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Full Length Article

Growth and Physiological Responses of Peanut Seedling to Salt Stress

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Abstract

Soil salinity plays a primary role in soil degradation and reducing agricultural productivity. This study was conducted to evaluate the effects of salinity stress on growth, photosynthesis and antioxidative enzyme activity in functional leaves of two peanut cultivars (Huayu 23 and Yueyou 40) were sown under five salinity levels *i.e*., 0.96, 2.35, 3.34, 4.82 and 6.70 dS/m; 0.96 dS/m being taken as control. With increasing salinity levels, peanut shoot and root dry weight significantly decreased in both cultivars. Chlorophyll contents, photosynthesis, the maximum fluorescence (F_v/F_m) and photochemical quenching (qP) declined with increasing soil salinity and decrease was more in salt-sensitive Yueyou 40 than salt-tolerance cultivar Huayu 23. Compared to salt-tolerance (Huayu 23), salt-sensitive cultivar Yueyou 40 observed more decrease of peanut growth. Moreover, SOD and CAT activity of peanut leaves was linearly increased with higher salinity in both cultivars. In contrast, non-photochemical quenching (NPQ) increased with increasing salinity levels, especially in salt-sensitive cultivar Yueyou 40. However, POD activity was not affected by soil salinity in Huayu 23, but significantly decreased by increasing salinity level in Yueyou 40. In conclusion, the salt-tolerance variety adapted well saline environment by reducing photoinhibition and diminishing capacity for electron transport and maintaining relatively high level of chlorophyll content and antioxidant enzyme activities.

Keywords: *Arachis hypogaea*; Salt stress; Photosynthesis; Reactive oxygen species; Leaf

Introduction

Salt stress is an important abiotic stress affecting plant growth and development in the world (Al-Maskri *et al.,* 2010; Muchate *et al*., 2016). Soil salinity affects plant metabolic disorder via osmotic stress, ion toxicity, nutrient imbalance and oxidative stress leading to cellular damage and even plant death (Hasegawa, 2000; Zhu, 2001; Farooq *et al*., 2015; Slama *et al*., 2015). The capacity of the plant to tolerance salinity is a complex trait consisting of multiple physiological and biochemical mechanisms, in particular by controlling the generation of reactive oxygen species (ROS) (Gong *et al*., 2013) and photosynthesis (Stefanov *et al*., 2016).

The photosystem I and II situated in the chloroplasts are the major sites to generate ROS such as superoxide anion radicals ($O_2\cdot^-$) and hydrogen peroxide (H_2O_2) during the electron transfer along the electron chain (Foyer *et al*., 1994). Soil salinity limited stomatal conductance (Bethke and Drew, 1992), carbon dioxide influx, regeneration of RubP (Munns, 2002; Degl'Innocenti *et al*., 2009), which in turn suppress the photosynthesis. This process is usually accompanied by excessive photo energy. The energy fills up the photosynthetic electron transport system (Niyogi, 2000) and cause the photosystem II (PSII) photo inhibition (Foyer and Noctor, 2005).

However, in order to suppress PSII photo inhibition, plants have developed a protective system in chloroplasts, which was noticed in NPQ of Chl florescence (Long *et al*., 1994; Kausar and Shahbaz, 2017). And the fluorescence parameters of barely and soybean were significantly affected by salt stress (Kao *et al*., 2003; Sayed, 2003). In addition, oxygen at PSI is photo reduced to hydrogen peroxide (H_2O_2), a superoxide ($O_2\cdot^-$) and hydroxyl radicals ($OH\cdot$) (Mittler, 2002). A complicated antioxidative defense system have been generated in order to reduce the oxidative damage (Noctor *et al.,* 1998). However, the tolerance of plant to different stresses may differ due to the various species, varieties, and even ecotypes (Ullah *et al*., 2008).

