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Seed biopriming mitigates terminal drought stress at reproductive stage of maize by enhancing gas exchange attributes and nutrient uptake

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Abstract: Maize (*Zea mays* L.) is an important cereal crop around the globe. Scarcity of water is one of the major abiotic factors reducing yields in this crop. The development of maize varieties with stress-tolerant traits is time-consuming and laborious work. There is a strong need to develop techniques that could have the effect of reducing irrigation requirements and mitigating water-stress conditions. Biopriming (seed priming with bacterial inoculation) is a newly emerging, simple, and easily adaptable strategy to mitigate drought stress for enhanced crop production. The current trial was executed using a randomized complete block design with factorial arrangements during the spring seasons of 2016 and 2017 at the research area of the Department of Agronomy, Bahauddin Zakariya University, Multan, Pakistan. The experiment consisted of two irrigation levels (normal irrigation and terminal drought stress at reproductive stage) and three seed priming techniques (control, hydropriming, and biopriming). Hybrid maize variety HC9091 was used as a test species. For hydropriming, seeds were soaked in distilled water (ratio 1:5) for 12 h. For biopriming, the hydroprimed seeds were inoculated with bacteria culture (*Rhizobium phaseoli*-RS-1 + *Pseudomonas* spp.) at the ratio of 1:5. Seeds were sown on ridges, maintaining a 75-cm row-to-row and 22.5-cm plant-to-plant distance. The results indicated an overall decline in agronomic and physiological attributes of the plants under terminal drought stress. However, seed biopriming considerably ameliorated the drought-induced deterioration in agronomic (plant height, cobs per plant, cob length, cob weight, grain yield, biological yield, and harvest index) as well as physiological (photosynthesis, transpiration rate, intrinsic water use efficiency, stomatal conductance, relative water content, and nutrient uptake) parameters of plants. It is concluded that seed biopriming is an easy, commercially feasible, cost-effective technique and an ecofriendly way to cope with drought stress at the reproductive growth stage of maize in order to enhance crop productivity.

Key words: Priming technique, water stress, physiological parameters, yield

1. Introduction

Global warming and sudden climatic fluctuations are the major causes of the onset of drastic abiotic stresses that are diminishing crop production worldwide. Among these stresses, drought is the most prominent hazard, affecting the growth and development of plants with a consequent decline in yield (Nawaz et al., 2017). Currently, the burgeoning demand for food by an increasing population has resulted in depletion of the world's freshwater resources. According to the Climate Change Vulnerability Index, Pakistan is at high risk of being affected by severe drought spells and frequent inundations (Saleem et al., 2007). Furthermore, unstable climatic conditions, coupled with a rising demand for water for industrialization and urbanization, will further aggravate the water crisis in the near future (Fereres and Soriano, 2007). Under limited water availability, plants cannot maintain their normal physiological processes due to oxidative stress and disturbances in the homeostasis of reactive oxygen species (ROS) at a cellular level (Li et al., 2009). A shortage of water can severely hamper plant growth events due to imbalanced nutrient uptake and disrupted metabolic activities. Maize is one of the crops most sensitive to drought stress and needs ample amounts of water during the entirety of its phenological development. Water deficit at the reproductive and grain-filling stages, known as terminal drought, may severely reduce the grain yield of maize (Farooq et al., 2014).

To cope with drought stress in maize scientists have been using different techniques and aspects at the field level (Maccaferri et al., 2011). Among these, biopriming has emerged as a sustainable and ecofriendly agronomic

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tool for mitigating the deleterious effects of drought with a consequent enhancement in crop productivity at the farm level. Biopriming is a technique in which imbibed seeds are inoculated with a bacterial culture (Kaymak et al., 2009). Through this method, a uniform and vigorous germination is achieved as well as additional protective measures against seed- and soil-borne pathogens. During hydropriming seeds are likely to be infected with pathogens, which may significantly impair the germination process (Naveed et al., 2014). Nevertheless, inoculation of seed with antagonistic microorganisms after seed hydropriming is a promising agronomic approach for solving this problem. A large group of *Rhizobia* are known to act as biocontrol agent/plant growth-promoting rhizobacteria (PGPR) by establishing synergetic associations with nodule-forming bacteria in the rhizosphere of legume crops (Grover et al., 2010). Information is now available on the role of PGPR in enhancing the growth of nonleguminous crops like maize under adverse growth conditions. In response to PGPR inoculation, plants may trigger various physiological processes for improving induced systemic tolerance, thereby boosting nutrient uptake, mitigating ethylene production by ACC-deaminase enzyme, maintaining antioxidant status against ROS, and regulating the synthesis of plant osmolytes (Nawaz et al., 2016).

Although various experiments have attempted to verify the significant potential of seed biopriming with bacterial inoculation, it has been difficult to find any investigation into the interactive effect of hydropriming and bacterial inoculation (biopriming) on nonlegume crops under terminal drought stress. Therefore, the current study was designed to evaluate the impact of seed biopriming on enhancing productivity in maize facing drought stress at the terminal (reproductive) growth stage under field conditions.

