# Seed germination, seedling survival, and physiological response of sunflowers under saline and alkaline conditions

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## Abstract

Salinization and alkalization of soil are widespread environmental problem and the alkali stress is more destructive than the effects caused by salt stress. To compare the mechanism of salt and alkali stresses, a sunflower variety (*Helianthus annuus* L. cv. Baikuiza 6) was tested under saline or alkaline conditions by mixing two neutral salts (NaCl and $Na_2SO_4$) or two alkaline salts ($NaHCO_3$ and $Na_2CO_3$). The results showed that saline conditions differed greatly from alkaline conditions in their threshold intensities where sunflower can germinate, survive and grow. Under saline conditions, the emergence time was delayed, and the emergence rate and seedling survival rate also decreased with increasing salinity. However, under alkaline conditions, the rate of seedling survival decreased sharply but the emergence time and emergence rate did not change. In addition, the damaging effects of alkali stress on growth and photosynthesis were more severe than those of saline. In shoots, the main inorganic osmolyte and cation was $K^+$ rather than $Na^+$; the primary organic osmolytes were organic acid and soluble sugar rather than proline. Organic acid, $NO_3^-$, and $Cl^-$ (only under saline condition) were the main source of anion. In addition, the osmotic adjustment and ion balance differed among sunflower roots, stems, and leaves. In conclusion, saline and alkaline conditions are two different stress conditions and there are special responses to two stress conditions for sunflower.

*Additional key words*: alkali stress; ionic balance; osmotic adjustment; salt stress.

## Introduction

Alkalization and salinization of soils have become global environmental problems and are important factors limiting agricultural productivity. Alkali stress has been clearly demonstrated as more severe than salt stress in a number of reports (Shi and Yin 1992, 1993, El-Samad and Shaddad 1996, Campbell and Nishio 2000, Shi *et al*. 2002, Shi and Sheng 2005, Shi and Wang 2005, Ma *et al*. 2007, Yang *et al*. 2007b, 2008a,d; Liu *et al*. 2008). When a saline soil contains $HCO_3^-$ and/or $CO_3^{2-}$, which elevate soil pH, plants experience damages from both salt and alkali stresses.

Salt stress in soil generally involves osmotic stress and ion-induced injury (Munns 2002); alkali stress exerts the same stress factors but with the added influence of high-pH stress (Shi and Yin 1993). The high-pH environment that surrounds the roots can cause metal ions and phosphorus to precipitate (Shi and Zhao 1997), greatly affect absorption of inorganic ions such as $Na^+$, $K^+$, $Cl^-$, $NO_3^-$, and $H_2PO_4^-$, and disrupt ionic balance and pH homeostasis in tissues (Yang *et al*. 2007b, 2008c). Thus, plants in alkaline soil must cope with both physiological drought and ion toxicity, and also maintain intracellular ionic balance.

Seed germination and seedling growth are two different growth stages. Different environmental conditions impact on seed germination and seedling growth and their adaptation to the environment may be different. The adaptability of plants to salt and alkali stresses not only depends on species (Katerji *et al*. 2000, 2001) but also on a reproductive stage. Generally, the tolerance of seedlings to salt and alkali stresses is lower than that of germinating seeds (Xie *et al*. 2000, Demir *et al*. 2003). It is a crucial stage that from seed germination to fully developed seedling and limit species distribution under saline and alkaline conditions. Therefore, the study not only has theoretical significance in physiological ecology, but also has a practical significance for crop production.

There are numerous reports on photosynthetic characteristics under salt stress (Qiu *et al*. 2003, Koyro *et al*. 2006, Wei *et al*. 2006). Generally, photosynthesis is

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*Abbreviations*: $C_i$ – intercellular $CO_2$ concentration; $E$ – transpiration rate; $g_s$ – stomatal conductance; $P_N$ – net photosynthetic rate.
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inhibited by salt stress (Ma *et al*. 1997, Sultana *et al*. 1999, Qiu *et al*. 2003, Koyro *et al*. 2006). Salt stress also affects photosynthetic components (Ma *et al*. 1997, Qiu *et al*. 2003) and chloroplast ultrastructure (Fidalgo *et al*. 2004). However, there are few reports on the effects of alkali stress on photosynthesis.

Sunflower is one of the salt-tolerant crops (Zhang *et al*. 2003), with cultivars that can be grown in saline areas. In spite of this, relatively little attention has been paid to physiological mechanisms of sunflower response to salt- and alkali stresses (Shi and Sheng 2005). In this paper, various saline or alkaline conditions were simulated initially in plastic pots before sowing seeds which was closer to natural conditions. The response characteristics of sunflower to saline or alkaline conditions and its physiological adaptive characteristics from germination to the seedling stage were investigated. The aim was to provide scientific basis for breeding, salt-tolerant species promotion and guide sunflower production in salt–alkaline soil areas.

## Materials and methods

**Plant materials**: A sunflower (*Helianthus annuus* L.) variety Baikuiza No. 6 was selected as experimental material due to its tolerance to saline–alkaline conditions. The seeds were provided by the Sunflower Institute, Jilin Province, China. All pots containing plants were placed outdoors and protected from the rain throughout the experiment. Temperatures during the experiment were 24–28°C during the day and 17–20°C at night. The relative humidity was 50–60% and plants were subjected to natural irradiation.

