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Pollen quality traits of cultivated (*Oryza sativa* L. ssp. indica) and weedy (*Oryza sativa* var. nivara) rice to water stress at reproductive stage

Ammini Amrina Saragih[1], Adam B. Puteh[1], Mohd Razi Ismail[1] and M. Monjurul Alam Mondal[1,2]*

[1]Department of Crop Science, Faculty of Agriculture, Universiti Putra Malaysia, 43400 UPM Serdang, Selangor D. E., Malaysia
[2]Crop Physiology Division, Bangladesh Institute of Nuclear Agriculture, Mymensingh, Bangladesh

***Corresponding author: ma_mondol@yahoo.com**

Abstract

Water stress during the early phase of the reproductive growth stage is a major constraint to yield of rice. The objective of this study was to evaluate the effect of pre-anthesis water stress on pollen quality of cultivated varieties and weedy rice strains. Two widely cultivated Malaysian varieties of MR219 and MR232 (*Oryza sativa* L. ssp. indica), and two weedy rice strains of Bertam and Ketara (*Oryza sativa* var. nivara) were grown in polybags in rice culture system-like situations. Water stress condition (no water supplied) was then applied for 10 days prior to anthesis phase. Plastic polybags (40 × 45 cm) were placed in an enclosed cage and arranged as completely randomized design with four replicates. Pollen quality traits were then determined such as pollen production, pollen viability and pollen load on stigma. The number of spikelets panicle^{-1} was also measured. Scanning Electron Microscopy was used to evaluate the morphology. Water stress reduced the pollen quality traits like pollen grain production, pollen viability and pollen load on stigma equally in both cultivated and weedy rice genotypes, resulting poor spikelet fertility and spikelet production. Observation of fluorescence microscopy indicated that water stress clearly affects pollen germination and pollen tube growth in both cultivated and weedy rice. Reduction of pollen viability and vigour appear to be the cause of reduction in pollen germinability and retardation in pollen tube growth, resulting poor fertilization and poor spikelets production in both cultivated and weedy rice genotypes under water stress. Weedy rice strains were comparatively more tolerant under water stress condition than cultivated rice varieties due to maintaining pollen quality traits. This suggests that weedy rices, Bertam and Ketara, may not heavily be influenced by water stress at reproductive growth stages.

Keywords: Pollen traits, water stress, weedy rice, yield components.
Abbreviations: IKI, iodine potassium iodide; NaOH, sodium hydroide; WR, weedy rice; WW, well water; WS, water stress.

Introduction

Rice is a major food crop in most of the Asian countries. Rice has been identified as water deficit susceptible crop, which undergo large yield losses in many Asian countries (Cha-um et al., 2010). The low land rice crop is a semi-aquatic plant. Thus, limitation of available water and drought will become a serious threat for rice cultivation. It was reported that in grain crops the reproductive stage is more sensitive to water stress than the vegetative. In other words, the presence of water stress during plant reproduction stage is detrimental to the reproductive organ (Saini, 1997). It is indicated that flowering phase is one of the most sensitive period to water stress in rice (Liu et al., 2006). Water stress is found to be disrupting anther and pollen grains development and function in rice (Liu and Bennet, 2010) and in chickpea (Fang et al., 2010). The physical and molecular effects of drought stress on reproductive development of cereal crops in general, and rice in particular, have been discussed explicitly elsewhere (Ekanayake et al., 1989; Saini and Lalonde, 1998; Nguyen and Sutton, 2009). Two stages of high sensitivity to water deficit have been well-documented in the literature. The first vulnerable stage to water deficit centres on anther meiosis, while the second one is during anthesis or flowering of the rice plant (Nguyen and Sutton, 2009). It is reported that environmental stresses cause a decline in pollen production, pollen number on stigma, pollen viability and pollen germination or retardation in pollen tube growth and those are the contributory factors to spikelet sterility (Khan and Abdullah, 2003; Prasad et al., 2006; Fang et al., 2010; Jagadish et al., 2010). Reduction of pollen quality traits under any stress condition might cause morphological disturbances on pollen (Fang et al., 2010). The reduction in the number of engorged pollen could be attributed to several reasons such as failure of young microspores to differentiate, decline in the number of dehisced anthers and repression of anther development (Satake, 1991). Consequently, this reduction in pollen grains will result in a decreased number of available pollen grains falling on stigma, leading to unsuccessful or poor pollination. This phenomenon is corresponds to the reduction of many key metabolic functions and physiological processes in plants (Tezara et al., 2002). Therefore, pollen quality plays important role in male fertility of crop plants and pollen grains can be used as an indicator of plant health as well as a screening tool for cultivar selection (Salem et al., 2007; Fang et al., 2010). Reduction of pollen quality traits in cultivated rice has been reported by many authors under water stress (Ekanayake et al., 1989; Liu et al., 2006; Nguyen and Sutton, 2009; Chu-um et al., 2010). However, based on our knowledge, no research work has been conducted on weedy rice in tropical region yet. Therefore, studies on pollen development in plants exposed to water stress are necessary to understand the effect of increasing water stress on pollen production, germination and other related characteristics for weed managements.

