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External potassium mediates the response and tolerance to salt stress in peanut at the flowering and needling stages

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Abstract

Potassium (K) is an essential macronutrient that plays an important role in abiotic stress tolerance. A pot experiment was carried out to identify the potential role of potassium fertilizer in alleviating salt stress in peanut. The results showed that salt stress significantly decreased plant height, dry mass, photosynthetic pigments, the photosynthetic rate, and stomatal conductance, but increased the Na^+/K^+ ratio, total sugars, and the leaf salinity hazard coefficient in two peanut varieties. However, the application of potassium significantly alleviated the harmful effect of salt by improving the contents of photosynthetic pigments and enhancing K^+/Na^+ ratios and osmolytes in both varieties. In general, HY25 showed a superior osmoregulation ability compared to that of HY33 and was less dependent on K^+ to maintain osmotic balance. Therefore, HY33 showed a better response to potassium application, and the treatment by 170 kg(K_2O) ha^{-1} was found to be the most effective in alleviating the harmful effects of salt. In conclusion, potassium reduced the toxic effect of salt and significantly enhanced salt tolerance.

Keywords: chlorophyll fluorescence; photosynthetic characteristics; salt tolerance; selective absorption and transport.

Introduction

Peanut (*Arachis hypogaea* L.), one of the five most important oilseed crops, serves as a good source of protein, calories, vitamins, and minerals (Sui *et al*. 2018, Zhuang *et al*. 2019). Due to insufficient farmland for food crops, the peanut is most often planted in arid and salinized sandy soils. Furthermore, extreme climate change and irrational human activities have caused the soil to be affected by secondary salinity (Munns and Tester 2008). Soil salinization affects approximately 10% of the land surface (950 million ha) worldwide, and this problem is expected to be exacerbated by the current climate change (Su *et al*. 2019). Peanut is considered a moderately salt-sensitive species (Cui *et al.* 2018), with many economic benefits. Under the currently used cropping structure, a cultivated peanut is a more appropriate alternative crop than others for salinized sandy land (Zhang *et al*. 2013). Therefore, improving the tolerance to salt stress and productivity of peanut by optimizing cultivation technology has important significance for ensuring the safe production of edible oil and the utilization of saline land.

Soil salinization is a major eco-environmental problem in agricultural development (Qiu *et al*. 2014), resulting in considerable crop yield losses worldwide (Negrão *et al*. 2016). The effects of salt stress on plant growth are extremely complex, involve ion toxicity, osmotic stress, and photosynthesis inhibition (Zhu 2002, Ahmad *et al*. 2012, Feng *et al*. 2014). It has been reported that salinity can decrease peanut seed germination and seedling growth (Singh and Prasad 2009, Salwa *et al*. 2010), induce Na^+ accumulation (Parida and Jha 2013), and inhibit photosynthesis (Qin *et al*. 2011). However, the accumulation of Na^+ in plants is often accompanied by a decrease in K^+ content (Shabala and Cuin 2008, Degl'Innocenti *et al*. 2009). Hence, the K^+/Na^+ ratio is considered an important parameter for assessing salt tolerance in plants (Cakmak 2005, Shabala and Cuin 2008). Nevertheless, the breeding of salt-tolerant varieties is currently of very limited success and requires a long time (Schubert *et al*. 2009). Thus, there is an urgent need to improve cultivation measures to effectively alleviate salt-induced inhibition in agricultural production.

Accordingly, external potassium is responsible for the maintenance of K^+ homeostasis and improves crop growth under salt stress (Dawood *et al*. 2014, Abbasi *et al*. 2015, Chakraborty *et al*. 2016). Among various macronutrients, K^+ plays a vital role in regulating plant physiological

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Abbreviations: Chl – chlorophyll; C_i – intercellular CO_2 concentration; F_0 – minimal fluorescence; F_m – maximum fluorescence; F_v – variable fluorescence; F_v/F_m – maximum quantum yield of PSII; g_s – stomatal conductance; L_s – stomatal limitation value; LSHC – leaf salinity hazard coefficient; NPQ – nonphotochemical quenching coefficient; P_N – net photosynthetic rate; Rfd – steady-state fluorescence decay rate; SA – Na^+, K^+ selective absorption; ST – Na^+, K^+ selective transport; STI – salt tolerance index; Φ_{PSII} – effective quantum yield of PSII photochemistry.
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processes and enables plants to survive under stressful conditions (Çolpan *et al*. 2013). The ability of crops to maintain a higher K^+/Na^+ ratio is a manifestation of salt tolerance (Abbasi *et al*. 2015), and balancing the K^+/Na^+ ratio is very important for stomatal function adjustment, enzymes activation, cell osmoregulation, photosynthesis, and turgor maintenance (Abbasi *et al*. 2014). Previous studies have shown that potassium plays an important role in alleviating salt stress. Salt stress causes significant decreases in the growth and productivity of crops, but the application of potassium was found to improve the growth and biomass yield of bean under salt stress (Dawood *et al*. 2014). Cheng *et al*. (2015) found that plant salt tolerance might be positively correlated with plant abilities for K^+ transport and retention, higher K^+ affinity may be a key factor for better P_{Nmax}/biomass yields of wheat under salt stress. Also, Chakraborty *et al*. (2016) reported that potassium had a significant effect on salt tolerance in peanut, which was reflected in reduced Na^+ uptake achieved by adjusting the tissue ionic balance and improving biomass production. To date, there have been relatively few studies on potassium improving the salt tolerance of peanut, and the mechanism is unclear.