**Formation of saline and alkaline conditions**: Thirty three 24-cm-diameter plastic pots were filled with washed sand. Before sowing, the control pots were thoroughly watered with 1,000 ml of nutrient solution per pot, in three portions, and the saline and alkaline pots with treatment solution, namely the nutrient solution containing the corresponding stress salts. In the present study, according to the salt components in the extant salt-alkaline soil of northeast China (Ge and Li 1990) and the tolerance of sunflowers, two neutral (NaCl and $Na_2SO_4$) or alkaline ($NaHCO_3$ and $Na_2CO_3$) salts mixed in molar ratios of 9:1 were used to prepare saline and alkaline treatment solutions, respectively. Based on a preliminary experiment, saline treatments consisted of five concentrations (40, 80, 120, 160, and 200 mM), and alkaline treatments also consisted of five concentrations (10, 20, 30, 40, and 50 mM). The pH of treatment solutions was 6.51, 6.52, 6.53, 6.55, and 6.57 for salt stress and 7.58, 8.16, 8.21, 8.51, and 9.01 for alkali stress, respectively.

After saline and alkaline treatments, seeds were sown equidistantly in six holes per pot and two seeds per hole (the germination rate of seeds is 99% above in distilled water). Each pot was considered one replicate, and each treatment had three replicates. After sowing, the pots were watered using the method above at around 17:00–18:00 h every 3 d. Each hole contained one seedling finally.

**Seedling emergence and survival monitoring**: After sowing, seedling emergence was recorded daily. It is defined as emergence when cotyledons were completely exposed, and the time was recorded. Germination rate was calculated from the number of seedlings and sown seeds. Seedling survival was defined as when a seedling remained alive and growing two weeks after emergence. Seedling survival rate was calculated according to the numbers of seedlings and surviving seedlings.

**Physiological indices measurements**: Net photosynthetic rates ($P_N$), stomatal conductance ($g_s$), intercellular $CO_2$ concentration ($C_i$) and transpiration rates ($E$) of leaves were determined during 8:30–10:30 h on fully expanded first blades, using a portable open-flow, gas-exchange system (*LI-6400*; *LICOR Biosciences*, Lincoln, USA) on the day before harvest. The respective results were expressed as μmol($CO_2$) $m^{-2}$ $s^{-1}$, mol($H_2O$) $m^{-2}$ $s^{-1}$, μmol($CO_2$) $mol^{-1}$ and mmol($H_2O$) $m^{-2}$ $s^{-1}$. The photosynthetically active radiation was 1,000 μmol $m^{-2}$ $s^{-1}$ (saturation light). The ambient $CO_2$ concentration was 360 ± 10 μmol $mol^{-1}$, the air temperature and humidity were about 24°C and 50%. Measurements were repeated five times for each blade, for five blades per pot, and the averages recorded.

All plants were harvested during the morning, 31 d after sowing and were first washed with tap water followed by distilled water. Roots, stems and leaves were separated per pot. At the same time, the leaf area of the first blades was determined by *1671-VHA* leaf area instrument. Then samples were oven-dried at 80°C for 15 min, vacuum-dried at 40°C to a constant mass and dry mass recorded.

Dry samples of plant material (100 mg) were treated with 10 ml of deionized water at 100°C for 60 min and the extract used to determine $Cl^-$, $SO_4^{2-}$, $NO_3^-$, and $H_2PO_4^-$ concentrations by ion chromatography (*DX-300* ion chromatographic system, *AS4A-SC* chromatographic column, *CDM-II* electrical conductivity detector, mobile phase: $Na_2CO_3/NaHCO_3$ = 1.7/1.8 mM; *DIONEX*, Sunnyvale, CA, USA). A flame photometer was used to determine $Na^+$ and $K^+$ concentrations (Wang and Zhao 1995), and complexometric titration to determine $Ca^{2+}$ and $Mg^{2+}$concentrations (Bao 1981).

The concentrations of proline and total soluble sugars were measured, respectively, using ninhydrin and anthrone (Zhu *et al*. 1983); the concentrations of organic acids were measured using the complexometric titration method (Jing and Ding 1981).

**Statistical analysis**: All experiments were based on three replicates. Data were analyzed by one-way analysis of variance (*ANOVA*) using the statistical software *SPSS 14.0* (*SPSS Inc*., Chicago, USA). The treatment mean values were compared by post hoc least significant difference (LSD) test. The term significant indicates differences for which $P \leq 0.05$.

## Results

**Emergence**: The emergence time was delayed, but the emergence rate and seedling survival rate did not decrease significantly for the first three treatments under saline conditions. For the remaining two treatments, not only was the emergence time significantly delayed, but the emergence rate and seedling survival rate also decreased significantly. Under alkaline conditions, the emergence rate did not change, but the emergence time delayed and the seedling survival rate decreased sharply with increasing alkalinity (Fig. 1*A–C*).

**Growth**: The dry mass of leaves, stems, and roots was decreased with increasing stress intensity, with the reductions under alkaline conditions greater than under saline conditions (Fig. 1*D–F*).