Weedy rice (*Oryza sativa* var. nivara) is an annual grass. It infest rice growing areas worldwide (Chung and Nam-Chon, 2003; Olsen et al., 2007; Hamid et al., 2007; Prathepha, 2009). It is morphologically similar to cultivated rice and usually grows in the same field (Mansor et al., 2012). The early and easy seed shattering is its main characteristic (Akasaka et al., 2011). Currently, it appears as one of the noxious weeds in rice cultivation due to its similar morphology and traits to cultivated rice varieties (Londo and Schaal, 2007). This study focuses on how weedy rice behaves under water stress during reproductive stage and compares it with the cultivated rice. So, the suitable genotypes and management practices can be developed to maximize rice production. This study was also aimed to compare the differences in pollen quality traits response to water stress during anthesis in cultivated rice varieties and weedy rice strains.

Results

Soil water content and leaf water potential

The changes in leaf water potential (LWP) and soil water content (SWC) in cultivated and weedy rice genotypes during the water stress period are shown in Figs. 1 and 2. After exposing to water stress, the SWC and LWP of the stressed plants, in both cultivated varieties and weedy rice ecotypes, reduced consistently with the increase time of withholding water. Meanwhile, the SWC and LWP of untreated plants were relatively constant. A positive correlation between SWC and LWP was demonstrated in each genotype (Figs. 1 and 2). Data showed that LWP decreased upon the reduction of SWC. The LWP in water stress plants remained constant in both cultivated varieties and weedy rice ecotypes at first five days after water withholding and then declined sharply to -16.2 MPa in MR 219, -18.1 MPa in MR 232, -20.3 MPa in WR Bertam and to -27.2 MPa in WR Ketara on day 10. During water stress period, LWP of well-watered plants remained constant (Fig. 1). From the results attained, it indicates that the stress period for 9 days was severe enough and caused extreme reduction in the leaf water potential in both cultivated varieties and weedy rice ecotypes.

