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Tolerant varieties and exogenous application of nutrients can effectively manage drought stress in rice

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ABSTRACT

Common abiotic stresses in rain-fed rice areas like drought can occur at any phase of crop growth and may occur periodically. Variation in intensity and severity of drought requires the use of different rice varieties and different nutrient management strategies. This study evaluated the morphological and physiological response of contrasting rice cultivars (Rajalaxmi, IR64, and Sahbhagidhan) to various nutrient combinations under water sufficiency and scarce conditions. Drought stress at vegetative stage significantly reduced tiller formation, dry matter remobilization, and photosynthesis, leading to around 41.6% yield reduction. The effect of drought stress was more evident in Rajalaxmi and IR64 by a yield reduction of 57.4% and 43.2% as against only 24.3% in Sahbhagidhan. The combined application of nutrients resulted in higher proline accumulation, chlorophyll and carbohydrate concentrations, and photosynthesis and antioxidant enzymes, ultimately better tolerance to drought. This is reflected in higher values of tolerance indices and low scores of leaf drying and leaf rolling, especially for Sahbhagidhan. The combined application of P, K, Ca, Zn, and Fe resulted in 52.9, 53.3, 48.9% higher yield over P or K application. Rice drought tolerance can be managed by combining breeding of drought-tolerant high yielding varieties with the proper application of fertilizer nutrients.

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KEYWORDS

Drought; drought tolerance indices; *Oryza sativa*; nutrient management; physiological traits

Introduction

Drought incidence in rain-fed areas is the major abiotic stress especially to rice growing in around 23 million ha areas in India, the dry spells of different intensities will be more common in coming years due to climate change (Wassmann et al. 2009). Out of the 21 million ha of rice in India, about 16 million ha is in eastern India and is prone to drought either in upland or in rain-fed lowlands (Pandey and Bhandari 2008; Raja et al. 2014). Water-deficit may occur early during the monsoon season or at any time from flowering to grain filling, and the intensity of the stress depends on the duration and recurrence of water paucity (Bunnag and Pongthai 2013). The most crucial stage in crop growth to any stress whether biotic or abiotic is reproductive, so, the dry spell at this stage may be detrimental and led to the failure of crop (Venuprasad et al. 2009). The challenges for crop production are even greater for crops such as rice, which is the staple food for more than half of world's population and is being

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grown under diverse environmental conditions (Dixit et al. 2014). Drought stress reduces growth, leaf area and biomass due to senescence and lower photosynthesis (Nooden 1988) and affects overall plant water relations leading to alteration in plant osmosis and membrane integration (Praba et al. 2009). Visible morphological responses like leaf rolling, wax deposition due to plant water deficit, helps in maintaining favourable water balance within plant tissues under paucity of water (Kumar et al. 2014). Apart from leaf rolling, proline accumulation in rice leaves under drought helps in maintaining intracellular osmolality (Madhusudan et al. 2002). The reactive oxygen species (ROS) scavenging system is the common defence against drought (Vranová et al. 2002) and to detoxify ROS, plants can inherently upregulate different antioxidant enzymes like superoxide dismutase, peroxidase, and catalase, to help in reducing oxidative damage and confer drought tolerance (Zain and Ismail 2016). Genotypes with higher antioxidant activity showed better tolerance to oxidative stress (Parida and Das 2005).

Sustainable production in drought-affected areas can only be achieved through genetic modification of cultivars (i.e. developing drought-tolerant varieties). Currently, most rain-fed areas are planted with high-yielding varieties like IR 36, IR 64, Sambha Mahsuri, TDK 1 and Swarna, which were originally bred for irrigated conditions. These varieties are high yielding but are highly susceptible to drought. In years with mild to moderate drought, these varieties show high yield losses, and in years of severe drought, which occur approximately once in five years in eastern India (Pandey and Bhandari 2008), these varieties may fail to flower and produce any grain (Vikram et al. 2011). Despite the internal resistance of the plants to drought stress, the detrimental effects of drought can be minimized by an adequate and balanced supply of mineral nutrients. Increasing evidence suggests that mineral-nutrient status of plants plays a critical role in increasing plant resistance to drought stress (Marschner 1995). Water deficit significantly affects the acquirement of nutrients by roots and their movements towards shoots that is why rice growth does not often respond to nutrient input. Drought stress leads to reduction in transpiration flow due to interference in uptake and unloading mechanisms may result in low absorption of nutrients (Garg et al. 2002). Optimal nutrition greatly affects water circulation within plants, which is a highly effective method of combating drought. Under low nutrient concentrations in soil, plants have to absorb more water to be able to take up the same amount of mineral nutrients for their metabolism than they would from the soil with satisfactory fertility. Hence, plant nutrients like P, K, Ca, Mg, etc. are an essential chemical for plant growth, metabolism and reproduction (Barker and Pilbeam 2007) and these nutrients are an integral part of organic compounds like amino acids, nucleic acids, phospholipids and proteins. However, rice genotypes may vary in their response to mineral nutrition under water stress. Notably, recently released drought tolerant rice cultivars may respond better to nutrient input, and growth and yield may be enhanced under drought, compared with susceptible varieties. The study was planned with the hypothesis that the plant performance under water stress conditions can be improved by internal tolerance combined with exogenous nutrient application. Therefore, the aim of the study was to find out the relevance of metabolic and morphological parameters and its phenotypic plasticity for drought tolerance in different cultivars of rice and exogenous application of different nutrients either alone or in combination. The objectives for conducting the study were kept in mind are; (1) to compare the drought tolerance of the popularly grown varieties in response to mineral nutrition; (2) to examine the combined effect of different nutrients and cultivars on drought tolerance in terms of morphological and metabolic characters and; (3) to confirm the hypothesis that the yield of tolerant cultivars can be further enhanced with exogenous nutrient application under drought conditions.

Materials and methods

Experimental setup

The experiment was conducted for consecutive 2 years during the dry season of 2014–2015 and 2015–2016 under controlled conditions at the Indian Council of Agricultural Research-National Rice Research Institute (ICAR-NRRI), Cuttack (20° 45'N, 85° 93'E; 24 m above mean sea level), Odisha, in

mini-plots of 2.25 m², having cemented bunds to prevent the lateral movements and losses of water and nutrient. The soil was sandy-clay-loam, with pH 6.8, EC 0.071 dSm⁻¹, and available N, P, and K of 126.4, 11.5 and 104.7 kg ha⁻¹, respectively. The experimental site is of the tropical climate, with annual precipitation of 1333.6 mm, of which 75–80% is received during monsoon (June to September). The whole crop received 136.7 mm rainfall, out of which only 30.6 mm was received during the drought stress period. Mean maximum and minimum temperatures were 32.5 and 21.1°C, respectively, during the cropping period and the mean temperature was 26.7°C. The experiment was arranged in a factorial randomized block design and replicated thrice. Pre-germinated seeds of IR64 (drought sensitive), Sahbhagidhan (drought tolerant) and Rajalaxmi (hybrid) were sown at a spacing of 20 × 15 cm. The varieties chosen for the study were popular among the farmers, IR64 and Rajalaxmi was preferred under irrigated condition due to their higher yield but if drought occurs, the varieties failed to perform. These varieties were taken in the study to find out whether the nutrient application can improve their yield under drought situations. Sahbhagidhan is gaining popularity among the farmers of the upland region due to its drought tolerance and short duration. 80, 40, 40, 70, 25, 25 kg N, P, K, Ca, Zn, Fe ha⁻¹ were applied, respectively, based on treatments. P, K, Ca, Zn, Fe and 1/3rd of N were applied as basal, remaining N was top-dressed at maximum tillering, and panicle initiation stage. Control plots were kept continuously flooded with 2–3 cm water after sowing throughout the growth period, while plots subjected to drought were irrigated upto 21 days (d) after sowing, then irrigation was subsequently withdrawn for one month. Life-saving irrigation was provided only when the soil water potential reached –60 KPa; monitored using tensiometers placed at soil depths of 20 cm depth.

