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Research article

External potassium (K^+) application improves salinity tolerance by promoting Na^+-exclusion, K^+-accumulation and osmotic adjustment in contrasting peanut cultivars

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ABSTRACT

Achieving salt-tolerance is highly desirable in today's agricultural context. Apart from developing salt-tolerant cultivars, possibility lies with management options, which can improve crop yield and have significant impact on crop physiology as well. Thus present study was aimed to evaluate the ameliorative role of potassium (K^+) in salinity tolerance of peanut. A field experiment was conducted using two differentially salt-responsive cultivars and three levels of salinity treatment (control, 2.0 dS m^{-1}, 4.0 dS m^{-1}) along with two levels (with and without) of potassium fertilizer (0 and 30 kg K_2O ha^{-1}). Salinity treatment incurred significant changes in overall physiology in two peanut cultivars, though the responses varied between the tolerant and the susceptible one. External K^+ application resulted in improved salinity tolerance in terms of plant water status, biomass produced under stress, osmotic adjustment and better ionic balance. Tolerant cv. GG 2 showed better salt tolerance by excluding Na^+ from uptake and lesser accumulation in leaf tissue and relied more on organic osmolyte for osmotic adjustment. On the contrary, susceptible cv. TG 37A allowed more Na^+ to accumulate in the leaf tissue and relied more on inorganic solute for osmotic adjustment under saline condition, hence showed more susceptibility to salinity stress. Application of K^+ resulted in nullifying the negative effect of salinity stress with slightly better response in the susceptible cultivar (TG 37A). The present study identified Na^+-exclusion as a key strategy for salt-tolerance in tolerant cv. GG 2 and also showed the ameliorating role of K^+ in salt-tolerance with varying degree of response amongst tolerant and susceptible cultivars.

1. Introduction

In today's context soil salinity happens to be one of the most important abiotic factors limiting plant growth and productivity globally. It encompasses almost 7% of world's total land area, which means about 800 million hectares of land is affected by soil salinity (Munns, 2005). Sodium, a natural constituent of earth crust, may promote growth in some plants at lower concentration but eventually become toxic to growth and development for most of the glycophytes if present in high concentration in growing medium (Munns and Tester, 2008). Although both Na^+ and K^+ bear high resemblance in ionic and physicochemical properties, but unlike Na^+, K^+ plays essential role in growth of all plant species (Schachtman and Liu, 1999). Many basic physiological processes are essentially dependent on K^+ and its specific transport and interactions with enzymes and membrane proteins (Britto and Kronzucker, 2008), which includes short-term maintenance of membrane potentials, pollen tube development and stomatal opening and closing in plants (Dietrich et al., 2001).

Under prolonged exposure to saline environment plants inclined to show K^+ deficiency symptoms due to reduced uptake and/or lesser tissue retention of K^+ in different plant parts along with a concomitant build-up of tissue Na^+ level (Munns et al., 2002). Thus under salt stress, it is very common to find plants with hindered growth and metabolism and skewed K^+/Na^+ ratio in actively growing plant tissues (Shabala and Cuin, 2008; Degl'Innocenti et al., 2009). Due to such imbalance, several interlinked

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physiological and biochemical processes are known to be suffered in plants. Previous reports suggested salinity induced decrease in photosynthetic activities as one of the major limiting factors for plant development in active growing phase and final productivity (Yan et al., 2012) owing to stomatal closure (Gama et al., 2009), destruction of chlorophyll pigment system (Parida et al., 2004), damage to the reaction centre of photosystem (Kalaji et al., 2011), either or all. Since, K^+ regulates the stomatal movements and in fact its higher supply found to improve plant water status and opening and closing of stomata under osmotic stress (Marschner, 2012). Hence, potassium is hypothesized to play an important role in alleviation of salinity stress. As very limited success had been achieved to develop salt-tolerant crop plants through breeding approaches (Schubert et al., 2009), thus utmost consideration should be given to physiological approaches *viz*. maintenance of K^+-homeostasis through altered crop management strategies (eg. external application of K^+) for the plants growing in saline environment.

Peanut (*Arachis hypogaea* L.), an important legume, consumed both as oilseed and confectionary purposes globally is known to be moderately salt sensitive. It shows restriction in growth and yield drop after crossing the threshold level of soil salinity (Meena et al., 2012). Although some previous studies reported that peanut could be grown with water having electrical conductivity (EC) up to 3.0 dS m^{-1}, but our recent studies showed the crop starts facing salinity stress above 2.0 dS m^{-1} EC value and significant plant mortality observed above 4.5 dS m^{-1} salinity level. Hence, soil salinity in the range of 3–4 dS m^{-1} during most of the cropping period was found to be ideal for screening of salinity tolerance in peanut (Singh et al., 2008).

Soil and water salinity has been a major threat in semi-arid agro-ecosystem from long past, either naturally or induced by poor quality (saline) irrigation. There is an emerging need to reclaim these saline lands and also to maintain a stable production and crop coverage by combating the salt stress. One of the feasible options lies in applying potassium fertilizers, which could be beneficial to plant growth by replacing Na^+ with K^+ in the exchangeable sites of clay particles. Also the adequacy of K^+ helps in well-functioning of enzymes and maintenance of cell turgor that ease the movement of water and solute in plants (Krauss, 2003), which proved to have beneficial role in overall physiology of the plants and stress tolerance (Cakmak, 2005). Thus higher availability of K^+ in saline environment induces enhanced activities of high-affinity potassium transporters (HKTs) and non-selective cation channels (NSCCs) resulting in increased K^+-uptake minimizing Na^+ uptake and preventing K^+ losses from the cell to maintain a K^+:Na^+ ratio optimum for plant metabolism (reviewed by Wakeel, 2013). However, to the best of our knowledge such beneficial effect of external K^+ application in salinity tolerance is yet to be tested in peanut crop in a systematic manner. Hence, the present study was carried with the hypotheses that (i) Does K^+ have any ameliorative effect on salinity stress tolerance in peanut? (ii) If yes, then how does the effect vary between tolerant and sensitive genotypes? And finally (iii) How K^+ improves salinity tolerance in this crop from overall physiological perspective. Thus in the present study we conclusively showed how the beneficial effect of supplementary K^+-application contributes to overall salt tolerance in sensitive and tolerant peanut genotypes and also the differential strategies for osmotic adjustment in these genotypes.

2. Material and methods

2.1. Study site and experimental condition

A field experiment was conducted in summer 2011 (February–May) in the research farm of ICAR-Directorate of Groundnut Research, Junagadh, India having soil classified as Vertic Ustochrepts, medium black, clayey, shallow and slightly alkaline (pH 7.8–8.0) in nature. The experiment was laid out in a split–split plot design with twelve treatment combinations and three replications by using three levels of saline irrigation water (I–0: control, I–1: 2.0 and I–2: 4.0 dS m^{-1}) as main plot, two peanut cultivars as sub plot and two levels of potassium treatment (K–0 = no potassium applied and K–30 = 30 kg K_2O ha^{-1} equivalent to 25 kg K^+ ha^{-1}) as sub–sub plot. The size of each plot was 7 m × 6 m where peanut seeds were sown at a spacing of 30 cm × 10 cm. The crop was grown following standard agronomic management practices and recommended doses of N (25 kg ha^{-1}) and P (50 kg ha^{-1}) fertilizers applied to all plots at the time of sowing. During the whole cropping season the plants were irrigated with an average interval of 10 days and salinity treatments were started in respective treatment combinations from 20 days after plants emergence (DAE). The irrigation water used for the present study belongs to the classes from C1S1 to C2S1 (USDA classification, Richards, 1954) having no sodium hazard (SAR< 10) and residual sodium carbonate (RSC< 1.00 me/l) with moderate soluble sodium percentage. The 2.0 (I–1) and 4.0 (I–2) dS m^{-1} salinity level in the irrigation water was created by dissolving required amount of commercially available sodium chloride salt (2.6 and 5.2 kg in 2000 L irrigation water to get 22 and 44 mM NaCl solution, respectively to achieve 2.0 and 4.0 dS m^{-1} salinity level).