Pollen quality traits

The effect of water regime on pollen traits such as number of pollens anther^{-1}, pollen viability and pollen load on stigma was significant (Table 1). Results showed that number of pollens anther^{-1}, pollen viability and pollen load on stigma was drastically decreased in water stress plant, compared to well-watered control. Results further revealed that the decreased of pollen number, pollen viability and pollen load were 63.2, 86.0 and 85.6%, respectively, under water stress conditions at reproductive stage, compared to well-water plants. These results indicate that pollen viability and pollen load on sigma are more sensitive than pollen production under water stress condition. Between the rice groups, weedy rice produced greater number of pollen anther^{-1} and pollen load on stigma but pollen viability was almost similar between cultivated and weedy rice. Among the genotypes, Weedy rice (WR) Bertam showed highest number of pollen anther^{-1} (904), pollen viability (55.94%) and pollen load on stigma (65.85) followed by WR Ketara (849, 54.50 and 65.32 for pollen number anther^{-1}, pollen viability and pollen load on stigma, respectively) with same statistical rank (Table 1). The cultivated variety MR232 showed the lowest pollen load on stigma (55.77). Other two pollen quality traits such as pollen number and pollen viability were almost similar between two cultivated varieties, MR219 and MR232. However, these varieties showed inferior pollen quality traits, compared to weedy rice strains. Season had no significant influence on pollen viability and pollen load on stigma but had significant influence on pollen production. The pollen production was greater in season 1 (955 anther^{-1}) than in season 2 (688 anther^{-1}). The interaction effect of genotypes and water regime on pollen quality traits was also significant (Table 2). Results showed that pollen quality traits were decreased in all the genotypes under water stress condition, compared to well-watered control. But the decline was not similar in all the genotypes. The lowest decrement of pollen grains anther^{-1} under water stress condition was recorded in the cultivated variety MR219 (51.12%), while the highest decrease was recorded in WR Ketara (65.02%), which was identical to cultivated variety MR232 (63.89%) and WR Bertam (62.93%). The decrease of pollen viability was lower in two weedy rice strains, Bertam and Ketara (average 84.19%) than the cultivated rice, MR219 and MR232 (average 87.96%). The lower decrease of pollen load on stigma was observed in cultivated variety MR232 (83.53%) and WR Ketara (84.13%) with being the lowest in MR232. The higher decrease of pollen load was observed in cultivated variety MR219 (87.61%) and WR Bertam (86.82%). Observations under fluorescence microscopy revealed that water stress clearly affects pollen germination and pollen tube growth both in cultivated rice varieties and weedy rice strains (Fig. 3). Under the water stress condition, the amounts of pollen grains on the stigma surface were few in all the studied genotypes. Meanwhile, the pollen tubes of pollen grains that germinated and grew through the style had shorter tube lengths than those in well water conditions. Fluorescence micrograph shows that some of the pollen grains did not germinate or failed to germinate under water stress condition. In contrast, under well water condition, large number of pollen grains attached to the stigma surface and germinated in both cultivated and weedy rice genotypes. However, under stress condition, the viable pollen grains of weedy rice genotypes were greater than the cultivated rice varieties.

Yield attributes

Spikelet number panicle^{-1} and spikelet fertility were greater in well-watered plants than water stress plants (Table 1). However, spikelet fertility was drastically reduced in water stress plants (25.73%) than well-watered control plants (90.86%). Between the rice groups, weedy rice produced greater number of spikelets panicle^{-1} (174.9) than cultivated rice (157.3) but no significant difference on spikelet fertility in rice group was observed. Among the genotypes, cultivated rice MR219 and WR Bertam produced higher number of spikelets panicle^{-1} with being the highest in WR Bertam (188.6). In contrast, the cultivated rice MR232 produced the lowest number of spikelets panicle^{-1} (129.3) with the highest spikelet fertility (62.23%). Other three genotypes showed alike in spikelet fertility (average 56.99%). Furthermore, season caused no significant difference in spikelet number and spikelet fertility. The interaction between genotypes and water regime on spikelet number panicle^{-1} and spikelet fertility percentage was significant (Table 2). Results showed that yield components decreased in all the genotypes under

Table 1. Effect of water regime, rice group and genotype on pollen traits and yield attributes in rice (Mean over two years).

Treatment		Pollen number anther^{-1}	Pollen viability (%)	Pollen load on stigma	Spikelet number panicle^{-1}	Spikelet fertility (%)
Water regime						
Well water		1183 a	95.72 a	108.5 a	186.0 a	90.86 a
Water stress		460 b	13.38 b	15.6 b	146.1 b	25.73 b
F-test		**	**	**	**	**
Rice group						
Cultivated rice		767 b	53.88	58.63 b	157.3 b	59.61
Weedy rice		877 a	54.78	65.59 a	174.9 a	56.99
F-test		**	NS	*	**	NS
Genotype						
Cultivated rice	MR219	766 b	53.69 b	61.49 a	185.3 a	56.98 b
	MR232	767 b	54.06 ab	55.77 b	129.3 c	62.23 a
Weedy rice	Bertam	904 a	55.94 a	65.85 a	188.6 a	56.97 b
	Ketara	849 ab	54.50 ab	65.32 a	161.1 b	57.01 b
F-test		*	*	**	**	**
Season						
2009		955 a	54.31	64.27	169.28	56.68
2010		688 b	54.78	59.95	162.87	59.91
F-test		**	NS	NS	NS	NS
CV (%)		17.03	4.36	21.97	9.77	4.67