Assessment of growth

Plant height and the number of tillers were measured at a 2-d interval from 21 to 60 days after sowing (DAS), and at the monthly interval after that, from all the treatments. Tillers producing panicles were denoted as effective tillers. Leaf area was measured from each treatment using a digital leaf-area meter. After recording leaf area at 30 and 60 DAS, the plant parts were subsequently divided into stem and leaf sheath, and in leaf, stem and panicle when recorded at 90 DAS and maturity. For calculating dry matter (DM) accumulation samples were dried at 70°C and its partitioning was calculated.

$$\text{DM remobilization (g)} = \text{DMW per tiller at flowering} - \text{DMW per tiller at maturity}$$

$$\text{DM remobilization efficiency(\%)} = (\text{DM remobilization} / \text{DMW per tiller at maturity}) \times 100$$

$$\text{DM conversion rate(\%)} = (\text{DM remobilization} / \text{grain weight per tiller at maturity}) \times 100$$

Photosynthetic rate and electrolyte leakage

Net photosynthetic rate (Pn) and stomatal conductance were measured with infrared gas analyzer (LI-6400, LI-COR, Lincoln, NE) from different treatments between 11:00 am and 2.00 pm. Electrolyte leakage is a measure of cellular membrane stability of leaf cells under water stress. Three fresh and fully developed leaves were taken from stress and normally irrigated treatments. Leaf samples were kept in 5 ml deionized water for measuring initial electrical conductivity (EC_i) and for measuring final electrical conductivity (EC_f) samples were kept in dark for 24 h. For estimating electrical conductivity (EC_i), the cells were ruptured by autoclaving the test tubes containing leaf pieces of around 1 mm for 15 min at 103 KPa. Electrolyte leakage was then calculated as per the formula given by Liu and Huang (2000)

$$\text{Electrolyte leakage}(\%) = \frac{EC_f - EC_i}{EC_t - EC_i} \times 100$$

Biochemical analysis and antioxidant enzymes

Chlorophyll, soluble sugar and starch concentrations were determined before and after stress imposition, following the procedures of Porra (2002) and Yoshida et al. (1976), respectively. Proline and epicuticular wax were quantified using the methods of Bates et al. (1973) and Haas et al. (2001), respectively. For enzyme analysis, 500-mg leaf sample from different treatments was homogenized in 10 ml of grinding medium. Activities of catalase (CAT), peroxidase (PER) and superoxide dismutase (SOD) were determined as per the methods described by Cakmak and Marschner (1992), Chance and Maehly (1955), Giannopolitis and Ries (1977) respectively.

Drought tolerance indices

The drought scores, leaf rolling (0 indicating healthy leaves and 9 for tightly rolled V-shaped leaves), leaf drying (0 indicates no symptom of drying and 9-all plants apparently dead, most leaves fully dried) and stress recovery (observed after 10 days following watering, score 1 for 90–100% plant recovery and 9 for less than 19% recovery) observations were assessed using the Standard Evaluation Scores (SES) method, on a scale of 0 to 9 (IRRI 1996). Drought tolerance is measured through different indices and some of them we have calculated here through yield under normal and stress situation.

Mean productivity index (MPI) is taken as the average of $(Yi)_{ww}$ and $(Yi)_{Ds}$,

$$\text{Mean relative performance (MRP)} = [(Yi)_{Ds}/(Y_{Ds})] + [(Yi)_{ww}/(Y_{Ds})]$$

$$(REI) = [(Yi)_{Ds}/(Y_{Ds})] \times [(Yi)_{ww}/(Y_{ww})],$$

$$\text{Stress tolerance level (TOL)} = (Yi)_{ww} - Yi_{Ds}$$

where $(Yi)_{ww}$ and $(Yi)_{Ds}$ are yields of the i^{th} genotype under well watered and drought stress conditions, respectively.

$$\text{Stress tolerance index (STI)} = [(Yi)_{ww} \times (Yi)_{Ds}]/(Y_{ww})^2$$

$$\text{Stress intensity (SI)} = 1 - (Y_{Ds}/Y_{ww})$$

Y_{Ds} and Y_{ww} represent an average yield of all varieties under well-watered and drought stress conditions, respectively.

$$\text{Drought tolerance efficiency (DTE}(\%)) = \frac{(\text{Yield under drought stress}/\text{yield under well watered condition})}{\times 100}$$

Relative water content (RWC)

Fully developed and expanded leaves were selected for RWC measurement and around 5 cm of the mid portion of the leaf was excised, and fresh weight (FW) was recorded. Leaf pieces were immersed in distilled water in dark for 4–6 h and the turgid weight (TW) was recorded. Then, samples were dried in the oven at 70°C, and dry weight (DW) was taken. RWC was then calculated as:

$$RWC(\%) = \frac{FW - DW}{TW - DW} \times 100$$

Statistical analysis

Analysis of variance (ANOVA) and correlation and regression analyses were performed in SAS version 9.3 for a factorial randomized block design for growth, biochemical parameters, drought indices, and yield. Fisher's least significant difference (LSD) was used to test the significance of the differences between various means at $P < 0.05$.

Results

Plant height

The well-watered plant exhibited healthy growth of the stems (i.e. plant height), only response of variety and nutrients was observed up to some extent. Under drought stress conditions, the plants showed a reduction in plant height throughout the growth period, but their reduction was more during the initial growth phase when drought was imposed (Appendix 1). Among the cultivars, Rajalaxmi was most affected due to drought as height was significantly reduced or the growth was nearly stopped during the drought period followed by IR64 (Appendix 2). Application of K, Ca, and Fe significantly improved the plant height of all the cultivars irrespective of the stage even under stress condition. Due to stress imposition, heights of Rajalaxmi, IR64, and Sahbhagidhan were reduced by 27.1, 14.5 and 14.0%, respectively, over the values of well-watered conditions.

Tiller occurrence dynamics

A number of tillers per plant under drought stress was found significantly lower than well-watered conditions (Figure 1). After the stress imposition, tiller occurrence was slightly lower in Sahbhagidhan followed by IR64 and completely stopped in Rajalaxmi. During the initial 20 days of stress imposition, tillers reduced by 35.6, 33.2, and 6.1% in Rajalaxmi, IR64, and Sahbhagidhan, respectively, compared to those of well-watered conditions. Tiller dynamics significantly varied with the nutrient application, irrespective of the cultivars and stress conditions. Tiller occurrence gradually improved with the addition of nutrients and combination of nutrients (Figure 2). Under drought stress conditions, combined role of P and K, and Ca and Fe was visible, as the highest number of tillers under both the condition was observed with the application of all the nutrients. Combined P and K application increased the number of tillers up to 13.7 and 22.6%; and the application of all the nutrients further improved tiller occurrence by 31.4 and 41.7% over K and P alone, irrespective of the cultivars and stress conditions.

Leaf area index (LAI)

The response of LAI to different nutrients and soil moisture treatments differed significantly among genotypes (Figure 3). Under well-watered conditions, all the genotypes showed healthy growth and response to nutrients, where Rajalaxmi recorded highest value of LAI followed by IR64. Whereas, under drought conditions, the LAI was in the order Sahbhagidhan > IR64 > Rajalaxmi. During initial growth (i.e. 30 and 60 DAS), the LAI was almost similar in Rajalaxmi and slightly higher in IR64 due to limited water conditions. The combined application of all the nutrients resulted in 26.5 and 43.8, 29.4 and 37.3, 20.1, and 30.3% increase in LAI in IR64, Sahbhagidhan, and Rajalaxmi under well-watered and stress condition over application of P or K alone, respectively.

