IN BRIEF

A New Mechanism for Starch Dephosphorylation: Insight from the Structure of LIKE SEX FOUR2

Starch granules are dense, insoluble structures made up of glucan chains that serve as both short- and long-term carbohydrate storage within plants (reviewed in Streb and Zeeman, 2012). It is thought that phosphorylation of glucosyl moieties within the glucan chains solubilizes the granule surface and facilitates starch degradation. Paradoxically, however, glucan phosphorylation also inhibits the activity of certain amylases that are required for starch breakdown. Therefore, in addition to glucan kinases, glucan phosphatases are needed for efficient starch degradation. Arabidopsis thaliana contains two chloroplastic glucan phosphatases, STARCH EXCESS4 (SEX4) and LIKE SEX FOUR2 (LSF2). SEX4 removes phosphate groups from both the C3 and C6 positions of glucosyl residues, whereas LSF2 is specific for phosphates at the C3 position (Santelia et al., 2011). Now, Meekins et al. (pages 2302–2314) report crystal structures of LSF2, revealing the basis of this specificity as well as of LSF2’s ability to bind glucan despite lacking a characteristic carbohydrate binding module.

Meekins et al. determined the structure of LSF2 both with and without bound products maltohexaose (a chain of six Glc residues) and phosphate. The fold of the LSF2 active site was similar to dual-specificity phosphatase domains of other members of the protein tyrosine phosphatase superfamily, including that of SEX4 (Vander Kooi et al., 2010). Furthermore, the catalytic triad within the active site was positioned to act on the C3 position of a glucosyl residue, nicely explaining LSF2’s positional specificity. Five aromatic residues that are conserved in plants made up an extended channel in the active site. When aromatic residues on each side of the channel were mutated, LSF2’s glucan phosphatase activity was nearly eliminated, although the mutant protein was still able to dephosphorylate a generic substrate. Thus, this aromatic channel is necessary for the glucan specificity of plant glucan phosphatases.

Interestingly, maltohexaose was bound not only in the active site but also at two other sites in the structure far removed from the active site (see figure). Mutating residues in these noncatalytic sites reduced both glucan binding and glucan phosphatase activity, and the effects were specific to glucans; the mutants displayed almost no reduction of phosphatase activity of a generic substrate. The importance of the secondary binding sites in LSF2 is emphasized by the fact that it took mutations in all three binding sites—the active site and both secondary binding sites—to abolish glucan binding and specific activity. Thus, this work from Meekins et al. reveals how LSF2 functions without the carbohydrate binding module that other glucan phosphatases use for substrate binding. The involvement of secondary binding sites in LSF2 activity brings to mind those found in starch-hydrolyzing enzymes (Cuyvers et al., 2012), broadening our view of potential starch binding mechanisms, as well as highlighting the need to understand the function of these noncatalytic substrate binding sites.

REFERENCES


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