In a column, either within water treatment or rice group or genotype or season, the figures bearing the same letter (s) do not differ significantly at $P \leq 0.05$ by DMRT; *, ** indicate significant at 5% and 1% level of probability, respectively; NS, not significant

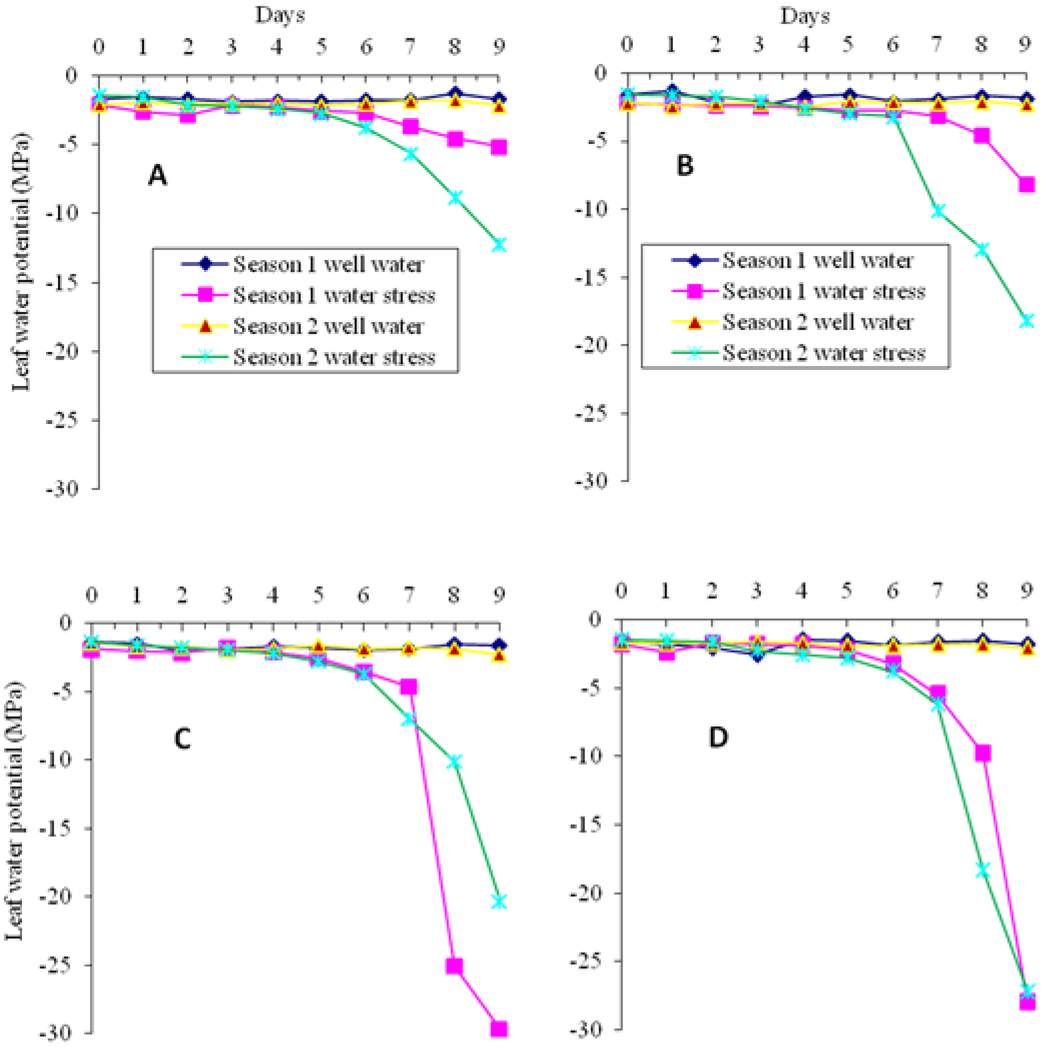

Fig 1. Changes in leaf water potential due to water stress (over time periods) in two cultivated varieties, MR232 (B) and MR219 (A) and two weedy rice genotypes, Bertam (C) and Ketara (D).

