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ミニレビュー

Root characteristics in salt tolerance

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Abstract: The mechanisms of salt tolerance in plants were reviewed focusing on root characteristics of salt-tolerant cultivars under saline conditions. The salt-tolerant traits were characterized as greater root growth, higher efficiency in water uptake, lower Na^+ permeability, better root osmotic adjustment, and higher root pressure. The roles of these characteristics in plant growth and crop production under saline conditions were discussed.

Keywords: root, salt tolerance, sodium (Na^+), water uptake,

1. Introduction

The warning to the rapid expansion of salt-affected soils can be recognized in all continents, especially in arid and semi-arid regions (Szabolcs, 1985, Fig. 1). The salt-affected soils contain excess salts which affect plants by decreasing the osmotic potential of the soil solution (osmotic stress), interfering with normal nutrient uptake, inducing ionic toxicity, and associating nutrient imbalances (Dudley, 1992).

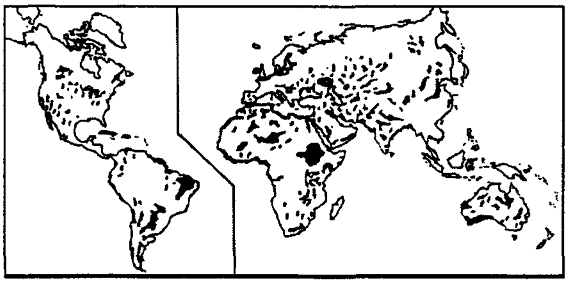

Fig. 1. Global distribution of salt-affected soils (Szabolcs, 1985)

The mechanisms of salt tolerance in plants have long been studied, and an array of mechanisms appears to be involved. To maintain turgor, plants grown under saline conditions undergo an osmotic adjustment that involves the net accumulation of solutes in cells as a response to the decline of environmental water potential (Blum *et al.*, 1996). In some cases, salt-tolerant cultivars synthesize more solutes for osmoregulation than the sensitive ones (Wyn Jones and Storey, 1981). Since the conservation of water within the plant may aid in decreasing translocation of salts to the leaves (Greenway and Munns, 1980), the sensitivity of stomata closure under saline conditions is related to the salt tolerance in plants (Robison *et al.*, 1997; Very *et al.*, 1998). Mayber and Lerner (1992) and Smith *et al.* (1996) emphasized the regulating role of plant hormones in the response of plants to salinity.

In the aspect of ionic relations, active limitation of sodium (Na^+) uptake is recognized as a significant trait for salt tolerance in some crop plants (Greenway and Munns, 1980) and the characteristics of potassium (K^+) and Na^+ transporters are determinant of the salt tolerance in plants (Benlloch *et al.*, 1994). It is generally accepted that

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increased K^+/ Na^+ selectivity and reduced Na^+ translocation from the root to the shoot contribute to the overall salt tolerance of glycophytes (Niu *et al.*, 1995). Another important ion associated with the salt-tolerance of plant is calcium (Ca^{2+}). Rengel (1992) and Garg (1998) reported that the presence of Ca^{2+} in root medium increased salt tolerance of plants, because of the function of Ca^{2+} in preserving K^+/ Na^+ selectivity (Zhong and Läuchli, 1994). In 1995, Niu *et al.* emphasized that the control mechanism of ion homeostasis (such as accumulation and intracellular compartmentation of ions predominant in the external environment), which also contributes to osmotic adjustment, is of paramount importance in salt tolerance of plants.

Since the salinity of the soils is detected first by the roots, Lacan and Durand (1995) pointed out that the primary and important processes of plant salt tolerance may reside in the roots. The following reports do support his opinion. By grafting experiments, Bernstein and Hayward (1958) showed that salt accumulation in leaves was controlled by roots. Naito *et al.* (1994) reported that the Na^+ exclusion, occurred at the exodermis and endodermis of the root, and the Na^+ and K^+ exchange was operated at the xylem/symplast interface in the roots (Lacan and Durand, 1996). The changes in the order of phosphatidylcholine acyl chains in the plasma membrane of the roots affected water permeability of the membrane under salinity (Schuler *et al.*, 1991). It is also demonstrated that the differences in plant growth in response to salinity are results of differences in root system structure (Lin and Sternberg, 1994).

