



Research Paper

A shoot based Na⁺ tolerance mechanism observed in pumpkin—An important consideration for screening salt tolerant rootstocks



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ABSTRACT

Ion accumulation and growth of 28 commercial pumpkin rootstocks and 16 inbred lines were investigated under saline conditions. Significant variation and correlations were observed in seven morphological traits and three ionic traits. 44 genotypes were clustered into three groups, namely, tolerant (low Na⁺ concentration in the shoot, low salt injury index, and high relative shoot dry weight), sensitive (high Na⁺ concentration in the shoot, high salt injury index, and low relative shoot dry weight) and intermediate (high Na⁺ concentration in shoot, low salt injury index, and high relative shoot dry weight) by three key traits. Na⁺ concentration in four parts of seedlings (root, stem, leaf veins, and mesophyll) were determined. Results indicated that different pumpkins groups show various Na⁺ distribution patterns (tolerant group restricted Na⁺ in roots, intermediate group restricts Na⁺ in their stems and leaf veins and sensitive group transported more Na⁺ to mesophyll tissues). Six genotypes were selected from three groups as rootstocks and grafted with a salt sensitive cucumber scion for evaluation the salt tolerance in grafting combinations. Results showed that Na⁺ concentration in the shoot of cucumbers grafted onto tolerant pumpkins was significantly lower than onto the sensitive and intermediate pumpkins. However, no significant differences were observed between the cucumbers grafted onto sensitive and intermediate group of pumpkins. These findings indicate that beside Na⁺ restriction in root, an alternative mechanism in shoot may be adopted by some pumpkin genotypes; if those genotypes are used as rootstocks they cannot perform as well as in self-root condition for their shoots have be replaced with cucumber scions. Our finding provides an insight into the screening of rootstocks tolerant to salinity.

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1. Introduction

Soil salinity is a global challenge affecting agricultural production worldwide. More than 800 million hectares of agricultural land suffer from soil salinity (Rengasamy, 2010). *Cucurbitaceae* plants, such as melon, watermelon, and cucumber, are a group of glyco-phytes that serve as major fruit vegetables, and most of these are sensitive to sodium (Na⁺) stress rather than chloride stress (Cl⁻) (Zhu et al., 2008). The increased Na⁺ concentration in shoots (SNa) significantly contributes to salinity stress. Excess Na⁺ in cell inter-

feres with the binding of potassium (K⁺) and with the activation of key enzymes involved in photosynthesis (Munns and Tester, 2008; Yue et al., 2012).

However, pumpkin which belong to the same family (*Cucurbitaceae*), is considerably more tolerant under saline conditions. Grafting onto *Cucurbita* plants to achieve increased salinity tolerance is a common agricultural practice in vegetable production. In China, Japan, Korea, and several other Asian countries, approximately 90% of watermelon and cucumber grown in greenhouses are grafted onto pumpkin or gourd rootstocks (Lee and Oda, 2010). A large number of pumpkin (*Cucurbita* spp.) cultivars have been bred as rootstocks for practical use in melon and cucumber production (Traka-Mavrona et al., 2000; Lee et al., 2010). The breeding for salt tolerant rootstock is crucial for grafted seedling production. In this process, screening of parents that show high tolerance to salinity in self-rooted condition is a common strategy. Salinity tolerance is controlled by polygene, several traits such as Na⁺ concentration, visual salt injury, biomass reduction, and mortality rate can

Abbreviations: SI, Salt injury index; SDW, Shoot dry weight; SL, Shoot length; LN, Leaf number; RSDW, Relative shoot dry weight; RSL, Relative shoot length; RLN, Relative leaf number; SNa, Na⁺ concentration in shoot; SK, K⁺ concentration in shoot; SK/Na, K⁺ concentration to Na⁺ concentration in Shoot.

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be used to screen salt-tolerant genotypes. However, better performance of non-grafted pumpkin does not mean tolerant behavior under grafting conditions, because grafting compatibility between the scion and the rootstock must be considered, moreover, high tolerance of pumpkin itself is not always attributed to the ability of Na^+ restriction.

It has been proved that the rootstock improved salt tolerance by restricting excess Na^+ in root (Huang et al., 2009; Colla et al., 2010; Edelstein et al., 2011). This mechanism claims that the pumpkin which is going to be used as the rootstock share the identical Na^+ restricting pattern and provide a clue for the screening of salt-tolerant pumpkin rootstocks. It is presumed that pumpkin that contains low Na^+ concentration in the shoot is a candidate rootstock. However, all of the pumpkin genotypes do not follow this pattern. Recently, a pumpkin genotype named N12 that shows a lower biomass reduction under salt condition while maintains a much higher Na^+ concentration in its shoot compared with a sensitive genotype (Xie et al., 2015). This finding suggests that different salt-tolerant mechanisms may exist in various pumpkin genotypes.