**Photosynthetic indices**: With increasing stress intensity, $P_N$, $g_s$, $C_i$, $E$, and leaf area all decreased under both saline and alkaline conditions, with greater reductions under alkaline conditions (Fig. 1*G–K*).

**Inorganic ions**

**Cations**: Under saline conditions, free $Mg^{2+}$ concentrations of leaves remained unchanged among treatments, but lower than controls. However, under alkaline conditions, free $Mg^{2+}$ concentrations were higher than controls except for the first treatment, and the concentrations increased with increasing alkalinity (Fig. 2*A*). Under saline conditions, free $Mg^{2+}$ concentrations of stems also remained unchanged; only at the 200 mM, the concentrations decreased sharply. Under alkaline conditions, when stress intensity < 30 mM, free $Mg^{2+}$ concentrations were significantly higher than control; however, when stress intensity increased, the concentrations were significantly lower than control (Fig. 2*B*). Under both saline and alkaline conditions, free $Mg^{2+}$ concentrations of roots increased with increasing stress intensity (Fig. 2*C*).

Free $Ca^{2+}$ concentrations of leaves did not significantly change under saline conditions, but under alkaline conditions they varied in a single-peak curve with increasing alkalinity; the value of free $Ca^{2+}$ was highest at 20 mM (Fig. 2*D*). With increasing stress intensity, free $Ca^{2+}$ concentrations of stems decreased, with greater reductions under alkaline than under saline conditions (Fig. 2*E*). However, under saline conditions, free $Ca^{2+}$ concentrations of roots did not increase with increasing salinity; the concentrations increased dramatically with increasing alkalinity under alkaline conditions (Fig. 2*F*).

With increasing salinity or alkalinity, $K^+$ concentrations in roots decreased, with reductions under alkaline conditions greater than under saline conditions (Fig. 2*I*). Opposite, the $K^+$ concentrations in leaves and stems increased with increasing salinity or alkalinity, and increment under alkaline conditions greater than under saline conditions (Fig. 2*G,H*). $Na^+$ concentrations in leaves, stems and roots increased with increasing salinity or alkalinity, and the increases were significantly higher under alkaline than saline conditions (Fig. 2*J–L*).

**Anions**: Under saline conditions, $Cl^-$ concentrations increased with increasing salinity; but under alkaline conditions, $Cl^-$ concentrations increased slowly (Fig. 3*A–C*). With increasing salinity, $NO_3^-$ concentrations in leaves, stems and roots decreased. However, with increasing alkalinity, $NO_3^-$ concentrations in leaves decreased, and varied in a single-peak curve in stems with the highest value at 20 mM. At 50 mM, $NO_3^-$ concentrations in roots increased sharply under alkaline conditions (Fig. 3*D–F*). he $SO_4^{2-}$ concentrations in leaves, stems, and roots all increased quickly under alkaline conditions (Fig. 3*G–I*); but under saline condition there were different trends, $SO_4^{2-}$ in leaves did not significantly change (Fig. 3*G*); $SO_4^{2-}$ in stems increased only at 200 mM and $SO_4^{2-}$ in roots increased with increasing salinity (Fig. 3*H,I*). The $PO_4^{3-}$ concentrations in leaves, stems, and roots all increased with increasing salinity. However, under alkaline conditions, the $PO_4^{3-}$ concentrations in leaves, stems and roots all dropped to similar values, and then raised abruptly at 50 mM (Fig. 3*J–L*).

**Organic solutes**: Under saline conditions, proline concentrations increased with increasing salinity. Under alkaline conditions, proline concentrations increased slightly with increasing intensity, but only at 50 mM proline concentrations increased sharply (Fig. 4*A–C*). Soluble sugars concentrations of leaves and roots increased with increasing salinity and alkalinity, with the increases higher under alkaline conditions (Fig. 4*D,F*). Soluble sugars concentrations of stems also increased with increasing salinity, but decreased with increased alkalinity (Fig. 4*E*). Organic acids concentrations of leaves, stems and roots increased with increasing intensity of both stress conditions; however, only at 40 mM organic acids concentrations were higher than control under alkaline conditions (Fig. 4*G–I*).

