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Review article

Root cell wall solutions for crop plants in saline soils

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ABSTRACT

The root growth of most crop plants is inhibited by soil salinity. Roots respond by modulating metabolism, gene expression and protein activity, which results in changes in cell wall composition, transport processes, cell size and shape, and root architecture. Here, we focus on the effects of salt stress on cell wall modifying enzymes, cellulose microfibril orientation and non-cellulosic polysaccharide deposition in root elongation zones, as important determinants of inhibition of root elongation, and highlight cell wall changes linked to tolerance to salt stressed and water limited roots. Salt stress induces changes in the wall composition of specific root cell types, including the increased deposition of lignin and suberin in endodermal and exodermal cells. These changes can benefit the plant by preventing water loss and altering ion transport pathways. We suggest that binding of Na^+ ions to cell wall components might influence the passage of Na^+ and that Na^+ can influence the binding of other ions and hinder the function of pectin during cell growth. Naturally occurring differences in cell wall structure may provide new resources for breeding crops that are more salt tolerant.

1. Introduction

Plant evolution has resulted in a large array of mechanisms to tolerate the stresses associated with increased soil salinity. However, for most cereal crops the growth of roots is disrupted when soil salinity exceeds 4 dS/m, equivalent to about 40 mM NaCl. Increased soil salinity exposes plants to ionic sodium (Na^+) and chloride (Cl^-), which leads to a cascade of responses in the plant due to the ionic and osmotic components of salt stress [1,2].

Salt stress can indirectly affect cell wall properties by causing changes in gene expression, but Na^+ can also physically interact with the cell wall components directly, and change their chemical properties [3]. An increase in soil salinity results in accumulation of Na^+ in the apoplast, which can lead to an increase in interactions between Na^+ and negatively charged sites within cell wall polymers, and also influence apoplastic pH. Salinity causes transient alkalinisation of the apoplast, and this could limit growth in the context of the acid growth theory [4,5]: Auxin activates plasma membrane H^+-ATPases and protons are extruded into the apoplast, apoplastic acidification induces cell wall loosening by activating expansins and other remodelling enzymes resulting in loosening of the cell wall. Hence, growth could be limited by a decrease in free apoplastic protons causing a shift in the apoplastic pH away from the range that favors cell-wall loosening [4], although in maize the inhibition of growth as a result of salinity was not associated with the capacity of the epidermal cells to acidify their walls [6].

Transcriptional analyses of many plant species to a variety of salt treatments show that the transcript levels of many cell wall related genes consistently change in response to salt stress. Transcriptional changes occur, for example, for genes linked to cell wall extensibility, lignin and suberin synthesis and genes associated with the modification of cell wall polysaccharides, such as xyloglucan endotransglycosylases [7–9]. One consequence of salt stress is often a reduction in the rate of cell elongation. Therefore, it is of no surprise that differential transcription of genes regulating the rate of cell wall loosening and stiffening is consistently observed. In this review, we concentrate upon the how, where and why of the affects of salt on cell wall modifications in response to a rise in soil salinity.

2. Na^+ can bind to cell wall constituents

Cell walls are negatively charged and reversibly bind cations such as Ca^{2+} and Na^+ [3,10]. There are examples where the ion binding is physiologically important. For example, the cross-linking of some pectin molecules is dependent on, and co-ordinated by, binding of Ca^{2+}

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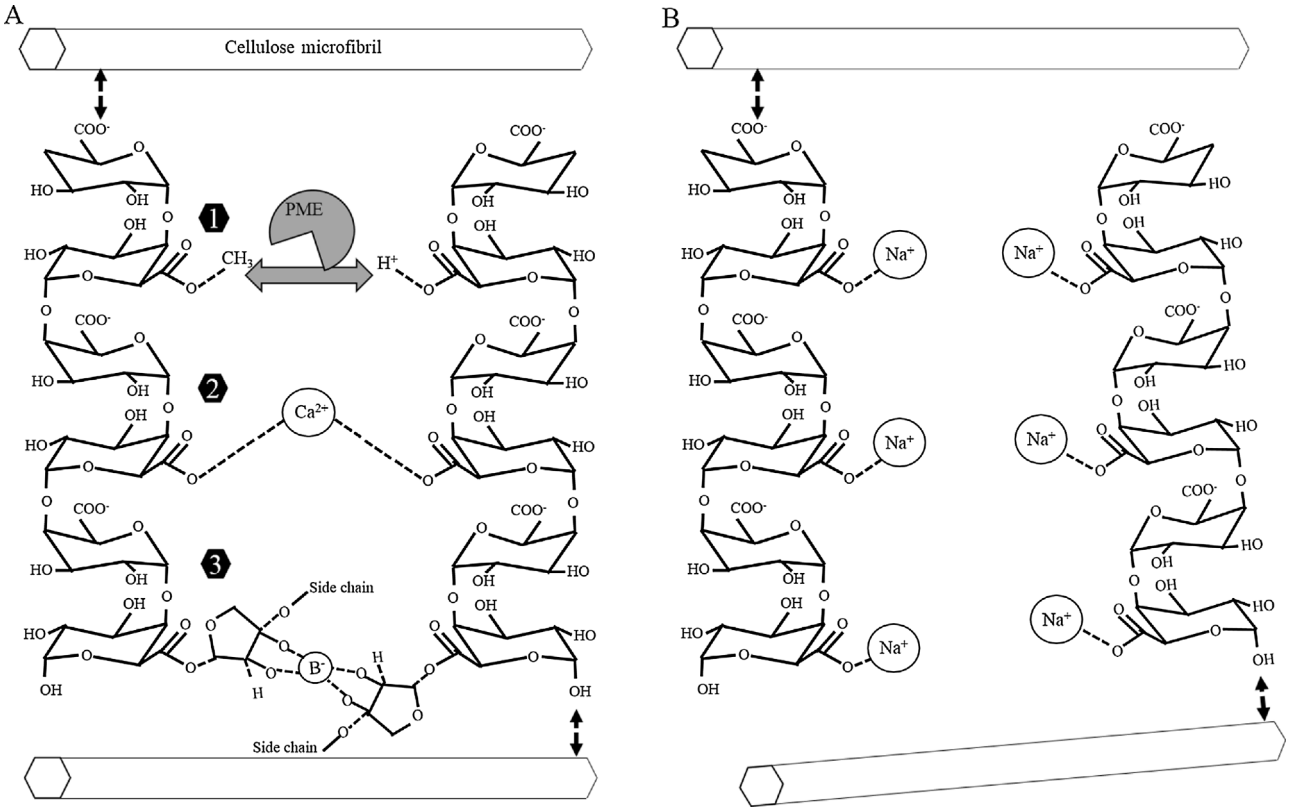