2. Materials and methods

2.1. Site and experimental description

The field experiment was conducted at the experimental area of the Department of Agronomy, Faculty of Agricultural Sciences and Technology, Bahauddin Zakariya University, Multan, Pakistan (30.2°N, 71.43°E; 122 m a.s.l.) during the second fortnight of February in 2016 and 2017. Multan is situated in a semiarid and subtropical climate zone. Meteorological data for the life cycle of the maize crop, for both years of study, are given in Figure 1. There were mild rain showers during both crop growth seasons that did not considerably affect the soil field capacity during the drought stress period. The soil is clay loam (EC 4.88 dS m^{-1}, pH 9.3) with low organic matter (0.42%), originating from the Sindh-Mianwali soil series, and it is fine-silty, mixed, hyperthermic, and classified as Sodic Haplocambid as per the classification of the US Department of Agriculture.

2.2. Experimental materials and treatments

Hybrid seeds of maize cultivar HC9091 were obtained from DuPont Pioneer, Pakistan. The trial consisted of two irrigation levels (normal irrigation and drought stress at reproductive stage) and three seed priming techniques (control, hydropriming, and biopriming). To maintain normal irrigation treatment, the plots were watered 4 times, i.e. at leaf development, inflorescence emergence, flowering, and fruit development stages, according to the extended BBCH scale (codes: 10, 51, 61, and 71). Terminal drought stress was imposed at reproductive stages by maintaining the soil moisture content at 50% of field capacity (V-Tech Soil Tensiometer) (Nawaz et al., 2016) until physiological maturity, by following the extended BBCH scale (codes: 61–89) (Enz and Dachler, 1997). A randomized complete block design was used with factorial arrangement and replicated thrice in the experiment. The soil samples were randomly collected on a weekly basis from three different locations at the experimental area at a depth of 15–30 cm for moisture content determination. Depending on the soil analysis, a measured quantity of water was applied to the relevant plots to maintain soil moisture content at 50% of field capacity. Seeds were treated with a hydropriming technique using a ratio of 1:5 (seed:water) for 12 h and allowed to dry at room temperature for 6 h (Nawaz et al., 2017). The hydroprimed seeds were stored at 25–30 °C until sowing. For biopriming treatment, the seeds were first hydroprimed as described above. However, before drying, the wet seeds were coated with slurry at a ratio of 1:5 (seed:slurry); slurry was prepared by mixing a sugar solution with bacterial inoculum (*Rhizobium phaseoli*-RS-1 + *Pseudomonas* spp.), which was purchased from the Soil Microbiology Laboratory of the University of Agriculture Faisalabad, Pakistan (Hussain et al., 2018). Treated seeds were kept overnight at laboratory temperatures (25–30 °C) before sowing. For the control treatment, dry seeds were used for sowing. The field was supplied with presoaking irrigation for seedbed preparation. After the soil attained a workable moisture content, the field was prepared by a cultivator followed by planking. All treated and untreated maize seeds were sown manually, keeping a 75-cm row-to-row and 22.5-cm plant-to-plant distance (approximately 25,466 plants per acre). Urea, diammonium phosphate (DAP), and muriate of potash (MOP) were applied at the recommended rates of 180, 140, and 90 kg ha^{-1}, respectively, after soil analysis. A full dose of phosphorus and potassium was applied at the time of soil preparation. Nitrogen was applied in two equal splits, as per crop requirements, at the 1st and 2nd irrigations. All other agronomic practices were uniformly performed to keep the field free from weeds, insects, and diseases.

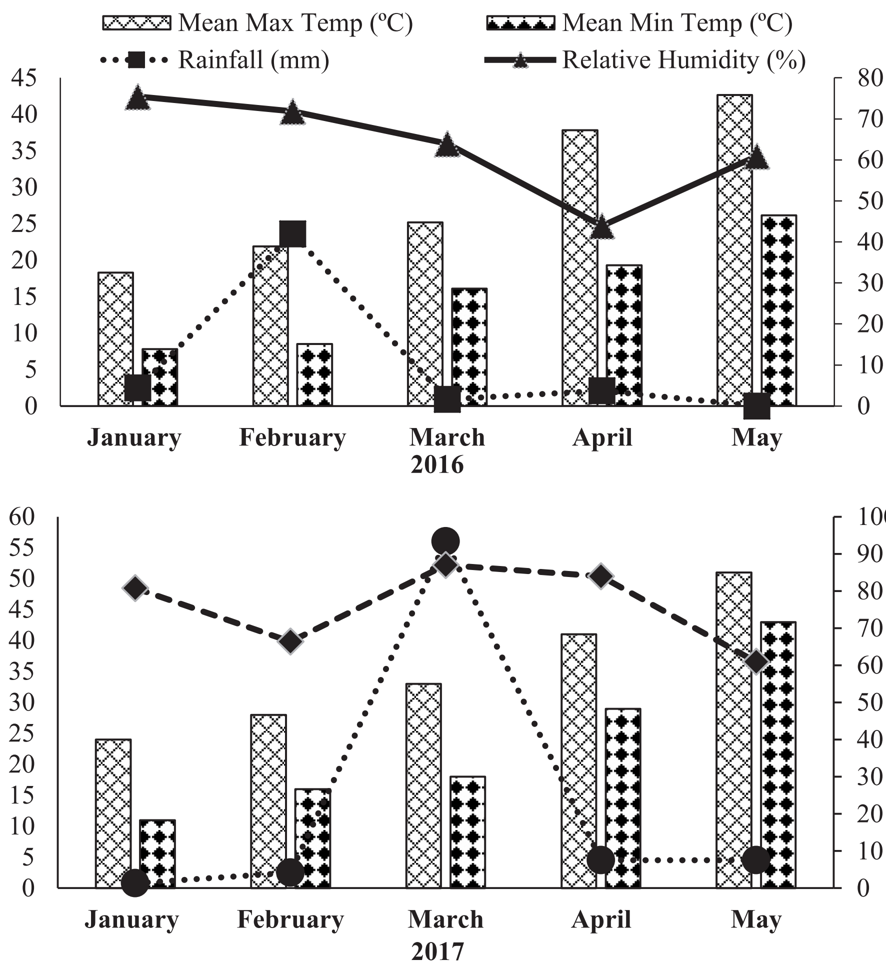

Figure 1. Meteorological data collected during maize phenological stages in 2016 and 2017.