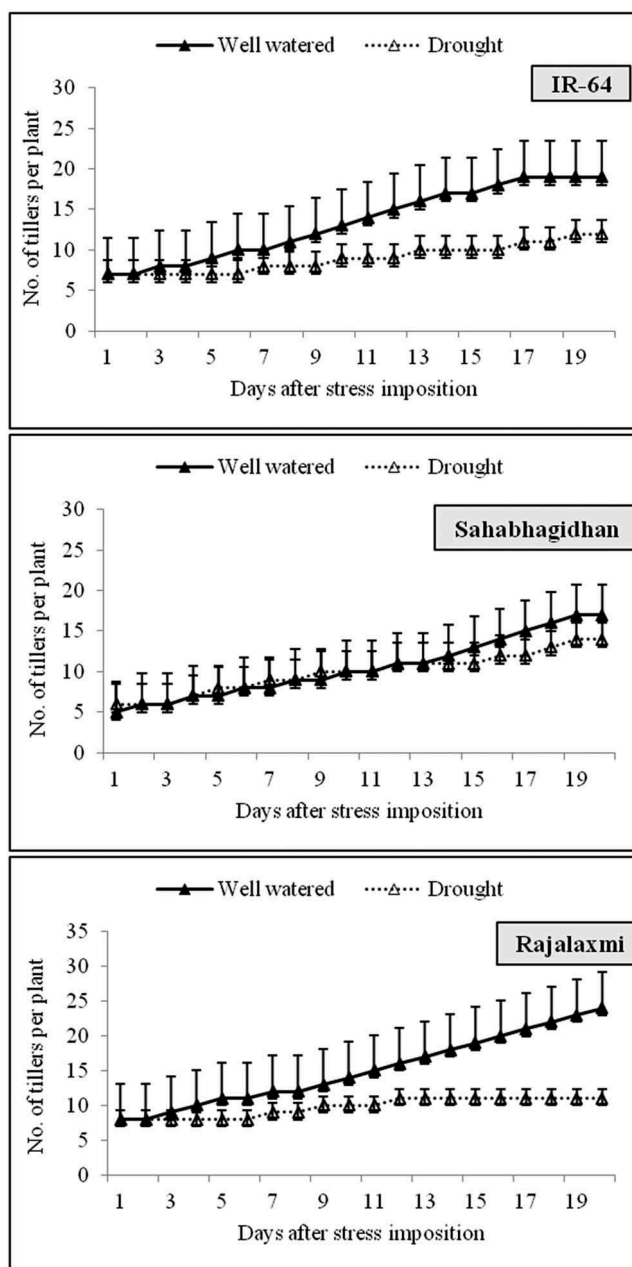


Figure 1. Tillering of different rice cultivars starting from stress imposition up to 20 days under well watered and drought conditions.

Chlorophyll concentrations and photosynthesis

Chlorophyll is one of the important pigments of photosynthetic apparatus, which absorbs light and transfers light energy to the reaction centre of the photosystem. Chlorophyll content of both, drought tolerant and intolerant varieties, decreased due to drought stress. Rajalaxmi recorded the highest concentrations of chlorophyll before stress imposition, and also experienced the maximum decrease due to drought, and lowest in Sahabhadhan (Figure 4). In the recovery period, the chlorophyll was regained in all the cultivars, but to a greater extent in Sahabhadhan (66.5%) followed by IR-64 (51.1%)

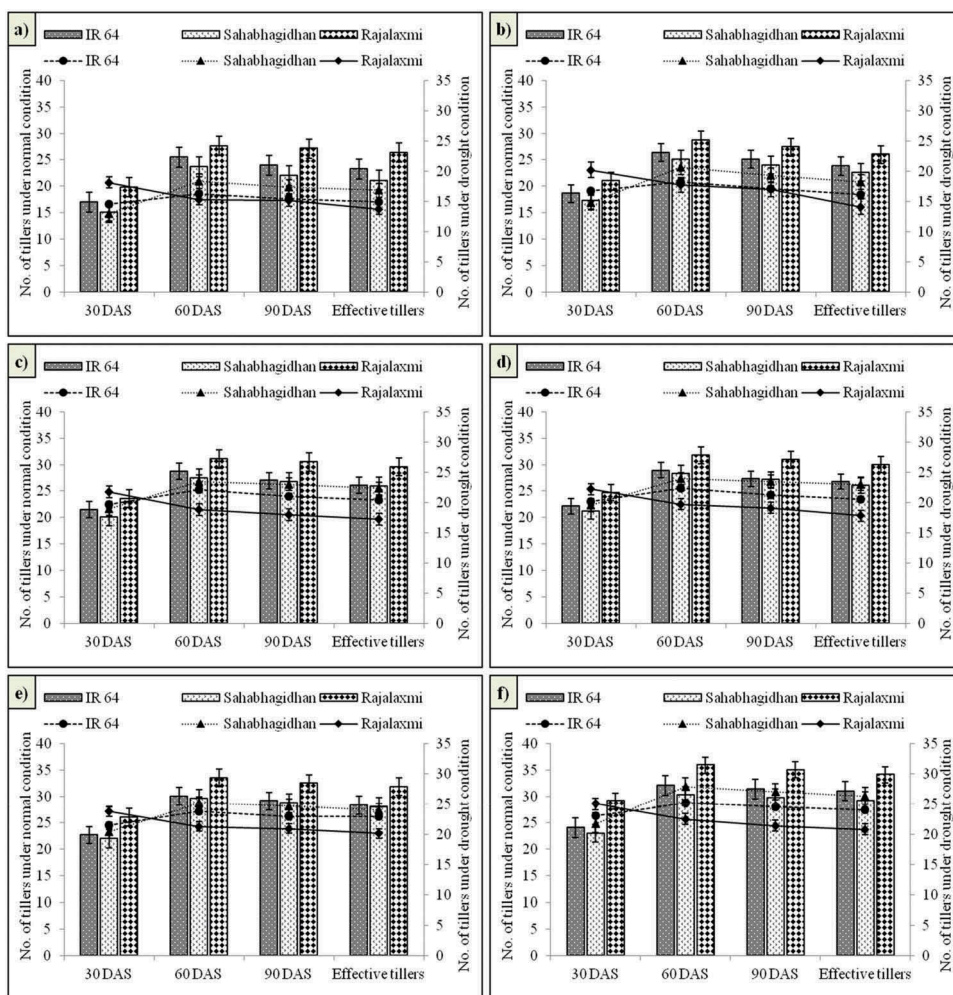


Figure 2. Effect of (a) P application, (b) K application, (c) P and K application, (d) P, K and Ca application, (e) P, K, Ca and Zn application, and (f) P, K, Ca, Zn and Fe application on tiller dynamics of different rice cultivars at 30, 60, 90 days after sowing (DAS) and at harvest under well watered and drought conditions (vertical bars in each column and line represents standard error). Column bars on primary axis represents number of tillers under well-watered condition and lines on secondary axis represents no of tillers under drought stress. Fertilizer application represents: F1: P; F2: K; F3: P+K; F4: P+K+Ca; F5: P+K+Ca+Zn; F6: P+K+Ca+Zn+Fe

and lowest in Rajalaxmi (41.2%). The nutrient application also played a significant role in resisting the chlorophyll damage and regain in chlorophyll; the role of Fe was most visible in all the cultivars followed by K and P. The decline in stomatal conductance was highest for Rajalaxmi and lowest for Sahabhabidhan. Stomatal conductance reduction was up to 61.7, 48.8 and 29.3% in Rajalaxmi, IR64, and Sahabhabidhan resulting in 62.6, 47.5 and 39.4% reduction in Pn rate, respectively (Figure 5). As in the chlorophyll concentrations, Fe and K along with other nutrient played a significant role in higher photosynthesis, especially under drought stress condition. The combined application of all the nutrients and application of Ca with P and K resulted in 11-and 9-fold gain in Pn rate over P alone.