2.2. Plant material and time of sampling

For the present study two contrasting *Spanish* bunch type peanut cultivars (TG 37A and GG 2), having similar crop duration was selected based on their differential sensitivity towards salinity stress. Most of the previous studies based on laboratory screening reported GG 2 as salt-tolerant cultivar, while TG 37A as salt-sensitive (Singh et al., 2008; Mungala et al., 2008). The cultivar thus selected was to define the role of external K^+ application in alleviating the salinity stress and their responses towards conjoint saline-K environment.

Both destructive and non-destructive sampling for estimation of different physiological and biochemical parameters and nutrient analyses were done between 60–65 DAE. Uniformly, the third fully matured leaf from the top was selected for measurement of leaf gas exchange parameters and SPAD reading from at least 10 similar looking plants from each replication. For destructive sampling (osmolyte accumulation and nutrient analyses), leaf samples were collected in triplicate from similar position of the plant from each experimental replication. The soil samples were also collected at the same time and were analyzed to see the changes in basic soil properties.

2.3. Agronomic parameter

The plant samples were collected at the maturity from each treatment combinations and dry biomass for both economic (pod) and non-economic (haulm) parts were recorded separately by taking mean of at least 5 individual plants from each replication.

2.4. Relative water content and leaf water potential

Leaf relative water content (RWC) was estimated by recording the fresh, turgid weight and dry weight following the formula: RWC = [(Fresh wt.–Dry wt.)/(Turgid wt.–Dry wt.)] × 100 (Weatherley, 1950). Mid-day leaf water potential (LWP) was measured from the representative leaf samples by thermocouple based psychrometric method (Rawlins, 1966). Briefly, random

samples were collected from each experimental plot and brought to the laboratory in sealed plastic bags. Small leaf disc (5 mm in diameter) were cut from the whole leaf, which were then placed in the leaf chamber attached to a water potential system (Psychrometer, Wescor, USA) by keeping adaxial surface of leaves upside touching the thermocouple. The leaf discs were kept inside the chamber for 20–30 min to attain equilibrium, before final readings were recorded.

2.5. Leaf-level gas exchange phenomena and SPAD reading

All the gas exchange measurements *viz.* net photosynthesis rate (P_N), stomatal conductance (g_s) and transpiration (E) were recorded using a portable photosynthesis system (Model LI-6400, LI-COR, USA) between 09:00–11:30 h local time. Temperature was set at ambient and giving a stable T_{leaf} reading. Photosynthetically active radiation (PAR) was set at 1650 $\mu mol_{(photon)}$ m^{-2} s^{-1} inside the cuvette, and CO_2 was supplied artificially and the concentration was kept at 400 μmol m^{-2} s^{-1} inside the chamber (Singh et al., 2014). The SPAD chlorophyll meter readings were recorded using SPAD-502 Plus (Konica Minolta, Japan) in the third leaf from top in the main axis uniformly for all the plants.

2.6. Estimation of organic solutes

Free proline content in the leaves was determined from homogenized leaf samples (0.5 g) in 5 mL of sulfo-salycylic acid (3%) following the method of Bates et al. (1973). Briefly, 2 mL of filtered extract was taken in test tube and to it 2 mL of glacial acetic acid and 2 mL of ninhydrin reagent were added. The reaction mixture was boiled in water bath at 100 °C for 30 min. After cooling the reaction mixture, 6 mL of toluene was added and then transferred to a separating funnel. After thorough mixing, the chromophore containing toluene was separated and absorbance read at 520 nm in UV–visible spectrophotometer (Model U3010, Hitachi, Japan) and finally proline content was determined by using pure L-proline as standard.

The glycine betaine (GB) content of the leaves was estimated following the method of Grieve and Grattan (1983) from 0.5 g of finely ground dry material. Finally GB content from the sample was determined by measuring the absorbance of peri-iodite crystals at 365 nm after 2.0–2.5 h of incubation in 1,2-dichloro ethane. The trehalose content was estimated spectrophotometrically at 620 nm from 10 mg of dried leaf sample using anthrone reagent (Ferreira et al., 1997).

For estimation of total sugar the leaf samples were boiled in 80% ethanol (v/v) at 80 °C for a brief period of 10 min, followed by its filtration and clarification to obtain final extract. The sugar content of this extract was measured spectrophotometrically using anthrone reagent method as described by (McCready et al., 1950) and was expressed in terms of glucose equivalent by using D-glucose as standard.

2.7. Nutrient analyses from leaf and soil samples

The oven-dried plants samples collected at 60 DAE were finely ground and dry materials were subjected to tri-acid digestion as separate plant parts. The K^+ and Na^+ content from leaf, root and stem samples were determined individually using flame photometer. For soil sample same methodology was followed except the extraction was done in neutral 1N ammonium acetate solution (Hanway and Heidel, 1952). The pH and electrical conductivity of soil samples were measured using portable Hanna-make pH-EC meter in saturation extract with distilled water at a ratio of 1:2.5.

2.8. Statistical analyses

All the data recorded were the mean values ± SEM of at least three independent experimental replications. The data was subjected to analysis of variance (ANOVA) appropriate to the experimental design and differences at $LSD_{P=0.05}$ were considered statistically significant (Gomez and Gomez, 1984). To emphasize on the ameliorative effect of K in salinity stress, secondary bar diagrams were illustrated for most of the studied parameters, where *k–0* and *k–30* are the combined mean(s) of both the cultivars under saline condition (the respective control values were excluded from the mean) with K-0 and K-30 treatments, respectively. Similarly; *i–0*, *i–1* and *i–2* are the combined mean(s) of both the cultivars under respective salinity level with K–0 treatment only.

3. Results

3.1. Salinity stress resulted in changes in external growing condition and leaf water status

Imposition of salinity stress resulted in significant changes in different soil parameters (Table 1). The electrical conductivity of saturated soil extract was increased from 1.13 (control) to as high as 4.41 dS m^{-1} in I–2: K–30 treated plot. Due to sole effect of Na^+ the salinity level rose to 3.34 dS m^{-1} due to continuous saline irrigation with no significant difference in soil pH. Salinity treatment was found to have significant impact on increasing the Na^+ content in soil under different salinity levels. On the other hand, the soil K^+ content was found to be unchanged with salinity treatment while it was increased with doses of external K^+ application.

