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Diversity of Exopolysaccharide Producing Bacteria and Applications of Exopolysaccharides

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Abstract: Bacteria produce diverse biopolymers with varied chemical properties using simple to complex monomer substrates. These bacterial biopolymers serve a range of biological functions, such as reserve material, protective capsules and slimes and biofilm matrix components. Several of them have chemical and material properties that are suitable for industrial and medical applications. The most important ones are bacterial exopolysaccharides that provide valuable sources for renewable, biodegradable and biocompatible materials that have high potential prospects to replace the non-renewable petro-based biopolymers. Bacterial exopolysaccharides are extracellular polysaccharides that exist either associated and covalently bound to the bacterial cell surface in the form of a capsule, or loosely bound to the bacterial cell surface in the form of slime. They have diverse applications in the food, pharmaceutical, nutraceutical, cosmeceutical, herbicides and insecticides industries. They do also have great prospects for applications as an anticoagulant, antithrombotic, immune-modulation, anticancer and as bio-flocculants. This review is written to show the diversity of these valuable bacterial genetic resources and discuss the various actual or potential applications that are derived from the exopolysaccharides they produce.

Key words: Diversity · Bacteria · Biopolymer · Exopolysaccharide and applications

INTRODUCTION

Biopolymers derived from biomass such as plants, animals and microbes have considerable economic and environmental values. Because of their values, extensive research has been done for the past few decades on polymers obtained from plants and animals. Currently, research related to bacterial biopolymers is rapidly expanding because bacterial exopolysaccharides have a number of advantages over synthetically produced and plant-derived polysaccharides. They are non-toxic, biodegradable, renewable, abundantly available and resistant to mechanical and oxidizing destruction, temperature and low pH values [1]. Moreover, there are easy methods being developed to grow and harvest them for use in numerous industrial and medical applications [2].

Since the beginning of twentieth century, technologies related to bacterial production of biomolecules like enzymes, antibiotics, metabolites and polymers have matured to a great extent. Currently, bacteria are used for commercial production of a wide variety of products such as pesticides, fertilizers and feed additives in agrochemical sector, food additives for their gelling, stabilizing or thickening properties in food industry sector, biopharmaceuticals and therapeutics in the healthcare sector, biopolymers and biofuels in the energy and environment sectors [3]. Particularly, bacterial extracellular polysaccharides besides the interest on their applications in the health (e.g. health promoting effects in the treatment of inflammatory diseases and cancer) and bio-nanotechnology sectors, they are also used as thickeners, bio-adhesives, stabilizers, probiotic and gelling agents in food and cosmetic industries and as emulsifier, bio-sorbent and bio-flocculant in the environmental sector [4].

Generally, bacterial biopolymers are classified into intracellular biopolymer (IBP), extracellular biopolymer (EBP) and structural biopolymer (SBP) depending on their cellular locations [5, 6]. In recent years, there is an increased demand for natural biopolymers for various industrial and biotechnological applications due to the

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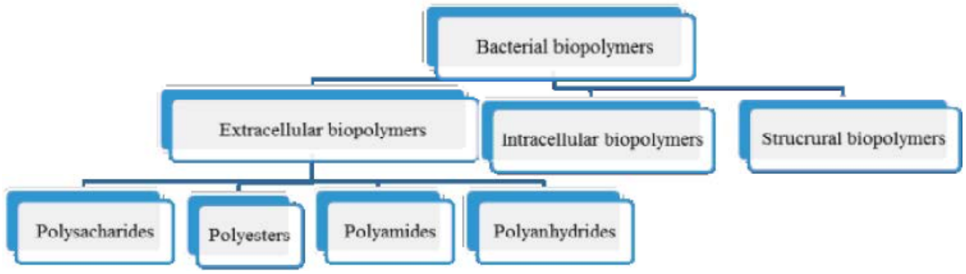

Fig. 1: Classification of bacterial biopolymers

environmentally unfriendly toxic petro-based polymers [7]. This high demand of renewable and biodegradable polymers has led to renewed interest in extracellular polymeric substances or extracellular biopolymer production by bacteria.