2.3. Observations

2.3.1. Gas exchange capacity

A portable infrared gas analyzer [IRGA (LCA-4) Germany] was used to determine photosynthesis, transpiration rate, and stomatal conductance between 11:00 am and 2:00 pm (20 ± 2 °C) after the last irrigation (on BBCH scale during reproductive fruit development stage; code: 89) (Enz and Dachler, 1997), keeping a standard value of photosynthetic photon flux density (1200–1400 µmol m^{-2} s^{-1}). Healthy plants with completely developed and extended leaf areas were selected. Water use efficiency and intrinsic water use efficiency were measured following the formula described by Ahmad et al. (2013):

Water use efficiency = Rate of photosynthesis / Rate of transpiration Intrinsic water use efficiency = Rate of photosynthesis / Stomatal conductance

2.3.2. Electrolyte leakage and relative water content

Maize flag leaves (n = 3) were collected from randomly selected healthy plants from each plot in the morning (20 ± 2 °C). To measure the electrolyte leakage (EL), leaf disc samples were taken and dipped in a test tube containing 10 mL of deionized (DI) water. Test tubes were kept in an orbital shaking incubator at 28 ± 1 °C and 100 rpm for 5 h. Electrical conductivity (EC) was checked after incubation using a Jenway conductivity meter (model 4070), and the samples were then autoclaved at 121 °C and 15 psi for 20 min. EC was then measured to calculate electrolyte leakage using the following equation (Jambunathan, 2010):

% Electrolyte leakage = (EC before autoclaving / EC after autoclaving) × 100

The fresh and turgid weights of maize leaf samples were determined after 16–18 h of incubation at 4 °C in DI water. Then the samples were dried in an oven at 72 °C for 24 h, and the relative water content was measured as described below (Mayak et al., 2004):

% Electrolyte leakage = ((Fresh leaf weight – Dry leaf weight) / (Turgid leaf weight / Dry leaf weight)) × 100

2.3.3. Nutrient contents

The selected dried grain and stalk samples after maturity (at harvest of the crop) were crushed into powder and digested (0.1 g) in a diacid mixture at a ratio of 2:1 (H_2SO_4 conc.:H_2O_2) (Wolf, 1982). Nitrogen content was calculated using a Kjeldahl apparatus followed by titration (0.01 N H_2SO_4) (Jackson, 1962). Phosphorus was determined in the digested sample using a UV-spectrophotometer (Carry 60, Agilent, USA) at 420 nm following the standard protocol as described by Richards et al. (1954). Potassium content was measured using a flame photometer (Jenway PFP-7, UK), according to Ryan et al. (2001).

2.3.4. Yield and related parameters

Ten plants were selected randomly at the physiological maturity of the crop and used to measure the plant height, cob length, cob weight, 100-grain weight, and number of grains cob^{-1}. The remaining plants were harvested and threshed manually to measure biological yield and grain yield on a per plot basis, followed by conversion to a per hectare basis.

2.3.5. Economic analysis

To measure the cost effectiveness and economic feasibility of seed priming techniques for enhancing maize grain yield under various irrigation regimes, an economic analysis was performed. Total expenditures related to maize production were calculated including cost of seed-priming techniques, experimental land rent, seedbed preparation, fertilizer usage rates, seed and sowing, irrigation regimes, protection measures, and crop harvested. Gross income was obtained by applying the current common market prices for maize grain and straw in the country. Moreover, net income and benefit/cost ratio (BCR) were determined by the given formulas:

Net income = Gross income – total expenses

Benefit/cost ratio = Gross income / total expenses

2.4 Statistical analysis

Data were analyzed using analysis of variance (ANOVA) following a randomized complete block design with equal two-way factorial arrangements (Steel et al., 1997). Precise and advanced statistic software (Statistix, v8.1) was used. The calculated means were compared using the least significance difference (LSD) test ($P \leq 0.05$). Microsoft Excel (2013) was used for the graphical representation of meteorological data.

3. Results

3.1. Morphological parameters

Terminal drought stress prominently reduced the morphological parameters of maize plants. However, bioprimed seeds significantly ($P \leq 0.05$) improved all agronomic traits in plants under both normal and water-deficit conditions. Biopriming showed the highest plant height, cob length, cob weight, and number of grains cob^{-1}, followed by hydropriming and control treatments, under reduced as well as normal irrigation during both years of the trial (Table 1).

3.2. Yield and related parameters

Seed treatments under different irrigation regimes significantly influenced the 100-grain weight. During the first year of the experiment, biopriming ensured the highest 100-grain weight as compared to hydropriming and the control under normal as well as stressed environmental conditions. Similarly, biopriming considerably improved the drought-induced decline in biological yield and grain yield during both years of study. The harvest index was not affected by drought and priming treatments (Table 2).