Peanut (*Arachis hypogaea* L.) is an important oilseed crop in China, which has been reported to be moderately salt tolerance (Singh *et al*., 2008). As a leguminous crop, it has an important role in ameliorating the soil fertility by fixing atmospheric nitrogen into the soil (Lal, 2008). Soil salinity depresses seed germination, development, dry matter production and peanut yield and quality (Nautiyal *et al*., 1989; Janila *et al*., 1999; Mensah *et al*., 2006; Salwa *et al*.,

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2010). Moreover, Chakraborty *et al*. (2016) identify the major ROS detoxification pathway in peanut under salinity stress. However, until now, limited information is available on the systematic investigation of the salt tolerance mechanism in peanut. Hence, the purpose of this research was to (1) assess the variation of the maximum fluorescence (F_v/F_m) and photochemical quenching (qP) and photosynthetic pigments of peanut leaves under soil salinity and (2) explore the effect of soil salinity on the activities of various antioxidant enzyme and scavenging capacity of ROS to better elucidate the possible physiological mechanism of salt tolerance during seedling stage. Information obtained will aid in the development of new peanut germplasm with high salinity stress tolerance.

Materials and Methods

Experiment Site and Plant Materials

Pot experiments were conducted in spring season of 2018 in a greenhouse at South China Agricultural University, Guangzhou, China. Two peanut cultivars of different salt tolerance, Huayu 23 (salt-tolerant) and Yueyou 40 (salt-sensitive) were used. Peanut seeds were sown in a plastic basin filled with 18 kg dry soil. The nutrient content of the soil and its physical and chemical properties are listed in Table 1.

Two peanut cultivars were sown under five salinity levels *i.e*., 0.96, 2.35, 3.34, 4.82 and 6.70 dS/m; 0.96 dS/m being taken as control. At seedling stage (one week after transplanting), NaCl were dissolved in 1000 mL water and then added to the pots, respectively, forming soils with five levels of salt stress. The experiment was arranged in a completely randomized design and every treatment had 12 replications. The plants were harvested at 2 weeks after salt treatment.

After two weeks of salt salinity application, the salt-tolerant cultivar Huayu 23 showed 100% survival in all salinity levels, but as the salinity exceeds 4.82 dS/m, the salt-sensitive cultivar Yueyou 40 died. The salt-sensitive cultivar survived only at low salinity (below 4.80 dS/m).

Growth Parameter Measurements

In every treatment, 10 plants were sampled and separated into root and shoot sections. The leaf areas of the functional leaves were measured. Meanwhile, chlorophyll content was measured through SPAD-502. Plant height, shoot and root dry weight were measured and averaged.

Leaf Photosynthesis and Chlorophyll Fluorescence Measurements

Net photosynthetic rate (Pn), stomatal conductance (gs) and transpiration rate (Tr) of the functional leaves were measured by using a photosynthesis system (Li-6400, Li-COR Inc., NE, USA) under 1500 μmol/m/s light intensity at 9:00–11:00 a.m.

Leaf chlorophyll fluorescence measurements were carried out using a pulse-amplitude-modulation fluorometer (PAM 2500, H. WALZ, Effeltrich, Germany). The method of measurement was according to the Zhang *et al*. (2013). After measurement, the leaf samples were immediately frozen in liquid N_2 and stored at -40^{o}C for other analysis.

Extraction and Assay of Antioxidative Enzymes

Superoxide dismutase activity was determined according to the methods of Foster and Hess (Foster and Hess, 1980). Total CAT activity was measured according to the method reported by Jr and Sizer (1952) with minor modifications. POD activity was analyzed according to the methods of Tan *et al.* (2008).

Statistical Analysis

OriginPro 7.5 was used for data processing and figures. Two ways ANOVA was performed using S.P.S.S. version 17.0 and the means were separated with LSD test. In all figures, data are represented as means ± standard errors.

Results

Root and Shoot Growth of Peanut

Shoot and root dry weights of both peanut cultivars (Huayu 23 and Yueyou 40) were decreased as soil salinity increased, but this reduction was more obvious in the salt-sensitive Yueyou 40 than the salt-tolerant cultivar Huayu 23 (Fig. 1). At the end of salt treatment, shoot dry weight decreased by 16.87, 23.92, 34.69 and 62.03% in Yueyou 40 and by 6.38, 15.45, 23.58 and 39.54% in Huayu 23, respectively at 2.35 dS/m, 3.34 dS/m, 4.82 dS/m and 6.70 dS/m salinity rate, compared to the control.