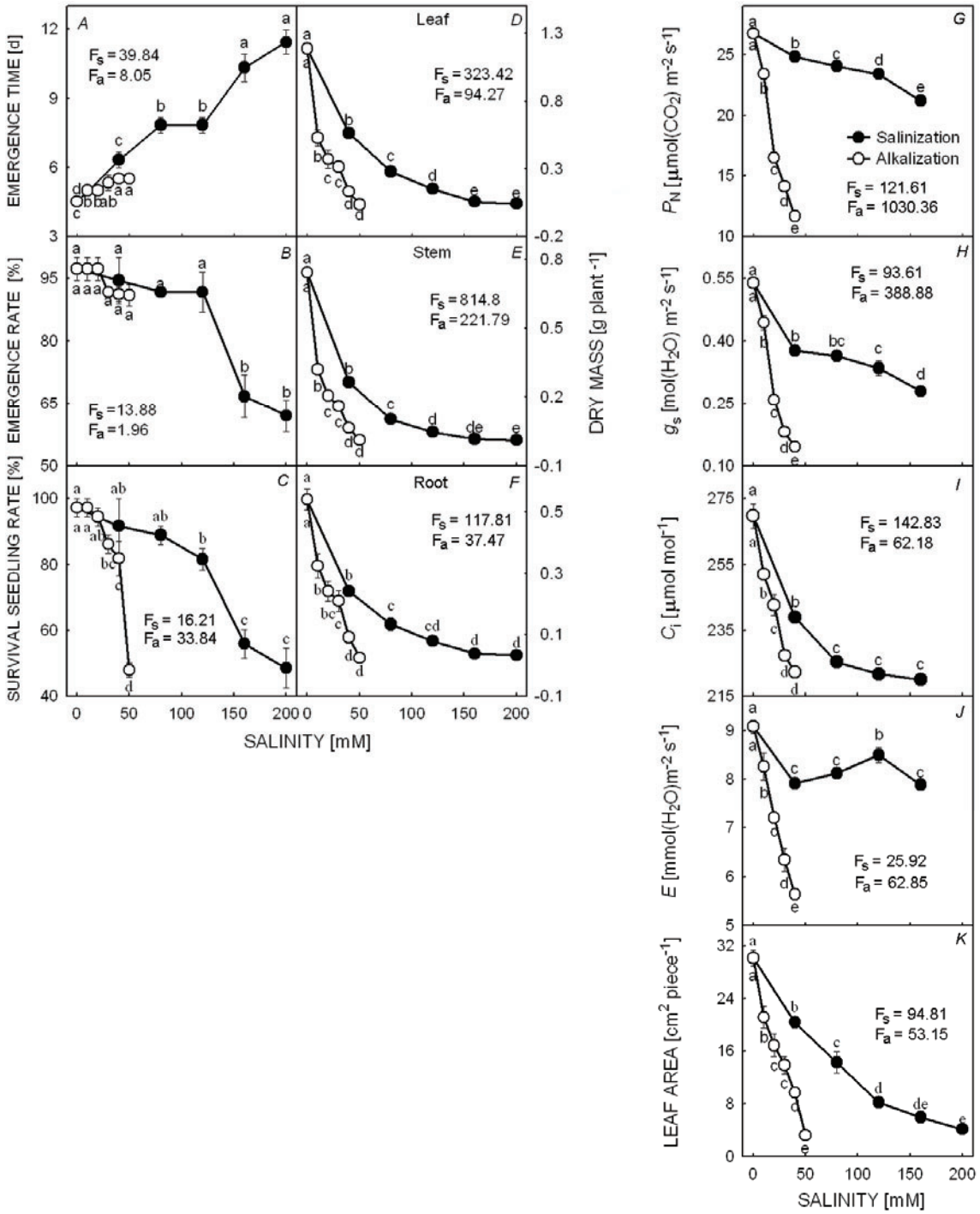


Fig. 1. Effects of saline and alkaline conditions on emergence time (*A*), emergence rate (*B*) and survival seedlings rate (*C*), dry mass of leaves (*D*), stems (*E*) and roots (*F*), net photosynthetic rate ($P_N$) (*G*), stomatal conductance ($g_s$) (*H*), intercellular $CO_2$ concentration ($C_i$) (*I*), transpiration rate (*E*) (*J*) and leaf area (*K*) of sunflowers. Sunflowers were treated with salt ($NaCl:Na_2SO_4$ = 9:1; 40–200 mM; pH 6.51–6.57) and alkali ($NaHCO_3:Na_2CO_3$ = 9:1; 10–50 mM; pH 7.58–9.01) stresses. Means (±S.E.) of three replicates. Different letters represent significant differences at the 5% level among the various concentration treatments of saline conditions or alkaline conditions, according to least significant difference (LSD) test. $F_a$ – F value for alkaline; $F_s$ – F value for saline.

## Discussion

**Seed germination and seedling survival**: The speed of seed germination depends on the speed of water absorption. At solute concentration < 0.4 M, seeds can very slowly absorb water from the solution (Ye and Liu 1994), thereby the emergence time was delayed (Fig. 1*A*). In this paper, the emergence time was delayed but the emergence rate and seedling survival rate were not significantly different among the first three saline conditions. When salinity increased the emergence time, the emergence rate and the seedling survival rate decreased significantly. It could be that salinity slowed the speed of water absorption and made cell membrane repair difficult during imbibitions and even aggravated the damage to membrane structure, leading to exudation of solutes from seed (Yang *et al*. 2007b) and even entry of toxic ions (*e.g*. $Na^+$). With increasing salinity and time, the damage became more obvious, and finally impacted on seed germination and seedling survival.

In the present study, the emergence time and the emergence rate did not change significantly under alkaline conditions; possibly the low alkaline salt concentration did not interfere with seed water absorption. However, with increased alkalinity, seedling survival rate decreased sharply. This phenomenon showed that high pH was a major factor limiting the seedling survival. When alkalinity was low, although high pH did not interfere with seed water absorption (Liu *et al*. 2008), radicel which broke through seed coat was injured markedly by alkaline salts, and thus seeds could germinate but would have difficulty forming normal seedlings that could survive.

