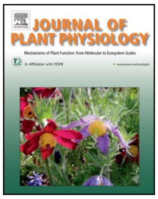
ARTICLE IN PRESS

Journal of Plant Physiology xxx (xxxx) xxx–xxx

Contents lists available at ScienceDirect

Journal of Plant Physiology

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



Suberized transport barriers in *Arabidopsis*, barley and rice roots: From the model plant to crop species

Tino Kreszies[a], Lukas Schreiber[a], Kosala Ranathunge[b,*]

[a] *Department of Ecophysiology, Institute of Cellular and Molecular Botany, University of Bonn, Kirschallee 1, 53115 Bonn, Germany*
[b] *School of Biological Sciences, University of Western Australia, 35 Stirling Highway, Crawley 6009, Perth, Australia*

ARTICLE INFO

Keywords:
Apoplast
Arabidopsis
Barley
Composite transport model
Hydraulic conductivity
Rice
Solutes
Suberin
Water transport

ABSTRACT

Water is the most important prerequisite for life and plays a major role during uptake and transport of nutrients. Roots are the plant organs that take up the major part of water, from the surrounding soil. Water uptake is related to the root system architecture, root growth, age and species dependent complex developmental changes in the anatomical structures. The latter is mainly attributed to the deposition of suberized barriers in certain layers of cell walls, such as endo- and exodermis. With respect to water permeability, changes in the suberization of roots are most relevant. Water transport or hydraulic conductivity of roots (Lp_r) can be described by the composite transport model and is known to be very variable between plant species and growth conditions and root developmental states. In this review, we summarize how anatomical structures and apoplastic barriers of roots can diversely affect water transport, comparing the model plant *Arabidopsis* with crop plants, such as barley and rice. Results comparing the suberin amounts and water transport properties indicate that the common assumption that suberin amount negatively correlates with water and solute transport through roots may not always be true. The composition, microstructure and localization of suberin may also have a great impact on the formation of efficient barriers to water and solutes.

1. Introduction

Plant roots are designed to take up water and nutrient ions from the surrounding soil and supplying them to shoots and leaves. It is well documented that the water moves through plants by water potential gradients set up by transpiration through the soil-plant-atmosphere continuum (SPAC) (Kramer and Boyer, 1995; Nobel, 2009; Steudle, 2000a, 2000b). Resistances in plant water uptake can be described by Ohm's Law using simple force and flow relations (Landsberg and Fowkes, 1978; Steudle, 2000b; van den Honert, 1948). The water and solute transport of roots are known to depend on (1) complex root anatomical features, which are species dependent, (2) different growth conditions, and (3) different growth stages/age of roots (Steudle, 2000b; Steudle and Peterson, 1998). Such factors also lead to a highly variable water and solute movement, which are not only related to permeability of root cell membranes but also to apoplastic barriers such as Casparian bands and the suberin lamellae (Hose et al., 2001; Steudle and Peterson, 1998; Steudle and Ranathunge, 2007). Suberin in cell walls can also be induced by plant exposure to different abiotic (drought, salinity, anoxia/hypoxia, organic acids, high nutrients etc.) and biotic (pathogens) stresses (Barberon et al., 2016; Enstone et al., 2002; Hose et al., 2001; Krishnamurthy et al., 2011, 2009; Ranathunge et al., 2011b; Shiono et al., 2014; Tylová et al., 2017). Induced suberin in cell walls is known to strengthen the barriers in order to minimize the entry of pathogens, toxic gases and organic acids into the roots (Lanoue et al., 2010; Lulai et al., 1998; Ranathunge et al., 2008; Thomas et al., 2007). Suberized cell walls also act as strong barriers to prevent radial oxygen loss (ROL) from roots to the substrate under anoxia/hypoxia and uncontrolled back flow of water and solutes from root to the surrounding soil/environment (Kotula et al., 2017, 2014, 2009a; Ranathunge et al., 2011b).