Our previous research revealed that peanut faced difficulties in emergence when the salt content of soil reached 3 g kg^{-1} (0.3% salt stress) (Zhang *et al*. 2013). The flowering and needling stages are the key phases for the transition of peanut from vegetative growth to reproductive growth, which is of great significance in ensuring the accumulation of photosynthates and the formation of yield. Thus, in the present study, different concentrations of potassium fertilizers were applied to evaluate the role of potassium in the salt tolerance of varieties differing in salt tolerance. Specifically, this study addresses the following questions: (*1*) Does potassium contribute to the peanut response to salt stress? (*2*) If so, how does the effect vary between tolerant and sensitive varieties? (*3*) Which are the underlying mechanisms for improving peanut salt tolerance? Our objectives were to identify the changes in peanut varieties differing in salt tolerance under salt stress, to discover the variation in photosynthetic characteristics elicited by potassium fertilizer application under salt stress, and to elucidate the physiological mechanism underlying the improvement in salt tolerance by external potassium application.

Materials and methods

Plant materials and experimental conditions: Two representative peanut varieties screened in our previous study, HY25 (tolerant to salt stress) and HY33 (sensitive to salt stress) (Zhang *et al*. 2013), were used in the present study. A pot experiment was conducted at the experimental field of Shenyang Agricultural University (41°82'N,123°56'E), Shenyang, China. The region has a temperate semi-humid continental climate, where annual mean temperatures range between 6.2 and 9.7°C, and rainfall ranges between 600–800 mm. Seed sowing was carried out on 12 May 2019, and harvesting was carried out on 18 September 2019. The soil was collected from the 0–20-cm cultivation layer of the experimental field and classified as brown soil with 96.70 mg(hydrolyzable N) kg^{-1}, 27.50 mg(available P) kg^{-1}, 117.9 mg(available K) kg^{-1}, 15.17 g(organic matter) kg^{-1}, 680 mg(soluble salt) kg^{-1}, and pH 6.5.

Experimental design and treatments: The experiment included four treatments: a control (CK) [0.00% NaCl + 0 kg(K_2O) ha^{-1}] and three potassium treatments, namely, T1 [0.25% NaCl + 0 kg(K_2O) ha^{-1}], T2 [0.25% NaCl + 85 kg(K_2O) ha^{-1}], and T3 [0.25% NaCl + 170 kg(K_2O) ha^{-1}]. Experiments were conducted according to a randomized complete block design with three replicates. Each pot contained two plants undergoing the same treatment, which were together considered a single experimental unit. The two peanut varieties were planted in a total of 90 pots.

Before sowing, the soil salt concentration was adjusted to 2.5 g(NaCl) kg^{-1} (purity: ≥ 99.5%, *Sinopharm Chemical Reagent*, Shanghai, China), and each pot (27-cm inside diameter, 34-cm depth) was filled with 20 kg of soil. The same dose of urea (N = 75 kg ha^{-1}) and superphosphate (P_2O_5 = 120 kg ha^{-1}) and a corresponding dose of potassium (K_2O = 0, 85 and 170 kg ha^{-1}) were applied as basal fertilizer, and then the moisture of the soil in each pot was adjusted to 60% of the maximum water-holding capacity by adding tap water. When the moisture level was suitable, the soil was mixed thoroughly to ensure the uniform distribution of salt and fertilizer. Five seeds were sown at a depth of 5 cm in every pot. After seed germination, two healthy seedlings were kept, and the others were eradicated. Throughout the growth period, field management followed normal agricultural practices.

Sample collection and agronomic parameter measurements: Sixty days after germination (beginning of the flowering and needle formation phases), fresh leaves were collected and stored in a –80°C freezer until use. Plant samples were collected and washed with sterile distilled water. The peanut plants were divided into roots, stems, and leaves, and plant height was measured. All plant parts were dried at 70°C for 72 h to record dry masses. The dried parts were ground and preserved. The salt tolerance index (STI) (Smitharani *et al*. 2014) was calculated by using the following formula: STI = total dry mass of salt-stressed plant/total dry mass of control plant × 100%.

Photosynthetic pigments and total sugars: Photosynthetic pigments [chlorophyll (Chl) *a* and *b*, total Chl, and carotenoids] were estimated following Lichtenthaler (1987). Fresh leaves were homogenized using ethanol (95%, v/v), and the absorbance of the supernatant was read at 665, 649, and 470 nm with a UV/visible spectrophotometer (*Lambda 365*, *PerkinElmer*, Waltham, MA, USA); the results were expressed as mg g^{-1}(leaf fresh mass, FM). Related parameters were calculated by using the following formulas: Chl *a* [mg g^{-1}(FM)] = (13.95 A_{665} – 6.88 A_{649}) × V/(1,000 × W), Chl *b* [mg g^{-1}(FM)] = (24.96 A_{649} – 7.32 A_{665}) × V/(1,000 × W), carotenoids [mg g^{-1}(FM)] = [(1,000 A_{470} – 2.05 Chl *a* – 114.8 Chl *b*)/245] × V/(1,000 × W), where A_{665}, A_{649}, and A_{470} are absorbances at 665, 649, and 470 nm, respectively, V is the total volume of the extract (10 mL), and W is the leaf fresh mass (0.1 g).

The sugar content of leaf samples was measured spectrophotometrically using the anthrone reagent method as described by McCready *et al*. (1950) and was expressed in terms of glucose equivalent by using D-glucose as a standard. The leaf salinity hazard coefficient (LSHC) (Fadl and El-Deen 1980) was calculated by using the following formula: LSHC = total sugars × carotenoids/Chl (*a*+*b*).

Photosynthetic parameters: Gas-exchange parameters were measured on the most recently fully expanded leaves using an infrared gas analyzer *CIRAS-2* (*PP Systems*, Hitchin, UK) 60 d after germination. The net photosynthetic rate (P_N), stomatal conductance (g_s), and intercellular CO_2 concentration (C_i) were recorded at a PPFD of 1,200 µmol m^{-2} s^{-1} from an internal light source in the leaf chamber. Relative humidity was maintained at 70%, leaf temperature was set at 25°C, and CO_2 concentration was maintained at 380 µmol mol^{-1} in the leaf chamber. All parameters were measured on five individual plants per treatment.

