Environment and Ecology 40 (2B) : 693—701, April—June 2022
ISSN 0970-0420

Leaf Thickness and Gas Exchange Parameters Render Differential Drought Tolerance in Rice (*Oryza sativa* L.) at the Flowering Stage

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Received 17 February 2022, Accepted 8 March 2022, Published on 17 April 2022

ABSTRACT

Leaf thickness plays a fundamental role in species strategies of resource use and acquisition. Gas exchange parameters and leaf thickness are important for maintaining drought tolerance in rice (*Oryza sativa* L.). A pot experiment was conducted by imposing drought stress (DS) on fourteen rice genotypes selected from a pool of 100 genotypes for determining drought tolerance. Five days before flowering, DS was imposed by withdrawing irrigation maintained at 50% field capacity, whereas non-stress pots were maintained at 100% field capacity. Our results showed that the genotypes Parijata, IC 516003, IC 516008 and IC 516149 were less affected by DS with higher values of specific leaf weight (SLW), leaf area (LA), membrane stability index (MSI), photosynthetic rate (Pn), stomatal conductance (gs), water use efficiency (WUE), intercellular CO_2 concentration (Ci) and carboxylation efficiency (CE) associated with better mechanism for DS tolerance. The genotype Prasad was most susceptible to DS with low in gas exchange and leaf growth parameters and genotypes Lalat, Pathara and IR 36 showed intermediate response. Overall, the parameters studied were found to be highly sensitive to DS and therefore can be used in breeding programs for screening drought tolerant genotypes.

Keywords Drought, Leaf thickness, SLW, Field capacity, WUE.

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INTRODUCTION

The interaction of plants and atmosphere is a continuous process in which water plays an important role. Due to the effects of ongoing climate change, the productivity of rainfed and rice is subjected to unpredictable shortage of water (Cal *et al.* 2019). Out of 159.7 million hectares of rice-cultivated area worldwide, around one fifth is DS prone area (Geda *et al.* 2019). In rainfed low lands, medium low lands and uplands, DS is the most vital factor that decreases the productivity of rice by affecting leaf thickness and leaf gas exchange parameters (Panda *et al.* 2019). However, the loss due to drought can be avoided by developing tolerant genotypes that are more resilient to DS in rice plants (Parida *et al.* 2021b). In fact, characterization of genotypes and trait identification with different mechanisms of drought tolerance would be a promising approach to substantiate DS tolerance in them (Parida *et al.* 2021c).

Lower SLA and higher SLW indicates thicker leaves which mean the genotypes having lower SLA usually have higher biomass per unit LA and therefore indicate greater photosynthetic capacity than thinner leaves (Songsri *et al.* 2009). Farooq *et al*. (2010) observed that LA is positively correlated with P_n and g_s under DS. The reduction in P_n indicates the decrease in the activities of CO_2 assimilation enzymes like ATP synthase or ribulose-1, 5-bisphosphate carboxylase/ oxygenase (RuBisCO) and increase in the activity of oxidative enzymes (Hayat *et al.* 2012 and Parida *et al.* 2021a). The genotypes maintaining higher P_n allowed better of gas exchange and higher photosynthetic efficiency, indicating greater tolerance to DS (Hungsaprug *et al.* 2020). The reduction in gs is attributed to reduction in gas exchange ability, hence low photosynthetic efficiency (Park *et al*. 2020). Reduction in P_n and g_s are positively significant associated with T_r (Zain *et al.* 2014). As completely closed stomata reduced T_r, conserved endogenous water and leading to enhanced adaptive tolerance mechanism against DS (Park *et al*. 2020). Further the escalation of WUE is directly and significantly associated to P_n and indicates the osmotic balance in the plants (Lidon and Cebola 2012). Earlier many researchers had suggested that reduction in P_n and T_r are well related with stomatal closure ensuing to an increase in WUE (Ruggiero *et al.* 2017). The genotypes were able to maintain higher WUE with lower C_i and higher CE allowed better amount of gas exchange and higher photosynthetic efficiency indicating greater tolerance ability under DS (Chen *et al.* 2019 and Yang *et al*. 2019). It is found that DS resilience in rice is associated with less reduction in P_n, g_s, T_r and CE with low C_i and high WUE is considered as tolerance mechanism under DS conditions (Kartika *et al.* 2020 and Xu *et al.* 2020). The objectives of the study were to reveal the impact of DS on leaf thickness, MSI, P_n, g_s, WUE, C_i and CE at flowering stage in ten rice genotypes.