water stress condition as compared to well-watered control, but the decline was not similar in all the genotypes. The lowest decline due to water stress of spikelet number was observed in MR219 (8.30%) while the highest decrease was recorded in WR Bertam (33.35%) followed by MR232 (24.63%). Again, MR219 showed the highest decrease in spikelet fertility due to water stress (77.44%) and other three genotypes showed the same trend in decrement of spikelet fertility under water stress. The relationship between water regime and pollen traits revealed that there was a strong negative correlation between water regime and pollen quality traits (Table 2).

Discussion

Water stress affects generative phase by reduction in number of pollen grains and markedly impairs their function (Fang et al., 2010). The findings of the study showed that pollen grains, pollen viability, pollen load on stigma and spikelet fertility in both weedy and cultivated rice reduced drastically after experiencing water stress at pre-anthesis phase for 10 days. This change due to water stress was clearly seen through *in vivo* pollen germination and pollen tube growth observation using fluorescence microscope. Reductions in pollen germination and inhibition of pollen tube growth caused by water stress might decrease the effectiveness of pollination and fertilization, and consequently change the quantity and quality of seed. Similar observations were reported in chickpea (Fang et al., 2010) and rice (Nguyen and Sutton, 2009). Therefore, pollen parameters would be good indicators in determining tolerance of plants to water stress at reproductive stage. Since pollen development during various phases of microsporogenesis is more sensitive to abiotic stresses such as water stress (Ekanayake et al., 1989; Saini, 1997; Saini and Lalonde, 1998; Liu et al., 2006), any factor that affects the pollen formation may result in pollen viability loss. Weedy rice genotypes produced more pollen grains and spikelets, showed greater pollen load on stigma than cultivated varieties. Pollen production is genotypic dependent, due to its weedy nature, in which weedy rice produced more pollen than cultivated rice genetically. High amount of pollen produced by weedy rice may play an important role in the pollen transfer by the wind. Pollen viability is important in successful pollination and formation of grain set. Therefore, reduction in pollen viability might affect seed set (Nguyen and Sutton, 2009). In the present experiment, no significant difference was found in pollen viability between weedy and cultivated rice genotypes under well-water condition. However, reduction of pollen viability was less in weedy rice (reduction 84.12%) over cultivated rice (reduction 87.96%), indicating weedy rice strains are more tolerant in pollen viability under water stress condition. Praba et al. (2009) also observed that pollen viability was seriously affected when water stress occurred at reproductive stage. Previous studies indicated that pollen inviability due to water stress is associated with starch deficiency for disturbance of carbohydrate metabolism (Datta et al., 2002), or enzyme activity (Boyer and Westgate, 2004). Similar phenomenon may be happened to lose leaf water content (Fig. 1), causing reduced pollen viability and decreased spikelet fertility under water stress condition. Nguyen and Sutton (2009) reported that reduction of many key metabolic functions and physiological processes in plants correlated with leaf water content. The finding obtained from *in vivo* pollen observation, using fluorescence microscope, supports the results of pollen viability attained from the staining test, indicating that reduction in pollen viability due to water stress consequently reduced germination ability and retardation of pollen tube growth. As a consequence, fertilization and subsequently development were inhibited. It is supported by the study of Fang et al. (2010) who reported that pollen from stressed plants have a short life and low vigor. Thereby, the pollen tube growth may occur but it fails to reach ovule, resulting no fertilization. The water stress treatment caused greater reduction (≥84%) in pollen load on stigma for all the rice genotypes. This might be due to production of less amount of pollen grain which usually leads to lower pollen deposition on the sigma surface. Theoretically, only a single pollen grain is needed for fertilization in every individual floret. In practice, a large number of engorged pollen is required for the successful pollination of a floret (Oliver et al., 2005). Therefore, more number of viable pollen grains is desirable. In the present study, results showed that under water stress condition weedy rice ecotypes produced greater number of viable pollens than the cultivated rice varieties, indicating weedy rice is comparatively more tolerant in maintaining pollen viability than cultivated rice. In conclusion, reduction in all pollen quality traits under water stress during early reproductive stage reduce the chances of fertilization and consequently become a contributory factor to spikelet sterility in both cultivated and weedy rice subjected to pre-anthesis water stress (for 10 days). Weedy rice strains were comparatively more tolerant under water stress condition than cultivated rice varieties mainly due to higher pollen quality traits. The exact physiological mechanisms affecting poor pollen germination at water stress needs further investigation.