**Growth**: Accumulated dry matter and leaf area are ideal indicators of sunflower growth. In this study, although dry matter accumulation and leaf expansion of sunflowers were inhibited under both saline and alkaline conditions, alkalinity was more severe (Fig. 1). This disparity between salinity and alkalinity increased with time. The reason that the effects of alkaline conditions on sunflower are more severe than the saline ones is closely related to the mechanisms of their action. Salinity generally involves osmotic stress and ion-induced injury (Munns 2002), whereas alkalinity exerts the same stress factors but with the added influence of high pH (Shi and Yin 1993). Many of the test data show high pH as a key factor in limiting plant growth and development under alkaline conditions (Yang *et al*. 2007b, 2008a,c; 2009). High pH clearly affects plant growth differently at various developmental stages. There was no obvious effect on seed germination, however, once germinated, it was a limiting factor to seedling growth and development. The high-pH environment surrounding the roots can seriously reduce mineral nutrition and oxygen supply around roots, and also directly damage root cell structure and function, resulting in ion imbalance (Thompson *et al*. 2007). This study showed that increasing alkalinity reduced seedling survival rate sharply and inhibited growth. These phenomena may result from nutritional damage, ion imbalance, and metabolic disorders caused by alkali stress (Li *et al*. 2009, Yang *et al*. 2009). The inhibition of plant growth was more serious under alkaline than saline conditions. Plant survival under alkaline conditions depends on the ability to cope with water stress and ion toxicity, and also resistance to high pH. Therefore, plants need to consume more energy and materials to adapt to alkaline conditions, than to adapt to saline conditions.

**Photosynthetic indices**: $P_N$ of plants usually decreases with increasing stress (Sultana *et al*. 1999, Koyro *et al*. 2006, Wei *et al*. 2006). In the present study, increasing stress intensity led to marked reduction in $P_N$ under alkaline compared to saline conditions (Fig. 1*G*). This phenomenon not only implied that saline and alkaline conditions are distinct stresses, but also revealed that the resistance of sunflower to saline conditions was stronger than to alkaline ones. Reduced plant $P_N$ values under higher salt stress are generally considered a result of either reduced intracellular $CO_2$ partial pressure caused by stomatal closure or nonstomatal factors (Bethke and Drew 1992). The nonstomatal factors mainly depend on the cumulative effects of leaf water potential and osmotic potential, biochemical constituents (Sultana *et al*. 1999), contents of photosynthetic pigments (Ma *et al*. 1997, Koyro *et al*. 2006), ion toxicities in the cytosol (James *et al*. 2006), and others. The $g_s$ and $E$ are closely correlated with changes in surrounding environment water potential under salt stress (Sultana *et al*. 1999, Koyro *et al*. 2006). Under saline and alkaline conditions, $g_s$ and $E$ of sunflower decreased with increasing stress intensity. This phenomenon showed that the changes of $g_s$ and $E$ of sunflower might be a response to decreased environment water potential. However, with increasing stress intensity, $g_s$ and $E$ were more reduced under alkaline than under saline conditions (Fig. 1*H,J*); this may be related to physiological drought that was caused by the reduction of water uptake by roots, which should be further investigated. High pH caused by alkaline conditions may seriously affect stomatal opening and closing and gas exchange. In addition, under the same stress intensity, leaf area was markedly smaller under alkaline than under saline conditions. Leaf area of sunflower directly affects photosynthetic production (Yang *et al*. 2008b), thereby affecting growth and metabolism (Sheng *et al*. 1999).

**Osmotic adjustment and ion balance**: The results showed that $K^+$ was the main inorganic osmolyte of sunflower under saline and alkaline conditions. This is different to other plants, such as wheat (Yang *et al*. 2008a, 2009). Usually $Na^+$ concentrations are obviously higher than $K^+$ concentrations in the plants under salt-

