Potassium fertilization mitigates the adverse effects of drought on selected Zea mays cultivars

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Abstract: In the present study, the role of potassium (K) in mitigating the adverse effects of drought stress (DS) on 2 maize (Zea mays L.) cultivars, ‘Shaandan 9’ (S9; drought-tolerant) and ‘Shaandan 911’ (S911; drought-sensitive), was assessed. K application increased dry matter (DM) across all growth stages and grain yield (GY) in both cultivars under DS, but not under control conditions. Drought-tolerant cultivar S9 was superior to drought-sensitive cultivar S911 under DS in terms of DM and GY regardless of K addition. Additionally, K application increased relative water content, nitrate reductase activity, and concentrations of potassium ion, free proline, soluble protein, and endogenous glycine betaine in both cultivars. These positive effects due to K fertilization under DS were greater for S911 than for S9. In contrast, the differences in the above parameters between K-treated plants and plants under control conditions were either nonsignificant or marginal. This study provides direct evidence of the beneficial physiological function of K fertilization in mitigating the adverse effects of DS by increased nitrate assimilation and osmotic regulation, but not due to its nutritive role.

Key words: Relative water content, nitrate reductase activity, osmotic solutes, Poaceae, potassium fertilizer

1. Introduction

Water shortage has become a significant limiting factor for agricultural production in most parts of the world, including China. Due to this problem, sustainable production of food requires new approaches to enhance the use efficiencies of all inputs, including water and nutrients. These approaches are vital not only to achieve enhanced agricultural productivity, but also to protect environmental quality (Zhang et al., 2009a; Saeidnejad et al., 2013). In recent years, the impact of frequent droughts on crop production in most parts of northern China has been tremendous (Ge et al., 2012). Maize (Zea mays L.), one of the most important cereal crops in this area, is frequently subjected to drought stress (DS), resulting in marked reductions in economic yields (Zhang et al., 2009a; Lopes et al., 2011; Ge et al., 2012).

DS, in fact, causes a multitude of biochemical and physiological changes as a consequence of osmotic stress. The imposition of osmotic stress causes a significant decline in chemical activity of water and a loss of turgor in plant cells (Taiz and Zeiger, 2002; Zhang et al., 2013; Yıldıztugay et al., 2014). These changes, in turn, may impair nitrate assimilation by reducing nitrate reductase activity (NRA) (Zhang et al., 2009b). Protein degradation also increases under DS due to enhanced protease hydrolysis activity. The net effect of these changes leads to reduced plant growth and/or plant death as well as reduced relative water content (RWC), the latter being an effective indicator of plant water status (Taiz and Zeiger, 2002; Zhang et al., 2009b).

Plants have evolved various strategies, the most promising one being osmotic regulation, to mitigate the negative effects of DS on nitrate assimilation. Furthermore, osmoregulation provides optimal conditions for plant growth (Ashraf and Foolad, 2007; Choluj et al., 2008; Ashraf, 2010). Plant cells can mitigate the adverse effects of osmotic stress by reducing the depletion of cellular water and regaining cell turgor, which is mediated by maintaining optimal NRA and accumulation of potassium ions (K+), as well as concentrations of endogenous glycine betaine (EGB), free proline (FP), soluble proteins (SP), and derivative products from N metabolism (Zhang et al., 2009a, 2009b). Therefore, changes in NRA and concentrations of K+, EGB, FP, and SP can determine the changes in nitrate...
assimilation and osmotic solute accumulation in response to DS (Choluj et al., 2008). Different reports have shown that changes in RWC, NRA, and osmotic solutes induced by DS were dependent on cultivars and growth stage as well as the intensity and duration of DS (Shao et al., 2006; Ashraf and Foolad, 2007; Choluj et al., 2008; Zhang et al., 2009a, 2009b; Ashraf, 2010; Zhang et al., 2013).