Sugar, starch, proline content and epicuticular wax

Sugar and starch concentrations varied significantly with nutrient application in all the three cultivars under well-watered and drought conditions (Table 1). Under the well-watered condition,

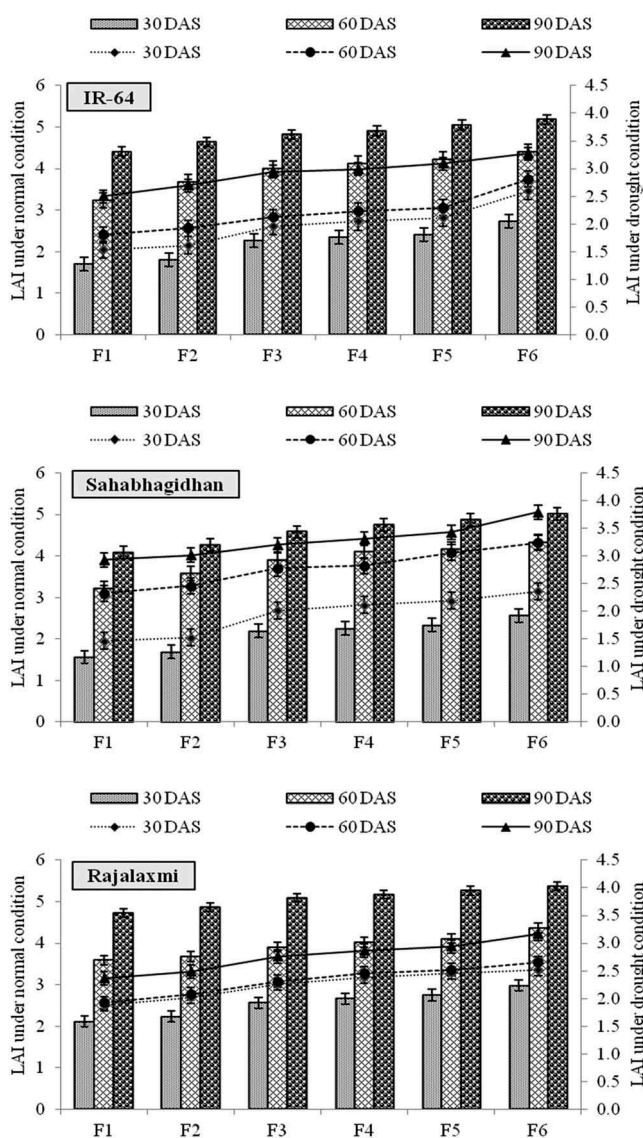


Figure 3. Effect of nutrient application on leaf area index (LAI) of different rice cultivars during 30, 60, and 90 days after sowing (DAS) under well watered and drought conditions (vertical bars in each column and line represents standard error). Column bars on primary axis represents leaf area index under well-watered condition and lines on secondary axis represents leaf area index under drought stress. Fertilizer application represents: F1: P; F2: K; F3: P+K; F4: P+K+Ca; F5: P+K+Ca+Zn; F6: P+K+Ca+Zn+Fe

the variations in concentrations were mainly due to varietal response and little effect of the nutrient application was observed. Whereas, under drought stress conditions, Sahbhagidhan maintained a high level of sugar and starch content in shoots than other two varieties, amounting to 32.1 and 61.4% higher sugar and 34.2 and 62.5% higher starch than IR64 and Rajalaxmi, respectively, irrespective of the fertilizer application. Effect of nutrients was somewhat visible under drought stress, as combined application of all the nutrients resulted in significantly higher concentrations of non-structural carbohydrates (Table 1). Proline acts as an osmolyte, and its accumulation contributes to better performance and drought tolerance. Sahbhagidhan was observed to have a high proline accumulation under drought stress, which was around 105 and 150% greater than IR64 and Rajalaxmi, respectively. The nutrient application also significantly

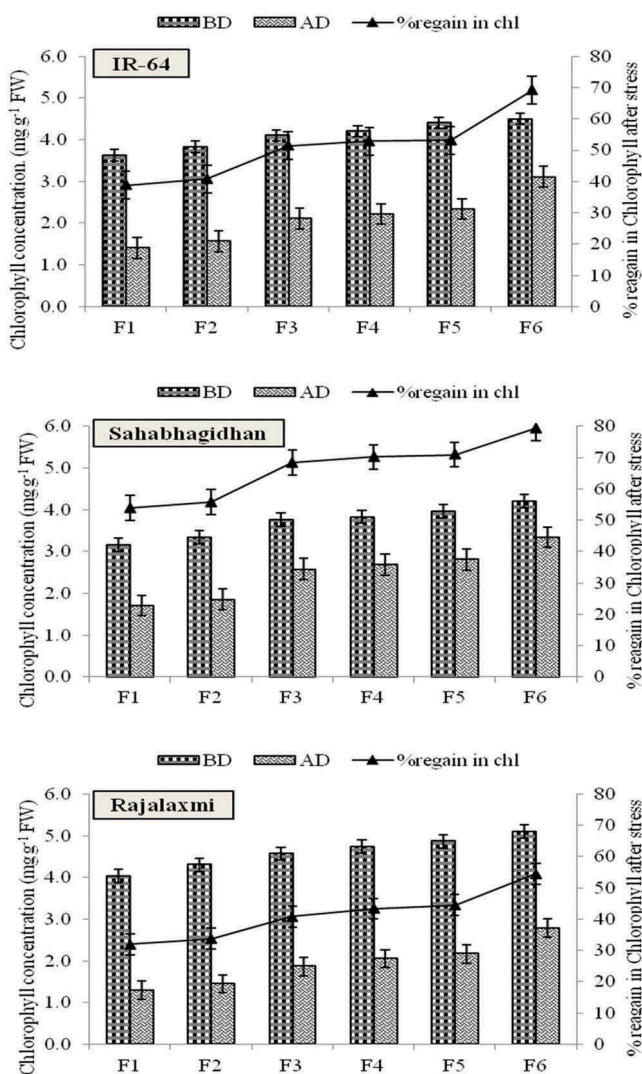


Figure 4. Effect of nutrient application on chlorophyll concentration (mg g^{-1} FW) before drought (BD) and after drought (AD) and % regain in chlorophyll after stress recovery for xx days. Column bars on primary axis represents chlorophyll concentration and lines on the secondary axis represent % regain in chlorophyll after recovery. Vertical bars in each column and line are \pm SE. Fertilizer application represents: F1: P; F2: K; F3: P+K; F4: P+K+Ca; F5: P+K+Ca+Zn; F6: P+K+Ca+Zn+Fe

contributed to higher proline accumulation, especially combined application of P, K, and all other nutrients (Table 1). Drought tolerant cultivar Sahbhagidhan resulted in maximum wax content over the leaves followed by IR64 (Figure 6). The role of nutrient was also registered in epicuticular wax deposition leading to be resistant to drought stress. The combined application of nutrients resulted in 33% higher and K alone 3.4% more wax deposition when compared to P alone, respectively, irrespective of the cultivars.