As soil salinity increased, plant height of both cultivars was decreased significantly; however, plant height of Yueyou 40 observed more reduction than Huayu 23 (Fig. 1). Compared to the control, Yueyou 40 and Huayu 23 showed reduction of plant height by 48.64 and 26.58% at the highest salt salinity, respectively. Within the soil salinity range from 0.96 dS/m to 6.70 dS/m salinity rate, a little decrease in leaf area of the functional peanut leaves was observed as soil salinity increased, and this reduction was more pronounced in Huayu 23 than Yueyou 40 (Fig. 1).

Chlorophyll Content

Chlorophyll concentration of both genotypes reacted differently to soil salinity. In salt-sensitive cultivar Yueyou 40, the chlorophyll concentration was decreased drastically with increased soil salinity (Fig. 2). However, in the salt-tolerant cultivar Huayu 23, chlorophyll concentration was increased with soil salinity up to 2.35 dS/m, and then decreased as soil salinity increased (Fig. 2).

Table 1: Nutrients contents, physical and chemical properties of the basic soil in the experiment in 2018

TNC ($mg \cdot kg^{-1}$)	APC ($mg \cdot kg^{-1}$)	AKC ($mg \cdot kg^{-1}$)	pH	BD ($g \cdot cm^{-3}$)	FWC (%)	EC ($dS \cdot m^{-1}$)
1.11×10^3	27.83	132.73	6.62	1.23	28.55	1.22

TNC: Total N content, APC: Available P content, AKC: Available K content, BD: Bulk density, FWC: Field water capacity, EC: Electrical conductivity

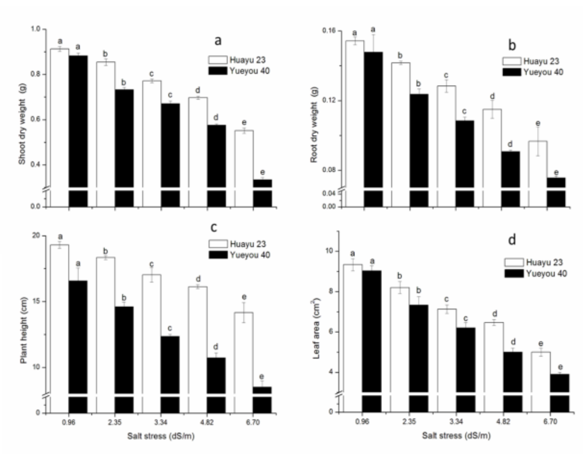

Fig. 1: Effects of soil salinity on shoot (**a**) and root (**b**) dry weights, plant height (**c**) and leaf area (**d**) of two peanut cultivars
Vertical bars represent means ± standard error (n = 3). Bars labelled with different lowercase letters on open-square bars or uppercase letters on closed-square bars represent significant differences ($P < 0.05$)

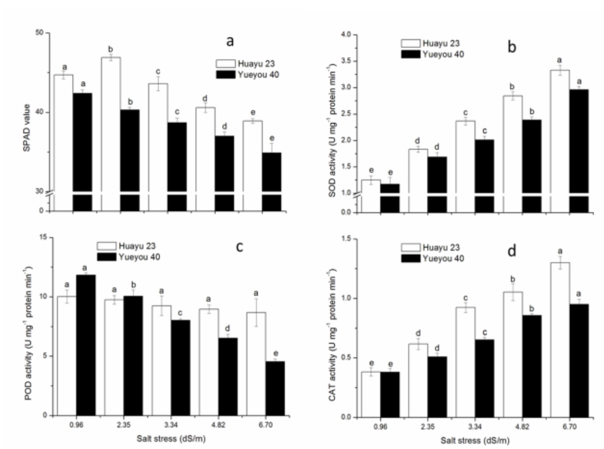

Fig. 2: Effects of soil salinity on chlorophyll content (**a**), superoxide dismutase (SOD, **b**), peroxide (POD, **c**), and catalase (CAT, **d**) activities of two peanut cultivars at seedling stage
Vertical bars represent ± standard error (n = 3). Bars labelled with different lowercase letters on open-square bars or uppercase letters on closed-square bars represent significant differences ($P < 0.05$)

