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Different effect of humidity on growth and salt tolerance of two soybean cultivars

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Abstract

Two soybean (*Glycine max* (L.) Merr.) cultivars, Tachiyutaka and Dare, were grown in pots at 30 and 70 % relative humidity (RH) and treated with 0 (control), 40 (moderate), 80 and 120 (severe) mM NaCl for 3 weeks. Increasing RH enhanced growth of salt sensitive cultivar, Tachiyutaka, but had no effect on salt tolerant cultivar, Dare, under control and moderate saline conditions. Both cultivars benefited from elevated humidity under severe saline conditions. Cultivar Tachiyutaka had poorer ability for controlling translocation of Na$^+$ to the leaves, lower Na$^+$ exclusion ability in the roots, and lower root activity under NaCl treatment, compared with cv. Dare. The increased growth of cv. Tachiyutaka at high RH was consistent with decreased Na$^+$ accumulation in the leaves, increased stomatal conductance and root activity, while the unchanged growth of cv. Dare was consistent with similar Na$^+$ accumulation in the leaves, and the decreased root activity.

Additional key words: *Glycine max*, Na$^+$ content, root exudate, stomatal conductance, transpiration.

Introduction

Saline soils occupy 47 % of the world's irrigated farmland (Lopez and Satti 1996) and induce water stress, ion toxicity and ion imbalance (Dudley 1992). Considerable efforts were invested in improving plant growth under saline conditions (Ali-Dinar *et al.* 1999, Hayashi *et al.* 1998, Lopez and Satti 1996, Mandeel 1996, Awad *et al.* 1990, Cramer *et al.* 1987). Increasing air humidity is one way to reduce the risks of the use of saline water (Salim 1989).

Increasing relative humidity (RH) ameliorated growth reduction in bean plants (Hoffman and Rawlins 1970), in mangroves (Ball *et al.* 1997), in *Albizia lebbek* (Kirdmanee *et al.* 1998), and in tomato (Paiva *et al.* 1998). However, RH has been reported to have no alleviation effect on cotton growth under saline conditions (Hoffman *et al.* 1971), or aggravated the growth reduction in soybean when RH increased at night (Stoyanova 1997). Moreover, salt tolerance was increased under conditions favoring high transpiration in *Phragmites australis* (Lissner *et al.* 1999a,b). RH affects plant growth primarily via its influence on the leaf to air vapour pressure deficient, as mediated by stomata (Hoffman *et al.* 1971, Grantz 1990). Na$^+$ accumulation in the leaves would inhibit stomatal opening (Perera *et al.* 1994, Robinson *et al.* 1997). Na$^+$ induced inhibition of photosynthesis resulted in the increase of intercellular CO_2 and then reduction in stomatal opening (Mansfield *et al.* 1990).

The interactions of transpiration, Na$^+$ uptake and translocation to the shoot have long been reported, but some contradictory reports have been found in the literature. Benjamin (1992) reported that Na$^+$ transport from the external solution to the cytoplasm depended on the electrochemical potential gradient of Na$^+$ and the presence of permeable Na$^+$ channels in the plasma membrane. Robinson *et al.* (1997) reported that Na$^+$ delivered from roots to shoots is mostly via the xylem stream. Regulation of transpiration controls Na$^+$

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translocation to the leaves. Passive ion uptake was related to transpiration in rice plant (Hirai *et al.* 1985), but Naito *et al.* (1994) showed that higher transpiration led to low Na^+ contents in shoot in rice plant. Models that relate salt absorption to transpiration were also provided (Dalton 1975, Dalton and Poss 1990). Salt tolerant *Euphorbia paralias* and sunflower had been reported to exhibit drought tolerance too (Ashraf and O'Leary 1996, Elhaak *et al.* 1997).