Drought tolerance indices

The plants in well-watered treatment maintained healthier leaves, but the degree of rolling and drying in their leaves became progressively more pronounced with increasing drought stress. Among the cultivars, Rajalaxmi showed the highest level of leaf rolling and drying followed by IR64 (Table 2). Stress recovery

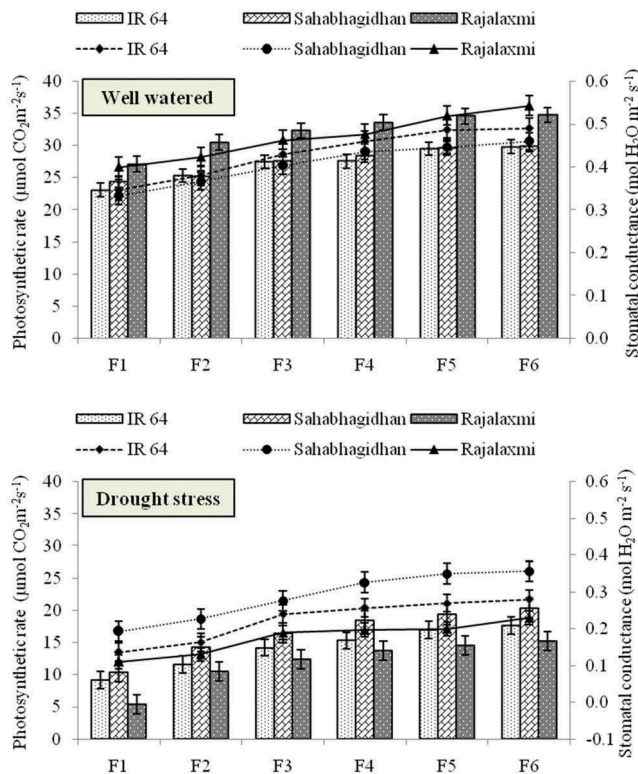


Figure 5. Effect of nutrient application on photosynthetic rate ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and stomatal conductance ($\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$) of different rice cultivars under (a) well watered and (b) drought conditions. Column bars on primary axis represents photosynthetic rate and lines on secondary axis represents stomatal conductance. Vertical bars in each column and line are \pm SE. Fertilizer application represents: F1: P; F2: K; F3: P+K; F4: P+K+Ca; F5: P+K+Ca+Zn; F6: P+K+Ca+Zn+Fe

after drought was maximum in Sahbhagidhan and with combined application of nutrients, especially P and K. Significant difference was observed between the mean grain yield of well-watered and drought stress conditions for all the cultivars, implying that performance of these cultivars under stress and well-watered conditions were considerably different, and also varied significantly with nutrient application (Table 2). On MRP and REI, no significant difference was observed among cultivars, because it is simply a summation or multiplication of yield under well-watered and drought conditions. Highest values of STI and DTE and the lowest values of TOL and SI were observed for Sahbhagidhan indicating its greater tolerance to drought. In the nutrient application treatments, highest values of MPI, MRP, REY and STI and DTE were observed with combined use of nutrients, which ultimately underlined the role of P, K, Ca, and other nutrients in enhancing drought tolerance.

Dry matter partitioning

The difference in dry weights was higher for leaves than stem and sheath, the gap between well-watered and drought conditions in the dry weight was widened as crop progressed towards maturity (Table 3). Dry matter remobilization (DMRE) amount was higher from leaves than from stem and sheath, in Sahbhagidhan, DMRE was almost similar from leaf and stem and the difference between drought, and well-watered conditions was also small. In Rajalaxmi and IR64, the difference between water regimes *w.r.t.* DMRE from stem and sheath was very high. Dry matter conversion rate (DMCR) was also highest for Sahbhagidhan, whereas the lowest for Rajalaxmi under drought stress condition. Rajalaxmi showed 77.6

Table 1. Effect of nutrient application on sugar, starch and proline concentrations in shoots of different rice genotypes under well-watered and drought stress conditions.

Fertilizer treatment	Well-watered			Drought stress		
	IR64	Sahabhadhan	Rajalaxmi	IR64	Sahabhadhan	Rajalaxmi
Sugar concentration (mg g⁻¹ DW)						
P	32.5	29.8	32.0	13.1	19.4	10.4
K	33.2	30.4	32.5	15.6	21.7	11.9
PK	34.5	31.6	33.1	18.3	23.2	14.8
PK+Ca	34.7	31.9	33.6	18.8	23.9	15.5
PK+Ca+Zn	34.8	32.2	33.9	19.2	24.5	16.1
PK+Ca+Zn+Fe	35.9	33.3	35.2	20.7	26.8	17.6
LSD_{0.05}				3.54		
Starch concentration (mg g⁻¹ DW)						
P	34.2	31.5	33.8	14.8	21.8	11.2
K	35.1	32.1	34.4	15.9	23.1	12.3
PK	36.8	33.6	35.7	19.1	24.9	15.7
PK+Ca	37.5	34.1	36.7	20.3	25.8	17.1
PK+Ca+Zn	37.9	34.8	37.1	20.8	26.5	17.9
PK+Ca+Zn+Fe	39.4	36.5	38.7	22.4	29.3	19.1
LSD_{p=0.05}				3.76		
Proline concentration (mg g⁻¹ FW)						
P	0.29	0.28	0.26	0.31	0.68	0.28
K	0.30	0.29	0.27	0.33	0.71	0.30
PK	0.32	0.32	0.29	0.39	0.79	0.35
PK+Ca	0.32	0.33	0.30	0.42	0.83	0.38
PK+Ca+Zn	0.33	0.33	0.30	0.44	0.85	0.39
PK+Ca+Zn+Fe	0.38	0.38	0.34	0.51	0.93	0.43
LSD_{p=0.05}				0.116		

and 56.8% higher DMCR under the well-watered condition, but 190.3 and 39.5% lower DMCR under drought conditions as compared to IR64 and Sahabhadhan, respectively (Table 4).

Enzymatic activities

Drought stress increased the anti-oxidant enzyme activity irrespective of the cultivars and nutrient application (Table 5). Highest SOD, CAT, and PER activity were observed in Sahabhadhan, which

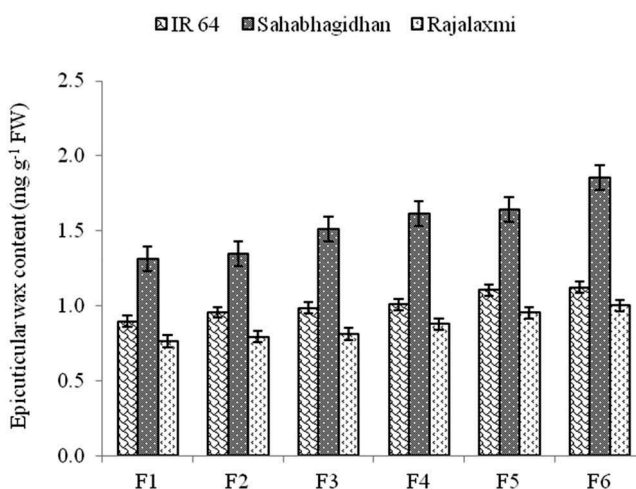


Figure 6. Effect of nutrient application on epicuticular wax concentration (mg g⁻¹ FW) of different rice cultivars under drought stress conditions. Vertical bars in each column and line are \pm SE.

Fertilizer application represents: F1: P; F2: K; F3: P+K; F4: P+K+Ca; F5: P+K+Ca+Zn; F6: P+K+Ca+Zn+Fe

Table 2. Effect of nutrient application on leaf rolling, leaf drying and different drought tolerance indices of rice cultivars under drought stress.

