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ORIGINAL ARTICLE

Variation in leaf photosynthetic response of rice genotypes to post-anthesis water deficit

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Abstract Variation in the response of six diverse rice genotypes to imposed water stress was investigated in terms of leaf photosynthetic traits and leaf water potential measurements (Ψ_{leaf}) during and following a period of water stress. The Ψ_{leaf} reduced from 0 days up to 6th day of irrigation deprivation and the reduction in Ψ_{leaf} was more pronounced in Swarna and minimum in PA-6201. A gradual recovery in Ψ_{leaf} was observed in all the tested varieties after re-irrigation. Similarly, water stress significantly reduced rate of photosynthesis (P_N), stomatal conductance (g_s), transpiration *(E)* and internal CO_2 concentration (C_i). Significant differences were noticed amongst the varieties in their response to water stress. The P_N partially recovered in all tested varieties after re-irrigation. Vandana recorded greater recovery (65 %), where as the recovery was only 32 % in Sugandha Samba. Water stress (6 days of irrigation deprivation) significantly decreased the mean Chl *a,* Chlb, total chlorophyll and total carotenoid content. However, a marginal increase in total chlorophyll was observed under water stress in Vandana and N-22. Water stress had no significant effect on maximum photochemical efficiency (F_v/F_m) for all the tested varieties. However, in Sugandha Samba and Swarna a significant reduction was noticed. Water stress reduced the efficiency of excitation capture (Φ_e), in vivo quantum yield of PSII photochemistry (Φ_{PSI}), coefficient of photochemical quenching (qP) and increased the coefficient of non-photochemical quenching (qN). The data on photosynthetic traits and chlorophyll fluorescence parameters indicate that Vandana, N-22, DRR-Dhan-38 and PA-6201 which maintained relatively higher, Ψ_{leaf}, P_N and g_s under water stress and could also maintain high values of photochemical efficiency (Fv/Fm, Φ_e, Φ_{PSI} and ETR) than Sugandha Samba and Swarna and the genotypic differences in the response of PSII activity could be exploited as traits for the selection of drought tolerant rice genotypes.

Keywords Gas exchange · Chlorophyll fluorescence · Photosynthesis · Stomatal conductance · Transpiration · Water stress

Introduction

Rice is one of the most important cereal crops in the world after wheat and is the primary source of calories for about half of mankind (Khush 2005). More than 75 % of the rice production comes from 79 million ha of irrigated lowland. Over 17 million ha of Asia's irrigated rice may experience "physical water scarcity" and 22 million ha may experience "economic water scarcity" by 2025 (Tuong and Bouman 2003). Impacts of climate change on freshwater supply are expected to be significant, with projected increases in water-stress already pronounced by 2050 in many regions (Tubiello and van der Velde 2002). Drought has become the most significant constraint for realizing the yield potential of rice across all agro-climatic zones and water stress is one of the most important abiotic stresses worldwide reducing average yields by as much as 50 % or more (Zhu 2002, Wang et al. 2003). Water stress results in reduction in relative water content (RWC), leaf water potential and turgor pressure, stomtatal closure and reduction in cell enlargement and

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growth (Toker and Cagirgan 1998). Photosynthesis is reduced in plants undergoing water stress as a result of water deficit in plant tissues. The ability to maintain photosynthetic activity under water stress is of major importance for drought tolerance (Zlatev and Yordanov 2004). Despite great progress in understanding the effects of water stress on photosynthesis, there is still no unified concept of the events which reduce photosynthetic efficiency (Lawlor 1995). Nayyar and Walia (2003) attributed genotypic variations in wheat in response to water stress to ABA-dependent solute accumulation in flag leaf and developing grain. The objective of this study was to investigate changes in photosynthesis under water stress in terms of gas exchange measurements in different rice varieties. The functionality of photosynthetic apparatus was assessed by chlorophyll fluorescence measurements.

Materials and methods

Plant material and culture conditions

Seeds of six popular rice varieties, viz., Vandana, PA-6201(hybrid), DRR Dhan-38, Sugandha Samba, Swarna and N-22 were sown in 12″ diameter earthen pots filled with soil collected from Directorate of Rice Research, Rajendranagar experimental farm. Two 7-days old seedlings of each variety were transplanted in eight 20″ diameter earthen pots. Recommended doses of N, P and K were applied @100, 60 and 40 kg ha^{-1}. All the pots were placed in a net house. Pots were watered with tap water throughout the experiment ensuring 2–3 cm standing water in each pot. Water stress was imposed immediately after anthesis by draining the standing water and withholding the irrigation in four pots and each pot was treated as separate replication. Remaining four pots received normal irrigation and were treated as control treatment. Care was taken to protect the pots from rain during the experiment by covering the net-house with transparent polythene sheet.

Measurement of leaf water potential (Ψ_w)

Mid-day leaf water status was measured using a portable Pressure Chamber *(Model 1000, PMS Instrument Company, USA*) at regular intervals after withholding water. Fully matured leaves from each variety and treatment were cut with a sharp blade and immediately enclosed in plastic bag. The time between leaf excision and Ψ_w determination was <60 s.

Leaf pigment extraction and quantification

Leaf pigments were extracted with mortar and pestle in cold 80 % acetone and a pinch of sea sand. The extract was centrifuged at 4 °C for 5 min and Chlorophyll and carotenoid content were determined spectrophotometrically by measuring the absorbance at 663.2, 646.8 and 470 with (*Spectrascan UV 2600, Toshniwal Instruments (India) Pvt. Ltd.)*. The pigment concentration was calculated according to Lichtenthaler and Wellburn (1983).

Gas-exchange measurements

Leaf photosynthetic characteristics of flag leaf were measured at regular time intervals after imposition of water stress between 10.00 and 13.00 h on fully matured leaves using *LI6400XT* portable photosynthesis measuring system (*LI-COR Environmental, USA)* connected to leaf chamber fluorometer *(6400-40, LI-COR, USA)*, which was used as a light source. During photosynthesis measurements leaf temperature was maintained at 30 °C and PAR was maintained at 1,100 µmol m^{-2} s^{-1}. Measurements were made at ambient CO_2 levels. The mean CO_2 concentration (C_a) during measurements was 387 ± 1.2 µmol mol^{-1}.