Abundant amounts of K are required by most plants. However, its uptake by plants is significantly affected by soil moisture content, which affects rates of root growth and of K+ diffusion from soil to the root. Hence, K uptake efficiency is rather low in dry-land regions. Thus, it becomes a major limiting factor for attaining optimal crop yield and quality (Ge et al., 2012). Despite acting as an essential macronutrient, K serves as a primary osmoticum to maintain turgor in plants, particularly under stressful environments. Therefore, abundant K+ accumulation in plant tissues under DS may play a vital role in water uptake from the soil (Cakmak, 2005). In view of several reports, it is now evident that the exogenous application of K can alleviate drought-induced negative effects on plant growth (Andersen et al., 1992; Abdelvahab and Abdalla, 1995; Sudama et al., 1998; Tiwari et al., 1998; Sangakkara et al., 2001; Singh and Kuhad, 2005; Fanæi et al., 2009; Ezzat et al., 2010; Mohammad and Mahmood, 2011).

K application can improve drought tolerance in plants by regulating a variety of processes, such as osmoregulation, charge balance, energy status, and protein synthesis (Maathuis and Sanders, 1996). Reduced water loss of plants grown under adequate K supply is dependent on the osmotic potential of mesophyll cells (Cakmak, 2005). Several studies, often under short durations of DS, have provided evidence of the role of K in mitigating DS by enhancement of NRA and accumulation of K+, glycine betaine, FP, and SP (Maathuis and Sanders, 1996; Fanæi et al., 2009; Ezzat et al., 2010; Mohammad and Mahmood, 2011).

Most past studies have dealt with the effects of K on plant physiological responses to mitigate DS during a single growth stage and a sudden simulated DS, mainly in terms of single factorial effects of a cultivar, water, or fertilizer. Hence, there is a need to investigate the influence of K supplementation on the response of maize cultivars exposed to long-term DS and to elucidate the specific role of K in modulating plant physiological responses to mitigate DS, as well as in the overall improvement of plant vigor by optimal K fertilization, which in turn facilitates enhanced tolerance to DS (Zhu et al., 2005; Fanæi et al., 2009; Ezzat et al., 2010; Mohammad and Mahmood, 2011). Keeping in view the above facts, we hypothesize that greater nitrate assimilation and osmotic regulation in the leaves of maize plants provides a mechanism of DS tolerance in different cultivars with application of K fertilizer. Thus, the primary objective of this study was to examine the mechanism of amelioration of negative effects of long-term DS by K nutrition in 2 maize cultivars with contrasting responses to DS.

2. Materials and methods

2.1. Plant material and experimental design

This study was conducted at the Northwest A & F University, Yangling (34°20’N, 108°24’E), Shaanxi Province, China. Two maize cultivars, Shaandan 9 (S9, drought-sensitive) and Shaandan 911 (S911, drought-tolerant) (Zhang et al., 2007), were used in the study. The soil used was a typical manural loessial clay-loam, which was sampled from a depth of 20 cm within Yangling, China. Selected properties of the soil used were determined using the procedures described by Miller and Keeney (1982): pH 8.13; organic matter = 11.8 g kg⁻¹ (potassium dichromate volume method); total N = 0.96 g kg⁻¹ (micro-Kjeldahl method); available N = 42.3 mg kg⁻¹ [2 mol L⁻¹ potassium chloride (KCl) extraction, autoanalyzer]; Olsen-P = 23.2 mg kg⁻¹ [0.5 mol L⁻¹ sodium bicarbonate (NaHCO₃), molybdenum blue method]; exchangeable K = 216 mg kg⁻¹ [1 mol L⁻¹ ammonium acetate (NH₄OAc) extraction, flame photometry]; water holding capacity (WHC) = 22.6% (Wilcox method).

