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Exopolysaccharide *Cepacia*: Structure, Biosynthesis and Role in Resistance to Stress Condition

Monika Sharma and Harish Kumar Dhingra*
Department of Biotechnology, Faculty of Arts, Science and Commerce, Mody Institute of Technology and Science, Lakshmangarh-332311

Keywords: Exopolysaccharides, chitoson, dextrane and genus *Burkholderia*.

Abstract

Many bacteria produce Exopolysaccharides (EPSs), which play a wide range of roles in their biology. EPSs are often important virulence determinants produced by pathogens of plants, animals, and humans. Various microbial exopolysaccharide like dextrane kefiran, alginate, cellulose, xanthan, leven and chitoson have commercial application. The genus *Burkholderia* are widespread in nature, gram-negative, non-spore-forming, aerobic bacillus; motile with a respiratory metabolism and typically catalase and oxidase positive; various non fluorescent pigments may be produced and poly-β-hydroxy alkanoates can be accumulated as reserve materials. One common feature across the genus is the ability to produce an exopolysaccharide (EPS) termed *cepacia*n. *Cepacia*n is composed of a branched acetylated heptasaccharide repeat unit with D-glucose, D-rhamnose, D-mannose, D-galactose and D-glucuronic acid. Genome sequence analyses of *Burkholderia* spp. shows presence of the bce-I gene cluster, named from bceA to bceK and bce-II gene cluster were named bceM to bceU and encode products putatively involved in nucleotide sugar precursor biosynthesis and repeat unit assembly, modification, and translocation across the cytoplasmic membrane. The ability of *Burkholderia strains* to withstand desiccation and metal ion stress was higher in the presence of *cepacia*n, suggesting that this EPS plays a role in the survival of these bacteria by contributing to their ability to thrive in different environments. It also provides resistance to bacteria in biological system via providing resistance against antimicrobial peptides. The significance of study on *Burkholderia* spp. has a huge area for future research to overcome its disadvantages and enhance its adventitious properties.

Corresponding author, **Harish Kumar Dhingra**, Department of Biotechnology, Faculty of Arts, Science and Commerce, Mody Institute of Technology and Science, Lakshmangarh-332311 Email: harishdhingra2000@gmail.com

Introduction

Polysaccharides, polymers based on sugar molecules (carbohydrates), are a major part of the annually produced biomass and only a very small percentage is currently used by man. Polysaccharides may be structural, secretary like exopolysaccharides. Exopolysaccharides (EPS) are high molecular weight polymers which are long chain composed of sugar residues and secreted by microorganisms into the surrounding environment. Exopolysaccharides are often found in the surrounding as the outer most structures of both prokaryotic and eukaryotic microbial cells. They may be closely associated with the cell in the form of discrete capsules or excreted as slime surface. EPS exist in a wide variety of unique and often complex chemical structures and they are believed to provide self protection against anti microbial substances (Kumon, 1994). The structure of many bacterial polysaccharides is relatively simple, comprising either homo polysaccharides (usually polymers composed of d-glucose) or hetero polysaccharides; the latter are normally composed of regular repeating units ranging in size from di-saccharides to octa-saccharides composed of 2–4 types of monosaccharide and many contain acyl groups as additional adornments. The commonest acyl substituents are acetate, esters and pyruvate, ketals and succinyl half esters are also a feature of some EPS. The presence of the ketals or of uronic acids, results in linear poly anionic macromolecules. Only bacterial alginates lack a regular structure. In these polymers, d-mannuronosyl and l-guluronosyl residues are found in random sequences and are normally heavily acetylated on the mannuronosyl groups. Some polysaccharides possess larger repeating units and other acyl substituents. These include succino-glycan produced by *Rhizobium* and *Agrobacterium* spp. It is composed of d-glucose and d-galactose in an octa-saccharide repeating unit and carries O-acetyl groups, O-succinyl half-esters and pyruvate ketals (Sutherland, 1996). Table given below contains different bacterial exopolysaccharide.