On the other hand, the damaging effects of salinity on roots have also been reported. The salt stress decreases root biomass and root density index (Krauss *et al.*, 1999), causes curling of root hairs and inhibit the elongation (Zahran and Sprent, 1986), and decrease the number of nodules (Tu, 1981). Because of the importance of roots for shoot growth under saline conditions (Lopez and Satti, 1996), some attempts have been made on roots to increase the salt-tolerance of the whole plants. Increasing root temperature was tested to promote salt tolerance, including active Na^+ exclusion (Schmutz and Ludders, 1998). Changing rootstocks to higher tolerant one successfully improved salt exclusion (Romero *et al.*, 1997). Bohnert and Jensen (1996) suggested that the control of water flux through the water channels in roots is one of the important steps for increasing salt tolerance of plants.

In general, growth, morphology and physiology of the roots change under salinity stress and the whole plant is then affected. Therefore, the responses and characteristics of the roots under saline conditions are of primary importance for plant salt-tolerance. The objective of this review was to evaluate the characteristics of roots working in salt tolerance of plants.

2. Root growth under salt stress

Salinity-induced changes in root morphology, anatomy, and ultrastructure as well as some physiological implications of the altered growth patterns have been reviewed by Poljakoff-Mayber (1988). Excess salinity has been reported to inhibit both root cell division and cell expansion (Zidan *et al.*, 1990), as shown in Table 1. Generally, in glycophytes, root growth is less affected by salinity than either vegetative shoot growth or fruit and seed production (Mass and Nieman, 1978). Depending on the species, the level of salinity stress, and the composition of the external solution, root growth may be stimulated (Waisel, 1985), inhibited (Setia and Narang, 1985), or unaffected (Delane *et al.*, 1982).

In our experiment, the NaCl treatments decreased root growth of two soybean cultivars, Dare and Tachiyutaka, and salt-sensitive melon cv. Revigal C-8 (Fig. 2). However, no inhibition of root growth was found in the salt-tolerant melon

Table 1. Effects of 100 mM NaCl on Root Growth Rate, Length of Elongation Zone, Length of Epidermal Cells, and Apparent Rates of Cell Production. Mean ± SD, n=6.

Treatment	Root Growth Rate (mm h^{-1})	Elongation Zone (mm)	Cell Length (μm)	Cell Production (h^{-1})
Control	1.6 ± 0.2	7.0 ± 0.0	195 ± 13	8.2
100 mM NaCl	0.4 ± 0.1	3.9 ± 1.0	104 ± 7	3.8

(Data based on Zidan *et al.*, 1990)

cv. Galia. In 40 mM NaCl, the growth of the roots decreased by 24% and 54% in cv. Dare and cv. Tachiyutaka, respectively. Generally, the relative root growth of NaCl-treated plants was higher for salt-tolerant cv. Dare than for the sensitive cv. Tachiyutaka in both NaCl concentrations. Similar results on root elongation of two melon cultivars differing in salt-tolerance has been reported (Yermiyahu *et al.*, 1997, Fig. 3). It is well known that the capacity to develop an extensive root system is related to the ability of plants to absorb both water and mineral nutrients from the soil (Taiz and Zeiger, 1991). So the better developed roots of the salt-tolerant cultivars under saline conditions may be related to their higher tolerance to salinity compared with the sensitive ones.

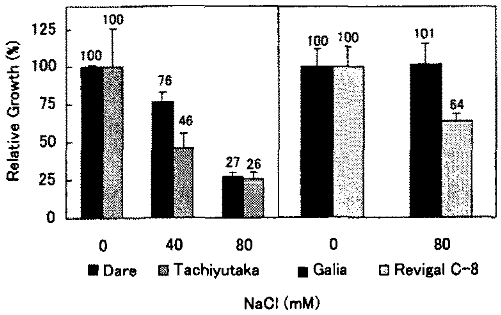

Fig. 2. Relative growth of the roots of two soybean cultivars, Dare (salt-tolerant) and Tachiyutaka (salt-sensitive), treated with 0, 40, and 80 mM NaCl for 3 weeks and two melon cultivars, Galia and Revigal C-8, treated with 0 and 80 mM NaCl for 15 days. Means ± SE, n=4. (Data based on An *et al.*, 2002a, b)