MATERIALS AND METHODS

Plant materials and treatments

The performance of fourteen rice genotypes including two controls (Sahabhagidhan as a tolerant and IR 64 as a susceptible control) which were selected from the vegetative stage drought screening during the dry season 2018 were studied in this experiment. Pot experiment took place during dry season 2019 at ICAR-National Rice Research Institute, Cuttack, India in two sets under well-watered (C) and drought stress (DS) conditions. Each pot was filled with a 4 kg mixture of farm yard manure (FYM) and dried dust farm soil in a ratio of 1:3 in Completely Randomized Design. Standard agronomic practices were followed, fertilizer (N, P and K) was kept at recommended levels and pesticides were applied as needed for the growing of healthy plants. Thinning was done after 15 days of germination to maintain single plant per pot. DS was imposed before the 5 days of flowering by withdrawing irrigation and maintaining 50% field capacity, while maintaining 100% for C. Sampling was done at flowering stage.

Leaf traits

At flowering stage the second leaf of the mother tiller was used to calculate the LA of rice plants. Leaves from each replication (ten leaves per replication) were collected and cleaned through the tissue paper. LA was measured using portable instrument LI-3100C (LI-COR, Lincoln, Nebraska, USA). After taking LA, oven dried the leaves at 70°c for 72 h.

SLA was calculated by underlying equation (Junior *et al.* 2019)

$$\text{SLA (cm}^2\text{ g}^{-1}) = \frac{\text{Leaf area (cm}^2)}{\text{Leaf dry weight (g)}}$$

SLW was calculated by underlying equation (Jumrani and Bhatia 2019).

$$\text{SLW (mg cm}^{-2}) = \frac{\text{Leaf dry weight (mg)}}{\text{Leaf area (cm}^2)}$$

Leaf gas exchange parameters

Leaf gas exchange parameters were measured between 8.00 AM to 12 PM under bright sunny days using LI-6400 (LI-COR, Lincoln, Nebraska, USA). Second leaf of the plant was placed in the leaf chamber to take observations at a PFD of 1000 µmol m^{-2} s^{-1}, leaf temperature was 28°C, ambient CO_2 concentration was 410 µmol CO_2 mol-1 air and vapor pressure deficit was 2.0 kPa. The parameters like P_n (µmol m^{-2} s^{-1}), gs (mol m^{-2} s^{-1}), Tr (m mol m^{-2} s^{-1}) and C_i (mmol m^{-2} s^{-1}) were recorded. WUE and CE were calculated as per the methods of Santosh *et al.* (2017). Photosynthetic rate (Pn).

(i) Water use efficiency WUE) =

$$\frac{\text{Photosynthetic rate } (P_n)}{\text{Transpiration rate } (T_r)}$$

(ii) Carboxylation efficiency (*CE*) =

$$\frac{\text{Photosynthetic rate } (Pn)}{\text{Intercellular } CO_2 \text{ concentration } (C_i)}$$

Leaf water potential (LWP)

In an attempt to measure the LWP, the second fresh leaves of rice pants were sampled for the purpose of using the water potential system (PSYPRO, Wescor). The sampling was performed between 12 noon to 2pm and data was taken using the protocol proposed by Barrs and Weatherley (1962).