3.3. Physiological components

Among different seed priming treatments, biopriming significantly improved the physiological performance of maize plants under normal as well as restricted irrigation during both years of the trial. The results revealed a clear reduction in photosynthesis, transpiration rate, water use efficiency (WUE), stomatal conductance, and the intrinsic WUE in drought-stressed maize plants. However, biopriming of seeds ameliorated the stress-induced effects on plants and improved all of the above-mentioned physiological attributes. The impact of biopriming was significantly better than that of hydropriming and control treatments during both years of the experiment (Table 3).

3.4. Electrolyte leakage and relative water content

Bioprimed seeds had improved electrolyte leakage and relative water content in maize leaves under applied terminal drought stress. Plants showed the lowest performance in the control (with seed treatment) under imposed terminal drought stress conditions, followed by normal irrigation levels, during the both years of the trial (Figure 2).

3.5. Nutrient uptake

Limited water supply reduced the NPK concentration in the grains and straw of maize plants. Nonetheless, among priming techniques, biopriming helped the plants withstand stress conditions through increased absorption of nutrients from the soil, followed by hydropriming, and then the control. A similar trend was observed during both years of the study (Figures 3 and 4).

3.6. Benefit/cost ratio (BCR)

Terminal drought stress at the reproductive stage of maize caused a drastic reduction in BCR values. Economic analysis illustrated that seed biopriming, as compared to other treatments, was a cost-effective technique for obtaining maximum profitability in terms of BCR under terminal drought stress conditions (Table 4).

4. Discussion

The aftermath of drought stress depends on its duration, intensity, and plant growth stage. It determines plant sensitivity and survivability against water deficit conditions. Moisture deficit at critical growth stages causes a significant

Table 1. Effect of biopriming on the growth characteristics of maize under terminal drought stress.

	2016		2017	
	Normal irrigation	Terminal drought	Normal irrigation	Terminal drought
	Plant height (cm)			
Control	198.70 bc ± 0.42	153.67 e ± 1.50	216.37 c ± 0.83	192.00 e ± 0.82
Hydropriming	204.87 b ± 1.24	181.67 d ± 1.29	227.00 b ± 1.25	205.37 d ± 1.27
Biopriming	216.00 a ± 0.98	193.33 c ± 2.28	239.00 a ± 1.09	210.33 cd ± 1.23
Year	191.37 B		215.01 A	
LSD 0.05 P	8.67		7.17	
	Cob length (cm)			
Control	16.96 b ± 0.50	12.79 c ± 0.42	25.23 a ± 0.32	17.47 d ± 0.62
Hydropriming	19.01 b ± 0.33	15.50 bc ± 0.87	15.35 d ± 0.24	17.83 cd ± 0.49
Biopriming	24.44 a ± 0.25	16.86 b ± 0.57	20.00 bc ± 0.25	20.58 b ± 0.15
Year	17.59 B		19.41 A	
LSD 0.05 P	3.52		2.52	
	Cob weight (g)			
Control	214.03 c ± 1.01	196.77 c ± 0.51	250.30 c ± 1.13	226.77 d ± 0.81
Hydropriming	237.53 b ± 0.85	204.67 c ± 0.72	293.99 b ± 1.97	231.07 cd ± 0.70
Biopriming	275.93 a ± 1.21	209.90 c ± 1.16	328.77 a ± 0.92	283.00 b ± 1.19
Year	223.14 B		268.98 A	
LSD 0.05 P	17.56		21.13	
	Number of grains cob^{-1}			
Control	420.74b c ± 0.35	390.26 d ± 0.99	512.93 c ± 1.22	425.50 e ± 0.82
Hydropriming	427.41 b ± 1.23	397.87 d ± 1.14	536.97 b ± 1.53	413.08 f ± 0.71
Biopriming	436.06 a ± 1.08	417.77 c ± 1.37	555.19 a ± 0.91	437.59 d ± 1.14
Year	415.02 B		480.21 A	
LSD 0.05 P	7.71		7.87	

Means not sharing the same letters in a group differ significantly at 5% probability level.

reduction in maize crop yield (Farooq et al., 2009). Several sustainable approaches have been investigated to mitigate the impact of abiotic stresses in plants. Among these, biopriming is an emerging seed treatment technique that may have the ability to rescue plants from drought stress by modulating their physiological activities (Hussain et al., 2014).

The results of the present study demonstrated a significant decline in yield in maize crops under drought stress at reproductive growth stages, as expected. However, the biopriming technique considerably alleviated the outcomes of water deficit, as illustrated by the morphological and physiological performance of plants (Ahmad et al., 2015). Terminal drought stress impaired growth- and development-related attributes of maize plants with a notable reduction in plant height, cob length, cob weight, and number of grains per cob. Trends of increase in the above-mentioned traits as a consequence of biopriming might be due to bacterial inoculation, which helps the plants survive under stressful environmental conditions through maximum utilization of available soil moisture (Ilyas et al., 2008). Biopriming has also been reported to reduce ethylene production, due to the presence of ACC-deaminase, which could enhance the chances for survival of plants under water deficit conditions (Lucy et al., 2004). Observations also revealed that biopriming treatment may enhance tolerance of water stress and modulate maize plant growth and development, producing better grain yield (Yang et al., 2009).

A notable improvement in maize grain yield under drought stress, which might be due to bacterial inoculation, was observed in seed biopriming (Zafar-ul-Hye et al.,

Table 2. Effect of biopriming on the yield components of maize under terminal drought stress.