Extracellular polymeric substances (extracellular biopolymer) are produced by both prokaryotic microbes (bacteria and archaea) and eukaryotic microbes (fungi and algae), but they occur widely, especially among prokaryotic species. They are produced by both free-living saprophytes and pathogenic prokaryotes to humans, animals and plants [5, 6]. Nevertheless, bacteria are the most prominent extracellular polymeric substances producer prokaryotes.

Extracellular polymeric substances produced by bacteria are natural, renewable and biodegradable. They can be used in the food, pharmaceutical, biomedical, bioremediation, waste water treatment and bioleaching fields due to their wide chemical, structural diversity and their physical, rheological and other unique properties [7]. Bacterial extracellular polymeric substances or exobiopolymers (EBP), for convenience of study, may be grouped into four major classes; exo-polysaccharides, exo-polyanhydrides, exo-polyesters and exo-polyamides [8-10]. This review focuses on bacterial exopolysaccharides (EPS). Different types of exopolysaccharides are produced by bacteria; alginate, dextran, gellan, pullulan and xanthan gum…etc. [7, 11]. They play important roles in various biological mechanisms such as immune response, adhesion, infection and signal transduction [6, 11].

Bacterial exopolysaccharides (EPS) exist either associated and covalently bound to cell surface in the form of capsule, or loosely bound to cell surface in the form of slime [12, 13]. The covalently bound EPS in the form of capsule is named as capsular EPS and the loosely bound to cell surface is known as slime EPS. Slime EPS comprises about 90% of bacterial exopolysaccharide as the main component [14].

Bacterial Biopolymers: Bacteria produce diverse biopolymers with varied chemical properties via utilization of simple to complex substrates [10]. These bacterial biopolymers serve a range of biological functions, such as reserve material, protective capsules and slimes and biofilm matrix components. Several of these polymers have chemical and material properties that are suitable for industrial and medical applications and many are therefore commercially produced, providing a valuable source for renewable, biodegradable and biocompatible materials [9, 10].

Bacterial biopolymers can be classified into intracellular biopolymer (IBP), extracellular biopolymer (EBP) and structural biopolymer (SBP) depending on their cellular locations (Fig. 1). The intracellular biopolymers are few and have very limited use; however, the types and range of applications of extracellular biopolymers (EBP) are vast [9, 10]. Structural biopolymers, e.g. cellulose, peptidoglycan etc., provide structural integrity which gives shape and firmness to the bacterial cell [15].

The main components of bacterial extracellular biopolymers are carbohydrates, proteins, nucleic acids, lipids and uronic acids along with substitutions by acetate, pyruvate, succinate and other acids. Proteins and carbohydrates are predominant components and comprises about 75-90% of the polymer. Other components, present relatively smaller amounts, are lipopolysaccharides, glycoproteins and lipoproteins [16, 17]. Bacterial EBP, for convenience of study, may be grouped into four major classes; exo-polysaccharides, exo-polyanhydrides (such as polyphosphates), exo-polyesters and exo-polyamides [9, 10], which have been collectively termed as extracellular polymeric substances or exobiopolymers [8].

As Rehm [9] depicted in a review, several bacterial exopolysaccharides and exo-polyhydroxyalkanoates are already commercially produced; the exo-polyamides and exo-polyanhydrides (e.g. polyphosphates) are not commercially produced by bacterial fermentation. However, recent advances in polyamide biosynthesis hold promise for future commercial synthesis.

Bacterial Exopolysaccharides: Bacterial exopolysaccharides (EPS) exist either associated and covalently bound to cell surface in the form of capsule, or loosely bound to cell surface in the form of slime [12, 13]. The covalently bound EPS in the form of capsule is named as capsular EPS and the loosely bound to cell surface is known as slime EPS. Slime EPS comprises about 90% of bacterial exopolysaccharide as the main component [14].

