Journal of Theoretical Biology 340 (2014) 1–10

Contents lists available at ScienceDirect

Journal of Theoretical Biology

journal homepage: www.elsevier.com/locate/yjtbi

On the competitive uptake and transport of ions through differentiated root tissues

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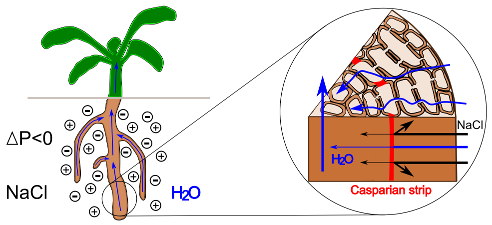
HIGHLIGHTS

- We model the uptake of ions in plant roots by forced diffusion and convection.
- The model includes differentiated root tissues with a focus on the Casparian strip.
- The Casparian strip is modelled via ion permeabilities and reflection coefficients.
- Reduced ion permeabilities affect ion concentrations in the pericycle and xylem.
- Higher reflection coefficients affect concentrations in the cortex and endodermis.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Received 15 April 2013
Received in revised form
30 July 2013
Accepted 4 September 2013
Available online 11 September 2013

Keywords:
Casparian strip
Ion permeability
Reflection coefficient
Salt stress
Salinity tolerance

ABSTRACT

We simulate the competitive uptake and transport of a mixed salt system in the differentiated tissues of plant roots. The results are based on a physical model that includes both forced diffusion and convection by the transpiration stream. The influence of the Casparian strip on regulating apoplastic flow, the focus of the paper, is modelled by varying ion diffusive permeabilities, hydraulic reflection coefficients and water permeability for transport across the endodermis–pericycle interface. We find that reducing diffusive permeabilities leads to significantly altered ion concentration profiles in the pericycle and vascular cylinder regions, while increased convective reflectivities affect predominantly ion concentrations in the cortex and endodermis tissues. The self-consistent electric field arising from ion separation is a major influence on predicted ion fluxes and accumulation rates.

1. Introduction

Salinity stress has been identified as one of the major factors affecting the growth and development of plants (Atwell et al., 1999; Munns and Tester, 2008; MacAdam, 2009). The consequences of salt stress range from decreased new shoot growth to premature senescence of older leaves. Furthermore, salt accumulation, particularly Na^+, in roots, shoots and leaves disrupts water movement in plants (Trapp et al., 2008); it disrupts protein synthesis for development and decreases yield in crops. These particulars are punctuated by the added fact that salinity affects one-fifth of the world's irrigated land (Finkel, 2009); all cereals are affected by salinity stress, with rice more so than barley, with wheat intermediate.

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http://dx.doi.org/10.1016/j.jtbi.2013.09.004

A plant's ability to tolerate salt is dependent on the mechanisms responsible for the transport of Na^+ and/or Cl^- through a plant. Reducing the amount of Na^+ in the transpiration stream by either reducing the initial influx of Na^+ into root epidermal and cortical cells or maximizing the efflux of Na^+ back to the soil, or both will reduce the amount of Na^+ crossing the endodermis to the root centre. Maximizing the influx of Na^+ into storage cells surrounding the xylem vessels, and minimizing the efflux of Na^+ from storage cells to the xylem, will further reduce the amount of Na^+ in the water travelling to the shoot via the xylem. Increased re-circulation of ions in the phloem from the shoot to other tissues will also help minimize accumulation of salt, while compartmentation of ions in the vacuoles of cells in both the root and the shoot will minimize toxic effects of both Na^+ and Cl^- on cellular processes.

Quantitative knowledge, even if incomplete, about how transport of nutrients and ions through a plant occurs is necessary for an understanding of the key points in the transport pathway that can be targeted to increase the chance of generating a salt tolerant crop.

Numerous quantitative models have appeared in the literature to describe the transport of a single neutral molecule (sucrose) in the phloem (Christy and Ferrier, 1973; Goeschl et al., 1976; Phillips and Dungan, 1993; Thompson and Holbrook, 2003) and less frequently of water and solute transport in the coupled xylem–phloem system (Hölttä et al., 2006, 2009). However, these and similar models are not directly suited to describe the transport of dissolved, freely mobile ions, especially mixtures of ions.

In an attempt to fill the gap we reported in a recent paper (Foster and Miklavcic, 2013) on a non-steady model of salt uptake and transport in plant roots, which was inspired to different degrees by the independent works of Steudle (1992) and Hölttä et al. (2006). In this model, the root was assumed to consist of five coaxial cylinders, representing the *epidermis*, the *cortex*, the *endodermis*, the *pericycle* and the *vascular cylinder*. Each tissue region was made theoretically distinct by assigning specific transport coefficients, which were, moreover, possible functions of position along the root (*i.e.*, functions of root age). One of our key findings was the importance of the self-consistent electric field, generated by the nonuniform distribution of ions through the discriminating tissues. Moreover, we found that significant competitive behaviour between co- and counter-ions ensues as a result of the inherently nonlinear ion densities coupling through the field.

