Annals of West University of Timişoara, ser. Biology, 2021, vol. 24 (1), pp.73-92

INFLUENCE OF SEED PRIMING ON YIELD, MORPHOLOGICAL AND PHYSIOLOGICAL CHARACTERISTICS OF WATER-DEFICIT STRESSED LOWLAND RICE

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Received 14 February, 2021; accepted 28 August 2021

ABSTRACT

One of the potential ways of increasing rice production to cater for ever increasing population of Malaysia is to extend the production area of lowland rice through its production as upland rice. Therefore, this research was conducted to determine the effects of seed priming in alleviating water deficit stress in lowland rice produced as upland rice. The treatments used were 100mM calcium chloride dihydrate for duration of 48hours and temperature of 25°C, 40% w/v polyethylene glycol (PEG) 6000 for a duration of 48hours and temperature of 25°C, 100ppm kinetin for a duration of 24hours and temperature of 4°C, 200ppm methyl jasmonate for a duration of 24hours and temperature of 4°C, stressed control (unprimed seeds) and the unstressed control (unprimed seeds with adequate irrigation). The experiment was laid out in randomized complete block design (RCBD) with three replications. Data were collected on classical growth parameters, germination pattern, gas exchange characteristics, yield and yield components. It was found that priming MR219 rice with PEG could enable the variety to be produced as upland rice with little yield reduction because PEG priming was the best in individual seed mass, final yield, harvest index and water use efficiency. It is, therefore, concluded that 48hours of *priming with 40%w/v polyethylene glycol at 25°C be used for MR219 rice seeds whenever MR219 rice variety is to be cultivated as upland rice.*

KEY WORDS: *seed priming, lowland rice, upland rice production, rice yield, water deficit.*

INTRODUCTION

The most important environmental factor for living organisms is moisture availability. It determines the habitat of different plants and animals as well as their survival. When water becomes a limiting factor of crop production, solving the problem becomes a sine qua none to have success in production of any crop of interest. For instance, the nature of rice plant with the exception of upland varieties is to grow it as a semi-aquatic plant because of its high water demand. Therefore, it is very sensitive to water deficit during its production. Problems that ensue from this situation are majorly physiological and, therefore, manifest morphologically in the plants. These problems have consequential effects on the final yield of the crop in question. The problem of water deficit is perennial in some places while it is ephemeral in others. Attempts to curb the problem of moisture stress have been made through breeding but the level of tolerance needed is yet to be achieved in the present improved germplasm. Since the target of tolerance is yet to be met through breeding, there is dire need for a better and simpler intervention which can induce tolerance in the plants without any repercussion. At present, the simplest and most effective technology for this is seed priming which has been established to be meeting the objective for which it was designed.

Seed priming is a potential technology against drought in rice but depends on cultivars and limited by severity of the drought (Yuan−Yuan et al., 2010). This is because severe drought can inhibit germination and kill emerging seedlings. Among the viable chemicals that can induce moisture stress tolerance in cereals is potassium hydrogen phosphate (KH_2PO_4). This has been proven to aid better germination and seedling establishment along with other germination attributes (Yagmur & Kaydan, 2008). This outcome of priming has been attributed to better mobilization of seed reserves through efficient water uptake by the germinating seeds (Soltani et al., 2006). Moreover, alleviation of drought stress effect on physiology of rice has been achieved through abscisic acid (ABA) priming (Majeed et al., 2011). The mechanism of operation here involves decrease in GA_3 concentration in the plant. This then maintains water budget, improves osmoregulation by increasing proline accumulation, increases stomatal resistance and aids early maturity through increase in the rate of grain filling (Majeed et al., 2011). Moreover, improvement of drought tolerance in rice has been achieved by priming rice seeds in 14% (w/v) potassium chloride solution (Du & Tuong, 2002). In the same vein, osmo-priming has been used for priming rice seeds in drought prone areas and it resulted in faster emergence with high uniformity which finally led to realization of higher yield (Harris & Jones, 1997). It could be summarily said that better seedling establishment that can confer better drought tolerance on rice plants could be achieved through seed priming technology. A proof of this is that when potassium hydrogen phosphate (KH_2PO4) was used for priming cereals like triticale, it induced drought tolerance on the treated cultivar (Yagmur & Kaydan, 2008) through better mobilization of seed reserve as a result of efficient water uptake by the germinating seeds (Soltani et al., 2006).

The problem of continuous shortage of water supply in the granary areas of Malaysia poses annual problems to rice farmers on the field. This forces them to have delay in planting which results in distortion of the plan for the main season. As this problem has become a perennial problem, the loss of income that accompanies it is a source of deficit to the national economy. Besides this, increased rice production could be achieved if non-granary areas are included in production. This is achieved by producing lowland rice as upland rice with supplementary irrigation as it is done for other cereal crops like maize. Through this method, water use efficiency would be guaranteed and judicious use of resources could come handy. However, the problem of water deficit that the crop will be suffering from when it is produced as upland rice should be solved. The promising solution to this problem of water deficit stress is seed priming. Therefore, this research was conducted to determine the effects of seed priming in alleviating water deficit stress in lowland rice produced as upland rice.