Relative water content (RWC) in the leaves of salinity treated plants showed significant reduction (Fig. 1A). Comparatively higher reduction in leaf RWC was observed in TG 37A (16 and 28% under I–1 and I–2, respectively) than GG 2 (11 and 20%) without application of external potassium. However, with application of K^+ (K–30), significant improvement in leaf RWC was observed particularly for TG 37A. The reduction in RWC was offset by ~7% (from 27.8 to 20.9%) and ~4% (from 20.4 to 15. 8%) in TG 37A and GG 2, respectively with supplementary dose of K. Similarly the leaf water potential (LWP) went down to more than −1.0 MPa due to salinity stress as compared to untreated control (~−0.6 MPa) (Fig. 1C) suggesting possible induction of osmotic adjustment mechanism in these cultivars. The supplementary dose of K^+ significantly improved LWP in both the cultivars (I–2 condition), with distinctly better effect in TG 37A (sensitive one). Thus a clear indication of osmotic adjustment and improvement of plant water status through additional K^+ supply was evident in the present study.

Table 1
Changes in selected soil properties over three salinity gradients (I–0, I–1, I–2) under potassium supplemented (K–30) and without potassium (K–0) conditions.

Salinity level	ECe (dS m^{-1})		pH		Na^+ content (%)		K^+ content (μg g^{-1})	
	K–0	K–30	K–0	K–30	K–0	K–30	K–0	K–30
I–0	1.13	1.13	7.97	8.07	0.029	0.034	82.2	85.3
I–1	1.69	2.27	8.00	8.00	0.037	0.041	81.5	87.0
I–2	3.34	4.41	8.13	8.00	0.057	0.055	80.0	87.3
$LSD_{0.05}$								
Salinity	0.42		NS		0.007		NS	
K	0.38		NS		NS		3.29	
Salinity × K	0.74		NS		NS		4.96	

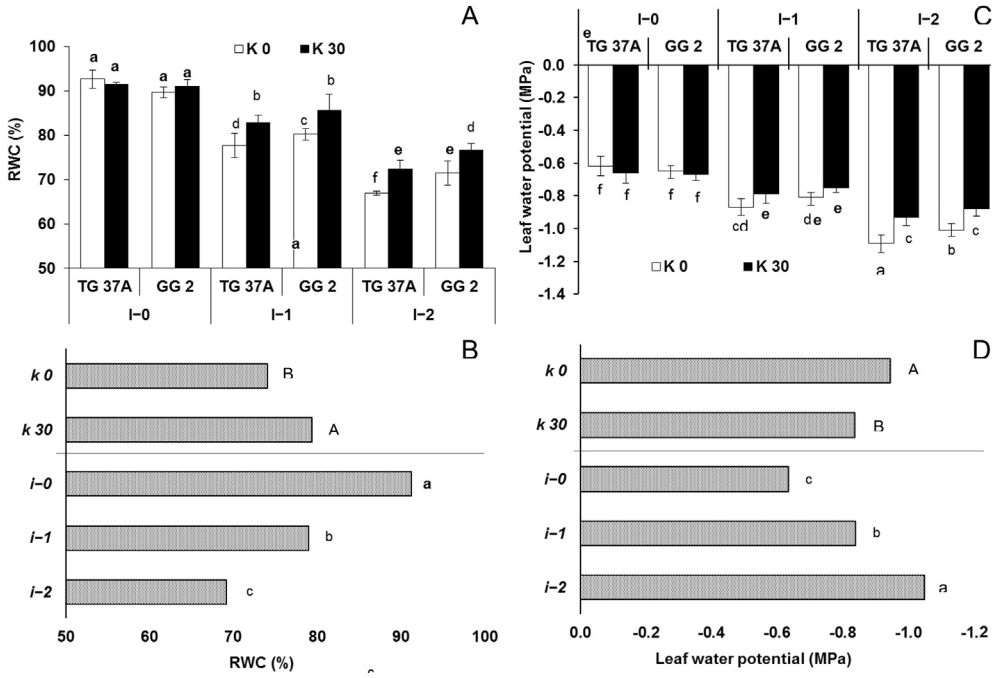

Fig. 1. Differences in (A) relative water content (RWC, %) and (C) leaf water potential (MPa) of two peanut cultivars (TG 37A, GG 2) over three salinity gradients (I–0: control, I–1: 2 dS m^{-1}, I–2: 4 dS m^{-1}) under potassium supplemented (K 30: 30 kg K_2O ha^{-1}) and without potassium (K 0: 0 kg K_2O ha^{-1}) conditions. Secondary bar diagram representing ameliorative effect of K in (B) RWC and (D) leaf water potential, where *k-0*, *k-30* and *i-0*, *i-1* and *i-2* are the derived mean values.

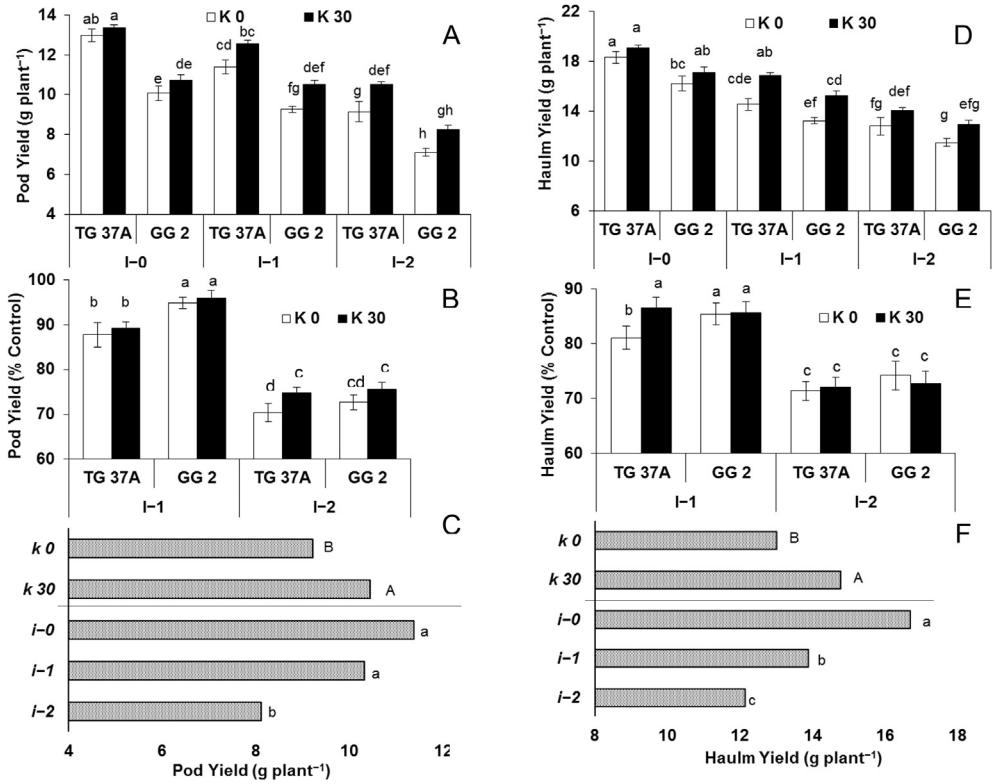

Fig. 2. Differences in (A) & (B) pod yield (g $plant^{-1}$) and (D) & (E) haulm yield (g $plant^{-1}$) of two peanut cultivars (TG 37A, GG 2) over three salinity gradients (I–0: control, I–1: 2 dS m^{-1}, I–2: 4 dS m^{-1}) under potassium supplemented (K 30: 30 kg K_2O ha^{-1}) and without potassium (K 0: 0 kg K_2O ha^{-1}) conditions; Secondary bar diagram representing ameliorative effect of K in pod yield (C) and haulm yield (F), where *k-0*, *k-30* and *i-0*, *i-1* and *i-2* are the derived mean values.