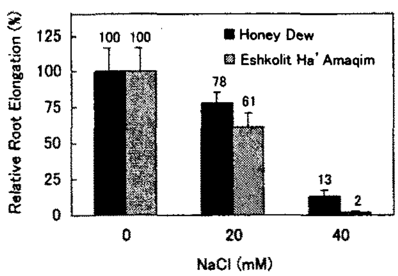

Fig. 3. Relative root elongation of two melon cultivars, Honey Dew (salt-tolerant) and Eshkolit Ha' Amaqim (salt-sensitive), treated with 0, 20, and 40 mM NaCl for 3 days. (Data based on Yermiyahu *et al.*, 1997)

3. Water uptake under salt stress

Water absorption by plant roots is generally viewed as a passive process which works only by differences in water potentials between plant and soil (Honert, 1948). However, when the volume of transpired water is much greater than the volume of the plant, the relative conductivity of roots to water is a significant factor necessary for salt tolerance (Shannon *et al.*, 1994). Martínez-Ballesta *et al.* (2000) demonstrated the effects of NaCl on root water conductance (Fig. 4) and attributed the decreased water conductivity of roots under saline condition to the decrease in the activity of water channel. They also showed the curing effect of Ca^{2+} on the NaCl-induced decrease in water conductivity. In our experiments, increasing the NaCl concentration to 40 mM decreased the water uptake rate in both soybean cultivars (Fig. 5), indicating a decrease in water conductivity in the roots. Leidi and Saiz (1997) reported that improved capacity of water uptake under salt stress led to a higher growth rate in cotton.

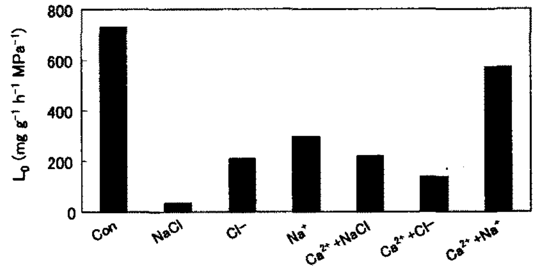

Fig. 4. Hydraulic conductance (L0) of melon roots treated for 3 days with 50 mM NaCl, Cl- (25mM KCl and 20 mM $MgCl_2$), Na+ (20 mM $NaNO_3$, 15 mM NaH_2PO_4 and 7.5 mM Na_2SO_4), and 10 mM $CaCl_2$ added 2 days before the above treatments. (Data based on Martínez-Ballesta et al., 2000)

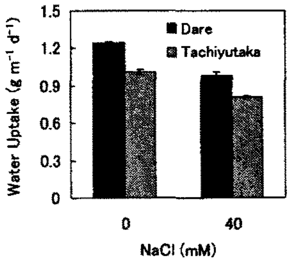

Fig. 5. Average water uptake rate per unit root length of two soybean cultivars, Dare (salt-tolerant) and Tachiyutaka (salt-sensitive), during 3-days on the 4th, 5th and 6th day after salinity treatment. Means ± SE, n=3. (Data based on An *et al.*, 2002a)

Figure 5 shows that cv. Dare had a higher water uptake rate per unit root length than cv. Tachiyutaka under both saline and non-saline conditions, indicating higher water conductivity in the roots of cv. Dare compared with cv. Tachiyutaka. Since the cell elongation rate is primarily determined by the amount of water absorption under salt stress (Nonami, 1998), it is conceivable that the higher water uptake in cv. Dare may contribute to its greater growth under saline conditions.

4. Na^+ permeability under salt stress

The Na^+ accumulation in the cytoplasm or apoplast interferes with plant metabolic functions (Greenway and Munns, 1980), such as photosynthesis (Seemann and Critchley, 1985; Yeo *et al.*, 1985). Therefore, keeping a low Na^+ concentration in the transpirations stream is important for reducing Na^+ entering the leaf. If we consider the whole root system composed of complex anatomical structure and functions as an interface between plant shoot and soil environment, the amount of Na^+ transported from external environment to the shoot will depend on the Na^+ permeability in the roots. Schubert and Läuchli (1990) reported that the plasma membrane in the root epidermis and cortex of the maize genotype with high salt tolerance had relatively low Na^+ permeability than the sensitive genotype.