The soil was ground well, sieved to 0.5 mm, and then air-dried. The soil was then added to each pot with 12 kg per pot. Each pot had a diameter of 28 cm and a height of 35 cm. All soil-filled pots were placed in a greenhouse. The soil moisture content before planting was 13%. The soil in each pot was supplemented with 0.15 g P kg⁻¹ and mulched with wheat straw to prevent water evaporation. In June, 5 seeds of each cultivar were planted in each pot. When the seedlings were at the 3-leaf stage they were thinned to 1 per pot. The treatments included 2 soil water regimes: 1) control, i.e. soil water content maintained at 19 ± 1% of water content (weight basis), which was equivalent to 85 ± 5% of WHC; 2) DS, maintained at 15 ± 1% of water content (weight basis), being equivalent to 65 ± 5% of WHC from seedlings at the 3-leaf stage to full maturity. The K treatments, applied as KCl, were: 1) 0 (K₀: no addition of K fertilizer); 2) 0.42 g K kg⁻¹ soil. Full doses of K and P fertilizers, together with one-third doses of N (0.5 g N kg⁻¹ soil), were added to the soil before sowing. The remaining N was added in 2 equal split doses at the beginning of the elongation stage and heading stage. The experiment was set up in a completely randomized design with 8 treatments and 17 replications. Soil water content was monitored referring to Zhang et al. (2007).

2.2. Sampling and measurement of different plant parameters

Between 1030 and 1100 hours, the third or fourth fully expanded leaf was sampled from each replicate at the
seedling, elongation, heading, and maturity stages at 25, 38, 65, and 95 days after planting, respectively, then stored in a bucket with dry ice during transportation to the laboratory. The leaf samples were washed with distilled water to remove surface dust. The leaf samples for NRA assay and osmotic solutes measurement were immediately placed in liquid N and stored at –40 °C until their use in experimentation.

The whole shoot was sampled from 4 replicates (pots) at each growth stage for measuring dry matter (DM). Grain yield (GY) was measured at the maturity stage after harvest.

RWC was determined using the following formula (Gao, 2000):

\[
\text{RWC} (\%) = [(\text{FW} – \text{DW}) / (\text{TW} – \text{DW})] \times 100,
\]

where FW is fresh weight of sample, TW is turgid weight of sample, and DW is dry weight of sample.

The measurement of NRA was carried out in vitro (Wray and Filner, 1970). Two portions of 0.25 g from each fresh leaf sample were taken. One was used for DM weight determination and the second portion was homogenized in 5 mL of 0.1 M phosphate buffer (pH 7.5) and 1 mM cysteine and then centrifuged. The reaction mixture containing 0.5 mL of enzyme extract, 0.01 mL of 0.1 M KNO₃, 0.5 mL of phosphate buffer (0.1 M, pH 7.5), 0.1 mL of 1 mM NADH, and 0.1 mL of double-distilled water was subjected to 30 °C for 45 min. The reaction was terminated by adding 1 mL of sulfanilamide (1% in 3 M HCl and 1 mL of 3% sulfosalicylic acid using a mortar and pestle. About 2 mL of extract was placed in a test tube and 2 mL of glacial acetic acid and 2 mL of ninhydrin reagent were added. The mixture was heated in boiling water bath for 1 h. After cooling the mixture in an ice bath, 4.0 mL of toluene was added to it. Absorbance of the colored mixture was read at 520 nm against a blank. Concentration of proline was estimated by referring to a standard curve of proline.

EGB concentration (EGBC) was measured following the method described by Greive and Grattan (1983) with some modifications. Leaf samples (finely ground, 0.5 g) were shaken with 20 mL of deionized water for 48 h at 25 °C. The samples were then filtered and the filtrate was diluted 1:1 with 2 M sulfuric acid. An aliquot (0.5 mL) of this mixture was transferred into a test tube, and then after cooling it for 1 h in an ice bath, cold potassium iodide-iodine reagent (0.2 mL) was added. The samples were centrifuged at 10,000 × g for 15 min at 0 °C, the supernatant was treated with 1,2-dichloroethane (reagent grade), and the absorbance was read at 365 nm. Reference standards of glycine betaine (50–200 µg mL⁻¹) were used for calibration and estimation of glycine betaine concentration in unknown samples.

