Response of three *Glycine* species to salt stress

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Abstract

Responses of leaf area, biomass, photosynthetic gas exchange and ion contents to four NaCl treatments, 0, 17, 51, and 85 mM NaCl, were examined for three wild soybean species (*Glycine soja*, *Glycine tomentella* and *Glycine tabacina*). In *G. soja*, NaCl treatment for 2 months reduced the photosaturated photosynthetic rate ($A_{\max}$), leaf area and biomass of NaCl treated plants relative to control treatments. Reductions were larger at higher NaCl concentrations. Similar changes were found in *G. tabacina*, however, the reductions were less than those in *G. soja*. In *G. tomentella*, significant reductions in $A_{\max}$ and biomass were found in 51 and 85 mM NaCl treated plants, but not in 17 mM concentrations. Results imply that the three species have differentiated in their sensitivity to salinity, with *G. soja* being the most sensitive, *G. tabacina* intermediate, and *G. tomentella* the least sensitive. The three species also differed in leaf tissue concentrations of Na and K. A negative correlation between Na accumulation in leaf tissue and salt tolerance was found that contrasted to a positive correlation between K concentration in leaf tissue and salt tolerance.

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1. Introduction

In glycophytes, plant growth and development are generally limited by salinity. Most of the world's crop species are glycophytes, hence they do not grow under high soil salinity. However, with increasing amounts of arable land undergoing salinization (Szabolcs, 1994) and increasing food demand from the growing human population, the need to develop salt-tolerant crop varieties is unavoidable. To develop salt-tolerant crops, it is necessary to identify the degree of salinity tolerance within crops and their wild-type relatives. Investigations of genetically based differences between closely related plants are particularly important because these studies provide necessary information to select traits for

breeding salt-tolerant crops (Tester and Davenport, 2003). Recent studies have found differences among rice (Lee et al., 2003), barley (Gorham et al., 1994; Flowers and Hajibagheri, 2001), maize (Fortmeier and Schubert, 1995) and wheat (Nagy and Galiba, 1995) cultivars in their response to salinity.

There are three wild soybean species in Taiwan, *Glycine soja* Sieb & Zucc., *Glycine tomentella* Hayata and *Glycine tabacina* (Labill.) Benth. Morphological and physiological differences in response to water availability have been reported previously for these three species, corresponding to differences in the water availability of their native habitats (Kao and Tsai, 1998). Plant responses to salt and water stress have much in common (Munns, 2002); however, they are not necessarily linked (Nagy and Galiba, 1995). *G. tomentella* is the only one of the species that has been found growing in seaside habitats (Huang and Ohashi, 1993). In this study, we test the hypothesis that in addition to their differences in response to drought (Kao and Tsai, 1998), the three wild soybeans have also differentiated in their sensitivity to salinity. If so, the wild soybean species might provide information

Abbreviations: $A_{\max}$, photosaturated photosynthetic rate; C_a , ambient CO₂ concentration; C_i , intercellular CO₂ concentration; g_s , stomatal conductance; HS, 85 mM NaCl; LS, 17 mM NaCl; MS, 51 mM NaCl; OS, 0 mM NaCl

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relevant to the selection of traits leading to more salt-tolerant soybean cultivars.

In addition to show reductions in growth, a typical response of glycophytic plants subjected to saline conditions is a reduction in photosynthetic rates (Bongi and Loreto, 1989; Brugnoli and Lauteri, 1991; Seemann and Critchley, 1985; Walker et al., 1981). Decreased photosynthetic rates may result from the closure of stoma, induced by osmotic stress, or from salt-induced damage to the photosynthetic apparatus (reduced efficiency of the electron transport chain and damage to the light harvesting complex). Accordingly, we conducted measurements of photosynthetic gas exchange to examine the comparative effects of salinity on net CO₂ assimilation and stomatal conductance among the three study species.

