SODIUM TRANSPORT AND DISTRIBUTION IN SWEET PEPPER DURING AND AFTER SALT STRESS

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Abstract

In hydroponic systems often saline water is used in nutrient solutions. Transpiration leads to a steady increase of the salt concentration. To avoid unfavourable salt conditions, solutions are renewed, regularly. So, plants are exposed to varying sodium concentrations. In this paper, the sodium distribution and its transport-profile in sweet pepper (*Capsicum annuum* L.) under stress conditions and the consequences of transfering the plants to a sodium-free nutrient solution will be discussed.

Plants can tolerate sodium stress very well. They appear to keep sodium out of the photosynthetic apparatus efficiently. Sodium is accumulated in the root cells and in the pith cells of the stem, mostly in the basal part. Almost no sodium is directed to the leaves and the fruits. Similar to the sodium profile of the pith cells, the sodium concentration of the xylem sap shows a concentration gradient decreasing towards the tip. A split root experiment, in which a pulse labelling with radioactive sodium was carried out, showed the involvement of phloem transport. During the salt stress period sodium is recirculated between phloem and xylem. Apparently, pith cells, the intermediates between the xylem and phloem veins, play a decisive role in the (re)circulation of sodium through the plant. After transferring the plants to a sodium-free solution a fast release of sodium occurs. In this paper, a model for a general transport mechanism will be presented. The consequences of sodium release into the nutrient solution after a refreshment will be calculated for the situation in greenhouses.

1. Introduction

Sweet pepper (*Capsicum annuum* L.) is an important, agricultural crop in the Netherlands. This crop is often grown on a hydroponic system in which a nutrient solution long circulate in order to minimize contamination of soil with nutrients. Since the introduction of this cultivation technique in greenhouse agronomy, the problem of mild salt stress has become actual. Near the coast, rain water or tap water containing some sodium chloride is often used for the preparation of nutrient solutions. Part of the sodium chloride in the solution is excluded by the plants, resulting in a steady increase of the salt concentration in the root medium. In order to avoid excessively high salt concentrations, solutions are regularly replenished, exposing plants to gradually increasing sodium concentrations and abrupt declines during cultivation. Sweet pepper is susceptible to mild sodium stress: When 11 mM sodium is present in the medium, fruit yield is diminished with *ca.* 5% (Post and Klein-Buitendijk, 1996a). Moreover, a simultaneous increase of the potassium concentration makes the fruits more sensitive to the occurrence of blossom-end-rot (Post and Klein-Buitendijk, 1996b).

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Most studies (recently reviewed by Adams *et al.*, 1995) focus on high salt stress as it poses serious limitations to agriculture by yield losses and crop damage in many areas. Several plant species show a special mechanism to correct for saline environments (Fernandez *et al.*, 1996; Nakamura *et al.*, 1996; Zhu *et al.*, 1997). Some plants avoid growth reduction or damage to the photosynthetic system by compartmentalisation of sodium in special organs, like glands or extracellular compartments (Barkla & Pantoja, 1996). Other species, like bean (Jacoby, 1979) and *Lupinus albus* (Munns, 1988; Munns *et al.*, 1988), show recirculation of sodium through xylem and phloem in the stem. In the case of recirculation, sodium has to be taken up into pith cells of the stem, followed by sodium efflux, mainly directed towards the phloem vessel.

The question arises how sweet pepper controls sodium levels in the medium during salt stress and after replenishment of the nutrient solution. Till now, less is known about the effect of changing mild saline conditions. Based on a sodium distribution pattern in sweet pepper during a sodium treatment and after refreshment of the nutrient solution, a transport model will be presented. Furthermore, the consequences of changing sodium concentrations in hydroponic systems will be discussed on the basis of a rough calculation for the situation in greenhouses during summer.