Chl fluorescence parameters: Sixty days after germination, the functional leaves were cut with scissors, wrapped in wet gauze, and dark-adapted for 30 min before the analysis. Chl fluorescence parameters of detached leaves were measured using a Chl fluorescence imaging system (*FluorCam FC800*, *Photon Systems Instruments*, Brno, Czechia). The measured parameters included minimal fluorescence (F_0), maximum fluorescence (F_m), the nonphotochemical quenching coefficient (NPQ), and the steady-state fluorescence decay rate (Rfd); the calculated parameters included variable fluorescence (F_v), the maximal quantum yield of PSII photochemistry (F_v/F_m), and the effective quantum yield of PSII photochemistry (Φ_{PSII}).

Measurement of K^+ and Na^+: For the determination of the K^+ and Na^+ concentrations, the dried root, stems, and leaf samples (0.3 g) were incubated in 10 mL of H_2SO_4. The samples were digested in a digestion furnace at 320°C for 30 min. During this period, H_2O_2 (30%) was added two times until the clarified solution was produced. The solution was brought to 100 mL with deionized water. The solution was analyzed using a flame photometer (*AP1200*, *AOPU Analytical Instrument*, Shanghai, China), and standard curves of K^+ and Na^+ were used for computation.

Na^+ and K^+ selective absorption (SA) and selective transport (ST) (Wang *et al*. 2002, 2004) were calculated by using the following formulas: SA = (rhizosphere soil Na^+/K^+)/(root Na^+/K^+), ST = (root Na^+/K^+)/(aboveground Na^+/K^+).

Yield and yield components: At the maturity stage, 12 representative plants were harvested to measure the pod number per plant, plump pod rate [%] (= the number of plump pod per plant/the number of total pod per plant × 100), 100-pod mass [g], 100-seed mass [g], shelling rate [%] (= total dry mass of peanut kernel/total dry mass of peanut pod × 100), and yield.

Statistical analysis: Data from each of the treatments with three replicates were subjected to one-way analysis of variance (*ANOVA*) and least significant difference (LSD) testing at $P<0.05$ by using *SPSS 19.0* software (*SPSS*, *Inc*., Chicago, IL, USA). *Origin 2017* software (*OriginLab*, Northampton, MA, USA) was used to produce graphs. The data in graphs were presented as the mean ± standard deviation.

Results

Growth and biomass production: Compared with CK, salt stress significantly reduced stem height by 39.1 and 39.3% in HY25 and HY33 (Fig. 1*A*), respectively. Similarly, dry mass (Fig. 1*B*) and the STI (Fig. 1*C*) were significantly reduced under the T1 treatment. Compared to those in CK, the dry masses of HY25 and HY33 were reduced by 37.3 and 41.6%, while the STIs were reduced by 37.2 and 41.5%, respectively. The T2 treatment significantly increased plant growth compared to that in the T1 treatment. However, the stem height of HY33 (but not HY25) significantly increased in the T3 treatment compared to the T1. The dry masses of HY25 in the T2 and T3 treatments were not significantly greater than those in the T1 treatment, whereas the mass of HY33 significantly increased in the T3 treatment; compared to T1, the T3 treatment significantly increased the STI of the two varieties.

Photosynthetic pigments: As shown in Table 1, salt stress caused significant decreases in the Chl *a*, Chl *b*, carotenoids, and total Chl contents compared with those in CK. Except for Chl *b*, the degree of reduction in other

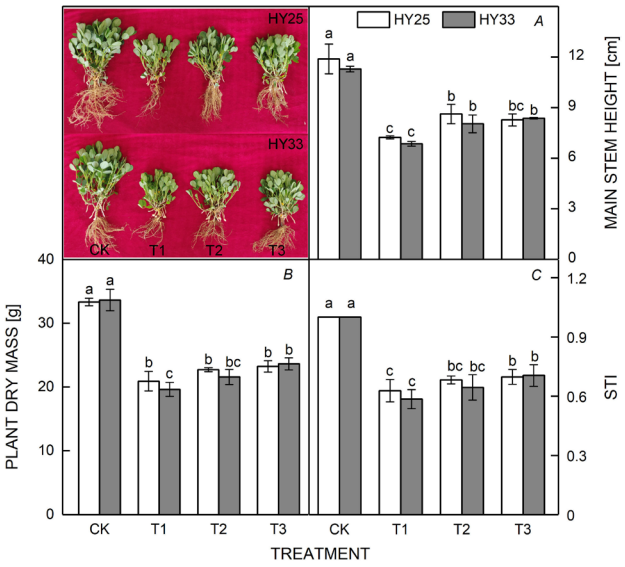

Fig. 1. Effects of salt stress and potassium fertilizer treatments on growth and biomass production in two peanut varieties. (*A*) Main stem height; (*B*) plant dry mass; (*C*) salt tolerance index (STI). CK – 0.00% NaCl + 0 kg(K_2O) ha^{-1}; T1 – 0.25% NaCl + 0 kg(K_2O) ha^{-1}; T2 – 0.25% NaCl + 85 kg(K_2O) ha^{-1}; T3 – 0.25% NaCl + 170 kg(K_2O) ha^{-1}. Data are the mean ± SD; $n = 3$. *Different lowercase letters* indicate significant differences between treatments at the 0.05 level. STI – salt tolerance index.

values was more obvious in HY33, with a range of 48.8 to 67.0%. Potassium application effectively improved the biosynthesis of photosynthetic pigments. Compared with T1 treatment, HY25 and HY33 showed an average increase of 27 and 75% in photosynthetic pigments content in the T2 treatment, respectively. However, HY25 and HY33 showed an average increase of 66 and 116% in the T3 treatment.