One mechanism associated with greater tolerance of moderately saline environments is the ability of plants to exclude Na from the shoot, and concurrently maintain high levels of shoot K (Schachtman and Munns, 1992; Gorham et al., 1994; Flowers and Hajibagheri, 2001). Salinity has been shown to interfere with K and Ca nutrition (Rengel, 1992) and this can cause nutrient deficiencies. In this study, we measured the K, Na and Ca ion contents of leaves from the three wild soybean species subjected to NaCl to investigate possible mechanisms for differential salt sensitivity among the species.

The main objective of this study was to determine whether there was variation among the three wild soybean species in their response to salinity.

2. Materials and methods

2.1. Plant materials

G. soja Sieb & Zucc. seeds were collected from Shih-men (25°02'N, 120°30'E) in northern Taiwan, *G. tomentella* Hayata from Hengchun (22°00'N, 120°44'E) in southern Taiwan, and *G. tabacina* (Labill.) Benth from Penghu island (23°34'N, 119°33'E) (Kao and Tsai, 1998). Seeds were germinated in Petri dishes, followed by transplanting of the seedlings to 2 L plastic pots. One seedling was planted in each pot, which was filled with a mixture of 1:1 vermiculite:soil by volume. Plants were grown in a glasshouse in natural daylight, watered every day, and fertilized using inorganic fertilizer (20 N:20 P:20 K) once every 2 weeks. The air temperature and relative humidity in the glasshouse was maintained between 30 and 35 °C and 70%, respectively. The salinity treatments began when plants were 4 weeks old. The pots were immersed in a modified Hoagland's solution (Haines and Dunn, 1976), containing 0, 17, 51, and 85 mM of NaCl, for 2 h every day, with four replicates per species for each salinity treatment. Final NaCl treatment concentrations were reached gradually by increments of 17 mM every 2 days. Then, plants were subjected to the final treatment concentration for 2 months before following measurements were taken.

2.2. Measurements

Photosynthetic gas exchange of the most recently expanded terminal trifoliate leaflet was measured between 8 a.m. and 5 p.m. using a steady-state open gas exchange system (Kao and Tsai, 1998). The system consisted of an infrared carbon dioxide analyzer (LI-6262, Licor, Lincoln, NE) and a leaf chamber (Pacsys 9900, DDG, La Jolla, CA) with integral temperature and humidity sensor. The rates of photosaturated photosynthetic carbon assimilation ($A_{\max}$) and stomatal conductance (g_s) were determined by enclosing the leaf in a cuvette under a photon flux of 1200 $\mu\text{mol m}^{-2} \text{s}^{-1}$, with light provided from a fibre illuminator (FL-440, Walz, Germany). Measurement conditions within the cuvette were: leaf temperature 30 °C, leaf-to-air water vapor pressure difference 1–1.2 kPa, and ambient CO₂ concentration $360 \pm 5 \text{ cm}^3 \text{ m}^{-3}$. After steady-state rates of $A_{\max}$ had been recorded (about 1 h), leaves were removed from the cuvette and excised leaf area was measured using a leaf area meter (LI-3100, Licor, Lincoln, NE). The leaf was then dried at 60 °C for at least 48 h and ground to powder for ion content analysis.

Ions were extracted from leaves at a temperature of 80 °C from a HCl (6 M) solution (Lambert, 1976). Potassium and Na contents were subsequently analyzed with a flame photometer (Model 410, Corning, England), and Ca analyzed by atomic absorption (Model 2380, Perkin-Elmer).

Plant shoots and roots were harvested after 2 months of salinity treatment, dried at 60 °C for 7 days and then weighed for determination of dry biomass.

All statistical tests were performed using the computer software SYSTAT (Statistical Solution Limited, Ireland). Means were compared using the least significant difference test. Significant levels are reported as $P < 0.05$.