As water passes through the roots, salts are selectively transported by transport proteins in plasma membranes. These transport proteins that mediate ion flux can be generally categorized as pumps, carriers, and channels (Sussman and Harper, 1989). Pumps (such as H^+—ATPase, H^+—PPase, Ca^{2+}—ATPase, Na^+—ATPase) directly utilize metabolic energy for transport, whereas carriers (such as Na^+/H^+ antiporter, K^+—H^+ symporter) couple uphill transport of one solute to the downhill movement of another, either in the same (symporter) or opposite (antiporter) direction. Channels (such as K^+ channel) mediate passive transport, i.e. movement down a free energy gradient. The Na^+ influx across the plasma membrane is passive and the efflux is active (Niu *et al.*, 1995), so the activity of export-proteins would be rather important in Na^+ exclusion.

The Na^+ permeability of the roots in different plant species was estimated by comparing the Na^+ accumulation in plant tissues. As shown in figure 6A, for example, Na^+ contents in the whole plant of cv. Dare was lower than those of cv. Tachiyutaka grown at the same NaCl level. The results suggest that the roots of cv. Dare either take up less Na^+ ions or exclude more Na^+. In addition, the higher rate of water uptake in cv. Dare compared with cv. Tachiyutaka (Fig. 5) may result in an increase in Na^+ concentration in the interface between roots and soil environment, and thus increase the influx electrochemical gradient of Na^+. However, less Na^+ accumulation in cv. Dare was found compared with cv. Tachiyutaka. This suggests that the proteins responsible for Na^+ exclusion in cv. Dare worked more effectively than cv. Tachiyutaka. The Na^+ concentrations in the root exudates of two melon cultivars differing in salt-tolerance (Fig. 6B) would lead to the same conclusion. The significantly lower Na^+ concentration was detected in the root exudates of salt-tolerant cv. Galia compared with the sensitive cv. Revigal C-8. This result also suggests that the roots of cv. Galia transport less Na^+ to the xylem stream and thus show a lower permeability to Na^+ than cv. Revigal C-8. Conclusively, characteristic low Na^+ permeability of the roots in the salt-tolerant cultivars primarily contribute to their greater growth under saline conditions.

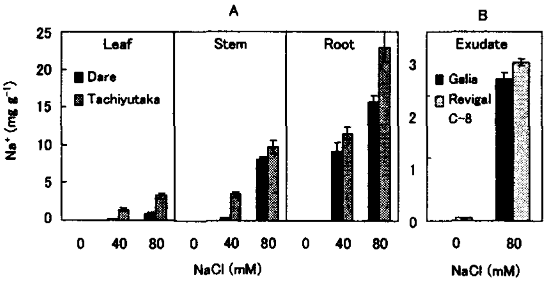

Fig. 6. A: Na^+ concentrations in leaf, stem, and root of two soybean cultivars, Dare (salt-tolerant) and Tachiyutaka (salt-sensitive), treated with 0, 40, and 80 mM NaCl for 3 weeks. B: Na^+ concentrations in exudate of two melon cultivars, Galia (salt-tolerant) and Revigal C-8 (salt-sensitive), after 15 days exposure to 0 or 80 mM NaCl. Means ± SE, n=4. (Data based on An *et al.*, 2002a, b)

5. Osmotic potential under salt stress

The osmotic adjustment *in vivo* helps the plants to decrease osmotic potential and thus maintain water balance (Blum *et al.*, 1996). As shown in figure 7, osmotic potentials of the roots of two soybean cultivars were decreased with increasing NaCl concentration. The osmotic potential within the cytoplasm is maintained by compatible solutes (polyols, glycerol, mannitol, sucrose, proline, and glycinebetaine) while inorganic salts accumulate inside the vacuole. It is reported that osmotic adjustment is more strongly dependent on compatible solute synthesis rather than ion accumulation in glycophytes (Shannon, *et al*, 1994).

In our experiment, both soybean cultivars showed similar osmotic potential, while significantly lower osmotic potential was developed in cv. Dare as compared with cv. Tachiyutaka at 40 and 80 mM NaCl levels (Fig. 7). The osmotic barrier in the roots has been suggested to have membrane-like properties such as ion-specific selectivity (Steudle and Frensch, 1989). So the low osmotic potential developed in the roots of cv. Dare may increase its ion selectivity, i.e. Na^+—specific exclusion and uptake of other ions. Besides, the lower osmotic potential in the roots of cv. Dare under saline condition may result in more effective water uptake than that of salt-sensitive cv. Tachiyutaka, as shown in figure 5.