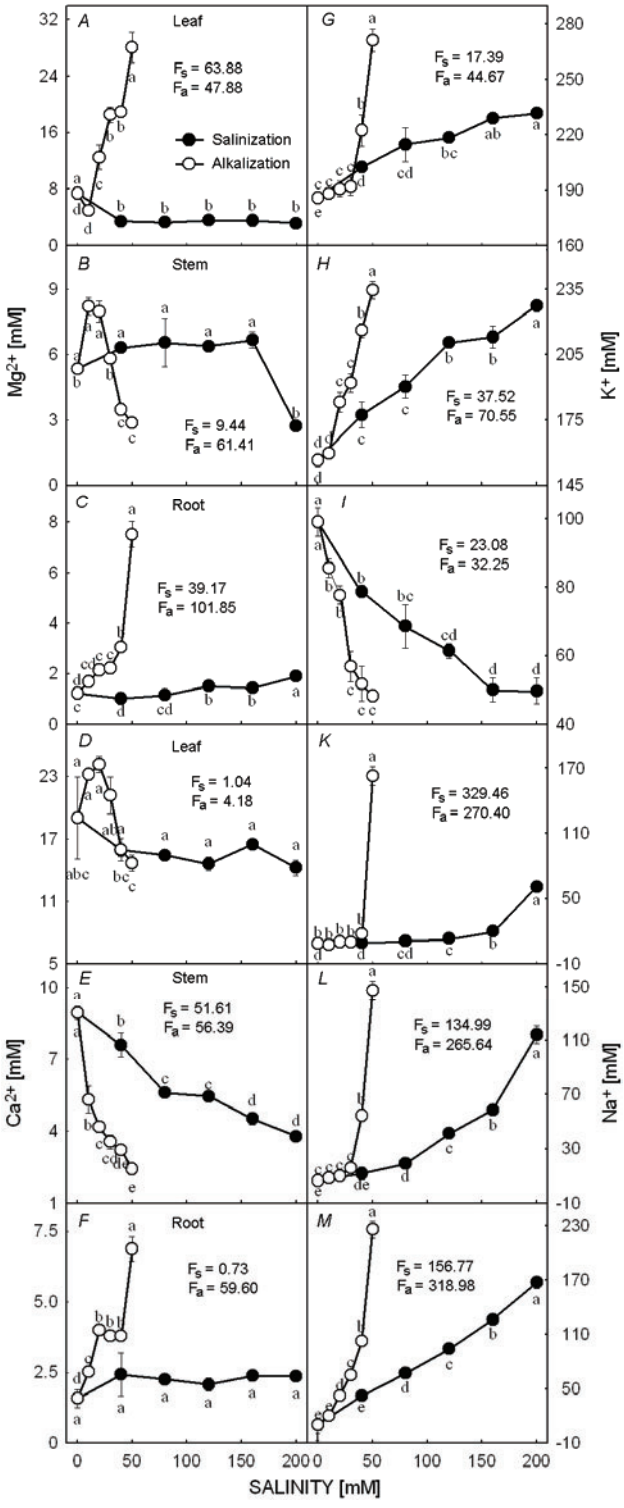


Fig. 2. Effects of saline and alkaline conditions on $Mg^{2+}$ (*A–C*), $Ca^{2+}$ (*D–F*), $K^+$ (*G–I*) and $Na^+$ (*J–L*) concentrations on leaves, stems and roots of sunflowers. Legend refers to Fig. 1.

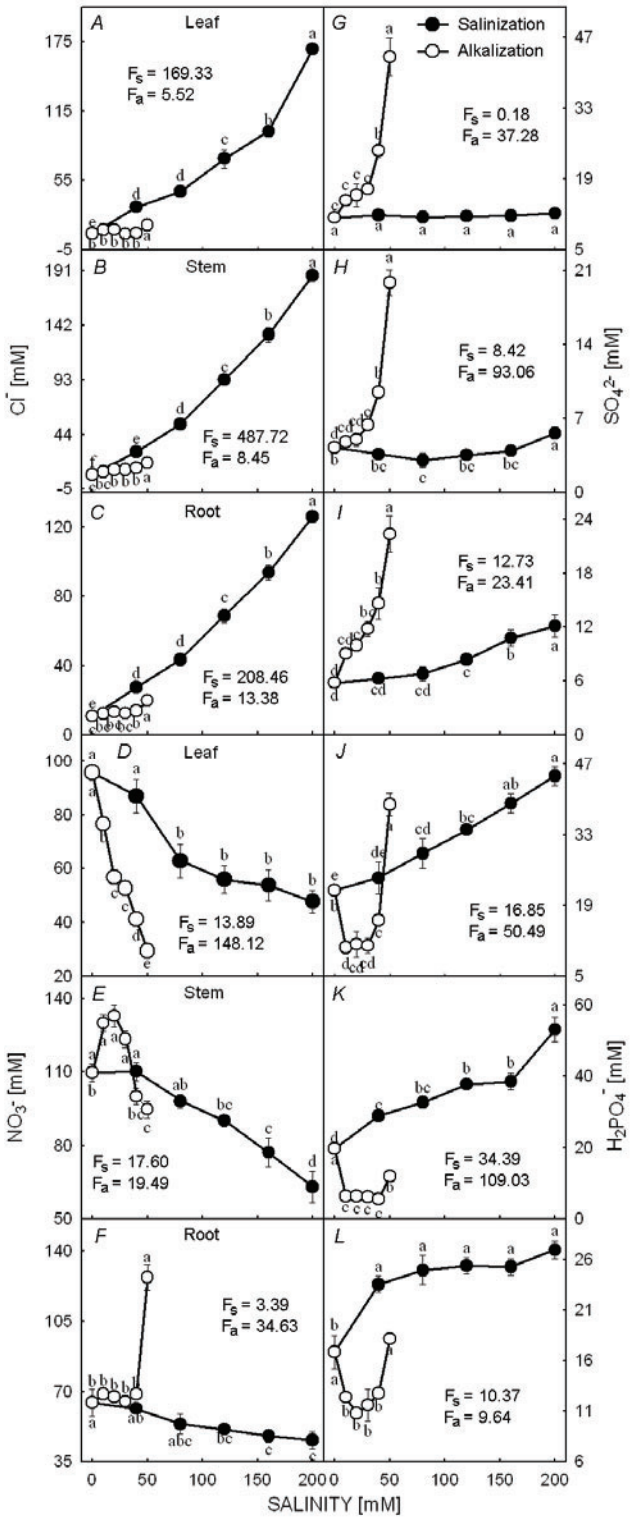


Fig. 3. Effects of saline and alkaline conditions on $Cl^-$ (*A–C*), $NO_3^-$ (*D–F*), $SO_4^{2-}$ (*G–I*) and $H_2PO_4^-$ (*J–L*) concentrations on leaves, stems, and roots of sunflowers. Legend refers to Fig. 1.

and alkali stresses. This result reflects a specific adaptability of sunflower under long-term stress. The plants accumulated a large amount $K^+$ instead of $Na^+$; this not only reduced the water potential to achieve osmotic adjustment, but also reduced $Na^+$ toxicity (Munns 2002).