Measurement of chlorophyll fluorescence parameters and light response curves

Chlorophyll fluorescence of flag leaf was measured with a portable *PAM-210 Fluorometer* (*Walz, Effeltrich, Germany*) connected to a portable computer on the 6th day after irrigation withdrawal. The minimal fluorescence level (F_0) and maximal fluorescence level (F_m) was recorded on attached leaf, dark adapted for 10 min on which the gas exchange was measured. The minimal fluorescence level in light adapted state (F'_0) was determined by illuminating the leaf with far-red light. By using fluorescence parameters determined on both light and dark-adapted leaves, the following parameters were calculated, the maximal quantum yield of PSII photochemistry F_v/F_m, the photochemical quenching coefficient $q_P = (F'_m - F'_t)/(F'_m - F'_0)$, non-photochemical quenching coefficient $q_N = 1 - (F'_m - F'_0)/(F_m - F_0)$, the efficiency of excitation capture by open PSII centers $\Phi_e = F'_v/F'_m$, in vivo quantum yield of PSII photochemistry $\Phi_{PSII} = \left(F'_v/F'_m \times q_p\right)$ and apparent photosynthetic electron transport rate ETR = Yield × PAR × 0.5 × 0.84, yield (Y) corresponded to the effective quantum yield of PSII in an illuminated leaf $\left(Y = (F'_m - F'_t)/F'_m\right)$, which is same as Φ_{PSII}, PAR corresponded to the flux density of incident photosynthetically active radiation measured in µmol quanta m^{-2} s^{-1}, transport of one electron requires absorption of two quanta, as two photosystems are involved (factor 0.5). It is assumed that 84 % of the incident quanta are absorbed by the leaf (factor 0.84). The absorption coefficient close to 0.84 has been reported for leaves of numerous species; this value depends on a number of other variables like leaf reflectance, chlorophyll content and spectral composition of incident light. These aspects could not be considered in this study. Light response curves were measured 24 h after the gas-exchange measurements with a portable PAM-210 Fluorometer (Heinz Walz, Effeltrich, Germany) connected to a laptop computer following the protocol developed by the manufacturers.

Statistical analysis

Two way analysis of variance (ANOVA) was performed on leaf photosynthetic characters and leaf pigments content using an open source software *R* (R Core Team 2012) with *agricolae* package (Felipe de Mendiburu 2012). Statistical significance of the parameter means were determined by performing the Tukey's HSD (honestly significant difference) test and standard errors (SE) were calculated and reported. For chlorophyll fluorescence parameters Fisher's LSD test was used to test the statistical significance.

Results and discussion

Leaf water potential is commonly used for determining the severity of drought stress (Jones 2007). Kim et al. (2012) reported a clear relationship between midday Ψ_{leaf} and leaf responses to drought and indicated that midday Ψ_{leaf} is a useful indicator of drought-stress severity. The Ψ_{leaf} began to decline gradually from 0 days up to 6th day of irrigation deprivation. The reduction in Ψ_{leaf} was observed in all the rice varieties. However, significant differences were observed among the varieties (Fig. 1). The reduction in Ψ_{leaf} was more pronounced in Swarna and least reduction was observed in PA-6201. The plants were re-irrigated on

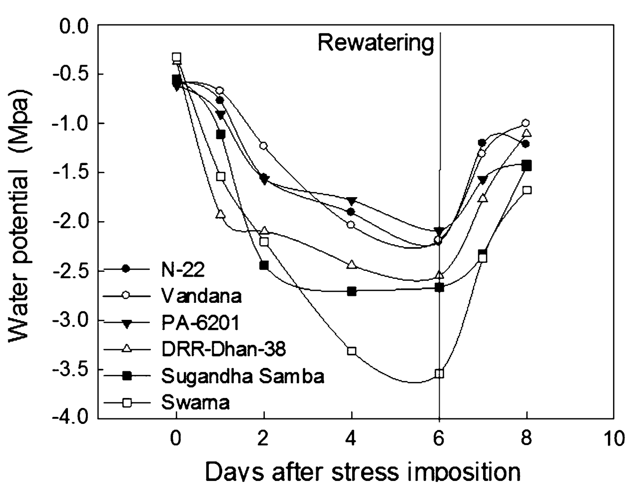

Fig. 1 Influence of water stress and recovery after re-watering on leaf water potential (Ψ_{leaf}) in different rice varieties. Each value represents the mean of four replications

