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Full Length Article



# Biomass, Gas Exchange and Chlorophyll Fluorescence in Wheat Seedlings under Salt and Alkali Stress

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# Abstract

Gas exchange and chlorophyll fluorescence are two very important physiological processes affecting plant growth. The experiment was simulated by salt and alkali stresses. Shoots biomass, gas exchange and chlorophyll fluorescence parameters of wheat were measured after 9 d of treatments. The shoot biomass and gas exchange indices decreased significantly with the increasing salt concentration, and more for alkaline stress at the same concentration, except for *Ci* concentration. Compared to saline and alkaline stresses with controls, the  $F_v/F_m$  was not changed under both stresses, but *qp* increased; PS II maximum efficiency ( $F_v$  ' / $F_m$ ') was not affected by salinity, but decreased under alkalinity; PS II efficiency ( $\phi_{PS II}$ ) and electron transport rates (ETR) only increased significantly at lower concentration (40 mmol/L) under salt stress, and didn't change at other concentration, but ETR decreased at higher concentration (120 mmol/L) under alkali stress;  $q_N$  did not change at salinity, but enhanced significantly at 120 mmol/L concentration under alkalinity. Therefore, photosynthetic performance response of wheat seedling to salt and alkali stresses was very different.  $P_N$  was affected by both stomatal and non-stomatal factors under salt and alkali stresses. Photo-protection caused by photo-inhibition happened at the highest level of alkali stress, depending on high pH and salinity. The wheat variety Jimai 3 in present stud y has tolerance to moderate salinity and alkalinity. © 2020 Friends Science Publishers

Keywords: Chlorophyll fluorescence; Gas exchange characteristics; Wheat; Salt stress; Alkali stress

# Introduction

Salt stress is one of the most serious abiotic stresses, which limit plant production in arid-semiarid region (Zhao *et al.* 2007). Saline-alkaline inland is a globally rare ecosystem, the soil of which is saline with the existence of  $CO_3^{2-}$  and  $HCO_3^{-}$ simultaneously. This kind of soil distributed widely in China and occupies one-tenth (9910.3×10<sup>4</sup> hm<sup>2</sup>) of total salinealkaline land areas in the world (Deng *et al.* 2006). West of Songnen Plain is the main distribution area of salinealkaline inland. In the past two decades, scientists have paid more attention on alkaline salt effects on plants and reported that alkaline stress were more destructive to plants, and the plants' responses are varied (Zhang and Mu 2009; Nadeem *et al.* 2018).

Photosynthesis (CO<sub>2</sub> assimilation) is the key process for which plants survived and gained high productivity in normal or stressed environments. In general, photosynthetic capacity decreases in plants under salt stress (Brugnoli and Bjorkman 1992; Dionisio-Sese and Tobita 2000; Farooq *et al.* 2015). The CO<sub>2</sub> assimilation was related to PS II operating efficiency, which could be estimated by Chl fluorescence measurements (Krall and Edwards 1991; Siebke *et al.* 1997) that can provide information on photosynthesis of plant at stress (Méthy *et al.* 1997). And maximum quantum efficiency decrease in Fv/Fm, such as in early salt-stressed mango trees (De-Lucena *et al.* 2012) have been reported. But some reports showed no significant change of Fv/Fm in other plants which respond to NaCl (Netondo *et al.* 2004). Other traits of Chl fluorescence, such as  $\Phi_{PSII}$ , Fv'/Fm', qP, qN and ETR can be determined and calculated under salt stress (Zribi *et al.* 2009). However, the change in traits was related to plants species and their tolerance to salinity.