	LR	LD	SR	MRP	REI	TOL	MPI	STI	SI	DTE
Variety										
IR 64	3.62	3.83	4.72	1.95	0.97	1.95	3.97	0.57	0.43	56.8
Sahabdagidhan	1.30	1.68	2.22	2.05	1.03	1.03	4.22	0.76	0.24	75.7
Rajalaxmi	5.02	5.27	6.50	1.93	0.93	3.65	3.68	0.43	0.58	42.6
LSD_{p=0.05}	0.56	0.31	0.89	0.05	0.04	0.11	0.10	0.05	0.07	3.26
Nutrient application										
P	3.60	4.00	5.20	1.70	0.70	2.58	3.44	0.47	0.53	46.7
K	3.60	3.90	5.07	1.81	0.78	2.41	3.62	0.52	0.48	52.2
PK	3.37	3.60	4.80	1.96	0.94	2.26	3.94	0.58	0.42	58.4
PK+Ca	3.17	3.47	4.30	2.03	1.04	2.08	4.08	0.63	0.37	63.1
PK+Ca+Zn	3.17	3.43	4.13	2.13	1.14	2.01	4.28	0.64	0.36	64.0
PK+Ca+Zn+Fe	2.97	3.17	3.37	2.21	1.24	1.93	4.47	0.66	0.34	65.8
LSD_{p=0.05}	0.63	0.48	1.04	0.15	0.09	0.19	0.14	0.06	0.08	5.67
V×N LSD_{p=0.05}	0.92	0.74	1.38	0.24	0.14	0.28	0.22	0.15	0.19	9.05

LR: leaf rolling; LD: lead drying; SR: stress recovery after drought; MRP: mean relative performance; REI: relative efficiency index; TOL: stress tolerance level; MPI: mean productivity index; STI: stress tolerance index; SI: stress intensity; DTE: drought tolerance efficiency.

Table 3. Above ground dry matter partitioning per tiller of different rice cultivars as influenced by nutrient application under well-watered and drought stress conditions.

	Maximum tillering			Panicle initiation			Maturity			
	Leaf	Stem and Sheath	Total	Leaf	Stem and Sheath	Total	Leaf	Stem and Sheath	Panicle	Total
Variety (V)										
IR 64	0.383	0.297	0.680	0.632	0.719	1.351	0.382	1.003	1.869	3.254
Sahabdagidhan	0.364	0.308	0.672	0.707	0.798	1.505	0.401	1.061	1.991	3.453
Rajalaxmi	0.368	0.291	0.659	0.651	0.724	1.375	0.416	1.241	1.851	3.508
LSD_{0.05}	0.009	0.003	0.021	0.018	0.054	0.081	0.011	0.063	0.062	0.132
Stress condition (S)										
Well-watered	0.402	0.319	0.721	0.759	0.834	1.593	0.457	1.354	2.105	3.916
Drought stress	0.341	0.281	0.622	0.568	0.659	1.227	0.342	0.849	1.702	2.893
LSD_{0.05}	0.008	0.002	0.019	0.016	0.049	0.072	0.009	0.058	0.053	0.110
Nutrient application (N)										
P	0.329	0.268	0.597	0.623	0.677	1.300	0.351	0.958	1.657	2.966
K	0.351	0.284	0.635	0.646	0.720	1.366	0.388	1.004	1.781	3.173
PK	0.378	0.308	0.686	0.661	0.760	1.420	0.402	1.084	1.899	3.385
PK+Ca	0.384	0.311	0.694	0.678	0.773	1.451	0.415	1.111	1.998	3.524
PK+Ca+Zn	0.392	0.312	0.704	0.683	0.777	1.460	0.418	1.196	2.028	3.642
PK+Ca+Zn+Fe	0.396	0.315	0.711	0.686	0.781	1.467	0.423	1.259	2.056	3.738
LSD_{0.05}	0.011	0.006	0.056	0.022	0.069	0.092	0.041	0.097	0.104	0.261
V×S	ns	ns	ns	0.036	0.081	0.102	0.058	0.104	0.113	0.283
V×N	ns	ns	ns	ns	ns	ns	0.075	0.121	0.129	0.311
S×N	ns	ns	ns	0.041	0.087	0.111	0.063	0.112	0.122	0.294
V×S×N	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

might have contributed to its drought tolerance. Nutrient use significantly influenced the anti-oxidant enzyme activity; it was lowest in the sole application of P and K, whereas, the combined application of P and K resulted in the significantly higher content of SOD, CAT, and PER. These activities further increased the application of Ca, Zn, and Fe, but were not significantly different from each other.

Electrolyte leakage, root dry weight, and relative water content

Leaf membrane rupture due to drought stress resulted in leakage of electrolytes from the leaf tissues; it was significantly lowest in the drought tolerant cultivar. Sahbhagidhan resulted in 51.7

Table 4. Dry matter remobilization of different rice cultivars as influenced by nutrient application under well-watered and drought stress conditions.

	Leaf			Stem and sheath		
	DMRA (g)	DMRE (%)	DMCR (%)	DMRA (g)	DMRE (%)	DMCR (%)
Variety (V)						
IR 64	0.308	22.50	16.40	0.203	18.31	10.01
Sahbhagidhan	0.316	21.60	15.80	0.238	22.38	11.94
Rajalaxmi	0.368	22.40	19.40	0.276	18.14	13.49
LSD_{0.05}	ns	ns	0.38	0.029	0.85	0.48
Stress condition (S)						
Well-watered	0.392	21.64	18.60	0.360	26.25	17.08
Drought stress	0.269	22.75	15.86	0.115	12.97	6.55
LSD_{0.05}	0.047	0.39	0.32	0.025	0.78	0.44
Nutrient application						
P	0.258	21.66	16.52	0.156	18.46	10.31
K	0.297	21.90	17.05	0.189	18.79	10.76
PK	0.328	22.23	17.30	0.233	19.54	12.07
PK+Ca	0.343	22.38	17.34	0.273	20.13	12.36
PK+Ca+Zn	0.375	22.41	17.43	0.284	20.35	12.52
PK+Ca+Zn+Fe	0.384	22.50	17.49	0.293	20.77	12.77
LSD_{0.05}	0.061	0.48	0.43	0.056	0.97	0.59
V×S	ns	ns	0.54	0.068	1.08	0.76
V×N	ns	ns	0.73	0.085	1.29	0.96
S×N	0.092	0.63	0.59	0.071	1.16	0.88
V×S×N	ns	ns	ns	0.096	1.47	1.18

DMRA: dry matter remobilization; DMRE: dry matter remobilization efficiency; DMCR: dry matter conversion rate.

and 50.5% lower electrolyte leakage over Rajalaxmi and IR64, respectively. Root dry weight/root growth was highest for Sahbhagidhan under drought condition, whereas it was maximum for Rajalaxmi under well-watered condition. Root dry weight did not differ significantly for the cultivars (Table 5). Effect of P was most significant on root dry weight; application of P alone contributed to 18.8% higher root dry weight over K alone, and it was 55.1% higher in combination. The RWC values were significantly higher for Sahbhagidhan as compared to other two cultivars; the value of RWC was 4.1 and 9.2% higher with the combined application of P and K over their sole application, respectively. The increase in RWC values was non-significant with the application of other nutrients.

Grain yield

Under well-watered conditions, Rajalaxmi being hybrid cultivar produced highest grain yield, which was 40.2 and 48.1% higher over IR-64 and Sahbhagidhan, respectively (Figure 7). With the imposition of drought stress, maximum decrease (57.4%) in grain yield was also observed in Rajalaxmi as compared to IR64 (43.2%) and Sahbhagidhan (24.3%) over those under well-watered conditions. Application of different nutrients contributed positively to grain yield under both the conditions, but the effect was more pronounced under drought condition. The combined application of P, K, Ca, Zn, and Fe resulted in 52.9, 53.3, 48.9% higher yield over P or K application alone under stress in IR64, Sahbhagidhan and Rajalaxmi, respectively (Figure 7).

Discussion

Water stress is one of the most undesirable factors of plant growth and productivity either in excess or in deficit and in today's changing climate, would be a severe menace to crop productivity. The dry spell of drought triggers a wide assortment of plant reactions, going from cell digestion to changes in development rates and harvest yields. Drought stress instigates are duction in plant development and improvement (Manikavelu et al. 2006). Cell development is seriously impeded, because of the decrease in turgor weight under stress leading to debilitates growth, development

Table 5. Effect of nutrient application on anti-oxidant enzyme activity, electrolyte leakage, root dry weight and relative water content of different rice cultivars under well-watered and drought stress conditions.