6th day and the changes in Ψ_{leaf} were measured 1 and 2 days after re-watering to study the pattern of recovery. Ψ_{leaf} recovered in all the tested varieties. However, the Ψ_{leaf} was not restored to the levels recorded at the beginning of the water stress treatment. Varietal differences were noticed in the extent of recovery amongst the rice varieties. The recovery was higher in Vandana, DRR-Dhan-38 and N-22 (Fig. 1). Differences in the extent of Ψ_{leaf} amongst different rice varieties have been reported by O'Toole and Cruz (1980). Several authors have reported that water stress resistant crop plants can maintain higher total leaf water potentials than the susceptible ones (Cortes and Sinclair 1986; Matin et al. 1989; Garcia et al. 2002; Subrahmanyam et al. 2006). Differential reduction in leaf osmotic potential as a response to water stress has been reported between susceptible and tolerant rice genotypes (Ji et al. 2012). The Swarna and Sugandha Samba, PA-6201 and DRR-dhan-38 were developed for the irrigated ecosystem and were never selected for drought tolerance hence the reduction in Ψ_{leaf} was more pronounced than N-22 and Vandana, which are drought tolerant varieties. Leaf Chlacontent was highest in DRR-Dhan-38, followed by PA-6201 under control treatment Water stress significantly decreased the mean Chl*a*, Chl*b* and total chlorophyll content (12.3, 7.7 and 11.1 % reduction over control). The reduction in Chlawas highest in Swarna, followed by Sugandha Samba, while the varieties N-22 and Vandana recorded a marginal increase in Chl*a* content. The Chl*b* content varied significantly from 0.76 (PA-6201) to 0.63 (Swarna) with a mean of 0.65 (mg g^{-1} fr. wt.) under control condition. The water stress induced reduction in Chlb content was more in Swarna, followed by Sugandha Samba. Water stress had no effect on Chlb content of PA-6201, where as a marginal increase was observed in Vandana (Table 1). Significant interaction was observed between treatment and varieties. Significant varietal differences were observed for total chlorophyll ($Chl_{(a+b)}$) content. The total Chl content was highest in DRR-Dhan-38, followed by PA-6201 and Sugandha Samba under control condition. Imposition of water stress resulted in significant reduction in the total Chl content in most of the varieties, with the exception of Vandana and N-22, which recorded a marginal increase (Table 2). A significant reduction of 12 % over control in the mean carotenoid (Car) content in all the varieties was observed under water stress condition. However, Sugandha Samba recorded a slight increase in Car content under water stress. The Car content varied significantly amongst the tested varieties both under control and water stress condition. The Car content varied between 0.78 (DRR-Dhan-38) and 0.51(N-22) with a mean of 0.62 (mg $g^{-}1$ fr. wt.) under water stress condition. However, under control PA-6201 had high Car content, followed by DRR-Dhan-38 (Table 2). The Chl *a/b*

Table 1 Influence of water stress on chlorophyll a and chlorophyll b content in different rice varieties during grain filling period

Variety	Chlorophyll *a* (mg g^{-1} fr. wt.)			Chlorophyll *b* (mg g^{-1} fr. wt.)		
	Control	Stress	Mean	Control	Stress	Mean
DRR Dhan-38	2.27 ± 0.030^{a}	2.01 ± 0.031^{abc}	2.14 ± 0.06^{a}	0.71 ± 0.020^{ab}	0.70 ± 0.047^{ab}	0.71 ± 0.21^{a}
N22	1.48 ± 0.021^{c}	1.58 ± 0.071^{abc}	1.53 ± 0.04^{c}	0.54 ± 0.015^{de}	0.52 ± 0.007^{de}	0.53 ± 0.01^{d}
PA-6201	2.15 ± 0.032^{ab}	2.08 ± 0.072^{abc}	2.12 ± 0.04^{a}	0.76 ± 0.014^{a}	0.76 ± 0.021^{a}	0.76 ± 0.01^{b}
Sugandha samba	2.10 ± 0.101^{abc}	1.51 ± 0.032^{bc}	1.81 ± 0.14^{b}	0.66 ± 0.051^{bc}	0.53 ± 0.011^{de}	0.60 ± 0.03^{c}
Swarna	1.54 ± 0.380^{bc}	0.72 ± 0.022^{d}	1.13 ± 0.25^{d}	0.63 ± 0.041^{bc}	0.45 ± 0.009^{e}	0.54 ± 0.04^{d}
Vandana	1.65 ± 0.182^{bcd}	1.90 ± 0.120^{abc}	1.78 ± 0.09^{bc}	0.60 ± 0.061 ^{cd}	0.65 ± 0.009^{bc}	0.63 ± 0.01^{c}
Mean	1.87 ± 0.98^{a}	1.64 ± 0.11^{b}	1.75	0.65 ± 0.018^{a}	0.60 ± 0.027^{b}	0.71
HSD (Treatment)	0.154**			0.020**		
HSD (Variety)	0.401**			0.054**		
HSD (T × V)	0.661**			0.089**		

Water stress was imposed by withholding water immediately after anthesis. Pigment content was estimated 5 days after withholding irrigation. Each value represents mean of four replications ± SE. Means with same letter are not significantly different
*($P < 0.05$), ** ($P < 0.01$)*

ratio did not differed significantly in water stressed plants. However, significant differences were noticed for Chl *a/b* amongst the rice varieties. The Chl *a/b* ratio varied between 3.19 (DRR-Dhan-38) and 2.74 N-22) with a mean of 2.86 under control condition. The interaction between treatment and varieties was found significant (Table 3). The Chl/Car ratio was not significantly affected by water stress treatment. However, significant variations were noticed among the varieties, both under control and water stress conditions. The interaction between the treatment and varieties was also found significant. Drought induced reduction in chlorophyll content has been reported earlier (Sikuku et al. 2010; Liu et al. 2011). The reduction in chlorophyll content due to water stress was attributed to reduction in antioxidant levels and increase in the levels of reactive active oxygen species (Jiang et al. 1994). In Vandana and N-22, total chl content was marginally higher under water stressed condition. Vandana is recommended for rainfed upland conditions, while N-22 is a traditional variety grown under drought prone conditions and is an important donor for heat and drought stress tolerance. Hu et al. (2009) reported that decrease in Chl content due to water stress in upland rice cultivar IRAT109 was about 1.23 % less than that of paddy rice Zhenshan97B. Pastori and Trippi (1992) reported that drought resistant genotypes of wheat and corn had higher chlorophyll content than sensitive genotypes under the oxidative stress conditions. Imposition of water stress had resulted in significant reduction in carotenoid content. Significant reduction in chlorophyll and carotenoid content under drought stress has also been reported in cotton genotypes (Parida et al. 2007). Bartoli et al. (1999), however, reported drought induced increase in leaf β-carotene content along with other anti-oxidant levels in wheat leaves.