MATERIAL AND METHODS

Experimental Site

An experiment to assess the efficacy of rice seed priming in overcoming the problem of incessant water shortage during the subsidiary season production or unexpected delay in commencement of rainfall in rice production was conducted in the glass house of Rice Research Centre Universiti Putra Malaysia (UPM), Serdang, Selangor, Malaysia (3^0 02' N, 101^0 42' E; elevation 31 m). The average monthly maximum and minimum temperature were 33.5 ^{0}C and 21.5 ^{0}C respectively while the relative humidity was 92.5 %. The sunshine hours was 6.6 hrs/day respectively while the average rainfall and evaporation were 9.8 mm/day and 4.6 mm/day respectively.

Plant Materials, Treatments and Experimental Design

The seeds used in this experiment were collected from the gene bank of the Faculty of Agriculture, UPM. Rice variety researched on was MR219. There were six experimental treatments. The treatments used were 100mM calcium chloride dehydrate for duration of 48hours and temperature of 25^{o}C, 40% w/v polyethylene glycol 6000 for a duration of 48hours and temperature of 25^{o}C, 100ppm kinetin for a duration of 24hours and temperature of 4^{o}C, 200ppm methyl jasmonate for a duration of 24hours and temperature of 4^{o}C, stressed control (unprimed seeds) and the flooded control (unprimed seeds). The priming treatments used were from our previous research (Kareem et al., 2019). Stressed control implies the control that was raised in aerobic condition like the primed rice instead of anaerobic one like the flooded control. The experiment was laid out in randomized complete block design (RCBD) with three replications.

Planting and Cultural Practices

Twenty-three kilogramme of soil from Kelantan was filled into each of the experimental pots. Twelve seeds were sown per pot and the germination pattern was observed. Enough water was added to maintain the soil at field capacity so as to pave the way for germination. After ten days, the plants were thinned to six per pot to give room for destructive sampling used for determining seedling vigour and classical growth parameters. Hand pulling was used to control weeds at regular interval to prevent interspecific competition. Plants were irrigated at an average interval of four days to maintain field capacity with the exception of the flooded control which was kept in anaerobic condition throughout the experiment.

Data Collection

Number of germinated seeds was recorded daily in the first ten days of sowing. From the data generated, germination percentage (GP), germination index (GI) and days to 50% germination were determined as follows:

Final germination percentages (GP) were calculated according to AOSA(1983) using the formula below:

$$GP = \frac{Number\ of\ germinated\ seeds\ at\ final\ count}{Total\ number\ of\ planted\ seeds} \text{x } 100$$

Germination index (GI) was calculated according to AOSA (1983) using the following formula:

$$GI = \frac{Number\ of\ germinated\ seeds}{Day\ of\ the\ first\ count} + \ldots + = \frac{Number\ of\ germinated\ seeds}{Day\ of\ the\ final\ count}$$

Day to 50% germination (T_{50}) was calculated according to the modified formula by Farooq et al. (2005) as follows:

$$T_{50\ =\ ti\ +} = \frac{(\frac{N}{2} - ni)(tj - ti)}{nj - ni}$$

Where N is the final number of germinated seeds and ni and nj are cumulative numbers of seed germinated by adjacent counts at time ti and tj (days) respectively. This is expressed in days.

Classical Growth Analysis

Two destructive samplings at an interval of seventeen days were carried out. Leaf areas of the samples were measured using leaf area meter Licor, inc. Lincoln (Nebraska, USA) and their dry masses after being oven-dried to constant masses were measured using analytical weighing balance. The area of land covered by plants was calculated using the following formula:

$$\text{Area} = \pi r^2$$

Where r is the radius of the pot used and π is a constant which is equal to 3.142

From these three parameters, leaf area index (LAI), absolute growth rate (AGR), crop growth rate (CGR), relative growth rate (RGR), net assimilation rate (NAR) and leaf area duration (LAD) were calculated as follows:

$$Leaf\,Area\ Index(LAI) = \frac{Leaf\ Area}{Area\ of\ Land\ Covered\ by\ the\ Plant}$$

Absolute Growth Rate (AGR) = $\frac{W2-W1}{t2-t1}$

Where W_1 and W_2 are plant dry masses at times t_1 and t_2 respectively.

Crop Growth Rate (CGR) = $\frac{1}{P} \times \frac{W2-W1}{t2-t1}$

Where W_1 and W_2 are plant dry masses at times t_1 and t_2 respectively and P is the area of land covered by the plant

Relative Growth Rate (RGR) = $\frac{loge\ W2-loge\ W1}{t2-t1}$

Where W_1 and W_2 are plant dry masses at times t_1 and t_2 respectively.