Genus *Burkholderia*

Bacteria from the genus *Burkholderia* are wide spread in nature, with *strains* being isolated from rhizosphere, aquatic environments, man-made environments and in association

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with hosts causing disease or beneficial interactions. One common feature across the genus is the ability to produce an exopolysaccharide (EPS) termed *cepacia*n (Ferreira, 2010). The general characteristics of *Burkholderia cepacia* include the following: gram-negative, non-spore-forming, aerobic bacillus, motile with a respiratory metabolism and typically catalase and oxidase positive, various non fluorescent pigments may be produced and poly-β-hydroxy alkanoates can be accumulated as reserve materials, the optimal temperature for growth is 30- 35°C (Palleroni, 1984). Recently, molecular analyses have provided scientific evidence that may account for the organism's impressive versatility, including multi locus linkage disequilibrium analysis of environmental populations (Wise, 1995) which suggested an extraordinarily high rate of recombination in *B. cepacia* relative to binary fission and demonstration of multiple replicons and insertion sequences in type *strains* (Cheng, 1994 and Rodley, 1995). The natural habitats of *Burkholderia cepacia* have been described as soil, water and vegetation (Holmes, 1986). However, it is a common but erroneous belief that *B. cepacia* is a ubiquitous saprophyte sharing similar environmental habitats with *Pseudomonas aeruginosa* and other pseudomonads. Extensive surveillance studies have shown that culture of *B. cepacia* from natural sources, including soil, water and plants, or from hospitals, food stores, restaurant salad bars and patients' homes is surprisingly difficult, with detection rates of only 1- 16% (Pitchford, 1987; Fisher, 1993; Butler, 1995; Mortensen, 1995 and Holmes, in press).

Biosynthesis pathway of Cepacain

Repeat-units of the polymer are assembled on a isoprenoid lipid carrier, in the cytoplasmic side of inner membrane in a reaction initiated by the BceB enzyme and continued by the other glycosyl transferases BceG, BceH, BceJ, BceK, and BceR and putative acyl transferases BceO, BceS and BceU. The lipid-linked repeat-units are translocated across the inner membrane by the putative BceQ membrane protein. Polymerization occurs at the periplasmic face of the inner membrane and is dependent on another membrane protein, the putative polysaccharide polymerase, BceI. Wzy-dependent polymerization and export requires the activity of the BceF tyrosine kinase. BceD is a protein tyrosine phosphatase enzyme responsible for dephosphorylating BceF. BceE forms a channel structure for export of EPS chains to the outside. BceP, putatively involved in polysaccharide degradation, is depicted as associated to the outer membrane, as one of its possible locations. Here abbreviations are elaborated like Glc, glucose; GlcA, glucuronic acid; Gal, galactose; Rha, rhamnose; Man, mannose; Fru, fructose; GDP, guanosine-5-diphosphate; UDP,uridine-5-diphosphate; PGM, phosphoglucomutase; UGP, UDP-glucose pyrophosphorylase; UGD, UDP-glucose dehydrogenase; UGE, UDP-glucose epimerase; PGI, phosphoglucose isomerase; PMI, phospho mannose isomerase; PMM, phosphomannomutase; GMP, GDP-D-mannose pyrophosphorylase; GRS, GDP-rhamnose synthase; ATP, adenosine-5-triphosphate; ADP, adenosine-5- diphosphate; YP, phosphorylated tyrosine residue; Pi, inorganic phosphate; IM, inner membrane; OM, outer membrane; PL, peptidoglycan layer (Ferreira, 2011).

Role of *Cepacia*n in Resistance in stress conditions

Bacterial extra cellular polysaccharides have been described as pathogenicity determinants in humans, livestock, and plant infections; as important in the establishment of symbiotic interactions between bacteria and plants; and as a barrier to harmful compounds (Fraysse, 2003; Lebeer, 2011; Nielsen, 2011). Depending on the ecological niche, exopolysaccharides help bacteria to colonize different environments. Given that *cepacia*n is ubiquitous in the genus *Burkholderia*, it would be expected that this exopolysaccharide plays an important role in bacterial adaptation to different conditions including host and bacteria interactions. Figure 5 summarizes the current knowledge on the relevance of exopolysaccharides in *Burkholderia*. Interaction between plants and bacteria is often correlated to the ability of bacteria to produce exopolysaccharides, regardless being pathogenic or symbiotic. In pathogenic interactions, exopolysaccharide contributes to the initial plant colonization and enhances bacteria survival within the plant host tissues during the course of infection, as described for *Agrobacterium*, *Erwinia*, and *Pseudomonas* (Denny, 1995). On the other hand, exopolysachharides are important in the establishment of symbiotic interactions such as in biological nitrogen fixation symbiosis between rhizobia and leguminous plants (Gonzalez, 1996). Since the first description of pathogenicity in the *Burkholderia cepacia* complex bacteria was based on sour skin rot of onion bulbs, (Bartholdson, 2008) investigated EPS production in *Burkholderia cepacia* complex isolates and the iron ion associated phenotype. Although the onion carbohydrates induced exopolysaccharide production, no correlation between exopolysaccharide production ability of the tested *strains* and tissue onion maceration was found. Therefore, a possible role of the exopolysaccharides in interaction between *Burkholderia* and host plants has yet to be demonstrated. Nevertheless, the observation that the endophytic *Burkholderia kururiensis* exopolysaccharides can be modulated under growth conditions is potentially significant in terms of a possible endophytic host plant interaction and further studies are needed (Hallack, 2010).