A gradual reduction in photosynthetic rate (P_N) was observed in all the varieties under water stress. The differences in P_N under control treatment amongst different varieties were not significant (Fig. 2). However, significant differences were observed between the varieties under water stress. After six days of irrigation deprivation the P_N was only 9.5 % of control in Sugandha Samba and 18.8 % of control in Swarna. The reduction in P_N was 71.1, 74.1 and 74.3 % with respect to control in PA-6201, N-22 and Vandana, respectively (Fig. 2). After 6 days of irrigation withdrawal, the plants received irrigation and the recovery in P_N was measured after 1 and 2 days of re-irrigation. The P_N recovered in all the varieties, though the recovery in P_N was not complete when compared to the initial values recorded before the imposition of water stress. Vandana recorded highest recovery (65 %), where as the recovery was only 32 % in Sugandha Samba (Fig. 2). A gradual reduction in stomatal conductance (g_s) was observed after imposition of water stress in all the varieties. After 6 days of water deprivation, the reduction in g_s was more pronounced in Swarna (83 % reduction over control) and SugandhaSsamba (75.5 % reduction over control), where as the reduction in g_s over control was 64, 63, 60.5 and 60 % in DRR-Dhan-38, PA-6201, N-22 and Vandana, respectively (Fig. 3). Partial recovery in g_s was observed in all the varieties, and greater recovery was observed in Vandana (79 %), followed by PA-6201 (60 %). The recovery was only 47.2 and 48.8 % in Swarna and Sugandha Samba, respectively (Fig. 3).

A gradual reduction in Transpiration rate (E) under water stress was observed in all the varieties. The water stress induced reduction was highest in Sugandha Samba (87 %), followed by Swarna (86.3 % reduction and least reduction (70 %) was observed in N-22 (Fig. 4). The

Table 2 Influence of water stress on flag leaf total chlorophyll and carotenoid content in different rice varieties during grain filling period

Variety	Total chlorophyll (mg g^{-1} fr. wt.)			Carotenoids (mg g^{-1} fr. wt.)		
	Control	Stress	Mean	Control	Stress	Mean
DRR Dhan-38	2.99 ± 0.039[a]	2.71 ± 0.040[abcd]	2.85 ± 0.07[a]	0.83 ± 0.029[ab]	0.78 ± 0.017[abc]	0.81 ± 0.02
N22	2.02 ± 0.034[e]	2.10 ± 0.062[cde]	2.06 ± 0.04[a]	0.56 ± 0.020[de]	0.51 ± 0.017[e]	0.54 ± 0.02
PA-6201	2.91 ± 0.029[ab]	2.84 ± 0.093[ab]	2.88 ± 0.05[b]	0.87 ± 0.009[a]	0.70 ± 0.025[abcde]	0.79 ± 0.04
Sugandha samba	2.77 ± 0.117[abc]	2.04 ± 0.026[de]	2.41 ± 0.17[b]	0.58 ± 0.025[cde]	0.64 ± 0.012[bcde]	0.61 ± 0.02
Swarna	2.17 ± 0.375[cde]	1.18 ± 0.022[f]	1.68 ± 0.28[c]	0.74 ± 0.131[abcd]	0.53 ± 0.015[d]	0.64 ± 0.08
Vandana	2.25 ± 0.181[bcde]	2.54 ± 0.016[abcde]	2.40 ± 0.10[d]	0.64 ± 0.023[bcde]	0.54 ± 0.025[de]	0.59 ± 0.03
Mean	2.52 ± 0.111[a]	2.24 ± 0.136[b]	2.38	0.70 ± 0.035[b]	0.62 ± 0.025[a]	0.66
HSD (Treatment)	0.157**			0.051**		
HSD (Variety)	0.406**			0.132**		
HSD (T × V)	0.669**			0.218*		

Water stress was imposed by withholding water immediately after anthesis. Pigment content was estimated 5 days after withholding irrigation. Each value represents mean of four replications ± SE. Means with same letter are not significantly different

*($P < 0.05$), ** ($P < 0.01$)*

Table 3 Influence of water stress on flag leaf pigment content in different rice varieties during grain filling period

Variety	Chl *a*/*b* ratio			Chl/Car ratio		
	Control	Stress	Mean	Control	Stress	Mean
DRR Dhan-38	3.19 ± 0.089[a]	2.91 ± 0.167[a]	3.05 ± 0.11[a]	3.60 ± 0.089[a]	3.47 ± 0.167[a]	3.54 ± 0.12[a]
N22	2.74 ± 0.056[a]	3.02 ± 0.148[a]	2.88 ± 0.09[a]	3.61 ± 0.056[a]	4.12 ± 0.149[a]	3.87 ± 0.05[a]
PA- 6201	2.84 ± 0.079[a]	2.74 ± 0.023[a]	2.79 ± 0.04[a]	3.34 ± 0.079[a]	4.06 ± 0.023[a]	3.70 ± 0.07[a]
Sugandha SAMBA	3.17 ± 0.092[a]	2.86 ± 0.113[a]	3.02 ± 0.09[a]	4.78 ± 0.092[a]	3.19 ± 0.112[a]	3.99 ± 0.05[a]
Swarna	2.45 ± 0.620[ab]	1.60 ± 0.070[b]	2.03 ± 0.34[b]	2.93 ± 0.621[ab]	2.23 ± 0.071[b]	2.58 ± 0.08[b]
Vandana	2.75 ± 0.283[a]	2.93 ± 0.059[a]	2.84 ± 0.14[a]	3.52 ± 0.283[a]	4.70 ± 0.059[a]	4.11 ± 0.12[c]
Mean	2.86 ± 0.116[a]	2.68 ± 0.124[a]	2.77	3.63 ± 0.116[a]	3.63 ± 0.125[a]	3.63
HSD (Treatment)	NS			NS		
HSD (Variety)	0.670**			0.670**		
HSD (T × V)	1.105*			1.100*		

Water stress was imposed by withholding water immediately after anthesis. Pigment content was estimated 5 days after withholding irrigation. Each value represents mean of four replications ± SE. Means with same letter are not significantly different

*($P < 0.05$), ** ($P < 0.01$)*

recovery in E after irrigation was highest in Vandana (75 %), followed by N-22 (63 %) and DRR-Dhan-38 (62.2 %). Sugandha Samba recorded lowest (32.8 %) recovery among all the varieties (Fig. 4). The internal CO_2 concentration (C_i) was gradually reduced after imposition of water stress in all the varieties. However significant varietal differences were observed in the extent of reduction. After 1 and 2 days of re-watering the C_i recovered in all the varieties. The recovery was relatively lower in Swarna and Sugandha Sambha (Fig. 5). The reduction in the C_i was mainly due to the reduction in g_s following imposition of water stress. Similar reduction in C_i has been reported by (Souza et al. 2004) in cowpea plants during water stress and recovery.