Concentration of K⁺ in the leaf samples was determined according to the method described by Bao (2000). Finely ground leaf biomass (0.2–0.3 g) was treated with 18 mol L⁻¹ concentrated sulfuric acid and 30 g L⁻¹ H₂O₂ at 300 °C for 4–5 h in a digestion tube using the wet ashing method. After wet digestion, the samples were diluted to 100 mL of final volume with deionized water. K⁺ concentration was determined by flame spectrometry.

The results of the above osmotic nitrides concentrations were expressed in µmol g⁻¹ DW based on mean of 4 replicates (n = 4). The relative contribution of a soluble nitride to osmotic adjustment was evaluated by comparing one mole concentration of one solute with another based on DW under DS referring to Zhang et al. (2009b).

2.3. Statistical analysis

The data of each variable were subjected to analysis of variance (ANOVA) separately using the SAS software package (SAS Institute Inc., 1996). Standard errors of the means were calculated. The significance of the treatment effect was assessed using the F-test, and significance of mean separation was worked out by Duncan’s multiple range test.

3. Results

3.1. Interactions between K and water regimes in 2 maize cultivars with respect to plant growth, water status, N assimilation, and osmotic solutes

ANOVA showed that the effects of water regime, maize cultivars, and K rates were significant on all measured parameters (Table 1). Two-way interactions among the treatments were also significant for all the parameters. The magnitude of mean squares across the above parameters was, in order: water regime > K rate > cultivar.
3.2. Plant growth and plant water status
DS caused a marked reduction in DM weight and GY as well as RWC in both cultivars, though this was more marked in S911 than in S9 (Figure 1; Table 2). The adverse effects of DS on the earlier mentioned parameters were significantly alleviated by exogenous K application. K application led to a significant increase in DM production, GY, and RWC in both cultivars under DS; such a K-induced positive effect was not observed in plant growth and water relations under control conditions. Applied K increased DM of S911 by 10.9%–18.5% and that of S9 by 4.1%–6.6%, and GR of S911 by 11.2% and that of S9 by 8.5% when exposed to DS. RWC also increased by 6.5% and 7.8% for S9 and S911, respectively (Figure 1; Table 2). The investigated parameters were higher in S9 than in S911 with addition of K fertilizer or no K application under DS.

3.3. Nitrate assimilation
The reduction in NRA of plants across different growth stages under DS as compared to that of the control plants was greater for the drought-sensitive cultivar S911 than in S9 (Figure 1; Table 2). The adverse effects of DS on the earlier mentioned parameters were significantly alleviated by exogenous K application. K application led to a significant increase in DM production, GY, and RWC in both cultivars under DS; such a K-induced positive effect was not observed in plant growth and water relations under control conditions. Applied K increased DM of S911 by 10.9%–18.5% and that of S9 by 4.1%–6.6%, and GR of S911 by 11.2% and that of S9 by 8.5% when exposed to DS. RWC also increased by 6.5% and 7.8% for S9 and S911, respectively (Figure 1; Table 2). The investigated parameters were higher in S9 as compared with S911 with addition of K fertilizer or no K application under DS.

3.4. Accumulation of osmotic solutes
The present study showed that K+ concentration, SPC, EGBC, and FPC were greater in plants of both cultivars under DS than in the controls (Figures 1 and 2). Furthermore, the magnitude of increase in concentrations of K+ and osmotic nitrides with K application was much greater in plants under DS than in those under control conditions. The concentrations of the above osmotic solutes were greater in S9 than in S911 across both K treatments. In the control treatment, no significant difference was evident between the 2 cultivars with respect to these osmotic solutes, except K+ concentration (Figure 2). Concentrations of osmotic nitrides increased from the seedling stage to the elongation/heading stage, followed by a decrease during the maturity stage, while K+ concentration continuously decreased through the entire growing period (Figure 3). The concentrations of K+ and osmotic nitrides in plants under DS increased with K application in both cultivars. With K application, the magnitude of increase in K+ concentration was much greater in plants grown under DS than that of the plants under control conditions (Figure 1). Across all treatments and both cultivars, K+ concentration and FPC were much greater than those of EGBC or SPC (Figures 1–3).