Membrane stability index (MSI)

Second fresh leaves of rice plant were taken, weighed and incubated at 30°C in water bath for 4 h. Initial electrical conductivity (EC) was taken by an EC meter, again the samples were incubated at 100°C for 15 minutes and final EC reading was taken. MSI was calculated as per protocol proposed by Sairam (1994).

$$\text{MSI (\%)} = 1 - \frac{(1- (T_1/ T_2))}{(1- (C_1 / C_2))} \times 100$$

Where,

T_1 and T_2 : Initial and final EC reading of stressed plant's leaves

C_1 and C_2 : Initial and final EC reading of control plant's leaves

Statistical analysis

Data were collected from six replications. The p-value and Pearson's correlation coefficient were calculated using Microsoft excel. The statistical data analysis was carried out using XLSTAT-2014 and Crop Stat 7.2 (IRRI 2009) statistical software. Analysis of variance (ANOVA) was calculated at 5% level of significance for treatments and genotypes.

RESULTS AND DISCUSSION

Induction of DS at flowering stage on rice plants resulted in significant reductions ($p<0.05$) of LA. With lower SLA and higher SLW, thicker leaves indicate greater photosynthetic capacity than thinner leaves. DS leads to significant reductions ($p<0.05$) in P_n, g_s, T_r, C_i, C_E, LWP and MSI. It was indicated that, the rice crop had experienced DS during flowering stage stress.

Leaf morphology

As a result of DS, plants lose leaf water content, diminution in cell division and elongation which can lead to a reduction in LA (Guendouz *et al.* 2016). As shown in Fig. 1, the DS significantly reduced the LA in all the studied genotypes when compared with C. In particular, susceptible control (IR64) (62.77%) exhibited sharp reduction in LA along with Prasad (60.05%), Naveen (51.25%) and Satabdi (50.99%) compared to tolerant control (Sahabhagidhan) (33.01%). However, the genotypes Parijata (29.35%), IC 516149 (30.5%) and IC 516130 (31.23%), showed less reduction than Sahabhagidhan under DS condi-

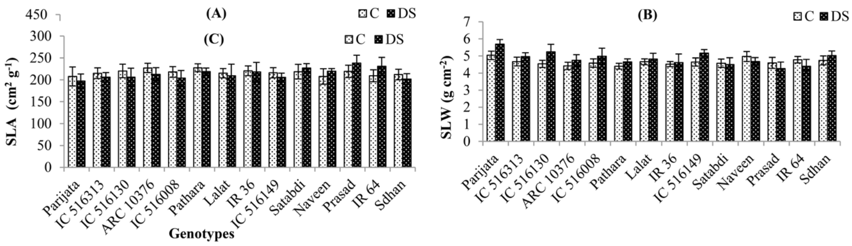

Fig. 1. Variation in (A) Leaf area, (B) Specific leaf weight (SLW) and (C) Specific leaf area (SLA) of fourteen rice genotypes under well watered (C) and drought stress (DS) condition. Sahabhagidhan (Sdhan) and IR 64 are drought tolerant and susceptible control respectively. Values are expressed as means of six biological replications ± SE at the 5% level.

tions. The SLW has a direct impact on dry matter accumulation and photosynthetic efficiency (Jumrani and Bhatia 2019). The SLW has been reported to be associated with drought tolerance, possibly indicating thicker leaves help in leaf water conservation. A significant positive correlation was observed between SLW with leaf gas exchange parameters. Under DS, the SLW was significantly increased in tolerant control (Sahahagidhan) (5.59%) but susceptible control (IR64) (8.00%) exhibited sharp reduction in SLW compared to C. The genotypes IC 516130 (13.24%), Parijata (11.49%) and IC 516008 (7.93%), showed higher increment of SLW whereas maximum reduction in SLW was observed in Prasad (7.28%), Naveen (5.75%) and Satabdi (1.61%). Tolerant genotypes with higher photosynthetic traits possess higher SLW with more adaptive mechanisms under DS conditions (Timung *et al.* 2017). The SLW and photosynthetic efficiency is negatively associated with SLA. This indicated that the genotypes with high SLW tended to give less SLA. In our study, the SLA was significantly decreased in tolerant control (Sahahagidhan) (4.84%) but the value was increased in susceptible control (IR64) (9.41%) compared to C. More significantly, the genotype IC 516008 (6.44%), IC 516130 (6.40%) and Parijata (5.09%) showed higher reduction of SLA than that of Sahabhagidhan and higher increment of SLA was noticed in Prasad (7.86%), Naveen (5.51%) and Satabdi (3.68%) under DS conditions. SLA was found to decrease in tolerant genotypes whereas it increased in susceptible genotypes may be due to the fact that tolerant genotypes were able to accumulate more photosynthates in less area with thicker leaves under DS (Kartika *et al.* 2020 and Abo *et al.* 2021).