Net Assimilation Rate (NAR) = $\frac{(W2-W1)(logeL2-logeL1)}{(t2-t1)(L2-L1)}$

Where L_1 and W_1 are respectively leaf area and dry mass of plant samples at time t_1 while L_2 and W_2 are respectively leaf area and dry mass of plant samples at time t_2

Leaf Area Duration (LAD) = $\frac{L1+L2}{2} \times (t_2+t_1)+\ldots+ = \frac{L1+L2}{2} \times(t_n+t_{n-1})$

Where L_1 is the leaf area at time t_1, L_2 is the leaf area at time t_2, L_n is the leaf area at time t_n and L_{n-1} is the leaf area at time t_{n-1}

Plant Phenology and Yield Data

Days to flowering was counted from the time of sowing to the appearance of panicle. Number of filled and unfilled grains or spikelets, mass of 100 seeds, final yield per treatment and harvest index were recorded after harvesting. Harvest index and water use efficiency were calculated as follows:

$$Harvest\ \ Index(HI) = \frac{Mass\ of\ Economic\ Yield}{Mass\ of\,Biological\ Yield} \text{ x } 100$$

$$Crop\ Water\ Use\ Efficiency = \frac{Plant\ Biological\ Yield}{Amount\ of\ Water\ Consumed\ by\ the\ Plant} \text{ x } 100$$

Leaf Gas Exchange Characteristics

Data on net photosynthetic rate (μmol m^{-2} s^{-1}), stomatal conductance (μmol H_2O m^{-2} s^{-1}), transpiration rate (mmol m^{-2} s^{-1}), and intercellular carbon dioxide (μmolCO_2m^{-1}) were taken with a closed infra-red gas analyser LICOR 6400 Portable Photosynthesis System (IRGA, Licor Inc., Lincoln, NE, USA) following Ibrahim and Jaafar (2012). Leaf surfaces were cleaned and dried using tissue paper before being enclosed in the leaf cuvette. Optimal conditions set for the measurements were 400 µmol mol^{-1} CO_2, 30°C cuvette temperature, 60% relative humidity with air flow rate of 500 cm^3 $min^{-1}$and modified cuvette conditions of 225, 500, 625 and 900 µmolm^{-2}

photosynthetic photon flux densities (PPFD) respectively. Gas exchange measurements were carried out when the sun was fully bright using fully expanded young leaves to record net photosynthesis rate (A).

Proline Determination

Fresh leaf samples (0.5 g) were collected from each experimental pot and were homogenized in 3% (w/v) sulfosalicylic acid. The mixture was then filtered using whattman filter paper. The filtrate was kept while the residue was discarded. The proline content was estimated colorimetrically using the acid ninhydrin method of Bates et al. (1973). The reacting mixture contained 2 ml glacial acetic acid, 2 ml ninhydrin (2.5% w/v ninhydrin in 60% v/v 6 M phosphoric acid) and 2 ml filtrate. The reacting mixture was incubated in a water bath at 95°C for 1 hour. The reaction was then stopped by incubating the reaction tube in an ice bath. After bringing the temperature of the tube to ambient the temperature, 4 ml of toluene was added to reaction mixture and mixed thoroughly by vortexing. The upper phase was carefully pipetted into a glass cuvette and absorbance was measured at 520 nm using spectrophotometer

RESULTS AND DISCUSSION

Leaf Area Index (LAI)

Leaf area indices (LAI) in all the priming treatments were lower than the unstressed control. Calcium chloride followed the unstressed control while the lowest value was from PEG. LAI from PEG treatment was 71.12% less than that of unstressed control (Table 1).

The size of assimilatory apparatus of plants is described by leaf area index (LAI). In addition to that, it is regarded as the primary factor for determining rate of dry matter production in plant systems. Furthermore, Addo-Quaye et al. (2011) quoted that leaf area index explained disparities in production efficiency among varieties of crops. The supremacy of calcium chloride priming over other priming media could be that it enhanced better vegetative growth which resulted in increase in leaf area and consequently leaf area index. This enhancement of vegetative growth might be through increase in cell division with inclusion of cell enlargement. It should be noted that LAI may not predict the yield because not all the leaves could trap enough solar radiation for photo-assimilate production. This is because mutual shading of leaves is not taken into consideration when measuring leaf area to determine leaf area index.

Absolute growth rate

Flooding increased absolute growth rate (AGR) above all the priming treatments and the stressed control. Methyl jasmonate was next to the unstressed control while the least was from PEG. PEG was 32.28% less than methyl jasmonate (Table 1).

Absolute growth rate (AGR) measures the rate of change in size of plant per unit time. This character is general to the whole plant system. It can be easily used to compare growth rate of two plants at a time without giving consideration to their initial masses. The edge of methyl jasmonate priming above other priming treatments could be attributed to improvement of root growth for better absorption of useful materials which resulted in higher luxuriant growth per unit time. This improvement might have resulted from multiplicity in cell production gingered by methyl jasmonate priming. With increase in number of cells, more nutrients are absorbed and better root and shoot growth are achieved.

Crop growth rate

Methyl jasmonate also had the highest value for crop growth rate (CGR) after the unstressed control while the lowest value was from PEG. PEG was 63% less than the unstressed control (Table 1).

Crop growth rate (CGR) measures dry matter accumulation per unit area and is considered a reasonable approximation for rate of canopy photosynthesis per unit ground area (Clawson et al., 1986). Its values vary according to the growth stage at which the data is taken (Addo-Quaye et al., 2011). The betterment of methyl jasmonate could be linked to its edge in absolute growth rate. Furthermore, it might be the result of reduction in photosynthates which could come in form of respiration and other catabolic activities. This because it has been established that dry matter accumulation has direct relationship with photosynthetic rate despite the fact that grain production is not associated with it (photosynthetic rate) (Murchie et al., 2002). However when there is judicious assimilate partitioning and mobilization to the economic part of the plant, photosynthetic rate could be attributed to grain yield.