Materials and methods

Planting materials and rice culture

The experiment was conducted at the field laboratory of Faculty of Agriculture, Universiti Putra Malaysia in 2011 and 2012. Two widely cultivated Malaysian rice varieties *viz*., MR219 **(***Oryza sativa* L. ssp. Indica var. MR219**)** and MR232 **(***Oryza sativa* L. ssp. Indica var. MR232**)** and two wild strains of weedy rice (WR) *viz*., WR Bertam (*Oryza sativa* var. nivara**)** (collected from Penang) and WR Ketara (*Oryza sativa* var. nivara**)** (collected from Terengganu) were used as planting material. Seeds of the cultivated varieties and wild strains of weedy rice were sown in black perforated plastic polybags of 40 × 45 cm size containing approximately 20 kg of soil obtained from a rice growing area. The soil was silty clay loam. Several pre-germinated seeds were sown in each polybag and plants were thinned to three about two weeks after sowing, keeping the main culm and first six tillers. All other tillers were removed as they appeared to achieve synchronized flowering in each replication and genotypes. The polybags were submerged in water of polythelene tanks (diameter 100 cm and height 56 cm). A total of eight polybags were housed in each polyethylene tank. The polyethylene tanks containing seedlings in polybags were placed in an enclosed cage and were arranged in a two factors completely randomized design with four replications. The treatments were four rice genotypes and two water regime (control and water stress just prior to anthesis). The standard procedures of rice growing culture were followed throughout the studies. Seedling growth and development were monitored daily.

Table 2. Interaction effect of genotype and water regime on pollen traits and yield attributes in rice (Mean over two years).

Interaction		Pollen number anther^{-1}	Pollen viability (%)	Pollen load on stigma	Spikelet number panicle^{-1}	Spikelet fertility (%)
Genotype	Water regime					
MR219	WW	1029 c	96.25 a	109.4 ab	193.4 b	92.99 a
	WS	403 d	11.13 c	13.55 c	177.3 b	20.98 e
		(61.12)	(88.55)	(87.61)	(8.30)	(77.44)
MR232	WW	1127 bc	96.00 a	95.76 b	147.4 c	95.50 a
	WS	407 d	12.13 c	15.77 c	111.1 d	28.96 c
		(63.89)	(87.36)	(83.53)	(24.63)	(69.68)
Bertam	WW	1319 a	96.50 a	116.4 a	226.4 a	87.97 b
	WS	489 d	15.38 b	15.34 c	150.9 c	25.96 d
		(62.93)	(84.06)	(86.82)	(33.35)	(70.49)
Ketara	WW	1258 ab	94.13 a	112.8 a	177.1 b	86.99 b
	WS	440 d	14.88 b	17.90 c	145.1 c	27.04 cd
		(65.02)	(84.19)	(84.13)	(18.07)	(68.92)
F-test		**	**	*	**	**
CV (%)		17.03	4.36	21.97	9.77	4.67

Figures bearing the same letter (s) within a column do not differ significantly at $P \leq 0.05$ by DMRT; *, ** indicate significant at 5% and 1% level of probability, respectively; WW = Well watered, WS = Water stress; figures in parenthesis indicate percent decreased over control.