Sugar content and LSHC: The total sugar content significantly increased by 36.3 and 30.3% in HY25 and HY33, respectively (Fig. 2*A*), in response to salt stress. Meanwhile, the results showed that salt stress increased the LSHC of HY25 and HY33 by 86.7 and 91.3%, respectively (Fig. 2*B*). Compared to the T1 treatment, the T2 treatment significantly reduced the total sugar content in HY25 but had no significant effect on that in HY33. The sugar content of HY25 was only slightly impacted by the T3 treatment, whereas that in HY33 was significantly reduced. The application of potassium decreased the LSHC of the two varieties, where the most significant reduction was observed in HY33 in the T3 treatment (40.1%).

Photosynthetic characteristics: Compared with CK, salt stress led to significant declines in P_N and g_s in the two varieties (Table 2). The P_N of HY25 and HY33 significantly decreased by 27.6 and 31.6% under salt stress compared to CK, respectively. Also, the T1 treatment decreased the C_i and increased L_s in HY25 but had the opposite effect in HY33. Potassium application (T2, T3) improved P_N and g_s in both varieties, especially in the T3 treatment, where the P_N of HY25 and HY33 significantly increased by 18.2 and 22.8% compared to that in the T1 treatment, respectively. Meanwhile, the T2 and T3 treatments increased C_i in HY25 and reduced it in HY33, but the difference was not significant. The effect of the T3 treatment on L_s was even more obvious in HY33, and the difference was significant.

Chl fluorescence parameters: As shown in Table 3, under salt-stress conditions, the F_m, F_v/F_m, and Φ_{PSII} of two varieties decreased compared to those in CK. However, the F_0 of HY33 was higher under salt stress than that in CK, while that of HY25 was lower. Also, NPQ and Rdf increased in the two varieties, and the increase in NPQ was more pronounced in HY25. Potassium application significantly increased the degree of PSII reaction center opening, improved the primary capture efficiency of light energy, and reduced photoinhibition compared to those in the T1 treatment. The images of F_v/F_m, NPQ, and Φ_{PSII} obtained through Chl fluorescence imaging intuitively showed obvious differences between the treatments (Fig. 3). Overall, marked increases in F_v/F_m were observed in HY25 in the T3 treatment, and marked decreases in NPQ and Rfd were observed in HY33.

Table 1. Effects of salt stress and potassium fertilizer treatments on photosynthetic pigments in peanut varieties. CK – 0.00% NaCl + 0 kg(K_2O) ha^{-1}; T1 – 0.25% NaCl + 0 kg(K_2O) ha^{-1}; T2 – 0.25% NaCl + 85 kg(K_2O) ha^{-1}; T3 – 0.25% NaCl +170 kg(K_2O) ha^{-1}. Data are the mean ± SD; n = 3. *Different lowercase letters* in the same column indicate significant differences between treatments at 0.05 level.

Cultivars	Treatments	Chlorophyll *a* [mg g^{-1}(FM)]	Chlorophyll *b* [mg g^{-1}(FM)]	Carotenoid [mg g^{-1}(FM)]	Chlorophyll (*a*+*b*) [mg g^{-1}(FM)]
HY25	CK	1.12 ± 0.23^{a}	0.38 ± 0.17^{a}	0.19 ± 0.04^{a}	1.49 ± 0.03^{a}
	T1	0.48 ± 0.12^{d}	0.11 ± 0.05^{c}	0.11 ± 0.10^{c}	0.59 ± 0.01^{d}
	T2	0.60 ± 0.18^{c}	0.14 ± 0.03^{c}	0.13 ± 0.04^{b}	0.75 ± 0.02^{c}
	T3	0.71 ± 0.09^{b}	0.25 ± 0.37^{b}	0.14 ± 0.02^{b}	0.96 ± 0.04^{b}
HY33	CK	0.94 ± 0.65^{a}	0.24 ± 0.19^{a}	0.20 ± 0.23^{a}	1.18 ± 0.08^{a}
	T1	0.33 ± 0.28^{c}	0.08 ± 0.20^{c}	0.11 ± 0.04^{d}	0.41 ± 0.03^{c}
	T2	0.61 ± 0.68^{b}	0.16 ± 0.25^{b}	0.14 ± 0.13^{c}	0.77 ± 0.09^{b}
	T3	0.69 ± 0.45^{b}	0.22 ± 0.18^{a}	0.17 ± 0.03^{b}	0.91 ± 0.06^{b}

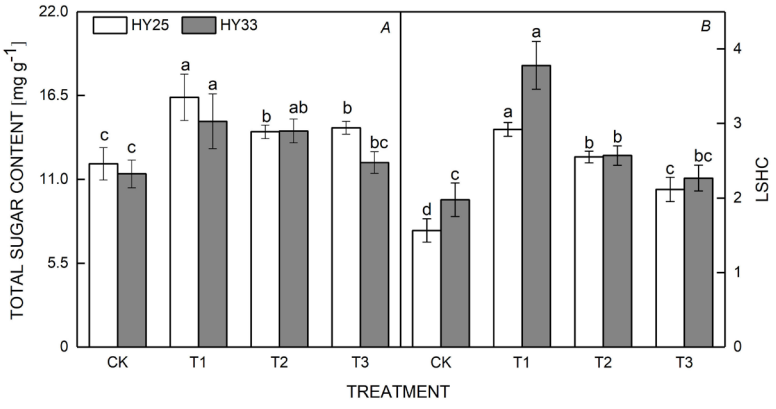

Fig. 2. Effects of salt stress and potassium fertilizer treatments on total sugar content (*A*) and leaf salinity hazard coefficient (LSHC) (*B*) in peanut varieties. CK – 0.00% NaCl + 0 kg(K_2O) ha^{-1}; T1 – 0.25% NaCl + 0 kg(K_2O) ha^{-1}; T2 – 0.25% NaCl + 85 kg(K_2O) ha^{-1}; T3 – 0.25% NaCl + 170 kg(K_2O) ha^{-1}. Data are the mean ± SD; n = 3. *Different lowercase letters* indicate significant differences between treatments at the 0.05 level.