Soybean is moderately salt tolerant, and the plant will die if the electrical conductivity (EC) of the irrigation water exceeds 6.7 dS m^{-1} (Ayers and Westcot 1984). Difference in salt tolerance in soybean cultivars has been reported (Velagaleti and Schweitzer 1992, Abd El-Samad and Shaddad 1997). The removal of Na^+ from the transpiration stream in the roots, limiting Na^+ access to the leaves, is associated with salt sensitivity of soybean (Lacan and Durand 1995). The inhibition of the shoot could be a function of the decreased hydraulic conductivity of the root (Lopez and Satti 1996). In this study, two cultivars, differing in salt tolerance, were selected from our previous studies (data not shown). The effects of RH on salt tolerance in relation with some physiological characteristics of these two cultivars were investigated.

Materials and methods

Plants and growing conditions: The experiment was carried out in two environmentally controlled growth chambers of the type GC-A (*Fuji Electric Co.*, Tokyo, Japan). Seeds of two soybean [*Glycine max* (L.) Merr.] cultivars, Dare and Tachiyutaka, were sown in small plastic pots and after one week, the seedlings were transplanted into big pots, containing 4 dm^3 light stones at the bottom of the pots for drainage and 9 dm^3 of sand and peat mixture (1:1). During the first and second week after transplanting, the seedlings were irrigated with 1/3 and 2/3 strength Hoagland and Arnon solution (Asagawa 1985), respectively, and full strength of the same solution was used for the rest of the experimental period.

Uniform plants were selected from each cultivar and transferred to growth chambers 23 d after sowing, when each plant was carrying about 12 leaves and had dry matter about 3 g. The photoperiod was 12 h and the photon flux density, measured by a portable photosynthesis system (*LC-6400*, *Li-Cor*, Lincoln, USA) at the canopy surface was 600 mol m^{-2} s^{-1}. The day/night temperature was 26/24 ± 0.1 °C. The RH of the two growth chambers was set at 30 (control) and 70 %, and the actual RH recorded continuously were 28 - 32 and 65 - 75 %, respectively. Four salinity treatments were applied using NaCl added to the nutrient solution to reach a concentration of 0 (control), 40 (moderate), 80 and 120 (severe) mM. EC of the solution extracted from soil medium on the second week after NaCl treatment was 1.60 ± 0.02, 5.52 ± 0.08, 8.60 ± 0.06, and 11.16 ± 0.12 dS m^{-1}, respectively. After starting with NaCl treatment, plant rooting media were flushed daily by excessive irrigation solution to secure salt leaching and avoid salt accumulation in the root medium. Five replications for each treatment were assigned randomly. The salinity treatments lasted 23 d.

Sap flow and transpiration: Sap flow in the stem was measured with the heat pulse method (Cohen *et al.* 1988) for the 2nd and 3rd weeks after NaCl treatment. The probe block (made at Institute of Soils, Water and Environmental Sciences, ARO, Bet Dagan, Israel) was used for the heat pulse velocity measurement. Two data loggers (*21X*, *Campbell Scientific*, Ogden, USA) were used to monitor the sensors and control the two boxes of relays operating the heaters. The probes were installed below the lowest branch in the main stem. Sixteen plants were measured simultaneously at 30-min intervals. This measurement was repeated for 3 times and the growing conditions of the plants were the same. Calibration coefficient of 1.0 (Cohen *et al.* 1993) was used to calculate transpiration from sap flow rate. Leaf area was measured weekly with a portable area meter (*LI-3000A*, *Li-Cor*). Stem diameter was also measured weekly. The increase in leaf area and stem diameter within one week was assumed to be linear.

Stomatal conductance: Stomatal conductance was measured on five fully developed leaves for each plant on 8th, 10th and 12th day during salinity treatment with a portable steady state porometer (*LI-1600*, *Li-Cor*) in the growth chambers. The average stomatal conductance of each plant and each treatment was calculated.

Dry matter and Na^+ content: At the end of the experiments, the plants were divided into leaf blades, stems plus petioles, and roots, and dried at 80 °C for 3 d. The dried plant samples were ground separately and Na^+ was measured as described by Ali *et al.* (1998) with an atomic absorption spectrophotometer (*ASC-6100*, *Shimadzu*, Kyoto, Japan).