The term exopolysaccharide (EPS) was coined by Sutherland [12] to describe high molecular weight carbohydrate polymers produced by many marine bacteria. Since then, EPS has also been used to designate more broadly defined compounds called extracellular polymeric substances [18]. The term extracellular polymeric substance is widely used for the polysaccharide materials present external to the cell-wall and/or cell membrane of the microbial cell and can be applied to polymers of very diverse composition and of different physical types. However, in strict definition the term extracellular polymeric substance includes not only the polysaccharide materials present external to the cell-wall and/or cell membrane of the microbial cell, which is named as exopolysaccharide, but also it includes other extracellular polymers, such as polyamides, polyesters and polyanhydrides. Thus, we would like to suggest that not to use the two terms: exopolysaccharides and extracellular polymeric substances interchangeably in scientific literatures which are indeed quite different in their meanings. We also recommend not to use the acronym EPS to represent both terms in the same literature, if not we suggest to write the full words and put the acronym EPS in bracket to avoid confusion. In this review, EPS stands only for exopolysaccharides.

Chemical Compositions of Bacterial Exopolysaccharides: Bacterial exopolysaccharides are a complex group of polymers containing a variety of monosaccharides and acyl and other substituents. They are essentially linear strands, many of which possess side-chains of one or more monosaccharides attached at regular interval to the chain. Almost all such exopolysaccharides are probably formed from repeating units of 2-6 monosaccharide residues, which are assembled from glycosyl donors on to a polyisoprenoid phosphate carrier by membrane-bound enzymes [12]. These metabolic products composed of a variety of organic and inorganic substances either accumulate on the cell surface of bacteria or secreted into the environment [6, 10]. Their composition and structure (Fig. 2) [19] is widely variable: they may be either homo-polysaccharides or hetero-polysaccharides in composition and of diverse high molecular weights (10 to 1000 kDa) [6, 10].

Homo-exopolysaccharides consist of single type of monosaccharide such as α-D-glucans, β-D-glucans, fructans and polygalactans, whereas, hetero-exopolysaccharides are formed of different types of monosaccharides including D-glucose, D-galactose, L-rhamnose and their derivatives [10, 20, 21]. Homo-exopolysaccharides possess differences with each other due to various important factors such as the primary structural skeleton including pattern of chain bonds, brand structures and molecular weights.

The polymers that belong to the microbial homo-polysaccharide group include cellulose, curdlan, dextran, alginate, mutans, levans, pullulan and scleroglucan. Curdlan and cellulose are linear homo-polysaccharide with (β 1>3 and β 1>4) glycosidic linkage but several others are branched homo-polysaccharides, including scleroglucan (β 1>3 and branch at β 1> 6) and pullulan (α 1>3 and branch at α 1>6). Dextran, another glucan, contains three different types of linkage (Fig. 2). Majority of the homo-polysaccharides are composed of neutral sugars however there are few exceptions like alginate that comprise of polyanionic acid called the polysialic acid (Fig. 2) [15, 22].

Hetero-polysaccharides of microbes comprise of three or four different monosaccharide units with different degree of branching. Components most usually found in EPS are pentoses (namely arabinose, ribose and xylose), hexoses (glucose, galactose, mannose, allose, rhamnose and fucose), amino sugars (D-Glucosamine and D-Galactosamine) or uronic acids (D-Glucuronic acids, D-Galacturonic acids). Organic or inorganic alternative such as sulfate, phosphate, acetic acid, succinic acid and pyruvic acid may also be present [23]. Most microbial exogenous layers contain neutral carbohydrates (mainly-hexose, seldom-pentose) and uronic acids. The commonest extracellular carbohydrates substituents are acetate esters, pyruvates, formates and succinates [24].

Physiological Role of Bacterial Exopolysaccharides: The specific functions and precise role of EPS in exopolysaccharide-producing bacteria is dependent on the structural units and different ecological niches of the microorganisms in the host or their natural environment [6, 25].