2. Materials and methods

2.1. Plant growth conditions

Seeds of *Capsicum annuum* L., cv Mazurka, were sown in Perlite and kept at 30 °C in the dark. After 9 days the seedlings were transferred to a hydroponic system containing a nutrient solution. The composition of the solution was: 3.73 mM $Ca(NO_3)_2$; 4.40 mM KNO_3; 0.97 mM KH_2PO_4; 1.92 mM $MgSO_4$; 0.89 mM K_2SO_4; trace elements and Fe-EDTA. Further growth occurred in a growth chamber at 20 °C, 70% RH and a photoperiod of 12 hours (150 μmol m^{-2} s^{-1}).

For pruning sweet pepper, the procedure used in commercial practice was followed: the largest of each dichotomic branch was retained, while the other was pruned just above its first leaf.

2.2. Sodium stress period.

Nine-week-old plants were transferred to pots containing nutrient solution supplemented with 10 mM NaCl or to 10 mM NaCl, followed by exposure to a sodium-free nutrient solution for an additional week. Plants were harvested at distinct intervals, as indicated in the text and divided into roots, stem, leaves, and fruits. The stem was subdivided into six internodal segments of *ca.* 5 cm and fresh and dry weights were determined. The plant parts were ground to powder and the sodium and potassium content was analysed by atomic absorption, using a Varian Techtron (AA4).

2.3. Statistical analyses

Differences between treatments were determined by analyses of variance (ANOVA) using GENSTAT 5 (Rothamsted Experimental Station, Harpenden, UK).

3. Results and discussion

3.1. Sodium uptake and distribution

Sweet pepper takes up sodium from the nutrient solution (Fig. 1), but the amount of sodium accumulated in the whole plant after one week is still lower than the external concentration. Moreover, the increase of sodium content in the plant levels off after about a week. This indicates that sodium uptake is very well regulated.

Sodium accumulates both in root and shoot (Fig. 2). In the shoot tissue, it preferentially accumulates in the pith cells of the stem, while hardly any sodium is directed to leaves and fruits. The figure shows that the sodium content is highest in the basal part of the stem (even two times higher than in the root). Towards the apex, the sodium content decreases. In the xylem sap the sodium concentration also decreases towards the shoot tip (Blom-Zandstra *et al.*, 1998). The concentration in the xylem sap is almost equal to that in the pith cells, indicating a well regulated exchange of sodium between both tissues.

3.2. Replenishment of the nutrient solution

When plants are transferred to a sodium-free nutrient solution, the amount of sodium in the pith cells of all stem segments decreases to about 50% in one week (Fig 2). The content still declines exponentially towards the apex, similar to that observed when plants remain on a sodium-containing nutrient solution. In contrast, plant transfer completely changes the situation in the xylem sap. The concentration gradient towards the apex disappears (Blom-Zandstra *et al.*, 1998), suggesting that the well regulated exchange between xylem sap and pith cells may have been altered. Transfer of plants to a sodium-free solution has also an effect on downward sodium fluxes within the plant. From a split-root experiment in which extra radioactive sodium was added to one root part (Blom-Zandstra *et al.*, 1998), it was shown that during a sodium-treatment no labelled sodium entered in the unlabelled root part. However, immediately after refreshment of the medium, sodium entered the unlabelled root part and was released from the plant into the medium. This phenomenon clearly indicates the involvement of phloem transport, which will be discussed in the following transport model.

3.3. Cellular transport model

It has been shown that the sodium content decreases exponentially towards the apex in both pith cells and xylem sap. Moreover, the sodium concentration in the pith cells is equal to that in the xylem sap. This is a clear indication for passive diffusion through the plasma membrane (Fig. 3A), which is proportional to the diffusion resistance for sodium influx through the plasma membrane. After one week a steady state situation has been reached (Fig. 1). Yet, the steep gradient towards the apex is maintained, also when plants are only harvested after two weeks. This indicates that the sodium that enters the pith cells is fast removed from the cytoplasm. This is only possible with an active pump system on the tonoplast (Fig. 3B), as earlier described for *Plantago maritima* L. (Staal *et al.*, 1991).