3.5. Correlations among parameters of plant growth, water status, N assimilation, and osmotic solutes
The correlation coefficients among different plant growth and physiological characteristics under DS and controlled growing conditions are presented in Table 3. In general, correlation coefficients among DM, GY, RWC, NRA, and osmolyte concentrations were greater for the plants under DS than for plants under control conditions (Figure 1). Across all treatments and both cultivars, K+ concentration and FPC were much greater than those of EGBC or SPC (Figures 1–3).

4. Discussion
Different crop cultivars maintain differential productivity, water status, N assimilation, and osmotic solute accumulation under DS, which can be altered by K.
The significant interactions in this study showed that choice of cultivar, optimal water, and K management are important to overcome the adverse effects of DS in terms of plant growth, water status, N assimilation, and osmotic solute accumulation. These results are in agreement with those of Zhang and Li (2005) and Zhang et al. (2007).

DS is generally characterized by a disorder in growth and a reduction in yield, which is dependent on the cultivar’s drought tolerance and nutrient supplies.

Figure 1. Effects of potassium application on relative water content (RWC), nitrate reductase activity (NRA), K⁺ concentration (KC), free proline concentration (FPC), endogenous glycine betaine concentration (EGBC), and soluble protein concentration (SPC) in 2 maize cultivars under drought stress (DS) or well-watered treatment (C). Cultivars Shaandan 9 and Shaandan 911 are represented by 9 and 911, respectively. Each value is the mean across 4 growth stages. Different letters at the top of histograms within each response variable indicate significant difference (P < 0.05).
(Cakmak, 2005). On the one hand, the drought-tolerant maize cultivar S9 had a greater DM production and GY regardless of K application (Table 2) and N application (Zhang et al., 2007). On the other hand, numerous studies have shown that the application of K fertilizer mitigates the adverse effects of DS on growth of different crops such as barley (Hordeum vulgare L.) (Andersen et al., 1992), faba beans (Vicia faba L.) (Abdelvahab and Abdalla, 1995), sugar cane (Saccharum officinarum L.) (Sudama et al., 1998), and rice (Oryza sativa L.) (Tiwari et al., 1998). K fertilization increased DM production and GY of both cultivars under DS to levels above those of plants with no K supply. However, K fertilization had no significant influence on the above parameters of both cultivars under nonstressed conditions (Maathuis and Sanders, 1996; Tabatabaii Ebrahimi and Yarnia, 2011; Table 2). The results demonstrate the beneficial effects of K in terms of mitigating the negative effects of DS on maize plants by its role in maintaining optimal water relations under DS conditions, which in turn support various physiological processes to enhance plant tolerance to DS; none of this is due to the nutritive role of K (Cakmak, 2005; Table 2).

RWC is an appropriate index of plant water status in terms of the physiological consequences of cellular water deficit. DS generally induces a decrease in RWC (Cakmak, 2005). Fanaei et al. (2009) reported a significant increase in RWC of 2 oilseed species with K fertilization across a range of DS. Similar responses to K were also reported in mung bean (Nandwal et al., 1998), maize (Premachandra et al., 1991), and wheat (Pier and Berkowitz, 1987) under DS. In both maize cultivars, the RWC of the plants under DS was greater with K fertilization than in the plants without K supply (Figure 1). However, this trend was not observed in nonstressed control plants. Application of K contributes to improved cell turgor through osmotic adjustment (Maathuis and Sanders, 1996). Plants absorb K from the soil to maintain normal growth and development under DS (Elumalai et al., 2002).

Nitrate reductase plays a key role in nitrate assimilation. Several crop species adapt to DS conditions by enhancing their NRA. Thus, NRA could be used as an index for assessing plant response to DS (Caravaca et al., 2003). Previously, it has been shown that changes in NRA under DS were dependent on the inherent capability of a given crop/cultivar to respond to DS and K supplies and growth stage (Zhang et al., 2011). DS was found to induce a greater reduction in NRA of the drought-sensitive cultivar S911 than of the drought-tolerant S9 at different growth stages (Figure 2). Guan et al. (1996) reported that NRA in corn leaves increased gradually from the elongation stage, reached maximum at blossoming, and then decreased considerably at the maturity stage. In contrast, NRA showed an increasing trend from seedling to elongation stage, and then a decreasing trend to the end of growth.