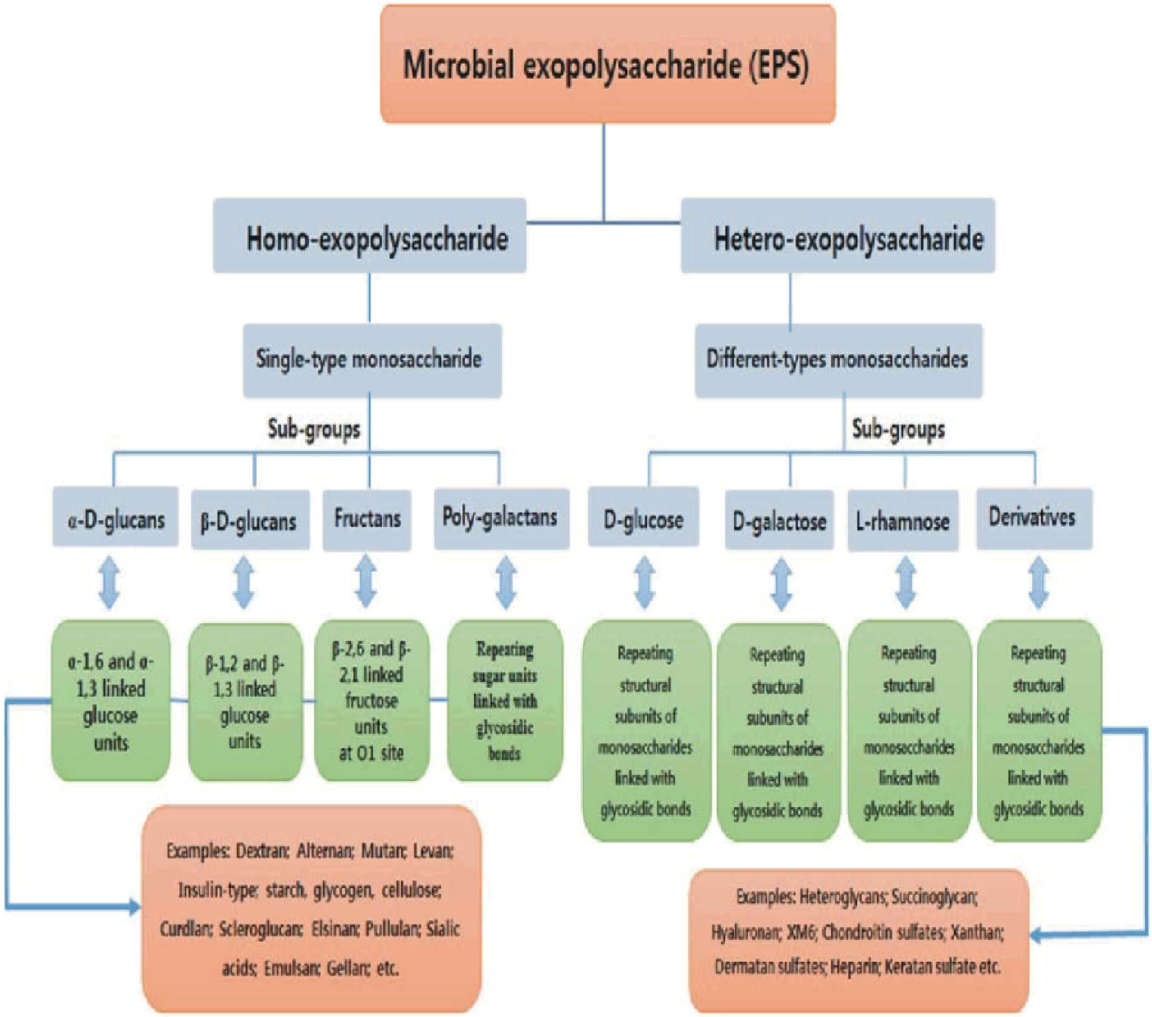

Fig. 2: Chemical classification of microbial exopolysaccharides

Bacterial exopolysaccharides occur in two basic forms. The first one is as a capsule (capsular polysaccharide, CPS, K-antigens) where the polysaccharide is ultimately associated with the cell surface and may be covalently bound and the second one is as slime polysaccharides which are loosely bound to the cell surface [6, 10, 25].