3.2. Changes in biomass production

Salinity treatment resulted in significant loss in total biomass production in both the cultivars, especially at the higher stress level (Fig. 2). Both TG 37A and GG 2 showed significant decline in pod (13 and 6% for TG 37A and GG 2, respectively) and haulm (21 and 18% for TG 37A and GG 2, respectively) yields even under I–1 treatment (Fig. 2A, D). But the more tolerant cv. GG 2 could able to maintain significantly greater pod yield (94 and 73% of control under I–1 and I–2 treatments, respectively) as compared to susceptible cv. TG 37A (Fig. 2B). Supplementary K^+ (K–30) resulted in definite improvement in pod yield, not so in case of haulm yield particularly in susceptible cv. TG 37A (Fig. 2B, E). Thus K–30 treatment seemed to have a greater impact in TG 37A over GG 2 for biomass production.

3.3. Effect on net photosynthesis and pigment system

Different levels of salinity treatment incurred negative impact on most important plant metabolic processes *viz.* photosynthesis and integrity of chlorophyll pigment system. Salinity treatment particularly at the higher level resulted in significant reduction in net photosynthesis rate (P_N) and chlorophyll content (SPAD reading) (Fig. 3). More prominent effect in P_N was observed in case of TG 37A, which showed 26 and 36% reduction from control to I–1 and I–2 treatments, respectively without the effect of supplementary K^+ (K–0), while under K–30 treatment the losses were reduced to 20 and 30%, respectively (Fig. 3A). In contrast, tolerant cultivar GG 2 showed relatively lesser magnitude of reduction at both K-0 and K-30. These results suggest that the ameliorative effect of K^+ is more pronounced in relatively susceptible cultivar TG 37A, than GG 2.

Salinity induced reduction of leaf chlorophyll content was observed in both the cultivars in present study, however significantly differing effect was observed between them (Fig. 3C). The tolerant cultivar GG 2 showed very little reduction (3–5% for I–1 and 10–12% for I–2), while susceptible cultivar TG 37A showed 13 and 19% reduction under I–1 and I–2 treatment level, respectively under K–0 condition. In K–30 treatment the loss was minimized to ~3–5% under both the salinity level. As far as the ameliorative effect of supplementary K^+ dose is concerned, it seemed to have greater effect on P_N than integration of pigment system under salinity stress (Fig. 3B, D). Thus the cultivar GG 2 possessed somewhat better tissue tolerance character, which eventually prevented the damage to the photosynthetic pigments and supplementary K^+ had very little role in preventing chlorophyll damage. But on the contrary, external K^+ application was found to improve P_N under saline condition (Fig. 3C) probably through improved stomatal regulation.

3.4. Changes in stomatal conductance and transpiration rate

Imposition of salinity stress resulted in severe reduction in stomatal conductance (g_s) and transpiration rate (E) possibly due to partial closure of stomata (Fig. 4). The extent of reduction was much higher in TG 37A, which showed ~35 and 47% reduction at I–1 and I–2 levels, respectively under K–0 condition (Fig. 4A). With external K^+ application (K–30) the extent of reduction was improved by 5–8% in both the cultivars. Similarly, significant reduction in transpiration rate was also observed, which showed maximum loss (~40%) in TG 37A under K–0 condition at the highest salinity level (Fig. 4C). Significant improvement in both g_s and E was observed with additional K^+ application in both TG 37A and GG 2 (Fig. 4B, D). This suggested that restricted gas exchange phenomena under salinity stress was more governed by stomatal factor in this cultivar, which was improved upon additional K^+ application.

3.5. Accumulation of organic solutes

Salinity stress resulted in significant increase in organic osmolyte content in the leaf tissue. Free proline content showed pronounced increase in response to salt stress with greater effect in tolerant cultivar GG 2 (Fig. 5A). Leaf proline content was increased by almost 2- and 4-fold under I–1 and I–2 treatments in GG 2 when no additional K^+ was applied (K–0), but the increase was comparatively less under K–30 condition (~80 and 130% increase

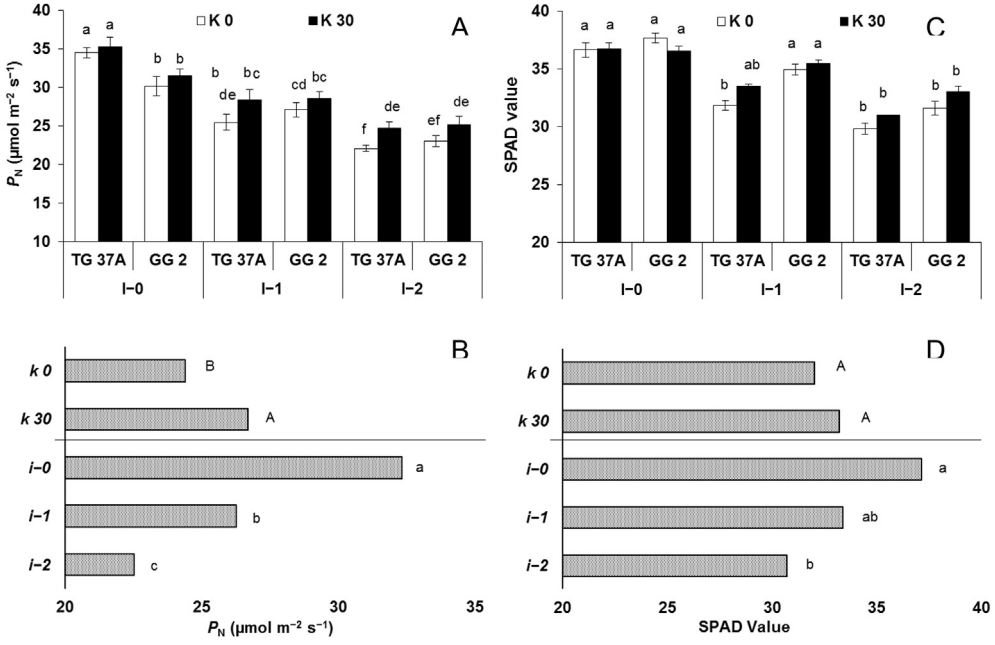

Fig. 3. Differences in (A) photosynthetic efficiency (P_N, µmol m^{-2} s^{-1}) and (C) SPAD value of two peanut cultivars (TG 37A, GG 2) over three salinity gradients (I–0: control, I–1: 2 dS m^{-1}, I–2: 4 dS m^{-1}) under potassium supplemented (K 30: 30 kg K_2O ha^{-1}) and without potassium (K 0: 0 kg K_2O ha^{-1}) conditions; Secondary bar diagram representing ameliorative effect of K in P_N (B) and SPAD (D), where *k-0*, *k-30* and *i-0*, *i-1* and *i-2* are the derived mean values.