	SOD (Unit min ⁻¹ g ⁻¹)	CAT (μmol g ⁻¹ min ⁻¹)	PER (μmol g ⁻¹ min ⁻¹)	Electrolyte leakage (%)	Root dry weight (g)	RWC (%)	Grain yield (t ha ⁻¹)
Variety (V)							
IR 64	26.80	0.25	2.63	21.24	10.64	69.67	3.57
Sahabdagidhan	62.83	0.55	3.98	10.50	11.18	76.65	3.79
Rajalaxmi	23.48	0.21	2.59	21.75	10.63	69.62	4.55
LSD_{0.05}	4.09	0.11	0.18	2.78	ns	1.86	0.19
Stress condition (S)							
Well-watered	13.74	0.11	2.02	2.84	12.47	92.02	5.08
Drought stress	61.63	0.57	4.12	32.81	9.16	51.95	2.87
LSD_{0.05}	3.55	0.10	0.15	2.55	1.12	1.51	0.24
Nutrient application (N)							
P	24.66	0.11	2.11	21.56	9.51	65.78	3.44
K	32.41	0.25	3.02	18.39	8.77	68.94	3.62
PK	41.91	0.41	3.24	16.97	10.92	71.78	3.94
PK+Ca	42.08	0.43	3.30	16.76	11.56	71.87	4.08
PK+Ca+Zn	42.33	0.44	3.35	16.67	11.76	72.12	4.28
PK+Ca+Zn+Fe	42.83	0.45	3.41	16.61	12.39	72.35	4.47
LSD_{0.05}	6.21	0.14	0.21	3.12	1.36	2.24	0.49
V×S	7.13	0.19	0.29	3.61	ns	2.86	0.67
V×N	7.89	0.31	0.48	4.06	ns	3.27	1.01
S×N	7.27	0.22	0.36	3.79	2.12	3.05	0.89
V×S×N	8.53	0.46	0.59	4.48	ns	4.15	1.22

SOD: superoxide dismutase; CAT: catalase; PER: peroxide; RWC: relative water content

and ultimately yield. When water stress arises, plants respond by backing off or ceasing their development. In this study, drought stress at vegetative stages significantly decreased the plant height, stem length, and tillering dynamics. It may be due to the reduction in elongation and extension of the cell which reduced plant tissue development. The diminishment in plant height could likewise be credited to declining in the cell extension and more leaf senescence in the plant prone to stress (Manivannan et al. 2007). Significant varietal differences in photosynthetic response to water stress have been reported in different crop plants (Subrahmanyam et al. 2006; Gautam et al. 2017). Photosynthesis is the primary metabolic process determining crop production and is seriously affected by drought stress (Yang et al. 2014). The factors constraining photosynthesis are the CO₂ diffusional impediment because of early stomatal closure, an abridged activity of photosynthetic enzymes, the biochemical components, stomatal and mesophyll conductance to CO₂ regularly diminishes in drought occurrence (Centritto et al. 2009). 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 CO₂ assimilation rate (A), stomatal conductance (gs), and transpiration rate (E) have been reported earlier in different crops (Lawlor and Cornic 2002; Gauthami et al. 2014). Flexas and Madrano (2002) opined that stomatal closure is the earliest response to drought and is the main limitation to photosynthesis under drought. Plants under water deficit reduce water losses through transpiration by reducing stomatal conductance. Drought also alters the PS II activity in rice, as reflected by a decrease in the values of Fv/Fm. This was probably because of the antenna pigments disorganization and a decrease of SPAD Chl index in the rice seedlings, as observed in drought stress (Mishra et al. 2018). Drought conditions also affect internal CO₂ transport of leaf, activities of enzymes and finally photosynthetic capacity. However, internal (metabolic and diffusive) as stress further increases, these imitations become predominant relative to stomata (Lawlor and Tezara 2009). Photo-oxidation induced chlorosis, chlorophyll molecule degradation, are the major source of oxidative stress the in a plant cell.

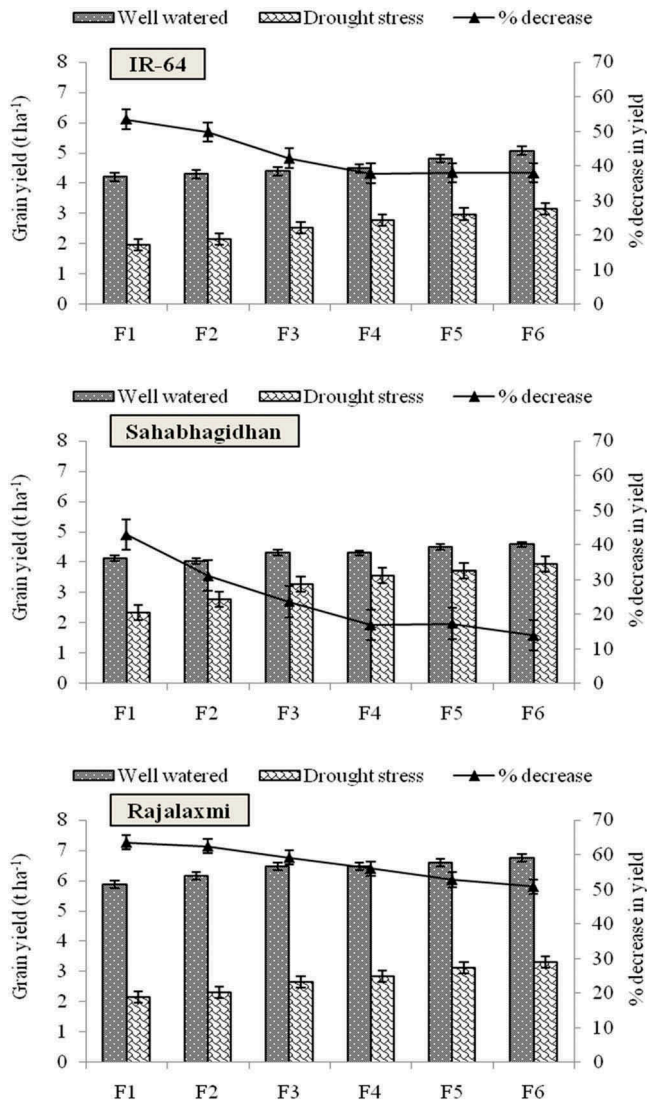


Figure 7. Effect of nutrient application on grain yield (t ha^{-1}) of different rice cultivars under well watered and drought conditions and % decrease in yield due to drought stress compared with control conditions. Column bars on primary axis represents grain yield and lines on the secondary axis represents % decrease in grain yield. Vertical bars in each column and line are \pm SE.

Under drought stress reduction in all the morpho-physiological parameters resulted in poor grain yield and this was reflected in the positive correlation of these parameters with yield (Figure 8).

Proline content builds more than other amino acids under stress, and this property has been used as a biochemical marker to select genotypes for providing drought resistance, proline accumulation may advance plant damage reparability by enhancing antioxidant defence (Fahramand et al. 2014). In the tolerant genotypes, better functioning of ROS-scavenging enzymes has been accounted, as compared to susceptible ones, proposing that the antioxidant system plays a vital part in plant resilience against environmental stress (Lum et al. 2014), as happened in Sahbhagidhan. This indicated that plants need to produce more CAT, SOD, and PER under drought conditions to remove the extra ROS in cells. In this study, drought tolerant cultivar Sahbhagidhan showed the highest proline and wax accumulation, like drought tolerance mechanisms along with high carbohydrates and chlorophyll concentration, growth, and photosynthesis under drought stress leading to maximum yield as compared to other cultivars.