Exudation: Growing conditions of the plants were the same as described above, but using Hoagland and Arnon solution culture (Asagawa 1985). Nutrient solution was replaced once a week. The pH of the solution was maintained at 5.5 by HCl or KOH. Sixty hours after starting with NaCl and RH treatments, shoots were cut 4 cm above the lower end of the stem. Plastic sleeves were sealed on the cut stems to collect the exudate. Five hours later, the exudate in the plastic sleeves was extracted by a syringe and the amount was determined.

Statistical analysis: Means and standard errors (SE) are presented. Significance of differences between the treatments was estimated using the *t*-test (Yonezawa *et al.* 1988).

Results

The two cultivars treated with 80 and 120 mM NaCl became chlorotic and wilted two weeks after the NaCl treatment. No visible damage symptoms were observed in the plants treated with 40 mM NaCl. With increasing NaCl concentration, the growth of the two cultivars decreased. This decrease was more pronounced in cv. Tachiyutaka than cv. Dare, irrespective of the RH and NaCl levels (Fig. 1). With increasing RH, the growth of cv. Tachiyutaka increased in control and at all NaCl concentrations. Increasing RH showed almost no effect on the growth of cv. Dare in control and at 40 mM NaCl (Fig. 1), while at 80 and 120 mM NaCl, the growth was improved for about 10 %.

With increasing NaCl concentration, root growth of the two cultivars decreased (Fig. 1). At 40 mM NaCl, this decrease was more pronounce in cv. Tachiyutaka than cv. Dare in each RH. With increasing RH, root growth was generally increased in cv. Tachiyutaka. However, in cv. Dare, this increase can be observed only at 80 and 120 mM NaCl.

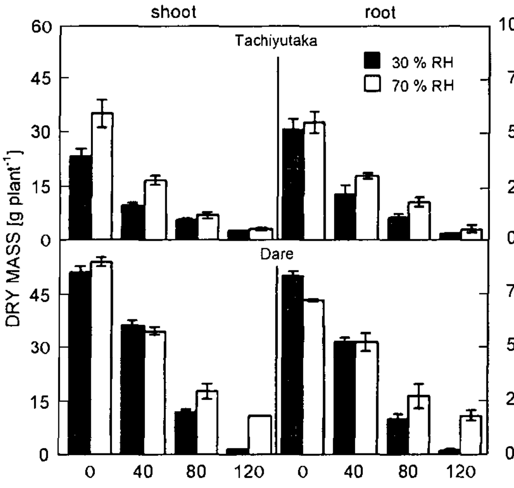

Fig. 1. Dry mass of the two soybean cultivars, Tachiyutaka and Dare, treated with three NaCl concentrations at two relative humidities (RH) for 3 weeks. Means ± SE, *n* = 3.

The control plants had a very low Na^+ content (0.001 mg g^{-1}). In the leaves, cultivar Tachiyutaka showed higher Na^+ contents than cv. Dare in each of the treatment (Fig. 2). Higher Na^+ contents in low than in high RH in 40 and 80 mM NaCl concentrations were observed in cv. Tachiyutaka. In cv. Dare, the differences in Na^+ content between the two RH treatments in each NaCl concentration were not significant, except Na^+ contents in the leaves at 120 mM NaCl. Root Na^+ contents was higher in cv. Tachiyutaka than cv. Dare in 40 and 80 mM NaCl at 30 % RH and in 80 mM at 70 % RH. Increasing RH showed no significant effect on root Na^+ contents in each cultivar.

Sap flow measurement was stopped at the 12th day after NaCl treatment in cv. Tachiyutaka treated with

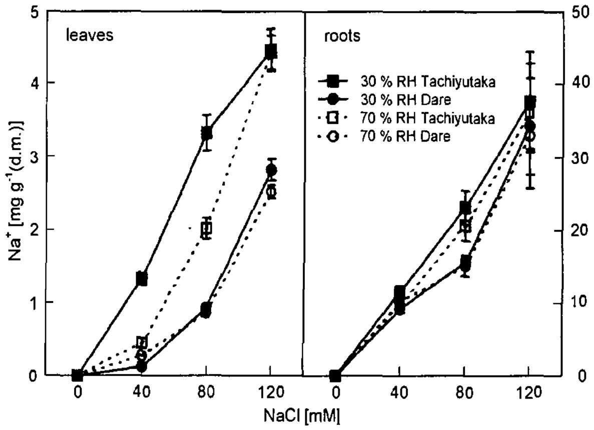

Fig. 2. Na^+ contents in the leaves and in the roots of the two soybean cultivars, Tachiyutaka and Dare, treated with three NaCl concentrations at two relative humidities (RH) for 3 weeks. Means ± SE, *n* = 3.