### Table 2. Dry weights and grain yield of 2 maize cultivars at different growth stages influenced by drought stress (DS) and potassium (K) application.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Cultivar</th>
<th>K rate</th>
<th>Seedling</th>
<th>Elongation</th>
<th>Heading</th>
<th>Maturity</th>
<th>Grain yield (g plant⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>DS</td>
<td>S9</td>
<td>K₀</td>
<td>4.81 b</td>
<td>47.86 b</td>
<td>72.80 b</td>
<td>85.06 b</td>
<td>44.01 b</td>
</tr>
<tr>
<td>DS</td>
<td>S9</td>
<td>K</td>
<td>5.13 a</td>
<td>50.72 a</td>
<td>76.65 a</td>
<td>88.56 a</td>
<td>47.74 a</td>
</tr>
<tr>
<td>DS</td>
<td>S₉₁₁</td>
<td>K₀</td>
<td>4.06 b</td>
<td>36.54 b</td>
<td>65.46 b</td>
<td>74.45 b</td>
<td>40.24 b</td>
</tr>
<tr>
<td>DS</td>
<td>S₉₁₁</td>
<td>K</td>
<td>4.81 a</td>
<td>42.67 a</td>
<td>72.64 a</td>
<td>83.13 a</td>
<td>44.76 a</td>
</tr>
<tr>
<td>Mean of S9</td>
<td></td>
<td></td>
<td>4.97 A</td>
<td>49.29 A</td>
<td>74.73 A</td>
<td>86.81 A</td>
<td>45.88 A</td>
</tr>
<tr>
<td>Mean of S₉₁₁</td>
<td></td>
<td></td>
<td>4.43 B</td>
<td>39.61 B</td>
<td>69.05 B</td>
<td>78.79 B</td>
<td>42.50 B</td>
</tr>
<tr>
<td>Control</td>
<td>S9</td>
<td>K₀</td>
<td>11.92 a</td>
<td>68.93 a</td>
<td>102.26 a</td>
<td>107.04 a</td>
<td>49.47 a</td>
</tr>
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<td>Control</td>
<td>S9</td>
<td>K</td>
<td>12.24 a</td>
<td>68.89 a</td>
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<td>108.54 a</td>
<td>51.60 a</td>
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<tr>
<td>Mean of S9</td>
<td></td>
<td></td>
<td>12.08 A</td>
<td>68.91 A</td>
<td>101.46 B</td>
<td>107.79 B</td>
<td>50.53 B</td>
</tr>
<tr>
<td>Mean of S₉₁₁</td>
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<td></td>
<td>12.43 A</td>
<td>70.71 A</td>
<td>106.67 A</td>
<td>114.94 A</td>
<td>59.46 A</td>
</tr>
</tbody>
</table>

K₀ = no K, K = 0.42 g K kg⁻¹ soil; Control = well-watered plants, DS = drought stress, S9 = Shaandan 9, S₉₁₁ = Shaandan 911. Means with different letters within a column are significantly different at P < 0.05. Lowercase letters: effects of K rates by each cultivar and water regime treatment. Uppercase letters: cultivar comparison means across both K rates by each water regime treatment.
Applied K exhibited a significant influence on NRA, as it increased in both cultivars under DS compared with NRA in control plants (Figure 1). These findings support the hypothesis that K is required for maintaining the activation of enzymes and protein synthesis in plants, because the whole structure of proteins and protein
activity needs high concentrations of K⁺ in the cytosol for optimum plant functions (Taiz and Zeiger, 2002; Cherel, 2004).