3. Results

3.1. Leaf size

Leaf size differed among species and with NaCl treatment (Table 1). Increasing NaCl concentration resulted in reduced leaf size for *G. soja*, as a consequence, plants received no NaCl had the largest and those with 85 mM the smallest leaf area (Table 1). In *G. tomentella*, no significant difference was found in leaf size among 0, 17 and 51 mM treated plants,

Table 1
Leaf area (mean $\pm$ S.E., $n = 4$, cm²) of the most recent, fully expanded trifoliate leaf of wild soybeans after 2 months of different NaCl treatments

Species	NaCl (mM)			
	0	17	51	85
<i>G. soja</i>	11.8 $\pm$ 0.6	6.6 $\pm$ 1.0	3.0 $\pm$ 0.3	2.1 $\pm$ 0.4
<i>G. tomentella</i>	10.2 $\pm$ 0.9	11.6 $\pm$ 0.7	10.0 $\pm$ 0.9	6.7 $\pm$ 1.9
<i>G. tabacina</i>	4.5 $\pm$ 0.2	4.4 $\pm$ 0.2	4.0 $\pm$ 0.3	4.2 $\pm$ 0.4

Fig. 1. Accumulated shoot (A) and root (B) biomass of three soybean species, *G. soja* (open bar), *G. tabacina* (closed bar), and *G. tomentella* (hatched bar), exposed to four NaCl treatments over 2 months. Vertical bars represent 1 S.E. of treatment ($n=4$).

however, 85 mM NaCl had significantly smaller leaf sizes compared to other treatments. No significant difference was found in leaf size among plants of *G. tabacina* in the four different regimes of NaCl (Table 1).

3.2. Biomass

Adding NaCl to culture medium significantly reduced both root and shoot biomass of *G. soja*, and the reduction increased with increasing salinity (Fig. 1A). NaCl treatments had no significant effect on root biomass of *G. tabacina* and *G. tomentella* (Fig. 1B). However, shoot biomass in 17, 51 and 85 mM NaCl treated *G. tabacina* were significantly lower than that of 0 mM plants (Fig. 1A). In *G. tomentella*, 17 mM treatment did not differ from controls for shoot biomass, however, 51 and 85 mM treatments resulted in significantly lower shoot biomass than controls and 17 mM treatments (Fig. 1A).

3.3. Photosynthetic gas exchange

Photosaturated photosynthetic rates were similar among the three species in the 0 mM treatment (Fig. 2A). However, stomatal conductance in this treatment was significantly higher in *G. soja* and *G. tomentella* than that in *G. tabacina*

Table 2

The ratio of C_i/C_a (mean $\pm$ S.E., $n=4$) of the most recent, fully expanded trifoliate leaf of wild soybeans after receiving different regimes of NaCl treatment

Species	NaCl (mM)			
	0	17	51	85
<i>G. soja</i>	0.67 ± 0.02	0.72 ± 0.01	NA	NA
<i>G. tomentella</i>	0.63 ± 0.01	0.57 ± 0.01	0.58 ± 0.01	0.58 ± 0.01
<i>G. tabacina</i>	0.60 ± 0.02	0.58 ± 0.02	0.57 ± 0.04	0.57 ± 0.02

NA: not available.

(Fig. 2B). A_{max} and g_s of the three species responded differently to the NaCl treatments. Leaves of *G. soja* in the 51 and 85 mM treatments were too small to conduct photosynthetic measurements, while those in the 17 mM treatment had significantly lower A_{max} and g_s than those of 0 mM treated plants. The reduction in A_{max} was relatively greater than that in g_s ; as a consequence, the ratio of intercellular to ambient CO_2 concentration (C_i/C_a) of 17 mM treated *G. soja* increased (Table 2). In contrast, 0, 17 and 51 mM NaCl treated *G. tomentella* and *G. tabacina* had similar A_{max} and g_s , with only 85 mM treated plants showing significantly lower A_{max} and g_s (Fig. 2). No significant differences were found in the ratio of C_i/C_a among *G. tabacina* plants from the four treat-

Fig. 2. Effect of four NaCl treatments on photosaturated photosynthetic rate (A_{max}) (A) and stomatal conductance (B) of three wild soybean species, *G. soja* (open bar), *G. tabacina* (closed bar), and *G. tomentella* (hatched bar). Vertical bars represent mean ($n=4$) $\pm$ S.E.