3.4. Whole plant transport model

The diffusion-controlled influx into the pith cells is responsible for the the maintenance of a steep gradient in the stem (Fig. 4A). This gradient can only be maintained when sodium is continuously supplied at the stem base and dependent on the local xylem concentration, is extracted from the xylem by the pith cells. This indicates the presence of an efflux system in the pith cells, which can not be directed towards the xylem sap (Fig. 4B). As described in the above mentioned split-root experiment (Blom-Zandstra *et al.*, 1998) radioactive sodium did not enter the unlabelled root part during the sodium treatment, but only when sodium was withdrawn from the nutrient solution. This can only be explained by a model in which sodium leaks from the phloem into the xylem again. A continuous supply at the stem base during the steady state (constant mild sodium treatment) suggests a constant supply of sodium into the xylem (Fig. 4C). This transport mechanism fits well in the Münch model for assimilates and nutrients (Esrich *et al.*, 1972). The sudden release into the medium after refreshment probably results from a change in the diffusion resistence for passive efflux from the pith cells, which is regulatory controlled by the sodium concentration in the medium.

4. Concluding remarks

4.1. Cultivation strategy

We conclude that sodium recirculation is strictly regulated: the external sodium concentration controls internal sodium fluxes. For growers these results have important consequences. A replenishment of the nutrient solution results in a rapid release of sodium into the nutrient solution, increasing the sodium concentration. Young plants grown on 15 mM NaCl in the nutrient solution for two weeks, will lose net 30 % of their accumulated sodium into the medium when they are transferred to a sodium-free solution during the third week of the experiment. With plants in a greenhouse that have reached a substantial size, refreshment of the nutrient solution may cause a considerable leakage of sodium into the medium. The amount of sodium leakage can easily be calculated. For a growers situation in June it can be supposed that: 1. plants have an average weight of 1500 grams, when a plant density of 3.12 m^{-2} is assumed (Gijzen, 1994) and 2. approximately 10 liters nutrient solution per plant is recirculating in the system (C. Stanghellini, personal communication). When the plants leak 2.25 mmol sodium in one week (according to the results measured with small plants), the sodium concentration in the hydroponic system will increase with 0.8 mmol/l. So, it is unfavorable when the sodium concentration varies too much. It has been shown (Fig. 1) that sodium uptake by sweet pepper reaches a steady state. Moreover, the amount of sodium accumulated in the plant will not exceed the external concentration. With a steady external concentration sodium uptake by the plant is only determined by growth. To compensate for an inevitable increase of the sodium concentration in the nutrient solution (especially in the summer), it is recommended to refresh only small parts of the nutrient solution to keep the variation of the sodium concentration within small margins.

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Figures

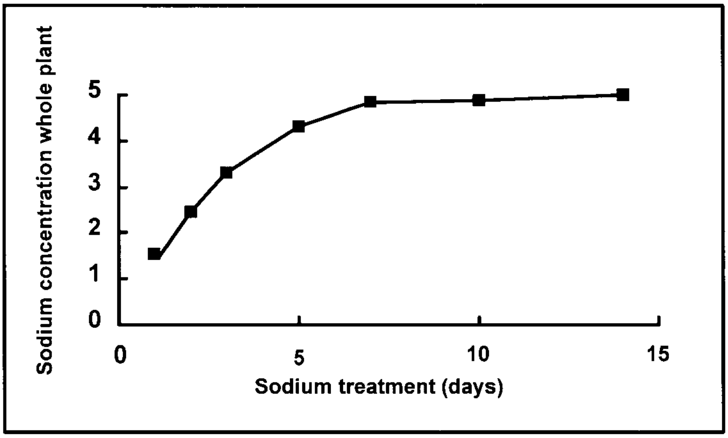

Fig. 1 Sodium concentration (mmol/kg FW) with time by sweet pepper grown on a nutrient solution with 10 mM NaCl