Wheat is an important crop world-wide and many studies have reported its responses to NaCl stress, such as ion changes (Ruan *et al.* 2007; Ehsanzadeh *et al.* 2009; Li *et al.* 2014) and antioxidant enzyme activities and osmotic solutes changes (Heidari and Mesri 2008). Comparison of salt-alkali

stress on wheat gas exchange characteristics (Guo *et al.* 2009) and ions balance (Li *et al.* 2009) had been studied. However, the photosynthesis capacity and its related PS II efficiency under alkali stresses are still unclear. Therefore, pot experiments with simulated saline and alkaline conditions were conducted to measure the PS II efficiency, Chl fluorescence attributes of wheat seedlings, biomass and gas exchange characteristics, and analyze the tolerance of wheat variety to salt-alkali stress condition. These results will provide supplement as the theory basis for utilizing saline-saline soil.

### **Materials and Methods**

### Pot experiments

Wheat (cv. Jimai 3) was used as the experimental materials. Fifteen wheat seeds were sowed in plastic pots. Hoagland's nutrient solution was added every day after seedlings emerged.

NaCl, Na<sub>2</sub>SO<sub>4</sub> and NaHCO<sub>3</sub>, Na<sub>2</sub>CO<sub>3</sub> were mixed in 9:1 (molar ratio), added to Hoagland's nutrition solution for salt-alkali stress, respectively (Li *et al.* 2009). Three concentrations were applied: 40 (S1 and A1), 80 (S2 and A2) and 120 (S3 and A3) mmol/L. The pH ranges were 6.27–6.45 and 9.10–9.17, respectively in salt and alkali stresses. The pots with only Hoagland's nutrition solution were used as controls.

Twenty-one pots were divided into 7 sets when seedlings were 10 d. One pot was a replicate and there were three replications in one treatment. Two hundred and fifty mL of stress solution were used to treat per pot daily at 16:30– 17:30 h. All pots were put in a greenhouse to protect against rain after treatments. The experiments were last for 9 days until the seedlings seemed died at the highest salinity under alkali stress.

#### Gas exchange characteristics

Before harvest of seedlings,  $P_N$ , E rates,  $g_s$  and Ci of leaves were measured on a fully expanded youngest leaf at 9:00, using a 1200  $\mu$ mol m<sup>-2</sup> s<sup>-1</sup> light illumination by a portable open flow gas exchange system LI-6400. The experiment was repeated for 5 times with 2 blades per pot and 6 leaves per treatment and the averages were calculated.

#### Chlorophyll fluorescence

The portable open gas exchange system LI-6400 with an integrated fluorescence chamber head (LI-6400-40 Leaf Chamber fluorometer) was used to measure leaf Chl fluorescence attributes. Seedlings were kept in darkness environment for at least 30 min before measuring. The  $F_0$  value was measured by a modulated light (< 1  $\mu$ mol m<sup>-2</sup> s<sup>-1</sup>). The  $F_m$  value was measured at 4200  $\mu$ mol m<sup>-2</sup> s<sup>-1</sup> light intensity for 0.8 s on dark-adapted leaves. Then  $F_v/F_m$  was

recorded. The  $F_m$  ' value in light-adapted leaves and  $\Phi_{PS II}$ were determined by a 0.8 s saturation pulses at 6000  $\mu$ mol m<sup>-2</sup> s<sup>-1</sup>, whereas the actinic light was 200  $\mu$ mol m<sup>-2</sup> s<sup>-1</sup> light intensity (Liu and Shi, 2010). All descriptions of Chl fluorescence parameters and calculated formulas of  $\Phi_{PS II}$ , ETR, qP and  $q_N$  were showed in Table 1.

## Harvest

After measuring the gas exchange characteristics and chlorophyll fluorescence parameters, all plants shoots were harvested and washed three times, then were oven-dried at 105 °C for 10 min. The biomass was recorded after oven-dried at 70 °C for 48 h.

#### Statistical analyses

The experimental parameters were analyzed by one-way analysis of variance (ANOVA) using S.P.S.S. 17.0 and plotted in a histogram using SigmaPlot 10.0. Means and standard errors were reported and compared by the least significant difference (LSD<sub>0.05</sub>) test if ANOVA tests were significant (P < 0.05).