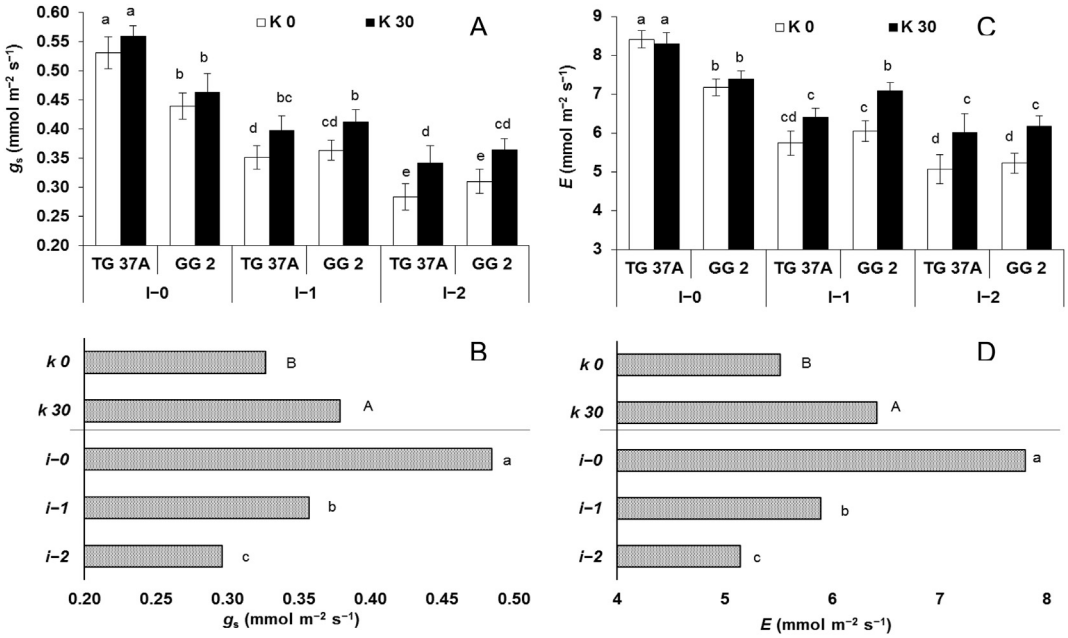

Fig. 4. Differences in (A) stomatal conductance (g_s, mmol m^{-2} s^{-1}) and (C) transpiration rate (E, mmol m^{-2} s^{-1}) of two peanut cultivars (TG 37A, GG 2) over three salinity gradients (I–0: control, I–1: 2 dS m^{-1}, I–2: 4 dS m^{-1}) under potassium supplemented (K 30: 30 kg K_2O ha^{-1}) and without potassium (K 0: 0 kg K_2O ha^{-1}) conditions; Secondary bar diagram representing ameliorative effect of K in g_s (B) and E (D), where *k-0*, *k-30* and *i-0*, *i-1* and *i-2* are the derived mean values.

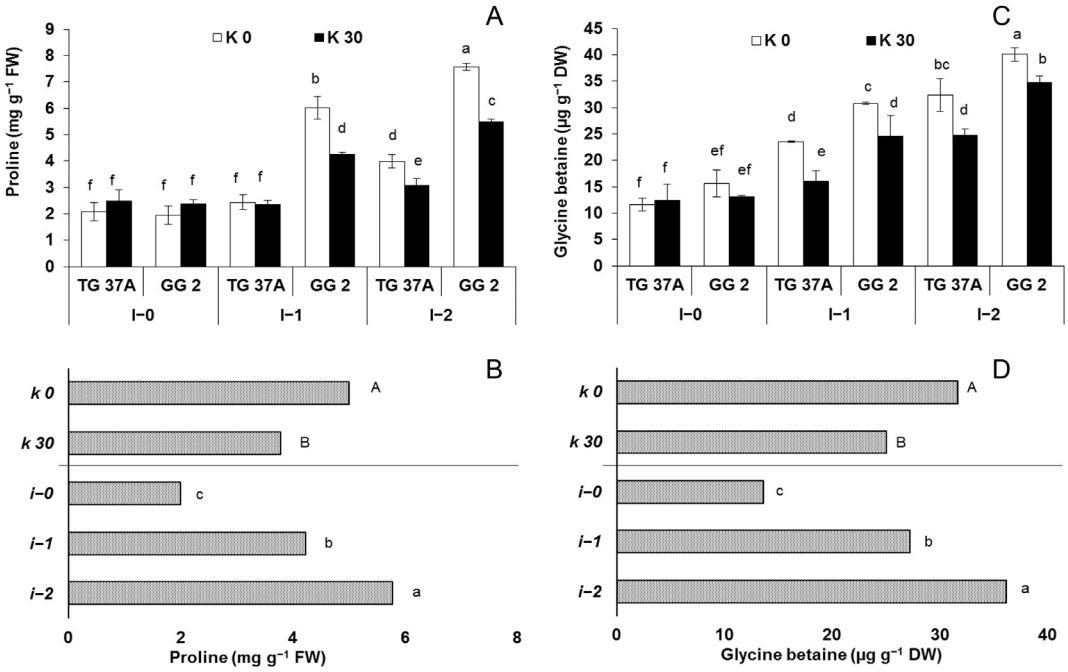

Fig. 5. Differences in (A) proline content (mg g^{-1} fresh weight) and (C) glycine betaine content (GB, µg g^{-1} dry weight) of two peanut cultivars (TG 37A, GG 2) over three salinity gradients (I–0: control, I–1: 2 dS m^{-1}, I–2: 4 dS m^{-1}) under potassium supplemented (K 30: 30 kg K_2O ha^{-1}) and without potassium (K 0: 0 kg K_2O ha^{-1}) conditions; Secondary bar diagram representing ameliorative effect of K in proline (B) and GB (D), where *k-0*, *k-30* and *i-0*, *i-1* and *i-2* are the derived mean values.

than control at I–1 and I–2, respectively). Non-significant change in proline content was observed in susceptible cultivar (TG 37A) at I–1 treatment, while it showed significant increase (92 and 24% under K–0 and K–30 condition) at the highest level of salt treatment. On an average salinity induced accumulation of proline was found to be less under K–30 condition than that of K–0 condition (Fig. 5B). Similarly, the glycine betaine content was increased with the increase in salinity level (Fig. 5C) and showed comparatively more increment in GG 2 and K–0 condition (Fig. 5D). Changes in glycine betaine content was more prominent under I–2 treatment, where it was increased by almost 3- and 2.5-fold, respectively for TG 37A and GG 2 as compared to control (I–0).

Other important cellular organic osmolytes (*viz.* trehalose and total sugar) were also increased in response to salt stress (Fig. 6). A gradual increase in trehalose content was observed in both the cultivars with slightly higher net content in the tolerant one. In GG