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Since many exopolysaccharides are high molecular weight polymers, they form a hydrated anionic matrix that surrounds the cell protecting bacteria against environmental stresses. Also, the hygroscopic properties of the EPS may reduce the rate of water loss from cells and provide bacteria with means to survive drying and desiccation (Potts, 1994). A study performed with B. xenovorans LB400 and B. *multivorans* ATCC 17616 isolates has shown that the external supplementation of *cepacia*n enhanced their desiccation tolerance when compared to a condition where no exopolysaccharide was present (Ferreira, 2010). *Cepacia*n also protects *Burkholderia* cells against metal ion stress, namely high concentration of Fe2+ and Zn2+ (Ferreira, 2010). The metal-binding properties of EPS might be due to the occurrence of carbonyl, carboxyl, and hydroxyl groups within the EPS matrix that can complex cations and scavenge metals (Potts, 1994). The ability of *Burkholderia strains* to with stand desiccation and metal ion stress in the presence of the *cepacia*n is an indication that this exopolysaccharide may play a role in survival, thus representing an advantage for bacteria to thrive in adverse environments. Another import role attributed to polysaccharides is them ediation of bacterial resistance against antimicrobial peptides produced by epithelial and phagocytic cells. A study involving the human antimicrobial peptides cathelicidin LL-37 and β-defensin hBD-3 as well as peptides from other mammals demonstrated that the antibacterial activity of these different peptides was considerably decreased in the presence of polysaccharides produced by the lung pathogens *P. aeruginosa*, *Klebsiella pneumoniae*, and *Burkholderia cepacia* complex members (Benincasa, 2009). Production of bacterial polysaccharides in the lungs of cystic fibrosis patients could contribute to a decreased efficacy of the host defense response and the concomitant establishment of a persistent infection by these bacteria. Exopolysaccharides, proteins and DNA are the main constituents of the mature biofilm matrix contributing for example to the persistence of chronic *P. aeruginosa* lung infections in cystic fibrosis patients (Hentzer, 2001). Bacterial biofilms cause chronic infections due to their increased tolerance to antibiotics and resistance to the immune system phagocytic cells. As a consequence, chronic inflammation develops, being the major cause of the lung tissue damage in cystic fibrosis (Hoiby, 2010). *Burkholderia cepacia* complex bacteria were also shown to produce biofilms in abiotic surfaces and on well differentiated human epithelial cells (Schwab, 2002) and the production of biofilms associated to a significant increase of resistance against the host immune system and antibiotic treatment in *Burkholderia* (Carahere, 2007). Mutants constructed on bce genes have confirmed the importance of *cepacia*n in the formation of mature biofilms. Mutants unable to produce *cepacia*n, such as a bceF insertion mutant, or mutants that produce a lower molecular weight form, such as bceD insertion mutant, exhibited a much thinner biofilm when compared to the one produced by the parental strain (Ferreira, 2007). Therefore, it has been hypothesized that by promoting the formation of mature biofilms, the EPS may enhance bacterial survival in cystic fibrosis lung, which leads to the impossibility to efficiently eradicate Bcc infections.