#### Results

Shoot biomass of wheat seedlings decreased significantly with the increasing salinity under both stresses (P < 0.05, Fig. 1). At the highest stress concentration (120 mmol/L), the decrements were about 31% and 47% respectively at salinity and alkalinity, comparing to controls. Alkali stress showed more decrease than salt stress.

 $P_{\rm N}$ ,  $g_{\rm s}$  and E (P < 0.05, Fig. 2) decreased significantly under both stresses, amounting to 82%, 50%, 71% under salt stress and 92%, 84%, 83% under alkali stresses, respectively at the highest concentration. More reductions were found in alkali stress than in salt stress. However,  $C_{\rm i}$  increased markedly only at the highest level under salt stress. The changes of  $C_{\rm i}$  were significant at all alkaline stress levels as compared to controls (P < 0.05, Fig. 2).

Chl fluorescence parameters were affected distinctly under salt and alkali stresses except of  $F_v/F_m$  (Table 2), the values of which were around 0.83 in all treatments.  $F_0$  and  $F_m$ of wheat leaves decreased significantly under both stresses. There was a decrease tendency in  $F_0$  ' and  $F_m$  ' with increasing salinity, but the significance was found only at higher concentration of salt (120 mmol/L) and alkali stresses (80–120 mmol/L) (Table 3). The change tendency of  $F_s$  was similar to  $F_0$  ' and  $F_m$  '. Then  $F_v$  '  $/F_m$  ' ratio didn't change under salt stress, but decreased markedly at the highest salinity under alkali stress (120 mmol/L).

 $\varphi_{\text{FS II}}$  and ETR were higher significantly at 40 mmol/L than controls and unchanged at other salinity under salt stress, but lower markedly at 120 mmol/L than controls and unchanged at other salinity under alkali stress (Fig. 3).  $q_N$  reduced significantly only at 40 mmol/L and kept a similar value with controls under salt stress, but increased significantly at 120 mmol/L under alkali stress.



**Fig. 1:** Shoot dry weight of wheat seedlings under salt (NaCl: Na<sub>2</sub>SO<sub>4</sub>) and alkali stresses (NaHCO<sub>3</sub>: Na<sub>2</sub>CO<sub>3</sub>), presented with means  $\pm$  standard error (n=3). CK is the control plants without treatments, S1-S3 are the salt-treated plants, A1-A3 are the alkali-stressed plants. Different letters showed the significant variances among treatments using the least significant difference (LSD) test (*P* < 5%)



**Fig. 2:** Photosynthetic parameters of wheat seedlings under salt (NaCl: Na<sub>2</sub>SO<sub>4</sub>) and alkali stresses (NaHCO<sub>3</sub>: Na<sub>2</sub>CO<sub>3</sub>), presented with means  $\pm$  standard error (n=4). CK is the control plants without treatments, S1-S3 are the salt-treated plants, A1-A3 are the alkali-stressed plants. Different letters showed the significant variances among treatments using the least significant difference (LSD) test (*P* < 5%)

Photochemical quenching (qP) increased markedly at 40 mmol/L then kept unchanged under salt stress, but increased markedly when salinity was equal or greater than 80 mmol under alkali stress.

 $Na^+/K^+$  ratio in wheat seedlings under alkali stress were much higher than those under salt stress at the same stress concentration, and the  $Na^+/K^+$  in the control group showed lowest (Fig. 4).

## Discussion

Soil salination and alkalization is becoming an increasing problem in world environments, which affected the



**Fig. 3:** Effect of salt and alkali stresses on actual PS II efficiency ( $\varphi$ PS II), non-photochemical quenching coefficient (qN), photochemical quenching coefficient (qp) and photosynthetic electron transport efficiency (ETR), presented with means ± standard error (n=4). CK is the control plants without treatments, S1-S3 are the salt-treated plants, A1-A3 are the alkali-stressed plants. Different letters showed the significant variances among treatments using the least significant difference (LSD) test (P < 5%)