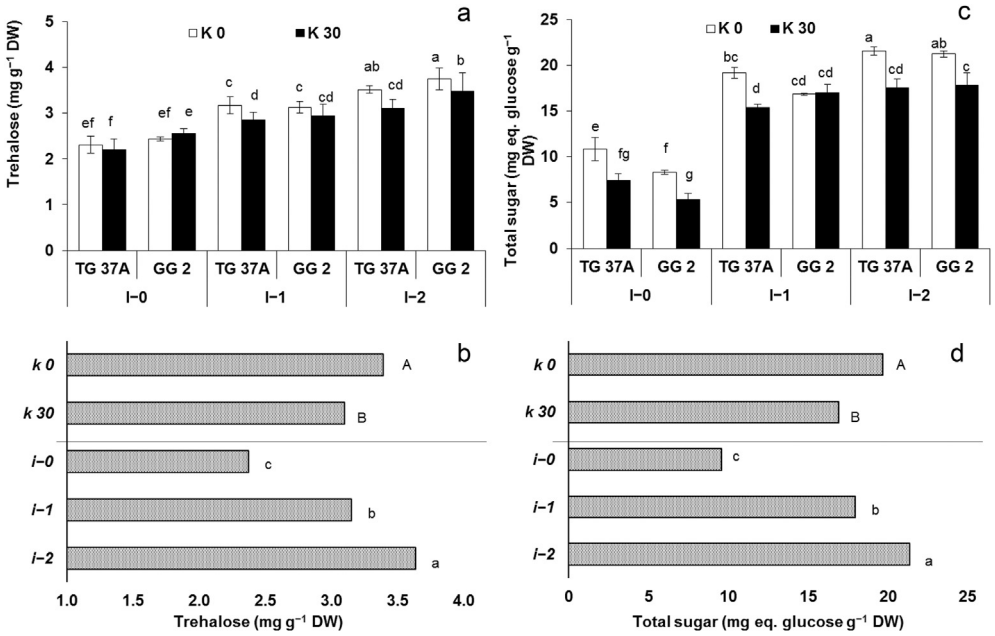

Fig. 6. Differences in (A) trehalose content (mg g^{-1} dry weight) and (C) total sugar (mg eq. glucose g^{-1} dry weight) of two peanut cultivars (TG 37A, GG 2) over three salinity gradients (I–0: control, I–1: 2 dS m^{-1}, I–2: 4 dS m^{-1}) under potassium supplemented (K 30: 30 kg K_2O ha^{-1}) and without potassium (K 0: 0 kg K_2O ha^{-1}) conditions; Secondary bar diagram representing ameliorative effect of K in trehalose (B) and total sugar (D), where *k-0*, *k-30* and *i-0*, *i-1* and *i-2* are the derived mean values.

2, the trehalose content was increased from 2.44 to 3.75 mg g^{-1} (on dry weight basis) at K–0 condition, whereas it rose to 3.48 mg g^{-1} at K–30 condition from a control value of 2.56 (Fig. 6A). The total sugar content was also increased following the similar trend of other organic solutes (Fig. 6C). Here also much prominent increase was observed in GG 2 than TG 37A, suggesting existence of more efficient organic osmolyte synthesis system in GG 2, which probably one of the reason for its better tolerance. The cultivar GG 2 showed 2- to 2.5-fold increase in total sugar content at the highest level of salinity treatment at K–0, while at K–30 it showed more than 3-fold increase. But overall, comparatively lesser salinity induced accumulation of total sugar was observed under K–30 treatment than K–0 treatment (Fig. 6D).

3.6. Effect of salinity stress on K- and Na-accumulation on different plant parts

Irrespective of the treatment effect, tissue K^+ concentration was found to be in the order of leaf > stem > root (Table 2). Salinity treatment resulted in significant decrease in tissue K^+ concentration with highest reduction observed in root tissue. The tolerant cultivar GG 2 showed comparatively less decrease (52 and 47% under K–0 and K–30 treatments, respectively) in root K^+ content at I–2 treatment, the susceptible cultivar TG 37A showed slightly higher degree of reduction with 60 and 54%, respective values. The extent of loss in tissue-K content was pretty much similar for both leaf and stem. A definite impact of external K^+ application was observed for better K^+-accumulation in both tolerant and susceptible cultivars. At K–30, the reduction in stem K^+ content was minimized to 40% only compared to ~55% reduction at K–0, which suggested an ameliorative effect of supplementary K^+ application in saline environment.

Unlike tissue K^+ content, the Na^+ content showed an opposite trend and a sequential increase in Na^+ uptake was observed with increasing level of salinity (Table 2). Differential accumulation of Na was observed under salinity stress in different plant parts and the tissue concentration was found in the order of root > leaf > stem. A sharp increase in root Na^+ content was observed under both the salinity levels especially in TG 37A, which showed 6.5- and 8-fold increase under I–1 and I–2 treatment, respectively without K^+ application. However external K^+ application (K–30) resulted in lowering down of Na^+ uptake by adjusting the tissue ionic balance to some extent in both the cultivars. As a whole, the tolerant cultivar (GG 2) showed relative greater resistance in Na^+ uptake and its further accumulation in different plant parts. Application of supplementary K^+ improved the overall stress tolerance resulting

Table 2
Variations in potassium (mmol) and sodium concentration (mmol) in different plant parts of two peanut cultivars (TG 37A, GG 2) over three salinity gradients (I–0, I–1, I–2) under potassium supplemented (K–30) and without potassium (K–0) conditions.

Treatments		Leaf				Stem				Root			
		K^+ Conc.		Na^+ Conc.		K^+ Conc.		Na^+ Conc.		K^+ Conc.		Na^+ Conc.	
		K–0	K–30	K–0	K–30	K–0	K–30	K–0	K–30	K–0	K–30	K–0	K–30
I–0	TG 37A	146.8^{a}	125.3^{a}	17.2^{g}	12.9^{g}	129.2^{a}	127.6^{a}	15.6^{e}	11.2^{e}	101.6^{b}	110.1^{a}	24.9^{f}	21.6^{f}
	GG 2	125.8^{c}	134.0^{b}	17.8^{g}	16.5^{g}	119.1^{b}	122.1^{b}	14.7^{e}	10.8^{e}	95.3^{c}	102.9^{b}	26.1^{f}	22.9^{f}
I–1	TG 37A	109.7^{d}	120.9^{c}	93.4^{c}	83.8^{d}	70.8^{d}	76.0^{c}	65.0^{c}	56.8^{d}	64.4^{f}	70.3^{e}	158.5^{b}	126.3^{d}
	GG 2	101.5^{d}	110.5^{d}	69.8^{e}	56.4^{f}	76.5^{c}	81.0^{c}	66.9^{c}	54.5^{d}	74.0^{e}	81.3^{d}	130.1^{d}	110.0^{e}
I–2	TG 37A	68.5^{f}	75.6^{e}	131.8^{a}	113.0^{b}	55.7^{f}	60.9^{e}	83.2^{a}	74.6^{b}	41.4^{h}	50.8^{g}	198.4^{a}	161.9^{b}
	GG 2	66.5^{f}	83.6^{e}	113.6^{b}	97.3^{c}	57.1^{ef}	62.47^{e}	76.3^{b}	68.1^{c}	46.1^{h}	55.0^{g}	164.7^{b}	145.2^{c}