	2016		2017	
	Normal irrigation	Terminal drought	Normal irrigation	Terminal drought
	100-Grain weight (g)			
Control	22.14 bc ± 0.66	18.66 d ± 0.26	25.55 d ± 1.23	27.19 cd ± 0.91
Hydropriming	23.59 b ± 0.38	20.33 cd ± 0.60	30.26 bc ± 0.44	29.62 b.d ± 0.83
Biopriming	29.33 a ± 0.54	21.74 b.d ± 0.29	37.22 a ± 0.37	32.23 b ± 0.83
Year	22.63 B		30.34 A	
LSD 0.05 P	3.16		4.61	
	Biological yield (t ha^{-1})			
Control	12.74 c ± 0.75	9.33 d ± 0.77	16.44 c ± 0.45	11.50 e ± 0.40
Hydropriming	18.63 b ± 0.44	8.99 d ± 0.41	22.76 b ± 0.46	12.82 de ± 0.56
Biopriming	24.66 a ± 0.80	12.03 c ± 0.73	27.11 a ± 0.18	15.14 cd ± 1.31
Year	14.40 B		17.63 A	
LSD 0.05 P	2.17		2.64	
	Grains yield (t ha^{-1})			
Control	5.07 c ± 0.18	4.26 d ± 0.31	5.07 c ± 0.04	4.64 cd ± 0.18
Hydropriming	6.30 b ± 0.19	4.07 d ± 0.58	5.21 bc ± 0.16	4.36 d ± 0.37
Biopriming	8.61 a ± 0.13	5.04 c ± 0.01	10.48 a ± 0.04	5.76 b ± 0.54
Year	5.56 B		5.92 A	
LSD 0.05 P	0.53		0.65	
	Harvest index (%)			
Control	40.55	45.47	31.58	40.81
Hydropriming	33.92	45.35	23.04	34.22
Biopriming	34.96	42.13	38.77	38.65
Year	40.39 A		34.51 B	
LSD 0.05 P	NS		NS	

Means not sharing the same letters in a group differ significantly at 5% probability level. NS = Nonsignificant.

2013). Maize is very sensitive to water deprivation in the reproductive growth stage. The increasing trend in plant growth and development indicators might be due to ACC-deaminase activity, which enhanced plant tolerance by converting ACC into ammonia and α-ketobutyrate, instead of ethylene (Zahir et al., 2011).

Biopriming mitigated the negative impact of terminal drought stress by improving gas exchange characteristics (Ahmad et al., 2015). In this study, the significant impact of biopriming might be ascribed to diminished activity of ROS, which improved the photosynthetic and transpiration rates in the leaves of maize plants under terminal drought stress (Anjum et al., 2011). Terminal drought did not influence the WUE and stomatal conductance, as yield reduction under stress was compensated by a decrease in water supply. However, biopriming improved the WUE against other treatments, which may be due to an increase in yield as even the water supply was different in the case of terminal drought and normal-irrigation water regimes (Ahmad et al., 2015). The drastic effect of terminal drought seems to be mitigated by bacterial inoculation that may have triggered a better antioxidant defense, which is responsible for sustaining the process of photosynthesis, transpiration rate, and intrinsic WUE under adverse conditions (Ahmadi and Siosemardeh, 2005). Moreover, due to early and synchronized emergence, healthy seedlings obtained by biopriming utilized the available resources more proficiently and performed better throughout the life cycle under normal as well as stressed environmental conditions (Hussain et al., 2016).

Table 3. Effect of biopriming on the physiological parameters of maize under terminal drought stress.

	2016		2017	
	Normal irrigation	Terminal drought	Normal irrigation	Terminal drought
	Photosynthesis rate (mmol m^{-2} s^{-1})			
Control	3.40 c ± 0.22	2.67 c ± 0.09	4.77 c ± 0.36	4.44 c ± 0.13
Hydropriming	5.18 b ± 1.27	4.99 b ± 0.41	6.30 b ± 0.53	5.01 c ± 0.15
Biopriming	8.00 a ± 0.24	5.70 b ± 0.26	8.44 a ± 0.32	5.96 b ± 0.12
Year	4.99 B		5.82 A	
LSD 0.05 P	1.30		0.72	
	Transpiration rate (mmol m^{-2} s^{-1})			
Control	1.07 d ± 0.06	0.87 e ± 0.07	1.17 bc ± 0.08	0.87 c ± 0.03
Hydropriming	1.35 b ± 0.08	0.76 e ± 0.05	1.51 b ± 0.06	0.97 c ± 0.40
Biopriming	1.90 a ± 0.01	1.20 c ± 0.02	1.95 a ± 0.04	1.35 b ± 0.15
Year	1.19 B		1.30 A	
LSD 0.05 P	0.12		0.36	
	Water use efficiency (WUE = A/E)			
Control	2.95 c ± 0.61	1.99 d ± 0.23	3.17 b ± 0.16	1.33 c ± 0.24
Hydropriming	2.72 c ± 0.43	3.06 c ± 0.03	3.65 ab ± 0.18	1.85 c ± 0.19
Biopriming	4.51 a ± 0.27	3.71 b ± 0.13	4.09 a ± 0.03	3.71 a ± 0.41
Year	NS			
LSD 0.05 P	0.63		0.53	
	Stomatal conductance (mmol m^{-2} s^{-1})			
Control	0.042 c ± 0.00	0.033 c ± 0.01	0.021 c ± 0.01	0.024 c ± 0.01
Hydropriming	0.051 bc ± 0.00	0.034 c ± 0.01	0.032 c ± 0.01	0.038 bc ± 0.00
Biopriming	0.081 a ± 0.01	0.061 b ± 0.01	0.091 a ± 0.00	0.056 b ± 0.01
Year	NS			
LSD 0.05 P	0.017		0.019	
	Intrinsic WUE (iWUE = A/g_s)			
Control	105.31 c ± 0.78	75.88 e ± 1.46	111.01 c ± 0.41	81.89 e ± 0.93
Hydropriming	123.02 b ± 1.76	85.73 d ± 0.91	125.08 b ± 1.08	83.12 e ± 0.85
Biopriming	132.14 a ± 1.46	93.39 d ± 0.98	138.20 a ± 0.81	95.13 d ± 0.76
Year	102.58 B		105.74 A	
LSD 0.05 P	9.00		5.09	