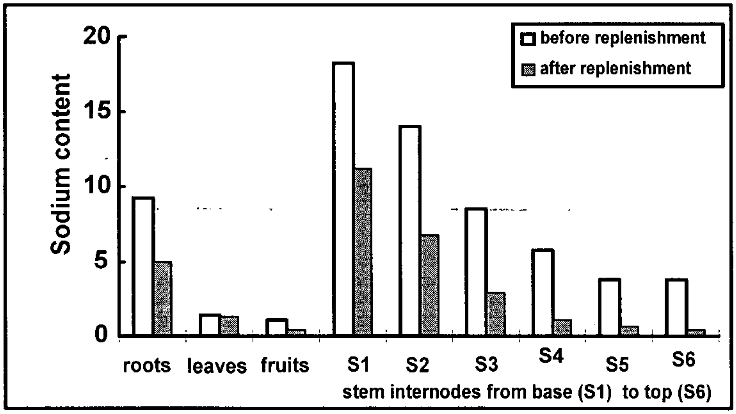

Fig. 2 Sodium content (mmol/kg FW) of different plant parts

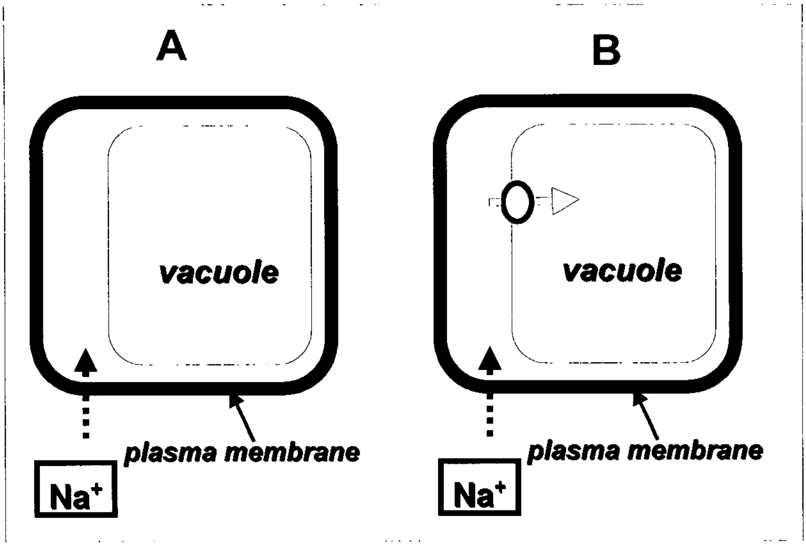

Fig. 3. Cellular sodium transport model with diffusion-controlled transport (⋯⋯▶) and energy-dependent transport (·O·▶).

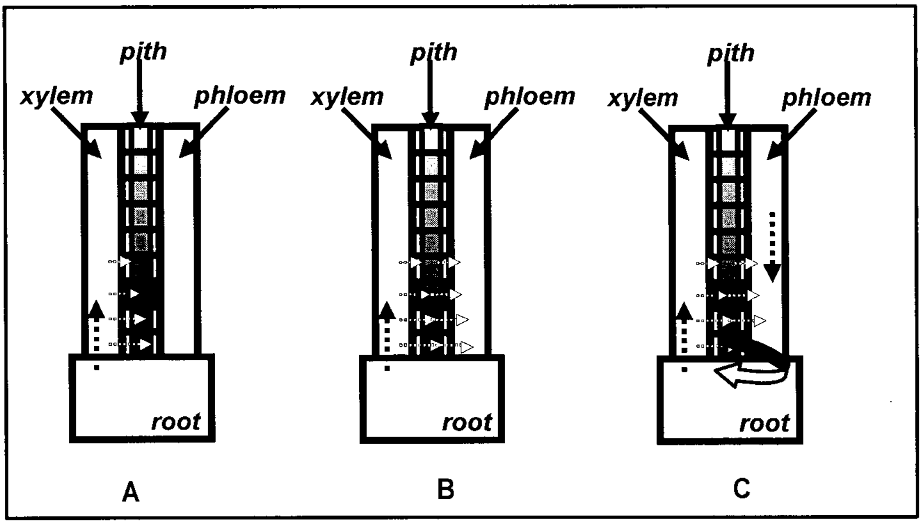

Fig. 4. Whole cell sodium transport model.