Conclusion

Exopolysaccharides exist in a wide variety of unique and often complex chemical structures and they are believed to provide self protection against anti microbial substances. *Cepacia*n is an exopolysaccharide produce by genus *Burkholderia* which is a genus of opportunistic bacteria which have important role in both plants and animals, it is pathogenic as well as have beneficial properties too. *Cepacia*n biosynthesis ability is comman feature among the *Burkholderia* genus. This genus has the genetic capacity to produce several different extracellular polysaccharides. Although some knowledge about the genes and enzymes involved in its biosynthesis already exists, the regulatory mechanisms for its production are almost unknown. The ability of *Burkholderia* to produce different exopolysaccharides raises questions on which environmental signals induce production of one polysaccharide verses others and their specific roles to provide a survival advantage in different ecological niches such as soil, water, or during host bacterial interactions. Cepecian exopolysaccharide provide resistance against desiccation, metal ion stress and antimicrobial peptides. The role of EPS in *Burkholderia* virulence remains an open issue. While some evidences point out to EPS as a virulence factor, others indicate a major role in persistence. Further study is required on genus *Burkholderia* to overcome its disadvantages in environment and enhance its adventitious properties.

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Table 1. Different Bacterial Exopolysaccharides Secreated by Various Bacteria

Sr. No.	Name	EPS	References
1.	*Lactic acid bacteria*	Dextran,	Cerning, 1990
2.	*Escherichia coli*	N-acetyl heparosan	Richard, 1996
3.	*Staphylococcus epidermidis*	N-acetyl glucosamine	Izano, 2008
4.	*Azotobacter spp.*	Alginate	Clementi, 1997
5.	*Rhizobium spp.*	Cyclosoporans	Scott, 1984
6.	*Xanthomonas compestris*	Xanthan	Carignatto, 2011
7.	*Bacillus subtilis*	Levan	Fernando, 2012
8.	*Mucorales spp.*	Chitosan	Amorim, 2001
9.	*Beinjerickia indica*	Indican	Daniels, 2009

Table 2. Overview of *Burkholderia cepacia* complex *species* and their sources of isolation

Sr. No.	Name	Habitat	References
1.	*B. cepacia*	Human (CF and non CF), Soil, Rhizosphere soil, Plant and Water	Vandamme, 1997
2.	*B. multivorans*	Human (CF and non-CF), Soil, Rhizosphere soil, plant	Vandamme, 1997
3.	*B. cenocepacia*	Human (CF and non-CF), animals, soil, rhizosphere soil, plant, water, industrial contaminant	Vandamme, 2003
4.	*B. stabilis*	Human (CF and non-CF), Rhizosphere soil, Hospital equipment	Coenye, 2001
5.	*B. vietnamiensis*	Human (CF and non-CF), Soil, Rhizosphere soil, plant material, animal	Coenye, 2001
6.	*B. dolosa*	Human (CF), plant material, Rhizosphere soil	Vermis, 2004
7.	*B. ambifaria*	Human (CF), soil, Rhizosphere soil	Coenye, 2001
8.	*B. anthina*	Human (CF), animals, soil, Rhizosphere soil, river water	Vandamme, 2002
9.	*B. anthina*	Human (CF), animals, soil, Rhizosphere soil, river water	Vandamme, 2002
10.	*B. pyrrocinia*	Human (CF and non-CF), soil, Rhizosphere soil, water	Vandamme, 2002
11.	*B. ubonensis*	Human (non CF), soil	Vanlaere, in press
12.	*B. latens*	Human (CF)	Vanlaere, 2008
13.	*B. diffusa*	Human (CF and non-CF), soil, hospital equipment	Vanlaere, 2008
14.	*B. arboris*	Human (CF and non CF),	Vanlaere, 2008
15.	*B. seminalis*	Human (CF and non-CF), Plant material, Rhizosphere soil	Vanlaere, 2008
16.	*B. metallica*	Human (CF)	Vanlaere, 2008
17.	*B. contaminans*	Human (CF and non CF), soil, animal, hospital	Vanlaere, in press
18.	*B. lata*	Human (CF and non CF), soil, plant material, water	Vanlaere, in press