Gas exchange parameters

DS at the flowering stage decreased gas exchange parameters (Haritha *et al.* 2017). The P_n of all the studied genotypes was significantly ($p<0.05$) reduced under DS conditions when compared with C. The susceptible control (IR64) (70.32%) exhibited sharp reduction in P_n compared to tolerant control (Sahabhagidhan) (31.18%) (Fig. 2). The genotypes IC 516130 (24.56%), Parijata (30.60%), IC 516149 (33.79%) had showed less reduction in P_n, whereas maximum reduction was observed in Prasad (73.10%), Satabdi (62.93%) and Naveen (60.55%) under DS conditions. The reduction of P_n was probably due to the stomatal closure and/or functional alternation of the photosynthetic apparatus (Yamori *et al.* 2020). P_n was strongly correlated with g_s. In our study, the value of g_s was significantly reduced in all the genotypes under DS over C. The genotypes IC 516008 (50.47%), Parijata (53.87%), and IC 516149 (55.97%) had showed less reduction in g_s than Sahabhagidhan, whereas maximum reduction was observed in Prasad (80.57%), Satabdi (74.65%) and Naveen (72.77%) under DS conditions. The reduction of g_s was probably due to the stomatal closure and CO_2 concentration in the chloroplast (Shanmugam *et al.* 2021). Stomatal closure reduces Tr and CO_2 availability makes the rice plants more susceptible to photo damage (Ouyang *et al.* 2017). The genotypes IC 516130 (50.89%), IC 516008 (52.07%) and IC 516149 (54.26%) showed less reduction in T_r, whereas maximum reduction was observed in Prasad (76.97%) followed by Satabdi (71.68%) and Naveen (69.73%) under DS conditions. The tolerant genotypes were able to maintain

Table 1. Correlation coefficient (r-value) between leaf morphological traits and leaf gas exchange parameters at flowering stage under DS conditions. Significant differences are indicated: *- p<0.05, **- p<0.01, ns- not significant. LA- leaf area, SLA-specific leaf area, SLW-specific leaf weight, P_n-photosynthetic rate, g_s-stomatal conductance, T_r-transpiration rate, WUE-water use efficiency, C_i-intercellular CO_2 concentration, CE-carboxylation efficiency, LWP-leaf water potential, MSI- membrane stability index.

	LA	SLA	SLW	Pn	gs	Tr	WUE	Ci	CE	LWP
SLA	-0.17ns									
SLW	0.17ns	-0.98**								
Pn	0.39*	-0.63**	0.62**							
gs	0.34*	-0.61**	0.63**	0.82**						
Tr	0.33*	-0.45*	0.44*	0.89**	0.71**					
WUE	0.36*	-0.60**	0.60**	0.78**	0.64**	0.53**				
Ci	-0.37*	0.59**	-0.58**	-0.91**	-0.81**	-0.86**	-0.68**			
CE	0.39*	-0.63**	0.63**	0.96**	0.84**	0.89**	0.78**	-0.94**		
LWP	0.34*	-0.41*	0.42*	0.80**	0.71**	0.67**	0.66**	-0.70**	0.79**	
MSI	0.42*	-0.48**	0.46*	0.72**	0.66**	0.67**	0.53**	-0.66**	0.70**	0.71**