In general, proline accumulation is a quick response to osmotic and ionic stresses (Yang *et al*. 2007b). Our

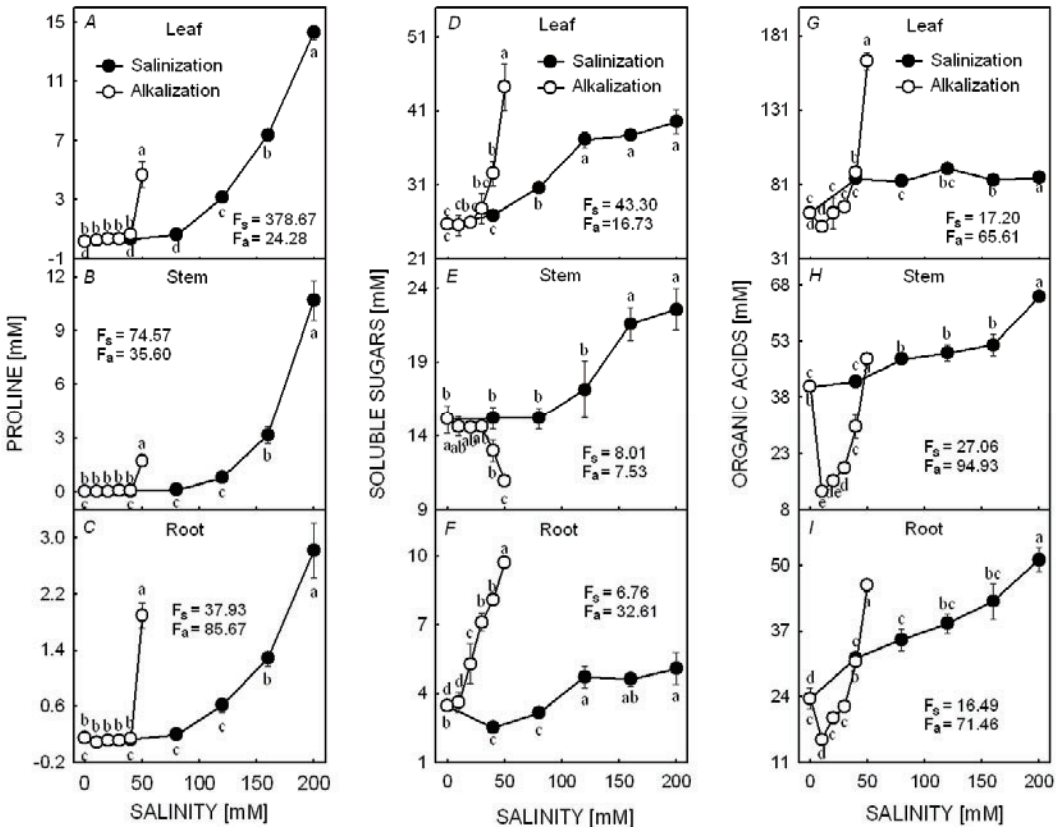


Fig. 4. Effects of saline and alkaline conditions on proline (*A–C*), soluble sugars (*D–F*), and organic acids' (*G–I*) concentrations on leaves, stems, and roots of sunflowers. Legend refers to Fig. 1.

Table 1. Percentage of each solute molarity to total molarity in sunflower leaves, stems, and roots under saline and alkaline conditions. OA – organic acid; SS – soluble sugar. The data are the averages of five treatments of saline or alkaline conditions.

| Treatment | | $Na^+$ [%] | $K^+$ [%] | $Ca^{2+}$ [%] | $Mg^{2+}$ [%] | $Cl^-$ [%] | $NO_3^-$ [%] | $SO_4^{2-}$ [%] | $H_2PO_4^-$ [%] | OA [%] | SS [%] | Proline [%] |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Leaf | Control | 1.94 | 41.60 | 4.26 | 1.65 | 1.96 | 21.42 | 2.54 | 4.92 | 13.90 | 5.76 | 0.04 |
| | Saline | 3.63 | 38.46 | 2.71 | 0.60 | 13.63 | 11.09 | 2.07 | 5.90 | 15.15 | 5.97 | 0.79 |
| | Alkaline | 6.00 | 42.87 | 4.27 | 3.17 | 2.34 | 11.25 | 4.32 | 3.19 | 16.22 | 6.19 | 0.19 |
| Stem | Control | 1.73 | 41.77 | 2.38 | 1.43 | 2.06 | 29.28 | 1.12 | 5.27 | 10.92 | 4.03 | 0.00 |
| | Saline | 7.77 | 36.84 | 1.03 | 1.09 | 16.22 | 16.70 | 0.70 | 6.75 | 9.22 | 3.27 | 0.42 |
| | Alkaline | 9.16 | 45.35 | 0.91 | 1.40 | 3.04 | 27.82 | 1.93 | 1.63 | 5.45 | 3.23 | 0.06 |
| Root | Control | 4.38 | 41.71 | 0.66 | 0.52 | 4.54 | 27.18 | 2.44 | 7.09 | 9.96 | 1.46 | 0.06 |
| | Saline | 7.77 | 36.84 | 1.03 | 1.09 | 16.22 | 16.70 | 0.70 | 6.75 | 9.22 | 3.27 | 0.42 |
| | Alkaline | 9.16 | 45.35 | 0.91 | 1.40 | 3.04 | 27.82 | 1.93 | 1.63 | 5.45 | 3.23 | 0.06 |