Means not sharing the same letters in a group differ significantly at 5% probability level. NS = Nonsignificant.

Terminal drought stress influenced electrolyte leakage and relative water content; however, stress was compensated by applied seed treatments including hydropriming and biopriming. In particular, the biopriming treatment improved drought tolerance of maize HC9091, mainly due to the decreasing need for water, as well as development of an improved source–sink relationship (Alexandre and Oliveira, 2013); hence, better plant moisture consumption was modulated. The improved source–sink relationship of water enhanced the growth and development of plants by converting ACC-deaminase into ammonia and α-ketobutyrate instead of ethylene (Zahir et al., 2011), which contributed to the improved drought-stress tolerance of maize in this study.

The results of this two-year field study clarified the supremacy of biopriming treatment in improving nutrient uptake (NPK) by maize HC9091 plants. The additional drought tolerance was attributed to the

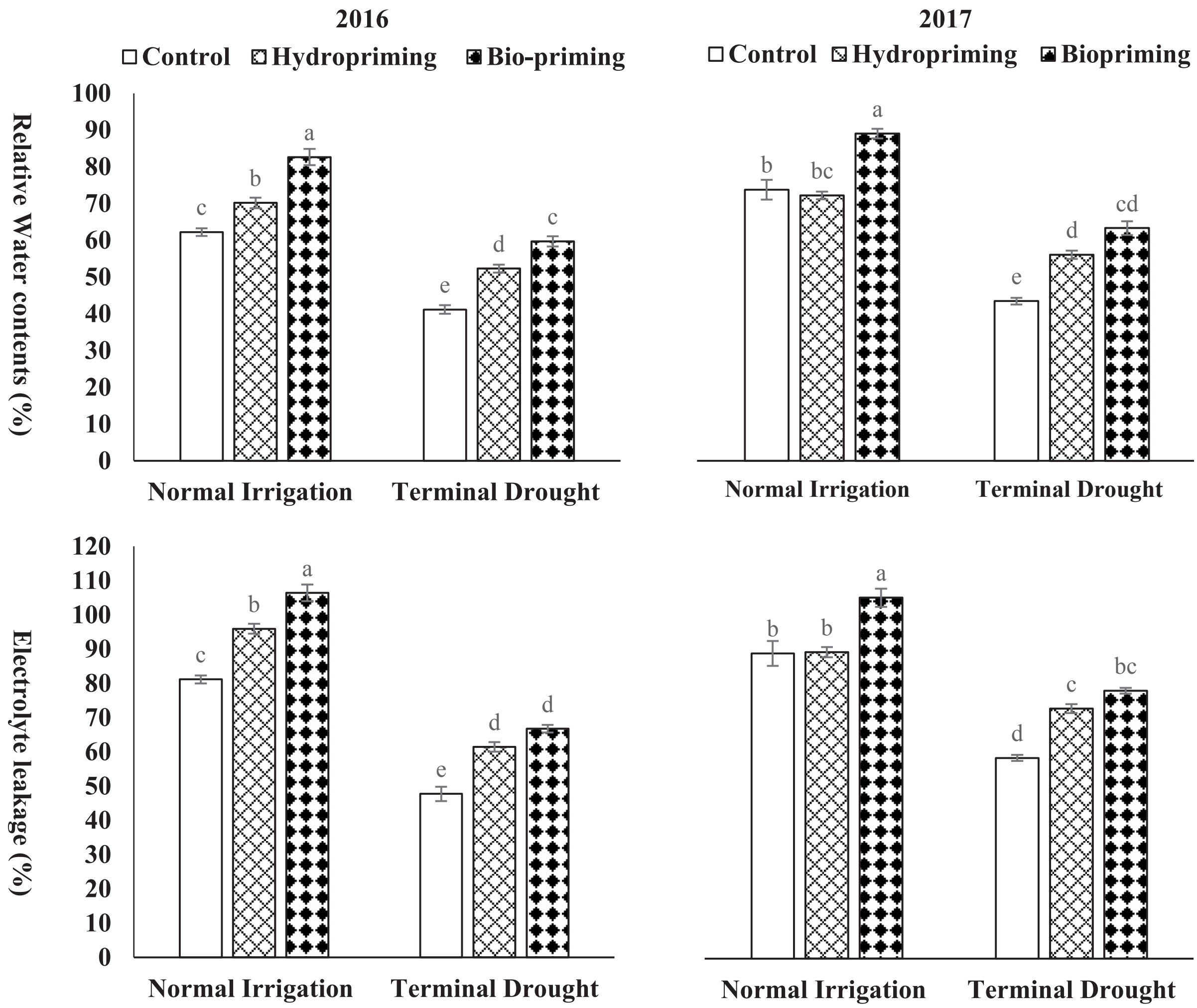

Figure 2. Effect of biopriming technique on relative water content and electrolyte leakage in maize leaves under terminal drought stress.