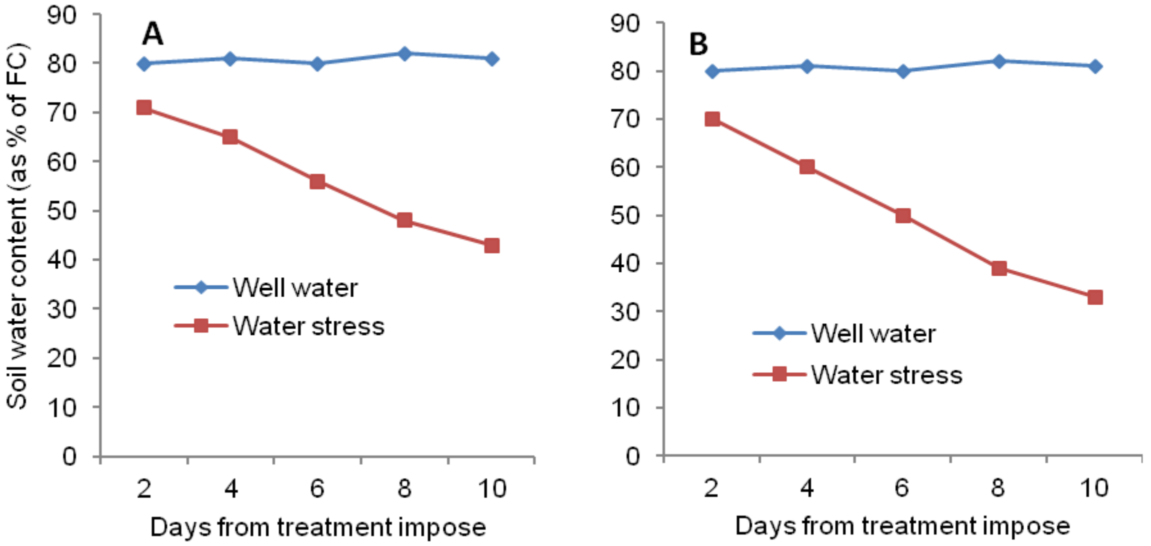

Fig 2. Changes in soil water content due to water stress in one cultivated rice MR219 (A), and one weedy rice Bertam (B) (over time periods).

Water stress treatment

When a panicle was protruded through the flag leaf from any tiller within a polyethylene tank, all the eight polyethylene bags were taken out to impose water stress treatment for days. Re-watering of stressed plants by putting back the plants into the polyethylene tank was done on day 11. The control plants were left in well-watered polyethylene tanks throughout the study. Within this imposition of water stress period, the polybags were placed under the shade in the glasshouse to avoid additional water from rain. A portable soil moisture meter (Irrometer, Model SR, Riverside, CA, USA) was inserted into each polybag of the stressed plants at a depth of 15 cm to monitor soil moisture during the water stress period (Fig. 2).

Determination of pollen quality

Pollen quality traits evaluated in this study were pollen number per anther, pollen viability and pollen load on stigma. Pollen number was counted by randomly collecting 10 matured anthers from 20-25 spikelets just before anthesis to determine the number of pollen grain produced per anther. The pollen number was estimated by placing a single anther on glass slide with grid. The anther was then squashed with a needle to disperse pollen grain on the slide. Finally pollen grain was observed and counted under a microscope (Hirox Hi-Scope KH-2700, Japan). Pollen viability was expressed as percentage and estimated using 1% Iodine Potassium Iodide (IKI) staining. Fresh flowers were collected from newly opened anther between 08:00 and 09:00 h and brought into the laboratory. Anthers and pistil were dissected from flowers on a glass slide and stained with IKI solution. Pollen viability was counted based on IKI staining pattern on pollen (Prasad et al., 2006). Pollen grains with bright red stain indicated viable pollen grains, pollen grains with pink stain indicate low viability pollen grains and unstained pollen grains indicate sterile pollen grain. To determine the pollen load, the stigma receptivity throughout the lifespan of the flower, pollen germination on stigmas was assessed. Flowers were