In this review, we compare the similarities and differences in root anatomy (first section), suberized apoplastic barrier development and its composition/biosynthesis (second section) between the model plant

---

Abbreviations: Lp_{hy}, hydrostatic hydraulic conductivity; Lp_{os}, osmotic hydraulic conductivity; PC, pressure chamberPC; ROL, radial oxygen loss; σ_{sr}, reflection coefficient; Lp_r, root hydraulic conductivity; rpp, root pressure probe; SPAC, soil-plant-atmosphere continuum; P_{sr}, solute permeability; diacids, α–ω dicarboxylic acids; ω-OH acids, ω-hydroxyl acids

[*] Corresponding author.

E-mail address: kosala.ranathunge@uwa.edu.au (K. Ranathunge).

https://doi.org/10.1016/j.jplph.2018.02.002
Received 5 December 2017; Received in revised form 31 January 2018; Accepted 2 February 2018

Please cite this article as: Kreszies, T., Journal of Plant Physiology (2018), https://doi.org/10.1016/j.jplph.2018.02.002

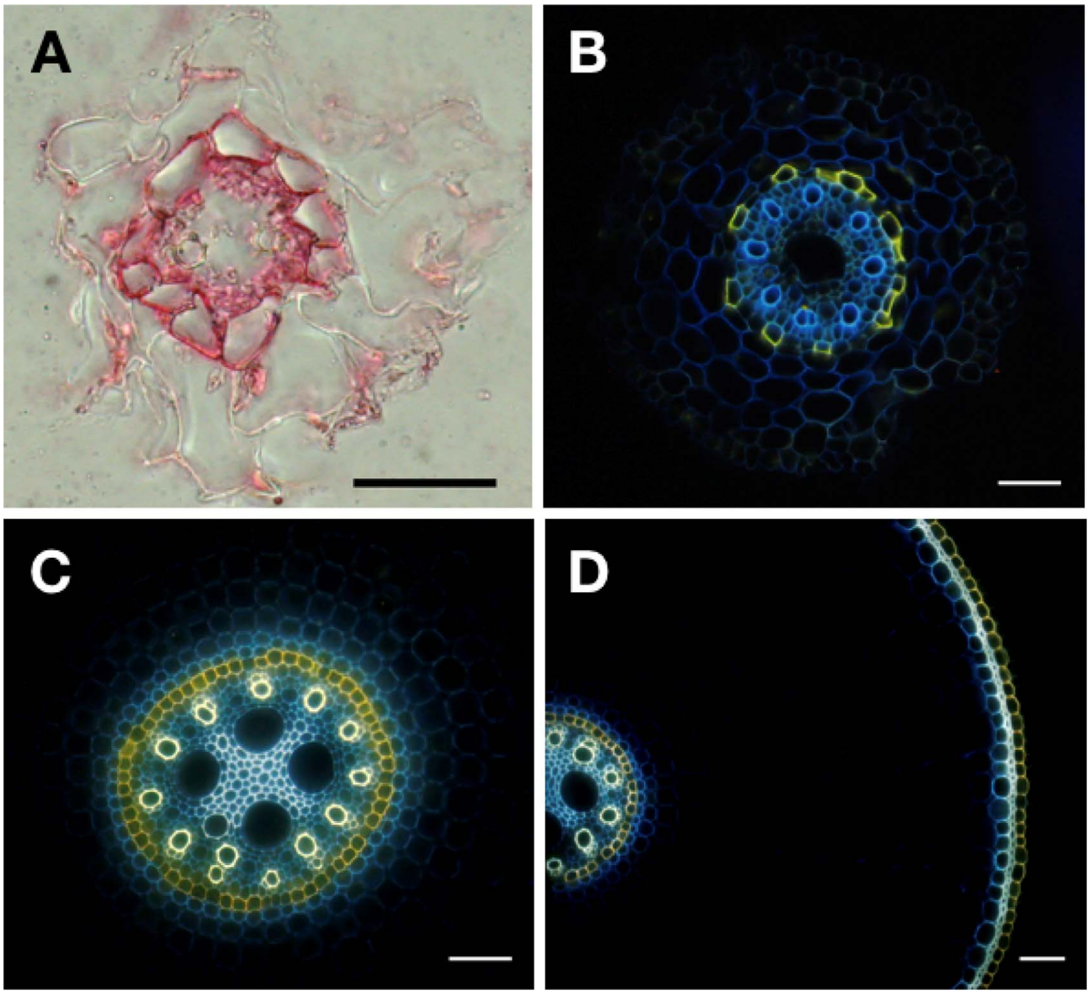


Fig. 1. Comparison of cross sections of *Arabidopsis*, barley and rice roots. (A) *Arabidopsis* root cross section stained with Sudan red 7B. The endodermis (red colour) shows suberized cells. Bar = 25 μm. (B) Barley seminal root cross section stained with fluorol yellow 088. The yellow fluorescence shows the suberized cells in the endodermis, whereas, unsuberized passage cells do not have yellow fluorescence. Bar = 50 μm. (C and D) Rice root cross sections stained with Fluorol yellow 088, in which intense yellow fluorescence shows suberized endo- and exodermis. Bars = 50 μm. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

of *Arabidopsis* (*Arabidopsis thaliana*) and crop plants, such as barley (*Hordeum vulgare*) and rice (*Oryza sativa*); and subsequently their influence on water and solute transport of roots (third section).

2. Anatomy/structure and suberized apoplastic barriers in roots

A comprehensive knowledge of root anatomy is essential to understand water and solute transport of roots. Different anatomical features as well as system architectures of roots from various plant species result in complex ways of water movement through roots (Steudle, 2000b; Steudle and Peterson, 1998).

