Using Cations to Probe the Question: How Do Roots Perceive, Respond to, and Modify their Environment?

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INTRODUCTION

Plant roots growing in soils face many chemical challenges with much research focused on how roots cope with such situations. Ten elements (Ca, Mg, K, Fe, Mn, Cu, Zn, Na, Co, and Ni), essential for the growth of plants, are absorbed by roots as cations, but must be present within limits so as not to be deficient or toxic. Non-essential cations (e.g. Al, Hg, and Ag) are of biological interest because of their toxicity at low to moderate levels. Cation effects on roots differ in their timing, magnitude, location, and the symptoms produced. Studying these phenomena provides an understanding of the mechanisms of perception, response, and modification of the rhizosphere.

METHODS

Cation effects on roots were studied in solutions that approximate the soil solution, with care taken to prevent precipitation and ensure realistic solution pH (Shaff et al., 2010). Estimates of cation activities in solution and at the outer surface of the plasma membrane assist in understanding effects on root elongation, intoxication, and alleviation of intoxication (Kinraide and Wang, 2010).

RESULTS AND DISCUSSION

Cations Binding Strongly to Hard Ligands (e.g. Carboxyl)

Based on rhizotoxic effects, this group includes Al(III), Ga(III), Gd(III), In(III), Ru(III), Sc(III), Cu(II), and Hg(II) (Kopittke et al., 2009) which accumulate in the rhizodermis. These cations reduce growth and rupture the rhizodermis of the elongation zone over an extended (e.g Al) or limited (e.g. Cu and La) range; interestingly, recovery differs among these cations (e.g. Al and Cu) (Fig. 1).

Exposure of Al-tolerant plants to soluble Al in the rhizosphere elicits the excretion of organic ligands (e.g. malate in wheat) (Delhaize et al., 1993). These ligands bind to Al in the apoplast and rhizosphere, thereby decreasing its toxic effects. Exposure of Al-tolerant plants to other metals (e.g. Cu, La) does not elicit organic ligand excretion. Increasingly, research has shown the importance of reactions of these cations (e.g. Al) with the cell wall (Horst et al., 2010).

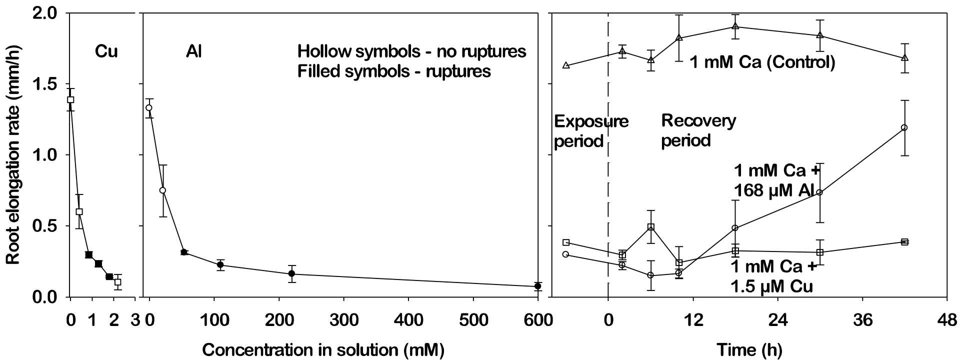

Fig. 1. Rhizotoxic effects of Al or Cu in cowpea and recovery after 24 h exposure to Al or Cu. Cations Binding Strongly to Soft Ligands (e.g. Sulfhydryl)

Cations in this group include Ca(II) (see below), Cd(II), Co(II), Mg(II), Mn(II,) Ni(II), Pb(II), Zn(II), Ag(I), K(I), Na(I), and Tl(I), some of which are highly toxic (e.g. Tl) through strong binding to S-rich enzymes. Others (e.g. K and Mg) are far less toxic. These cations, other than Ag, do not rupture roots in the elongation zone. Relatively high concentrations of these cations are found in the inner cortex and stele for ready translocation to the shoots.

Calcium is a Special Case

In the face of changes in soil solution Ca, close control of Ca in the apoplast and cytoplasm is needed (Stael et al., 2012) for cell wall integrity and signalling. Seedlings transferred from 1 to ≤ 0.1 mM Ca rapidly attained a high root elongation rate (RER) of > 2.0 mm h^{-1} in contrast to 0.5 mm h^{-1} at ≥ 5 mM Ca, recovering slowly over 24 h to ca. 80 % of that at low Ca. (Fig. 2). The detrimental effect of high Ca on root growth was ameliorated by ≥ 0.5 mM K. Decreased solution pH accompanied all cases of initial high RER as found with roots transferred to solutions at < pH 4 (Winch and Pritchard, 1999). The gradual increase in RER at high Ca was not accompanied by solution acidification (Fig. 2).

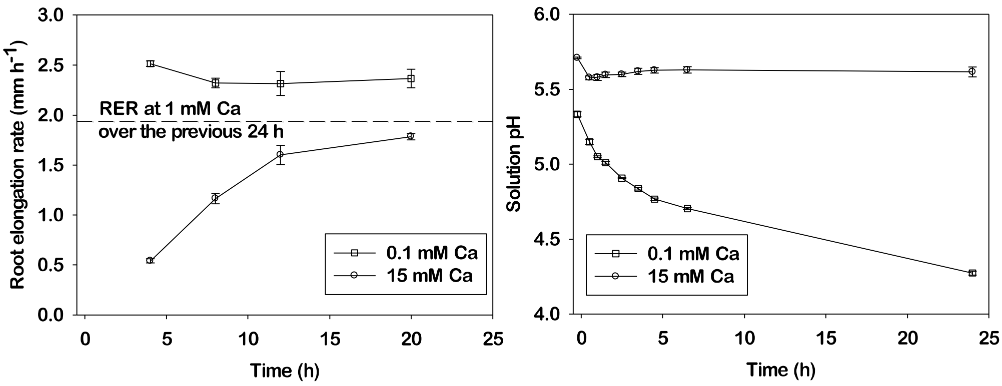

Fig. 2. Solution Ca affects cowpea root growth and solution pH over 24 h.

Many effects of cations at toxic and non-toxic concentrations occur within a few minutes of exposure (e.g. Al, Ca) while others have delayed effects (e.g. La). We propose that cations which bind strongly to hard ligands induce rhizodermal ruptures by inhibiting cell wall loosening; except for Ag, other cations do not. General mechanisms of perception are related to their strength of binding to hard or soft ligands, in turn affecting root responses and rhizosphere modification.

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