minimum reduction in g_s and T_r with higher WUE (Shanmugam *et al*. 2021). Here in, DS led to significant increase in WUE in all the studied genotypes at flowering stage. The genotypes IC 516130 (34.67%) had showed maximum increment in WUE followed by Parijata (34.49%) and IC 516313 (31.24%) than Sahabhagidhan, while minimum increment was observed in Prasad (14.11), Satabdi (22.54) and Naveen (23.69%). In tolerant genotypes, lower g_s results in reduced T_r, contributing to higher WUE (Yang *et al.* 2019). Improved WUE under DS also contribute to maintaining Pn for sustainable crop production (Chen *et al.* 2019). The reduction in P_n due to stomatal closure led to increase in C_i under DS conditions. In particular, the susceptible control (IR64) (40.74%) exhibited maximum increased in C_i compared to tolerant control (Sahabhagidhan) (23.31%) (Fig 2). However, the genotypes IC 516130 (12.74%), IC 516008 (16.11%) and IC 516149 (16.41%) exhibited minimum significantly (p<0.05) increased in C_i, whereas maximum was observed in Prasad (38.37%), followed by Satabdi (37.33%) and Naveen (35.57%) under DS conditions. The value of C_i was negatively correlated with CE. Compared to C, DS leads to a significant (p<0.05) decrease in CE at flowering stage in all the studied genotypes (Fig. 2). The genotype IR64 (82.35%) exhibited sharp reduction in CE compared to Sahabhagidhan (46.95%). The genotypes IC 516130 (33.77%), Parijata (42.66%) and IC 516149 (44.76%) had less reduction in CE, whereas maximum reduction was observed in Prasad (83.44%), Satabdi (76.67%) and Naveen (74.51%) under DS conditions. The reduction of CE is probably due to the stomatal closure, structural damage of photosynthetic apparatus and reduction in LWP (Panda *et al.* 2020 and Parida *et al.* 2021a). The ability of the genotypes to maintain P_n, g_s, T_r and CE is the major importance for stress tolerance under DS conditions (Mishra *et al.* 2018).The genotypes Parijata, IC 516130, IC 516008 and IC 516149 showed higher value of leaf gas exchange parameters compared with Prasad. The genotypes Pathara, Lalat and IR 36 showed intermediate behavior under DS conditions.

LWP and MSI

As a result of DS, plants lose leaf water content, reducing membrane stability which can lead to a reduction in LWP (Hussain *et al*. 2018). As shown in Fig. 3, the DS significantly (p<0.05) reduced LWP in all the studied genotypes when compared with C. The susceptible control (IR64) (65.08%) exhibited sharp reduction in LWP compared to tolerant control (Sahabhagidhan) (44.65%). The genotypes Parijata (42.35%), IC 516149 (45.95%) and IC 516130 (49.15%) showed less reduction in LWP, whereas maximum reduction was observed in Prasad (66.38%), Naveen (62.21%) and Satabdi (60.88%) under DS conditions. The ability of the genotypes with minimum reduction in LWP is the major importance for stress tolerance under DS conditions (Yang *et al.* 2019). Higher membrane stability helps to maintain cell turgor and maintain higher