Fig. 1. A model for how excess Na^+ might influence cell wall pectin properties.
A. Cellulose microfibrils are linked by pectins (rhamnogalacturonan I, II and homogalacturonan), and also by xyloglucan (not shown). Pectin links are important for cell wall strength. Pectin can contain up to 17 different monosaccharides, it has a backbone of 1,4-linked α-D-GalpA residues, these residues can be methyl-esterified and where there are unesterified sections Ca^{2+} cross-links occur (reviewed by O'Neill, Ishii, Albersheim and Darvill [10], Vincken, et al. [116]. Black arrows represent complex layers of pectin molecules and black dashed lines represent ionic bonds (not to scale). The distribution of side chains remains to be established. Two rhamnogalacturonan II molecules can complex with boron forming a borate-diol ester and Ca^{2+} promotes this dimer formation. Apiofuranosyl residues of 2-*O*-methyl-D-Xyl-containing side chains participate in the cross-linking. Excess Na^+ may displace the Ca^{2+} and hinder dimerization. Newly deposited pectins are methyl esterified: (1) Pectin methylesterases (PMEs) regulate the removal of methyl esters. Carboxyl groups on de-methesterified pectin interact with ions. (2) Interaction of Ca^{2+} with the carboxyl groups (Ca^{2+} bridges) is important for stabilising pectin. (3) Borate diol ester cross links can form between two rhamnogalacturonan molecules via apiofuranosyl residues, this is thought to require more than nine Ca^{2+} bridges. B. Na^+ binds polygalacturonic acid [117]. When there is excess salt in the apoplasm Na^+ can interfere with PME function, the interaction of Ca^{2+} with the carboxyl groups and the formation of borate diol ester cross links.

to the negatively charged residues (Fig. 1A) [11]. If the ratio of Na^+: to Ca^{2+} is high, Na^+ could displace Ca^{2+} from these binding sites, so reducing pectin crosslinking (Fig. 1B) and subsequently slowing down cell elongation [12]. We suggest that this may contribute to how root elongation is reduced in saline soil. Na^+ interference in pectin cross-linking could reduce the stabilising influence of pectin in the cell wall. Detection of the initial loss in stability is likely to trigger mechanisms to rigidify the cell wall. Proteins such as wall associated kinases (WAKs), Feronia and arabinogalactan proteins are possible candidates for recognising these changes [13,14].

The cell wall changes due to the physical interaction of Na^+ with cell wall components as a result of salt stress are less well documented than the changes in gene expression. Yet a physical interaction between Na^+ and the cation exchange sites on the cell wall might be a key reason why the chemical composition of the cell wall changes when Na^+ is present. There are notable differences in cell wall composition between different cell types and different species which we propose might reflect different strategies to cope with excess salt. The strategy used might depend on the developmental stage of the cell. For example, in the growing regions there may be changes in cell wall components that result in a tighter binding of Ca^{2+} that helps to maintain growth; or in the fully expanded regions there may be upregulation of negatively charged cell wall components that "trap" Na^+ and restrict its movement to the stele and ultimately to the shoots. The ability of the cell wall components to bind Na^+ ions might greatly influence the passage of Na^+ [15]. For example, it has been suggested that cell walls in the stele of citrus plants might influence root Na^+ transport by acting as Na^+ traps [16]. Genetic variation for Na^+ binding of root cell walls has been reported in barley (*Hordeum vulgare* L.), where a two-fold greater Na^+ adsorption was observed for a salt tolerant variety relative to a salt sensitive variety [17]; however, it is currently unknown how much Na^+ could be trapped in the apoplast or whether this would make a significant contribution to sequestering Na^+ in root tissue or affect accumulation in the shoot. At present there are few reports detailing how compositional variation in different cell wall polymers influences Na^+ binding, or how this would influence potassium (K^+) passage or the binding and passage of Ca^{2+} in roots.

3. Changes in the chemical composition of root cell walls in response to salt treatments

It is difficult to measure the changes in cell wall composition that occur in response to salt treatments. This is because the chemical composition of root tissues already varies significantly across many cell layers, and changes during development [18]. Additionally, the growing zones of the root contract with salinity, complicating direct comparison when tissues are measured as distance from the root tip [19,20]. All plant cells are surrounded by an extensible primary cell wall, which contains cellulose, pectin and non-cellulosic polysaccharides. Secondary cell walls are produced when the cell stops expanding, and are more rigid and thicker than the primary wall [21]. They generally contain more cellulose and can accumulate lignin and