Leaf Photosynthesis and Chlorophyll Fluorescence

After two weeks of salt stress application, Pn in functional peanut leaves of both cultivars was decreased gradually as soil salinity increased (Table 2). And the reduction of Pn was more obvious in Yueyou 40 than Huayu 23 at any given soil salinity. Stomatal conductance (gs) was decreased in both cultivars as soil salinity increased; However, the decrease rate of gs in salt-tolerance Huayu 23 observed less reduction than Yueyou 40. Transpiration (Tr) also decreased as soil salinity increased, and reaching 56.76 and 68.78% of reduction in Huayu 23 and Yueyou 40, respectively, at the highest soil salinity (Table 2).

Maximum quantum yield of PSII photochemistry (F_v/F_m) was decreased gradually as soil salinity increased at the end of the study. And the salt-sensitive cultivar showed a more pronounced reduction than salt-tolerance in fluorescence (Table 2). F_v/F_m dropped by 14.81% in Yueyou 40 and by 11.11% in Huayu 23 compared to their respective controls. Photochemical quenching coefficient (qP) value in both cultivars was decreased as soil salinity increased. Unlike the Qp, the non-photochemical quenching

Table 2: Effect of soil salinity on photosynthesis and chlorophyll fluorescence in the leaves of two peanut cultivars

Cultivars	Soil salinity (dS/m)	Pn	Tr	gs	F_v/F_m	qP	NPQ
Huayu 23	0.96	21.63 ± 0.42 a	7.40 ± 0.10 a	423.33 ± 5.69 a	0.81 ± 0.01 a	0.93 ± 0.03 a	0.29 ± 0.02 e
	2.35	19.52 ± 0.48 b	6.50 ± 0.20 b	393.00 ± 4.36 b	0.80 ± 0.00 b	0.85 ± 0.02 b	0.35 ± 0.02 d
	3.34	15.86 ± 0.85 c	5.50 ± 0.20 c	372.33 ± 7.02 c	0.77 ± 0.01 c	0.77 ± 0.01 c	0.41 ± 0.01 c
	4.82	13.21 ± 0.40 d	4.53 ± 0.15 d	337.33 ± 4.16 d	0.74 ± 0.01 d	0.59 ± 0.04 d	0.53 ± 0.02 b
	6.70	11.88 ± 0.49 e	3.20 ± 0.17 e	293.00 ± 11.36 e	0.72 ± 0.00 e	0.46 ± 0.03 e	0.63 ± 0.03 a
Yueyou 40	0.96	21.58 ± 0.46 a	7.27 ± 0.21 a	413.67 ± 7.77 a	0.81 ± 0.01 a	0.91 ± 0.03 a	0.30 ± 0.03 e
	2.35	17.70 ± 0.67 b	6.10 ± 0.10 b	375.33 ± 9.29 b	0.79 ± 0.00 b	0.82 ± 0.02 b	0.41 ± 0.02 d
	3.34	13.78 ± 0.37 c	4.90 ± 0.10 c	339.67 ± 3.21 c	0.76 ± 0.01 c	0.70 ± 0.02 c	0.51 ± 0.01 c
	4.82	11.25 ± 0.22 d	3.50 ± 0.10 d	305.00 ± 4.58 d	0.72 ± 0.00 d	0.51 ± 0.02 d	0.58 ± 0.02 b
	6.70	8.77 ± 0.70 e	2.27 ± 0.15 e	265.00 ± 9.17 e	0.69 ± 0.01 e	0.38 ± 0.02 e	0.71 ± 0.03 a
	Cultivar (C)	84.96 **	120.31 **	86.35 **	43.86 **	38.65 **	63.77 **
	salt stress (S)	442.15 **	826.97 **	350.42 **	278.97 **	411.70 **	316.49 **
	C × S	6.34 **	8.68 **	3.03 *	3.58 *	1.87 ns	5.01 **