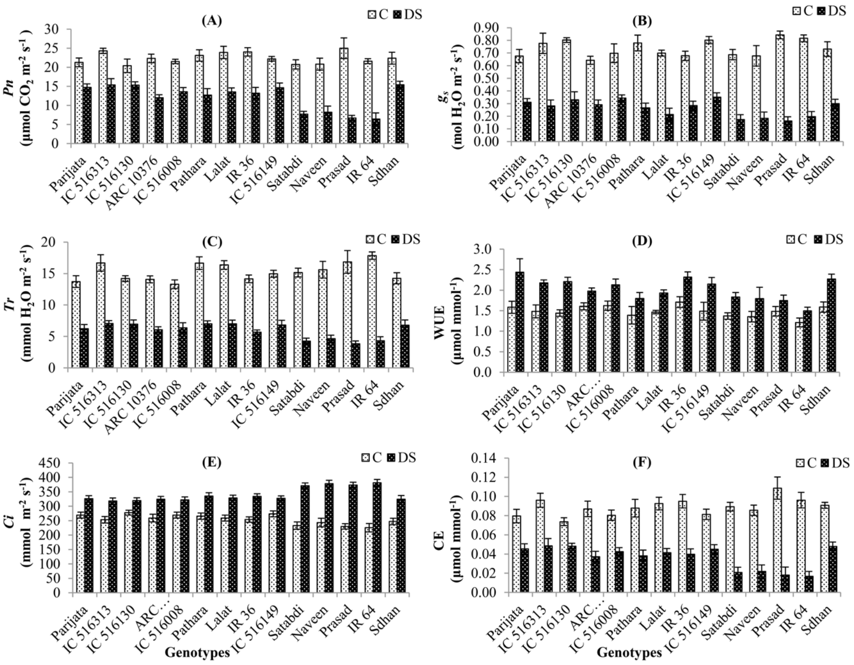

Fig. 2. Variation in (A) photosynthetic rate (P_n) (B) stomatal conductance (g_s), (C) transpiration rate (T_r), (D) water use efficiency (WUE), (E) intercellular CO_2 concentration (C_i) and (F) carboxylation efficiency (CE) of fourteen rice genotypes under well watered (C) and drought stress (DS) condition. Sahabhagidhan (Sdhan) and IR 64 are drought tolerant and susceptible control respectively. Values are expressed as means of six biological replications ± SE at the 5% level.

P_n and g_s (Choudhary *et al.* 2017). Similarly, MSI was significantly reduced ($p<0.05$) in all the studied genotypes under DS. The susceptible control (IR64) (61.45%) exhibited sharp reduction in MSI compared to tolerant control (Sahabhagidhan) (32.87%). The genotypes IC 516008 (27.37%), IC 516149 (30.58%) and Parijata (31.23%), had showed less reduction in MSI as compared to tolerant control, whereas maximum reduction was observed in Prasad (55.63%), Satabdi (53.77%) and Naveen (51.50%) under DS conditions. Our study revealed that with higher LWP the cell membranes of Parijata, IC 516130, IC 516008 and IC 516149 are more stable than Prasad, Satabdi and Naveen. Again, the genotypes Pathara, Lalat and IR 36 showed intermediate behavior in terms of LWP and MSI. The genotypes that can modulate the thicker leaves (higher SLW), higher photosynthesis, higher LWP and sustain membrane stability through osmoregulation are capable of withstanding under DS conditions than those which cannot (Rao and Chaitanya 2019 and Huang *et al*. 2019).

Relationship between leaf morphological traits and leaf gas exchange parameters

In the present study (Table 1), SLA was negatively significant correlated with SLW ($r= -0.98$, $p<0.01$). Leaf P_n, g_s, T_r, WUE and CE ($r= 0.62$, 0.63, 0.44, 0.60 and 0.63) were positively correlated with SLW whereas, C_i ($r= -0.58$, $p<0.01$) was negatively significant influenced by SLW. A strong positive correlation between Leaf P_n with g_s, T_r, WUE and CE ($r= 0.82$, 0.89, 0.78, and 0.96 respectively, all $p<0.01$) was observed whereas, P_n was highly negative correlated with C_i ($r= -0.91$, $p<0.01$). Further, a positive correlation between LWP with SLW, P_n, g_s, T_r, WUE and CE ($r= 0.42$, 0.80, 0.71, 0.67, 0.66 and 0.79) was observed.

