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Structure of Extracellular Polysaccharides (EPS) Produced by Rhizobia and their Functions in Legume–Bacteria Symbiosis: — A Review

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ABSTRACT

The symbiotic diazotrophs comprise with a very diverse group of Gram negative soil bacteria, collectively called as rhizobia found in nodule of legume plant. Rhizobia adopt themselves in different environment including soil, rhizosphere and grown within legume roots, where they fix nitrogen. The establishment of symbiosis is a very complicated process involving a coordinated exchange of signal between legume plants and the symbionts. The nodule development requires synthesis of signal molecules such as Nod factors that are important for induction of nodule development. There are different types of surface polysaccharides such as lipopolysaccharides, capsular polysaccharides, neutral and acidic polysaccharides found in rhizobia. The production of symbiotically active polysaccharides may allow rhizobial strains to adapt themselves to changing environmental conditions and interact efficiently with legume plants. Despite extensive research, the actual molecular function of the surface polysaccharides of rhizobia in symbiosis remains unclear. This review emphasized on the structural composition of extracellular polysaccharide of different rhizobia isolated from different legume plants. The compositions of extracellular polysaccharides are different in different rhizobia. The various compositions of extracellular polysaccharides produced by the symbionts are considered as the signaling molecules essential for determining host plant specificity. The present status of the biological functions of the exopolysaccharide in symbiosis such as host specificity, successful invasion, formation of infection thread and induction of nodule formation in legume plants is also summarized here.

Contents

Abbreviations: EPS, extracellular polysaccharide; CPS, capsular polysaccharide; LPS, lipopolysaccharides; CG, cyclic beta glucan; KPS, K-antigen polysaccharide; NP, neutral polysaccharide.

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Introduction

Polysaccharide is the most abundant organic macromolecules in nature. The biosyntheses of polysaccharide are found in different organisms ranging from bacteria to eukarya, including plants. Gram negative soil bacteria belonging to (α and β-proteobacteria) have the ability to produce root nodule by symbiosis with legume plants (Skorupska et al., 2006). This interaction is initiated by the exchange of signal by diverse molecules between the two partners. Among them, plants liberate flavonoids into the rhizospheric region that upregulate rhizobial genes responsible for nodule formation (Spaink, 2000; Schulze et al., 1998). Recognition of the symbiont is made possible through the exchange of nod factor perception and Ca^{2+}/calmodulin-dependent protein signaling (Geurts and Bisseling, 2002; Oldroyd and Downie, 2004). The establishment of successful symbiosis in legume plant was made by the production of nod factor signal and exposure of the correct surface and/or extracellular polysaccharide.

This signal exchange between the two partners seems to work at a distance in the rhizosphere and before binding of rhizobial symbiont to the host root hairs, to induce morphogenetic changes in plant roots. These signal molecules, the Nod factors, are sufficient for initiation of root hair changes, bacterial cell entry for infection, thread formation and activation of cortical cell division Schulze et al. (1998) to generate the nodule primordium (Nod) (Kijne, 1992). Rhizobia colonize with plant root hairs, develops infection, the bacteria multiply to form infection thread. In this thread the bacteria encircled by the peribacteroid membrane of plant origin that differentiate into bacteroids (Fisher and Long, 1992).

Bacteroids were found to fix nitrogen by synthesizing the nitrogenase enzyme and other proteins. In return, plant supplies carbohydrates to bacteria as a source of carbon and energy. The establishment of symbiosis is stringently controlled through a complex network of signaling cascades Schulze et al. (1998). This process is partner specific and signifies that the rhizobial species can only nodulate a limited but defined range of legume plants.

The key factors for the interaction are a number of rhizobial genes which are responsible for production of different types of cell-surface polysaccharides such as capsular polysaccharide (CPS) that form as adherent cohesive layer on the cell surface. However, the term exopolysaccharides (EPS) is used for polysaccharides with little or no cell association (Becker and Pühler, 1998). Cyclic beta-(1-2)-glucan is concentrated in periplasmic space of rhizobia, which plays an important role in osmotic adaptation of bacteria Breedveld et al. (1993). Lipopolysaccharides (LPS) are anchored in outer membrane and consist of lipid A, a core polysaccharide and repeating O-side antigen polysaccharides. Despite extensive research, the precise role of surface polysaccharides in symbiosis remains unclear. So the role of rhizobial polysaccharide has been the goal of many studies.

The present review describes the production and structure of different exopolysaccharides of rhizobia isolated from legume root nodule. Attempts were also made to discuss the possible role of the exopolysaccharide in legume — rhizobia symbiosis and nodule formation.

Structural Features of Rhizobial Exopolysaccharides

Rhizobial cell produces different types of surface polysaccharides into environment or retained at the cell surface. They comprise extracellular polysaccharide (EPS), lipopolysaccharide (LPS), capsular polysaccharide (CPS), cyclic beta glucan (CG), K-antigen polysaccharide (KPS), neutral polysaccharide (NP), gel-forming-polysaccharide (GPS), and cellulose fibrils. They are species as well as strain-specific heteropolymers and consisting of repeating units containing mainly common monosaccharides (D-glucose, D-mannose, D-galactose, L-rhamnose, D-glucuronic and D-galacturonic acids) (Table 1). A large diversity in EPS chemical structures can be found among rhizobia, concerning sugar composition, linkage of subunit, repeating unit size and degree of polymerization as well as non-carbohydrate decoration (Table 1) (Laus et al., 2005; Skorupska et al., 2006; Downie, 2010; Janczarek, 2011). EPS are mainly two types, succinoglycan (EPS I) and galactoglucan (EPS II) produced by several rhizobial strains (Reinhold et al., 1994) (Fig. 1). EPS-I composed of octasaccharide repeating units containing one galactose and seven glucose residues (in molar ratio 1:7), joined by β-1,3; β-1,4 and β-1,6 glycosidic linkages whereas EPS II is a polymer of disaccharide repeating unit and joined by α-1,3 and β-1,3 glycosidic bonds (Her et al., 1990; Zevenhuizen, 1997).

Single repeating unit is decorated by different non-carbohydrate such as acetyl, pyruvyl and succinyl groups. Both EPS I and II are secreted in two major fractions — High Molecular Weight (HMW) consisting of hundreds to thousands of repeating units and Low Molecular Weight (LMW) that represents monomers, dimers and trimers in a case of EPS I and oligomers (15–20) in the case of EPS II (Gonzalez et al., 1996, 1998; Wang et al., 1999). The pattern of non-carbohydrate modifications of EPS may be different in various strains of the same species and depend on the phase of bacterial growth and culture medium. Non-carbohydrate modifications located in the side chain of the EPS units proved to be very important for the signaling properties of EPS in the symbiosis (Ivashina and Ksenzenko, 2012; Janczarek et al., 2014).

Production of Exopolysaccharides in Culture by Rhizobia

Rhizobium spp. are able to produce large amount of EPS in culture rather than EPS produced in symbiotic condition (Table 2). The growth environment was very important for maximum exopolysaccharide production (Sutherland, 1972). Utilization of different carbon sources for the growth and EPS production by *Rhizobium* sp. was reported earlier (Stowers, 1985; Breedveld

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