The primary functions of exopolysaccharide are of a protective nature. The ability of a microorganism to surround itself with a highly hydrated exopolysaccharide layer may provide it with protection against desiccation and predation by protozoans. Also, the presence of a gelled polysaccharide layer around the cell may have paramount effects on the diffusion properties, both into and out of the cell [26]. For instance, cells buried within a polymer matrix would be inaccessible to antibiotics. Anionic exopolysaccharide may also bind and affect the penetration of both useful and toxic metal ions through the cell surface. This type of interaction assumes practical importance in the corrosion of metallic surfaces.

The production of exopolysaccharide in the form of capsules is eminent in pathogenic bacteria, wherein the pathogenicity of an organism depends on the rate of synthesis and the amount of exopolysaccharide synthesized. Capsules enable evasion of phagocytosis. A noteworthy fact is that all capsular polysaccharides do not activate the immune system, which is due to the fact that their chemical structures may mimic the host cell surface components [6].

Exopolysaccharides play a principal role in the formation of cell aggregates, initiation of flocculation and similar processes. This property is vital for wastewater treatment and soil aggregation [27]. The presence of exopolysaccharide in adherent biofilms on inert and biological surfaces has been recognized for some time. However, the widespread incidence of these biofilms and their commercial implications in microbiological problems are as divergent as fouling of pipelines and the onset of dental caries [28].

Physical Properties and Applications of Bacterial Exopolysaccharides: The possession of unique properties by the exopolysaccharides of bacteria, which may not be found in other traditional (plant, algae and animal) polysaccharides, resulted into high-value applications [5, 6, 10]. Virtually lack of toxicity problems, comparably the easiness to manipulate bacterial genome and metabolic pathways than higher organisms, the environment and green technology in addition to their chemical and structural diversity and versatility of functions of the different exopolysaccharides produced by bacteria are making them preferable for quality product production in the market [15].

Ever since the discovery of "dextran", the first microbial polysaccharide in 1880, continued search for novel polysaccharides from microbial resources have resulted in the discovery of a number of extracellular polymers. Some of them have been commercially accepted, while others are at various stages of development [5, 29]. Their wide range of potential applications with respect to human utilization extends mainly in pharmaceutical products, cosmetics, health devices, food industries and environments.

Advances in the application of bacterial exopolysaccharides in medicine and biotechnology have seen uses to include bacterial alginate in cell microencapsulation, such as microsphere vectors for drug delivery, making dental impressions, as an active ingredient in absorbent dressings and anti-reflux therapies [30]. Likewise, dextran, produced by *Leuconostoc mesenteroides*, have been used to prepare one of the most effective plasma substitutes for application in shock and the loss of blood [31]. Sulphated forms of alginate have been thought to serve as an alternative to glycosaminoglycan heparin, the drug of choice in the prevention and treatment of thromboembolic disorders, with enhanced activity. Nonetheless, other therapeutic activities attributed to sulphated forms of alginate includes; anticoagulant, antithrombotic, anti-atherosclerotic, anti-angiogenesis, anti-metastatic and anti-inflammatory [32].

Xanthan gum produced by *Xanthomonascampestris* enjoys broad industrial application. The industrial applications are broad and include areas such as in foods, toiletries, oil recovery, cosmetics and as water-based paints among other. Superior rheological properties shown by xanthan gum allow it to be used as rheological control agent in aqueous systems and as stabilizer for emulsions and suspensions [33]. In the agriculture sector, the flow ability in fungicides, herbicides and insecticides has been improved by the addition of xanthan to uniformly suspend solid component in formulations [34]. Furthermore, the petroleum industry uses xanthan gum in oil drilling, fracturing and pipeline cleaning [33] and due to its excellent compatibility with salt and resistance to thermal degradation, it is also useful as an additive in drilling fluids. The functions and properties of a few other bacterial exopolysaccharides have been summarized (Table 1).

Diversity of Exopolysaccharide Producing Bacteria

Habitats of Exopolysaccharide Producing Bacteria: Exopolysaccharides producing bacteria are found in various ecological niches. Environment offering a medium with high carbon/nitrogen ratio are known to contain microorganisms producing polysaccharides, for example, effluents from the sugar, paper or food industries as well as wastewater plants [35]. In addition, milk and milk products are also well known sources of EPS producing bacteria.