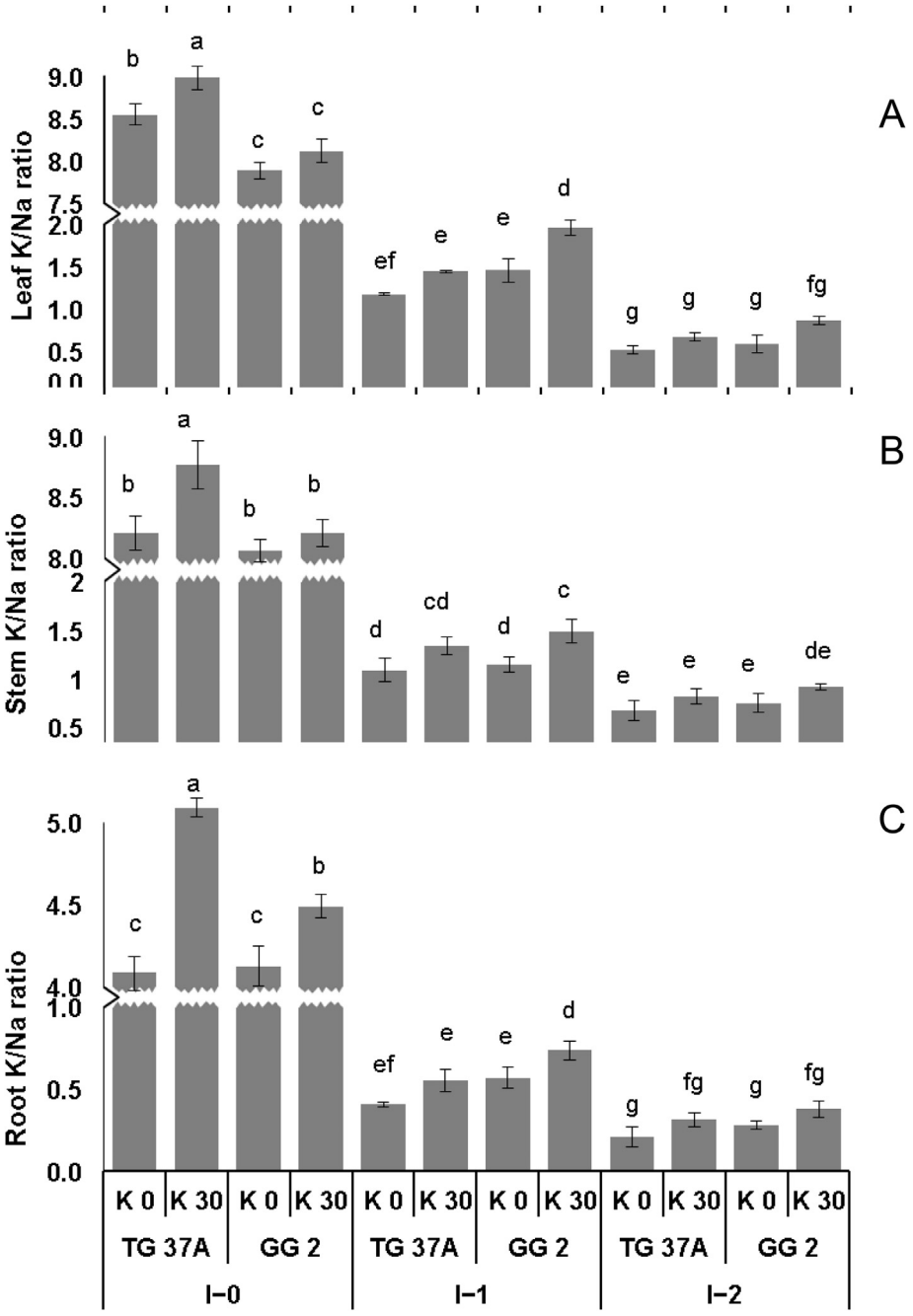

Fig. 7. Differences in ionic (K^+/Na^+) ratio in (A) leaf, (B) stem and (C) root tissues of two peanut cultivars (TG 37A, GG 2) over three salinity gradients (I–0: control, I–1: 2 dS m^{-1}, I–2: 4 dS m^{-1}) under potassium supplemented (K 30: 30 kg K_2O ha^{-1}) and without potassium (K 0: 0 kg K_2O ha^{-1}) conditions.

in comparatively lesser Na^+ build-up in both the tolerant and susceptible cultivars.

Salinity treatment resulted in significant alteration in K^+/Na^+ ratio in different plant parts (Fig. 7). The leaf K^+/Na^+ ratio reduced from 8.55 to 1.17 and 0.52 in TG 37A under I–1 and I–2 treatments, respectively, while the changes were 7.89 to 1.46 and 0.59 in case GG 2 at K–0 condition (Fig. 7A). Similar drastic reduction was observed in stem and root tissues as well with a more prominent effect on root tissue (Fig. 7B, C). The tissue K^+/Na^+ ratio was found to be improved under K–30 than K–0 condition in all the plant parts with no obvious difference in improvement between tolerant and susceptible cultivars.

4. Discussion

Taken together our results from the present study suggested imposition of salinity stress (particularly I–2 treatment) had deleterious effect on overall plant growth and physiological processes. Significantly different response and adaptability to stressful environment was observed in two different peanut cultivars, which showed varying sensitivity towards salt stress. Being more tolerant cultivar GG 2 showed relatively lesser metabolic and physiological changes under salinity stress, while the effects were much pronounced in TG 37A. For most of the physiological parameters studied, external application of K^+ (K–30) resulted in improved salt tolerance, more so in susceptible cultivar TG 37A. Thus in the

present study we are focussing on the differential response in ameliorative effect of supplementary K^+-application under salt stress in tolerant and susceptible genotypes.

4.1. Application of external K^+ has differential impact of stress alleviation in tolerant and susceptible cultivar

Salinity stress generally hinders plants growth initially due to its osmotic effect and later on because of more deleterious specific ion toxicity effect. Thus under the Phase I stage of soil salinity plants started to show altered plant water status without much effect on cell turgor (Munns, 1993). Under salinity stress significant loss in relative water content (RWC) was observed in both tolerant and susceptible cultivars (Fig. 1A). With concurrent fall in RWC with increasing salinity level, the leaf water potential (LWP) dropped significantly in the present study (Fig. 1C). Decrease in LWP and its maintenance under prolonged exposure to salt stress below the threshold value indicates turgor maintenance and induction of osmotic adjustment in the tissue (Tyerman, 1990). With supplementary doses of K^+, improvement in LWP was observed, which was clearly more pronounced in sensitive genotype. Thus it is clear from the present study that external application of K^+ definitely helped to improve plant water status as a whole. For number of crop plants salinity mediated reduction in plant water status was reported in earlier studies (Kaya et al., 2001a; Chakraborty et al., 2012a), while a few studies also reported external K^+ application helped to improve plant water status under salinity (Kaya et al., 2001b) and drought (Wei et al., 2013) stress. Potassium, a key regulatory element in plant metabolic processes seemed to improve plant water uptake by regulating the osmotic potential and hydraulic conductivity of membranes via induction of hyperactive response of plasma membrane bound aquaporins and specific K^+ channels in the root tissue under osmotic stress condition aroused due to drought or salinity (Heinen et al., 2009).

In plants, salt tolerance is usually associated with comparative loss of biomass in saline versus non-saline condition over fairly long period of time (Munns et al., 2002). It was also observed that the genotypes with lower biomass production potential under non-saline condition was proven to be relatively more salt tolerant under saline condition (Tejera et al., 2006). In the present study, we found significantly less biomass production (both pod and haulm yield) in tolerant cultivar GG 2 under non-saline (I–0) condition than susceptible cultivar TG 37A (Fig. 2A, d), but interestingly with imposition of salinity stress the reduction of biomass was also less in GG 2 compared to TG 37A (Fig. 2B). This may be due to the higher metabolic cost for imparting inherent tolerance character in GG 2 resulted in sacrificing total biomass under control condition. External application of K^+ resulted in offsetting the salinity induced yield loss (Fig. 2C, F) and the effect was comparatively higher in TG 37A than GG 2, when external K^+ was applied. This result suggested under K–30 condition higher availability of K^+ even in saline condition helped both the cultivars to maintain better physiological status may be through higher uptake of K^+ or better retention of tissue-K^+ than K–0 condition. In saline condition, the availability of nutrients to plants including that of K^+ is often hampered, hence sufficient availability of K^+ in growing environment is absolutely essential for plant growth (Ashraf and Sultana, 2000; Munns, 2005). In earlier studies exogenously applied K^+ has found to promote growth and biomass production in diverse group of crops (Kaya et al., 2001ab; Ikeda, 2005; Akram et al., 2009). It is possible that in the saline environment where there is presence of high salt concentrations, the amount of naturally occurring K^+ may suppress plant growth (Chen et al., 2007). Increasing K^+ concentration in growing medium in such situations may improve K^+ absorption and therefore counterbalance the adverse effect of salt stress (Zheng et al., 2008).