Table 2. Effects of salt stress and potassium fertilizer treatments on photosynthetic characteristics in peanut varieties. CK – 0.00% NaCl + 0 kg(K_2O) ha^{-1}; T1 – 0.25% NaCl + 0 kg(K_2O) ha^{-1}; T2 – 0.25% NaCl + 85 kg(K_2O) ha^{-1}; T3 – 0.25% NaCl + 170 kg(K_2O) ha^{-1}. Data are the mean ± SD; $n = 3$. *Different lowercase letters* in the same column indicate significant differences between treatments at the 0.05 level. C_i – intercellular CO_2 concentration; g_s – stomatal conductance; L_s – stomatal limitation value; P_N – net photosynthetic rate.

Cultivars	Treatments	P_N [μmol m^{-2} s^{-1}]	g_s [mmol(H_2O) m^{-2} s^{-1}]	C_i [μmol(CO_2) mol^{-1}]	L_s
HY25	CK	23.03 ± 1.60^{a}	253.82 ± 11.34^{a}	254.49 ± 13.87^{a}	0.42 ± 0.03^{b}
	T1	16.67 ± 0.90^{c}	196.88 ± 12.66^{b}	216.00 ± 16.58^{b}	0.51 ± 0.04^{a}
	T2	18.33 ± 1.02^{bc}	215.45 ± 17.44^{b}	220.53 ± 16.69^{b}	0.50 ± 0.04^{a}
	T3	19.70 ± 1.49^{ab}	230.55 ± 17.43^{ab}	237.37 ± 8.66^{ab}	0.46 ± 0.02^{ab}
HY33	CK	20.73 ± 1.49^{a}	223.45 ± 17.09^{a}	208.78 ± 9.67^{a}	0.52 ± 0.02^{a}
	T1	14.19 ± 0.71^{c}	155.26 ± 9.77^{c}	238.89 ± 20.66^{a}	0.40 ± 0.06^{b}
	T2	16.50 ± 0.63^{bc}	179.33 ± 10.53^{bc}	215.48 ± 24.49^{a}	0.48 ± 0.04^{ab}
	T3	17.43 ± 1.20^{b}	190.59 ± 12.77^{ab}	214.85 ± 13.78^{a}	0.50 ± 0.03^{a}

Table 3. Effects of salt stress and potassium fertilizer treatments on chlorophyll fluorescence parameters in peanut varieties. CK – 0.00% NaCl + 0 kg(K_2O) ha^{-1}; T1 – 0.25% NaCl + 0 kg(K_2O) ha^{-1}; T2 – 0.25% NaCl + 85 kg(K_2O) ha^{-1}; T3 – 0.25% NaCl + 170 kg(K_2O) ha^{-1}. Data are the mean ± SD; $n = 3$. *Different lowercase letters* in the same column indicate significant differences between treatments at 0.05 level. F_0 – minimal fluorescence; F_m – maximum fluorescence; F_v – variable fluorescence; F_v/F_m – maximum quantum yield of PSII; NPQ – nonphotochemical quenching coefficient; Rfd – steady-state fluorescence decay rate; Φ_{PSII} – effective quantum yield of PSII.

Cultivars	Treatments	F_0	F_m	F_v/F_m	Φ_{PSII}	NPQ	Rfd
HY25	CK	37.23 ± 1.56^{a}	237.71 ± 1.22^{ab}	0.83 ± 0.02^{a}	0.33 ± 0.01^{a}	1.27 ± 0.02^{c}	2.38 ± 0.01^{c}
	T1	34.08 ± 1.29^{b}	206.65 ± 3.04^{c}	0.76 ± 0.04^{a}	0.31 ± 0.01^{a}	1.61 ± 0.02^{a}	2.80 ± 0.02^{a}
	T2	36.71 ± 0.49^{a}	229.55 ± 9.32^{b}	0.82 ± 0.04^{a}	0.30 ± 0.03^{a}	1.59 ± 0.10^{ab}	2.61 ± 0.02^{b}
	T3	36.81 ± 0.98^{a}	243.56 ± 1.28^{a}	0.83 ± 0.01^{a}	0.32 ± 0.02^{a}	1.44 ± 0.06^{bc}	2.59 ± 0.09^{b}
HY33	CK	35.02 ± 1.06^{b}	233.84 ± 1.63^{a}	0.83 ± 0.03^{a}	0.43 ± 0.00^{a}	0.31 ± 0.01^{b}	2.06 ± 0.15^{b}
	T1	37.75 ± 0.73^{a}	214.96 ± 9.64^{c}	0.73 ± 0.02^{b}	0.41 ± 0.04^{a}	0.39 ± 0.05^{a}	2.91 ± 0.20^{a}
	T2	34.97 ± 0.79^{ab}	226.77 ± 4.75^{ab}	0.79 ± 0.06^{ab}	0.44 ± 0.02^{a}	0.31 ± 0.02^{b}	2.41 ± 0.07^{b}
	T3	34.78 ± 1.45^{ab}	222.13 ± 6.77^{bc}	0.82 ± 0.04^{ab}	0.43 ± 0.05^{a}	0.29 ± 0.02^{b}	2.14 ± 0.31^{b}