**Fig. 4:** Na<sup>+</sup>/K<sup>+</sup> in the shoot of wheat seedlings under salt (NaCl: Na<sub>2</sub>SO<sub>4</sub>) and alkali stresses (NaHCO<sub>3</sub>: Na<sub>2</sub>CO<sub>3</sub>), presented with means ± standard error (n=3). CK is the control plants without treatments, S1-S3 are the salt-treated plants, A1-A3 are the alkali-stressed plants. Different letters showed the significant variances among treatments using the least significant difference (LSD) test (P < 5%)

production of crops seriously. Alkali stress inhibited the growth of wheat seedlings more significant than salt stress (Li *et al.* 2009). Plants usually maintain photosynthetic carbon gain and lessen transpiration under salt stress by decreasing stomatal conductance (Läuchli and Lüttge 2002; Benlloch-González *et al.* 2008). Clark *et al.* (1999) indicated that the reductions of stomatal and transpiration represented the physiological responses to cope with salt condition. The

Parameter	Description	Mathematical expression
F <sub>0</sub>	minimal Chl a fluorescence in dark-adapted	
$F_0'$	minimal Chl a fluorescence in light-adapted	
$F_{\rm m}$	maximal Chl a fluorescence in dark-adapted	
$F_{ m m}'$	maximal Chl a fluorescence in light-adapted	
$F_{\rm s}$	steady-state Chl fluorescence	
$F_{\rm v}/F_{\rm m}$	maximum quantum efficiency of PS II photochemistry	
Fv'/Fm'	PS II maximum efficiency	
$arPhi_{ m PSII}$	quantum yield of PS II (actual PS II efficiency)	$\Phi_{\rm PSII} = (F_{\rm m}' - F_{\rm s})/F_{\rm m}'$
$q_{\rm P}$	photochemical quenching	$q_p = (F_m' - F_s)/(F_m' - F_0')$
q <sub>N</sub>	non-photochemical quenching	$q_N = (F_m - F_m')/(F_m - F_0)$
ETR	electron transport rate	$ETR = \Phi_{PS II} \times PFDa \times 0.5$

Table 1: Summary of Chl fluorescence outputs parameters with general descriptions and where applicable, mathematical expressions

	Table 2: ANOVA results of salt	(NaCl: Na <sub>2</sub> SO <sub>4</sub> ) and alkal	i (NaHCO3: Na2CO3	(a) treatments on chloroph	yll fluorescence p	arameters
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Parameters	F <sub>0</sub>	F <sub>m</sub>	$F_v/F_m$	F <sub>0</sub> ′	F <sub>m</sub> ′	Fs	$F_v'/F_m'$	$\Phi_{ m PSII}$	ETR	qP	qN
Treatments	*	*	ns	*	**	**	**	*	***	**	**
Note: the meanings of chlorophyll fluorescence parameters refer to Table 1											

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Table 3: The major fluorescence parameters of wheat seedlings under salt (NaCl: Na<sub>2</sub>SO<sub>4</sub>) and alkali stresses (NaHCO<sub>3</sub>: Na<sub>2</sub>CO<sub>3</sub>)

Concentration (mn	nol/L)	F <sub>0</sub>	Fm	$F_v/F_m$	$F_0'$	F <sub>m</sub> '	Fs	$F_v'/F_m'$
control	0	73.38a	428.98a	0.83a	75.50a	213.98a	116.13a	0.64a
Salt	40	62.25b	367.35b	0.83a	68.85ab	210.20ab	103.05ab	0.67a
Stress	80	64.25ab	376.58b	0.83a	65.48ab	187.45abc	94.80bc	0.65a
	120	60.43b	363.95b	0.83a	58.65b	163.20c	85.08c	0.64a
Alkali	40	72.58a	429.60a	0.83a	69.33ab	188.60abc	103.15ab	0.63a
Stress	80	62.38b	367.30b	0.83a	61.95b	174.93bc	88.50bc	0.65a
	120	64.90ab	374.68b	0.83a	62.65b	152.35c	85.10c	0.59b

Notes: Difference letters showed the significant difference among different treatments (P < 5%)

reductions of  $g_s$  and E increased with increasing salinity, indicating the photosynthetic adaptation of wheat seedlings to both salt and alkali stresses.