In roots, there are three major radial pathways for transport of water and solutes across the cylinder: (1) the apoplastic path around the protoplast, where water and solutes can move towards the stele through free spaces and cell walls of the rhizodermis and cortex, (2) the symplastic pathway, in which transport occurs through plasmodesmata from one cell (protoplast) to the other using cytoplasmic continuum, and (3) the transmembrane pathway, where water and solutes move through cell walls and aquaporins/transporters localized in the cell membrane (Peterson and Cholewa, 1998; Steudle, 2000a, 2000b; Steudle and Peterson, 1998). To date, there are no simple and straightforward experimental approaches to separate the latter two components. Therefore, these two pathways together are summarized as a ‘cell-to-cell’ or ‘protoplastic’ component (Steudle, 2000b). Water transport across roots should be considered as radial, in which water has to cross series of cell layers such as rhizodermis, cortex (including endodermis and/or exodermis) and stele. Once water entered into the vascular tissue of the root, its direction is longitudinal through the xylem vessels towards the shoot. The apoplast can be interrupted by Casparian bands and suberin lamellae in endodermal and exodermal cell walls. This blockage can only be bypassed in young root zones close to the tips, where these structures are not yet fully developed and also through lateral roots, which emerge from pericycle cells and directly grow through the endodermis thus disturbing the continuity of endodermal barrier (Krishnamurthy et al., 2011; Steudle, 2000b; Steudle and Jeschke, 1983; Steudle and Peterson, 1998).

Over the length of the root, from the root tip to the base, roots can be divided into developmental stages which exhibit different apoplastic modifications with suberin. At stage I, close to the root apex, Casparian bands are deposited in the transverse and radial cell walls of the endodermis (Chen et al., 2011; Karahara et al., 2004; Krishnamurthy et al., 2009; Ma and Peterson, 2003). It was shown that Casparian bands can block the movement of ions and fluorescents dyes through the apoplastic pathway (Peterson, 1987; Singh and Jacobsen, 1977). At stage II, the suberin lamellae start to lay down interior to the primary cell walls but outside of the plasma membrane of some endodermal cells, which increases the blockage of the apoplast. The transition zone from Casparian bands to a fully developed suberized endodermis is called patchy suberin lamellae. This patchy suberin lamellae is not a perfect barrier, because unsuberized passage cells allow movement of