TABLE 1: Effect of seed priming on leaf area, absolute growth rate and crop growth rate of rice grown under water deficit condition

Treatment	Leaf Area Index	Absolute Growth Rate (g day^{-1})	Crop Growth Rate (g (crop)m^{-2}day^{-1})
Calcium Chloride	1.9296	0.3238	10.3810
Polyethylene Glycol	1.211	0.2356	7.5550
Kinetin	1.4179	0.2838	9.0990
Methyl Jasmonate	1.6444	0.3479	11.1560
Stressed Control	1.4347	0.2658	8.5240
Unstressed control	3.5702	0.6388	20.4820
LSD0.05	1.2065	0.2923	9.37230

Relative Growth Rate

The highest value of relative growth rate (RGR) was from methyl jasmonate followed by kinetin while the lowest value was from $CaCl_2$ which was 18% less than that of methyl jasmonate (Table 2).

Relative growth rate (RGR) is used to determine the rate of increase in plant mass per unit plant mass already present in the plant. Highest value of RGR recorded from methyl jasmonate among all the priming media could be attributed to enhancement of absorption of the needed nutrients from the soil which resulted in higher relative mass-gain in the tested plants. Furthermore, other parameters (net assimilation rate and net photosynthesis) which result in mass-gain could be responsible for the highest value of RGR recorded from methyl jasmonate priming in this work.

Net assimilation rate

The highest net assimilation rate (NAR) was from $CaCl_2$ followed by PEG, methyl jasmonate and the stressed control while the lowest value was from kinetin. $CaCl_2$ was 38% better than kinetin (Table 2).

Net assimilation rate measures the rate of increase in plant mass per unit leaf area. It is could be a useful trait in measuring photosynthetic rate. The betterment found in calcium chloride priming could be attributed to better leaf architecture which allowed for greater part of the leaves to be available for trapping solar energy as revealed by the value of NAR.

Leaf area duration

The unstressed control had the highest value for leaf area duration followed by $CaCl_2$ while the lowest value was from PEG. The unstressed control was 63% better than PEG (Table 2).

Leaf area duration is a measure of retention of photosynthetically active leaf over a period of time. It takes care of both duration and the extent of activeness of photosynthetic tissue of the canopy. The result from calcium chloride priming could be attributed to delay in senescence and abscission of leaves which resulted from reduction in severity of water stress conferred by calcium chloride. This resembles continuous water supply through flooding (like our unstressed control) as shown in this work. This delay in leaf senescence and abscission resulted in retention of much more green leaves over time by the plants. It should be noted that leaf area and leaf area duration are the main causes of yield differences not photosynthesis or net assimilation rate (Abayomi et al., 2007) quoting Watson (1947).

Table 2: Effect of seed priming on relative growth rate, net assimilation rate and leaf area duration of rice grown under water deficit condition

Treatment	**Relative Growth Rate** (mg $g^{-1}day^{-1}$)	**Net Assimilation Rate** (g (crop)$m^{-2}day^{-1}$)	**Leaf Area Duration** ($m^2day\ m^{-2}$)
Calcium Chloride	0.0987	0.0016	3445.2000
Polyethylene Glycol	0.1062	0.0014	2514.6000

Kinetin	0.1094	0.0010	2532.6000
Methyl Jasmonate	0.1199	0.0014	3133.6000
Stressed Control	0.1059	0.0014	2630.7000
Unstressed control	0.1058	0.0011	6770.9000
LSD0.05	0.0536	0.0012	2057.8000

Germination Percentage

Kinetin had the highest value followed by methyl jasmonate treatment as well as the stressed control that had the same magnitude with it. The lowest GP was from the unstressed control which was 37% lower in performance than kinetin (Table 3).

The betterment of kinetin priming over other priming and non-priming treatments might have resulted from faster completion of pre-germination metabolic activities which ensured rapid radicle protrusion through multiplication of radicle cells soon after sowing by accelerating the imbibition process (Basra *et al*., 2005). However, germination percentage is generally increased by priming treatments in many occasions (Basra *et al*., 2005). This is further proved by the observation of Ashraf and Rauf (2001) that final germination percentage, fresh and dry weight of corn seed were significantly increased by seed priming.

Days to 50% Germination

The shortest duration to achieve 50% germination was found in the unstressed control while the longest duration was found in methyl jasmonate and calcium chloride. The unstressed control was 3days faster than methyl jasmonate to have 50% of the planted seeds germinated (Table 3).

Early emergence indicated by lower days to 50% germination in kinetin primed seeds could be the result of rapidity in production of germination metabolites (Lee and Kim, 2000; Basra *et al*., 2005) along with swift synthesis of RNA, DNA and proteins indicating better genetic repair (Bray *et al.*, 1989).

Germination Index

Uniformity of germination as measured by germination index was better improved by kinetin than the unstressed control. Kinetin was 58% more uniform in germination than the seeds from the unstressed control (Table 3).