On the other hand, the osmotic adjustment generally cost metabolic energies for making organic solutes and ion transport (Schwarz and Gale, 1981; Stavarek and Rains, 1985; Yeo, 1983). It has been estimated that the energy costs associated with the use of salts as osmoticum may be much lower than the use of organic solutes (Raven, 1985).

6. Root pressure under salt stress

The water potential difference between the culture medium and xylem develops root pressure (Hirasawa 1994). Under saline condition, the water potential of the culture medium is decreased by salinity, while the accumulation of ions or solutes for osmotic adjustment decreases the water potential of xylem. So, the extents of the decreases in water potential of the culture medium and xylem determine the root pressure under saline condition. It is reported that the root pressure is closely related with physiological activity of roots and affects root exudation rate. Higher the exudation rate, higher the root pressure and physiological activity (Katou, 1998).

Soybean and melon cultivars show a decrease in root exudation with NaCl treatment (Table 2), indicating a decrease in root pressure under salt stress. In soybean plants treated with 40 mM NaCl, the amount of exudates decreased by 90% in cv. Dare, and by 99% in cv. Tachiyutaka. The salt-tolerant cultivars Dare and Galia had significantly higher amount of root exudates than the salt-sensitive cultivars Tachiyutaka and Revigal C-8 under NaCl treatments, respectively.

Table 2. Amount of exudate (mg g-1 root f.m.) from the roots of two soybean cultivars, Dare (salt-tolerant) and Taciyutaka (salt-sensitive), after 3 days exposure to 0, 40, and 80 mM NaCl and two melon cultivars, Galia (salt-tolerant) and Revigal C-8 (salt-sensitive), after 15 days exposure to 0 or 80 mM NaCl. Means ± SE, n=4.

Cultivar	NaCl (mM)		
	0	40	80
Dare	54.5 ± 0.1	5.68 ± 0	0
Tachiyutaka	54.3 ± 0.2	0.32 ± 0.01	0
Galia	70.3 ± 5.0	—	4.78 ± 0.38
Revigal C-8	80.6 ± 3.7	—	2.68 ± 0.31

(Data based on An *et al.*, 2002a,b)

These results indicate that salt-tolerant cultivars develop a higher root pressure. It is conceivable that the lower osmotic potential in the roots of cv. Dare (Fig. 7) contributed to its higher root pressure. According to Martinez-Ballesta *et al.* (2000), the higher root pressure in salt-tolerant cultivars indicates a higher hydraulic conductivity, which improves the water uptake by the roots and thus improve the overall water relations of the plants under saline conditions.

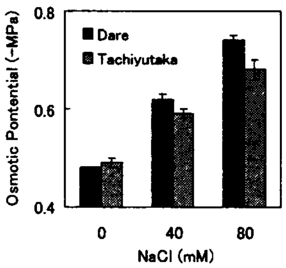

Fig. 7. Root osmotic potentials of two soybean cultivars, Dare (salt-tolerant) and Tachiyutaka (salt-sensitive), after 23 days exposure to 0, 40, and 80 mM NaCl. Means ± SE, n=4. (Data based on An et al., 2002a)

7. Conclusions

Salinity is intricately meshed with water and nutrient uptake by plants. Salinity effects at low and moderate concentrations are so ubiquitous that it has become one of the most severe and insidious limiters of crop growth and production. Plant growth is suppressed when specific ion concentrations exceed their thresholds and become toxic. Due to the selective ion absorption by roots, the ion concentrations transported to the shoot are significantly different from those in the external medium. Therefore, the characteristics of roots in ion and water absorption are critically important in salt tolerance of plants.

Basically, the greater root growth under saline condition improves all the functions in the roots that response to salinity. The observed higher water uptake in the roots of the tolerant cultivar compared with the sensitive ones suggests the importance of water uptake ability of the roots under salinity condition. Since the ionic concentration range suitable for the normal physiological function of cell is very narrow, the controlling ability for Na^+ permeation into xylem stream through the roots may critically determine the salt tolerance. This Na^+ permeability in the roots depends on the activity of the proteins for Na^+ exclusion, which may be related with the physiological activity of roots. The ions or solutes accumulations in the roots result in a decrease in osmotic potential and thus create root pressure. The higher root pressure and lower root osmotic potential might be correlated with higher physiological activity of roots and lower Na^+ permeability, which lead to higher salt tolerance as indicated by greater growth.

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