4.2. Supplementary K^+ improves salinity tolerance by modulating stomatal behaviour and leaf-level gas exchange

For majority of the glycophyte species salinity stress resulted in severe limitation for photosynthesis and other leaf-level gas exchange phenomena, but the actual cause of such photosynthetic limitation may be more than one dimensional (Kalaji and Łoboda, 2009). Non-stomatal factor such as damage to photosynthetic apparatus was reported under salinity stress in many plant species *viz. Triticum aestivum* (Perveen et al., 2010), sunflower, *Heliantus annuus* (Akram and Ashraf, 2011), *Brassica juncea* and *B. campestris* (Chakraborty et al., 2012a). Such destruction of chlorophyll pigments under saline condition is mainly attributed to the Na^+ toxicity (Munns et al., 2002; Pinheiro et al., 2008). In most of the cases salinity stress is reported to reduce leaf chlorophyll pigment, but often the response is variable among salt-tolerant and susceptible species as the tolerant genotypes showed minimum pigment loss even under significantly higher stress (Akram and Ashraf, 2011). In the present study, though salinity stress considerably reduced the chlorophyll pigments (SPAD reading) may be because of cytotoxic effect of high Na^+ concentration in salt stressed plants, but we found significantly lesser chlorophyll loss in tolerant cultivar GG 2 with no apparent impact of external K^+ application (Fig. 3C). This finding suggested minimal role of tissue K^+ in protecting pigment system of mesophyll tissue in both the cultivars.

On the other hand, more severe decline in stomatal conductance was observed due to imposition of salinity stress particularly under K–0 condition (Fig. 4A), suggesting relatively greater impact of salinity induced stomatal limitation in peanut cultivars than due to non-stomatal limitation (damage to pigment system). Externally applied K^+ was found to be beneficial to improve both stomatal conductance (g_s) and transpiration (E). The tolerant genotype seemed to improve both g_s and E under saline condition. Salinity stress is known to reduce conductance mainly due to loss of sufficient turgor pressure in the guard cells of mesophyll tissue resulting in partial closure of stomata which often attributed for reduced photosynthesis under salt stress (Debez et al., 2008). Although, potassium plays crucial role in turgor regulation of stomatal guard cells and eventually governs opening and closing of stomata by a large extent (Marschner, 2012), but under saline condition loss of cell turgor is negligible (especially during early and mid-stage) (Munns, 1993), hence the improvement in stomatal conductance and other photosynthetic characters in the present study may well be due to improved plant growth with K^+-supplementation resulting in decreased feedback down-regulation of photosynthesis.

4.3. Balance between organic and inorganic osmolyte is the key for salt-tolerance in peanut

Accumulation of organic solute is one of the major strategies adapted by tolerant group of plants to counterbalance the salinity induced osmotic stress and protection of cellular structure (Hasegawa et al., 2000). Cellular dehydration and drop in osmotic potential under salinity stress usually resulted in reduced water uptake and turgor loss in glycophytes (Zhu, 2001). Salinity induced accumulation of both organic and inorganic solutes were observed in the present study. Relatively higher accumulation of organic osmolytes *viz.* proline, glycine betaine, trehalose etc. was recorded in tolerant genotype GG 2. But interestingly, with supplementary dose of K^+, the increase in organic osmolyte accumulation was significantly lower in both the cultivars (Figs. 5 and 6). It suggested

that higher dose of K^+, which might improve the tissue K^+ level, resulted in relatively lesser dependence of organic osmolyte in both the cultivars towards osmotic adjustment. This might be related to significant saving of metabolic energy in peanut for synthesis of energy intensive organic osmolytes for osmotic adjustment. Accumulation of number of organic solutes consisting of simple sugars (mainly fructose, glucose and sucrose), sugar alcohols (glycerol and methylated inositols) and complex sugars (trehalose, raffinose and fructans), amino acids and their derivatives were reported to be induced under salinity stress (Bohnert and Jensen, 1996; Nuccio et al., 1999). Salinity induced accumulation of proline, glycine betaine and other organic solutes were also reported in earlier studies (Ahmed, 2009; Chakraborty et al., 2012b). Muthukumarasamy and Panneerselvam (1997) showed close relation between proline and glycine betaine accumulation, and increase in osmotic pressure in peanut under saline condition.

Being a primary inorganic osmoticum K^+ is one of the major players in cellular osmotic adjustment whenever the plants face osmotic stress (Wang et al., 2013). Due to similar physicochemical properties of K^+ and Na^+ in the growing environment, plants often face K^+ deficiency under saline condition (Shabala and Cuin, 2008). Earlier studies reported reduction in tissue K^+ content in plants grown under saline condition for prolonged period (Chakraborty et al., 2012a). Thus, maintaining a high cytosolic K^+/Na^+ ratio in metabolically active tissues are critical for plant growth and salt tolerance (Wang et al., 2013). Previous studies suggested under saline condition maintenance of cytosolic K^+ concentration at a constant level is important for plant metabolism, while vacuolar K^+ concentrations may vary dramatically (Shabala and Cuin, 2008; Wu et al., 2014). Under K^+-deficient situation especially due to reduced uptake of K^+ under salinity stress results in constant consumption of vacuolar K^+ in order to maintain a uniform cytosolic K^+ concentration (Wang et al., 2013). On the same note, we also found reduced K^+ uptake under increasing salinity level and concomitant rise in Na^+ uptake and accumulation (Table 2). A clear cut difference in tissue K^+ retention and Na^+ accumulation was observed between GG 2 and TG 37A. The more tolerant GG 2 showed significantly lesser decrease in K^+ level and also Na^+ accumulation in different plant parts, however, the scenario was completely opposite in susceptible cultivar TG 37A. This gives us the indication that probably GG 2 (tolerant) used greater proportion of organic solutes and K^+ for osmotic adjustment, whereas TG 37A (susceptible) relied more on cytotoxic Na^+ as osmoticum under salinity stress. This may well be the reason for better response of TG 37A to supplementary dose of K^+ by improving tissue K^+/Na^+ ratio and overall physiological performance.

5. Conclusion

It can be concluded from the present study that supplementary application of K^+ had significant effect in salt tolerance in peanut, although the responses varied between two cultivars owing to differential salt-sensitivity. The cultivar GG 2 had basic salt tolerance character, which was evident from its capacity to exclude Na^+ from uptake and lesser accumulation particularly in metabolically active mesophyll tissue and also relied more on organic solute for osmotic adjustment. This ultimately resulted in better plant water status and imparted relatively favourable physiological condition in this cultivar. On the other hand, TG 37A allowed more Na^+ accumulation particularly on the leaf tissue and depended more on inorganic solute for osmotic adjustment under saline condition hence showed more susceptibility to salinity. Additional dose of K^+ seemed to nullify the negative effect of salinity in both the cultivar, but the effect was better in TG 37A, the susceptible one. Hence, the present study clearly defines the role of K^+ in ameliorating salinity stress in peanut, although the response may vary depending upon the salt-sensitivity of the genotype studied.

Conflict of interest

The authors declare that they have no conflict of interest.

Author contribution

KC conceptualized the whole study and HM designed the experiment and performed field trials. KC and DB drafted the manuscript, analysed the data and done the statistical analysis. DB carried out the nutrient analysis, KK had done the gas exchange studies and KC performed the biochemical studies.

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