It has been reported that decreased photosynthetic rate exposure to salt for long-term might be due to reduced  $g_s$ (Ouerghi et al. 2000). Stomatal closure (Abbruzzese et al. 2009; Shahbaz and Zia 2011; Ashraf and Ashraf 2012; Farooq et al. 2017) and non-stomatal factors (Ai-Abdoulhadi et al. 2012) could result in a lower  $C_i$  and then led to the reduction of  $P_{\rm N}$  under stress conditions, thereby causing reduction in growth. However,  $C_i$  of wheat seedlings increased when gs and  $P_{\rm N}$  decreased with increasing salinity, especially  $P_{\rm N}$  remarkable decreased only when salinity over 80 mmol/L in the present study (Fig. 2). The decreases of  $g_s$ and  $P_{\rm N}$  values with increasing of  $C_{\rm i}$ , suggesting that nonstomatal factor was dominant for inhibiting of photosynthesis (Yan *et al.* 2012). Thus,  $P_N$  were affected by both stomatal non-stomatal factors in salt and alkali stressed wheat seedlings.

PS II was the importance stage to fix  $CO_2$  in the photosynthetic process, which could be estimated by Chl fluorescence measurements. Chl fluorescence attributes were affected by salt stress in salt-sensitive genotypes (Atlassi *et al.* 2009; Baker and Rosenqvist 2004). Ashraf and Ashraf (2012) reported that salt stress declined the activity of PS II of wheat during all the growth stages. However, Perveen *et al.* (2013) hold a contrary opinion, which indicated most Chl fluorescence attributes of wheat remained unaffected under salt stress. In present study, both stress types affected Chl

fluorescence attributes significantly except of  $F_{\nu}/F_m$  (Table 2). Usually, Chl fluorescence was negatively correlated to photosynthesis. The concentration of CO<sub>2</sub> in leaves will increase going with the decreasing fluorescence intensity. Although  $F_m$  and  $F_m'$  decreased and  $C_i$  increased at saltalkali stress, there was no significant correlation between  $C_i$  and  $F_m$  (R<sup>2</sup>=0.34, P > 0.05),  $C_i$  and  $F_m'$  (R<sup>2</sup>=0.59, P > 0.05).

Some reports showed that  $F_{\nu}/F_{\rm m}$  wasn't affected in tolerant plant cultivars, such as wheat (Zair et al. 2003), rice (Dionisio-Sese and Tobita 2000), sorghum varieties (Netondo et al. 2004) and maize (Shabala et al. 1998). When compared NaCl and NaHCO3 effects on tomato, the ratio of  $F_{\nu}/F_m$  declined with increasing levels and the reduction was more significant in later (Gong et al. 2013). There, no photoinhibition happening in present wheat seedlings under salt stress. Our experimental material (Jimai 3) was a salttolerant line of wheat varieties. Higher Fv'/Fm' was beneficial to improve the transformed efficacy of light energy in plants, accelerating the carbon assimilation and organic solutes accumulation (Baker and Rosenqvist 2004). Wheat seedlings under both stresses could keep the similar Fv'/Fm' value with controls in most stress concentration except of the highest alkalinity, proved the maintain mechanisms of wheat seedlings under stresses and higher tolerance.

Plants had developed certain photo-protective mechanisms to dissipate excess excitation energy which protected the photosynthetic apparatus to avoid photodamaging PS II (Qiu *et al.* 2003).  $q_P$  in leaves are the most sensitive photosynthetic characteristics for measuring salinity tolerance in maize (Shabala *et al.* 1998). In wheat seedlings,  $q_P$  didn't decreased even increased significantly at some salinity. Both  $\varphi$ PS II and  $q_P$  increased at lower concentrations of saline stress and  $P_N$  maintain a stable value as the same as control. This result proved that higher  $\varphi$ PS II and  $q_P$  value could accelerate the photosynthetic activity, which may be the adaptation of wheat to salt stress.