Thermophilic niches which include volcanic and geothermal areas (terrestrial, subterranean and marine hot springs), solfataric areas, sun heated refuse, oil reservoirs and manmade habitats are the source of isolation for (hyper) thermophilic exopolysaccharides producing bacteria [36].

Rhizosphere soil is also another important natural site where EPS producing bacteria reside by inhabiting the vicinity of the plant roots. EPS produced by these bacteria form the water stable micro-aggregates responsible for maintaining physico-chemical properties of the soil suitable for plant growth [37]. In addition, there are some pathogenic EPS producing bacteria which live by infecting plants and animals' tissues. For example, well known commercialized EPS-xanthan is a product from the plant pathogen *Xanthomonas campestris* [11].

Exopolysaccharide Producing Bacteria Genera/species: Exopolysaccharides have been isolated from different genera of Bacteria and Archaea, mainly belonging to mesophilic, thermophilic and halophilic groups.

Mesophilic Group of Exopolysaccharide Producing Bacteria: Lactic acid bacteria (LAB) are generally recognized as safe (GRAS) microorganisms and are capable of producing EPSs with wide diversity of

Table 1: Bacterial exopolysaccharides with their physical properties and applications

S.No.	EPS	Bacteria	Properties	Applications	References
1	Alginate	*Pseudomonas spices* and *Azotobacter vinelandii*	Gelling capacity, film forming	For the production of micro-or nanostructures suitable for medical applications (i.e. surgical dressings, wound management and controlled drug release) and Food hydrocolloid	[11; 5; 2; 10; 15]
2	Cellulose	*Acetobacter xylinum* and other, mainly Gram-negative, bacterial species	Purity and orientation of fibrils, high tensile strength	Wound dressings, temporary skin substitute, high-quality acoustic diaphragm membrane	[11; 2]
3	Curdlan	*Agrobacterium biobar* and *Alcaligenesfaecalis, Rhizobium meliloti, Cellulomonas* spp and *Agrobacterium radiobacter*	Gel-forming ability, water insolubility, edible and non-toxic biological activity	Foods, pharmaceutical industry, heavy metal removal and concrete additive, Food additive (for example, as a thickener or a gelling agent)	[11; 5; 2; 10; 15]
4	Dextran	*Leuconostoc mesenteroides, Lactobacillus spices* and *Steptococcus mutans.*	Non-ionic, good stability Newtonian, fluid behavi or	Foods, Pharmaceutical industry (Blood volume expander) and Chromatographic media. It is also used in healthy beverages	[11; 5; 2; 10; 15],
5	Gellan	*Pseudomonas elodea, Aureomonas elodea* and *Sphingomonas paucimobilis*	Anionic charge, Hydrocolloid, Stability over wide P^H range, Gelling capacity	This is used primarily as a gelling agent, alternative to agar, in microbiological culture	[11; 5; 2; 15]
6	Hyaluronan (Hyaluronic acid)	*Streptococcal species, Pasteurella multocida* and *Bacillus subtilis*	Biological activity, Highly hydrophilic, An ionic charge	Dermal Filles: Reduce Facial wrinkles, Regenerist Micro-Sculpting Cream: An anti -aging treatment for sagging skin	[11; 5; 2; 15]
7	Levan	*Alcaligenes viscous, Halomonas eurihalina, Zymomonas mobilis* and *Bacillus subtilis*	Neutral charge, Low viscosity, High water solubility, Biological activity: Anti-tumor activity and Anti-inflammatory, Adhesive strength, Film-forming capacity	For use in medical application such as tissue engineering and drug delivery and as well in the food and biotechnology	[2; 15]
8	Succinoglycan	*Agrobacterium radiobacter, Agrobacterium tumefaciens* and *Rhizobium meliloti, Alcaligenes fecalis* var. myxogenes	Anionic charge, High viscosity and acid stability	Food and oil recovery	[2;10; 15]
9	Xanthan	*Xanthomonas* spp. *(Xanthomonas campestris)*	High viscosity, Stable over a wide temperature, pH and salt concen rations ranges	Foods, petroleum industry, Pharmaceuticals,cosmetics and personal care products. It is used as rheology modifier and food additive	[11; 5; 2; 10; 15]

