Up-scaling salt effects in cucumber: trade-off between photosynthesis and toxic ion accumulation

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Highlights: A dynamic cucumber FSPM, describing the effects of salinity on the plant morphology and the pattern of sodium accumulation in leaves, is parameterized and evaluated. This model is a first step in exploring mechanisms which improve plant tolerance and WUE at canopy level under salinity stress.

Keywords: Salinity stress, Na^+ accumulation, toxic effect, L-Cucumber, photosynthesis, transpiration

INTRODUCTION

Under salinity stress, concentrations of Na^+ and Cl^- ions in the xylem sap increase significantly (Wolf and Jeschke, 1987) and these two ions accumulate excessively in mature leaves (Munns and Tester, 2008). Once the cells in leaves become incapable of compartmentalising those ions in the vacuole, chlorosis or even necrosis appears (Stępień and Kłobus, 2006). Plants attempt to maximize carbon assimilation and minimize water loss, but there is a trade-off between transpiration and carbon assimilation. Optimization of this trade-off can be interpreted mathematically as the maximization of water use efficiency (WUE, assimilation per unit of water loss). Since the toxic ions are transported by the transpiration stream, an increase in WUE indicates a lower uptake of toxic ions per unit of carbon assimilated under salinity. This means that plants with higher WUE may delay the accumulation of ions to a toxic level which is in line with experimental results showing an inverse relation between Na^+ accumulation and WUE in a comparison of tomato cultivars (Al-Karaki, 2000). Moreover, inhibition of photosynthetic ability caused by accumulated toxic ions diminishes WUE further (Stępień and Kłobus, 2006). Therefore, a low WUE under salinity stress may even result in a negative feedback on plant growth. Since WUE and transpiration is closely related to leaf morphology and leaf distribution within canopy, functional-structural plant models (FSPM) should be a proper tool to study how WUE can be improved under salinity stress. The aim of this work is to construct and to parameterize the first FSPM describing Na^+ accumulation and its toxic effect on physiological functions.

MATERIALS AND METHODS

Experiments and measurements

Cucumber (*Cucumis sativus* L.), a salt sensitive crop, was chosen. Cucumber seedlings ('Aramon' Rijk Zwaan, De Lier, the Netherlands) were grown in three growth chambers in the Institute of Biological Production Systems, Leibniz Universität, Hannover, Germany. Cucumber plants were grown hydroponically under a 12-h photoperiod of 350 µmol $m^{-2}s^{-1}$ PPFD (photosynthetic photon flux density) with 24/20°C day-night temperature and 380 ppm CO_2 concentration with four salinity levels, 0, 28, 56 and 84 mM NaCl in solution. In experiment 1, light response curves of gas-exchange parameters (photosynthesis, stomatal conductance and transpiration) were measured between days 8-10 after salinity start using a Li-6400 gas analyzer (LI-COR Inc., Lincoln, NE, USA). Final organ size (leaf, petiole and internode) was measured and dry masses of plant materials were weighed after drying at 70°C for 72 hours. Thereafter, plant samples were ground for Na^+ analysis. Sodium concentration in the transpirational stream was estimated by total Na^+ accumulated in the shoot over total transpiration. These data were used for model parameterization. In the experiment 2, cucumber plants were grown at the same environmental condition and data were used to evaluate the model.

Model description

Cucumber architecture model is based on *L-Cucumber* (Kahlen and Stützel, 2011). Influences of salinity stress on plant morphology and physiology are sketched in Fig. 1. Final internode length (*FIL*) is reduced proportionally with salinity level S_s:

$$FIL(S_s) = FIL(1-0.0017S_s) \qquad (1)$$

Stomatal conductance (g_s) is a function of PPFD (I_{Inc}) with additional influence by S_s and ion concentration in leaves (S_{leaf}):

$$g_s = f(S_{leaf})(g_{s\_min} + b\, I_{Inc})(1-\alpha S_s) \qquad (2)$$

where minimum g_s (g_{s_min}) is 0.26, b and α are 0.0001 and 0.0065 respectively. $f(S_{leaf})$ is the function described in Fig.2. Light conversion efficiency (LCE) is influenced by I_{Inc}, osmotic restriction and S_{leaf}