Rate of photosynthesis directly affects the biomass production and yield of crops. In rice, higher leaf photosynthetic efficiency was reported to be correlated with greater biomass. Drought affects leaf photosynthesis either through stomatal closure or by metabolic impairment (Lawlor and Cornic 2002). A Significant negative effect of drought on leaf net CO_2 assimilation rate (A), stomatal conductance (g_s), and transpiration rate (E) have been reported earlier in different crops (Lawlor and Cornic 2002; Centritto et al. 2009; Kim et al. 2012). Flexas and Madrano (2002) opined that stomatal closure is the earliest response to drought and is the main limitation to photosynthesis under mild and moderate stress condition. Plants under water deficit reduce water losses through

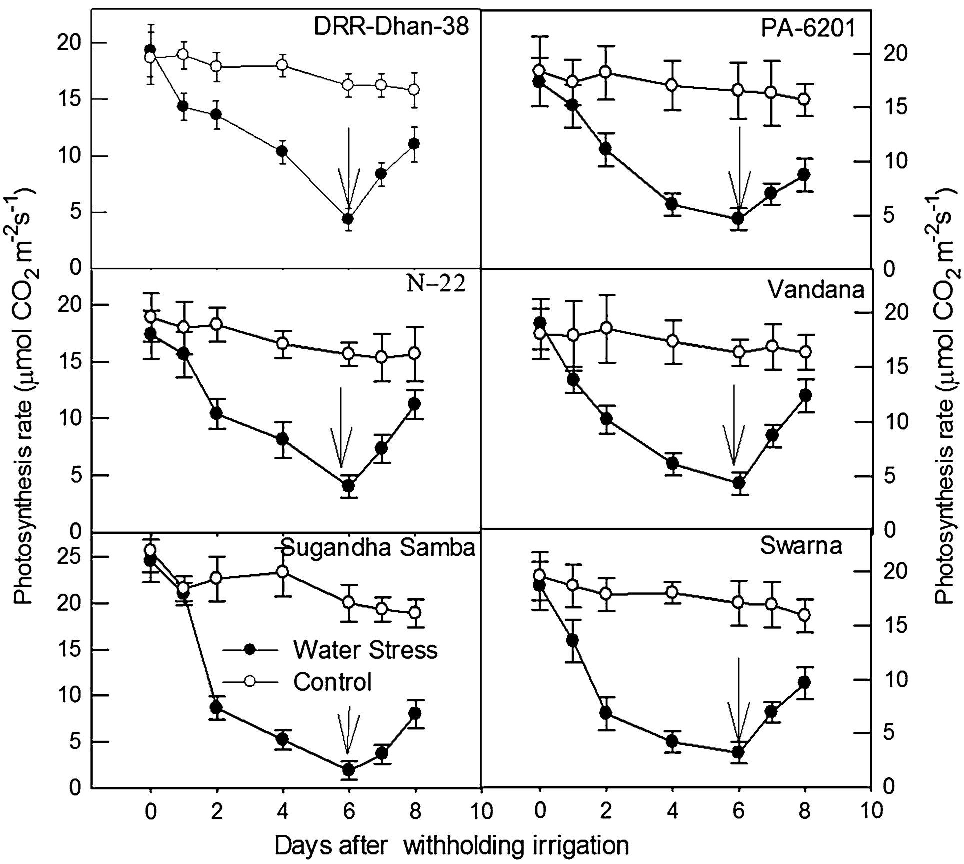

Fig. 2 Influence of water stress and recovery after re-watering on rate of photosynthesis (P_N) in different rice varieties. Each value represents the mean of four replications ± SE

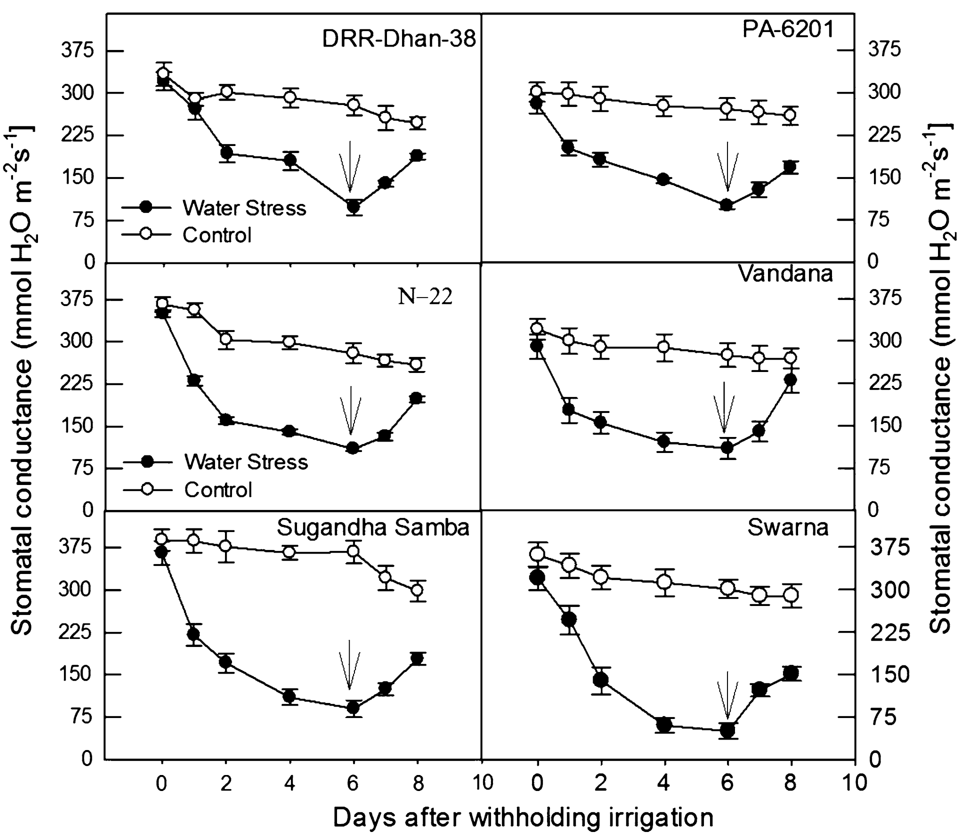

Fig. 3 Influence of water stress and recovery after re-watering on stomatal conductance (g_s) in different rice varieties. Each value represents the mean of four replications ± SE