Fig. 3. The correlation between leaf Na (A), K (B) and Ca (C) contents and NaCl treatment for *G. soja* (square), *G. tabacina* (triangle), and *G. tomentella* (circle). Solid lines are significant regressions fit to the pooled data from all NaCl treatments.

ments (Table 2). In *G. tomentella*, all NaCl treatments above 0 mM resulted in significant reductions in C_i/C_a , although there was no further decrease with increased NaCl concentration (Table 2).

3.4. Leaf Na, K and Ca contents

No significant difference was found in leaf Na contents among the three species in the 0 mM NaCl treatment (Fig. 3A). The Na concentration in leaves of the three species increased with increasing NaCl, resulting in positive correlations between leaf Na content and NaCl concentration in all three species. *G. soja* accumulated more Na than *G. tomentella* and *G. tabacina*.

No significant difference in leaf K contents was measured among the three species in 0 mM NaCl treatment (Fig. 3B). Increasing NaCl concentration in the treatments decreased leaf K contents in *G. soja* and *G. tabacina*, with the degree of reduction higher in *G. soja* than in *G. tabacina*. As a result, leaf K contents were highest in *G. tomentella*, intermediate in *G. tabacina*, and lowest in *G. soja*.

Fig. 4. The correlation between the ratio of Na/K in leaves and NaCl concentration in four different treatments for *G. soja* (square), *G. tabacina* (triangle), and *G. tomentella* (circle). Solid lines are significant regressions fit to the pooled data from all NaCl treatments.

No significant difference was found in leaf Ca contents among the three species on the 0 mM NaCl treatment (Fig. 3C). Increasing NaCl concentration in the treatments increased leaf Ca contents in *G. soja*, however, no correlations were found in *G. tabacina* and *G. tomentella*.

No significant difference was found in the ratio of Na/K in leaves for the three species in the 0 mM NaCl treatment (Fig. 4). The ratio of Na/K in leaves of all three species increased significantly with increasing treatment NaCl concentration, with the greatest increment in *G. soja*, the least in *G. tomentella*.

4. Discussion

Results from this study showed that 85 mM NaCl treatment caused reductions in growth of all three wild soybean species (Table 1; Fig. 1). This is consistent with previous reports that soybeans are glycophytes (Läuchli and Wieneke, 1979). However, our results also showed that the susceptibility to salt stress differed among the three species. *G. soja* appeared to be the most salt sensitive, with reduced leaf expansion (Table 1), photosynthetic rates (Fig. 2), and biomass (Fig. 1) in response to exposure to NaCl. These reductions increased with increasing NaCl concentration. The response of *G. tomentella* and *G. tabacina* to NaCl treatment differed from that of *G. soja*. Though their growth was also reduced at the highest NaCl concentrations used (51 and 85 mM), a slight or no decrease in biomass was found between 17 and 0 mM treated plants. This result supports the hypothesis that the three wild soybeans in Taiwan have differentiated in their sensitivity to salinity, with *G. soja* the most, *G. tabacina* intermediate, and *G. tomentella* the least sensitive. This corresponds to field observations that *G. tomentella* is the only species found growing in seaside habitats.

The reductions in growth due to NaCl treatment (Table 1; Fig. 1) were consistent with differences in the sensitivity of A_{max} among the species (Fig. 2). However, the inhibition of A_{max} may be due to different mechanisms in different