Better uniformity of growth conferred by kinetin priming treatment could be as a result of the completion of pre-germination metabolic activities which ensured rapid radicle protrusion through multiplication of radicle cells soon after sowing by accelerating the imbibition process (Basra *et al.*, 2005). Furthermore, reduction in imbibition lag time and build-up of germination-enhancing metabolites (Basra *et al.* 2005) might also contribute to early emergence of primed seeds. In another view, higher and synchronized emergence could have resulted from rapid development of embryo, genetic, structural repair (Arif *et al.*, 2008) and reduction of seed bulk physiological non-uniformity through priming process (Still and Bradford, 1997).

TABLE 3: Effect of seed priming on germination percentage, germination index and days to 50% germination of rice under water deficit condition

Treatment	Germination Percentage (%)	Germination Index	Days to 50% germination (Days)
Calcium Chloride	63.89	9.91	4.00
Polyethylene Glycol	63.89	10.18	2.00
Kinetin	83.33	13.33	3.00
Methyl Jasmonate	66.67	8.12	4.00
Stressed Control	66.67	11.48	2.00
Unstressed Control	52.78	5.65	1.00
LSD0.05	63.81	5.41	3.00

Number of Tillers

The highest number of tillers was from methyl jasmonate followed by $CaCl_2$ while the lowest number was from PEG. Methyl jasmonate was just 10% better than PEG. All the priming treatments except PEG were better than the unstressed control (Table 4).

Tiller production is an equivalent of branching in non-grass species. It shows success of vegetative growth of grass families like rice and can predict, to an appreciable extent, the yield of the plants because it relates to the number of productive tillers that the plants will eventually produce. From the results of this work, methyl jasmonate was better than all other priming treatments with inclusion of the unstressed control. Better performance of methyl jasmonate priming could be attributed to better biochemical and physiological repairs that occurred during the priming operation. Completion of metabolic activities during priming period (Sadeghi et al., 2011) gives the resulting plants a head start for harnessing available growth resources to produce higher number of tillers as well as panicle-producing tillers (Harris et al., 2002).

Productive tillers

The highest number of productive tillers was from the unstressed control followed by methyl jasmonate while the lowest number from PEG. The unstressed control flooded control was 30.77% higher than PEG. All the priming treatments were lower than the unstressed control. However, methyl jasmonate was the best among all the priming treatments (Table 4).

Panicle bearing tillers are the important tillers because of their link with the final yield. If panicle productivity is high, there is high probability of getting high yield at the end of a production cycle. Better performance of methyl jasmonate priming might be attributed to the repair done to the embryo at the priming stage which then translated to better seedlings after germination and produced higher number of productive tillers. Furthermore, mobilization of nutrients by the plants from seed priming (methyl jasmonate priming) (Sakakibara, 2005) could have highly contributed to the betterment in the performance of the plants. Finally, biochemical repairs at the priming stage during imbibition (Shakirova et al., 2003) might have well enhanced the performance of all the priming treatments.

Plant height

The unstressed control produced the tallest plants. The unstressed control plants were 19.86% taller than those from the stressed control (the shortest plants). So, all the priming treatments performed better than the stressed control. The closest of all the treatments to the un-stressed control was PEG (Table 4).

In this work, all the priming agents produced plants that were taller than those from the stressed control. The advantage that polyethylene glycol had over the stressed control might be the result of enhancement of meristematic activities (Werner et al., 2001) of the shoot apex which is responsible for increase in plant height. Furthermore, it could be attributed to betterment of physiological activities of the plants during morphogenesis which is believed to have been induced by priming treatments (Igari et al., 2008). In the same vein, height gain could be linked to better absorption of water and nutrients enhanced by development of efficient roots as a result of priming treatments. The absorption of the required growth materials then led to luxuriant growth of the shoot with consequential height increase.

TABLE 4: Effect of seed priming on number of tillers, productive tillers and plant height of rice under water deficit condition

Treatment	Number of Tillers(no/pot)	Productive Tillers(no/pot)	Plant Height(cm)
Calcium Chloride	41.00	33.00	78.67
Polyethylene Glycol	34.00	27.00	83.33
Kinetin	41.00	33.00	80.83
Methyl jasmonate	45.00	35.00	81.33
Stressed control	40.00	34.00	78.17
Unstressed Control	40.00	39.00	98.17
LSD0.05	12.21	8.52	6.52

Net Photosynthesis

The highest photosynthetic rate was from plants resulting from PEG priming followed by plants from $CaCl_2$ priming treatment while slowest rate was from the stressed control. PEG was 51.68% higher than the stressed control. Only PEG and $CaCl_2$ priming treatments were higher in rate than the unstressed control (Table 5).

Betterment of photosynthetic rate in plants resulting from PEG priming might be attributed to maintenance of guard cell turgidity through tolerance to water deficit. This was equally evident in stomatal conductance which had the highest value among all the treatments. However, this photosynthetic enhancement alone cannot guarantee better yield in rice production (Murchie et al., 2002). The contribution of photosynthesis is directly on the dry matter production which can be at the detriment of the filling grains except if there are better assimilate partitioning and remobilization of photo-assimilate from the vegetative parts to the filling grains. This could be clearly determined through better harvest index which reveals the proportion of the economic yield to the whole biological yield. It can be inferred that there was judicious assimilate partitioning in this work because plants from PEG priming had the highest yield and harvest index among all the priming treatments used (Tables 9 and 10).