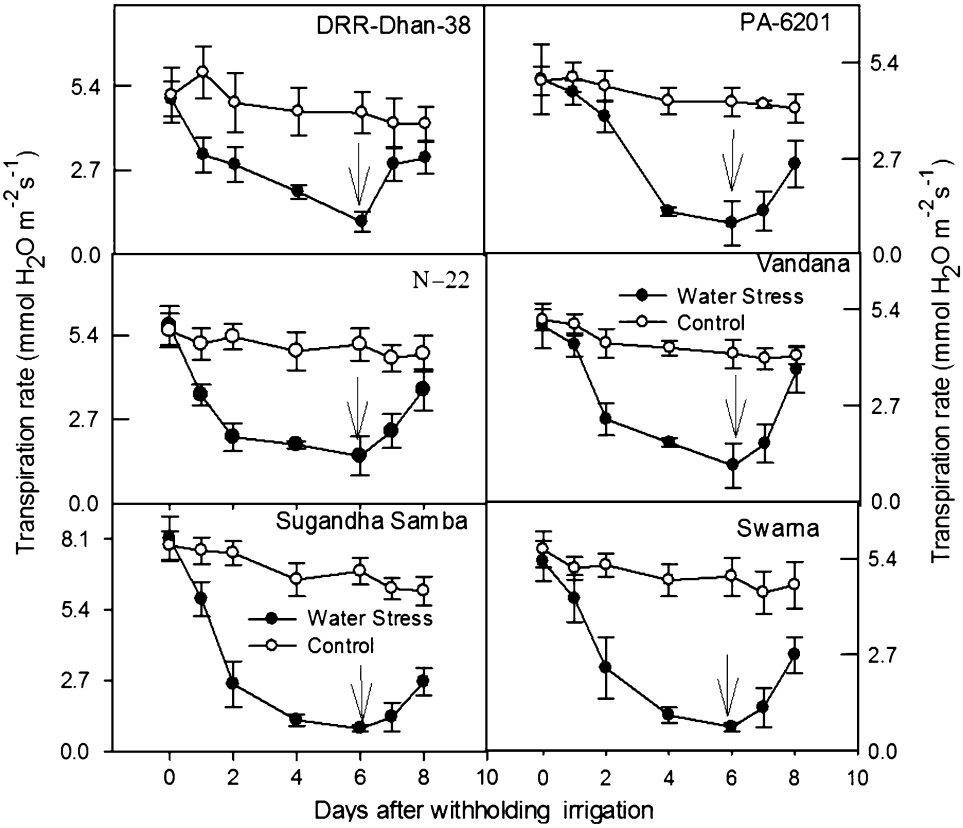

Fig. 4 Influence of water stress and recovery after re-watering on Transpiration rate (*E*) in different rice varieties. Each value represents the mean of four replications ± SE

transpiration by reducing stomatal conductance. Water stress also affects internal CO_2 transport of leaf, activities of enzymes and finally photosynthetic capacity (Ghannoum 2009; Lawlor and Tezara 2009). However internal (metabolic and diffusive) limitations become predominant relative to stomatal limitation as water stress further increases (Galmes et al. 2007; Tezara et al. 2008; Ghannoum 2009; Lawlor and Tezara 2009). Significant varietal differences in photosynthetic response to water stress have been reported in different crop plants (Subrahmanyam et al. 2006; Cruz de Carvalho et al. 2010). Differences amongst the varieties in recovery of photosynthesis parameters has also been reported in maize cultivars (Cruz de Carvalho et al. 2010). Ghannoum (2009) opined that the differences in stomatal and non-stomatal contributions to the limitation of photosynthesis could be due to the species-specific differences. Significant varietal differences were noticed for recovery of photosynthesis after re-watering. Complete recovery of gas exchange parameters 3 days after re-watering have been reported in cowpea (Souza et al. 2004). Water stress had no significant effect on mean F_v/F_m ratio in all the varieties, except Sugandha Samba and Swarna (Table 3) indicating that water stress did not influence the primary photochemistry of PSII and energy distribution within the light harvesting complex (Subrahmanyam et al. 2006; Lu and Zhang 1999). However, significant varietal differences were observed. The F_v/F_m ratio is generally very resistant to stress conditions. da Silva and Arrabaça (Marques da Silva and Arrabaca 2004) reported that in *Setaria sphacelata* F_v/F_m was not affected even when the leaf RWC decreased to 50 %. Similarly, Souza et al. (2004) reported that during the initial phases of water stress the photochemical activity was not affected as revealed by lack of alterations in fluorescence parameters associated with PSII activity. However, under severe stress conditions a reduction in F_v/F_m was observed in cowpea. Differential Inhibition of F_v/F_m in maize cultivars has been reported by Cruz de Carvalho et al. (2010), and they attributed this to differences concerning PSII function and susceptibility to photoinhibition amongst the maize varieties. F_v/F_m ratio reflects the maximal efficiency of excitation energy captured by "open" PSII reaction centers. A decrease in this parameter by moisture stress in Sugandha Samba and Swarna indicates down regulation of photosynthesis (Öquist et al. 1992). The Φ_e (F_v'/F_m') representing the efficiency of excitation transfer by open PSII centres was reduced by water stress. The mean Φ_e for all varieties was reduced by 9.6 % over control by water stress treatment. The reduction in Φ_e was relatively higher in Sugandha Samba (14 %) and Swarna (11.6 %). The reduction was <10 % in the remaining varieties. The in vivo quantum yield of PSII photochemistry (Φ_{PSII}) was significantly