Values are the mean of 3 replicates ±S.E. Means followed by different letter within a column for each cotton species are significantly different at $P < 0.05$ according to student's LSD test

*, **: significant at 5 and 1% probability levels, respectively; NS: non-significant; Pn: net photosynthetic rate; Tr: transpiration rate; gs: stomatal conductance; F_v/F_m: maximum quantum yield of PSII photochemistry; qP: photochemical quenching coefficient; NPQ: non-photochemical quenching

(NPQ) value was drastically increased as soil salinity increased. Nevertheless, this increase was more obvious in the salt-sensitive cultivar Yueyou 40 than in the salt-tolerant cultivar Huayu 23 (Table 2).

Antioxidant Enzyme Activities

The SOD and CAT activity of peanut leaves was linearly increased as soil salinity levels were increased in both cultivars; however, increase was more pronounced in Huayu 23 than Yueyou 40 (Fig. 2). The POD activity was not affected by soil salinity in Huayu 23, but significantly decreased by increasing salinity level in Yueyou 40 (Fig. 2).

Discussion

Soil salinity affected biometric response, hampered growth and led to significant reduction in biomass, which was due to the inhibition of cell elongation (Xianzhao *et al*., 2013; Pompeiano *et al*., 2016; Alejando *et al*., 2017; Bacha *et al*., 2017). In this research, relative growth of shoot and root in salt-tolerance cultivar Huayu 23 was less inhibited than that in salt-sensitive cultivar Yueyou 40 under different soil salinity, which was similar to the results in rice (*Oryza sativa* L.) (Hussain *et al*., 2018), centipedgrass (*Eremochloa ophiuroides* Hack.) (Li *et al*., 2018) and tomato (*Lycopersicon esculentum* Mill.) (Bacha *et al*., 2017). The growth inhibition was also accompanied with morphological changes related to leaf area and plant height (Fig. 1). The possible reason might be related to the inaugural influence of osmotic stress happening after salt shock, which hamper the root and shoot growth (Thameur *et al.*, 2012).

When plants grow under soil salinity conditions, photosynthesis is particularly reduced by severe impairments in photosynthetic activities and the photosynthetic apparatus (Mao *et al*., 2007). Soil salinity caused greater chlorophyll content reduction in cultivar Yueyou 40 than in cultivar Huayu 23, which revealed that the biosynthesis of pigment degradation was influenced more clearly in salt-sensitive cultivar than salt-tolerance cultivar by soil salinity. As chlorophyll content correlates directly with the growth and development of plant, the reduction of chlorophyll content suggested substantial damage to the photosynthetic mechanism in Yueyou 40, which were similar to the findings in wheat (*Triticum aestivum* L.) (Shirao *et al*., 2013), rice (Kibria *et al*., 2017) and tomato (Bacha *et al*., 2017) grown in saline conditions.

Soil salinity affected chlorophyll content, suppressed the PSII activity, and led to the restraining of photosynthetic rate, which induced by initial osmotic stress and the photosynthetic apparatus damage caused by soil salinity (Mehta *et al.*, 2010; Farooq *et al*., 2015). The decreasing rate of Pn was more obviously in Yueyou 40 cultivar than Yuhua 23 cultivar, indicating that the Huayu 23 cultivar was more salt-tolerant than the Yueyou 40, which was consistent with their growth characteristics under soil salinity. Previous studies have revealed that soil salinity may influence the net photosynthesis and stomatal conductance through either the stomata closure, or altering the biochemical mechanisms of CO_2 fixation (Chaves *et al*., 2003). However, in this study, as soil salinity increased, gs and Tr was dramatically decreased in both peanut cultivars, indicating that Pn might be affected by non-stomatal factors, especially in cultivar Yueyou 40.