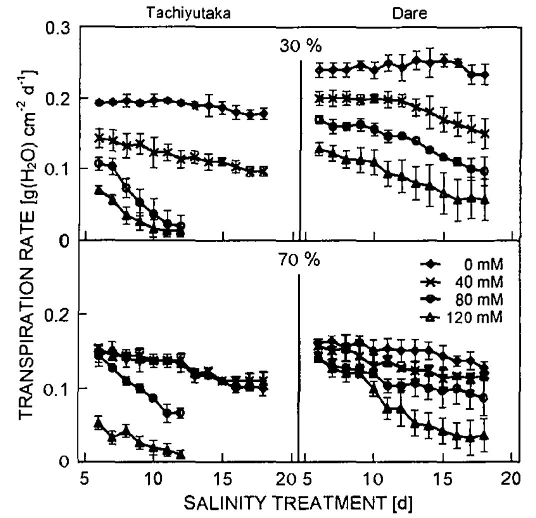

Fig. 3. Daily mean transpiration rates of the two soybean cultivars, Tachiyutaka and Dare, treated with three NaCl concentrations at two relative humidities (RH), during the 2nd and 3rd weeks of the treatment. Means ± SE, *n* = 3.

80 and 120 mM NaCl, when the transpiration rates of these plants were almost 0 (Fig. 3). In the low RH, transpiration rates decreased with increasing NaCl concentration in both cultivars. The decreasing tendency was more remarkable for cv. Tachiyutaka than cv. Dare. Cv. Dare showed higher transpiration rate than cv. Tachiyutaka in control and each NaCl concentration. At the high RH (Fig. 3), no significant difference in transpiration rate was found between the control and the plants treated with 40 mM NaCl in cv. Tachiyutaka, and among the control and the plants treated with 40 and 80 mM NaCl in cv. Dare. However, the transpiration of the plants treated with 80 and 120 mM NaCl in cv. Tachiyutaka and the plants treated with 120 mM in cv. Dare remarkably decreased.

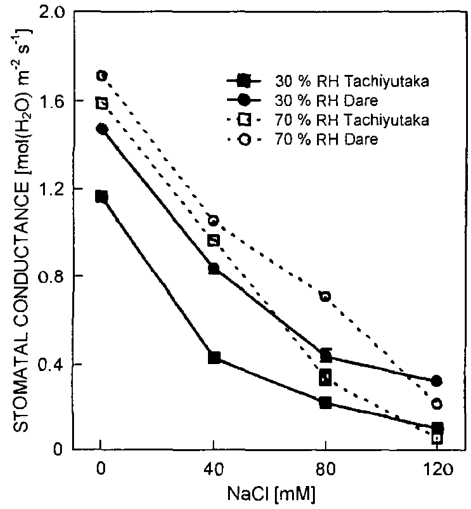

Fig. 4. Stomatal conductance of the two soybean cultivars, Tachiyutaka and Dare, treated with three NaCl concentrations at two relative humidities (RH). Data show the mean of 8th, 10th and 12th days of five plants in each treatment, and *vertical bars* represent SE (not shown when lower than size of points).

Stomatal conductance of cv. Dare was higher than that of cv. Tachiyutaka in each treatment. Stomatal conductance of both cultivars increased with increasing RH at control and each NaCl concentration, except at 120 mM NaCl. This increase was more marked in cv. Tachiyutaka than cv. Dare at control and 40 mM NaCl, while in 80 mM NaCl, it was more marked in cv. Dare.