CONCLUSION

Besides the identification of tolerant genotypes, attention has been inclined to the recognition of

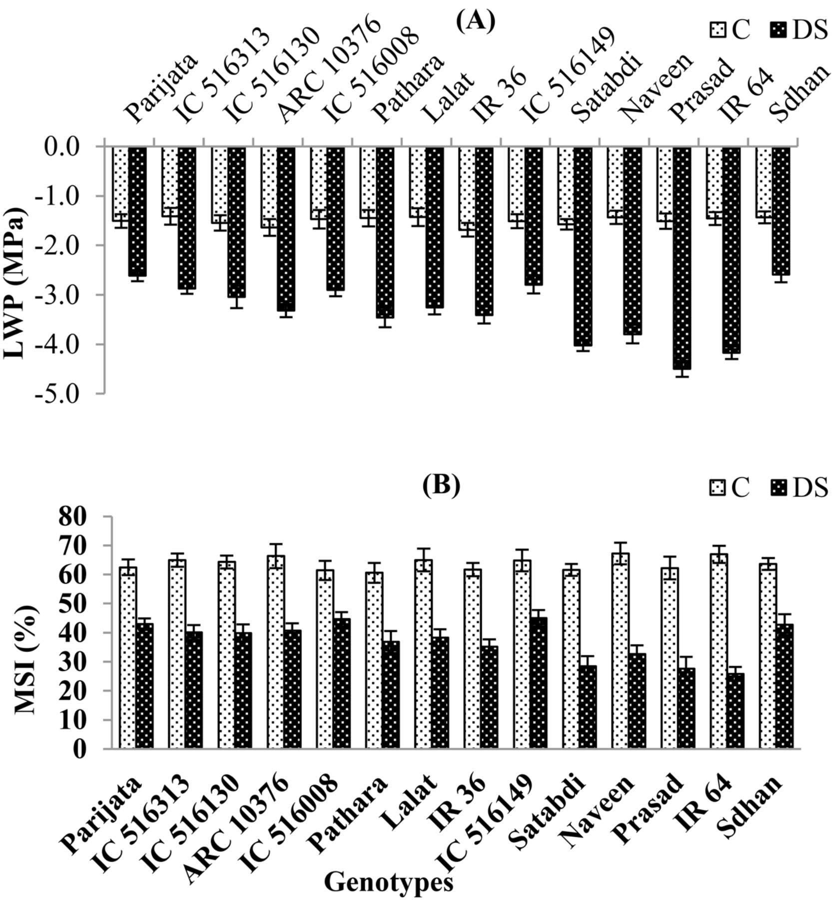

Fig. 3. Variation in (A) leaf water potential (LWP) (B) membrane stability index (MSI) of fourteen rice genotypes under well watered (C) and drought stress (DS) condition. Sahabhagidhan (Sdhan) and IR 64 are drought tolerant and susceptible control respectively. Values are expressed as means of six biological replications ± SE at the 5% level.

appropriate techniques with suitable traits that can precisely differentiate between tolerant and susceptible genotypes under DS conditions. An informative study of leaf thickness and gas exchange parameters was found very sensitive and provided significant information regarding genotypic sensitivity levels. The results showed that SLW, Pn, gs, Tr, WUE, C_i and CE provide accurate information on the genotypes based on their tolerance level. A strong correlation between SLW, with P_n, g_s, T_r, WUE, C_i and CE suggested that these parameters should be studied in the association while evaluating tolerant genotypes under DS conditions. However, the genotypes Parijata, IC 516130, IC 516149 and IC 516008 confer significantly tolerance to DS and could be introduced into large scale evaluation programs aiming at designing and developing drought tolerance lines.

ACKNOWLEDGEMENT

Authors express their gratefulness to the NICRA (National Innovation on climate resilient Agriculture) project, ICAR-National Rice Research Institute, Cuttack and Odisha University of Agriculture and Technology, Bhubaneswar, Odisha for providing necessary facilities.

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