results showed an insignificant contribution of proline to osmotic adjustment (Table 1), meaning that proline (Fig. 4*A–C*) accumulation might not be a response to osmotic stress, similar to the conclusions of Yang *et al*. (2007). Under both stresses, especially alkalinity, soluble sugars (Fig. 4*D–F*) accumulated as the main organic osmolyte (Table 1).

Under salt stress, plants accumulate cations such as $Na^+$ (Khan *et al*. 2000, Parida and Das 2005, Shi and Sheng 2005, Yang *et al*. 2007a), and simultaneously accumulate inorganic anions such as $Cl^-$ (Ghoulam *et al*. 2002, Santa-Cruz *et al*. 2002), $NO_3^-$, and $SO_4^{2-}$ or synthesized organic anions (Sagi *et al*. 1997) to keep ion balance. The present results indicated that sunflowers accumulated organic acids (Fig. 4*G–I*) and inorganic anions (Fig. 2) to maintain intracelluar ion balance and adjust pH under saline and alkaline conditions. However, the contributions of organic acids and inorganic anions to total negative charge were different between saline and alkaline conditions, as well among the various plant parts (Table 2). The results indicated that organic acids' accumulation correlated closely with changes in inorganic anions' contents. Under alkaline conditions, the organic acids synthesized in sunflower might be utilized

Table 2. Percentage of the contribution of various free ions of total charge in sunflower leaves, stems, and roots under saline and alkaline conditions. OA – organic acid. The data are the averages of five treatments of saline conditions or alkaline conditions. Percentage is calculated according to actual charge.

| Treatment | | Cation [%] | | | | Anion [%] | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | $Na^+$ | $K^+$ | $Ca^{2+}$ | $Mg^{2+}$ | $Cl^-$ | $NO_3^-$ | $SO_4^{2-}$ | $H_2PO_4^-$ | OA |
| Leaf | Control | 3.51 | 75.14 | 15.38 | 5.97 | 3.21 | 35.02 | 8.31 | 8.03 | 45.43 |
| | Saline | 7.67 | 78.77 | 11.09 | 2.47 | 21.14 | 16.93 | 6.36 | 9.09 | 46.48 |
| | Alkaline | 9.43 | 67.31 | 13.40 | 9.85 | 4.08 | 19.77 | 14.85 | 5.47 | 55.82 |
| Stem | Control | 3.38 | 81.72 | 9.32 | 5.59 | 3.39 | 48.24 | 3.70 | 8.69 | 35.99 |
| | Saline | 16.12 | 75.26 | 4.19 | 4.43 | 27.38 | 27.96 | 2.34 | 11.34 | 30.97 |
| | Alkaline | 14.53 | 77.34 | 3.18 | 4.96 | 6.47 | 58.18 | 8.36 | 3.46 | 23.52 |
| Root | Control | 9.03 | 86.10 | 2.74 | 2.13 | 7.13 | 42.73 | 7.68 | 11.14 | 31.31 |
| | Saline | 56.16 | 39.33 | 2.84 | 1.66 | 27.46 | 22.31 | 7.12 | 10.54 | 32.56 |
| | Alkaline | 46.80 | 44.55 | 5.04 | 3.62 | 7.89 | 42.62 | 14.30 | 7.22 | 27.97 |

to supplement the deficiency of negative charge caused by decreased inorganic anion content. The metabolic regulation of organic acids is very complex and related to carbon assimilation (Backhausen *et al*. 1994, Tian *et al*. 2001), nitrogen metabolism (Scheible *et al*. 1997), and other biochemical pathways. Therefore, the regulation mechanism of organic acids' accumulation deserves further investigation.

**Conclusions**: The damaging effects of alkalinity on germination, growth, and photosynthesis were more severe than those of salinity. Under saline or alkaline conditions, the transportation of $Na^+$ from roots to leaves was markedly inhibited, such that leaves maintained a low $Na^+$ and high $K^+$ status, which may be an important feature of sunflower tolerance of salinity. $K^+$ was the main inorganic osmolyte and cation in the stems and leaves of sunflower; the primary organic osmolytes were organic acids and soluble sugars. In addition, the characteristics of osmotic adjustment and ion balance differed among sunflower roots, stems and leaves.

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