species. Analysis of gas exchange measurements revealed that decreased photosynthesis in *G. tomentella* might not be caused by ion toxicity but by salinity-induced reductions in g_s (a greater relative reduction in g_s than in $A_{\max}$ and concomitantly a lower ratio of C_i/C_a) (Fig. 2; Table 2). Similar results were found in the salt-sensitive species, *Phaseolus vulgaris* L. (Seemann and Critchley, 1985; Brugnoli and Lauteri, 1991) and spinach leaves (Downton et al., 1985) in response to salinity. In contrast, the greater relative reductions in $A_{\max}$ than in g_s and consequently higher ratio of C_i/C_a (Table 2) measured in *G. soja* suggests that non-stomatal inhibition of photosynthesis, caused by direct effects of NaCl on the photosynthetic apparatus independent of stomatal closure, might be responsible for the reduction in photosynthetic rate of NaCl treated *G. soja*. Non-stomatal inhibition of photosynthesis by salinity has also been reported for several plant species (Seemann and Critchley, 1985; Ball and Anderson, 1986). This inhibition of photosynthetic capacity may result from a reduced efficiency of ribulose-1,5-bisphosphate (RuBP) carboxylase, or a reduction of RuBP regeneration capacity, or to the sensitivity of PSII to NaCl (Ball and Anderson, 1986). The C_i/C_a ratio declined slightly in NaCl treated *G. tabacina* compared to 0 mM treatments, however, no significant difference was detected in this ratio as NaCl increased from 17 to 85 mM (Table 2). This implies that the reduction of $A_{\max}$ by salinity treatment in this species was caused by both stomatal and non-stomatal factors.

Results from this study showed a different ranking among the three soybean species in their sensitivity to salinity compared to their susceptibility to low water availability. While *G. soja* was the most susceptible to both salinity and low water availability, *G. tabacina* and *G. tomentella* reversed positions (Kao and Tsai, 1998). Thus, similar to the finding in wheat (Nagy and Galiba, 1995), drought and salt tolerance are not necessarily linked among these three species of wild soybean.

Differences in the accumulation of Na and K in leaves of the three species (Fig. 3A and B) may contribute to their differential responses. A negative correlation between Na accumulation in leaves and salt tolerance was found (Figs. 1 and 3A), with the most sensitive species, *G. soja*, accumulating the most, and the least sensitive species, *G. tomentella* accumulating the least (Fig. 3A). This is consistent with findings in many crop species (Hajibagheri et al., 1987; Schachtman and Munns, 1992).

Salinity can interfere with K and Ca nutrition (Rengel, 1992). Potassium is an activator of many enzymes that are essential for photosynthesis and respiration, and deficiencies in K would result in inhibition of photosynthesis and eventually reduction in growth (Salisbury and Ross, 1992). The maintenance of a high K content may be crucial to sustain the integrity of the photosynthetic system under high salinity (Chow et al., 1990) and thus an important pre-requisite for salinity tolerance. Results from present investigation showed higher Na and lower K contents in the leaf tissue of *G. soja* compared to *G. tomentella* and *G. tabacina* (Fig. 4). This

result implies that the differential accumulation of leaf Na and K might be responsible for the different sensitivity of the three wild soybeans to NaCl treatment. Similarly, Gregorio and Senadhira (1993) found that in rice varieties the higher the level of salinity tolerance the lower the Na content and the higher the K content in the shoot.

Salinity impairs the uptake of Ca by plants (Cramer et al., 1987). Suhayda et al. (1992) and Huang and Redmann (1995) suggested that salinity-induced symptoms in cultivated barley may be the result of a Ca deficiency. In this study, we found no significant effect of salinity on Ca contents in *G. tomentella* and *G. tabacina* (Fig. 3C). In contrast, there were increases in Ca content in the most salt-sensitive species, *G. soja*, in response to salinity treatment (Fig. 3C). Sweet clover, which showed no effect of salt on Ca uptake, actually increased Ca uptake during the reproductive phase (Romero and Maranon, 1994). Accordingly, salinity-induced deficiency of Ca was not evident in the wild soybeans measured.

In conclusion, growth and photosynthesis of three wild soybean species differ in their response to NaCl treatments. *G. soja* was the most sensitive species, *G. tabacina* intermediate, and *G. tomentella* the least to NaCl treatment. Differences among species in leaf accumulation of Na and K might be responsible for the differential sensitivity to NaCl treatments.

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