$$LCE = f(S_{leaf})f(I_{Inc})(1-\beta S_s) \qquad (3)$$

where $f(S_{leaf})$ is the function described in Fig. 2, $f(I_{Inc})$ is described in Wilson *et al.* (1992) and β (0.0047) is the osmotic effect on LCE derived from measured data. Transpiration (E) is linearly related to g_s ($E = 8.93g_s + 0.08$), and ion accumulation (S_{acc}) is the product of the ion concentration in the xylem sap (S_{xy}) and E. S_{xy} is calculated by S_s:

$$S_{xy} = 0.51e^{(0.05\, Ss)} \qquad (4)$$

and 38% of S_{acc} was partitioned to the supporting tissues. The relationship between the Na^+ concentration and gas-exchange parameters was derived by normalizing and refitting corresponding published data (James *et al.*, 2002, Fig. 2). The reduction of leaf area due to salinity is determined by the dry weight partitioned to the leaves and specific area (290 cm^2 g^{-1}, not influenced by salinity).
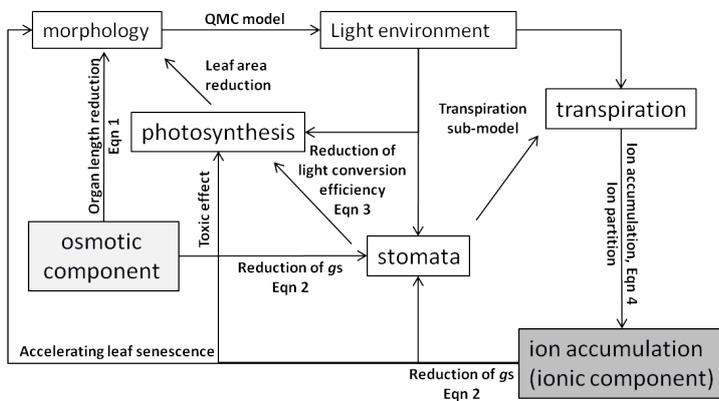

Fig. 1 Model structure representing effects of different components of salinity on morphology and function.

RESULTS AND DISCUSSION

In this model, a reduction of leaf area under salinity stress is due to the decrease of light conversion efficiency and then the dry mass partitioned to the leaves. In comparison with the control plants, leaf area at slight and high salinity stress (28 and 56 mM NaCl) was reduced about 15-20% and 50-60% respectively. The simulated results are quite in agreement with the measurements (Fig. 3).
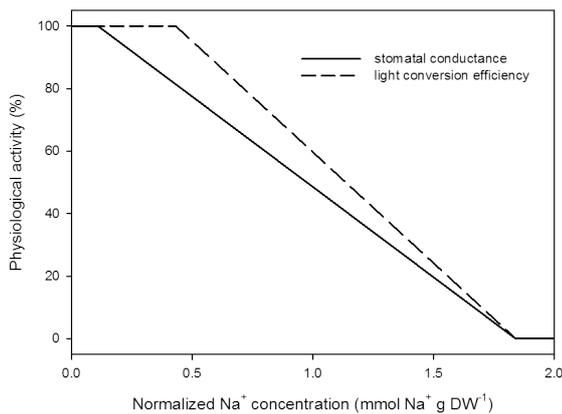

Fig. 2 Effects of Na^+ concentration on stomatal conductance and light conversion efficiency. The equations are obtained by refitting the data from James et al. (2002), which are normalized by the threshold Na^+ concentration of cucumber (1.84 mmol Na^+ g DW^{-1}).
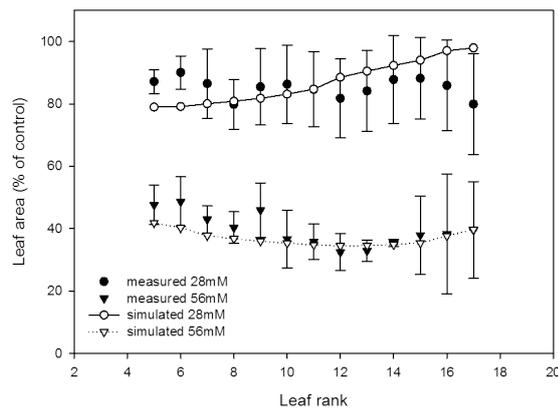
Fig. 3 Measured and simulated reduction of leaf area at 28 and 56 mM NaCl (n=3).