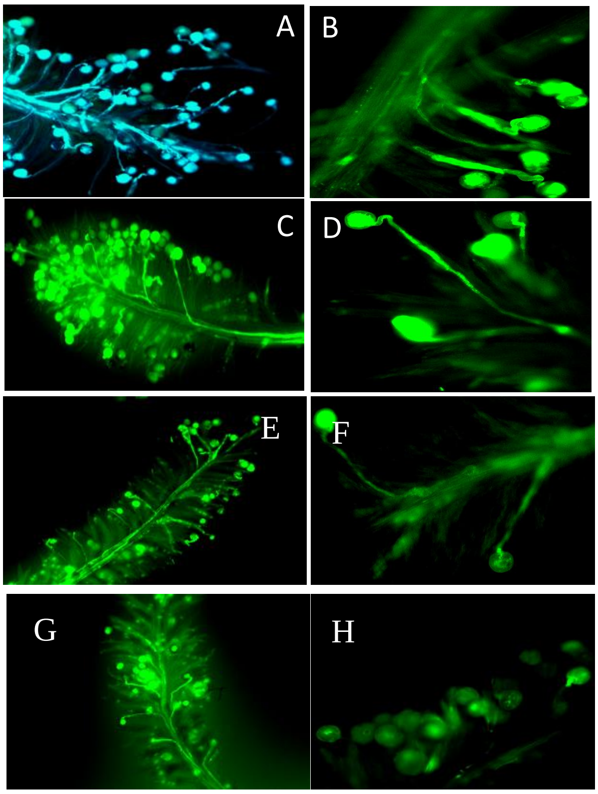

Fig 3. Fluorescence microscopy images of pollen germination and pollen tube growth of (A, C) well water, (B, D) water stress condition of MR219 and MR232; pollen germination and pollen tube growth of (E, G) well water, (F, H) water stress condition of weedy rice Bertam and Ketara.

collected one day after pollination and kept in 70% ethanol at room temperature for subsequent examination of pollen tube development. They were macerated in 1 N sodium hydroxide (NaOH) for 2h, rinsed in distilled water, and then stained for 3h with 0.05% aniline blue in 0.1 NK_3PO_4. The pistils were mounted onto a staining medium on a glass slide with a drop of 50% glycerin and then covered with another glass cover slip. Pollen germination was determined by direct microscopic observation (Nikon Scientific, Kanagawa, Japan). A total of 100 pollens were evaluated for germination for each variety. A pollen grain was considered germinated when pollen tube length was at least equal to or greater than the pollen grain diameter (Kakani et al., 2002). The number of pollen tube penetrating through the stigmatic papillae and style was recorded.

Measurement of in vivo pollen germination and pollen tube growth

Pollen germination and pollen tube growth were observed by fluorescence microscope. The spikelets were collected approximately one hour after anthesis, after lemma and palea closed, and immediately fixed in one part of glacial acetic acid and three parts of absolute alcohol (1:3 glacial acetic acid: absolute alcohol) for overnight. The fixed spikelets were dissected to isolate the pistils. The pistils were transferred to 8N NaOH for two hours and subsequently washed in distilled water and then placed overnight in 0.1% aniline blue in 50 mol m^{-3} NaH_2PO_4 (pH 8.2). Next, the stained pistils were mounted on microscope slide in a drop of 50% glycerine. Afterwards germinated pollen and pollen tube growth were observed under fluorescence microscope (Leica II DMRA Florescence).

Measurement of leaf water potential

Leaf water potential was determined daily from freshly cut flag leaves from five plants per treatment during the water stress period for nine days. A potentiometer (model WP4-T, Decagon Devices, Inc, Pullman, Washington) was used for leaf water potential measurement (Fig. 1).

Yield components

At harvest, when the seed reached full maturity, 10 undisturbed panicles from each experimental unit were randomly selected for the determination of seed yield components. The panicles were cut and then the spikelets were threshed from the panicles by hands. From each panicle, filled and unfilled spikelets were separated. Spikelet sterility was estimated as the ratio of unfilled grains or sterile florets to total number of reproductive florets or spikelets and expressed as percentage.

Statistical analyses

All data were analyzed statistically appropriate to the applied design following the two way analysis of variance technique and the mean differences were compared with Duncan's Multiple Range Test using the statistical computer package programme. Microsoft excel was used for graphical presentation.

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