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Changes in cell wall polysaccharides during water stress in wheat genotypes varying in drought tolerance

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SUMMARY – The *in vivo* changes of cell wall polysaccharides were studied in apical root segments excised from water-stressed and unstressed wheat seedlings (*Triticum durum*, Desf.) cv. 'Capeiti' "drought tolerant" and cv. 'Creso' "drought sensitive". In both cv., the total amount of cell wall matrix polysaccharides (pectins and hemicelluloses), sequentially solubilised with CDTA/Na₂CO₃ and KOH, and of the insoluble residue (α -cellulose) was unaffected by the stress. However, a reduction in the amount of solubilised pectins in favour of an increase of hemicelluloses was evidenced in stressed cv. 'Capeiti'. Stress determined little variations in the glycosyl residue composition of pectins, hemicelluloses and α -cellulose of root apical segments of both cv., nevertheless, the glycosidic linkage analyses indicated that the root apex of the "drought tolerant" cv. 'Capeiti' subjected to water stress, synthesises cell wall polysaccharides with a higher capability of binding water which could play an important role in water stress tolerance.

Introduction

Water stress represents one of the most important factor limiting plant crop production worldwide. The availability of water for agriculture is destined to decrease because the priority is people, industry and, finally, agriculture. Naturally, these difficulties will be particularly pronounced in semi-arid agricultural zones. In the light of this, the hope for the future is to obtain genetically engineered crop plants which possess the capability to perform high productivity in condition of drought stress. This explains the numerous studies related to the effect of water stress on growth (Shimazaki *et al.*, 2005), gene expression (Bray, 2002), signaling pathways (Chaves *et al.*, 2003), respiration (Ribas-Carbó *et al.*, 2005), stomatal closure, reduction of photosynthesis rate and accumulation of osmolytes within the cells (Taiz and Zeiger, 2002).

Water stress and cell growth

Undoubtedly, plant cell growth is the most sensitive indicator of water stress in plants. In particular, under water stress, shoot growth is more inhibited than root growth (Westgate and Boyer, 1985). This differential growth between shoot and root is extremely important for plant survival because leads the roots to better explore the moisture of the soil (Serraj and Sinclair, 2002). Thus, the root represents the first organ of a plant in sensing soil water stress and, in particular, the root tip is the primary site for such perception. In primary roots of maize (*Zea mays*), water stress induces a marked reduction of the root tip growth mainly due to a decrease in cell expansion rather than in cell division (Shimazaki *et al.*, 2005). This decrease in root elongation at low water potential has been attributed to changes in cell wall extensibility and/or yield threshold, as well as to a reduction in the hydraulic conductivity of cells or tissues (Wu *et al.*, 1996).

Although numerous investigations on root growth have been carried out, studies examining the effect of water stress on cell wall polysaccharides are few. This surprisingly contrasts with the important role of cell wall as the first cellular compartment that interacts with the protoplast.

Water stress and cell wall polysaccharides

Although changes on composition and molecular mass of cell wall polysaccharides of squash (*Cucurbita maxima* Duch.) hypocotyls (Sakurai *et al.*, 1987) and wheat (*Triticum aestivum* L.) coleoptiles (Wakabayashi, 1997) under water stress have been reported, little is known on the role of

cell wall polysaccharides in roots of water stressed seedlings. In our previous study, we investigated the *in vivo* changes in the biosynthesis of cell wall polysaccharides in apical (5 mm starting from the root cap) and subapical (5-10 mm starting from the root cap) root segments isolated from water stressed and unstressed wheat seedlings (*Triticum durum* Desf.) cv. 'Capeiti' "drought tolerant" and cv. 'Creso' "drought sensitive" (Piro *et al.*, 2003). The drought susceptibility index (DSI) for the two cv. was determined by Flagella *et al.* (1995). Water stress inhibited markedly the growth of wheat seedlings cv. 'Capeiti' "drought tolerant" and cv. 'Creso' "drought sensitive". In both cv., the growth of coleoptile was inhibited by approximately 75% whereas that of root by approximately 50%. Our biosynthetic studies were performed in the presence of D-[U-¹⁴C]-glucose as radioactive tracer. We have demonstrated that during water stress, the newly synthesised cell wall matrix polysaccharides, namely pectins and hemicelluloses, were differentially decreased in the apical and subapical root segments of both cv. Root segments (apical and subapical) of cv. 'Creso' were more affected than those corresponding to cv. 'Capeiti'. In addition, on both cv., this decrease was greater in the subapical region than in the apical one. In water stressed apical root segments of cv. 'Creso' "drought sensitive", all radioactive glycosyl residues incorporated into matrix polysaccharides were drastically reduced whereas, in cv. 'Capeiti' "drought tolerant", some glycosyl residues were perceptually slightly reduced (uronic acids and xylose), some others (galactose, rhamnose and arabinose) remained almost unchanged. These data indicate that, under water stress, cv. 'Capeiti' "drought tolerant" has the capability to sustain the synthesis of cell wall polysaccharides which are able to influence the hydration gelling properties of the wall. These properties are important to protect cells from desiccation. The polysaccharides involved in conferring cell wall hydration are homogalacturonan (HGA), rhamnogalacturonan-II (RG-II) and rhamnogalacturonan-I (RG-I) with lateral chains of arabinans, galactans and highly branched arabinogalactans. These pectins, although are minor components of primary cell walls of monocot, play multiple functions in plant growth and development (Willats *et al.*, 2001). Although a sequential chemical solubilisation of cell wall polysaccharides was performed in isolated wheat root segments, it was difficult to obtain a clear distinction between pectins and hemicelluloses on the base of glycosyl residue composition of both polymers. There is evidence for the existence of a significant proportion of xyloglucan (XyG) covalently linked to the pectic network through arabinan/galactan of RG-I (Thompson and Fry, 2000; Popper and Fry, 2005). The hemicellulosic components of primary wall of monocot are thought to be mainly glucurono-arabino-xylan (GAX) with a little amount of XyG. An appropriate interaction of the hemicelluloses with pectins may modulate the gelling properties of cell wall matrix polysaccharides.