The patterns of Na^+ accumulation in the 6th leaves after leaf appearance (Fig. 4A) and the patterns of Na^+ concentration along the leaf rank after exposing to salinity for 28 days (Fig. 4B) can be simulated, but not very accurately, especially at high salinity level. Interestingly, the Na^+ concentration was overestimated at higher leaf rank but underestimated at lower leaf rank in both salinity levels (4B). Two arguments stated in

the literature could explain this model error: 1) S_{xy} should not be constant but decrease along the leaf rank, as described in the literature (Wolf and Jeschke, 1987) or 2) Na^+ reaching young leaves could be transported to old leaves via the phloem (Wolf *et al.*, 1991). However, the changes of S_{xy} along the stem are difficult to estimate accurately and could be influenced by the plant age and the length of stem (Wolf *et al.*, 1991). To estimate the re-translocation of Na^+ from young leaves to old leaves experimentally is even more difficult. Munns and Tester (2008) stated that this re-translocation is an important mechanism to avoid the damage of young leaves, but some authors suggest that Na^+ export has no significant contribution to the reduction of leaf Na^+ (Wolf *et al.*, 1991, Watson *et al.*, 2001). Our model framework could allow us to answer the following questions: 1) what are important mechanisms of Na^+ transport in plant? 2) How important is the Na^+ re-translocation to salt tolerance? 3) How to improve WUE by plant management strategies to avoid the toxic ion accumulation in leaves. To our knowledge, this is the first model up-scaling the Na^+ accumulation from leaf level to whole plant level and we expect that model improvement could provide insight to the and plant tolerance to ionic stress.
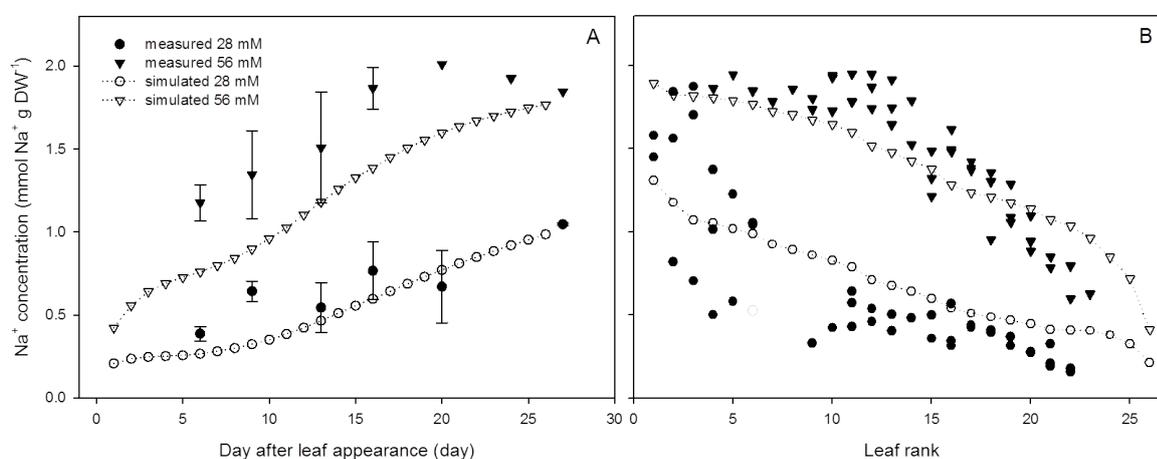
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Fig. 4 Measured and simulated Na^+ concentration in the cucumber leaves at 28 and 56 mM NaCl. (A) Increase of the Na^+ concentration in the 6th leaves with days after leaf appearance and (B) the Na^+ concentration along the leaf rank after exposing to salinity for 28 days.

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