Stepien and Johnson (2009) concluded that increasing salinity resulted in a substantial increase in nonphotochemical quenching (NPQ) in Arabidopsis thaliana. Moradi and Ismail (2007) reported no significant difference in quantum yields of PS II ( $\Phi_{PS II}$ ) were observed with increasing salinity levels at vegetative stages in rice, but NPQ increased significantly. The NPO increase is suggested to occur of photo-protection to dissipate excess excitation energy (Demmig-Adams and Adams 1992; Yan et al. 2012), in which a higher proportion of absorbed photons are lost as thermal energy instead of being used to drive photosynthesis (Shangguan et al. 2000). In the wheat seedlings of present research,  $\Phi_{PS II}$  was not affected but non-photochemical quenching  $(q_N, similar like NPQ)$  increased significantly at the highest salinity under alkali stress (Fig. 3). High pH from alkali stress may have caused a series of harmful effects including destruction of photosynthetic machinery and primary electron acceptors, weakening PS II activity, and a reduction in the photochemical reaction. This resulted in plants being exposed to photo-inhibition, which then activated photo-protection by increasing NPQ (Liu and Shi 2010). It was concluded that the photo-protection caused by photoinhibition would happen depending on high pH and salinity. Under such conditions, increasing  $q_N$  could play a key role in excess energy dissipation to keep photosynthetic machinery from being destroyed.

#### Conclusion

Although shoot biomass of wheat seedling decreased significantly under both salt and alkali stresses, the photosynthetic performance response mechanisms were quite different between them. The inhibition of  $P_N$  was related to stomatal and non-stomatal factors under both stresses. According to the Chl fluorescence parameters, Jimai 3 was a kind of tolerant line wheat for some extent of salinity and alkalinity. There was no photo-inhibition observed under salt stress. Photo-protection caused by photo-inhibition happened at the highest level of alkali stress, depending on high pH and salinity. Based on Chl fluorescence parameters, Photosystem II response of wheat seedlings to salt and alkali stresses was different.