Exposure to DS may induce osmotic stress, resulting in detrimental effects on plant growth and development. Therefore, maintenance of osmotic homeostasis is vital for plant adaptation to DS. Osmoregulation in plants is achieved by the absorption, transportation, and compartmentation of water and solutes, including K⁺, which is an important ion present in large amounts in cells for maintaining membrane potential and turgor and for the regulation of osmotic pressure (Taiz and Zeiger, 2002; Cherel, 2004; Ashraf and Foolad, 2007; Choluj et al., 2008; Ashraf, 2010; Yildiztugay et al., 2014). An increased accumulation of K⁺ in the cytosol is needed for optimal plant function (Taiz and Zeiger, 2002; Cherel, 2004).

Figure 3. Effects of drought stress (DS) on relative water content (RWC), nitrate reductase activity (NRA), K⁺ concentration (KC), free proline concentration (FPC), endogenous glycine betaine concentration (EGBC), and soluble protein concentration (SPC) in maize at different growth stages. Control represents well-watered treatment. Each value is the mean across 2 cultivars and 2 K treatments. Different letters at the top of histograms across all growth stages indicate significant difference (P < 0.05).
was observed under DS in tropical grasses, soybean, and maize for osmotic adjustment to help retain water (Taiz and Zeiger, 2002; Cakmak, 2005). For this reason, tissue K+ concentration of plants under DS is much greater than the recommended optimal K concentration for plants under controlled growing conditions (Cakmak, 2005).

Ma et al. (2004) reported that Brassica napus accounted for about 25% of drought-induced changes in osmotic adjustment from K+ accumulation in the expanding leaves in 2 genotypes.

The accumulation of soluble osmotic nitrides is an expected response of plants under DS, as derivative products from N metabolism are proposed to counteract the dehydration caused by DS. Therefore, the levels of K+ and soluble osmotic nitrides in plant tissues are an indication of responses to DS. These compounds contribute to osmoregulation and hence osmotolerance to maintain desirable RWC and mitigate the adverse effects of DS (Taiz and Zeiger, 2002; Ashraf and Foolad, 2007; Chołuj et al., 2008; Ashraf, 2010; Zhang et al., 2013; Yıldıztugay et al., 2014). Drought may induce synthesis and accumulation of organic osmolytes such as SP, EGB, and FP as well as K+, which vary between and within plant species (Zhang et al., 2009a, 2009b; Figures 1 and 2). The above responses were greater for both cultivars with K application under DS than for those under control conditions. They were also greater for drought-sensitive S911 than for the tolerant cultivar S9. Contents of the osmotic solutes were greater in the drought-tolerant cultivar (S9) than in the sensitive cultivar S911 under DS, irrespective of K treatments. However, the 2 cultivars showed similar contents of these osmotic solutes, except for K+ in control plants (Figure 2).

This is clear evidence of the role of K+ and osmotic nitrides in mitigating the effects of DS, particularly in the case of a DS-tolerant cultivar (Figures 1 and 2).

Accumulation of osmotic nitrides in maize plants varied with different growth stages, which followed an increasing trend from seedling to elongation/heading stage and then a decreasing trend towards the maturity stage. Inorganic osmolytes such as K+ decreased across the whole period (Figure 3). This trend was also observed in some previous studies (Zhang et al., 2002, 2009). DS-induced accumulation of certain osmotic solutes, mostly in the cytoplasm, can protect cell membranes, proteins, and metabolic machinery and consequently preserve subcellular structures from damage under cell dehydration caused by DS (Taiz and Zeiger, 2002).

Adequate supply of K to crop plants may cause osmotic adjustment, in which leaf water potential of the cells is reduced to maintain turgor pressure. This facilitates DS toleration in plants by improving plant growth and increasing yield (Cakmak, 2005). The addition of K application could strengthen the accumulation of K+ and osmotic nitrides in plants, especially for a drought-sensitive cultivar under DS (Figure 1). Additionally, the comparison of all osmoles measured in this study indicated the relative contribution of K+ and FP to osmotic adjustment in all treatments and both cultivars had reasonably high amounts of EGB and SP (Zhang et al., 2009; Figures 1–3).