The mechanisms of tolerance to Na^+ stress fall into two categories (Munns and Tester, 2008), namely, Na^+ exclusion and tissue tolerance. Na^+ exclusion is an indispensable mechanism of salinity tolerance among glycophytes, such as *Arabidopsis thaliana* (Moller et al., 2009), *Zea mays* (Fortmeier and Schubert, 1995), *Triticum turgidum* (James et al., 2006), and *Poncirus trifoliata* (Walker, 1986). In these mechanisms, Na^+ is restricted in the roots or excluded from the roots to ensure that Na^+ does not accumulate up to the toxic levels in the shoot. Tissue tolerance is another mechanism that requires compartmentalization of Na^+ at the cellular level to prevent Na^+ from causing damage. High Na^+ concentration in shoot can be tolerated through vacuole partitioning or through secretion through salt glands. This mechanism is widely observed in halophytes, such as *Suaeda maritima* (Wang et al., 2007), *Puccinellia peisonis*, and *Spartina townsendii* (Koyro and Stelzer, 1988). Recently, some reports suggest that Na^+ exclusion is not the only mechanism involved in glycophytes. Australian bread wheat varieties (*Triticum aestivum*) (Genc et al., 2007) and *Triticum monococcum* (Rajendran et al., 2009), maintain a relatively high Na^+ in their shoots, demonstrating the lack of correlation between shoot Na^+ and salt tolerance. A study on *Arabidopsis* has shown the absence of inverse relationship between shoot Na^+ accumulation and salinity tolerance in different *Arabidopsis* genotypes, whereas *AtAVP1* expression is positively correlated to tolerance, indicating that some *Arabidopsis* genotypes use mechanisms that involve tolerance of tissue to Na^+ (Jha et al., 2010).

Does the mechanism of tissue tolerance exist in pumpkin? If the answer is yes, it may cause a misjudgment when a candidate pumpkin rootstock adopted the way of tissue tolerance rather than Na^+ restriction in the root. In this case, pumpkin may exhibit salt-tolerant behavior under non-grafted conditions but sensitive when used as a rootstock under grafted conditions. A large number of studies have investigated Na^+ restriction mechanism of pumpkin under grafted conditions, however, a few studies have investigated the relationship between SNa and salinity tolerance in non-grafted pumpkins. Furthermore, the evaluation of pumpkin salt tolerance before and after grafting is necessary. This study aims (1) to compare the salt tolerance of 44 pumpkin genotypes, (2) to evaluate different selectable traits to screen the salinity tolerance of pumpkin rootstocks, particularly to determine the relationships among leaf injury, Na^+ concentration in the shoot, and growth parameters under salt stress, and (3) to compare the salt tolerance of selected pumpkin rootstocks when salt-sensitive scion is grafted onto these rootstocks, as well as the possible mechanism involved.

2. Materials and methods

2.1. Experiment 1: self-rooted screening

2.1.1. Plant material

The plant materials used in self-root screening experiment consisted of 28 commercial rootstocks and 16 inbred lines of pumpkin obtained from the Key Laboratory of Horticultural Plant Biology (Ministry of Education, Wuhan, People's Republic of China). More information on the pumpkins used in this study can be found in **Table S1**.

2.1.2. Growth conditions and NaCl treatment

The experiment was conducted in a greenhouse at the National Center of Vegetable Improvement, Huazhong Agricultural University, Central China (latitude 30°27'N, longitude 114°20'E at an altitude of 22 m above the sea level). The seeds of 44 pumpkin genotypes were soaked in water for 6 h and incubated in the dark at 30 °C until germination. Then the seeds were sown in 50 hole plug trays (54 cm × 28 cm, volume = 60 cm³ per hole) filled with a 2:1 (v/v) mixture of peat and perlite (bulk density = 0.3 g/cm³, total porosity = 80%, pH = 6.2). After the pumpkins developed two true leaves, the seedlings were transferred into pots (with 12 cm diameter) filled with the same substrate used in plug trays. The plants were irrigated with 100 mL of full-strength Hoagland solution (Hoagland and Arnon, 1950). To avoid salt shock, NaCl was added to the nutrient solution by gradually increasing its concentration by 50 mM per day until the final concentration (150 mM) was reached. This concentration of 150 mM NaCl was chosen through a multi-concentration gradient NaCl preliminary test and we observed that under 100 mM most of the plant material showed modest salt injury while under 200 mM most of them withered. Control plants were simultaneously irrigated with identical nutrient solutions but without NaCl application. The experiment was conducted at a mean temperature of 27.6 °C/18.8 °C (day/night), mean relative humidity of 76.8%/84.4% (day/night), and CO₂ concentration of 360 μmol mol⁻¹. The average daily photosynthetic active radiation inside the greenhouse was 26.6 mol m⁻² day⁻¹ with a maximum radiation of 1570 μmol m⁻² s⁻¹. The experiment was conducted according to randomized complete block design. Each genotype was represented by 30 plants with 3 replications under NaCl stress or controlled condition, respectively.

2.1.3. Salt injury index (SI) and growth parameter

Salt injury index (SI) was determined 20 days after treatment (DAT), and classification of the standard and calculation of the SI were performed according to the method described by Zhen et al. (2010) with some modifications. Leaf injury ratings of the second leaf above the base of the seedling were determined based on a score of 1–4. An injury score of 1 was assigned to leaves showing no yellowing or damage; a score of 2 is assigned to slightly yellowish or slightly damaged leaves; a score of 3 is assigned to leaves showing moderate yellowing or damage; and a score of 4 is assigned to leaves showing severe yellowing or damage. SI was calculated as follows and 10 seedlings for each triplicate were used:

$$SI = \sum_i \frac{(\text{score value} \times \text{number of plants})}{\text{total number of plants}}$$

Six plants from the total 30 plants (two uniform seedlings from each replicate) were selected for data collection in each treatment. The shoot of plants from the salt-treated and control plants were harvested 20 DAT (The part above the cotyledonary leaves or grafting union was considered as "shoot" in this study, and the leaf number of all entirely expanding leaves (LN) and shoot length from the bottom of shoot to the tip of newest leaf (SL) was recorded. The shoots were subsequently placed in a forced air oven at 65 °C for

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