Stomatal conductance

The peak of stomatal conductance was from PEG followed by the unstressed control while lowest conductance was from methyl jasmonate. Methyl jasmonate was 49.79% lower than PEG. Here, only PEG was better than the unstressed control though $CaCl_2$ was close to it (Table 5).

Plants from PEG priming had better stomatal opening resulting from turgid guard cells. This might have resulted from prevention of excessive water loss from the leaves which was conferred by PEG priming. Better stomatal conductance translated to higher photosynthetic rate in this work because stomatal opening is the entry channel for photosynthetic raw material (CO_2) and exit route for its by-product (O_2). In the same vein, there should be stomatal closure and suppression of mesophyll conductance to have photosynthetic rate reduction (Flexas et al., 2004). So, stomatal conductance regulation is very important in plants because it plays a vital role in CO_2 assimilation on which photosynthesis depends and controls evapotranspiration on which cooling as well as desiccation of plants depends (Medici et al., 2007).

TABLE 5: Effect of seed priming on net photosynthesis and stomatal conductance of rice under water deficit condition

Treatment	Net Photosynthesis(µmolCO_2m^{-2}s^{-1})	Stomatal Conductance (molH_2O m^{-2}s^{-1})
Calcium Chloride	11.30	0.11
Polyethylene Glycol	12.50	0.12
Kinetin	9.60	0.08
Methyl Jasmonate	6.21	0.06
Stressed Control	6.04	0.07
Unstressed Control	10.00	0.11
LSD0.05	0.0200	0.0001

Intercellular Carbon dioxide

The highest CO_2 volume was found the stressed control plants followed by the unstressed control while the lowest volume was from kinetin treatment. Kinetin was 30.16% lower in CO_2 level than the stressed control. So, the unstressed control performed better than any of the priming treatments (Table 6).

Despite the fact that PEG priming enhanced higher stomatal conductance, plants resulting from it had the lowest intercellular CO_2 volume. With the highest volume of CO_2 in the unstressed control, the photosynthetic rate was so low and incommensurate with the amount of the useful CO_2 gas found in the inter-cellular space. This shows that photosynthetic rate and intercellular CO_2 have indirect relationship. So, if the volume of intercellular CO_2 is increased, there will be low photosynthetic rate and vice versa. This is simply because when carbon dioxide is higher in the intercellular space, further assimilation of such gas is hampered because of saturation. So, when less volume of the gas is available in the intercellular space, assimilation by the process of photosynthesis occurs and better utilization results. In the same vein, having higher photosynthetic rate does not lead to higher grain yield except if better partitioning of assimilate is found (Murchie et al., 2002). Therefore, photosynthetic parameters should be used for interpretation of dry matter production and not the economic yield. Nevertheless, it should be realized that dark respiration and photorespiration determine the net dry matter production which is the leftover after removal of the consumption of both dark respiration and photorespiration from the total photo-assimilate production.

Transpiration Rate

The flooded control had the highest transpiration rate followed by PEG while methyl jasmonate had the slowest rate. Transpiration rate in the unstressed control was 39.88% better than what was found in plants resulting from methyl jasmonate treatment (Table 6).

Transpiration determines how cool the plants are. This is based on the basic Physics principle that evaporation causes cooling. This depends on the stomatal opening, the level of moisture in the rhizosphere, ambient temperature and wind speed. We expected plants from PEG priming to have the highest transpiration rate because they had the highest level of stomatal conductance but they were lower in transpiration rate than the unstressed control. Despite the advantage of cooling the plants through evapotranspiration, it predisposes plants to wilt when the rate of evapotranspiration exceeds absorption as a result water deficit in the rhizosphere. Therefore, the best priming treatment for transpiration rate was methyl jasmonate because it had lowest transpiration rate which is an indication of better water conservation to withstand moisture stress.

Proline Content

The highest proline concentration was found in plants from polyethylene glycol priming followed by kinetin treatment while the lowest was found in the unstressed control (Table 6). Water stress increases amino acids like proline in the stressed plants (Shehab et al., 2010) because high level of proline can do scavenging function in the removal of reactive oxygen species (Türkan and Demiral, 2009). Higher proline accumulation found in polyethylene glycol priming was an indication of better tolerance to moisture stress. This is because accumulation of proline has a protective role in stressed plants because of its involvement in osmotic adjustment as well as increase in concentration of other osmolytes (Cha-um and Kirdmanee, 2008). Proline contributes to mitigation of negative impact of dehydration (Bandurska, 2004) because it helps plants in getting adapted to stress by making genes which protect cells against dehydration to express. Moreover, high proline concentration in drought-stressed plants could lead to relative maintenance of water and malondialdehyde level with consequent preferable growth performance (Chutipaijit et al., 2012). The manifestation of drought tolerance by PEG was showcased by having higher water use efficiency (Table 8) and yield than other priming treatments (Table 9)