The decline of photosynthetic rate of plant under soil salinity was associated with the reduction in gs, carbon dioxide availability and CO_2 assimilation, which resulting in pronounced reduction of photosynthetic electron transport chain in chloroplasts. Chlorophyll fluorescence is sensitive and shown an immediate response of the plants subjected to salt stress conditions (Wu *et al*., 2015). The only exception was the F_v/F_m, which seems to be sensitive to only the highest salinity level and the last time point. Our results is similar to the result of Shu *et al.* (2012) where F_v/F_m was decreased significantly as soil salinity increased. The results stating that photoinhibition and a diminish capacity for electron transport may partly elucidate the mechanism of the retarding effect of soil salinity on peanut growth. However, some researches shown that soil salinity had no influence on the chlorophyll fluorescence (Percival, 2005), which suggest that different plant species may perform difference under soil salinity. Moreover, there was a sharp decreasing trend in the chlorophyll content and F_v/F_m of two peanut cultivars after two-week salt stress, with the cultivar Yueyou 40 decreased greater than the Huayu 23 at the same treatment, which further approved thee non-stomatal factors mediated Pn decrease in both peanut cultivars.

Simultaneously, as soil salinity increased, the qP exhibited a significant decrease trend in both peanut cultivars indicated that soil salinity reduce the CO_2 assimilation rates and the Calvin cycle activity (Catatayud and Barreno, 2001), which in turn reduced the re-oxidiz Q_A ability, suggested soil salinity induce the pressure on PSII and bring out the PSII reaction center closed. Moreover, the quick response of the NPQ seems to be a usual reaction of plants able to offset the harmful influence of soil salinity, which defending the plant against the latent ruinous influence of absorbed excess light energy under salt stress (Roban, 2015). In this research, the increasing rate of NPQ value was more obvious in the salt-sensitive cultivar Yueyou 40 than in the salt-tolerant cultivar Huayu 23, which stated that the salt stress-induced increase of NPQ in Huayu 23 is likely expected to provide with improved protection for high photosynthetic activity during the salt stress. The increase NPQ in salt treated of Huayu 23 may provide a good standard in investigating how salt-tolerant cultivars cope with soil salinity. Thus, the maintenance of fairly high rates of electron transport at PSII corresponding with the increase in NPQ in salt stressed plants was able to impede nonreversible hurt to PSII. Moreover, leaf F_v/F_m significantly decrease and NPQ increased as soil salinity increased, suggesting that soil salinity caused serious inhibition of photosynthesis to peanut and an improvement in the thermal dissipation in PSII.

Another consequence of soil salinity in plant is the generation of ROS, and the oxidative stress in stressed plants results from a shortfall in ROS scavenging due to a decrease in scavenging enzymes activity (Mittler, 2002; Slama *et al*., 2002). Oxidative stress SOD activities depress the risk of ·OH radical formation, and may bring about serious hurt to membrane and protein (Bowler *et al*., 1992). The more salt-tolerant cultivar Huayu 23 maintained higher levels of SOD and CAT activity than Yueyou 40, which allowed it to keep a better balance between ROS formation and detoxification, and similar to the results of Gong *et al.* (2014) and Liu *et al.* (2016), revealing that the salt-tolerant cultivar Huayu 23 has a better O_2^- radical scavenging capacity than salt-sensitive cultivar Yueyou 40 (Qian *et al.*, 2009). In addition, the higher activity of CAT in Huayu 23 suggesting that it had a higher ability for resolving the H_2O_2, which generated by SOD. Therefore, our results reveal that SOD activity assorted with CAT activity play a significant role in scavenging O_2^- and H_2O_2 content (Liang *et al*., 2003; Badawi *et al*., 2004) and might be the important mechanisms for peanut in elucidating tolerance against soil salinity. Moreover, as soil salinity increasing, POD activity decrease significantly in Yueyou 40, but remained unchanged in Huayu 23, which was different from results of rice (Kibria *et al*., 2017), peanut (Chakraborty *et al*., 2016) and cotton (Zhang *et al*., 2014). This divergence is because of the difference in the species, length of the experiment as well as with the intensity of stress.

Conclusion

Salt-tolerant cultivar observed higher salt tolerance due to reduced photoinhibition and diminishing capacity for electron transport, and maintained relatively more chlorophyll contents and antioxidant enzyme activities. Information obtained in this study will aid in developing of new peanut germplasm with high salinity stress tolerance.

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