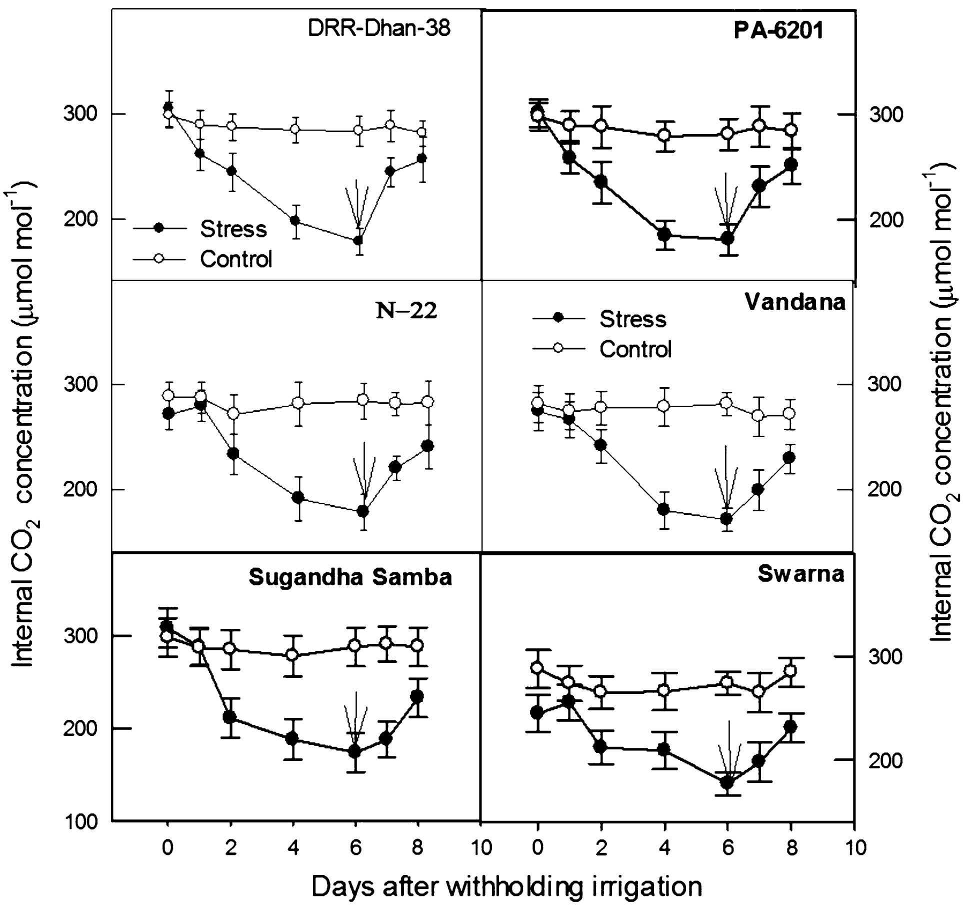

Fig. 5 Influence of water stress and recovery after re-watering on internal CO_2 concentration (C_i) in different rice varieties. Each value represents the mean of four replications ± SE

reduced by water stress. The mean Φ_{PSII} of all the varieties was reduced by 22 % by severe water stress. The reduction was higher in PA-6201(32 %), Swarna (26.2 %), Sugandha Samba (24.9 %) and N-22 (24.8 %), where as reduction was lowest in Vandana (6 %) followed by DRR-Dhan-38 (16.3 %). The quantum yield of PSII (Φ_{PSII}) and the efficiency of excitation capture by open PSII centers (Φ_e) were significantly reduced by water stress. The reduction in Φ_{PSII} is mainly due to the reduction in Φ_e (F_v'/F_m'). The reduction in F_v'/F_m' may reflect the light-induced non-photochemical quenching. Zhang (1999) reported that PS II photochemistry in light-adapted leaves was modified in water-stressed plants. This was shown by the decrease in the efficiency of excitation energy capture by open PS II reaction centres and the quantum yield of PS II electron transport and a significant increase in non-photochemical quenching.

Water stress significantly reduced the apparent electron transport rate (ETR) in all the varieties, and the mean reduction in ETR for all the varieties was 21.9 % over control plants (Table 4). The reduction in ETR was 31.5 % in PA-6201, 24.9 % in N-22 and Sugandha Samba. However, in Vandana the reduction was only 7 % with respect to control. The ETR increased gradually with increasing PAR both in irrigated control and water stressed plants in all the varieties (Fig. 6). However the ETR reached saturation point at lower PAR levels in water stressed plants in all the varieties. Significant reductions in ETR due to water stress has been reported in two Mediterranean tree species (Rincón et al. 2008).

Imposition of water stress significantly reduced (11 %) the mean coefficient of photochemical quenching (q_P) for all the varieties as compared to irrigated control. The reduction was higher in Sugandha Samba (18.9 %) and PA-6201 (14.7 %). The reduction in q_P was lower in Vandana (5.3 %) and DRR-Dhan-38 (8.2 %). Conflicting results have been reported in the literature regarding the effect of water stress on q_P. A linear reduction in q_P with decreasing RWC has been reported earlier (Havaux et al. 1988; Marques da Silva and Arrabaca 2004; Flagella et al. 1994). However, water stress marginally increased the coefficient of non-photochemical quenching (q_N) in all the varieties. The increase in q_N was higher in PA-6201, Swarna, DRR-Dhan-38 and comparatively less in Vandana and N-22 (Table 4). Significant varietal differences were observed, which suggested that the genotypic differences in the response of PSII activity could be exploited as traits for the selection of drought tolerant genotypes.