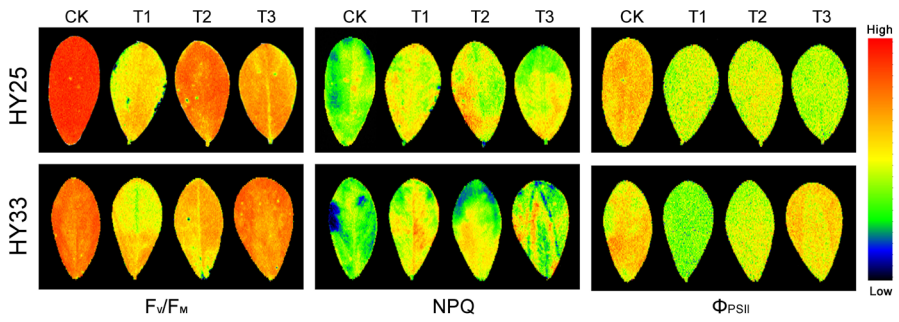

Fig. 3. Effects of salt stress and potassium fertilizer treatments on chlorophyll fluorescence images (F_v/F_m, NPQ, and Φ_{PSII}) in peanut varieties. CK – 0.00% NaCl + 0 kg(K_2O) ha^{-1}; T1 – 0.25% NaCl + 0 kg(K_2O) ha^{-1}; T2 – 0.25% NaCl + 85 kg(K_2O) ha^{-1}; T3 – 0.25% NaCl + 170 kg(K_2O) ha^{-1}. F_v/F_m – maximum quantum yield of PSII; NPQ – nonphotochemical quenching coefficient; Φ_{PSII} – effective quantum yield of PSII.

Na^+ and K^+ SA and ST, and Na^+/K^+: Salt stress significantly affected the Na^+/K^+ in the plant organs (Fig. 4*A–C*). Na^+/K^+ increased significantly in the roots and stems of the two varieties whereas Na^+/K^+ was markedly higher in HY25 than that in HY33 under salt stress. HY33 showed a higher leaf Na^+/K^+ ratio than that of HY25, but no significant differences were observed between treatments. Potassium application resulted in a decrease in the Na^+/K^+ ratio under salt stress in the two varieties. The effect of potassium application in the T3 treatment compared to T1 treatment was stronger than that in the T2 treatment, and the highest potassium concentration (T3) maintained a lower Na^+/K^+ ratio in the stems of HY33. The T2 and T3 treatments reduced the Na^+/K^+ ratio in the leaves of the two varieties, but this effect was not statistically significant. Also, the SA values of the two varieties significantly decreased under salt stress (Fig. 4*E*); that in HY25 decreased by 65.2%, while that in HY33 decreased by 45.8%. The ST value of HY25 was higher in the T1 treatment than that in the CK, whereas that of HY33 showed the opposite effect (Fig. 4*D*).

The application of potassium effectively improved the SA and ST values in the two varieties under salt stress. The ST value of HY25 significantly increased in the T2 treatment compared to the T1 treatment, but that of HY33 did not significantly change. The opposite trend was observed in the T3 treatment, where the ST value of HY25 did not change and that of HY33 significantly increased. The SA value significantly increased under potassium treatment, especially in the T3 treatment.

Yield and yield components: Under salt stress, the yield per plant significantly decreased in both varieties (Table 4). Compared with those in CK, the yields of HY25 and HY33 under salt stress decreased by 73.0 and 76.0%, the pod number per plant decreased by 61.5 and 64.0%, the 100-pod mass decreased by 35.6 and 39.8%, and the 100-seed mass decreased by 38.3 and 44.0%, respectively. Therefore, the decrease in yield was mainly caused by the decreases in pod number, 100-pod mass, and 100-seed mass under salt stress. The T2 and T3 treatments had a positive effect on yield. The effect of the T3 treatment compared with the T1 treatment was more obvious than that of the T2 treatment, with yields of HY25 and HY33 significantly increasing by 54.0 and 89.4%, respectively. Besides, potassium fertilizer significantly increased the pod number, 100-pod mass, and 100-seed mass, and the growth rate of HY33 was higher in the T3 treatment than that in the T1 treatment.

Discussion

Soil salinization has become a global problem limiting agricultural production and causing considerable yield and economic losses to agricultural production every year. The inhibition of plant growth by salt stress is an effect of both osmotic and ionic stress (Ahmad *et al*. 2016), which can negatively affect many morphological and physiological traits of plants. A large number of studies used exogenous substances, such as calcium (Wasti *et al*. 2017, Ahmad *et al*. 2018), potassium (Ahmad 2014, Dawood *et al*. 2014, Chakraborty *et al*. 2016, Jan *et al*. 2017), and phytohormones (Kaur *et al*. 2018, Alam *et al*.

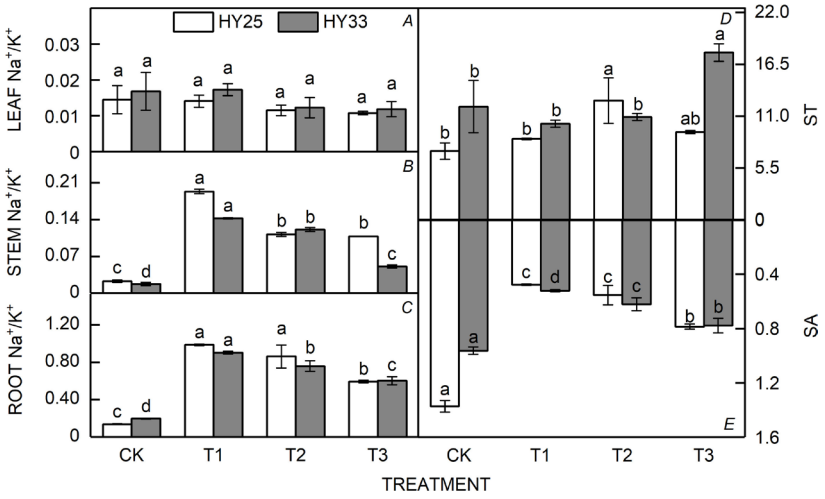

Fig. 4. Effects of salt stress and potassium fertilizer treatments on Na^+/K^+ in different organs, SA and ST. CK – 0.00% NaCl + 0 kg(K_2O) ha^{-1}; T1 – 0.25% NaCl + 0 kg(K_2O) ha^{-1}; T2 – 0.25% NaCl + 85 kg(K_2O) ha^{-1}; T3 – 0.25% NaCl + 170 kg(K_2O) ha^{-1}. Data are the mean ± SD; $n = 3$. *Different lowercase letters* indicate significant differences between treatments at the 0.05 level. SA – Na^+, K^+ selective absorption; ST – Na^+, K^+ selective transport.