Note: CF: Cystic fibrosis

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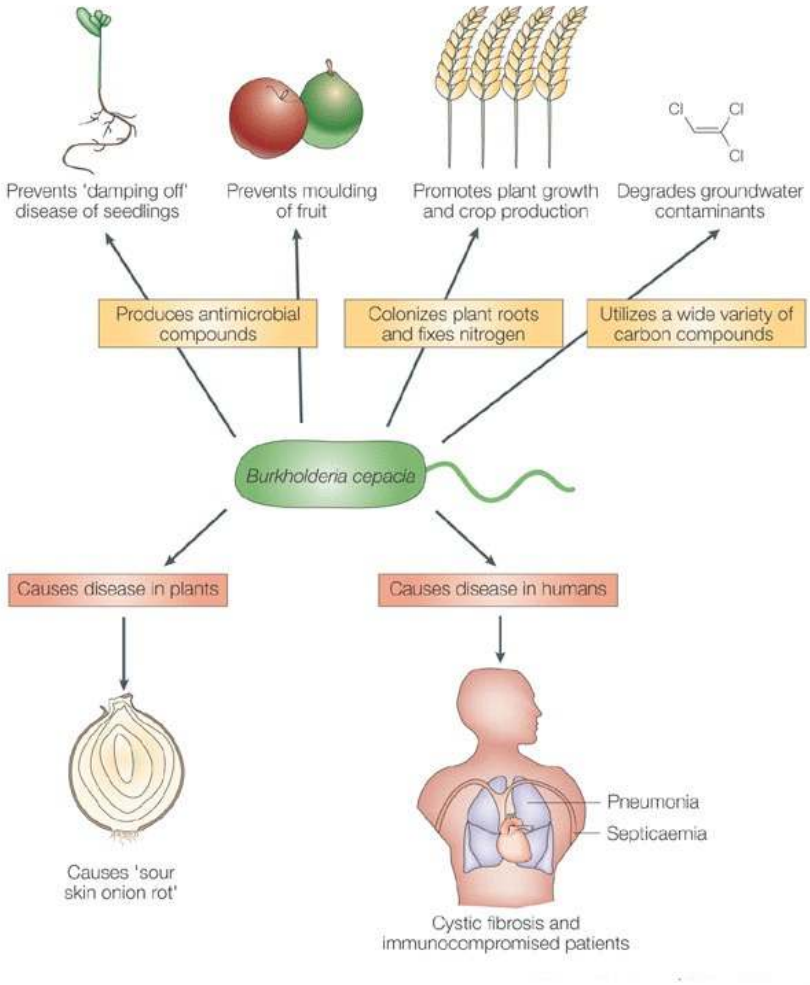
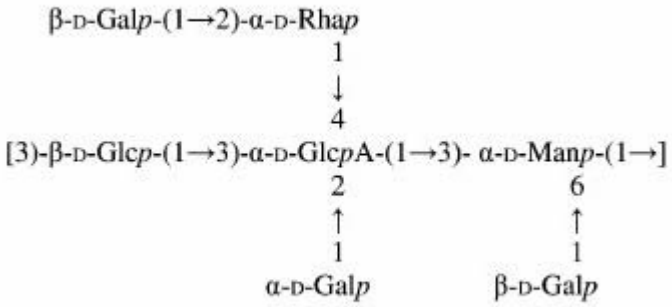
Figure 1. Beneficial effects of the *Burkholderia cepacia* complex (Mahenthiralingam, 2005)



Exopolysaccharide: *Cepacia*n

Figure 2: Structure of exopolysaccharide produced by *Burkholderia cepacia* strain (Cerantola, 2000)



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Gene cluster involved in *cepacia*n biosynthesis

Figure 3. Genetic organization of the bce gene cluster directing the biosynthesis of *cepacia*n by *Burkholderia* bacteria.
The *bce* genes are clustered together in the same genomic region as shown in (a) is represented by *strains* of *species B. xenovorans, B. phymatum* and *B. graminis.* while, the *bce* genes are split into two regions 155 to 314 kb apart in (b) which is represented in *strains* of *Burkholderia cepecia* complex comprising *B. pseudomallei, B. oklahomensis* and *B. thailandensis. Strains* from *B. mallei* have the *bce-II* cluster only (Ferreira, 2011).