TABLE 6: Effect of seed priming on intercellular carbon dioxide and transpiration rate of rice under water deficit condition

Treatment	Intercellular Carbon dioxide (µmol$CO_2$$m^{-1}$)	Transpiration Rate (mmolH_2O $m^{-2}s^{-1}$)	Proline Content (µM)
Calcium Chloride	203.60	3.09	22.89
Polyethylene Glycol	194.75	3.32	29.64
Kinetin	182.12	2.73	25.50
Methyl Jasmonate	203.64	2.11	24.86
Stressed Control	237.05	2.30	23.67
Unstressed Control	226.71	3.51	21.56
LSD0.05	0.4324	0.0015	

Number of spikelets per panicle

The highest number of spikelets was from the unstressed control followed by kinetin and calcium chloride priming while the lowest number was from the stressed control. The betterment of the unstressed control over the stressed one was 32%. All the priming treatments were better than the stressed control (Table 7).

The number of spikelets produced by a panicle determines the maximum number of grains that could be produced per panicle. However, panicle architecture determines grain weight and quality because the superior spikelets get filled first while the inferior ones are either poorly filled or remain blank (empty). It should be understood that increasing panicle size or height to increase the number of spikelets and consequently the number of grains could be detrimental to light interception and photosynthetic rate of the source leaves that are positioned beneath the panicle for the supply of assimilates to the grains during grain filling (Setter et al., 1996). It has been established that the number of grains per panicle in rice is determined by panicle length and the filled grains per panicle length (Sheehy et al., 2001). Therefore, final grain yield per unit area is dependent on the population of spikelets produced by panicles per unit area. The result here reveals the inherent potential of seed priming especially the use of growth regulators like kinetin in increasing the number of spikelets per panicle. It further confirms the role of growth regulators on growth and development of the plant reproductive phase.

Number of Filled Grains

The number of filled grains per panicle did not follow the same pattern as that of spikelet production except for the unstressed control. Instead, PEG priming produced the highest number of filled grains per panicle (35). The highest percentage of filled grain was also from PEG priming while the lowest percentage was recorded from calcium chloride priming (Table 7). Although kinetin and calcium chloride priming had the highest number of spikelets, they did not have the highest number of filled grains except that of unstressed control. This is because having large panicle size with higher number of spikelets will significantly increase the number of poorly filled grains while most of the grains in the inferior spikelets will become source-limited (Kato, 2004). This might be because poor partitioning and inefficient translocation of assimilates from the source leaves and stems during grain filling could not sustain the development and filling of a large number of spikelets (Yang et al., 2002). Moreover, starch synthesis in the endosperm cells of inferior spikelets is poor (Umemoto et al., 1994) and assimilates partitioned to them (inferior spikelets) remain unused. In addition to that, superior spikelets on the upper part of the panicle flower early, exert dominance, accumulate higher level of starch and produce better quality grains than inferior spikelets that flower late (Yang et al., 2006).

TABLE 7: Effect of seed priming on number of spikelets and number of filled grains of rice under water deficit condition

Treatment	Number of Spikelets (no)	Number of Filled Grains (no/panicle)
Calcium Chloride	79.00	22.44
Polyethylene Glycol	76.00	34.56
Kinetin	79.00	32.67
Methyl Jasmonate	76.00	22.89
Stressed Control	70.00	26.89
Unstressed Control	104.00	52.78
LSD 0.05	24.00	24.43

Percentage of Filled spikelets

The percentage of the filled spikelet was at its peak in the unstressed control followed by PEG while the lowest percentage was from $CaCl_2$. All the priming treatments were better than the stressed control except $CaCl_2$ and methyl jasmonate. (Table 8).

Despite the fact that other treatments had higher number of spikelets than PEG, their percentages of filled spikelets were low compared to that of PEG priming with the exception of unstressed control. This result led to better grain yield produced by the plants resulting from PEG priming.

It should be noted that water stress might lead to considerable increase in secondary rachis branch abortion which leads to reduced number of filled spikelets per panicle (Katoa et al., 2008). In the same vein, slow and poor filling of the inferior spikelets resulting from moisture stress may even result in sterile spikelets or non-consumable grains which contribute majorly to low yield production in rice (Ishimaru et al., 2005). However, increase in number of filled grains could be a result of increase in photosynthetic rates that leads to higher assimilate production which is effectively partitioned into the developing grains with consequent increase in the final yield (Xu and Zhou, 2007) and harvest index.

Water Use Efficiency

The highest WUE was from the unstressed control followed by the PEG priming while lowest was from kinetin priming. The edge of the unstressed control over kinetin was 51%. The stressed control was next to PEG priming while the rest treatments were below the stressed control (Table 8).

Water use efficiency depicts the amount of water used in producing 1kg of dry matter in a plant. This implies that despite the stress of the plants, PEG primed seeds could still produce rice plants that used little water to produce 1kg of dry matter. Better use of water has led to better production of yield despite the stress condition in which the plants were grown.