bacterial colonization in the root zone of these plants, which allowed the plants to absorb relatively higher amounts of nutrients from the soil as compared with the control (Grover et al., 2010). The increase in the nutrient uptake mainly took place due to modification of the root morphological behavior by the biopriming involving PGPR. Inoculation with PGPR after seed priming increased nutrient uptake by increasing the root surface area. The modification of root development characteristics supported the functional traits of the root as well as other organs of the maize HC9091 plants, contributing to an overall improvement in drought-stress tolerance (Hussain et al., 2018). Furthermore, seed priming with inoculation of PGPR accelerated the activity of oxidase enzyme and enhanced production of exopolysaccharides and auxins, which may have improved nutrient absorption by maize plants for greater yield under terminal drought stress (Anjum et al., 2011).

The effectiveness of any new innovation or technique is based on easy adoptability, commercial feasibility, and environmental sustainability at field level (Farooq et al., 2014). Economic analysis indicated an increase in the profitability of maize crops through the biopriming of seeds under normal as well as deficit moisture conditions as compared with the control treatment.

In conclusion, in the current study we observed that terminal drought stress significantly decreases maize productivity; however, biopriming of maize seeds showed promising results in modulating plant physiological behavior, improving nutrient uptake, and mitigating grain-yield losses that occur due to drought stress observed during flowering and grain development. An examination of proteinaceous banding profiles and characteristics at a molecular level through SDS-PAGE, after application of the seed biopriming technique, is needed to further investigate the effects of seed biopriming.

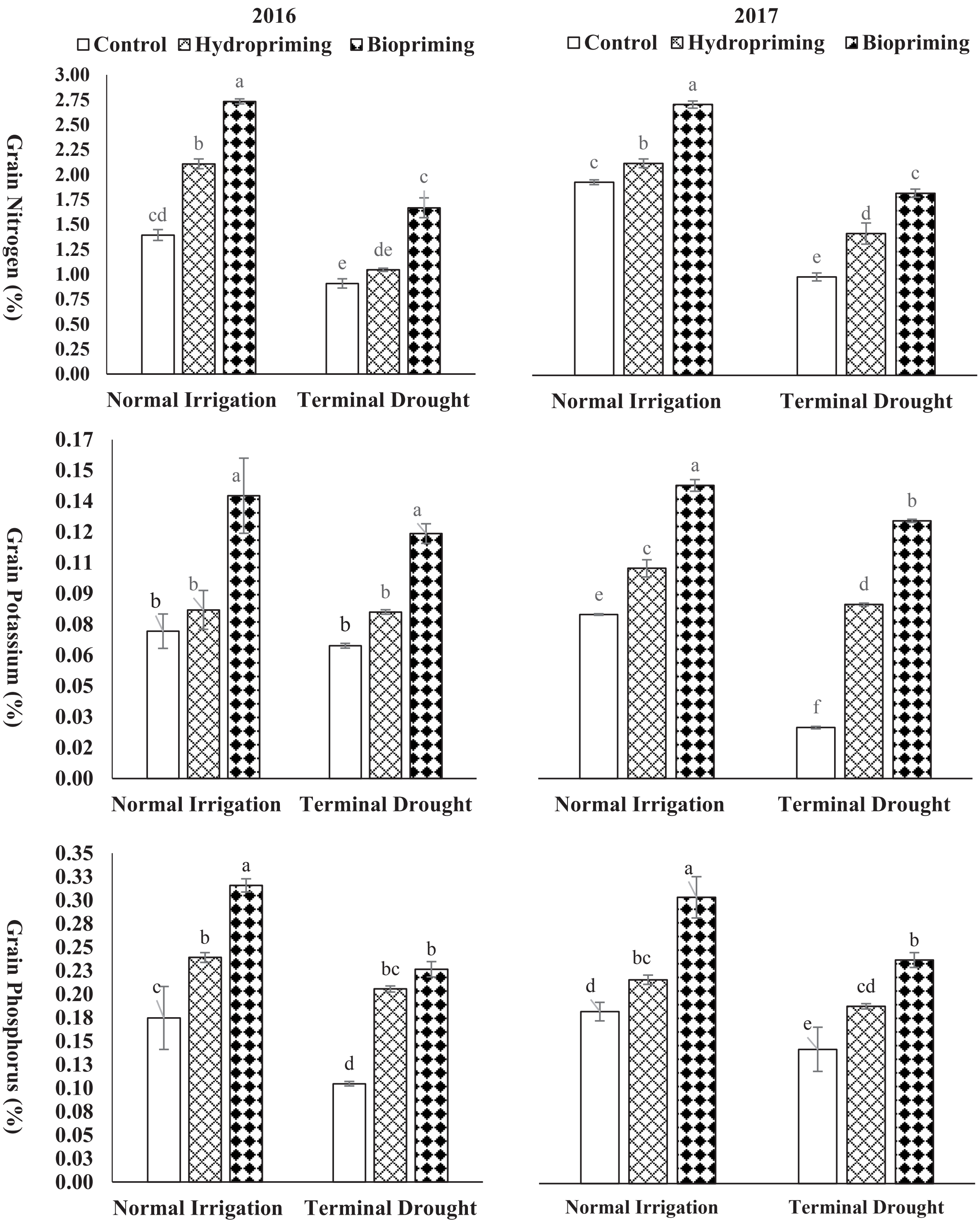

Figure 3. Effect of biopriming technique on nutrient contents in maize grains under terminal drought stress.