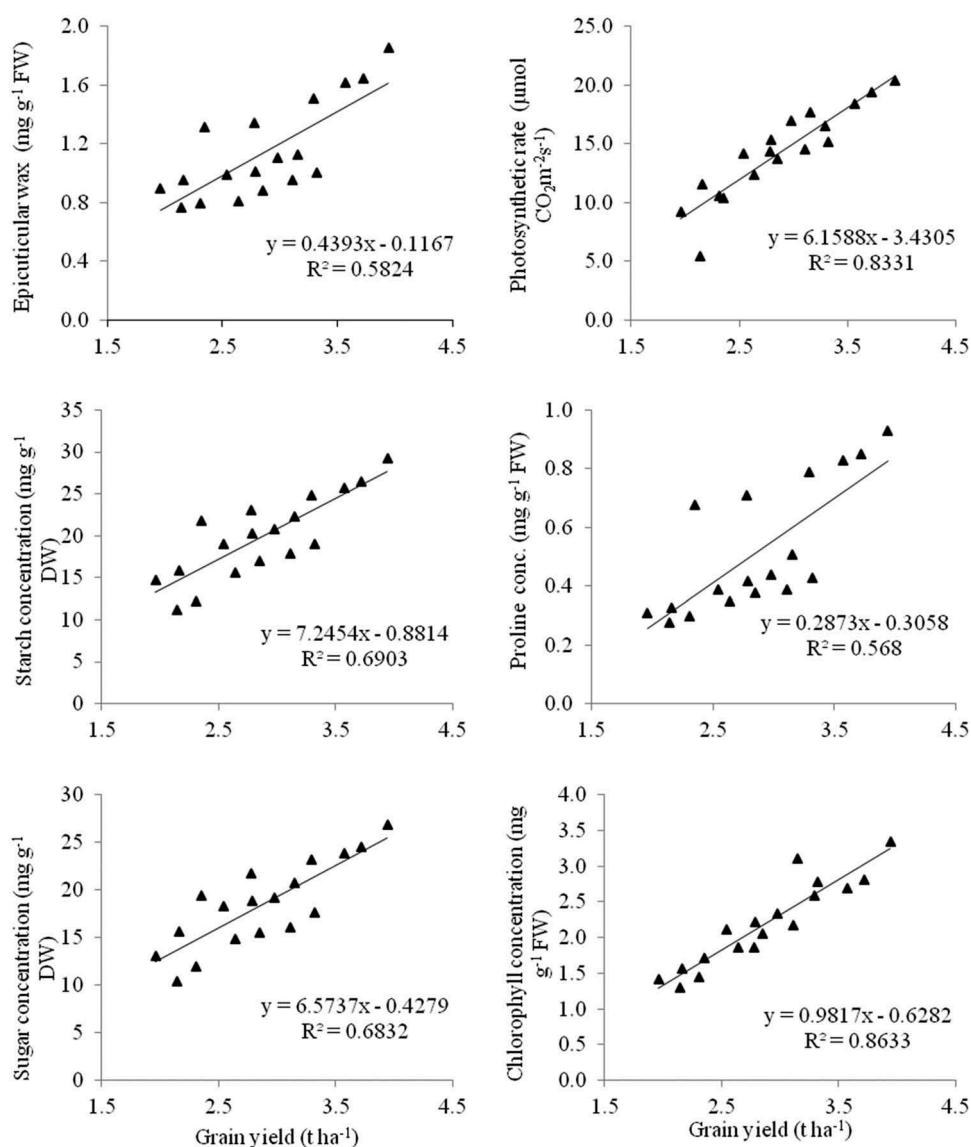


Figure 8. Relationship between grain yield (t ha^{-1}) with different physiological and biochemical parameters.

Rice genotypes having lowest STI and TOL values had minimal yield decrement (Raman et al. 2012; Kumar et al. 2014), in this study also Rajalaxmi has the lowest value of tolerance indices, also reflected in the lesser output of grain yield.

Drought stress influences the normal physiology and growth of plants in many ways. It results in an increase of solute concentration outside the roots compared to the internal environment of the root and causes reverse osmosis. As a result, the cell membrane shrinks from the cell wall and may eventually lead to the death of the cell. Mineral elements have numerous functions in plants including maintaining charge balance, electron carriers, structural components, enzyme activation, and providing osmoticum for turgor and growth (Waraich et al. 2011). The low nutrient uptake, under drought, was related to low transpiration rate leading to the nutrient deficiency in the plant. Application of these nutrients under drought may improve the drought tolerance as happened in this experiment. Phosphorus improves the root growth and maintains high leaf water potential and increases the activity of nitrate reductase which

improves the assimilation of nitrate under drought condition. It also maintains the cell turgidity which in turn increases the stomatal conductance and photosynthetic rate under drought. Phosphorus is the imperative part of moderating cell vitality, conserving and transferring energy in the cell metabolism (Jin et al. 2006). According to Gutiérrez-Boem and Thomas (1998), P application increased the growth parameters like leaf appearance, leaves per plant and leaf area in wheat under moisture stress conditions as supply of ample P enables plant to deal with stress environment. Phosphorus supply enhances the uptake and translocation of P in seed also help in mitigate the undesirable effects of water stress on growth attributes (Jin et al. 2006). Potassium is essential for many physiological processes, such as photosynthesis, translocation of photosynthates into sink organs, maintenance of turgescence, activation of enzymes, and reducing excess uptake of ions such as Na and Fe in saline and flooded soils (Marschner 1995; Mengel and Kirkby 2001). The reason for the enhanced need for K by plants suffering from environmental stresses appears to be related to the fact that K is required for the maintenance of photosynthetic CO₂ fixation (Gautam et al. 2016). According to Ruiz-Lozano and Azcon (1996), different nutrients play important role in drought tolerance; in particular, K is the cationic solute responsible for stomatal movement describing its role in providing the ability to survive under moisture stress. Elevated K level induced drought tolerance in maize plant (Premachandra et al. 2008). Calcium is considered to play a role in mediating stress response during drought, and acclimation of plants to stress (Palta 2000). Ca is necessary for recovery from drought by activating the plasma membrane enzyme ATPase which is required to pump back the nutrients that were lost in cell damage (Palta 2000). Zinc plays an important role in increasing auxin levels which enhances the root growth which in turn improves the drought tolerance in plants (Bennett and Skoog 2002). In our study, the combined application of P, K, Ca, Zn, and Fe resulted in highest growth, tillering, the concentration of carbohydrates, proline, which led to around 50% yield enhancement under drought stress over P or K application alone in all the cultivars. Many researchers also found that water stress decreased the availability of Ca, Zn and Fe (Sardans et al. 2008), and also play a significant role in carbohydrate metabolism, synthesis of protein, the metabolism of auxins, stomatal conductance and plant water relations (Broadley et al. 2007). Nutrient input would benefit drought-tolerant cultivar (Sahbhagidhan) more than drought-susceptible irrigated rice cultivars (Rajalaxmi and IR64).

Conclusion

Our 2-year study revealed that imposition of drought during active growth period significantly influenced the performance of all the rice cultivars but yield penalty was lower in tolerant cultivar i.e. Sahbhagidhan. The differential response of cultivars regarding growth, tillering dynamics, physio-biochemical parameters, drought tolerance indices to imposed stress indicated their drought tolerance ability, which was highest in Sahbhagidhan. Besides the tolerant cultivar, application of nutrients also helped the rice plants to overcome the drought stress and its after-effects. The maximum growth, photosynthesis, chlorophyll, proline, anti-oxidants production, and yield was obtained with combined application of nutrients, especially P and K. As possible technological alternatives, the use of drought-tolerant cultivars associated with extraneous supply of nutrients, which are not available due to water deficit, may help cope with or at least ameliorate this problem. Though our insight into how rice plant reacts to stress is increasing, the comprehension of how these changes convert into plant development and yield level contrasts in execution under drought falls behind, so more endeavours ought to be made to examine these reactions on nutrient management.

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