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#### References

- Abbruzzese G, I Beritognolo, R Muleo, M Piazzai, M Sabatti, GS Mugnozza, E Kuzminsky (2009). Leaf morphological plasticity and stomatal conductance in three *Populus alba* L. genotypes subjected to salt stress. *Environ Exp Bot* 66:381–388
- Ai-Abdoulhadi IA, HA Dinar, G Ebert, C Büttner (2012). Influence of salinity stress on photosynthesis and chlorophyll content in date palm. *Afr J Agric Res* 7:3314–3319
- Ashraf MA, M Ashraf (2012). Salt-induced variation in some potential physiochemical attribute of two genetically diverse spring wheat (*Triticum aestivum* L.) cultivars: photosynthesis and photosystem II efficiency. *Pak J Bot* 44:53–64
- Atlassi PV, M Nabipour, M Meskarbashee (2009). Effect of salt stress on chlorophyll content, Fluorescence, Na<sup>+</sup> and K<sup>+</sup> ions content in Rape plants (*Brassica napus* L.). Asian J Agric Res 3:28–37
- Baker NR, E Rosenqvist (2004). Applications of chlorophyll fluorescence can improve crop production strategies: an examination of future possibilities. *J Exp Bot* 55:1607–1621
- Benlloch-González M, O Arquero, JM Fournier, D Barranco, M Benlloch (2008). "K<sup>+</sup> starvation inhibits water-stress-induced stomatal closure. *J Plant Physiol* 165:623–630
- Brugnoli E, O Björkman (1992). Growth of cotton under continuous salinity stress: influence on allocation pattern, stomatal and non-stomatal components of photosynthesis and dissipation of excess light energy. *Planta* 187:335–345
- Clark H, PCD Newton, DJ Barker (1999). Physiological and morphological responses to elevated CO<sub>2</sub> and a soil moisture deficit of temperate pasture species growing in an established plant community. J Exp Bot 50:233–242
- De-Lucena CC, DL De-Siqueira, HEP Martinez, PR Cecon (2012). Salt stress change chlorophyll fluorescence in mango. *Rev Bras Fruticult* 34:1245–1255
- Demmig-Adams B, WW Adams (1992). Photoprotection and other responses of plants to high light stress. Annu Rev Plant Physiol Plant Mol Biol 43:599–626
- Deng W, SW Qiu, ZW Liang (2006). Background of regional ecoenvironment in Da'an sodic land experiment station of China. Science Press, Beijing, China
- Dionisio-Sese ML, S Tobita (2000). Effects of salinity on sodium content and photosynthetic responses of rice seedlings differing in salt tolerance. J Plant Physiol 157:54–58
- Ehsanzadeh P, MS Nekoonam, JN Azhar, H Pourhadian, S Shaydaee (2009). Growth, chlorophyll, and cation concentration of tetraploid wheat on a solution high in sodium chloride salt: Hulled versus free-threshing genotypes. J Plant Nutr 32:58–70
- Farooq M, N Gogoi, M Hussain, S Barthakur, S Paul, N Bharadwaj, HM Migdadi, SS Alghamdi, KHM Siddique (2017). Effects, tolerance mechanisms and management of salt stress in grain legumes. *Plant Physiol Biochem* 118:199–217
- Farooq M, M Hussain, A Wakeel, KHM Siddique (2015). Salt stress in maize: effects, resistance mechanisms and management. A review. Agron Sustain Dev 35:461–481
- Gong B, D Wen, K VandenLangenberg, M Wei, FJ Yang, QH Shi, XF Wang (2013). Comparative effects of NaCl and NaHCO<sub>3</sub> stress on photosynthetic parameters, nutrient metablism, and the antioxidant system in tomato leaves. *Sci Hortic* 157:1–12
- Guo R, LX Shi, YF Yang (2009). Germination, growth, osmotic and adjustment and ionic balance of wheat in response to saline and alkaline stresses. *Soil Sci Plant Nutr* 6:1747–1765
- Heidari M, F Mesri (2008). Salinity effects on compatible solutes, antioxidants enzymes and ion content in three wheat cultivars. *Pak J Biol Sci* 11:1385–1389
- Krall JP, GE Edwards (1991). Environmental effects on the relationship between quantum yield of carbon assimilation and *in vivo* PS II electron transport in maize. *Aust J Plant Physiol* 18:267–278

- Läuchli A, U Lüttge (2002). Salinity in the soil environment. In: Salinity: Environment-Plants-Molecules, pp: 21–23. Tanji KK (Ed.). Kluwer Academic Publishers, Boston, Massachusetts, USA
- Li XY, CS Mu, JX Lin, Y Wang, XJ Li (2014). Effect of alkaline potassium and sodium salts on growth, photosynthesis, ions absorption and solutes synthesis of wheat seedlings. *Exp Agric* 50:144–157
- Li XY, JJ Liu, YT Zhang, JX Lin, CS Mu (2009). Physiological responses and adaptive strategies of wheat seedlings to salt and alkali stresses. *Soil Sci Plant Nutr* 55:680–684
- Liu J, DC Shi (2010). Photosynthesis, chlorophyll fluorescence, inorganic ion and organic acid accumulations of sunflower in responses to salt and salt-alkaline mixed stress. *Photosynthetica* 48:127–134
- Méthy M, D Gillon, C Houssard (1997). Temperature-induced changes of photosystem II activity in *Quercus ilex* and *Pinus halepensis*. Can J For Res 27:31–38
- Moradi F, AM Ismail (2007). Responses of Photosynthesis, Chlorophyll Fluorescence and ROS-Scavenging Systems to Salt Stress During Seedling and Reproductive Stages in Rice. Ann Bot 99:1161–1173
- Nadeem MK, SJ Rasool, M Ikram, A Jahanzab, MF Maqbool, H Ahmad, R Habib (2018). Management of wheat production in saline soils through multi-strain bacterial inoculation. J Glob Innov Agric Soc Sci 6:135–142
- Netondo GW, JC Onyanqo, E Beck (2004). Sorghum and salinity: II. Gas exchange and chlorophyll fluorescence of sorghum under salt stress. *Crop Sci* 44:797–805
- Ouerghi ZG, M Roudani, A Ayadi, J Brulfert (2000). Effect of NaCl on Photosynthesis of Two Wheat Species (*Triticum durum* and *T. aestivum*) Differing in Their Sensitivity to Salt Stress. J Plant Physiol 156:335–340
- Perveen S, M Shahbaz, M Ashraf (2013). Influence of foliar-applied triacontanol on growth, gas exchange characteristics, and chlorophyll fluorescence at different growth stages in wheat under saline conditions. *Photosynthetica* 51:541–551
- Qiu NW, QT Lu, CM Lu (2003). Photosynthesis, photosystem II efficiency and the xanthophyll cycle in the salt-adapted halophyte Atriplex centralasiatica. New Phytol 159:479–486
- Ruan YF, SE El-Hendawy, YC Hu, U Schmidhalter (2007). Differential effect of moderate salinity on growth and ion contents in the main stem and subtillers of two wheat genotypes. *Soil Sci Plant Nutr* 53:782–791