The amount of exudate (Table 1) from the roots was similar in the control plants, but higher in cv. Dare than cv. Tachiyutaka at 40 mM NaCl in each RH. With increasing RH, amount of exudate increased significantly in cv. Tachiyutaka, but decreased in cv. Dare. Under 80 and 120 mM NaCl, no exudation was observed.

Table 1. Amount of exudate [mg g^{-1}(root f.m.)] from the roots of two soybean cultivars, Tachiyutaka and Dare, after 60 h exposure to 0 or 40 mM NaCl in the nutrient solution at RH 30 or 70 %. Means of 3 plants ± SE.

Cultivar	RH [%]	0 mM NaCl	40 mM NaCl
Tachiyutaka	30	54.3 ± 0.15	0.32 ± 0.01
	70	54.4 ± 0.18	0.53 ± 0.01
Dare	30	54.5 ± 0.10	5.68 ± 0.00
	70	54.2 ± 0.20	3.31 ± 0.05

Discussion

The higher growth of cv. Dare as compared with cv. Tachiyutaka under NaCl at each RH (Fig. 1), indicates that cv. Dare is more tolerant to salt than cv. Tachiyutaka, according to the salt tolerance criteria (Maas 1986). Roots growth of the two cultivars (Fig. 1) were consistent with the shoot growth, indicating that plants respond to salinity and RH as a whole. Less Na^+ translocation to the leaves in cv. Dare, compared with cv. Tachiyutaka (Fig. 2), can be supposed to be one of the reasons resulting in better growth of cv. Dare under salinity. Na^+ accumulation in the leaves is determinant for salt sensitivity (Lacan and Druand 1996), and salt accumulation interfere with photosynthesis (Seemann and Critchley 1985, Yeo *et al.* 1985).

Cultivar Dare showed higher ability on maintaining transpiration rate under stress conditions, compared with cv. Tachiyutaka (Fig. 3). The different transpiration rates (Fig. 3) and the similar Na^+ accumulation in the leaves at the two RH in cv. Dare (Fig. 2), suggest that increasing RH did not affect Na^+ uptake and translocation to its leaves. However, Na^+ in the leaves in 120 mM is an exception. It can be supposed, therefore, that Na^+ uptake and translocation to the leaves in cv. Dare is mostly not a passive transport regulated by transpiration. Less Na^+ accumulation in the roots of cv. Dare compared with cv. Tachiyutaka at 30 % RH (Fig. 2) indicates that cv. Dare has higher Na^+ exclusion ability of the roots than cv. Tachiyutaka, which is determinant for plant salt tolerance (Schubert and Läuchli 1990).

In contrast to cv. Dare, cv. Tachiyutaka showed lower ability in Na^+ exclusion by the roots (Fig. 2), and increasing RH decreased Na^+ uptake and translocation to the leaves. This is consistent with previous reports that Na^+ delivered from the roots to the shoots is regulated by transpiration (Robinson *et al.* 1997). Therefore, it can be supposed that the decreased transpiration rate at the high RH resulted in less Na^+ accumulation in the leaves of cv. Tachiyutaka, and might contribute to the amelioration of the reduction in stomatal conductance (Fig. 4). The improved growth of cv. Tachiyutaka at high RH (Fig. 1) might result from the above two consequences.

Higher exudation of cv. Dare compared with cv. Tachiyutaka at 40 mM NaCl in each RH (Table 1) suggests that cv. Dare had higher root activity, according to Katou (1998). The two cultivars showed opposite change in the amount of exudate with increasing RH, which needs to be further studied.

Transpiration rates and stomatal conductance of both cultivars were better maintained in high than in low RH under salinity (Figs. 3, 4), indicating that the effect of NaCl is smaller in high than in low RH. The different response in plant growth to high and low RH between the two cultivars in 0 and 40 mM NaCl concentraitons (Fig. 1), suggests that cv. Dare is also more tolerant to air drought than cv. Tachiyutaka under control and moderate salinity.

It is suggested therefore that salt tolerance of soybeans could be increased by increasing RH only in salt sensitive plants, but RH may give no effect for salt tolerant plants.

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