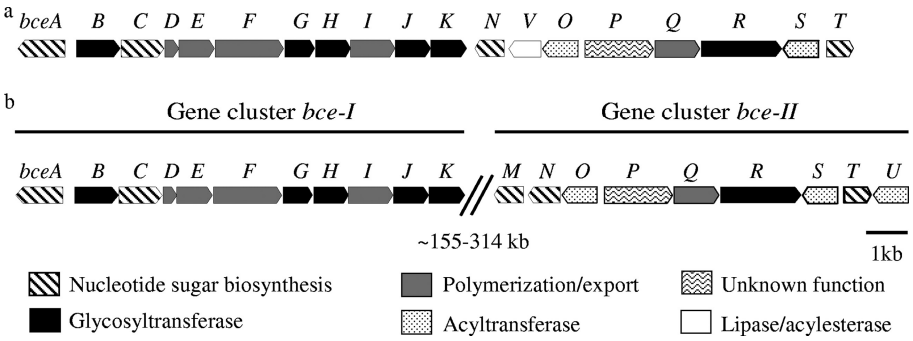
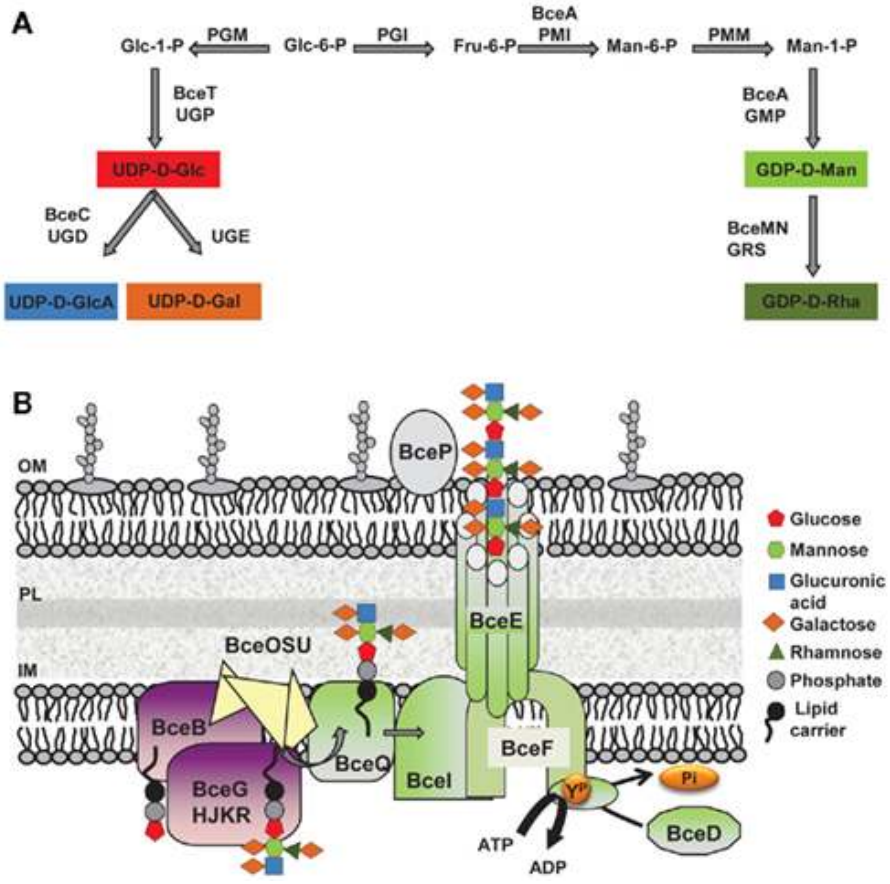


Figure 4. Biosynthesis of the exopolysaccharide *cepacia*n by *Burkholderia*.
(A) Metabolic route toward the synthesis of the various activated sugar nucleotide precursors required for *cepacia*n repeat-unit biosynthesis. (B) Schematic representation of enzymes involved in *cepacia*n biosynthesis.



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Monika Sharma
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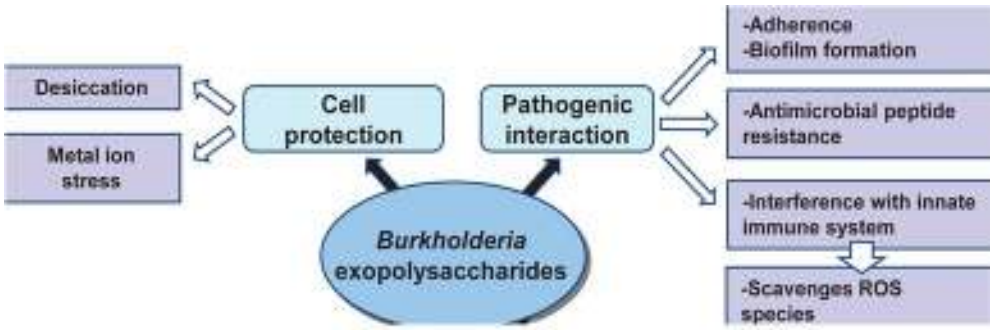
Figure 5. Roles of *Burkholderia* exopolysaccharides in the adaptation to different stress conditions.



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