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Variability in root apoplastic barriers relates with variability of cadmium uptake and translocation

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ABSTRACT

Root apoplastic barriers, endodermis and exodermis represent cell layers with specific wall modifications. One of their functions is regulation of radial transport of water and ions. In response to cadmium influence these layers mature closer to the root tip. Differences in the development of endodermis were found in clones of the same species differing in cadmium translocation from the root to the shoot. Specific additional layer of lignified cells the peri-endodermal layer is formed in one of the hyperaccumulator species *Thlaspi caerulescens* syn. *Noccaea caerulescens*. Suberinization, lignification and cell wall thickening may occur in reaction to Cd treatment in roots of various plant species. Even wound periderm in monocot roots can be formed.
KEYWORDS: apoplast, cadmium, endodermis, exodermis

1. INTRODUCTION

Two major barriers of apoplastic transport are developed in majority of roots of angiosperms, the endodermis and exodermis. Both endo- and exodermis may mature in three ontogenetic stages: Casparian band development, suberin lamellae deposition and thick secondary cell wall formation. Cell wall modifications occurring during these stages are important in regulation of radial transport processes in roots. The development of these tissues is highly variable and may start close to or relatively far from the root apex. This variability results in variability of apical zone of unhindered apoplastic transport into the vascular cylinder. Both species-specific and intra-specific differences exist in the distance of individual developmental stages from the root apex. The variability is increased by the differences between various types of roots of the same plant and by the effect of external conditions.

2. MATERIALS AND METHODS

Plants of various species including crop species maize (*Zea mays*), radish (*Raphanus sativus*), wheat (*Triticum durum*) and model plants of cadmium hyperaccumulators (*Thlaspi caerulescens* syn. *Noccaea caerulescens*), accumulators (*Silene vulgaris*) and non-accumulating sensitive species (*Thlaspi arvense*, *Arabidopsis thaliana*) as well as some woody plants (*Salix spp*., tea plant *Camellia sinensis*) and some South African bulb species were studied in their reaction to cadmium treatment. Plants were grown mostly hydroponically in controlled conditions of growth chambers, or on agar media and treated with cadmium in the form of $Cd(NO_3)_2 . 4H_2O$ in several concentrations from 5 µM up to 100 µM.

For structural observations the root samples were prepared as hand sections stained by berberine or Fluorol Yellow 088 for visualization of suberin in exo- and endodermis (Lux et al. 2005). For lignin histological determination phloroglucinol reaction was used. Other samples were embedded in Spurr resin and semi-thin sections were compared and proportion of tissues were quantified in light microscope using image analysis by Lucia (v.4.8, laboratory imaging Praha). For detail observations TEM and SEM or cryo-scanning electron microscopy were used. The Cd concentrations were determined by flame atomic absorption spectroscopy (AAS) (PerkinElmer #1100), or ICP-MS (Elan 6000, Pe Sciex, Canada).

3. RESULTS AND DISCUSSIONS

Experimental results show that the differences in the development of root apoplastic barriers are related with the uptake and translocation of cadmium. Willow clones with variable accumulation and translocation of cadmium and tolerance to this toxic metal exhibited differences especially in suberin lamellae deposition in endodermis with more distant development of this wall modification in clones with high Cd translocation (Lux et al. 2004). In maize (*Zea mays* cv. Jozefina) cadmium treatment induced earlier development of endodermal suberin lamellae, closer to the root apex, when compared with the root of control plants. Silicon addition to cadmium containing solution alleviated cadmium inhibitory effects in these plants. This phenomenon was connected with a shift of development of complete endodermis suberin lamellae to the region more distant from the root apex when compared with the Cd treatment. Moreover, the Cd content was also elevated in both root and shoot of cadmium plus silicon treatment in comparison with the Cd treatment (Vaculik et al. 2009).

In cadmium hyperaccumulator species *Thlaspi* (*Noccaea*) *caerulescens* endodermal maturation starts close to the root apex. This is in contrast with relatively late endodermal maturation in closely related, sensitive non-accumulating species *Thlaspi arvense*. In *T. caerulescens* in addition to endodermis a specific peri-endodermal layer is formed, externally adjacent to endodermis (Broadley et al. 2007, Zelko et al. 2008). This layer was non-correctly interpreted as additional endodermal layer. However, peri-endodermal layer does not develop characteristic wall modifications, neither Casparian bands nor suberin lamellae. In this layer irregularly thickened secondary walls with lignin deposition are formed close to the apex. The function of these modifications is recently unknown. However, we may speculate, that these protective layers, formed close to the root tip in hyperaccumulator species, may increase the retention of cadmium ions in peripheral root tissues. It corresponds with the finding about long deposition of cadmium in root apoplast after Cd treatment in this species (Zhao et al. 2002).
Modifications of cell walls, wall thickening, lignification and suberinization, were observed after cadmium treatment in roots of various species. Recently a wound periderm formation was found in response of one South African medicinal monocots (unpublished results) to cadmium treatment. All these modifications represent part of the plant reaction to toxic effects of cadmium.

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