TABLE 8: Effect of seed priming on percent filled spikelets and water use efficiency of rice under water deficit condition

Treatment	Percent Filled Spikelets (%)	Crop Water Use Efficiency (kg fresh weight/Litre of water used)
Calcium Chloride	27.98	0.18
Polyethylene Glycol	45.48	0.34
Kinetin	41.16	0.23
Methyl Jasmonate	29.35	0.23
Stressed Control	38.22	0.31
Unstressed Control	48.94	0.46
LSD 0.05	18.26	0.18

Mass of 100 seeds

The heaviest seeds were from the unstressed control followed by the stressed control. The lightest seeds were from $CaCl_2$ priming. The percent difference in weight between the unstressed control and $CaCl_2$ was just 13%. All the priming treatments were slightly below the stressed control (Table 9).

The mass of individual grain indicated by mass of 100 seeds is the major contributor to the final yield. The size and mass of a grain depend on the spikelet's position on the panicle. If the spikelet is a superior one, the grain will be better filled. Otherwise, the spikelet is either poorly filled or remains blank. This aspect of grain filling is not directly affected by photosynthesis (Virk et al., 2004). Moreover, it has been made evident that many spikelets still remain poorly filled or blank even when there are very heavy panicles (Mohapatra et al., 2011).

Yield

The highest grain yield was produced by the unstressed control. This was followed by PEG priming. The lowest yield was recorded from $CaCl_2$. $CaCl_2$ was 66% lower than the unstressed control. All the priming treatments produced less than the stressed control with the exception of PEG (Table 9).

Higher grain yield from the unstressed control could be attributed to better assimilate partitioning as depicted by higher HI (Table 10). Grain yield depends on effective partitioning of photo-assimilates. So, if there is effective partitioning, the economic yield will have substantial share which will consequently lead to having appreciable harvest index. The yield increase in PEG priming over other treatments with the exception of the unstressed control might be attributed to better moisture and nutrient absorption by plants from PEG priming might have led to better fertilization and final higher yield (Anwar et al., 2012). This could have equally resulted from better utilization of water in producing dry matter as depicted by the value of water use efficiency. In the same vein, Farooq et al. (2006) made it evident that kernel improvement, increase in straw yield as well as harvest index could be enhanced by better and effective assimilate partitioning to the grains. In addition to that, reduction in the number of sterile spikelets, abortive as well as the opaque seeds could account for yield increase. Furthermore, increase in number of filled grains could be a result of increase in photosynthetic rates that leads to higher assimilate production which is effectively partitioned into the developing grains with consequent increase in the final yield (Xu and Zhou, 2007) and harvest index.

TABLE 9: Effect of seed priming on 100 grain mass and yield of rice under water deficit condition

Treatment	100 Grain Mass (g)	Yield (g/pot)
Calcium Chloride	3.22	11.00
Polyethylene Glycol	3.29	21.50
Kinetin	3.36	14.05
Methyl Jasmonate	3.24	14.15
Stressed Control	3.41	19.20
Unstressed Control	3.72	62.37
LSD0.05	0.45	17.63

Harvest Index

Harvest index followed the trend of the yield. So, the highest value of harvest index was from the unstressed control followed by PEG while the lowest value was from $CaCl_2$. The difference between the highest and the lowest was 64%. Like the case of grain yield, all the priming treatments with the exception of PEG were lower than the unstressed control (Table 10). Harvest index (HI) measures effectiveness in assimilate partitioning. In this research, PEG priming that had the highest grain yield among all the priming treatments still had the highest harvest index. This could be attributed to better assimilate partitioning with very little or no relationship at all with light saturated-photosynthesis (Murchie et al. 2002).

Biological yield

The highest biological yield was from the unstressed control followed by methyl jasmonate priming while the lowest was from kinetin priming. The difference between kinetin and the unstressed control was 53%. With the exception of methyl jasmonate, all the priming treatments had lower biological yield than the flooded control (Table 10).

The results of biological yield in this experiments show that though most of the treatments had higher biological yield, they did not have better assimilate production except that of unstressed control. The plants from PEG priming produced less biological yield but there was judicious assimilate production as shown by higher harvest index. That was what led to higher grain yield among all the stressed plants raised through priming treatments. The implication is that a farmer who is interested in straw production will give preference to all the treatments that produced higher biological yield in this work leaving plants from PEG and kinetin priming aside.

TABLE 10: Effect of seed priming on harvest index and biological yield of rice under water deficit condition

Treatment	Harvest Index (%)	Biological Yield (g/pot)
Calcium Chloride	10.73	102.41
Polyethylene Glycol	21.75	99.85
Kinetin	16.22	96.30
Methyl Jasmonate	13.20	107.96
Stressed Control	17.78	106.66
Unstressed Control	29.70	206.46
LSD0.05	10.93	40.51

CONCLUSION

From this work, it was found that priming MR219 rice with PEG could enable the variety to be produced as upland rice with little yield reduction because PEG priming was the best in individual seed mass, final yield, harvest index and water use efficiency. It is, therefore, concluded that 48hours of priming with 40%w/v polyethylene glycol at 25^{o}C be used for MR219 rice seeds whenever MR219 rice variety is to be cultivated as upland rice.

Acknowledgement. The authors acknowledge the support of Malaysia Ministry of Education Long Term Research Grant Scheme (LRGS)-Food Security through Enhancing Sustainable Rice Production- for financing this project.

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