The simulations performed by Foster and Miklavcic (2013) assumed uniform transport properties across the root tissues, although they may have differed for different ions. In the present paper we focus greater attention on the effects on transport of distinct transport coefficients for differentiated tissues, although we again consider ions of different permeabilities. This is easily accommodated in the model. In particular, we examine one of the major influences on solute transport that has been documented in the literature, the Casparian strip. It has been observed and established by experiment that the Casparian strip is critical in hindering undesired nutrients from entering the root and simultaneously preventing loss of water once taken up by the root.

We summarise the physical and mathematical model in Section 2. This is followed in Section 3 by a presentation of our main results. Section 4 provides a discussion of our findings, with concluding statements given in Section 5.

2. Model of ion transport

The simplest system possessing the essential physical features characteristic of real roots is that of a flat ended, rigid, right cylinder of length L and radius R. We assume that the root-cylinder is aligned with the gravitational field. Each of the root tissue regions is identified by a value of the parameter α: the epidermis $(\alpha=1)$, cortex $(\alpha=2)$, endodermis $(\alpha=3)$, pericycle $(\alpha=4)$ and vascular cylinder $(\alpha=5)$ (see Fig. 1). Each region α occupies an annular cylinder of cross-sectional (*i.e.*, radial) thickness, d_α.

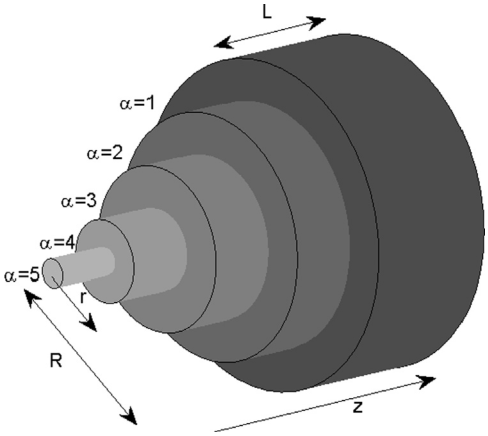

Fig. 1. A schematic, in expanded longitudinal view, of the physical model of concentric cylinders representing the five different tissues of the root that are modelled. The tissues are epidermis $(\alpha=1)$, cortex $(\alpha=2)$, endodermis $(\alpha=3)$, pericycle $(\alpha=4)$ and vascular cylinder $(\alpha=5)$. The respective tissue thicknesses, d_1–d_5, and overall root dimensions are given in Table 1. The coordinate system (r,z) is as shown. Gravity force is in the direction of decreasing z.

For convenience, we assume axial symmetry so that structural and functional features in the tissues are independent of angle around the central axis, and thus depend only on the radial and axial coordinates, (r,z).

The uptake of water and solutes is modelled as a coupled system of mass–balance and convective equations. Axial flow of water and solutes is assumed to occur only in the vascular bundle, which for simplicity occupies the entire central region of the cylinder (from $r=0$ to $r=d_5$). As the model focuses on the transport of solutes up into the plant, we will assume that the transpiration stream occurring in the xylem is the dominant function of the vascular bundle. Lateral (*i.e.*, radial) and longitudinal (*i.e.*, axial) flows of water and solutes occur due to both osmotic and hydraulic pressure gradients. Consequently, both radial and axial flows of solutes are driven/retarded by local concentration differences, electric field effects and convection, the latter is effected by a hydraulic pressure gradient set up by the transpiring plant.

For rigid and completely water-filled compartments, volume conservation of solution requires the condition

$$[(Q_{ax,in}-Q_{ax,out})\delta_{vascular\ \ cylinder}+(Q_{rad,in}-Q_{rad,out})]|_{(r,z)}=0 \tag{1}$$

where $Q_{ax,in}$ $(Q_{ax,out})$ is the *axial* volume flow rate of solution into (out of) position (r,z), $Q_{rad,in}$ $(Q_{rad,out})$ is the *radial* volume flow rate into (out of) position (r,z); $\delta_{vascular\ \ cylinder}=1$ for the vascular cylinder/vascular cylinder tissue and 0 otherwise. This ensures that axial flow takes place only in the vascular cylinder $(\alpha=5)$.

The concentration of solute species m at position (r,z) is analogously given by a conservation equation:

$$\frac{dC_m}{dt}=[(S^m_{ax,in}-S^m_{ax,out})\delta_{vascular\ \ cylinder}+S^m_{rad,in}-S^m_{rad,out}]\frac{1}{V_{sol}}, \tag{2}$$

where V_{sol} is the solution volume, C_m is the concentration of species m, $S_{ax,in}$ $(S_{ax,out})$ is the *axial* flux of solute m into (out of) position (r,z) and $S_{rad,in}$ $(S_{rad,out})$ is the *radial* flux of solute m into (out of) position (r,z).

The axial flow in the vascular bundle can be modelled as linearly proportional to the hydraulic pressure gradient, given by