structures without health risk [36]. They are well-known mesophilic group of EPS producers. Among them; *Bacillus* spp., *Lactobacillus bulgaricus*, *Lactobacillus helveticus, Lactobacillus brevi, Lactococcus lactis, Leuconostoc mesenteroides and Streptococcus* spp are good EPS producing lactic acid bacteria [7]. The highest EPS production levels from LAB reported so far is from the mesophilic strains *Lactobacillus rhamnasus* (1200 mg/L) and *Lactobacillus sakei* (1375 mg/L) [36]. The other potential mesophilic EPS producers are *Pseudomonas* spp., *Acetobacter*s pp., *Aureobasidiums* pp., *Sinorhizobium* spp., *Escherichia* spp. and *Acetobacter* spp. In the contrary, there are harmful pathogenic bacteria to plants and animals which are mesophilic in nature and produce EPS. For example, *Xanthomonas campestris* from plant pathogens and *Streptococcus pneumoniae* from human pathogens are among other EPS producers.

Thermophilic Group of Exopolysaccharide Producing Bacteria: Thermophilic bacteria are extremophilic bacteria which are able to grow at comparatively high temperatures, between 45 and 122°C [38]. Thermophilic microorganisms can be found in every phylum of Archaea and Bacteria and have been isolated from various thermophilic environments: marine hot springs, both deep and shallow and terrestrial hot springs that have served as sources for isolation of microbial EPS producers [7, 38]. Suggested groups of thermophiles are: facultative thermophiles growing up to 50°C, obligate thermophiles able to grow between 50 and 70°C and optimally at 55-65°C, extreme thermophiles growing in the range 65-80°C and hyperthermophiles-optimum is higher than 80°C [7, 38].

Thermophilic bacteria belonging to obligate thermophilic genera *Bacillus, Geobacillus, Brevibacillus* and *Aeribacillus,* extremely thermophilic genus *Thermus* and hyperthermophilic genus *Thermotoga* are reported as good thermophilic producers of EPSs [38]. For example, thermophilic bacteria *Bacillus thermantarcticus*, *Geobacillus thermodenitrificans* and *Bacillus licheniformis* isolated from continental hot springs or shallow marine vents as extremely thermophilic fermentative anaerobe are good producers of large amounts of EPS [38]. Among the thermophilic archaeal genera, *Thermococcus* and *Sulfolobus* produce EPS and *Archaeoglobus fulgidus* and *Thermococcus litoralis* accumulate significant amounts of EPS as biofilms [7].

Halophilic Group of Exopolysaccharide Producing Bacteria: Halophylic bacteria are salt loving bacteria which can be categorized into slight, moderate and extreme halophiles depending on their salt dependence and salt tolerance [29]. The main EPS producers of halophiles so far reported are represented by members of the family Halomonadaceae and Alteromonadaceae. The most common halophilic EPS producing bacteria belongs to the genus *Halomonas*, most importantly *H. maura, H. eurihalina, H. ventosae* and *H. anticariensis* [39]. EPS synthesized by *Halomonas* strains unusually consists of high sulphate content and a significant amount of uronic acids determining their good jellifying properties [7, 29]. Many halophilic Archaea are also described as being EPS producers such as *Haloferax*, *Haloarcula*, *Halococcus*, *Natronococcus* and *Halobacterium*.

CONCLUSION

Bacteria produce diverse exopolysaccharides with varied chemical and physical properties using simple to complex monomer substrates. These polymeric substances have actual and potential applications in industrial, medical and environmental sectors. Since EPS producing bacteria are found in/on different environmental habitats and organisms, the exploration and isolation of EPS producing bacteria for extraction of targeted EPS must be done in deep care. The search for specific bacteria should be based on the type of exopolysaccharide in need and the sources where that particular EPS producing bacteria is potentially found.

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