Table 4. Effects of salt stress and potassium fertilizer treatments on yield and yield components in peanut varieties. CK – 0.00% NaCl + 0 kg(K_2O) ha^{-1}; T1 – 0.25% NaCl + 0 kg(K_2O) ha^{-1}; T2 – 0.25% NaCl + 85 kg(K_2O) ha^{-1}; T3 – 0.25% NaCl + 170 kg(K_2O) ha^{-1}. Data are the mean ± SD; $n = 3$. *Different lowercase letters* in the same column indicate significant differences between treatments at the 0.05 level.

Cultivars	Treatments	Yield [g per plant]	Pod number per plant	Plump pod rate [%]	100-pod mass [g]	100-seed mass [g]	Shelling rate [%]
HY25	CK	22.60 ± 1.63^{a}	20.83 ± 0.73^{a}	78.57 ± 2.52^{a}	180.50 ± 8.16^{a}	61.83 ± 3.24^{a}	68.49 ± 0.49^{a}
	T1	6.11 ± 0.89^{c}	8.35 ± 0.33^{c}	69.73 ± 3.43^{b}	116.23 ± 5.72^{c}	38.13 ± 4.60^{c}	65.39 ± 4.71^{a}
	T2	6.17 ± 1.03^{c}	11.17 ± 1.63^{b}	71.43 ± 2.95^{b}	125.23 ± 5.73^{bc}	46.27 ± 0.82^{bc}	69.08 ± 3.76^{a}
	T3	9.41 ± 0.82^{b}	12.75 ± 0.27^{b}	71.93 ± 1.14^{b}	135.50 ± 3.22^{b}	48.50 ± 3.30^{b}	69.96 ± 9.21^{a}
HY33	CK	20.77 ± 1.63^{a}	20.17 ± 0.51^{a}	78.66 ± 1.88^{a}	170.47 ± 6.53^{a}	59.23 ± 3.27^{a}	69.30 ± 5.01^{a}
	T1	4.98 ± 0.82^{c}	7.27 ± 0.56^{c}	67.47 ± 3.80^{b}	102.67 ± 3.27^{d}	33.16 ± 0.82^{c}	64.96 ± 11.62^{a}
	T2	7.35 ± 1.25^{b}	10.73 ± 0.83^{b}	70.12 ± 2.31^{b}	119.97 ± 4.90^{c}	39.66 ± 3.27^{c}	66.45 ± 8.17^{a}
	T3	9.43 ± 0.94^{b}	12.50 ± 0.99^{b}	71.73 ± 1.24^{b}	137.23 ± 7.35^{b}	46.56 ± 0.82^{b}	68.37 ± 9.63^{a}

2019, Ahanger *et al*. 2020), to improve plant salt tolerance. However, the mechanism by which potassium improves the salt tolerance of peanut is less understood. Hence, the responses of different peanut varieties to potassium application under salt stress were examined in the present study.

Previous studies have revealed that salt stress inhibits plant growth and decreases the accumulation of photosynthates, which leads to a decrease in crop yield (Bai *et al*. 2011, Rasool *et al*. 2013, Ke *et al*. 2018). Salinity reduces the ability of peanut to acquire water, which reduces the growth rate (Désiré *et al*. 2010). In the present study, salt stress significantly reduced the main stem height of HY25 and HY33, and the decreases were of similar magnitudes (approximately 39%). However, there were large differences in dry mass between HY25 and HY33. Meanwhile, the STI showed that HY25 had a higher salt-tolerance capacity than that of HY33 under salt stress. This also explained why the salt-tolerant variety HY25 was able to maintain higher biomass under salt stress. However, potassium application improves growth and biomass production in diverse groups of crops. Several studies have shown that potassium also plays an important role in plant adaptive responses to adverse environments, especially by alleviating salt stress (Abbasi *et al*. 2015, Wei *et al*. 2015, Chakraborty *et al*. 2016). In the present study, increases in the main stem height and dry mass were observed in HY25 and HY33 in the T2 and T3 treatments, which suggested that the application of potassium fertilizer restored plant growth. Increasing the K concentration in the growing medium may improve K^+ absorption and therefore counterbalance the adverse effects of salt stress and improve salt-stress tolerance.