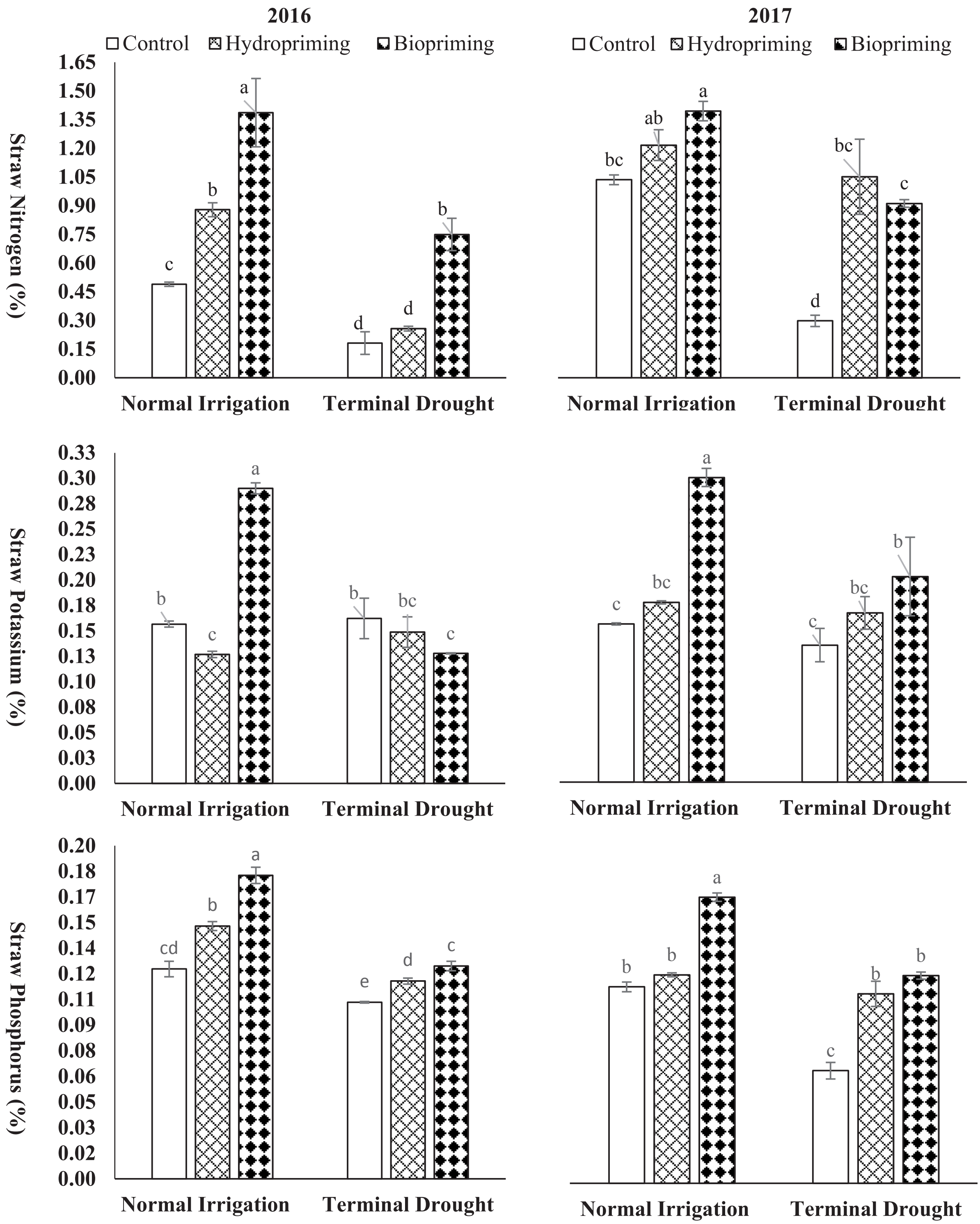

Figure 4. Effect of biopriming technique on nutrient contents in maize straw under terminal drought stress.

Table 4. Comparative benefit/cost ratio (BCR) by seed treatment in maize under terminal drought stress.

	Total expenditure (US$ ha^{-1})		Gross income (US$ ha^{-1})		Net income (US$ ha^{-1})		Benefit/cost ratio	
	Normal irrigation							
	2016	2017	2016	2017	2016	2017	2016	2017
Control	655	647	1082.33	1167.99	427.06	521.44	1.65	1.81
Hydropriming	655	647	1229.78	1209.92	574.51	563.37	1.88	1.87
Biopriming	669	661	1489.42	1506.53	820.42	845.98	2.23	2.28
	Terminal drought							
Control	612	626	791.71	743.78	179.71	117.96	1.29	1.19
Hydropriming	612	626	786.56	841.43	174.56	215.61	1.29	1.34
Biopriming	630	631	933.09	949.79	303.09	319.24	1.48	1.51

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