The β -glucans are well known growth specific cell wall polysaccharides (Carpita *et al.*, 1996). During water stress, in apical and subapical root segments of both cv. the radioactive glucosyl residues incorporated in β -glucan-based polysaccharides were markedly decreased. This reduced synthesis of β -glucan-based polysaccharides is not correlated to the characteristic of "drought tolerance" of cv. 'Capeiti' and "drought sensitivity" of cv. 'Creso'. It is probably connected to the inhibition of root growth under water stress. Similar conclusion may be reached about the reduced biosynthesis of α -cellulose in apical and subapical root segments of both cv. under water stress. Numerous investigations have also evidenced the decrease of cellulose synthesis, under water stress, in different tissues and organs (Zhong and Läuchli, 1993; Sweet *et al.*, 1990; Sakurai *et al.*, 1987; Muñoz *et al.*, 1993). Thus, the study on the biosynthesis of cell wall polysaccharides in water stressed and unstressed roots of wheat seedlings has given an indication of how the polysaccharide synthases located on the plasma membrane (cellulose synthase complex) and Golgi apparatus (pectin and hemicellulose synthases) are differentially modulated in cv. 'Capeiti' "drought tolerant" and cv. 'Creso' "drought sensitive".

We have also studied the chemical structure of cell wall polysaccharides of the root of both cv. For these experiments 5-mm apical root segments were used. From the purified cell walls of the apical segments pectins (CDTA+Na₂CO₃), hemicelluloses (different concentrations of KOH) and the remaining insoluble residue (α -cellulose) were sequentially solubilised. Each polysaccharide was then analysed for the glycosyl residue composition and subjected to linkage analysis (York *et al.*, 1986). In apical root segments of both cv. grown under water stressed and unstressed conditions, the total amount of cell wall matrix polysaccharides (pectins and hemicelluloses) and α -cellulose remained almost unchanged. However, in cv. 'Capeiti' "drought tolerant", grown under water stress, the amount of solubilised pectins was reduced in favour of an increase of the amount of hemicelluloses. In apical root segments of both cv., 2/3 of cell wall are matrix polysaccharides and 1/3 α -cellulose.

In water stressed and unstressed apical root segments of both cv., the glycosyl residue

composition of pectins and hemicelluloses remains very much similar with only slightly variations. Xylose, glucose and arabinose were the main glycosyl residues, whereas mannose, galactose and galacturonic acid were minor components. In apical roots, the qualitative and quantitative similarities between pectins and hemicelluloses have let us to consider these polymers a complex interacting network.

The glycosyl linkage analysis of neutral cell wall polysaccharides solubilised as pectins and hemicelluloses was performed on root apical segments of both cv. grown under water stress and unstressed condition. From these analyses it was possible to calculate the amount of the main cell wall polysaccharides solubilised from the wall of wheat root segments of the two cv. In cv. 'Capeiti' "drought tolerant", water stress increased the mol % of side chains of RG-I and RG-II and slightly affected the mol % of xyloglucans, arabinoxylans and β -glucans. About four fold increase in the mol % of HGA, determined by the method of Blumenkrantz and Asboe-Hansen (1973), was also observed during water stress. In cv. 'Creso' "drought sensitive" the mol % of all polysaccharides remained unaltered with the exception of the amount of HGA (mol %) which increased approximately two fold under water stress. Altogether these data confirm that cv. 'Capeiti' "drought tolerant" has the capability to synthesise HGA and side chains (arabinans, galactans and arabinogalactans) of RG-I and RG-II which contribute to cell wall porosity as plasticizer and water-gelling agents.

Conclusions

Our studies indicate that a way to improve drought tolerance in roots can be achieved through an overexpression of the genes involved in the synthesis of matrix polysaccharides (pectins and hemicelluloses). There are two strategies available for the enhancement of matrix polysaccharides in plants: (i) traditional plant breeding / varietal difference; and (ii) genetic engineering.

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