For plants, photosynthesis is the cornerstone of growth and yield. Photosynthetic pigments are an important physiological/biological attribute directly related to the photosynthetic rate in plants (Ma *et al*. 2012). Salt stress may restrict plant photosynthesis through stomatal limitation, by degrading Chl, and/or by accelerating senescence processes (Ahmad *et al*. 2019). In this study, salt stress caused significant decreases in pigment contents in both varieties, which might have contributed to the reduction in their photosynthetic activity. The decrease in Chl pigments in stressed plants is mainly attributed to higher Na^+ toxicity (Munns *et al*. 2002). The g_s is known to be the most sensitive plant gas-exchange attribute to environmental stress (Vaghar and Ehsanzadeh 2018). Salt, drought, and osmotic tolerance are correlated with a decline in stomatal conductance in many plant species (Najafabadi and Ehsanzadeh 2017, Bouzroud *et al*. 2020). However, stomatal closure has the disadvantages of limiting the entry of CO_2 and reducing the photosynthetic rate. We observed that salt stress significantly reduced the P_N and g_s in the two varieties. Interestingly, C_i decreased and L_s increased in HY25 under salt stress, while the reverse was true in HY33. Notably, the reduction in g_s was accompanied by an increase in C_i in HY33, suggesting that the photosynthetic machinery was seriously damaged by salt stress. Hence, the decrease in photosynthesis in HY25 was mainly driven by stomatal closure, whereas that in HY33 was due to salt-induced damage to the photosynthetic apparatus.

In addition to the photosynthetic pigments and gas-exchange parameters, PSII could be the target of harmful stress effects (Shafeiee and Ehsanzadeh 2019). The present study showed reductions in F_m, F_v/F_m, and Φ_{PSII}, and an increase in NPQ suggesting that salt stress induced severe damage to the photosynthetic apparatus and photosynthetic electron transfer in two varieties of peanut. Furthermore, distinct changes in F_0 in two varieties, F_0 of HY33 increased under salt stress compared with CK, while the opposite was observed in HY25, indicate that the PSII reaction center of HY33 was more susceptible to damage or reversible inactivation under salt stress.

Potassium application effectively improves the biosynthesis of photosynthetic pigments. Particularly, the Chl *a*, Chl *b*, carotenoids, and total Chl contents were significantly higher in the T3 treatment than that in other treatments. The higher Chl content may stimulate photosynthesis and then promote plant growth (Sarwat *et al*. 2016). Meanwhile, stomatal regulation during photosynthesis is critically important, and it is significantly moderated by the amount of K retained in the plant (Sarwar *et al*. 2019). In this study, potassium regulated gas exchange and prevented photoinhibition, resulting in enhanced photosynthesis. In the T3 treatment, such modulation was much more evident in the salt-sensitive variety HY33 than in the salt-tolerant variety HY25. Moreover, the proper application of potassium effectively improved the F_v/F_m and Φ_{PSII} and reduced the NPQ of peanut under salt stress. Therefore, we concluded that potassium prevented salt-induced inhibition of photosynthesis by ensuring a dynamic balance of photosynthetic pigments and maintaining the conformational stability of PSII reaction centers and accelerated photosynthetic electron transfer under salt stress.

In addition to the impact on the growth and photosynthesis of plants, salt stress also hinders K^+ transport in plants due to a large amount of Na^+ absorption (Maathuis *et al*. 2014), which eventually leads to a Na^+/K^+ imbalance in plants. Thus, maintaining a relatively low Na^+/K^+ is critically important for plants to survive under salt stress (Wang *et al*. 2013). Numerous studies have reported that the K^+ content of plants is reduced under salt stress. It is generally accepted that maintaining K^+ homeostasis in plant cells depends on the selective uptake of K^+ and the cellular compartmentalization and distribution of Na^+ and K^+ in various organs (Carden *et al*. 2003). Thus, K^+ and Na^+ SA and ST in plants strongly correlate with salt tolerance (Liu *et al*. 2016). The results showed that under salt stress, the Na^+ content significantly increased in various organs, and the uptake of K^+ decreased, thus increasing the Na^+/K^+ in each organ. Under salt stress, the reduction in the SA value in HY25 was more than twice that in HY33. Moreover, the ST value of HY25 was higher under salt stress than that in CK, while that of HY33 was lower. These results indicated that the salt-tolerant variety HY25 could not only control Na^+ absorption under salt stress but also reduce Na^+ transport to the shoots through self-regulation, which reduced excessive damage. However, the salt-sensitive variety HY33 showed a poor self-regulation

ability. Osmotic adjustment is an essential property of plant salt tolerance, and the accumulation of compatible organic solutes is one of the main strategies by which salt-tolerant plants balance salt-induced osmotic stress and maintain normal cell structure (Hasegawa *et al.* 2000). Under salt stress, excessive Na^+ accumulation in vacuoles leads to osmotic imbalance, such that the synthesis of many organic osmolytes or the uptake of inorganic osmolytes is needed to maintain osmotic balance. As a major inorganic osmolyte, potassium ion plays an important role in cell osmoregulation when plants are under osmotic stress (Wang *et al*. 2013). External potassium application improves soil potassium availability. Thus, plants can drive K^+ transport and compete with Na^+ through osmotic-mediated cell expansion and turgor pressure under salt stress, which improves the SA and ST of K^+ while reducing the Na^+/K^+ ratio in various organs. In particular, the decrease in Na^+/K^+ in the stem was more pronounced in the salt-sensitive variety HY33 (64.2%) than that in the salt-tolerant variety HY25 (44.1%) in T3 treatment. These results showed that the salt-tolerant variety could synthesize more organic osmolytes that cooperate with K^+ for osmotic adjustment, while the salt-sensitive variety relied more on cytotoxic Na^+ as an osmolyte under salt stress. Therefore, the salt-sensitive variety requires a large number of inorganic osmolytes (K^+) to maintain Na^+/K^+ homeostasis under salt stress.

Conclusion: Salt stress negatively influenced the morphology, osmotic balance, and photosynthetic characteristics of peanut, causing a reduction in biomass. However, the application of potassium enhanced salt tolerance in peanut plants. On the one hand, external potassium maintained the ion homeostasis by involving osmotic adjustment. On the other hand, potassium enhanced the photosynthetic capacity by increasing concentrations of photosynthetic pigments, ultimately promoting photosynthate accumulation and pod yield formation. Therefore, it is clear that the reasonable application of potassium fertilizer under salt stress can effectively improve the salt tolerance of crops.

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