Table 4 Influence of post-anthesis water stress on leaf chlorophyll fluorescence parameters in different rice varieties

Variety	Fv/Fm		Φ_e (*Fv′/Fm′*)		Φ_{II} (*Fv′/Fm′* × qP)		Apparent electron transport rate (ETR)		Coefficient of photochemical quenching (qP)		Coefficient of non-photochemical quenching (qN)	
	Control	Stress	Control	Stress	Control	Stress	Control	Stress	Control	Stress	Control	Stress
DRR Dhan-38	0.78	0.78	0.66	0.61	0.480	0.402	69.30	55.61	0.73	0.67	0.4	0.55
N-22	0.79	0.78	0.70	0.64	0.670	0.504	92.08	69.13	0.95	0.84	0.39	0.46
PA-6201	0.80	0.79	0.71	0.61	0.530	0.360	73.10	50.09	0.78	0.69	0.40	0.57
S. samba	0.80	0.74	0.69	0.61	0.610	0.458	84.87	63.76	0.88	0.75	0.40	0.49
Swarna	0.81	0.75	0.70	0.64	0.520	0.384	68.00	52.67	0.74	0.60	0.39	0.54
Vandana	0.79	0.79	0.70	0.65	0.530	0.494	73.70	68.54	0.76	0.72	0.41	0.46
Mean	0.80	0.77	0.69	0.63	0.56	0.43	76.84	59.97	0.81	0.71	0.40	0.51
LSD (*P* < *0.05*)	0.036		0.033		0.094		3.273		0.025		0.012	

Each value represents the mean of four replications

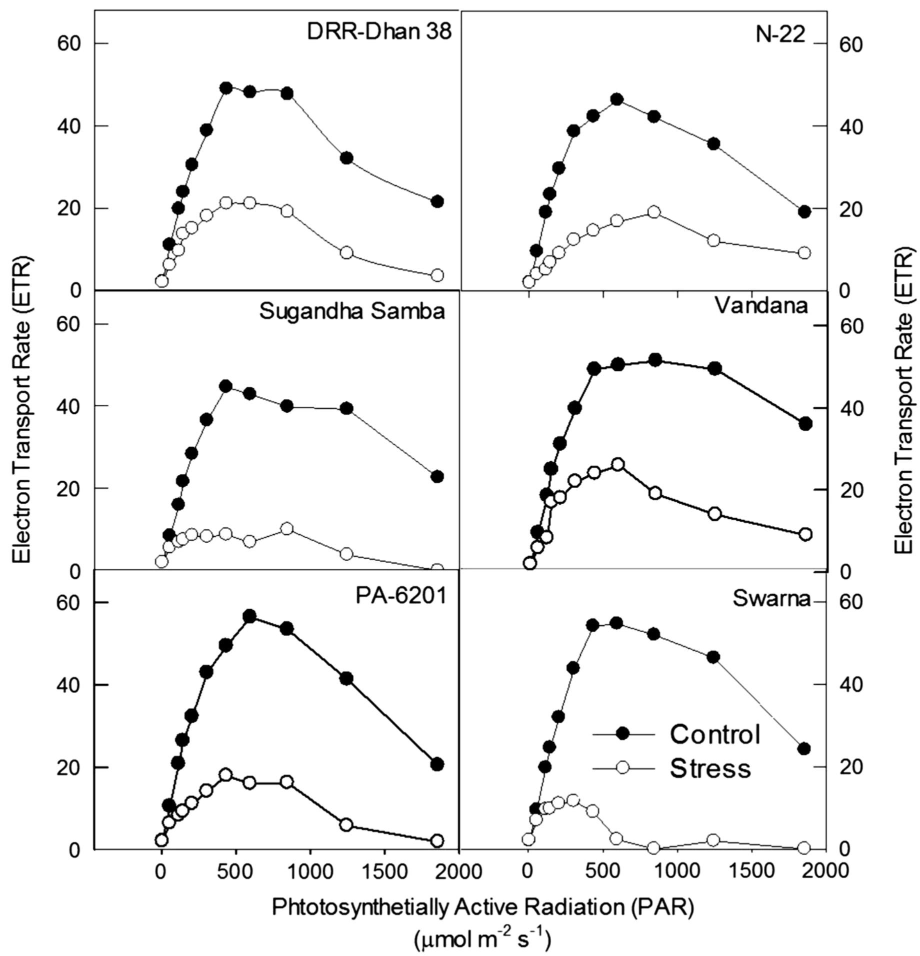

Fig. 6 Influence of water stress and recovery after re-watering on electron transport rate (ETR) as a function of photosynthetically active radiation (PAR) in different rice varieties. Each value represents the mean of two replications

In conclusion the data on leaf photosynthetic traits and leaf water potential measurements (Ψ_{leaf}) and chlorophyll fluorescence parameters indicate significant differences amongst the tested rice varieties under water stress. The water stress induced reduction in Ψ_{leaf} was more pronounced in Swarna and Sugandha Samba as well as re-recovery in Ψ_{leaf} after re-watering was lower in both these varieties and relatively higher in Vandana, DRR-Dhan-38 and N-22. Imposition of water stress resulted in significant reduction in rate of photosynthesis, stomatal conductance, transpiration and internal CO_2 concentration in all the varieties. After re-watering the photosynthetic traits recovered and the recovery was higher in Vandana, N-22, PA-6201 and lower in Sugandha Samba and Swarna. Water stress has non-significant effect on maximum photochemical efficiency (F_v/F_m) in most of the varieties, with the exception of Sugandha Samba and Swarna. Water stress decreased the efficiency of excitation capture (Φ_e), in vivo quantum yield of PSII photochemistry (Φ_{PSI}), coefficient of photochemical quenching (qP) and increased the coefficient of non-photochemical quenching (qN). The data on photosynthetic traits and chlorophyll fluorescence parameters indicated that varieties like Vandana, N-22, DRR-Dhan-38 and PA-6201 are relatively tolerant to water stress as they maintained relatively higher, Ψ_{leaf}, P_N, g_s and high values of photochemical efficiency (Fv/Fm, Φ_e, Φ_{PSI} and ETR) and these parameters are useful for differentiating drought susceptible and tolerant genotypes. Significant recovery of Ψ_{leaf} and photosynthetic parameters indicated that imposition of water stress did not result in irreversible damage to photosynthetic apparatus.

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