Correlations between different sets of parameters show that those among DM, GY, and most of the parameters measured under DS were stronger than the correlations under well-watered treatments. In particular, significant positive correlations were found between RWC and K+ concentration, NRA, FPC, EGB, and SPC under DS; the same correlations were nonsignificant under control

<table>
<thead>
<tr>
<th>Character</th>
<th>DM</th>
<th>GY</th>
<th>RWC</th>
<th>KC</th>
<th>NRA</th>
<th>FPC</th>
<th>EGBC</th>
<th>SPC</th>
</tr>
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<tbody>
<tr>
<td>DM</td>
<td>0.925***</td>
<td>0.977***</td>
<td>0.810***</td>
<td>0.701**</td>
<td>0.677**</td>
<td>0.904***</td>
<td>0.898***</td>
<td></td>
</tr>
<tr>
<td>GY</td>
<td>0.874***</td>
<td>0.956***</td>
<td>0.874***</td>
<td>0.781**</td>
<td>0.786**</td>
<td>0.917***</td>
<td>0.925***</td>
<td></td>
</tr>
<tr>
<td>RWC</td>
<td>0.461</td>
<td>0.440</td>
<td>0.869***</td>
<td>0.771**</td>
<td>0.756**</td>
<td>0.930***</td>
<td>0.938***</td>
<td></td>
</tr>
<tr>
<td>KC</td>
<td>0.608*</td>
<td>0.616*</td>
<td>0.493</td>
<td>0.982***</td>
<td>0.980***</td>
<td>0.976***</td>
<td>0.981***</td>
<td></td>
</tr>
<tr>
<td>NRA</td>
<td>0.641*</td>
<td>0.741**</td>
<td>0.337</td>
<td>0.687**</td>
<td>0.996***</td>
<td>0.936***</td>
<td>0.938***</td>
<td></td>
</tr>
<tr>
<td>FPC</td>
<td>0.649*</td>
<td>0.648*</td>
<td>0.503</td>
<td>0.444</td>
<td>0.603*</td>
<td>0.924***</td>
<td>0.928***</td>
<td></td>
</tr>
<tr>
<td>EGBC</td>
<td>0.373</td>
<td>0.489</td>
<td>0.429</td>
<td>0.253</td>
<td>0.593*</td>
<td>0.743**</td>
<td>0.944***</td>
<td></td>
</tr>
<tr>
<td>SPC</td>
<td>0.624*</td>
<td>0.636*</td>
<td>0.513</td>
<td>0.374</td>
<td>0.827***</td>
<td>0.476</td>
<td>0.924***</td>
<td></td>
</tr>
</tbody>
</table>

* , ** , ***: Significant at 5%, 1%, and 0.1 %, respectively.

DM, Dry matter; DS, drought stress; EGBC, endogenous glycine betaine concentration; FPC, free proline concentration; GY, grain yield; KC, K+ concentration; NRA, nitrate reductase activity; RWC, relative water content; SPC, soluble protein concentration; S9, Shaandan 9; S911, Shaandan 911.
conditions. Thus, it appears that K⁺ and these organic osmotic solutes play an important role in improving plant growth, water status, and N assimilation in plants tissues under DS (Zhang et al., 2007; Mohammad and Mahmood, 2011).

The mechanism of K-induced DS tolerance was found to be due to an increase in RWC, NRA, K⁺ concentration, FPC, EGBC, and SPC in maize cultivars. The beneficial effects of K were greater on the drought-sensitive cultivar (S₉₁₁) than on the drought-tolerant cultivar (S₉). Thus, accumulation of K and osmotic nitrides appeared to improve plant water status and N assimilation under DS, which increased plant growth and yield.

In conclusion, this study demonstrated that the negative impacts of DS on plant growth could be significantly mitigated by adequate K supply, which, in turn, can improve plant water status, N assimilation, and osmotic adjustment, though not due to its nutritive role. The positive responses to the application of K under DS were greater in the drought-sensitive S₉₁₁ than those in the drought-tolerant S₉. Leaf water status of the plants, N assimilation, and osmotic adjustment parameters under DS were greater in the drought-tolerant cultivar (S₉) than in the drought-sensitive one (S₉₁₁).

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References


