacity, thus enabling the plant to photosynthesize in non-extreme water stress condition though stomatal limiting condition as well as turgor-related growth inhibition may be present.

WUE is important indicator to translate plant adaptation and productivity in water-limited areas (Liu & Hsiao, 2004). Therefore, better WUE could sustain a better agricultural development under an aerobic condition where water is limited.

An interesting potential was seen in the Malaysian rice varieties MRQ74 and MR253, where characteristics such as enhanced drought tolerance would be highly desirable for optimal growth and production (Mahmod *et al*., 2014; Herman *et al*., 2015; Shamsudin *et al*., 2016). This varieties have shown great adaptability to aerobic condition which may influence a high yield in rice crop.

Conclusion

Adaptation of MRQ74 and MR253 to aerobic or non-flooded condition coupled with mulching treatments (PM or SM) exhibited effective diurnal physiological performance, i.e. higher levels of photosynthesis rate and WUE compared to the control (NM). In term of photosynthesis rate, PM suits the MRQ74 very well during maturation stage. The highest WUE was achieved at the midday of tillering stage by using PM in MRQ74 cultivation. Both PM and SM increased WUE in MRQ74 and MR253 though not as high as found in tillering stage. Thus, the mulching treatment would be a better practise for farmers if implemented in appropriate regions (soil and environment condition), at suitable growth stages, and using specific rice variety. Further investigations are needed on physiological, molecular, and biochemical processes. The latter can be for instance a study on metabolomics or metabolic alteration to elucidate the mechanism of diurnal responses of aerobic rice and mulching treatments. With all of this knowledge, a better understanding and precise agricultural practices can be implemented for aerobic rice cultivation.

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