- Shabala SN, SI Shabala, AI Martynenko, O Babourina, IA Newman, (1998). Salinity effect on bioelectric activity, growth, Na<sup>+</sup> accumulation and chlorophyll fluorescence of maize leaves: a comparative survey and prospects for screening. *Aust J Plant Physiol* 25:609–616
- Shahbaz M, B Zia (2011). Does exogenous application of glycine-betaine through rooting medium alter rice (*Oryza sativa* L.) mineral nutrient status under saline conditions? J Appl Bot Food Qual 84:54–60
- Shangguan Z, M Shao, J Dyckmans (2000). Effects of nitrogen nutrition and water deficit on net photosynthetic rate and chlorophyll fluorescence in winter wheat. J Plant Physiol 156:46–51
- Siebke K, SV Caemmerer, M Badger, RT Furbank (1997). Expressing an RbcS antisense gene in transgenic *Flaveria bidentis* leads to an increased quantum requirement for CO<sub>2</sub> fixed in photosystems I and II. *Plant Physiol* 105:1163–1174
- Stepien P, NG Johnson (2009). Contrasting responses of photosynthesis to salt stress in the glycophyte arabidopsis and the halophyte thellungiella: Role of the plastid terminal oxidase as an alternative electron sink. *Plant Physiol* 149:1154–1165
- Yan H, X Hu, F Li (2012). Leaf photosynthesis, chlorophyll fluorescence, ion content and free amino acids in *Caragana korshinskii* Kom exposed to NaCl stress. *Acta Physiol Plantarum* 34:2285–2295
- Zair I, A Chlyah, K Sabounji, M Tittahsen, H Chlyah (2003). Salt tolerance improvement in some wheat cultivars after application of *in vitro* selection pressure. *Plant Cell Tiss Org Cult* 73:237–244
- Zhang JT, CS Mu (2009). Effects of saline and alkaline stresses on the germination, growth, photosynthesis, ionic balance and anti-oxidant system in an alkali-tolerant leguminous forage *Lathyrus quinquenervius. Soil Sci Plant Nutr* 55:685–697
- Zhao GQ, BL Ma, CZ Ren (2007). Growth, gas exchange, chlorophy II fluorescence, and ion content of naked oat in response to salinity. *Crop* Sci 47:123–131
- Zribi L, G Fatma, R Fatma, R Salwa, N Hassan, RM Nejib (2009). Application of chlorophyll fluorescence for the diagnosis of salt stress in tomato "Solanum lycopersicum (variety Rio Grande)". Sci Hortic 120:367–372